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The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States

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The skull of *Postosuchus kirkpatricki* Chatterjee 1985 is known from the holotype and paratype specimens along with disassociated skull elements from several Triassic localities in the southwestern and eastern United States. Recent preparation of the holotype skull allows for more careful examination of the cranial elements and comparison with related taxa. This description indicates that *Postosuchus* shares several previously unrecognized synapomorphies with crocodylomorphs, including fossae and foramina in the dermatocranium that are not present in other basal pseudosuchians. The sutural arrangements of the skull of *Postosuchus* presented in this paper differ considerably from previous descriptions, due in part to the reassignment of what was previously considered the prefrontal to the palpebral bone. Also, further preparation of skull elements revealed morphologies that differ from previous descriptions. This new description also indicates a close relationship with *Polonosuchus silesiacus* Sulej 2005. The only autapomorphic characters of the skull are a distinct, rounded lateral ridge on the maxilla and a foramen present in a large fossa on the anteromedial surface of the maxilla.

INTRODUCTION

"Rauisuchians" were pseudosuchian archosaurs with a near cosmopolitan distribution during the Middle and Late Triassic Period. Rauisuchians were likely the apex predators of their ecosystems during the Late Triassic, representing the largest land carnivores and reaching lengths of at least 9 meters (Alcober 2000). The term Rauisuchia/rauisuchian is applied to the paraphyletic grouping of poposaurids plus those taxa referred to as rauisuchids in the literature. Rauisuchids include those taxa more closely related to *Postosuchus*, *Saurosuchus* and *Batrachotomus* than to *Poposaurus* or *Arizonasaurus*, for example, but do not include crocodylomorphs. The term Rauisuchia has been supplanted by the taxon Paracrocodylomorpha, a monophylum that includes all those taxa plus crocodylomorphs (Weinbaum and Hungerbühler 2007).

Postosuchus has been a taxonomic enigma since its discovery. Although named and described by Chatterjee in 1985, elements of *Postosuchus* have been known as early as 1922, when Case described a braincase of *Coelophysis* (Case 1922) and a "new form of phytosaur pelvis" (Case 1943), both of which are referable to *Postosuchus kirkpatricki* (Chatterjee 1985, Weinbaum 2002). The holotype (TTUP 9000) and paratype (TTUP 9002) of *Postosuchus kirkpatricki* consist of disarticulated but associated cranial and postcranial material representing approximately 75% of the skeleton from the Post Quarry in the Cooper Canyon Formation, Garza County, Texas (Chatterjee 1985, Weinbaum 2002, 2007). A diverse vertebrate assemblage has been found at the Post Quarry (MOTT 3624), including *Postosuchus kirkpatricki*, temnospondyls, therapsids, poposaurids, aetosaurs, phytosaurs, crocodylomorphs, dinosauromorphs, dinosaurs, and a variety of enigmatic diapsids (Small 1989, Lehman and Chatterjee 2005, Nesbitt and Chatterjee 2008). Long and Murry (1995) later described new cranial and postcranial *Postosuchus* material from Arizona (e.g., *Placerias* Quarry UCMP A269, and Petrified Forest National Park, Arizona e.g., UCMP V82040) and New Mexico (e.g., Whittaker/*Coelophysis* Quarry, Ghost Ranch).

Chatterjee (1985) described *Postosuchus kirkpatricki* from the remains of twelve individuals: two large specimens (estimated length 4–6 meters) and ten smaller individuals (estimated length 2–3 meters) that he concluded were juveniles of the same species. Chatterjee (1985) noticed several morphological differences between the large and small individuals but attributed this variation to ontogeny and sexual dimorphism. Long and Murry (1995) determined that the differences in the anatomy between the two morphs were too great to be ontogenetic or the result of sexual dimorphism, and referred the smaller animals to a new taxon, *Chatterjeea elegans.* Furthermore, they suggested that the skeleton of *C. elegans* belonged to the skull of *Shuvosaurus inexpectatus* Chatterjee 1993, which Chatterjee (1993) and Rauhut later (1997) identified as a theropod dinosaur. Additionally, some of the *Chatterjeea* material was found in the jacket containing *Shuvosaurus* (Chatterjee 1993). Gower (2000) and Weinbaum (2002) concurred that there are significant differences between *Postosuchus* and *Chatterjeea*, and that *Chatterjeea* is most likely a distinct taxon from *Postosuchus.* Weinbaum (2002) also suggested that there are only two individuals of *Postosuchus* from the Post Quarry, that are morphologically distinct from the *Chatterjeea* material.

Nesbitt and Norell (2006) and Nesbitt (2007) recently published the description of a new poposaurid named *Effigia okeeffeae* Nesbitt and Norell 2006, which appears to be very closely related to *Shuvosaurus* (Nesbitt 2007). The skull of *E. okeeffeae* was found in near articulation with a partial postcranial skeleton that is almost indistinguishable from

Chatterjeea, providing strong support for the referral of the *Chatterjeea* postcrania to *Shuvosaurus.* Chatterjee (1985) initially placed *Postosuchus* in the family Poposauridae based on the inclusion of material from *Chatterjeea* and *Poposaurus* (=*Lythrosuchus*) in his description (Long and Murry 1995). Long and Murry (1995) removed *Postosuchus* to the Rauisuchidae and put *Chatterjeea* in the new family Chatterjeeidae without an explicit phylogenetic analysis of the material they examined. More recently a new species of *Postosuchus* from North Carolina was described, *Postosuchus alisonae* Peyer et al. 2008, which possesses at least one autapomorphic character: a deep groove on the first metacarpal and a corresponding flange on the second metacarpal. However, this is the only significant difference between the type *Postosuchus* material and all corresponding specimens of UNC-15575, so UNC-15575 is considered to be at least congeneric with *Postosuchus kirkpatricki.* The few cranial elements preserved (e.g., opisthotics, prootic, nasals, supraoccipital, palpebral, articular) are relatively indistinguishable from the type material and any differences can be attributed to individual variation.

Recent phylogenetic analyses (Benton and Clark 1988, Parrish 1993, Juul 1994, Clark et al. 2000, Gower and Walker 2002, Nesbitt and Norell 2006, Nesbitt 2007, Brusatte et al. 2008) included character codings based on previous descriptions of *Postosuchus* (i.e., Chatterjee 1985, Long and Murry 1995). These characters should be viewed with caution because many details of the holotype specimen of *Postosuchus kirkpatricki* (TTUP 9000) were obscured by plaster, wire mesh, and paint during the restoration of the skull. Here, I describe in detail the skull and braincase of *Postosuchus*, which, after preparation, have proven to be mostly complete, well preserved, and differ substantially from the original description. No phylogenetic analysis is included in this study as detailed and accurate anatomical data are required before accurate codings are possible.

Institutional abbreviations: GBIT, Institute of Geology and Palaeontology, University of Tübingen; **MCCDP**, Mesalands Community College Dinosaur Museum, Tucumcari, New Mexico; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; **PEFO**, Petrified Forest National Park; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart; **TTUP**, Museum of Texas Tech, Lubbock, Texas; **UCMP**, University of California, Berkeley, California; **UMMP**, University of Michigan, Ann Arbor, Michigan; **UNC**, University of North Carolina, Chapel Hill, North Carolina.

Anatomical abbreviations: a, surface/facet for articulation with; **al**, tooth alveolus; **an**, angular; **aof**, antorbital fenestra; **aofo**, antorbital fossa; **ar**, articular; **bo**, basioccipital; **bs**, basisphenoid; **bpt**, basipterygoid process; **bt**, basal tubera; **bv**, bulla vestibularis; **c**, coronoid; **cp**, cultriform process; **cr**, lagenar/cochlear recess; **d**, dentary; **dhv**, dorsal head vein; **en**, external naris; **eo** exoccipital; **f**, frontal; **fm**, foramen magnum; **fo**, fenestra ovalis; **for**, foramen; **fos**, fossa; **fr**, floccular recess; **g**, groove; **hf**, hypophyseal (pituitary) fossa; **ic**, internal carotid; **idp**, interdental plates; **imp**, impression; **itf**, inferior infratemporal fenestra; **j**, jugal; **l**, lacrimal; **lmf**, lateral mandibular fenestra; **lc**, lateral canal; **lch,** lateral chamber; **ls**, laterosphenoid; **m**, maxilla; **ma**, matrix; **mc**, meckelian canal; **mf,** metotic foramen; **mp**, medial process of articular; **mpr**, medial pharyngeal recess; **mr**, median ridge; **mxp**, palatal process of maxilla; **n**, nasal; **o**, orbit; **ob**, olfactory bulb; **ot**, olfactory tract; **of**, orbital fossa; **pa**, parietal; **pal**, palatine; **pb**, palpebral; **pf**, postfrontal; **pmx**, premaxillae; **po**, postorbital; **pp**, paroccipital process of opisthotic; **pr**, prearticular; **prf**, prefrontal; **prot**, prootic; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qf**, quadrate foramen; **qj**, quadratojugal; **r**, ridge; **rap**, retroarticular process; **rp**, resorption pit; **rr**, rugose ridge; **rt**, replacement tooth; **sa**, surangular; **sg**, stapedial groove; **sitf**, superior infratemporal fenestra; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **sqp**, posterior process of squamosal; **st**, supratemporal fenestra; **su**, suture; **ug**, unossified gap; **v**, vomer; **V**, foramen for trigeminal nerve; **V1**, passage of optic branch of trigeminal nerve; **VI**, foramen for abducens nerve; **VII**, position of passage of facial nerve; **XII**, foramen for hypoglossal nerve; **vcd**, venae capitis dorsales; **vg**, vessel grooves.

MATERIALS AND METHODS

Preparation of the holotype skull (TTUP 9000) provides new information regarding the morphology, sutural arrangements, and potential phylogenetic relationships of *Postosuchus.* Parts of the paratype of *Postosuchus kirkpatricki* (TTUP 9002) were also prepared, and several new elements of the braincase and skull were identified. Peyer et al. (2008:364) recently suggested that the skull is the only definite material referable to *Postosuchus kirkpatricki* and that most knowledge of *Postosuchus* rests on "non-type material" (Peyer et al. 2008:378). This is refuted by: (1) the close association of the skull to the postcranial material for both the holotype and paratype (documented by maps in Chatterjee (1985) and photos of the excavation provided by the author); (2) left and right elements for each specimen are of the same size with no element duplication (e.g., only one right humerus); and (3) size differences in all elements are consistent between the holotype and paratype (the paratype femora are not only the same size, but are smaller and more gracile than the holotype femora, as are both humeri, the skull elements, etc.). Roughly 75% of the skeleton is represented by type material (TTUP-9000, TTUP-9002), and the only elements not well represented are the osteoderms, ribs and gastralia.

I examined the holotype and paratype of *Postosuchus kirkpatricki*, other associated Post Quarry specimens, fossils from other TTU localities, referred material, and pseudosuchian taxa. The Texas Tech University specimens are from the Cooper Canyon Formation, Garza County, and the Tecovas Formation, Crosby County, Texas (see Long and Murry 1995 for a detailed list of fossils). The postcranial skeleton, including TTUP-9002 and TTUP-9002, will be described in a subsequent paper.

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA Cope 1869 sensu Gauthier 1986
SUCHIA Krebs 1974
PARACROCODYLOMORPHA Parrish 1993 sensu Weinbaum and Hungerbühler 2007
Postosuchus Chatterjee 1985

Type species—*Postosuchus kirkpatricki* Chatterjee 1985 (by monotypy).

Holotype—TTUP 9000 *Postosuchus kirkpatricki*: almost complete skull, assorted teeth, third cervical centrum, partial cervical centrum with spine table, mid-dorsal vertebral centrum, left and right scapulae, left and right humeri, left and right ulnae, partial left and right radii, carpals, phalanges, unguals, ischia, left femur, proximal left tibia, and partial left fibula.

Paratype—TTUP 9002 nearly complete skull, mostly complete skeleton missing the cervical vertebrae, ribs, gastral elements, and most of the tail.

Referred material—MCCDMP 1654, left frontal from the Trujillo Formation of eastern central New Mexico; the following UCMP material is from the Chinle Formation, *Placerias* Quarry in Arizona: UCMP A369/27492, right articular; UCMP A269/27572, left and right premaxillae; UCMP A269/27441, right squamosal; UCMP A269/140035, right palpebral; UCMP A269/124586, left maxilla; UCMP A269/27481, left and right nasals; UCMP A269/27440, left squamosal; UCMP A269/27478, left and right frontals; UCMP A269/27447, right quadrate; UCMP A269/27449, left quadrate; UCMP A269/27450, left quadrate; UCMP A269/27485, left surangular and articular; PEFO 34044, postorbital, Sonsela Member, Chinle Formation, Arizona; UMMP 7473, braincase, Tecovas Formation, Dockum Group, West Texas; UNC 15575, assorted skull elements from Lithofacies II of the Durham sub-basin of the Deep River basin, Newark Supergroup, North Carolina.

Revised diagnosis—Paracrocodylomorph archosaur with the following autapomorphies: A prominent rugose, rounded ridge on the lateral surface of maxilla, and a foramen present on the ventral surface of a triangular fossa on the anteromedial surface of the ascending process of the maxilla. These are the only apparent autapomorphies of the skull.

Differential diagnosis—*Postosuchus kirkpatricki* differs from all other rauisuchians in the possession of a distinct fossa on the anteromedial surface of the maxilla (shared with *Polonosuchus* and *Luperosuchus fractus* Romer 1971); a highly reduced prefrontal with a descending process (shared with *Polonosuchus*); a maxilla with a sinuous lower margin in lateral view (shared with *Polonosuchus*); a frontal-postfrontal with lateral excavations and associated foramina (possibly shared with *Polonosuchus*); presence of a palpebral bone (shared with *Polonosuchus*); frontal does not contact lateral margin of orbit (shared with *Polonosuchus*); infratemporal fenestra divided by forward projecting squamosal and quadratojugal contacting the postorbital (shared with *Polonosuchus*, and possibly *Tikisuchus romeri* Chatterjee and Majumdar 1987); quadratojugal large and plate-like; dorsomedial process of lacrimal separates prefrontal and nasal (possibly shared with *Polonosuchus*); and long, deep ventrally projecting basipterygoid (shared with *Tikisuchus*). *Postosuchus* differs from *Polonosuchus* in that it has a shallower anterior maxilla and a more prominent rugose ridge on the lateral margin of the maxilla.

DESCRIPTION

Skull reconstruction

The skull of *Postosuchus* has been reconstructed twice, first by Chatterjee (1985) in the original description, and again by Long and Murry (1995). The majority of differences between these two restorations result from the inclusion of *Postosuchus* material with a more robust morphology described by Long and Murry (1995) from the *Placerias* Quarry. However, as noted by Long and Murry (1995:118) and Gower (2000, 2002), most of the diagnostic details of the holotype skull were covered by the plaster and paint used in the reconstruction, preventing any thorough description.

For this study the *Postosuchus kirkpatricki* holotype skull was prepared, revealing a well-preserved skull approximately 90% complete, with slight post-mortem distortion and some damage from initial preparation or excavation. An updated reconstruction of the skull is provided in Figure 1. The fairly complete re-prepared paratype skull has also aided in completing the restoration (Figs. 2, 11). The more gracile paratype skull is not as well preserved as the holotype.

The elements in both skulls exhibit no fusion, although the maxillae and jugals are firmly sutured together in the holotype. The length of the holotype skull is approximately 540 mm in length, and the paratype skull is approximately 470 mm long. The skull is narrow in dorsal view (Fig. 1A), but not nearly as narrow as reconstructed by Chatterjee (1985:406) and Long and Murry (1995:121). The maxillae are clearly visible along their entire length in dorsal view (contra Chatterjee 1985:402).

Differences between the past restorations of the skull and the one presented in this study include the morphology of several of the elements and their sutural arrangements as discussed below.

