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The Ancestry of Reptiles

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THE ANCESTRY OF REPTILES

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[Plates 62 and 63, and pull-out diagrams

CONTENTS

Reptiles of several distinct lineages have been described from the lower part of the Upper Carboniferous. Neither reptiles nor any plausible ancestors are known from earlier beds. The nature of the amphibian–reptilian transition must be studied on the basis of relicts of earlier groups which are contemporary with true reptiles.

Several genera from the Middle Pennsylvanian locality of Nýřany, Czechoslovakia, have been considered closely related to the ancestry of reptiles. The incomplete nature of the original descriptions of *Diplovertebron*, *Gephyrostegus* and *Solenodonsaurus* has led to considerable confusion as to their taxonomic distinction and phylogenetic significance. Subsequently these taxa have been variously synonymized and considered as being alternately embolomeres, primitive anthracosaurs, seymouriamorphs, extremely primitive reptiles and captorhinomorphs. On the basis of redescription of type material from museums in Berlin, Prague and Cambridge as well as more recently discovered specimens, it is possible to establish the identity of these forms and to describe them in considerable detail.

The type of *Diplovertebron punctatum* can be identified as a small embolomere. The material on which it is based can be distinguished from the types of *Solenodonsaurus* and *Gephyrostegus*.

The type of *Gephyrostegus bohemicus* is a primitive anthracosaur. On the basis of this and other material, description of almost the entire skeleton is possible. The vertebral column has 24 presacral segments, each consisting of a large U-shaped pleurocentrum and a smaller, crescentic intercentrum. This genus is an almost ideal relict of the anthracosaur group which gave rise to reptiles. It is clearly distinct from the Permian seymouriamorphs, and could not have given rise to any known members of that group. *Eusauropleura digitata* from a deposit of equivalent age at Linton, Ohio, is a related, but somewhat more primitive form. The body proportions of these genera indicate that they were terrestrial in habit, with no specifically aquatic adaptations.

The type of *Solenodonsaurus janenschi* is a very primitive reptile. This form retains an otic notch and labyrinthine infolding of the enamel, but the postcranial skeleton is very close to the pattern of romeriid captorhinomorphs. Material of a very immature specimen assigned to this genus by Pearson has a typically reptilian palate and skull roof pattern, but anthracosaurian dorsal and ventral scales.

Material (designated by them as specimen I) assigned to the genus *Gephyrostegus* by Brough & Brough actually pertains to a romeriid captorhinomorph.

On the basis of this material, the ancestry of captorhinomorph reptiles from the gephyrostegid anthracosaurs can be firmly established. The families Solenodonsauridae and Limnoscelidae are relicts of more primitive, but still reptilian, lineages which retain a number of anthracosaurian characteristics.

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INTRODUCTION

It has long been recognized that reptiles evolved from Paleozoic amphibians, but the exact nature of the relationship has not been established. Among the known genera, only the anthracosaurs (Romer 1947, 1963, 1964; Panchen 1964, 1966) have the cranial and vertebral anatomy consistent with close relationship to the reptiles. Within this group, the seymouriamorphs (White 1939; Špinar 1952; Olson 1965) resemble reptiles in their general body proportions and apparent terrestrial adaptations. No members of this group are known before the Lower Permian, however, at least an entire period subsequent to the appearance of true reptiles in the Lower Pennsylvanian. Although the known seymouriamorphs may be relicts of a group which gave rise to reptiles, they are specialized in a number of features not expected in the ancestors of the class. Their late appearance and specialized anatomy indicates that it is inappropriate to consider the known seymouriamorphs as examples of the group which gave rise to reptiles.

Among the poorly known forms from the Middle Pennsylvanian coal swamp faunas of Nýřany, Czechoslovakia, and Linton, Ohio, are two genera which much more closely approximate the morphology expected in the group which was ancestral to reptiles. Although these deposits are still considerably later than those from which the earliest reptiles are known (Baird & Carroll 1967; Carroll 1964*a*) they are considerably earlier than those of the oldest known seymouriamorphs, and the genera are far less specialized.

The close relationship of the Nýřany genus *Gephyrostegus* (Jaekel 1902) and the Linton genus *Eusauropleura* (Romer 1930) to reptiles was recognized by their initial describers, but their phylogenetic position has been obscured as a result of the incomplete original descriptions and subsequent taxonomic confusion. By the use of new techniques of preparation and casting (Baird 1955) much more complete and detailed knowledge of the original specimens is now available. In addition, new material of both genera has recently been discovered. For these reasons we have a much better understanding of *Eusauropleura*, and detailed description of almost the entire skeleton of *Gephyrostegus* is now possible. Description of these genera provides the first adequate knowledge of the anatomy of amphibians which were close to the ancestry of reptiles and furnishes a basis for considering the anatomical changes which occurred in the amphibian-reptilian transition.

Specimens from different institutions are indicated by the following abbreviations:

AMNH	American Museum of Natural History, New York.
DMSW	D. M. S. Watson Collection, Cambridge University.
MB	Humboldt Museum, Berlin.
MCZ	Museum of Comparative Zoology, Harvard.
PU	Princeton University, Princeton, New Jersey.
WM	Walker Museum, University of Chicago.

GEPHYROSTEGUS BOHEMICUS

Gephyrostegus bohemicus (Jaekel 1902, p. 127)
Diplovertebron punctatum (Watson 1926, p. 239)
Gephyrostegus watsoni (Brough & Brough 1967*c*, p. 158)

Gephyrostegus bohemicus is known from three specimens:

(1) The type. Counterpart blocks in the Humboldt Museum, Berlin, showing the skull in

dorsal and ventral views and scattered elements of the anterior postcranial skeleton (figures 1 and 5). (Figures 1 and 2 are on a pullout at the end of the paper.)

(2) MB1901.1378 a+b. Counterpart blocks in the Humboldt Museum, Berlin; a well articulated postcranial skeleton, lacking only the tail and a few phalanges (figure 2).

(3) DMSW B.65, Cambridge University. The skeleton of an immature individual, lacking only the tail. Referred to by Watson (1926) as *Diplovertebron punctatum*, and by Brough & Brough (1967*c*) as the type of a new species, *Gephyrostegus watsoni* (figures 3 and 4A, plate 62).

Other specimens attributed to this genus by Brough & Brough (1967*c*) are reptiles, which will be discussed later in this paper.

Size

The skull of the type is 63 mm in length as measured from the quadrate to the tip of the premaxilla, parallel with the long axis of the skull. Comparison of common postcranial elements indicates that the second Berlin skeleton is from an individual of almost exactly the same size. Any possible difference in size is within the margin of error expected in the measurement of individual bones. The length of the trunk region, from the atlas arch to the sacral vertebra, as restored, is 142 mm. The degree of ossification of the tarsals and articulating surfaces of the limb bones suggests that these specimens are of essentially mature individuals. The skull of Watson's specimen is only 34 mm in length. The vertebrae are only weakly ossified and the carpals and tarsals remain totally cartilaginous. Although small and immature, it possesses few of the features typifying the larval stage of discosauriscid seymouriamorphs (Špinar 1952). Despite the obvious immaturity of this specimen, the morphology is clearly very similar to that of the type and provides no basis for distinction as a separate species.

Skull

The skull of the type is preserved in such a way as to show the roof, palate and cheek region very clearly, allowing restoration (figure 6) with little chance of serious error. The length is approximately twice the width, as measured at the quadrates. The height at the back of the skull table is roughly one half the width. The orbits are located midway in the length of the skull, face primarily laterally and are approximately 17 mm in diameter. The skull table is movable on the cheek region. There are shallow, typically amphibian otic notches, accentuated by long tabular horns. The skull table is narrower than that of embolomeres and seymouriamorphs, and the frontals enter the margin of the orbits. The general proportions of the skull of *Gephyrostegus*, despite the presence of an otic notch, resemble those of the romeriid captorhinomorphs more than those of other anthracosaurs.

The bones of the skull table are marked by pustular ornamentation, not reported in any other carboniferous tetrapods. The cheek bones and the more anterior skull roof elements are marked by faint grooves radiating from the centres of ossification. The premaxillae are evenly pitted. No lateral line canal grooves are visible.

The pattern of the bones of the skull corresponds with that of anthracosaurs in general. The posterior margin of the skull roof is markedly concave, as a result of the extent of the tabular horns. As in other anthracosaurs and the primitive reptile *Limnoscelis*, these bones extend ventromedial processes to support the paroccipital processes of the braincase. The supratemporals are very large elements which extend lateral to the tabulars, almost to the ends of these bones. Posteroventral processes extend behind the dorsal margin of the squamosal, with which there was apparently a ligamentous attachment. The postparietals face almost entirely dorsally,

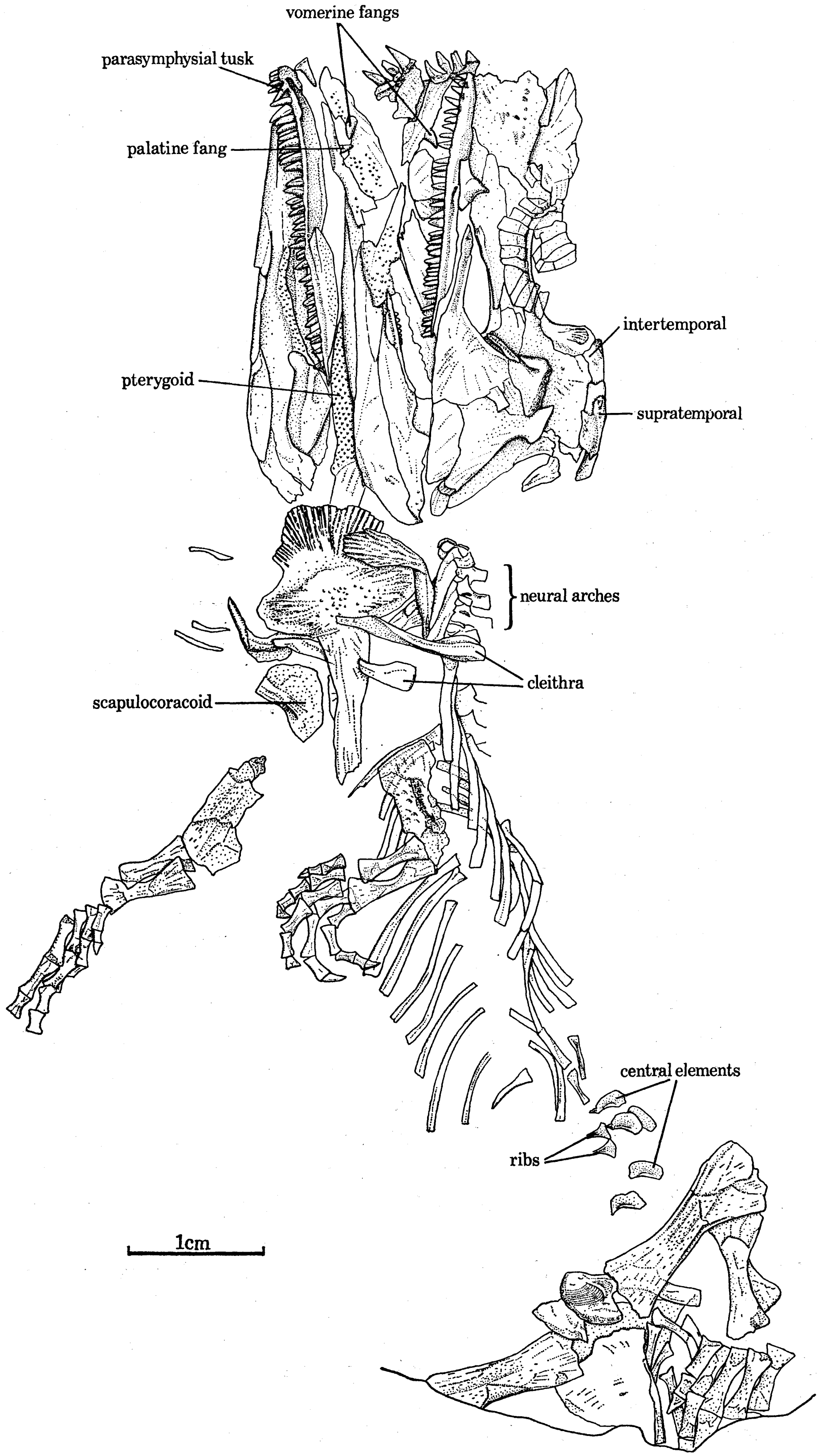
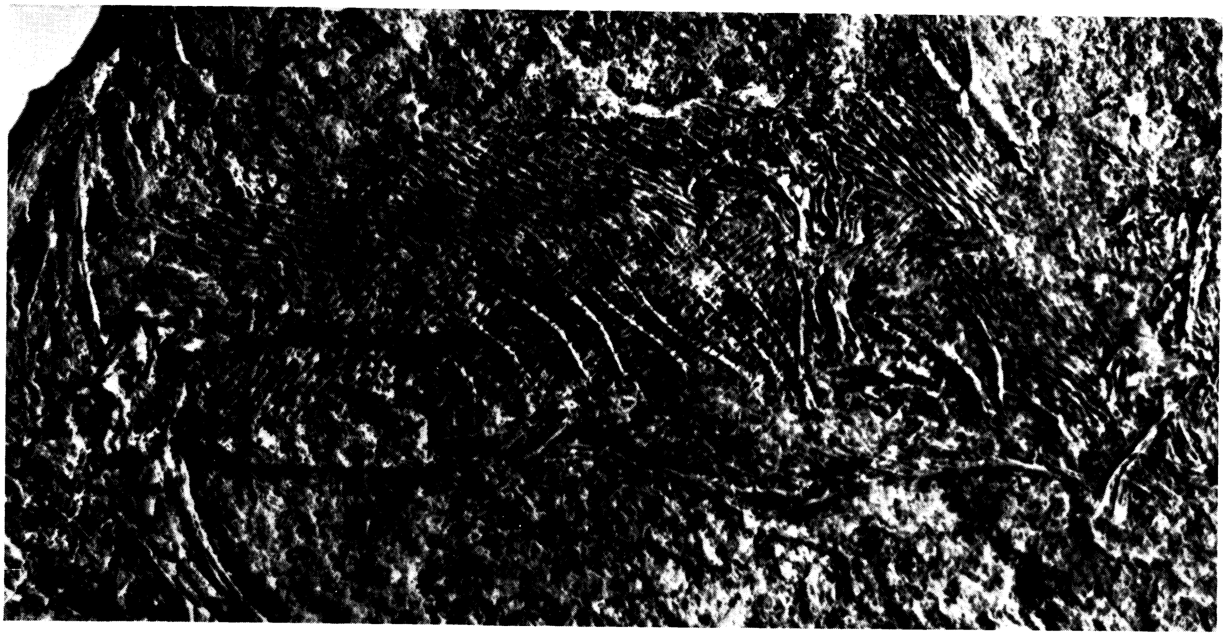


Figure 3. *Gephyrostegus bohemicus*. DMSW B.65. Skeleton.

FIGURE 4. A, *Gephyrostegus bohemicus*. DMSW B.65. Skeleton.

B



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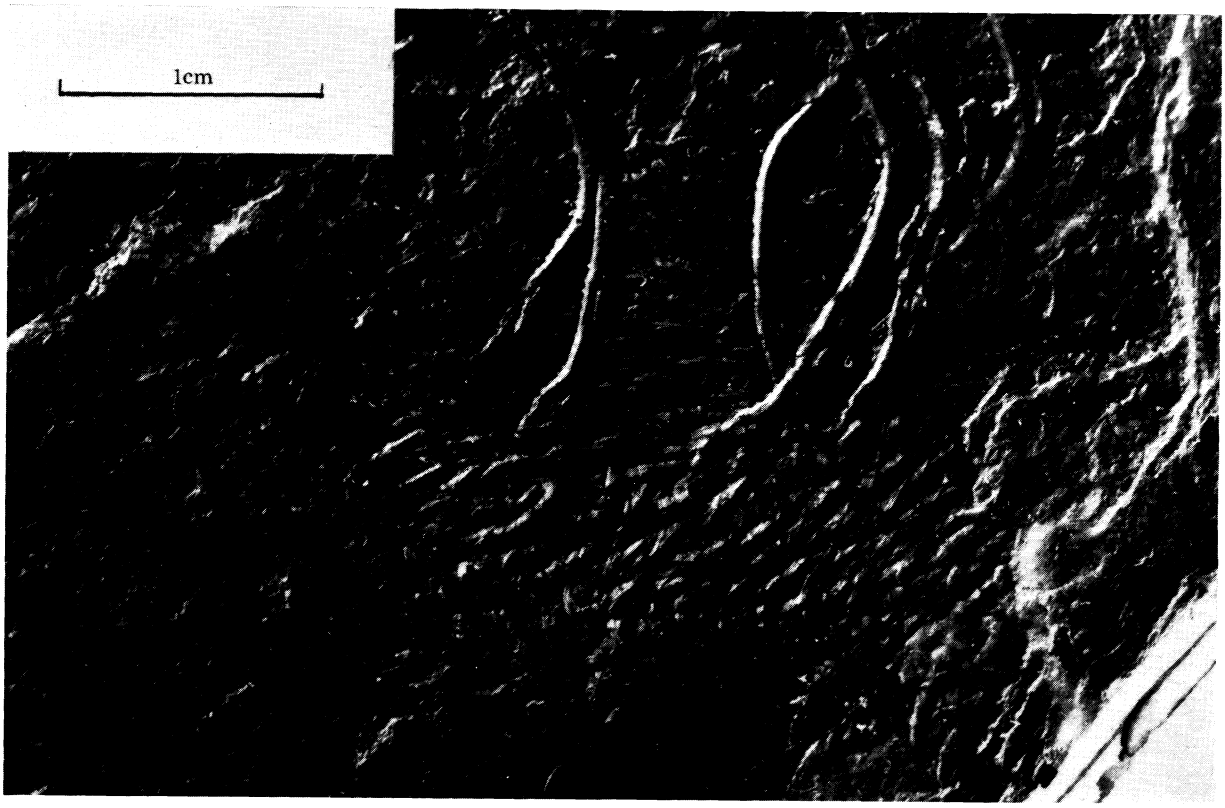


FIGURE 4. B, *Gephyrostegus bohemicus*. DMSW B. 65. Detail of scales. The anterior end of the animal is to the right.
FIGURE 4. C, *Eusauropleura digitata*. AMNH 6960. The anterior end of the animal is to the right.

with little occipital exposure. As in other anthracosaurs, intertemporal bones are retained. Despite their considerable dorsal exposure, they appear as primarily superficial elements, resting on extensive ventral lappets from the surrounding bones. This is particularly evident in Watson's specimen, in which the skull roof is exposed in ventral view. Laterally, the intertemporals still form a movable contact with the postorbitals. Except for the limited exposure of the frontal in the margin of the orbit, and the greater relative length of the nasals, there is little to differentiate the more anterior roofing bones from those of captorhinomorphs.

The posterior margin of the squamosal slopes posteroventrally at an angle of approximately 40° from the vertical, not appreciably more than in romeriids, and less than in some pelycosaurs.

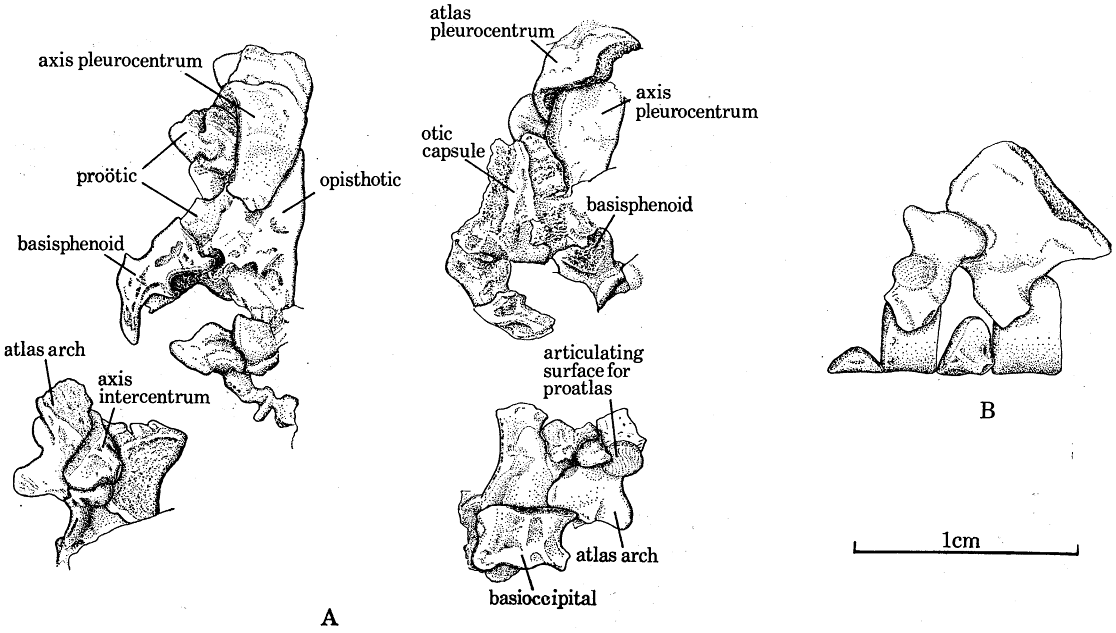


Figure 5. *Gephyrostegus bohemicus*. A, Brain case and elements of atlas-axis complex counterparts from the type. B, Reconstruction of atlas-axis complex, based on the type. Atlas intercentrum from MB. 1901 1378 a + b.

Near the posterior margin of the bone is a faint groove which presumably marked the line of anterior attachment of the tympanum. This membrane was probably supported dorsally by the supratemporal; unfortunately the posteroventral margin of this bone is not preserved on either side. A narrow quadratojugal separates the jugal from the margin of the cheek. The jugal extends a narrow process beneath the orbit to the lacrimal. The lacrimal apparently did not reach to the border of the external naris, but was separated from it by a superficial exposure of the septomaxilla. That bone is not preserved. The outline of the nasolacrimal duct is visible on the external surface of the left side as a result of crushing. It runs along the maxillary margin of the bone. The openings of this duct in the orbital margin are not visible.

The maxillae are very narrow; in the type specimen, 29 teeth are present on the right side, plus 18 empty alveoli (room for a total of 47 teeth). On the left side, 29 are present, with room for 16 additional (a total of 45). The right premaxilla has four teeth, and one empty alveolus. All five teeth are in place on the left side. Watson's specimen has 35 teeth in place in the left maxilla, with 12 additional alveoli. Four of the five premaxillary teeth are present on this side. Only three are visible on the right side. The similarity in number of the marginal teeth in these specimens of such different size indicates the value of the feature as a quantitative means of differentiating *Gephyrostegus* from other Nýřany genera with which it has been confused (see table 2, p. 284).

Except for a slight diminution in the size of the most posterior maxillary teeth, all the marginal teeth are of approximately the same size. There are certainly no 'canines' of the type described in romeriids or primitive pelycosaurs, nor is there any noticeable increase in the length of the anterior maxillary teeth. All of the teeth are in the form of pointed, slightly recurved, cones.

