A new araeoscelid reptile, Zarcasaurus tanyderus, from the Cutler Formation (Lower Permian) of north-central New Mexico

Donald B. Brinkman, David S. Berman, and David A. Eberth

This page is intentionally left blank to maintain order of facing pages.

A new araeoscelid reptile, *Zarcasaurus tanyderus*, from the Cutler Formation (Lower Permian) of north-central New Mexico

by *Donald B. Brinkman*, Curator, Tyrrell Museum of Palaeontology, Drumheller, Alberta, *David S Berman*, Associate Curator, Section of Vertebrate Fossils, Carnegie Museum of Natural History, Pittsburgh, PA, and
David A. Eberth, Graduate Student, Department of Geology, University of Toronto, Toronto, Ontario

A new genus and species of araeoscelid reptile, *Zarcasaurus tanyderus*, is described on the basis of a partial jaw and disarticulated postcranial elements from the Cutler Formation (Lower Permian) of north-central New Mexico. It is the first representative of this family to be reported from that state, and it is considered closely related to *Araeoscelis*. *Z. tanyderus* possesses a combination of primitive and derived features with respect to *Araeoscelis*, indicating that they could not have had a direct ancestor–descendant relationship.

Introduction

The phylogenetic positions of *Araeoscelis* and *Petrolacosaurus* are important to our understanding of the early diversification of diapsid reptiles. *Araeoscelis* is a small, lightly built reptile from the Lower Permian of Texas and Oklahoma (Vaughn, 1955; Simpson, 1979). In the most recent detailed description of *Araeoscelis*, Vaughn (1955) concluded that it is best considered a lizard-like experiment of the anapsid captorhinomorph reptiles. He argued that, except for such features as the upper temporal fenestra, specialized dentition, elongate limbs, and elongate cervical vertebrae, *Araeoscelis* resembles in most respects the primitive members of the group. On the basis of better preserved early captorhinomorphs, Carroll (1969) agreed with Vaughn's assessment. Romer (1956, 1966, 1967), on the other hand, placed *Araeoscelis* with a number of poorly known, early (Permian and Triassic) forms generally referred to as protorosaurs, which he regarded as ancestral to the sauropterygians (plesiosaurs, nothosaurs, and placodonts). The protorosaurs, as defined by Romer, are now believed to be a rather diverse assemblage of distantly related forms (Kuhn-Schnyder, 1967; Brinkman, 1981; Chatterjee, 1980; Carroll, 1981), and there is little evidence to suggest that *Araeoscelis* is closely related to any of them (Vaughn, 1955).

The controversy of the phylogenetic affinities of *Araeoscelis* has seemingly been resolved with the demonstration of its close relationship with *Petrolacosaurus*, a diapsid reptile of lizard-like proportions from the Late Pennsylvanian of Kansas. *Petrolacosaurus* was originally described by Peabody (1952), who believed it to be closely related to the eosuchians, the most primitive group of diapsid reptiles, with strong ties with the captorhinomorphs. Vaughn (1955) recognized the close similarity between *Araeoscelis* and *Petrolacosaurus* and even suggested that they may belong to the same family, thereby implying

that *Petrolacosaurus* was related to the captorhinomorphs. It also has been argued that *Petrolacosaurus* belongs to a group of archaic edaphosaurs of the early mammal-like reptile pelycosaurs (Stovall, Price, and Romer, 1966). Most recently, a redescription of *Petrolacosaurus* by Reisz (1977, 1981) has established firmly both its position as a primitive diapsid and its close relationship with *Araeoscelis*. Previously undescribed specimens of *Araeoscelis* presently under study (Reisz, Berman, and Scott, in preparation) have provided additional information that greatly expands upon our assessment of the phylogenetic relationships of *Araeoscelis*, a summary of which can be given here. Current evidence indicates that *Araeoscelis* shares a more recent common ancestor with—that is, it is more closely related to—*Petrolacosaurus* than with the captorhinomorphs, and that both genera share a more recent common ancestor with eosuchians than with the captorhinomorphs.

Together, *Araeoscelis* and *Petrolacosaurus* represent the earliest, most primitive known stage in the adaptive radiation of the diapsid reptiles. This relationship is strongly supported by their postcranial skeletons that exhibit only minor differences, but, most importantly, they share numerous derived features. Cranial differences between the two genera, on the other hand, are more marked. They are recognized as providing *Araeoscelis* with a more massive, sturdily constructed

skull, and are interpreted as an adaptation to a specialized diet that probably included invertebrates protected by a heavy exoskeleton. Most importantly, this theory is extended to suggest that the absence of a lower temporal fenestra in *Araeoscelis* may be the result of a secondary closure. These conclusions prompted a somewhat revised classification in which *Araeoscelis* was assigned to the Araeoscelidae Williston, 1910, and *Petrolacosaurus* to the Petrolacosauridae Peabody, 1952; both families were united under the suborder Araeoscelidia Williston, 1913. Other genera that have been included in this suborder, but which are considered too poorly known to be assigned to either family, are *Kadaliosaurus* Credner, 1889, and *Dictybolus* Olson, 1970.