Dermal bones of the skull roof

Premaxilla—Premaxillae are present in both type specimens (TTUP 9000 and 9002) of *Postosuchus* (Fig. 3) but they are best preserved and most complete in the holotype. Both premaxillae are also preserved in UCMP 27572. The main body of the premaxilla is sub-rectangular in lateral view, slightly longer than tall, with long anterior and maxillary processes, similar to *Saurosuchus galilei* Reig 1959, *Rauisuchus tiradentes* Huene 1942, *Polonosuchus* (Sulej 2005) and *Fasolasuchus tenax* Bonaparte 1981. The anterior ascending process rises from the body of the premaxilla and curves posteriorly to meet the nasal. There are two small raised prominences on the dorsal surface of the body of the premaxilla posterior to the anterior ascending process. These prominences are separated by a groove on the dorsolateral surface. A tooth resorption pit is present on the lateral surface of the anterior prominence. Posterior and lateral to this prominence is a groove that separates the anterior half of the premaxilla from the posterior half. The anterior prominence forms the dorsal extent of the articular surface between the two premaxillae, extends posteromedially to the posterior prominence, and terminates at the base of the maxillary process. The maxillary process extends from the posterior prominence posterodorsally to separate the maxilla from the external naris. The anterior, anterodorsal, posterior, and ventral borders of the external naris are formed by the premaxilla, with only a small contri-

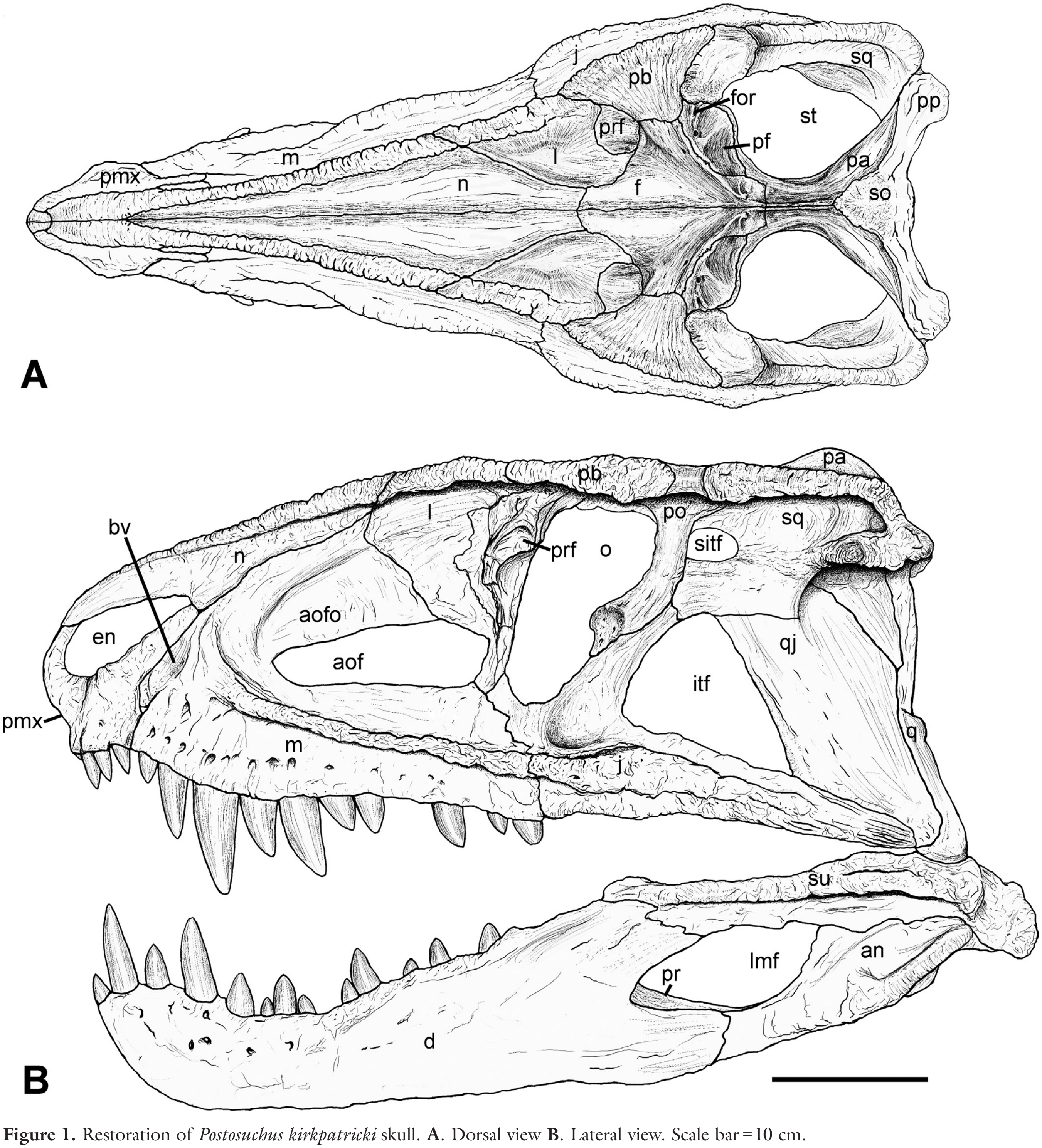

Figure 1. Restoration of *Postosuchus kirkpatricki* skull. **A**. Dorsal view **B**. Lateral view. Scale bar = 10 cm.

bution posterodorsally from the nasal. The external naris is subterminal and ovate in shape. The anteroventral margin of the naris is bordered by a shallow fossa as in *Batrachotomus kupferzellensis* Gower 1999, *Fasolasuchus* (Bonaparte 1981), *Saurosuchus* (Sill 1974), and *Polonosuchus* (Sulej 2005). Ventromedial to the maxillary process, a smooth, flattened area on the premaxilla is overlapped by the corresponding palatal process of the maxilla dorsally (Fig. 3A).

A deep groove extends posteriorly on the medial surface of the premaxilla to the posterior edge, just ventral to the symphysis of the premaxillae and posterior to the first alveolus. Chatterjee (1985) identified this and a corresponding groove and hollow on the maxilla as forming a recess for Jacobson's organ (vomeronasal organ). However, because no extant archosaurs possess a Jacobson's organ (Romer 1956), the extant phylogenetic bracketing hypothesis argues against such an interpretation (see Witmer 1995). *Polonosuchus* (Sulej 2005), *Batrachotomus* (Gower 1999), *Saurosuchus* (Sill 1974), and *Fasolasuchus* (Bonaparte 1981) all possess an identical groove.

There are four alveoli in all premaxillae of *Postosuchus,* a character state also present in *Rauisuchus* (Huene 1942), *Polonosuchus* (Sulej 2005), *Fasolasuchus* (Bonaparte 1981), *Saurosuchus* (Sill 1974), and *Batrachotomus* (Gower 1999). All known premaxillae of *Postosuchus* have what appear to be tooth resorption pits on the dorsolateral surface between the ascending and maxillary processes of the premaxillae.

Maxilla—Many *Postosuchus* maxillae are known, including both type specimens (TTUP 9000 and 9002) and several partial maxillae from the *Placerias* Quarry; the holotype elements are the best preserved among them. The maxilla of *Postosuchus* is a large, laterally compressed and elongate bone (Fig. 3), and is similar to other paracrocodyliform maxillae like that of *Ticinosuchus ferox* Krebs 1965, *Teratosaurus suevicus* Meyer 1861, *Polonosuchus* (Sulej 2005) *Fasolasuchus* (Bonaparte 1981), *Saurosuchus* (Sill 1974), *Saltoposuchus connectens* Huene 1921, and *Hesperosuchus agilis* Colbert 1952. The ventral margin is sinuous in lateral view as in *Polonosuchus.* The ventrolateral surface of the maxilla possesses two to three nutrient foramina per tooth alveolus that form an anteroposterior row (Fig. 3B).

The maxilla forms the entire anteroventral and most of the dorsal border of the long, dorsoventrally compressed antorbital fenestra. The antorbital fenestra is wedge-shaped, tapering anteriorly and expanding dorsoventrally towards the posterior end of the element, as in other paracrocodyliforms, including *Ticinosuchus* (Krebs 1965), *Teratosaurus* (Galton 1985), *Polonosuchus* (Sulej 2005), *Fasolasuchus* (Bonaparte 1981), *Saurosuchus* (Sill 1974), *Saltoposuchus* (pers. obs. of SMNS 12597), *Hesperosuchus* (Clark et al. 2000), and *Dromicosuchus* (Sues et al. 2003). A shallow antorbital fossa present on the maxilla extends dorsally onto the ascending process and is bordered ventrally by a rugose, rounded ridge that continues from just anterior to the margin of the antorbital fenestra (near the third alveolus) and trends posteroventrally onto the jugal. In contrast, the maxillae of poposauroids such as *Arizonasaurus* (Nesbitt 2005), *Lotosaurus adentus* Zhang 1975 (Parrish 1993), *Shuvosaurus* (Chatterjee 1993), *Effigia* (Nesbitt 2007), and possibly *Poposaurus* (Weinbaum and Hungerbühler 2007) have an anteroposteriorly shorter, anteriorly rounded antorbital fenestra and fossa.

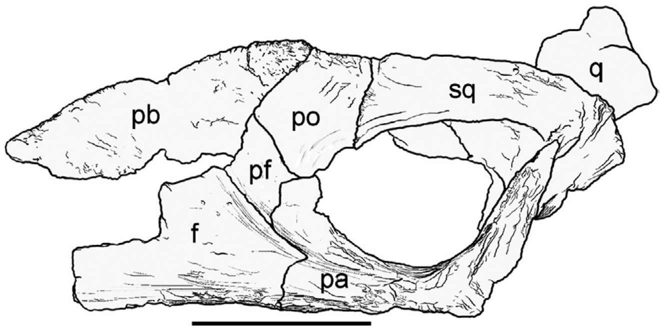

Figure 2. *Postosuchus kirkpatricki* (TTUP 9002) skull roof in dorsal view. Scale bar = 5 cm.

Anteromedially, a notch is formed by the palatal process and the anterior part of the main body of the maxilla. A large foramen is present on the lateral side of the anterior portion of the maxilla; this feature is present in both *Teratosaurus* (Galton 1985:fig. 1E) and *Polonosuchus* (Sulej 2005:fig. 4A–D). The premaxilla overlaps the maxilla laterally forming the small subnarial fenestra. Dorsomedial to the foramen is a shallow groove in the maxilla where the maxillary process of the premaxilla articulates, excluding the maxilla from the external naris. The subnarial fenestra created by the articulation of the premaxilla and maxilla is much smaller than originally figured by Chatterjee (1985:fig. 2). This is because in Chatterjee's (1985) reconstruction, which is based on the holotype, TTUP 9000, the palatal processes on both the left and right maxillae are broken and missing their anterior ends. Therefore the process does not articulate with the maxillary process of the premaxilla as it should, causing the fenestra to appear to be approximately twice its natural size. When the premaxilla and maxilla are properly articulated, the fenestra is a small and ovate opening. The palatal process of the right maxilla of the paratype is relatively complete, and shows the extent to which the process extends medially. A deep depression, approximately 35 mm long on the anterolateral surface of the maxilla and just dorsal to the notch where it meets the premaxilla, resembles a depression in the same position in theropods, and referred to by Witmer (1997) as the bulla vestibularis (see Figs. 1, 3).

A hollow connected to a groove extends anteriorly to meet a corresponding groove in the premaxilla, and dorsally enters a large foramen that opens into a large, triangular fossa on the ventral surface of the palatal process. The function of this fossa and associated foramen is unknown, but it may be a pneumatic diverticulum of the craniofacial sinus system similar to those described by Witmer (1997) in theropods. The palatal process is mediolaterally compressed and extends beyond the anterior margin of the maxilla. In contrast, the palatal process of *Batrachotomus* is expanded mediolaterally (SMNS 52970 pers. obs.). The medial surface of the palatal process has two thin ridges separated by a groove, which appears to be the anterior articulation for the vomer. A smooth surface above the dorsal ridge presumably articulated with the

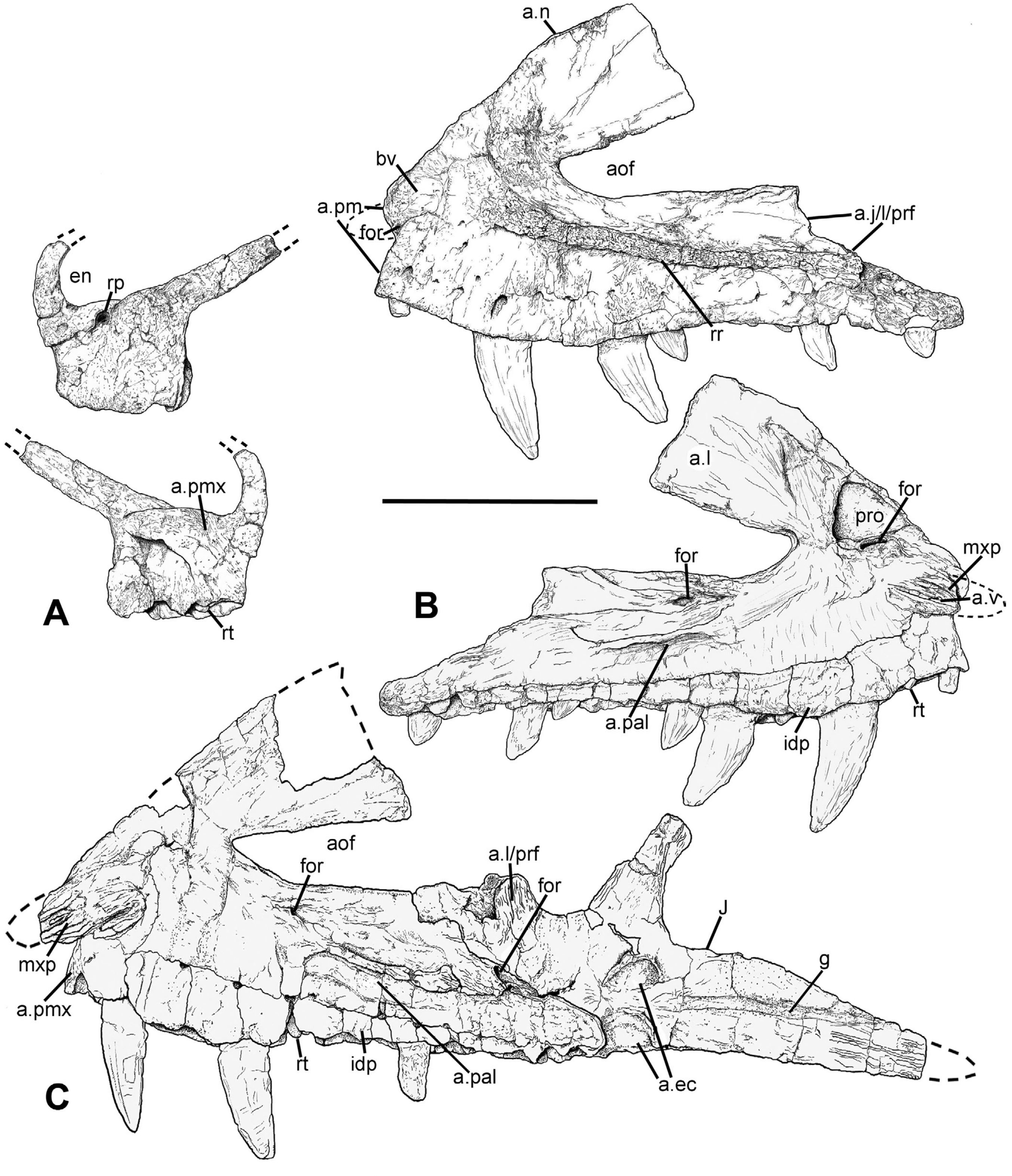

Figure 3. *Postosuchus kirkpatricki* (TTUP 9000) **A**. Left premaxilla in lateral and medial view. **B**. Left maxilla in lateral and medial view. **C.** Right maxilla and jugal in medial view. Scale bar = 10 cm.

corresponding palatal process on the other maxilla.

The ascending process of the maxilla projects posterodorsally at roughly a 45° angle to the body of the maxilla. The ascending process is thin and plate-like, and, as mentioned above, possesses a large fossa at the base on the medial surface, as in *Polonosuchus* (Sulej 2005:fig. 1D), *Luperosuchus* Romer 1971 (Desojo and Arcucci 2009) and similar to the theropod *Allosaurus* Marsh 1877 (Madsen 1993, Witmer 1997). The maxilla of *Arganasuchus* has a small foramen on the medial surface of the maxilla posterior to the palatal process (Jalil and Peyer 2007:fig. 3), which may be homologous with the fossae of other taxa. A "promaxillary fenestra" was also reported in the aetosaurs *Desmatosuchus* (Small 2002) and *Stagonolepis* (Witmer 1997). *Batrachotomus* has a depression on the medial surface of the ascending process (SMNS 52970), though it is not clear if other pseudosuchians have a foramen or hollow in this area. A large foramen present on the ventral surface of the fossa in *Postosuchus kirkpatricki* may be part of the craniofacial sinus system (Witmer 1997).

The ventral surface of the descending process of the nasal fits into a shallow and narrow groove on the ascending process of the maxilla, and both the process and the groove continue posteriorly to meet the lacrimal. Here, the ascending process overlaps the lacrimal laterally. The posterior-most part of the ascending process is broken in all type maxillae; however, there appears to be a suture line on the lacrimal indicating that the process has a V-shaped articular surface where it meets the lacrimal. The posterior portion of the maxilla overlaps the jugal laterally in a tight, jagged suture, and also overlaps part of the medial surface of the jugal. The posterior part of the main body of the maxilla contacts the descending process of the lacrimal.

On the medial surface of the maxilla, a deep shelf ventral to the antorbital fenestra extends from approximately the sixth tooth alveolus to the tenth alveolus posterior. Just ventral to this shelf is the articulating facet for the palatine. An alveolar ridge separates the dorsal portion of the maxilla from the tooth-bearing area. Like *Teratosaurus* (Galton 1985), *Polonosuchus,* (Sulej 2005), *Arganasuchus* Jalil and Peyer 2007 and *Fasolasuchus* (Bonaparte 1981), just ventral to this ridge there are distinct interdental plates on the medial surface of the maxilla. The maxilla of *Postosuchus* contains 13 alveoli. There appears to be a posteriorly-opening foramen on the medial surface, ventral to the antorbital fenestra as in *Batrachotomus* (Gower 1999) and *Teratosaurus* (Galton 1985, Sulej 2005), although this area in both holotype maxillae is somewhat deformed by postmortem crushing, and the medial surface of the right maxilla of TTUP 9002 is covered by the displaced, diagenetically attached prearticular, making it difficult to assess whether the foramen was in fact present. Anterior and dorsal to the terminal end of the posterior process, there are two large foramina that open into a groove, which wraps around posteriorly and laterally to the jugal, where it continues posteriorly between the ectopterygoid heads.

