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THE ANATOMY OF *EFFIGIA OKEEFFEAE* (ARCHOSAURIA, SUCHIA), THEROPOD-LIKE CONVERGENCE, AND THE DISTRIBUTION OF RELATED TAXA

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ABSTRACT

Effigia okeeffeae is named based on a well-preserved nearly complete skeleton from the Upper Triassic (?Rhaetian) "siltstone member" at Ghost Ranch, northern New Mexico. The skull is described and compared to other suchian and basal archosaurs. The maxilla and premaxilla are edentulous, and a rhamphotheca was possibly present in life.

Effigia conclusively indicates that the skull of *Shuvosaurus* and the postcrania of "*Chatterjeea*" belong to the same taxon. Furthermore, the close relationship between *Shuvosaurus* and *Effigia* indicates that both taxa are nested within the suchian clade and not within Ornithomimisauria. However, the similarity in features in the skull and postcrania of *Effigia* and ornithomimids suggests extreme convergence occurred between the two clades.

A clade containing *Arizonasaurus*, *Bromsgroveia*, *Poposaurus*, *Sillosuchus*, *Shuvosaurus*, and *Effigia* is suggested based solely on shared derived character states. Additionally, a clade (Clade Y) containing *Sillosuchus*, *Shuvosaurus*, and *Effigia* is well supported by further derived character states. The distribution and temporal pattern of members of Group Y suggest that members of Group Y are present in the early Middle Triassic through the Latest Triassic of North America, and one member of the clade, *Sillosuchus*, was present in South America.

INTRODUCTION

Archosauria diverged into two major lineages in the Triassic, the crocodile-line, archosaurs more closely related to crocodiles, and the bird-line archosaurs, more closely related to birds (Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Parrish, 1993; Juul, 1994; Benton, 1999). Most of the crocodile-line archosaurs, including the stagonolepidids, "rauisuchians", and parasuchians, originated, radiated, and went extinct during the Triassic. Relationships among these groups are currently poorly understood (Gower and Wilkinson, 1996). Moreover, "rauisuchian" relationships are in a state of confusion, and their systematic position or positions are intimately related to the systematic positions of the stagonolepidids, parasuchians, and crocodylomorphs. "Rauisuchians" may be monophyletic, paraphyletic, or even made up of several unrelated clades (Gower, 2000; Nesbitt, 2005a).

A complete robust phylogenetic analysis of "rauisuchians" must await complete detailed morphological revisions for all of the included taxa (Gower, 2000; Nesbitt, 2005a). For example, poorly known proposed "rauisuchian" groups such as the "poposaurs" and the "chatterjeeids" need reexamination and detailed descriptions. Fortunately, new discoveries (Nesbitt, 2005a; Sen, 2005; Sulej, 2005) and descriptions (Gower, 1999, 2002; Weinbaum, 2002) have allowed new comparisons. The purpose of this work is to describe the anatomy of the relatively complete articulated skeleton and referred material of *Effigia okeeffeae* from the "siltstone member" of the Chinle Formation of New Mexico and compare it to other "rauisuchians" and basal archosaurs (see appendix 1). A well-preserved skull allows a first look at the distribution of character states among "rauisuchians" with skull material and character convergences with theropod dinosaurs. Additionally, the occurrences of members of Group Y in the southwest United States and the character states that members of Group Y share are discussed.

MATERIALS AND OCCURRENCE

The holotype material was recovered in 1947 during the first few weeks of excavation of the Ghost Ranch *Coelophysis* Quarry (Whitaker Quarry) at Ghost Ranch, New Mexico. The quarry is located in the "siltstone member" in the upper portion of the Triassic sequence at Ghost Ranch (Stewart et al., 1972). Correlation of the "siltstone member" with other units in the Chinle Formation and the Dockum Group remains controversial. Some consider the "siltstone member" an equivalent to the top of the

