Results of Prof. E. Stromer's Research Expeditions in the Deserts of Egypt

II. Vertebrate remains of the Baharîja Stage (lowest Cenomanian)

5. The *Simoliophis* Remains

by

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with a Foreword
by
E. Stromer

Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens
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5. Die *Symoliophis*-Reste
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Foreword by E. Stromer

In April 1914 the natural-history collector R. Markgraf had closed the fossil excavation in the Baharîja Oasis, planned according to my instructions, with quite good success, and after his return packed the booty for despatch. But the Anglo-Egyptian authorities, which in previous years had constantly been very forthcoming, quite unexpectedly made difficulties for the exportation, and the Survey of Egypt in July 1914 put the impossible demand to be able to take out duplicates from the collection for the time being just as they liked. During the negotiations over the export license came the World War and the distinguished collector died at the beginning of 1916. At the request of his widow, who in her difficulties was no longer able to help herself, the Director of the Geological Survey of Egypt, Dr. Hume, took the 12 large cases with the fossils for safe-keeping and thus saved them from probable destruction.

But after the war the Anglo-Egyptian authorities wanted to confiscate the whole collection. It required very long negotiations, in which I was supported by the Präsidium of the Bayerisch Academy of Sciences and the Bayerisch Foreign Office, and the intervention of befriended foreign colleagues as well as neutral governments, especially Messrs. W.D. Matthew in New York, the Director of the Natural History Museum in London, Sir A. Smith Woodward, and the Swedish embassy in Cairo, as well as finally the German Legation there, until the collection was given completely free. Hence it was only in summer 1922 that it could be sent here, where I donated it like the earlier ones to the State Palaeontological Collection. The consignment itself was only made possible by the magnanimous expenditure of 72 Pounds Sterling by my pupil, colleague and friend Dr. B. Peyer, Privatdozent of Zoology and Palaeontology at the University in Zurich.

All persons and authorities who, in the ways mentioned, have deserved it by saving the fossils, be in this place most heartily thanked!

The administration of the Survey Museum in Cairo had had the carefully packed fossils unpacked, and unfortunately not tightly enough repacked. Hence everything was rather badly smashed up. Much is irrecoverably destroyed or at least heavily damaged. It took endless trouble and work to repair the damage to some extent. The preparation, carried out with my supervision and assistance, could for this reason, and also because of the long illness of the collection preparator, not be substantially completed until this spring.

Now at last it can be seen that the material collected in 1914, obtained in earlier excavations and which I briefly listed (Wirbeltierreste der Baharîje-Stufe. 1. Einleitung, S. 4/5. These proceedings **27**(3), Munich 1914), was not only added to in a most valuable manner, but substantially enriched by skeletal remains of entirely new forms of fish, dinosaurs and crocodiles. Due to the abovementioned death of the ideal collector Markgraf, the present situation of the Germans in Egypt and the total devaluation of the private funds, which were principally raised by the good services of the late President of the Academy of Sciences, Excellency vom Heigel, a continuation of the excavation is of course out of the question. The description of the included materials, which must occur in easy stages, and in which, I am pleased to say, numerous colleagues are sharing, will take years and show that despite all of the difficulties the undertaking has been richly worthwhile, for a wealth of scientifically totally new and highly interesting fossil material has been brought to light and made accessible by careful working-up.

I. Introduction

Among the more interesting petrifactions discovered by Professor Stromer in the Egyptian Cenomanian belong those small vertebrae which he identified as belonging to *Simoliophis* and as which he has already mentioned them (Stromer 1914, pp. 27, 28 and 42). Due to my previous involvement with a primitive snake of the Neocomian, Professor Stromer and Professor Broili had the great goodness to set aside the material in the Bayerisch State palaeontological collection in Munich for me to work on, and send it to Vienna. The following work contains the description of the material transferred and its scientific evaluation. I wish to thank Messrs Professor Stromer and Professor Broili with all my heart for the confidence which honours me, [and] which they have shown by leaving the material for me to work on. I also wish to thankfully remember the curator of the herpetological collection of the natural history museum in Vienna, Dr. O. Wettstein, for he allowed me to investigate some skeletons of pygopodids, so important for the understanding of snakes.

With the cooperation of Professor Diener, Professor Schaeffer and the administration of the geological Landesanstalt in Vienna, small rib fragments of one of the *Pachyophis* specimens in the Vienna natural history museum, of the *Adriosaurus* specimen of the Vienna University collection, and of the *Pontosaurus* and *Opetiosaurus* specimens in the geological Landesanstalt were removed and worked up as thin sections. Admittedly we are dealing, in view of the preciousness of the objects, with only minute fragments, whose orientation and sectioning were only possible due to the well-known outstanding skill of Herr Horvath, the preparator at the mineralogical department of the Vienna Natural History Museum. I do not know how best to thank especially Herr Horvath for the interest that he brought to the mounting of these difficult thin sections.

The microphotographs of thin sections of the ribs of *Simoliophis* and *Pachyophis* included in the work were taken by Frl. Lotte Adametz in the mineralogical department of the Vienna Natural History Museum; the permission to use the microphotography equipment was given to me by the Director of this department, Dr. Michel.

II. The material

The material includes:

1. Two cervical vertebrae, nine trunk vertebrae, four distal caudal vertebrae, one rib (registration 1912. VIII 26)
2. Three cervical, nine trunk, two distal caudals, one long rib (1912. VIII 27)
3. Two cervicals, one trunk (1912. VIII 25)
4. Two trunk vertebrae (1922. X 38)
5. One posterior trunk vertebra (1922. VIII 28)

6. Two cervicals, 12 smaller and one very large trunk vertebrae, one distal caudal, several rib fragments (1912. VIII 29)
7. Five trunk vertebrae (1922. X 39)
8. One cervical, one distal caudal (1912. VII 11)
9. One posterior trunk vertebra (1912. VIII 24)
10. One trunk vertebra (1922. X 41)
11. Four cervicals, 12 trunk, two distal caudals, five rib fragments (1922. X 40)

In total we thus have before us 14 cervical, 52 trunk and 11 caudal vertebrae, and they show a certain regular proportion in that, in all those places where several trunk vertebrae were found, cervical and caudal vertebrae were also found. From this circumstance one can conclude with a certain security that the cervical and caudal vertebrae do in fact belong to *Simoliophis*, and moreover, that at each locality more or less the remains of a single individual were found. Naturally the proportion of the discovered vertebrae is important as a basis for the reconstruction of *Simoliophis*.

