

AN EARLY PERMIAN VARANODONTINE VARANOPID (SYNAPSIDA: EUPELYCOSAURIA) FROM THE RICHARDS SPUR LOCALITY, OKLAHOMA

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ABSTRACT—Description of the first varanodontine varanopid material from the highly fossiliferous limestone fissure fill deposits at Richards Spur (Dolese Brothers Limestone Quarry), Oklahoma, is based on elements of at least three individuals recovered from two separate blocks of sedimentary rock. One block, which yielded associated cranial and postcranial bones from both adult and juvenile individuals, includes two well-preserved parabasisphenoid complexes, vertebrae, forelimb, pelvic girdle, and hind limb bones. An isolated maxilla fragment from another block preserves the diagnostic dorsal process characteristic of varanodontines. Preserved cranial and postcranial material is virtually identical to the varanodontine *Varanops brevirostris*. Taxonomic assessment of this new material in the context of the most comprehensive phylogenetic analysis of Varanopidae to date indicates the Richards Spur varanodontine is referable to *Varanops brevirostris* based on distinctive characters of the maxilla and the parabasisphenoid. The large size of *Varanops* suggests it was one of the top predators of the Richards Spur ecosystem. The Richards Spur locality records the only known co-occurrence of a mycterosaurine and a varanodontine varanopid at a single locality, and varanopids are the most common synspsids in the assemblage. As generally rare components of the more typically preserved lowland environments, the relative abundance and diversity of varanopids at Richards Spur suggests that they may have been more common components of the upland ecosystems in the Early Permian.

INTRODUCTION

The Richards Spur locality, located near the town of Richards Spur, Oklahoma, continues to be one of the most productive Early Permian tetrapod fossil localities in the world. Exposure of fossiliferous clay-rich fissure fill during the continuous excavation of the Ordovician limestone of the Arbuckle Formation by the Dolese Brothers Limestone Quarry operation frequently turns up new fossils. As a result, the faunal list of the Richards Spur locality continues to grow (Kissel et al., 2002; Anderson and Reisz, 2004; Reisz, 2005). Currently, the fauna comprises 25 taxa (Sullivan and Reisz, 1999; Sullivan et al., 2000; Anderson and Reisz, 2004; Reisz, 2005). Although stratigraphically isolated due to their unique geological context, the fossil assemblage of the Richards Spur fissure fills is thought to represent an Early Permian upland ecosystem, probably distant and distinct from the more frequently preserved lowland fluviodeltaic environments typical of North American Permian fossil deposits (Olson, 1971; Kemp, 1982; Sullivan and Reisz, 1999; Eberth et al., 2000; Sullivan et al., 2000).

In contrast to the more typical lowland assemblages from the Early Permian, the fissure fills are typified by the presence of relatively small, terrestrial forms. The captorhinid reptile *Captorhinus aguti* dominates the assemblage, and terrestrially adapted dissorophoid temnospondyls and seymouriamorphs are also common (Sullivan and Reisz, 2000). Synspsids, represented by a mycterosaurine varanopid (Reisz et al., 1997) and a basal caseosaur (Reisz, 2005), are generally rare.

Here we report on previously undescribed varanodontine varanopid material from the Richards Spur assemblage. All of the bones but one, a partial maxilla, were found within a single block of fissure fill matrix that had eroded out and was found near the base of the quarry wall. The new material is significantly larger than any previously known varanopid material from the assemblage, and adds to the faunal list of this important locality.

This discovery contributes to our knowledge of the Richards Spur paleocommunity structure, and has implications for the biostratigraphic correlation of the fissure fill deposits.

Institutional Abbreviations—FMNH (WM, UR, UC), Field Museum of Natural History, Chicago, IL; OMNH, Oklahoma Museum of Natural History, University of Oklahoma, Norman, OK.

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA Osborn, 1903
EUPELYCOSAURIA Kemp, 1982
VARANOPIIDAE Romer and Price, 1940
VARANODONTINAE Reisz and Berman, 2001
VARANOPS Williston, 1914
VARANOPS cf. *BREVIROSTRIS* (Williston, 1911)

Type Species—*VARANOPS BREVIROSTRIS* (Williston, 1911)

Diagnosis—As for type species.

Holotype—FMNH (WM) 644, from the *Cacops* bonebed, Indian Creek, west of Coffee Creek, Baylor County, Lower Permian.

Referred Material—Disarticulated but associated cranial and postcranial bones (Figs. 1–6) recovered from a single block of fissure fill sediment that includes: two parabasisphenoid complexes (OMNH 73157, 73158); axial neural arch (OMNH 73159); two cervical vertebrae (OMNH 73160, 73161); five mid-dorsal vertebrae (OMNH 73162–73166); one caudal vertebra (73167); one sacral rib (OMNH 73177); three partial humeri (OMNH 73168–70); partial ulna (OMNH 73171); complete radius (OMNH 73172); metacarpal IV (OMNH 73173); ilium (OMNH 73174); two tibiae (OMNH 73175, 73176); and a single metatarsal (OMNH 73178). One isolated maxilla fragment (OMNH 73156) found in proximity to the aforementioned block at the base of the quarry wall (Fig. 1). At least three individuals are represented, as indicated by the presence of two parabasisphenoid complexes in one block and the maxilla from another non-associated block.

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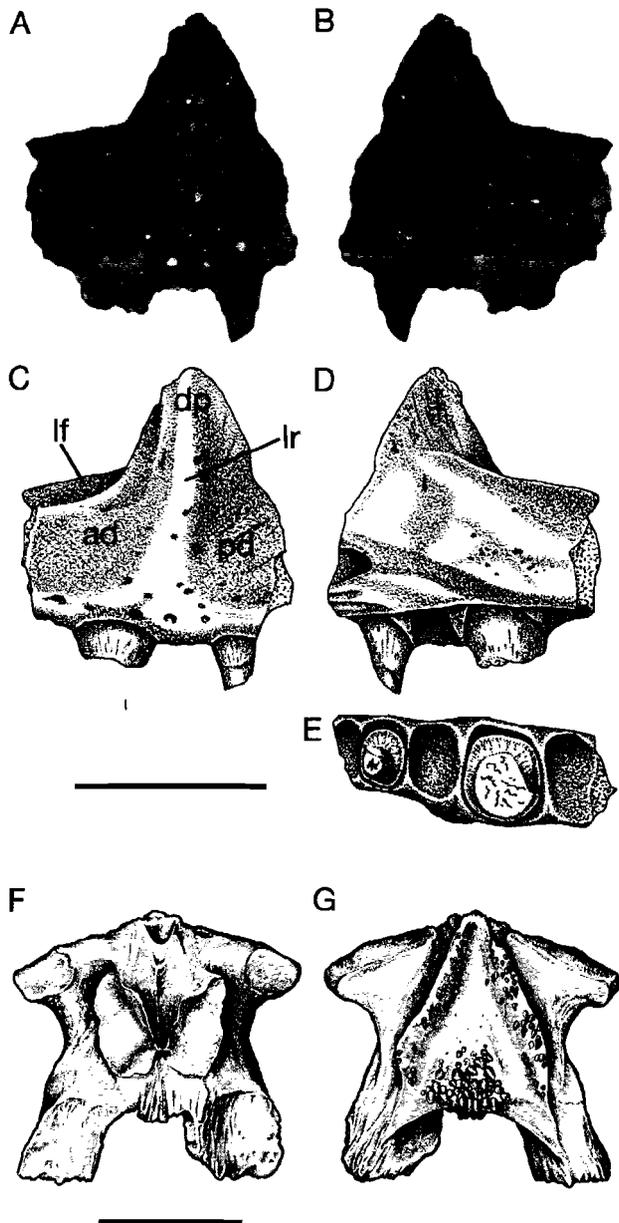


FIGURE 1. Cranial elements of the Richards Spur varanodontine varanopid. A and B, photographs and C and D, illustrations of the partial maxilla (OMNH 73156) of the Richards Spur varanodontine varanopid in medial and lateral views, respectively, and E, ventral view. The parabasisphenoid complex (OMNH 73157) in F, dorsal and G, ventral views, where anterior is toward the top of the page. Abbreviations: ad, anterior depression; dp, dorsal process; lf, lacrimal facet; lr, lateral ridge; pd, posterior depression. Scale bar equals 1 cm.