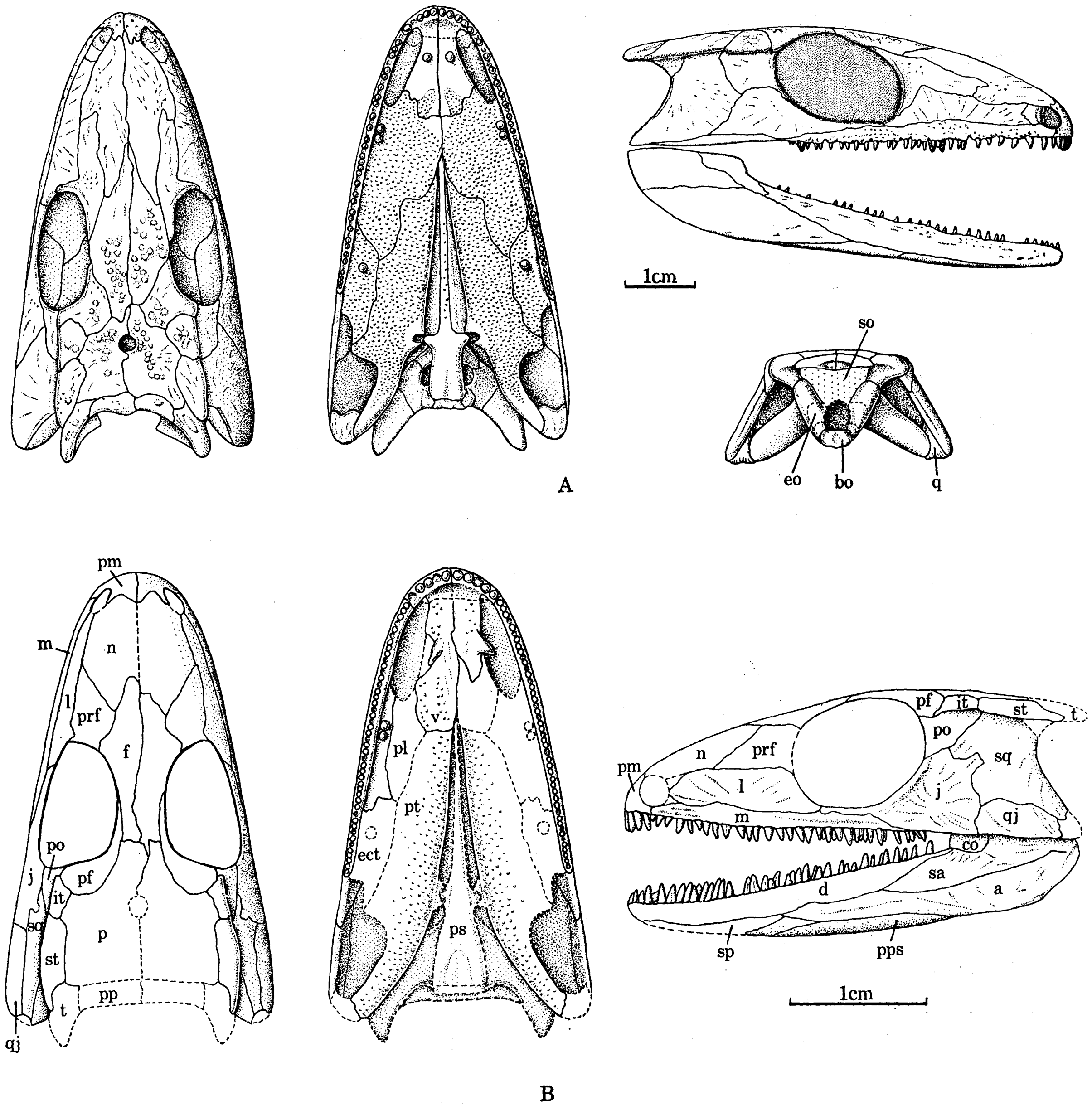


FIGURE 6. *Gephyrostegus bohemicus*. Restoration of skull. A, Type in dorsal, palatal, lateral and occipital views. Probable extent of supraoccipital indicated by coarse stipples. B, DMSW B.65 in dorsal, palatal and lateral views. Abbreviations: a, angular; bo, basioccipital; co, coronoid; d, dentary; ect, ectopterygoid; eo, exoccipital; f, frontal; it, intertemporal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf, postfrontal; pl, palatine; pm, premaxilla; po, postorbital; pp, postparietal; pps, postsplenial; ps, parasphenoid; prf, prefrontal; pt, pterygoid; q, quadrate; qj, quadratojugal; sa, surangular; so, supraoccipital; sp, splenial; sq, squamosal; st, supratemporal; t, tabular; v, vomer.

Many of those in the type specimen show vertical grooves near their base indicative of labyrinthine infolding of the enamel. This feature is less obvious in the smaller specimen described by Watson.

The palate, best shown in the type, follows the pattern of primitive labyrinthodonts. The basicranial articulation is movable, the pterygoids closely approach the parasphenoid and the ectopterygoids, palatines and vomers bear pairs of fangs. This is a more primitive configuration than that of embolomeres, in which the vomers lack fangs, or *Seymouria*, in which the ectopterygoids lack fangs. Fangs are of course not present on any of the palatal bones in reptiles. The fangs in *Gephyrostegus* are of approximately the same length as the marginal teeth. Labyrinthine structure can be clearly seen at the base of a broken palatine fang. All of the paired bones bear a shagreen of tiny denticles, randomly arranged. The denticles on the vomers are primarily limited to a narrow band extending anteriorly from the palatine.

Table 1

specimens	no. presacral vertebrae	diameter of centra	linear unit ($r^{2/3}$*)	average vertebral length		humerus		length of radius	
				mm	l.u.†	mm	l.u.	mm	l.u.
Gephyrostegus (second Berlin specimen)	24	5	1.84	5.8	3.2	28	15.2	14	7.6
Archeria (MCZ 2045)	40	22	5	—	—	65.5	13	35	7
Eogyrinus (DMSW 28)	40	48	8.32	36	4.33	—	—	—	—
Paleothyris (MCZ 3482)	32	1.4	0.79	3	3.8	15	19	9	11.4
Varanosaurus acutirostris (AMNH 4174)	27	14	3.65	15	4.1	73	20	52	14.3
Ophiacodon mirus (WM 671)	27	19	4.48	20	4.45	102	22.8	73	16.3

specimens	length of ulna		femur		tibia		fibula		length of presacral column	
	mm	l.u.	mm	l.u.	mm	l.u.	mm	l.u.	mm	l.u.
Gephyrostegus (second Berlin specimen)	19.5	10.6	33	17.8	23	12.5	24	13	140	76
Archeria (MCZ 2045)	54	11	85.5	17	45.5	9	50.5	10	—	—
Eogyrinus (DMSW 28)	—	—	134	16	—	—	—	—	1500	180
Paleothyris (MCZ 3482)	10	12.6	15.5	19.6	10	12.6	11	14	96	121
Varanosaurus acutirostris (AMNH 4174)	—	—	87	23.8	70	19.2	—	—	405	111
Ophiacodon mirus (WM 671)	—	—	125	27.8	100	22.3	103	23	540	121

* r = radius of centrum. † l.u. = linear units.

The quadrate ramus of the pterygoid forms a gently curving medial wall to the temporal fossa. There is no development of a transverse flange, so significant in the origin of reptiles (Carroll 1969*c*). The parasphenoid is largely covered by the left lower jaw. A row of denticles are visible protruding through the jaw, outlining the extent of the stem. The posterior portion of the parasphenoid is narrow, like that of typical primitive reptiles and embolomeres, rather than extending laterally as in seymouriamorphs.

The quadrate resembles in relative size and general proportions that of romeriid captorhinomorphs. It has a massive triangular base supporting the articulating surface. Anteriorly, this area is covered medially by the quadrate ramus of the pterygoid. Dorsally the bone extends as a fairly thin plate. It bears a narrow ridge, extending at about 40° from the vertical, marking the anterior limit of the area which is overlapped by a medial extension of the squamosal. There is no recess to receive the stem of the stapes. The epipterygoid is not exposed.

The anterior, sphenethmoid, portion of the braincase is not visible. The general outline of the otic-occipital region of the braincase can be judged by the relative position of the parasphenoid and the paroccipital processes of the tabulars. Endochondral bones from this area are disarticulated and lie, somewhat scattered, behind the skull. Although some of the elements are lost, and the identity of others is uncertain, the general configuration follows the pattern of the embolomere *Palaeogyrinus* (Panchen 1964) and is certainly distinct from that of either seymouriamorphs or typical captorhinomorphs.

What appears to be the right otic capsule lies between the cheek region and skull roof, showing nothing but its posterior margin. The left capsule is displaced to lie behind the right side of the skull. Its lateral surface is visible on the block showing the palate; and the medial, or internal, surface on the block showing the skull roof. Both views are enlarged in figure 5. The posterior portion of the paroccipital process is obscured by the atlas and axis pleurocentra. The anterior portion, formed by the pro-otic, extends above the pro-otic incisure. The pro-otic and opisthotic are closely united. Their ventral margin is of unfinished bone where they surround the fenestra ovalis. The anterior margin of this opening is formed by a dorsal extension of the basisphenoid, which overlaps the pro-otic. As in typical early reptiles and embolomeres, the fenestra ovalis is medially placed, in contrast with the condition in seymouriamorphs. The interior surface of the otic capsule is entirely unfinished bone. A large groove crosses the dorsal process of the basisphenoid longitudinally, apparently exiting from the braincase shortly anterior to the fenestra ovalis. In analogy with *Captorhinus* (Price 1935) this groove may have provided passage for the palatal branch of the VIIth nerve.

No element is exposed which can be identified as a supraoccipital. This bone is small in *Palaeogyrinus* and may have remained unossified in *Gephyrostegus*. The elaboration of this bone is one of various features which distinguishes the braincase of early reptiles. Exoccipitals have not been definitely recognized, although material lying below the posterior margin of the left opisthotic might be a partially exposed left exoccipital.

The entire ventral surface of the basioccipital is exposed just posterior to the left atlas arch. The condylar surface was apparently poorly ossified, since it is not exposed posterior to the ventral area of finished bone. The dorsal surface is exposed on the left side, behind the axis intercentrum. A large bone, one side of which shows an extensive unfinished surface, lies just above the basioccipital. Its identity cannot be determined. It might be part of the basisphenoid. The reconstruction of the occiput (figure 6) is somewhat speculative.

No element can be identified as the stapes. The position of the fenestra ovalis, relative to the probable area of the tympanum, is such that dorsolateral orientation of the stapes would appear to be much more likely than ventrolateral. A dorsolaterally directed stapes would need to be only about one half the length of one directed ventrolaterally, to reach the tympanum.

The lower jaws are exposed both medially and laterally in the type and Watson's specimen. Their most surprising feature is the possession of parasymphysial fangs. These are known among the anthracosaurs only in Mississippian embolomeres (Romer 1963). This is an unexpectedly primitive character in a generally advanced form. The surangular, angular and splenials are large, relative to the dentary and their surface is only lightly sculptured. The dentary is marked by deep pits, most numerous near the symphysis. There is no convincing evidence that these are remnants of a lateral line canal groove system. There are two splenials, a feature noted in at

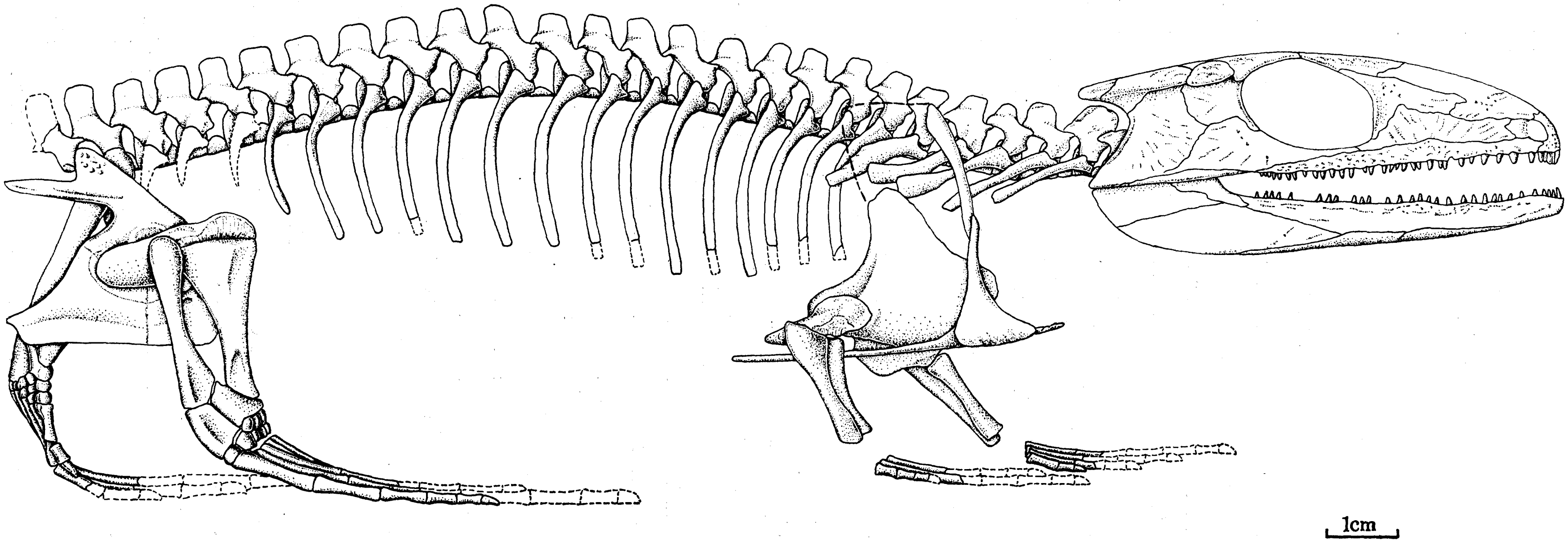


FIGURE 7. *Gephyrostegus bohemicus*. Restoration of skeleton. Based on the type and MB. 1901.1378 a+b.

least some romeriids, although there is only a single one in most reptiles. The three coronoids are covered by a shagreen of tiny teeth. The prearticular extends well over half the length of the jaw. The inframeckelian fossa occurs at the point of its juncture with the postsplenial. The adductor fossa extends less than one fourth the length of the jaw. The articular resembles very closely that of romeriid and captorhinid reptiles, with a prominent medial extension of the articular surface from the body of the jaw.

Vertebrae

A series of anterior arches and scattered centra are preserved in the type. In the very immature specimen described by Watson a few neural arches are visible, and some very incompletely ossified central elements. All of the latter appear to be more or less crescentic in shape, suggestive of the schizomerous structure of the centra in very immature specimens of discosauriscids (Špinar 1952). The entire precaudal vertebral column is preserved, with the arches in almost continuous articulation, in the second Berlin specimen. There are 24 presacral vertebrae. A short gap occurs between the 10th and 11th arches, but there is no reason to suppose that any additional elements had been present. There is a single vertebra which bears a sacral rib. The first caudal vertebra is preserved in this specimen. Nothing more of the tail is known in the currently available specimens of this genus.

In all the vertebrae, the neural arches are weakly attached to large intercentra and pleurocentra which have typically become separated. The neutral arches are not swollen. The zygapophyses are close to the midline, as is the case in primitive captorhinomorphs and most pelycosaurs, and in contrast with seymouriamorphs, limnoscelids and diadectids. The two sides of the arches are frequently slightly displaced. The spines are in general quite long and high, in contrast to the condition in early romeriid captorhinomorphs. Large spines, embedded in the axial musculature, presumably helped to stabilize the column in which the arches were not firmly attached to the centra. The arches have well developed transverse processes for attachment of the tuberculum of the ribs. As seen in medial view, the pedicel of the arch has a large area for attachment to the pleurocentra.

The intercentra are openly crescentic elements which appear roughly triangular in lateral view in the articulated column. Their midventral length is approximately as great as that of the pleurocentra. Apparently none of the intercentra supported the neural arches. As preserved in the second Berlin specimen, only a few show their lateral surface at all clearly. Surprisingly, only the axis intercentrum and one just anterior to the sacrum show specialized areas for attachment of the capitulum of the ribs. In the centre of the trunk region the area of rib articulation was apparently not distinct from the area of unfinished bone at the posterior surface of the centrum, or else occupied an unossified dorsal extension of the bone.

The pleurocentra have the configuration, when viewed end on, of horseshoes with a very large opening for the notochord. None are complete cylinders. They have large areas, facing anterodorsally, for support of the pedicel of the arch.

In reconstruction of the vertebral column (figure 8) large gaps are evident dorsal to the intercentra. It is probable that this element was supplemented by cartilage in the living animal. This suggestion is supported by the presence of an area of articulation at the posterodorsal margin of the pleurocentrum. It is possible that the intercentrum was fully cylindrical in life. The very large notochordal canal in the pleurocentra was probably also partially filled with cartilage, making this element very similar to that of embolomeres.

The basic structure of the vertebrae of *Gephyrostegus* is similar to that of embolomeres (Panchen 1966, figures 3 and 5), but ossification is more extensive in the latter group, even in individuals of very small size. In the embolomere *Calligenethlon* (Carroll 1967*a*) both pleurocentra and intercentra are complete, although thin walled, cylinders in vertebrae with a diameter as small as 4 mm. The notochordal canal is almost occluded in centra with a diameter of 7 mm. The average diameter of the centra in the Berlin specimens of *Gephyrostegus* is between 5 and 6 mm. It is possible that larger specimens of *Gephyrostegus*, or other gephyrostegids, might be more completely ossified, and thus have a structure which would be difficult if not impossible to differentiate from that of embolomeres. This raises the possibility that some large, isolated centra attributed to embolomeres actually pertain to gephyrostegids. The number of presacral vertebrae allow the two groups to be clearly differentiated, but articulated specimens of anthracosaurs seem much more the exception than the rule.

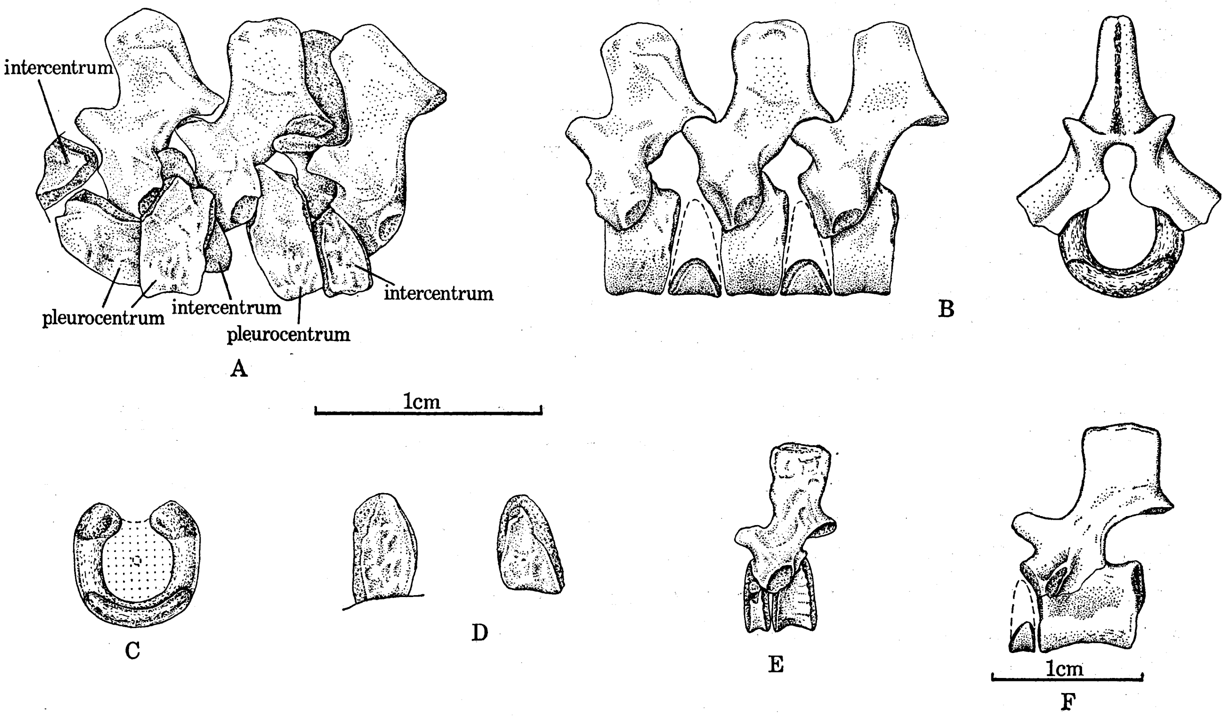


Figure 8. *Gephyrostegus bohemicus*. Vertebrae. A, Vertebrae 8, 9 and 10 from MB 1901.1378 a+b. B, Reconstruction based on A, lateral and anterior views. Probable cartilaginous extension of intercentra indicated by broken lines. C, Anterior view of centra. Possible cartilaginous extension of pleurocentra indicated by coarse stipples. D, Intercentra from the 14th and 21st presacral vertebrae. E, Vertebra of the embolomere *Eogyrinus* (from Panchen 1966, p. 203). F, Vertebra of a romeriid captorhinomorph. MB 1901.1379. Probable cartilaginous extension of intercentrum indicated by broken lines.

The differences between the vertebrae of *Gephyrostegus* and those of seymouriamorphs are considerably greater, since they involve a considerable structural modification of the arch, as well as fusion to the centra.

Surprisingly, there is not a very great difference between gephyrostegid vertebrae and those of primitive reptiles. The neural arch is fused to the pleurocentrum, but the line of attachment, in essentially the same position as that of gephyrostegids, is frequently still evident. Although the length of the intercentrum in relation to the pleurocentrum is always reduced, the former element may retain a structural function, and in some cases the bony crescent was obviously supplemented by a cartilaginous portion which extended for much of the height of the pleurocentrum. The dimensions of this dorsal extension diminish considerably in all advanced groups.

It has been repeatedly suggested that the reptilian vertebral structure is comparable with that of microsaurs (Westoll 1942; Vaughn 1962; and most recently Brough & Brough 1967*a*, *b*, *c*), and that this similarity indicates close relationship. The confirmation of haemal arches in the tail of the microsaur *Pantylus*, and the lysorophid *Lysorophus* (Carroll 1968) presumably establishes the homology of the trunk centra in those groups with the pleurocentra in labyrinthodonts and amniotes. Although the reports of trunk intercentra in microsaurs are based on equivocal evidence (see Romer 1968, p. 101), they presumably existed in some members of that group, or among their ancestors, if they are in any way related to labyrinthodonts, or even to their ancestors among the rhipidistians.

The probable homology of the centra in microsaurs and reptiles is definitely not sufficient to indicate close relationship, however. As has been recently shown in a comprehensive investigation of all described microsaurs (Carroll & Baird 1968), the pattern of the skull roof and palate and the relation of the occipital condyle to the atlas–axis complex are consistent among microsaurs, and fundamentally different from the structure known in primitive reptiles. The resemblances in vertebral structure and general body proportions between microsaurs and reptiles are clearly due to convergence and do not reflect a close common ancestry. Although the structure of the centra in seymouriamorphs and embolomeres is quite different from that of reptiles, knowledge of the vertebrae of *Gephyrostegus* indicates the relatively minor modification necessary to transform the primitive anthracosaurian vertebral structure into a reptilian pattern.