All remains come from the deeper layers of the fluviomarine Baharîja Stage (Vraconian, lowest Cenomanian) in the northern part of the Baharîja Basin. The pieces no. 8 were collected there by Prof. Stromer himself, all the others on his instructions by the collector R. Markgraf. Only the somewhat weathered vertebra no. 5 was found 3.5 km east of Gebel el Dist in the deepest (Main Dinosaur) Level, but obviously only on the surface; it is thus surely only transported. For almost all the others, namely nos 1-4, 6, 7 and 11 from the plateau at the base of Gebel el Dist and Maghrafe and to the east of Ain Murûn, come from a level 12-15 m high above the main dinosaur and *Ceratodus* levels, mostly from green, fine sandy muds, from stratigraphic stage 7n of Prof. Stromer (1914, p.27), in which very numerous remains of elasmobranchs, ganoid fish, procoelous unarmoured crocodiles, and plesiosaurs appear, so that it is to be considered essentially marine. Also the vertebra no. 10, which was found 10 km north of Ain Harra, 8 m below the main sandstone there, comes from green muds obviously of the same age (Lebling, these proceedings Vol 29, 1919, p.7). The vertebrae no. 8 were found at Locality A at Gebel Mandische (Stromer 1914, p.30-31) together with obviously marine fish, exogyres and fusids, and no. 9 at the same hill 15 m below its basalt cap, thus equally in a lower level of the Baharîja stage.

In what follows all specimens, as far as they are easily recognisable, are cited using the number of the summary list, and similar pieces from the same locality are differentiated using Roman letters.

As the literature concerning recent and fossil snakes has already been cited by Janensch in his work on the Palaeophidae and even more thoroughly by me in my work on *Pachyophis* (1923), and no new relevant publication has appeared since (for the lizards there is the very valuable work of Camp), here it can suffice to mention that in what follows the works listed in my *Eidolosaurus-Pachyophis* work are used, especially numbers 1 (Andrews), 16 (Janensch), 30 (Owen), 32 (Rochebrune) and 36 (Sauvage) in the list of literature cited there. The histological works used in this work are cited in the relevant section.

III. Description of the material

1. The cervical vertebrae: I regard as cervical vertebrae those pieces on which an indication of a hypapophysis is present. These pieces are all relatively small. The longest cervical in no. 11 is only 12 mm long, a middle-sized one 9.5 mm and a shorter one 7.5 mm; in no. 3 a cervical of 15 mm and another of 11.5 mm have been found; from locality 6 there is just one cervical of 8 mm; hence one sees that they are smaller than the trunk vertebrae, and that the size of the cervicals decreases conspicuously anteriorly.

Already from this one can recognise that the merely 7.5 mm long vertebra from no. 11 (Fig. 1) is **the most anterior cervical vertebra so far known**. Seen from below the centrum of this vertebra is anteriorly somewhat flattened and quite broad, further posteriorly it narrows quite significantly and becomes transversely convex. It shows traces of a very weak keel which extends to the posterior condyle, where it is set off from the condyle by a slight constriction. As in the snakes we are dealing in this case with an outgrowth of the vertebral centrum and not a separately ossified piece, such as is present in numerous squamates. The small condyle is prominent; it is almost circular and hemispherical, and faces as strongly dorsally as posteriorly. From the side a blunt ridge runs anteriorly from the condyle to the pleurapophysis, which forms a small (preserved only on the left) but well developed round lump. It lies at the same level as the lower edge of the articular cavity of the centrum, circular below but becoming somewhat narrower above. The flanks of the centrum and of the lower part of the neural arch are flat. The arch, narrowing in the middle, is bordered on both sides by a sharp keel, which joins the pre- and postzygapophysis. -- Above the lateral keel the neural arch forms a quite steep roof, that lies 5.5 mm above the base of the vertebra in the middle, and rises posteriorly behind the middle; here the roof merges with a neural spine. Unfortunately the neural spine is not preserved, but on the basis of the broken surface it seems not improbable that it was thin and slender. The zygosphene is located dorsomedially at the anterior edge of the arch, forming a projecting bone lamella sloping downward and outward on both sides. While the prezygapophyses are oriented at scarcely more than 30˚ above [horizontal], the small facets of the zygosphene are nearly vertical. The transverse diameter of the zygosphene measures only 2.3 mm, that of the cotyle 3 mm; the zygosphene is thus relatively small. As Camp (1923) states, a zygosphene is generally absent in terrestrial limbless squamates (a rudimentary one is found only in *Bachia*), so its presence in *Dolichosaurus*, but especially in *Pachyophis* and *Simoliophis*, is of considerable biological importance. In a development of the same kind as in the animals named and the mosasaurs, a zygosphene is otherwise present only in snakes. By the orientation of the neural spine, its roof-shaped neural arch, the lateral crest joining the pre- and postzygapophyses, and the proportion of length to width of the neural arch, this vertebra is reminiscent of *Pachyophis*. It differs from this form in that the prominent shallow grooves, present in *Pachyophis* on the arch behind the zygosphene and in front of the neural spine, are absent.

A cervical vertebra from no. 2 (Fig. 2) can be distinguished from the preceding vertebra in that the ridge running from the pleurapophysis towards the condyle is doubled, for one ridge runs to the pleurapophysis itself, the other to the tuber projecting below the articular facet. In contrast to this the median keel disappears anteriorly, while the hypapophysis itself remains as a well developed knob. On this vertebra, as on all the following non-pachyostotic vertebrae, the zygosphene is just as wide as the cotyle. This vertebra from locality 2 is also significant for being among the few anterior cervicals which show intact prezygapophyses. While the prezygapophyses of most recent snakes are strongly directed laterally and have nearly horizontal articular facets, the bases of the prezygapophyses on vertebra no. 2 are directed very steeply upwards, so that the prezygapophyses do not stand far apart. Moreover their articular facets face obliquely inwards and upwards; they have transversely elliptical outlines. A similar orientation of the prezygapophyses as in our fossil is found among snakes only in *Pachyophis*, the palaeophids, and pythonids [?!]. A mamillary process projecting below the prezygapophysis, such as characterises all Alethinophidia (for this term cf. Nopcsa 1923), is absent in *Simoliophis*, but also in *Palaeophis*. Surely this vertebra, on account of the smallness of its condyle and its relatively great length, belongs anterior to the pieces to be described from localities 6 and 11. But it must come from a relatively large *Simoliophis*.

A cervical vertebra from locality 6 (Fig. 3) is similarly built. But it is already somewhat broader than the vertebrae described above from nos 11 and 2. The lower processes of the pleurapophyses, developed as in snakes, converge somewhat ventrally and extend deep below the centrum. The zygosphene projects up very high, so that in lateral view it almost gives the impression of a small neural spine in a far anterior position, but with a transverse diameter of only 2.5 mm it is narrower than the cotyle of the circular [sic] centrum, whose diameter is 4 mm. The base of the vertebra is similar to those of the preceding, namely there is an indication of a hypapophysis posteriorly; further forward the base becomes very strongly concave transversely, as ridges extend from each of the ventral processes of the pleurapophyses towards the end of the vertebra, but only weakly concave longitudinally. Unfortunately the posterior part of the neural arch of this specimen is damaged.

