PELYCOSAURIAN REPTILES FROM THE MIDDLE PENNSYLVANIAN OF NORTH AMERICA

ABSTRACT

New pelycosaurs from the Middle Pennsylvanian of Florence, Nova Scotia are described. Two of these pelycosaurs are the oldest representatives of the order whose taxonomic position can be exactly determined. Archeothyris florensis is found to be a well ossified primitive ophiacodont, closely related to the genus Ophiacodon. Echinerpeton intermedium, represented by a small immature specimen, was found to have some ophiacodont and some sphenacodont characteristics.

The taxonomic position of the Lower Pennsylvanian pelycosaur Protoclepsydrops haplous is reconsidered in the light of new finds.

The origins and the interrelationships of the Pelycosauria are discussed along with the reconsideration of the taxonomic position of the genus Varanosaurus.

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PELYCOSAURS FROM THE MIDDLE PENNSYLVANIAN OF N. AMERICA

TO THE READER

This thesis has been written and organized according to the style and format of the Journal of Paleontology.

Much of the explanatory information usually included in a thesis has been omitted in order to have the entire manuscript acceptable for publication.

The figures are reproduced here at the scale at which they would be published.

PELYCOSAURIAN REPTILES FROM THE MIDDLE PENNSYLVANIAN OF NORTH AMERICA

by

ROBERT REISZ

A thesis presented to the Faculty of Graduate Studies and Research of McGill University in partial fulfillment of the requirements for the degree of Master of Science.

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PELYCOSAURIAN REPTILES FROM THE MIDDLE PENNSYLVANIAN OF NORTH AMERICA

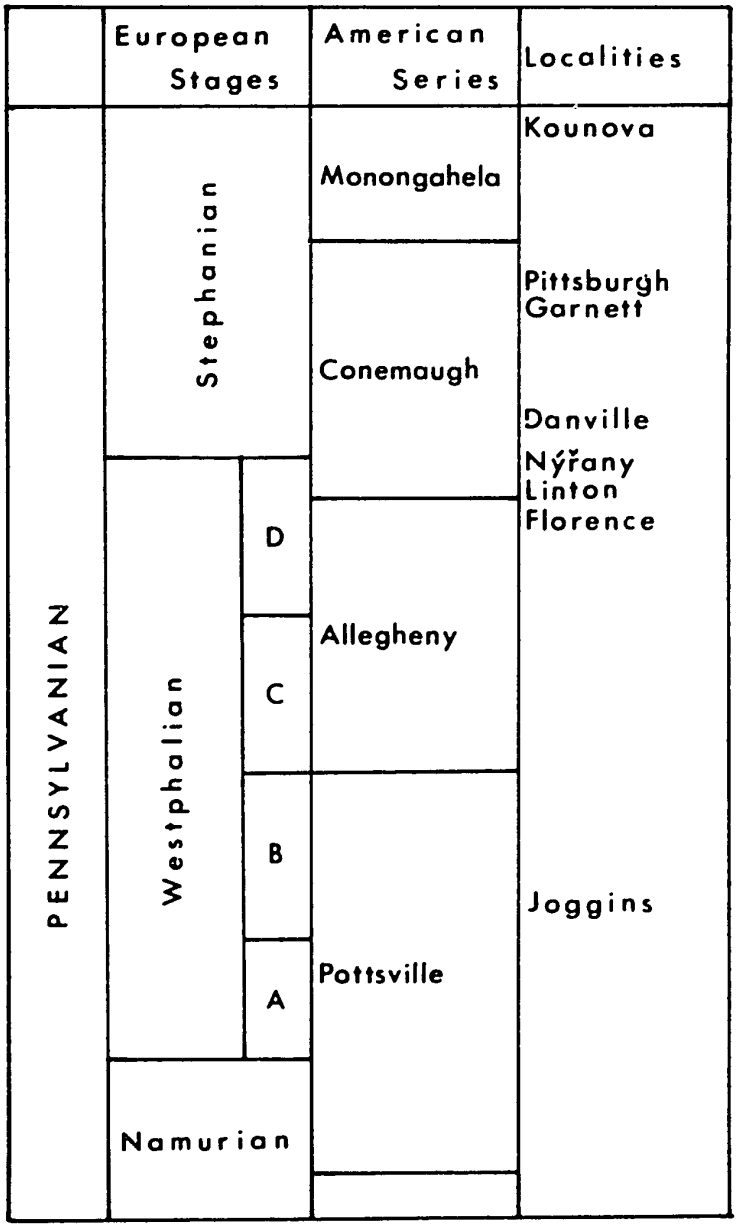
INTRODUCTION

The Order Pelycosauria represents the earliest stage in the evolution of mammal-like reptiles. The early work on the 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 terrrestrial carnivores;
3. Suborder Edaphosauria - specialized swamp-dwelling herbivores.

Most pelycosaurs are known from the Lower Permian (Autunian)of North America and Europe (see chart of geological horizons, text-figure 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:



Text-figure 1. Pennsylvanian stratigraphy. The chart is based on Moore et al. (1944).

1. The McLeansboro Formation near Danville, Illinois; fragmentary skeletal elements of a single ophiacodont genus, Clepsydrops (Cope, 1875).

2. The Matoon Formation of Illinois; numerous fragments of a varanopsid sphenacodont, Milosaurus mccordi (DeMar, 1970).

3. The Round Knob Formation of the Conemaugh group near Pittsburgh, Pennsylvania; Edaphosaurus (Romer and Price, 1940), and a large ophiacodont pelycosaur, Clepsydrops magnus (Romer, 1961).

4. The Upper Pennsylvanian of Garnett, Kansas; a complete presacral vertebral column belonging to an edaphosaur designated as Edaphosaurus ecordi, an ophiacodont pelycosaur similar to Clepsydrops (Peabody, 1957), and an undescribed sphenacodont.

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 sphenacodont, 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, p. 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, p. 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 Protoclepsydrops and identified as a very primitive pelycosaur. Since the age of this deposit is Westphalian B, Protoclepsydrops 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 Protoclepsydrops was mainly based on the nature of the humerus.) The affinities of Protoclepsydrops will be discussed later in this paper.

Between the Joggins deposits and the Danville bonebed, there is a great gap in time. The extensive pelycosaurian fauna found in Florence, Nova Scotia provides considerable information about the representatives of the order living during this time interval. The subject of this paper is the description of the new fauna. The Florence locality was discovered by a field party from Harvard

University under the direction of Dr. 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, p. 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 Nyrany.

Five tree stumps were collected in all, but most of the vertebrates came from one tree. 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), as well as several skulls of the edopoid amphibian Cochleosaurus have been found. The tree was 12 to 15 feet in height, with four blocks at successively lower levels, indicated as A, B, C, and D, with intermittent layers of unproductive shale in between. Block D was collected in 1965 by a McGill-Princeton field party, and might belong to a different (but adjacent) tree.

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 (Protoclepsydrops is too fragmentary in nature to be of value in bridging the great morphological gap between the romeriids and the Lower Permian ophiacodonts). Two pelycosaurs which 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 of 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);

CGH, 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, Sachsiches Geologisches Landesamt, Leipzig;

WM, Walker Museum, Chicago University;

YPM, Yale Peabody Museum.

Acknowledgements. I wish to thank Dr. 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 pelycosaurs and captorhinomorphs, and a high standard for all students of vertebrate paleontology. 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 Patterson of the Museum of Comparative Zoology, Dr. Ostrom of the Peabody Museum and Dr. Gaffney of the American Museum of Natural History who allowed me to examine the collections of pelycosaur material in Harvard, Yale and the American Museum. I also wish to thank Dr. 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 ARCHEOTHYRIS n. gen.

