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THE ANATOMY AND RELATIONSHIPS OF THE LOWER PERMIAN REPTILE *ARAEOSCELIS*

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ABSTRACT—Two recently discovered skeletons of the enigmatic Lower Permian reptile *Araeoscelis* provide important, additional information on its osteology and permit a reassessment of its phylogenetic relationships. A combination of primitive and derived characters shared by *Araeoscelis* and *Petrolacosaurus* justifies their inclusion in the suborder Araeoscelidia as members of separate families and indicates that they represent the earliest, most primitive known stage in the adaptive radiation of the diapsid reptiles. *Araeoscelis* exhibits a suite of unusual cranial features resulting in a massive, sturdily constructed skull, which is interpreted as an adaptation to a specialized diet that probably included invertebrates protected by heavy exoskeletons. This theory is also used to explain the absence of a lower temporal fenestra in *Araeoscelis* as the result of secondary closure. Some cranial features are noted that support this hypothesis.

INTRODUCTION

Araeoscelis, a small, lizard-like reptile with an elongate neck and long slender limbs, is best known from three Lower Permian localities in north-central Texas. Seven skull fragments and a considerable amount of postcranial material, including three partial articulated postcranial skeletons, were collected by S. W. Williston from the Arroyo Formation, Clear Fork Group, at the famous Craddock bonebed, Craddock Ranch, Baylor County, and described by him (1910, 1914) as *Araeoscelis gracilis*. Two partial skulls and associated postcranial material were collected by E. C. Case from the Admiral Formation, Wichita Group, near the mouth of Godwin Creek, Archer County. These were originally referred to *Bolosaurus striatus* (Cope, 1878) by Case (1907), later assigned to a new genus and species, *Ophiodeirus casei* Broom (1913), and finally reassigned by Vaughn (1955) to *Araeoscelis*, as *A. casei*. Five *Araeoscelis* specimens, including skulls, skull fragments, and associated but mainly disarticulated postcranial elements were collected by L. I. Price between 1934 and 1937 from the Belle Plains Formation, Wichita Group, at the Bar X Ranch, Baylor County. On the basis of these specimens Vaughn (1955) determined that *Ophiodeirus* is a junior synonym of *Araeoscelis*. Even though Vaughn was unable to distinguish between the two species anatomically, he reluctantly retained them on the grounds of stratigraphic separation—*A. casei* being from the Wichita Group and *A. gracilis* from the overlying Clear Fork Group. Thus, the specimens collected by Price were assigned to *A. casei*. Despite this distinction, however, Vaughn's description treated *Araeoscelis* as if represented by a single form, which is also followed here.

The above materials were used by Vaughn (1955) in the latest redescription of *Araeoscelis*, one of the most thorough studies of a Paleozoic reptile. Although it would appear that a sufficient number of specimens was available for a complete osteological description, Vaughn was seriously hindered by the poor quality of the cranial remains and the lack of well preserved, articulated postcranial skeletons. Thus, almost all of the figures presented by Vaughn are composites that utilize specimens assigned to both species of *Araeoscelis*. Two excellently preserved, partial, articulated skeletons of *Araeoscelis* that were part of the collections made by Price from the Belle Plains Formation, but not prepared until recently, add to our knowledge of the anatomy of this important animal and permit a reassessment of its phylogenetic relationships.

Abbreviations used in figures are as follows: **a**, angular; **ac**, anterior coracoid; **ar**, articular; **as**, astragalus; **ati**, atlantal intercentrum; **ax**, axis; **c**, calcaneum; **c5** and **c17**, caudal vertebrae; **cl**, clavicle; **cm**, medial centralia; **co**, coronoid; **cth**, cleithrum; **d**, dentary; **f**, frontal; **fcor**, coracoid foramen, **fe**, femur; **g**, glenoid; **h**, humerus; **icl**, interclavicle; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, pterygoid; **pa**, parietal; **pc**, posterior coracoid; **pf**, postfrontal; **pm**, premaxilla; **po**, postorbital; **pop**, paroccipital process; **pra**, prearticular; **prf**, prefrontal; **q**, quadrate; **qj**, quadratojugal; **r**, radiale; **ra**, radius; **s**, splenial; **s1** and **s2**, first and second sacral ribs; **sa**, surangular; **sc**, scapulocoracoid; **sq**, squamosal; **st**, supratemporal; **t**, tibia; **ta**, tabular; **u**, ulna; **ul**, ulnare; **v5–v20**, presacral vertebrae; **I–V**, metacarpals and metatarsals; **1–5**, distal carpals and tarsals.

Acknowledgements—We are indebted to the Museum of Comparative Zoology, Harvard University,



FIGURE 1. *Araeoscelis* skeletons MCZ 4380 and MCZ 8828 (referred to in text as MCZ I and MCZ II, respectively) seen mainly in dorsal view.