Two further small vertebrae, which are approximately 9 mm long and 4.5 mm wide, obviously belong to the same animal as the small vertebra described. As in the preceding vertebrae they have a posteriorly narrowed centrum. Also the neural arch shows essentially the same structure, but the whole arch is higher than on the preceding vertebrae; specifically the height of the ridge of the neural arch anterior to the neural spine comes to 8 mm. Thus this vertebra is reminiscent of the vertebra described from locality 6. A further difference from the previously described specimens is seen in a larger specimen from no 11 in the form of the centrum (Fig. 4). It is quite strongly concave longitudinally at the base, but rather flat transversely and shows a well developed longitudinal keel in the midline. Anteriorly this keel has a small and insignificant, and posteriorly a quite conspicuous knob, a blunt hypapophysis. It repeats *in nucleo* the structure of the palaeophids. To both sides of the median keel and approximately in the middle of the centrum there are small subvertebral foramina; but they are asymmetric, for on the left side two small openings lie close together and quite far from the midline, on the right there is just one foramen and this close by the median keel. The other middle cervical vertebra from no. 11 partly approaches the first described vertebra by its very weak indication of a median keel. On this one the very small subvertebral foramina lie more symmetrically. On both vertebrae, lateral to the anterior small lump, the well developed pleurapophyses project forward, and on this vertebra they even extend somewhat deeper than the ventral edge of the hemispherical cotyle. The zygosphene on this vertebra is much more strongly developed than on the smaller one, it is also broader, but extends less far anteriorly. With a cotyle diameter of 5 mm, the maximum transverse diameter of the zygosphene is almost the same. The circular condyle, whose diameter on the smallest vertebra was just 2 mm, here has a diameter of nearly 4 mm. It faces less strongly upwards than on the preceding vertebrae, and is bordered all round by a narrow, thin, but well-developed constriction.

On a **cervical vertebra from no. 3** (Fig. 5), on which traces of the anterior hypapophysis are still present, the doubling of the lateral edges of the centrum appears less marked, but on the other hand the median keel is doubled. Thus this region of *Simoliophis* seems to very significantly; but to erect new species for the different isolated vertebrae seems to me premature.

An **11 mm long vertebra from no. 6** and a 12 mm long vertebra from no. 11 (Fig. 6) are the most posterior cervical vertebrae that we know. Unfortunately only the centrum of both specimens is preserved. In the smaller, the hypapophysis still ends anteriorly in a small keel, in the other it is limited to a blunt knob. Common to both vertebrae is the strong development of the processes lying below the pleurapophyses, between which the flattened centrum seems as if sunken in. As the thick pleurapophyses project far anteriorly, a sharp furrow [=paracotylar depression] is formed around the concave and deep cotyle, which borders the projecting rim of the cotyle on both sides. On the specimen from no. 11 the transverse diameter of the condyle is 6 mm. The condyle itself faces strongly posteriorly and only slightly upward.

A vertebra from locality 3 (Fig. 7) can be regarded as a transitional vertebra between neck and trunk. **The centrum of this vertebra** still shows the lateral keels running posteriorly from the pleurapophyses, and between them a posteriorly narrowing, longitudinally concave, transversely flat surface with a median blunt keel. The pleurapophyses lie lateral to the hemispherical cotyle and somewhat higher than on the preceding vertebra. The zygosphene is broad, its articular facets are parallel to those of the prezygapophyses. The latter face quite significantly upwards. The roof of the neural arch [not '*Neurapophyse*'] is much wider and flatter than in the preceding vertebrae, at last the neural spine is no longer limited only to the posterior part of the arch. With a centrum length of 10 mm, the width of the neural arch is 9 mm; the vertebra is thus almost as broad as long, in contrast to the anterior, strongly elongated cervical vertebrae. The condyle of the centrum faces almost directly posteriorly, its diameter is 5.5 mm.

The transitional vertebra from no. 3 is of significance, for it is the most anterior larger vertebra on which the neural spine is known. This neural spine consists of an obliquely rising, thin anterior portion, to which is adjoined a thicker part. The posterior thicker part is 'insignificantly' [= 15-20˚] tilted posteriorly, becomes somewhat thickened dorsally and ends dorsally in a rounded knob. Posteriorly the neural spine is weakly furrowed along its length. The zygantrum lies below the neural spine and still extends deep into the neural arch. As on all the preceding, on this vertebra too the horizontal and vertical diameters of the condyle are equally large.

2. Trunk vertebrae. Five vertebrae from no. 1 and one vertebra from no. 2 could be regarded as the most anterior trunk vertebrae. They are quite well differentiated from the preceding vertebrae by the posterior end of the centrum not being narrowed basally.

The centrum of the **first vertebra of the series from no. 1** (Fig. 8) is 11 mm long, basally it is still pronouncedly concave longitudinally and still somewhat narrowed posteriorly, but on the following vertebrae the concavity and narrowing disappear progressively. In particular the posterior part of the centrum becomes visibly flatter. The development of the breadth of the basal part of the centrum occurs through the development of two small mounds below and lateral to the condyle [JS: 'paired hypapophyses' cf. Madtsoiidae], from each of which a ridge runs to the base of the postzygapophysis. The zygantrum on the first vertebra of this series is still located in a spacious triangular hole, but on the more posterior vertebrae, e.g. the one from no. 2 (Fig. 10) it becomes less and less deep and eventually is reduced to two [separate] pits which receive the two articular facets of the zygosphene. One sees this difference clearly from a comparison of Fig. 8 with Fig. 10. The form of the zygantrum restricted to two pits is characteristic of all the following vertebrae. In contrast to the cervical vertebrae, the prezygapophyses of these vertebrae spread apart more strongly dorsally, and consequently in these specimens also the bases of the prezygapophyses are placed less steeply. The articular facets of the prezygapophyses themselves have a transversely elongate outline, their slope is the same as on the cervical vertebrae. Also on these vertebrae, there is no noticeable trace of a mamillary process projecting below the prezygapophysis. The structure of the prezygapophysis reached in these vertebrae remains characteristic for the greatest part of the vertebral column, differences first appear on the many smaller caudal vertebrae. The upper part of the neural arch (the 'roof' on the preceding vertebrae) is on the anterior trunk vertebrae an almost horizontal surface, out of which the strong neural spine rises quite suddenly. The neural spine itself, as in the preceding vertebrae, anteriorly rises obliquely and is narrow, is thicker posteriorly and ends in an anteriorly stepped knob. It stands no longer obliquely, but is vertical. The vertical groove running on its posterior side is much more strongly developed than on the preceding vertebrae. The pleurapophyses are hemispherical projections to both sides of the ventral edge of the cotyle. They face laterally, but also somewhat posteriorly. As on all the vertebrae so far described, here too the pre- and postzygapophyses are joined on each side by a sharp ridge.