The new araeoscelid described here as *Zarcasaurus tanyderus* consists of a partial, disarticulated skeleton collected by the authors during the summer of 1982 from the Cutler Formation (Lower Permian) near the village of Arroyo del Agua in Rio Arriba County, north-central New Mexico (Fig. 1). The discovery was reported in a preliminary paper on the sedimentology and paleontology of the Lower Permian red-bed deposits of north-central New Mexico (Eberth and Berman, 1983). *Z. tanyderus* represents the first record of an araeosceloid from New Mexico. It is more closely related to *Araeoscelis* than to *Petrolacosaurus* and is, therefore, assigned to the Araeoscelidae.
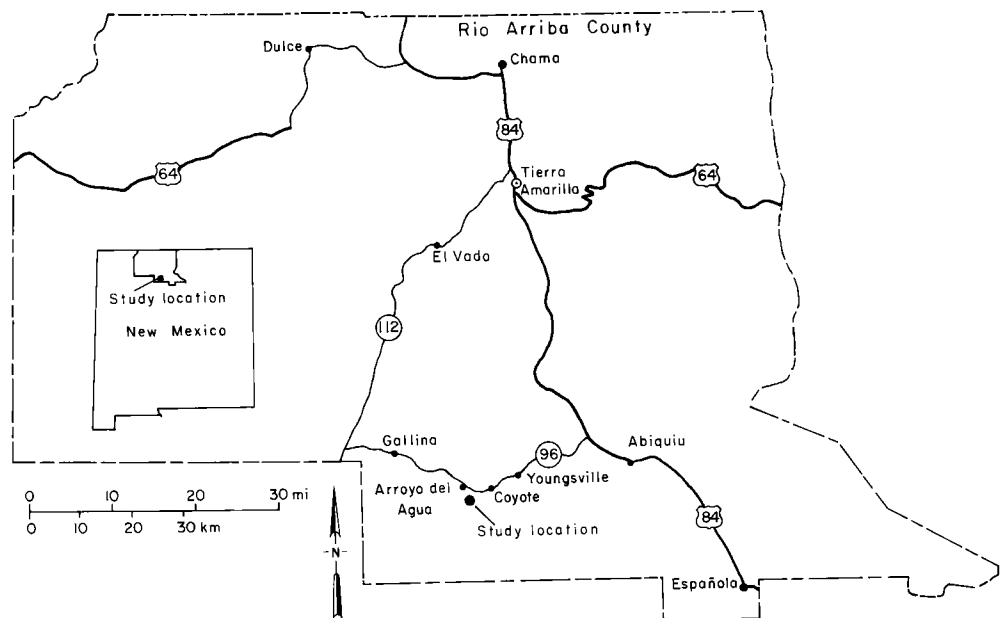

FIGURE 1—Locality of *Zarcasaurus tanyderus*, Rio Arriba County, north-central New Mexico.

Systematic paleontology
Class Reptilia
Suborder Araeoscelidia Williston, 1913
Family Araeoscelidae Williston, 1910
Zarcasaurus, new genus
Type species: *Zarcasaurus tanyderus* n.sp.

Etymology—Refers to the Agua Sarca, a small creek about 3 km northwest of the type locality; pronounced Zarca and spelled as such on early maps and publications (Langston, 1953).

Diagnosis—A small araeoscelid closely related to *Araeoscelis* and characterized by the following derived features: cervical vertebrae are longer, with central lengths exceeding those of the dorsals by as much as two times; absence of a prominent notch on the distal edge of the astragalus that separates the articular facets for the fourth distal tarsal and centrale. Primitive features that distinguish *Zarcasaurus* from *Araeoscelis* include: the humerus lacks ectepicondylar foramen; a supracondylar process is present on the posterior condyle of the femur; a concave area of finished bone separates the lateral and medial articular surfaces on the proximal end of the tibia; the tibial facet of the astragalus is convex and not developed into a ridge-and-trough pattern.

Zarcasaurus tanyderus, new species

Etymology—Derived from the Greek *tany*, long, and *deros*, neck, referring to the specimen's very long cervical vertebrae.

Holotype—CM 41704 (collections of the Carnegie Museum of Natural History, Section of Vertebrate Fossils) is a partial, disarticulated skeleton consisting of the following elements: a short section of the left ramus of the lower jaw just anterior to the adductor fossa; three cervical, including axis, and five dorsal vertebrae, and fragments of centra; the distal ends of both humeri; the proximal and distal ends of the left femur and a fragment of the proximal end of the right femur; the proximal and distal ends of both tibiae; the left astragalus; several metapodials and phalanges; and numerous indeterminate fragments.

Horizon and locality—Cutler Formation (Lower Permian: Wolfcampian), about 1 km southeast of the small village of Arroyo del Agua in Rio Arriba County, north-central New Mexico (exact locality data on file at the Carnegie Museum of Natural History). The holotype, as is the case with the majority of vertebrate fossils from the Cutler Formation of the Arroyo del Agua area, is from the extensive, well-known deposits commonly referred to as lake or pond deposits (Langston, 1953). Preliminary investigations of these deposits (Eberth and Berman, 1983), as well as adjacent lithofacies, have revealed that they are discrete, U-shaped bodies of interbedded mudstones and minor sandstones and have a very limited extent. Their close lateral association with U-shaped, low-sinuosity channel fills consisting of vertically accreted, medium to coarse sandstones more properly suggests that they are actually remnants of crevasse channel fills in an anastomosed reach

of an ancient river system. The limited extents of the crevasse channels suggest the proximity of interchannel pond and/or marsh environments where such channels would quickly lose their U-shape morphology.

Diagnosis—Same as for the genus.

Description and comparison

All of the elements assigned to the holotype, CM 41704, were collected from the surface and had eroded out of a single slope. Although only two elements (dorsal vertebrae) were articulated, all the elements were found closely associated. None of the parts is duplicated and all are of an appropriate size to have belonged to a single individual. No bones were found associated with CM 41704 that would indicate the presence of another form of similar size. For these reasons, CM 41704 is considered to represent a single individual that probably was represented originally by a greater part of articulated skeleton.

Lower jaw—The lower jaw is represented by a short section of the left ramus just anterior to the adductor fossa (Fig. 2). It includes the posterior end of the dentary, which includes one empty socket and two incomplete teeth. The more complete tooth is missing only its tip; this is possibly a result of wear. The tooth is stout, like those of *Araeoscelis*, rather than like the slender teeth of *Petrolacosaurus*, though it lacks the lateral, incipient cusp seen in the cheek teeth of *Araeoscelis*. Little of the bases of the teeth can be seen in the lateral view of the jaw due to the low level of implantation of the teeth on the medial surface of the dentary. In this feature, *Zarcasaurus* more closely approaches *Petrolacosaurus* than *Araeoscelis*.