Type species. - Archeothyris 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 (9 mm long and 6.5 mm high at the posterior end). Neural arches are not swollen, the neural spines are 10 mm high, and 6 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.

ARCHEOTHYRIS FLORENSIS n. sp.

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

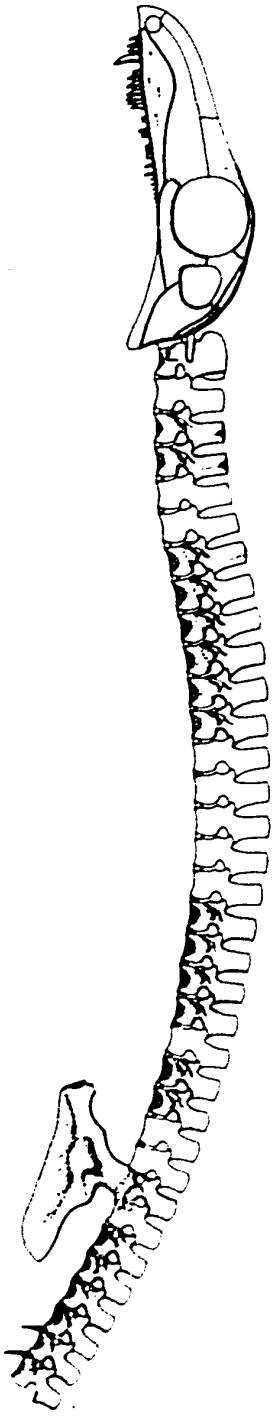
Holotype. - Museum of Comparative Zoology, Harvard MCZ 4079, block B.-1, partial skull, several vertebrae, humerus, cervical ribs.

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, close to the Lloyd Cove coal seam, equivalent to the 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.

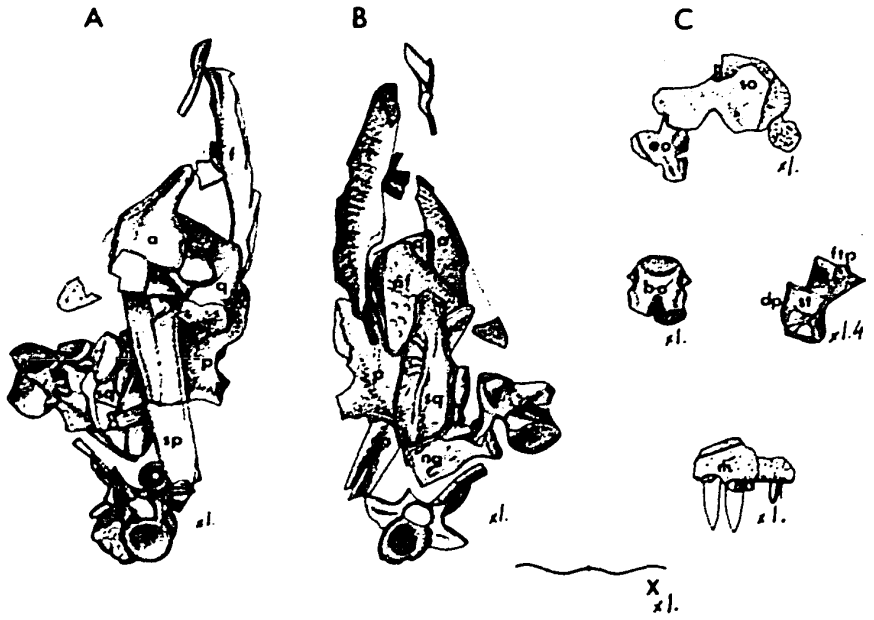
Description: Skull. - On the basis of the material from block B (MCZ 4079) and D (RM 10056), a reconstruction of the skull has been attempted (text-figure 2). The skull resembles that of



Text-figure 2. Archeothyris florensis, partial reconstruction. X 0.5.

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 (text-figure 3), the right frontal, postfrontal, parietal, and squamosal are found in close association - only slightly 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% 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



Text-figure 3. Type of Archeothyris florensis, MCZ 4079.

A, Skull and vertebral elements in ventral view;

B, Dorsal view of A; C, isolated skull elements.

Abbreviations used in figures: a, angular; bo, basioccipital; d, dentary; eo, exoccipital; f, frontal; ha, haemal arch; m, maxilla; p, parietal; pf, postfrontal; q, quadrate; so, supraoccipital; sp, splenial; sq, squamosal; st, stapes; x, outline of dorsal surface of the frontal.

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 Archeothyris 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 text-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. This is unlike the condition in Ophiacodon, in which the dorsal orbital margin is much more strongly curved.

The posterior margin of the frontal and postfrontal extend over the parietal and fit within dorsal grooves which provide an extended surface of attachment. The parietal is 16 mm in length

at the midline. The pineal foramen is located towards the posterior end of the parietal. The foramen is well developed, probably housing a functional pineal organ in life. On the underside there is an invagination around the foramen that probably housed the greater part of the pineal 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 ends 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% of the margin of the temporal fenestra. Anteroventrally, the squamosal is in contact with the jugal, which it overlaps for a considerable 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 inward 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 surface of the lateral border of the supraoccipital (Romer and Price, 1940, p. 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.

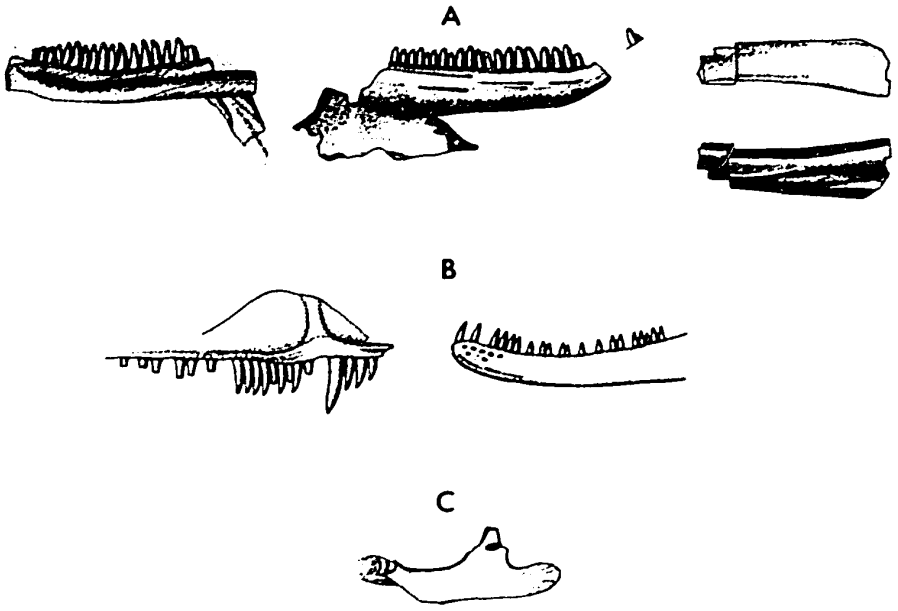
An almost complete maxilla is found in block D (RM 10056). A small fragment of this bone is also found in block B.-8. The maxilla in block D is 40 mm long and 10 mm high at its highest point. The lower margin is almost straight while in the genus Ophiacodon and in sphenacodonts, the convexity of the 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 shelf above the tooth row which is continuous 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 Archeothyris 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 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, p. 89) the length of the maxilla is determined by the dentition and not vice versa. There are only 3 precanine teeth in RM 10056, a number indicative of strongly developed canines, while in Ophiacodon there are from 5 to 7 teeth

present anterior to the canines (Romer and Price, 1940, p. 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 (text-figure 4). There is nothing in the features of this bone that would prevent it from belonging to the type of Archeothyris except its smaller size. It is about 50% too small to fit the skull as it has been restored. 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 in length and 10 mm high at the postorbital 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



Text-figure 4. Archeothyris florensis. A, MCZ 4085, lower jaw elements from block B; B, RM 10056, maxilla in medial view and dentary in lateral view; C, MCZ 4089, jugal in lateral view. All X 1. See text-figure 3 for key to abbreviations.