Locality and Horizon—Richards Spur locality (Dolese Brothers Limestone Quarry) near Fort Sill, Comanche County, Oklahoma. Lower Permian. The site is designated OMNH locality V51.

Revised Diagnosis—A varanodontine varanopid diagnosed by the following autapomorphies: maxilla with a dorsal process that has both anterior and posterior depressions of subequal depth on the lateral surface; long trough-like lacrimal facet ex-

tending anteriorly from the base of the dorsal process along the anterodorsal margin of the maxilla. Differs from non-varanodontine varanopids in the presence of a posterior dental field on the parasphenoid and the tall triangular dorsal process of the maxilla.

DESCRIPTION

Cranium

The isolated fragment of a left maxilla (OMNH 73156) consists of the diagnostic dorsal process and the caniniform region of the marginal dentition (Fig. 1A–E). The dorsal process is triangular in lateral view and overlaps the lateral surface of the lacrimal. A similar process occurs in other varanodontines, but is absent in *Archaeovenator*, and mycterosaurines. Anterior to the dorsal process, the lacrimal facet extends along the dorsal margin of the maxilla. The location and morphology of the lacrimal facet is identical to that in *Varanops*, but differs from that in *Varanodon*, where it is located on the more vertical anterior margin of the dorsal process. A low vertical ridge on the lateral surface of the dorsal process separates two shallow depressions. This morphology is also seen in *Varanops* and *Varanodon*, but is unknown in any other varanopid. Ventrally the ridge curves anteriorly, as in *Varanops brevirostris* (FMNH UC 644). The posterior depression is slightly deeper, but more restricted anteroposteriorly than the anterior depression beneath the posterior end of the external naris, as in *V. brevirostris*. *Varanodon* differs from OMNH 73156 and *Varanops* in the possession of a much deeper, pocket-like posterior depression. The incomplete ventral alveolar ramus preserves four alveoli, the largest of which is directly beneath the lateral ridge. The broken bases of two incomplete teeth are present, and as a result the degree of distal recurvature of the marginal dentition is unknown.

Two parasphenoid-basisphenoid (parabasisphenoid) complexes were recovered from the same block. One is approximately 20% larger (OMNH 73157; Fig. 1F, G) than the other (OMNH 73158; not shown), but the two are otherwise identical in morphology. The parabasisphenoid complex is subtriangular in ventral view, except for the large, laterally-projecting basiptyergoid processes, which have transversely elongate, anteriorly facing articular facets. The processes are relatively large compared to those in *Archaeovenator*, mycterosaurines, and *Aerosaurus*. The ventral parasphenoid plate gradually increases in width posterior to the basiptyergoid processes. A similar gradual increase in width is seen in *Mycterosaurus* (Berman and Reisz, 1982) and *Archaeovenator* (Reisz and Dilkes, 2003). In *Aerosaurus* and *Mesenosaurus*, the increase is abrupt (Langston and Reisz, 1981; Reisz and Berman, 2001), giving the parasphenoid plate a bell-shaped outline.

Parasphenoidal dentition extends from the base of the cultriform process to the posterior margin of the parasphenoid plate, but is concentrated into three fields, including a well-developed posteromedial field that is also present in *Varanops*, *Aerosaurus*, and *Varanodon*, but absent in *Archaeovenator* and mycterosaurines, including *Mycterosaurus* (= *Basicranodon*, Reisz et al. 1997). The other two dental fields extend along the entire, ventrally-raised, lateral margins of the parasphenoid plate. A deep median sulcus lies between them and the ventrally expanded basiptyergoid processes. The larger of the parabasisphenoids has relatively larger, more densely packed dental fields, and the margins of the parasphenoid plate project further ventrally. These differences may be attributable to ontogenetic growth, indicating both adult and juvenile material is present in the sample.

Postcranial Axial Skeleton

Nine varanopid vertebrae were recovered. Several smaller vertebrae exhibit poor fusion between the neural arch and the centrum (not shown), again indicating the presence of age classes.