Cervical vertebrae are preserved in both Berlin specimens. Elements of the atlas-axis complex are intimately associated with the braincase in the type (figure 5). They are better articulated in the second Berlin specimen, but show less detail. In that specimen, the anterior face of the atlas arch and the posterior surface of the atlas intercentrum are obscured by a bone which is presumably the proatlas. This oval element is poorly preserved, but has what appears to be an articulating surface at one end. The left side of the paired atlas arch is exposed both medially and laterally in the type. As in romeriids and pelycosaurs, it bears no spine. It has a conspicuous raised area anteriorly for articulation with the proatlas. There is a large area on the anteromedial surface for articulation with the pleurocentrum. The atlas intercentrum, exposed in the second Berlin specimen, is a small, barely crescentic element showing areas for articulation with the occipital condyle and the pleurocentrum. The posterior ventral margin is partially obscured by the proatlas, but there are paired, low, longitudinal ridges which presumably terminate, as in *Ophiacodon* (Romer & Price 1940, figure 44E), in articulating facets for the capitulum of the first cervical rib. The atlas pleurocentrum is visible from the left side, just above the left otic capsule in the type. It is U-shaped, with the anterodorsal margin incised to receive the arch.

The axis intercentrum partially surrounds the atlas arch. It is a low sided crescent, showing, in exception to most trunk intercentra, a well developed articulating surface for the capitulum of the rib. The axis pleurocentrum is wrapped about the paroccipital process of the opisthotic. It is in the shape of a very high sided crescent. The area for articulation with the arch is exposed in the second Berlin specimen. Both the atlas and axis pleurocentra have very large notochordal canals. The spine of the axis arch is very large, overhanging the zygapophyses and much of the atlas arch anteriorly. Posteriorly it is marked by a vertical groove for attachment of interspinous ligaments or muscles. The neural spine of the third vertebra is of approximately the same dimensions as those of the fifth and more posterior thoracic vertebrae. Like the axis, it is grooved posteriorly. The spine of the fourth vertebra is shorter and more narrow, anteroposteriorly, than those adjacent. It is apparent that, like the reduced neural spine in *Eryops*, the small size facilitated dorsal flexure of the neck. A similar specialization of the third cervical vertebra occurs in an undescribed romeriid from the Middle Pennsylvanian of Linton, Ohio. Other Pennsylvanian romeriids do not show this specialization since none of the neural arches is sufficiently large to interfere with flexure.

The general anatomy of the cervical vertebrae is exactly what would be expected in an ancestor of the romeriids and pelycosaurs, and very distinct from that of *Seymouria*.

Ribs

Ribs were present throughout the column, although the first cervical is not preserved in the well articulated second Berlin specimen. The head of the second cervical rib is not well preserved, but the tuberculum and capitulum of both of the anterior ribs must have been distinctly separated, judging by the distance between the articulating surfaces of the atlas and axis intercentra and arches. More posteriorly, the heads of the ribs are definitely closely set, like those of embolomeres and captorhinomorphs and in contrast with the condition in seymouriamorphs. The shafts of the cervical ribs are narrow and apparently extended posteriorly as well as ventrally. Those beneath the shoulder girdle also extended posteriorly, and are broadly flattened. Similarly shaped ribs are present in this region in *Seymouria*, *Limnoscelis* and *Diadectes* and are presumably related to the large size of these forms in contrast with the romeriids. Large pelycosaurs, however, do not show such specialization of the ribs beneath the shoulder girdle. The ribs in the mid-region, from the seventh to the twentieth vertebrae, have narrow shafts and end bluntly, suggesting the attachment of a cartilaginous sternum, at least anteriorly. The immediately presacral ribs, seen in Watson's specimen, are very short and sharply pointed.

Both sacral ribs are visible in the second Berlin specimen. They have well developed, separate surfaces for articulation with the transverse process and the intercentrum of the sacral vertebra. The blade is bent sharply into a vertical plane and is oval in outline. The immediately postsacral ribs, preserved only in the immature specimen described by Watson, are large, not fused to the centra, and extend posteriorly to lie alongside the tail. In reptiles these ribs are short and fused to the centra.

Appendicular skeleton

The pectoral girdle is known in all three specimens. The dermal elements are all well developed. The cleithrum has a long, rather narrow, flattened stem, recessed anteriorly for reception of the clavicular stem, and with a posterior flange for attachment to the dorsal portion of the scapular blade. The dorsal end is not expanded appreciably. This area is smaller than that of limnoscelids (Carroll 1967*b*), but comparable with that of the romeriid described from Nýřany, Czechoslovakia, by Brough & Brough (1967*c*, figure 10). The clavicles follow the general pattern of all primitive tetrapods. The ventral blade is expanded to a greater extent than that of captorhinomorphs and pelycosaurs, but is smaller than that of embolomeres and *Seymouria*. It is sculptured in a similar fashion to that of *Archeria*. The anterior plate of the interclavicle is very large and recessed ventrally for reception of the clavicular blades. The anterior border is striated both dorsally and ventrally, and the more posterior ventral surface is finely sculptured. There is a long posterior stem.

The endochondral shoulder girdle, generally resembling that of the embolomere *Archeria*, is ossified as a unit. It lacks the peculiarities attributed to that of *Seymouria*. In Watson's specimen, the ossified portion is very small. Even in the other much larger specimens there must have been a considerable cartilaginous dorsal expansion of the scapular blade, to judge from the height of the top of the cleithrum. The glenoid is very large and appears to extend close to the posterior margin of the coracoid. The supraglenoid buttress is pierced by the supraglenoid foramen. The ventral portion of the coracoid area is not well exposed in any of the specimens. The outline of the medial surface is shown in the type, but little detail is visible.

The humerus is too poorly ossified in Watson's specimen for comparison with other forms. It is well ossified in the other specimens and resembles in general that of embolomeres. The left humerus is exposed dorsally in the type and the right can be seen in both dorsal and ventral views in the second Berlin specimen. The bone is 28 mm in length, equivalent to the length of approximately five anterior vertebrae. The expanded proximal area is somewhat crushed in both specimens. The dorsal surface appears to have been vaguely hemispherical, as in embolomeres. Although somewhat distorted, the proximal articulating surface, as in *Archeria*, faces primarily proximally. Anteriorly, the shaft is extended, as in *Archeria*, by a prominent lateral keel which continues for much of the length of the bone. Unlike the condition in *Archeria*, there does not appear to be a distinct deltopectoral crest at the proximal end of this structure. These distinctive features are among the characteristics by which *Gephyrostegus* may be recognized as a close relative of the Linton, Ohio, genus *Eusauropleura*. A prominent ectepicondylar ridge runs along the dorsal surface of the shaft to its distal extremity, rising well above the articulating surface. There is an extensive, but thin, squarish entepicondylar region, pierced at its proximal margin by the entepicondylar foramen. The entire bone is flattened into a single plane, making it difficult to establish the degree of twisting of the proximal and distal areas in the living animal. Except for the ectepicondylar ridge, the dorsal surface of the area of distal expansion is flat, without the longitudinal groove reported in *Archeria*. The distal articulating surfaces are considerably better defined than those of *Archeria*, with a distinct hemispherical knob to receive the head of the radius. The area for articulation with the ulna, which is continuous with that of the radius, extends around the end of the bone onto the dorsal surface. The distal end of the entepicondylar ridge also bears an unfinished surface.

Romer (1957, p. 122) associated the configuration of the humerus of *Archeria* with aquatic habits. Although there might be some doubt as to the proportions of time spent on land and in the water by *Gephyrostegus*, the general body proportions—shortness of vertebral column, proportionately large and well ossified limb bones—suggest a more terrestrial habit than those of the long-bodied, short-limbed, poorly-ossified embolomeres. The similarities of the humeri in *Archeria* and *Ichthyostega*, cited by Romer, and that of *Gephyrostegus* suggest rather that this pattern is typical of early tetrapods, regardless of particular habits. Certainly *Parioxys*, which Romer cites as also having the humeral characteristics of *Archeria*, appears to be strongly specialized toward terrestrial habits in other features of its anatomy (Moustafa 1955; Carroll 1964*b*).

The radius, which is slightly more than one half the length of the humerus, is a simple, cylindrical bone, with slightly flattened areas of proximal and distal expansion. Both articulating surfaces are at right angles to the shaft, the proximal being somewhat wider. Except for its slightly greater relative length and the absence of rugose areas, it is very similar to that of *Archeria*. The ulna is likewise similar in structure and proportions. The shaft slightly exceeds that of the radius in length, but the total length of the bone, including a well ossified olecranon, is about 40 % greater. Romer & Price cite the ossification of the olecranon as indicative of adult

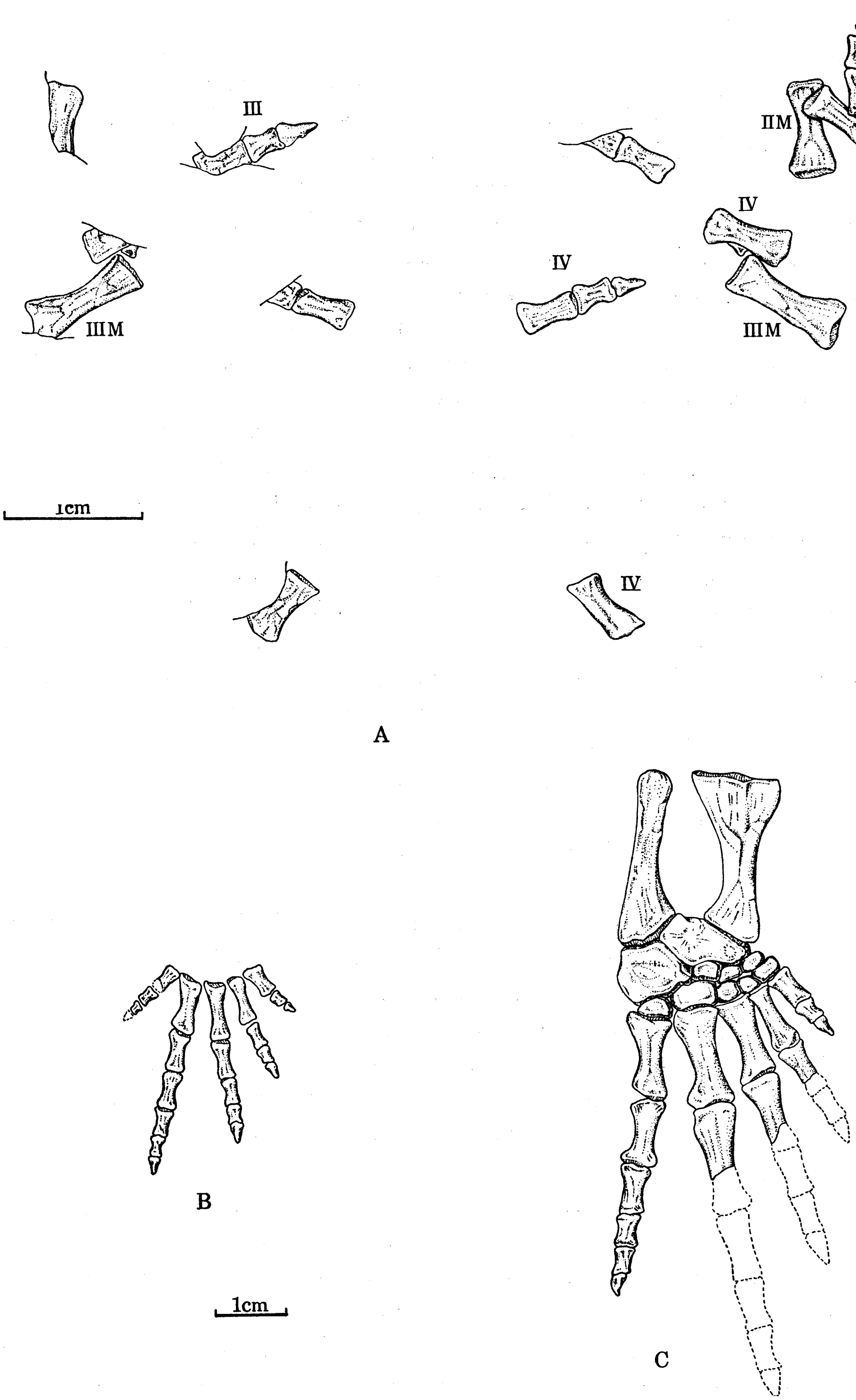


FIGURE 9. *Gephyrostegus bohemicus*. A, Metacarpals and phalanges from the type; counterparts. B, Restoration of the hand. Metacarpals and proximal phalanges from MB 1901.1378 a+b, distal phalanges from the type. C, Restoration of the foot, based on MB 1901.1378 a+b. Digits indicated by Roman numerals. M, metacarpal.

status among pelycosaurs (1940, p. 146). If that criterion can be used here, then the Berlin specimens of *Gephyrostegus* must be fully mature.

Two carpal bones are preserved in the second Berlin specimen near the distal ends of the epipodials. Although they are not articulated, they may tentatively be identified as the radiale and intermedium. The small width of the distal end of the radius indicates that, as in *Archeria* and early reptiles, this bone did not articulate with a proximal centrale. A number of articulated metacarpals and phalanges from the right hand are present in this specimen. All of the metacarpals are in their natural position, although the distal end of the fifth is missing. Proximal phalanges of all but the third digit are in place, as is the first ungual, and the second phalanx of the fifth digit. In the type, a number of metacarpals and phalanges lie clustered to the left of the body, approximately 7 cm from the head of the left humerus. To save space, they have not been illustrated with the remainder of the skeleton, but are shown separately in figure 9. They are probably all from one hand. By comparison with the proximal elements in the second Berlin specimen, the identity of many of the elements can be specified. Only two metacarpals are present, the second and the third. Three digits are represented by the distal three phalanges. None compares with the first or fifth in the other specimen, so they must be from the second, third and fourth. One further phalanx is of the small size expected from the penultimate of the first or fifth. The other large phalanges are presumably the first of the third digit, and the first and second of the fourth. Only a single phalanx, the fifth ungual, is not represented in either specimen. As reconstructed, the phalangeal count is 2, 3, 4, 5, 3, as in typical primitive reptiles.

Both hands are preserved, more or less in articulation, in Watson's specimen. The left appears to have a phalangeal count of 2, 3, 3, 3, 4. The phalanges of the right hand are somewhat jumbled, but there is no evidence for a higher count. Considering what is known of the other specimens of *Gephyrostegus*, anthracosaurs in general, and *Eusauropleura* (see below), it is obvious that this particular specimen is exceptional in this regard. Considering the similarities in other features of the anatomy to the type of *Gephyrostegus*, it is not probable that this is a taxonomically significant feature.

The pelvic girdle is shown in its mature form in the second Berlin specimen, with the three elements firmly attached. In the immature specimen described by Watson, the pubis is not ossified, and the ilium is not attached to the ischium. The iliac blade is well exposed in the former specimen, and its outline can be determined in the latter, where the femur has been deformed over it. In both specimens the blade has both dorsal and posterior processes, as in ichthyostegids and embolomeres, but they are not as clearly demarcated as in these forms. The general pattern appears to be approaching the condition noted in primitive reptiles in which there is a single posterodorsally oriented blade, with a slight anterodorsal expansion. In *Gephyrostegus*, the anterior margin of the dorsal process extends posteriorly at approximately a 45° angle, rather than directly vertically, as in *Archeria* or the type of *Diplovertebron* (see below). A recessed area is visible on the medial surface of the blade for attachment of the sacral rib. Fairly deep longitudinal grooves extend the length of the ventrolateral surface of the posterior prong. The acetabulum is poorly preserved on both sides of the girdle in the Berlin specimen. The pubis, although not clearly visible, resembles in general that of *Archeria*. The ischium, however, is notably shorter.

The femora in the second Berlin specimen resemble in general those of *Archeria*, but the extremities are more completely ossified. Except for *Limnoscelis*, the femur appears considerably stockier than in most primitive reptiles, although this may be somewhat accentuated by crushing. The area of the internal trochanter is obscured on both sides. It is certainly not a massive, rugose structure as in *Archeria*. It continues distally as the adductor ridge which extends to the distal extremity. There is no fourth trochanter. The entire distal end of the bone has an unfinished surface. A place for attachment of joint ligaments or for the ischiotrochantericus and the puboischiofemoralis internus muscles is marked by a triangular area of unfinished bone on the posterior dorsal surface, essentially continuous with the area of proximal articulation.

The tibia and fibula are shown dorsally and ventrally in the same specimen. They resemble in general those of *Archeria*, but are somewhat more lightly built, and the articulating surfaces less extensive. The degree of twisting of these surfaces cannot be determined because of the essentially two-dimensional preservation. The cnemial crest is prominent. The tibia has a single, distal articulating surface, in contrast to two separate areas in *Archeria*, corresponding with the single articulating surface formed by the fused tibiale and intermedium. The distal extremity of the tibia is reduced in relative size in the successively advanced reptilian genera *Hylonomus* and *Paleothyris*. The proximal end of the fibula is considerably less expanded than is that of *Archeria*. The distal end is also smaller and has distinct areas for articulation with the calcaneum and intermedium.

The tarsals are preserved in almost their natural position in the second Berlin specimen. They show a pattern intermediate between that of primitive amphibians and typical captorhinomorphs. In typical amphibians, as for example *Archeria* (Romer 1957, figure 15), the tarsus consists of four proximal elements, fibulare, intermedium, tibiale, and proximal centrale. There are two distal centralia, and five distals. In typical early reptiles, there are two proximal elements, a calcaneum, equivalent to the fibulare, and an astragalus which Peabody (1951) has shown develops ontogenetically from a fusion of the tibiale, intermedium and proximal centrale. In *Gephyrostegus*, the tibiale and intermedium are fused dorsally, although the originally separate centres of ossification are represented by radiating patterns of fine striations. Ventrally the bones are suturally united, but not fused. The proximal centrale remains an independent centre of ossification, but articulates closely with the intermedium and tibiale. A notch for the perforating artery is evident on the medial margin of the calcaneum, adjacent to the line of juncture of the intermedium and proximal centrale. There are two distal centralia of approximately equal size. The distals follow the typical pattern seen in both anthracosaurs and reptiles. The metatarsals, at least the proximal portion of all proximal phalanges, and the distal phalanges of digits 1 and 5, are in place. As in *Archeria*, the fifth digit has five phalanges. The first has, typically, two. The remaining three digits are restored (figure 9) as having a reptilian count. The metatarsals and proximal phalanges are also preserved in Watson's specimen. As restored, the foot is approximately twice the length of the hand. Such a disparity is common in other Carboniferous tetrapods. The structure of the proximal tarsals appears as an ideal preliminary to that of typical captorhinomorphs. Surprisingly, the most primitive forms which are classified as reptiles, *Limnoscelis* (Romer 1946) and *Tseajaia* (Vaughn 1964), have a more primitive pattern with four separate proximal tarsals. On the other hand, an astragalus has independently evolved in at least two microsaur genera, *Pantylus* (Carroll 1968) and *Tuditanus* (Carroll & Baird 1968).

Limb proportions

The limb elements in *Gephyrostegus* appear quite large relative to the length of the trunk region. In order to obtain a more objective comparison, use was made of what Romer (1957, p. 151) referred to as an 'orthometric linear unit', based on the diameter of the trunk vertebrae.

According to Romer & Price (1940, pp. 7–9), this dimension (or more specifically, the radius of the centra raised to the power of $\frac{2}{3}$) should be directly correlated with the total weight of the animal, and so should provide a more meaningful standard than any other linear dimension. The pertinent measurements are given in table 1, page 273, together with comparative values for embolomeres, a romeriid and two pelycosaurs. The values in linear units, for *Gephyrostegus*, are comparable with those of embolomeres, somewhat less than those of the captorhinomorphs, and substantially less than those of *Ophiacodon*. This is in marked contrast to comparision with other linear measures. Comparison with the length of the individual vertebrae and the total presacral column gives quite the reverse picture. Although these values may not be as directly related to the bulk of the animal as is the vertebral diameter, they should be in general agreement.

TABLE 2. COMPARISON OF ANTHRACOSAURS AND REPTILES OF THE NÝŘANY FAUNA

		length of skull	total no. of maxillary teeth	tooth structure	vertebral structure
Gephyrostegus bohemicus	type	63	47	labyrinthine no canines	proto-embolomerous
	Watson's specimen	34	47	labyrinthine no canines	very poorly ossified
Solenodonsaurus janenschi	type	140	35	labyrinthine no canines	reptilian
	Pearson's specimen	58	33	labyrinthine no canines	incompletely ossified reptilian
Brough's specimen I		35	*ca.* 26	non-labyrinthine canines	reptilian

Romer (1957) expressed some hesitation in applying this basis of comparison to the embolomere *Archeria* since that genus was clearly of aquatic habits, with the weight of the body supported by the buoyancy of the water. A second, equally important, reason to question the advisability of comparison with embolomeres is the nature of the vertebral structure. Since the centra are composed of two loosely articulating elements, neither of which is solidly attached to the neural arches, the vertebrae are structurally weaker than those of reptiles. If this weakness were compensated for by greater width of the individual centra, this would alter the basis on which the comparison is made. The apparently small size of the limbs in *Gephyrostegus*, as measured in comparison with the radius of the centra, could just as well be interpreted as indicating the large size of the vertebrae.

The use of such a standard 'orthometric linear unit' may be a valid basis for comparison within a particular group such as the pelycosaurs, but even here the difference in overall vertebral structure, as between the long spined *Ophiacodon*, and the short spined *Varanosaurus*, should be considered. Between groups with such distinct vertebral structure as embolomeres and reptiles the comparison has little meaning. Comparison may be relevant between embolomeres and gephyrostegids, however. Although the ossification of the centra is more extensive in the former group, there is not a great deal of difference in structure, particularly in the relation between the pleurocentra and the arches. If this is a valid assumption, it is interesting to note that the relative size of the limbs in *Gephyrostegus*, as measured in this manner, is just slightly greater than that of *Archeria* and *Eogyrinus*. The relative length of the presacral vertebral column in the latter genera, in contrast, is at least 50 % greater. This indicates a considerably greater bulk relative to the size of either limbs or vertebral diameter. The fact that the central diameter is much greater, relative to the length of the vertebral column, in *Gephyrostegus*, may be explained by its terrestrial habits and hence its need for additional support, in contrast to the aquatic embolomeres.

Scales

Large, oblong ventral scales, of the pattern common to embolomeres, are conspicuous features of all three skeletons. In Watson's specimen (figure 4) they are in place, in the typical chevron pattern, extending between the girdles. The scales become more circular in the lateral rows. In the Berlin specimens they are scattered, showing their individual structure more clearly. Dorsal scales are present in the two Berlin specimens. They apparently had had the configuration of the dorsal scales in discosauriscids (Špinar 1952), *Eusauropleura* and *Solenodonsaurus* (see below), but they are very insubstantial and tend to be mashed together so that they are not practical to illustrate. They are most clearly shown where they are in contact with the medial surface of the scapulocoracoid in the type.