Brusatte et al. (2009) discussed differences in the alignment of the foramina above the alveoli, along the dental groove on the medial surface of the maxillae of *Teratosaurus* and *Polonosuchus.* The anterior-most alveolus of *Teratosaurus* is much smaller than the following alveoli, while this is not the case in *Polonosuchus.* In *Postosuchus*, the replacement teeth foramina follow a similar pattern to that of *Teratosaurus*, which also has a first alveolus that is much smaller than those that follow. Brusatte et al. (2009:228) claimed that the maxilla of *Polonosuchus* is differentiated from *Postosuchus* by a sinuous and convex ventral margin; however, this feature is also present in the maxilla of *Postosuchus.*

Nasal—Several nasals of *Postosuchus* have been recovered, including those of the type specimens, several *Placerias* Quarry specimens, and a partial nasal from UNC 15575. The best preserved are those of TTUP 9000 (Fig. 4A–D). The *Postosuchus* nasal is narrow, elongate and highly sculptured with a rugose lateral ridge. The ridge continues onto the lacrimal, palpebral and squamosal along the dorsolateral margin of the skull roof, similar to *Polonosuchus* (Sulej 2005) and *Batrachotomus* (Gower 1999). The anterior end of the nasal overlaps the ascending process of the premaxilla and the descending process of the nasal contacts the dorsal margin of the maxillary process of the premaxilla posteriorly. The nasal forms a majority of the dorsal border of the external naris (Fig. 4A). The medial surface has a distinct, rugose suture for articulation with the opposite nasal (Fig. 4B).

The ventral surface of the descending process of the nasal has a shallow distinctive groove where it overlaps the ascending process of the maxilla (Fig. 4D). The nasal tapers posteriorly where it meets the lacrimal and frontal. The posteroventral surface of the nasal possesses a shallow, triangular depression for articulation with the lacrimal (Fig. 4D). Anteriorly, the ventral surface of the nasal is hollowed and may be a passage for the olfactory tract.

Lacrimal—The lacrimal is best preserved on the left side of TTUP 9000 (Figs. 5, 6). It is a large, thin, plate-like bone with a highly rugose, thickened dorsolateral ridge that continues along the skull roof. The lacrimal forms the posterodorsal margin of the antorbital fenestra ventrally. The ascending process of the maxilla overlaps the anterior part of the lacrimal laterally. Anteromedially, the lacrimal is overlapped by the nasal, which fits into a large subtriangular depression on the dorsal surface of the lacrimal that tapers posteriorly into a narrow groove. In dorsal view, the lacrimal lies between the nasal anteromedially, the frontal posteromedially, and the palpebral and prefrontal posteriorly, separating the prefrontal from any articulation with the nasal. The lacrimal expands posteromedially, as in *Polonosuchus* (Sulej 2005).

The descending process of the prefrontal overlaps the descending process of the lacrimal posteriorly. The lacrimal fits into a groove on the prefrontal and this arrangement excludes the lacrimal from bordering the orbit. On the posteromedial surface, the conjunction of the lacrimal, prefrontal and frontal form a deep fossa, the function of which is unknown, as in *Sphenosuchus* Haughton 1924 (Walker 1990:fig. 5E, see Fig.

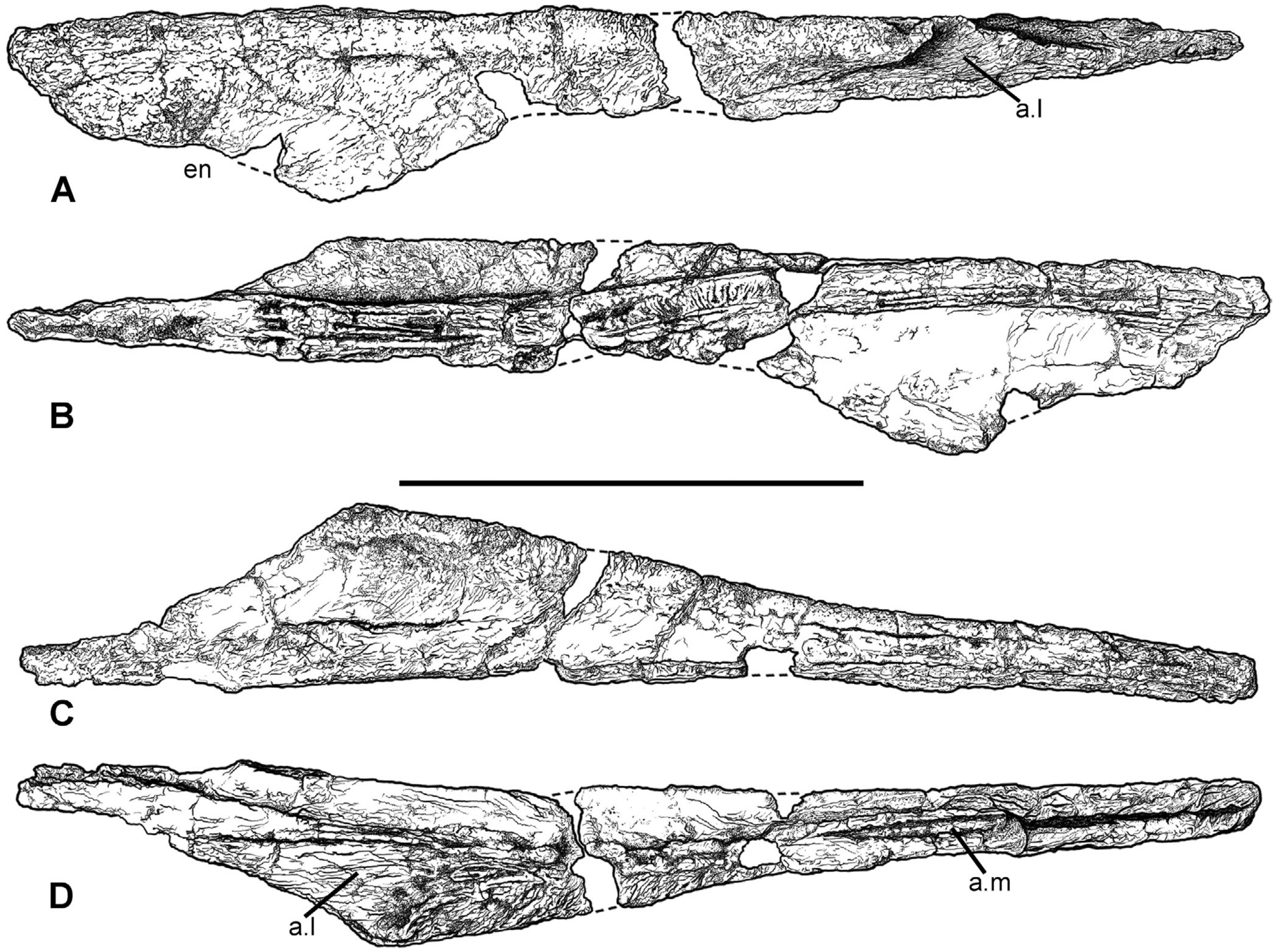

Figure 4. *Postosuchus kirkpatricki* (TTUP 9000) left nasal. **A**. Lateral view. **B**. Medial view. **C**. Dorsal view. **D**. Ventral view. Scale bar = 10 cm.

6), and similar to *Batrachotomus* (Gower 1999, pers. obs. of SMNS 80269). This fossa expands onto the medial surface of the lacrimal, where it becomes a wide, shallow impression that extends for most of the length of the bone. The fossa is bordered dorsally by a low, anteriorly trending ridge, and ventrally by the antorbital fenestra. The nasolacrimal duct is not readily identifiable.

Prefrontal—The prefrontal was previously identified by Chatterjee (1985) as a large, triangular wedge of bone that bordered the entire dorsal margin of the orbit. This would be a very unusual configuration for any archosaur, and for most reptiles (Romer 1956). However, upon preparation of the holotype and paratype skulls, it was found that there are separate sutural contacts between the lacrimal, a small wedge of bone co-ossified to the lacrimal (the actual prefrontal), and a large triangular bone, the palpebral (see below).

The prefrontal (Figs. 5, 6) consists of two parts: a small wedge of bone visible on the dorsal surface of the skull between the palpebral and lacrimal (see Fig. 1) and an ornately sculptured, ventral descending process that overlaps the lacrimal in a tongue-in-groove articulation. The prefrontal forms the anterior margin of the orbit. This configuration is very similar to that in *Saurosuchus* (Alcober 2000) and *Polonosuchus* (Sulej 2005:fig. 1B, C). The dorsal-most portion of the descending process overlaps approximately one third of the anteroposterior length of the lacrimal, but narrows ventrally from this point and continues to a small suture visible on the medial surface of the anterior ascending process of the jugal (Fig. 12). The anteromedial surface of the prefrontal is deeply excavated, forming a deep fossa with the lacrimal and frontal. A small, round depression containing a foramen is present on the posteromedial surface of the dorsal portion of the prefrontal. This foramen appears to connect to the anterolateral edge of the frontal, just lateral to the fossa that continues onto the prefrontal and lacrimal.

Palpebral—After re-preparation of the holotype, it is apparent that the large triangular element described by Chatterjee (1985) as the prefrontal is in fact a palpebral (supraorbital) bone (Figs. 2, 7). This assignment is supported by the sutural arrangement between that element and the lacrimal,

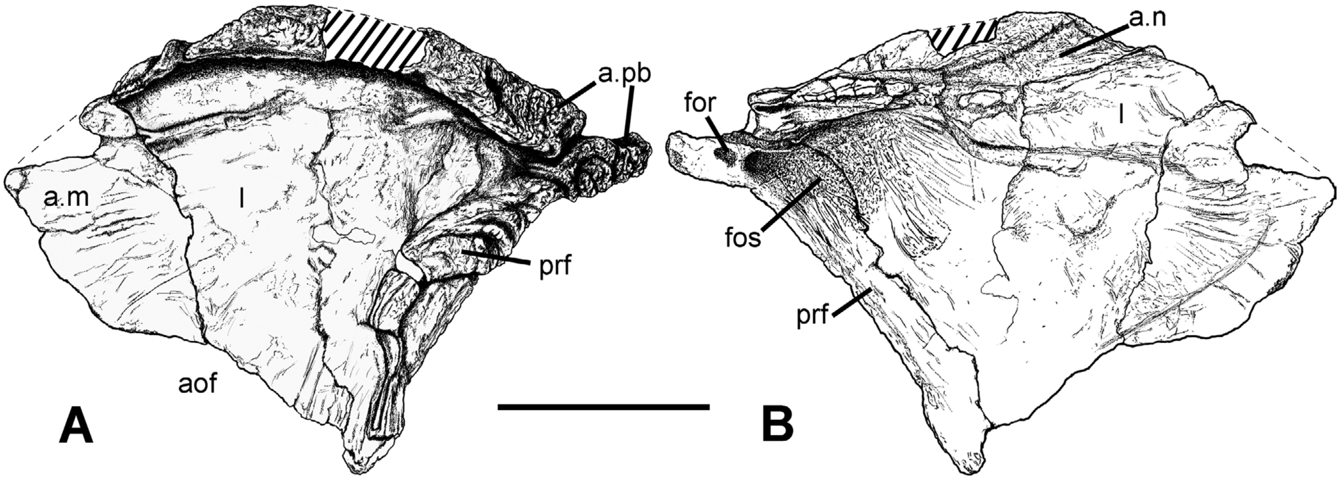

Figure 5. *Postosuchus kirkpatricki* (TTUP 9000) left lacrimal and prefrontal. **A**. Lateral view. **B**. Medial view. Scale bar = 40 mm.

prefrontal, and frontal bones. There are also several examples of the palpebral in other *Postosuchus* specimens (e.g., UCMP A269/140035 and UNC 15575). Examination of a recently discovered frontal bone (MCCDMP 1654) of *Postosuchus* by A. Hungerbühler (pers. comm.), confirmed this interpretation. The phylogenetic significance of this bone in *Postosuchus* will be discussed in a subsequent publication.

The unusual configuration of this region of the skull accounts for the mis-diagnosis of the lateral (triangular wedge) portion of the bone as the prefrontal by Chatterjee (1985), Long and Murry (1995), and subsequently in *Polonosuchus* by Sulej (2005:fig. 4E, F). No other known non-crocodyliform pseudosuchian besides *Polonosuchus* possesses a palpebral bone that completely blocks the frontal from contact with the orbital margin.

The exclusion of the dorsal portion of the prefrontal from exposure on the lateral surface of the skull is an unusual character, shared only with *Polonosuchus* (Sulej 2005:fig. 1B, C). If the palpebral is removed from the restoration of the skull, a typical dorsal skull configuration is present, with the prefrontal exposed laterally. The orbital portion of the frontal in most pseudosuchians is concave (e.g., phytosaurs, aetosaurs, poposauroids and most rauisuchids), but the palpebral in *Postosuchus* and *P. silesiacus* (Sulej 2005:fig. 4E, F) has a convex orbital margin strikingly similar to that in *Sebecus*, an Eocene crocodyliform (Colbert 1946:fig. 5A). A new *Postosuchus* frontal from New Mexico (MCCDMP 1654) also supports this interpretation (see below).

The palpebral is a wide and relatively thick subtriangular bone with a rugose, thickened lateral ridge that overhangs the orbit and continues as a dorsolateral ridge along the upper skull margin that is also formed by the nasal, lacrimal postorbital, and squamosal. The dorsal surface is convex and possesses many vascular foramina. The lateral edge of the ventral surface has many small canals, some of which lead to small nutrient foramina. The rest of the ventromedial surface of the palpebral is mostly smooth, with a few small foramina. It has a concave, circular depression, the lateral margin of the optic fossa, which is continuous with the depression on the frontal and the posterolateral edge of the prefrontal. In dorsal view, the lateral edge of the palpebral has a small depression about a third of the way down from the anterior edge that separates the anterior and posterior portions of the bone. The anteromedial surface articulates with the lacrimal, prefrontal and frontal, and the posteromedial surface articulates with the postfrontal and postorbital.

Frontal—The frontal of *Postosuchus* is known from several specimens including a nearly complete left frontal in the holotype (Fig. 8), and nearly complete left and right frontals from the paratype. UCMP 27478 consists of partial left and right frontals from the *Placerias* Quarry in Arizona, and a

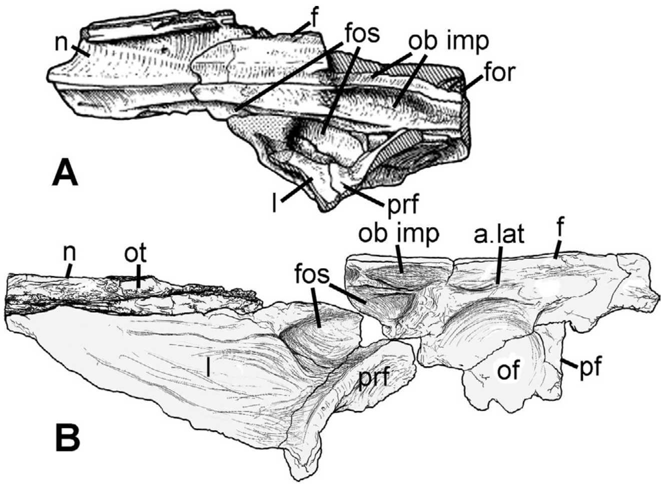

Figure 6. A. Ventral view of conjoined nasals, frontals, lacrimal and prefrontal of the holotype of *Sphenosuchus acutus* (modified from Walker 1990) indicating the large fossa that appears to be homologous with that of *Postosuchus*. **B**. Same elements; view of *Postosuchus kirkpatricki* (TTUP 9000). Anterior is to the left. Not to scale.

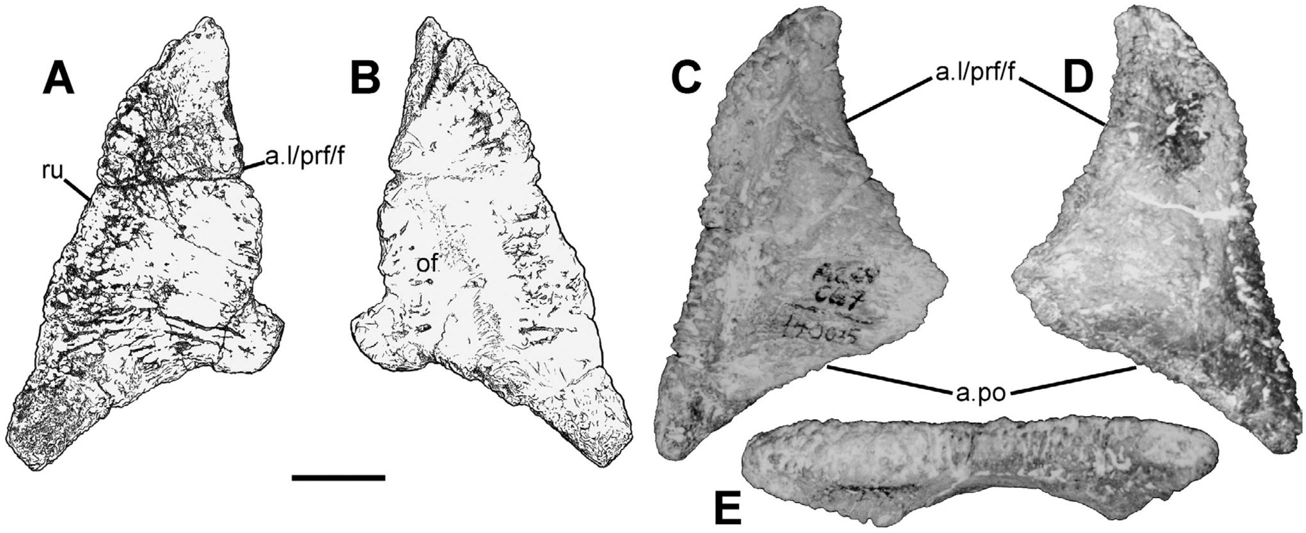

Figure 7. *Postosuchus kirkpatricki* (TTUP 9000) left palpebral. **A**. Dorsal view. **B**. Ventral view. **C–E**. UCMP A269/140035 left palpebral. **C**. Dorsal view. **D**. Ventral view. **E**. Lateral view. Scale bar = 20 mm.