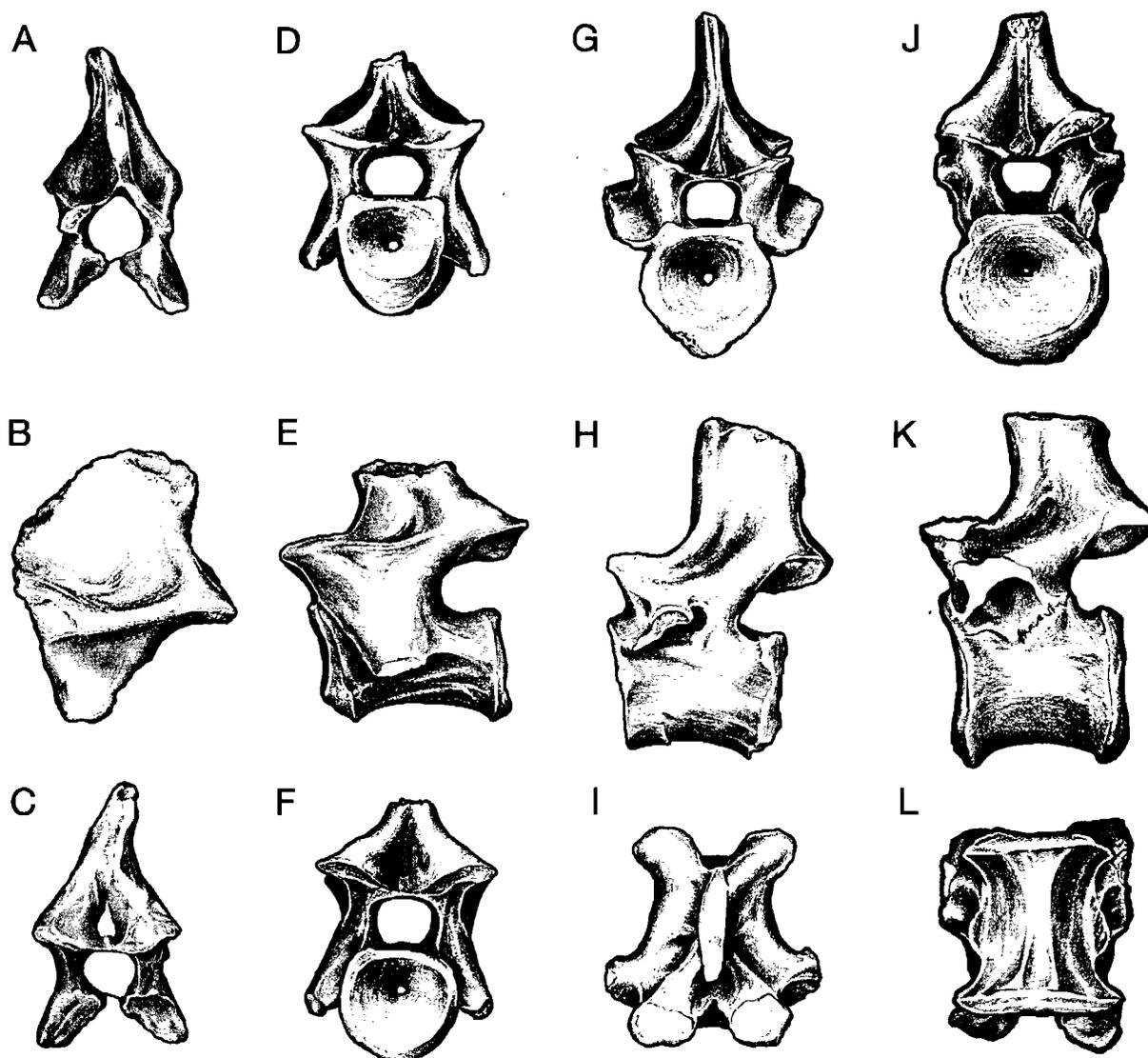


FIGURE 2. Vertebral elements of the Richards Spur varanodontine varanopid. Axial neural arch (OMNH 73159) in A, anterior; B, left lateral; and C, posterior views. Anterior cervical vertebra (OMNH 73160) in D, anterior; E, left lateral; and F, posterior views. Mid-dorsal vertebra (OMNH 73162) in G, anterior; H, left lateral; and I dorsal with anterior toward the top of the page. Another mid-dorsal vertebra (OMNH 73163) in J, posterior; K, left lateral; and L, ventral with anterior toward the top of the page. Scale bar equals 1 cm.

The axis is represented by a nearly complete neural arch (OMNH 73159; Fig. 2A–C). It has an anteroposteriorly expanded neural spine that is longer in this dimension than the spine height, although the dorsal margin is broken. The posterior margin of the spine projects slightly above the postzygapophyses. The angle formed between the posterior margin of the spine and the postzygapophyseal lamina is larger than in *Mycterosaurus* from the same deposit (Reisz et al., 1997), but is similar to that in *Varanops* (FMNH UR 2423). In ophiacodontids, the posterior margin of the axial neural spine is vertical (Romer and Price, 1940). The preserved right prezygapophysis has an articular facet for the atlantal postzygapophysis that faces posterodorsally. A distinct lateral ridge at the base of the neural spine connects the pre- and postzygapophyses. There is a slight depression dorsal to the midpoint of the ridge. The postzygapophyseal articulations

diverge slightly and face ventrolaterally. The postzygapophyseal laminae converge on the neural spine and border a deep median depression (Fig. 2C).

The anterior cervical vertebrae (OMNH 73160, 73161) have ventrolaterally projecting transverse processes and elongate centra (Fig. 2D–F). The centrum is amphicoelous and has a weakly developed midventral ridge. There is a large anterior facet for the intercentrum. The anterior articular face of the centrum is offset slightly dorsally relative to the posterior face, indicating that the neck extended upwards from the level of the dorsal series of the vertebral column. Prezygapophyses extend anteriorly beyond the centrum and have large articulation surfaces that are wider than long. The postzygapophyses form bell-shaped structures that border a deep midline depression between the dorsally projecting posterior laminae. The base of the neural

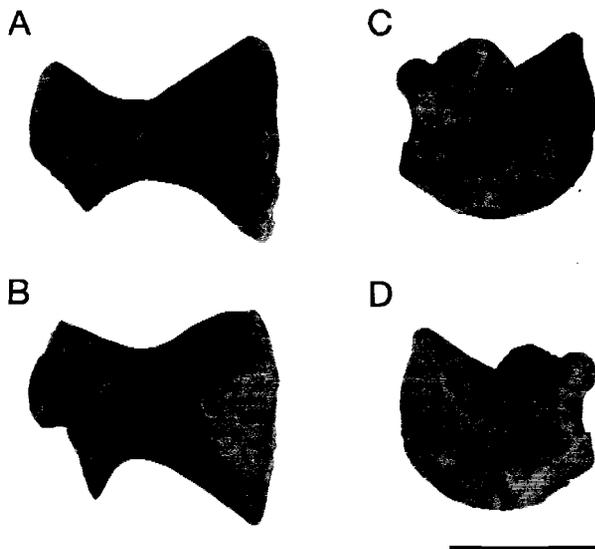


FIGURE 3. Axial element of the Richards Spur varanodontine varanopid. First sacral rib (OMNH 73177) in A, anterior; B, dorsal; C, proximal; and D, distal view. Scale bar equals 1 cm.

spine is located over the posterior half of the centrum. Unfortunately, the neural spine is broken off at its base and its height cannot be determined.

All five mid-dorsal vertebrae (OMNH 73162-73166) exhibit features that resemble those of several other varanodontine varanopids (*Varanops*, *Varanodon*, and *Watongia*) in their general shape and proportions (Fig. 2G-L). In detailed morphology, the dorsals more closely resemble those of *Varanops* than those of *Watongia* (Reisz and Laurin, 2004) and *Varanodon* in that the lateral excavations of the neural arch at the base of the neural spines are particularly deep and elongate anteroposteriorly. The midventral keel of the centrum does not exhibit the sharp ventral keel as in sphenacodontids, and is similar in morphology to those in *Varanops* and *Watongia* (Reisz and Laurin, 2004). The only dorsal vertebra that preserves a significant portion of the neural spine shows that it is taller than the centrum.

The only preserved caudal vertebra (OMNH 73167; not figured) has an elongate centrum with a slight midventral ridge. Both pre- and postzygapophyses are small and circular in outline, and their articular surfaces are angled medioventrally. A thin ridge-like keel extends posterodorsally from the posterior margin of the prezygapophyses to become continuous with the anterior margin of the neural spine. The neural spine is positioned caudally on the arch, with its posterior margin in line with the level of the posterior margin of the centrum. In lateral view, the neural spine narrows from its base towards its incomplete dorsal margin.

Cervical and dorsal ribs were not identified in the sample. The first sacral rib is hourglass-shaped and robust (OMNH 73177; Fig. 3). There are three distinct but conjoined articular facets for articulation with the vertebral column. The dorsalmost and anteriormost facet articulates with the base of the neural arch, whereas the remaining two join the centra. The anterior facet also contacts the centrum of the preceding dorsal vertebra. The distal articulation surface matches perfectly the corresponding facet on the preserved ilium. In distal view the iliac articulation surface is crescentic, with its concave margin facing dorsally, and there is a posterior facet for the articulation with the succeeding sacral rib.

Appendicular Skeleton

The appendicular bones closely resemble those of *Varanops*, and again can be divided into two size classes. Three incomplete humeri are present: proximal portions of two right humeri (OMNH 73168, 73169) and the distal portion of a left humerus (OMNH 73170). The two partial proximal humeri, the larger of which (Fig. 4A-C) is approximately 30% larger than the other (not shown), are distinctly varanopid based on the presence of a greatly expanded width of the head relative to the shaft and a deltopectoral crest that has two accessory ridges separated by an intervening flattened shelf (Reisz and Laurin, 2004). The first ridge extends from the anterior tip of the deltopectoral crest along the dorsal margin to the proximal articular surface. The second ridge, not as well defined, is located on the ventral surface between the deltopectoral crest and the proximal articulation. The partial left distal humerus (Fig. 4D, E) is of the same size class as the smallest proximal humerus, and both may represent juvenile individuals due to their small size compared to the morphologically identical large humerus in the sample. The distal margin is smooth and subtly bilobate in dorsal and ventral views, as in *Varanops* (Romer and Price, 1940) and *Aerosaurus*. This is in contrast to the scalloped or rugose margin of ophiacodontids and sphenacodontids, although the possibility that this feature is ontogenetic cannot be discounted. The smooth, broad entepicondyle has a large entepicondylar foramen, and there is no evidence of an ectepicondylar foramen, also absent in *Watongia* (Reisz and Laurin, 2004). The supinator process, sharply differentiated from the ectepicondyle, is relatively shorter than that of *Aerosaurus*.

