

PELYCOSAURIAN REPTILES FROM THE MIDDLE PENNSYLVANIAN OF NORTH AMERICA

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ABSTRACT. At least five species of pelycosaurs have been found in the Middle Pennsylvanian terrestrial deposit of Florence, Nova Scotia. *Archaeothyris florensis* is a primitive but typical ophiacodont, while *Echinerpeton intermedium* is an ophiacodont with some sphenacodont characteristics, including elongate neural spines. Vertebral material from three other pelycosaurs is also present. The occurrence of this rich fauna in the Middle Pennsylvanian permits reconsideration of the taxonomic interrelationships of primitive pelycosaurs. Although ophiacodonts did not diverge as drastically from the ancestral romeriid pattern as sphenacodonts or edaphosaurs, none of the known early ophiacodonts could be ancestral to the other suborders. Even if pelycosaurs evolved from a single romeriid species, the separation of the major pelycosaurian lineages must have occurred early in the evolution of the order, probably at about the time of the formation of the Joggins deposits. Comparison of romeriid captorhinomorphs and the

earliest pelycosaurs indicates that the temporal opening developed in response to selection for more efficient use of the jaw musculature in forms of increasing body size.

INTRODUCTION

The Order Pelycosauria represents the earliest stage in the evolution of mammal-like reptiles. Early work on forms from the Lower Permian redbeds of Texas and New Mexico by Cope (1877, 1878), Case (1907), Williston (1911), and von Huene (1925) demonstrated the prominence of the group among primitive fossil reptiles.

Our current understanding of the order is based primarily on the work of Romer and Price (1940). This extensive study indicated that the Pelycosauria comprised a large order with at least three major lineages: 1) Suborder Ophiacodontia—primitive amphibious piscivores; 2) Suborder Sphenacodontia—advanced terrestrial carnivores; 3) Suborder Edaphosauria—specialized swamp-dwelling herbivores. Most pelycosaurs are known from the Lower Permian (Artinskian) of North America and Europe (see chart of geological horizons, Fig. 1). In the Pennsylvanian, fossil remains are limited both in variety and numbers, but are sufficient to show that pelycosaurs were already highly diversified. Upper Pennsylvanian (Stephanian) localities from which pelycosaurs are known are limited to: 1) The McLeansboro Formation near Danville, Illinois: fragmentary skeletal elements

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	EUROPEAN STAGES		AMERICAN SERIES	LOCALITIES
PENNSYLVANIAN	Stephanian		Monongahela	Kounova Jasper County
			Conemaugh	Pittsburgh Garnett Danville
	Westphalian	D	Allegheny	Nýřany Linton Florence
		C		
		B	Pottsville	Joggins
		A		
	Namurian			

Figure 1. Pennsylvanian stratigraphy. The chart is based on Moore et al. (1944).

of a single ophiacodont genus, *Clepsydrops* (Cope, 1875). 2) The Matoon Formation of Jasper County, Illinois: numerous fragments of a varanopsid sphenacodont, *Milosaurus mccordi* (DeMar, 1970). 3) The Conemaugh Group near Pittsburg, Pennsylvania: *Edaphosaurus* (Romer and Price, 1940) just below the Ames Limestone, and a

large ophiacodont pelycosaur, *Clepsydropus magnus* (Romer, 1961), just above the Ames Limestone. 4) The Upper Pennsylvanian Round Knob Formation of Garnett, Kansas: a complete presacral vertebral column belonging to an edaphosaur designated as *Edaphosaurus ecordi*, an ophiacodont pelycosaur similar to *Clepsydropus* (Peabody, 1957), and an undescribed spheonacodont. 5) The late Stephanian of Kounova, Bohemia: a small *Edaphosaurus* similar to that from the Round Knob Formation, and a number of bones of a large spheonacodont, *Macromerion schwarzenbergii* (Romer, 1945).

Indications are that, by the time of deposition of the Danville bonebed (the oldest of the above localities), considerable differentiation of the pelycosaur groups had already taken place, and that the ophiacodonts had already entered upon a stage of structural stability (Romer and Price, 1940: 34). This idea is supported by other finds in the Stephanian indicating the presence of highly evolved members of all three pelycosaur suborders. From this evidence, it is inferred that the Pelycosauria must have originated well down in the Pennsylvanian, at least in the early Pottsville or Namurian.

Romer and Price (1940: 34) pointed out the need to discover and investigate "fossiliferous beds of early and middle Pennsylvanian (Westphalian) age of a more terrestrial type than the coal swamp deposits" so typical of the age, in order to establish a better understanding of the origins of the Pelycosauria.

In 1964, Carroll described a fossil from the upright lycopod tree stumps of Joggins, Nova Scotia, which he named *Protoclepsydropus* and identified as a very primitive pelycosaur. Since the age of this deposit is Westphalian B, *Protoclepsydropus* would be the oldest known pelycosaur. The affinities of this animal are open to question, however, because of the similar nature of the humerus to that of the subsequently described romeriid captorhinomorph, *Paleothyris* (Carroll, 1969). (The original identification of *Protoclepsydropus* was mainly

based on the nature of the humerus.) The affinities of *Protoclepsydropus* will be discussed later in this paper.

Between the Joggins deposit and the Danville bonebed there is a great gap in time. An extensive pelycosaurian fauna from Florence, Nova Scotia, which will be described in this paper, provides considerable information about the representatives of the order living during this time interval. The Florence locality was discovered by a field party from Harvard University under the direction of Dr. A. S. Romer in 1956. As at Joggins, the vertebrates are found within the stumps of upright lycopods of the genus *Sigillaria*. The trees, rooted above the Lloyd Cove coal seam of the Morien Group, were exposed by strip mining. The age of the locality was established by Bell (1966: 62) to be equivalent to the Westphalian D. The Florence locality is hence younger than the Joggins deposit, where the earliest reptiles were found, and about the same age as the traditional Pennsylvanian coal swamp deposits of Linton, Ohio, and Nýřany, Czechoslovakia. As at Joggins, the fauna consists almost entirely of terrestrial vertebrates, rather than swamp and pond dwellers common to Linton and Nýřany.

Five tree stumps were collected in all, but most of the vertebrates came from one tree, No. 3. In addition to the pelycosaurs to be described in this paper, at least 18 specimens of a romeriid captorhinomorph (Carroll, 1969), a single specimen of a small limnoscelid (Carroll, 1967), and several skulls of the edopoid amphibian *Cochleosaurus* have been found. The tree was 12 to 15 feet in height, with three blocks at successively lower levels, indicated as A, B, and C, with intervening layers of unproductive shale. The base of a tree stump was collected in 1965 by a McGill-Princeton field party. According to Dr. Baird's field notes, this tree (designated as block D for convenience) stood between the still recognizable cavities left by trees No. 3 and 5, so it is part of the Harvard party's tree No. 4.

Several types of pelycosaurs were found

in the tree, with the greatest amount of material being located in block B. These finds represent the earliest adequately known pelycosaurs whose affinities can be definitely established. They add very much to our knowledge of the anatomy of the early members of this group. Two pelycosaurs that are almost complete will be described first; some fragmentary pelycosaurian material will be discussed later.

The manner of preservation of these pelycosaurs makes systematic description difficult. Most the specimens are badly disarticulated, even to complete separation of the component skull bones. The bones in block D are particularly poorly preserved.

The following abbreviations are used in this paper:

AMNH American Museum of Natural History, New York

BM(NH) British Museum (Natural History)

ČGH National Museum, Prague

CM Carnegie Museum, Pittsburgh

DMSW private collection of D. M. S. Watson, Cambridge University

MB Humboldt Museum, Berlin

MCZ Museum of Comparative Zoology, Harvard University

RM Redpath Museum, McGill University, Montreal

SGL Sächsisches Geologisches Landesamt, Leipzig

WM Walker Museum, Chicago University

YPM Yale Peabody Museum

ACKNOWLEDGMENTS

I wish to thank Dr. A. S. Romer for the loan of this material to the Redpath Museum. His contribution goes far beyond the discovery of these particular specimens, however; his painstaking study of the Lower Permian reptiles provides an indispensable background for the study of both pelyco-

saur and captorhinomorphs, and a high standard for all students of vertebrate palaeontology. I also thank Dr. R. L. Carroll, of the Redpath Museum, McGill University, who encouraged me to study the material described here and who also gave me considerable guidance and advice. This study owes much to Professor B. Patterson of the Museum of Comparative Zoology, Dr. J. H. Ostrom of the Peabody Museum and Dr. E. S. Gaffney, of the American Museum of Natural History, who allowed me to examine the collections of pelycosaur material in Harvard, Yale, and the American museums. I also wish to thank Dr. D. Baird of Princeton University for his very helpful advice. The study was partially supported by grants from the National Research Council of Canada.

SYSTEMATIC DESCRIPTIONS

Class *REPTILIA*

Subclass *SYNAPSIDA*

Order *Pelycosauria*

Suborder *Ophiacodontia*

Family *OPHIACODONTIDAE*

Genus *Archaeothyris* n. gen.

Type species. *Archaeothyris florensis* new species.

Known distribution. Middle Pennsylvanian of eastern North America.

Diagnosis. Small ophiacodont pelycosaur with well-ossified skeleton. Skull resembles that of *Ophiacodon uniformis*, except for the relative shortness of the antorbital region and the horizontal ventral margin of the maxilla. The mid-dorsal centra are elongate. Neural arches are not swollen; the neural spines are 9 ± 3 mm high and 6 ± 1 mm wide at the top. The humerus has a deep groove running proximally above the entepicondylar foramen and the entepicondyle is not expanded. The ectepicondyle is at 85 degrees to the plane of the distal end. The supinator process is stout. The pubic tubercle is well developed. Metatarsals and phalanges are elongate.

Archaeothyris florensis n. sp.

Etymology. Greek *archaeo*, ancient, plus *thyris*, window, in reference to the earliest evidence of a temporal opening. *Florensis*, from the name of the locality, Florence.

Holotype. Museum of Comparative Zoology, Harvard, MCZ 4079, block B.-1, partial skull, several vertebrae, humerus, cervical ribs.

Paratypes. MCZ 4080, block A, pelvis, sacral vertebra, axis; MCZ 4081, block B, caudal vertebrae; MCZ 4082, block B, anterior dorsal vertebrae; MCZ 4083, block B, assorted postcranial elements; MCZ 4084, block B, caudal vertebrae, articulated; MCZ 4085, block B, lower jaw elements, frontal; MCZ 4086, block C, metacarpals; MCZ 4087, block C, presacral vertebrae; RM 10056, block D, maxilla, dentary, presacral and caudal vertebrae, interclavicle, calcaneum.

Horizon and locality. Morien Group, within 25 feet above the Lloyd Cove coal seam, equivalent to the Westphalian D of Europe. Dominion Coal Co., strip mine No. 7, two miles north of Florence, Cape Breton County, Nova Scotia.

Diagnosis. Same as for genus.

Description. Skull: On the basis of the material from block B (MCZ 4079) and D (RM 10056), a reconstruction of the skull has been attempted (Fig. 2). The skull resembles that of *Ophiacodon* except that the antorbital region is not strongly elongated. The approximate length of the skull is 92 mm; the orbit is about 21 mm in diameter. The posterior rim of the orbit is 31 mm from the posterior tip of the quadrate. The maximum height of the skull (25 mm) is reached in the region of the orbit. The skull is relatively narrow and has a well-developed temporal opening bounded by the postorbital, squamosal, and the jugal. The sculpturing resembles that seen in other pelycosaurs. It is more pronounced on the dorsal surface than on the lateral.

Of the skull roof (Fig. 3), the right frontal, postfrontal, parietal, and squamosal are found in close association—only slightly

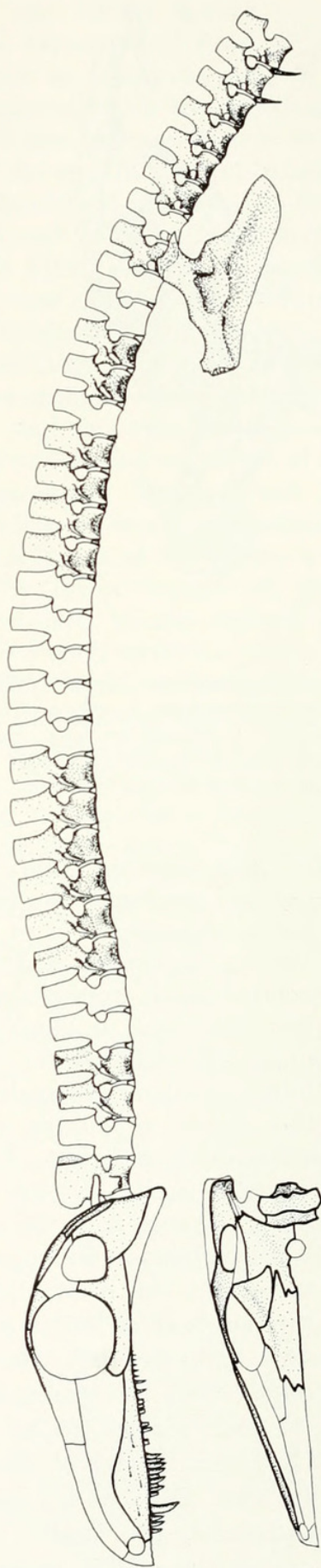


Figure 2. *Archaeothyris florensis*, partial reconstruction. The angle of the occiput to the skull table is uncertain. $\times 0.5$.

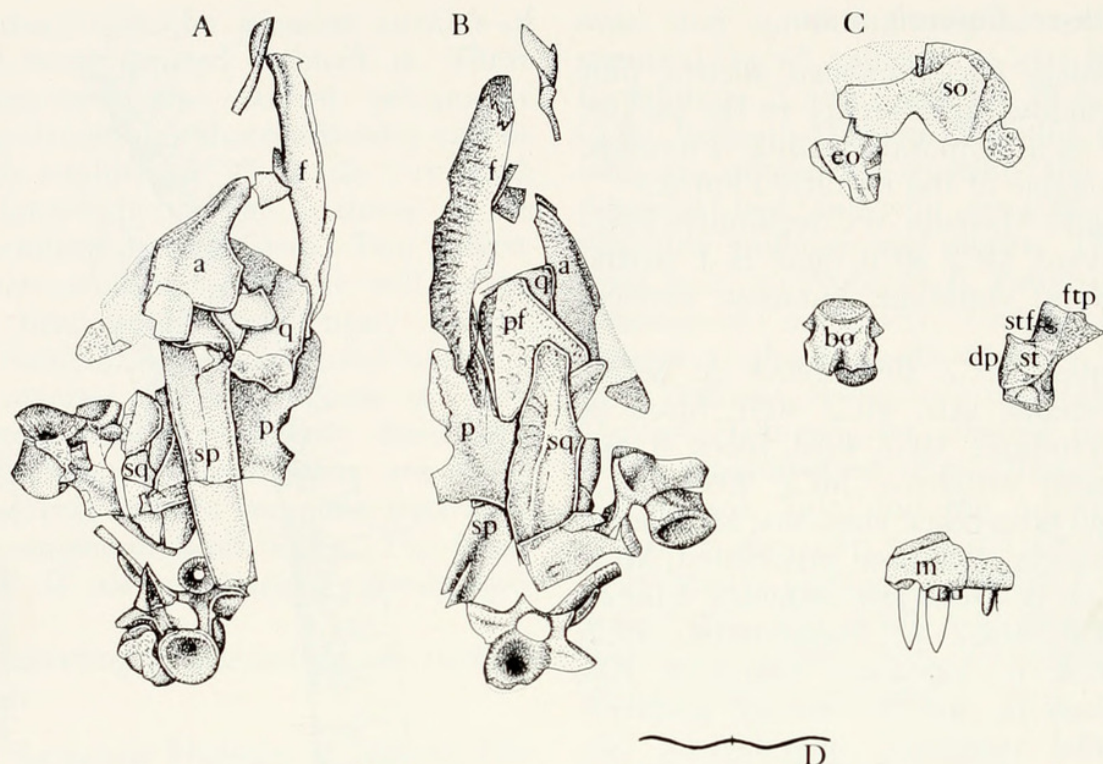


Figure 3. Type of *Archaeothyris florens*, MCZ 4079. A, skull and vertebral elements in ventral view; B, dorsal view of A; C, isolated skull elements; D, outline of dorsal surface of the frontal. Stapes $\times 1.4$. All others $\times 1$. Abbreviations used in figures: a, angular; bo, basioccipital; d, dentary; dp, dorsal process; eo, exoccipital; f, frontal; ftp, footplate; ha, haemal arch; m, maxilla; p, parietal; pf, postfrontal; q, quadrate; so, supraoccipital; sp, splenial; sq, squamosal; st, stapes; stf, stapedial foramen.

disarticulated, but showing their surfaces of attachment and overlap. The frontal is only moderately elongated: it is 33 mm in length, with a maximum width of 11 mm. A second frontal, approximately 20 percent larger than that in block B.-1, is found in block B.-22 (MCZ 4085). In comparison with that of other ophiacodonts, the frontal in this animal is shorter and also wider in the supraorbital region. The ratio of median length of the frontal to the median length of the parietal in *Ophiacodon uniformis* is 3:1, while in this genus it is only 2:1. Anteriorly, the frontal interdigitates with the nasal, extending 1 to 3 mm underneath it. Anterolaterally, the frontal comes in contact with the prefrontal over a length of 11 mm. The prefrontal is missing in block B.-1, but the area of attachment can be readily seen. Between the prefrontal and the postfrontal, the frontal extends laterally to reach the orbital margin over

a length of 5 mm. This part of the orbital margin is relatively straight, but the posterior end of it reaches further laterally than its anterior end. In this feature *Archaeothyris* is different from *Ophiacodon*, in which the orbital margin is concave, and the anterior and posterior margins extend equally far from the midline. Dorsally the bone is marked by fine sculpturing on the orbital margin (these marks are different from the general sculpturing of the skull). The curved nature of the frontal in cross section is shown in Figure 3. This curvature is followed with great fidelity by the postfrontal, creating a swelling over the orbital region.