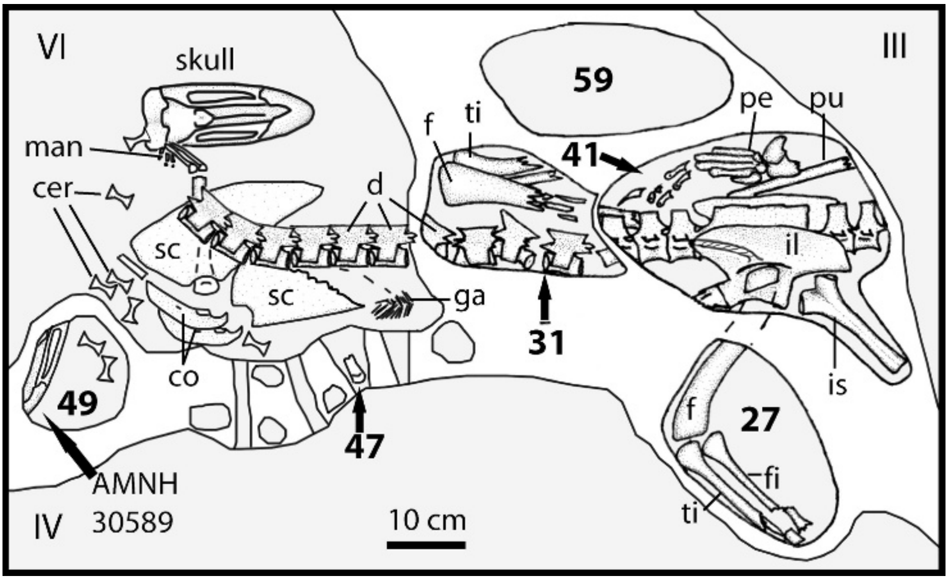


Fig. 1. Reconstruction of the association of the holotype of *Effigia okeeffeae* from jackets and unpublished maps from Edwin Colbert's original fieldnotes (courtesy of AMNH). The roman numerals refer to the large blocks removed in 1947 (see fig. 6 of Colbert, 1989). The original edge of the quarry is to the right. White space indicates rock that was not collected. The bold numbers refer to original field numbers given to the smaller jackets taken out between the large blocks. Abbreviations are spelled out in appendix 3.

Petrified Forest Member (Colbert, 1974; Schwartz and Gillette, 1994) or correlate it to a post-Petrified Forest Member unit of the Chinle Formation (Dubiel, 1989; Hunt and Lucas, 1989a, 1989b, 1991, 1993; Lucas and Hunt, 1992). Correlation with a post-Petrified Forest Member is preferred here based on lithology, superposition, and biostratigraphy. Lucas and Hunt (1992) correlate the "siltstone member" to the Rock Point Member of the Chinle Formation based on the presence of the parasuchian *Redondasaurus* in both.

Although the material was collected in 1947 within blocks containing *Coelophysis* skeletons, it was only partially prepared and it remained unstudied until late 2004. The posterior half of an articulated skeleton of a single individual, AMNH FR 30587, was recovered in three small jackets (numbered 27, 31, 42) that were removed between two of the large blocks (VI and III; fig. 1). Colbert's original detailed unpublished quarry map allowed easy reconstruction of the three jackets and the relative positions of the bones belonging to AMNH FR 30587 (fig. 1).

The relations of the bones of AMNH FR 30587 in three small jackets (27, 31, 41) led to the discovery of the upper half of the skeleton in block VI, one of the larger blocks. The articulated dorsal vertebrae of jacket number 31 continued into block VI. This suggests that portions of block III should contain the tail of AMNH FR 30587; however this block (see fig. 6 of Colbert, 1989) is unprepared. Multiple skeletons of the theropod *Coelophysis*, a skull and disarticulated skeleton of a juvenile parasuchian, and an unidentified small reptile also occur within block VI; however, the easily distinguishable morphology, partial articulation, lack of duplicated elements, and association of AMNH FR 30587 clearly indicates that it belongs to a single individual. The skull of AMNH FR 30589 was found in a small jacket (49) next to block VI along with two cervical vertebrae (fig. 1). Four articulated vertebrae found under AMNH FR 30587 may belong with the skull of AMNH FR 30589, but it is not clear. The whereabouts of the rest of the skeleton of AMNH FR 30589 is unknown.