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, indicating 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 postorbital 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 in 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 postfrontal 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, p. 61). Posteroventrally, the bone changes from a sheet-like nature into a more massive structure which 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 allows it to be associated with Archeothyris. 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 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 text-figure 3. The occipital condyle is 5.5 mm in width. Laterally, close to the condylar area, the connecting surface with the exoccipital is seen. Between this area and the ventral ramus of the bone there is a

notch not observed in Ophiacodon uniformis. The 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. 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 part 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 the 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 or 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 consequence of the scattering of the bones, the exact number of presacral vertebrae cannot be

determined. Romer and Price (1940, p. 93) give 27 as the number of presacrals for ophiacodonts and sphenacodonts. Primitive romeriid captorhinomorphs have from 26 to 32 presacral vertebrae, but Archeothyris is close enough in time and osteology to the other known pelycosaurs to expect a presacral count of 27 or very close to it. 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 of this animal 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.

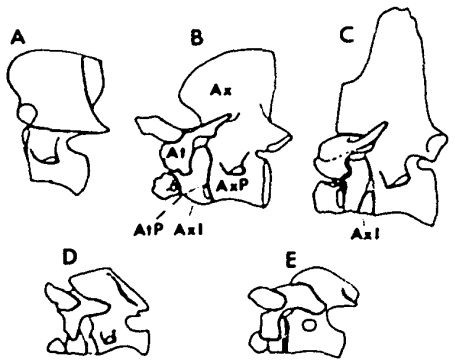
The vertebral elements found in block D are of the same size as in other blocks so that the level of maturity would be expected to be similar to those found above them. The reason for finding separate centra and neural arches in block D can be found in the nature of the preservation in this block. The matrix is not as consolidated as in the other blocks 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 Archeothyris it is insignficant.

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

nearly a 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 which would have articulated with the uppermost part of the atlas centrum, indicating that the axis intercentrum is located immediately below the atlas centrum (text-figure 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 to the height of the atlas centrum. Immediately above this articulating area are the anterior zygopophyses. Between



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

the zygopophyses and the top of the anterior central connecting surface there is a recess which is also present on the Ophiacodon axis. There is also a deep groove extending from the lowermost edge of the anterior zygopophyses to the ventral edge of the posterior zygopophyses.

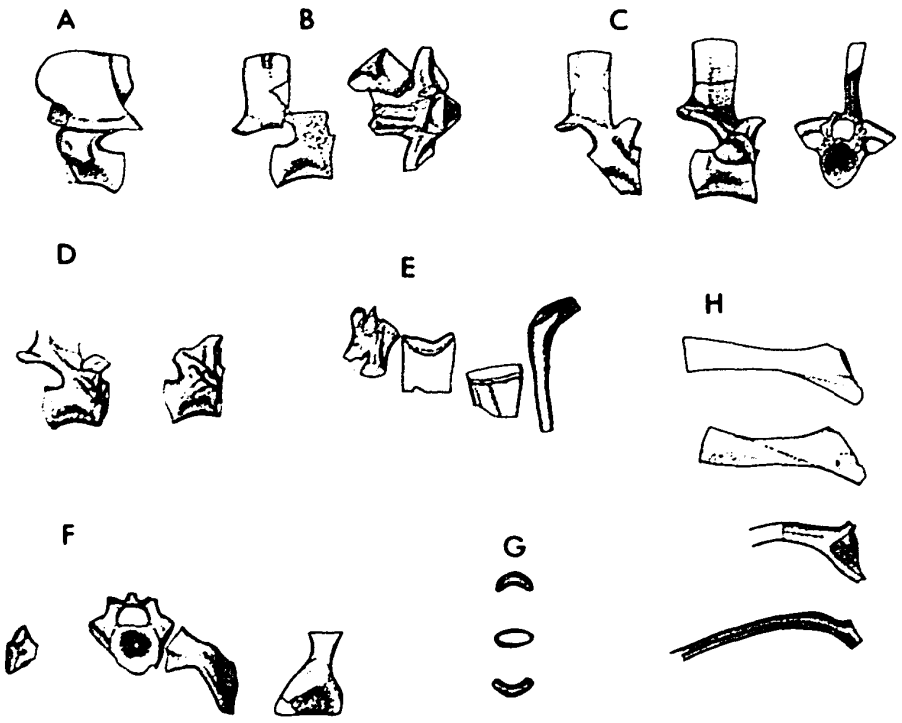
The transverse process is very stout and has a large articulating surface. There is a little "webbing" seen anteroventrally. The transverse process extends without a break to the upper margin of the centrum. In anterior view the transverse process extends far laterally and downward at about 65 degrees to the vertical axis of the vertebra. The neural spine is moderately tall, and extends anteriorly and posteriorly beyond the level of the zygopophyses. 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 Archeothyris. 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% 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



Text-figure 6. Archeothyris florensis, postcranial skeletal elements. A, axis in lateral view, MCZ 4080; B, two cervicals, incomplete, 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 are also shown, 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 X 1.

from a high position on the arch, almost level to the zygopophysial surface and extend almost 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 only seen in the trunk region of other ophiacodonts. No "webbing" is present in sphenacodonts 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 mid-dorsals the capitular head articulates with the intercentrum but there is a tendency for it to move on to the anterior rim of the same centrum in the lumbar, sacral and anterior caudal vertebrae.

As in other ophiacodonts, the anterior zygopophyses are supported by buttresses extending upward and forward beyond the pedicels of the neural arch. These buttresses are quite prominent. The posterior zygopophyses are braced by paired supports descending and expanding from the base of the neural spine. The zygopophyseal surfaces extend laterally to the limits of the centra and are moderately tilted. Romer and Price (1940, p. 103) emphasize the importance of the angle of the zygopophyses in separating the different suborders of

pelycosaurs and in distinguishing pelycosaurs from other early reptiles. In Archeothyris this angle is difficult to establish exactly because:

1. the number of presacral vertebrae is small;

2. the actual articulating surfaces are not straight, but oval in outline;

3. 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 sphenacodonts 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.