Identification of the sutures on the lateral surface of the jaw fragment presents no serious problems. However, with the exception of the coronoid, the interpretation of the sutures on the medial surface is uncertain. Though the coronoid of *Zarcasaurus* is incomplete, its relative depth, as in *Araeoscelis*, was obviously much greater than in *Petrolacosaurus*. Identification of a narrow splint of bone contacting the anterior end of the coronoid as the anterior coronoid, or precoronoid, is

Vertebra	1	2	3	4	5	6
Axis	—	2.8	3.5	—	—	7.5
Midcervical	11.2	4.0	4.6	3.5	3.8	8.5
Posterior cervical	8.6	3.5	3.7	3.1	3.9	4.3
Dorsal	5.9	2.8	3.9	3.2	3.9	3.4
Dorsal	5.0	3.4	3.5	3.3	4.0	3.4

tentative, as is identification of the prearticular–angular contact near the ventral margin of the jaw fragment. In its possession of a precoronoid, *Zarcasaurus* would more closely approach *Araeoscelis* than *Petrolacosaurus*. There is no evidence of a postsplenial in *Zarcasaurus*. The postsplenial is absent in *Araeoscelis*, but is present in *Petrolacosaurus* as a moderate-sized element wedged between the angular and prearticular at the level of the coronoid.

Vertebrae—Three cervical and five dorsal vertebrae of varying degrees of completeness and fragments of centra comprise the vertebral elements. Two of the dorsal vertebrae were preserved in articulation. The three cervicals (Fig. 3A–C) include an axis, midcervical, and posterior cervical. Determination of their serial positions has been based on successive changes in the cervical series of *Araeoscelis* and *Petrolacosaurus*.

As in *Araeoscelis* and *Petrolacosaurus*, the cervical vertebrae of *Zarcasaurus* are conspicuously elongate. The centrum of the midcervical, the longest and most complete of the three cervicals, is 1.9 and 2.2 times the length of the longest and shortest of the preserved dorsals (Table 1). The neural spine, nearly preserved in its entirety only in the midcervical, is very low. In the axis and midcervical vertebrae, the pedicle of the neural arch extends about three-fourths of the length ☞
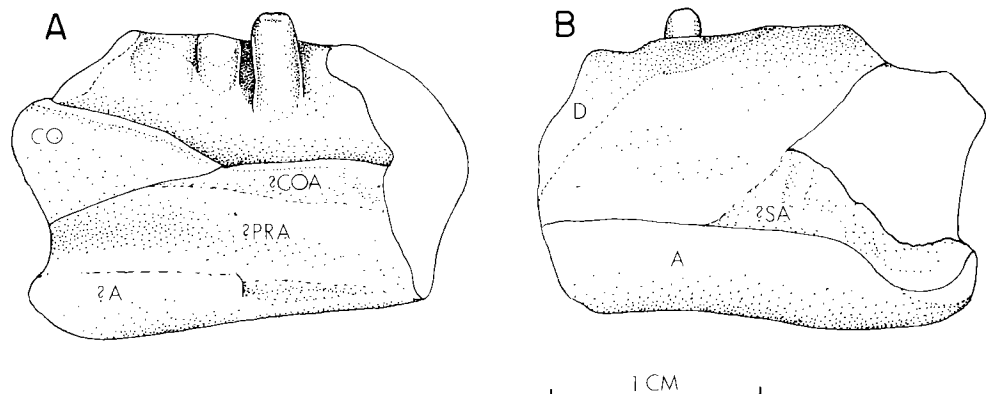

FIGURE 2—*Zarcasaurus tanyderus* gen. et sp. nov., CM 41704. **A** is the medial and **B** is the lateral view of a portion of the left mandible; angular **(A)**, coronoid **(CO)**, anterior coronoid **(COA)**, dentary **(D)**, prearticular **(PRA)**, and surangular **(SA)** indicated.

of the centrum, and in the posterior cervical the pedicle is restricted to the anterior half of the centrum. The zygapophyses of the axis and midcervical are narrowly separated and extend very little beyond the lateral margin of the centrum. The axial prezygapophyses are much smaller than those of the midcervical, face nearly as much laterally as dorsally, and the facets are convex. The prezygapophyses of the midcervical extend beyond the end of the centrum, whereas the postzygapophyses do not. At the base of the neural arch, there is a shallow, lateral excavation. The anterior ends of the centra are strongly beveled to accommodate the intercentra (not found); in the axis, this feature has been exaggerated by breakage. The transverse processes of the axis and midcervical vertebrae consist of a very small, horizontal ridge near the anterior end of the centrum; a small costal facet is present near the anterior end of the process. The transverse process of the posterior cervical differs from the more anterior vertebrae in several features: its base extends posterodorsally from the anterior rim of the centrum to the midlength of the base of the neural arch; it extends much farther laterally; and the length of the costal facet is nearly equal to that of the base of the process and expands somewhat posterodorsally. The ventral longitudinal keels of the axial and midcervical centra are V-shaped in cross section, whereas that of the posterior cervical is U-shaped.

Several features demonstrate that the cervical vertebrae of *Zarcasaurus* more closely approach those of *Araeoscelis* (Fig. 3D) than those of *Petrolacosaurus* (Fig. 3E). The most noticeable feature is that the neural arch pedicles of the axis and midcervical vertebrae of *Zarcasaurus* and the cervicals of *Araeoscelis* extend for about three-fourths of the length of the centrum. In *Petrolacosaurus*, on the other hand, the pedicles of all the cervicals are restricted to the anterior half of the centrum, as in the posterior cervical of *Zarcasaurus*. The cervical zygapophyses diverge more widely and extend more laterally beyond the margin of the centrum in *Petrolacosaurus* than in *Zarcasaurus* or *Araeoscelis*. The neural spine of the midcervical of *Zarcasaurus*, as in the cervicals of *Araeoscelis*, is little more than a low ridge, whereas in *Petrolacosaurus*, the cervical spines are moderately high and blade-like.