The postfrontal is relatively large; its anterior and inner surfaces connect to the frontal (except for the posterior portion of its inner surface where it is separated by a thin strip of the parietal). Viewed from above, the orbital margin of the postorbital curves gently, following the arch of the

frontal. In *Ophiacodon* the dorsal orbital margin is much more strongly curved.

The posterior margin of the frontal and postfrontal extends over the parietal and fits within dorsal grooves that provide an extended surface of attachment. The parapineal foramen is located towards the posterior end of the parietal. On the underside there is an invagination around the foramen that probably housed the greater part of the parapineal organ and its accessory structures. The parietals cover a large part of the table and are bounded on the sides by the postorbitals. Posterolaterally the parietal extends far backwards, a notch at the end receiving the anterior portion of the supratemporal. The dorsal surface of the skull ends with the parietals, the interparietal and the tabulars being part of the uppermost region of the occiput. The concavity at the end of the table is interrupted at the midline by a slight backward projection of the parietals, offering attachment to the nuchal ligament. There are no tabular bones preserved in the tree.

The squamosal occupies a large area in the posterior part of the cheek region. It forms almost 50 percent of the margin of the temporal fenestra. Anteroventrally, the squamosal overlaps the jugal for a considerable portion of its length. Above the temporal opening, the squamosal is in contact with the postorbital, extending slightly underneath it. The squamosal-parietal contact is not strong (the skull roof is not firmly attached to the cheek region). The posterodorsal margin of the squamosal forms the main component of the ridge sloping down from the skull table to the quadrate. The dorsal portion of the posterior margin of the squamosal is covered superficially by the supratemporal, as indicated by a groove, and the lateral portion of the tabular. The squamosal extends inwards beneath these elements so that it underlies the posterolateral corner of the parietal. The area of the squamosal that lies underneath the tabular is so extensive that it is expected to come in contact with the paroccipital process and the inner sur-

face of the lateral border of the supraoccipital (Romer and Price, 1940: 56). It is difficult to assess the area of contact of the squamosal with the quadratojugal because of the incompleteness of the lower edge of the squamosal and because there is no quadratojugal preserved in the tree.

An almost complete maxilla is found in block D (RM 10056). A small fragment of this bone is also found in block B. The maxilla in block D is 40 mm long and 10 mm high at its highest point. The lower margin is almost straight, while in the genus *Ophiacodon* and in most sphenacodonts, the convexity of the lower margin of the maxilla is conspicuous. The internal surface of the maxilla is more important from the taxonomic point of view than is the lateral one. The lower margin of the bone is thickened and turned inward to form a continuous shelf with the palate. This shelf is striated posterior to the canines for attachment to the palatine and the ectopterygoid and is considerably thickened above the canines. Immediately above this area of swelling, the maxilla is braced by a ridge extending to the top of the bone. In other ophiacodonts the maxilla is strengthened by a well-formed vertical ridge, while in sphenacodonts this area is thickened but without the development of a definite ridge. This type of buttressing in *Archaeothyris* and sphenacodonts may be more primitive than that observed in ophiacodonts. It is also observed in another pelycosaur from Florence and in some primitive romeriid captorhinomorphs. The highest point on the upper expansion of the maxilla is reached 15 mm from the anterior end of the bone, 6 mm posterior to the region of the canines.

There are 21 teeth implanted in the subthecodont manner on the maxillary shelf. There is place for at least seven more teeth. The number of teeth in this maxilla is low in comparison with that in other ophiacodonts: *Varanosaurus acutirostris* has 46 teeth, *Ophiacodon mirus* (37), *Ophiacodon uniformis* (32), and *Ophiacodon retroversus* (36). In relationship to this low

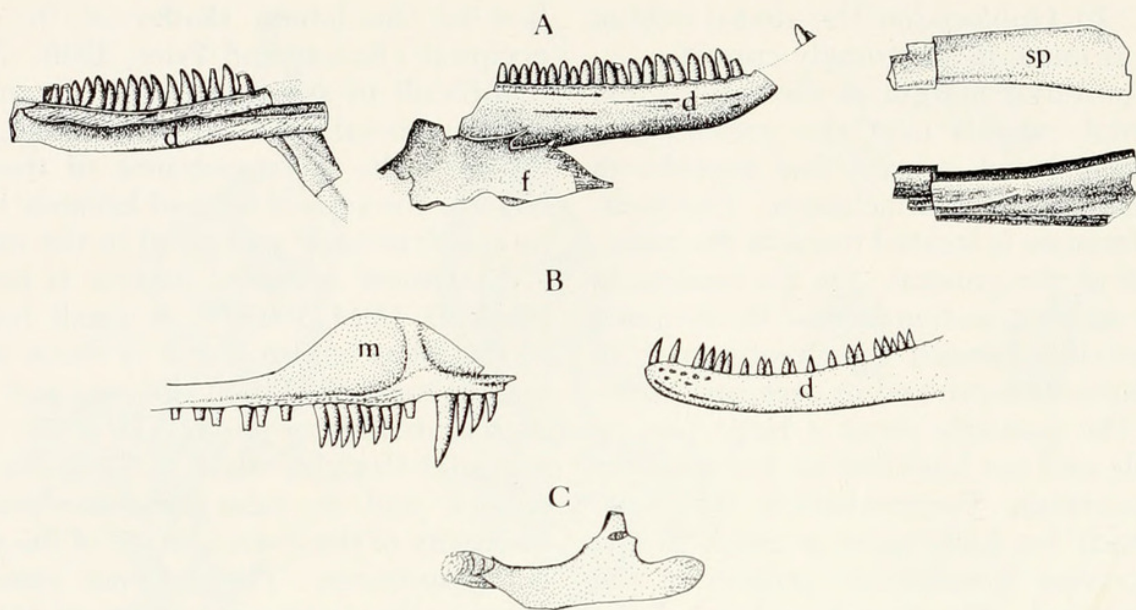


Figure 4. *Archaeothyris florens*. A, MCZ 4085, medial and lateral views of the dentary and of the splenial; B, RM 10056, maxilla in medial view and dentary in lateral view; C, MCZ 4089, jugal in lateral view. All $\times 1$. See Fig. 3 for key to abbreviations.

number of teeth, the maxilla is relatively shorter than in other ophiacodonts and as a consequence of this the snout region is less elongated. According to Romer and Price (1940: 89), the length of the maxilla is determined by the dentition and not vice versa. There are only three precanine teeth in RM 10056, a number indicative of strongly developed canines, while in *Ophiacodon* there are from five to seven teeth present anterior to the canines (Romer and Price, 1940: 89). The canine (only one is in place, a second is being replaced) is strongly developed (7 mm in length). The teeth are simple structures, slightly compressed, and sharply pointed. Towards the tip, the teeth bend slightly backwards and are serrated on the medial surface. This serration occurs only on the inside half of the tooth and only towards the tip. It is unlike the labyrinthine infolding seen in the Ophiacodontidae, in which there are deep grooves at the base of the teeth.

An isolated jugal is present in block A, MCZ 4089 (Fig. 4). There is no feature of this bone that would prevent it from belonging to the type of *Archaeothyris* except its small size. It is about 50 percent too small to fit the skull as it has been re-

stored. It is essentially a triradiate structure with long anterior and moderately developed dorsal and posterior rami surrounding a well-developed temporal opening. It is 22 mm long and 10 mm high at the post-orbital bar. The anterior process extends far forward under the orbit and articulates with the lacrimal over a width of 2 mm. It extends a further 5 mm beneath the posterior limit of the lacrimal. The ventral surface for articulation with the maxilla is 11 mm long. At the end of this surface, the jugal reaches the lower edge of the skull, as indicated by the ventral curvature of the bone at this point. The extent of exposure to the ventral border of the skull is less here than in any other pelycosaur with the exception of *Varanops*, in which the jugal does not reach the margin of the skull at all. More posteriorly, the jugal is bounded by the quadratojugal. Articulating marks on the lateral surface of the posterior ramus indicate that the jugal was covered by the squamosal dorsally and the quadratojugal ventrally. Dorsally the posterior and anterior processes form part of the temporal opening and the orbit respectively. The jugal extends only 4.5 mm under the orbit and 3.5 mm under the temporal opening, in-

dicating that the skull was low in outline and that the orbit occupied most of the lateral side of the skull. The dorsal process of the jugal forms roughly half of the post-orbital bar. The upper portion of this process has been lost. It can, however, be established that the type of infolding seen on the *Ophiacodon* dorsal process is not present on this jugal. A somewhat similar jugal has been found at Garnett, belonging to an undescribed sphenacodont pelycosaur (from the Redpath Museum collection). This type of jugal is generally primitive in character and is also found in *Varanosaurus*.

A fragment of one of the palatal elements is also found in block B.-1. Since it bears denticles, it is either part of the pterygoid, the palatine, or the ectopterygoid. In ophiacodonts the palatal elements are covered by single rows of teeth, while this particular fragment is completely covered by teeth. This kind of palatal dentition is found only in sphenacodonts and on the transverse flange of the pterygoid in primitive romeriid captorhinomorphs. Since this fragment is the only known element of the palate, a reconstruction of this area is not possible.

Wedged in between the frontal, the post-frontal, and the angular in block B.-1, MCZ 4079, is the quadrate with a fragment of the pterygoid next to it. The dorsal portion of the quadrate is a sheet of bone about 1.5 mm thick, applied to the outer side of the pterygoid. It extends laterally as well as posteriorly to come in contact with the quadratojugal. Dorsally, the ossified portion of the quadrate is not large enough to reach the squamosal or the paroccipital process. A cartilaginous extension of the quadrate may have reached these areas to complete the posterior wall of the chamber containing the temporal muscles (Romer and Price, 1940: 61). Posteroventrally, the bone changes from a sheetlike nature into a more massive structure that bears the articular surface for the lower jaw. Just dorsal to this area, the lateral surface is indented to form the internal margin of the quadrate foramen. Ventrally, the articulating surface is broken, but it can be seen that

it originally consisted of two rounded ridges, possibly separated by a longitudinal depression as in other pelycosaurs. The inner ridge is smaller than the outer one.

The following bones from the occipital region of the skull are present in the type: the supraoccipital, the exoccipital, the interparietal, and the stapes (MCZ 4079). A basioccipital was found in block B.-21, but the size and characteristics of this bone allow it to be associated with *Archaeothyris*. As in *Ophiacodon*, the bones of the braincase are only suturally articulated, whereas in all other pelycosaurs they tend to fuse.

The supraoccipital is 20 mm wide and 11 mm tall. The only feature that differentiates this bone from the one in *Ophiacodon uniformis* is its more rounded lateral margins. A partial exoccipital is found suturally attached to the supraoccipital. Its articulating surface for the proatlas is placed more laterally than in *O. uniformis*. The bone extends further laterally than in *Ophiacodon*, occupying the whole of the ventral margin of the supraoccipital. A portion of the connecting surface for the basioccipital is seen on the ventral margin of the bone. Laterally, the exoccipital extends slightly under the opisthotic. The ventral surface of the basioccipital is seen in Figure 3. The occipital condyle is 5.5 mm in width. Laterally, close to the condylar area, the connecting surface of the exoccipital is seen. Between this area and the ventral ramus of the bone there is a notch not observed in *Ophiacodon uniformis*. This small fragment of the interparietal indicates that there was only one postparietal element, which is similar to the one seen in *O. uniformis*.

The stapes is typically pelycosaurian in its configuration. The shaft, however, is extremely short. It was probably continued in cartilage. The distal portion of the shaft, as preserved, is compressed to a thin sheet of bone. The dorsal process extends laterally at 90 degrees to the shaft, as in the primitive romeriids *Paleothyris* and *Hylonomus*, to form an oval articular surface that is roughly parallel to the longitudinal axis of the shaft. The relative proportions of the

footplate and the dorsal process are about intermediate between those seen in *Ophiacodon* and those of *Dimetrodon*. In *Ophiacodon* the footplate is much larger than the dorsal process, while in *Dimetrodon* the reverse is the case. In this stapes, however, the two structures are about the same size.

Three fragments of the lower jaw are present in block B, and an incomplete dentary is found next to the maxilla in block D. The description to follow is a composite of all three specimens. The dentary carries the single lateral tooth row on its upper border and forms a large part of the outer surface of the jaw. Anteriorly it forms the major part of the jaw and is bounded ventrally by the splenial. It bears the type of sculpturing seen in *Ophiacodon uniformis*. Posteriorly the dentary is bounded by the splenial and angular successively (Fig. 4). There are 16, 20, and 22 teeth respectively in the three fragmentary jaws, but a total number of at least 25 is expected in a complete dentary. The teeth are similar to those seen on the maxilla, except for the absence of canines. The dentary bends upward at its front end and the second and third teeth are slightly larger than the remainder. The splenial forms the internal surface of the jaw, connecting dorsally to the internal ridge of the dentary that bears the teeth. Ventrally it connects to the outer side of the dentary, extending down to enclose the Meckelian canal. The splenial does not extend to the outer surface of the jaw as in other ophiacodonts. The angular is a large bone forming part of both the internal and external surface of the jaw. In the area of the Meckelian fossa it forms the ventral portion of a lateral fenestra, as in some other ophiacodonts. On the posterior part of the jaw this bone becomes very thin where it was succeeded by the surangular. Neither surangular, articular, nor coronoid bones have been identified in the tree.

The axial skeleton. Although most of the known elements of the axial skeleton are disarticulated and found at four different levels in the tree, their affinity with this genus is reasonably certain. As a conse-

quence of the scattering of the bones, the exact number of presacral vertebrae cannot be determined. Romer and Price (1940: 93) give 27 as the number of presacrals for ophiacodonts and sphenacodonts. Primitive romeriid captorhinomorphs have from 26 to 32 presacral vertebrae, but *Archaeothyris* is close enough in time and osteology to the other known pelycosaurs that a presacral count of 27 or very close to it is expected. It is also expected that this animal would have had two sacral vertebrae. There is no direct evidence for this, but the shape of the iliac blade fragment in block A, MCZ 4080, suggests that there were only two sacral ribs. Presumably the tail was comparable in length to that of later pelycosaurs, which have 50–70 segments.

