

CARBONIFEROUS STEM-REPTILES OF THE FAMILY ROMERIIDAE

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ABSTRACT. The Family Romeriidae is ancestral to most, if not all, advanced reptilian groups. This family is known from the early Pennsylvanian to the early Permian. The species *Hylonomus lyelli* and *Paleothyris acadiana* are well represented among tree stump faunas in deposits of early and middle Pennsylvania age. Four additional species are known from individual but nearly complete specimens from Middle Pennsylvanian coal swamp deposits: *Cephalerpeton ventriarmatum*, Westphalian D of Mazon Creek, Illinois; *Anthracodromeus longipes* (new genus), latest Westphalian D of Linton, Ohio; and *Brouffia orientalis* and *Coelostegus prothales* (both new genera) from deposits of equivalent age from Nýřany, Czechoslovakia. Other members of this group are represented by less complete remains. Several distinct lineages may be recognized within this family, characterized by differences in patterns of the bones of the skull roof, the dentition, the number and configuration of the vertebrae, and the proportions of the limbs. The diversity within the group suggests the initial differentiation of the later, more specialized reptilian groups. All romeriids are small, insectivorous forms that ap-

parently lived in a fairly wide range of terrestrial environments. The family was the most numerous and diverse in the Middle Pennsylvanian; by the early Permian the group was largely replaced by more specialized descendants.

INTRODUCTION

The earliest mammals are known primarily from very incomplete material—teeth and even fragments of teeth, edentulous jaws, and partial skulls. The relationship among the various groups of Mesozoic mammals is subject to continuing revision, and the specific ancestry of the Tertiary orders is equally contentious. Despite the much greater age of the relevant fossils, there is a surprisingly good record of the early reptiles. Fortunately, the best known group is the family Romeriidae, which is ancestral to most, if not all, higher reptilian taxa. Specimens have been described recently from the Lower Pennsylvanian of Joggins, Nova Scotia (Carroll, 1964), and the Middle Pennsylvanian of Florence, Nova Scotia (Carroll, 1969a). From these forms the basic anatomy of the family is well established. Numerous other genera can now be recognized as belonging to this group. They indicate a considerable range of variability in the patterns of the skull roof, the nature of the dentition, the shape of the vertebrae, and especially in limb proportions. The specializations seen within this group may presage the more significant adaptive changes that occurred within the early evolution of the higher reptilian

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lineages. It is therefore of considerable importance to describe the various romeriids in detail. At least a dozen genera are known, from the Lower Pennsylvanian to the Lower Permian of North America and Europe. For various reasons, it is more practical to consider the Pennsylvanian and Lower Permian genera separately. Only the earlier members of the group will be described in this paper.

The best known of the Pennsylvanian romeriids were discovered in upright tree stumps at Joggins and Florence, Nova Scotia. In these localities, romeriids are relatively common members of the fauna. Romeriids can also be recognized in the coal swamp localities of Linton, Ohio, and Nýřany, Czechoslovakia, and from Mazon Creek, Illinois. Here romeriids are very rare, with no more than a single specimen of any particular species being recognized. Several of the romeriids from these localities have been described previously, but their anatomy typically was not known in sufficient detail to establish their identity. New techniques of preparation and an increase in knowledge of other Paleozoic reptiles makes revision of these forms necessary.

Museum abbreviations. Specimens from various institutions are indicated by the following abbreviations: AMNH: American Museum of Natural History; BM(NH): British Museum (Natural History); ČGH: National Museum, Prague, Czechoslovakia; MB: Humboldt Museum, Berlin, German Democratic Republic; MCZ: Museum of Comparative Zoology, Harvard; MP: Mestké Museum Historicté, Pilzen, Czechoslovakia; YPM: Yale Peabody Museum.

ACKNOWLEDGMENTS

All of the specimens described in this paper were preserved, to a greater or lesser extent, as natural molds in coal shale or ironstone and have been studied by the use of latex casts. We are very grateful for permission to prepare and cast material from various institutions. Dr. and Mrs. James

Brough were very kind in permitting the senior author to study specimens from Czechoslovakia that were in their possession, and for allowing additional casts to be made. Dr. A. Charig arranged for these casts to be prepared by the British Museum (Natural History), after obtaining permission from the museums in Prague and Pilzen, Czechoslovakia, from which they had originally been borrowed. Dr. J. T. Gregory, then of Yale University, permitted the junior author to prepare a cast of the type specimen of *Cephalerpeton ventriarmatum*. Dr. E. H. Colbert, then of the American Museum, allowed the type of *Anthraco-dromeus longipes* to be prepared with hydrochloric acid and cast in latex. Dr. H. Jaeger of the Humboldt Museum was very helpful in allowing the senior author to prepare casts of numerous specimens from the Carboniferous coal swamp fauna of North America and Europe. The specimens have been painstakingly drawn by Mrs. Pamela Gaskill. The photographs were prepared by David C. Stager. Several drafts of the manuscript were typed by Mrs. D. Alison. The work was supported by grants from the National Research Council of Canada, the American Philosophical Society, the Jeffries Wyman Fund of Harvard University, and the William Berryman Scott Research Fund of Princeton University.

SYSTEMATIC DESCRIPTIONS

Class *REPTILIA*

Subclass *ANAPSIDA*

Order *COTYLOSAURIA*

Suborder *CAPTORHINOMORPHA*

Family *ROMERIIDAE*

Genus *Cephalerpeton* Moodie, 1912: 349

Species *Cephalerpeton ventriarmatum* Moodie, 1912: 350

Holotype. Yale Peabody Museum No. 796. This is the only known specimen.

Horizon and locality. Mazon Creek, Grundy Co., Illinois. Francis Creek Shale above Morris (no. 2) Coal, Carbondale

Formation, Westphalian D, Middle Pennsylvanian.

Revised diagnosis. Romeriid captorhinomorph, known at present from a single, incomplete, immature specimen. Teeth of upper jaw much larger and fewer in number than in other romeriids. Sixteen teeth in maxilla, four "pre-canines," two "canines," and ten "cheek" teeth. Size of cheek teeth variable, with some larger than canines. Approximately 24 teeth in dentary, which are smaller than those in maxilla and alternate with them in length. Large teeth show labyrinthine plication of enamel. Palatal bones covered with shagreen of denticles. Longer denticles arranged in three rows radiating from basicranial articulation. Number of presacral vertebrae not established, 28 estimated. Tall neural spines, rectangular in outline. Neural arches sutured to centra. Intercentra large crescents, which may have been continued in cartilage to form complete rings. Scapulocoracoid ossified in three units. Humerus equal in length to five trunk vertebrae. Neither supinator process nor ectepicondylar ridge ossified. Ulna and radius two-thirds the length of the humerus.

Description. Like the Joggins romeriid *Hylonomus*, the Mazon Creek genus *Cephalerpeton* was originally described as a microsauro, and has repeatedly been cited as indicating that this group was ancestral to reptiles. In the initial description (1912 and 1916), Moodie compared the genus with a wide range of forms, most of which are now considered as temnospondyl labyrinthodonts, and placed it in the "microsaurian family Amphibamidae." This classification was followed by Hay (1929).

Gregory (1948) accepted Moodie's assignment of the genus to the Microsauria, but interpreted its anatomy as indicating reptilian affinities. Following Romer's (1950) re-evaluation of the microsauro concept, Gregory (1950) placed *Cephalerpeton* in the captorhinomorph family Protothyrididae [*sic*] (essentially synonymous with Romeriidae). Gregory's work very ably

illustrated the basic anatomy of this genus. High-fidelity latex casts, however, provide sufficient additional detail to warrant a new drawing of the specimen (Fig. 1) and information from recently described romeriids from other localities suggests some modifications in his restoration of the skull. A revised reconstruction of the skull was published by Baird (1965, fig. 6), who first formally assigned the genus to the Romeriidae.

The remains include most of the skull, the first 23 presacral vertebrae, the pectoral girdle, fore limbs and the ventral scales. Outlines of the limbs can be seen in the matrix, indicating the extent of the soft tissue and the texture of the skin. The bone itself was represented by a very soft, clay-like material that had been removed from the hard, ironstone matrix. The resulting cavities were cast with liquid latex, giving a detailed impression of the original structure (Baird, 1955).

Skull. The skull is preserved so as to expose the inside surface of the roofing bones and the ventral surface of the palate. None of the bones of the posterior margin of the skull roof are visible. The configuration of the supratemporal, tabular, and postparietal can be restored only by analogy with other romeriids. The parietals are present only in part, so that their extent must be judged from the configuration of the other parts of the skull. The cheek, outer portion of the skull roof, and snout are preserved so that the skull as a whole can be readily restored.

As restored (Fig. 2) the skull appears relatively deeper and shorter than in other romeriids. The very large circular orbit is slightly posterior to the middle of the skull. The nature of preservation precludes determination of the pattern of the sculpturing. The position of the sutures shown in the restoration is based almost entirely on their appearance in internal view. The configuration of the bones is close to that seen in other romeriid genera, although the pre- and postfrontals very nearly meet beneath the frontals. In dorsal view, how-

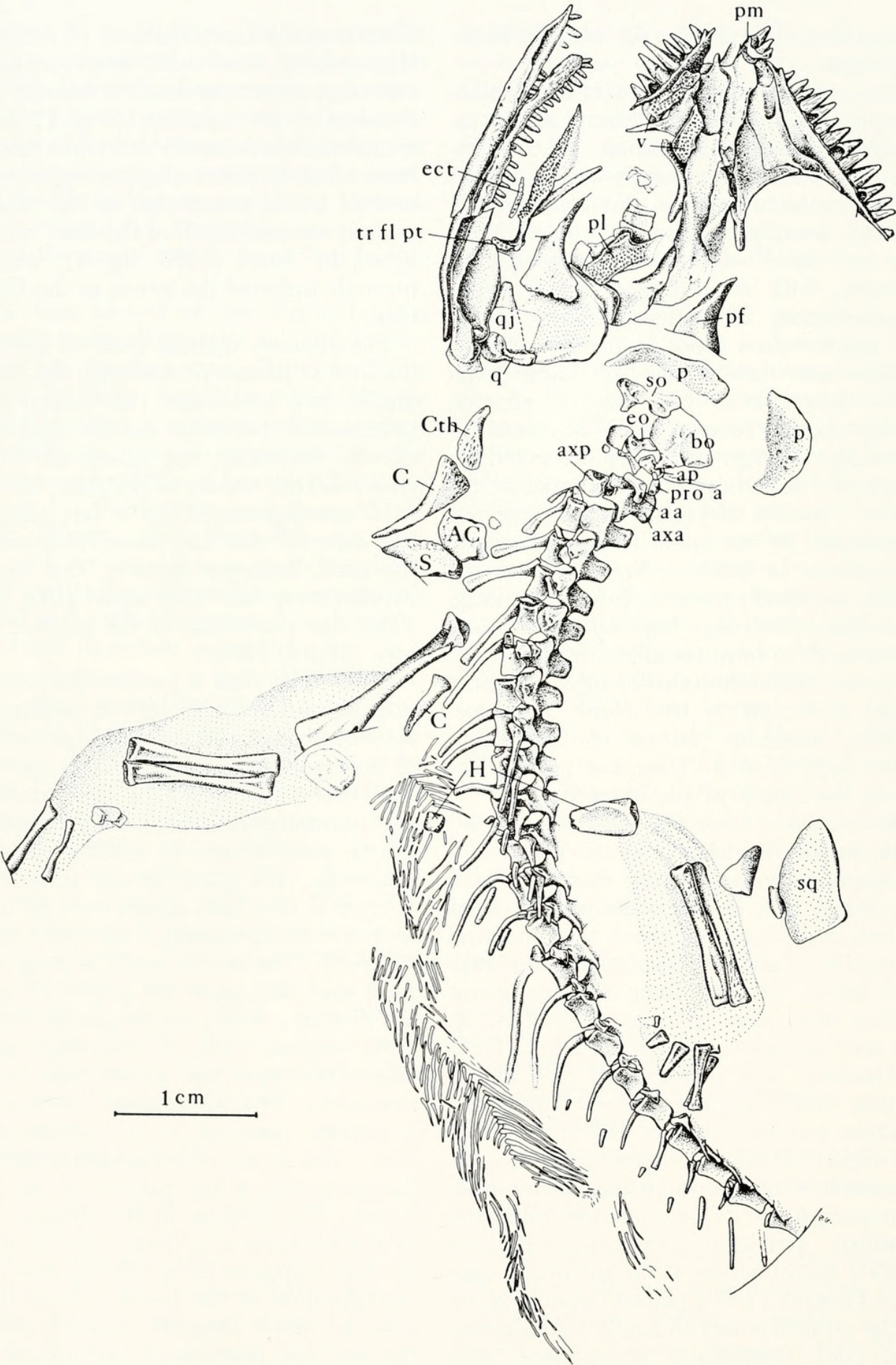


Figure 1. Skeleton of *Cephalerpeton ventriarmatum*. Type YPM 796. $\times 2$. For abbreviations see page 325.

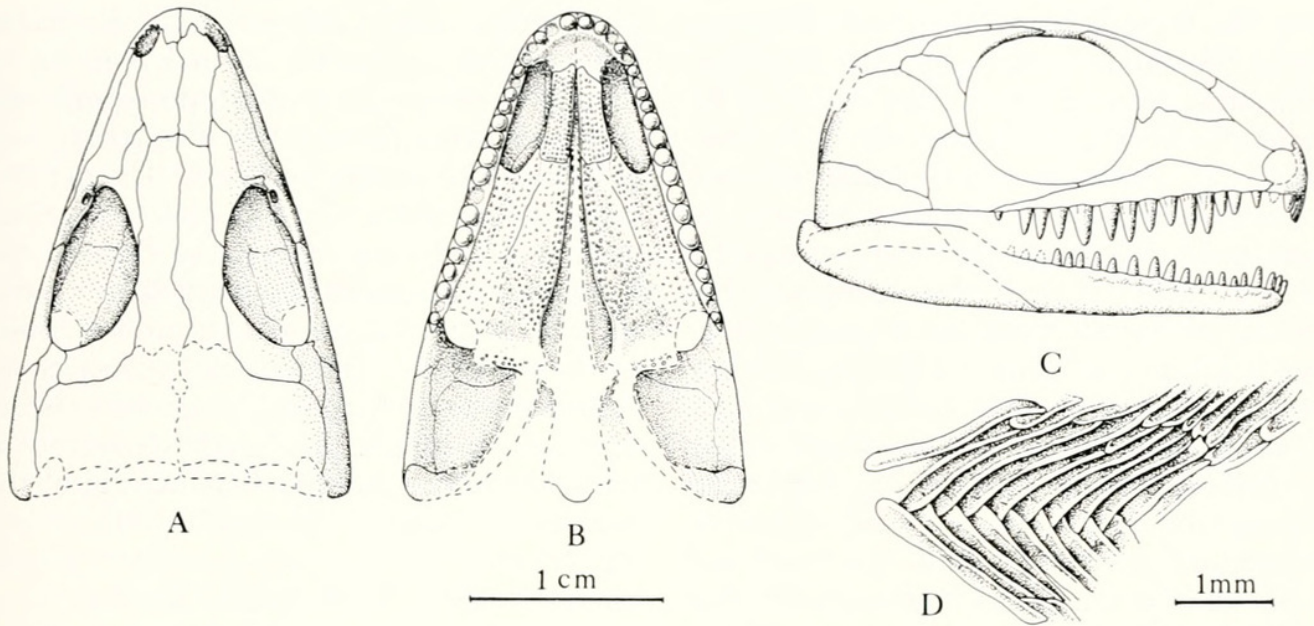


Figure 2. Restoration of skull of *Cephalerpeton ventriarmatum* in A. dorsal; B. palatal; and C. lateral views. $\times 2$. D. Detail of ventral scales in ventral view (somewhat schematic). $\times 10$.

ABBREVIATIONS

AXIAL SKELETON

a—articular
 aa—atlas arch
 ai—atlas intercentrum
 ap—atlas pleurocentrum
 axa—axis arch
 axp—axis pleurocentrum
 bo—basioccipital
 d—dentary
 ect—ectopterygoid
 eo—exoccipital
 f—frontal
 j—jugal
 l—lacrimal
 m—maxilla
 n—nasal
 o—otic capsule
 p—parietal
 pf—postfrontal
 pl—palatine
 pm—premaxilla
 po—postorbital
 pp—postparietal
 prf—prefrontal

proa—proatlas
 ps—parasphenoid
 pt—pterygoid
 q—quadrate
 qj—quadratojugal
 sa—surangular
 so—supraoccipital
 sq—squamosal
 SR—sacral rib
 st—supratemporal
 tr fl pt—transverse flange of pterygoid
 v—vomer

APPENDICULAR SKELETON

A—Astragalus
 AC—Anterior coracoid
 C—Clavicle
 Ca—Calcaneum
 Cth—Cleithrum
 F—Fibula
 H—Humerus
 I—Ilium
 IC—Interclavicle
 P—Pubis
 S—Scapula
 T—Tibia

ever, the frontals have fairly wide exposure above the orbits. One apparent difference from other genera is the great width of the parietals. This is not sufficiently well established to be strongly emphasized, however. A number of typical sclerotic plates can be seen in the right orbit. The most significant feature of the skull is the dentition. The entirety of the left maxilla is exposed. Fourteen teeth are in place with room for two others. This is far below the number in *Hylonomus* (36) or *Protorothyris* (30). Even *Romeria* has room for 21. Like these genera, the most anterior teeth (four in this genus) of *Cephalerpeton* are small, and the next two are large "canines." The remaining teeth are not uniformly small, but of large diameter and variable length. The sixth from the rear is the largest of all. All the teeth are conical and bluntly pointed. The largest show definite labyrinthine infolding at their bases. This feature indicates clearly that the presence or absence of plication of the enamel is not significant to the origin of reptiles. This feature apparently is related primarily to the size of the teeth. *Limnoscelis* and *Solenodonsaurus* have large teeth with labyrinthodont infolding. Most romeriids have small teeth that lack this feature. *Cephalerpeton* might be said to be the exception that proves the rule. The sixth, ninth, and twelfth teeth are deeply eroded at the base, preparatory to replacement.

The premaxillae are not well exposed. Their general configuration can be determined from the restoration of other parts of the skull. There was room for approximately five teeth. Two are present on the left side. They are longer than the most anterior maxilla teeth but smaller than the "canines." In an earlier restoration (Baird, 1965, fig. 6) *Cephalerpeton* is figured as having an overhanging premaxilla, as in *Romeria* and the captorhinids. The configuration of the remainder of the skull makes such a restoration unlikely.