A proximal half of a right ulna (OMNH 73171) and a complete right radius (OMNH 73172) pertain to the smaller size class in the sample. The shape of the ulna is identical to that in *Varanops brevirostris* and *Varanodon* (Fig. 5A, B). The olecranon is relatively larger in *Aerosaurus* (Langston and Reisz, 1981), as well as ophiacodontids and sphenacodontids (Romer and Price, 1940), and appears to be reduced in *Watongia* (Reisz and Laurin, 2004). Romer and Price (1940) note that the ossification of the olecranon likely occurred late in ontogeny, and the morphology of this region is highly variable and ontogeny-dependent in early synapsids.

The radius has a shaft strongly bowed dorsally (Fig. 4H-K). *Watongia* exhibits a greater degree of bowing than *Varanops*, and the Richards Spur varanopid is very similar to *Varanops* in this aspect. A narrow ridge extends down the medial edge of nearly the entire length of the bone. This ridge is present in the varanodontines *Watongia*, *Varanodon*, and *Varanops*, as well as in the mycterosaurine *Mesenosaurus*. The lateral surface has a low ridge that extends along the distal half of the bone. This ridge is also present in *Varanops* and *Watongia*, but indeterminate in *Varanodon*, *Aerosaurus*, and *Mesenosaurus*. The proximal and distal ends are moderately expanded in comparison to ophiacodontids, and they also lack the surrounding rugosities described by Romer and Price (1940) in ophiacodontids and some sphenacodontids, although this feature may also be ontogeny dependent. The proximal end is semicircular in outline and the articular surface has a central depression for articulation with the humerus (Fig. 4F). The distal end is roughly ovoid in outline and the articular surface is gently concave (Fig. 4G).

A single complete juvenile left metacarpal (OMNH 73173) is identified as that of digit IV by the presence of a distinctive lip on the lateral side of the proximal end (Fig. 5C, D), which is also seen in *Varanodon* and *Watongia*. The ventral surface of the lip is slightly concave, and the bone tapers into a very slender shaft relative to the expanded ends. The distal articular surface is convex for articulation with the first phalanx.

A single, almost complete ilium (OMNH 73174; Fig. 5G, H) closely resembles that of *Varanops*. The size is proportionally

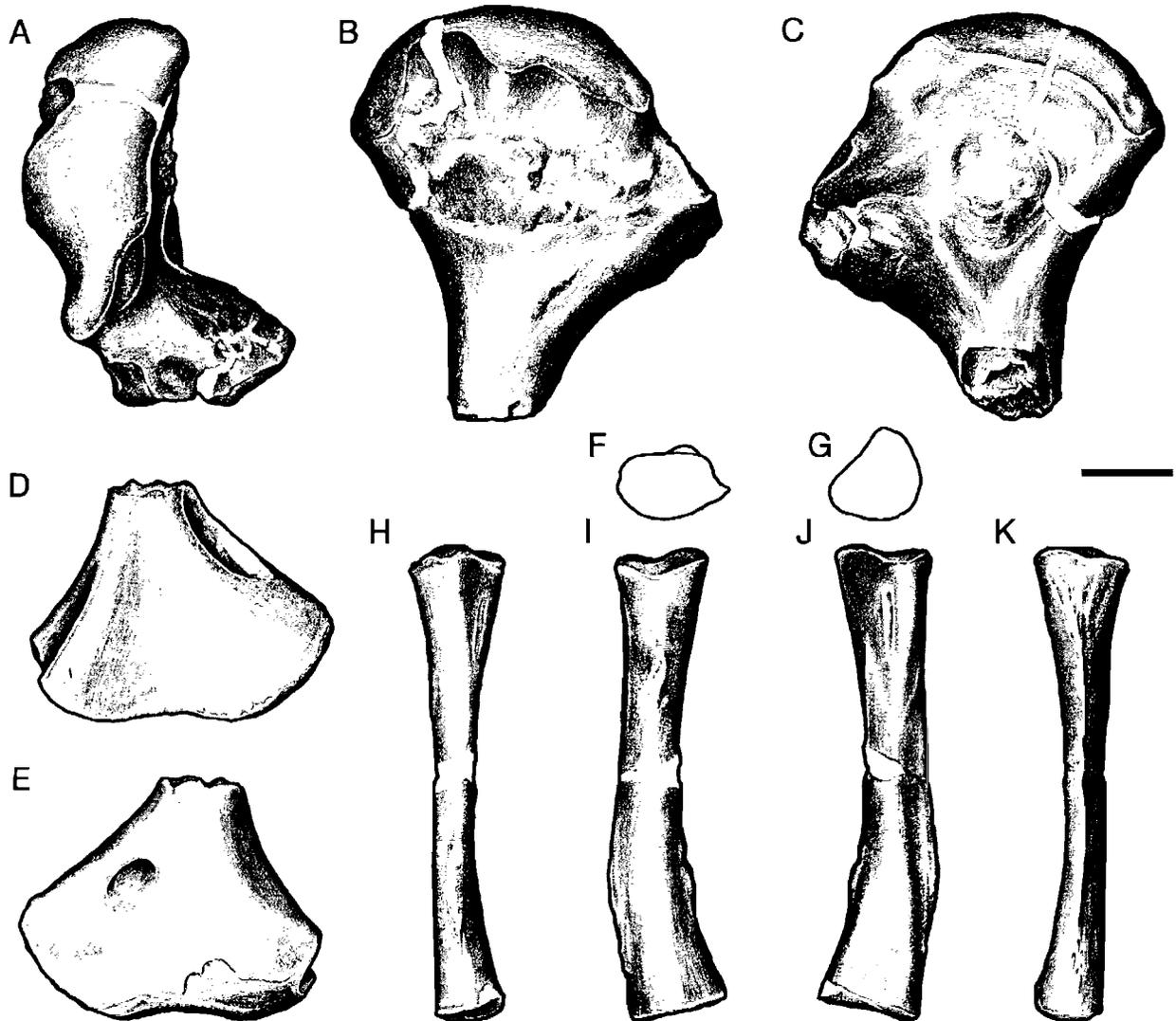


FIGURE 4. Appendicular skeletal elements of the forelimb of the Richards Spur varanodontine varanopid. Proximal end of a right humerus (OMNH 73168) in A, proximal view of the articular surface; B, dorsal and C, ventral view. Distal end of left humerus (OMNH 73170) in D, dorsal and E, ventral views. Complete right radius (OMNH 73172) in H, lateral; I, dorsal; J, ventral; and K, medial views with outlines of the proximal and distal views for F and G. Scale bar equals 1 cm.

consistent with the other juvenile material in the sample. Above the acetabulum the ilium extends as a thin, posteriorly tapering blade. Both the dorsal and ventral margins of the blade are sharply edged (i.e., acuminate in cross section). The anterior margin of the iliac blade ascends abruptly above the midpoint of the acetabulum, and is subvertical as characteristic of varanopids. The horizontal dorsal margin of the blade extends posteriorly at right angle to the anterior margin. The ilium is thickest around the anterior and superior margins of the acetabulum and lacks a prominent posterior acetabular buttress seen in *Aerosaurus* and ophiacodontids (Romer and Price, 1940; Langston and Reisz, 1981). The ischiac peduncle is considerably larger than the pubic peduncle. Medially a large, rugose region at the base of the blade and posterior to the medial flange indicates the area of attachment for the sacral rib.