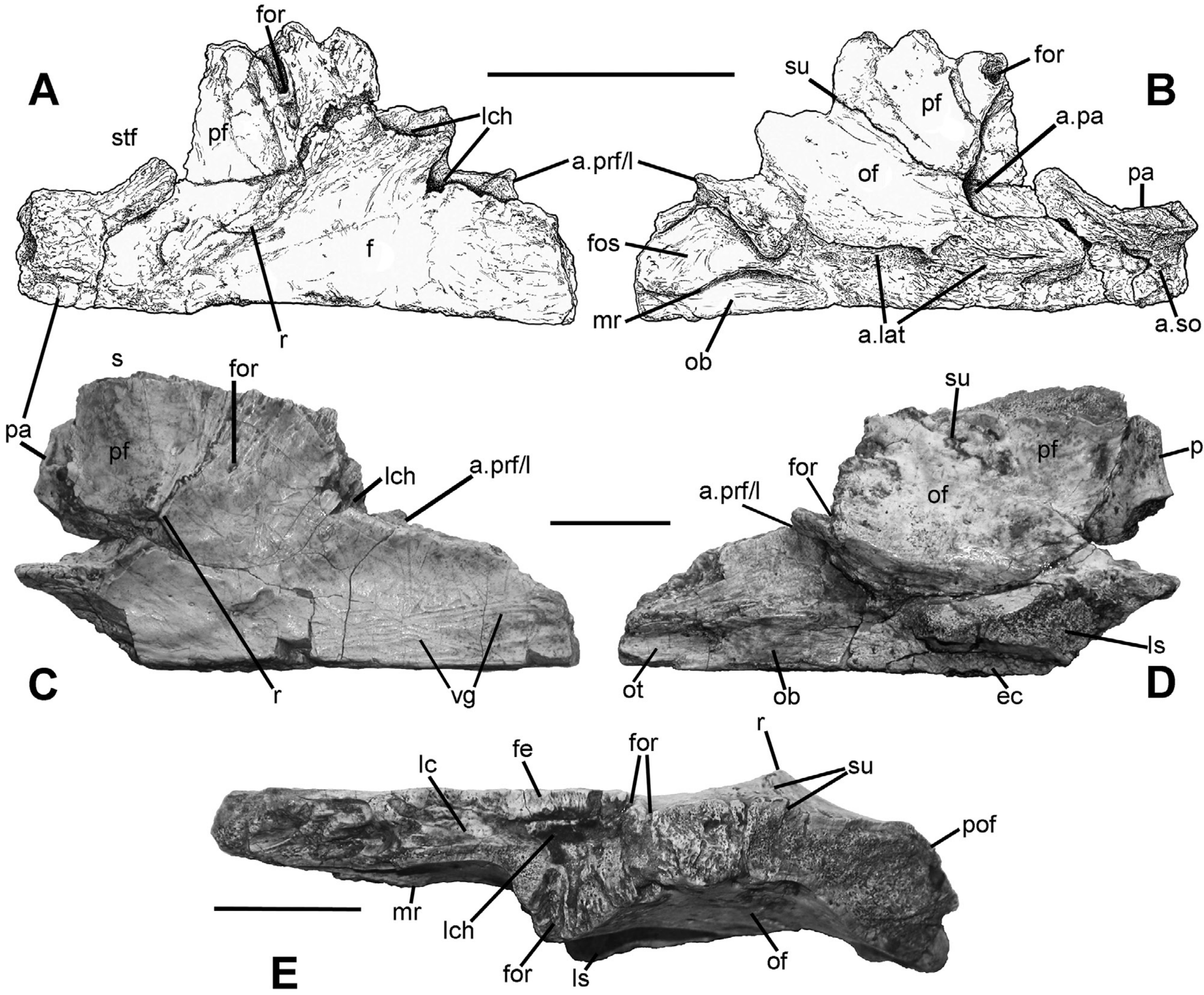

Figure 8. *Postosuchus kirkpatricki* (TTUP 9000) left frontal-postfrontal. **A**. Dorsal view. **B**. Ventral view. **C–E**. MCCDM 1654 left frontal-prefrontal. **C**. Dorsal view. **D**. Ventral view. **E**. Lateral view. Scale bar for **A** and **B** = 40 mm, scale bars for **C–E** = 20 mm.

well-preserved left frontal (MCCDMP 1654) from the Trujillo Formation of eastern New Mexico recently identified by A. Hungerbühler (pers. comm.) clarifies many details of the element (Fig. 8). The paratype frontals are not as well preserved as in the holotype or MCCDMP 1654.

The frontal of *Postosuchus* is a thick, broad wedge of bone similar in general morphology to the frontal in other archosaurs, most notably *Sphenosuchus* (Walker 1990). The dorsal surface of the frontal has many small nutrient foramina, and on MCCDMP 1654, distinct impressions of small blood vessels are present, some leading into foramina. Most of the small foramina are concentrated on the posterolateral edge of the dorsal surface, surrounding the suture between the frontal and prefrontal. The anterior dorsal surface has a shallow, elongate depression that rises gently toward the midline of the skull, and more sharply toward the lateral margin. Posteriorly, a large crest trends anterolaterally from the posterior midline of the bone and separates the frontal from the postfrontal, which are firmly sutured to one another. This crest forms the anterior margin of the supratemporal fossa, an arrangement that is most similar to that of *Hesperosuchus* (Clark et al. 2000), *Dromicosuchus grallator* Sues et al. 2003 and *Sphenosuchus* (Walker 1990) among paracrocodylomorphs.

The nasal overlaps the frontal anteriorly and the lacrimal and prefrontal overlap the frontal anterolaterally. The frontal is overlapped by the parietal posteromedially, with part of the parietal fitting into a deep depression on the ventral portion of the conjoined frontal and postfrontal. The anteromedial portion of the parietal is partly fused to the posteromedial portion of the frontal in the holotype and paratype, and the anterolateral parietal is partly fused to the depression in the underside of the frontal-prefrontal in MCCDMP 1654 (Fig. 8).

The frontal does not have a finished lateral edge typical of tetrapods, nor does the frontal enter into the orbit or the supratemporal fenestra. Instead, several small chambers excavate the lateral margin of the frontal, which may be part of a craniofacial sinus system (Witmer 1997). Although TTUP 9000 possesses all of the following characters, the excellent preservation of MCCDMP 1654 clarifies many of the details that were not previously apparent in the holotype. The largest chamber (lateral frontal chamber) is slightly dorsal and posterior to the beginning of the fossa that extends onto the prefrontal and lacrimal. This chamber feeds into several channels that trend posterodorsally toward the dorsal surface of the bone, ventrally into the orbit, and anteriorly toward the prefrontal and lacrimal. The chamber is approximately 12 mm long with an exposed depth of at least 5 mm, but the medial extent of the chamber is obstructed by hematitic matrix. A 2.5 mm thick natural edge of bone is present dorsal to the chamber. The lateral canal is the largest channel leading from this chamber and opens to about 3.5 mm at its widest path. The lateral canal trends anteriorly toward the medial edge of the lacrimal, emptying into a groove on the ventral surface of the posteromedial portion of the lacrimal. This groove overhangs the deep fossa created between the lacrimal and prefrontal and wraps around the medial edge of the lacrimal and into the articular surface for the nasal bone. Several more channels open ventrally into the anteromedial margin of the orbital fossa, just posterolateral to the depression for the olfactory bulb, and several open directly into the anterior portion of the orbital fossa (Fig. 8).

The ventral surface of the frontal is dominated by the large optic fossa, occupying most of the ventrolateral surface. Several nutrient foramina are present in the fossa. The posterolateral edge of the optic fossa is formed by the confluence of frontal and postfrontal bones, with a distinct suture separating the two elements. Anteromedially, the optic fossa curves ventrally, and where it meets the prefrontal, the anterolateral edge opens into the lateral chamber mentioned above. Several small channels (approximately 2 mm wide at maximum) lead from this fossa into the orbit between the frontal and prefrontal bones, similar to *Sphenosuchus* (Walker 1990:fig. 6D). Medially, the optic fossa is bordered by a deep groove with a distinct suture for the laterosphenoid bone, which separates the optic fossa from the olfactory bulb. A piece of the laterosphenoid is fused to this suture on MCCDMP 1654, clearly indicating that the laterosphenoid extends anteriorly to the posterolateral edge of the fossa that continues onto the prefrontal and lacrimal. The impression of the dorsal surface of the olfactory bulb on the anteromedial surface of the frontal occupies about one third the length of the bone. It widens mediolaterally before constricting into a narrow channel separated from the olfactory tract anteriorly by a rounded "step." The depression for the olfactory bulb is bordered laterally by a large fossa and separated by a low, median ridge. This fossa is part of the fossa on the prefrontal and lacrimal. Walker (1990:90) speculated that the channels in the frontal of *Sphenosuchus* served to house salt glands similar to those in sea birds, but found no homolog in extant crocodylians or other crocodylomorphs. However, because paracrocodyliforms were terrestrial animals that lived near freshwater sources, this seems unlikely.

Postfrontal—The postfrontal in *Postosuchus* is a small, thick element firmly attached to the posterolateral edge of the frontal, with several fossae on the lateral surface like those in the frontal (Fig. 8). On the dorsal surface of the skull, the suture between the frontal and postfrontal continues along the posteromedially trending ridge that forms the anterior margin of the supratemporal fossa.

A large foramen continues into a deep, posterolaterally trending groove that descends ventrally into a small chamber within the posterolateral edge on the lateral margin of the postfrontal. This configuration appears to be virtually identical to that of *Sphenosuchus* (Walker 1990:fig. 6D). It is not clear if other crocodylomorphs possess this same type of potential pneumatization shared between *Postosuchus* and *Sphenosuchus* in the frontal region of the skull, or if it simply has not been described for other taxa.

Parietal—The right parietal is mostly complete in TTUP

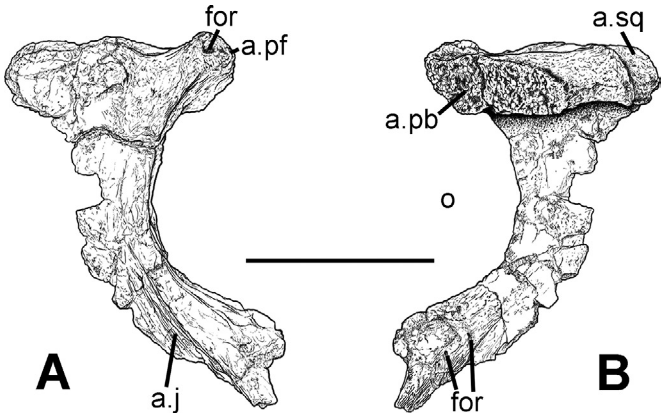

Figure 9. *Postosuchus kirkpatricki* (TTUP 9000) left postorbital. **A**. Medial view. **B**. Lateral view. Scale bar = 5 cm.

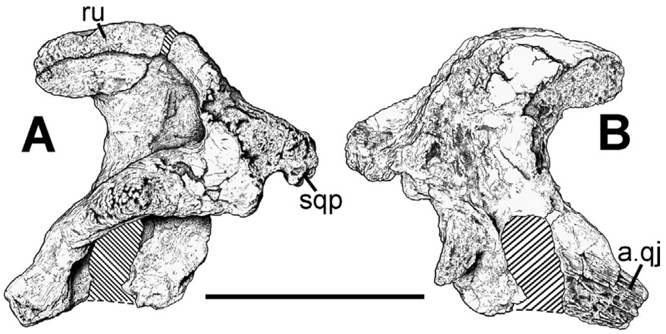

Figure 10. *Postosuchus kirkpatricki* (TTUP 9000) left squamosal. **A**. Lateral view. **B**. Medial view. Scale bar = 5 cm.

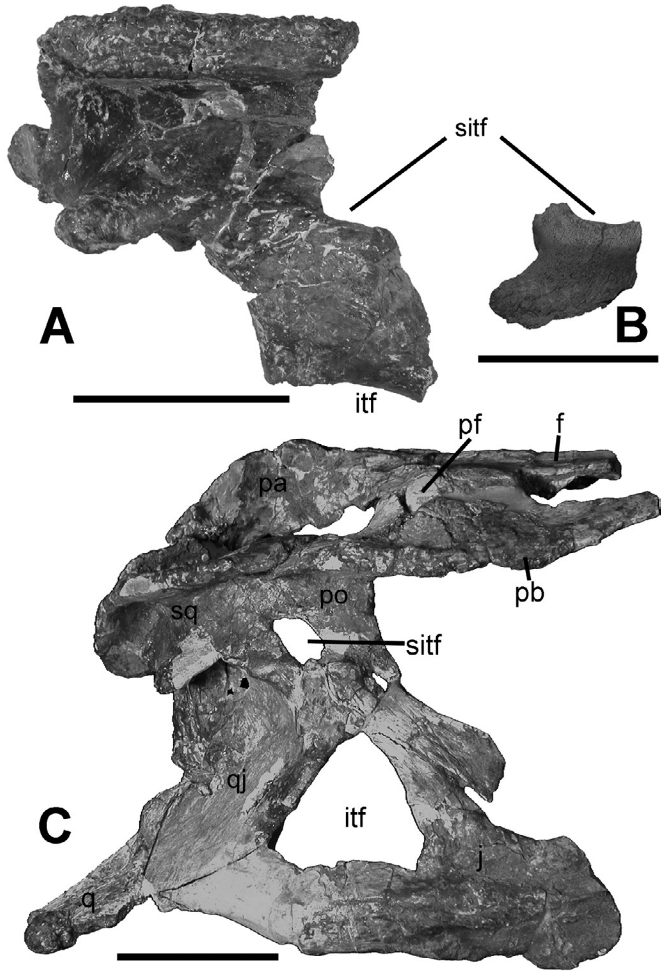

Figure 11. *Postosuchus* right squamosals showing bifurcated lateral temporal fenestra in right lateral view. **A.** UCMP 27441 right squamosal. **B.** UNC 15575 partial right squamosal. **C.** TTUP 9002 partial skull in right lateral view. Scale bars = 5 cm.

9002, with part of the left parietal fused to the left frontal (see Figs. 1, 2). In MCCDMP 1654, a small piece of the anterolateral parietal is fused to the frontal-postfrontal element. The bone is a relatively narrow and slender element, similar to the condition in closely related taxa (e.g., *Saurosuchus*, *Batrachotomus* and *Sphenosuchus*). The anterior arm of the parietal is bifurcated, much like the parietal in *Batrachotomus* (Gower 1999), with a medial portion that overlaps the posterior edge of the frontal, and a lateral part that fits into a deep slot on the ventral surface of the frontal and postfrontal. Posterolaterally the parietal articulates on the posteromedial surface of the squamosal. Dorsally, the parietals form a narrow crest with a shallow groove in the center that continues anteriorly onto the posterior region of the frontals. The anterior ventral surface of the parietals contains part of the endocranial cavity and the articulation for the supraoccipital is posterior to the endocranial cavity.

Postorbital—The configuration of the postorbital is typical of rauisuchids, in forming a keyhole-shaped orbit where the descending process of the postorbital projects forward into the orbit (Fig. 9). The dorsal process of the postorbital is thickened and rugose, and articulates with the palpebral anterolaterally in a rugose suture, and anteromedially with the postfrontal. Posteriorly, the postorbital is overlapped by the squamosal. The posteroventral surface of the postorbital descending process fits into a grooved suture on the anterolateral edge of the jugal. The confluence of these bones creates an accessory superior infratemporal fenestra (discussed below). The quadratojugal does not contact the postorbital in *Postosuchus* and is separated by a forward projection of the squamosal. Postorbital-quadratojugal contact does not appear to reflect a phylogenetic signal linking suchians, as suggested by Parrish (1993), since among aetosaurs, it is apparent only in *Aetosaurus* (Schoch 2007), and the relationship of these elements in other pseudosuchians is unclear (Schoch 2007). Together, the postorbital and the ascending process of the jugal form the posterior border of the orbit. The posteromedial surface of the dorsal process forms the anterolateral corner of the supratemporal fossa.

The body of the postorbital is expanded laterally, overhangs the descending process, and creates a deep recess ventrolaterally. The postorbital participates in the formation of a continuous dorsolateral ridge along the length of the skull. The descending process of the postorbital is "stepped", or curved anteriorly about halfway down its length, like other rauisuchids and the poposauroid *Arizonasaurus* (Nesbitt 2005, pers. obs. of MSM 4590). The descending process is triangular in cross-section with the anterior edge transversely flattened and posteriorly tapered. The lateral surface is slightly concave along its length. A depression on the lateroventral surface of the descending process is not as deeply excavated as in *Batrachotomus* (Gower 1999, pers. obs. of SMNS 52970, 80260). The lateroventral surface of the postorbital also has numerous small nutrient foramina.