Neither the parasphenoid nor any of the anterior portion of the braincase is

preserved. Both vomers and the right palatine, as well as the medial portions of the right pterygoid and ectopterygoid, are present. From these bones the palate can be almost completely restored. The general pattern resembles that of other romeriids. As was noted by Gregory, the base of the transverse flange of the pterygoid is clearly visible. A very interesting feature is evident in the pattern of the denticles. They cover the vomers and palatine bones in uniform rows. Most of the pterygoid is covered as well, but not uniformly. The margin of the transverse flange is outlined in large denticles. The anterior surface is only sparsely covered. Those on the palatal ramus appear to be uniform, but close examination shows that those on the medial margin of the bone and those extending in a line running anterolaterally from the area of the basipterygoid articulation are slightly raised above their surroundings. This is evidently an early stage in the evolution of the distinct radiating ridges of denticles seen in *Paleothyris*, *Protorothyris*, and most members of other primitive reptilian groups.

Only the posterolateral portion of the right quadrate is preserved. The articulating surface resembles that of other small captorhinomorphs. The epipterygoids are not preserved.

Behind the skull can be seen elements of the rear of the braincase: supraoccipital, basioccipital, and exoccipital. None are sufficiently well exposed for detailed comparison with other early reptiles. All appear to follow the general pattern seen in other romeriids.

The anterior end of the left lower jaw is exposed in lateral view. The dentary is sculptured in a pattern of shallow irregular pits. The right lower jaw is seen in medial aspect. The most notable feature is the presence of a retroarticular process extending one or two millimeters behind the articulating surface. Eighteen teeth can be seen in the left dentary. There is room for approximately four more in this series. About two additional teeth were probably present

at the rear of the jaw to correspond with those in the maxilla. A total of 24 teeth in the lower jaw is three more than the number suggested for the maxilla and premaxilla. The length of the teeth in the lower jaw alternates with that seen in the upper. The most anterior dentary teeth are short. The length increases to fit into a series of short teeth at the front of the maxilla. The length of successive teeth decreases to accommodate the long canine fangs and then increases behind them. This arrangement probably served as a very efficient device for holding and piercing the bodies of small invertebrates.

Postcranial skeleton. Twenty-three vertebrae are in position behind the skull. The greater number (25 or 26) suggested by Gregory apparently resulted from inclusion of some of the occipital elements among the cervical series. Nothing of the pelvic girdle or rear limb is preserved. In other romeriids, the last five or six pairs of trunk ribs are conspicuously shorter than are those further anterior. The last preserved rib (the 22nd) in *Cephalerpeton* is similar in size and shape to those just anterior to this short series. This would suggest approximately six more pairs. A count of 28 presacral vertebrae is intermediate between that observed in *Hylonomus* (26) and *Paleothyris* (32). Such a count is consistent with a constant head/trunk ratio of approximately 1:3.1 in these three genera. (Two romeriid genera from Nýřany, Czechoslovakia, however, have a head/trunk ratio of approximately 1:2.8.) The first two vertebrae are specialized cervicals, very similar to those described in *Paleothyris*. The right proatlas, seen more or less in its natural position, is a small oval bone. The atlas intercentrum is not recognizable. It may be represented by a small bone fragment below the right atlas arch. The atlas centrum can be seen just anterior to the right proatlas. It is a flat-ended cylinder, indented dorsally for the neural canal. It apparently incorporates the tissue that, in pelycosaurs, develops as a separate axis in-

tercentrum. The paired atlas arches are small, L-shaped bones. They do not appear to have had very extensive areas of contact with the centrum. The area of attachment for the tuberculum of the first cervical rib is not preserved. The anterior margin of the axis centrum is not complete. This is the longest centrum in most primitive reptiles. Restoration of the remainder of the cervical region in *Cephalerpeton*, however, indicates that it is no longer than the immediately successive centra. The axis neural arch is very long and high. It is only suturally attached to the centrum, not fused as in other early reptiles. This is probably the result of the immaturity of this particular specimen.

The remaining trunk vertebrae follow a standard pattern. There are large, high-spined neural arches, suturally attached to cylindrical centra. The intercentra are fairly wide crescents. The anterior margin of the arch somewhat overlaps the anterior dorsal margin of the centrum, in a similar fashion, but to a lesser degree than that noted in *Gephyrostegus* (Carroll, 1970a). This feature suggests that the intercentra were probably continued in cartilage to form narrow cylinders.

No ribs are present in association with the atlas. They are present on all more posterior vertebrae. All are clearly double headed, but without the great degree of separation noted in *Seymouria*. The anterior ribs have flattened, but not expanded, blades, which extend posteriorly as well as ventrolaterally. More posteriorly, the shaft is cylindrical and extends primarily ventrally. The length increases to about the tenth rib and then decreases gradually as far as the last preserved presacral.

The pectoral girdle lies in the area of the third to fifth vertebrae. The interclavicle is not preserved. The right clavicle lies in essentially its natural position relative to the endochondral shoulder girdle. The left is posterior to the right humerus. The bones are small, with the blades well sculptured with radiating grooves. Near the right clavicle is another sculptured bone. It

might conceivably be a displaced supratemporal, but it is considerably larger than that element in other romeriids. More probably it is the blade of the cleithrum. It is unusually large for this bone also but it is more or less in the correct area. It is sculptured in a similar manner to the clavicle.

Three elements of the endochondral shoulder girdle are preserved, two in the area of the clavicle, and the third at the distal end of the right humerus. Those near the clavicle are unquestionably the right scapula and anterior coracoid in almost their natural positions relative to one another (although upside down relative to the remainder of the skeleton). The entire girdle can be reconstructed according to the pattern of the pelycosaurs. The third element is not well enough preserved to establish its identity. It might be either the left procoracoid, or one of the posterior coracoids. These elements are very incompletely ossified, suggesting that *Cephalerpeton* was very immature. The dorsal end of the scapula is buried in the matrix. It must have been much more extensive both dorsally and anteriorly in the mature animal. A foramen pierces the bone just above the glenoid. The procoracoid is roughly circular in outline. The posterior margin is largely occupied by the anterior face of the glenoid. Beneath this structure is the coracoid foramen. The scapulocoracoid in most romeriids that have been described is preserved as a single ossification. The tripartite structure as seen in *Cephalerpeton* probably has no taxonomic significance. The presence of one or more coracoids in pelycosaurs, procolophonids, and other reptiles may have resulted from prolongation of the pattern of development seen originally only in immature animals.

The humerus, despite the incomplete ossification of the articulating surfaces, is the length of five trunk centra. It is a lightly built bone with the distal extremity expanded flatly. The entepicondylar foramen is an elongate opening. The ulna and radius are present in close association on both

sides. As a result of the low degree of ossification they appear almost identical. They are approximately the length of four trunk vertebrae. The ends are almost equally expanded. The shaft of the ulna is slimmer than that of the radius. There is little, if any, ossification in the area of the carpals. There is one element that might be a distal, but could also be a fragment of a metacarpal or phalanx.

The largest metacarpal is almost half the length of the ulna or radius. Neither the digital nor phalangeal formula can be established. The elements present indicate that the hand was very long, as are all elements of the forelimb.

Skin and scales. The skin impressions along the forelimb have a slightly pebbly texture—rougher than the limb bones but smoother than the broken surface of the matrix. There is no evidence of discrete scales. An indication of epidermal scales would be expected in this type of preservation, if they were present in the animal. This suggests that this specimen of *Cephalerpeton* lacked epidermal scales. Some indication of dorsal dermal scales appears in the reptilelike anthracosaurs *Gephyrostegus* and *Eusauropleura*. Dermal scales are apparently lost early in reptilian evolution. Unfortunately, epidermal scales can only be recorded as impressions and this type of preservation is rare and apparently not reported in other Paleozoic reptiles. There is no record sufficiently early to indicate the time at which epidermal scales evolved. There may have been a period during which dermal scales were completely lost, but epidermal scales had not yet evolved.

The ventral dermal scales are preserved in this specimen of *Cephalerpeton*. The overall pattern is similar to that of other primitive reptiles: a series of overlapping scales forming a chevron pattern, the apex of which points anteriorly. The detailed configuration and pattern of overlap is somewhat difficult to see in either of the photographs (Plates I and II) or the draw-

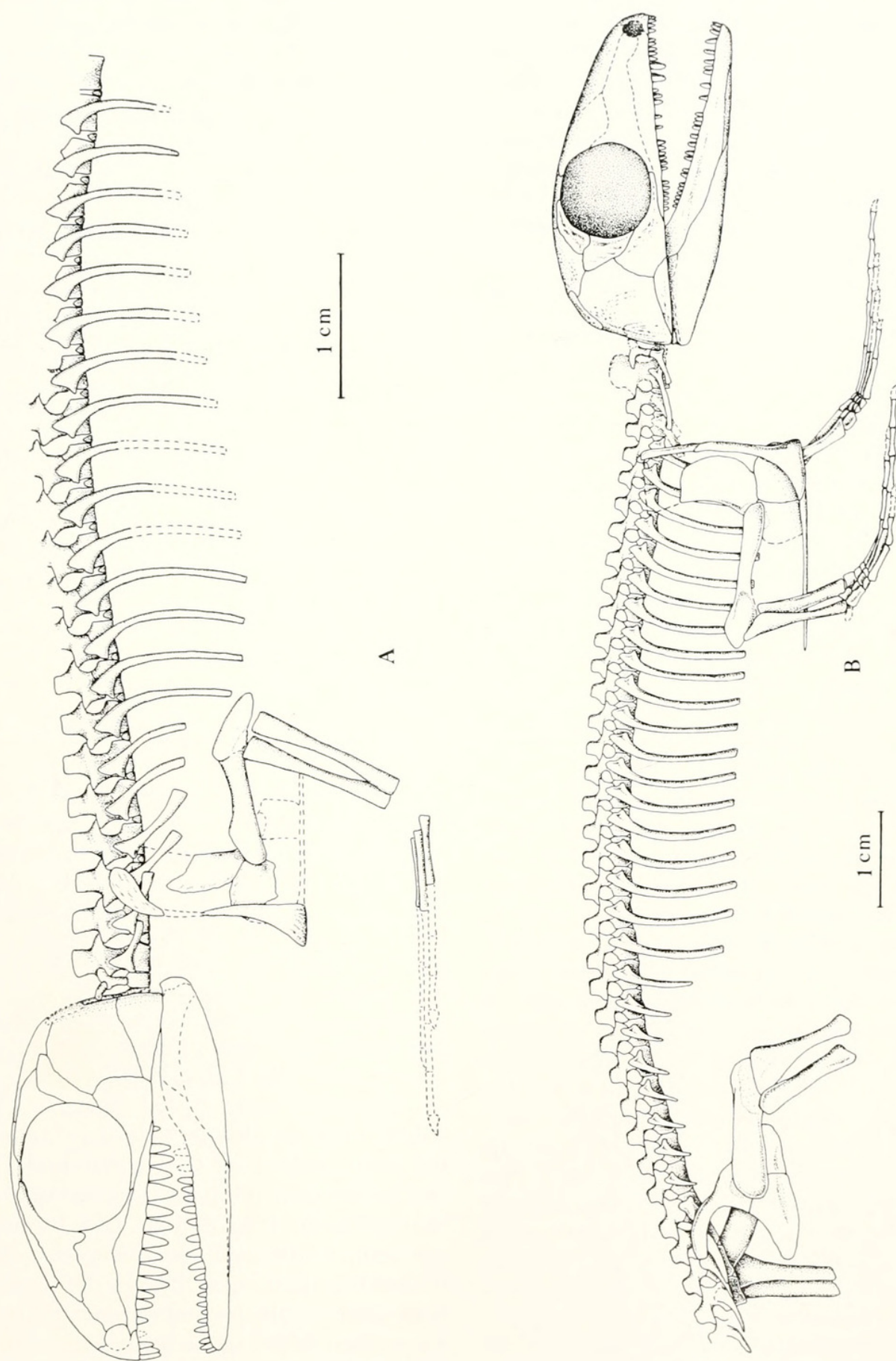


Figure 3. A. Restoration of the skeleton of *Cephalerpeton ventriarmatum*, $\times 2$. B. Restoration of *Brouffia orientalis*, $\times 1.33$.

ings, owing to the nature of preservation. The narrow rodlike structures that are visible are the posterior ridges of the scales, and the remainder of the surface is largely covered by matrix.

Small sections of the squamation have been illustrated in a slightly schematic manner in Figure 2D. The covering of scales is contiguous, in fact overlapping, rather than in the form of an open lattice. The medial ends of the scales overlap in an alternate fashion at the midline. The distal end of the medial scales overlaps the proximal end of the more lateral ones. Posteriorly, there are isolated scales that come from a third row.

Discussion. The absence of the posterior portion of the skull roof, the pelvic girdle, and the rear limb as well as the immaturity of the only known specimen make it difficult to compare *Cephalerpeton* with other romeriids. The most notable feature is the dentition, which immediately distinguishes this genus from all other members of the family (except *Anthracodromeus*, in which the dentition is not known). The reduction in the number of teeth and the increase in size of the postcanines indicate a significant change in diet from the primitive pattern. The cheek teeth in most romeriids were presumably employed primarily to hold and squash the prey. In *Cephalerpeton* they would be efficient for piercing the prey as well. A similar dentition is developed in the small and primitive eothyridid pelycosaurs. No later romeriids have such a pattern. This suggests that this particular feeding specialization may have been usurped by small pelycosaurs that had the advantage of a more sophisticated jaw musculature. The primitive distribution of the palatal denticles and the structure of the vertebrae suggest that the ancestors of *Cephalerpeton* diverged from the main romeriid lineage early in the Pennsylvanian. This genus might have evolved directly from *Hylonomus* or possibly from a slightly more primitive form. The dentition is too specialized for *Cephalerpeton* to have given

rise to any of the known genera from the later Pennsylvanian or Permian.

Anthracodromeus n. gen.

Type species. *Anthracodromeus longipes* (Cope), new combination.

Known distribution. Middle Pennsylvanian of North America.

Etymology. Greek: *anthracos*, coal, plus *dromeus*, runner.

Diagnosis. Romeriid captorhinomorph. Thirty-one presacral vertebrae. One pair of sacral ribs. Neural arches anteroposteriorly elongate, lateral surfaces "sculptured." Pattern of bones of the posterior skull roof and nature of sculpturing very similar to those of *Paleothyris* and *Protorothyris*. Blade of ilium very long. Limbs long relative to body size; humerus and femur equal in length to eight trunk centra; radius and tibia equal in length to four trunk centra. Hands and feet very long.

Anthracodromeus longipes

Sauropleura longipes Cope, 1874: 270.

Tuditatus longipes Cope, 1875: 398–399, pl. XXVI, fig. 2; Moodie, 1916: 89–91, fig. 20.

Holotype. American Museum of Natural History (AMNH) 6940. Almost complete skeleton preserved in counterpart blocks. This is the only known specimen.

Horizon. Canneloid shale underlying Upper Freeport Coal, Allegheny Group, Middle Pennsylvanian, equivalent to the latest Westphalian D of Europe.

Locality. Diamond Mine, Linton, Saline Township, Jefferson County, Ohio; NE corner, sect. 13, T.9N., R.2W.

Diagnosis. Same as for genus.

Description. Although the Linton fauna has been studied for over a hundred years and scores of amphibian genera have been described, no true reptiles had been recognized. *Tuditatus punctulatus* has been referred to that class by several workers, but recent study has established that it is unquestionably a microsauro (Carroll and Baird, 1968). It is not surprising that reptiles

are rare at this locality, considering the nature of the deposition and the aquatic and semi-aquatic adaptations of the amphibians. Judging from our knowledge of events leading up to the origin of reptiles (Carroll, 1967 and 1970b), the early members of that group were apparently primarily terrestrial in habit. Some aquatic lineages may have evolved later among primitive reptiles, but none are known in the Middle Pennsylvanian. As a result of a large-scale, systematic effort to prepare all material that has been found from the Linton locality, several specimens have been discovered that are definitely reptilian. Most of these are pelycosaurs and are being studied by Reisz; the single known romeriid consists of an almost entire skeleton preserved in counterpart blocks. The method used for preparing this material has been described by Baird (1955).

Like many of the specimens from Linton, this genus has a complex taxonomic history. It was initially described by Cope (1874) as one of numerous species of the genus *Sauroplesura*, the type species of which is a nectridean. Cope was no doubt led to this initial identification by the configuration of the neural spines. He later placed it in the ill-defined genus *Tuditanus*. Moodie, in his 1916 monograph, accepted Cope's identification as a species of *Tuditanus* and noted the presence of ventral chevrons. In 1930, Romer identified the specimen as a coelacanth, largely on the basis of undoubted coelacanth scales that lie close to it on the block. Upon preparing the specimen, Baird (1958) diagnosed it as a romeriid reptile on the basis of skull characters, noting its close affinities to the Permian genus *Protorothyris*; he assigned the species tentatively to *Cephalerpeton* pending further study. Analysis of the specimen has been difficult, however, because extreme crushing has reduced the bones to paper-thinness. Mrs. Pamela Gaskill has contributed greatly to this work by her careful drawing of the specimen (Fig. 4). The skeleton is virtually complete,

lacking only the skull anterior to the orbits, the ventral portion of the shoulder girdle, and the end of the tail.

Skull. The posterior portion of the skull is crushed so that the dorsal skull roof is exposed in one block and the right cheek region is seen in the other. None of the dentition can be seen and the posterior portion of the palate is completely covered by other bones. The bones at the posterior margin of the skull roof have a configuration similar to those seen in *Protorothyris*. The parietal extends a narrow lateral lappet over the top of the squamosal. Posteriorly the bone is deeply embayed for the supratemporal, tabular, and postparietal. These bones are spread out behind the skull roof. The supratemporal is in the shape of an elongate oval superficially sculptured, which must have extended ventrally over the posterior margin of the squamosal. The tabular was overlapped dorsomedially by the postparietal. Ventrally it is notched where it surrounds the posttemporal fenestra. The postparietals are simple oblong bones, smooth-surfaced like the tabulars. The supraoccipital is displaced slightly to the left of the midline behind the skull. It is incised laterally for the posttemporal fenestra. Dorsally the bone is marked by indentations where it was overlapped by the postparietals. Medially a narrow ridge extends dorsally between these bones. The dorsal margin of the foramen magnum is covered by the right exoccipital. The left exoccipital overlies the left margin of the supraoccipital, with the medial surface uppermost. The basioccipital is not visible. The right otic capsule may be represented by an ill-defined ossification visible behind the squamosal. The stapes may also be crushed into this area. The occipital surface may be restored according to the pattern of the other, better articulated romeriids.