The dorsal vertebrae of *Zarcasaurus* (Fig. 3E), as in *Petrolacosaurus* and *Araeoscelis*, are considerably shorter than the cervicals. The lengths of the centra are about equal to, or slightly less than, the widths. With the marked exception of an isolated neural arch, the height of the dorsal neural spines is far greater than that of the midcervical. The difference in spine height of the dorsal vertebrae may be a result of gradual change along the column or of a regular pattern of alternation in height of successive spines; the latter feature has been reported not only in *Araeoscelis* (Reisz, Ber-

man, and Scott, in preparation) and *Petrolacosaurus* (Reisz, 1981), but in other Paleozoic tetrapods as well (Vaughn, 1970). The dorsal neural arches of *Zarcasaurus* and *Araeoscelis* differ from those of *Petrolacosaurus*: they are slightly wider, have a somewhat swollen appearance, and they possess much lower neural spines. None of the neural spines show any signs of the mammillary processes that have been described in *Araeoscelis* (Vaughn, 1955) and *Petrolacosaurus* (Reisz, 1981). The neural arches exhibit prominent lateral excavations. The zygapophyses are smaller than those of the cervicals and extend very little beyond the lateral margin of the centrum. The prezygapophyses extend only to the anterior end of the centrum, whereas the postzygapophyses extend beyond the posterior end. The zygapophyseal planes diverge only slightly from the horizontal. The small transverse processes are situated just below the base of the prezygapophyses near the anterior rim of the centrum and project only a short distance laterally. The elongate axis of the base of the process, as well as its costal surface, is inclined about 45° from the horizontal, and neither the process nor its costal surface exhibit any signs of a capitular–tubercular division. There is no beveling of the ventral rim of the anterior and posterior ends of the centra to accommodate the intercentra (not found). The ventral halves of the centra are laterally compressed, forming a narrow, ventral, longitudinal ridge that is U-shaped in cross section.

APPENDICULAR ELEMENTS—Preserved elements of the appendicular skeleton include: the distal ends of both humeri; the proximal and distal ends of the left femur and a fragment of the proximal end of the right femur; the proximal and distal ends of both tibiae; the left astragalus; and isolated metapodials and phalanges. The terminology used in orienting the hind-limb elements is that proposed by Rewcastle (1980).

The humerus of *Zarcasaurus* (Fig. 4), as in *Petrolacosaurus* and most primitive reptiles, possesses a well-developed, distally-directed supinator process which in dorsal view is separated from the ectepicondyle by a deep ectepicondylar groove. Both the supinator process and ectepicondyle are covered by finished bone, indicating a late adult stage of development. In *Araeoscelis* the ectepicondylar groove is bridged over distally to form the ectepicondylar foramen. Just distal to the supinator process a prominent, hemispherical radial condyle projects ventrally and slightly distally from the distal margin of the humerus.

Enough of the femur is represented to indicate that it was very slender (Fig. 5). For most of its length the shaft is subcircular in cross section. The proximal end of the femur is turned strongly upward, and the entire bone probably had a pronounced sigmoidal flexure. In this feature and in its slender proportions, the femur of *Zarcasaurus* is more like that of *Araeoscelis* than *Petrolacosaurus*. As in *Petrolacosaurus*, but in contrast to *Araeoscelis*, the adductor ridge does not terminate proximally in a distinct internal trochanter;
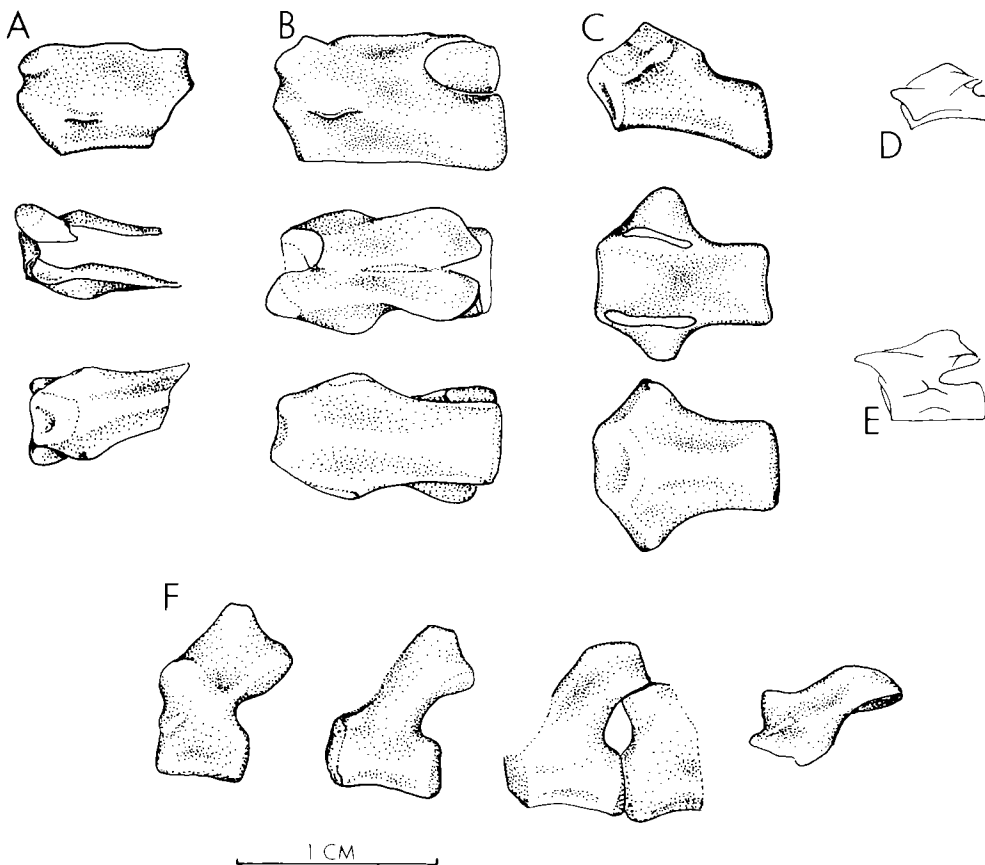

FIGURE 3—A is the axis, B is the midcervical, and C is the posterior cervical vertebrae of *Zarcasaurus tanyderus* gen. et sp. nov., CM 41704, in lateral, dorsal, and ventral views; D and E are diagrammatic lateral views (not to scale) of posterior cervicals of *Araeoscelis* (after Vaughn, 1955) and *Petrolacosaurus* (after Reisz, 1981), respectively; F are lateral views of dorsal vertebrae (relative serial positions unknown) of *Z. tanyderus*.

rather, the adductor ridge, which is represented on the shaft of the femur by a faintly visible line, extends proximally as a sharp crest along the anterior bounding ridge of the intertrochanteric fossa. The length of the intertrochanteric fossa is greater than the width of the femur head. This compares well with *Araeoscelis*, but differs from *Petrolacosaurus* where the two measurements are about equal. As in primitive reptiles generally, a distinct ischiotrochanteric tuberosity is present near the posterior margin of the dorsal surface of the femur head.