A complete right tibia (OMNH 73175; Fig. 6A–C) and proximal third of a left tibia (OMNH 73176; not shown) were recovered, of which the latter is approximately 20% larger than the

former (juvenile), but both are almost identical in morphology to that of *Varanops*. The wide, mediolaterally expanded tibial head is reniform in proximal view (Fig. 6C) and tapers distally into a narrow shaft. The complete tibia demonstrates the slight medial bowing that is seen in *Varanops*, and contrasts with the strongly bowed tibia of *Aerosaurus*. The angle between the medial and lateral condyles is less than in ophiacodontids, but greater than in sphenacodontids.

The dorsal surface of the left calcaneum (OMNH 73179; Fig. 6D–F) is gently concave due to well-developed marginal articular surfaces for the fibula, astragalus, and 4th distal metatarsal, whereas the ventral surface is nearly flat. The canal for the perforating artery is located on the medial side of the calcaneum and is larger on the dorsal surface than on the ventral surface. In varanopids the canal is gradually excluded from the ventral surface during ontogeny (Shinya et al., 2003). The level of exclusion of the perforating artery canal in OMNH 73179 is intermediate and consistent with the presence of a juvenile in the sample.

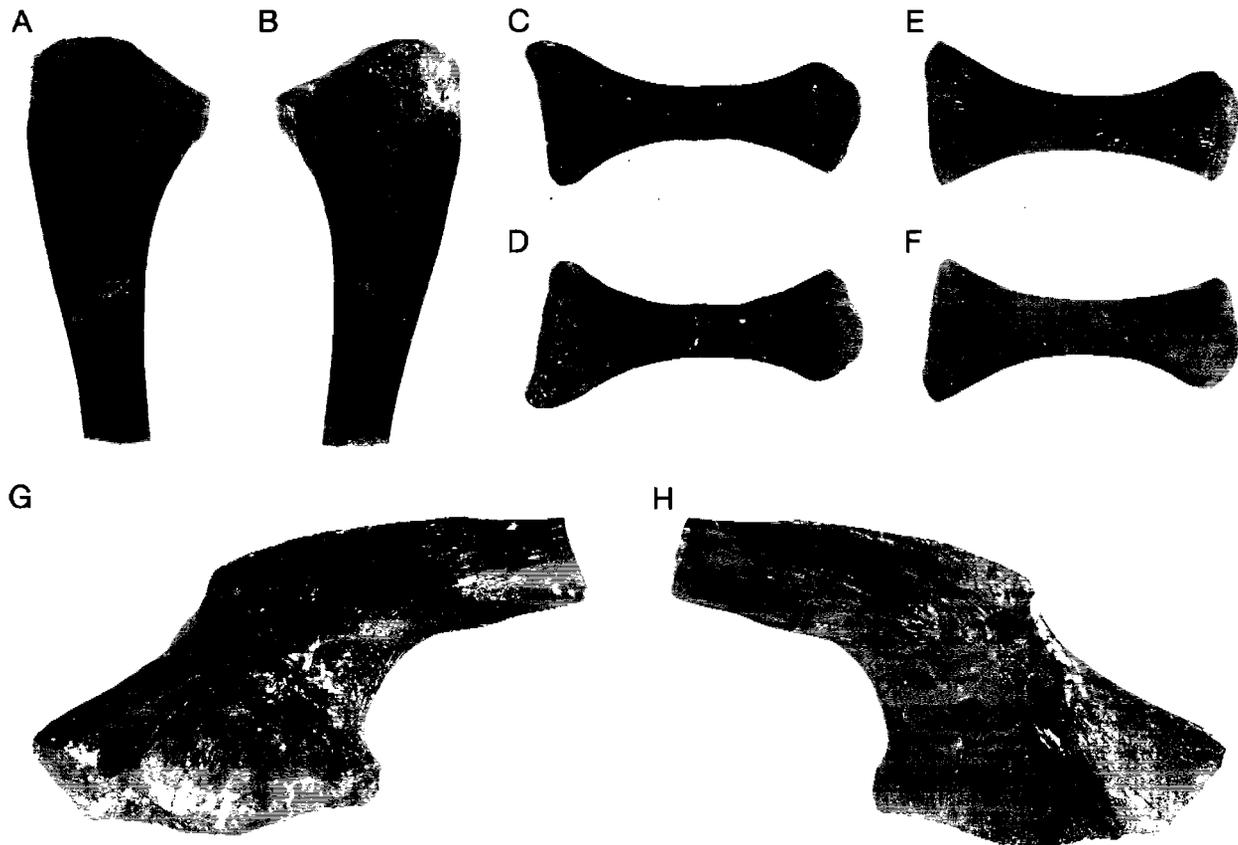


FIGURE 5. Appendicular skeletal elements of the Richards Spur varanodontine varanopid. Proximal portion of right ulna (OMNH 73171) in **A**, dorsal and **B**, ventral views. Left metacarpal IV (OMNH 73173) in **C**, dorsal and **D**, ventral views. Right metatarsal, digit II, III, or IV, (OMNH 73178) in **E**, dorsal and **F**, ventral views. Nearly complete left ilium (OMNH 73174) in **G**, lateral and **H**, medial views. Scale bar equals 1 cm.

However, the assignment of this bone to *Varanops* is equivocal because its dorsal outline does not resemble closely the typical subcircular shape seen in adult *Varanops* specimens (L. Tsuji, pers. com. 2006). Rather, OMNH 73179 has an ovoid outline, being longer in the proximodistal direction. In addition, the perforating artery is more proximally positioned than that of *Varanops*. We are unable to confidently attribute these differences to ontogeny alone due to the seemingly conservative nature of the shape of this bone throughout ontogeny in varanopids (Williston, 1911; Romer and Price, 1940). Furthermore, the shape of OMNH 73179 is similar to that in *Casea*, and a caseid has recently been reported from the same locality (Reisz 2005). On the basis of this uncertainty, we do not refer OMNH 73179 to the Richards Spur varanodontine at this time.

A single metatarsal (OMNH 73178; Fig. 5E, F) that pertains to the smaller of the two size classes is from either digit II, III, or IV of the right pes. It has a more robust shaft relative to the expanded ends than the metacarpal described previously (OMNH 73173). The proximal end is especially expanded, although not as greatly as in the metacarpal, and the proximal articulation surface is far more flattened.

PHYLOGENETIC ANALYSIS AND TAXONOMIC ASSIGNMENT

To confirm varanodontine affinities and determine the systematic position of the new Richards Spur varanopid material, we

conducted a phylogenetic analysis based on the previous work of Reisz and Dilkes (2003), Reisz and Laurin (2004), and Anderson and Reisz (2004). Reisz and Laurin (2004) duplicate a character in their matrix (presence of a supraglenoid foramen, characters 29 and 54). We have replaced character 54 in their matrix with character 54 of Anderson and Reisz (2004). Five new characters were also added to the matrix to determine the relationships of the Richards Spur varanodontine within Varanopidae and the characters are listed in anatomical order. We follow Anderson and Reisz (2004) and omit the problematic South African varanopid represented by BP/1/5678 (Modesto et al., 2001) until further study. Reptilia was designated as the outgroup in this analysis and four other taxa, included as outgroups in Reisz and Laurin (2004), were also used in this analysis (Appendices 1 and 2).