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

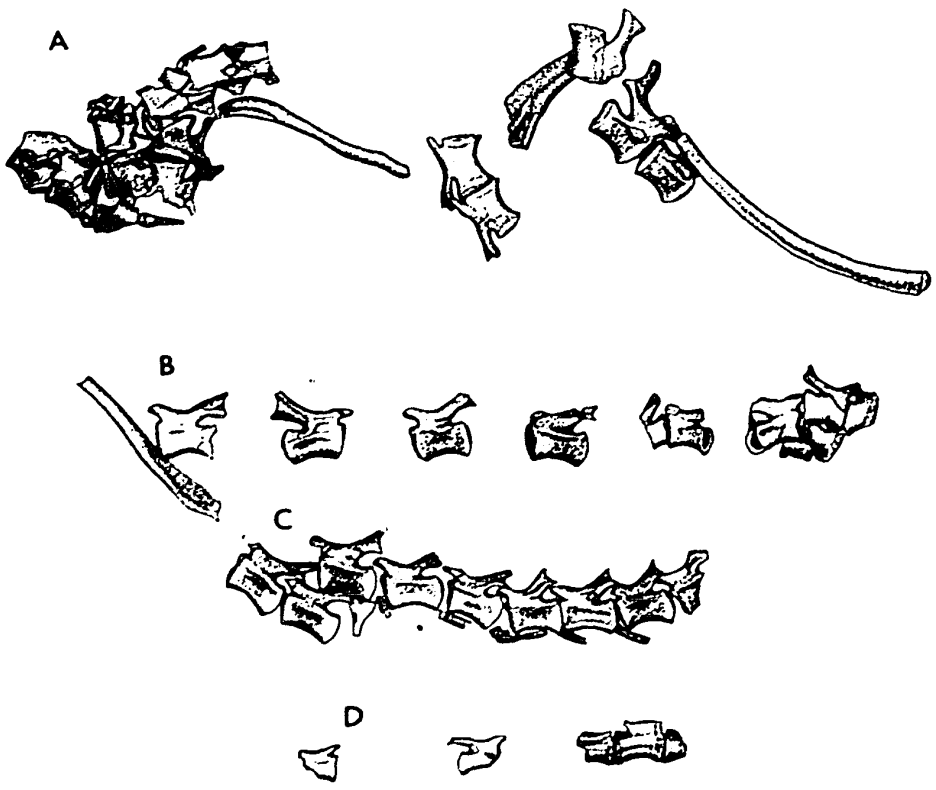
surface, expanding the head even more at this point. More posteriorly along the column, the spines tend to become blade-like structures. Towards the sacrum, the neural spines become shorter, yet their width remains the same.

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). The spine and the posterior zygopophyses 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 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 rim. Neither the second 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

caudal 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, Archeothyris is very primitive. Other pelycosaurs have their caudal ribs fused to the centra (Romer and Price, 1940, p. 110). The length of the zygopophyses 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 text-figure 7 where two normal intercentra are seen between 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



Text-figure 7. Archeothyris florensis. 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 X 1.

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) (text-figure 6), and one in block B.-20 (MCZ 4081) (text-figure 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, p. 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.

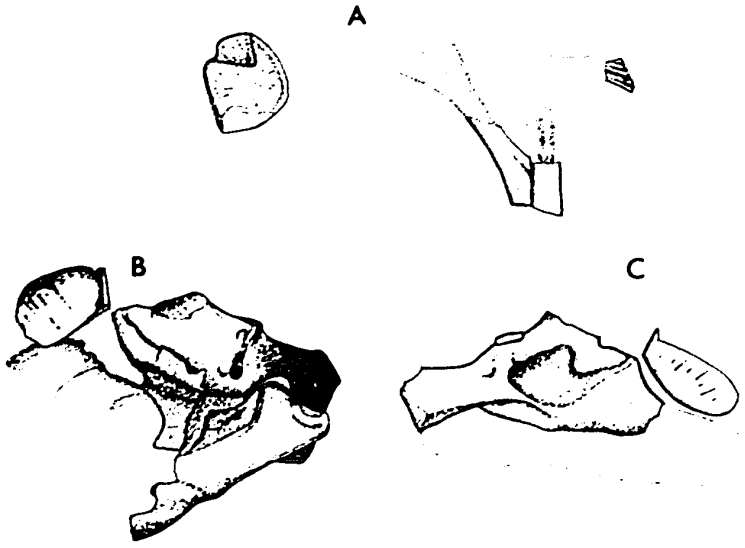
In typical dorsal ribs, the head is greatly expanded dorsoventrally with the tubercular and capitular heads connected by a thin sheet of bone. The main body of the rib is circular in section, with a ridge running along its postero-dorsal margin. The curvature of the ribs indicates that the trunk was 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 head 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 short and very massive; the plate is not as wide as is 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 sacrals. 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. There are no ribs preserved in the tree which can be identified as the second sacral. The general similarity of Archeothyris 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

Archeothyris, 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 the 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 to the ones seen in the more primitive ophiacodonts. In sphenacodonts there is less constriction. Hence it is probable that only two sacral ribs were present in this animal and not three sacrals as in sphenacodonts, in which the iliac blade is greatly expanded. The articular surface of the acetabular cavity is similar in configuration to that of Clepsydrops colletti (Romer and Price, 1940, p. 127). It is only in the ventral rim of the acetabulum that the pelvis in block A differs from that of Clepsydrops. In Archeothyris the acetabular rim describes a semicircle with the dorsal tip of the acetabulum being the centre. In Clepsydrops, however, this lower rim is practically straight.



Text-figure 8. Archeothyris florensis. A, fragmentary interclavicle, unidentified limb bone, calcaneum, RM 10056; B, pelvic girdle material, MCZ 4080; C, lateral view of B. All X 1.

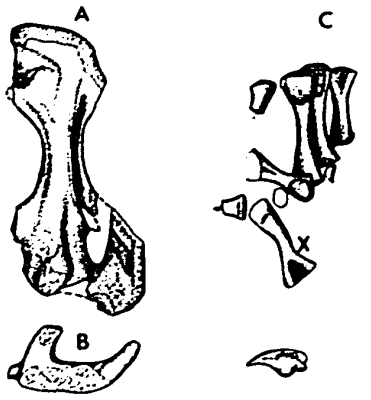
On the whole, the acetabulum faces rather more dorsally than in the more advanced pelycosaurs and in this it resembles that of Clepsydrops. The pubic and ischiadic parts of the acetabulum turn sharply outward close to the rim.

The dorsal margin of the pubis forms a thickened ridge which runs to the tip of this element and slants downward. This ridge bears, close to the anterior limit, a prominent lateral pubic tubercle which provides attachment for the inguinal ligament and pubotibialis muscle. This tubercle tends to be of small size in the genus Ophiacodon. The tubercle in Archeothyris is comparable in size to those of Clepsydrops 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 blade-like ventral process of the pubis, immediately underneath the acetabulum.

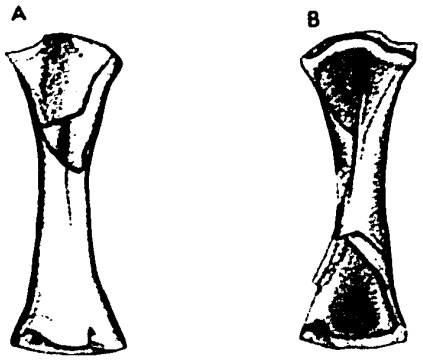
The ischium is thickened immediately behind the acetabulum and forms a thinner, ridged upper margin posteriorly. This ridge overhangs the plate-like region below it and, as it passes backwards, the upper margin of the ischium turns downward towards the symphysis.

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



Text-figure 9. Archeothyris florensis. A, humerus in distal dorsal view, MCZ 4079; B, outline of distal end of A; C, metacarpals, MCZ 4083, and claw, MCZ 4083; X, femur of a small romeriid. All X 1.



Text-figure 10. Archeothyris florensis, RM 10056. A, femur in dorsal view; B, ventral view of A. X 1.

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 heads -- 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. In block B.-22.15, the distal end of another femur is seen, but this fragment is also weakly ossified.