The description of the individual vertebrae of this animal is based on several specimens. In general, the vertebrae resemble those in the most primitive members of the Ophiacodontia. They have large pleurocentra, small crescentic intercentra, strong and well-developed transverse processes, unswollen neural arches, and high neural spines, in comparison with those of most romeriids. The arches are firmly attached to the centra, the line of suture between them indicated by a rugose ridge posterior and ventral to the transverse process. The centra and neural arches are always found attached to each other in blocks A, B, and C, but the few vertebral elements found in block D have their centra and neural arch elements separated. The vertebral elements found in block D are of the same size as in other blocks, so that the level of maturity would be expected to be similar to those found above them. The reason for finding separate centra and neural arches in block D can be found in the nature of the preservation in this block. The matrix is poorly consolidated and is full of plant material. It is probable that material in this part of the tree accumulated more slowly than in the remainder, and allowed more weathering of the bones.

Of the atlas-axis complex, only the axis is preserved, with arch and centrum firmly

fused. This element was found in block A (MCZ 4080), immediately underneath the first sacral vertebra. It is of a rather primitive nature; the general proportions are intermediate between those of some romeriids and those of the most "primitive" pelycosaurs, the ophiacodonts. The centrum is 8 mm long and 5.5 mm high at the posterior rim. In most pelycosaurs the bevelling for the intercentrum is extensive in the cervical region, but in *Archaeothyris* it is insignificant.

Pelycosaurs typically have a ridge of bone to strengthen the ventral side of the centrum. The level of development of this ridge, or keel, varies among different pelycosaurs, as well as in different regions of the vertebral column of a single animal. In the axis, this ridge extends ventrally, forming a nearly straight line between the ends of the centrum. The ventral margin is slightly rounded. The lateral surface of this ridge at the lower middle of the centrum is concave in section.

Above the anterior rim of the centrum there are paired facets that would have articulated with the uppermost part of the atlas centrum, indicating that the axis intercentrum is located immediately below the atlas centrum (Fig. 5) and possibly fused to it. Here, as in all ophiacodonts, the atlantal centrum is not expected to reach the ventral surface of the column. In sphenacodonts and edaphosaurs, on the other hand, the axial intercentrum is large and is positioned posterior to the atlas centrum. The atlantal centrum reaches the ventral surface of the column, but this ventral exposure is quite narrow. (In the Middle Pennsylvanian romeriid *Paleothyris*, the atlantal centrum is indistinguishably fused to the axis intercentrum. On the other hand, the configuration in *Hylonomus*, the most primitive romeriid, resembles that seen in sphenacodonts and edaphosaurs.) The presence of the axis intercentrum underneath the atlantal centrum necessitates the formation of paired accessory connecting surfaces above the rim of the axis centrum, because the height of the axis intercentrum is added

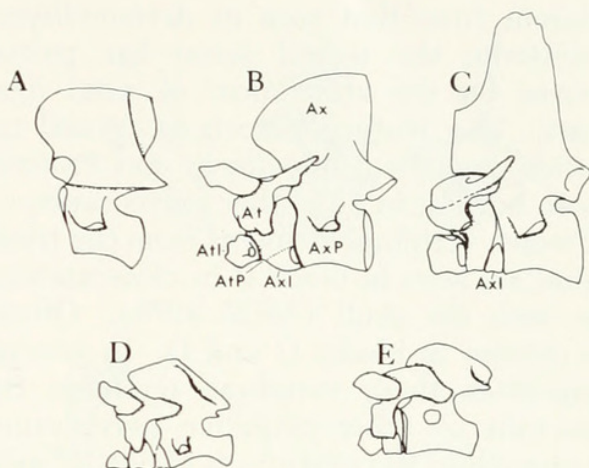


Figure 5. Comparison of the atlas-axis complex in three pelycosaurian and two romeriid genera to show the position of the axis intercentrum. A, *Archaeothyris florensis*, MCZ 4080, $\times 1$; B, *Ophiacodon retroversus*, MCZ 1121 (Romer and Price, 1940, text-fig. 44), $\times 0.25$; C, *Dimetrodon limbatus*, MCZ 1347 (Romer and Price, 1940, plate 23), $\times 0.25$; D, *Hylonomus lyelli*, BM(NH) R.4168, (Carroll, 1964, text-fig. 2), $\times 2$; E, *Paleothyris acadiana*, MCZ 3484 (Carroll, 1969, text-fig. 5), $\times 2.5$. Abbreviations used in the figure: At, atlas neural arch; Atl, atlas intercentrum; Ax, axis neural arch; AtP, atlas pleurocentrum; AxI, axis intercentrum; AxP, axis pleurocentrum.

to the height of the atlas centrum. Immediately above this articulating area are the anterior zygapophyses. Between the zygapophyses and the top of the anterior central connecting surface there is a recess that is also present on the *Ophiacodon* axis. There is also a deep groove extending from the lowermost edge of the anterior zygapophyses to the ventral edge of the posterior zygapophyses.

The transverse process is very stout and has a large articulating surface. There is a little "webbing" seen anteroventrally. The transverse process extends without a break to the upper margin of the centrum. In anterior view the transverse process extends far laterally and downward at about 65 degrees to the vertical axis of the vertebra. The neural spine is moderately tall, and extends anteriorly beyond the level of the zygapophyses. A similarly shaped anterior extension is seen in the primitive romeriid captorhinomorph *Hylonomus*. In *Ophiacodon* the neural spine also extends far anteriorly, but the shape of this process is

different from that seen in *Archaeothyris*. Posteriorly, the neural spine has paired grooves for the attachment of axial ligaments. This feature is seen in several romeriids, including *Paleothyris* and *Protorothyris*, but not in any other pelycosaurs.

Twelve vertebral elements from the trunk region are seen in block B in close association with the skull (MCZ 4079). Others are present in blocks C and D. In general proportions these vertebrae resemble the presacrals of other primitive pelycosaurs. The length of the centrum is almost 40 percent greater than its height. In later and larger ophiacodonts there is a tendency for the width and the height of the centrum to increase at a greater rate than the length, so that the relative length decreases. The configuration of the ventral ridge (keel) varies throughout the column. It is most pronounced in the cervical region. The sacrals are stout and more rounded in contour and there is little keel development in the caudal region. There is a tendency for the posterior edge of the centrum, as viewed laterally, to have a slightly convex outline, and for the anterior edge to be slightly concave. In end view, the centra have the configuration of a laterally compressed oval, pierced above the midline for the passage of the notochord.

An intercentrum located in block B is crescentic in outline; its outer surface describes an arc of almost 90 degrees. Since this intercentrum is well developed, it seems probable that the intercentral space was larger than in other pelycosaurs. It is also probable that in life the intercentra had large cartilaginous extensions, reaching high up between the ends of the centra.

The nature of the transverse process is very important in associating this genus with the Ophiacodontia. The processes on the cervical and anterior dorsal vertebrae are markedly shorter than in other suborders. In the mid-dorsal region they arise from a high position on the arch, almost level to the zygapophyseal surface, and extend directly laterally. The

articulating surface of the transverse process is narrow. A thin portion of the surface extends anteroventrally toward the front of the centrum. This anteroventral extension of the transverse process is separated from the surface for the capitulum by only a slight gap for the passage of the segmental artery. This type of anteroventral extension of the articulating surface is seen only in the trunk region of other ophiacodonts. No "webbing" is present in spenacodonts or edaphosaurs. The head of the rib is formed in such a manner that there is complementary webbing between the tubercular and capitular heads. In the mid-dorsals the capitular head articulates with the intercentrum but there is a tendency for it to move onto the anterior rim of the same centrum in the lumbar, sacral, and anterior caudal vertebrae.

As in other ophiacodonts, the anterior zygapophyses are supported by buttresses extending upward and forward beyond the pedicels of the neural arch. These buttresses are quite prominent. The posterior zygapophyses are braced by paired supports descending and expanding from the base of the neural spine. The zygapophyseal surfaces extend laterally to the limits of the centra and are moderately tilted. Romer and Price (1940: 103) emphasize the importance of the angle of the zygapophyses in separating the different suborders of pelycosaurs and in distinguishing pelycosaurs from other early reptiles. In *Archaeothyris* this angle is difficult to establish exactly because the number of presacral vertebrae is small; the actual articulating surfaces are not straight, but oval in outline, and a little crushing can change the angle considerably. An approximate angle of 25 ± 5 degrees can, however, be established for the anterior dorsal vertebrae. In most ophiacodonts the angle is around 30 degrees in the dorsals; in most spenacodonts and edaphosaurs the figure is higher, frequently close to 45 degrees. In the anterior cervicals the angle is less; in the sacrals and caudals it tends to be greater.

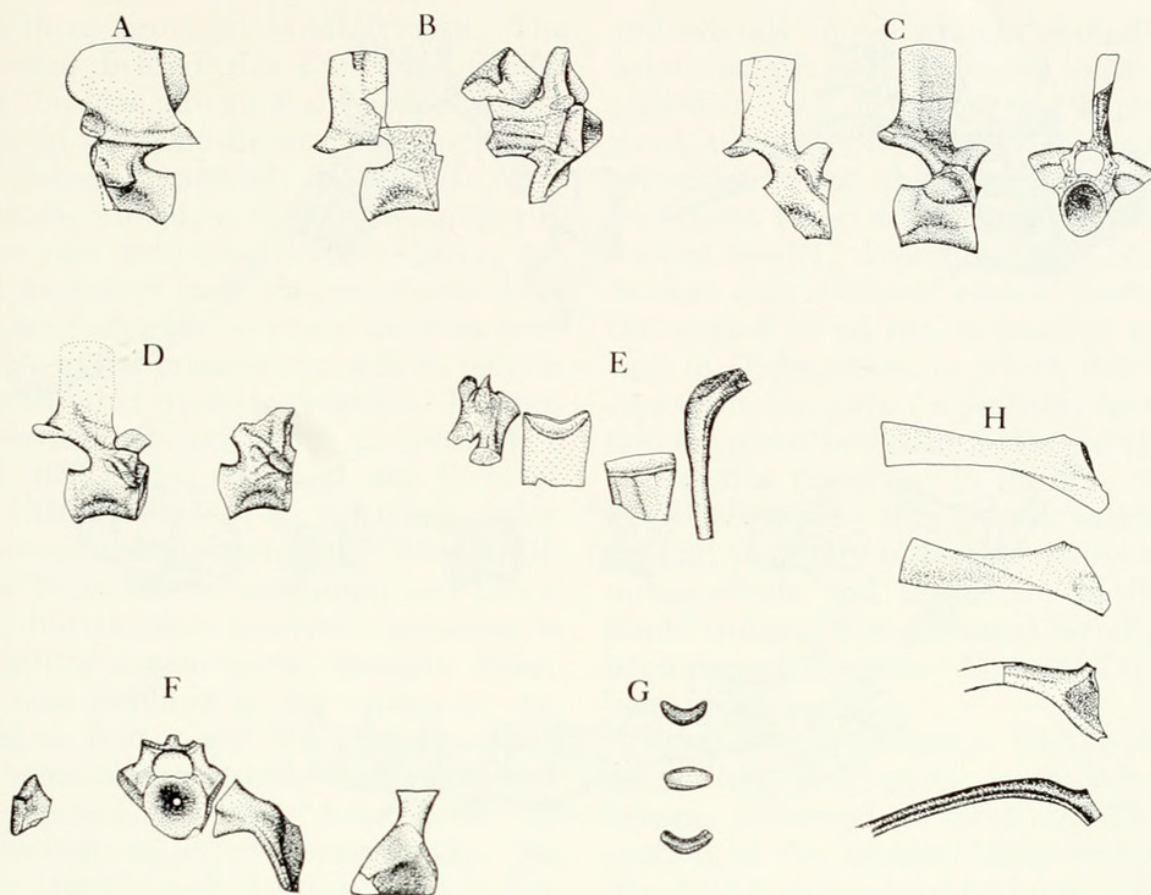


Figure 6. *Archaeothyris florensensis*, postcranial skeletal elements. A, axis in lateral view, MCZ 4080; B, cervicals, in lateral and dorsal view, MCZ 4079; C, three dorsal vertebrae in lateral and anterior views, MCZ 4082; D, two posterior dorsal vertebrae in lateral view, MCZ 4083; E, two fragmentary neural spines together with a rib and a caudal vertebra, MCZ 4083; F, first sacral vertebra with its ribs in anterior view, the articular surface of the right rib, and the anterior and lateral views of the right rib, MCZ 4080; G, presacral intercentrum in anterior, ventral, and posterior views, MCZ 4083; H, cervical, MCZ 4079, anterior, MCZ 4081, and posterior dorsal ribs, MCZ 4083. All $\times 1$.

The neural spines are well developed. They are greatly expanded anteroposteriorly to more than half the length of the centrum. Towards the top the spine expands further, so that the ends are nearly in contact. The spines are typically narrow transversely. The spine is situated towards the back of the vertebra, with the posterior margin in line with the posterior end of the centrum. The proportions of the neural spines vary in different areas of the vertebral column. The spines on the anterior dorsals expand laterally towards the top as well as transversely. When viewed from above the spine looks barrel-shaped. The unfinished end of the spine invades the lateral surface, expanding the head even more at this point. More posteriorly along the column, the spines tend to become

bladelike structures. Towards the sacrum, the neural spines become shorter, yet their width remains the same.

The nature of the iliac blade indicates that only two sacral ribs come in contact with it, as in ophiacodonts in general. The first sacral vertebra with its rib is preserved in block A (MCZ 4080) (Fig. 6). The spine and the posterior zygapophyses have been lost. The sacral rib is almost complete. The centrum is stouter than that of the presacrals—a feature commonly seen in pelycosaurs. The ventral keel on the centrum is rounded in cross section. The transverse process is located on the extreme anterior portion of the vertebra and extends farther down the body of the centrum than in presacrals; it is very massive and extends little laterally. The capitular facet is located on

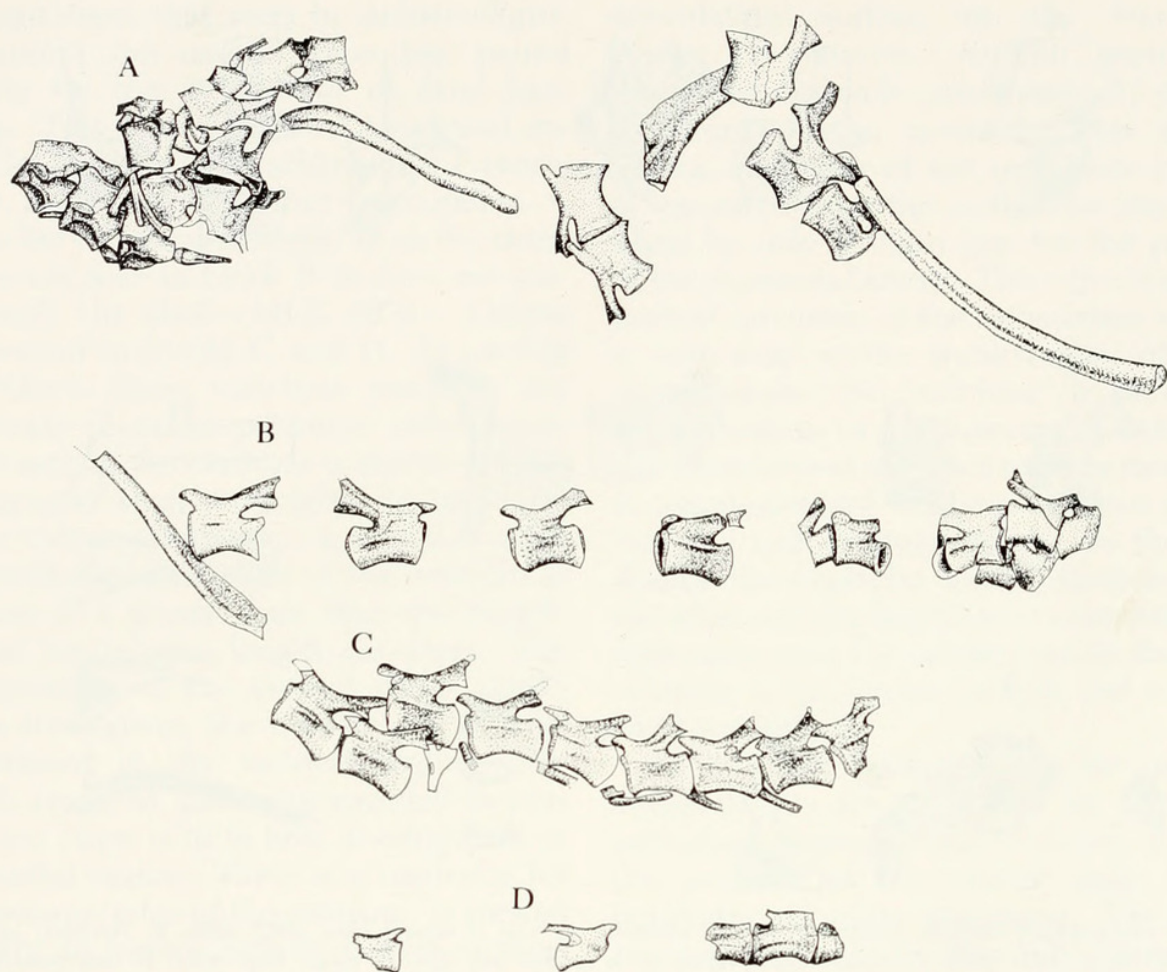


Figure 7. *Archaeothyris florens*. A, proximal caudal vertebrae, one cervical rib, and two isolated presacral ribs, MCZ 4081; B, mid-caudal vertebrae, not in articulation, and an isolated presacral rib, MCZ 4083; C, mid-caudal vertebrae, in articulation, MCZ 4084; D, posterior caudal vertebrae, MCZ 4081. All $\times 1$.

the body of the centrum, in close proximity to the transverse process. The two articulating facets are separated only by a small groove. The capitular facet is triangular in shape, with its tip pointing ventrally, almost reaching the ventral margin of the anterior central rib. Neither the second sacral vertebra nor its rib have been found in the tree.