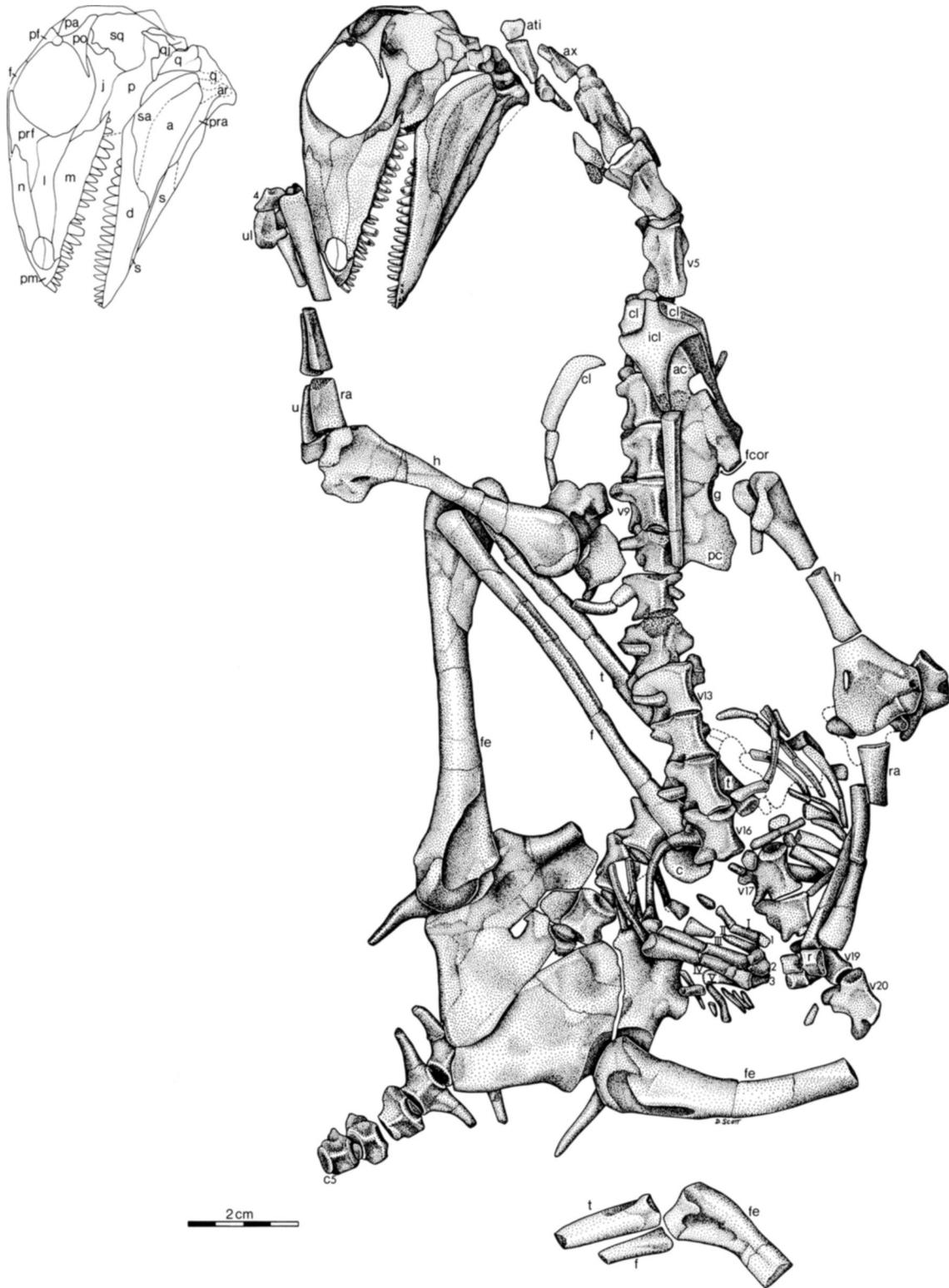


FIGURE 2. *Araeoscelis* skeletons MCZ 4380 and MCZ 8828 (referred to in text as MCZ I and MCZ II, respectively) seen mainly in ventral view.

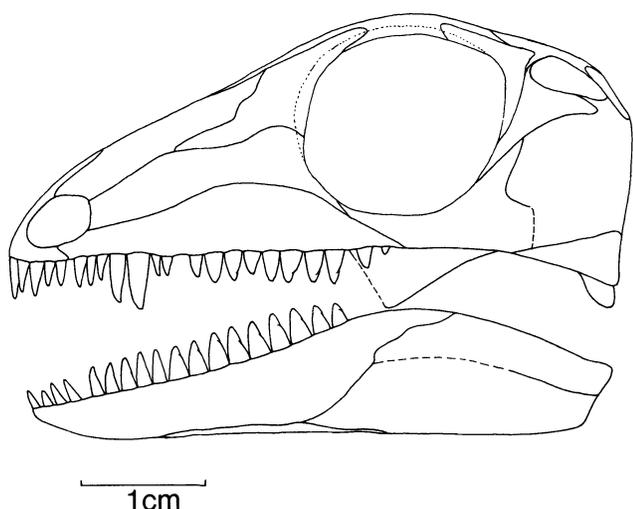


FIGURE 3. Restoration of *Araeoscelis* skull MCZ 4380 (MCZ I of text).

for the loan of the specimens described herein and referred to by the abbreviation MCZ. Thanks are also due Drs. P. P. Vaughn and E. C. Olson of the University of California, Los Angeles, for critically reading the manuscript.

DESCRIPTION

The two *Araeoscelis* skeletons described here were contained in a single block. Using wax and polyethylene glycol, or carbowax, it was possible to expose in sequence both dorsal and ventral sides of the skeletons (Figs. 1, 2). The dispositions of the skeletons and their abrupt terminations at the edges of the block strongly suggest that they were originally complete and well articulated, and that their missing portions were lost by erosion or possibly left in situ. At the time the two skeletons were collected, it may have been thought that they represented the anterior and posterior portions of a single specimen. The smaller of the two specimens, MCZ 4380, includes the skull, vertebrae 1 through 20 with some associated ribs, portions of the pectoral girdle, right forelimb with a partial carpus, left forelimb and a partial manus, partial right femur, tibia and fibula, and a complete right pes. The skeleton MCZ 8828 includes the vertebral series from presacral vertebra 20 to caudal 17 with some associated ribs, pelvic girdle, right hindlimb and pes except for the phalanges, and proximal half of the left femur. The following description is limited almost entirely to those aspects of the osteology of *Araeoscelis* in which MCZ 4380 and MCZ 8828 either correct or expand upon Vaughn's (1955) description. For convenience, in the remainder of the text MCZ 4380 and MCZ 8828 will be referred to as MCZ I and MCZ II, respectively.