Reconstruction

There is little problem in restoring either the skull or the postcranial skeleton (aside from the carpals, phalanges and the tail) on the basis of the Berlin material. Watson's specimen confirms the association of such an anthracosaurian skull with a short trunk region. The posture of the limbs is established on the basis of the typical pattern in primitive tetrapods. The amount of crushing undergone by these specimens precludes accurate determination of the shape and orientation of the articulating surfaces. The size of the limbs relative to the trunk region gives the animal a very stocky appearance, actually rather comparable to *Ichthyostega*.

Except for the presence of five phalanges on the fifth digit in the rear foot, *Gephyrostegus* shows no specialization suggestive of aquatic habits. Although the configuration of the humerus and femur resemble in general those of *Archeria*, the articulating surfaces are better ossified and suggest a posture like that of *Eryops* or pelycosaurs, with the limbs used more for support than for swimming. No superficial lateral line canal grooves are present on the skull. The high degree of development of the atlas–axis complex and the elongation of the tabular horns would assist in stabilizing the very large head when it would not be supported by the buoyancy of the water.

The degree of ossification of the articulating surface of the limb bones and particularly the specialization of the tarsus are adaptations for terrestrial life. The large size of the skull and the loose attachment of the vertebral elements, however, are primitive traits which indicate a lower degree of terrestrial specialization than that of contemporary reptiles. It may be assumed that *Gephyrostegus* retained, like the morphologically similar forms *Seymouria* and discosauriscids, aquatic reproductive habits. How much of its adult life this species spent on land and how much in the water cannot be demonstrated, but it would presumably show more specifically aquatic adaptations if it spent a large proportion of its life in the water.

Taxonomic position

On the basis of its vertebral and cranial anatomy, *Gephyrostegus* appears to be a relict of an early stage in the evolution of anthracosaurs. In these features it is more primitive than either embolomeres or seymouriamorphs, but a logical ancestor to both. The general body proportions, with a small number of presacral vertebrae and well developed limbs, may also be primitive features. Only the embolomeres and *Pholidogaster* (Romer 1964), among labyrinthodonts, have a large number of trunk segments. According to Panchen (1966), the elongate vertebral column, which may be associated with aquatic adaptation in these forms, is a secondary specialization from a primitively more terrestrial ancestry. The similarities in body proportions of *Gephyrostegus*, *Ichthyostega* and *Seymouria* suggest that this is the primitive pattern for anthracosaurs.

In addition to having a morphological pattern expected in an ancestor of other anthracosaurs, *Gephyrostegus* is also an almost ideal morphological antecedent to the reptiles. Its general proportions are similar to those of *Seymouria*. It is somewhat more primitive in some respects, but more importantly, it lacks the peculiarly non-reptilian specializations of that genus. The otic notch is not exaggerated; the configuration of the squamosal resembles that of romeriid captorhinomorphs. The fenestra ovalis is close to the midline, in contrast to the lateral position in seymouriamorphs. The neural arches are not swollen, and the zygapophyses are close to the midline, rather than being laterally placed. As a consequence of the vertebral structure, the heads of the ribs of *Gephyrostegus* are close together as in embolomeres and most primitive reptiles, rather than being widely separated.

The few features in which *Gephyrostegus* may be considered specialized approach the condition in reptiles. Most notable is the structure of the atlas–axis complex and the tarsus. The presence of five phalanges on the fifth digit of the foot is the only feature which shows specialization in a non-reptilian direction.

The morphology of *Gephyrostegus* is almost exactly what would be expected in a reptilian ancestor, sometime in the middle or late Mississippian.

The principal morphological differences between *Gephyrostegus* and the earliest known romeriid captorhinomorph *Hylonomus* are in the modification of the individual vertebrae: fusion of pleurocentrum and arch and reduction of the intercentrum; and in the skull: reduction in relative size, elimination of tabular horn, and modification of the palate (Carroll 1969*c*).

From what is known of primitive captorhinomorphs and pelycosaurs, there is probably a reduction in absolute body size between primitive amphibians and primitive reptiles and apparently an increase in the number of presacral vertebrae.

DIPLOVERTEBRON PUNCTATUM

Diplovertebron punctatum (Fritsch 1889, p. 11, plates 50, 52 and 53)

Although Brough & Brough (1967*c*) recognized that *Diplovertebron punctatum* was probably an embolomere and not closely related to the specimen which Watson (1926) assigned to this genus, the taxonomic problems involving these forms make it advisable to consider the type of *Diplovertebron* in more detail. Fritsch based the genus on material in several blocks from the gas coal of Nýřany, Czechoslovakia. Steen (1938, p. 239) designated specimens 96 and 126, in the collection of the National Museum in Prague, as types. Through the kindness of Dr Zázvorka, I have been able to study a cast of specimen 96 (figure 10).

Unlike the specimens of *Gephyrostegus*, all of which are preserved as natural casts which may be studied by the use of latex molds, the material of *Diplovertebron* is represented by the bone itself which has been badly damaged in attempts to prepare it mechanically. Because of this, the specimen appears a great deal less well preserved than those of *Gephyrostegus*. Specimen 96 includes much of the left half of the pelvic girdle, viewed medially, the right humerus, viewed ventrally, a radius, several ribs and the right premaxilla. Since all of these bones are anthracosaurian in pattern, and are of common size, it seems probable that they came from a single individual. Although there are several bones (not illustrated) whose identity is uncertain, none of the material is obviously extraneous. These bones together form an acceptable basis for considering the nature of *Diplovertebron punctatum*.

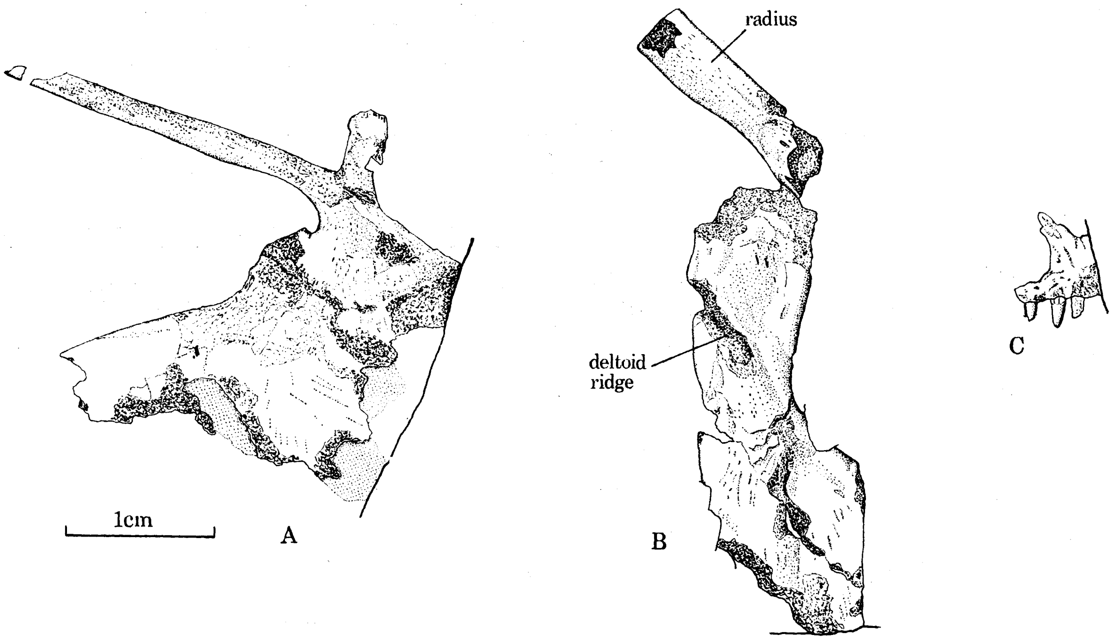


FIGURE 10. *Diplovertebron punctatum*. Type. A, Pelvis. B, Humerus and radius. C, Premaxilla.

The individual bones are very similar in size and proportions to those of the second Berlin specimen of *Gephyrostegus*, which facilitates comparison. The most distinctive bone is the ilium, in which the dorsal and posterior processes are clearly separate. This feature, as well as the great length of the posterior process, matches the pattern of the embolomeres *Archeria* and *Calligenethlon* (Carroll 1967*a*). In the clear distinction of the blades, *Diplovertebron* somewhat resembles *Eusauropleura* (see below), but is clearly distinct from *Gephyrostegus*.

The humerus has a generally similar configuration to that of *Gephyrostegus* and *Archeria*. As in the latter genus, but not in *Gephyrostegus*, there is a prominent ridge on the ventral surface, running from the middle of the shaft to the deltopectoral crest. Except for slight differences, reasonably attributed to crushing and/or immaturity, the radius resembles that of *Gephyrostegus* and *Archeria*.

The premaxilla resembles that of *Gephyrostegus* in having room for approximately five teeth. Those in place are bluntly pointed cones, lacking the distinctive chisel shape of those of *Archeria*. They show labyrinthine infolding at the base.

The ribs are of the pattern common to embolomeres, gephyrostegids and reptiles. The vertebrae which were figured by Fritsch in plate 52 are not present in this block. As illustrated by

Fritsch and Steen, the vertebrae attributed to *Diplovertebron* are embolomerous in pattern. These vertebrae are clearly from the caudal region, since they include haemal arches. They resemble those of embolomeres, in general, and are better articulated than the trunk vertebrae in *Gephyrostegus*. Unfortunately, the caudal vertebrae of that genus are not known.

On the basis of this specimen, it is clear that the type of *Diplovertebron punctatum* does not belong to the same genus as the type of *Gephyrostegus bohemicus*; it is probably an embolomere. In terms of size and dental similarity, *Diplovertebron* appears most closely related to the Joggins embolomere *Calligenethlon*.

Differences between this specimen of *Diplovertebron* and *Eusauropleura* are less clear cut. In both, the humeri are essentially embolomerous in pattern. Like *Diplovertebron*, *Eusauropleura* has distinct anterodorsal and posterior processes of the iliac blade. General proportions of the pelvic girdle of *Diplovertebron* are more similar to the typical embolomerous pattern than are those of *Eusauropleura*.

Dr Panchen is currently preparing a review of the embolomeres to be published in *Handbuch der Paläoherpetologie*. In that publication he is designating the ilium figured here as the lectotype of *Diplovertebron*.

In addition to the material which has been mentioned as appearing in close association with the type ilium, Fritsch described a number of other, isolated bones, some of which apparently belong to the genus *Gephyrostegus*. In particular, a pleurocentrum (plate 53, figure 9), and an interclavicle (figure 10), appear very similar to those of the type of *Gephyrostegus bohemicus*, and differ from the pattern of typical embolomeres.

EUSAUROPLEURA DIGITATA

Sauropleura digitata (Cope 1868, p. 216)

Eusauropleura digitata (Cope) (Romer 1930, p. 135)

Although most of our knowledge of the Gephyrostegidae is based on the material from the Middle Pennsylvanian of Nýřany, Czechoslovakia, a related form is known from beds of very similar age in North America. *Eusauropleura* has been recognized as a distinct element in the fauna at Linton, Ohio, since the review paper of Romer in 1930. As with *Gephyrostegus*, much more information is now available as the result of new techniques of preparation.

Two specimens may be confidently attributed to this taxa:

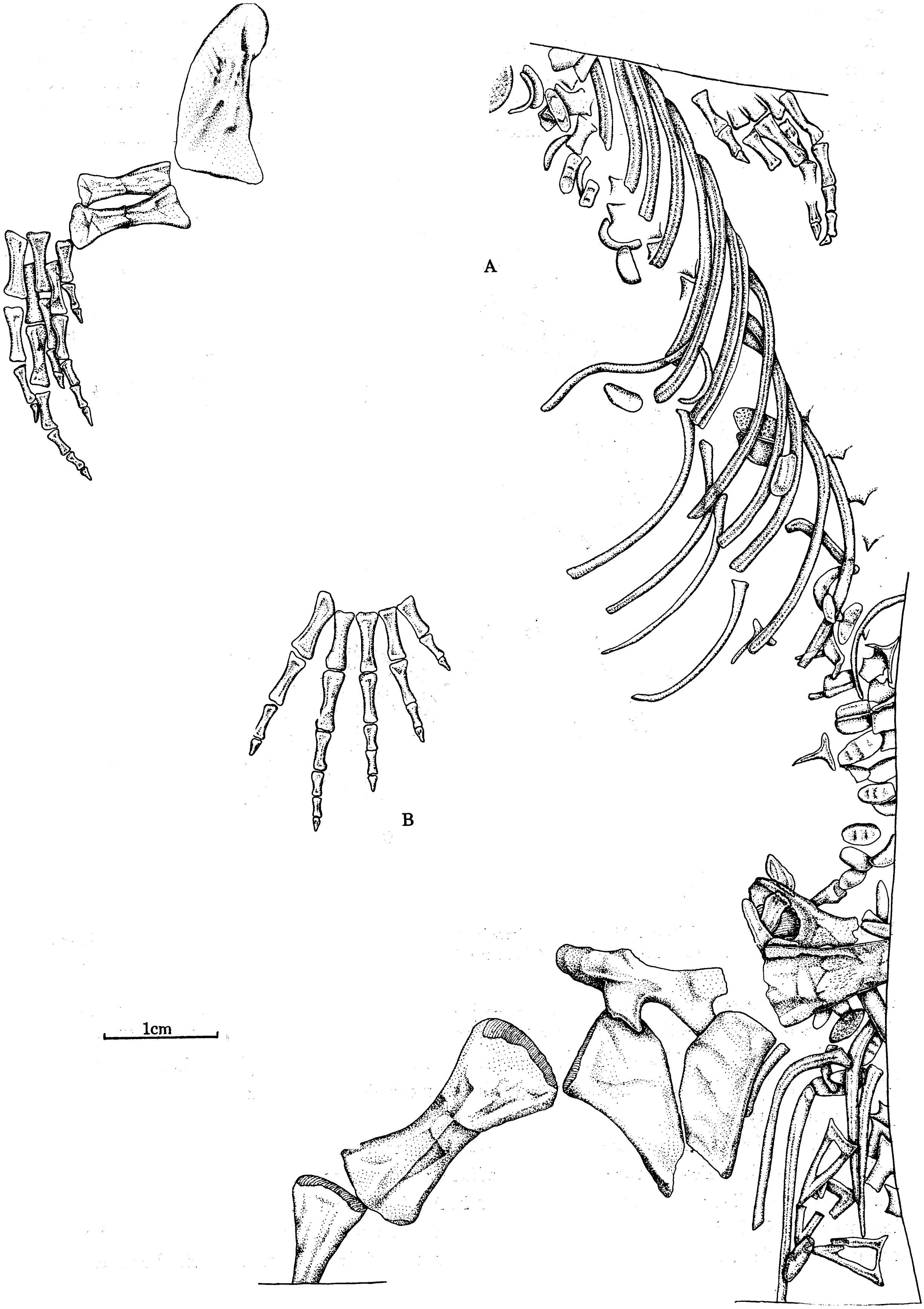
(1) The Type. AMNH 6865. Trunk region, forelimbs, pelvic girdle and rear limbs, proximal end of tail (figure 11).

(2) AMNH 6960. Described by Moodie (1909, p. 355). Trunk region, forelimbs, pelvic girdle and femora, proximal end of tail (figures 4 *c* and 12).

Description

These specimens are considerably smaller and obviously less mature than the Berlin specimens of *Gephyrostegus*. Since no cranial material is present, there might be some question as to the validity of comparison. Despite some difference in detail, however, the general anatomy of the trunk region, and particularly its proportions, indicate membership in the same family.

Although the vertebrae are too badly articulated in both specimens to give an accurate count, the trunk region is clearly short in proportion to the size of the limbs. The number of ribs indicates approximately 16 segments between the pectoral and pelvic girdles, comparable with the



RE 11. *Eusauropleura digitata*. Type. AMNH 6865. A, Skeleton. Right forelimb drawn 2 cm to the right of its actual position. B, Restoration of right manus.

number in *Gephyrostegus*. Cervical vertebrae are not preserved. Although less well ossified, the trunk vertebrae resemble those of *Gephyrostegus*. The pleurocentra are U-shaped, with the dorsal ends expanded to support the neural arch. The intercentra are low sided crescents. Most are marked ventrally by paired, longitudinal ridges. Both of the central elements are very thin walled, and would have formed little more than a husk around a large notochord. The neural arches, better shown in AMNH 6960, are weakly fused at the midline and all have separated from the centra. The arches are narrow, with the zygapophyses close to the midline. The spines are squarish in outline. The centra of the anterior caudals are well displayed in AMNH 6960. The first two have intercentra like those of the trunk region. Several large haemal arches are present in the type.

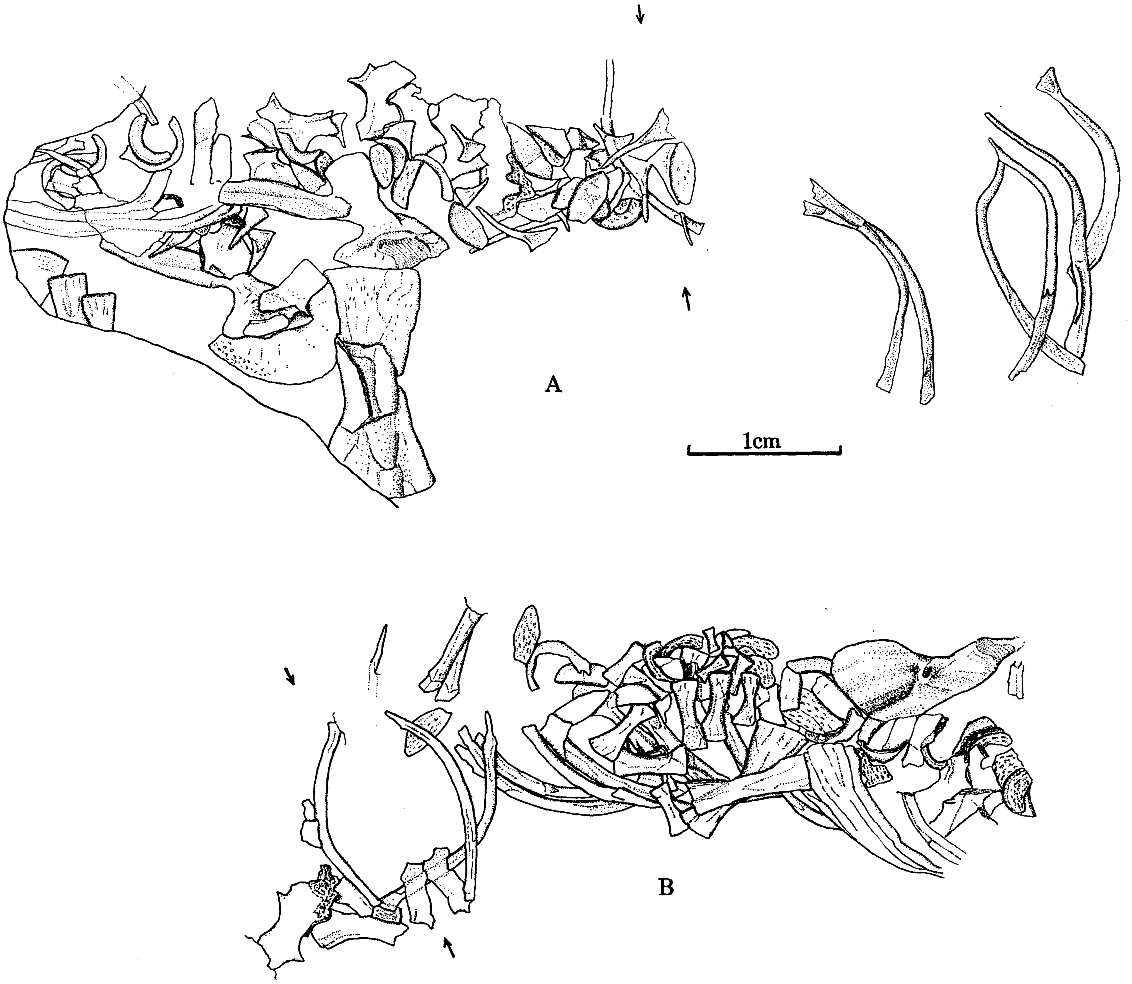


FIGURE 12. *Eusauropleura digitata*. AMNH 6960. Drawings from counterpart blocks. A, Posterior section viewed from the right. B, Anterior section viewed from the left. Arrows indicate approximate line of overlap.

The trunk ribs resemble those of *Gephyrostegus* in general shape, although the heads are nowhere well ossified. Two or three pairs immediately anterior to the sacrum are very short and sharply pointed. Sacral ribs are well displayed in AMNH 6960. The left is visible medially, in its natural articulation with the ilium. The right, displaced posteriorly to lie beneath the posterior prong of the blade, is visible laterally. It is not possible to determine whether these ribs have separate heads for articulating with the arch and centrum of the sacral vertebra. The blade is oval and covers the entire medial surface of the anterior blade of the ilium. An anterior vertical ridge overlaps its margin. The anterior caudal ribs are very long and, like those of Watson's specimen of *Gephyrostegus*, bend posteriorly to lie alongside the caudal vertebrae. In contrast to early reptiles, they are not fused to the vertebrae.

PU 16815 (figure 13) is an isolated endochondral girdle which may be associated with this taxa. It resembles that of *Gephyrostegus* in being ossified in a single unit, in the shape of the glenoid, and in the fact that the supraglenoid foramen opens within the area of the supraglenoid buttress. The medial surface shows a large subscapular fossa. Like those of *Gephyrostegus* and *Archeria*, the anterior margin of the scapular blade is expanded anteriorly at its base. Unfortunately none of these features is sufficiently diagnostic to differentiate this bone from those of temnospondyls. It comes from a considerably larger individual than the other material of *Eusauropleura*, and is even larger than the Berlin specimens of *Gephyrostegus*.

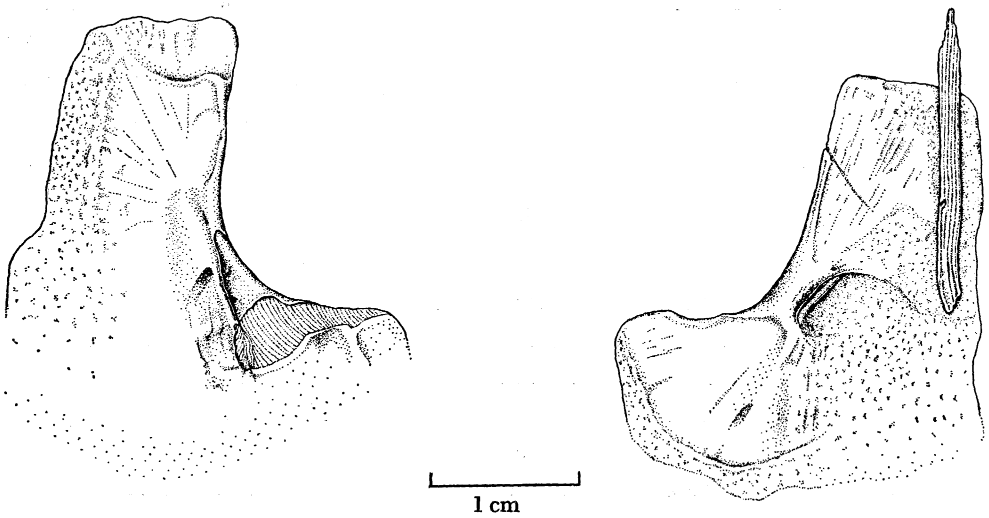


FIGURE 13. Scapulocoracoid possibly attributable to *Eusauropleura digitata*. PU 16815.