Over forty caudal vertebrae were observed in the four blocks, representing all the regions of the tail. The anterior vertebrae are only slightly less stout than the sacral known from block A. They possess a ventral keel that disappears by the end of the rib-bearing series, where the lower surface of the centrum becomes flattened. The tubercular and capitular facets are present on the proximal caudals but are eliminated posteriorly, indicating the loss of the ribs.

The capitular facets are not visible on the centrum beyond the sixth caudal. By the twelfth caudal, only stubby lateral projections are visible, and they may simply be transverse processes. As indicated by the nature of the tubercular and capitular articulating areas, the anterior ribs are not fused to the centra. In this feature, *Archaeothyris* is very primitive. Other pelycosaurs have their caudal ribs fused to the centra (Romer and Price, 1940: 110). The length of the zygapophyses in the caudal region exceeds their width. The neural spines decrease in size in the caudal region and are not present on the distal portion of the tail beyond about the 35th caudal. Normal intercentra continue back into the proximal caudal region. This is seen in Figure 7 where two normal intercentra are seen be-

tween three proximal caudal centra. The intercentra behind the first four caudal centra develop into typical haemal arches, as seen in the same figure. The first chevron is already completely developed.

With the exception of the first sacral rib, all the ribs belonging to this genus are found separated from the vertebrae. Ribs are typically present on every vertebra from the atlas to the proximal caudals in pelycosaurs and other primitive reptiles. There is one cervical rib preserved in block B.-1 (MCZ 4079) (Fig. 6), and one in block B.-20 (MCZ 4081) (Fig. 7), lying underneath some caudal vertebrae. Webbing is present between the capitulum and tuberculum, but because transverse processes in the cervical region point strongly downward, this webbing is not extensive. According to Romer and Price (1940: 110), other ophiacodonts lose the connecting web in the cervical ribs. The head of the rib is moderately expanded dorsoventrally. The shaft is straight and the distal end is flattened and expanded in the shape of a paddle as in other ophiacodonts and romeriids.

In typical dorsal ribs, the head is greatly expanded dorsoventrally with the tubercular and capitular heads connected by a thin sheet of bone. The main body of the rib is circular in section, with a ridge running along its posterodorsal margin. The curvature of the ribs indicates that the trunk was rather high and narrow, as in most primitive carnivorous reptiles. Towards the posterior dorsal region the ribs become much shorter and there is a tendency for the transverse process to move onto the centrum. The heads of the ribs become much smaller with a corresponding reduction of the webbing.

The first sacral rib, preserved in block A (MCZ 4080), is almost complete. It was in articulation with the vertebra, but not fused to it. The rib is very short and massive; the plate is not as wide as that of *Ophiacodon*. The rib expands laterally for about 5 mm, then changes direction sharply

and extends almost straight ventrally. The outer margin of the lateral expansion is angled in such a manner that it points towards the posterior sacra. The downward projection of the rib is slightly cupped and terminates in an almost straight horizontal ventral border. Posteriorly, the rib seems to have only a limited area of contact with the second sacral rib, in contrast with the case in *Ophiacodon*, in which this area of contact is extensive (a probable accommodation to greater body size and weight). There are no ribs preserved in the tree that can be identified as the second sacral. The general similarity of *Archaeothyris* to other ophiacodonts and the extent of the iliac blade suggest that a second sacral rib had been present however. No caudal ribs have been found.

Appendicular skeleton. Of the shoulder girdle, only a fragmentary interclavicle is known, preserved in block D. The right portion of the anterior blade and part of the shaft is represented by bone. The parts in between are known only as an impression. The major part of the shaft is preserved as a separate fragment in the same block. The configuration of the anterior portion of the shaft is important diagnostically. In *Archaeothyris*, as in other ophiacodonts, the head constricts strongly, to make the shaft relatively constant in width. In sphenacodonts, however, the anterior portion of the shaft is wide so that the head and shaft are not clearly differentiated.

An almost complete pelvis is preserved in block A. The major parts of the three elements are preserved either as bone or as impression on the right side, except that the iliac blade is broken off at its base. Fragments of the left ischium and pubis are also preserved. As in most tetrapods, the ilium is fused to the pubis and ischium and forms the upper part of the acetabulum. The sutures between the bones are represented by slight rugosities in the areas outside the acetabulum. The ilium constricts strongly into the neck above the acetabulum. This constriction is closely comparable

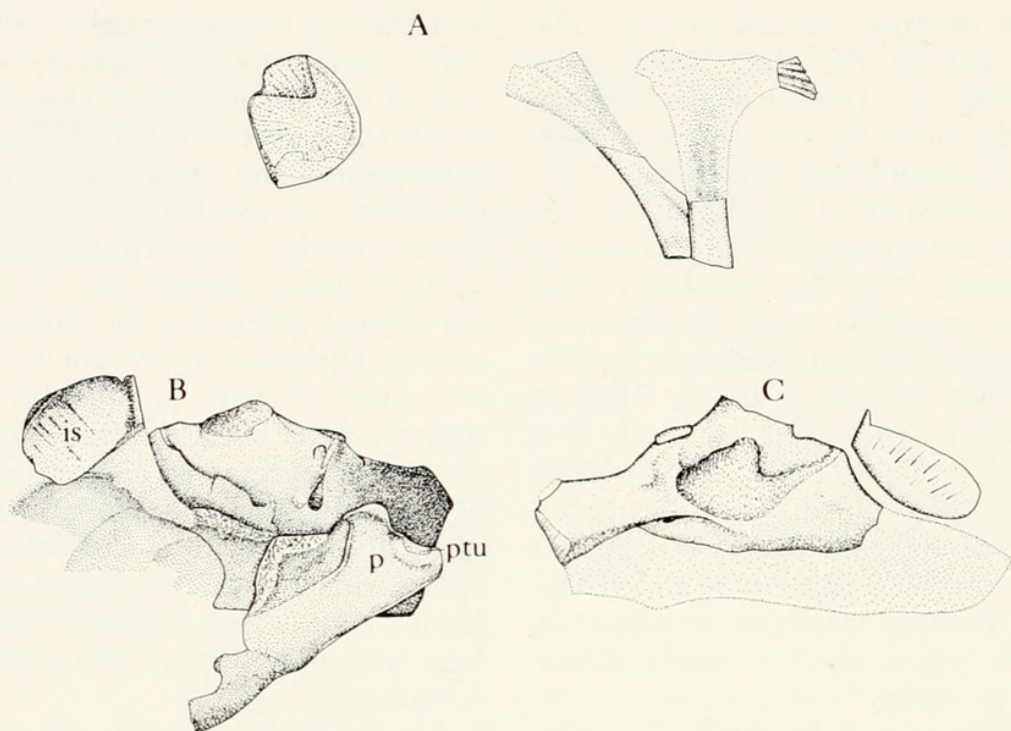


Figure 8. *Archaeothyris florens*. A, calcaneum, RM 10056, unidentified limb bone, fragmentary interclavicle; B, pelvic girdle material, MCZ 4080; C, lateral view of B. All $\times 1$. Abbreviations used in figure: is, ischium; p, pubis; ptu, pubic tubercle.

to the ones seen in the more primitive ophiacodonts. In spenacodonts there is less constriction. Hence it is probable that only two sacral ribs were present in this animal and not three sacrals as in spenacodonts, in which the iliac blade is greatly expanded. The articular surface of the acetabular cavity is similar in configuration to that of *Clepsydropus colletti* (Romer and Price, 1940: 127). It is only in the ventral rim of the acetabulum that the pelvis in block A differs from that of *Clepsydropus*. In *Archaeothyris* the acetabular rim describes a semicircle, with the dorsal tip of the acetabulum being the center. In *Clepsydropus*, however, this lower rim is practically straight. On the whole, the acetabulum faces rather more dorsally than in the more advanced pelycosaurs and in this it resembles that of *Clepsydropus*. The pubic and ischiadic parts of the acetabulum turn sharply outward close to the rim.

The dorsal margin of the pubis forms a thickened ridge that runs to the tip of this element and slants downward. This ridge

bears, close to the anterior limit, a prominent lateral pubic tubercle that provides attachment for the inguinal ligament and pubotibialis muscle. This tubercle tends to be of small size in the genus *Ophiacodon*. The tubercle in *Archaeothyris* is comparable in size to those of *Clepsydropus colletti* and *Varanosaurus wichitaensis*. The anterior margin of the pubis is wider than in ophiacodonts in general and has a large area of unfinished bone at the end. The obturator foramen is situated on the bladelike ventral process of the pubis, immediately underneath the acetabulum.

The ischium is thickened immediately behind the acetabulum and forms a thinner, ridged upper margin posteriorly. This ridge overhangs the platelike region below it and, as it passes backwards, the upper margin of the ischium turns downward towards the symphysis.

The left humerus was found in the proximity of the skull. It is only 38 mm in length (approximately 40 percent of the length of the skull). The twist of the distal upon the

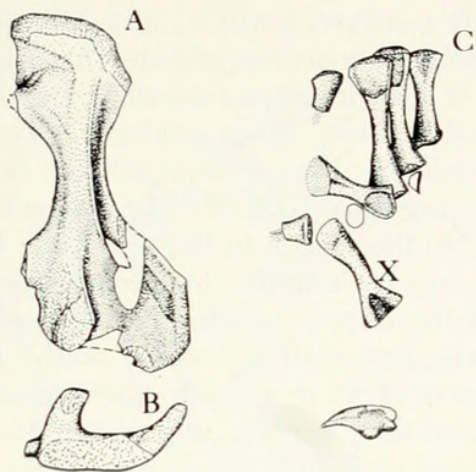


Figure 9. *Archaeothyris florensis*. A, humerus in dorsal view, MCZ 4079; B, distal end of A; C, metacarpals, and claw, MCZ 4083; X, femur of a small romeriid. All $\times 1$.

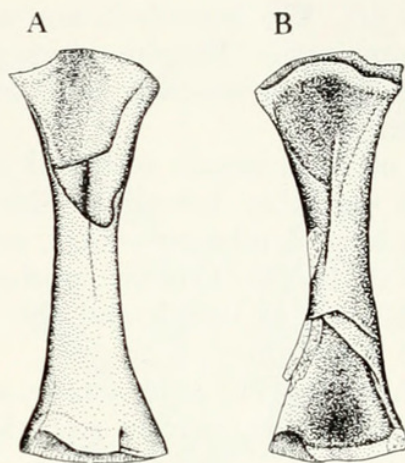


Figure 10. *Archaeothyris florensis*, RM 10056. A, femur in dorsal view; B, ventral view of A. $\times 1$.

proximal plane is about 65 degrees, a very primitive condition. In other pelycosaurs this angle ranges from about 35 to 60 degrees—the higher figures being found in ophiacodonts. In general proportions, this humerus resembles that of *Varanosaurus* and *Clepsydropus*, although it is smaller. Since the head is very little expanded, the articular surface occupies the entire extent of the proximal end of the humerus. There is little curvature seen on this articulating surface. The latissimus tubercle corresponds well in size to that seen in primitive ophiacodonts in general. The shaft of the humerus is short and very massive. The entepicondyle is little developed in comparison to that seen in Lower Permian ophiacodonts. The entepicondylar foramen is located within a deep groove that extends along the dorsal surface of the humerus to the proximal end. Such a groove is not seen in any other pelycosaurian humerus, with the possible exception of *Protoclepsydropus*, in which there is a slight deepening close to the entepicondylar foramen. There is extensive rugosity on the entepicondyle indicating the area of attachment of the flexor musculature. The ectepicondyle slopes very sharply dorsally from the general distal surface. The angle between the ectepicondyle and the plane of the distal end is about 80 degrees. The

summit of this ridge is about 5 mm above the general dorsal surface. The anterior margin of the supinator process projects sharply from the general surface of the bone. The distal surface of this process is blunt and faces forward. It is at about the level of the entepicondylar foramen, as in all pelycosaurs, but well beneath the ectepicondyle and separated from it by a deep ectepicondylar groove. The ectepicondylar notch is relatively shallow. The radial articulation was broken off and only a small part of the ulnar articulating surface is seen.

In block D there is a femur that can be associated with this animal. This bone, 42 mm in length, seems to have belonged to an immature individual, since neither the proximal nor the distal head—so important in characterization—are well ossified. A rudimentary adductor crest is visible on the ventral side of the femur. Even in this immature state, this femur is longer than the humerus in block B. There are few features in this particular femur to compare with the femora in other pelycosaurs.

An almost complete calcaneum is found in the same fragment in block D as the interclavicle (RM 10056). This element is weakly ossified and the proximal end is crushed in such a manner that this region is shifted to the right. The area where the perforating foramina would be expected

is broken off. The bone is 12 mm in length and 10 mm wide. In general proportions this calcaneum resembles that found in *Varanosaurus*.

A set of metacarpals is found in block C. They probably belong to this genus. They are long slender structures, indicative of small size. The longest (probably the 4th) is 15 mm in length and the shortest one (1st) is 9.5 mm.

No other limb elements whose affinities with this genus are certain were found in the tree.

Discussion. On the basis of the material found in the four blocks of the tree, a partial reconstruction of the skeleton has been made (Fig. 2). *Archaeothyris* is a relatively small pelycosaur with a well-ossified skeleton. This degree of ossification and the nature of preservation suggests a terrestrial habitat. Members of the genus *Ophiacodon* are less well ossified and come from coal-swamp and deltaic deposits. It has been suggested by Romer and Price (1940) that *Ophiacodon* was an amphibious animal. The size of the skull and the nature of the teeth indicate that *Archaeothyris* had the capability to feed on larger invertebrates than did the romeriids, and it is also probable that it could have preyed on the smaller tetrapods.