Analysis of the matrix in PAUP* 4.0b10 (Swofford, 2002) using the Branch and Bound algorithm resulted in three equally parsimonious trees, each with a tree length of 100 steps, a consistency index of 0.73 (rescaled CI=0.61), a retention index of 0.83, and a Homoplasy Index of 0.27 (Appendix 2). The strict consensus tree (Fig. 7) has a single polytomy at the base of Varanopidae. The incompletely preserved *Pyozia* is phylogenetically problematic, and re-examination of the material does not rule out the possibility that it may not be a member of the clade. Although the Richards Spur varanodontine can only be scored for 18% of the characters, its phylogenetic position within Varanodontinae is resolved as the sister taxon of *Varanops breviro-*

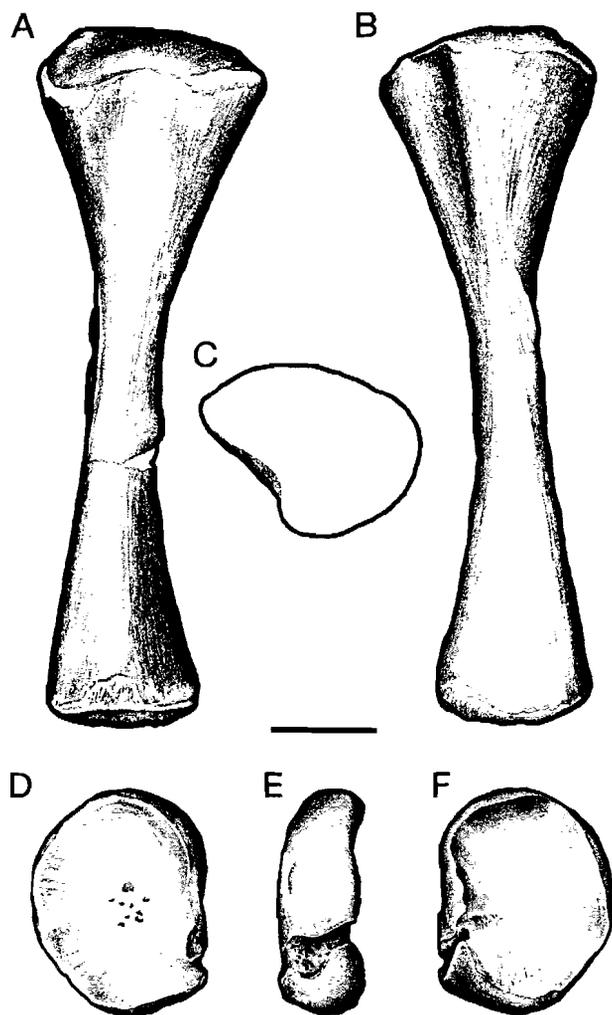


FIGURE 6. Complete right tibia of the Richards Spur varanodontine varanopid (OMNH 73175) in A, dorsal and B, lateral view; and C, showing the outline of the proximal surface. Left calcaneum (OMNH 73179) in D, ventral; E, medial; and F, dorsal views. Scale bar equals 1 cm.

iris and all available data are consonant with an assignment to *Varanops* (see subsequent discussion).

A Bremer decay analysis and a bootstrap analysis (1000 replicates using the Branch and Bound algorithm) were performed to assess the robustness of the tree. The results (Fig. 7) show that some clades are relatively robust, with bootstrap frequencies above 90% and decay indices of at least 3. Varanodontine clades are particularly well supported, including the least inclusive clade containing *Aerosaurus* and *Varanops*, and the clade comprised of *Varanodon*, *Watongia*, *Varanops*, and the Richards Spur varanodontine. The sister-group relationship between *Varanodon* and *Watongia* is also robust. The position of the Richards Spur varanodontine as the sister taxon of *Varanops* is supported by relatively low Bremer (1) and bootstrap (70%) values for the tree.

DISCUSSION

The material described here, although fragmentary, are resolved as the sister taxon of *Varanops brevirostris*. In fact, all of the material in this sample is virtually indistinguishable from *V. brevirostris*. One of the most diagnostic bones of the derived

varanopids is the maxilla. The morphology of the dorsal process is identical to that in *Varanops* (FMNH UC 644, FMNH UR 2423) and differs from *Varanodon* in the depth of the lateral depressions and the position of the anterior lacrimal facet. Critical areas of the maxilla are not preserved in *Watongia* or *Aerosaurus*, but parabasisphenoid morphology of the latter precludes assignment of the Richards Spur material to that taxon. The parabasisphenoid complex of the Richards Spur varanopid is also indistinguishable from that in *Varanops*. Based on the phylogenetic results and anatomical similarity, we tentatively refer the Richards Spur varanodontine material to *Varanops*, as *V. brevirostris*.

Uncertainty surrounds the precise age and correlation of the Richards Spur deposits, as summarized by Sullivan and Reisz (1999). They note that biostratigraphy is key to correct chronostratigraphic correlation due to the stratigraphically isolated nature of fissure fill deposits. The general biostratigraphic pattern indicates contemporaneity with the Arroyo Formation of Texas; however, the presence of *Mycterosaurus longiceps* and *Captorhinus laticeps* in the Richards Spur assemblage conflict with this assignment (Sullivan and Reisz, 1999). Review of the material referred to *M. longiceps* confirms the presence of a small mycterosaurine. In the absence of a skull the species-level identification to *M. longiceps* is equivocal. In addition, the material from Richards Spur originally referred to as *Eocaptorhinus* (= *Captorhinus*) *laticeps* (Heaton, 1979) has a complicated taxonomic history. Most recently the material has been reassigned to *C. magnus* (see Kissel et al., 2002). The '*C. laticeps*' material from the geologically older Wichita Group of Texas may also be referable to *C. magnus*, but Kissel and colleagues (2002) consider it to be too fragmentary for a positive assignment. Therefore, both *M. longiceps* and *C. laticeps* are no longer considered conflicting data.

Sullivan and Reisz (1999) report that the presence of *Cacops* in the Richards Spur deposit may suggest an age younger than that represented by the Arroyo Formation. Despite isolated occurrences of humeri from the Choza Formation (Olson, 1956), *Cacops* is otherwise known only from the '*Cacops* bonebed' site, near Indian Creek, Texas. *Varanops*, reported here for the first time from the Richards Spur locality, is also otherwise known exclusively from the *Cacops* bonebed. The stratigraphic assignment of the *Cacops* bonebed is unclear in the literature (Romer, 1958; Olson, 1954). Sullivan and Reisz (1999) considered the bonebed to occur within the lowermost part of the Vale Formation (Romer, 1958; Olson, 1954), but the *Cacops* bonebed is in fact considered to be within the Arroyo Formation by most authors (Romer and Price, 1940; Kemp, 1982; Reisz, 1986). Olson (1968) points out that the *Cacops* bonebed cannot be confidently assigned to either formation because it occurs in a red shale layer above the typical Arroyo beds and below the coarse clastic beds typical of the Vale Formation. After re-evaluation of the biostratigraphic data, there is no indication that the Richards Spur deposits are older than the age of the Arroyo Formation, and the evidence suggesting the deposit is significantly younger than lower Vale equivalency is scant. Therefore we concur with Sullivan and Reisz (1999) that the Richards Spur deposit is most likely temporally equivalent to that of the upper Arroyo Formation (mid-Leonardian).

