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

HILLARY C. MADDIN, DAVID C. EVANS, and ROBERT R. REISZ*
Department of Biology, University of Toronto at Mississauga, 3359 Mississauga Rd., Mississauga, Ontario, Canada, L5L 1C6; hillary@utm.utoronto.ca, devans@utm.utoronto.ca, rreisz@utm.utoronto.ca

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 synapsids 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 deposits during the continuous excavation of the Ordovician limestone of the Arbuckle Formation by the Dolese Brothers Limestone Quarry 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 fill 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 diapsid synapsid families also are common (Sullivan and Reisz, 2000). Synapsids, represented by a mycterosaurine varanopid (Reisz et al., 1997) and a basal caseasaur (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 sediment 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
VARANOPIDAE 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.

*Corresponding author.
DESCRIPTION

Cranium

The isolated fragment of a left maxilla (OMNH 73156) consists of the diagnostic dorsal process and the caniniform region 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.

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 extending 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.

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.
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 *Mycerossaurus* from the same deposit (Reisz et al., 1991), but is similar to that in *Varanops* (FMNH UR 2421). 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 amphicoelus 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
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) and Varanodon in that the cortical bone of the arch at the base of the neural spines is 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) 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 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 (OMNH 73177; Fig. 3) 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 deltoid process 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 deltoid process along the dorsal margin of the prezygapophyses to become continuous with the first phalanx. The second ridge, not as well defined, is located on the ventral surface between the deltoid process 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 subely bicipital 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 ophiacodontid and sphenacodontid humeri, although the possibility that this feature is ontogenetic cannot be discounted. The smooth, broad entepicondylar process has a large entepicondylar foramen, and there is no evidence of an ectepicondylar foramen, also present in Watongia (Reisz and Laurin, 2004). The epicondyle process, sharply differentiated from the entepicondyle, 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 mстерosaurs *Watongia*. The articular 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 dorsal 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 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.
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 Aerasaurus 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 Aerasaurus. 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.
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/155878 (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 *Pyrozia* 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 brevirostr-
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 *Aerossaurus*, 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 *Capito rhinus laiceps* 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 mysticetosaurine. 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 (= Capito rhinus) laiceps* (Heaton, 1979) has a complicated taxonomic history. Most recently the material has been reassigned to *C. magnus* (see Kissel et al., 2002). The 'C. laiceps' 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. laiceps* 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, 1958), *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 (Cacops bonebed 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 Morz nitzia, Russia; *Varanops* from the Cacops bonebed, Texas; *Elliotsmithia* from the Abrahamskraal locality near Price Albert, South Africa; and *Archaeorvenator* from the Hamilton Quarry, Kansas. One notable deviation from this pattern is the co-occurrence of the derived varanodontines *Varanodon agilis* and *Watongia meieni*, both from the same horizon (level of the middle Flowerpot) of the Chickasha Formation, Blaine County, Okla.

**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

**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.
The numerical dominance of small-bodied tetrapods in the Richards Spur deposits suggests that there is either a preservation bias against large bones or that large-bodied taxa were uncommon in the paleocommunity (Sullivan et al., 2000). This location 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 synapids 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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LITERATURE CITED

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

1. Marginal dentition: conical and slightly recurved (0); strongly recurved and medially compressed for over 2/3 of its length (1). (Modified from R-1 and RD-34)

2. Maxillary tooth row: 23 maxillary teeth or fewer (0); 26 maxillary teeth or more (1). (R-28)

3. Serrations on teeth: absent (0); present (1). (M-32, added to ROB)

4. Septomaxilla: lateral, sheet-like exposure absent (0); present (1). (RD-6)

5. Premaxillary rostral process: absent (0); present (1). (RDB-2)

6. 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)

7. Dorsal and lateral surfaces of postorbital: form smooth curve (0); slender, in parietal and squamosal trough (1). (RD-22)