Taxonomic position. On the basis of the known skeletal elements, *Archaeothyris* appears to be a very primitive pelycosaur, with characteristics that suggest a close relationship to the genus *Ophiacodon*. The similarities of *Archaeothyris* to the well known members of the Ophiacodontidae enable us to place this genus in the same family. It is sufficiently differentiated by certain primitive and specialized features, however, for it to be recognized as a distinct genus.

The following features in *Archaeothyris* are primitive: 1) The length of the pre-frontal and maxilla indicate that the skull is less elongated than in *Ophiacodon*. The lower edge of the maxilla is straight, as in all romeriid captorhinomorphs (in the more advanced pelycosaurs there is a tendency

towards a curved maxilla). 2) The type of buttressing above the canines in *Archaeothyris* is seen in some romeriids, but is also retained among spenacodonts. In later ophiacodonts, a more specialized type of buttressing is present. 3) The stapes is very similar to those seen in the romeriids *Paleothyris* and *Hylonomus* in the relative position of the dorsal process. In other pelycosaurs the articulating surface of the dorsal process is at 45 degrees to the articulating surface of the footplate, whereas in *Archaeothyris* and romeriids the angle between the two articulating surfaces is about 90 degrees. 4) The nature of the centra, inter-centra, transverse processes (with webbing), and high neural spines confirms the association of *Archaeothyris* to the most primitive members of the family Ophiacodontidae. The width of the neural spines (in mid-dorsals) is greater than in other ophiacodonts. Wide neural spines are directly associated with long centra, a very primitive feature in pelycosaurs. As in romeriids, the proximal caudal ribs are not fused in *Archaeothyris*; they are fused in later pelycosaurs. 5) The pelvic girdle is very similar to the type of pelvis seen in such primitive ophiacodonts as *Clepsydropus* and *Varanosaurus*. It has a pubic tubercle seen only in the most primitive ophiacodonts. 6) The humerus is like those of *Clepsydropus* and *Varanosaurus*, the most primitive ophiacodonts. *Ophiacodon* humeri tend to be more advanced in the size of their entepicondyle.

The following features in *Archaeothyris* are specialized: 1) The blade of the first sacral rib is not as wide as in the genus *Ophiacodon*. It is therefore suggested that the second sacral rib also came into contact with the iliac blade, whereas in *Ophiacodon* the second sacral rib only supports the first one. 2) The humerus has a very stout supinator process and a deep groove on the dorsal surface running from the entepicondylar foramen to the proximal head. 3) The canines on the maxilla are very well developed and there are only three precanine teeth.

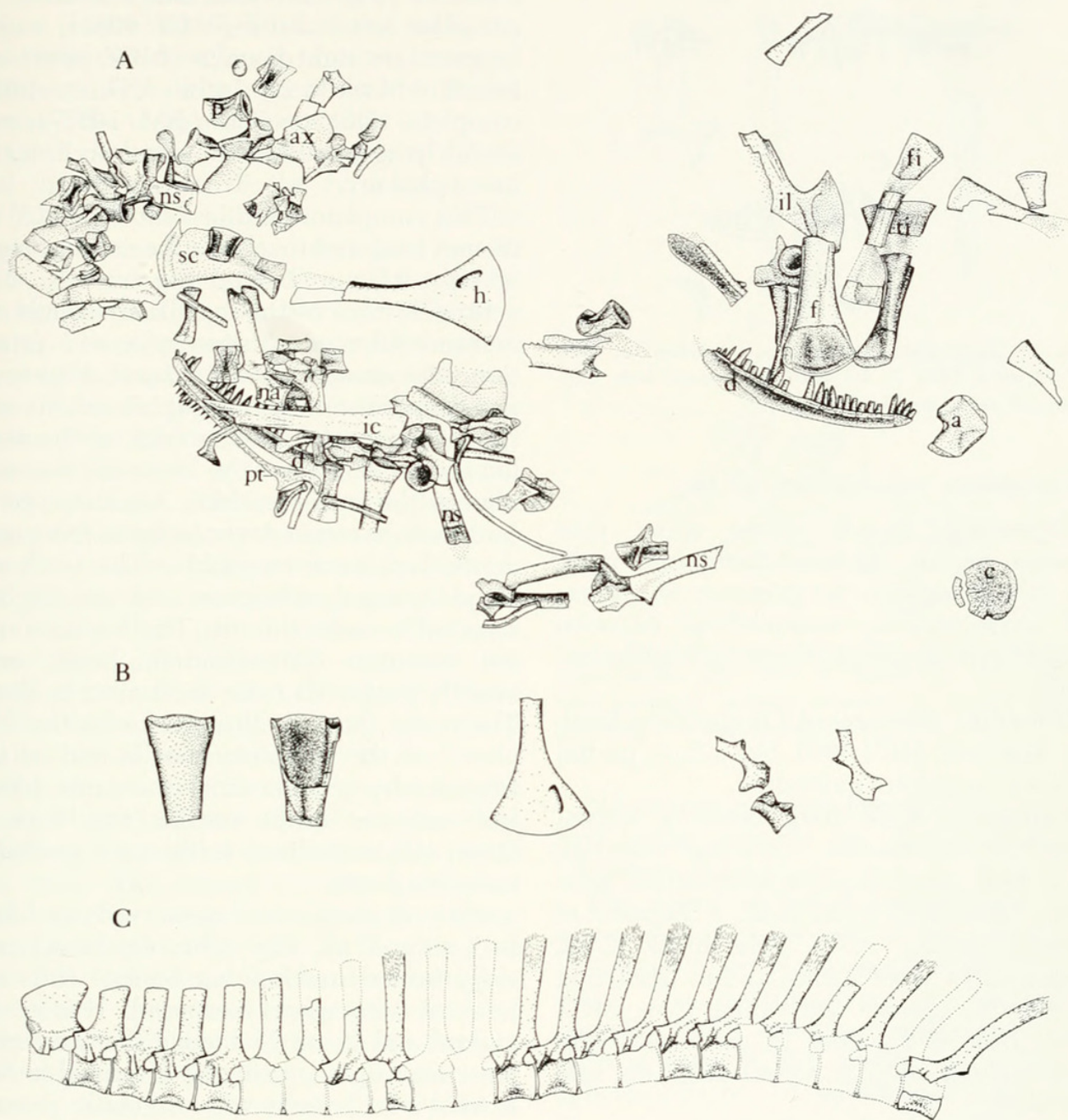


Figure 11. Type of *Echinerpeton intermedium*, MCZ 4090. A, partial skeleton; B, other skeletal elements belonging to the type specimen, dorsal and ventral view of femur, humerus, and two proximal caudal vertebrae; C, partial reconstruction. $\times 1$. Abbreviations used in the figure: a, astragalus; ax, axis neural arch; d, dentary; f, femur; fi, fibula; h, humerus; ic, interclavicle; il, ilium; na, neural arch; ns, neural spines; p, pleurocentrum; pt, pterygoid; sc, scapula; ti, tibia.

Genus *Echinerpeton* n. gen.

Type species. *Echinerpeton intermedium* new species.

Known distribution. Middle Pennsylvanian of eastern North America.

Diagnosis. Very small ophiacodont pel-

ycosaur, with very high neural spines. Ratio between height and width of mid-dorsal neural spine—7:1. Primitive axis vertebra. Neural arches not swollen. Webbing present on the transverse processes of the dorsal vertebrae. Primitive iliac blade.

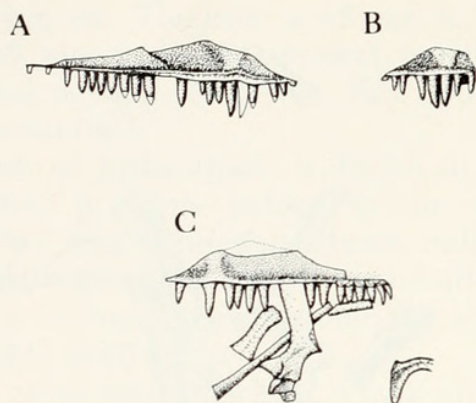


Figure 12. *Echinerpeton intermedium*. Maxillae: A, MCZ 4092; B, MCZ 4093; C, RM 10057 (also neural arch, fragmentary rib and phalanx). All $\times 1$.

Echinerpeton intermedium n. sp.

Etymology. Greek *echino*, spiny, plus *erpeton*, reptile. *Intermedium*, intermediate, in reference to the presence of numerous characteristics intermediate between those of typical ophiacodonts and sphenacodonts.

Holotype. Museum of Comparative Zoology, Harvard, MCZ 4090, block B.-1, partial skeleton, immature individual.

Paratypes. MCZ 4091, block A, almost complete interclavicle, vertebral material; MCZ 4092, block B.-22, a left maxilla, complete; MCZ 4093, block B.-22, a fragment of a right maxilla; MCZ 4094, block C.-12, fragments of three neural arches belonging to a more mature individual than MCZ 4090; RM 10057, block D, an almost complete right maxilla, a neural arch, rib, and a phalanx.

Horizon and locality. Morien Group, within 25 feet above the Lloyd Cove coal seam, equivalent to the late Westphalian D of Europe. Dominion Coal Co., strip mine No. 7, 2 miles north of Florence, Cape Breton County, Nova Scotia.

Diagnosis. Same as for genus.

Description. Much of the description is based on a single, somewhat scattered skeleton (MCZ 4090) (Fig. 11). Isolated material from five additional individuals can be questionably associated.

Skull. The only skull elements that can be associated with this genus are three

maxillae (Fig. 12) and two dentaries. A complete left maxilla (MCZ 4092), and a fragmentary right maxilla (MCZ 4093) are found in block B.-22. In block D, an almost complete right maxilla (RM 10057) was found lying close to the neural arch, a rib, and a phalanx.

The complete maxilla (block B.-22) is 28 mm long and reaches a maximum height of only 3.5 mm behind the canines. The ventral surface of the maxilla is straight, as in romeriid captorhinomorphs and primitive pelycosaurs (*Archaeothyris*, *Varanops*, and *Haptodus*). In most ophiacodonts and sphenacodonts, the lower edge of the maxilla is curved. Above the "canines" the maxilla, on the inside surface, has the type of buttressing seen in *Archaeothyris*, sphenacodonts, and some romeriids. The teeth are simple conical structures and are slightly serrated towards the tip. The "canines" are not strongly differentiated, being only slightly longer than the teeth next to them. There are three teeth anterior to the "canines" on the complete maxilla and on the fragmentary maxilla from the same block, but only one on the maxilla from block D. Here, the other two teeth were probably lost after death.

Both dentaries are preserved in block B.-1 (Fig. 11), the right one being partially buried under other bones, while the left one is completely exposed. It is gently curved and bears 23 teeth. The posterior-most margin is missing; it is probable that a total of 25 teeth was originally present on this element. The extent of the outside surface of the dentary indicates that the lower jaw was quite narrow. The teeth are implanted on a ridge that extends medially from the upper side of the dentary. The variation of tooth length in the dentary complements that of the maxilla. This type of variation in the tooth length is very similar to that seen in primitive romeriids. The anterior three teeth are not perpendicular to the upper edge of the dentary but point slightly forward. In some advanced pelycosaurs (*Sphenacodon ferocior*, *Dimetrodon milleri*, *Dimetrodon limbatus*), a simi-

lar situation exists but the anterior teeth are larger than those behind them, while in *Echinerpeton* these teeth are not strongly differentiated. At the posterior end of the dentary, the teeth are very small.

Axial skeleton. The incomplete nature and disarticulation of the type specimen, MCZ 4090, makes determination of the exact number of presacral vertebrae impossible. Partial reconstruction of the skeleton has been attempted, however (Fig. 11). On the basis of this reconstruction there must have been at least 23 presacral vertebrae. Since the typical number of presacrals in the great majority of pelycosaurs is 27, it is probable that at least four are missing in this specimen. The vertebrae in the anterior portion of the column are found in close association with each other but are not articulated, and the centra have separated from their neural arches. The mid-dorsal and anterior dorsal vertebrae are found scattered all over the block. There is also some vertebral material of a very similar nature in blocks C and D.

The centra are not elongated. In the cervical and anterior dorsal regions they are 5 mm long and 4 mm high at the posterior rim. The centra in the mid-dorsal and posterior dorsal vertebrae are about equal in length and height. In the primitive romeriid *Hylonomus* and in *Archaeothyris*, the centra are more elongated. In later ophiacodonts, however, the centra tend to be compressed; this shortening of the centrum is most strongly marked in *Ophiacodon retroversus*. The keel development, more prominent in the anterior region of the column, never reaches the levels found in advanced sphenacodonts in which prominent ventral keels are present and the centra have strongly excavated lateral margins.

In *Echinerpeton* the ventral lip of the centra is not strongly bevelled for the reception of the intercentra, indicating that there were wide intercentral spaces. Dorsally, the wedges into which the neural arch pedicels fit are conspicuous and extend along two-thirds of the length of the centrum.

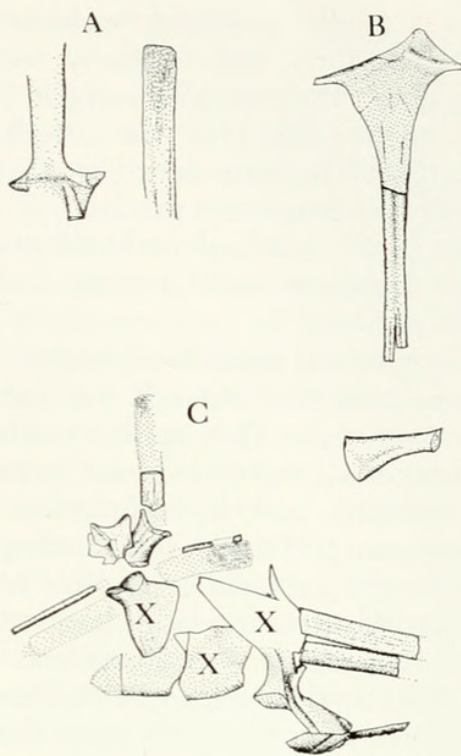


Figure 13. *Echinerpeton intermedium*. A, two fragmentary neural arches, MCZ 4094; B, interclavicle, MCZ 4091; C, three presacral vertebral elements; X, skeletal elements belonging to a small romeriid, MCZ 4091. All $\times 1$.

No intercentra were found in the deposits that could possibly be identified as belonging to this genus.

The neural arches do not show the type of excavation at the base of the spines seen in the more advanced sphenacodonts (Fig. 13). The zygapophyses do not have strongly tilted articular surfaces, nor are they as close to the midline as in typical sphenacodonts. In mid-dorsals, the angle of the zygapophyses is estimated to be about 35 degrees. In most ophiacodonts the angle is approximately 30 degrees, while in most sphenacodonts it is about 45 degrees.

The transverse processes are relatively high on the anterior portion of the neural arch. In the cervicals they tend to point strongly downward, so that they appear as lateral bulges on the neural arch. From the anterior dorsal region to the 23rd presacral, all the transverse processes extend far laterally, and tip gently downward. Their tubercular facets are shaped in a fashion similar to that seen in ophiacodonts,

showing a small amount of "webbing" that extends anteriorly and ventrally from the main head of the articular surface. In the caudal region (Fig. 11), the articular surface for the rib is on the centrum; the neural arch bears no transverse process.

There is no vertebral material from the posterior trunk or sacral regions and little from the caudal.

The axis neural spine is a strongly developed structure that extends far anteriorly and posteriorly. The spine reaches its highest point at its posterior end, as in many sphenacodonts, and it is broadest along its dorsal margin, as in ophiacodonts and some romeriid captorhinomorphs. In sphenacodonts the greatest lateral expansion is reached well before the dorsal end of the spine. The condition seen in *Echinerpeton* is probably more primitive than that seen in pelycosaurs in general.

The most striking feature in this animal is the length of the neural spines in the trunk region. Along the known parts of the column they vary considerably, and reach proportions comparable to those seen in *Sphenacodon*. The neural spines reach their greatest length around the 15th presacral vertebra, at which point they also increase in width towards the top.