Lying beneath the anterior margin of the scapular blade, in the position of the cleithrum, is a rod-shaped structure, showing prominent longitudinal fluting. It is quite unlike the cleithrum of *Gephyrostegus*, or for that matter any Carboniferous tetrapod. It is probably extraneous.

Humeri are present in both the type and AMNH 6960. They are fairly well ossified, but are partially obscured by matrix and overlying bones and scales. An important feature by which the humerus of AMNH 6960 can be differentiated from those of *Gephyrostegus* is in the presence of a longitudinal groove, extending alongside the ectepicondylar ridge on the dorsal side of the area of distal expansion. This is a feature which it shares with embolomeres. The humerus in the type is exposed ventrally. In neither specimen are the articulating surfaces exposed. The radius and ulna resemble their counterparts in other anthracosaurs. Carpals are not ossified in either specimen. Much of both hands is present, more or less in articulation, in the type. The right is shown in its entirety. As preserved, the phalanges exhibit a count in successive digits of 2, 4, 3, 5, 3. Clearly there has been some transposition. If the entire second and third digits are interchanged, the metacarpal and proximal phalanx of the second are longer than those of the third. This does not agree with the pattern in the opposite hand, nor in Carboniferous tetrapods in general. By comparison with these other forms, it seems more probable that only the terminal phalanges have been interchanged. On this basis the hand has been restored (figure 11); it appears to differ from that of *Gephyrostegus* in the greater relative length of the fifth digit.

The pelvic girdle is exposed in both specimens. The pubis is not ossified in either, nor the ilium and ischium attached. The iliac blade differs from that of *Gephyrostegus*, but resembles that of embolomeres, in having clearly separate anterior and posterior processes. In this it also resembles *Diplovertebron*, although the entire ilium seems more strongly built than in that genus.

The femur is large, but the extremities are incompletely ossified. The only significant feature evident is an adductor ridge extending to the distal end. Of the distal elements of the posterior limb, only the proximal end of the tibia is preserved in the type, and the proximal ends of three metatarsals in AMNH 6960.

Scales, both dorsal and ventral, are conspicuous in these specimens. The body was protected by heavy, oblong scales, overlapping to form a chevron pattern, between the pelvic and pectoral girdles (figure 4, C). Were they not associated with the skeleton, they would be difficult to distinguish from those of embolomeres. Laterally the scales assume a more oval outline, become thinner, smaller and less extensively overlapping. The dorsal scales are small, thin and round. Where worn, all the scales exhibit a pattern of fine ridges, running parallel with the margins. These form a pattern of concentric ridges in the dorsal scales, similar to that of discosauriscids. Except for the heavier ossification of the dorsal scales, those of *Eusauropleura* are generally similar to those of *Gephyrostegus*.

Discussion

The structure of the vertebrae and the shortness of the trunk region indicate that *Eusauropleura* may be included in the same family as *Gephyrostegus*. There are several features which support generic distinction of these forms, however. Both the configuration of the humerus and the iliac blade in *Eusauropleura* are close to the pattern of embolomeres. The nature of the scales and the proportions of the hand also differ. These genera indicate a certain range of variability within this family. If the known genera are but relicts of a group which first differentiated in the Mississippian, a considerably greater range of variability would be expected once earlier members are discovered.

SOLENODONSAURUS JANENSCHI

The gephyrostegids, particularly *Gephyrostegus*, illustrate the morphology expected in the group of anthracosaurs which gave rise to reptiles. They are still typically amphibian in their cranial and vertebral anatomy, however, and in some features are even more primitive than the seymouriids. There is a considerable morphological gap between these anthracosaurs and the romeriid captorhinomorphs and pelycosaurs. This gap is partially bridged by the limnoscelids, usually classified as captorhinomorphs but far more primitive than romeriids or captorhinids. The limnoscelid *Romeriscus* (Baird & Carroll 1967) is currently the oldest known reptile, Westphalian A in age. All known members of this group show features, such as the pattern of the skull roof and occiput, which indicate a prior divergence from the lineage which gave rise to romeriids and pelycosaurs.

An additional lineage of primitive reptiles is represented by *Solenodonsaurus*, another form from the gas coal of Nýřany, Czechoslovakia, long confused with *Gephyrostegus*. The type of *Solenodonsaurus* was originally described by Broili (1905) on the basis of a specimen in the Munich Museum. The vertebrae were poorly exposed, but the skull showed well developed otic notches. This characteristic led Broili to classify it as a member of the labyrinthodont genus

Cochleosaurus. He later studied the counterpart of the same specimen in the Humboldt Museum in Berlin. The vertebrae were here represented by natural casts which Broili studied by the use of gutta-percha moulds. Their structure suggested that the animal was a cotylosaur, which Broili (1924) designated *Solenodonsaurus janenschi*. The significance of this specimen has been generally overlooked, probably due to the fact that the skull and vertebral column were separately illustrated in Broili's two papers.

In 1924, Pearson described a second specimen from Nýřany, DMSW R. 15, as *Solenodonsaurus*. On the basis of her material, which was from a much smaller and less mature individual, she concluded that this genus was a seymouriamorph, rather than a reptile. Recently, Brough & Brough (1967*c*) attributed both of these specimens to *Gephyrostegus*, although without further description of either.

On the basis of the literature it was apparent that further study of these specimens would contribute to our understanding of the origin of reptiles. Through the kindness of Dr Parrington, I was able to prepare and make new casts of Pearson's specimen. During a recent visit to the Humboldt Museum I was able to study Broili's type. Unfortunately, the counterpart, which had been in Munich, has not been located since the Second World War. The counterpart of Pearson's specimen, not previously described, was found in the Berlin Museum, as well as a further specimen similar in size to the type. As with much of this material, association of various individuals with a single taxon is often questionable. For that reason, each of these specimens will be described separately.

Description

The type is a large animal, the skull exceeding 15 cm in total length. The drawing of the skull (figure 14) is based on a plaster mould which may have been made from the Munich specimen, in which the skull was represented by a natural cast. The bone itself is present in the Berlin specimen, but it is badly preserved and shows much less detail than the cast. Except in the most significant area, the back of the skull table and temporal region, the pattern of the roofing elements can be readily determined. The sutures outlining the lateral and posterior margins of the parietal and the supratemporal were established on the basis of overall similarity with Pearson's specimen. Like other specimens from Nýřany, this skull is crushed into a single plane. If the cheek region is restored to its original position, the skull appears triangular in dorsal view, in contrast with that of the type of *Gephyrostegus*. The surface is marked by irregular pits and grooves, more or less in the pattern of some of the larger pelycosaurs, and clearly distinct from the pustular ornamentation of *Gephyrostegus*. A groove which might be interpreted as a remnant of a system of lateral line canals can be seen on the jugal, but this could also be attributed to *post mortem* deformation. The orbits are located slightly posterior to the middle of the skull. As in *Limnoscelis*, they do not intersect the frontal. Both pre- and postfrontal are somewhat displaced to overlap the dorsal border of the orbit. The jaw articulation is well behind the posterior margin of the skull roof. The squamosals are incised to form conspicuous otic notches. The border of the notch has a ridge which presumably supported a tympanum. Apparently the quadrate was of small size, as in amphibians in general, and restricted to the undersurface of the squamosal. The skull roof and cheek region appear to be more firmly attached than in embolomeres and gephyrostegids, but they may not have been solidly fused. The postorbital appears to be restricted to the cheek region. Except for the great length of the frontals and nasals, the pattern of the anterior roofing bones is not distinct from that of typical Carboniferous amphibians and reptiles. The lacrimal appears to reach the margin of the external naris. The maxilla has space for roughly 33–35 teeth, of which approximately 26 are in place. Many show a vertical groove at the base, indicative of labyrinthine infolding of the enamel. All are simple, cylindrical pegs, pointed at the tip. The length of the teeth gradually increases to reach a peak

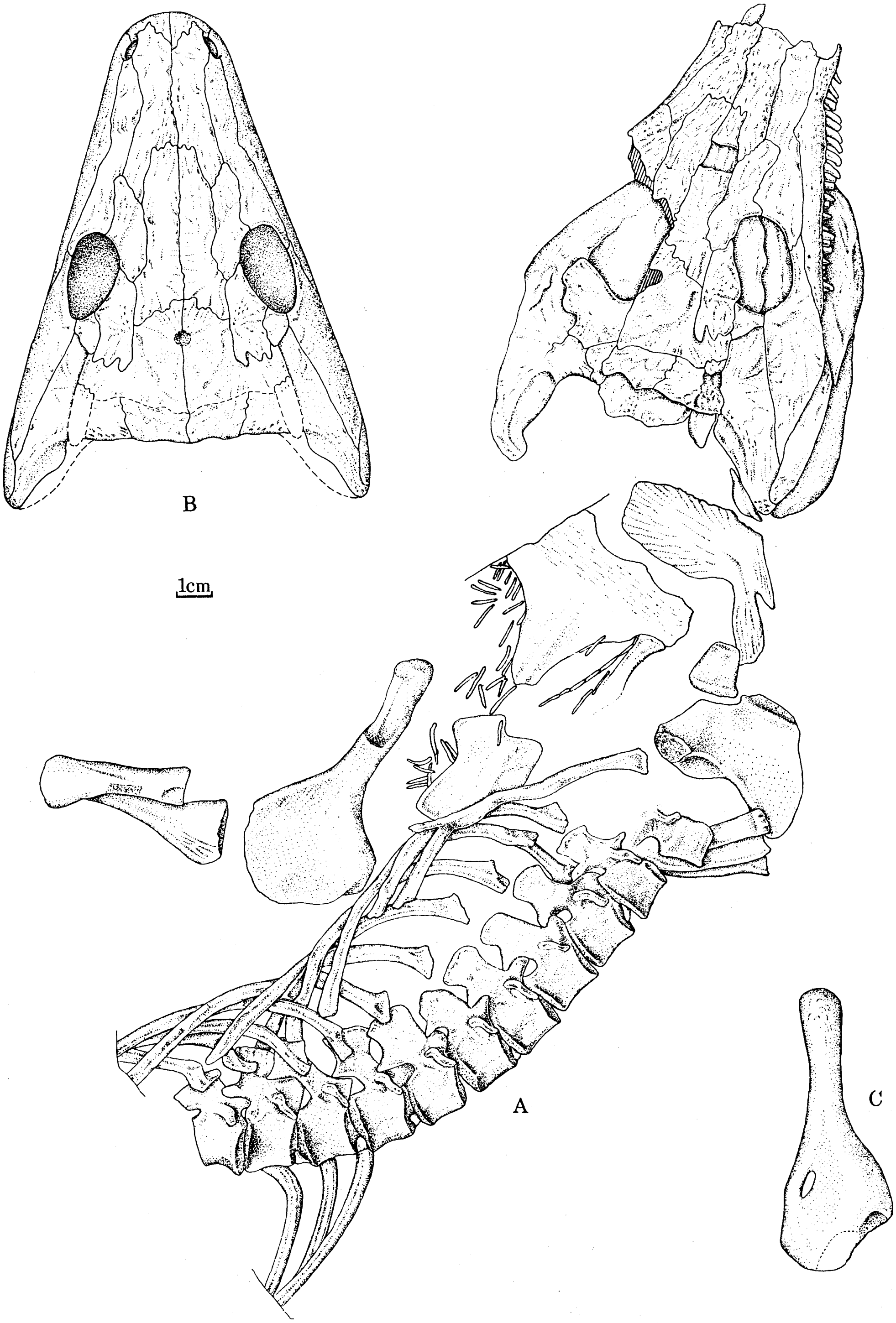


FIGURE 14. *Solenodonsaurus janenschi*. Type. A, Skeleton based on the Berlin specimen. B, Restoration of skull, anterior portion based on drawing of Munich counterpart. C, Humerus in ventral view, from drawing of Munich counterpart.

just anterior to the middle of the bone, and then diminishes slightly. None can be termed 'canine'.

Unfortunately it is not practical to prepare the palate in this specimen. As preserved, the skull is anthracosaurian in possessing otic notches, but is clearly distinct from any known embolomeres, seymouriamorphs or gephyrostegids in its proportions.

The postcranial skeleton is entirely reptilian in aspect. Unfortunately, the anterior cervical vertebrae are not exposed. Twelve vertebrae are visible, all from the trunk region. In all, the pleurocentrum is a large cylindrical element, solidly fused to the neural arch. In some a swollen area indicates the line of fusion. The arch is narrow, with the zygapophyses close to the midline. The transverse processes extend a short distance laterally, as in romeriid captorhinomorphs. They evidently supported both the capitular and tubercular heads of the ribs. These arches are in marked contrast to the swollen structures of limnoscelids, seymouriamorphs and diadectids. The neural spines are roughly square in outline and somewhat crenulated dorsally. Several small, crescentic intercentra are present between the pleurocentra. They are too small to have articulated with the capitulum of the rib. The vertebral structure is very similar to that of the romeriid *Cephalerpeton* (Gregory 1950) although the elements are of much greater size.

The ribs are of the general pattern typical for embolomeres, gephyrostegids and primitive reptiles. The heads are not greatly expanded. The capitulum and tuberculum appear to form a continuous articulating surface for attachment to the transverse process.

The scapular and coracoid portions of the endochondral shoulder girdle are preserved separately. This suggest that they may have ossified in two units. There is a stout supraglenoid buttress. The dermal shoulder girdle shows a pattern similar to anthracosaurs and primitive reptiles.

Except for its considerably greater size, the humerus resembles in general that of *Captorhinus*. The ventral surface is shown in the Munich specimen, and the dorsal surface in the Berlin counterpart. In contrast to gephyrostegids, limnoscelids, seymouriamorphs and embolomeres, there is neither an ectepicondylar ridge nor a supinator process. The expanded ends of the bone are twisted at right angles to one another. The entepicondylar foramen is not visible dorsally, but apparently entered on the posterior margin of the bone, as is the case in some romeriids. It is a conspicuous feature on the ventral surface. The ulna and radius are well ossified, but considerably shorter than the humerus. None of the wrist or hand is preserved.

A number of scales of typically reptilian pattern are preserved behind the shoulder girdle.

The anatomy of the postcranial skeleton of this specimen is that of a much overgrown romeriid captorhinomorph. It is clearly distinct from that of both anthracosaurs and limnoscelids.

A further specimen (MB 1901.1380) from the same deposit, which almost surely belongs to this genus, includes a series of four posterior trunk vertebrae, a sacral, and four anterior caudals (figure 15). They are from an individual of approximately the same size as the type. The trunk vertebrae are very similar in morphology to those further forward. The neural spines become more triangular in outline posteriorly. The arches of the caudal vertebrae appear to shift slightly forward in position. This may presage a condition, seen in more posterior caudal vertebrae in *Seymouria* but not in any typical primitive reptiles, in which the neural arches are intercentral in position. The most posterior in the series shows very clearly the suture between the arch and centrum. Ribs are not found in association with the posterior trunk vertebrae. The left sacral rib is more or less in position, partially obscured by the sacral vertebra. The capitular head, which must have articulated with the body of the centrum judging from the small size of the sacral intercentrum, is visible just beneath the vertebra. The tubercular head is completely covered. Caudal ribs are visible beneath the sacral vertebra and adjacent to the next two centra. They are of large size, and evidently extended posteriorly to lie alongside the vertebrae. They were not fused to the centra. The caudal ribs are free in Paleozoic amphibians, but typically fused in primitive reptiles. Intercentra are present between the second and third caudals, but a large haemal arch is present between the third and fourth.

It is somewhat difficult to compare these specimens with that which Pearson described because of the difference in size and degree of ossification. The skull which she described is approximately half the length of the type skull. It is roughly comparable in size to the type of *Gephyrostegus* and the Broughs' specimen I. Since the latter specimens are much better ossified, they clearly reached maturity at a considerably smaller size than did the taxon to which Pearson's specimen (figures 16 and 17) belongs.

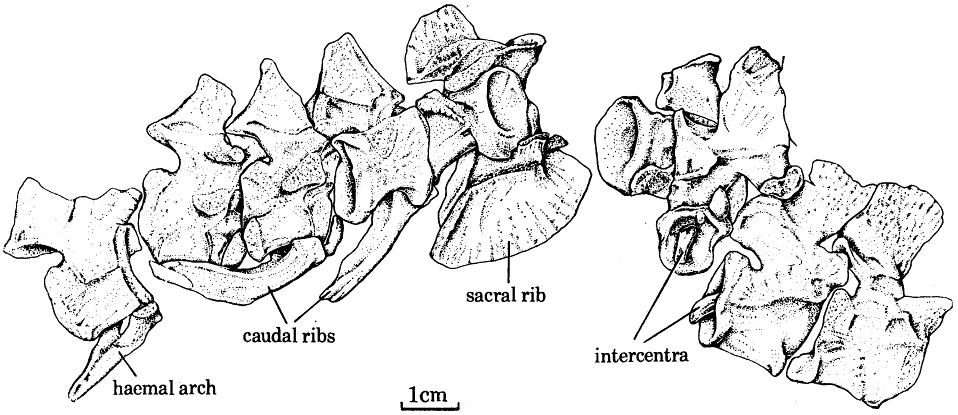


FIGURE 15. *Solenodonsaurus janenschi*. MB 1901.1379. Posterior trunk vertebrae, sacral and anterior caudals.

Although much of the cheek region and palate are not preserved, the skull has been restored in order to facilitate comparison with other, better known forms. The preorbital portion of the skull is quite long. The sculpturing consists of irregular grooves, radiating from the centres of ossification. There are no lateral line canal grooves. Unlike the condition in the type, the prefrontal is very narrow above the orbit. It may not have made contact with the postfrontal. This difference might be a result of the immaturity of this specimen. The parietals are displaced in the Berlin counterpart of Pearson's specimen. The left lies beneath the interclavicle, and only the margins are visible. The right overlaps the back of the frontals. This bone appears to have maintained its correct orientation, and shows a lateral lappet, more or less as in romeriids, separating a long posterior groove which received the supratemporal from anterior recesses for the frontal and postfrontal. The bone apparently extended laterally to overlie the squamosal. If this interpretation is correct, this arrangement of bones is distinct from that of both limnoscelids and all anthracosaurs, but resembles that of romeriids and pelycosaurs. Unfortunately neither tabulars, supratemporals nor postparietals are visible.

Pearson described a series of bones as coming from the cheek region and indicating the presence of an otic notch. Unfortunately this area is not preserved. The bones so identified are actually from the palate. On the basis of the bones preserved, the skull roof is apparently considerably shorter than the lower jaw, as in the type of *Solenodonsaurus*. This suggests that an otic notch may have been present, but this cannot be proven. The anterior margin of the lacrimal

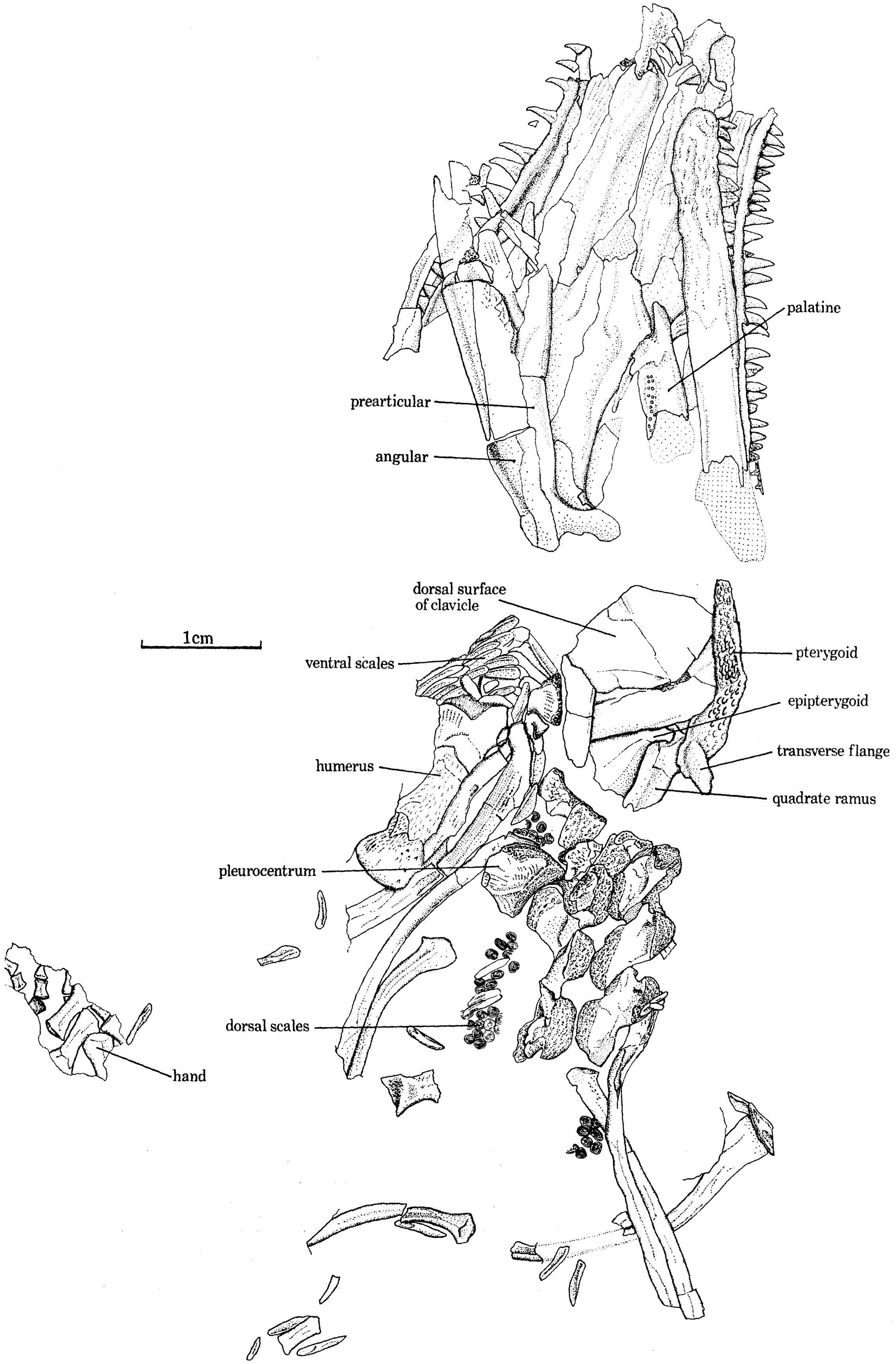


Figure 16. Specimen attributed by Pearson to *Solenodonsaurus janenschi*. DMSW R.15. Ventral surface of skull roof and associated postcranial elements.

is uneven, suggesting that it did not reach the margin of the external naris. This indicates that, as in *Gephyrostegus*, the septomaxilla was exposed superficially. There is room for approximately