Squamosal—The squamosal is a complex bone that forms the back of the skull roof and radiates into five separate processes: anterior and posterior, ventromedial, ventrolateral, and lateral (Figs. 10, 11). The anterior and posterior projections of the squamosal form most of the lateral and part of the posterior border of the supratemporal fenestra, which is roughly ovate and tapers to the posterolateral edge of the skull roof.

The dorsolateral margin of the squamosal is thickened and rugose, forming the posterior terminal point of the

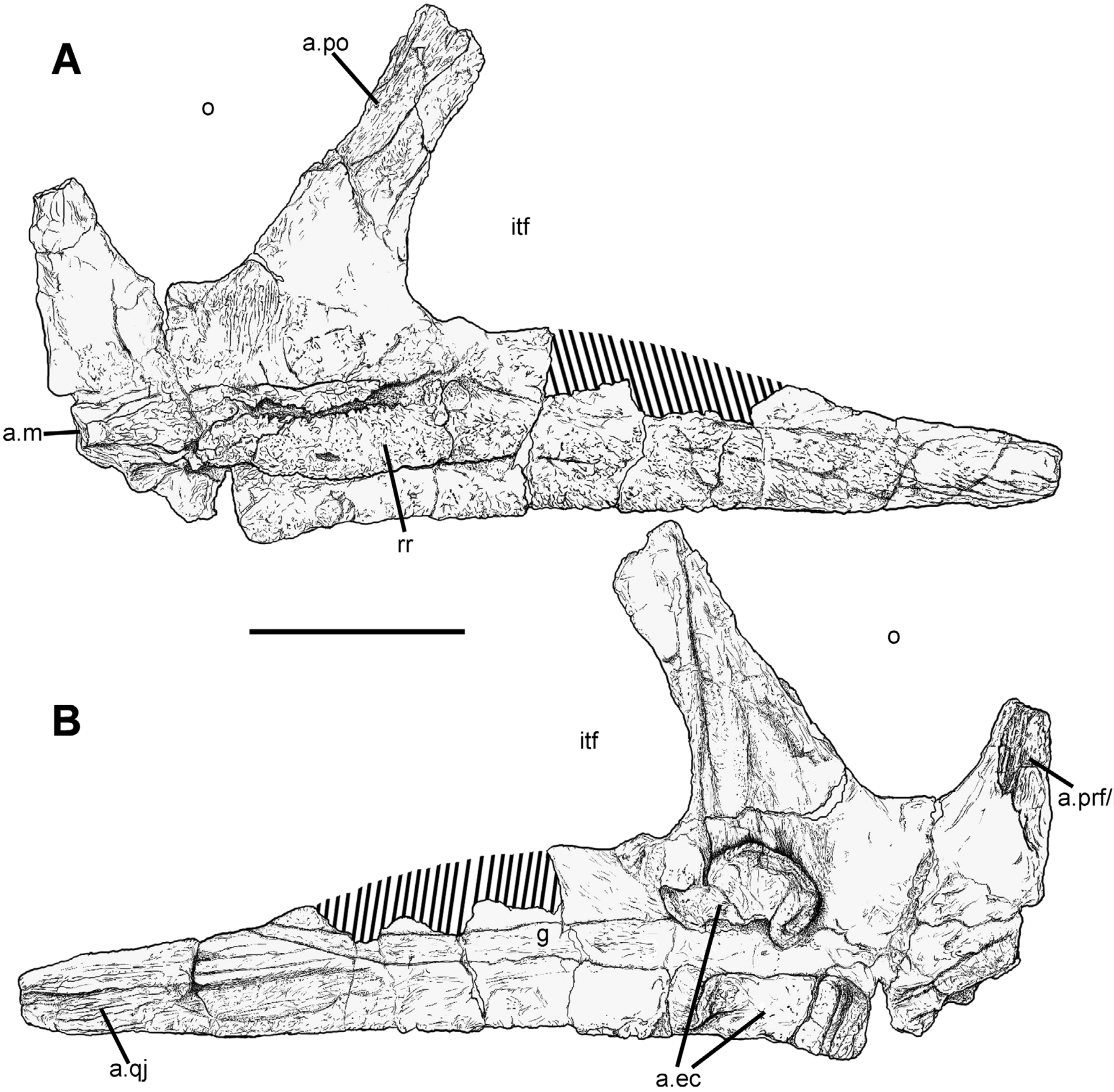

Figure 12. *Postosuchus kirkpatricki* (TTUP 9000) left jugal. **A**. Lateral view. **B**. Medial view. Scale bar = 5 cm.

rugose ridge that continues along the entire dorsolateral skull roof, identical to *Polonosuchus* (Sulej 2005) and similar to *Batrachotomus* (Gower 1999). Posteriorly, this ridge curves ventrally, then anteriorly and laterally, forming a deep concavity anteriorly and laterally. Posterior to the ridge, the ventromedial opisthotic process overhangs the head of the quadrate, as in other archosaurs.

The anterior ramus of the squamosal overlaps the postorbital. The posterior ramus of the squamosal curves medially to articulate with the parietal, and a cup-shaped depression receives the quadrate head ventromedially. Dorsal to the articulation for the quadrate, an articular surface is surrounded by a low ridge for the reception of the paroccipital process of the opisthotic on the medial side of the squamosal. The ventrolateral descending process tapers to a point and is wedged between the quadrate posteriorly and the quadratojugal anteriorly.

The squamosal forms the dorsal, posterior and ventral borders of the small, round superior infratemporal fenestra (see description of postorbital), that is ventral and posterior to the articulation with the postorbital (Fig. 11). This is identical to the configuration in *Polonosuchus* (Sulej 2005:fig. 4G), and is similar to that in *Saurosuchus* (Alcober 2000:figs. 1, 2; pers. obs. of cast of PVSJ 32) in which this process divides the infratemporal fenestra. The forward projection of the squamosal forms an incipient accessory lateral temporal fenestra. This could be an apomorphy of rauisuchids, although this cannot be determined for *Batrachotomus* because most of the quadratojugal is unknown and part of the squamosal is broken in SMNS 80260.

Jugal—The triradiate jugal forms the ventral margins of the orbit and almost the entire anterior and ventral margins of the subtriangular lower infratemporal fenestra (Figs. 3C, 12). The rugose ridge that continues from the maxilla develops a large swelling on the lateral surface of the jugal before it tapers posteriorly. The posterior process of the maxilla overlaps the anterior ramus of the jugal in a sinuous suture that traverses the rugose ridge. A suture on the medial surface of the anterior ascending process indicates where the descending process of the prefrontal articulates. An elongate and distinct suture on the anterodorsal surface of the posterior ascending process of the jugal articulates with the ventral process of the postorbital bar. The jugal tapers posteriorly and fits into a long, deep groove on the ventrolateral surface of the quadratojugal. The lateral surface of the jugal is extremely rugose, with distinct vascular grooves.

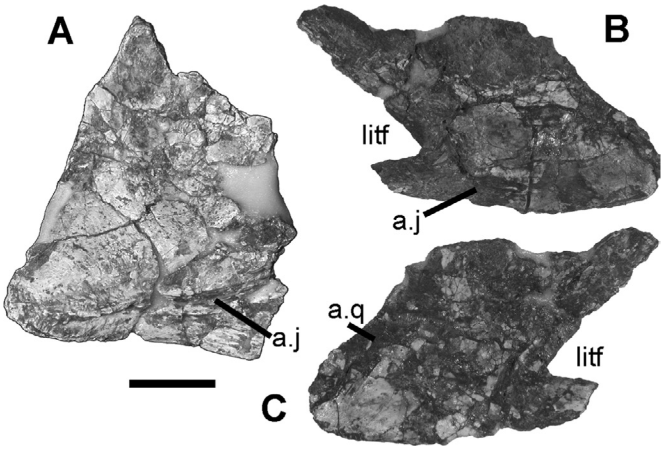

Figure 13. *Postosuchus kirkpatricki* type quadratojugals. **A**. TTUP 9000 partial right quadratojugal in lateral view. **B**. TTUP 9002 partial left quadratojugal in lateral view. **C**. TTUP 9002 partial left quadratojugal in medial view. Scale bar = 20 mm.

A socket for reception of the ectopterygoid on the medial surface of the jugal lies just ventral to the margin of the orbit.. The socket is bifurcated into dorsal and ventral components (a condition also present in *Sphenosuchus, Batrachotomus* and *Polonosuchus*), separated by a deep groove that originates just posterior to a large foramen on the maxilla, and continues posteriorly until it curves gently upward onto the quadratojugal. The dorsal socket is formed by a raised semicircular ridge that arcs posteriorly, while the ventral socket, the smaller of the two, is more rectangular in shape and opens ventrally. Grooves on the sockets correspond to large and smaller grooves that continue onto the ectopterygoid.

Quadratojugal—The quadratojugal is a large, plate-like bone that is firmly sutured to the squamosal dorsally and posterodorsally, and overlaps the quadrate posteriorly (Fig. 13). The quadratojugal is deeply excavated on the lateral surface, just ventral to the overhang of the squamosal.

Anteroventrally, the quadratojugal possesses a deep groove into which the jugal articulates. There is a quadrate foramen at the quadratojugal-quadrate contact just ventral to the descending process of the squamosal that is present in saurians such as proterosuchids (e.g., Cruikshank 1972), *Euparkeria capensis* Broom 1913 (Ewer 1965), aetosaurs (e.g., Walker 1961), and other rauisuchids like *Batrachotomus* (Gower 1999). This quadrate foramen is not present in *Erythrosuchus africanus* Broom 1905 (Gower 2003) or the crocodylomorphs *Hesperosuchus* (Clark et al. 2000) and *Sphenosuchus* (Walker 1990).

The anterodorsal region of the quadratojugal projects anteriorly with the anteroventral portion of the squamosal to articulate with the postorbital, dividing the infratemporal fenestra into two separate fenestrae: a small, ovate upper

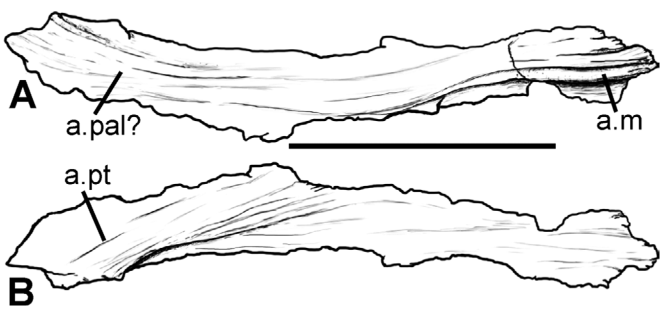

Figure 14. *Postosuchus kirkpatricki* (TTUP 9002) right vomer. **A**. Dorsal view. **B**. Ventral view. Scale bar = 5 cm.

fenestra (superior infratemporal fenestra) and a large, subtriangular lower fenestra (inferior infratemporal fenestra). This configuration is also observed in *Polonosuchus* (Sulej 2005:fig. 4G), and a similar condition is present in *Saurosuchus* (Alcober 2000:figs. 1–2, pers. obs. of cast of PVSJ 32). This fenestra has been one of the more contentious issues regarding the cranial anatomy of *Postosuchus* (Parrish 1993, Long and Murry 1995). Diapsid reptiles (including most archosaurs) typically have a single infratemporal fenestra on the lateral surface of the skull surrounded by the postorbital, squamosal, quadratojugal and jugal (Romer 1956). In *Postosuchus* (Chatterjee 1985), *Polonosuchus* (Sulej 2005), and possibly *Tikisuchus* (in Sulej 2005:81) however, this fenestra is divided at the dorsal margin, creating an accessory infratemporal fenestra. As noted by Chatterjee (1985), partial division of the fenestra was developed independently in tyrannosaurids (Holtz 1994).

When plaster was removed from the upper infratemporal fenestra of TTUP 9002, the original bone surface was revealed, confirming a second infratemporal opening. UCMP A269/27441, a right squamosal from the *Placerias* Quarry, and a partial squamosal from UNC 15575, also clearly show a bifurcated lateral temporal fenestra.

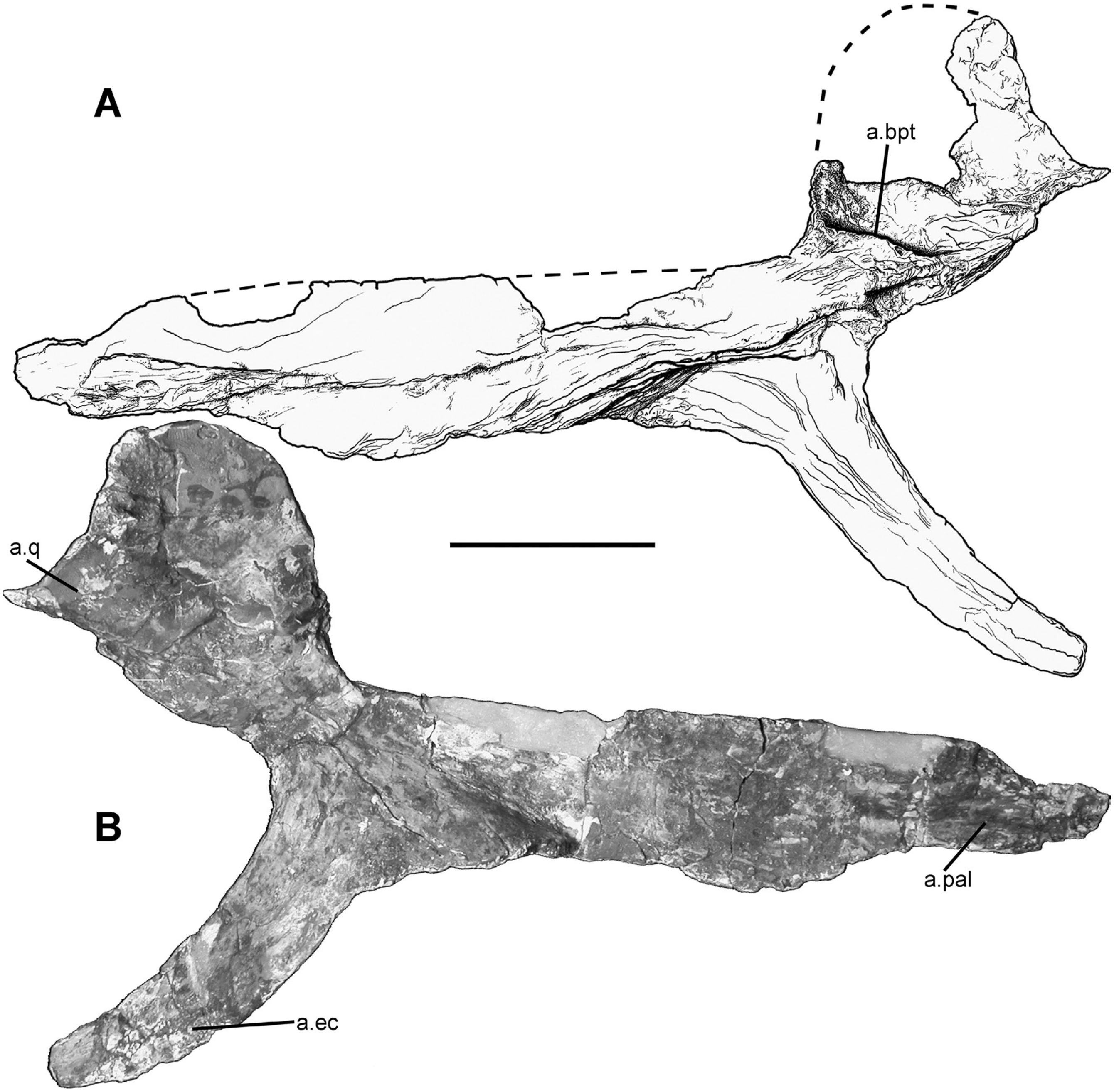

Figure 15. *Postosuchus kirkpatricki* (TTUP 9000) right pterygoid. **A**. Medial view. **B**. Lateral view. Scale bar = 5 cm.