The dorsal portion of the neural spine is very thin in cross section and is strongly fluted. The spines do not have a definite dorsal ending but become so thin at the top that it becomes difficult to establish whether they are broken or not. A neural spine from block C (Fig. 13) is larger than the ones in block B; here the dorsal tip of this spine ends definitely, indicating a higher level of ossification. This spine also becomes very thin towards the tip, however. On the basis of the relatively smaller size and lower degree of ossification, it is probable that the animal in block B.-1 is an immature individual. It is, therefore, expected that in mature individuals the neural spines of the dorsals would be even taller than those seen in the type specimen.

As shown by the anterior caudals found in block B.-1 (MCZ 4090), the neural spines

in the caudal region lose height quite rapidly. The spines of the two vertebrae are already short and lateral, and transverse spread has also decreased markedly.

Numerous ribs are found scattered in block B.-1 (Fig. 11), and a fragment of a rib is found in block D (Fig. 12). The tubercular and capitular heads are connected by a thin sheet of bone that corresponds to the webbing seen on the transverse processes. This type of webbing is seen only in ophiacodonts and never in Permian sphenacodonts. In typical ophiacodonts the mid-dorsal ribs have extensive webbing. In this animal the webbing is not strongly developed because the ventral edge of the rib comes close to the centrum and only then turns down towards the intercentrum. The capitulum extends far ventrally to reach the small intercentrum. A complete mid-dorsal rib, found in block B.-1, indicates that the body of the animal was high and narrow.

Appendicular skeleton. Of the shoulder girdle, only the interclavicle and the scapula are known. The head of the interclavicle from block A (Fig. 13) is 15 mm wide; the shaft is 30 mm long and its width varies greatly along its length. These general proportions fit well with those found in pelycosaurs in general. Romeriids have relatively wider heads. Anteriorly, the shaft is 9 mm in width but diminishes gradually to 2.5 mm midway in its length. It is two-pronged at the end. In ophiacodonts, the shaft does not vary so greatly in width; in sphenacodonts, the shaft is somewhat similar to that of *Echinerpeton*, but there is no definite point where the head ends and the shaft begins. A fragmentary scapula is found in block B.-1 (Fig. 11). Exposed in medial view, the width of the blade at the dorsal end is 9 mm and the dorsoventral height of the bone is 16 mm. These proportions are intermediate between those of typical ophiacodonts and sphenacodonts.

The distal part of both humeri are present in the type specimen (Fig. 11). The fragment of the right humerus is 26 mm long, while the left one is 16 mm long. The

distal ends of both humeri are 12 mm wide. The bones are weakly ossified and almost featureless, as are the humeri of the immature sphenacodont *Haptodus* (Gaudry, 1886). The distal head is essentially a triangular structure with an arc for the base. The typical pelycosaurian structures present on more mature humeri are not visible here. There is no ectepicondyle or supinator process and the entepicondyle does not have the shape comparable to that in mature pelycosaurs. Only a very simple entepicondylar foramen is present, its lower margin being only 2 mm from the end of the bone. The shaft is long, slender, and almost round in section. The part of the proximal head visible on the right humerus indicates that the bone was strongly twisted. It is estimated that the complete humerus in the type specimen was 28 mm in length.

Of the pelvic girdle only the ilium is present (Fig. 11). It is very primitive. The iliac blade is narrow and points posteriorly, as in ophiacodonts and romeriids in general. In sphenacodonts the blade is strongly expanded anteriorly to receive the three sacral ribs. The area that might have shown a trough for the dorsal musculature is not preserved.

The heads of both femora are present in the type specimen (Fig. 11). These fragments are about the same size and are immature and primitive. A simple adductor crest is present on the shaft. The tibia, lying close to the fibula and the femur, is not complete, but shows that it has a broad proximal end (9 mm wide), a narrow shaft, and a relatively small distal end (4 mm wide). The bone is 20 mm long. The fibula is also incomplete, but shows the same elongation as the tibia and has well-developed distal and proximal heads. The astragalus is an essentially L-shaped structure as in typical ophiacodonts. The surface of the astragalus that connects to the calcaneum shows the beginnings of a foramen towards its distal end. The calcaneum, also found in the type specimen, is poorly ossified. It is an almost round disc, but shows the corresponding margin of the foramen

on its connecting surface with the astragalus.

Four of the metatarsals are also found in block B.-1. They are long elements when compared to the rest of the skeleton, but this is typical of small primitive reptiles. In romeriids of similar size, the hands and feet are large and the metatarsals as well as the phalanges tend to be elongate.

Some other distal limb elements are also found in block B.-1 and in other blocks. The association of these elements with the genus *Echinerpeton* is not certain, however.

Discussion. On the basis of the immature type specimen (MCZ 4090), a partial reconstruction has been made (Fig. 11). This reconstruction shows that *Echinerpeton* is a small reptile with very high neural spines. The more mature specimens are up to 50 percent bigger than the type. From the dentition and size, it is probable that *Echinerpeton* (at least in its immature state) fed on small invertebrates, such as the millipedes found in the same tree.

The affinities of this pelycosaur are harder to establish than those of the ophiacodont pelycosaur described above. This is because the most complete specimen is very immature, many of the most diagnostic portions of the skeleton are not known, and because the animal is so primitive that it is difficult to establish which features are simply primitive and which can be used to establish its affinities.

The following features in *Echinerpeton* indicate its primitive nature: 1) The lower edge of the maxilla is straight, as in *Archaeothyris*, *Haptodus*, and *Varanops*. The buttressing above the canines is similar to that seen in *Archaeothyris* and some romeriids (in sphenacodonts this primitive feature is retained). The teeth are simple conical structures, canines are not very strongly differentiated (spenacodonts have greatly differentiated canines). 2) The centra are simple structures; the bevelling for receiving the intercentra is not strongly developed. 3) The transverse processes on the cervical vertebrae are similar to those seen in some romeriid captorhinomorphs. 4) The

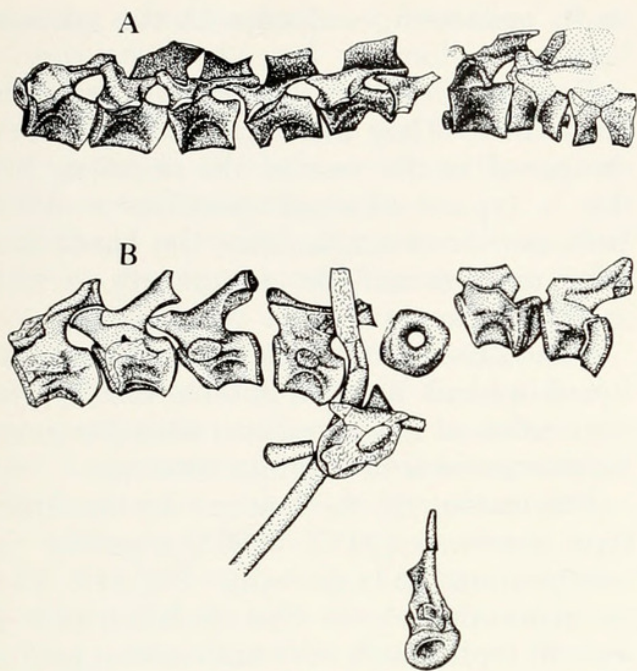


Figure 14. Unnamed pelycosaurs. A, 9 presacral vertebrae, MCZ 4088; B, 9 proximal caudal vertebrae, fragmentary rib and phalanx, MCZ 4095. All $\times 1$.

iliac blade is extremely primitive in nature, rather similar to those found in romeriids. It is probable that there were only two sacral ribs, as in some romeriids and all ophiacodonts.

The following features of *Echinerpeton* show its affinities to ophiacodonts: 1) In the trunk region the transverse processes have the type of webbing seen only in ophiacodonts. The neural spines do not have the type of excavation at the base as that seen in sphenacodonts. 2) The centra are slightly compressed anteroposteriorly, a tendency followed in ophiacodonts. 3) The zygapophyses are only moderately tilted. 4) The astragalus and calcaneum are similar to those seen in primitive ophiacodonts.

The following features in *Echinerpeton* suggest affinities with sphenacodonts: 1) The neural spines are very high, narrow, bladelike structures. Similarly high neural spines are found in some primitive sphenacodonts, e.g., *Sphenacodon*. There is, however, no reason to believe that only sphenacodonts and edaphosaurs developed high neural spines. 2) The nature of the axis neural spine is somewhat similar to that in

sphenacodonts in that its highest point is reached at its posterior end. On the other hand, the spine is similar to those in ophiacodonts in that it is broadest along its dorsal margin.

This particular pelycosaur shows the close relationship between primitive ophiacodonts and sphenacodonts. There is actually little in the features of this animal that prevents it from being close to the ancestry of sphenacodonts.

OTHER PELYCOSAURIAN MATERIAL FROM FLORENCE, NOVA SCOTIA

Other material, of a generally pelycosaurian nature, is present in tree No. 3, but cannot be associated with the previous two genera. These specimens are too incomplete to be given generic names. They are worth describing, however, because they show the extent of radiation pelycosaurs had undergone by the Middle Pennsylvanian.

I. An articulated series of nine anterior dorsal vertebrae, including three intercentra (Fig. 14), is preserved in block B (MCZ 4088). The centra are about 6 mm long on their ventral side and 5 mm high at the posterior rim. They are strongly keeled. The ventral region of the keel is very thin in cross section, although still rounded at the margin. In comparably developed sphenacodonts, the keel has a sharp ventral margin. In side view, the ventral margin of the keel shows little concavity, whereas in other pelycosaurs the concavity tends to be greater. The centrum is strongly concave in cross section, a feature seen only in strongly keeled forms. Here we have a very specialized type of ventral strengthening of the centrum. It is questionable whether the nature of the ventral ridge is diagnostic in such early forms as described in this paper. The use of this particular feature (see Romer and Price, 1940: Fig. 17) in separating the three pelycosaur suborders is justifiable only when these three major lineages have become fully differentiated in the Lower Permian.

The ends of the centra are formed in such a manner that there are large intercentral spaces ventrally. Dorsally the anterior and posterior ends of the centra touch. This type of bevelling for the intercentra is probably very primitive, and is seen in some very primitive romeriids (Carroll, 1970: fig. 8f). The intercentra are well developed, but do not show the lateral facets where the capitulum would be expected to articulate. The nature of the intercentral spaces suggests that the intercentra had cartilaginous dorsal extensions.

The transverse processes have the type of webbing seen in typical ophiacodonts; however, it does not extend as far ventrally as in other members of the family. Dorsally, the articulating surface of the transverse process is not as rounded in section as in other ophiacodonts. The zygapophyses, which extend far beyond the anterior and posterior margins of the centrum, are moderately tilted. The angle of this tilt is estimated to be more than 35 degrees, a condition seen in spenacodonts. The zygapophyses are close to the midline. The neural spines are different from the type usually seen in pelycosaurs. They are only 5 mm high, yet are extremely wide. At the base they are 6.5 mm wide; dorsally they constrict to 5.5 mm and then expand again to become as wide at the top as they are at the base.

Although the specimen shows some primitive as well as ophiacodont and spenacodont characters, the determination of its exact taxonomic position among pelycosaurs has to await the discovery of more complete specimens.

II. Eight caudal vertebrae (Fig. 14) are found in block B (MCZ 4095). The centra are massive structures solidly fused to the neural arches. The anterior and posterior articulating surfaces of the centra are strongly developed and on the ventral region there is marked bevelling to accommodate the intercentra.

The neural arches are not swollen, but are stoutly built. The transverse processes are broken off on the first two vertebrae, but

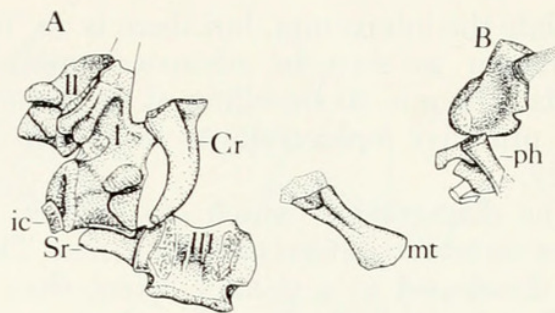


Figure 15. Unnamed spenacodont pelycosaur. A, three sacral vertebrae and a caudal rib, MCZ 4096; B, astragalus and other distal limb elements, MCZ 4097. $\times 1$. Abbreviations used in the figure: ic, intercentrum; mt, metatarsal; ph, phalanx; Cr, caudal rib; Sr, sacral rib; I—1st sacral vertebra, II—2nd sacral vertebra, III—3rd sacral vertebra.

the broken surfaces indicate that both the capitular and tubercular heads of the ribs were attached to the centrum. The transverse process on the 3rd vertebra is intact, but has only one articulating surface—the diapophysis. This articulating surface indicates that the caudal ribs are not fused to the transverse process. The articulating surfaces are smaller on the 4th and 5th vertebrae and are completely lost by the 6th.

Here there is only a very slight swelling where the transverse process would have been.

The anterior and posterior zygapophyses extend far beyond the rims of the centra. The angle between the articulating surface of the zygapophyses is slight—about 30 degrees (in ophiacodonts the tilt in the caudal region is greater). The neural spines are very small and occupy the extreme posterior region of the neural arch. The spine in the isolated caudal is 5 mm long and only 1 mm in diameter. The affinities of this string of caudals are difficult to assess.

III. Three closely associated sacral vertebrae and a caudal rib are found in block C (MCZ 4096) (Fig. 15). Among pelycosaurs, only advanced spenacodonts have three sacrals. They are stoutly built and have different proportions than the vertebrae in *Archaeothyris*. The centra are 8 mm long and 8 mm high at the posterior rim. There is no keel. In the ventral region of the central rims there is bevelling to accom-

modate the intercentra, but there is no "lip" formation as seen in advanced ophiacodonts. There is no bevelling of this type in the primitive ophiacodonts from this locality.

The diapophyses, which are huge in all three vertebrae, extend onto the centra. They are developed to a greater extent than in *Archaeothyris*, being 5 mm long and up to 3 mm in height. There are slight differences in the shape of these articulating surfaces from centrum to centrum. The presence of these surfaces indicates that the ribs did not fuse to the transverse process, as is the case in advanced spenacodonts. The parapophyses are located on the centrum directly underneath the diapophyses. They are essentially triangular in shape and are separated from the diapophyses by a small groove. The parapophysis on the 3rd sacral is not as strongly developed as in the 1st and 2nd ones; it is only 2 mm long and 3 mm tall. The parapophyses on the other sacrals are 4 mm long and 5 mm tall. They are all located close to the anterior rim of the centrum.

The neural arches on the 2nd and 3rd sacral vertebrae are broken off, but there is an almost complete neural arch on the first sacral. It is typically spenacodont in nature, being strongly excavated above the transverse process. The zygapophyses are well developed, but only the anterior ones extend well beyond the anterior margin of the centrum. The posterior ones extend only to the level of the central rim, as in *Dimetrodon* (Romer and Price, 1940, plate 25). In *Ophiacodon*, the anterior and posterior zygapophyses extend well beyond the respective central rims (Romer and Price, 1940, text-fig. 45). The articulating surfaces of the zygapophyses are strongly tilted (40 degrees) and are close to the midline. The angle of this tilt is close to that seen in the sacral region of *Dimetrodon limbatus*. Although the top of the neural spine is missing, it can be seen that the spine is not bladelike in nature as in ophiacodonts, but diminishes in width towards the top.

The 3rd sacral vertebra has preserved in position its left rib, which is only 8 mm long. The body of the rib is bladelike in nature and is slightly cupped on the dorsal surface. The distal end of the rib has an unfinished area 5 mm long and 1.5 mm wide that probably provided attachment to the 2nd sacral rib. The manner of attachment is similar to that of the two sacral ribs in *Ophiacodon retroversus* (Romer and Price, 1940, text-fig. 45). This type of attachment is more primitive than the one seen in *Dimetrodon*, where all three ribs make contact with the iliac blade. In the specimen under discussion, the third rib does not make contact with the iliac blade; it only supports the other two sacral ribs.