The dorsal surface of the distal end of the femur is marked by a deep intercondylar fossa. The dorsal surface of the posterior condyle extends distally a short distance beyond the level of the tibial facet below it as a distinct, lip-like process, here termed the supracondylar process. A narrow strip of finished bone, continuous with that of the intercondylar fossa, separates this process from the tibial facet. Ridges on the dorsal surface of the supracondylar process mark the site of attachment of the extensor musculature of the lower leg. In contrast to *Zarcasaurus*, the intercondylar fossa is shallower, and the supracondylar process is absent in *Araeoscelis*. The intercondylar fossa of *Petrolacosaurus* is well developed. Although the femur figured by Reisz (1981, fig. 22) does not show a supracondylar process, an extensive area of unfinished bone at this site may indicate that its absence is due to the immaturity of the specimen. The popliteal area on the ventral surface of the distal end of the femur is a smooth, broadly concave depression. As in *Araeoscelis*, the posterior limited ridge of the popliteal area is low; in *Petrolacosaurus* it is a relatively high, sharp crest.

The proximal articular surface of the tibia (Fig. 6) is triangular in outline with a large, oval-shaped, lateral articular surface for the posterior (fibular) condyle of the femur and a small, mesial articular surface that faces somewhat laterally and posteriorly for the anterior (tibial) condyle of the femur. The anterior corner of the proximal end of the tibia forms a knob-shaped cnemial crest similar to, but less strongly developed than, *Araeoscelis*; the tibia of *Petrolacosaurus* lacks such a crest. Between these three areas of the proximal articular surface is a deep, concave area of finished bone. A similar area of finished bone has not been described in *Araeoscelis*, nor has it been observed in those *Araeoscelis* specimens examined during the course of this study that are presumed to be adults on the basis of the complete ossification of their skeletons. The proximal articular surface of the tibia of *Petrolacosaurus* has not been described in detail. The preserved proximal ends of the tibiae of *Zarcasaurus* suggest that the bone is concave laterally. This is a primitive feature seen in *Petrolacosaurus* and primitive reptiles generally, but not in *Araeoscelis* where the great elongation of the limbs has resulted in the tibia being straight or slightly concave medially. A ridge on the lateral surface of the tibia presumably marks the site of attachment of the interosseous ligament. The distal articular surface

of the tibia is divided into two areas—a flat, lateral area and a convex, ventrally projecting, mesial area—that are separated by a shallow groove. A similar arrangement is seen in *Araeoscelis* and *Petrolacosaurus*.

The left astragalus (Fig. 7) is complete, and the L-shape is typically reptilian, although the neck is short. The astragalus of *Petrolacosaurus* is also L-shaped, but the neck is much longer; in *Araeoscelis* it is not L-shaped, although the neck is similarly short. A notch near the distal end of the calcaneal articular surface forms the mesial portion of the perforating foramen. The distal articular surface of the astragalus is divided subequally into a lateral (fibular), convex, condylar-like area and a mesial (tibial), concave, socket-like area. Presumably the convex area articulated with the fourth distal tarsal, and the concave area articulated with the centrale. This arrangement is unlike the condition in either *Araeoscelis* or *Petrolacosaurus*, where a notch in the distal edge of the astragalus separates a lateral condyloid process (the articular surface for the fourth distal tarsal) from a mesial convex area (the articular surface for the centrale). The tibial articular facet of the astragalus of *Zarcasaurus* is a simple convex surface, with no ridge-and-trough pattern like that

seen in *Araeoscelis* and *Petrolacosaurus*. Of the isolated phalanges, one is strongly curved and claw-like.

Discussion

The assessment of *Zarcasaurus tanyderus* as a member of the suborder Araeoscelidia is based on its elongate cervical vertebrae, lateral excavations of the neural arches, the structure of the distal articular surface of the tibia, and the long, slender proportions of the limb elements. All of these features are shared by *Araeoscelis* and *Petrolacosaurus*. The astragalus is the only element that does not conform to the basic structural pattern of the araeosceloids. Apart from this, the holotype does not possess any features that would prevent its assignment to the suborder.

It is clear from the previous section that *Zarcasaurus* more closely approaches *Araeoscelis* than *Petrolacosaurus* in overall structure. Among the more important features shared by *Zarcasaurus* and *Araeoscelis*, but absent in *Petrolacosaurus*, are the shape and position of the cnemial crest of the tibia, the presence of stout teeth, and the great length of the pedicles of the cervical neural arches. The former two features are interpreted as shared,
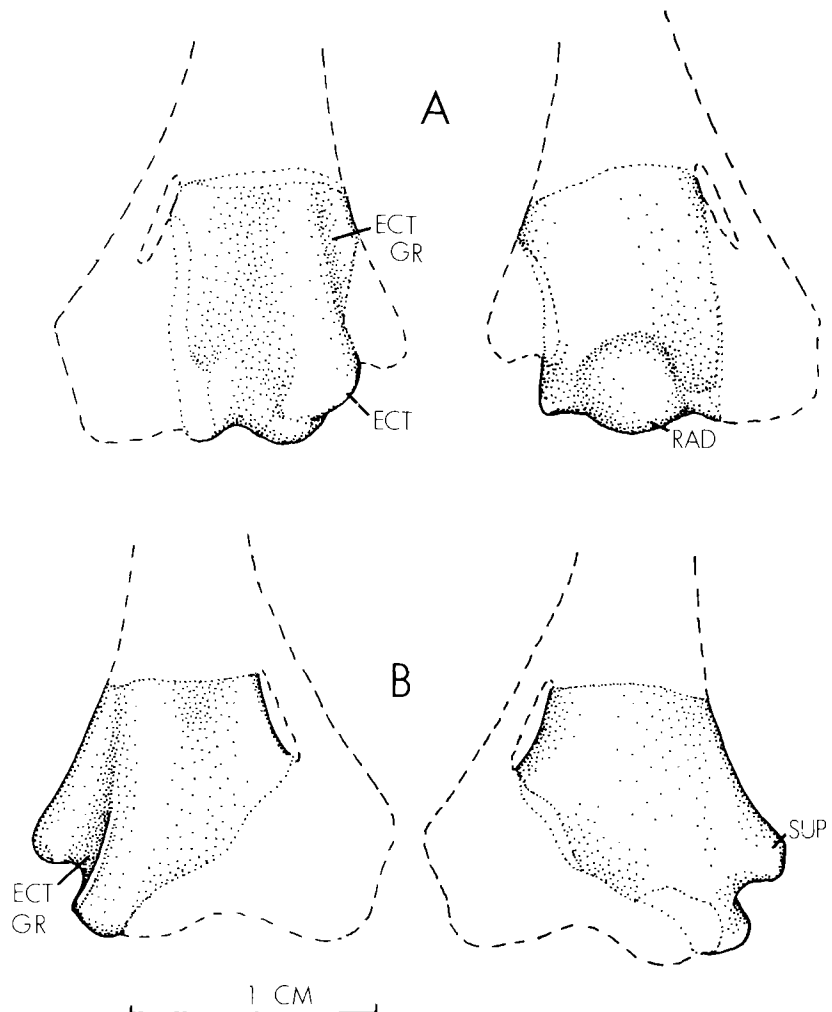