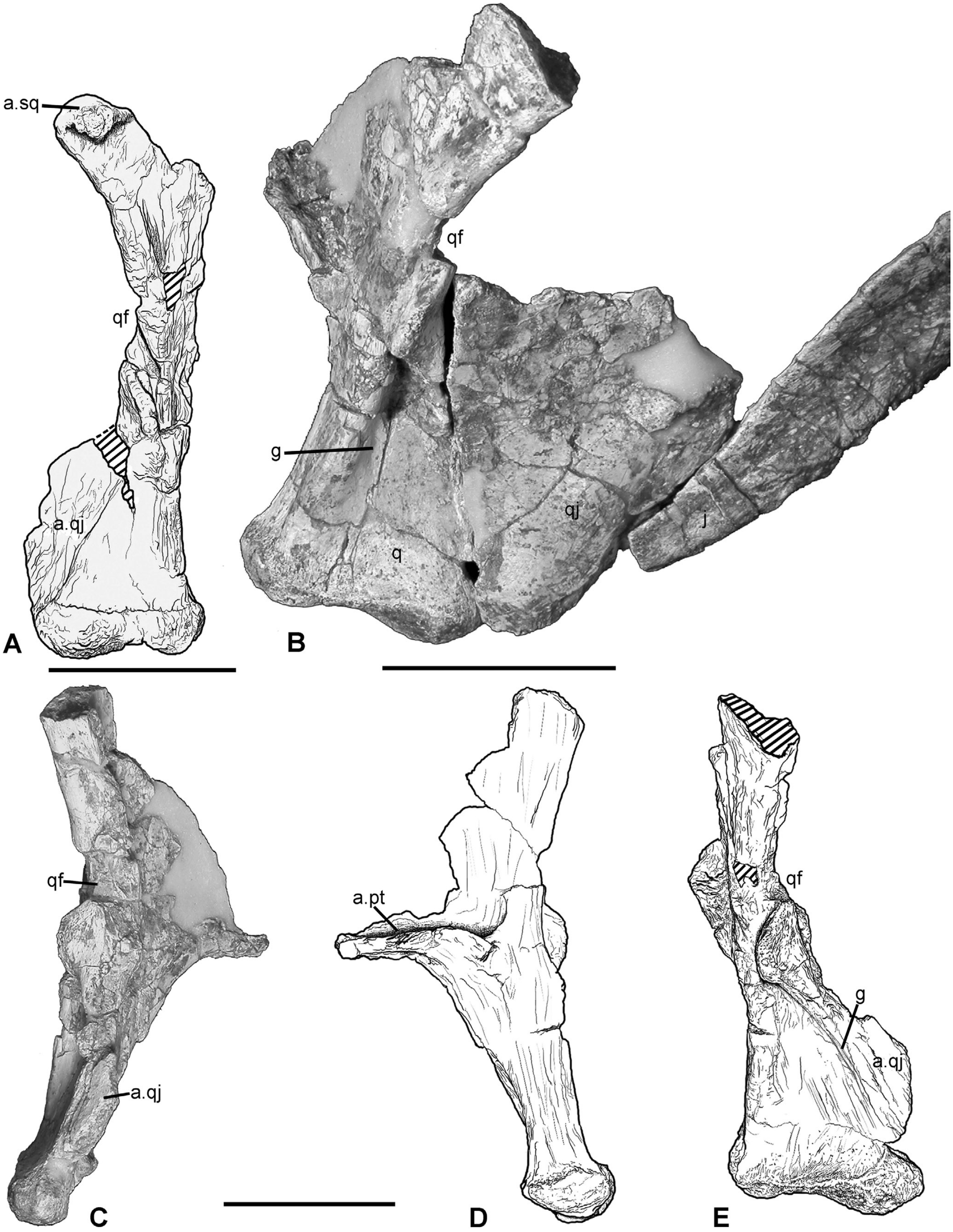

Figure 16. *Postosuchus kirkpatricki* (TTUP 9000) quadrates. **A**. Left quadrate in posterior view. **B**–**E**. Right quadrate with quadratojugal and jugal. **B**. Posterolateral view. **C**. Lateral view. **D**. Medial view. **E**. Posterior view. Scale bars = 5 cm.

Palatal complex

Vomer—Although a complete vomer from *Postosuchus* has not been recovered, TTUP 9002 does have a portion of the right vomer (Fig. 14). It is long and narrow, and extends anteriorly from the posteromedial edge of the palatine to meet the palatal process of the maxilla.

There are two articulating facets on the anterodorsal surface of the vomer, separated by a median ridge that begins on the lateral margin, and curves posteromedially to the medial edge. The lateral facet is overlapped by the medial edge of the palatine, whereas the medial facet is overlapped by the thin, anterior ramus of the pterygoid.

Palatine—Chatterjee (1985:405, 407, fig. 6E) described an element as the palatine, but provided a limited description, stating the palatines "are small and articulate with the pterygoid posteriorly," and that "each bone takes part in the formation of choana and palatal fenestra". It is unclear if the bone he described is a palatine because the element could not be located during later examination of the material.

Pterygoid—The pterygoid is long, triradiate (Fig. 15) and similar in morphology to that of many archosauriforms (e.g., other pseudosuchians and erythrosuchids). The anterior ramus is transversely narrow, expands slightly dorsoventrally, and tapers anteriorly. A ridge on the medial surface extends the length of the anterior ramus. The anterior ramus articulates with the palatine anterolaterally and vomers anteriorly. The two anterior rami are in contact along most of their length, reducing the length of the interpterygoid vacuity at the anterior end.

The quadrate ramus extends posterodorsally where it meets the pterygoid flange of the quadrate. At the base of the quadrate ramus, the medial surface possesses a cup-shaped depression into which the basipterygoid process of the basisphenoid articulates. This ball-in-socket joint may have allowed limited movement between the pterygoid and braincase.

A medial ridge on the large posteroventral ramus of the pterygoid is the attachment site of *M. pterygoideus ventralis*. Laterally, the dorsal surface of the posteroventral ramus is overlapped by the ectopterygoid.

Quadrate—Examples of the quadrate are known from the type material and from the *Placerias* Quarry; the most complete element is from TTUP 9000 (Fig. 16). The quadrate is similar in morphology to that of many archosaurs. It is high, with a rounded head that articulates with a depression on the ventral surface of the squamosal. A ridge begins on the medial articular condyle and continues dorsolaterally, terminating in the head of the quadrate. Ventrolateral to the head of the quadrate is a ridge that fits into a groove on the descending

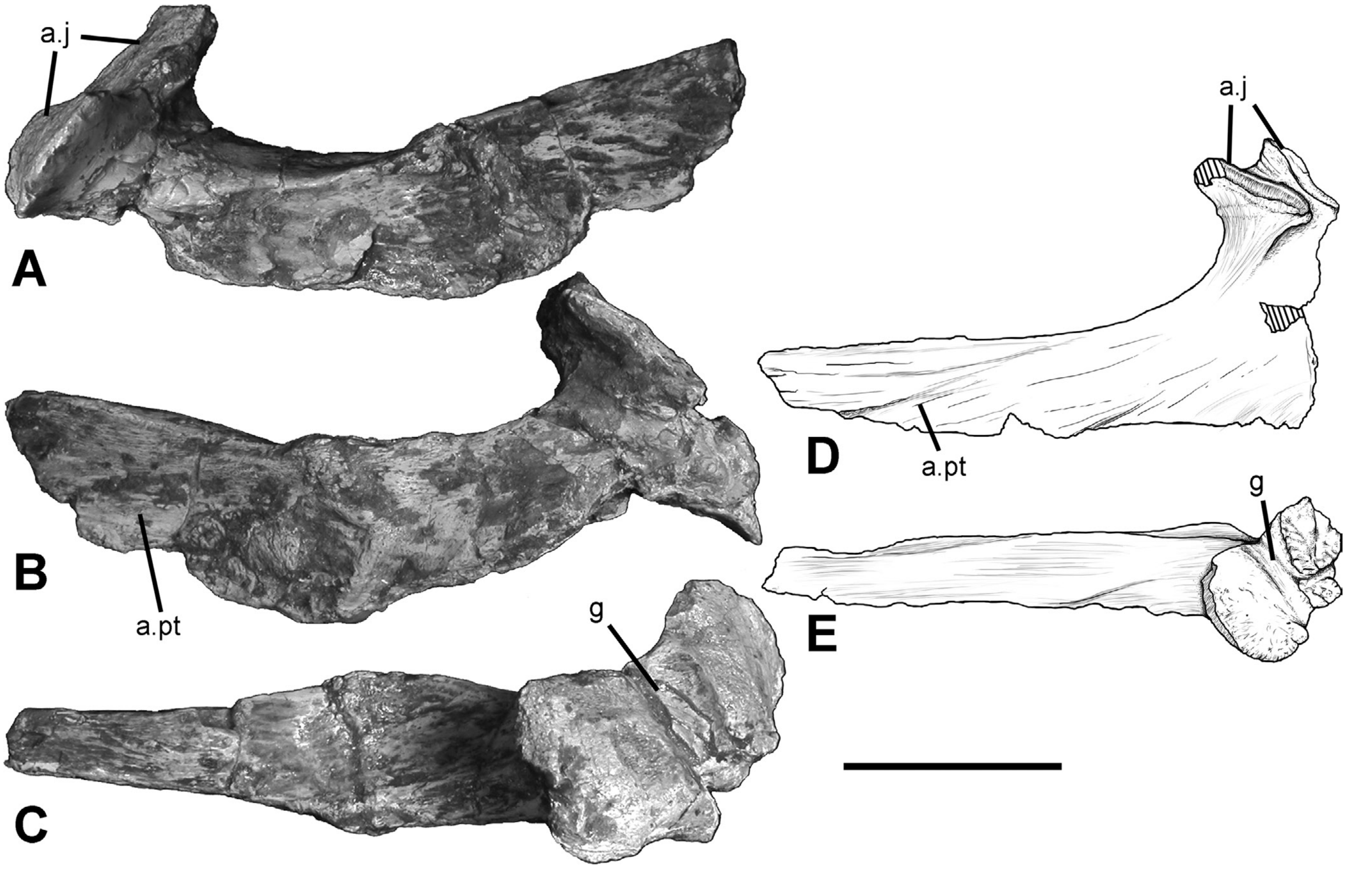

Figure 17. *Postosuchus kirkpatricki* (TTUP 9000) right ectopterygoid. **A**. Dorsal view. **B**. Ventral view. **C**. Lateral view. **D**, **E**. TTUP 9002 right ectopterygoid. **D**. Ventral view. **E**. Lateral view. Scale bar = 30 mm.

process of the squamosal. A quadrate foramen is present approximately halfway along the length of the quadrate formed by a medial emargination of the quadrate along its anterolateral articulation with the quadratojugal. Although Chatterjee's (1985:fig. 3C) illustration of the holotype left quadrate indicates a foramen ventromedial to the actual position of the quadrate foramen, this is an artifact of preparation. This is supported by the fact that no other *Postosuchus* quadrate possesses a foramen in the area figured by Chatterjee, including the right quadrate from the same specimen. A distinct facet is separated by a ridge where the quadratojugal articulates on the lateroventral surface of the quadrate.

The ventral articular surface of the quadrate has two well-defined condyles separated by a shallow groove that trends anteromedially. The pterygoid process begins about halfway up the medial surface of the quadrate and extends anteromedially. A groove on the surface of the pterygoid process that articulates with the quadrate ramus of the pterygoid. A faint groove on the posterior surface of the quadrate extends ventromedially from the quadrate foramen to the medial surface of the quadrate just above the medial condyle, similar to the configurations in *Batrachotomus* (Gower 1999) but more pronounced in *Sphenosuchus* (Walker 1990).

Ectopterygoid—The ectopterygoid is known from several well-preserved examples: a left and right from TTUP 9000, a right and partial left from TTUP 9002 (Fig. 17), a well preserved right ectopterygoid from an unnumbered specimen in the Texas Tech collection, and several uncataloged specimens in the UCMP *Placerias* Quarry collections. The ectopterygoid is a large J-shaped bone with a distinct thickened anterior head and a long tapering posterior process with a facet on the dorsal surface of the arm for articulation with the descending ramus of the pterygoid. It is very similar in morphology to the ectopterygoid of *Batrachotomus* (Gower 1999).

The head of the ectopterygoid is divided by a large, deep groove into two distinct processes, dorsal and ventral, which fit into corresponding sockets on the jugal. The dorsal process is slightly smaller, and is divided again by a small groove that enters a foramen, which exits onto the dorsal surface of the ectopterygoid. The ventral head is larger and its anteroventral edge has another groove that continues onto the ventral surface. The only other suchians known to possess a double-headed ectopterygoid are *Sphenosuchus* (Walker 1990), *Batrachotomus* (Gower 1999), and *Polonosuchus* (Sulej 2005).

The articulation of the ectopterygoid with the jugal forms a large foramen between the two elements that continues as a groove onto the medial surface of the jugal. The articulation between the ectopterygoid and jugal also forms two smaller foramina that exit anterodorsally and anteroventrally.

Mandible

The lower jaw of *Postosuchus* is robust and is similar in form to the mandible of other paracrocodylomorphs, including *Arizonasaurus*, *Fasolasuchus*, *Batrachotomus*, *Saurosuchus* and *Hesperosuchus*.

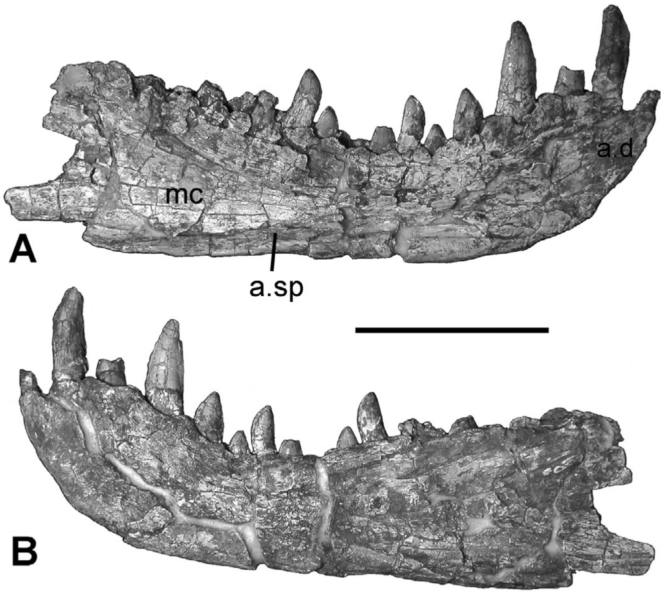

Figure 18. *Postosuchus kirkpatricki* (TTUP 9000) left dentary. **A**. Medial view. **B**. Lateral view. Scale bar = 5 cm.

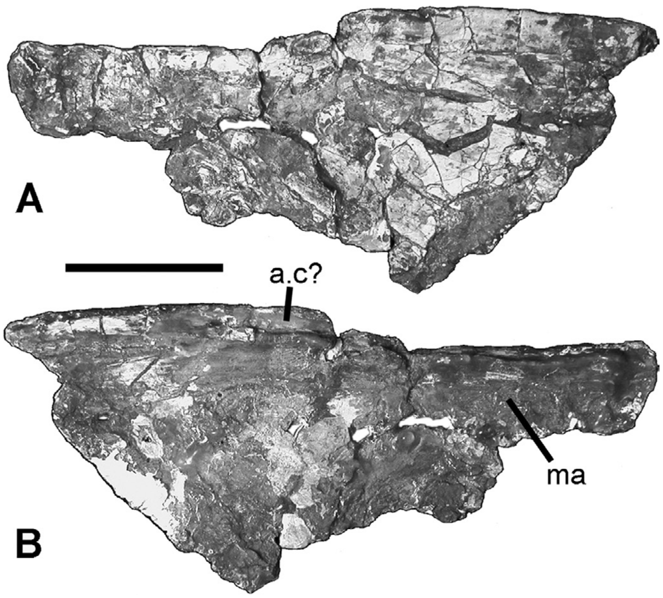

Figure 19. *Postosuchus kirkpatricki* (TTUP 9000) left splenial. **A.** Lateral view. **B.** Medial view. Scale bar = 5 cm.

Dentary—Both dentaries are preserved in the type specimens and the left dentary of TTUP 9000 is nearly complete (Fig. 18). The dorsoventral expansion at the anterior end is more apparent in TTUP 9002 than in TTUP 9000. This expansion is typical of other rauisuchids such as *Fasolasuchus*, *Batrachotomus*, and *Saurosuchus*, as well as in crocodylomorphs, e.g., *Sphenosuchus* (Walker 1990), *Hesperosuchus* (Clark et al. 2000). The central part of the dentary is slightly compressed dorsoventrally then expands again posteriorly where it meets the surangular and angular laterally, and

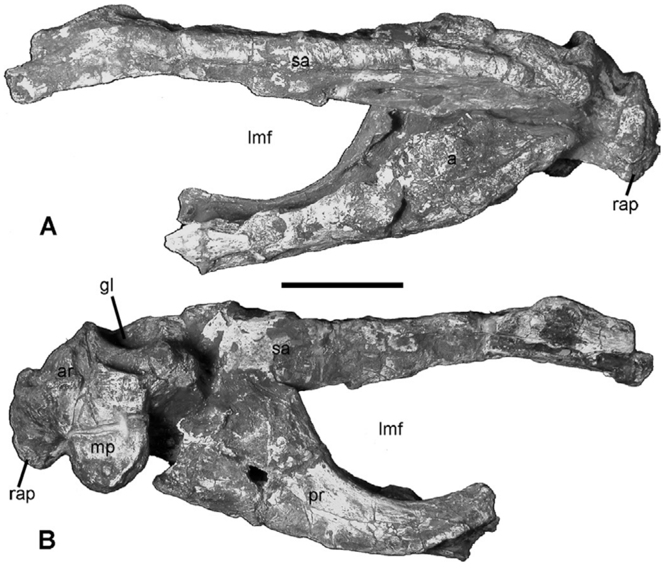

Figure 20. *Postosuchus kirkpatricki* (TTUP 9000) left surangular, angular, prearticular and articular. **A.** Lateral view. **B.** Medial view. Scale bar = 5 cm.