The caudal rib lying close to the three vertebrae is short and curves posteriorly, as in all pelycosaurs. The presence of articulating surfaces on the tuberculum and capitulum indicates that this rib was not fused to the transverse process.

The structural differences between these sacrals and the vertebrae of *Echinerpeton* are too great for them to belong to a mature specimen of that genus.

There is in block C an astragalus (MCZ 4097) that also may be a spenacodont. It is fairly well ossified, 10 mm long and 8 mm wide at the distal end. In spite of this great distal width, the astragalus is not L-shaped as in ophiacodonts and in *Varanops*. It is somewhat intermediate between the condition in the above genera and the condition in *Dimetrodon* (Romer and Price, 1940, text-fig. 41).

Protoclepsydrops haplous

A possible pelycosaur from the Westphalian B of Joggins, Nova Scotia, has been described by Carroll (1964: 79–82). *Protoclepsydrops* (Fig. 16) was assigned to the Order Pelycosauria on the basis of the configuration of the humerus. The other skeletal elements in the type, RM 3166, were not particularly indicative of pelycosaurian affinities. They are extremely small, poorly defined, and badly preserved. The humerus

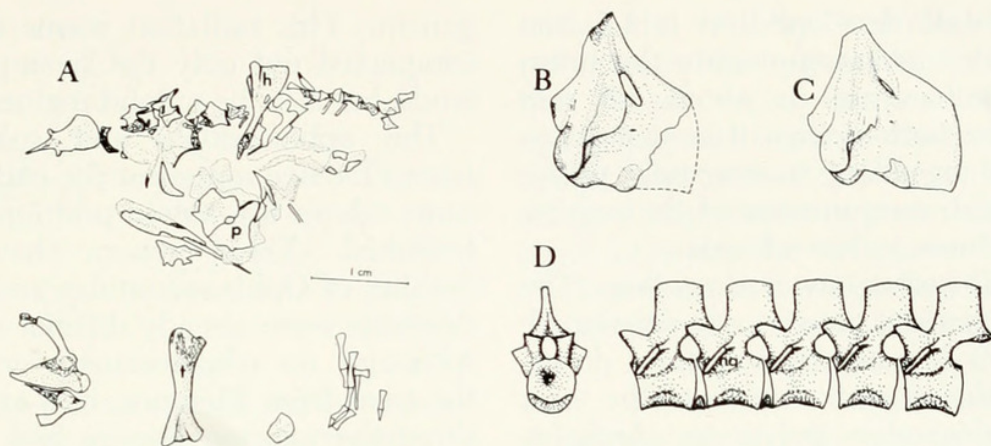


Figure 16. *Protoclepsydropus haplous*. A, type specimen, RM 3166 (Carroll, 1964; text-fig. 13). B, distal end of the humerus, DMSW B.239; C, distal end of humerus, BM(NH) R.5778 (Carroll, 1964; text-fig. 14); D, anterior and lateral view of presacral vertebrae, RM 12202. All $\times 1$. Abbreviations used in the figure: h, humerus; f, femur; na, neural arch; p, parietal.

in the type specimen has a prominent supinator process, distinguishing it from most captorhinomorph humeri. Two other humeri with supinator processes were associated with the genus, although they were of much larger size. Subsequently, a romeriid captorhinomorph, *Paleothyris*, from the Westphalian D of Florence, Nova Scotia, was described by Carroll (1969) as having a well developed supinator process, and the humerus as a whole was very similar to that in the immature type specimen of *Protoclepsydropus*. The supinator process in *Paleothyris* and in the type specimen of *Protoclepsydropus* is located very close to the distal articulating surface of the humerus, whereas in all well known pelycosaurs the supinator process is located much higher up the distal head of the humerus, close to the level of the entepicondylar foramen. Considered by itself, there is little to justify the inclusion of the type specimen of *Protoclepsydropus haplous* in the Order Pelycosauria.

The two larger humeri designated as paratypes of *Protoclepsydropus haplous* are more pelycosaurian in nature. They are very similar to the humerus in *Archaeothyris* in the nature and relationship of the entepicondyle and ectepicondyle. More significantly, the supinator process on the humerus of DMSW B.239 is stoutly built and

is in a position comparable to that in *Archaeothyris*. On the other hand, the supinator process of the humerus of BM(NH) R.5778 is in an intermediate position between that seen in the type specimen of *Protoclepsydropus* and that seen in *Archaeothyris*. This humerus is considered less mature than DMSW B.239 because the entepicondylar foramen is smaller and the supinator process is not as stout. It is highly probable that these three specimens represent growth stages in a single species.

In the Redpath Museum collection there are six anterior trunk vertebrae (RM 12202) whose size fits well with that of the large humeri of *Protoclepsydropus haplous*. They (Fig. 16) are well ossified, with the centra and neural arches fused, but with the line of attachment indicated by a rugose ridge running below the transverse process. In the more advanced pelycosaurs and in most romeriids, the anterior and posterior articulating rims of the vertebrae are part of the centrum. In these vertebrae, however, as in *Archaeothyris*, the upper region of the anterior rim is part of the neural arch. Such a condition is apparently very primitive, reflecting the condition noted in *Gephyrostegus* (Carroll, 1970).

The centra are 5 mm long in the ventral region and 4 mm high at the posterior rim. There is no keel. The only known inter-

centrum is well developed; it is 1.5 mm long. In order to accommodate the inter-centrum, the centrum is about 1.5 mm shorter at the bottom than it is at the top. This type of bevelling is extremely primitive, but is also seen in some of the pelycosaurs from Florence, Nova Scotia.

The neural arches are not swollen. The transverse processes are strongly developed, extending far laterally and slightly downward as in the anterior dorsals of the most primitive ophiacodont pelycosaur *Archaeothyris*. The articulating surface of the transverse process is straight and extends antero-ventrally. The width of the articulating surface remains constant, forming a long, fairly thin facet for the articulation with the tuberculum of the rib. This type of articulating surface is directly antecedent to the type seen in the primitive ophiacodonts.

The zygapophyses extend beyond the lateral limits of the centrum and the surfaces are tilted at only about 20 degrees (this angle is less than in any other primitive pelycosaur). The neural spine is well developed; it is 5.5 mm tall and 4.5 mm wide at the base. This width in relation to the length of the centrum is comparable to that seen in *Archaeothyris*; in romeriids the spines tend not to be so wide.

The extremely primitive nature of *Proto-clepsydropus haplous* prevents the determination of its exact taxonomic position within the Pelycosauria. The nature of the humerus and of the transverse processes on the newly described vertebrae indicates possible association of this genus with the Suborder Ophiacodontia (see Fig. 17).

INTERRELATIONSHIPS OF PRIMITIVE PELYCOSAURIA

The discovery of this new material requires reconsideration of interrelationships of primitive pelycosaurs. The pelycosaurs found in the early to middle Pennsylvanian deposits of Joggins and Florence, Nova Scotia, confirm the idea that there was extensive radiation of this order long before the appearance of the well-known Autunian

genera. This radiation seems to have encompassed not only the swamps and lowlands, but also the upland regions.

The ophiacodonts and sphenacodonts from Florence represent the earliest pelycosaurs whose taxonomic position can be established. These genera show that the families of Ophiacodontidae and Sphenacodontidae were already distinct at this time. Although no edaphosaurs were found in the trees from Florence, it is expected that this pelycosaurian lineage had also differentiated by the middle Pennsylvanian. The genus *Archaeothyris* is a fairly typical member of the family Ophiacodontidae. There are actually no features in this genus that would prevent it from giving rise to the genus *Ophiacodon*. Although it is the most primitive member of the Ophiacodontidae, it is already too specialized to have been ancestral to any of the other pelycosaurian lineages present in the Lower Permian. Labeling of the Suborder Ophiacodontia as "primitive" is unacceptable in light of the specialized characteristics seen in all known genera. The configuration of the atlas-axis complex and the nature of the transverse processes prevent even its earliest known members from being ancestral to the sphenacodonts or the edaphosaurs. The type of diapophyses seen in ophiacodonts, sphenacodonts, and edaphosaurs can be derived from the type seen in primitive romeriids (see Fig. 17). The type of diapophyses in sphenacodonts and edaphosaurs cannot, however, be easily derived from those seen in even the earliest ophiacodont.

The specialized nature of these structures in the earliest known ophiacodonts raises the possibility of separate derivation of the major lineages of pelycosaurs from the romeriids. The question is whether only a single romeriid species that had developed a temporal opening gave rise to all pelycosaurs, or whether the different lineages of pelycosaurs developed from different romeriid species. The second alternative implies that the pelycosaurian temporal opening developed several times. Although the conservative nature of the temporal opening

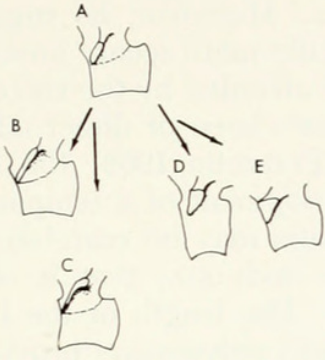


Figure 17. Evolution of the transverse processes in pelycosaurs. A, the primitive romeriid pattern, based on MB 1901.1379 (Carroll, 1970; Text-fig. 8); B, *Protoclepsydraps haplous*, RM 12202; C, pattern seen in ophiacodonts, based on *Archaeothyris florensis*, MCZ 4079; D, the sphenacodont pattern, based on MCZ 1347 (Romer and Price, 1940, plates 24 E); E, the edaphosaur pattern, based on MCZ 1531 (Romer and Price, 1940, plate 36C).

in all pelycosaurs suggests that it was developed only once, it will require a considerable increase in the knowledge of Pennsylvanian pelycosaurs to confirm or deny the monophyly of the group. In any case, the possibility of polyphyly of the Pelycosauria within the Romeriidae does not pose any significant phylogenetic problem, because the possible ancestors were closely related and formed only a single adaptive assemblage. Comparison of early ophiacodonts and sphenacodonts shows great similarities between the two groups. *Echinerpeton* is somewhat intermediate between the two suborders.

The usually accepted taxonomic position of the genus *Varanosaurus* may be questioned on the basis of its vertebral structure. Romer and Price (1940: 216–222) suggested that *Varanosaurus* is a very primitive ophiacodont pelycosaur. The type of neural arch seen in this genus, however, is not present in any other pelycosaur or any romeriid. This suggests that *Varanosaurus* is not primitive but specialized. There is considerable increase in size from early romeriids. *Varanosaurus* solved the problems involved in strengthening the vertebral column to support more weight in a different way from other pelycosaurs, and also developed a different type of movement

within the vertebral column. In all other pelycosaurs the zygapophyses are tilted so that forces acting perpendicular to the zygopophyseal surfaces meet in the neural spine. The neural spines are strongly developed to provide support. Limited movement between the vertebrae can occur in all directions. In *Varanosaurus*, however, the zygapophyses are not tilted, and the forces acting on these surfaces are oriented vertically. Therefore, a large amount of bone is necessary directly above the zygapophyses in order to resist this force. The extra amount of bone gives the swollen appearance to the neural arches. The angle of the zygapophyseal surfaces in *Varanosaurus* greatly limits the axial rotation of the vertebral column, but enhances the amount of lateral undulatory movement.

The configuration of the vertebrae indicates that *Varanosaurus* must have separated very early from the main line of pelycosaurian evolution. The type of neural arch seen in *Varanosaurus* also developed independently in the Lower Permian captorhinids, limnoscelids, diadectids, and Seymouriamorphs in response to increase in size.

THE ORIGIN OF PELYCOSAURS

On the basis of the known Lower Permian pelycosaurs and cotylosaurs, Romer and Price (1940: 178) supported Watson's suggestion that the captorhinomorphs were ancestral to the pelycosaurs. They noticed the great similarities between pelycosaurs and two small romeriid captorhinomorphs, *Romeria* and *Protorothyris* (Price, 1937). On the basis of our present knowledge of the early romeriids and of the Westphalian pelycosaurs described in this paper, a more exact relationship between these two groups can be established.

The family Romeriidae, thought to be ancestral to most, if not all, advanced reptilian groups, is represented in the Pennsylvanian by the following genera: *Hylonomus* and *Archerpeton* (Carroll, 1964), from the Westphalian B of Joggins, Nova Scotia;

Cephalerpeton (Gregory, 1950), from the Westphalian C of Mazon Creek, Illinois; *Paleothyris* (Carroll, 1969), from the Westphalian D of Florence, Nova Scotia; and three others of about the same age, from Nýřany, Czechoslovakia, and Linton, Ohio (Carroll, 1972). The morphological differences between Pennsylvanian romeriids are slight. They are all small, well-ossified reptiles with similar body proportions and dental patterns. These features suggest that they all fed on small invertebrates and were terrestrial in habit.

Although the pelycosaurs are thought to have arisen well before the formation of the Joggins deposits (probably in pre-Westphalian time), it is worth while to compare the earliest romeriid, *Hylonomus*, with the earliest known ophiacodont pelycosaur, *Archaeothyris*. The morphological similarities between these genera are so great that their common ancestry among earlier romeriids is unquestionable. The suggestion that pelycosaurs evolved from anthracosaurs, independent of captorhinomorphs (Hotton, 1970), is not supported by the evidence.

The differences between the earliest romeriids and the primitive pelycosaurs are related to the development of the temporal opening and the subsequent pelycosaurian radiation into different adaptive zones. The classical explanation for fenestration offered by Gregory and Adams (1915) and Case (1924) is based on the premise that open spaces in the skull permit bulging of the closing jaw musculature. This explanation did not, however, take into consideration the adaptive value of fenestration before it reached the size to function in this manner. In a more comprehensive study of the problems involved in fenestration, Frazzetta (1968) proposed that thickened and thinned areas of the skull were produced by the patterns of muscular stress. Selection may have achieved areas of stress sufficiently reduced at the junction of the bones of the cheek region that these elements failed to meet, thus giving rise to the initial stage of

fenestration. Moreover, he suggested that the potentially more secure areas of muscle attachment afforded by the rim of an opening may have been of direct adaptive significance (Frazzetta, 1968: 156).

The development of a temporal opening in pelycosaurs may be correlated with the increase in body size that is observed in this group. The length of the humerus in romeriids and pelycosaurs provides a good indication of the size of the respective genera (Fig. 18). Pelycosaurs between the Westphalian B and the Upper Stephanian show exponential increase in size.

Romeriids, however, retain essentially the same body size from the Lower Pennsylvanian into the Lower Permian.

The following changes are observed as pelycosaurs increase in size:

1. There is considerable change in the skull to trunk ratio. As primitive pelycosaurs increase in snout-vent length from 20 to 120 cm, the skull to trunk ratio increases from 34 to 64 percent (Fig. 19). The increase in the ratio of skull to trunk length with greater size is related to the fact that the body volume increases in proportion to the third power of linear dimensions, whereas the mouth area increases only to the square. The jaw mechanics and method of feeding are apparently very similar in primitive pelycosaurs and their direct ancestors, the romeriids. With increase in body bulk, a proportionately greater area of jaw surface is necessary in order that the larger animal may obtain an equivalent amount of food. In specialized sphenacodonts and edaphosaurs the mechanism of feeding is so different from that seen in primitive pelycosaurs and romeriids that the criteria used in comparing the earlier forms do not apply.