There are **two slender, slightly curved, thin ribs** (Fig. 19) originally more than 60 mm long and only slightly thickened proximally, found with the anterior vertebrae from no. 1 and no. 2, and obviously belong in the anterior thoracic region of *Simoliophis.* One of these ribs has a well preserved proximal end. This end is cut off somewhat obliquely and bears in the middle a shallowly concave, circular cotyle of ca. 3 mm diameter. Adjoining this dorsally and posteriorly is a tiny little tuberculum costae, though it can barely be pointed out on the photograph. A small dorsal tuberculum costae is found in *Ophisaurus*, further in the Amphisbaenidae and also in the Ophidia. At the tuberculum the dorsoventral diameter of the rib is ca. 5 mm, then it soon narrows to 4 mm, though following a dorsal excrescence it swells again rapidly to 4.5 mm. From there on towards the lower end of the rib it decreases only very gradually. About 6 mm from the lower end the dorsoventral diameter of the rib is still 3 mm. The anteroposterior diameter is greatest at the upper articular facet (5 mm) and reduces without interruption, uniformly and gradually to 3 mm.

The splendidly preserved **small vertebra 11a** (Fig. 11) mediates the connection of the vertebrae so far described to the other, strongly pachyostotic vertebrae of different examples. Its form can be seen in the figure. The centrum, almost rectangular in outline, shows the two previously described mounds anterior and lateral to the condyle. The pleurapophyses lie quite far from the round and deep cotyle, and at the level of its lower half. Below the pleurapophyses the centrum is inflated, and as this inflation paired with a roughened surface extends to the posterior end of the centrum, the condyle of the posterior end sits on a base projecting on both sides.

The upper part of the neural arch slopes down only slightly on both sides, its width reaches a full 14 mm with a vertebral length of 11 mm; the arch is thus broader than long. The neural spine is very peculiarly placed. It is formed by the upper surface of the neural arch turning quite suddenly upward, and extends from one end of the arch to the other. It is quite thick anteriorly, but still thicker posteriorly. Its anterior edge, seen from above, is formed by a sharp ridge, which forks at half-height into two ridges diverging ventrally in the form of a Y, which extend down to the zygosphene. Posteriorly the neural spine, as on the preceding vertebrae, is bounded by a broad, shallow, flat vertical groove, and the upper end of the neural spine, as a result of this groove, shows a concave, U-shaped outline. Right at the top the end of the spine also broadens anteriorly to both sides of the anterior narrow ridge, and so the outline of the upper end of the neural spine is here quadrangular. As on the preceding vertebrae the posterior part of the neural spine rises somewhat higher than the anterior end, but at the same time it is smooth dorsally, whereas the more anterior, wider part forms a concave pit with trapezoidal outline around the midpoint of the neural spine. The pit is crossed by several irregular *Riefen* [cracks?] and as a result of these the lateral edges of the pit are jagged. It makes the impression as if at this place a bone-core (an epiphysis?) still used to sit on the neural spine. A strengthening of the dorsal end of the neural spine appears numerous times in snakes. The zygosphene and zygantrum are well developed, they stand far apart, but are relatively small.

Through a whole series of transitions such as vertebrae 11b, 11c, 11d, 6a and 6f, this delicate type of vertebra is associated with a type in which strong pachyostosis is present. Many of the vertebrae discovered belong to this type.

Two vertebrae d and f from locality 6 and the isolated vertebra no. 10 can count as **typical of the pachyostotic vertebrae**. As differences from vertebra 11a it is principally to be noted on 6d (Fig. 12a-e) that the small thickening which appears behind the pleurapophyses on vertebra 11a is strongly enlarged, and runs on the flanks of the vertebra almost to the postzygapophyses. -- Below the dorsal edge of the pleurapophysis this exostotic growth divides a horizontal, shallow furrow into an upper and lower part. A further strong exostotic growth appears above the edge that runs from the prezygapophysis to the postzygapophysis. As this exostotic growth attains quite significant dimensions, especially lateral to the zygosphene, it almost overgrows the whole zygosphene. This hence appears shallow. Also the upper part of the arch lateral to the neural spine seems inflated due to this exostotic growth, and as a consequence of this inflation of the neural arch the prezygapophyses each lie at the bottom of a deep pit opening anteriorly. The neural spine of this vertebra is thick, posteriorly wider than anteriorly, and not especially high. Again it bears dorsally a flat pit, which is transversely crossed by irregular *Riefen*; the posterior, smooth, higher process is missing. The length of this vertebra comes to scarcely 11 mm, while the width of the arch at the narrowest place is 19 mm. In vertebra 6f illustrated in Fig. 13, the length is 11.5 mm, the width 21 mm. The illustration gives an idea of the size of the condyle and the strong development of the hemispherical pleurapophyses of this vertebra. What is not apparent from the illustration is the development of the subvertebral foramina. The position and development of these foramina is quite different. Without exception they are very small; at times only one foramen is present on each side, appearing at the lateral edge of the basal surface of the centrum, but sometimes one lies more medially than the other and this produces a significant asymmetry. At times numerous, irregularly distributed, small holes are present. As is well known, something similar is found in snakes, in the embryos of which the foramina are still large. The larger vertebra 6f illustrated in Fig. 14 is, as one sees, yet more strongly inflated than 6d.

A very large vertebra (Fig. 14a-e), the largest, which was found together with the other specimens from 6, is placed between the vertebral types of 11a and 6f in the scheme so far worked out. The proportion of length to width is 36:21 [vice versa!]; it thus lies between 11a and 6f and corresponds somewhat to vertebra d from no. 11. The egg-shaped, very well preserved pleurapophyses of this vertebra are unusually large and their diameter (9 mm) remains only a little less than the diameter of the condyle (12 mm). The zygosphene still projects strongly, but the bone surface of the zygosphene is overgrown with roughness. In the same way the part of the neural arch adjacent to the zygosphene shows strong exostotic growth all over. Unfortunately the distal parts of the postzygapophyses are missing from this vertebra, but it can be concluded from the form of 11b that they bore prominent, long and narrow articular facets. They were also reconstructed correspondingly on the large vertebra 6 [in Fig. 14]. The exostotic growth on the flanks of the vertebra is relatively moderate, there is a part of the arch behind the postzygapophyses not yet affected by it. The neural spine, as is to be expected in a vertebra still lying relatively far forward in the trunk, has a triangular cross-section, and as in vertebra 11a there is a dorsoposterior part that is still smooth.

A peculiar phenomenon, which also appears, though less distinctly developed, in the preceding vertebrae, draws the attention particularly in this large vertebra; this is the ornamentation of the pre- and postzygapophyses. Instead of being flat, as is the case in most reptiles, the articular facets show a series of stripes parallel to its lateral edge, which can be compared well with the growth-lines on the outside of a *Unio* or another smooth bivalve. As these 'ornamentations', obviously conditioned by the hyperostosis, are also found on the smaller vertebrae of pachyostotic specimens, we are not dealing with an individual phenomenon. They indicate that no vertical motion at all took place.