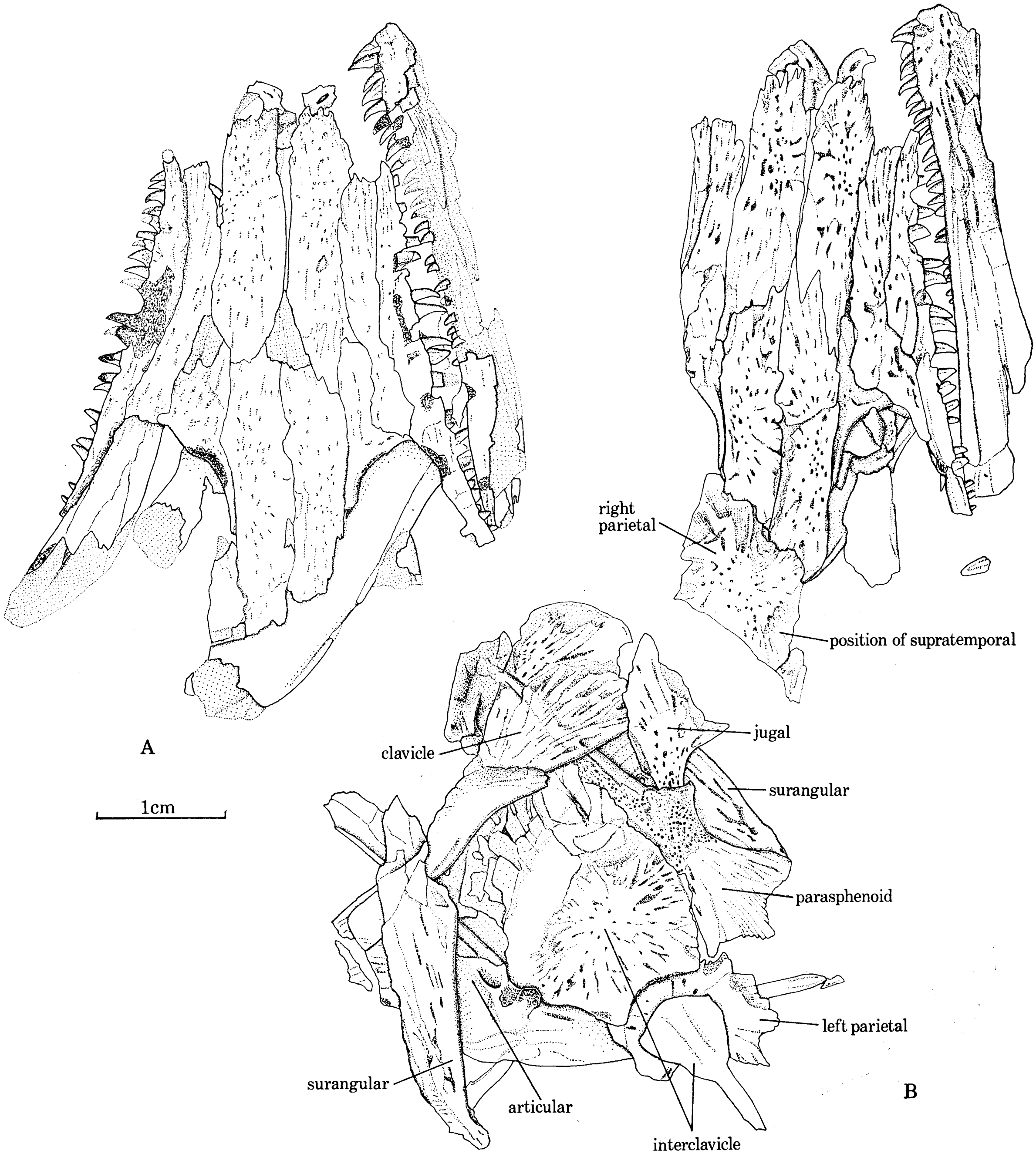


FIGURE 17. Specimen attributed to *Solenodonsaurus janenschi*. A, DMSW R. 15. Dorsal surface of skull roof. B, Cast made of counterpart. MB 1898.1038.

33 teeth in each maxilla. Nineteen are present on the right side and 21 on the left. Their structure and size distribution are very similar to those of the type. All five teeth are present in the right premaxilla, and three in the left. They are approximately as long as the longest maxillary teeth.

The palate is only very incompletely known, but what is present is very important for determining the taxonomic position of the form. The bone termed squamosal by Pearson is actually the posterior portion of the pterygoid (compare with plate 8 in Romer & Price 1940), and associated epipterygoid. What she thought represented the area for ligamentous attachment to the skull roof is actually the rows of teeth which run along the medial margin of the palatal ramus of the pterygoid. The area termed tabular is the proximal portion of the transverse flange of the pterygoid. A pterygoid of this structure is typically reptilian and occurs in no anthracosaurs. A second palatal bone, the palatine, was exposed in preparing the underside of the skull roof. It bears a row of denticles, exactly as in romeriids and pelycosaurs, rather than having large fangs as in anthracosaurs. The parasphenoid is present in the Berlin counterpart. It resembles that of both reptiles and gephyrostegids, and lacks the peculiar lateral processes associated with the otic capsules which are present in seymouriamorphs.

Both dentaries are close to their normal position. They are deeply pitted anteriorly. The postdentary bones are displaced. The medial bones of the back of the left jaw are visible medially through the right orbit and behind the frontals. The same bones are visible laterally (as if from within the adductor fossa) on the opposite side of the same specimen. Other jaw elements lie near the dermal shoulder girdle.

Several incompletely ossified vertebrae with the elements disarticulated lie behind the skull. One very poorly preserved bone is apparently a fairly large pleurocentrum. Despite its incomplete ossification, it is certainly more massive than those of *Gephyrostegus*. The neural arches are paired. Pearson referred to them as swollen, in analogy with those of *Seymouria*, but the zygapophyses are situated near the midline, rather than laterally. The area of the neural spines is not exposed. The immaturity of these vertebrae makes comparison with the type difficult, but they show no features which allow the two to be differentiated. The heads of the ribs are poorly ossified, but give no evidence of being widely expanded. The shafts are flattened cylinders. One of those more anterior in position appears to be somewhat wider than the remainder.

The endochondral shoulder girdle is not preserved. The right clavicle and the interclavicle lie amidst the parasphenoid and posterior elements of the lower jaws. Both have broad, conspicuously sculptured ventral plates. The plate of the interclavicle tapers to a short stem posteriorly. These elements appear more primitive in their large size and conspicuous sculpturing than their counterparts in primitive reptiles. The shape of the interclavicle in the type of *Solenodonsaurus* is comparable, but since it is exposed only dorsally, the nature of the sculpturing cannot be determined. The clavicle of the type appears smaller in dorsal view, but may be incomplete in that specimen.

The humerus is very incompletely ossified. It appears to be simple, like that of the type. The area of the entepicondylar foramen is not exposed. A few metacarpals and phalanges are present. It is not possible to give a phalangeal count, but the hand was apparently quite short, judging from the small size of the unguals and penultimate phalanges.

A patch of articulated ventral scales lies just behind the skull. Others are scattered throughout the block. They resemble those of embolomeres and gephyrostegids in general, although they may be somewhat narrower, approaching the typical reptilian condition. Dorsal scales are visible among the vertebral elements. They resemble closely those described in discosauriscids, and follow the general pattern of the dorsal scales in gephyrostegids. Such dorsal scales have not been described in any typical reptiles.

Discussion

Pearson's specimen combines a series of features common to primitive reptiles and advanced anthracosaurs. On the basis of the palate alone, this specimen can be classified as a reptile. This identification is supported by the apparent absence of an intertemporal bone. The presence of labyrinthine infolding of the enamel and the possible existence of otic notches suggest close affinities with the anthracosaurs. Both dorsal and ventral scales are anthracosaurian in pattern. The dermal shoulder girdle is primitive, but the vertebral structure appears more like that of reptiles than any anthracosaurs.

The only important feature by which this specimen can be distinguished from the type of *Solenodonsaurus* is the lesser extent of the prefrontal above the orbit. This and other minor points of distinction might be attributed to the difference in age, and/or individual variation. Although there may be some argument as to the validity of its association with the type, the two specimens certainly illustrate similar stages in evolutionary development. These specimens most assuredly are not closely related to *Gephyrostegus* or the Broughs specimens I and II.

If the three specimens described here can be attributed to a single taxon, *Solenodonsaurus* combines a series of characteristics which allow it to be classified as a reptile, with unquestionably anthracosaurian traits. The palate of Pearson's specimen and the trunk vertebrae of the type are reptilian in all features. The nature of the marginal teeth and the otic notch in the type, and the dorsal scales in Pearson's specimen, are amphibian characteristics. Taken individually or together, these specimens provide substantial evidence of the anthracosaurian origin of reptiles.

The lineage or lineages represented by these specimens is clearly distinct from the limnoscelids. The zygapophyses are close to the midline, and the humeri are simple. The presence of an otic notch indicates a more primitive level of development, but most of the postcranial features suggest closer relationship to romeriids and pelycosaurs. The pattern of bones in the temporal region exhibited in Pearson's specimen (and not contradicted in the type) is also similar to that of romeriids. It is apparent that the different patterns of the temporal bones in limnoscelids and romeriids resulted from separate ways of strengthening the attachment between the skull roof and the cheek region. In romeriids, the parietal extends a lappet to the margin of the skull roof to overlap the squamosal. The postorbital remains small and is primarily restricted to the cheek region. In limnoscelids, the parietal remains fairly small, and does not reach the margin of the skull roof. The postorbital, however, extends dorsally onto the skull roof. In both groups the intertemporal is lost, but the area which it occupied is differently incorporated into the surrounding bones. *Solenodonsaurus* may represent an independent development of the romeriid pattern. The similarity of postcranial features, particularly the structure of the vertebrae and the humerus, to the romeriid pattern suggests that they may be more closely related to each other than are either to the limnoscelids.

Clearly, a genus such as *Solenodonsaurus* from the Middle Pennsylvanian must be a relict of a considerably earlier phase of reptilian evolution. At the time when the true ancestors of the romeriids and pelycosaurs might be expected to have gone through a solendonsaurid-like stage in their evolution, some time in the late Mississippian, the difference between primitive limnoscelids, primitive solenodonsaurids and primitive romeriids might have been very slight. It is probable that some reptilian characteristics were achieved separately among subsequent members of all of these lineages. At present, we can be no more definite in the assignment of the limnoscelids and solenodonsaurids than to consider both as separate lineages of essentially reptilian grade which diverged from the central reptilian stock at an early stage.

One important feature in which *Solenodonsaurus* is specialized over the Middle Carboniferous genera which gave rise to romeriids and pelycosaurs is its large size. The earliest known fossils of these groups were of much smaller animals and it is probable that such small size was directly related to the achievement of reptilian reproductive habits (Carroll 1969*a*, *c*). Such cranial features as the large area of contact between the pre- and postfrontal in the type, and the conspicuous nature of the otic notches may be attributed more to large size than to the primitive nature of this genus.

'*GEPHYROSTEGUS*', SPECIMENS I AND II

In their paper entitled 'The Genus *Gephyrostegus*' Brough & Brough (1967*c*) devoted most of their attention not to the type material of the genus but to two specimens from the same locality which had not been previously described. These they designated specimens I and II. On the basis of the current study of the type of *Gephyrostegus*, it is apparent that these specimens do not belong to this taxon. They are not primitive anthracosaurs, but members of the reptilian family Romeriidae. Although these specimens do not contribute directly to the question of the ancestry of reptiles, they will be considered briefly, since it is important to clarify their taxonomic position.

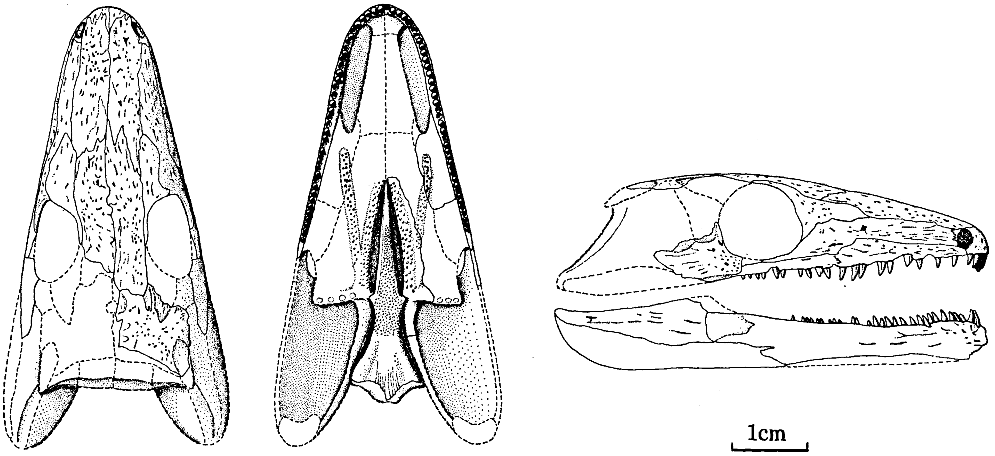


FIGURE 18. Restoration of skull attributed to *Solenodonsaurus janenschi*. Based on DMSW R.15 and MB 1898.1038.

Of the two, specimen I is by far the more complete, and will serve as the primary basis for this discussion. Although clearly a primitive reptile of generally romeriid characteristics, there are some features of specimen II which suggest that it may belong to a different genus than does specimen I.

There are a number of features whereby specimen I can be differentiated from the type of *G. bohemicus*, now that the palate and postcranial skeleton of the latter specimen have been described. The palate of specimen I (as can be seen in Broughs's figures 2 and 10; and re-illustrated here in figure 19) is typically reptilian in the possession of a transverse flange on the pterygoid, and discrete rows of denticles radiating out from the area of the basicranial articulation. The pterygoid in *G. bohemicus* forms a smooth medial wall to the temporal fossa, with no development of a transverse flange. The palatal bones are covered with a continuous shagreen of teeth. The marginal teeth in specimen I lack labyrinthine infolding, are fewer in number, and are distinguished by the presence of prominent 'canines'.

Most of the features of the skull roof which led to comparison of this form with the type of *Gephyrostegus* are a result of the occipital surface being flattened into the plane of the roof. Because of this, the postparietals and tabulars appear to have a large area of dorsal exposure, rather than being more occipital in position. Further, the posterior extent of the tabular and supratemporal give the appearance of forming the dorsal border of an otic notch. Restoration of these bones to their natural position gives a configuration almost identical with that of a romeriid captorhinomorph of comparable age, *Paleothyris*, from Sydney, Nova Scotia (Carroll 1969*a*). The bone which was identified as an intertemporal is a broken area of the parietal. Another feature of the skull which confirms association with the romeriids is the fine surface ornamentation of the bone, in sharp contrast with the pustular nature of *Gephyrostegus*, or the deep linear grooves of *Solenodonsaurus*. A plate-like supraoccipital lies just behind the skull.

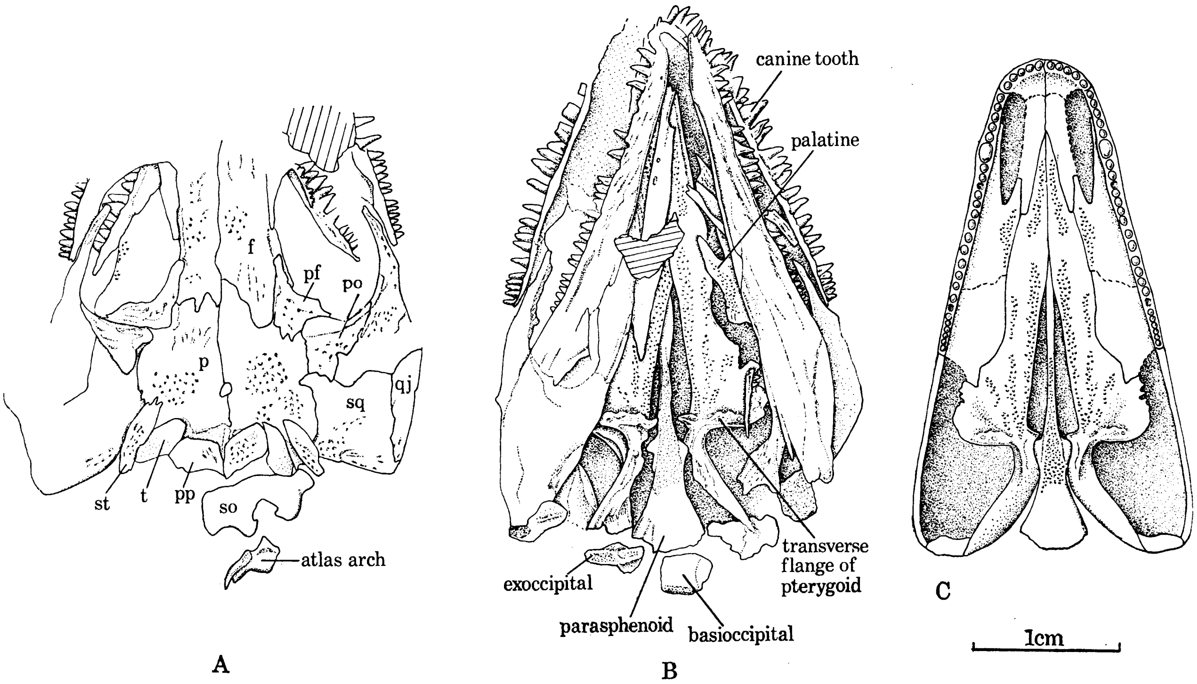


FIGURE 19. Romeriid captorhinomorph. Specimen I attributed by Brough & Brough to *Gephyrostegus bohemicus*. A, Posterior portion of skull roof. B, Palate. C, Restoration of palate. Abbreviations: f, frontal; p, parietal; pf, postfrontal; po, postorbital; pp, postparietal; qj, quadratojugal; so, supraoccipital; sq, squamosal; st, supratemporal; t, tabular.

In the postcranial skeleton, the structure and number of presacral vertebrae are in sharp contrast with *Gephyrostegus*. Although the skull of specimen I is only 35 mm in length, 55 % that of the type of *Gephyrostegus*, and approximately 60 % that of Pearson's specimen of *Solenodonsaurus*, the vertebrae are fairly well ossified, and have a typically reptilian structure with large pleurocentra suturally attached to the neural arches. The intercentra are small crescents. There are 31 or 32 presacral vertebrae in both specimens I and II. This number is matched in the romeriids *Paleothyris* and an unnamed genus of equivalent age from Linton, Ohio. The articulated postcranial skeleton here attributed to *Gephyrostegus* has only 24 presacral vertebrae. In the Broughs' restoration (figure 10D), the iliac blade is shown as having separate dorsal and posterior blades. This is not evident in specimen I, in which the ilium has a typically romeriid configuration. Apparently they based their restoration of this bone on Watson's specimen of *Gephyrostegus*.

Judging from the incomplete ossification of the girdles and limb elements in specimen I, the mature adult was probably somewhat larger. The immaturity of the specimen explains some apparent difference from other romeriids, all described on the basis of better ossified material. The scapula and coracoid are separately ossified, and the neural arches have in some cases become separated from the centra. A large cleithrum and fairly large ventral scales are slightly primitive features of these specimens.

Broughs' specimen I is significant in being the first member of the family Romeriidae to be described from outside North America. This supports our general understanding of a cosmopolitan reptilian fauna during the late Paleozoic.

Table 3. Taxonomic history of Nýřany anthracosaurs and reptiles

specimens	Watson 1926	Brough & Brough 1967*c*	Carroll 1969*b*	Carroll 1969*c* and this paper
type of *Diplovertebron punctatum* Fritsch 1889	*Diplovertebron*, an embolomere	*Diplovertebron*, an embolomere	*Diplovertebron*, an embolomere	*Diplovertebron*, an embolomere
type of *Gephyrostegus bohemicus* Jaekel 1902	Junior synonym of *Diplovertebron*	*G. bohemicus*, a seymouriamorph	*G. bohemicus*, a primitive anthracosaur	*G. bohemicus*, an anthracosaur close to the ancestry of reptiles
type of *Solenodonsaurus janenschi* Broili 1924	*Solenodonsaurus*	*Gephyrostegus bohemicus*, a seymouriamorph	*Solenodonsaurus*, an advanced anthracosaur, close to the ancestry of reptiles	*Solenodonsaurus*, a primitive reptile
Pearson's *Solenodonsaurus* DMSW R.15	*Solenodonsaurus*	*Gephyrostegus bohemicus*, a seymouriamorph	position uncertain	*Solenodonsaurus*
DMSW B.65	*Diplovertebron*	*Gephyrostegus watsoni*, a seymouriamorph	*G. bohemicus*	*G. bohemicus*
specimen I of Brough & Brough 1967		*Gephyrostegus bohemicus*, a seymouriamorph	*Solenodonsaurus*	a romeriid captorhinomorph

Conclusions

Until recently, consideration of the ancestry of reptiles has been based primarily on genera from no earlier than the Lower Permian (Watson 1954, 1957; Vaughn 1955; Parrington 1958; Olson 1962). From this material it has been established that most, if not all, advanced reptilian groups may be traced to either the captorhinomorphs or the pelycosaurs (Romer 1966). The specific ancestry of the Chelonia, Ichthyopterygia and Euryapsida remains subject to question, but the divergence of these groups, all of which are first known in the Triassic, apparently occurred subsequent to the original differentiation of the class. The similarity of early captorhinomorphs and primitive pelycosaurs indicates that all major reptilian groups have a common ancestry.

Even in the Lower Permian, however, there are a number of distinct reptilian lineages: three suborders of pelycosaurs; the mesosaurs; captorhinomorphs belonging to the families Romeriidae, Captorhinidae, and Araeoscelidae; limnoscelids, *Tseajaia* and the diadectids (figure 20). A further possibly reptilian form, *Bolosaurus*, is too poorly known to establish its relationship with these forms or even to assure its classification as a reptile.

In addition to the typical captorhinomorphs and pelycosaurs, it has been assumed that other apparently reptilian groups known in the Lower Permain also share a common ancestry. Despite the absence of earlier, less specialized forms intermediate between captorhinomorphs and mesosaurs, it is apparent that they too have arisen from the central romeriid stock. The position of the family Diadectidae has recently been subject to much speculation. The postcranial skeleton appears generally reptilian, but the skull is so highly specialized that it cannot be compared with any typical members of that class. Romer (1966) and Olson (1966) have allied this family with the seymouriamorphs, but there is no more evidence to support assignment to that group than to the cotylosaurs (Carroll 1969*a*). Although their relationship to other taxa cannot be judged without knowledge of more primitive members of the family, diadectids will be referred to here as reptiles.

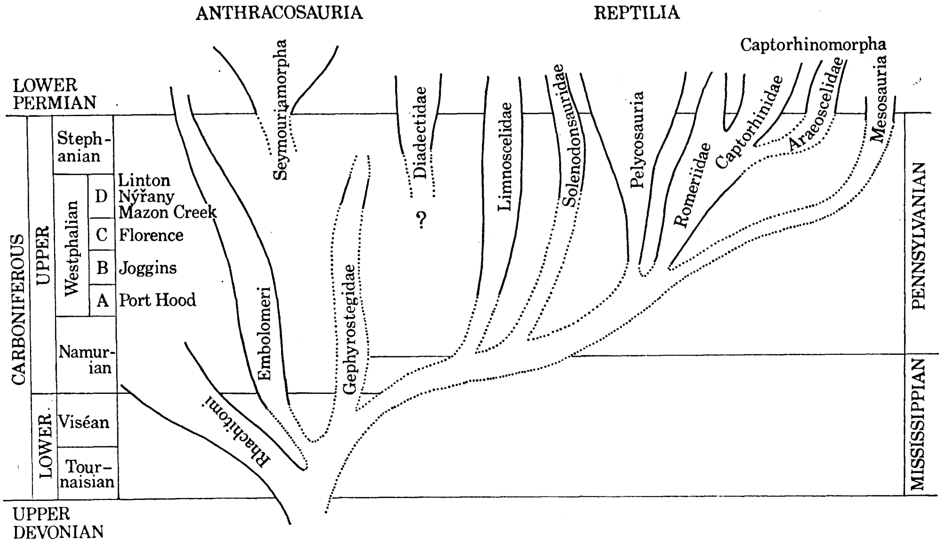


FIGURE 20. Phylogeny of Paleozoic reptiles and anthracosaurs. Relative age of pertinent fossil localities and geological subdivisions indicated.