The configuration of the bones of the cheek region and posterior parts of the jaw is essentially similar to that seen in other romeriids. The right quadrate has been forced out behind the quadratojugal. As in

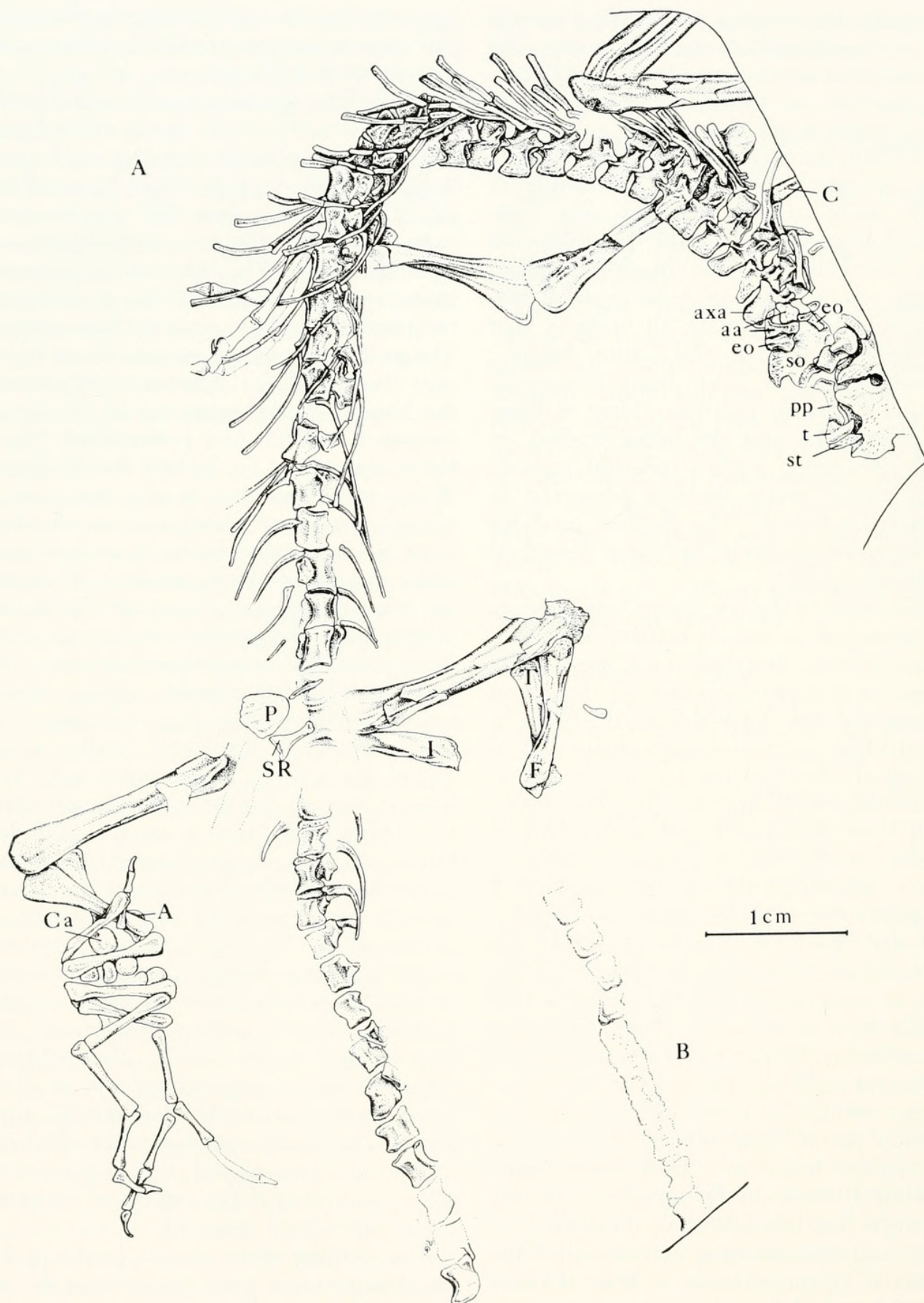
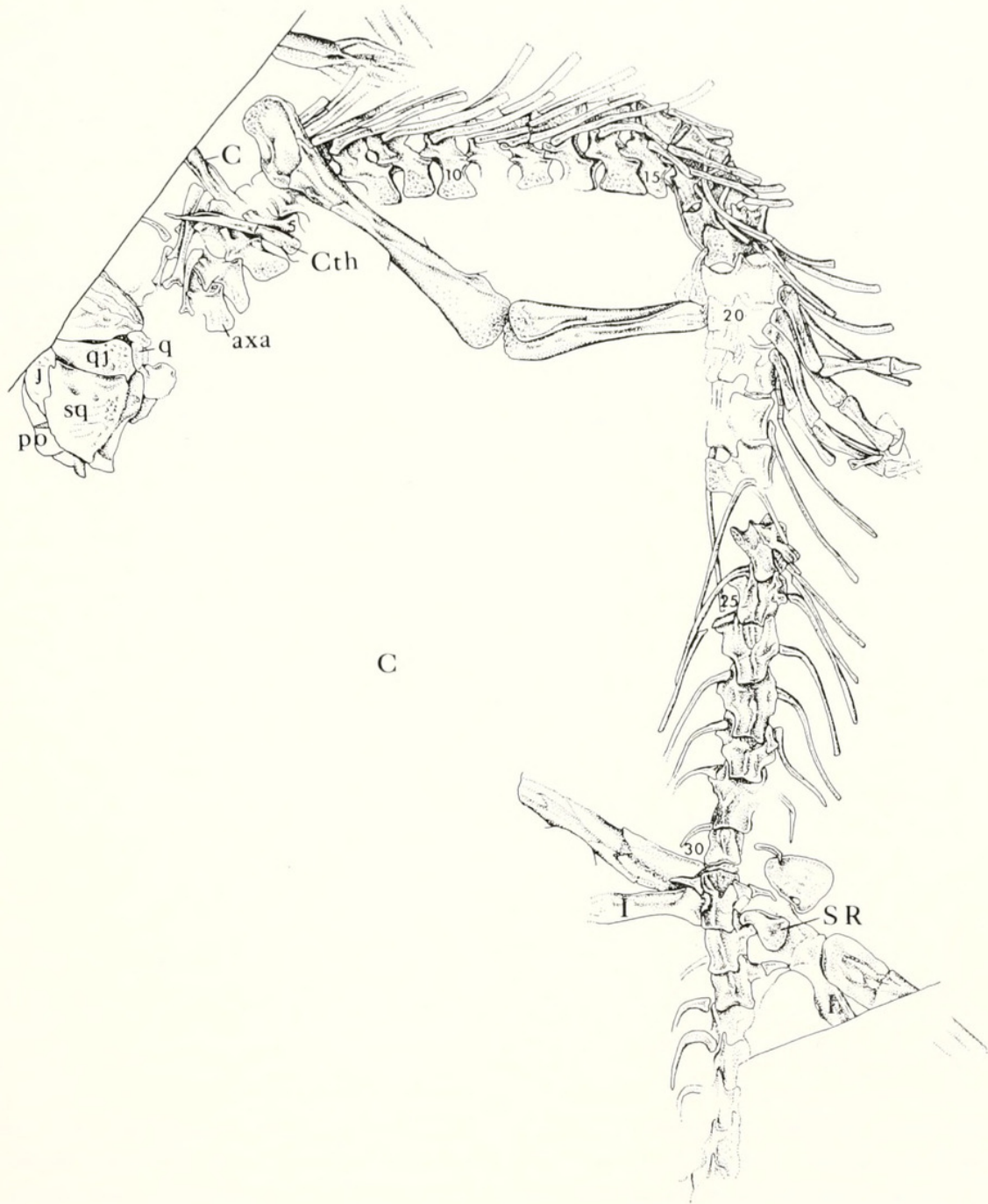


Figure 4. A-C. Counterparts of skeleton of *Anthracodromeus longipes*. Type AMNH 6940. $\times 2$. B. Distal end of tail.



Protorothyris, the ventrolateral margin of the articulating surface was probably exposed laterally beneath this bone. The posterior margin of the squamosal was exposed on the occipital surface and is clearly demarked from the lateral surface. The sculpturing seen on the cheek region and dorsal surface of the posterior skull roof is very similar to that seen in *Protorothyris*, a series of relatively uniform, shallow pits. The outline of the skull may be restored on the basis of the known posterior portion and

the general pattern of other romeriids. It may reasonably be reconstructed as having a length equivalent to that of nine or ten trunk vertebrae. There is no way of judging the nature of the dentition.

Postcranial skeleton. The vertebral column lies in more or less natural articulation behind the skull and extends to approximately the 24th caudal. There are 31 pre-sacral vertebrae and one sacral. The tail probably had at least 12 more segments posterior to those that are present.

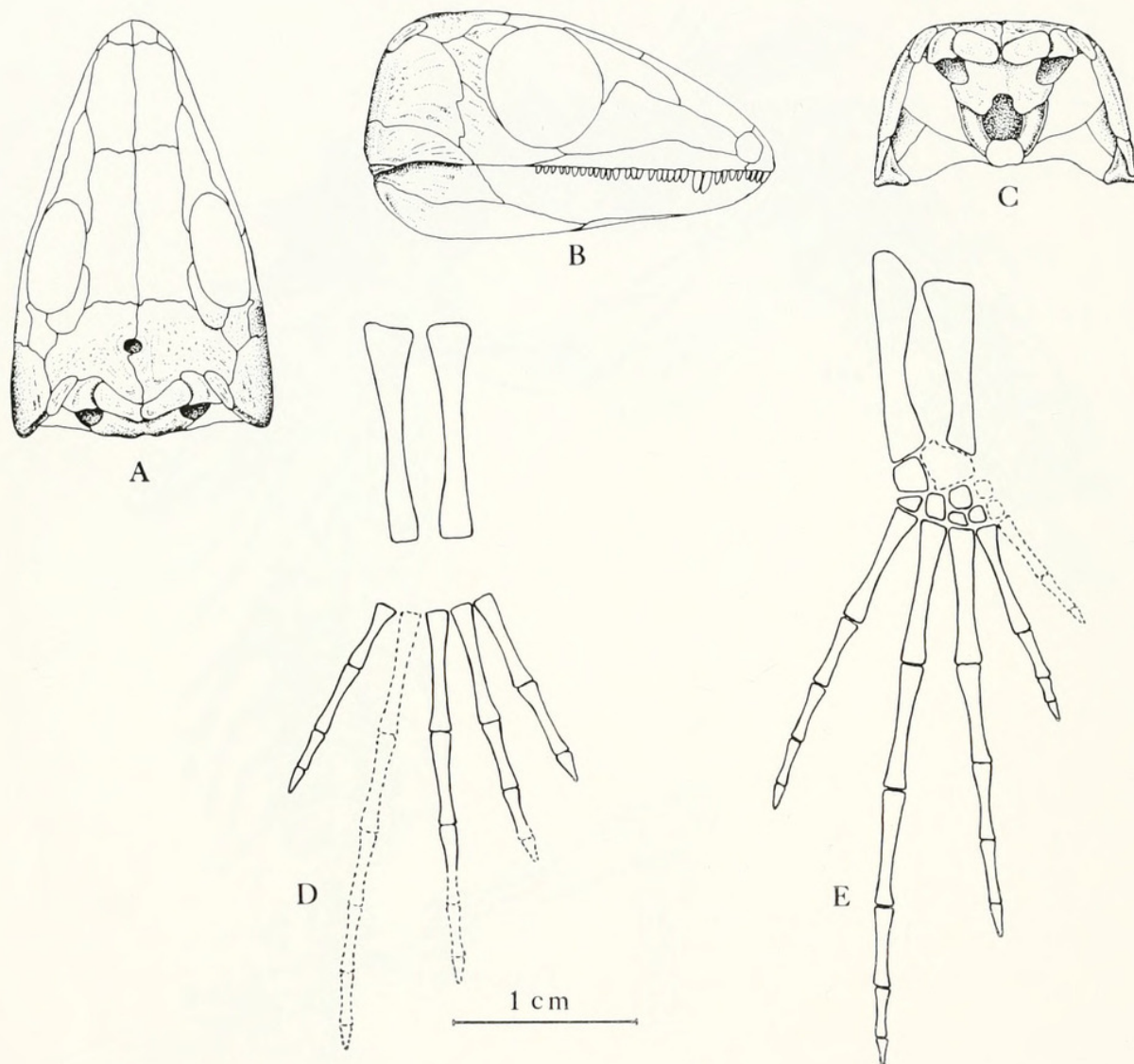


Figure 5. *Anthracodromeus longipes*. Restoration of skull in: A. dorsal; B. lateral; and C. occipital views. Unshaded areas are hypothetical. D. and E. Restoration of hand and foot. $\times 2$.

The elements of the atlas-axis complex are somewhat disarticulated and partially obscured by the scattered bone of the occipital complex. The proatlas is not evident. The left atlas arch is preserved in essentially its normal position although its lateral surface is obscured by an unidentified bone fragment. Ventrally there is a well-developed lateral ridge that ends distally in an area for the articulation of the tuberculum of the first rib. The right atlas arch can be seen in medial view anterior to the dorsal margin of the axis neural spine. Ventrally there is a distinct surface for articulation with the centrum. Posteriorly there is an elongate portion that articulates

with the anterior zygapophysis of the axis. As in other romeriids, the atlas lacks a spine. Neither the atlas intercentrum nor pleurocentrum can be identified. The axis, like that of other romeriids, has a large spine, fused to the centrum and overhanging the posterior margin of the atlas. The spine of this and all subsequent trunk vertebrae is narrow from side to side and marked by delicate pitting. All the spines have the appearance of metal, gently tapped by a ballpeen hammer. An identical pattern has been observed on an unnamed (but probably closely related) form from the Lower Permian of Texas (MCZ 1474). The large size of the neural spines probably contrib-

uted to the stability of the vertebral column by being deeply embedded in the axial musculature. Posterior to the twenty-third vertebra, the arches and spines are crushed down into the neural canal. The hatchet-shaped outline observed in the anterior segments probably continued at least to the sacral region, but there is no evidence for the more posterior elements. The arches are very narrow at the base with no evidence of the swelling noted in later captorhinomorphs. The transverse processes of the anterior vertebrae are narrow and extend a considerable distance ventrolaterally from the arch. More posteriorly the length diminishes and the configuration corresponds more closely to that seen in other Pennsylvanian romeriids. In none of the vertebrae is the area for articulation with the capitulum of the rib evident. The neural arches are strongly attached to the centra throughout the column. Only where there has been severe crushing have the elements been disarticulated. Where this has occurred, the typical line of sutural attachment in other primitive reptiles has been disclosed. Throughout the column, the pleurocentra are elongate cylinders, deeply indented at the ends for the notochord. The anteroventral margin is notched for the reception of the intercentrum, which appears as a narrow crescent. This element is rarely visible. It is unlikely that this bone continued dorsally in cartilage, as has been suggested for *Cephalerpeton*.

The sacral vertebra is specialized only in the larger size of its transverse process. A thin piece is broken from the dorsal block, so that posterior to the sixth caudal the tail is visible only ventrally. Well-developed intercentra are visible anterior to the first four caudals. No intercentral elements are evident in the succeeding three segments. Between the seventh and eighth is a typical haemal arch. No other haemal arches can be recognized. The first eleven caudal centra resemble those in the trunk region, except for their gradually diminishing size. More posteriorly, the preservation is too

poor for even the number of segments to be determined with any assurance.

Ribs are present throughout the column. The first three pairs of cervical ribs have flattened blades and extend posteriorly as well as ventrolaterally. They are clearly double-headed. More posteriorly, the ribs extend primarily ventrolaterally and the shafts are essentially cylindrical, although they are crushed flat in the specimen. The length of the shaft increases rapidly to the eighth rib and then remains approximately the same back to the 24th segment, after which it decreases. The last three pairs of ribs are particularly short. The last several pairs of presacral ribs are short in all romeriids, but the specific number of short ribs varies from genus to genus.

There is only a single pair of sacral ribs. The tubercular head is much thicker than that of other ribs. The area of the capitular head is not visible. The blade is short and spatulate, like that of *Paleothyris*. Unlike that genus, the next succeeding rib does not contribute to the attachment of the pelvis. The first six caudal vertebrae have fused ribs which extend posteriorly to lie alongside the column. The length increases from the first to the third and then decreases rapidly. The sixth is only a short nubbin.

The endochondral shoulder girdle is not preserved. The general configuration is restored according to the pattern of other romeriids. There is no way of judging whether it developed as a single bone, or from two or more initially separate areas of ossification. The ventral portion of the dermal shoulder girdle is lost beyond the edge of the blocks. Nothing of the interclavicle is visible, and only the dorsal end of the stem of the clavicle. The right cleithrum is clearly exposed. It is in the shape of a long, narrow rod. The dorsal end is flattened but only slightly expanded, anteroposteriorly. The ventral end is pointed and notched posteriorly for attachment to the stem of the clavicle or the scapular blade. The anterior margin of the shoulder

girdle, as preserved, is at the level of the fifth vertebra.

The humerus is a long, narrow bone, with the extremities well ossified. In general it resembles that of *Araeoscelis*. It is equivalent in length to eight trunk centra. The shaft is long and narrow. There is neither a supinator process nor an entepicondylar ridge. The distal articulating surfaces are obscured as a result of crushing. The outline of the entepicondylar foramen can be seen in dorsal view on the right humerus, although the posterior border is broken away.

The ulna and radius are long, lightly built bones. The olecranon is poorly ossified, but otherwise these bones are similar to their counterparts in other romeriids.

The carpals are lightly ossified. Their original configuration is impossible to determine. This area is crushed into the vertebral column on the right side and missing from the block on the left. Much of the proximal part of the right manus is in natural articulation. One of the digits and its metacarpal (apparently number four) is missing. The longer metacarpals are more than half the length of the radius. The proximal phalanges are only slightly shorter. The unguals of digits one and five are short and sharply pointed. They do not appear to bear a well-developed keel such as is reported in *Paleothyris*. If the manus is restored according to the pattern of other romeriids, it would be slightly longer than the humerus.