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 metatarsals are 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 (text-figure 2). Archeothyris 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 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 Archeothyris 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, Archeothyris appears to be a very primitive pelycosaur, with characteristics that suggest a close relationship to the

genus Ophiacodon. The similarities of Archeothyris to the well known members of the Ophaicodontidae 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 Archeothyris are primitive:

1. The length of the prefrontal 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 Archeothyris is also seen in some romeriids, but is also retained among sphenacodonts. In 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 Archeothyris and romeriids the angle between the two articulating surfaces is about 90 degrees.

4. The nature of the centra, intercentra, transverse processes (with webbing), and high neural spines confirm the association of Archeothyris 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 Archeothyris; they are fused in later pelycosaurs.

5. The pelvic girdle is very similar to the type of pelvis seen in such primitive ophiacodonts as Clepsydrops and Varanosaurus. It has a pubic tubercle only seen in the most primitive ophiacodonts.

6. The humerus is like those of Clepsydrops and Varanosaurus, the most primitive ophiacodonts. Ophiacodon humeri tend to be more advanced in the size of their entepicondyle.

The following features in Archeothyris 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 3 precanine teeth.

Suborder OPHIACODONTOIDEA

Family OPHIACODONTIDAE

Genus ECHINERPETON n. gen.

Type species. - Echinerpeton intermedium new species.

Known distribution. - Middle Pennsylvanian of eastern North America.

Diagnosis. - Very small ophiacodont pelycosaur, 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.

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.

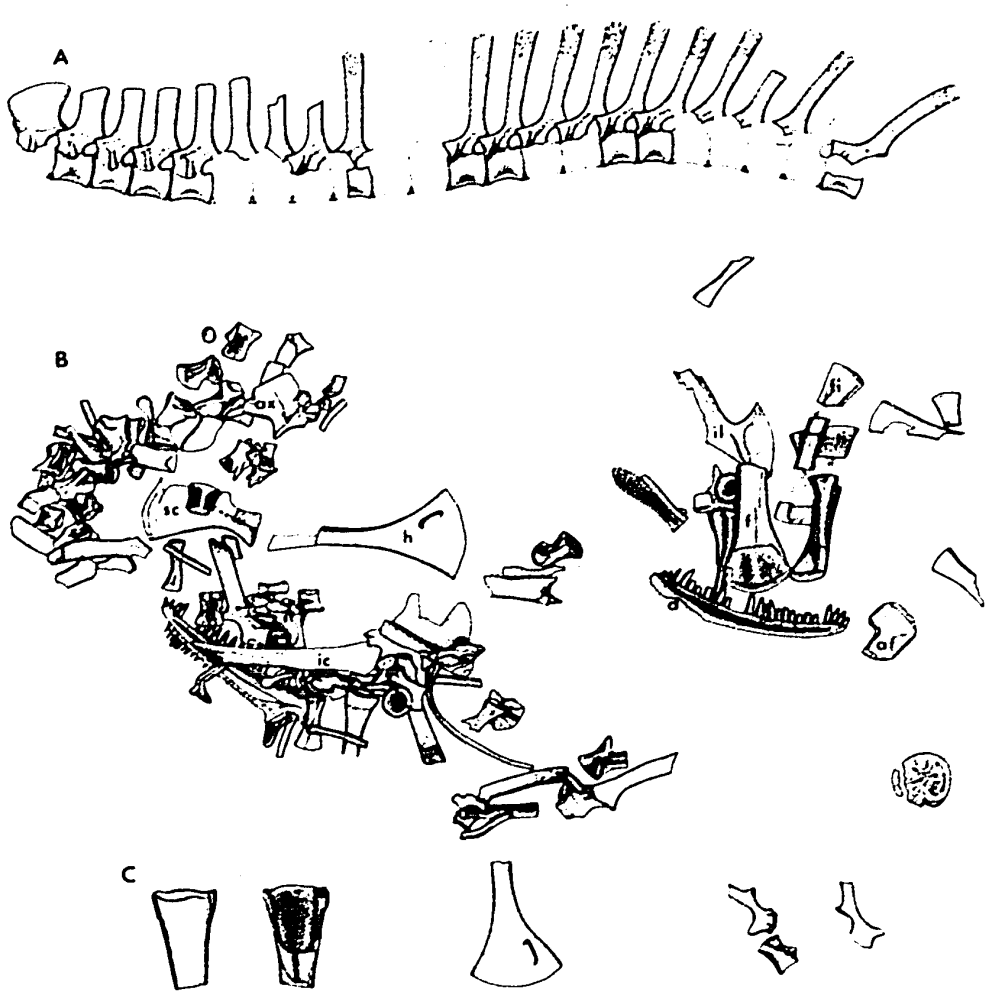
Holotype. - Museum of Comparative Zoology, Harvard MCZ 4090, block B.-1, partial skeleton, immature individual.

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



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

belonging to a more mature individual than MCZ 4090.
RM 10,057, block D, an almost complete right maxilla, a neural arch, rib, and a phalanx.

Horizon and locality. - Morien Group, 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) (text-figure 11). Isolated material from 5 additional individuals can be questionably associated.

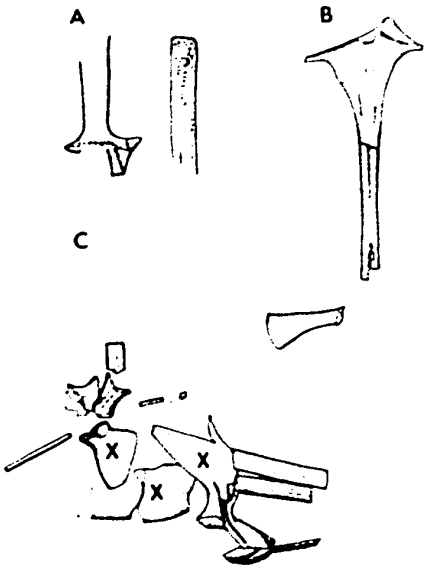
Skull. - The only skull elements that can be associated with this genus are three maxillae (text-figure 12) and two dentaries. A complete left maxilla (MCZ 4092), as well as a fragmentary right maxilla (MCZ 4093) are found in block B.-22. In block D, an almost complete right maxilla (RM 10,057) was found 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 (Archeothyris, Varanops and Haptodus). In other pelycosaurs (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 also seen in Archeothyris, 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 (text-figure 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 were 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,

Text-figure 12. Echinerpeton intermedium. Maxillae: A, MCZ 4092; B, MCZ 4093; C, RM 10,057 (also neural arch, fragmentary rib and phalanx). All X 1.



Text-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 X 1.

Dimetrodon milleri, Dimetrodon limbatus) a similar 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 (text-figure 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 Archeothyris, the centra are more elongated. In later pelycosaurs, 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 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.

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 (text-figure 13). The zygopophyses do not have strongly tilted articular surfaces, nor are they as close to the midline as in typical sphenacodonts. In the mid-dorsals, the angle of the zygopophyses 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 angles noted in the anterior cervicals are less than 35 degrees, and in the lumbars, sacrals and caudals they are greater.

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 (text-figure 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 which 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. It is probable that the condition seen in Echinerpeton is 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. The 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 (text-figure 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 (text-figure 13) 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 (text-figure 11), and a fragment of a rib is found in block D (text-figure 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 (text-figure 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 (text-figure 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 (text-figure 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 (text-figure 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 which might have shown a trough for the dorsal musculature is not preserved.