With the redescription of the Joggins fauna, and the discovery of other reptiles in the Lower and Middle Pennsylvanian, our knowledge of romeriids, pelycosaurs and limnoscelids has been extended nearly an entire period earlier. Description of these earlier forms confirms many of our suppositions based on the Permian genera, but raises some new problems. Romeriid captorhinomorphs and pelycosaurs from the early Pennsylvanian are clearly closely related to one another, and probably share a common ancestry within the very lowest Pennsylvanian. The limnoscelids, in contrast, are a separate and distinctly more primitive lineage. *Solenodonsaurus* represents yet another separate lineage, which may include the Permain genus *Tseajaia*.

We can recognize at least four distinct reptilian lineages in the early Pennsylvanian; the common ancestors of the romeriids and pelycosaurs, limnoscelids, the ancestors of the diadectids, and the solenodonsaurids. On the basis of the fossil record of the reptiles themselves, it is not yet possible to determine how these groups are interrelated, or whether they share a common ancestry above the amphibian level.

Description of *Gephyrostegus* provides us with a basis for considering the morphology of reptilian ancestors. Although this genus may be somewhat specialized from its late Mississippian progenitors, it nevertheless represents the morphological pattern expected in the group of anthracosaurs which gave rise to reptiles. Almost certainly the ancestry of romeriid captorhinomorphs, pelycosaurs, limnoscelids and solenodonsaurids may be traced to forms with this general morphology, and presumably to genera which could be included in this particular family. Unfortunately, there is still a sufficient morphological gap between gephyrostegids and even the most primitive reptilian genera that we cannot determine the specific relationship of the two groups. It is quite possible that each of the four primitive reptilian lineages evolved separately from gephyrostegids. In all probability, the Diadectidae may be ultimately traced to the Gephyrostegidae also. It is somewhat easier to attribute the many reptilian characteristics of that family to a common ancestry with captorhinomorphs and pelycosaurs, but it is possible that they were achieved separately from an amphibian level.

Knowledge of gephyrostegids and solenodonsaurids requires revaluation of the criteria by which reptiles are defined and differentiated from amphibians. The early pelycosaurs and romeriids are sufficiently similar to primitive living reptiles in their morphology that they can be assumed to be reptilian in their physiology as well. Although known limnoscelids and solenodonsaurids are obviously not themselves ancestral to higher reptiles, they are included within the class on the basis of their overall similarity to romeriids, and their obvious distinction from any unequivocal amphibians. *Gephyrostegus*, on the other hand, is, in most features of its anatomy, comparable with Paleozoic amphibians. Although the reproductive pattern of this genus is not established, it is presumably like that of the discosauriscid seymouriamorphs, which are known to have aquatic larval stages.

On the basis of Lower Permain reptiles and seymouriamorphs, the following morphological features have been indicated as differentiating reptiles from anthracosaurs.

(1) Loss of intertemporal bone.
(2) Reduction in size of supratemporal, tabular and postparietal.
(3) Loss of palatine fangs and development of transverse flange on pterygoid.
(4) Loss of labyrinthine infolding of enamel.
(5) Absence of otic notch.
(6) Development of specialized atlas-axis complex.
(7) Reduction in relative size of trunk and caudal intercentra.
(8) Development of astragalus.
(9) Wheat shaped ventral scales; absence of ossified dorsal scales.

Limnoscelis has long been known to retain an amphibian condition in features 2, 4 and 8. *Tseajaia* (Vaughn 1964) is also primitive in these features. The otic notch described in that genus appears to be specialized in the manner of *Diadectes* and higher reptiles, rather than having a labyrinthodont pattern. The Lower Pennsylvanian limnoscelid, *Romeriscus* (Baird & Carroll 1967) may retain a primitive notch, however. Consideration of *Gephyrostegus* and *Solenodonsaurus* forces us to revaluate other features as well. The structure of the atlas-axis complex in *Gephyrostegus* differs from that in reptiles only in the relatively large size of the axis intercentrum, and the loose attachment of the axis arch and pleurocentrum. Although the proportions of the trunk vertebrae remain primitive, their basic structure is close to the reptilian pattern. The tarsus in this genus is actually closer to the reptilian pattern than is that of *Limnoscelis* and *Tseajaia*. *Solenodonsaurus*, while a reptile in regards to its postcranial anatomy, definitely retains a primitive otic notch. Consideration of the relative development of the parietal and postorbital in limnoscelids and other early reptiles suggests that the intertemporal bone may have been lost separately in the two groups. Pearson's specimen of *Solenodonsaurus* retains ossified dorsal scales and the ventral scales differ little from those of embolomeres.

Among all the structural features which have been used to differentiate primitive reptiles from their ancestors among the amphibians, only the configuration of the palate remains a valid point of distinction. Whether or not the modification of this structure occurred at the same time, and was directly associated with a change in reproductive patterns has not been established with certainty. Their general synchrony, however, seems very probable. Moreover, the modification of the palate appears to be a sufficiently distinct change to be used as a practical morphological criterion of the achievement of reptilian status.

Considering the parallel development of other reptilian features among several (albeit closely related) lineages, there is the possibility that the reptilian palatal construction was also developed in more than a single lineage. If so, use of this particular morphological criterion would indicate the polyphyletic origin of reptiles, at the level of the family, and would reflect a horizontal pattern of classification. This matter might be simplified by specifically excluding all lineages from reptilian status which achieved reptilian morphological characteristics separately from the romeriids and pelycosaurs. MacIntyre (1967) suggests an equivalent scheme of eliminating all nontherian mammals from the Class Mammalia.

At the present time, however, there is no evidence that the reptilian palatal structure did develop in more than a single lineage. With the exception of the diadectids, all adequately known groups may be classified unequivocally as either reptiles or amphibians.

With description of *Gephyrostegus*, *Eusauropleura* and *Solenodonsaurus*, all known genera from the Upper Carboniferous which may be expected to contribute directly to our understanding of the amphibian–reptilian transition have been studied. Further knowledge of this transition now awaits discovery of the new material in the lowermost Pennsylvanian or Mississippian. On the basis of the described deposits of this age, it is unlikely that any will yield new specimens which will contribute to this problem. In all cases, the fauna and nature of deposition point to an aquatic environment. It is clear from our understanding of both the early reptiles and their closest relatives among the anthracosaurs, that this group originated among terrestrial forms (Carroll 1967*b*, 1969*a*, *c*). Further knowledge of the ancestry of reptiles requires the discovery of new Mississippian localities reflecting a terrestrial environment.

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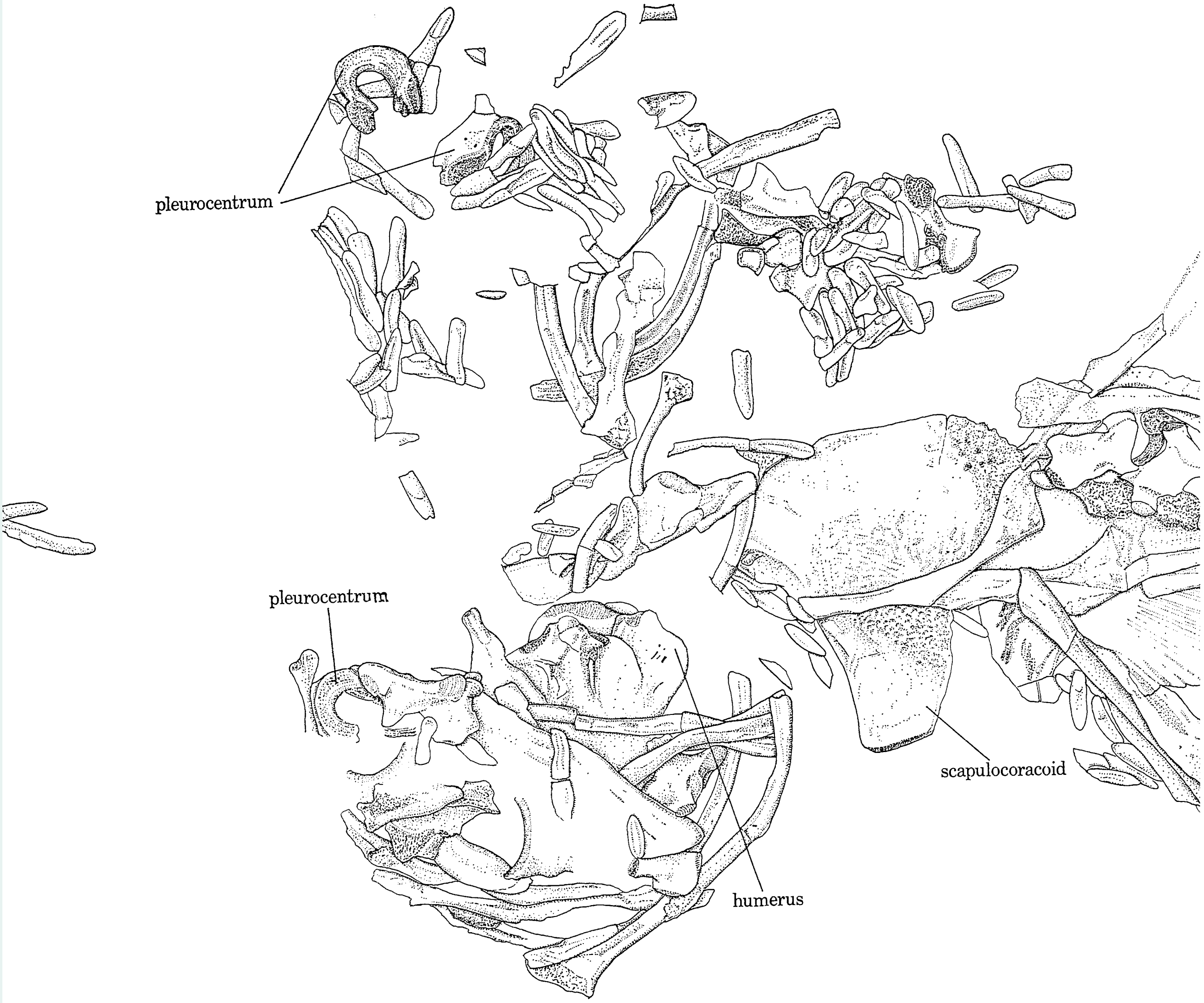

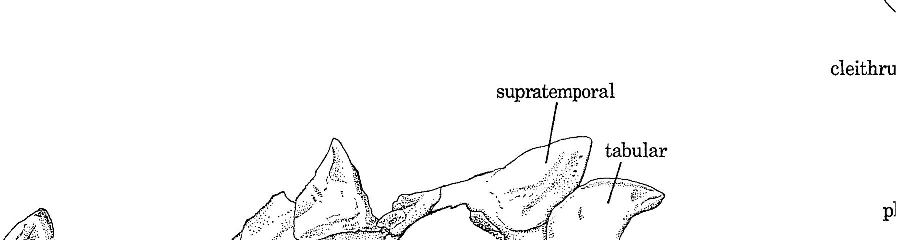

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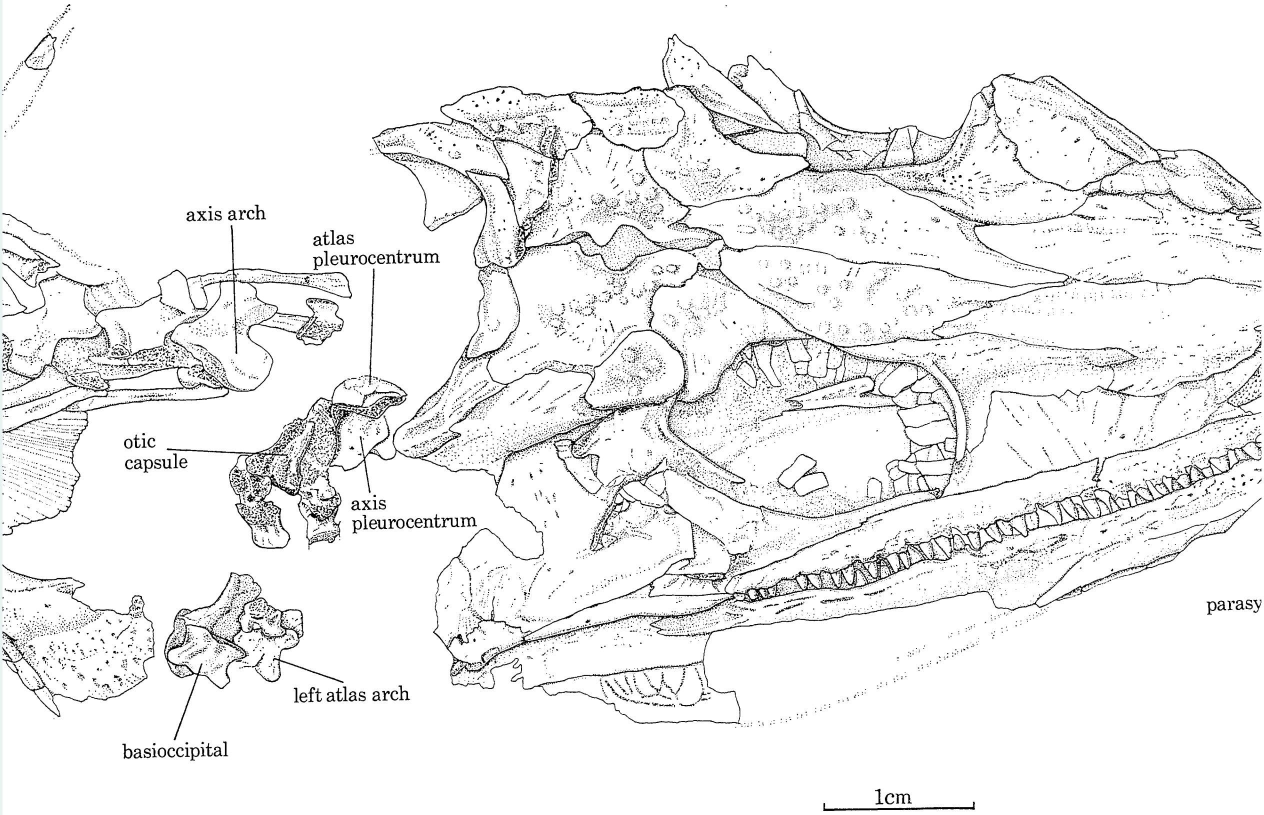
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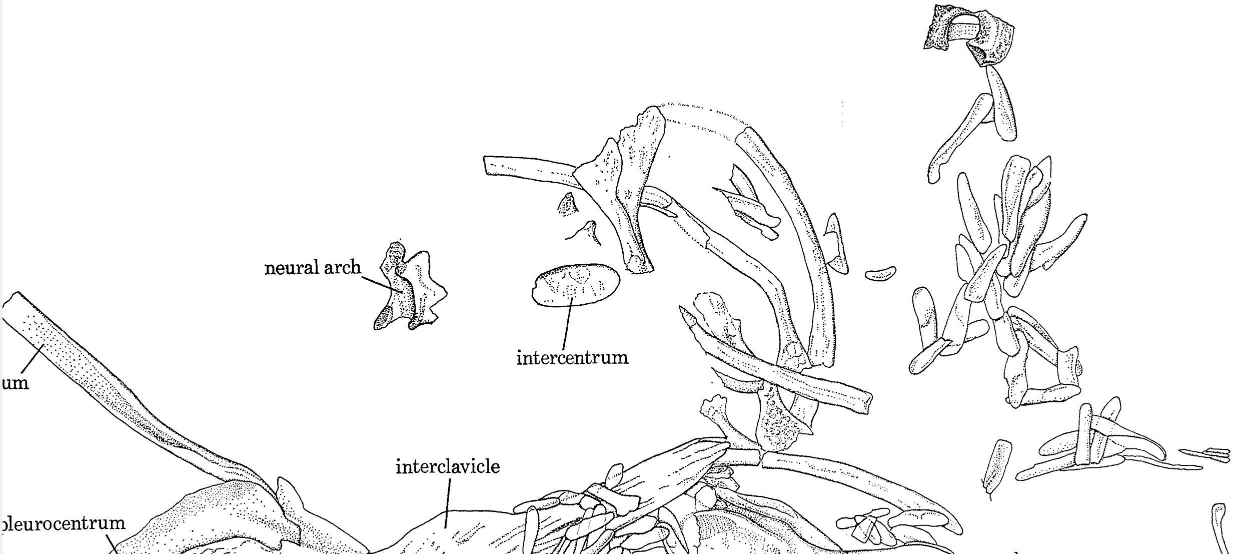
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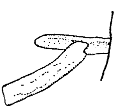

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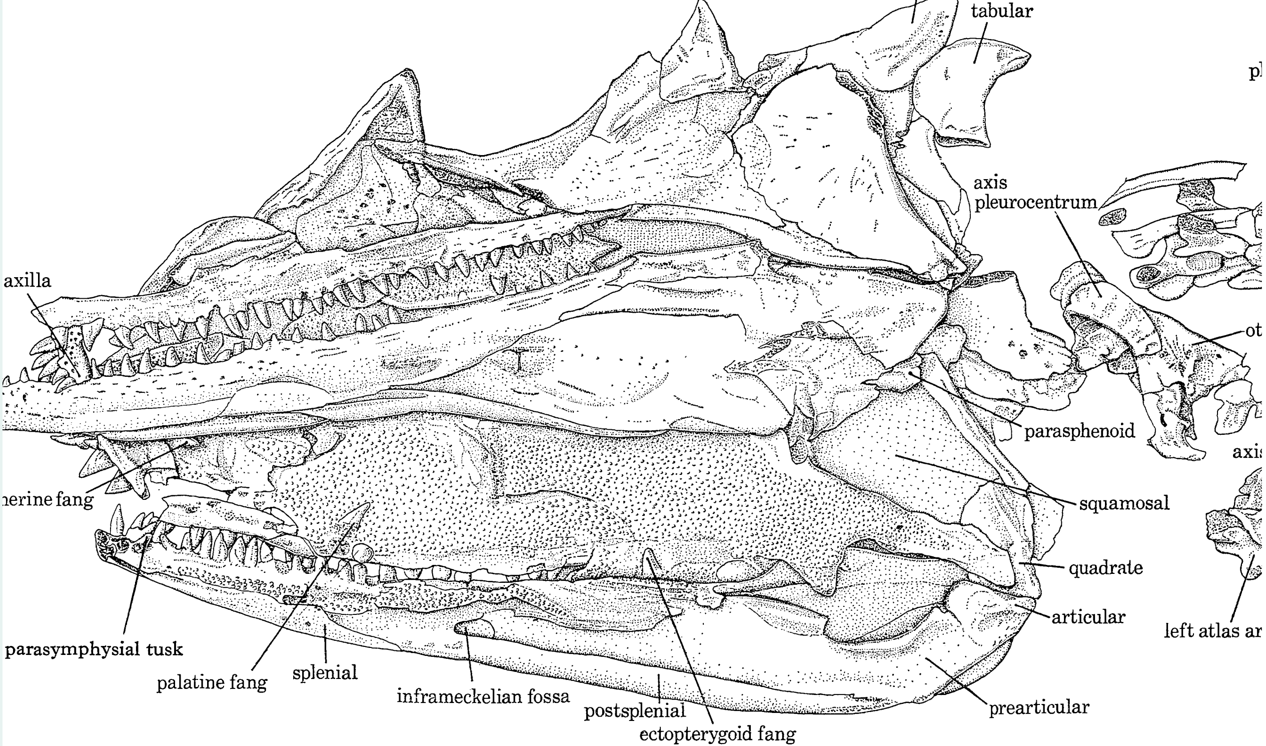
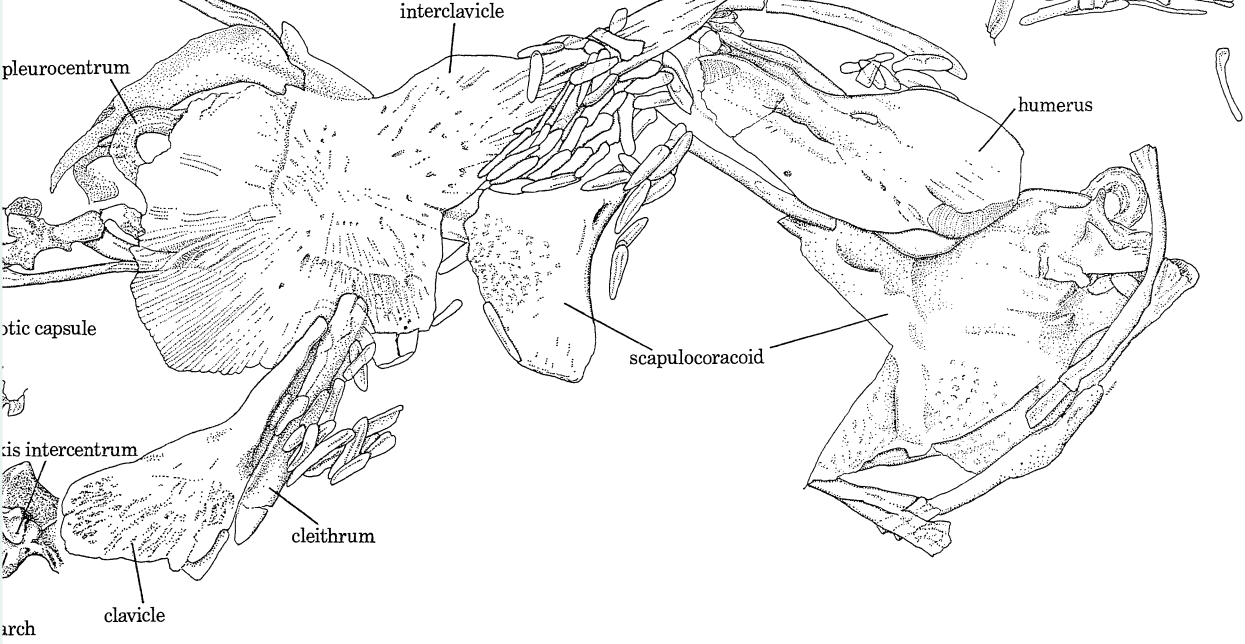


FIGURE 1. *Gephyrostegus bohemicus*.



s. Type. Skeleton in dorsal and ventral views. *(F* *acing p.* 308)