8. Maxilla-prefrontal contact: contact absent (0); contact present (1). (RDB-6)

9. Maxilla dorsal process: absent (0); present, forms extensive overlap with lacrimal medially (1). (RD-5 REDEFINED)

10. Parietal: extension over orbital region absent (0); present (1). (RD-37)

11. Supratemporal: broad element of skull table (0); slender, in parietal and squamosal trough (1). (RD-22)

12. Squamosal-occipital shelf: occipital process of squamosal present and extends to corner between posterior and anteroventral processes of postorbital (1). (RDB-8)

13. Frontal: posterolateral process short or absent (0); posterolateral process long and narrow, matching length of postfrontal, and between parietal and postfrontal (1). (RD-4)

14. 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)

15. Maxilla, lacrimal facet: anterior base of dorsal process: absent (0); present (1), present on vertical edge of anterior margin (2). (NEW)

16. External narial shelf on nasal: absent (0); present (1). (R, listed as 49 in RD)

17. Nasal: longer: shorter or equal to frontal (0); longer than frontal (1). (B-9)

18. Lacrimal duct: lacrimal duct opens on posterior edge of lacrimal (0); opens laterally near posterior edge of lacrimal (1); opens laterally on concave surface of lacrimal (2). (RD-19)

19. Frontal 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)

20. Frontal: posterolateral process short or absent (0); posterolateral process long and narrow, matching length of postfrontal, and between parietal and postfrontal (1). (RD-4)

21. Frontal: orbital border: frontal contribution to orbit absent or narrow (0); frontal contribution to orbit broad and forms most of dorsal edge (1). (RD-13)

22. Parietal: extension over orbital region absent (0); present (1). (RD-16)

23. Pinnae foramen: located on anterior or mid-region of midline palatine suture (0); pinale located in posterior region of midline palatine suture (1). (RDB-17)

24. Postorbital: long posterior process present, extending over temporal fenestra (0); long posterior process absent (1). (RD-23)

25. Caniniform region: absent (0), present (1), present with canine tooth (2). (RD-39)

26. Premaxillary rostral process: absent (0); present (1). (R, listed as 51 in RD)

27. 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)

28. Septomaxilla: lateral, sheet-like exposure absent (0); present (1). (RD-42)

29. Maxilla-prefrontal contact: contact absent (0); contact present (1). (RDB-6)

30. Orbital margin: conical and slightly recurved (0); strongly recurved and medially compressed for over 2/3 of its length (1). (Modified from R-1 and RD-34)

31. Maxillary tooth row: 23 maxillary teeth or fewer (0); 26 maxillary teeth or more (1). (R-28)

32. Serrations on teeth: absent (0); present (1). (M-32, added to ROB)

33. Premaxillary rostral process: absent (0); present (1). (RDB-2)

34. 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)

35. Premaxillary rostral process: absent (0); present (1). (RDB-2)

36. Premaxilla dorsal process: absent (0); present, forms extensive overlap with lacrimal medially (1). (RD-5 REDEFINED)

37. Parietal: extension over orbital region absent (0); present (1). (RD-16)

38. Pinnae foramen: located on anterior or mid-region of midline palatine suture (0); pinale located in posterior region of midline palatine suture (1). (RDB-17)

39. Postorbital: long posterior process present, extending over temporal fenestra (0); long posterior process absent (1). (RD-23)

40. Dorsal and lateral surfaces of postorbital: form smooth curve (0); dorsal and lateral surfaces sharply divided (1). (RD-25)

41. Postorbital: lateral boss at orbital margin absent (0); present (1). (RD-37)

42. 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 antecoronal processes of postorbital (1). (RDB-8)

43. Squamosal occipital shelf: occipital process of squamosal present and contributes to occipital surface of skull (0); narrow (1), absent (2). (RD-15)

44. Squamosal: contact with jugal absent anterodorsally (0); squamosal-jugal contact present on postorbital bar (1). (RD-24)

45. Squamosal postorbital process: absent (0); present (1). (M-33, added to RD)

46. Supratemporal: broad element of skull table (0); slender, in parietal and squamosal trough (1). (RD-22)
APPENDIX 2. Data matrix in PaUP* 4.0b10 (Swofford, 2002) using the Branch and Bound algorithm.

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