The heads of both femora are present in the type specimen (text-figure 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 (text-figure 11). This reconstruction shows that Echinerpeton is a small reptile, with long slender limbs, and very high neural spines. The more mature specimens are up to 50% 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 millipeds 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 Archeothyris, Haptodus and Varanops. The buttressing above the canines is similar to that seen in Archeothyris and some romeriids (in sphenacodonts this primitive feature is retained). The teeth are simple conical structures, canines are not very strongly differentiated (sphenacodonts 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 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 only seen in ophiacodonts. The neural spines do not have the type of excavation at the base as is seen in sphenacodonts.

2. The centra are slightly compressed anteroposteriorly, a tendency followed in ophiacodonts.

3. The zygopophyses 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, blade-like 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.

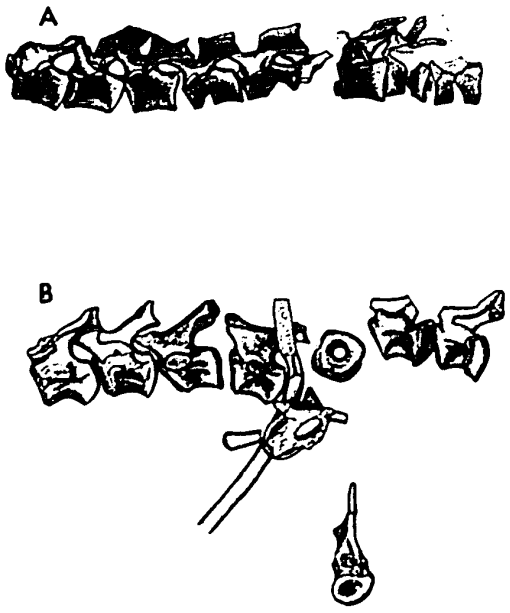
2. The nature of the axis neural spine is somewhat similar to those in sphenacodonts in that its highest point is reached at its posterior end. On the other hand, the spine is similar to those in ophiacodonts in that it is broadest along its dorsal margin.

This particular pelycosaur shows the close relationship between primitive ophiacodonts and sphenacodonts. There is actually little in the features of this animal that prevent 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 this tree, 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 (text-figure 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



Text-figure 14. Unnamed pelycosaurs. A, 9 presacral vertebrae, articulated, MCZ 4088; B, 9 proximal caudal vertebrae, partially articulated, also fragmentary rib and phalanx, MCZ 4095.

described in this paper. The use of this particular feature (see Romer and Price, 1940, text-figure 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, text-figure 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 zygopophyses, 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 sphenacodonts. The right and left zygopophyses are placed 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 that this pelycosaur has some primitive as well as ophiacodont and sphenacodont characters, the determination of its exact taxonomic position among pelycosaurs has to await the discovery of more complete specimens.

II. Eight caudal vertebrae (text-figure 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.

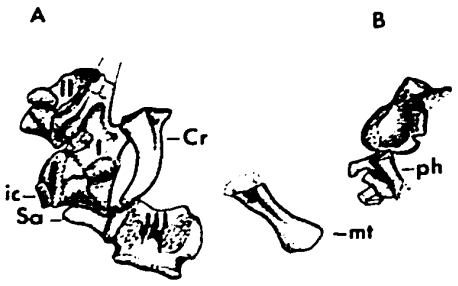
The neural arches are not swollen, but are stoutly built. The transverse processes are broken off on the first two vertebrae, but the broken surfaces indicate that both the capitular and tubercular heads of the ribs were suturally attached to the centrum. The transverse process on the 3rd vertebra is 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 slight

swelling where the transverse process would have been.

The anterior and posterior zygopophyses extend far beyond the rims of the centra. The angle between the articulating surface of the zygopophyses is slight -- about 30 degrees (in ophiacodonts the tilt in the caudal region is slightly 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) (text-figure 15). Among pelycosaurs, only advanced sphenacodonts have three sacrals. They are stoutly built and have different proportions than the vertebrae in Archeothyris. The centra are 8 mm long and 8 mm tall at the posterior rim. There is no keel. In the ventral region of the central rims there is bevelling to accommodate the intercentra, but there is no "lip" formation as seen in advanced ophiacodonts. There is no bevelling in the primitive ophiacodonts from this locality.

The diapophyses, which are huge in all three vertebra, extend onto the centra. They are developed to a greater extent than in Archeothyris, being 5 mm long and up to 3 mm in height. There are slight differences in the shape of these



Text-figure 15. Unnamed sphenacodont pelycosaur.

A, three sacral vertebrae and a caudal rib, MCZ 4096;

B, astragalus and other distal limb elements, MCZ 4097.

X 1. Abbreviations used in the figure: Cr, caudal rib;

ic, intercentrum; mt, metatarsal; ph, phalanx;

sr, sacral rib; I, first sacral; II, second sacral;

III, third sacral.

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 sphenacodonts. 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 sphenacodont in nature, being strongly excavated above the transverse process. The zygopophyses 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 zygopophyses extend well beyond the respective central rims (Romer and Price, 1940, text-figure 45). The articulating surfaces of the zygopophyses 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

blade-like 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 blade-like 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-figure 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 indicate that this rib was not fused to the transverse process.

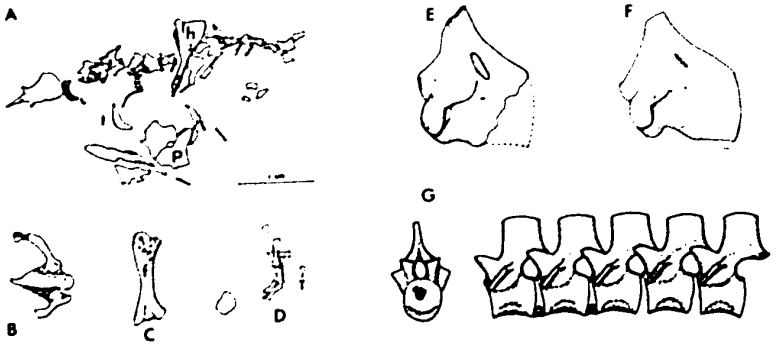
It has been found necessary to describe this sphenacodont material separately from Echinerpeton. The structural differences between them are too great for these sacrals to belong to a mature specimen of that genus.

There is in block C an astragalus (MCZ 4097) that also may be a sphenacodont. 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-figure 41).

PROTOCLEPSYDROPS HAPLOUS

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



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

Order Pelycosauria.

The two larger humeri designated as paratypes of Protoclepsydrops haplous are more pelycosaurian in nature. They are very similar to the humerus in Archeothyris 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 Archeothyris. 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 Protoclepsydrops and that seen in Archeothyris. This humerus is considered less mature than the one from DMSW B.239 because the endepicondylar 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 Protoclepsydrops haplous. They (text-figure 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 Archeothyris, 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 intercentrum is well developed; it is 1.5 mm long. In order to accommodate the intercentrum, 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 Archeothyris. The articulating surface of the transverse process is straight and extends anteroventrally. 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 zygopophyses 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 Archeothyris; in romeriids the spines tend not to be so wide.

The extremely primitive nature of Protoclepsydrops 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 string of vertebrae indicate possible association of this genus with the suborder Ophiacodontia (see text-figure 17).