Skull

Preservation of the skull of MCZ I is such that detailed comments can be made only on the dermal bones

of the skull roof and lateral surface of the lower jaw. The skull and mandibles have been severely crushed laterally, concealing much of the occiput and most of the palate. This has resulted in an enlarged lateral exposure of the premaxillae and most of the antorbital region of the skull. The temporal region has also undergone great compression, dislocating to some extent the elements of the cheek and suspensorium. Thus, the quadratojugal and quadrate have been displaced ventrally toward the mandible by the collapsed occiput, and the squamosal, postorbital, and jugal have been moved slightly, exaggerating the anteroposterior and dorsoventral dimensions of the cheek. A reconstruction of the skull of MCZ I in lateral view is presented in Figure 3.

The premaxillae are unusually large; each carries five teeth, forms nearly one-half of the external naris, and has a very long dorsal process that penetrates deeply between the anterior ends of the nasals. The first premaxillary tooth is preserved only on the left side and, though incomplete, appears to be larger than the other four. The maxilla reaches its maximum dorsal expansion just in front of the orbit, then quickly tapers to the ventral rim of the skull at about the level of the midlength of the orbit. The right maxilla carries 19 teeth, whereas the left has 17 and spaces for two more. Teeth 1 through 3 and 6 through 8 are small, similar in size to the posterior premaxillary teeth, whereas 4 and 5 are noticeably longer than any of the others and can be regarded as caniniform. The remaining maxillary teeth increase progressively in height and width posteriorly, becoming nearly as large as the caniniform teeth at about tooth positions 11 or 12 of the right maxilla and 14 or 15 of the left, then decrease in size to the end of the series. The cheek teeth exhibit a lateral shoulder.

The lacrimal is wide throughout its length and makes a substantial contribution to both the posterior margin of the external naris and the anterior margin of the orbit. Though the lacrimal-jugal suture is rather narrow, the maxilla is well separated from the anteroventral margin of the orbit. In lateral view the prefrontal and jugal are widely separated from each other by the lacrimal. It is possible, nevertheless, that the narrow, posteroventral process of the prefrontal, exposed on the right side of the skull, extended medially to the lacrimal to contact the jugal. The jugal is a large, tri-radiate element. Below the orbit it forms a substantial portion of the ventral rim of the skull and separates widely the maxilla and quadratojugal. Posterior to the orbit the jugal is distinctly bifurcated into a broad posterior sheet and a narrow posterodorsal process. Anteriorly the jugal terminates in a broad flange that not only contacts the medial surface of the maxilla above the alveolar shelf, but is in turn at least partly overlapped medially by the lacrimal. The quadratojugal is roughly triangular in outline. Though its extension along the ventral margin of the skull is at least twice as long as that along the occiput, it does not form a long, attenuated anterior process. The anteroventral process

of the triradiate postorbital narrowly separates the postfrontal and jugal to contribute to the orbital margin. A posterior process contributes to the ventral border of the temporal fenestra, inserting in a distinct groove on the external surface of the squamosal. These two elements are slightly disarticulated on the left side of the skull and their tongue-and-groove relationship is clearly revealed. The squamosal is a large sheet of bone covering most of the cheek above the quadra-tojugal. Anteriorly it has an extensive overlapping suture with the jugal. A narrow strip of bone displaced a short distance laterally from the right side of the occiput is identified as the tabular. A small fragment of bone lying in a slot on the posterolateral wing of the right parietal is the supratemporal. It appears to have been a very small element separated from the temporal fenestra by a very narrow exposure of the parietal.

The right dentary possesses 16 teeth with spaces for one or two more, whereas the left dentary appears to have a full complement of 18 teeth. The teeth increase in height posteriorly, reaching a maximum at about the sixth tooth. Continuing posteriorly, the height of the teeth remains about the same until tooth number 14, then decreases to the end of the series. The posterior half of the series exhibits a marked increase in tooth width accompanied by a substantial shoulder on the lateral surface of each tooth, similar to that seen on the posterior maxillary teeth.

Axial Skeleton

Vaughn (1955) estimated that *Araeoscelis* had 31 presacral vertebrae, including nine cervicals and 22 dorsals. In the absence of a complete neck in any of the specimens available to him, his restoration of the number, serial arrangement, and lengths of the cervical vertebrae was based mainly on four partial cervical series that also included the first few dorsals, and on isolated cervicals. Distinction between cervical and dorsal vertebrae was based primarily on two features: 1) greater elongation of the cervicals, and 2) cervical ribs single-headed and their costal area of attachment not divided into distinct capitular and tubercular areas. In reconstructing the neck Vaughn interpolated three vertebrae between the axis and the first element of one of the four cervical–dorsal series that includes dorsals 1 through 3 and the four preceding cervicals. The presence of isolated cervicals longer than any of those in the articulated series indicated to Vaughn the existence of such a gap. Thus, three vertebrae of appropriate sizes were added in order to bring the serial changes in the lengths of the cervicals in line with that typically found in living and fossil, long-necked reptiles. Vaughn clearly admitted the uncertainty of his analysis. It is, therefore, gratifying that MCZ I confirms his estimate of nine cervicals in *Araeoscelis*, which is the largest number found in any known terrestrial Paleozoic reptile. The posteriormost cervical rib in MCZ I is associated with the ninth vertebra; its holocephalous head quickly constricts to a very short, narrow shaft. Unfortunately, changes in the costal articulations in the region of the

cervical–dorsal transition are not visible in MCZ I. Despite having to estimate the lengths of some of the cervicals of MCZ I, it is still obvious that most of the serial changes in length do not match proportionally those of Vaughn's reconstruction. For example, it is apparent that in Vaughn's reconstruction cervical 2 is too short, whereas 4 and 5 are too long.