Varanopids are generally rare components of Paleozoic terrestrial vertebrate assemblages. Typically, varanopids are represented by a single taxon per locality: *Mesenosaurus* from Morznitz, Russia; *Varanops* from the *Cacops* bonebed, Texas; *Elliot-smithia* from the Abrahamskraal locality near Price Albert, South Africa; and *Archaeovenator* from the Hamilton Quarry, Kansas. One notable deviation from this pattern is the co-occurrence of the derived varanodontines *Varanodon agilis* and *Watongia meieri*, both from the same horizon (level of the middle Flowerpot) of the Chickasha Formation, Blaine County, Okla-

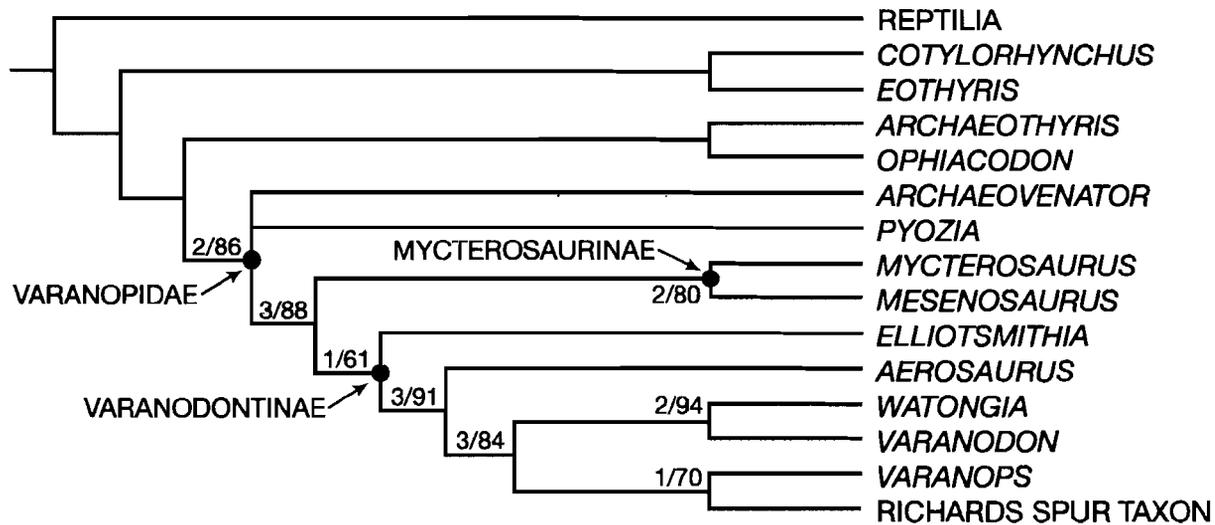


FIGURE 7. Strict consensus cladogram of three most-parsimonious trees for varanopid relationships (Tree Length = 100). At each varanopid node, the Bremer decay values are indicated on the left-hand side of the virgule and bootstrap support values are indicated on the right-hand side.

homa (Olson, 1965; Reisz and Laurin, 2004). These two varanodontines are sister taxa that differ greatly in size, raising the possibility that they may represent ontogenetic stages of the same taxon. At the Richards Spur locality, varanopids are the most commonly found synapsids (Reisz et al., 1997), and they are taxonomically diverse compared to other assemblages. Two taxa, the mycterosaurine *Mycterosaurus* sp. and the varanodontine *Varanops* discussed here, have been described, and a third, recently discovered new taxon is currently under study by R. Reisz and others. Recognition of a varanodontine in the Richards Spur assemblage marks the only known co-occurrence of a mycterosaurine and a varanodontine at a single locality. The presence of multiple varanopid taxa in the Richards Spur fissure fills, which likely represent an upland environment (Kemp, 1982; Olson, 1991; Sullivan and Reisz, 1999; Eberth et al., 2000), suggests that these agile predators may have been more common in upland communities than in the widely sampled lowland fluviodeltaic assemblages of Laurasia.

The Richards Spur varanodontine is considerably larger than all other varanopid material recovered from this locality, and the largest predator known in the assemblage. The largest humerus and tibia are much larger than those in the holotype of *Varanodon* and approach those in *Watongia*, the largest known varanopid. The Richards Spur varanodontine appears to have been the top predator in the upland ecosystem represented by the Richards Spur locality.

The numerical dominance of small-bodied tetrapods in the Richards Spur deposits suggests that there is either a preservational bias against large bones or that large-bodied taxa were uncommon in the paleocommunity, or both (Olson, 1971; Kemp, 1982). Sullivan and colleagues (2000) reported a femur from the trematopid amphibian *Acheloma* that is approximately 10 cm in length, and argued that this size class of material is in the range of that previously considered to be excluded due to preservational bias. The estimated restored length of the largest varanodontine humerus described here is 9 to 9.5 cm. If this bone was not broken prior to deposition, as suggested by the autochthonous nature of the fissure fill assemblage (Sullivan et al., 2000), this second example of relatively large tetrapod remains at the Richards Spur locality supports the hypothesis that the rarity of large forms is ecological in origin and indicative of the true composition of the paleocommunity (Sullivan et al., 2000).

CONCLUSIONS

Varanopid synapsids are represented at the Richards Spur locality by both large and small forms. The varanodontine cranial and postcranial material described here is virtually indistinguishable from *Varanops brevirostris* from the Arroyo Formation of Texas. A new comprehensive phylogenetic analysis of Varanopidae recovers a sister taxon relationship between the Richards Spur varanodontine and *V. brevirostris*, supporting referral of the new material to this taxon.

The Richards Spur assemblage records the only known co-occurrence of mycterosaurine and varanodontine varanopids, and varanopids are the most common synapsids at this locality. As generally rare components of the more typically preserved lowland environments, the diversity and abundance of varanopids at the Richards Spur locality suggests that they may have been more common components of upland ecosystems in the Early Permian.

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APPENDIX 1. Description of characters used in the phylogenetic analysis.

- Marginal dentition: conical and slightly recurved (0); strongly recurved and mediolaterally compressed for over 2/3 of its length (1). (Modified from R-1 and RD-34)
- Maxillary tooth row: 23 maxillary teeth or fewer (0); 26 maxillary teeth or more (1). (R-28)
- Serrations on teeth: absent (0); present (1). (M-32, added to RDB)
- Caniniform region: absent (0), present (1), present with canine tooth (2). (RD-39)
- Premaxillary teeth: five or more (0), four or fewer (1). (RD-41)
- Premaxillary rostral process: absent (0); present (1). (R, listed as 51 in RD)
- Premaxillary narial shelf: ventral shelf of external naris separated from sculptured lateral surface (0); rounded ventral narial shelf that extends smoothly to ventral edge of skull (1). (RDB-2)
- Septomaxilla: lateral, sheet-like exposure absent (0); present (1). (RD-42)
- Maxilla dorsal process: absent (0); present, forms extensive overlap joint with lacrimal medially (1). (RD-5 REDEFINED)
- Maxilla-prefrontal contact: contact absent (0); contact present (1). (RDB-6)
- Maxilla dorsal process: laterally flat (0); has an external ridge at confluence of subequally deep anterior and posterior depressions (1); has an external ridge with posterior depression deep and pocket like (2). (RDB-10 REDEFINED and NEW)
- Maxilla, lacrimal facet at anterior base of dorsal process: absent (0); present (1), present on vertical edge of anterior margin (2). (NEW)
- External narial shelf on nasal: absent (0); present (1). (R, listed as 49 in RD)
- Nasal length: shorter or equal to frontal (0); longer than frontal (1). (B-9)
- Lacrimal duct: lacrimal duct opens on posterior edge of lacrimal (0); duct opens laterally near posterior edge of lacrimal (1); opens laterally on concave surface of lacrimal (2). (RDB-19)
- Prefrontal contribution to orbit: restricted to anterodorsal corner of orbit (0); long ventral process of prefrontal extends ventrally to reduce lacrimal contribution to orbit (1). (RD-7)
- Frontal: posterolateral process short or absent (0); posterolateral process long and narrow, matching length of postfrontal, and between parietal and postfrontal (1). (RDB-4)
- Frontal-orbital border: frontal contribution to orbit absent or narrow (0); frontal contribution to orbit broad and forms most of dorsal edge (1). (RDB-13)
- Parietal: extension over orbital region absent (0); present (1). (RD-16)
- Pineal foramen: located on anterior or mid-region of midline parietal suture (0); pineal located in posterior region of midline parietal suture (1). (RDB-17)
- Postorbital: long posterior process present, extending over temporal fenestra (0); long posterior process absent (1). (RDB-23)
- Dorsal and lateral surfaces of postorbital: form smooth curve (0); dorsal and lateral surfaces sharply divided (1). (RDB-25)
- Postorbital: lateral boss at orbital margin absent (0); present (1). (RD-37)
- Anterodorsal process of squamosal: absent or short and does not extend along entire length of posterior process of postorbital (0); present and extends to corner between posterior and anteroventral processes of postorbital (1). (RDB-8)
- Squamosal occipital shelf: occipital process of squamosal present and contributes to occipital surface of skull (0); narrow (1); absent (2). (RDB-15)
- Squamosal: contact with jugal absent anterodorsally (0); squamosal-jugal contact present on postorbital bar (1). (RDB-24)
- Squamosal posterodorsal process: absent (0); present (1). (M-33, added to RD)
- Supratemporal: broad element of skull table (0); slender, in parietal and squamosal trough (1). (RDB-22)