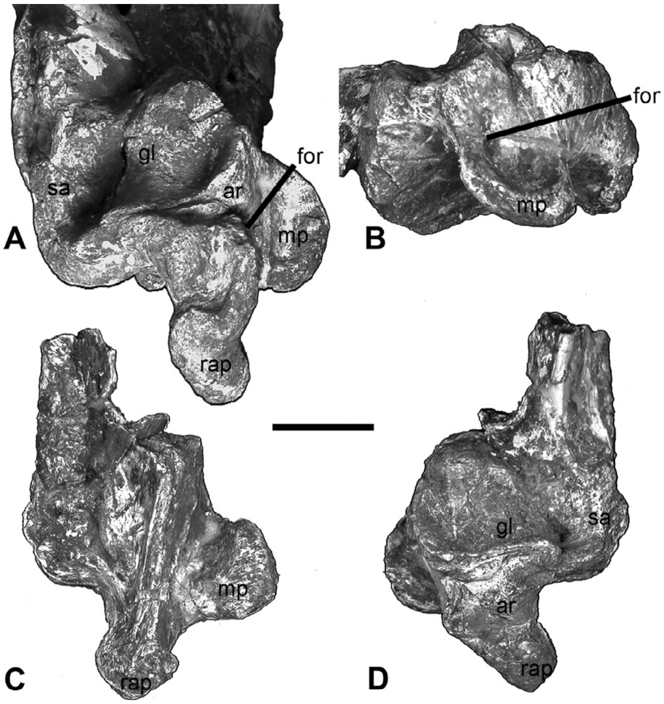

Figure 21. *Postosuchus kirkpatricki* (TTUP 9000) left surangular-articular. **A.** Oblique posterodorsal view. **B–D**. TTUP 9000 right surangular-articular. **B**. Medial view. **C**. Ventral view. **D**. Dorsal view. Scale bar = 30 mm.

the prearticular and coronoid medially. The medial surface reveals resorption pits ventral to the alveolar margin and interdental plates. The ventromedial surface of the dentary possesses a flange for articulation with the splenial, and covers the Meckelian canal. In TTUP 9002, the Meckelian canal terminates about two thirds of the way toward the anterior end of the dentary. The anterior medial surface possesses a small dorsoventrally oriented symphyseal facet for articulation with the other dentary.

Splenial—The only known specimen of the splenial is a single element preserved in TTUP 9000. This long, thin, and plate-like bone forms the medial wall of the Meckelian canal, and also covers much of the medial surface of the dentary (Fig. 19). It is shaped roughly like an elongate triangle, tapering toward the anterior end of the dentary. A thickened ridge on the dorsomedial surface of the splenial has a narrow dorsal groove extending along its length, as in *Batrachotomus* (Gower 1999). Chatterjee (1985:409) mentioned a foramen in the middle of the splenial "indicates the outlet for the mandibular ramus of the fifth nerve." However, it is not clear if this "foramen" actually exists, as it may just be part of a matrix-filled crack in the bone.

Coronoid—The bone Chatterjee (1985:409) identified as the coronoid could not be located for this study. Chatterjee (1985) described the coronoid as a "small triradiate bone forming the anterior rim of the adductor fossa" lying behind the dentary, and between the surangular and prearticular, but this cannot be confirmed without re-examination of the missing element.

Angular—The angular is well preserved in TTUP 9000. It is a large mediolaterally thickened bone that curves and tapers anteroventrally, and forms the ventral margin of the lateral mandibular fossa (Fig. 20). A deep anteroposteriorly trending groove on the medial surface of the angular forms part of the lateral surface of the Meckelian canal. Just ventral to this groove is a thin flange of bone that separates it from a shallow depression. The ventral surface of the angular is thickened and rugose. Anteriorly, the angular meets the dentary, and posterodorsally it contacts the surangular.

Surangular—The elongate and mediolaterally compressed surangular is well preserved in TTUP 9000 and in several examples (e.g., UCMP 27492, 27485) from the UCMP collections (Figs. 20, 21). It articulates tightly with the articular, forming the lateral third of the glenoid. Anteriorly, the surangular is a thin blade that forms the dorsal margin of the mandibular fenestra. Posteriorly, the ventral margin of the surangular bifurcates into a sharp medial flange and a thickened, rugose lateral ridge. These two ventral surfaces are separated by a groove that extends anteriorly. About four-fifths of the way toward the anterior end of the bone, the two ventral surfaces merge and become a single, sharp ventral edge that continues toward the dentary. Anterior to where these two surfaces merge, a foramen opens into a deep groove on the medial surface on the ventrolateral surface of the surangular. Anterolaterally, the surangular is overlapped by the dentary. A facet on the dorsomedial surface of the surangular appears to articulate with the coronoid.

Prearticular—The prearticular is an elongate bone that curves posterodorsally, and forms the ventromedial edge of the lateral mandibular fenestra (Fig. 20). The posterior end is expanded dorsally where it contacts the posteromedial surface of the articular and a deep groove on the lateral surface contributes to part of the Meckelian canal. The prearticular contacts the angular ventrolaterally.

Articular—The articular is a thickened wedge of bone that forms five distinct radiating processes: anterior, medial, ventral, posterior (retroarticular process), and ascending (Figs. 20, 21). Morphologically, it resembles other paracrocodylomorph articulars, including *Polonosuchus* (Sulej 2005), *Batrachotomus* (Gower 1999) and *Fasolasuchus* (Bonaparte 1981). The anterior process of the articular forms the medial two thirds of the glenoid, and the surangular forms the remaining third. This condition is also found in *Batrachotomus* (Gower 1999) and *Fasolasuchus* (Bonaparte 1981), but not *Arizonasaurus* (Nesbitt 2005), in which the articular forms the entire glenoid. This characteristic may differentiate poposauroids from rauisuchids, but more material is necessary for confirmation. The medial surface of the articular is angled posteroventrally and has a greatly thickened, rugose edge. The center of the medial process is pierced by a large foramen, interpreted by Chatterjee (1985) as the chorda tympani branch of the facial nerve. A similar foramen is present in other suchians, such as *Polonosuchus* (Sulej 2005), *Batrachotomus* (Gower 1999), *Fasolasuchus* (Bonaparte 1981), *Arizonasaurus* (Nesbitt 2005), and *Hesperosuchus* (Parrish 1991). This foramen may be homologous to the posterior surangular foramen of the aetosaur *Desmatosuchus* (Small 2002). A groove originates from this foramen and trends toward the posterolateral edge of the medial process onto the dorsal surface of the anterior process posterior to the glenoid. The ventral process is a thickened ridge that continues posteriorly to form the ventral surface of the posterior (or retroarticular) process. The thickened and highly rugose retroarticular process trends ventrolaterally. The ascending process of the articular lies posterior to the glenoid, dorsal and anterior to the retroarticular process, and is thickened and rugose for attachment of the *M. depressor mandibulae.*

Dentition

The teeth of *Postosuchus* are slightly more heterodont (Fig. 22) than other rauisuchians for which fairly complete dentitions are known (e.g., *Saurosuchus* and *Batrachotomus*), and possesses four distinct crown types. Three of the four crown types bear symmetrical crowns (the carinae are in line with each other and not offset at an angle as in phytosaurs) that are characteristic of all premaxillary, maxillary and posterior dentary teeth. The fourth crown type in the second alveolus of the dentary in TTUP 9000 is asymmetrical and indistinguishable from those of the premaxillary teeth of some phytosaurs, such as *Leptosuchus* and *Psuedopalatus* (see Hungerbühler 2000). It is unclear if this condition is typical for *Postosuchus* or if it is an aberration of TTUP 9000. All teeth have serrations on the anterior and posterior carinae (~3 serrations/mm), although occasionally, some premaxillary teeth have serrations on only the posterior margin.

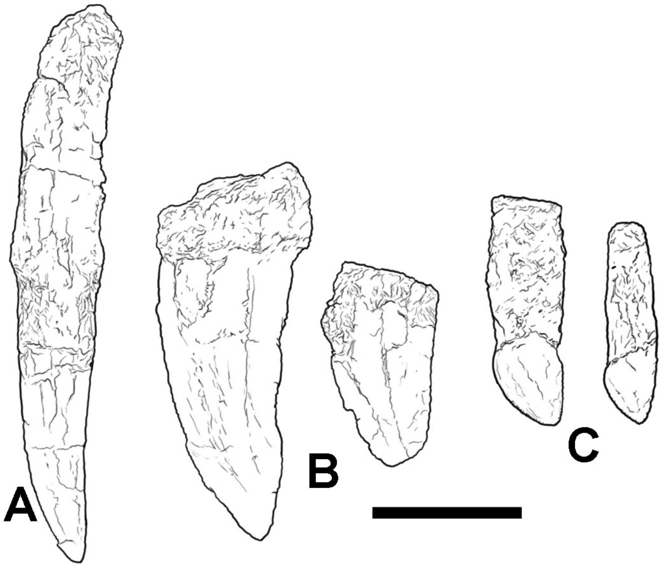

Figure 22. *Postosuchus kirkpatricki* (TTUP 9000) teeth. **A**. Premaxillary tooth. **B**. Anterior maxillary teeth. **C**. Posterior maxillary teeth. Scale bar = 20 mm.

The premaxillary teeth are round in cross-section, slightly recurved and serrated, and only slightly laterally compressed. The anterior-most maxillary tooth has the same morphology as the premaxillary teeth and is much smaller than subsequent maxillary teeth, which are large and blade-like, with curved anterior margins and relatively straight posterior margins. These teeth are also mediolaterally compressed and are relatively typical of most known rauisuchids , such as *Batrachotomus* (Gower 1999) and *Saurosuchus* (Sill 1974). The teeth of the poposauroid *Arizonasaurus* (Nesbitt 2005), and those of a possible poposaurid maxilla (Weinbaum and Hungerbühler 2007) are very similar, but are not as recurved as rauisuchid teeth. The posterior maxillary teeth of *Postosuchus* are smaller and are constricted at the base of the crown, similar to the teeth of crocodylomorphs such as *Sphenosuchus* (Walker 1990) and *Hesperosuchus* (Colbert 1952, Clark et al. 2000).

The teeth of the dentary follow the same pattern as the maxilla, only differing in the morphology of the second dentary tooth previously mentioned. This tooth is indistinguishable from the posterior premaxillary and anterior maxillary teeth of phytosaurs, which makes identification of an isolated tooth of this morphology untenable.

Neurocranium

Chatterjee's (1985) restoration of the braincase is generally correct in overall proportions, but incorrect in details of the sutural arrangement. This was addressed in part by Gower (2002) in his thorough description of the braincase of *Batrachotomus.* The braincase of *Postosuchus* is similar in overall morphology to many suchians, exclusive of poposauroids (e.g., *Arizonasaurus* and *Shuvosaurus*), which retain a more plesiomorphic archosaurian morphology (see Gower and Nesbitt 2006).

The braincases of TTUP 9000 and TTUP 9002 are well preserved (Figs. 23, 24). The braincase of TTUP 9000 was originally partly reconstructed with plaster, but preparation revealed that it is relatively complete and undistorted. It is missing the right paroccipital process and the basipterygoid process, which may have been lost during excavation or initial preparation since there is a clean break at the base of the basipterygoid. The right prootic-supraoccipital is preserved as a separate element, which does not articulate cleanly with the rest of the braincase. The braincase of TTUP 9002 is missing the supraoccipital, left prootic and right basipterygoid process, but is otherwise relatively complete.

Case (1922) initially described UMMP 7473 (Fig. 25) as *Coelophysis*, but Chatterjee (1985) correctly recognized it as *Postosuchus*. Gower (2002) later inferred that this specimen is not *Postosuchus*, based on the position of the external foramen for the hypoglossal nerve. However, while the paratype braincase is damaged in this area, the same configuration of the foramen is present in the holotype braincase, and the UMMP specimen is otherwise identical to the type specimens except for the more extensive fusion between elements. UMMP 7473 is a very well preserved braincase from a large individual, and assigned here to *Postosuchus kirkpatricki* based on the morphology of the occipital condyle, shape of the foramen magnum, position and shape of all foramina exiting the braincase, shape and depth of the median pharyngeal recess, apparent extended basipterygoid process, and the possession of several distinct anteroposteriorly trending ridges on the parasphenoid. UMMP 7473 is from the Tecovas Formation, which is Adamanian in age, as is the lower part of the Cooper Canyon Formation where the Post Quarry is located (Lehman and Chatterjee 2005; Martz 2008), making it contemporaneous with the type material. The size of the specimen and the fact that all sutures between the braincase elements are fused, suggest that this was an ontogenetically older animal than the Post Quarry specimens. Most of the basipterygoid and both paroccipital processes are missing. None of the above specimens possess any trace of laterosphenoid.

A well-preserved prootic was found during preparation of the paratype. This bone shows some of the morphology of the posterior brain as well as the articulation with the

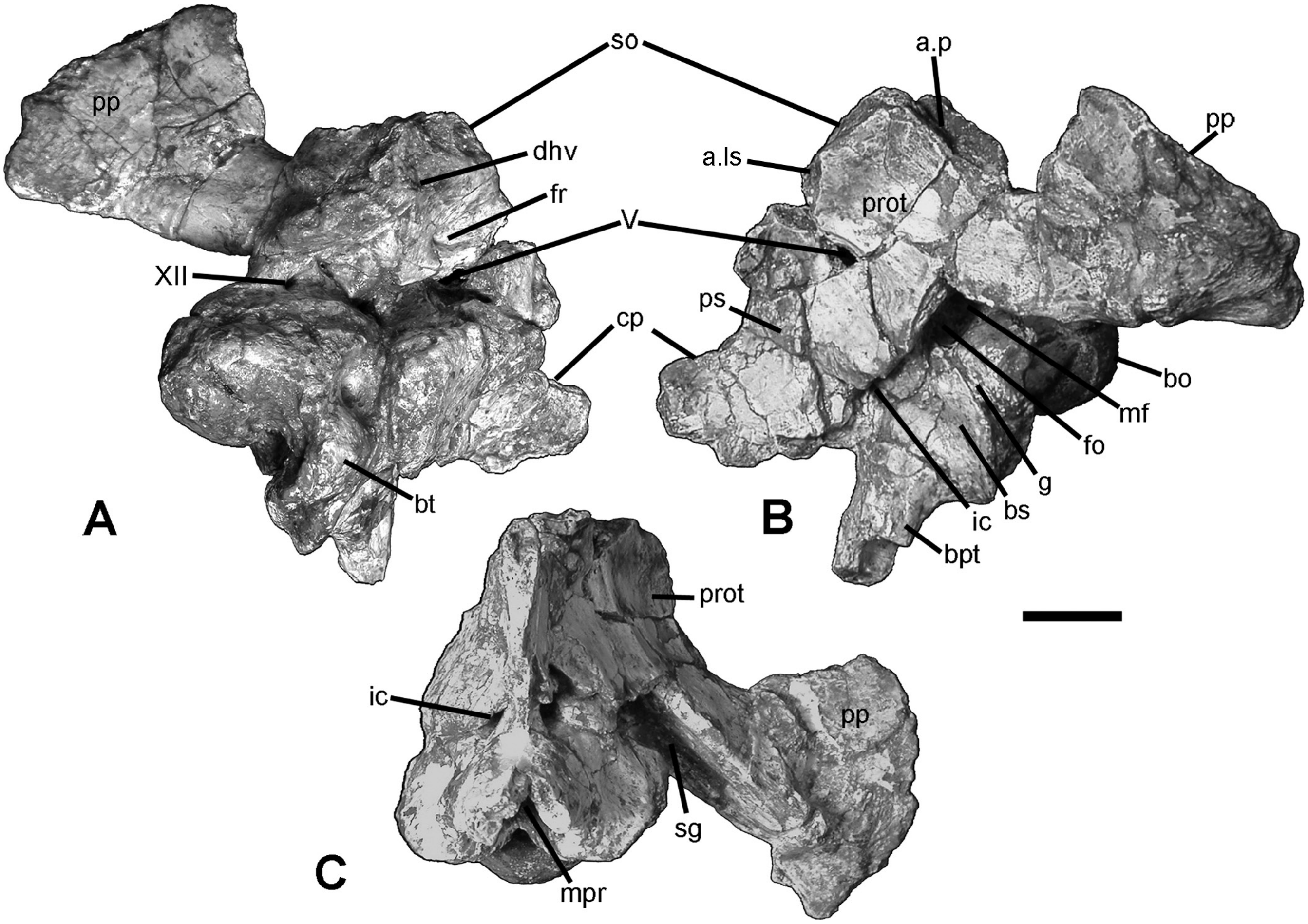

Figure 23. *Postosuchus kirkpatricki* (TTUP 9000) braincase. **A**. Oblique right lateral view. **B**. Left lateral view. **C**. Ventral view. Scale bar = 20 mm.

opisthotic, basisphenoid and laterosphenoid. Contra Gower (2002), the prootics were not preserved *in situ* in the braincase of TTUP 9002, but as noted above, the right prootic was found fused to one of the nasal bones during preparation.

Description of *Postosuchus* braincase

Basioccipital—The basioccipital forms the majority of the occipital condyle, with a small contribution dorsolaterally from each of the exoccipitals. The neck of the occipital condyle is short, slightly overhangs the basioccipital, and two small nutrient foramina are present on the ventral surface. Ventral to the occipital condyle, the basioccipital diverges into two flat plates that meet with the basisphenoid to form the basal tubera. On TTUP 9002, an indentation on the outer edge of the basioccipital portion of the basal tubera is similar to that of *Batrachotomus* (Gower 2002:fig. 1). A deep groove between the suture of the two bones continues dorsally toward the floor of the endocranial cavity. The groove is similar to, but better defined than in *Batrachotomus*, which Gower (2002:51) referred to as the unossified gap. The groove is clearly visible on the left side of TTUP 9000 (Fig. 23B). No "basioccipital recess" is present between the basioccipital portion of the basal tubera of TTUP 9000 as in *Batrachotomus* (Gower 2002:fig. 1).