With the small pachyostotic vertebrae from 6 as well as with those from 11, numerous proximally **club-shaped, thickened ribs** (cf. Fig. 20) have been found. Unfortunately not one is complete. Whereas an anterior, non-pachyostotic rib is more than 60 mm long, 60 mm can also be assumed to be the minimum measurement for the pachyostotic ribs. The swelling up of the rib, which reaches 8 mm in a thick example, decreases rapidly towards the lower end, so that even this thick rib, 25 mm from its upper end, has a diameter of no more than 4 mm. The pachyostotically thickened ribs reach their greatest thickness not immediately at the upper end, but rather a few millimetres further ventrally. The diameter of the circular cotyle measures ca. 4 mm in the thickest ribs and, in those thickened to just 6 mm, falls to 3.5 mm; the diameter thus remains relatively constant. On the lateral ridge of the thick ribs is found in some cases a shallow longitudinal groove, but otherwise the cross-section of these quite irregularly formed ribs is nearly circular. Not the slightest trace of a tuberculum costae is recognisable. As the section regarding Histology touches on the study of some thin sections taken from ribs, refer to this section for further details.

3. Caudal vertebrae. Just as it was expedient to begin the description of the anterior portion of the vertebral column with the description of those vertebrae whose hypapophyses characterise them as cervicals, so it is, as we are dealing with a serpentiform animal, expedient to start the description of the posterior half of the animals with those almost microscopically small vertebrae which obviously come from the end of the tail. Four distal caudal vertebrae lie before us from locality no. 1 and one somewhat larger one from locality no. 6.

The **smallest well-preserved vertebra** (Fig. 15), whose discovery gives eloquent testimony to the painstaking collecting of its discoverer Herr Markgraf, is only three millimetres long and just as wide. The almost rectangular base is flattened and traversed by two deep, sharp longitudinal furrows, whereby it falls apart into three strips of nearly equal width. Both the lateral strips narrow somewhat anteriorly and are sharply set off laterally from the small pleurapophyses. Seen from behind, the centrum gives the impression of a cube, on which the well-developed condyle sits. The neural arch is low and roof-shaped, the zygosphene and zygantrum are relatively strongly developed. The complete ossification of the well-developed vertebra speaks with considerable force for this vertebra not being that of a very young *Simoliophis*, but otherwise, as the vertebra shows essentially the same structure as three further, somewhat larger vertebrae from the same locality, its more detailed description is not necessary.

In **one of the three larger vertebrae** (Fig. 16), whose flattened centrum is equally cubic, the condyle is relatively small. The neural spine is low, remains restricted to the posterior part of the neural arch, and anteriorly passes into a low ridge not even reaching the zygosphene. On a somewhat larger vertebra (Fig. 16) the neural spine is somewhat higher, tilted backwards, sharp anteriorly, convex posteriorly (thus not concave as in the anterior trunk vertebrae) and flattened dorsally. The small condyle has a diameter of scarcely 2 mm, with a transverse diameter of the vertebra of almost 5 mm. This vertebra also has well developed articular facets for freely movable ribs.

Approximately the same structure is seen in an unfortunately quite badly damaged, 5.5 mm long vertebra from no. 6 (Fig. 17). Also on this one, the somewhat posteriorly sloping neural spine forms a sharp ridge anteriorly. Moreover, on this vertebra the condyle is relatively larger, with respect to the centrum itself, than in the minute vertebrae.

Similarly built to these small vertebrae but much larger specimens, whose preservation unfortunately leaves much to be desired, have been found at no. 2, no. 6 and no. 11, and one can regard these 9, 10 and 12 mm long specimens as vertebrae of that region of the body in which pachyostosis again decreases caudally, and the anteriorly high neural spine is again rooflike. Due to these changes the anterior caudal vertebrae of *Simoliophis* (Fig. 18) are strongly reminiscent of the anterior trunk vertebrae of this reptile, and hence an identification of isolated vertebrae of this region is almost impossible. At best, one can differentiate these posterior vertebrae from the anterior ones by the greater transverse diameter of the cotyle.

A similar return to the *Bauplan* of the anterior thoracic vertebrae in the caudal region of a reptile, which strikes us from this description, also occurs in *Pachyophis*.

It is important and hence especially to be emphasised that on all posterior vertebrae and even the smallest vertebrae of *Simoliophis*, haemapophyses are absent, on the contrary free trunk ribs are found on them. This extremely peculiar stroke, it seems, is common to *Simoliophis* and *Pachyophis*. Further, as is evident from the measurements shared in the preceding text and stands out still more when one measures all the available vertebrae, it is seen that also the proportion of length to breadth of the neural arch of this animal is almost the same in the different regions of the body.

In *Pachyophis* the arches of the most anterior cervicals are only somewhat longer than wide, then their relative length increases around the 10th preserved vertebra and thereafter decreases again. By the 33rd known vertebra the length and width are equal, then the width begins to predominate and reaches approximately the proportion 10:7, whereon this proportion persists up to the neighbourhood of the 100th vertebra. At the 113th vertebra length and width become equal again, and finally from the 115th to 122nd vertebrae the length is greater than the width. Towards the extreme end of the tail the length decreases again. The last caudal vertebrae of *Pachyophis* are unfortunately buried in the rock.

In *Simoliophis* one finds similar proportions. In specimens no. 2 and no. 11 the arches of the most anterior cervical vertebrae are longer than wide, and in the posterior cervicals and most anterior trunk vertebrae in no. 1, approximately the proportions 10:10 can be determined. -- The pachyostotic dorsal vertebrae are in all specimens very wide: their approximate proportions vary in no. 11 between 6:10 and 8:10, in no. 6 between 6:10 and 5:10, and in one vertebra known from no. 2 it measures 7:10. Behind these conspicuously broad vertebrae again follow somewhat narrower, non-pachyostotic vertebrae, which show the proportions 7:10 and 9:10 in no. 1; in no. 2, 7:10 to 10:10; in no. 11, similarly 8:10 and 10:10; and finally in the tiny little vertebrae of the end of the tail the length is again approximately equal to the width. -- The approximate measurements and proportions of some remains found together, and probably in part belonging together, are to be seen in the following Table.

Vertebrae whose proportions or measurements stand out more strongly from the rest, and which perhaps belong to other specimens, have been placed in square brackets. Particularly in localities 2 and 6 we seem to be dealing with the remains of two examples. Smaller differences are to be attributed to inaccuracy in the measurement or the unfavourable state of preservation of the specimens concerned. -- The numbers in round brackets indicate the proportion of arch-width to arch-length according to the formula 10:x, where the first part of the formula is left out. The parallelism of proportions of *Pachyophis* and *Simoliophis*, as well as the common features yet to be discussed, let us conclude by and large that the total number of vertebrae was also approximately equal, and we can hence reconstruct *Simoliophis* with ca. 140-160 vertebrae, which also corresponds to the total number of trunk vertebrae of many recent snakes.