In the absence of a well exposed, complete, articulated dorsal series of vertebrae, Vaughn was able to provide only an estimate of the number of dorsals in *Araeoscelis*. He first determined the positions of the girdles relative to specific vertebrae of the column. This was done using several specimens that consisted of only short strings of dorsals with which either the pectoral or pelvic girdle was preserved in its presumably correct serial position. From these specimens it was established that the center of the glenoid cavity lies at about the level of the point of articulation between dorsals 2 and 3, and that the anterior rim of the pubis lies at about the level of the anterior surface of the second to last presacral vertebra. With this information he located these two serial positions in two nearly complete dorsal series (exposed only in ventral view). Then, after calculating the number of missing vertebrae from a few small gaps, a total of 22 dorsals in both specimens was arrived at. Williston (1914), using the same two specimens as Vaughn, simply recognized the anterior-most dorsal in both columns by their position relative to the scapular blades and counted the number of dorsals in each specimen as 19 or 20. For several reasons, we are more inclined to accept Williston's rather than Vaughn's estimate.

A possible error in Vaughn's calculation of the number of dorsals may stem from his attempt to determine the exact serial relationship of the pectoral girdle to the vertebral column. This procedure, inaccurate even under the best circumstances because there is no bony connection between the pectoral girdle and the axial skeleton, gives a different result if applied to MCZ I. The scapulocoracoid in MCZ I is as much as two or three vertebrae farther anteriorly along the column than that determined by Vaughn and, thus, the dorsal or presacral series would be shorter by this number if calculated as he did. The morphology of the neural spines also suggests that Vaughn overestimated the number of presacrals. The mammillary processes of the neural spines are present in MCZ I from the sixth vertebra posteriorward, whereas according to Vaughn's interpretation of the vertebral column they first appear on the eighth vertebra. MCZ I offers one other indirect line of evidence on the number of presacral vertebrae in *Araeoscelis*. On the assumption that the missing portion of the MCZ I skeleton was not seriously disrupted, a rough estimate can be made of its total number of presacral vertebrae. If the right femur is restored to its proper length, and knowing that its proximal end would have occupied a common transverse plane with the first sacral vertebra as in MCZ II, an approximation of no more than eight or nine missing dorsal vertebrae can be made; this would bring its total number of

presacrals to 28 or 29 (19 or 20 dorsal vertebrae). Circumstantial evidence supporting the estimate of 28 or 29 presacral vertebrae is also provided by the Late Pennsylvanian diapsid reptile *Petrolacosaurus*. Numerous similarities in the postcranial skeletons of *Araeoscelis* and *Petrolacosaurus* (discussed below) include several shared derived characters of the vertebral column (Reisz, 1981). The earlier occurring and apparently more primitive *Petrolacosaurus* nevertheless has only six cervicals of 26 presacral vertebrae. If the only major feature differentiating their vertebral columns is the three additional cervical vertebrae in *Araeoscelis*, then its presacral count would be expected to be 29.

The dorsal vertebrae of both MCZ I and MCZ II exhibit a regular pattern of alternation in the height of the neural spines. This phenomenon is not uncommon in Lower Permian reptiles (Vaughn, 1970; Reisz, 1981), but has not been previously described in *Araeoscelis*. The pattern of alternation is noticeable between vertebra 17 and the sacrum. The arrangement in MCZ II is such that the sequence of tall neural spines ends with an unusually tall and massive spine on the first sacral vertebra.

MCZ II has 17 caudal vertebrae preserved in articulation with the sacrum. In most respects these caudals resemble those of *Petrolacosaurus* (Reisz, 1981). The first nine caudals possess distinct transverse processes, but only the anteriormost two still have ribs attached to them. The shape of the remaining series of transverse processes indicates that only the anterior four of five processes could have carried ribs. Intercentra, rather than chevrons, can be seen as far posteriorly as caudal 5; fragmentary evidence suggested to Vaughn that the first chevron may occur between the second and third caudals.

Appendicular Skeleton

The pectoral girdle is incomplete in MCZ I, but preserved parts of the elements provide additional information to Vaughn's description. The morphology of the clavicle and interclavicle indicates that the clavicles did not meet at the ventral midline of the diamond-shaped head of the interclavicle. The dorsal stem of the clavicle is long and slender. A long, narrow bone lying to the right of vertebrae 8 and 9 appears to be the cleithrum; this element has not been previously reported in *Araeoscelis*. Although the posterior coracoid is not well preserved, it appears that the thumb-like process for the triceps muscle is not as narrow as indicated by Vaughn (1955, fig. 7). The pelvic girdle is completely preserved in MCZ II. The dorsolateral border of the ischium is slightly convex, rather than concave, in lateral view, and has a pointed, rather than rectangular, posterior end. In contrast to Vaughn's description, the lateral pubic tubercle is smaller and has a rectangular, rather than rounded, outline. Both specimens described here differ from those studied by Vaughn in that the fourth and fifth tarsals are distinct

elements rather than being fused with only a vestigial suture visible on the ventral surface.

SKELETAL RECONSTRUCTION

The skeletal reconstruction of an average-sized "adult" *Araeoscelis* and the tabulation of its pertinent measurements presented by Vaughn (1955, fig. 15 and pp. 389–390) were by necessity based largely on articulated portions of skeletons and isolated elements. The two partial, articulated *Araeoscelis* specimens described here provide an opportunity to re-evaluate Vaughn's composite reconstruction. Toward this purpose we use relevant measurements of MCZ I, MCZ II, and Vaughn's average-sized adult (Table 1), and the skull and postcranial reconstructions of Figures 3 and 4, which are based almost exclusively on MCZ I.