Exoccipitals—Dorsal to the occipital condyle, the exoccipitals meet along the midline and ascend dorsolaterally to form the floor of the posterior endocranial cavity and lateral sides of the strongly mediolaterally ovate foramen magnum. The anterior ends of the exoccipitals are tapered and form a steep drop to the floor of the endocranial cavity as in *Batrachotomus* (Gower 2002) and similar to *Arizonasaurus* (Gower and Nesbitt 2006). The hypoglossal nerve (XII) exits the exoccipital from a single foramen, which is ventrolateral to the foramen magnum and posterior to the descending process of the exoccipital (contra Gower 2002). A foramen on the anteromedial-most part of the exoccipital continues through a groove into another foramen dorsally, interpreted as a passage for vessels possibly corresponding with the venae capitis dorsales (see Walker 1990). The exoccipitals are firmly fused to the opisthotics with no discernible suture.

Supraoccipital—The anteriorly sloping supraoccipital is tall and plate-like (Fig. 25). It forms the dorsal margin of

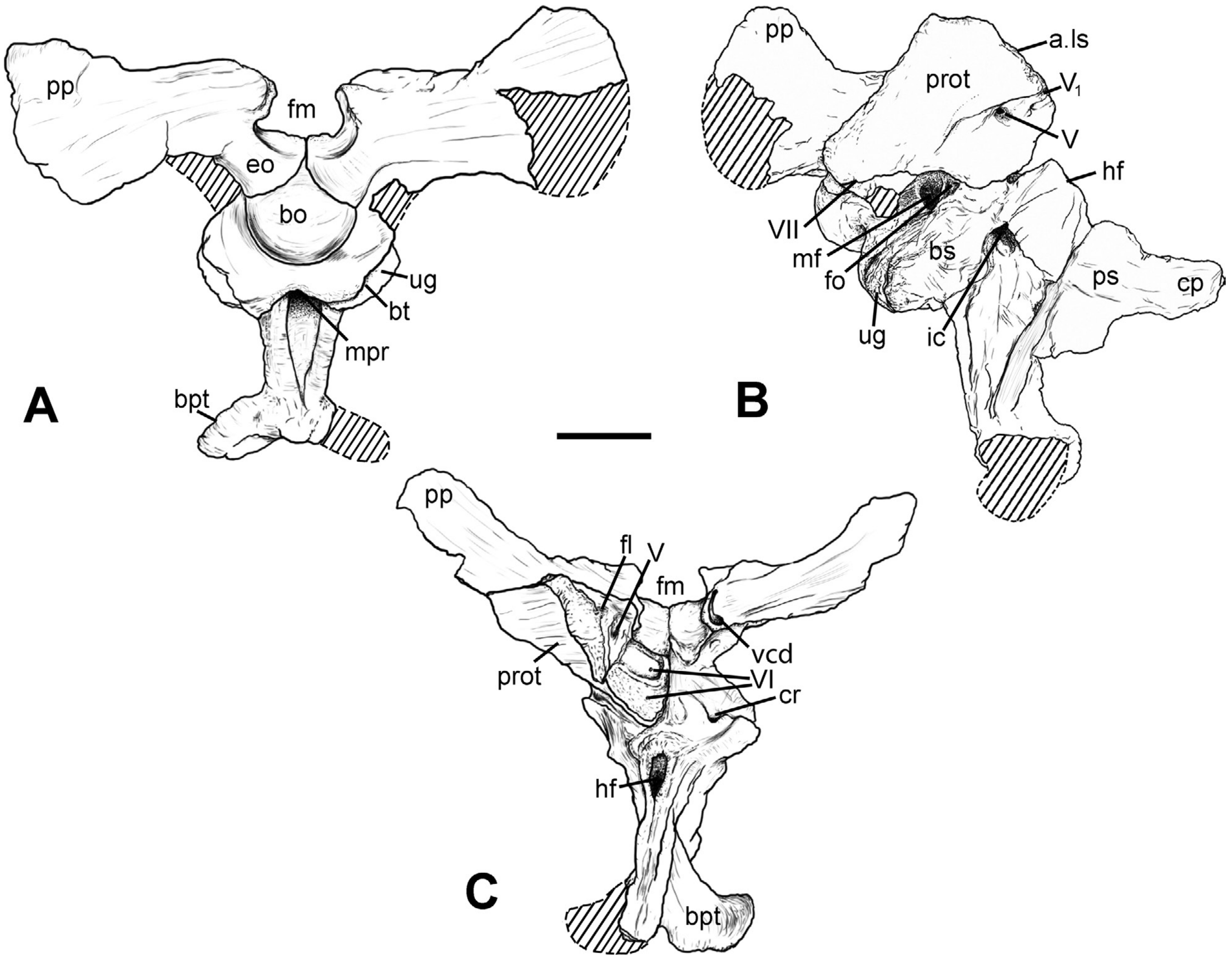

Figure 24. *Postosuchus kirkpatricki* (TTUP 9002) braincase. **A**. Posterior view. **B**. Right lateral view. **C**. Anterior view. Scale bar = 20 mm.

the foramen magnum and articulates with the exoccipitals posteroventrally, the prootic anteroventrally, and the parietal dorsally. The parietals possess a distinct facet for articulation with the supraoccipital. There are recesses for the dorsal head vein on the dorsomedial surface. No supraoccipital is preserved in the paratype. In the holotype however, part of the left supraoccipital is fused to the prootic and opisthotic, and the left supraoccipital and prootic are preserved separately. The supraoccipital is completely preserved in UMMP 7473 (Fig. 25).

Opisthotics—The opisthotics are wing-like structures with distal, dorsoventral expansions for articulation with the ventromedial ramus of the squamosal and form the majority of the paroccipital processes. This articulation creates a small, slit-like post-temporal fenestra. Most of the anterior surface of the opisthotic is covered by the prootic. The anterior of the opisthotic in TTUP 9002 possesses two small foramina separated by a dorsoventrally trending groove, presumably for the passage of the posterior cerebral/cephalic vein. The anteroventral surface of the opisthotic forms half of the tympanic groove and the prootic forms the remainder.

Prootic—The prootic is a roughly triangular wedge of bone that forms most of the lateral wall and the entire floor of the endocranial cavity. The entrance for the abducens (VI) nerve is on the anterior prootic and the exit is on the floor of the prootic. The exit for the trigeminal (V) nerve is completely enclosed by this bone with no apparent contribution from the laterosphenoid (contra Chatterjee 1985). Dorsal to the exit for the trigeminal nerve is a strong, anteriorly projecting ridge. The posterior process of the prootic contacts the anterior paroccipital process and forms a deep tympanic groove ventrally that leads to the fenestra ovalis anteriorly and to the metotic foramen posteriorly, through which cranial nerves IX-XI and the jugular artery are conducted. The exit for the facialis (VII) nerve lies just anterior to the tympanic groove on the posteroventral surface of the prootic. This exit expands dorsoventrally into separate grooves that continue onto the lateral surface of the prootic and basisphenoid respectively. Large floccular (auricular) recesses are present on the anteromedial walls of the prootic dorsal to the exit for the trigeminal nerve. Dorsally, the prootic is capped by the supraoccipital and by the laterosphenoid anterodorsally.

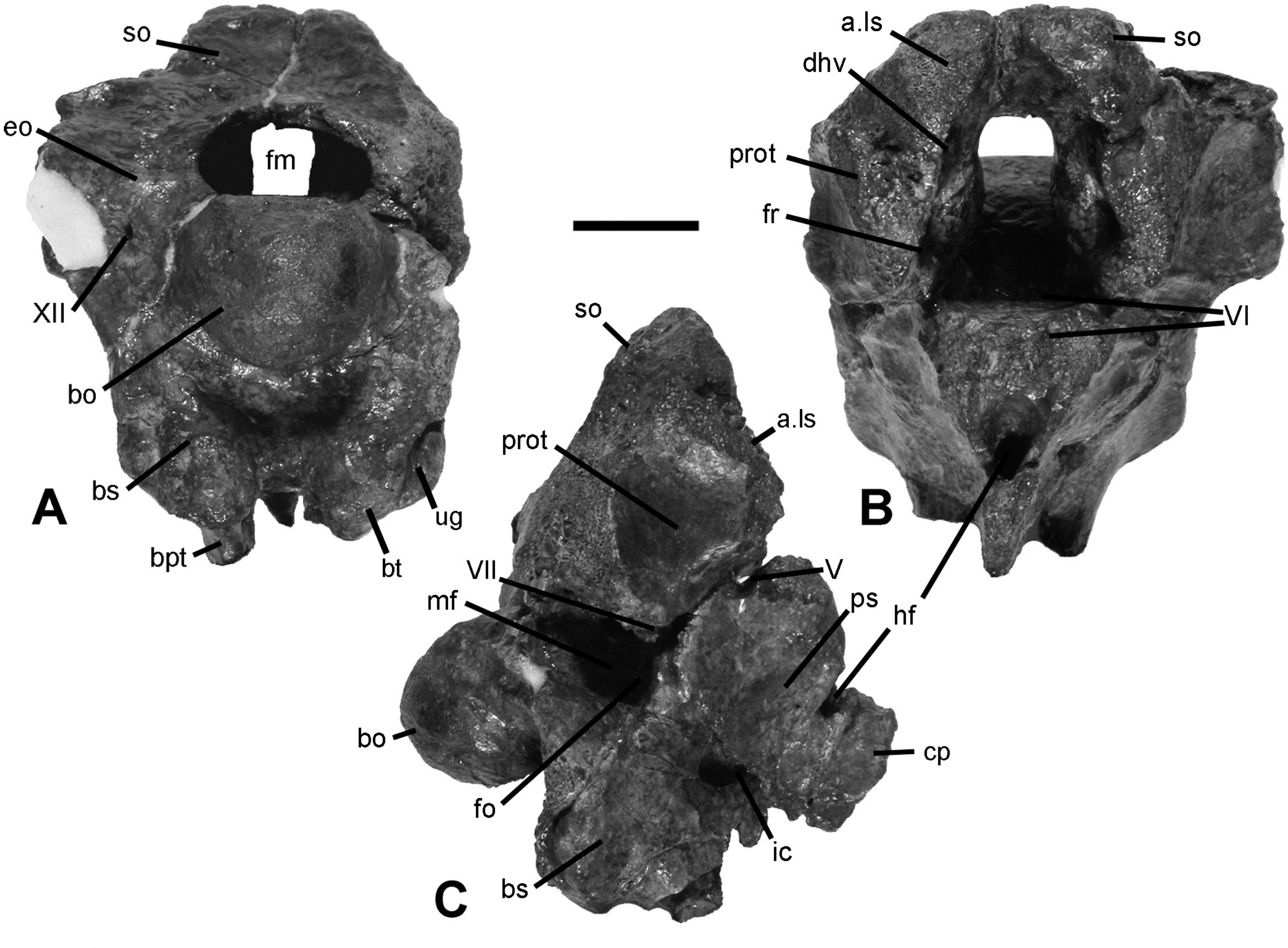

Figure 25. *Postosuchus* (UMMP 7473) braincase. **A.** Posterior view. **B**. Anterior view. **C**. Right lateral view. Scale = 20 mm.

Parasphenoid—The parasphenoid sheaths the basisphenoid posteriorly and continues anteriorly to form a deep, narrow, plate-like cultriform process. Although the process is partly damaged, it appears to be relatively complete in both TTUP 9000 and TTUP 9002. This process differs from the basal paracrocodylomorphs (poposauroids, or "clade X" from Nesbitt 2005) *Arizonasaurus* and *Shuvosaurus* in being shorter and less "rod-like" (Gower and Nesbitt 2006, Chatterjee 1995). The cultriform process of *Arizonasaurus* and *Shuvosaurus* is approximately twice as long as the main body of the basisphenoid, whereas in *Postosuchus* it is roughly half as long. This may be a viable character for phylogenetic analysis (see Weinbaum and Hungerbühler 2007). Posteriorly, the dorsum sellae contains an opening for a large hypophyseal (pituitary) fossa. Although usually fused, the parasphenoid is distinguishable from the basisphenoid by a distinct posteroventrally trending ridge, which separates the two bones in both type specimens.

Basisphenoid—The basisphenoid forms a V-shaped descending process anteroventrally with a deep, dorsal recess. This recess was considered by Parrish (1993) and Alcober (2000) to be the entrance for the eustachian tubes. However, as discussed by Gower (2002), there is no opening present within this dorsal recess that might communicate with either the inner ear or throat regions. Witmer (1997) called this the median pharyngeal recess. The ventral portion of the basisphenoid terminates with large, diverging basipterygoid processes that are anteroposteriorly elongate with a rounded ventral surface. These articulate with the cup-like depression on the pterygoids. A large opening for the internal carotid occurs just ventral to the overlap between the basisphenoid and parasphenoid and anterior to the basal tubera. A well-defined lagenar/cochlear recess on the floor of the endocranial cavity (Fig. 24B) was also noted by Gower (2002). Anteriorly, the basisphenoid is sheathed extensively by the parasphenoid.

Laterosphenoid—The frontal-postfrontal MCCDMP 1654 possesses the dorsal-most part of the laterosphenoid on its ventral surface within a groove lateral to the orbital fossa. Unfortunately, most of the element is missing, but enough remains to indicate its anteroposterior extent, from the anteromedial portion of the parietal to the junction of the prefrontal-lacrimal. A laterosphenoid is not present in any of the type *Postosuchus kirkpatricki* material or UMMP 7473; however, the same groove present on MCCDMP 1654 is also on the ventral surface of both the holotype and paratype frontals.

Presphenoid—Chatterjee (1985) described a presphenoid in *Postosuchus*, but there is no evidence for the presence of this bone in any known *Postosuchus* material.

DISCUSSION

The relationships of rauisuchian archosaurs are still not fully resolved, but several recent phylogenetic analyses indicate a closer relationship with crocodylomorphs than with aetosaurs and phytosaurs (Nesbitt and Norell 2006, Nesbitt 2007, Weinbaum and Hungerbühler 2007). Alternatively, Gower (2002) and Gower and Nesbitt (2006) presented phylogenetic hypotheses based solely on braincase characters that placed aetosaurs closer to crocodylomorphs than rauisuchians. However, several braincase characters that are now apparent in *Postosuchus*, but were unclear prior to preparation to the aforementioned authors (e.g., Gower 2002:characters 2, 15, 16, 23, 25) may change the topology of that tree. Brusatte et al. (2008) also proposed a phylogeny that placed aetosaurs closer to crocodylomorphs and poposauroids and ornithosuchids as the sister group to rauisuchids, but again, several characters were miscoded for *Postosuchus* (Brusatte et al. 2008 supporting material, e.g., characters 2, 9, 11, 16, 35, 42). An analysis by Weinbaum and Hungerbühler (2007), using characters of *Postosuchus* based in part on this description, suggested that poposaurids are a monophyletic taxon separate from rauisuchids or Paracrocodyliformes, and that the latter group includes crocodylomorphs.

Rauisuchids possessed certain homologous characters (Gower 1999, 2000), such as the subnarial foramen or fenestra, tapered antorbital fenestra, and various characters of the pelvis. A wedge-shaped parasphenoid rostrum, described by Parrish (1993) as a diagnostic character, may also be valid, although it is not well preserved in many presently known taxa. The cultriform process of *Arizonasaurus* and *Shuvosaurus* is approximately twice as long as the main body of the basisphenoid. Nesbitt (2007:64) described this as a "slightly anteriorly elongated and horizontally oriented parabasisphenoid" possessed by *Arizonasaurus*, *Shuvosaurus,* and *Effigia*. However, in *Postosuchus* and *Sphenosuchus,* the cultriform process is roughly half as long. Some basal archosaurs like *Fugusuchus hejiapanensis* (Gower and Sennikov 1996) and basal dinosaurs (e.g., *Herrerasaurus*, Sereno and Novas 1993) also possess an elongate cultriform process, so the shortening of the process could potentially be a significant apomorphy within Paracrocodyliformes. Another potentially important cranial character is the palpebral. Possession of a supraorbital bone is not an unusual feature for archosaurs. Although none have been previously identified in any poposauroids or rauisuchids, supraorbitals have been found in *Aetosaurus* Fraas 1877 (Walker 1961, Schoch 2007), crocodylomorphs (Clark et al. 2000), and various ornithodiran groups (e.g., pterosaurs and dinosaurs).

Although *Postosuchus* has been considered problematic in the understanding of the relationships of the rauisuchian archosaurs (e.g., Gower 2000), *Postosuchus* clearly belongs to a clade of archosaurs more closely related to crocodylians than to aetosaurs and, most likely poposauroids as well.

CONCLUSIONS

Rauisuchians have long been considered an enigmatic group of archosaurs (e.g., Gower 1999, 2000, Nesbitt 2005, Peyer et al. 2008). However, over the past several years, new descriptions of taxa pivotal to the understanding of this group have been published (Alcober and Parrish 1997, Gower 1999, Alcober 2000, Gebauer 2004, Nesbitt 2005, 2007, Sulej 2005, Sen 2005, Weinbaum and Hungerbühler 2007, Peyer et al. 2008, Gower and Schoch 2009). *Postosuchus* clearly shares many characteristics with *Polonosuchus* and based on apomorphies, it is evident that these animals are closely allied with crocodylomorphs (Weinbaum and Hungerbühler 2007: e.g., wedge-shaped antorbital fenestra, double-headed ectopterygoid, broad lateral expansion of squamosal, and extra neural spine on caudal vertebrae).

The reexamination of the holotype and other *Postosuchus* skull material provides new information that will help to polarize cranial character states for pseudosuchians. The only apparent autapomorphic characters of the skull of *Postosuchus* are the rounded ridge on the maxilla and the foramen within the fossa on the medial surface of the ascending process of the maxilla. A forthcoming detailed description of the postcrania, combined with this study of the skull and cranial elements, should help to further clarify the phylogeny of pseudosuchian archosaurs.

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