The proportion of length to height of *Simoliophis* vertebrae is circa 5:10 at midbody, and seems to climb to 7:10 at the anterior and posterior ends; as the neural spines are known in only a few vertebrae, more exact data are not possible.

In *Pachyophis* the ribs at mid-trunk are circa five times longer than at the neck, and as the neural spines of *Simoliophis* are much higher than in *Pachyophis*, and also the trunk ribs show a stronger pachyostosis, one may assume that the proportion of rib length between neck and trunk slips [*sich verschob*] at most in favour of trunk rib length; one may thus expect at least the same proportions in *Simoliophis* as in *Pachyophis*.

After these points, we can proceed to a reconstruction of *Simoliophis*. First of all, we come to the fact that even the smaller examples of *Simoliophis* may have been about one metre long; the neck may have been as thick as a thumb; the trunk at its thickest part, if one takes into account the posterior slant of the ribs, may have reached a diameter of at least 9 cm , and to this ungainly body was appended a relatively short tail. Text-figure A can give an approximate concept of the type of this and similar pachyophidians, though the genus *Pachyophis* may have been somewhat more slender, and *Simoliophis* itself somewhat thicker than the type reconstructed here.

The pachyostosis of ribs and vertebrae, associated with osteosclerosis, according to our experience appears only in totally or half-aquatic vertebrates (*Mesosaurus, Pachypleura, Proneusticosaurus, Adriosaurus, Eidolosaurus, Pachyophis*, whales and sirenians), so we may assume that *Simoliophis* was a water-inhabiting animal. This assumption can also be supported with geological arguments, for the relatively common remains are found in near-coastally deposited marine or fluvio-marine sands. Due to the abundance of the remains, that they were washed in is not to be considered, and so it could at most only on account of the presence of *Mycelites* on some bones, seem improbable that *Pachyophis* [JS: lapsus for *Symoliophis*] inhabited the sea. As traces of *Mycelites* are also found on some *Plioplatecarpus* bones described by Seitz, even its presence forms no counterargument.

4. Histology. The histology of the bones of *Simoliophis* was investigated in a longitudinal section and two transverse sections of a thickened rib from locality 6. Already at weak magnification one can distinguish on the elliptical cross-section three zones built up of numerous lamellae. -- On the outside lies a layer arranged like onion-shells, crossed radially by long, straight, primary blood vessels, forking slightly towards the outside, penetrating from the periost. Inward from this zone there follows a second, strongly eccentrically deposited, elliptical, cylindrical, uniformly thick zone, in which the blood vessels are less marked; and internal to this elliptical zone one can finally distinguish a core of massive bone which has been laid down to quite uniform thickness around an eccentrically placed, round opening. The general arrangement of the three different zones is recognisable from Text-figure B.

Obviously the elliptical zone corresponds to the true cranio-caudally compressed rib, before it was distorted by the pachyostosis of the outer zone, and the core to the original marrow cavity, which was filled by remodelling (?) of the bone.

In very strong magnification one sees the following: after a very thin (ca. $^{1}/_{100}$ mm), dense outer layer with weakly corrugated outer edge follows, towards the inside of the bone, a $^{1}/_{12}$ mm thick spongy-honey-comb layer, crossed by numerous large lacunae showing rounded outlines and in part tubular [and?] looping. These lacunae reduce the true bone substance to a delicate scaffolding. The approximate diameter of individual lacunae measures $^{1}/_{100}$ mm. This layer surrounds the whole rib uniformly and probably owes its existence to the destructive effects of *Mycelites ossifragus*. In some of the tubes, according to this hypothesis produced by this 'hair-fungus', one sees collections of small granules showing a diameter of some $^{1}/_{500}$ mm diameter, which could perhaps be spores of this fungus.

Adjoining the layer chewed up by *Mycelites* is the layer, varying regionally and growing in the manner of onion-skin, for which we will use, for short, the term 'onion-skin-layer' (Zwiebelschalenschicht). From the combination of the results obtained from the cross-section and longitudinal section of the rib one can recognise that the individual onion-skins become thinner not only towards the ventral side of the rib, but also towards the lower end. This shows that the pachyostosis produced in this manner proceeds from the dorsal and proximal part of the rib. -- This rapid remodelling of the bone on the outer and upper parts is hence less conspicuous than it could seem at first glance, for precisely in the ribs is, also during the growth of human ribs something analogous noticeable, as "through the surging thoracic organs on the inner surface the whole periosteal bone is resorbed, so that the *'enchordale'* [endochondral?] is exposed, and in part is also destroyed. Hence one finds in cross-sections through ribs of older foetuses and children a thick layer of periosteal bone on the outside. Such is completely absent on the inside, here the 'enchordalen' 'bone-beamlets' with their enclosed remains of the cartilaginous ground-substance are directly covered by periost" (Schaffer 1922).

In the onion-skin-layer, transparent, light brown layers poor in bone-cells alternate with opaque, dark ones richer in bone-cells. In both layers there appear, through enrichment in bone-cells, zones which run parallel to the colour-bands. The bone-cells themselves are likewise oriented with the long axis of their cross-sections parallel to the colour bands. In longitudinal section the bone-cells show themselves as quite long but very thin hollow spaces, and thus one sees that they had the form of long, elliptical tubes. Their canaliculi are somewhat undulating, numerous, and in longitudinal section oriented at right angles to the long axes of the cells. In cross-section their course is less regular, they thus mainly undulate parallel to the cross-section.

...

IV. Systematic position and importance of *Simoliophis*

After this quite detailed description of the peculiar Egyptian Cenomanian reptile, its relationships must be determined. As was already said in the introduction, it was identified by Prof. Stromer as *Simoliophis*, and this identification proved to be correct. Not only that all the characters known from the Egyptian material are also found in the generic definition given by Rochebrune, even the dorsally flattened neural spine, but one can even see on the illustrations given by Rochebrune the separation of the base of the centrum into three longitudinal parts, which characterises the anterior thickened vertebrae of the Egyptian species and which Rochebrune did not once mention. Apart from France, *Simoliophis* vertebrae are also known through Sauvage from the Cenomanian of Portugal, and have been provided with a species name of their own; but as the vertebrae in the different body regions of *Simoliophis* vary very strongly, and as moreover there are probably also quite significant individual variations, the specific difference of the Egyptian, French and Portuguese *Simoliophis* vertebrae can hardly be determined in practice [*vorderhand*]. Hence it seems best for the time being to use the oldest name, *Simoliophis rochebrunei* Sauvage, for the three different species of *Simoliophis*. The genus *Simoliophis* can be characterised by a very small head, in any case; rather elongate, procoelous, delicate cervical vertebrae; procoelous, robust, short, broad, pachyostotic trunk vertebrae; and short, but less wide, procoelous caudal vertebrae. The neural spine of the anterior vertebrae was restricted to the posterior part of the neural arch, and thin; that of the middle vertebrae was, especially posteriorly, thick, high, strong, expanded dorsally (and provided with an epiphysis?); the neural spine of the caudal vertebrae was again more delicate, thinner and lower. -- All vertebrae bore well-developed zygosphenes and zygantra, these being somewhat reduced in the middle trunk vertebrae on account of the pachyostosis. The cervical vertebrae bore a basal keel, sometimes just indicated, on some vertebrae duplicated, otherwise the base of the vertebral centrum was flat. The position and development of the subvertebral foramina varied. All known vertebrae, even the very small caudal vertebrae, bore single-headed, freely moveable ribs, which articulated to a hemispherical pleurapophysis. The articulation surfaces of the centrum were circular in the anterior portion of the body and transversely elliptical posteriorly. The most anterior ribs were thin and hollow and had a minimal dorsoposterior tuberculum costae, those of mid-trunk were, in correspondence to the vertebrae to which they articulated, hyperostotically thickened and massive. A tuberculum costae is not present on the thickened ribs.