The reinterpretation of the skull of *Araeoscelis* in lateral view presented here (Fig. 3) differs in several ways in its gross morphology from that given by Vaughn (1955, fig. 1). Differences in the skull openings of the reconstructed MCZ I include a much larger external naris, a nearly circular, rather than oval, orbit, and a mainly dorsally, rather than laterally, facing upper temporal fenestra. Further contrasts can be made between the profiles of the two skull reconstructions. The reconstructed skull of MCZ I is more dome-shaped above the orbit, the occipital margin is more nearly vertically truncated, and the degree of posteroventral angulation of the ventral margin of the cheek and the resultant displacement of the jaw articulation below the level of the tooth row are not as great. The latter two features have contributed to a reduction in the extent of the postorbital region in the reconstruction of the MCZ I skull.

Even a casual comparison between the postcranial skeleton of Vaughn's reconstruction of an average-sized adult *Araeoscelis* and that of MCZ I presented here reveals large proportional differences. Except for restoring the radius and ulna too large, in Vaughn's reconstruction the relative length differences between the pro- and epipodials of both limbs, and between the fore- and hindlimb, excluding the manus and pes, appear to be accurate. Among the materials available to Vaughn, he was able to calculate (p. 366) the humerus/femur and tibia/femur length ratios (0.89 and 0.97, respectively) from associated elements of two specimens. Using these ratios, the lengths of the femur and tibia of MCZ I in Table 1 have been calculated. If the average length of a dorsal vertebra is used as a standard for comparing the relative sizes of various portions of Vaughn's composite skeleton with those of the reconstruction of MCZ I, inconsistencies of varying magnitudes become evident. On this basis, in order to make Vaughn's reconstruction conform with that of MCZ I, the length of the skull should be increased about 6.5% (to 45 mm), whereas decreases should be made in the lengths of the cervical series of vertebrae of about 9% (to 95 mm), the dorsal series of vertebrae of about 9% (to 161 mm), the scapulocoracoid of about

TABLE 1. Measurements (in mm) of *Araeoscelis* specimens MCZ 4380 (MCZ I of text) and MCZ 8828 (MCZ II of text), and Vaughn's (1955:389–390) composite skeletal reconstruction of an average-sized adult *Araeoscelis*. c = calculated.

	Vaughn's (1955) reconstruction	MCZ 4380 (MCZ I)	MCZ 8828 (MCZ II)
Skull			
Length	42.0	52.0	
Height at orbit	13.0	18.5	
Height at jaw articulation	17.0	24.5	
Mandible			
Height at coronoid process	9.5	10.0	
Vertebrae			
Length of vertebra			
2	10.6	15.0	
3	12.5	14.4	
4	15.7	14.6	
5	15.7	14.0	
6	13.0	13.8	
7	12.0	12.5	
8	10.0	11.8	
9	9.5	10.0	
10	8.5	9.0	
13	8.0	9.5	
17	8.0	9.5	
22	8.0		10.5
Length of average dorsal vertebra	8.0	9.3	
Pectoral girdle			
Length of scapulocoracoid	39.0	40.7	
Forelimb			
Length of humerus	57.0	50.0	
Length of radius	?52.0	44.8	
Length of ulnare	6.3	7.2	
Length of third metacarpal	12.0	17.2	
Length of fourth metacarpal	?15.0	20.8	
Pelvic girdle			
Length of puboischiadic plate	42.0	c34.6	47.0
Distance between acetabula	25.0		30.8
Hindlimb			
Length of femur	64.0	c56.2	77.8
Length of tibia	62.0	c54.5	75.5
Length of fibula			75.5
Length of calcaneum	7.5	9.0	10.0
Length of fourth metatarsal	25.0	19.6	

11.5% (to 35 mm), the forelimb (without manus) of about 21% (to 86 mm), and the hindlimb (without pes) of about 24.5% (to 96 mm).

In the absence of a pelvic girdle in MCZ I, its reconstructed size was calculated from the puboischiadic plate/femur length ratios of MCZ II and two partial specimens figured by Williston (1914, figs. 1, 2), which range from about 0.60 to 0.63. On the basis of this ratio, the length of the puboischiadic plate in MCZ I should be about 35 mm, whereas that in Vaughn's reconstruction should be reduced about 20% (to 34 mm), using a corrected length of 55 mm for the femur. Where comparisons are possible, similar calculations suggest a wide range of length changes in the elements of the manus and pes of Vaughn's reconstruction: increases in the lengths of the ulnare, third and fourth

metacarpals, and calcaneum of about 16% (to 7.5 mm), 41% (to 17 mm) and 36% (to 20.5 mm), and 17% (to 9 mm), respectively; and a decrease in the length of the fourth metatarsal of about 23% (to 19 mm). However, rough measurements of the overall lengths of the restored manus and pes in his reconstruction are very close to those estimated.

In Vaughn's reconstruction of *Araeoscelis* the neck appears to be proportionally much longer than is suggested by its comparison with the reconstruction of this study. This is largely due to the positioning of the pectoral girdle at a more anterior level along the vertebral column in the reconstruction of MCZ I, the approximate level at which it was preserved. It should also be noted that the relative length of the trunk, or dorsal series of vertebrae, in Vaughn's reconstruction