The pelvic girdle is poorly preserved. The most notable feature is the great length of the iliac blade. It is a narrow, flat structure oriented at approximately 15 degrees from the vertical. The ventral portion is poorly preserved, but appears to be quite small. The right pubis is visible medially; the margins are poorly defined, but it is roughly quadrangular in shape. The ischia are crushed against the ventral surface of the vertebrae so as to obscure their original shape. Only the general extent can be determined.

The femur has a long, narrow shaft. It

is slightly shorter than the humerus—a very surprising feature among primitive tetrapods. Few structural details are evident. The tibia appears to be slightly shorter than the radius. Unfortunately the limits of the articulating surface are difficult to establish because of the extreme crushing. The tarsals are weakly ossified and scattered among the metatarsals of the right foot so that their specific configuration is impossible to determine, but they can be restored according to the general pattern observed in other romeriids. The astragalus and calcaneum are represented by roughly circular blobs. Most of the foot bones are present, but their manner of association is subject to various interpretations. The first digit appears to be missing. The remaining metatarsals are in essentially their original position relative to one another. The longest is approximately 80 percent as long as the tibia and at least 20 percent longer than the longest of the metacarpals. The posterior epipodials may be shorter than the anterior, but the rear foot as a whole is not shorter than the manus, although the first two digits of the pes are shorter than those of the manus. All the phalanges of the fourth digit are seen in contact with one another. Together with the metatarsal it is more than half again as long as the femur. A series of three short phalanges can reasonably be associated with the second metatarsal. Other phalanges can be attributed to the third and fourth digits. The series probably associated with the fifth is very poorly preserved and the number and configuration of the phalanges is difficult to establish. There may have been four.

Ventral scales are present in large numbers in the specimen. Crushing makes it impractical to illustrate them with the rest of the skeleton. They are considerably wider than those in the Joggins and Florence romeriids, but this may be accentuated by crushing. The lateral extent of the squamation of ventral scales appears to be greater than in these genera as well. No dermal dorsal scales are evident.

Age-Habits. It is difficult to judge the degree of maturity of the type of *Anthracodromeus* because of the nature of preservation. The poor definition of the articulating surfaces of the limb bones, carpals, and tarsals can be attributed either to incomplete ossification or extreme crushing. This specimen may be less mature than the material of *Paleothyris* or *Hylonomus*, but it is certainly more mature than the only known specimen of *Cephalerpeton* or the Czechoslovakian genera. The neural arch and centrum of the vertebra are firmly united and there is certainly some degree of ossification of the carpals and tarsals.

The great length of the limb bones and feet suggests a somewhat different habit than that of more conservative romeriids. Such long limbs and feet are seen in a number of modern lizards that are terrestrial or arboreal in habit. It would not be unreasonable to assign *Anthracodromeus* to such adaptive zones. To judge from the body and limb proportions, it was presumably an agile form. In the absence of any information on the dentition, there is little evidence of possible feeding habits.

Taxonomic position. The pattern of the bones of the skull roof and the structure of the postcranial elements indicate that *Anthracodromeus* is a member of the family Romeriidae. The configuration of the neural arches and the great relative length of the limb bones distinguish this form from all other described genera.

The presence of one pair of sacral ribs indicates that the ancestors of the genus evolved from the primary romeriid stock separately from *Paleothyris*, which has two.

It shows no close affinity with *Cephalerpeton* or the forms from Czechoslovakia. *Anthracodromeus* is probably directly ancestral to an, as yet, undescribed form from the Putnam Formation, Lower Permian of Texas, which has similarly shaped vertebrae and elongate limb elements. It shows no specific affinities with other, more advanced reptilian groups.

Brouffia n. gen.

Type species. *Brouffia orientalis* new species.

Known distribution. Middle Pennsylvanian of Central Europe.

Diagnosis (based on a single, immature specimen). Romeriid captorhinomorph, pattern of skull roof and dentition similar to *Paleothyris*, except for smaller number (26) of maxillary teeth. Four rows of denticles on pterygoid. Thirty-one presacral vertebrae, one sacral. Neural spines squarish in lateral view, not elongate. Scapulocoracoid is ossified from more than one unit. Limbs and feet not greatly elongate. Carpals ossified.

Brouffia orientalis n. sp.

Etymology. Generic name is in honour of Dr. Margaret Steen Brough, who initially recognized the specimen on which this genus is based. The species name emphasizes the presence of the family Romeriidae in Europe.

Holotype. Counterpart blocks including the natural cast of an almost complete skeleton. Dorsal surface from the Czechoslovakian National Museum in Prague ČGH III B.21.C.587 and the ventral surface from the Natural History Museum in Pilzen MP 451. This is the only recognized specimen.

Horizon and locality. Middle Pennsylvanian, Westphalian D, of Nýřany, Czechoslovakia.

Diagnosis. Same as for genus.

Description. Although the type specimen of *Anthracodromeus* is the only reptile currently recognized from the coal swamp deposit of Linton, Ohio, a number of forms are known from Nýřany, Czechoslovakia, a locality of roughly equivalent age and generally similar ecology.

The exact taxonomic position of *Solenodonsaurus* (Carroll, 1970a) remains subject to controversy, but it has attained an essentially reptilian level of development. Three additional specimens will be discussed here that are apparently members

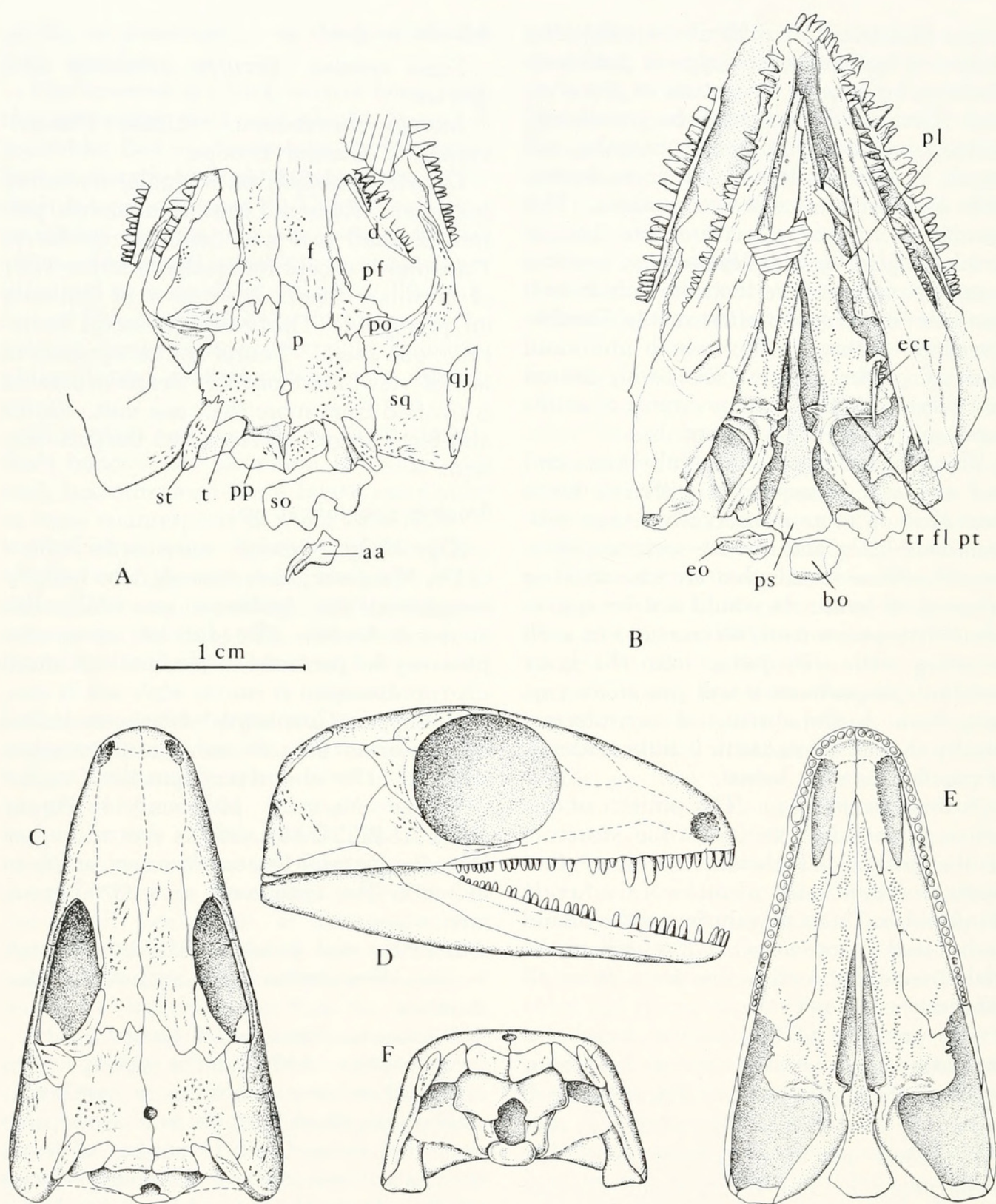


Figure 6. Type of *Brouffia orientalis*. A. Dorsal surface of skull ČGH 111B.21.C.587. B. Ventral surface of skull MP. 451. Restoration of skull in: C. dorsal; D. lateral; E. palatal; and F. occipital views. $\times 2$.

of the family Romeriidae. The most completely known specimen is a skeleton preserved in counterpart blocks from the museums in Prague and Pilzen, described by

Brough and Brough (1967) as *Gephyrostegus bohemicus* specimen I. It is an almost complete skeleton of an immature animal. Considerable attention has already

been paid to the fact that this specimen does not belong to the genus *Gephyrostegus* (a taxon now much better known than it was at the time of the publication of the Broughs' work). The pattern of the bones of the skull roof and the morphology of the palate are comparable to the North American genera of the family Romeriidae. This is especially noteworthy, since this is the first recognized member of this family in Europe.

The specimen is preserved as a natural mold in coal shale. The cavities have been cast in latex. The restoration of the postcranial skeleton (Fig. 3B) is based primarily on drawings (their figs. 10A and B) made by the Broughs. The skull (Fig. 6) has been redrawn from the original latex casts.

Skull. The pattern of the bones of the skull roof and the nature of the sculpturing in *Brouffia* is very similar to that of the contemporary genus *Paleothyris*. The skulls would be very difficult to differentiate in dorsal or lateral views. The parietal is broadly in contact with the squamosal and postorbital. The postfrontal does not extend as far posteriorly as that of *Protorothyris*, nor is the posterior margin of the parietal as deeply embayed for the tabular and postparietal as in *Anthracodromeus*. Several features that distinguish this skull from that of *Paleothyris* (Fig. 10) can be noted in palatal view. There are significantly fewer marginal teeth: *Brouffia* has room for 26 teeth in the maxilla, in contrast with 35 in *Paleothyris*. The presence of a single pair of "canines" in the type of *Brouffia*, rather than two pairs, is probably not significant since the number is variable in *Paleothyris*. *Brouffia* has room for approximately five teeth in the premaxilla. *Paleothyris* and members of the most primitive reptilian groups have two rows of denticles on the pterygoid, radiating out from the area of the basicranial articulation, anterior to the transverse flange; *Brouffia* has three rows. The ectopterygoid may also be seen to bear large denticles. The pterygoids extend an-

teriorly to the level of the "canines," separating the vomers for most of their length. A further, minor difference is the presence of a carpet of fine denticles on the ventral surface of the parasphenoid, rather than a single or double row of larger teeth.

Most of the occipital elements are spread out behind the skull. A large, platelike supraoccipital is visible dorsally. It lacks the well-developed recesses to accommodate the postparietals, characteristic of *Anthracodromeus*, nor does it bear a prominent medial keel. The basioccipital is displaced, so that the entire ventral surface is exposed behind the parasphenoid. The more anterior position of the exoccipitals indicates that such a posterior position did not occur in life. The exoccipitals (termed stapes by Brough and Brough) are badly crushed and extend primarily laterally as the skull is preserved. The opisthotics have not been recognized. The occipital surface can be restored according to the general pattern seen in other romeriids.

Postcranial skeleton. There are 31 presacral vertebrae, one sacral and four caudals preserved. The elements of the atlas-axis complex are disarticulated and not all can be recognized. The proatlas has not been identified. The atlas arch is paired and had a long posterior process for articulation with the axis arch. Neither the atlas pleurocentrum nor intercentrum can be distinguished. The axis centrum is only slightly longer than the more posterior elements. The arch was suturally attached rather than fused and has become separated. The extent of the spine cannot be determined. The more posterior trunk vertebrae also have a distinct suture between the arch and centrum and most of the elements are at least slightly displaced. The left and right halves of the neural arches are also displaced at the midline. The neural spines are squarish in outline, but without the elongation noted in *Cephalerpeton*. No intercentra are observed in the column, but the ventral margins of the pleurocentra are bevelled for their reception.

Only a single vertebra, the 32nd, bears a sacral rib. The vertebra itself is little modified, except for the large size of the transverse process. No haemal arches are present among the four anterior caudal vertebrae preserved.

Double-headed ribs are present throughout the column. The first two pairs are specialized cervicals with flattened shafts that extend posteriorly, as well as ventrolaterally. The configuration of the next two pairs cannot be established. Those in the remainder of the column have cylindrical shafts that extend primarily ventrolaterally. Their length increases rapidly to the 8th rib, remains essentially constant to the 22nd, and then diminishes rapidly. The last six pairs of presacral ribs are very short. The sacral rib has a simple, spatulate blade, which apparently was not in contact with either of the adjacent ribs. The anterior caudal ribs are fused to the vertebrae, and extend posteriorly to lie alongside the tail.

The dermal elements of the shoulder girdle are all clearly exposed. The cleithrum is a flattened rod of bone, with little elaboration of the dorsal blade. The clavicle resembles that of other romeriids in having a small, neatly sculptured blade. The interclavicle has a long stem and a smoothly rounded anterior margin. The endochondral shoulder girdle is ossified in three separate units, as is the case in *Cephalerpeton*. The scapula is illustrated by the Broughs. Its margins must have been considerably extended by cartilage in the living animal. One of the anterior coracoids is visible just dorsal to the left scapula. It is vaguely oval in outline. The posterior element has not been recognized. It may have been slow to ossify.

The forelimb is not well ossified; only the general configuration and proportions of the bones can be established. The size of the humerus, ulna, and radius relative to the length of the trunk vertebrae is similar to the condition in *Paleothyris*. The limbs are relatively shorter than those of *Cephalerpeton* and *Anthracodromeus*. Con-

sidering the small degree of ossification in the shoulder girdle and limbs, the carpals are surprisingly well ossified. Because they are somewhat jumbled, their exact configuration is obscured, but their pattern closely resembles that seen in *Paleothyris*.

The manus is not complete and the elements are somewhat disarticulated. Nevertheless, the number of digits and the phalangeal formula is almost certainly similar to that noted in other romeriids. Brough and Brough restored the hand in this specimen on the basis of Watson's specimen of *Gephyrostegus bohemicus* (which they designated the type of a new species *G. watsoni*). As has been demonstrated by the senior author (1970a), Watson's specimen is an anthracosaur, not at all closely related to the specimen under consideration here.

The three elements of the pelvic girdle are only weakly attached to one another. The configuration of the ilium resembles that of *Hylonomus* and *Paleothyris*. It certainly lacks the peculiarities of *Anthracodromeus*. The outline of the pubis is roughly oval. The ischium is quite small.

The rear limb is poorly ossified. The tibia is primitive in having a broad distal articulating area like that of *Hylonomus* but in contrast to *Paleothyris*. Nothing remains of the tarsus or rear feet.

Many ventral scales are present in the blocks. They are quite broad, rather than being narrowly wheat-shaped, as has been considered typical in early reptiles. A faint impression of dorsal scales is evident also, but these are too insubstantial to illustrate.

Discussion. One of the most notable features of *Brouffia* is the incomplete nature of the ossification. Although the presacral length of the type is approximately 123 millimeters, the limbs and endochondral shoulder girdle are much less well ossified than are these elements in *Paleothyris acadiana*. The type specimen of that species has a presacral length of 118 millimeters, and other specimens are considerably smaller. Presumably *Brouffia* grew to a con-

siderably greater adult size before ossification was completed. Alternatively, this genus may have retained a low degree of ossification as an adult. The larger size of the skull, relative to the trunk region (Table 1), suggests that the adult was larger than the typical North American Pennsylvanian romeriids.

Owing to obvious immaturity of the only known specimen, the generic distinction of *Brouffia* from more mature romeriids, particularly *Paleothyris*, is subject to some doubt. Until we have more knowledge of changes that occur ontogenetically, as well as more information on variability within species and genera, it is not possible to state positively what differences are required to define genera. The presence of only a single pair of sacral ribs, the broad distal articulating surface of the tibia, and possibly the extra row of palatine denticles are primitive features that might be expressed also in an immature member of a more advanced species. The smaller number of maxillary teeth and other minor differences might indicate differentiation from *Paleothyris acadiana* only at the level of the species. Even if all members of the Family Romeriidae are considered, however, there is relatively little variability within the group. If the features that can be observed in this immature specimen also characterize the adult, this animal would be as different from *Paleothyris* as are other forms recognized as distinct genera. On this basis, a new genus is named to include this specimen.

The presence of the romeriids in Europe immediately suggests comparison with primitive eosuchians, which are (on present knowledge) restricted to the Old World. There is little to preclude the evolution of a genus such as *Millerosaurus* (Watson, 1957) from *Brouffia*. There are no specialized features, however, that favour this genus over other generalized romeriids for such an ancestral position. There is no evidence for the development of an otic notch formed from the quadrate. The posterior

margin of the squamosal may be more nearly erect than in other early romeriids, but the jaw suspension definitely lies posterior to the rear margin of the skull roof. One feature that might be considered of significance in deriving millerosaurs directly from such romeriids is the smaller size of the skull relative to vertebral length in the known eosuchian genera.

Coelostegus prothales

Brough and Brough described as belonging to the same species as the preceding animal, a second specimen that they termed *Gephyrostegus bohemicus* specimen II. It consists of the axial skeleton, girdles, and proximal portions of the humeri and right femur of an animal in which the trunk region was approximately 17 percent longer. It is almost as poorly ossified, however. The skull (Fig. 7) shows only superficial similarities to the type of *Brouffia*. The pineal opening is larger and the postfrontal extends posteriorly so that a distinct lateral lappet of the parietal is formed. The posterior margin of the parietal is much more deeply embayed for the tabular and postparietal. These differences cannot be attributed to growth. Although the remains are incomplete, this animal certainly belongs to a genus other than *Brouffia*.