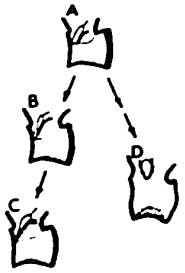
SOME OF THE INTERRELATIONSHIPS OF THE PELYCOSAURIA

Consideration of the interrelationships of all pelycosaurs is beyond the scope of this work. Nevertheless, the discovery of this new material requires some reconsideration of the more primitive members of the group. The pelycosaurs found in the 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 suborders of Ophiacodontia and Sphenacodontia 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 this time. The genus Archeothyris 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. The

labeling of the suborder Ophiacodontia as "primitive" is unacceptable in light of some of its specialized characteristics. The specialization of the atlas-axis complex and the nature of the transverse processes prevent even its earliest known members 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 text-figure 17). The type of diapophyses in sphenacodonts and edaphosaurs cannot, however, be easily derived from those seen in even the earliest ophiacodont, because the latter lineage evolved in a completely different direction.

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 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



Text-figure 17. Possible manner of derivation of the pelycosaurian transverse processes. A, the original romeriid pattern, based on MB 1901.1379 (Carroll, 1970, text-figure 8); B, the type of transverse process in Protoclepsydrops haplous, RM 12202; C, pattern seen in ophiacodonts, based on Archeothyris florensis, MCZ 4079; D, the sphenacodont and edaphosaur pattern, based on MCZ 1347 and MCZ 1531 (Romer and Price, 1940, plates 24 E, and 36C).

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 the early ophiacodonts and sphenacodonts show great similarities between the two groups. Echinerpeton is in a position somewhat intermediate between ophiacodonts and sphenacodonts. The sphenacodont material from Florence, MCZ 4096, shows that members of the family Sphenacodontidae were already differentiated.

The taxonomic position of the genus Varanosaurus may be questioned on the basis of its greatly swollen neural arches. Romer and Price (1940, p. 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 early romeriid. This suggests that Varanosaurus is not primitive but specialized. There is considerable increase in size from early romeriids. Varanosaurus not only solved the problems involved in strengthening the vertebral column to support more weight in a different way from other pelycosaurs, but also developed a different type of movement within the vertebral column. In normal pelycosaurs the zygopophyses are slightly tilted so that forces acting perpendicular to the zygopophyseal surfaces meet in the neural spine. The neural spines are strongly developed to

provide further support for the vertebral column. Limited movement between the vertebrae can occur in all directions. In Varanosaurus, however, the zygopophyseal surfaces are not tilted, and the perpendicular forces acting on these surfaces are oriented vertically. Therefore, a large amount of bone is necessary directly above the zygopophyses in order that the latter may be able to resist the forces acting on them. This extra amount of bone gives the swollen appearance to the neural arches. The nature of the zygopophyseal surfaces in Varanosaurus greatly limits the axial rotation of the vertebral column, but enhances the amount of lateral undulatory movement of the column.

This suggests that Varanosaurus must have separated very early from the main line of pelycosaurian evolution. The type of neural arch seen in Varanosaurus also developed in the Lower Permian captorhinids, limnoscelids, diadectids, and seymouriamorphs in response to increase in size.

THE ORIGINS OF THE PELYCOSAURS

On the basis of the known Lower Permian pelycosaurs and cotylosaurs, Romer and Price (1940, p. 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 as yet undescribed romeriids of about the same age, from Nýřany, Czechoslovakia and Linton, Ohio. At least four romeriid lineages can be recognized in the Pennsylvanian. The central stock consists of the genera Hylonomus and Paleothyris. The morphological differences between Pennsylvanian romeriids are slight. They are all well ossified reptiles with similar body proportions, levels of limb development, and dental pattern. These features suggest that they all fed on small invertebrates and were

terrestrial in habitat.

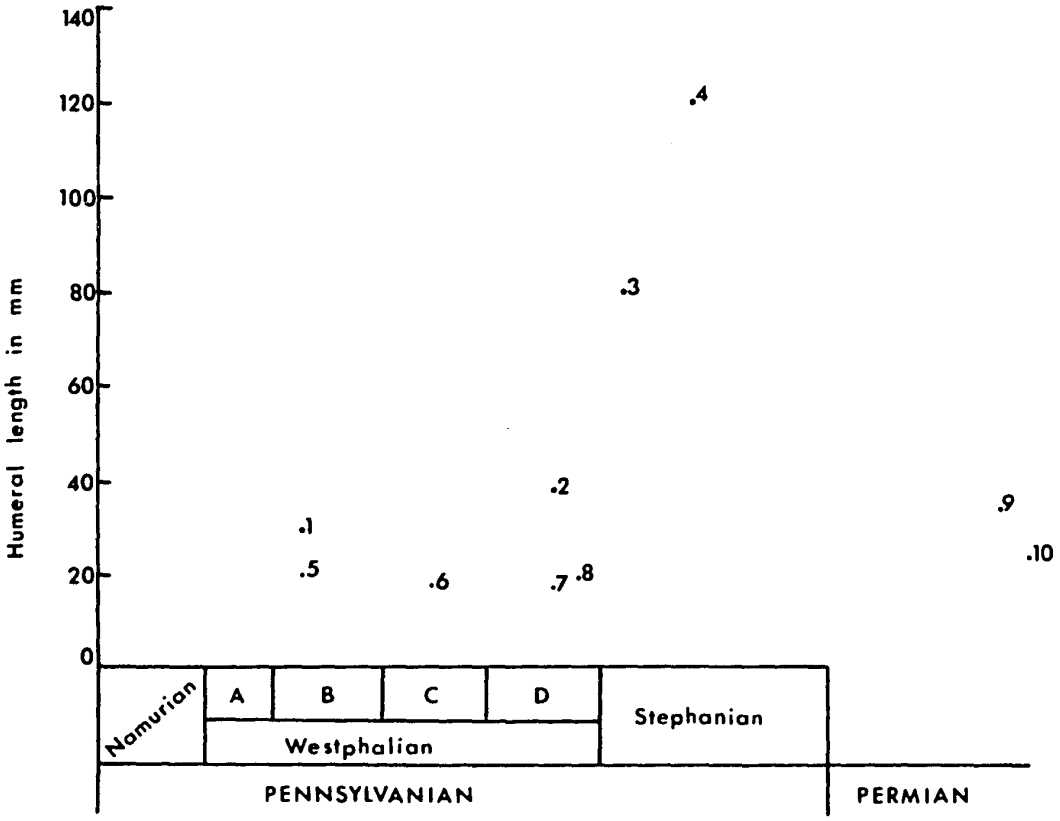
Although the pelycosaurs are thought to have arisen well before the formation of the Joggins deposits (probably in the Lower Namurian) it is worth while to compare the earliest romeriid, Hylonomus, with the earliest known ophiacodont pelycosaur, Archeothyris. The morphological similarities between these genera are so great that their common ancestry among earlier romeriids is unquestionable. With the exception of the genus Cephalerpeton, all Pennsylvanian romeriids would make good ancestors for pelycosaurs. 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 the thickened and thinned areas of the skull were produced by the pattern of muscular stresses on them. Selection may have achieved sufficiently reduced areas of stress 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, p. 156). It is suggested that this particular change in the skull structure allowed pelycosaurs to increase greatly in size and to develop other specializations permitting them to occupy niches different from those filled by primitive romeriids. The length of the humerus in romeriids and pelycosaurs provides a good indication of the size of the respective genera (text-figure 18). Pelycosaurs between the Westphalian B and the Upper Stephanian show exponential increase in size. Romeriids, however, do not increase greatly in size.