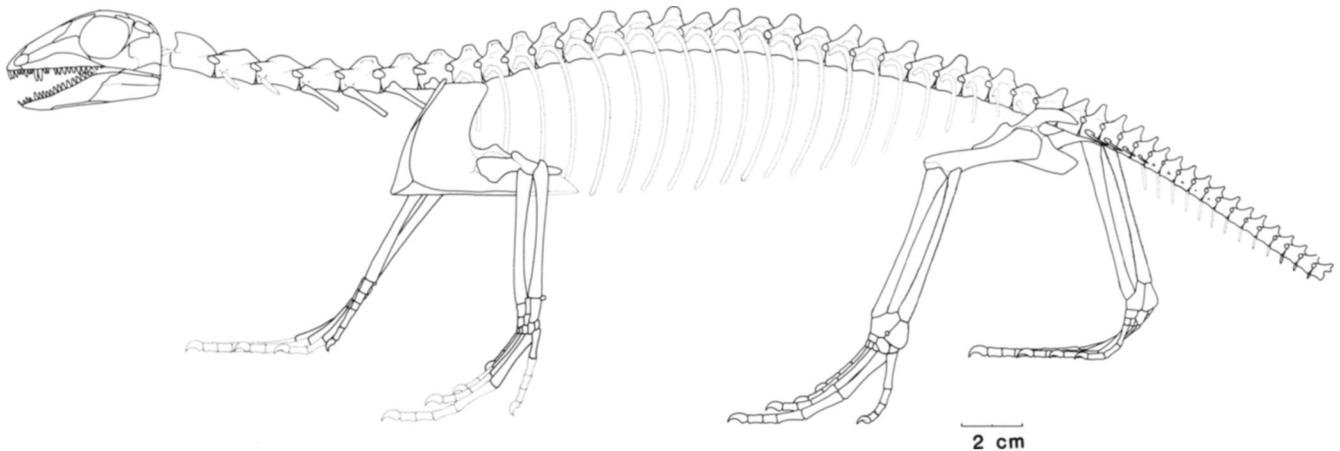


FIGURE 4. Restoration of *Araeoscelis* skeleton based mainly on MCZ 4380 (MCZ I of text). Dorsal ribs, as preserved in the specimen, are too fragmentary to allow a precise reconstruction. Consequently, it was decided to represent them as dotted lines, on the basis of other specimens of *Araeoscelis*.

would be equal to that in the MCZ I reconstruction if it were restored with 20 vertebrae, rather than 22, as recommended here. Admittedly, because animals of different sizes were used in the reconstructions, allometric growth could account for some proportion of their relative size differences noted above. However, both reconstructions are based on adult specimens and, therefore, the possible magnitude of error due to this factor could only be negligible. It might also be suggested (Currie, 1978) that a better standard of measurement for comparing the relative size differences between the two reconstructions would be the employment of the orthometric linear unit formulated by Romer and Price (1940). In that scheme linear measurements are expressed in values relative to the animal's overall size by dividing them by the specimen's orthometric linear unit—defined as equal to the radius of the average-sized dorsal centrum to the $2/3$ power. This procedure could not be used, however, because neither the transverse diameters of the dorsal centra were provided by Vaughn for his composite skeleton, nor can they be accurately obtained from the specimens studied by us. Despite these problems, and although the reconstruction presented here depicts *Araeoscelis* as having a slender and lightly built skeleton, it can still be safely concluded that it was not as highly derived in its proportions as indicated by Vaughn's reconstruction, in which it is given an especially spindly appearance by the exaggerated lengths of the fore- and hindlimbs, neck, and trunk.

Somewhat different interpretations are given here to the orientation of the scapulocoracoid and the configuration of the pes. In Paleozoic reptiles the area of the coracoids below the glenoid cavity faces mainly ventrally. The coracoids, together with the enlarged head of the clavicle and the interclavicle, form a massive, ventral shield for the ribcage. Vaughn's reconstruction of the scapulocoracoid shows a large coracoid plate

having mainly a lateral exposure. In the reconstruction presented here the lateral exposure of this plate has been reduced. The peses of MCZ I and MCZ II exhibit a structural pattern similar to that seen in *Petrolacosaurus* (Reisz, 1981), in which the tarsals and metatarsals form a tight, transversely narrow complex. As in modern cursorial lizards, but in contrast to Vaughn's reconstruction (see also his fig. 14), the proximal heads of the metatarsals overlap one another extensively so that the first tarsal does not extend beyond the level of the medial edges of the centrale and astragalus.

PHYLOGENETIC RELATIONSHIPS

Since its discovery, *Araeoscelis* has occupied a prominent position in discussions of reptilian phylogeny. In the original description of *Araeoscelis*, Williston (1910) refrained from making any statements on its position among the reptiles until the skulls could be prepared and studied; however, in a later paper that described for the first time the peculiar configuration of the temporal region of *Araeoscelis*, Williston (1913) suggested that it was ancestral to the lizards. He felt that the lizard type of skull fenestration probably arose from that seen in *Araeoscelis* by reduction of the squamosal (emargination of the cheek) and the acquisition of streptostyly. In 1933 Romer allied *Araeoscelis* with nothosaurs and plesiosaurs rather than with lizards, a position he continued to reinforce in subsequent publications (Romer, 1956, 1966, 1967). Colbert (1955, 1969) agreed with this association, providing illustrations of *Araeoscelis* and *Nothosaurus* to demonstrate the similar structure of their temporal regions. Vaughn (1955), in a thorough discussion of the phylogenetic relationships of *Araeoscelis*, concluded that it should be associated with the anapsid reptiles (captorhinomorphs) despite the presence of a temporal fenestra. He felt that, in the absence of any clear-cut association

between *Araeoscelis* and other reptile groups, the temporal fenestra should not be used as the sole diagnostic criterion for assignment at the level of subclass. Vaughn recognized, however, the close similarity between *Araeoscelis* and the Late Pennsylvanian and oldest known diapsid reptile *Petrolacosaurus*, despite the fact that at that time many important osteological features of the latter were either unknown or inadequately documented (Peabody, 1952). Carroll (1969) supported Vaughn's thesis and suggested that *Araeoscelis* may be considered simply as a somewhat specialized captorhinomorph. Recently, Reisz (1977, 1981) has given a detailed account of the osteology of *Petrolacosaurus*, which underscores its close similarity to *Araeoscelis*. The specimens described here provide even greater documentation of this resemblance.