Coelostegus n. gen.

Type species. *Coelostegus prothales* new species.

Known distribution. Middle Pennsylvanian of Central Europe.

Diagnosis. Large romeriid captorhinomorph. Parietals deeply embayed for postparietals and tabulars. Distinct lateral lappet of parietal. Frontals and postfrontals marked with deep grooves. Frontals shorter than nasals. Numerous, small posterior maxillary teeth; enlarged canines. Twenty-nine presacral vertebrae. Two sacral vertebrae. Vertebral centra relatively short. In the only known specimen (which is immature) the scapulocoracoid is ossified from

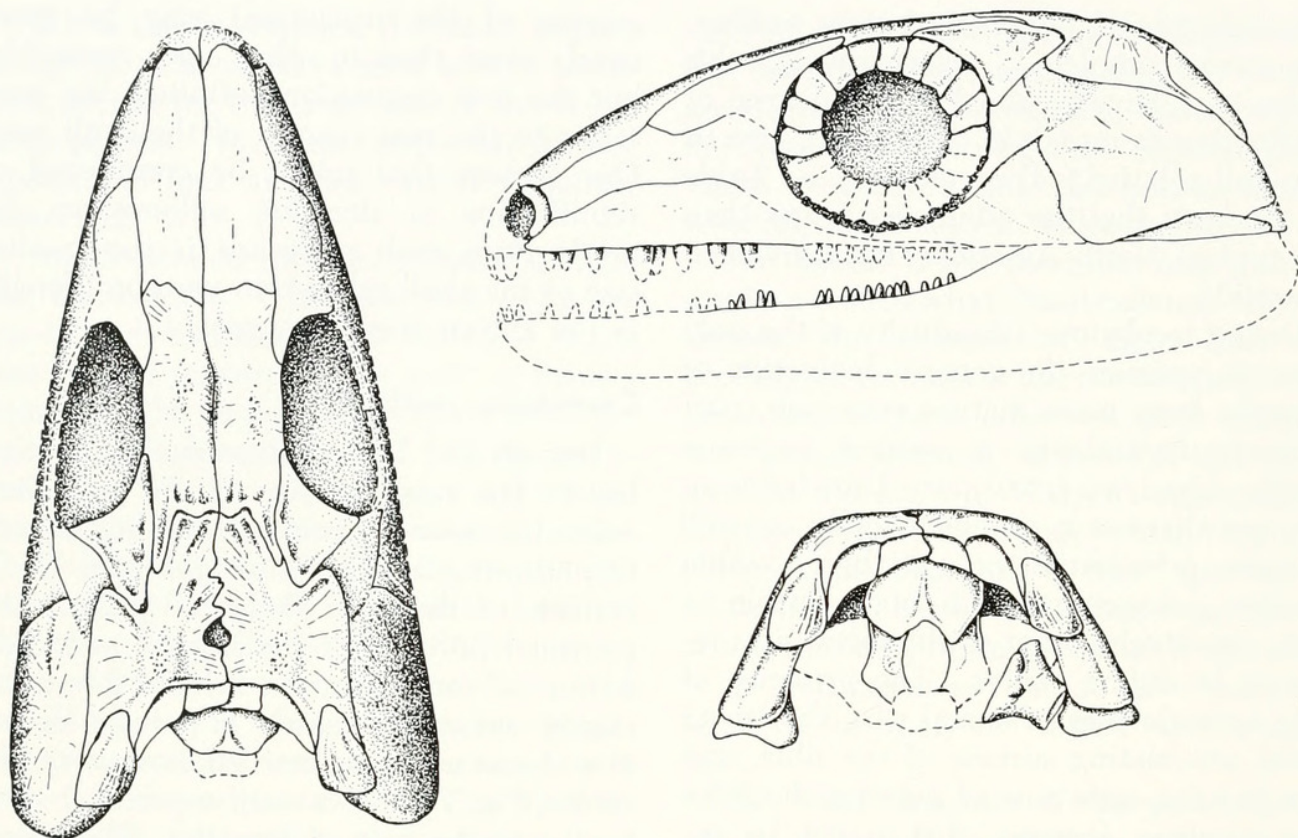


Figure 7. Reconstruction of skull of *Coelostegus prothales* in dorsal, lateral, and occipital views. $\times 2$.

more than one unit, and neural arches are suturally attached to the centra.

Coelostegus prothales n. sp.

Etymology. Greek *coelo*, embayed; plus *stegos*, roof; in reference to the deep embayment of the parietals. *Prothales*, from the Greek, meaning precocious, in reference to the early attainment of embayed parietals and large size.

Holotype. National Museum of Prague, Czechoslovakia, ČGH 3027. Axial skeleton and girdles of an immature individual. This is the only specimen that can definitely be assigned to this taxon.

Horizon and locality. Middle Pennsylvanian, Westphalian D of Nýřany, Czechoslovakia.

Diagnosis. Same as for genus.

Description. Much of the dorsal surface of the skull roof and the left cheek region are preserved. The area anterior to the left orbit is folded under, so that the bone is visible in medial rather than lateral view.

The skull can be restored in dorsal and lateral views, but the exact angle between the skull roof and the cheek region cannot be established without more knowledge of the palate. The bones of the skull roof are conspicuously sculptured. There are fine pits near the centre of ossification of the parietal, and radiating grooves extending to the periphery. There are deep grooves at the posterior margin of the frontal and on the lateral portion of the postfrontal. The squamosal and quadratojugal, in contrast, are almost smooth.

The most conspicuous feature of the skull roof is the deep posterior embayment of the parietals. In this character *Coelostegus* resembles the Lower Permian romeriid *Protorothyris* more than it does any of the other Pennsylvanian genera. The postfrontal extends posteriorly, demarcating a conspicuous lateral lappet. The marginal bones of the skull roof, supratemporal, tabular, and postparietal have slipped from the parietal and are mixed with displaced elements of

the palate, occiput, and cervical vertebrae. There is a large sheet of bone behind the right parietal that is probably the displaced right squamosal. The supratemporal fitted into a deep groove in the posterolateral corner of the parietal, which extends superficially beyond the deeper medial recess for the tabular. The supratemporal is much wider than in other romeriids, and sculptured by linear grooves. There is a wide triangular shelf of the parietal that extended underneath the tabular and postparietal. A bone that is probably the left tabular is visible just medial to the supratemporal. Its extent is difficult to determine since the margins are overlapped by surrounding bones. The postparietal is also only questionably identified. Near the midline, just behind the posterior margin of the superficial portion of the parietal is an oblong bone that may be so designated.

The frontal has a broad margin above the orbit and extends narrow processes posteriorly between the parietals and postfrontals. The nasal is apparently longer than the body of the frontal. The left maxilla, lacrimal, and prefrontal are exposed in medial view. The maxillary teeth are almost entirely covered by the nasal. The ridge bearing the teeth is swollen anteriorly, as is the case in other romeriids at the level of the canines. There are four teeth anterior to this area. The tooth count cannot be accurately established. The lacrimal comes to a point anteriorly, indicating that the posterior margin of the external nares was formed by a superficial expression of the septomaxilla. That bone lies just anterior to its normal position relative to the maxilla and lacrimal. Its posterior margin is rounded. Approximately a dozen roughly rectangular sclerotic plates can be seen in the area of the left orbit.

The squamosal is displaced laterally and posteriorly from its normal position. Dorsally, the margin of the bone curves medially to pass beneath the parietal. The skull roof simply overlaps the cheek region, apparently without any firm attachment. The

rear margin of the squamosal slopes ventrally at an angle of approximately 40 degrees from the vertical. The supratemporal would have extended approximately halfway down this slope. The quadratojugal is a narrow bone, pointed at both ends. The postorbital is not preserved, but its posterior extent may be judged by an area for its reception on the anterior portion of the squamosal. The dorsal portion of the jugal is visible in medial view, having been folded beneath the skull roof. Although the anterior portion of the bone is not preserved, restoration of the skull indicates that the suborbital extension must have been narrow, in contrast with the condition in Lower Permian romeriids.

The quadrate is exposed where it was forced dorsally from beneath the squamosal. The articulating surface is not visible. The dorsal portion is a fairly thin plate of bone extending nearly to the top of the squamosal.

The occipital elements are scattered and obscured by other bones. The central portion of the supraoccipital is visible above the atlas pleurocentrum. It has a median ridge, extending dorsally from the rim of the foramen magnum. The lateral margins of the bone cannot be accurately established. The dorsal portion of the left exoccipital can be seen just medial to the left tabular. The lateral and ventral portions are covered by other bones. A fragment of bone lying just below the right side of the supraoccipital may be part of the right exoccipital. Neither the basioccipital nor otic bones are visible. The otic bones are probably incompletely ossified, since they are not clearly shown in any of the Pennsylvanian romeriids. Because of the poor preservation of this area, the restoration of the occiput (Fig. 7) is only tentative.

The stapes is visible between the atlas intercentrum and the quadrate. It has a very short stem, ending in a broad surface of unfinished bone. The dorsal process (extending posteriorly, as preserved) is proportionately large, as is the footplate. Ex-

cept for the incomplete ossification of the stem, the stapes resembles closely that of other romeriids.

The quadrate rami of both pterygoids are exposed dorsally, lying among the bones of the occiput. As in other romeriids, they are wide but very thin plates of bone that would have been oriented vertically. They helped support the quadrates and formed an almost complete medial wall to the area of temporal musculature. The anterior portion of the left pterygoid is visible through the orbit. The area of the basicranial articulation is crushed flat. This bone is too incompletely known to attempt a restoration of the palate.

The left lower jaw is folded medially beneath the skull. A portion of the tooth row is visible through the orbit and much of the margin is indicated by deformation of the bones of the overlying skull roof and cheek region. The thickened rim of the adductor fossa can be seen through the very thin squamosal, with part of the surangular and the most posterior portion of the dentary visible between that bone and the postfrontal. Sixteen small teeth can be seen lateral to the frontal. More anteriorly, the tooth row interdigitates with that of the maxilla. Unfortunately, this area is almost completely obscured by the left nasal bone. The articulating surface of the articular bone is visible behind the quadrate, retaining its normal orientation relative to the skull roof.

The vertebral column is fairly well articulated from the skull back to the 13th caudal. There are 29 presacrals and two sacral vertebrae. The centra and neural arches are separately ossified throughout the column, but the general configuration is typical of other romeriid captorhinomorphs.

The atlas-axis elements are somewhat disarticulated, but obviously follow the pattern seen in other romeriids. A very thin, oval bone, flattened onto the posterior notochordal pit of the atlas pleurocentrum, is apparently the proatlas. It lies just anterior to the appropriate articulating surface of

the atlas arch. The atlas intercentrum is a broad, openly crescentic bone. It probably bears processes for the attachment of the capitula of the first ribs, but these are not exposed. The atlas pleurocentrum is partially obscured by the left atlas arch and the supraoccipital. It appears to be basically cylindrical, but deeply recessed dorsally. There is a large notochordal canal that was probably much more restricted in the adult. The posteroventral margin appears somewhat recessed, as if to accommodate an axis intercentrum. Such an element is typically absent in advanced romeriids, and is not visible in this specimen.

The left atlas arch is displaced slightly ventrally from its normal relationship with the axis. It closely resembles its counterpart in *Ophiacodon* in having a sharp spine projecting behind the posterior articulating surface.

The centrum of the axis and the next three vertebrae are missing. In view of the generally low degree of ossification in this specimen, it is probable that the atlas arch and centrum were not fused, although they are in the adults of other romeriid species. The neural spines of all the vertebrae are poorly ossified, and have very irregular outlines. This is particularly evident in the axis. The arch and spine are obviously large, as in most primitive reptiles, but the outline cannot be accurately established. The transverse processes of all the anterior vertebrae are quite long, so that the two heads of the ribs are separated by a wide gap.

The arches and centra are loosely attached and variably disarticulated throughout the column. The neural spines are poorly defined, but have a generally rounded outline. This is almost certainly not their normal adult configuration. The length of the neural spines and the transverse processes gradually decrease posteriorly. The centra are crushed flat, making it difficult to estimate their original proportions. As preserved, the height is equal to, or even greater than, the length. Although

no accurate measure can be given, the centra appear unusually short for a primitive reptile. Unless the nature of preservation is significantly different, these vertebrae seem to be proportionately much shorter than those of *Brouffia*.

Numerous intercentra are visible in the trunk region. All are very thin, narrow crescents. The bases of the centra are slightly notched for their reception. Unlike the condition in *Cephalerpeton* and MB 1901.1379 (described below), there is no evidence that the intercentra formed a structurally significant part of the column, or had extensive dorsal cartilaginous components. Neither the intercentra nor the anterior or posterior rims of the centra exhibit specialized areas for the articulation of the capitular rib heads.

It is difficult to establish the number of sacral vertebrae. The column is slightly bent in this area, and the elements are disarticulated. In restoring the column, it appears that all of the neural arches are present, but that at least three pleurocentra are missing. Trunk ribs can be associated with the first 28 presacral vertebrae. The next arch has a small transverse process that almost certainly bore a small presacral rib. As the Broughs pointed out, the transverse processes of arches 30 and 31 are considerably larger. They are in a position, relative to the iliac blade, expected for sacral vertebrae. The arch of the 32nd vertebra is so crushed that the transverse processes cannot be seen. Immediately adjacent lies a well-developed sacral rib. It is of smaller size than would be expected for the principal sacral rib and has a slightly more posterior position. Dorsal to the arch of the 31st vertebra is a poorly preserved bone of somewhat larger size. It might be interpreted as the principal sacral. In restoring the skeleton, the size and orientation of the iliac blade makes it extremely unlikely that there were more than two pairs of sacral ribs. Both must have been displaced posteriorly, and the most anterior caudal rib lost or obscured by other bones.

The 13 caudal vertebrae are badly crushed. The neural arches are similar in configuration to those in the trunk region. The ventral region of the centra is not visible.

Ribs are present throughout the column. The heads of the cervical ribs are conspicuously double-headed. The shaft of the first is narrow, fairly short, and flattened. The second through fifth are increasingly long and spatulate. They evidently all extended posteriorly, more than ventrally. They rather resemble the anterior ribs of *Seymouria*. The third and fourth ribs in the type specimen of *Brouffia* are not preserved. The fifth is apparently similar to those more posterior. In *Coelostegus*, the sixth through 19th are of more or less uniform length. The next six are progressively shorter and the last four are very short. The only well-preserved sacral rib has conspicuously separated heads and a narrowly expanded blade. The most anterior caudal rib is apparently missing. The next six curve sharply posteriorly to lie alongside the tail.

Elements of the shoulder girdle lie alongside vertebrae two through seven. The cleithrum is a long, narrow rod, slightly expanded along the anterodorsal margin. The blade and lower portion of the stem of the clavicle are considerably expanded, although not beyond the range that might be expected of romeriids. The interclavicle underlies the anterior portion of the column. The anterior margin is fimbriated. The remainder of the outline is difficult to establish, but apparently conforms to the typical romeriid pattern. The scapula is considerably better ossified than its counterpart in the type of *Brouffia*. There is a well-defined supraglenoid buttress, within which, apparently, opened a supraglenoid foramen. The ventral margin of the bone extends anteriorly from the centre of the glenoid area. One or more coracoid elements must have ossified separately. Very limited portions of the proximal articulating surface of both humeri are present. No diagnostic

features are evident. None of the distal elements of the fore limb are present.

The three elements of the pelvic girdle are disarticulated. The margins are partially obscured by other bones, but they resemble in general their counterparts in other early reptiles. The medial surface of the iliac blade shows a series of linear grooves for the attachment of epaxial musculature. The size and configuration of the ilium corresponds almost exactly with that of an isolated pelvic girdle from Florence, Nova Scotia (Fig. 14D). This is definitely distinct from the ilium of *Paleothyris* in the width of the blade. This suggests the presence of a second, rare, romeriid genus within the tree stump fauna. Only the proximal portion of the femur is preserved. The texture of the surface indicates an immature stage of development. Enough of the shaft is present to indicate that the total length did not exceed 20 cm, roughly equivalent to the length of five trunk centra.

The numerous ventral scales are similar to those observed in the type of *Brouffia* and *Cephalerpeton*. They form a continuous, wide, but thin covering from the pectoral to the pelvic girdle. There are at least five rows of scales on each side. There is no trace of dorsal scales.

Discussion. The configuration of the posterior bones of the skull roof and the proportions of the vertebral centra suggest that this specimen is taxonomically distinct from all other Pennsylvanian romeriids. It resembles the Lower Permian genus *Protorothyris* in some features of the skull, but the vertebrae appear quite different. The specific phylogenetic position of *Coelostegus* is difficult to establish on the basis of this specimen, since it is immature and lacking most of the limb elements.

Although immature, the trunk region alone is 120 millimeters in length. If the low degree of ossification is indicative of immaturity, the adult size would probably be in excess of that in all other Pennsylvanian romeriids but comparable to that of the Lower Permian members of the family.

Humboldt Museum 1901.1379

A further specimen which came from the Nýřany locality may be discussed here. It consists of 16 posterior trunk vertebrae, the sacral and associated ribs and limb material (Fig. 8). This specimen (No. 1901.1379) from the Humboldt Museum in Berlin, is from a much larger animal than any of the previously described Pennsylvanian romeriids and even exceeds the size of the Lower Permian members of the family. The bones are well ossified, suggesting an adult condition. As restored, this section of the presacral column would be 120 mm in length. Given a typical romeriid length of 31 or 32 presacra, the entire trunk region would be approximately 240 mm long.

Despite being well ossified, the vertebrae display a distinct suture between arch and centrum. The neural arch is squarish in outline, as might be expected in adult specimens of the preceding two species, but the two sides are solidly fused at the midline. The arches are not swollen. The transverse processes extend a short distance laterally from the base of the pedicel. The articulating surfaces face obliquely ventrolaterally. The centra are well-developed, deeply amphicoelous cylinders. Laterally, they are deeply concave. Ventrally they are notched to provide space for large, crescentic intercentra. The dorsal area of the posterior rim of the more posterior centra is recessed to receive the anterior margin of the next succeeding vertebra. As restored there is a considerable gap between the intercentrum and this dorsal articulating area. It is probable that the sides of the intercentra extended a considerable distance dorsally in cartilage. This form illustrates an advanced stage in the reduction of the intercentra from the condition in anthracosaurs to the definitive reptilian configuration.