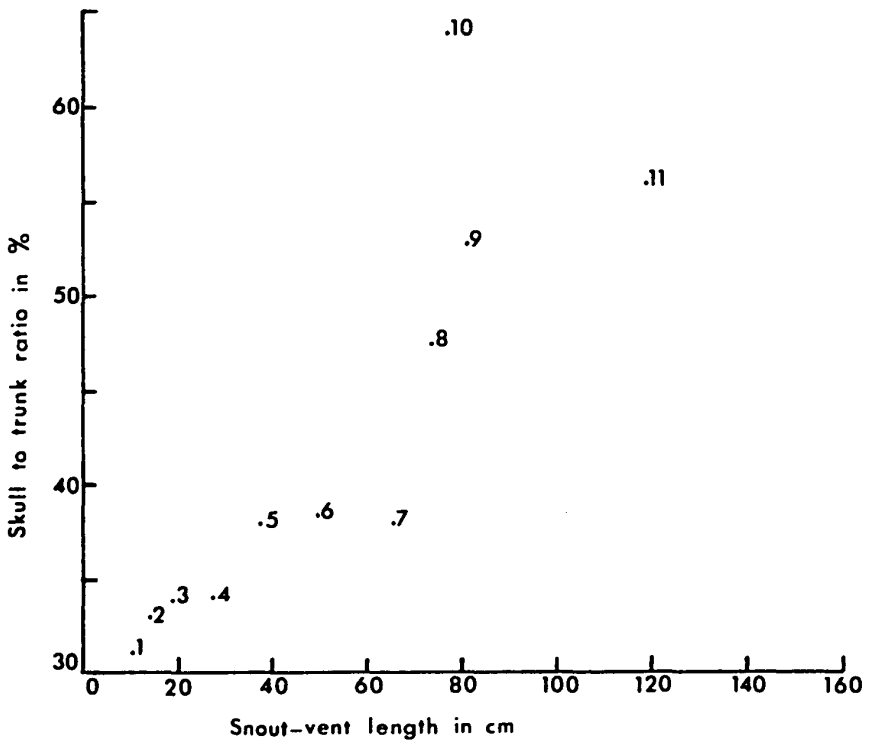
The following changes are observed as pelycosaurs increase in size:

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 ratio of the skull to trunk ratio increases 34 to 64% as seen in text-figure 19. 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 in these suborders. The increase in the ratio of the skull to trunk length with increase in body size is related to the fact that the body volume increases



Text-figure 18. Relationship between humeral length and relative age of the following genera:

1. Protoclepsydrops haplous, DMS W.B. 239, pelycosaur.
2. Archeothyris florensis, MCZ 4079, pelycosaur.
3. Clepsydrops colletti, WM 6542, pelycosaur.
4. Clepsydrops magnus, CM 13942, pelycosaur.
5. Hylonomus lyelli, RM 21126, BM(NH) R.4168, BM(NH) R.443, romeriid.
6. Cephalerpeton ventriarmatum, VPM 796, romeriid.
7. Paleothyris acadiana, MCZ 3482, MCZ 3485, MCZ 3487, romeriid.
8. "Cephyrostegus bohemicus", CGH III B21.C.587, romeriid.
9. Undescribed, MCZ 1474, advanced romeriid.
10. Undescribed, MCZ 1478, advanced romeriid.



Text-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. Archeothyris 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.

in proportion to the third power of linear dimensions, whereas the mouth area increases only as 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.

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 one. In Archeothyris, on the other hand, the ratio between 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 of the skull. 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 (text-figure 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 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 may be of direct advantage. It would serve to allow the jaw muscles to bulge laterally and may also provide more secure attachment of the muscles on its margins.

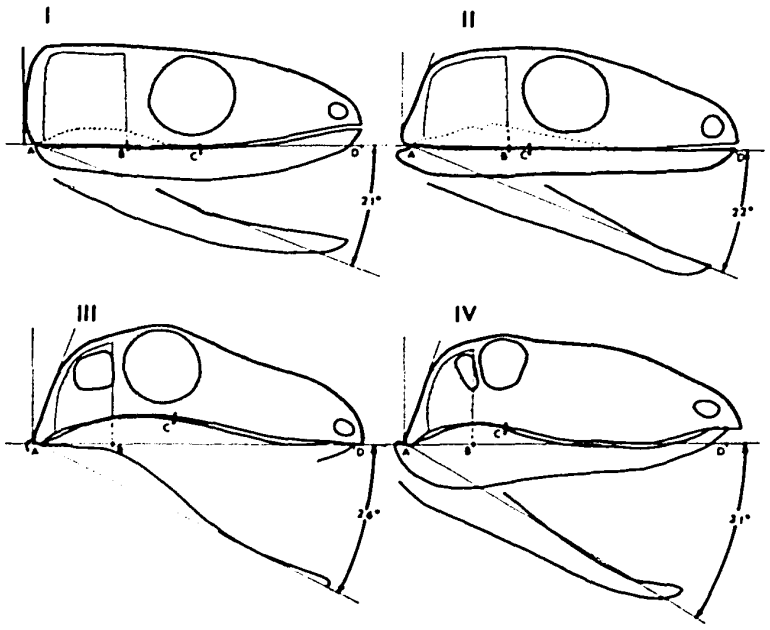
The advantages provided by these changes in the jaws are manifold:

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 (text-figure 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 must have 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



Text-figure 20. Comparison of the jaw mechanisms in the following genera:

I. Hylonomus lyelli, RM 12016. X 1.2 (Carroll, 1964, text-fig. 1).

II. Paleothyris acadiana, MCZ 3483. X 1.6 (Carroll, 1969, text-fig. 12).

III. Archeothyris florensis, MCZ 4079. X 0.5.

IV. Ophiacodon uniformis, MCZ 1366. X 0.25 (Romer and Price, 1940, plate I).

A = fulcrum of lever.

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

$\frac{AB}{AD}$ = mechanical disadvantage in jaw mechanism.

CD - length of tooth row.

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

[ ] - area of location of adductor mandibulae externus musculature.

also that it is the absence of a specialized temporal region that limited the size of romeriids as such (text-figure 18).

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 have 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 descendents, 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 groups, in relationship to the origin of mammals.

Other differences between romeriid and pelycosaurian skulls can be associated with the development of the temporal opening. 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. The sloping nature of the

posterior margin of the cheek is probably related to the necessity of having large areas of attachment for the jaw musculature.

In the postcranial skeleton the differences between the romeriids and pelycosaurs are the result of the retention of some primitive characters in pelycosaurs, as well as adjustments to a considerable increase in size. The Pennsylvanian romeriids show certain advances in their postcranial skeleton not seen in pelycosaurs, providing evidence that pelycosaurs must have separated very early from the romeriids in order to have retained some of these primitive characteristics. In pelycosaurs, 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. Changes in the configuration of the limb bones in pelycosaurs are directly associable with increase in size.

SUMMARY

This study has shown that there are at least five species of pelycosaurs in the Middle Pennsylvanian terrestrial deposit of Florence, Nova Scotia. Two of these pelycosaurs were described in detail. Archeothyris florensis is a primitive but typical ophiacodont, while Echinerpeton intermedium is an ophiacodont with some sphenacodont characteristics.

Vertebral material from three other pelycosaurs was also described, but not named. The presence of this rich fauna in the Middle Pennsylvanian permits reconsideration of the taxonomic interrelationships of primitive pelycosaurs. It was concluded that although ophiacodonts did not differentiate 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.

The taxonomic position of the genus Varanosaurus was also reconsidered, and it was concluded that this genus represents a very specialized vertebral adaptation.

Recent investigations of the ancestral romeriid stock, in addition to the pelycosaurian finds described in this paper, also permits consideration of the problems and functional changes involved in the origins of the Order Pelycosauria. The study of this problem showed that it was the development of the temporal opening in a small romeriid that permitted pelycosaurs to diversify and increase greatly in size.

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