Two hypotheses of relationships presented and tested here are illustrated in Figure 5. The first is that *Araeoscelis* shares a more recent common ancestor with (is more closely related to) *Petrolacosaurus* than with the protorothyridid captorhinomorphs, as exemplified by *Paleothyris*. This hypothesis is tested by the postcranial characters 1–11 listed below. *Paleothyris* provides the best basis for comparison with the protorothyridids because it is the most primitive and best known member of this Middle Pennsylvanian to Early Permian group (Carroll, 1969) and is very similar to *Petrolacosaurus* (Reisz, 1981). The second hypothesis tested in Figure 5 is that *Araeoscelis* and *Petrolacosaurus* share a more recent common ancestor with the eosuchians, as exemplified by *Youngina*, than with the protorothyridid captorhinomorphs. This hypothesis, tested by the cranial characters 12–16 listed below, is an expanded version of one previously presented and tested (Reisz, 1981). *Youngina* was chosen as representative of the eosuchians because it is the best known early member of the group (Gow, 1975; Carroll, 1977), and because of its closeness in structure to *Petrolacosaurus* (Reisz, 1981).

Resemblances between *Araeoscelis* and *Petrolacosaurus* are greatest in their postcranial skeletons; if only their postcranial skeletons were well known, they would undoubtedly be placed within the same family. In addition to similarities that are the result of the common possession of primitive reptilian features, the postcranial skeletons of *Araeoscelis* and *Petrolacosaurus* share the following derived characters that set them apart from all protorothyridids:

- 1) elongate cervical vertebrae and hence a long neck;
- 2) strongly developed longitudinal ventral keels on cervical and anterior dorsal vertebrae;
- 3) swollen neural arches with deep lateral excavations on posterior cervical, dorsal, and sacral vertebrae;
- 4) mammillary processes on neural spines of posterior cervical and anterior dorsal vertebrae;
- 5) small accessory anterolateral processes on anterior cervical ribs;
- 6) long, slender second sacral rib supports expanded

first sacral rib from below while abutting against ilium;

- 7) long tail with elongate midcaudal vertebrae;
- 8) enlarged coracoid process for the triceps muscle;
- 9) greatly enlarged lateral and distal pubic tubercles;
- 10) elongate limb bones with very slender proximal and distal ends;
- 11) radius nearly equal in length to humerus, and tibia nearly equal in length to femur.

The few differences between the postcranial skeletons of *Araeoscelis* and *Petrolacosaurus* have been discussed previously (Reisz, 1981:64–65); with one exception, the presence of an ischiadic notch (an apomorphic feature) in *Petrolacosaurus*, they are all relatively minor differences, with the geologically younger *Araeoscelis* being somewhat more derived. As examples, *Araeoscelis* is more advanced than *Petrolacosaurus* in its even greater elongation of the neck and limbs, fusion of the axial intercentrum to the atlantal centrum, and greater ossification of the supinator process of the humerus to form the ectepicondylar foramen.

The skull of *Araeoscelis*, as reinterpreted here, also resembles closely that of *Petrolacosaurus*. Similarities in the sutural patterns of most areas and in the general skull proportions can be attributed to the common possession of a suite of primitive reptilian features. The following characters are seen in the skulls of *Araeoscelis* and *Petrolacosaurus*, as well as in Late Permian and Triassic diapsids, but are not found in captorhinomorphs or any other Pennsylvanian or Early Permian reptiles:

- 12) upper temporal fenestra;
- 13) similar shape and interrelationships of the circumfenestral elements;
- 14) well developed suborbital fenestra;
- 15) temporal region of skull reduced in length (shorter than in all captorhinomorphs and small, primitive pelycosaur such as *Eothyris*);
- 16) relative size of skull reduced, as indicated by the skull/trunk length ratio.

Araeoscelis, however, possesses several apomorphic cranial features which are not only absent in *Petrolacosaurus*, but can be immediately recognized as reflecting an adaptation to a specific type of diet that requires a more massive, sturdily constructed skull. In *Araeoscelis* the stout, bluntly pointed marginal teeth with incipient cusp development in the cheek region are in sharp contrast with the more numerous, narrow, sharply pointed marginal teeth of *Petrolacosaurus*. The greater depth of the cheek and displacement of the jaw joint below the level of occlusion of the upper and lower tooth rows in *Araeoscelis* are features typical of forms having molar-like dentitions, such as the cotylosaurian amphibian *Diadectes*, the questionable captorhinomorph *Bolosaurus*, and the protosaur *Triphosaurus*. In *Araeoscelis* the posterodorsal process of the premaxilla is exceptionally long, the occiput is

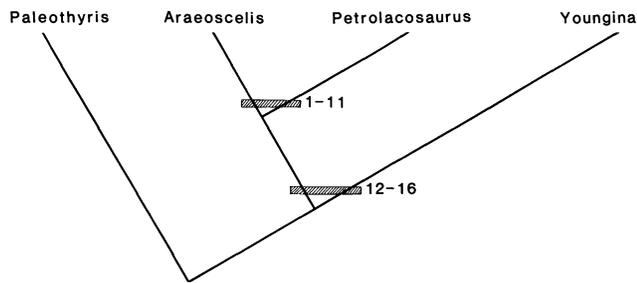


FIGURE 5. Cladogram illustrating hypotheses of relationships of *Araeoscelis*. Shared derived characters 1–16 listed in text.

more massive, and the posterior process of the post-orbital is unique in being a long, tapered projection that inserts in a groove on the squamosal along the ventral border of the upper temporal fenestra. All these cranial features are consistent with an adaptation permitting a diet not restricted to soft-bodied invertebrates. The precise preferred diet of *Araeoscelis* is of course difficult to define in the absence of stomach contents or associated invertebrates, but it is likely that it could feed on invertebrates with unusually thick chitinous exoskeletons.