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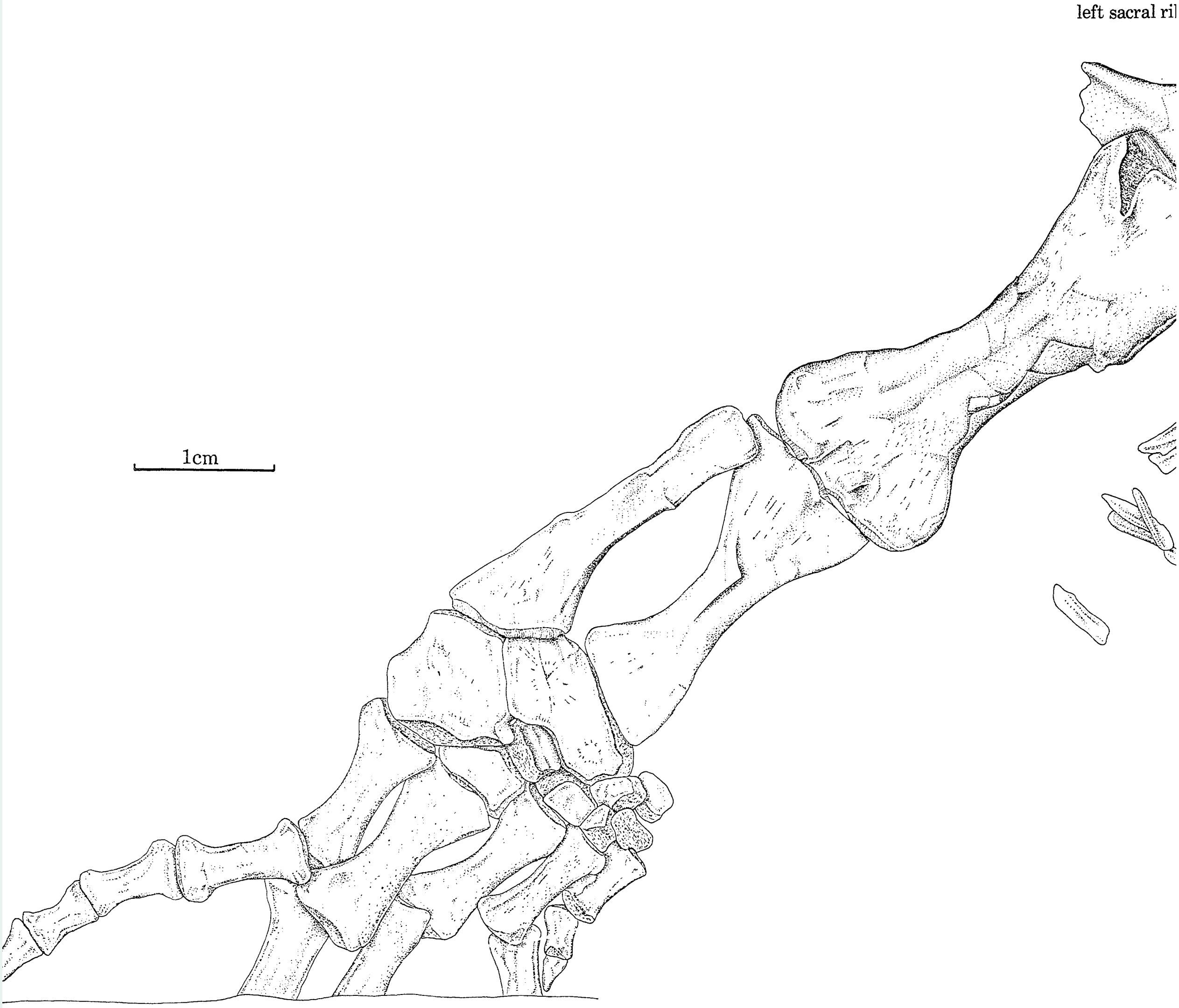

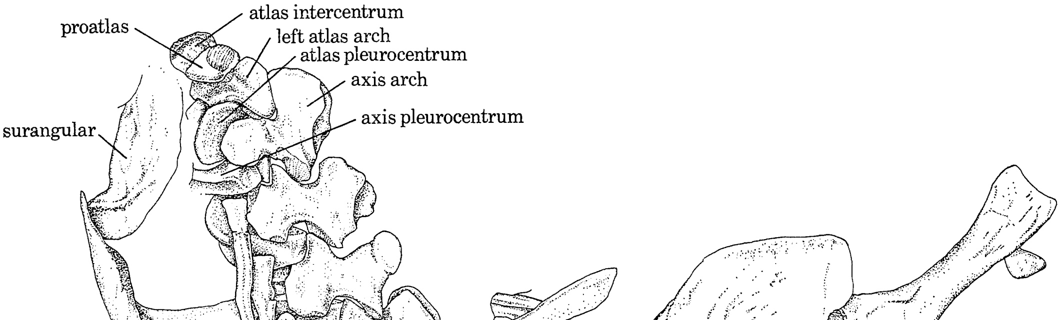


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sacral vertebra
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right sacral rib

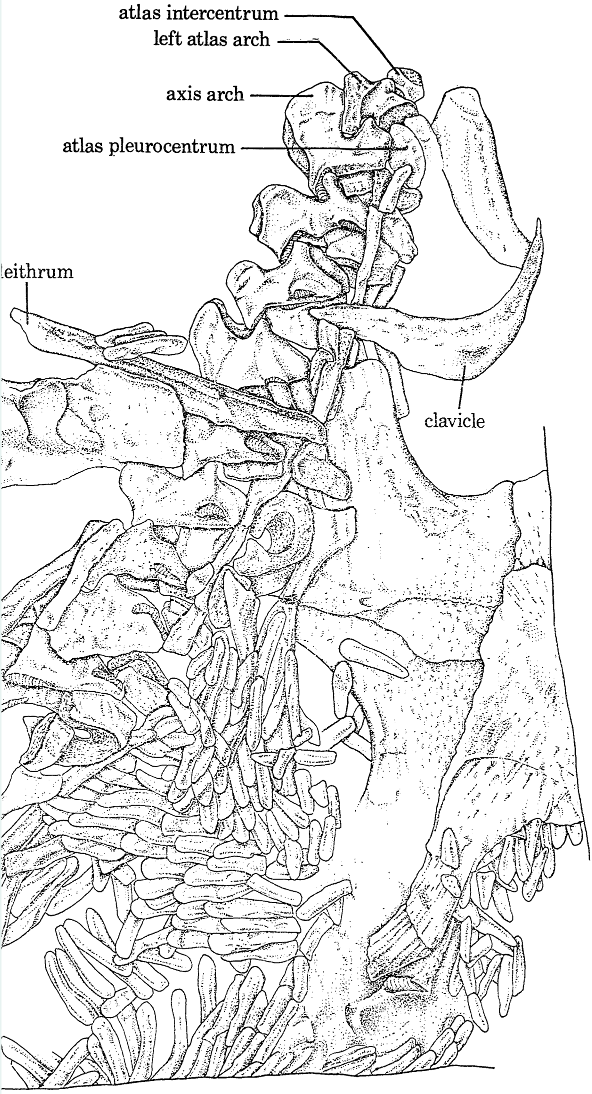
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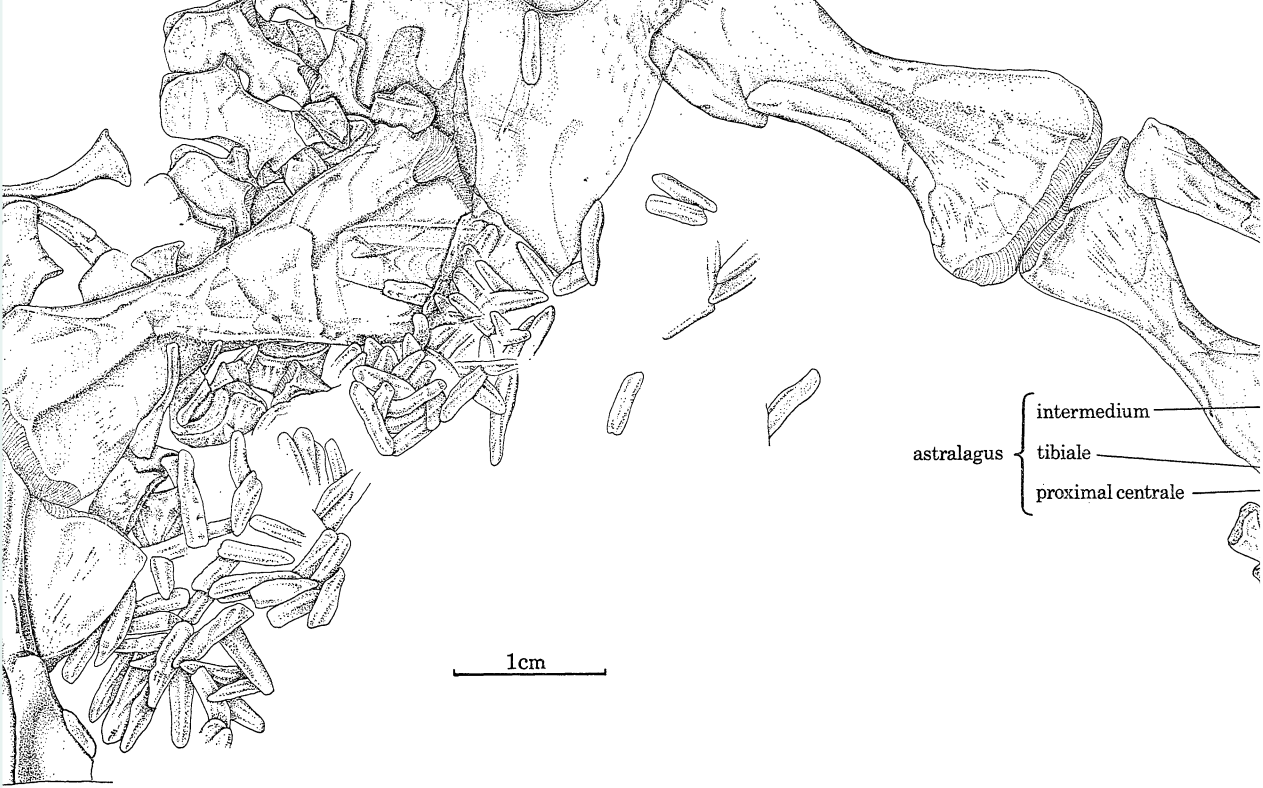
FIGURE 2. *Gephyrostegus bo*



ohemicus. MB1901.1378 a+b. Postcranial skeleton in counterpart blocks.

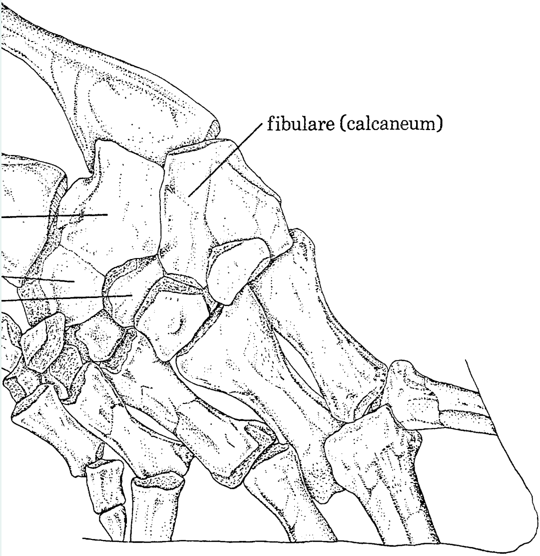

fibulare (calcaneum)

FIGURE 4. A, *Gephyrostegus bohemicus*. DMSW B.65. Skeleton.

B

C

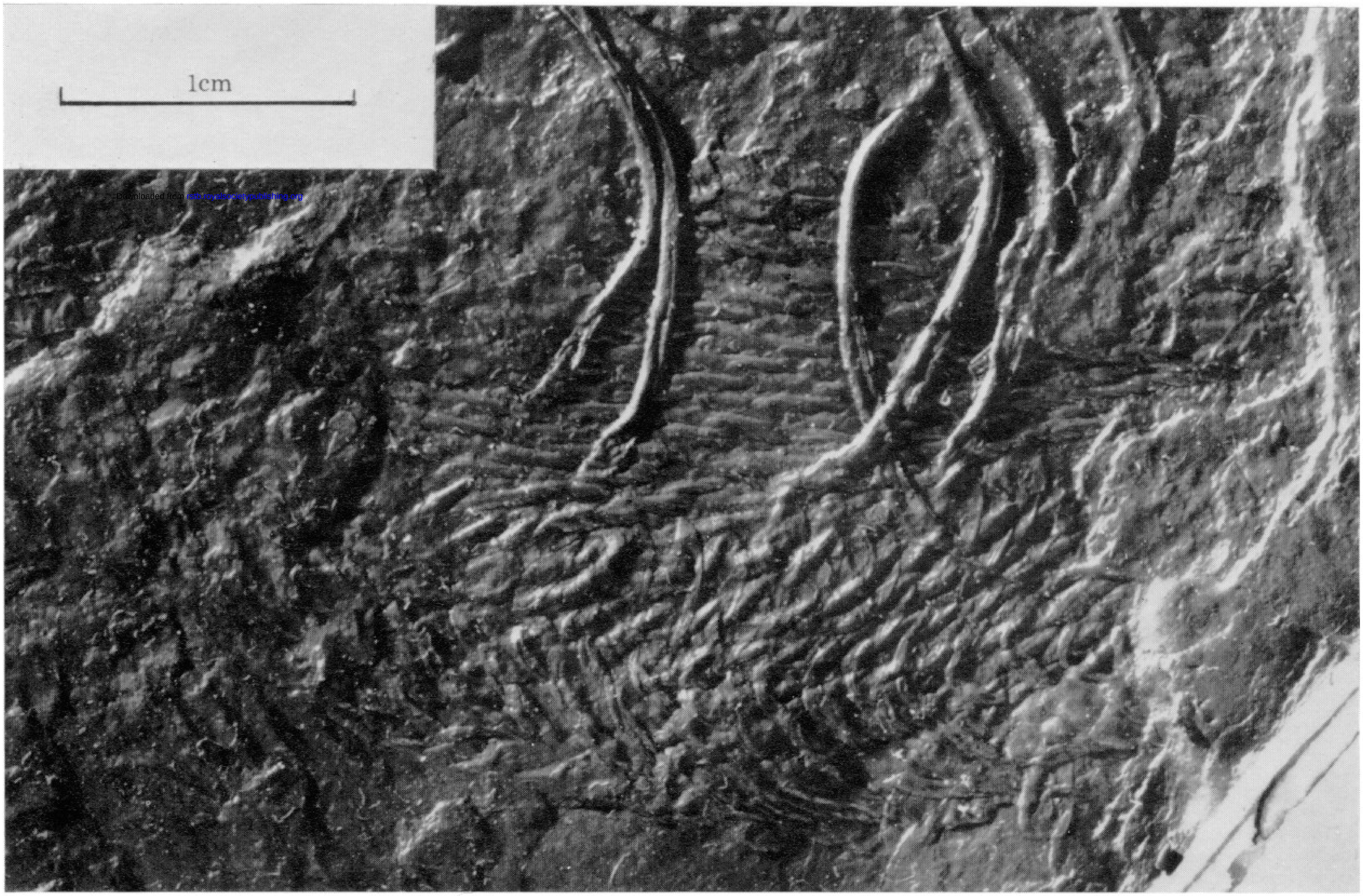


FIGURE 4. B, *Gephyrostegus bohemicus*. DMSW B. 65. Detail of scales. The anterior end of the animal is to the right.

FIGURE 4. C, *Eusauropleura digitata*. AMNH 6960. The anterior end of the animal is to the right.

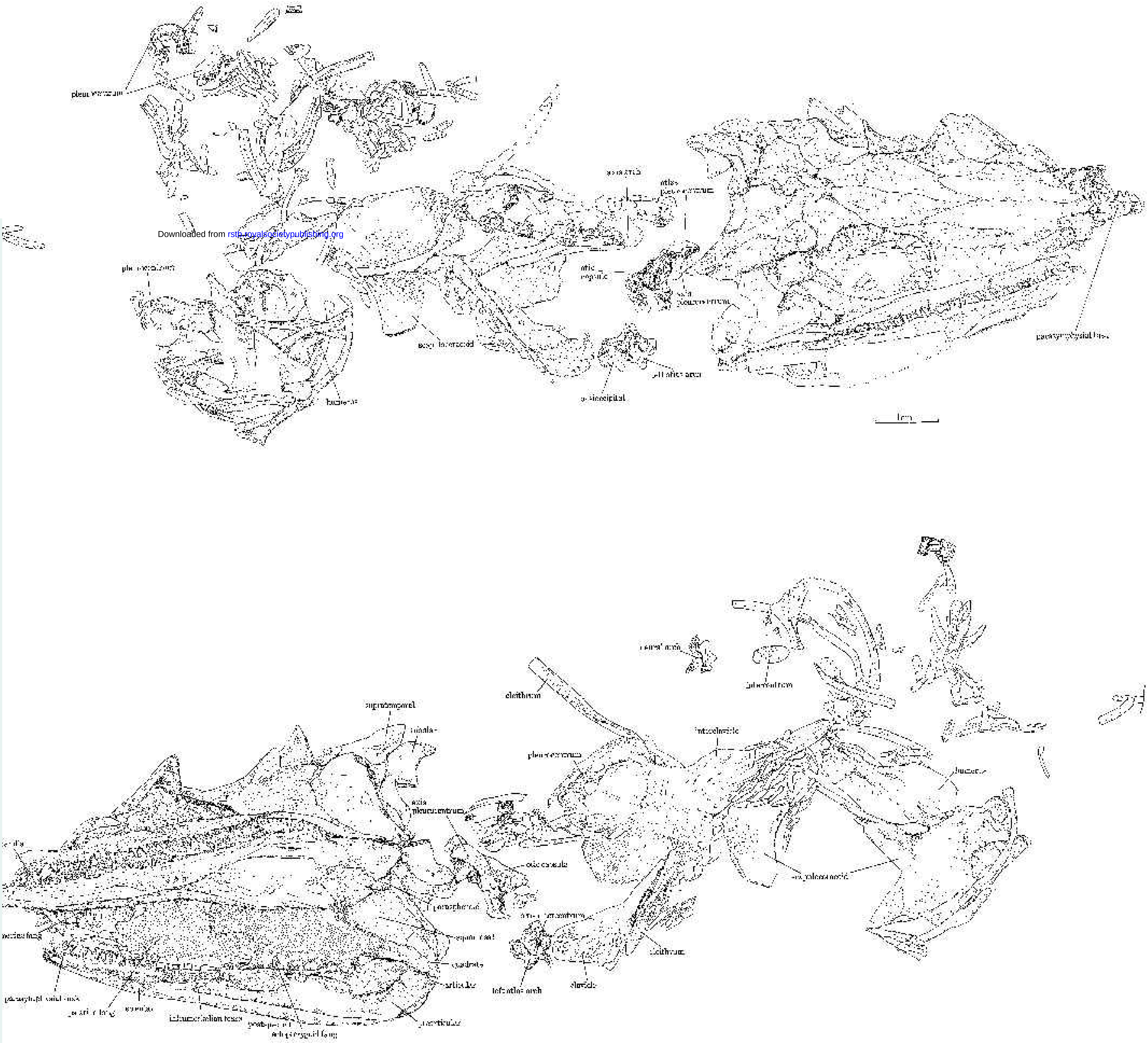


Figure 1. *Gephyrostegus bohemicus.* Type. Skeleton in dorsal and ventral views.

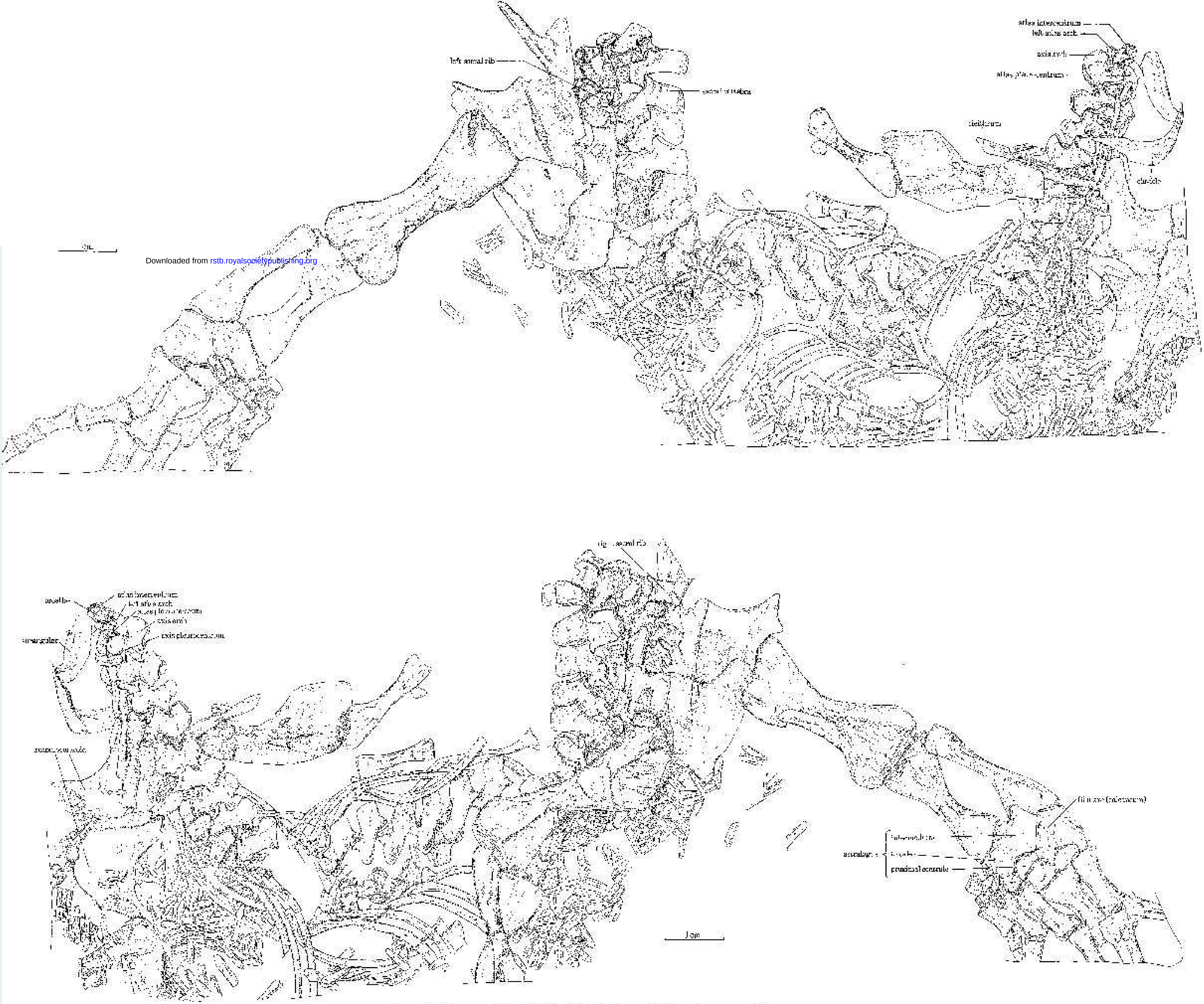


Figure 3. *Gephyrostegus bohemicus.* NM1901.1078 a, b. Postcranial skeleton in counterpart blocks.