FIGURE 4—*Zarcasaurus tanyderus* gen. et sp. nov. Dorsal and ventral views of distal ends of the right, **A,** and the left, **B,** humeri; ectepicondyle (**ECT**), ectepicondylar groove (**ECT GR**), radial condyle (**RAD**), and supinator process (**SUP**) indicated.

derived characters and, therefore, underscore the close relationship between *Zarcasaurus* and *Araeoscelis*. *Zarcasaurus* possesses several features that are widespread among primitive reptiles and can be considered primitive with respect to the condition in *Araeoscelis*: there is no ectepicondylar foramen on the humerus; a distinct supracondylar process on the posterior condyle of the femur is present; a concave area of finished bone separates the lateral and medial articular surfaces on the proximal end of the tibia; and the simple tibial facet of the astragalus, which is a convex surface lacking a ridge-and-trough configuration, is present. An additional feature that may be considered primitive within the Araeoscelidia is the absence of a distinct internal trochanter of the femur. This character state is not typical of primitive reptiles, but is present in *Petrolacosaurus*, which in other respects is considered to be the most primitive member of the suborder Araeoscelidia (Reisz, Berman, and Scott, in preparation).

Zarcasaurus exhibits two derived features not seen in either *Araeoscelis* or *Petrolacosaurus*. One is the great length of the cervical vertebrae of *Zarcasaurus*, the centra of which are as much as two times longer than the dorsal centra, whereas in *Araeoscelis* the maximum is 1.61 times (Reisz, Berman, and Scott, in preparation) and in *Petrolacosaurus* 1.55 times (Reisz, 1981). The second derived feature of *Zarcasaurus* is the structure of the distal articular surface of the astragalus. The astragali of *Petrolacosaurus* and *Araeoscelis*, as in *Captorhinus* (Peabody, 1951), have a deep notch in the distal articular border. This notch separates a condyloid-like structure at the laterodistal corner of the astragalus from a convex surface mesial to this. The distal notch corresponds to the suture between the proximal fourth centrale and the tibiale of the amphibian tarsus (Peabody, 1951). The absence of the distal notch in *Zarcasaurus* is therefore viewed as a derived character. Although closely related to *Araeoscelis*, the existence in *Zarcasaurus* of both primitive and derived features with respect to *Araeoscelis* rules out the possibility that they had an ancestor–descendant relationship.