Numerous ribs are present in the block. At least as far back as the fourth vertebra anterior to the sacrum, they are similar to those in the trunk region of most early

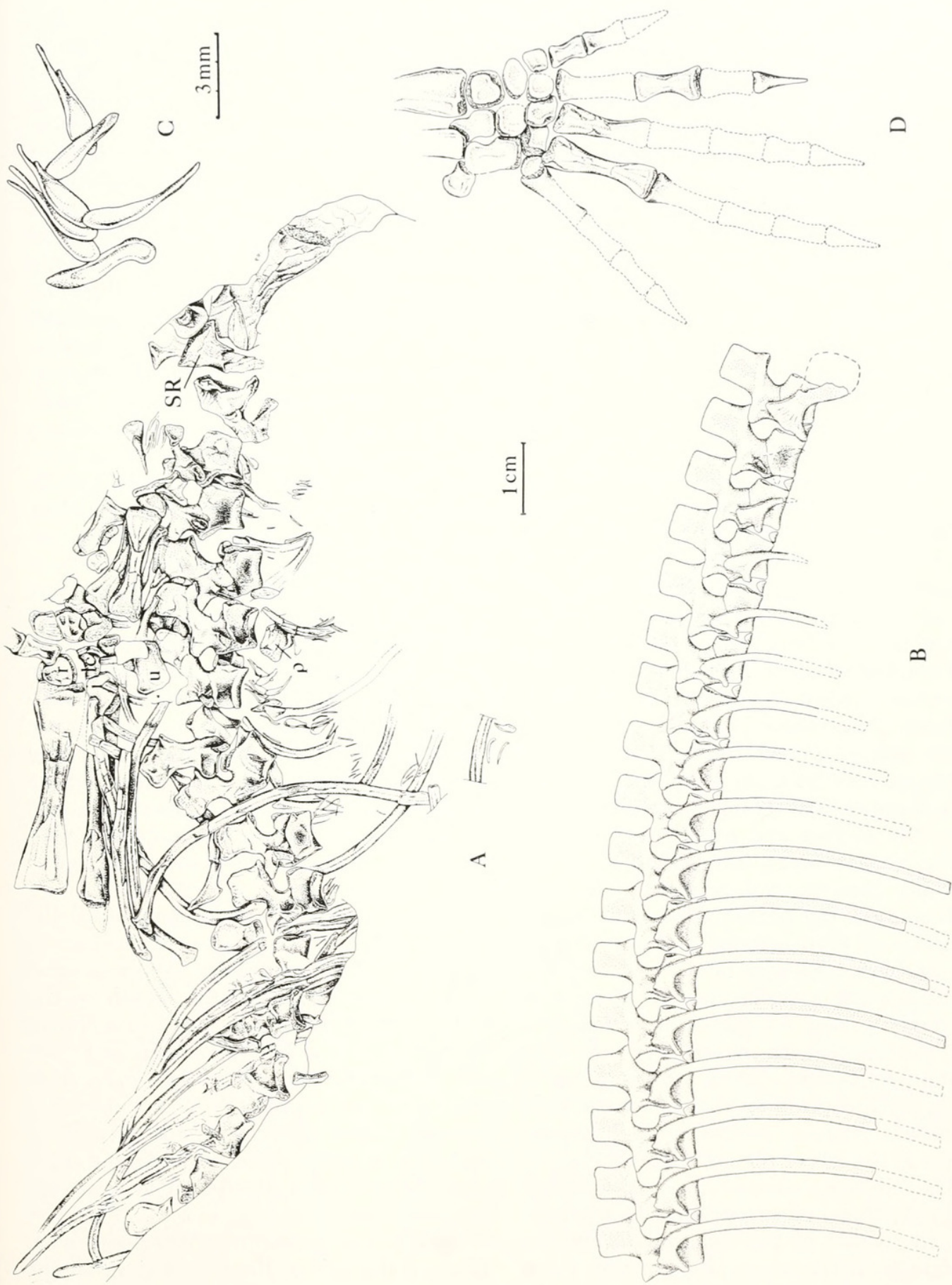


Figure 8. MB 1901.1378: A. Partial skeleton. $\times 1$. B. Restoration of posterior portion of axial skeleton. $\times 1$. C. Detail of scales. $\times 4$. D. Restoration of hand. $\times 1$. Abbreviations: i, intermedium; lc, lateral centrale; p, pisiform; r, radiale; u, ulnare; SR, sacral rib.

tetrapods. In their great length relative to the size of the vertebrae, they resemble those of pelycosaurs more than those of typical romeriids. The length of the posterior ribs shortens gradually. The last presacral rib is apparently only slightly longer than a single centrum. Where present the rib heads are typically double-headed. The capitulum must have articulated with the dorsal, cartilaginous portion of the intercentrum. A single massive sacral rib is preserved. The head has two articulating surfaces set at a slight angle to each other and separated by only a short gap. The shaft narrows only slightly before expanding again as a simple blade. Its natural orientation and distal extent is obscured by crushing. The first presacral vertebra is visible only in anterior view, so it is not possible to determine the nature of the articulation of the capitular head of the sacral rib.

Neither any part of the shoulder girdle nor the humerus is preserved. The radius and ulna resemble those of *Cephalerpeton* and *Anthracodromeus* in being long, lightly built, and with the articulating surfaces ill defined. The radius is the length of four trunk centra. The ends are flattened and expanded to about an equal extent. The ulna is only slightly longer and the olecranon little ossified and poorly preserved.

The carpal bones are preserved in essentially their natural position. They are well ossified, but crushing has made determination of their original outlines difficult to establish. Eleven bones can be recognized. The specific identity of some is in doubt owing to partial disarticulation and the fact that the margins are somewhat obscured by other bones. A bone that is probably the pisiform is the furthest from its natural position, lying more than a centimeter to the left of the other bones.

The elements can be reassembled with little likelihood of serious error to a pattern similar to that of the romeriid *Paleothyris* and most pelycosaurs (Romer and Price, 1940, fig. 40). The configuration of the

individual bones is distinct from that of *Paleothyris*, but without more knowledge of the range of variability in the configuration of the carpus in romeriids, it is not possible to establish whether the pattern seen in this specimen is sufficiently different to suggest assignment to a different family.

The radiale is oval in outline, the dorsal surface somewhat flattened. The distal articulating surface of the radius is slightly concave and considerably wider than the radiale, with the lateral portion apparently resting on the intermedium. As in other primitive reptiles, the intermedium has distinct articulating surfaces for the radius and ulna, which are set at approximately a 45-degree angle to one another and separated by a notch. The ulnare is by far the largest carpal. The proximal articulating facet is obscured, but was probably essentially horizontal. The medial surface is incised to form the margin of the perforating foramen. In contrast with the condition in *Paleothyris*, this opening is bordered medially by the intermedium, rather than by the lateral centrale. The ulna articulates with the lateral centrale by a well-developed, medially facing facet. Little of the lateral centrale is visible, but this bone appears to be relatively smaller than its counterpart in *Paleothyris*. The medial centrale is only tentatively distinguished from a number of distal bones.

At least the proximal portions of all the metacarpals can be seen in their normal sequence. The fourth is complete and slightly more than half the length of the radius. The first is very short. A tentative restoration of the hand is shown in Figure 8D, although fragments of only four phalanges are visible. A single ungual is seen in ventral view. It is sharply pointed and has a pronounced keel ending in a large knob for the attachment of ligaments for retraction.

Except for a fragment of bone lying beneath the end of the femur, none of the pelvic girdle is preserved. The femur itself

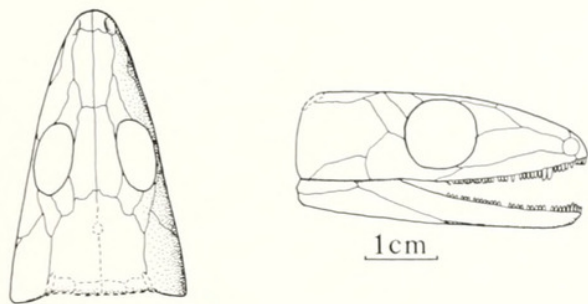


Figure 9. Skull of *Hylonomus lyelli*, in dorsal and lateral views. $\times 0.75$.

is very incomplete. It was clearly heavily built, but no structural details can be ascertained.

Scales are scattered throughout the block. They appear quite large, but not surprisingly so for such a large animal.

Discussion. The taxonomic position of this specimen is difficult to establish. Since there are still comparatively few reptiles known from the Carboniferous, it seems worthwhile to publish this account even though the remains are very incomplete and the affinities of the animal uncertain. There is little question but that this specimen is a reptile, at least as that term is broadly used. The relatively large size of the animal suggests comparison with *Solenodonsaurus*. Although the general vertebral proportions are similar, the intercentrum was apparently not greatly extended in

cartilage in *Solenodonsaurus*, nor are there special articulating surfaces on the dorsal margins of the pleurocentra. The proportions of the ulna and radius are entirely different in the two forms.

The proportions of the radius and ulna also distinguish it from *Brouffia*. It is more difficult to compare it with *Coelostegus prothales* because of the paucity of corresponding elements. The low degree of ossification of the vertebrae in that specimen makes it difficult to compare their configuration with the more mature animal from the Berlin Museum. The extent of the intercentra and the proportions of the pleurocentra are quite different, but these might change with increasing maturity. The position of the articulating facet for the capitulum is apparently similar in the two forms. Since there are few corresponding elements in the appendicular skeleton, there is not sufficient evidence to establish whether or not they might be included in the same genus.

Outside the Nýřany fauna, perhaps the closest comparison can be made with *Cephalerpeton*, which also had extensive intercentra, squarish neural spines, and long epipodials. The vertebral features are typical of a wide range of primitive tetrapods, and long epipodials have evolved in many

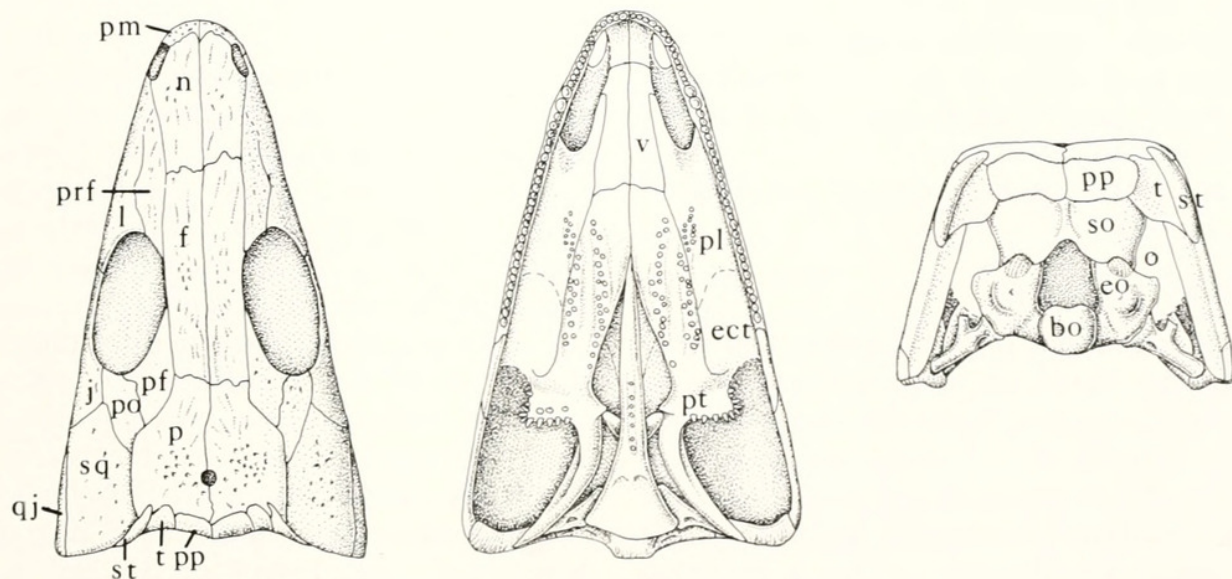


Figure 10. Skull of *Paleothyris acadiana* in dorsal, palatal, and occipital views. $\times 2$.

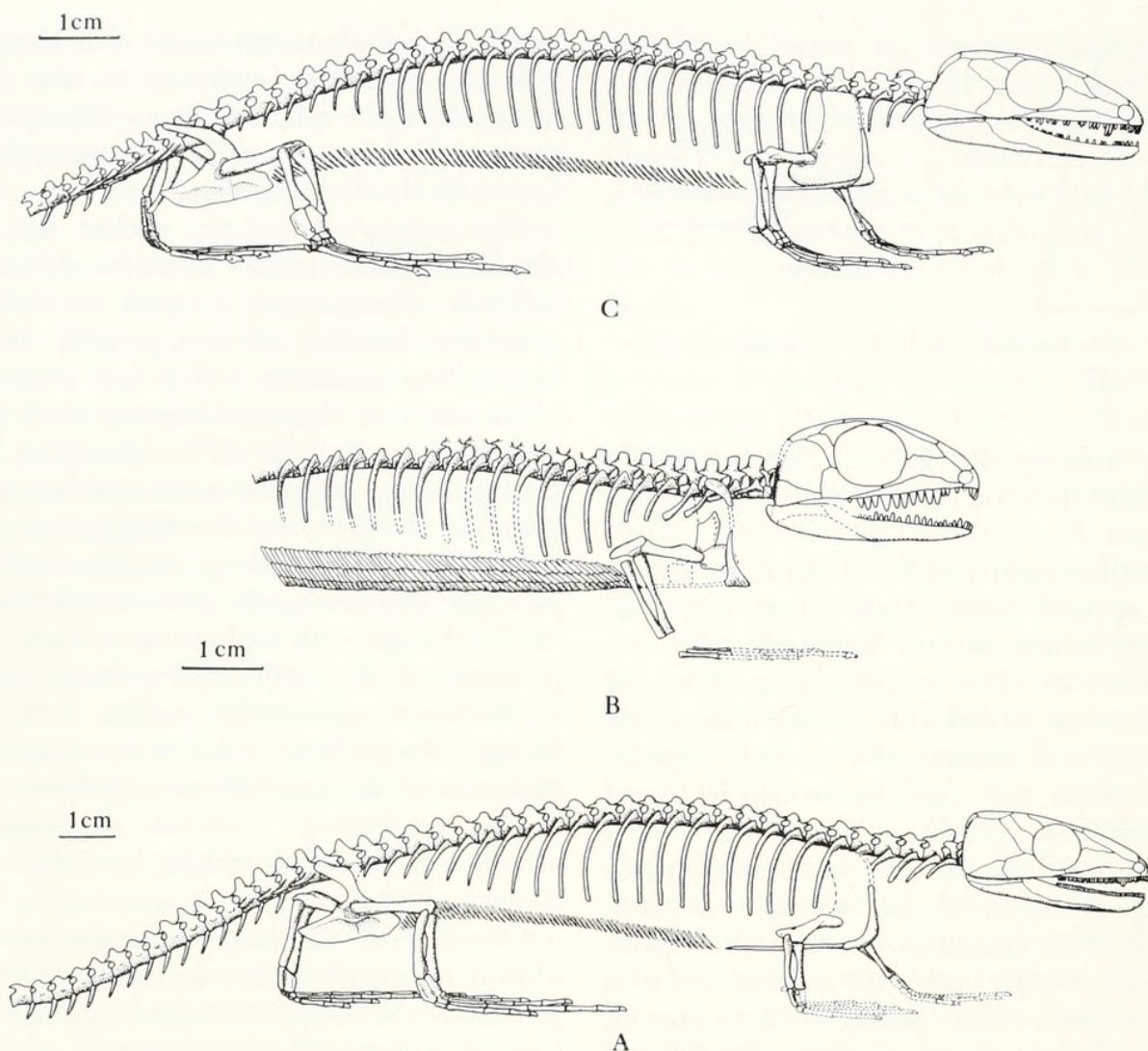


Figure 11. Skeletal reconstruction of Pennsylvanian romeriids. A. *Hylonomus lyelli*—Westphalian D. B. *Cephalerpeton ventriarmatum*—Westphalian D. C. *Paleothyris acadiana*—Westphalian D. D. *Anthracodromeus longipes*—Westphalian D. E. *Brouffia orientalis*—Westphalian D. F. *Coelostegus prothales*—Westphalian D. Scale indicated on figures.

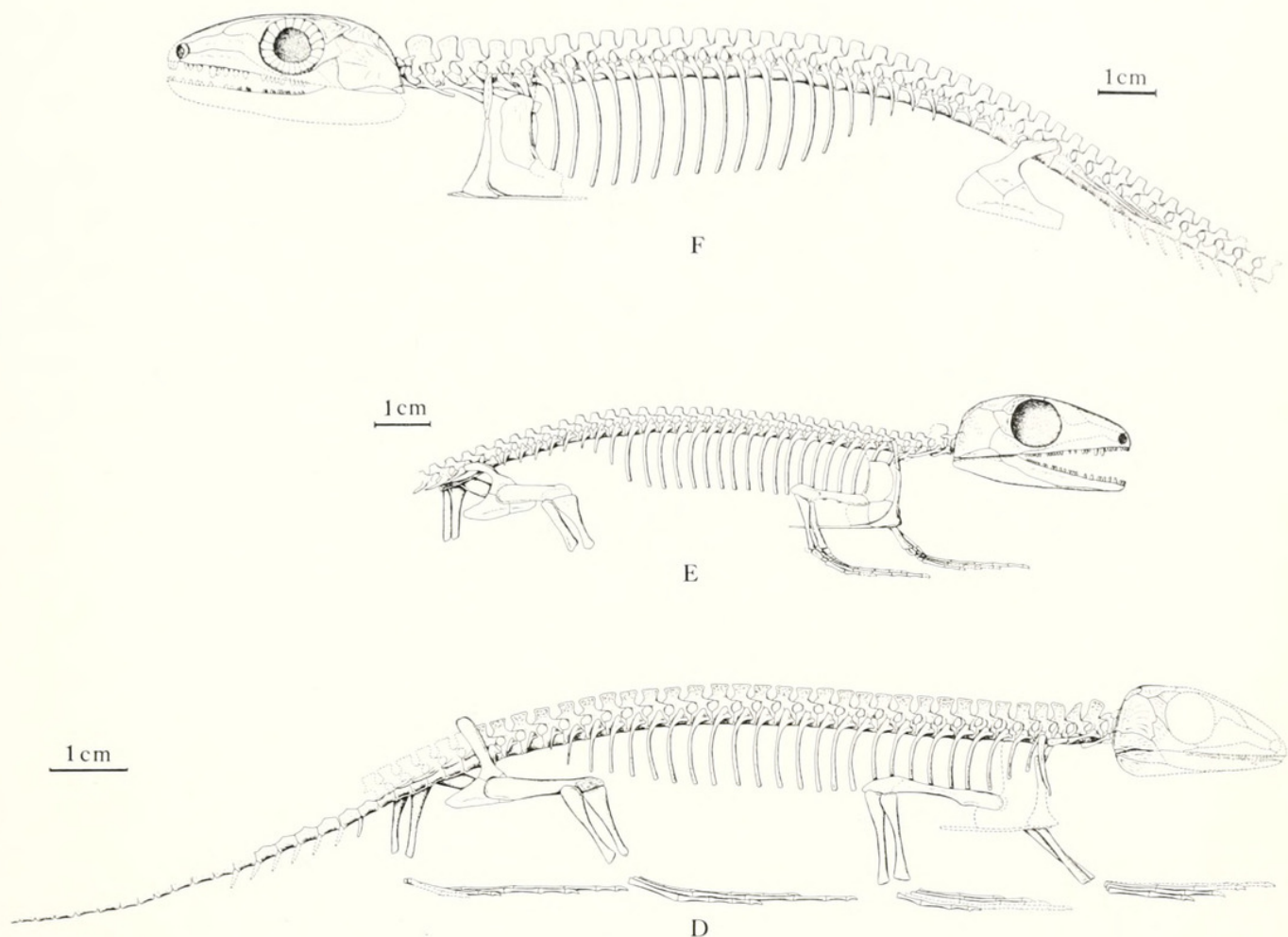
groups. The relatively great size suggests comparison with pelycosaurs, but no significant similarities with any member of that group have been recognized. Without cranial material, not even the order to which this specimen belongs can be established with certainty.