- 29. Tabular: large sheet-like (0); narrow, slender (1). (RD-46)
- 30. Quadratojugal: contribution to fenestra absent (0); present (1). (RDB-11)
- 31. Quadratojugal: superficial anterodorsal process absent (0); present (1). (RD-35)
- 32. Anterior extent of quadratojugal: equal to anterior extent of ventral portion of squamosal (0), quadratojugal longer extending anterior to ventral portion of squamosal (1). (RD-36)
- 33. Dimensions of paroccipital process: tall, blade-like, and attached dorsolaterally to tabular (0); narrow, blade-like, and unattached (1). (RDB-26)
- 34. Quadrate: occipital margin with anterior slope greater than 60° (0); occipital edge with anterior slope 50° or less (1). (RDB-27)
- 35. Teeth on transverse flange: single row on edge (0); additional teeth anterior to single row (1). (RDB-30)
- 36. Expansion of parasphenoid plate posterior to basicranial articulation: gradual (0); or abrupt (1). (NEW)
- 37. Parasphenoid basal plate: relatively flat (0); marginal dental fields raised (1). (NEW)
- 38. Parasphenoid dentition posterior to level of anterior base of basicranial articulation: absent (0), present along edges (1), present on edges and posterior body (2). (RD-45 modified)
- 39. Basipterygoid processes: short, broad, with short articulating facets facing anterolaterally (0); wing-like, with articulating facets facing anteriorly (1); basipterygoid processes with hypertrophied, mediolaterally elongate articular facets (2). (RD-20 modified)
- 40. Angular posteroventral edge: ridged, or keeled (0); rounded (1). (RD-38)
- 41. Retroarticular process present and formed by articular, angular and surangular: absent (0); present (1). (AR-54)
- 42. Nasal posteroventral expansion: absent (0); present, but modest, pinched between nasal and maxilla (1); greatly enlarged, between nasal and lacrimal (2). (RD-43)
- 43. Antorbital region: broad antorbital region, nasal largely dorsal element (0); antorbital region narrow and tall, nasal has nearly vertical contribution to snout (1). (RDB-12)
- 44. Circumorbital ornamentation: tuberos ornamentation on prefrontal and jugal absent (0); present (1). (RD-14)
- 45. Lateral temporal fenestra: absent (0); present (1). (RD-3)
- 46. Temporal fenestra shape: subcircular (0); posteroventral expansion

- resulting in triangular outline of fenestra (1); oval, height greater than length (2); key-hole shape (3). (RD-9 modified)
- 47. Lower temporal bar: zygomatic arch or subtemporal bar tall, occupying at least 30% of skull height (0); bar narrow, occupying less than 20% of postorbital skull height (1). (RDB-18)
- 48. Ventral margin of postorbital region: straight (0); concave (1). (B-42)
- 49. Hyoid: short, directed to quadrate (0); long, directed posteriorly beyond skull (1). (RD-40)
- 50. Dorsal centra midventral margin: rounded (0); ridged but without keel (1); strongly pinched with keel (2). (RD-44)
- 51. Vertebral neural spine excavation: absent (0); present, but shallow and anteroposteriorly restricted (1); present, deep and elongate (2). (RD-47 modified)
- 52. Neural spine height of mid-dorsal vertebrae from base of zygapophysis / maximum centrum height: equal or less than 1 (0); 1.5 or greater (1). (RD-31)
- 53. Sacral ribs: two unequal (0); two equal (1); three (2); four (3). (R, listed as 48 in RD)
- 54. Clavicular head: large (0); slender and pinched (1). (RL-55)
- 55. Radiale maximum width/length ratio: subequal or <1 (0); >1(1). (RL-56)
- 56. 5th/4th metacarpal length ratio: 0.65 or more (0); less than 0.65 (1). (RL-57)
- 57. 4th metacarpal:ulna length ratio: less than 0.5 (0); greater than 0.5 (1). (NEW)
- 58. Distal phalanx length/width ratio: >1.5 (0); 1 or <1 (1). (RL-58)
- 59. Supraglenoid foramen: present (0); absent (1). (RDB-29)
- 60. Dimensions of femur: broad and short, maximum length/distal width ratio less than 3:1 (0); femur long and slender, length/distal width ratio more than 3:1 (1). (RDB-21)

Character list is taken from Reisz and Laurin (2004), which was built from Reisz and Dilkes (2003) and added to by Anderson and Reisz (2004). Character descriptions that have been modified are also indicated. Characters are polarized with respect to Reptilia as the outgroup. All characters are unordered. Following the last character state for each character is a citation for the source of the character. Citations are in the form: (author initials-character number). **Abbreviations for authors:** AR, Anderson and Reisz (2004); B, Berman et al. (1995); M, Modesto et al. (2001); R, Reisz (1986); RD, Reisz and Dilkes (2003); RL, Reisz and Laurin (2004); RDB, Reisz et al. (1998).

APPENDIX 2. Data matrix in PaUP* 4.0b10 (Swofford, 2002) using the Branch and Bound algorithm.

Taxon	1	10	20	30	40	50	60
Reptilia	0000100000	0000000100	00000?000?	0010/00000	00000?0000	0000000000	0000000000
<i>Cotylorhynchus</i>	0000110010	0010000000	0000101001	0100100000	0000101100	0030000110	0030000110
<i>Eothyris</i>	0001110000	0010000000	0000001000	0100100?00	00001000??	??????????	??????????
<i>Archaeothyris</i>	0101?0??00	0001001101	010000?100	0?10000?00	00101001?1	010?????00	010?????00
<i>Ophiacodon</i>	01/1000000	0001001101	0100000100	0110000000	0010130101	0101000000	0101000000
<i>Mycterosaurus</i>	1011001?11	0000111111	011010?110	0010?0011?	?1111210?1	111?????11	111?????11
<i>Mesenosaurus</i>	1011001?11	0000111111	0110101110	0010110110	1111121011	1010?00011	1010?00011
<i>Elliotmuthia</i>	1?1???????	??0??11111	0111101110	01110?????	1??111101?	??????????	??????????
<i>Aerosaurus</i>	1001001110	0?00201111	11?121?111	1101011211	1210111011	1120010001	1120010001
<i>Varanops</i>	11?1001110	1100201111	110121?111	11011?1211	1210111011	2120110101	2120110101
<i>Varanodon</i>	1101001110	2200201111	111121?111	11011???11	1210111012	11211111?1	11211111?1
<i>Archaeovenator</i>	0100101100	0000011111	010010?110	00?0000000	02101210?1	0010????0?1	0010????0?1
<i>Watongia</i>	1?0???????	?????11???	??1?????1?	1?????1???	?????111???	11?11111???	11?11111???
RS varanopid	?????????1?	11?????????	???????????	?????0122?	?????????1?	21?????????	21?????????
<i>Pyozia</i>	01001?1???	???????????	???????????	????1?????	?????1?1?1	???????????	???????????