It is worth noting that araeosceloid remains may be present among the isolated limb elements described by Reisz (1980) from the Early Permian at Fort Sill, Oklahoma, and referred by him to the Protorothyrididae. This assessment was made solely on the basis of primitive features, particularly the presence on the humerus of a prominent,
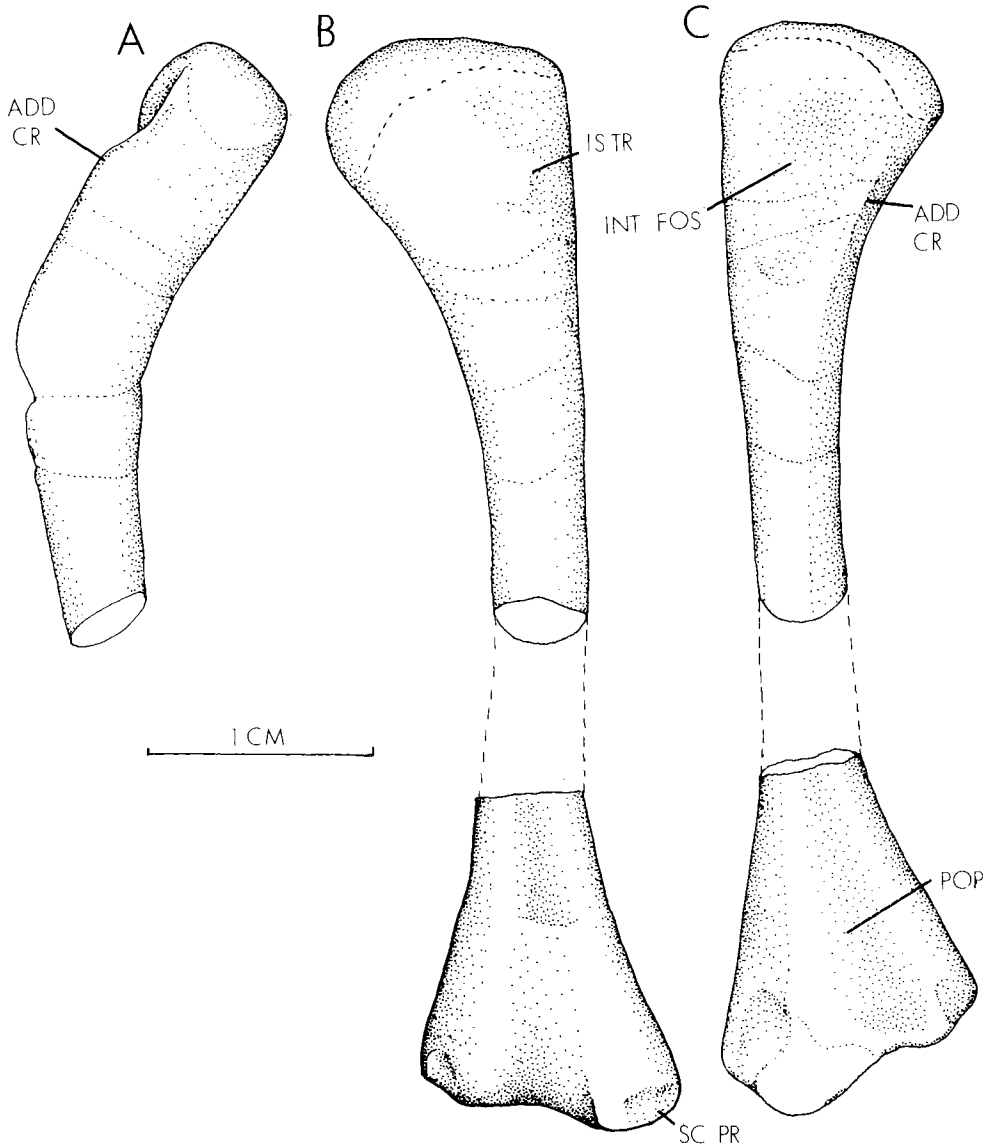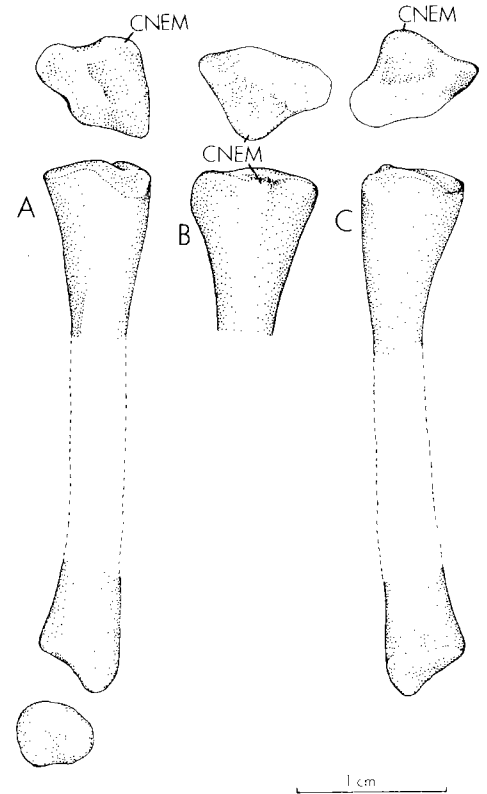
FIGURE 6—Left tibia of *Zarcasaurus tanyderus* gen. et sp. nov. **A** are the posteromedial and articular surface views of the proximal and distal ends, **B** are the anterior and articular surface views of the proximal end, and **C** are the posterolateral and proximal articular surface views of the proximal and distal ends; cnemial crest **(CNEM)** indicated.
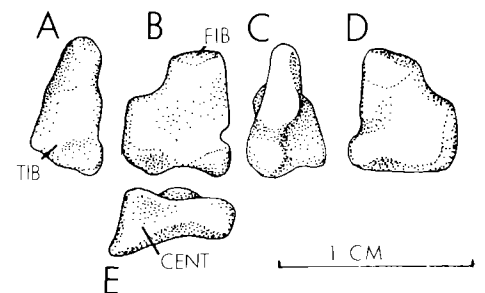
FIGURE 5—Left femur of *Zarcasaurus tanyderus* gen. et sp. nov. **A** is the anterior view of the proximal end; **B** is the dorsal view and **C** is the ventral view of the proximal and distal ends; adductor crest **(ADD CR)**, intertrochanteric fossa **(INT FOS)**, ischiotrochantericus tuberosity **(IS TR)**, popliteal area **(POP)**, and supracondylar process **(SC PR)** indicated.

FIGURE 7—Left astragalus of *Zarcasaurus tanyderus* gen. et sp. nov. **A** is the medial, **B** is the anterior, **C** is the lateral, **D** is the posterior, and **E** is the distal view; articular surface for centrale **(CENT)**, articular surface for fibula **(FIB)**, articular surface for tibia **(TIB)** indicated.

distally-directed supinator process located just proximal to the radial condyle. Reisz noted that the Fort Sill humerus and femur are surprisingly similar to humeri and femora of *Petrolacosaurus* and *Araeoscelis*, but he rejected their assignment to an araeoscelid because in the protorothyridids, as in the Fort Sill elements, the epipodials are considerably shorter than the propodials, whereas in *Petrolacosaurus* and *Araeoscelis* they are subequal in length. This comparison, though valid, cannot be applied here with any confidence because there is no assurance that the Fort Sill limb bones are from individuals of equal size, or that they represent a single, or even closely related, species. On the other hand, the very slender proportions of the humeri and femora of the Fort Sill form, *Petrolacosaurus*, and *Araeoscelis* can be considered a shared, derived character that sets them apart from the protorothyridids. The possibility that some of the Fort Sill limb elements described by Reisz may pertain to an araeosceloid is reinforced by Carroll's (1968) description of an isolated parietal from the same deposit that indicates the presence of a well-developed, upper temporal opening. In retrospect, his conclusion that this parietal may belong to a form structurally, if not phylogenetically, intermediate between primitive captorhinomorphs and eosuchians now appears even more plausible.

References

Brinkman, D. B., 1981, The origin of the crocodiloid tarsi and the interrelationships of thecodontian archosaurs: Breviora, no. 466, pp. 1–23.

Carroll, R. L., 1968, A ?diapsid (Reptilia) parietal from the Lower Permian of Oklahoma: Postilla, no. 117, pp. 1–7.

———, 1969, A Middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles: Journal of Paleontology, v. 4, pp. 151–170.

———, 1981, Plesiosaur ancestors from the Upper Permian of Madagascar: Royal Society of London, Philosophical Transactions, Ser. B, v. 293, pp. 315–383.

Chatterjee, S., 1980, *Malerisaurus,* a new eosuchian reptile from the Late Triassic of India: Royal Society of London, Philosophical Transactions, Ser. B, v. 291, pp. 163–200.