The only procoelous reptile that resembles this definition to any extent is the Neocomian *Pachyophis*. *Pachyophis* is also, as was already said earlier, like *Simoliophis* in its small skull, procoelous, elongated cervical vertebrae provided with slender neural spines; procoelous, short, broad, pachyostotic trunk vertebrae; and characterised by the procoelous vertebrae, again becoming more lightly built towards the end of the body, bearing free ribs almost to the end of the body. Differences are present in that the neural spines in the trunk of

Pachyophis are very low, but high in *Simoliophis*; further that the trunk vertebrae of *Pachyophis* are much less wide than in *Simoliophis*. The maximum proportion of width to length in *Pachyophis* is ca. 10:7, in *Simoliophis* ca. 10:5. The specific, indeed the generic difference of *Simoliophis* and *Pachyophis* is sufficiently well grounded by these differences, but a common *Bauplan* can still be recognised; in any case the specialisation of the Cenomanian form is so much further advanced than that of the Neocomian, that it recommends creating a separate subfamily or family for each of these forms, Pachyophidae and Simoliophidae.

A question which automatically arises is that of the relationship of the Cenomanian Simoliophidae to the Eocene Palaeophidae. There are differences, but also similarities.

The differences are:

1. The more or less well developed pterapophyses in the palaeophids.
2. The much stronger development of hypapophyses in the palaeophids.
3. The lack of pachyostosis and osteosclerosis in the palaeophids.
4. The higher neural spine in the palaeophids.
5. The greater vertebral length in the palaeophids.

The similarities are:

1. In both groups the transverse diameter of the zygosphene of the cervical vertebrae is smaller than that of the cotyle, in the trunk vertebrae both diameters are equally large.
2. The presence of two hypapophyses on the base of some vertebrae, one anterior and one posterior.
3. The strikingly high development, for snakes, of the neural spine of the trunk vertebrae.
4. The different anteroposterior extent of the neural spine on the cervical and trunk vertebrae.
5. The position of the pleurapophyses.
6. The presence of a lateral longitudinal keel joining pre- and postzygapophyses.
7. The steep position of the prezygapophyses and lack of a processus mamillaris.
8. The presence of small, strongly elongated anterior cervical vertebrae (*Palaeophis 'longus'*)
9. The lack of typical, snakelike caudal vertebrae.
10. The lack of a tuberculum costae on the trunk ribs.

As one sees, the palaeophids differ from the simoliophids essentially in characters analogous to those which differentiate *Simoliophis* and *Pachyophis*. With the exception of the pachyostosis being absent in *Palaeophis*, all the differences are only gradual and indeed such as are produced by the stronger development of the dorsal part of the arch and the strengthening of the hypapophyseal ligaments. This shows well in the following summary:

1. Properties of the neural arch:
    - a) *Pachyophis*; neural spine short.
    - b) *Simoliophis*; neural spine high.
    - c) *Palaeophis*; neural spine very high, pterapophyses low.

d) *Pterosphenus*; neural spine very high, pterapophyses high.

2. Properties of the centrum.

a) *Pachyophis*; two hypapophyses (?*)

b) *Simoliophis*; an indication of a second hypapophysis.

c) *Palaeophis*; one small and one large hypapophysis.

d) *Pterosphenus*; ditto.

*[Footnote] The possibility that the pieces identified by me as such were rib fragments, seems to me subsequently to be not completely excluded.

Obviously the greater elongation of the dorsal vertebrae of the palaeophids is also associated with the different structure of their neural arches showing greater mobility, and even though the palaeophids can in no way be constructed as the direct descendants of the simoliophids, yet the similarities appearing between these three forms entitle one, as was already done by me in 1923, to bind them together as Cholophidia. It seems better to separate the archaeophids from the cholophidians, on the grounds of the definition given by Janensch, and to place them in Alethinophidia as their own family.

The sharper circumscription of the concept Cholophidia allows its relationship to the alethinophidians to be more clearly recognised. As far as skull structure is concerned, since no new material is available, one must refer to what was said in 1923; but in the following all the new features recognised in vertebral structure will be discussed in detail.

The **similarities to snakes** in the vertebral column of the specialised cholophidians are:

1. The numerous rib-bearing vertebrae.
2. The long, delicately built cervical region.
3. The development of a quite large zygosphene and zygantrum.
4. The development of downward-projecting processes below the articular mounds for the ribs.
5. The strong hypapophyses appearing on very numerous vertebrae.

In the primitive cholophidians [i.e. *Pachyophis*] points 4 and 5 seem to be absent.

The **differences from snakes** of all cholophidians are:

1. The pronounced regional differentiation of the vertebral column.
2. The lack of a Processus mamillaris on the prezygapophysis.
3. The doubled hypapophyses.
4. The persistence of ribs to the end of the tail and the lack of all characteristic features of the snake tail.
5. The lack of a Tuberculum costae.

It is important and interesting that the primitive cholophidians of the Neocomian, as far as their presacral vertebrae are concerned, are **still closely connected to the dolichosaurs**, whereas the presacral vertebrae of the Cenomanian and Eocene forms already show almost all of those features which characterise snakes today; it is important as well that true snakes are first found in the Tertiary. If one proceeds from the assumption, supported by the chronological succession, that the similarity of the presacral vertebrae of the specialised cholophidians and the alethinophidians is not simply a convergence phenomenon, but rather is genetically conditioned, then one sees positively how the origin of snakes proceeds, **though not on land, rather in a shallow near-coastal sea**, from Neocomian to Eocene gradually [and] cranio-caudally, and is only half-attained in the Cenomanian. In any case, in the primitive predatory cholophidians the slenderness and length of the neck was a compensation for the massive pachyostotic trunk, and this explains well to us why the lightly built and mobile, if also limbless squamates constantly lack a long, slender neck. In contrast to the limblessness of the terrestrial squamates, in which the body always remains mobile, the origin of snakes from some mud-inhabiting dolichosaurs of the Mesozoic obviously occurred by the anterior portion of the body, due to pachyostosis of the lung region conditioned by aquatic life as in the sirenians, becoming elongated and, in compensation, highly mobile, and later, after pachyostosis stopped, this elevated mobility extended caudally.