RECONSTRUCTIONS

Reconstructions of the skeleton and flesh have been made of the six, more or less completely known, Pennsylvanian romeriids (Figs. 11 and 12). In terms of body size and general proportions, all fall within the range exhibited by small, iguanid lizards (excepting *Phrynosoma*). This is reflected in the restorations. Feeding patterns and

general ecology were probably broadly comparable as well. The only feature that is shown as distinguishing these genera from lizards is the nondivergence of the fifth digit of the foot. Since the footprints of some Paleozoic forms (*e.g.*, *Dromopus*) show a divergence of the fifth digit, romeriids may have resembled modern lizards in this feature as well.

The known body proportions of romeriids appear to follow a sufficiently restricted range of variation that missing elements (*e.g.*, the rear limbs of *Cephalerpeton* and the distal extremities of *Coelostegus*) can be restored with a fairly high degree of confidence. The extent of the tail is not known in any romeriids. In analogy with



typical pelycosaurs and modern lizards, it is shown approximately as long as the trunk region. All are shown lacking epidermal scales, since they are known to be missing in *Cephalerpeton*.

The particular poses are copied from a variety of iguanids illustrated in Smith's *Handbook of Lizards* (1946). The nature of preservation and generally low degree of definition of the extremities of the limbs and articulating surfaces of the girdles make it impossible to define the range of limb positions in the romeriids, but the postures exhibited here could be assumed without doing violence to the known anatomy.

DISCUSSION

Variation among Pennsylvanian Romeriids

Six romeriid genera from the Pennsylvanian are known from almost complete skeletons. The remains of *Archerpeton*

(which are substantially smaller than those of other Pennsylvanian romeriids) and MB 1901.1379 (which are significantly larger) are much less complete, and will not be included in this discussion. The position of *Brouffia orientalis* is considered on the basis of the characters shown in the single, immature specimen, although it is conceivable that they are altered somewhat in the adult.

With the possible exception of the relative skull size, in which the Czechoslovakian genera differ from the North American forms, there is no consistent pattern evident in terms of either geographic or temporal distribution, at least among the characters listed (Table 1). The presence of a single pair of sacral ribs is certainly more primitive than two pairs, and a large number of maxillary teeth is more primitive than a reduced number. On the basis of the known specimens, there are no consistent

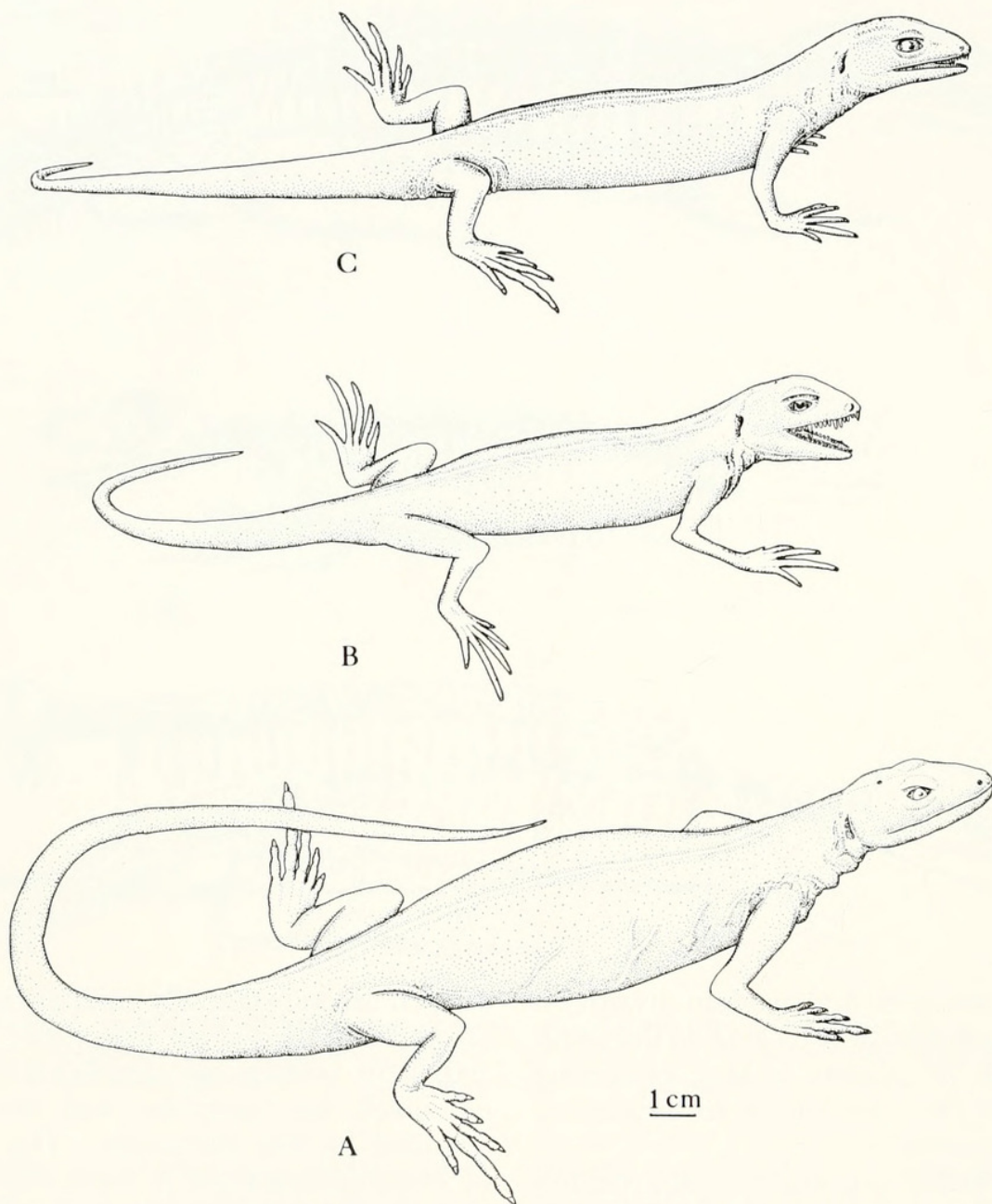
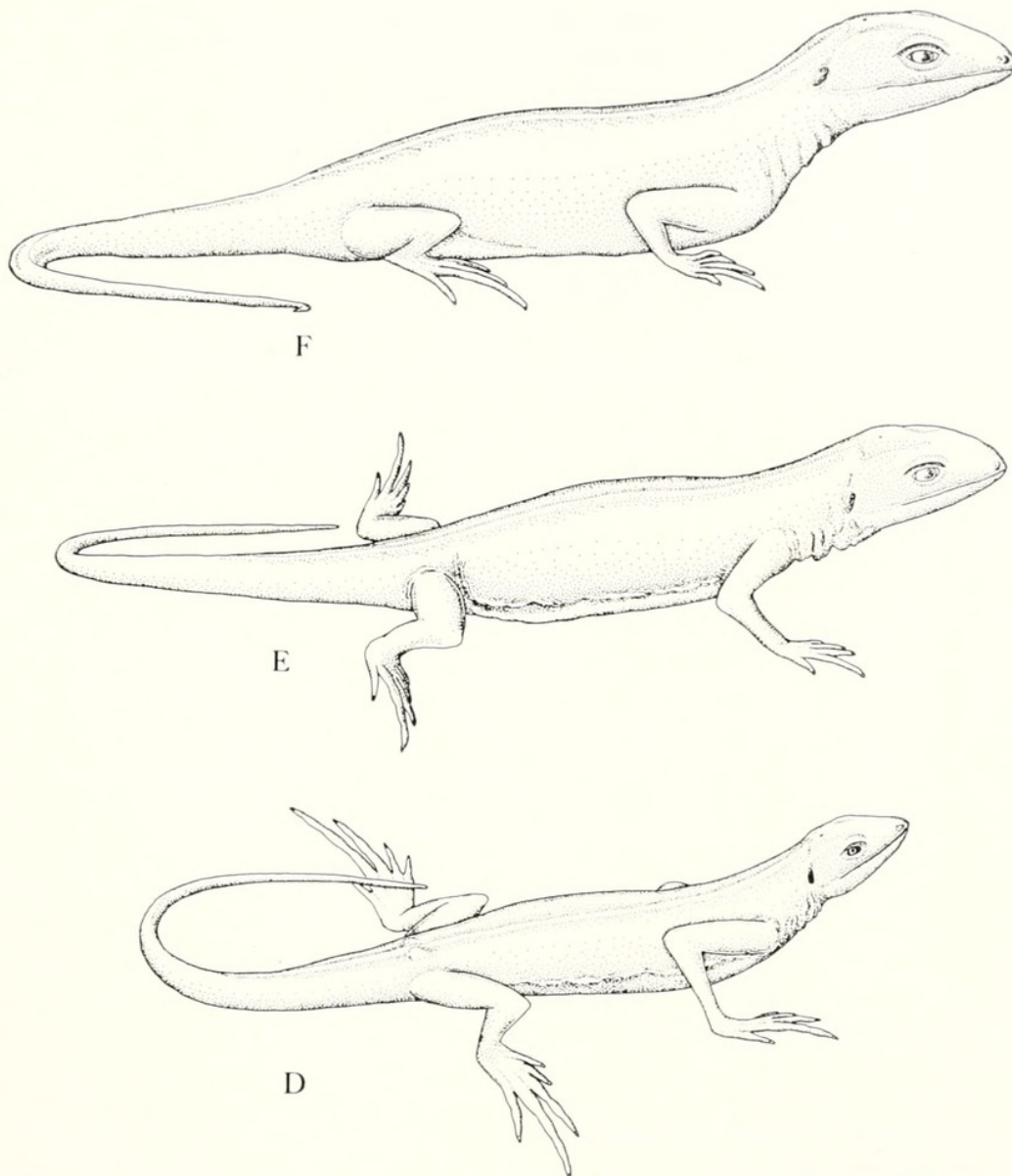


Figure 12. Flesh reconstruction of Pennsylvanian romeriids. A. *Hylonomus lyelli*; B. *Cephalerpeton ventriarmatum*; C. *Paleothyris acadiana*; D. *Anthracodromeus longipes*; E. *Brouffia orientalis*; F. *Coelostegus prothales*. $\times 0.5$.

trends evident in either overall body size or in the specific number of presacral vertebrae. If a low degree of ossification can safely be correlated with immaturity and body size significantly less than that of adults, mature specimens of *Cephalerpeton*, *Brouffia*, and *Coelostegus* may be considerably larger than the ones known. The proportionately larger skull size in the latter two genera may also be correlated with the larger absolute body size. The pelycosaurs, for instance, typically have proportionately

larger skulls than romeriids. If early Permian romeriids are considered as well, the family does show a general increase in size through time. Mature skulls from the Redbeds of Texas range from 50 to 60 mm in length. Very roughly, there is a doubling in size throughout the history of the family.

In comparison with size increase observed among pelycosaurs during a comparable time interval, romeriids appear quite conservative. It is probable that the definable features of the family are closely related



to absolute body size. Adjustments for great increase in bulk would probably lead to sufficiently extensive reorganization of the skeleton for support and of the skull in relationship to feeding that the resultant form would have to be recognized as a member of a distinct family.

Early pelycosaurs (see Reisz, 1972) may be considered romeriids grown large. It is probable that once pelycosaurs had differentiated in the early Pennsylvanian, specialization by simple increase in size was strictly limited in later romeriids.

Within the limits of small, insectivorous primitive reptiles, the most significant specialization among romeriids occurred in

the dentition and limb proportions. Both may be associated with pursuit and capture of particular prey. There is no consistent correlation between particular specializations of any of the romeriid genera and their specific mode of preservation.

The pattern of the skull roof is very conservative. The most significant change is seen in *Coelostegus*, in which the posterior margin is deeply embayed. This may be correlated with an anterior extension of the axial musculature to give more efficient control to movement of the head. An analogous, but not exactly equivalent, specialization is seen in the Lower Permian genus *Protorothyris*.

TABLE 1. MEASUREMENTS OF PENNSYLVANIAN ROMERIIDS (BASED IN ALL CASES ON THE TYPE SPECIMENS).
 Archerpeton and MB 1901.1379 not included.

	Number of maxillary teeth	Number of pre- sacral vertebrae	Pairs of sacral ribs	Length of presacral column (mm)	Length of skull (mm)	Skull/trunk	Humerus (mm)	Humerus ²	Radius (mm)	Ulna (mm)	Femur (mm)	Tibia (mm)	Fibula (mm)
<i>Hylonomus lyelli</i> BM (NH) R.4168	35	26?	1	108	33	31%	20	5	—	—	22	11	12
<i>Cephalerpeton</i> ¹ <i>ventriarmatum</i> YPM 796	16	—	—	—	25.5	—	15	6	10	10	—	—	—
<i>Paleothyris</i> <i>acadiana</i> MCZ 3481	35	32	2	89	27.2	31%	13	5	8	8.5	14	9	9+
<i>Anthracodromeus</i> <i>longipes</i> AMNH 6940	—	31	1	80	—	—	20.5	8	10.2	11.3	18.5	10	12
<i>Brouffia</i> <i>orientalis</i> ¹ ČGH IIIB. 21.C.587 MP 451	26	31	1	89	32.4	36%	14.6	5	10	11.2	15.8	11.6	13.1
<i>Coelostegus</i> <i>prothales</i> ¹ ČGH 3027	26+	29	2	104	40	38%	—	—	—	—	—	—	—

¹ Poorly ossified, presumably immature specimen.
² Length of humerus measured in terms of number of trunk vertebrae.

Stratigraphic Distribution and Depositional Environment of Romeriid Fossils

Romeriids are known from at least three basic depositional environments: *Hylonomus* and *Paleothyris* from upright trees; *Cephalerpeton*, *Anthracodromeus*, *Brouffia*, and *Coelostegus* from coal swamp deposits; and the Lower Permian genera from the redbeds of a huge delta complex. The relative abundance of the specimens in each type of deposit is significant. The tree stump genera are relatively common elements in their respective faunas. All of the genera from the coal swamps are represented by single specimens. Tetrapods of any sort are rare at Mazon Creek, so the presence of a single reptile is no measure of its original frequency. The deposits at Linton, Ohio, and Nýřany, Czechoslovakia,

are extremely rich in aquatic and semi-aquatic forms, suggesting that the few romeriids are exotics, preserved by chance. Five romeriid genera may be recognized in the Lower Permian of Texas (see Watson, 1954). Three are known from unique specimens. *Romeria* is known from two individuals, and *Protorothyris* from five, all from a single locality. In comparison with the rich fauna of both reptiles and amphibians in the Texas beds, romeriids are very rare elements.

Numerous specimens of *Melanothyris* are known from a single locality in the Dunkard Group of Pennsylvania, roughly equivalent in age to the Wichita beds in Texas. All the individuals are small, presumably immature, and come from a single block of freshwater limestone. Except for

the smaller size of the specimens, *Melanothyris* is very similar to *Protorothyris* and may not be generically distinct. The presence of a large number of individuals in a definitely aquatic deposit is difficult to explain, in light of the apparent terrestrial habits of all the other members of the group.

The frequency of early romeriids in tree stump faunas certainly reflects their terrestrial habits. The relative diversity in terms of genera, but rarity of individuals in later, essentially aquatic deposits suggests that the family remained a dominant element of the Middle Pennsylvanian fauna, but probably remained more common in a more terrestrial environment. The complete absence of romeriids in the Stephanian deposits of aquatic and deltaic nature is surprising. Reptiles and even amphibians of that age are comparatively rare, but most faunal elements are represented, at least by fragments.

The subsequent rarity of romeriids in the Wichita Group and their absence in the later Clear Fork Group of the Texas Lower Permian apparently indicate a marked reduction from their original frequency in the early and middle Pennsylvanian. The generalized reptilian habitus originally defined by the romeriids was apparently usurped by a host of derivative groups, each more successful in some portion of the environment. Romeriids may, however, have remained relatively common in more upland environments than are represented in either the typical Stephanian or Lower Permian deposits. Certainly some lineages must have survived into at least the Middle Permian to give rise to eosuchians and possibly to ancestral archosaurs.

The absence of romeriid fossils prior to the early Pennsylvanian Joggins horizon may be attributed to the absence of any deposits reflecting a sufficiently terrestrial environment in the latest Mississippian or earliest Pennsylvanian. The slightly more primitive features of *Hylonomus*, particularly in the structure of the atlas-axis com-

plex and in the absence of well-defined tooth rows on the palatal elements, suggest that the group had only recently evolved from some distinguishably more primitive family of reptiles. The subsequent evolution of the family is consistent with differentiation of all major lineages no earlier than the early Pennsylvanian.