Credner, H., 1889, Die Stegocephalen und Saurier aus dem Rothliegenden des Plauen'schen Grundes bei Dresden, VIII, Theil, *Kadaliosaurus priscus* Cred.: Zeitschrift der deutschen geologischen Gesellschaft, v. 41, pp. 319–342.

Eberth, D. A., and Berman, D. S., 1983, Sedimentology and paleontology of Lower Permian fluvial redbeds of north-central New Mexico—preliminary report: New Mexico Geology, v. 5, no. 2, pp. 21–25.

Kuhn–Schnyder, E., 1967, Das problem der Euryapsida: Colloque Internationaux du Centre National de la Recherche Scientifique, no. 163, pp. 335–348.

Langston, W., Jr., 1953, Permian amphibians from New Mexico: University of California, Publications in Geological Sciences, v. 29, pp. 349–416.

Olson, E. C., 1970, New and little known genera and species of vertebrates from the Lower Permian of Oklahoma: Fieldiana, Geology, v. 18, pp. 359–434.

Peabody, F. E., 1951, The origin of the astragalus of reptiles: Evolution, v. 5, pp. 339–344.

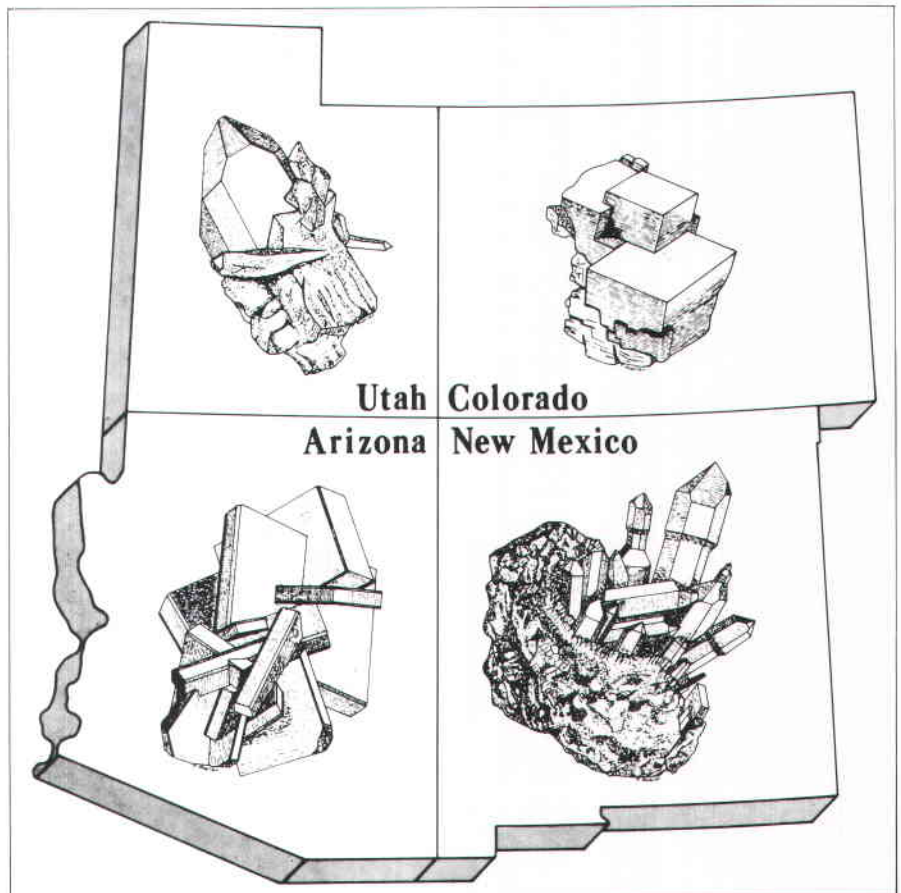———, 1952, *Petrolacosaurus kansensis* Lane, a Pennsylvanian reptile from Kansas: University of Kansas Paleontological Contributions, Vertebrata, Art. 1, 44 pp.

Reisz, R. R., 1977, *Petrolacosaurus,* the oldest known diapsid reptile: Science, v. 196, pp. 1,091–1,093.

———, 1980, A protorothyridid captorhinomorph reptile from the Lower Permian of Oklahoma: Royal Ontario Museum, Life Sciences Contributions, no. 121, pp. 1–16.

———, 1981, A diapsid reptile from the Pennsylvanian of Kansas: University of Kansas, Museum of Natural History Special Publications, no. 7, 74 pp.

Reisz, R. R., Berman, D. S, and Scott, D., The anatomy and relationships of the Lower Permian reptile *Araeoscelis,* in preparation.

Rewcastle, S. C., 1980, Form and function in lacertilian knee and mesotarsal joints—a contribution to the analysis of sprawling locomotion: London, Journal of Zoology, v. 191, pp. 147–170.

Romer, A. S., 1956, The osteology of the reptiles: University of Chicago Press, 772 pp.

———, 1966, Vertebrate paleontology, 3rd edition: University of Chicago Press, 468 pp.

———, 1967, Early reptilian evolution re-viewed: Evolution, v. 21, pp. 821–833.

Simpson, L. C., 1979, Upper Gearyan and Lower Leonardian terrestrial vertebrate faunas of Oklahoma: Oklahoma Geology Notes, v. 39, pp. 3–19.

Stovall, J. W., Price, L. I., and Romer, A. S., 1966, The postcranial skeleton of the giant Permian pelycosaur *Cotylorhynchus romerii:* Museum of Comparative Zoology, Bulletin, v. 135, pp. 1–30.

Vaughn, P. P., 1955, The Permian reptile *Araeoscelis* restudied: Museum of Comparative Zoology, Bulletin, v. 113, pp. 305–467.

———, 1970, Alternation of neural spine height in certain Early Permian tetrapods: Southern California Academy of Sciences, Bulletin, v. 60, pp. 80–86.

Williston, S. W., 1910, New Permian reptiles—rhachitomous vertebrae: Journal of Geology, v. 18, pp. 585–600.

———, 1913, An ancestral lizard from the Permian of Texas: Science, v. 38, pp. 825–826. ☐

Scepter quartz from Kingston, New Mexico; rhodochrosite from Silverton, Colorado; topaz from the Thomas Mountains, Utah; and barite from Superior, Arizona, represent minerals from the four-corners states. Artist: Teresa Mueller