Those vertebrates that capture their prey simply by grabbing with the head which sits on an elongate neck (e.g. *Trionyx, Elasmosaurus*) one can call **cephalotropic** forms, whereas for those forms which move the whole body in order to seize prey (e.g. *Chelone, Trinacromerum*) the term **somatotropic** recommends itself. All the limbless squamates are somatotropic, the snakes on the other hand are principally, if not exclusively, cephalotropic.

The loss of the posterior temporal arch characterising snakes likewise occurs in cephalotropic aquatic forms like *Hydromedusa*, though also in the pygopodids and eventually also pronouncedly fossorial forms, as e.g. in numerous limbless squamates. A difference is present in so far as the aquatic forms, like the snakes, generally have strong cervical muscles, which in contrast are mostly absent in the fossorial squamates which mostly have a posteriorly expanded skull. The strong M. longissimus dorsi of the cephalotropic snakes corresponds to the M. testocervicalis lateralis of the cepalotropic turtles, their M. articulospinalis to the M. testocervicalis medius. The M. testocapitis lateralis of the somatotropic turtles, which inserts on the squamosal, stiffens the neck and conditions the existence of the posterior temporal arch of these animals, is absent in the cephalotropic testudinates. Between the skull of the pygopodids and that of the snakes, though, there is, as far as the posterior part is concerned, an undeniable similarity, but the zygosphenal articulation of the snake vertebra is a further feature which indicates a marine stage in the previous life [Vorleben] of the snakes.

Strong zygosphenal articulations develop without respect to the general body form, principally in all those procoelous, mobile, aquatic reptiles in which, as in the dolichosaurs and mosasaurs, the vertebral column requires particular stabilisation due to the impact of waves during swimming; then they are found, but less marked, in those long-tailed, quadrupedal terrestrial reptiles, likewise possessing convexo-concave vertebral centra, in which due to the weight of their bodies particular demands are placed on the vertebral column during their somewhat undulating locomotion, among which are the large forms among the squamates and the quadrupedal sauropods. In contrast to this **there is not one limbless, terrestrial reptile** apart from the snakes in which a zygosphenal articulation develops. Even *Bachia*, which probably descends from a teiid possessing zygosphenes, now shows only a rudimentary zygosphene, and this shows sufficiently that limblessness acquired on land does not only not promote a zygosphenal articulation, but directly hinders it. As the most primitive cholophidians that we know have large zygosphenes, but are marine, one can well put the hypothesis that they too acquired their zygosphenal articulation **as a consequence** of their aquatic life. As the zygosphene is partially suppressed again in the dorsal region of *Simoliophis* as a consequence of pachyostosis, its acquisition must have occurred before that of pachyostosis. So the zygosphene is an important marine character of the cholophidians.

Also the appearance together of tail-reduction and limblessness in the cholophidians, while at the same time the skull modifications typical for fossorial forms fail to appear, make it very hard to conceive them as a group of properties acquired on land. In arboreal [lapsus for 'terrestrial'!?] forms limblessness, as in the pygopodids, particularly *Lialis*, never goes hand in hand with truncation of the tail, on the contrary rather an elongation of the tail; in fossorial forms by contrast, where a tail reduction does in fact occur, it is accompanied by the skull modifications typical for these forms. All this is not the case in the cholophidians. Only among aquatic animals are a few sparse forms, like *Amphiuma*, which are limbless and yet at the same time have a pointed skull and a somewhat reduced tail. Abel's assumption that the cholophidians had passed through a primarily terrestrial, limbless phase of development, is for the time being proved by nothing; but as limblessness appears more often on land than in the sea, Abel's hypothesis can not simply be flatly denied. To that extent, the possibility is not completely excluded that the cholophidians descend from a limbless, somatotropic, long-tailed reptile that was forced to a life in water by the Neocomian transgression. This animal thereupon first acquired a zygosphene, at any rate in the sea, and then, like any primitive aquatic vertebrate, it became pachyostotic and cephalotropic. In any case the true terrestrial snakes came from this ungainly form by the assumption of a secondarily terrestrial way of life. The eel and the dipneusten [dipnoans], gravitating to snake-form, show clearly that the assumption of a secondary, terrestrial way of life sometimes also occurs in an animal adapted to life in water.

The recent pygopodids give us some information about the last, terrestrial stage of development of snakes. The only limbless terrestrial squamates whose skull can be compared to some extent with that of the snakes, are the grass- and undergrowth-inhabiting pygopodids. The pygopodids, though, have just four elements in the lower jaw, a long fragile tail and, like all other terrestrial limbless squamates, a short neck and no zygosphene, and hence they can not belong to the genealogical series of the snakes, but in the forms which have an elongate skull (*Lialis*), as in snakes a second coronoid process is recognisable far back on the lower jaw, which is obviously in correlation with a limited facility of dilatation of the mouth. As this process is absent in the short-skulled pygopodids (*Pygopus*), it shows that while this is just a convergence phenomenon with snakes, but whose importance lies in the fact that it partly well demonstrates to us, in a recent example, the last phase of development of the snake skull, that of becoming secondarily terrestrial. Also the quadrate suspension of the pygopodids is so far identically built to that of snakes, that also in them there is only one, anteriorly chip-shaped bone intervening between the parotic process and the quadrate, which lies against the posterior part of the lateral surface of the parietal and is surely identical with the bone which in snakes - whether correctly or incorrectly remains to be seen - is called the squamosal. This bone is surely not identical with the bone of *Varanus* called the squamosal by most authors (but by Watsom the quadratojugal), rather with the bone in *Varanus* which Broom has recently called the tabular, but Watsom the squamosal. This is a second important feature common to snakes and pygopodids; and finally there is also yet in the pygopodids a noticeable enclosure of the anterior part of the brain cavity by the frontals. In this way they too initiate the complete bony enclosure of the brain cavity which characterises snakes. As the pygopodids, as a consequence of the grounds previously mentioned, can not be considered as the ancestors of snakes, so must all these features common to them and snakes be considered as convergence phenomena; whereby one is forced to the assumption of a secondary terrestrial development phase in the origin of snakes.

On this point of view, the tail of snakes, showing such peculiar haemapophyses, presents a problem in so far as a rejuvenation must be assumed; but as the tree snakes have conspicuously many caudal vertebrae and a secondary increase in vertebral number has surely taken place in them, and moreover, as was already known to Rathke (1839), a posterior increase in the number of caudal vertebrae also occurs in the course of development in the grass-snake, arguments for such a rejuvenation are also available.