Geographical Distribution

The discovery of romeriids from Czechoslovakia very much extends the range of a group that was originally known only from North America. Although *Brouffia* and *Coelostegus* are clearly distinct from all described New World genera, they are not particularly closely related to each other, nor give any evidence that their evolution had proceeded in isolation from that undergone by the North American forms. There is, in fact, no consistent correlation between the geographic distribution of the known specimens and their taxonomic relationship. Genera from Texas, Illinois, Ohio, Pennsylvania, Nova Scotia, and Czechoslovakia appear to represent a single evolving complex that was essentially worldwide in range. No romeriids are known from anywhere in the southern hemisphere. In view of the rarity of other tetrapods during the appropriate period of time, this is hardly surprising. Indirect evidence of the family in the land masses now recognized as South America and Africa is provided by the presence of mesosaurs, which certainly evolved from primitive romeriids, as well as primitive eosuchians.

Interrelationships of Pennsylvanian Romeriids

Several lineages may be recognized among the Pennsylvanian romeriids (Fig. 13). A central stock consists of the genera *Hylonomus* (Figs. 9 and 11A) from the Westphalian B and *Paleothyris* (Figs. 10 and 11C) from the Westphalian D, which gave rise to the early Permian forms *Melanothyris* and *Protorothyris*. The denti-

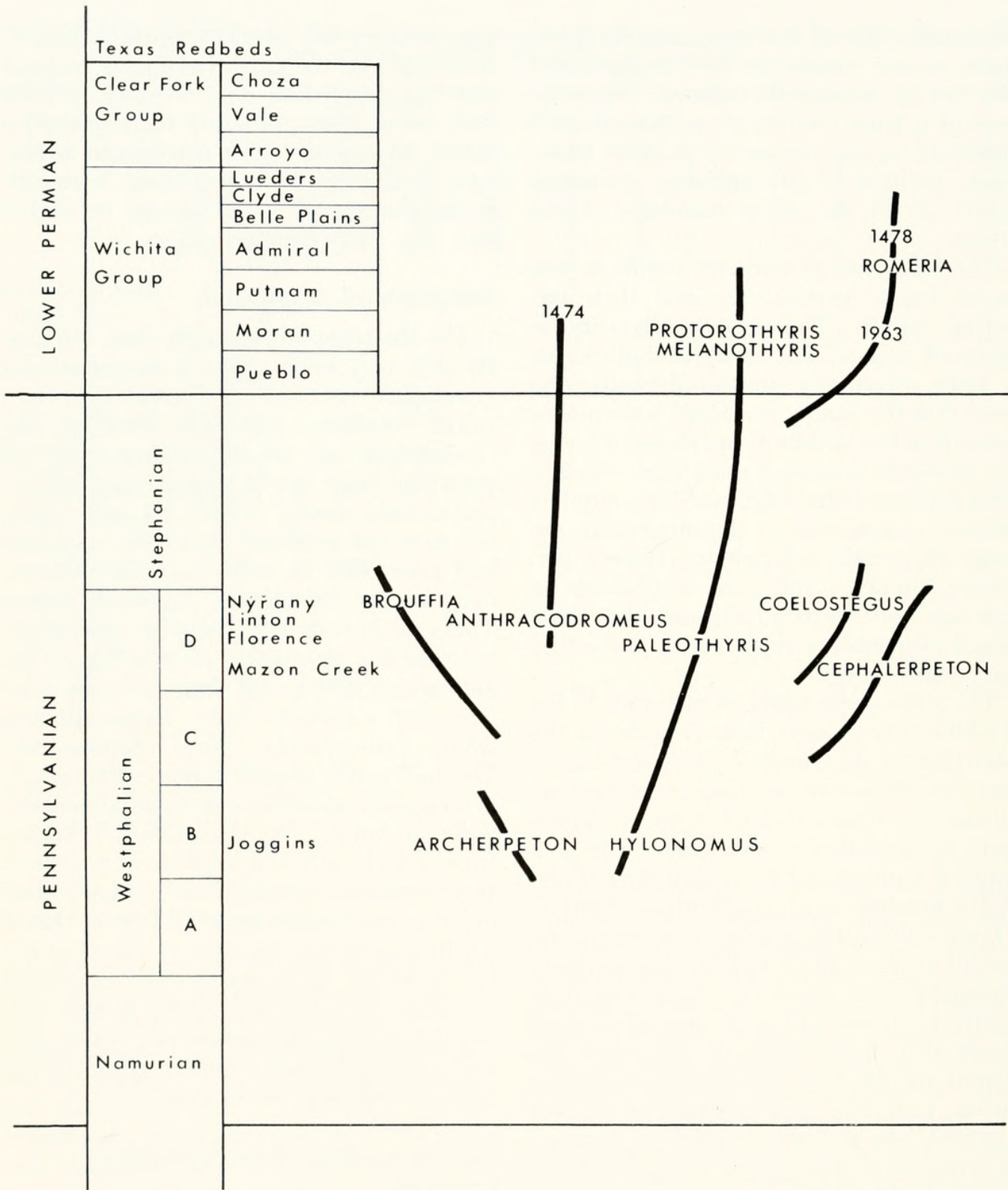


Figure 13. Phylogeny and stratigraphic distribution of romeriids. Numbers indicate unnamed MCZ specimens.

tion remains similar throughout this group. The overall body size increases and the neural spines become elongate. The relative length of the limb elements increases somewhat. The presence of only a single sacral rib and a primitively large distal

articulating surface of the tibia suggest that *Brouffia* diverged from this lineage in the early Pennsylvanian. *Coelostegus*, in contrast, appears as advanced as the Permian members of the family. The apparent shortness of the vertebral centra and the large

size of the supratemporal and small post-parietal indicate that it is not directly ancestral to these forms, however.

The dentition of *Cephalerpeton* clearly distinguishes this genus from all other members of the family. It presumably evolved from *Hylonomus* or other early Pennsylvanian members of the central lineage. The dentition is too specialized to suggest the ancestry of any later forms. It is comparable with that seen in some of the small carnivorous pelycosaurs.

Anthracodromeus represents another divergent group. The peculiar nature of the

neural spines and the great elongation of the limbs is matched in an undescribed specimen from the Lower Permian of Texas. There is no evidence that this particular lineage gave rise to any later reptilian groups. The relationships of romeriids with other primitive reptiles was discussed with the descriptions of *Paleothyris* (Carroll, 1969a) and *Batropetes* (Carroll and Gaskill, 1971). The knowledge of additional Pennsylvanian romeriids does not substantially alter the conclusions reached in those papers.

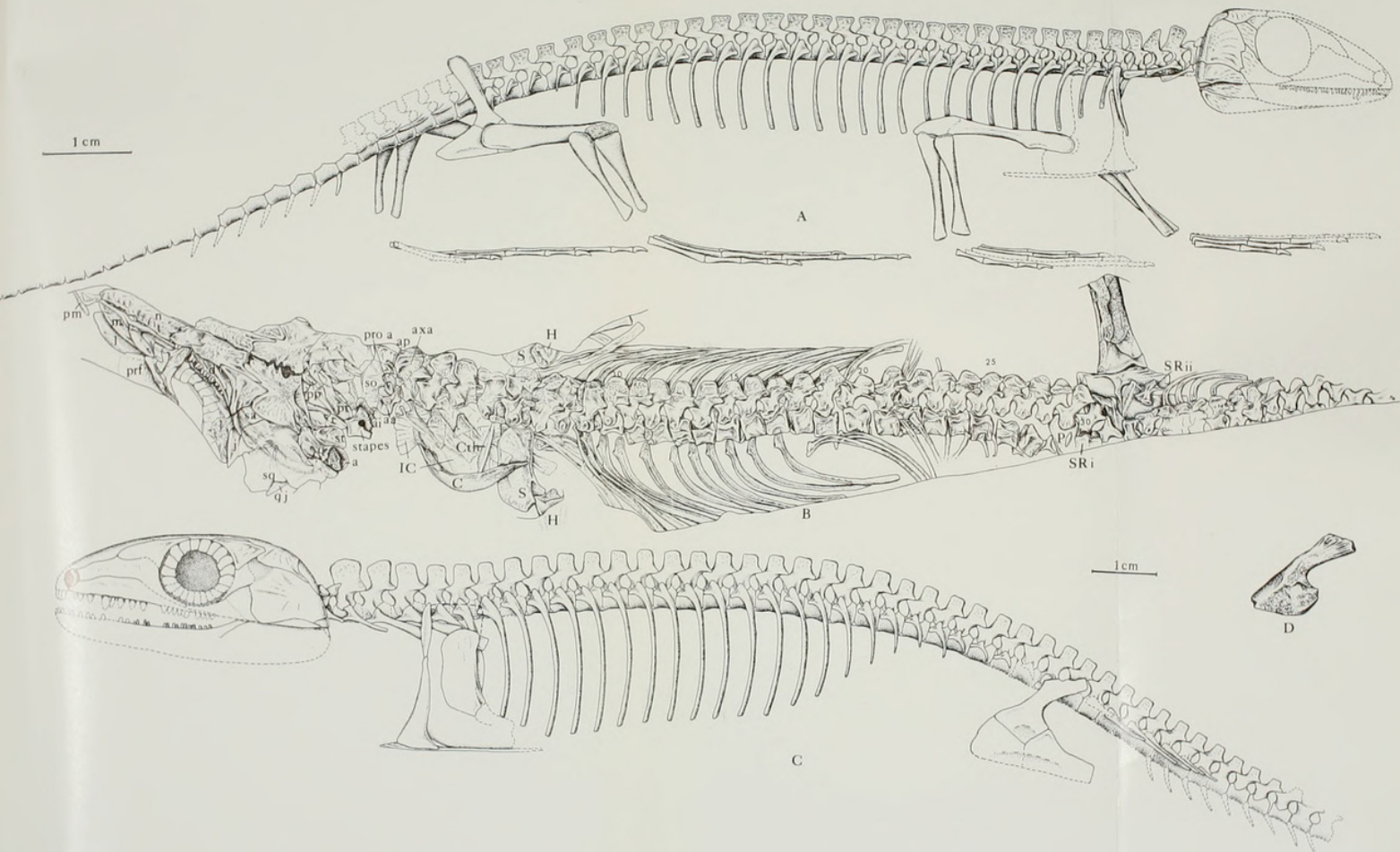


Figure 14. (Fold out). A. Restoration of the skeleton of *Anthracodromeus longipes*. $\times 2$. B. *Coelostegus prothales* type CGH 3027. $\times 1.5$. C. Restoration of axial skeleton and girdles of *Coelostegus prothales*. $\times 1.5$. D. Ilium of romerid from Florence, Nova Scotia, MCZ 4109. $\times 1.5$.

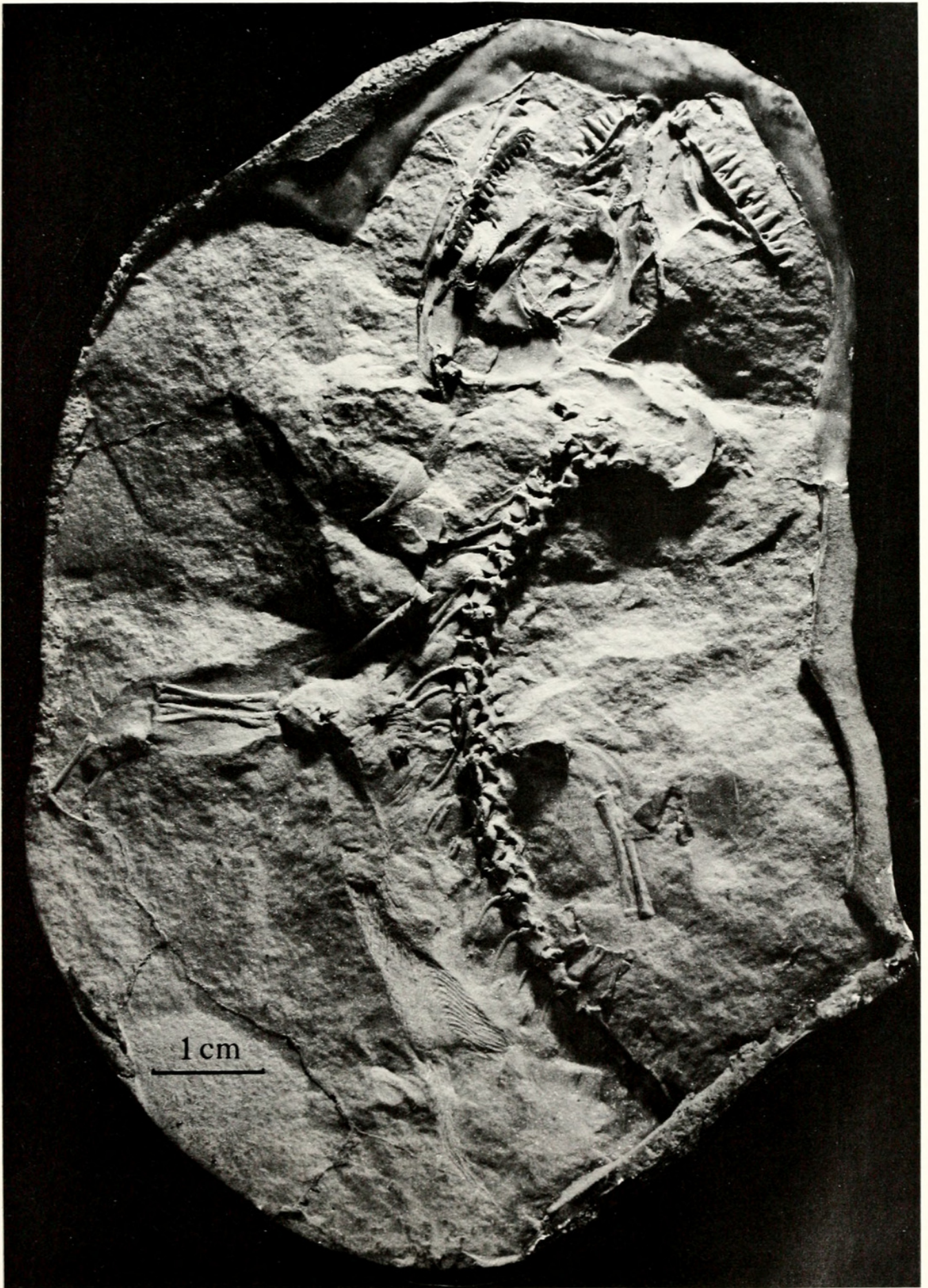


Plate 1. Latex cast of *Cephalerpeton ventriarmatum*. Scale indicated on figure.

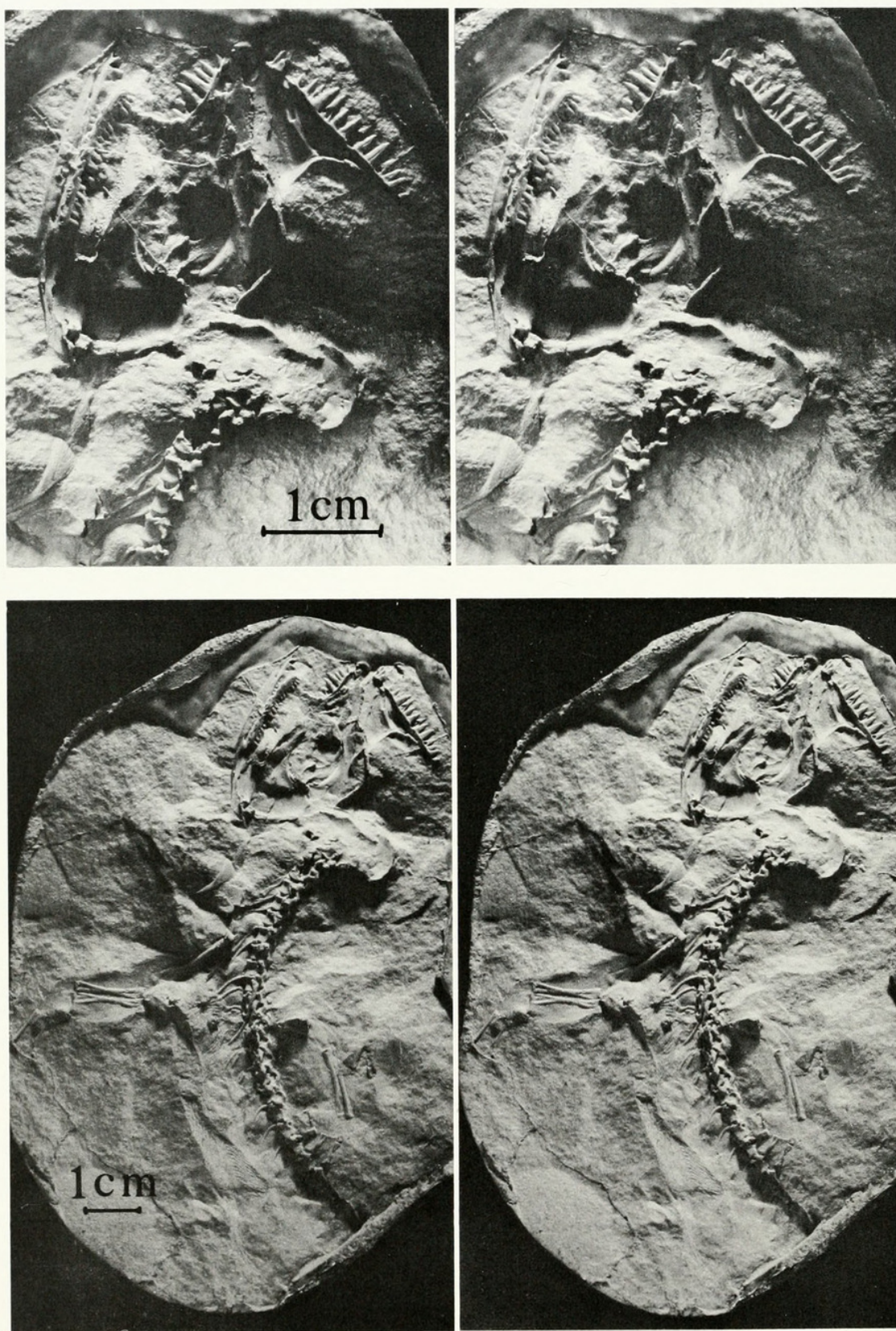


Plate 2. Stereo pairs of *Cephalepion*. Upper, Skull; Lower, Skeleton. Scale indicated on figure.

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