Clearly *Araeoscelis* and *Petrolacosaurus* are more closely related to each other than to any other early reptile, but with the former being specialized for a diet necessitating a stronger, more massive skull. In this regard, it might then be asked if the absence of a lower temporal fenestra in *Araeoscelis* is yet another feature of its adaptation to an unusual diet. If true, then the differences in the fenestration of the temporal regions of *Araeoscelis* and *Petrolacosaurus* can be most reasonably interpreted in only two ways: (a) both genera evolved from a reptile having only an upper temporal fenestra and, while *Araeoscelis* retained this condition, the line leading to *Petrolacosaurus* developed a lower temporal fenestra; or (b) *Araeoscelis* evolved from a diapsid reptile by a secondary closure of the lower temporal fenestra as an adaptation to an unusual diet (Reisz, 1981). Considering the phylogenetic relationships proposed here (Fig. 5), the same number of morphological changes are required in both hypotheses. The first hypothesis (a) requires the parallel development of the lower temporal fenestra in the lines leading to *Petrolacosaurus* and *Youngina* (Fig. 6A), whereas the second hypothesis (b) requires a character reversal in the line leading to *Araeoscelis* (Fig. 6B). There is, however, osteological evidence to support the latter (b), reversional event hypothesis.

All the specimens of *Araeoscelis* in which the temporal region is preserved were studied, and it was observed that even in immature individuals the postorbital and jugal have a distinctly triradiate configuration, a condition normally found only in reptiles possessing a lower temporal fenestra. Further, in *Araeoscelis* the posteroventral edge of the postorbital is smooth and

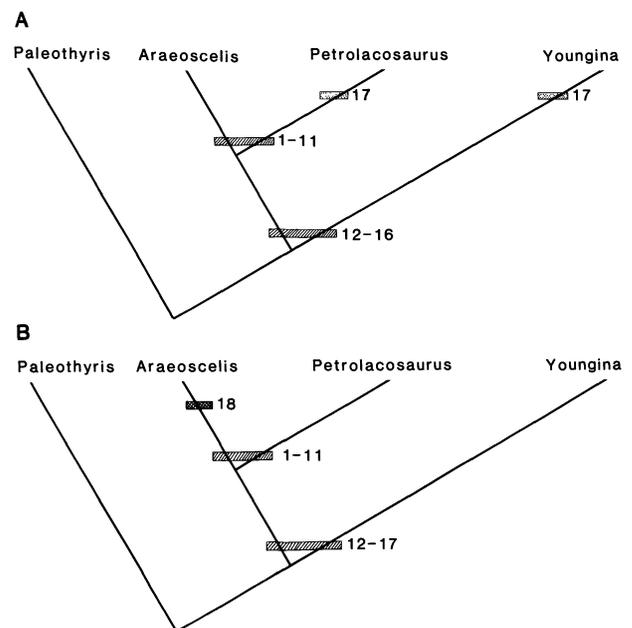


FIGURE 6. Cladogram as in Figure 5, but with two alternative hypotheses to explain absence of lower temporal fenestra in *Araeoscelis*: **A**) lower temporal fenestra acquired, character 17, independently in lines leading to *Petrolacosaurus* and *Youngina* (and all eosuchians); **B**) lower temporal fenestra in ancestor common to *Araeoscelis*, *Petrolacosaurus*, and *Youngina*, but secondarily lost, character 18, in line leading to *Araeoscelis*.

concave, and the posterior and dorsal processes of the jugal are separated by a smooth, concave notch. Both these features are typical of reptiles having a well developed lower temporal fenestra. The area between the posterior margins of the jugal and postorbital, normally occupied by the lower temporal fenestra, is covered by the squamosal in *Araeoscelis*. An anteroventral extension of the squamosal overlaps the lateral surface of the posterior process of the jugal.

It can also be pointed out that, although the upper temporal fenestra of *Araeoscelis* is like that found in diapsid reptiles, the suborbital and post-temporal fenestrae are very much reduced (Vaughn, 1955, figs. 3, 4). As in the absence of a lower temporal fenestra, this may be an adaptive response for a more massive, sturdily constructed skull.

In summary, the available evidence supports the inclusion of *Petrolacosaurus* (family Petrolacosauridae) and *Araeoscelis* (family Araeoscelidae) in the suborder Araeoscelidia (Williston, 1913). Although the former is a diapsid and the latter appears to be derived from a diapsid reptile, they are more primitive than the eosuchians, protorosaurs, or other diapsids in the absence of at least two cranial features: (1) a well developed ventrolateral parietal flange on the medial border of the upper temporal fenestra, and (2) a lateral exposure of the dorsal process of the quadrate. The parietal flange permits the extension of the adductor mus-

culature into the fenestra, whereas the lateral exposure of the dorsal process of the quadrate is the first stage in the reduction of the squamosal and the development of the reptilian otic notch. Despite certain specializations, *Petrolacosaurus* and *Araeoscelis* apparently represent a primitive stage in the adaptive radiation of the diapsid reptiles.

The exact taxonomic position of the Lower Permian reptile *Kadaliosaurus* from the German Rothliegende (Credner, 1889), considered closely related to *Araeoscelis* by Vaughn (1955), cannot be determined. This form, known only from a greater part of the postcranial skeleton, is preserved in a relatively hard, fine-grained sandstone as damaged bone without finished surfaces. Until this material is restudied, we can only state that *Kadaliosaurus* is assigned to the Araeoscelidia merely on the basis of its general skeletal proportions and outlines of its limbs, and that it is impossible to say whether it is more closely related to *Petrolacosaurus* or *Araeoscelis*. Olson (1970) has described a new araeosceloid, *Dictybolus*, on the basis of isolated elements of numerous individuals from the Lower Permian of Oklahoma. Although it can justifiably be considered an araeosceloid, it is too poorly known to be assigned with certainty to either the Araeoscelidae or the Petrolacosauridae.

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