2. In order to have a greater area of jaw surface, the skull of pelycosaurs not only becomes larger, but the antorbital region of the skull becomes relatively longer. In romeriids, the antorbital region is about equal in length to the postorbital. In *Archaeothyris*, on the other hand, the ratio be-

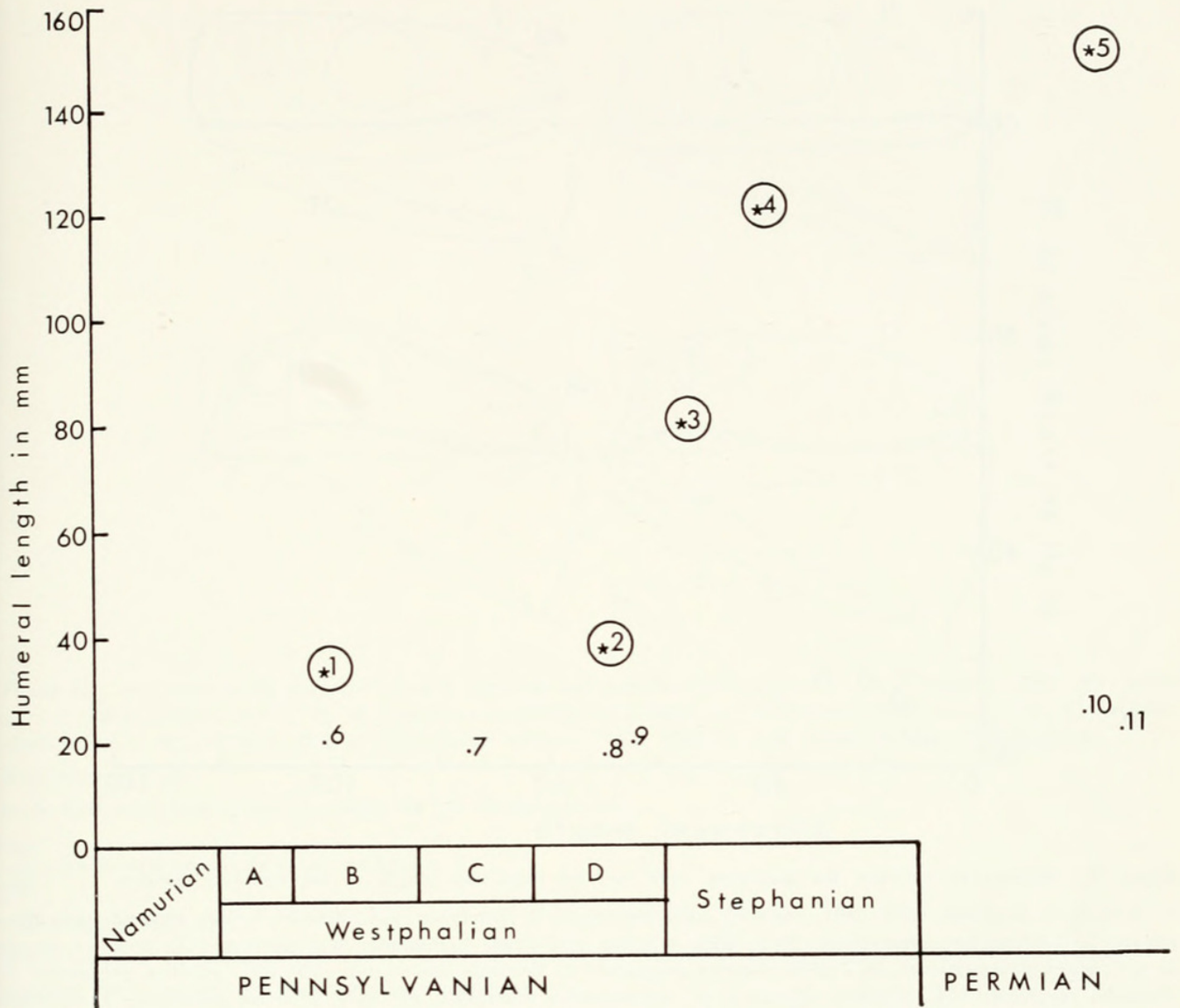


Figure 18. Relationship between humeral length and relative age of the following genera:

1. *Protoclepsydraps haplous*, DMS W.B. 239, pelycosaur; 2. *Archaeothyris florensis*, MCZ 4079, pelycosaur; 3. *Clepsydraps colletti*, WM 6542, pelycosaur (Romer & Price, 1940, Table 4); 4. *Clepsydraps magnus*, CM 13942, pelycosaur (Romer, 1961); 5. *Ophiacodon retroversus*, MCZ 1426, pelycosaur (Romer & Price, 1940, Table 4); 6. *Hylonomus lyelli*, RM 21126, romeriid (Carroll, 1964); 7. *Cephalerpeton ventriarmatum*, VPM 796, romeriid; 8. *Paleothyris acadiana*, MCZ 3482, romeriid; 9. "Gephyrostegus bohemicus," ČGH III B21.C.587, romeriid; 10. Undescribed, MCZ 1474, advanced romeriid; 11. Undescribed, MCZ 1478, advanced romeriid.

tween the two regions is about 2:1; in larger Permian ophiacodonts the ratio is even greater. In *Ophiacodon mirus* and *Ophiacodon uniformis* the ratio is 3.5:1.

3. The jaws in romeriids and pelycosaurs function as simple levers. The fulcrum of the lever is at the point of articulation of the lower jaw with the quadrate. The force is supplied by muscles that are limited to the postorbital region in general and the subtemporal fossae in particular.

These muscles work at a mechanical disadvantage; the greatest amount of force is applied at the point of articulation between the jaws rather than at the teeth. In pelycosaurs, the mechanical disadvantage of the jaw-lever system is even greater than in the romeriids because the muscles are closer to the fulcrum (Fig. 20). This means that greater power has to be applied by the jaw muscles of pelycosaurs than of romeriids in order to provide the same amount of force

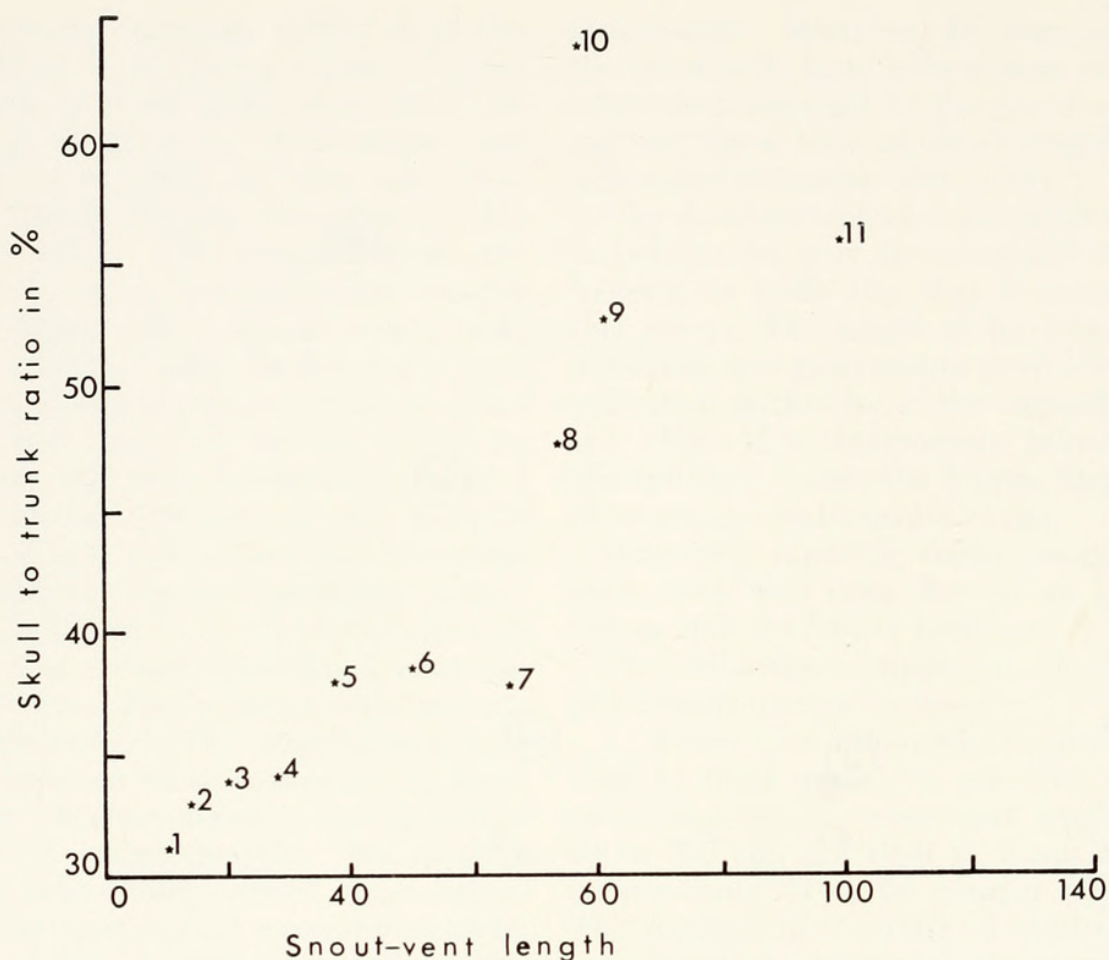


Figure 19. Relationship between the skull-trunk ratio and the snout-vent length in the following genera:

1. *Paleothyris acadiana*, MCZ 3481, romeriid captorhinomorph; 2. *Hylonomus lyelli*, BM(NH) R.4168, romeriid captorhinomorph; 3. *Echinerpeton intermedium*, MCZ 4090, primitive pelycosaur; 4. *Haptodus longicaudatus*, SGL, primitive pelycosaur; 5. *Archaeothyris florensis*, MCZ 4079, primitive pelycosaur; 6. *Varanops brevirostris*, WM 606, primitive pelycosaur; 7. *Haptodus saxonicus*, SGL, primitive pelycosaur; 8. *Varanosaurus acutirostris*, AM 4174, primitive pelycosaur; 9. *Ophiacodon mirus*, WM 671, pelycosaur; 10. *Ophiacodon uniformis*, MCZ 1366, pelycosaur; 11. *Ophiacodon retroversus*, WM 458, pelycosaur.

at the anterior tip of the jaws. In order to be able to exert greater force, either a greater mass of jaw muscle is necessary or more efficient use of a limited amount. This is where a temporal opening would be of direct advantage.

There are several other changes in jaw structure between romeriids and pelycosaurs that may be noted:

1. The length of the tooth-bearing portion of the jaw becomes relatively greater.

2. Because the area of insertion of the jaw musculature on the lower jaw is closer to the fulcrum in pelycosaurs than in romeriids, the animal could open its mouth wider with the same amount of muscular

distention, to accommodate larger prey (Fig. 20).

3. At the same time, more rapid motion at the tip of the jaw is possible, a definite advantage in catching prey.

These arguments suggest that the original development of the temporal opening occurred in romeriids that were initially of small size. After the temporal opening developed and became stabilized, these forms, which could now be termed pelycosaurs, could diversify and increase substantially in size. This suggests also that it is the absence of a specialized temporal region as such that limited the size of romeriids (Fig. 18).

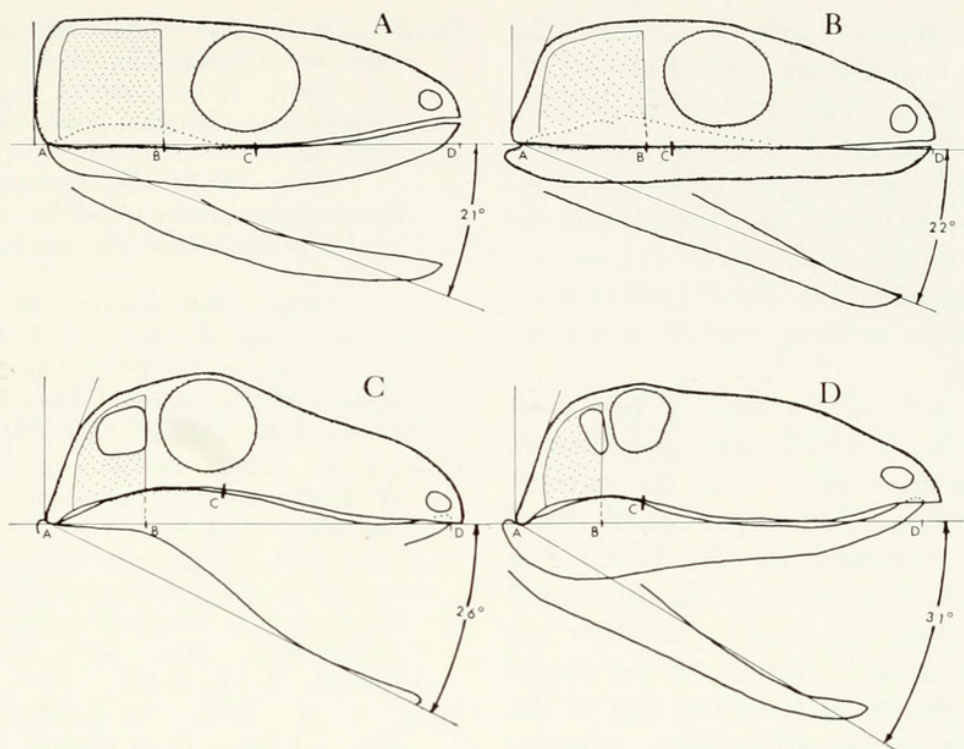


Figure 20. Comparison of the jaw mechanisms in romeriids and primitive ophiacodontids. A. *Hylonomus lyelli*, RM 12016. $\times 1.2$ (Carroll, 1964; text-fig. 1); B. *Paleothyris acadiana*, MCZ 3483. $\times 1.6$ (Carroll, 1969; text-fig. 12); C. *Archaeothyris florensis*, MCZ 4079. $\times 0.5$; D. *Ophiacodon uniformis*, MCZ 1366. $\times 0.25$ (Romer & Price, 1940, plate 1).

A—fulcrum of lever.

B—furthest point from fulcrum on which the jaw muscle can act.

AB
—mechanical advantage in jaw mechanism.

AD

CD—length of tooth row.

Angle shown is the angle of opening of the jaw when jaw muscles extend by 50 percent of their original length.

Stippled area—location of adductor jaw musculature.

Although the Limnoscelidae and the Captorhinidae do not develop temporal openings, they show an increase in size similar to that seen in pelycosaurs. Limnoscelids are very primitive in nature and have little to do with the ancestry of other more advanced reptiles. They seem to have solved the problems involved with increase in size by developing great lateral expansion of the temporal region to accommodate a greater mass of jaw musculature. The captorhinids represent another sterile lineage that has solved this problem in a similar fashion. On the other hand, pelycosaurs retain the narrow configuration of the skull observed in romeriids, but develop a temporal fenestra. This temporal opening enabled the pelycosaurs to reach a position of

dominance in the Lower Permian. The same basic pattern is retained in their descendants, the primitive therapsids, which were dominant terrestrial vertebrates for much of the later Permian and the Triassic. The entire system of jaw musculature was again reorganized in the later group in relationship to the origin of mammals.

Other differences between romeriid and pelycosaurian skulls can also be associated with the changes in the temporal musculature. In romeriids the postorbital and the supratemporal bones do not come into contact. In pelycosaurs, the postorbital extends posteriorly to reach the supratemporal in order to strengthen the cheek region above the temporal opening. Primitive pelycosaurs tend to have the position of jaw

articulation well posterior to the back of the skull roof, so that the margin of the cheek slopes posteriorly. This feature may have developed primarily to increase the area available for jaw musculature. The resulting change in orientation of the muscles might also serve to modify the nature of jaw mechanics as suggested by Olson (1961) from a static pressure system toward a kinetic inertial system.

There are several features of the postcranial skeleton in which early pelycosaurs are more primitive than even the earliest known romeriids. Two equal-sized distal centralia are retained in the foot. The lateral centrale has become the dominant element in even the most primitive romeriids. The neural arch forms the dorsal part of the anterior articulating rim of the vertebra in primitive pelycosaurs, whereas in most romeriids all of the anterior articulating rim is formed by the centrum. A distinct axis intercentrum is retained in all pelycosaurs, although this element became partially fused to the atlas centrum in ophiacodonts. This element is lost or indistinguishably fused in all romeriids except *Hylonomus*. These features are of minor anatomical significance, but they indicate that pelycosaurs diverged from the primitive reptilian stock prior to the appearance of the earliest known romeriids.

The structure of the limbs and girdles in early pelycosaurs can be considered more specialized or advanced than that observed in the romeriids. These changes from the primitive reptilian pattern can be attributed to accommodation to the greater body size achieved by even the earliest known pelycosaurs.

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