AMNH FR 30588 was found in a box pieced together with plaster with little information indicating its position within the *Coelophysis* Quarry. A handwritten note with the specimen indicates that it was collected in 1948, one year after AMNH FR 30587, AMNH FR 30589, and AMNH FR 30590 were collected. Therefore, it is clear that AMNH FR 30588 is not part of the holotype or the two other referred specimens. The whereabouts of the rest of AMNH FR 30589 is unknown.

All of the *Effigia* specimens were deposited with or just after the deposition of most of the articulated *Coelophysis* skeletons, because the skeletons lie below and on top of *Coelophysis* remains.

INSTITUTIONAL ABBREVIATIONS

AMNH: American Museum of Natural History, New York, New York; **BMNH**: British Museum of Natural History, London, England; **CFMNH**: Chicago Field Museum of Natural History, Chicago, Illinois; **CM**: Carnegie Museum of Natural History, Pittsburg, Pennsylvania; **GI**: Geological Institute, Academy of Sciences of the Mongolian People's Republic, Ulaan Bataar, Mongolia; **IGM**: Mongolian Institute of Geology, Ulaan Bataar, Mongolia; **ISI**: Indian Statistical Institute, Calcutta; **IVPP**: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; **MNA**: Museum of Northern Arizona, Flagstaff, Arizona; **MSM**: Mesa Southwest Museum, Mesa, Arizona; **NMMNH**: New Mexico Museum of Natural History, Albuquerque, New Mexico; **PVL**: Instituto Miguel Lillo, Tucuman, Argentina; **PVSJ**: Division of Paleontology of the Museo de Ciencias Naturales de la Universidad Nacional de San Juan, Argentina; **SAM**: South African Museum, Cape Town, South Africa; **SMNS**: Staatliches Museum fur Naturkunde, Stuttgart, Germany. **TMM**: Texas Memorial Museum, Austin, Texas; **TTUP**: Texas Tech University Museum, Lubbock, Texas; **UCMP**: University of California Museum of Paleontology, Berkeley, California; **UNC**, Department of Geological Sciences, University of North Carolina at Chapel Hill, North Carolina; **UW**: University of Wisconsin, Madison Wisconsin; **ZPAL**: Institute of Paleobiology of the Polish Academy of Science, Warsaw, Poland.

METHODS

The grouping of basal archosaur taxa into the "rauisuchians" or "poposaurids" is varied and confusing in the literature because different definitions of the same taxa are used, the same taxa are not consistently compared, and many taxa are differently covered or constituted, sometimes erroneously. In this article, the terms "rauisuchian" and "poposaurid" will not be used without a specific named taxon and specimen number in parentheses. Instead, to avoid confusion in future revisions of taxonomy, specimen-to-specimen comparisons are used. Each taxon usually refers to a specific specimen (see appendix 1).

The skull of AMNH FR 30587 was CT scanned on a GE Systems Lightspeed 16 scanner at Stony Brook University Hospital in late March 2005. The skull was scanned in air after final preparation was completed. Original scans were done in the coronal plane with a slice thickness of 0.625 mm, an interslice spacing of 0.310 mm, and a field of reconstruction of 96.0 mm. The original DICOM files were converted to TIFFs using Adobe Photoshop 7.0 (levels: 35, 1.00, 150). Stack movies and additional manipulation and visualization of the dataset were done using VG Studio and the ImageJ software package available as freeware from NIH.

The parsimony analysis consisted of equally weighted heuristic searches with 100 random addition (RA) replicates and tree bisection and reconnection (TBR) branch-swapping run using PAUP* v4.0b10 (Swofford, 2002). Nodal support was examined using nonparametric bootstrapping, with 1000 bootstrap replicates, TBR branch-swapping, and 10 RA sequences. Decay indices were calculated using TreeRot v2c (Sorenson, 1999).

SYSTEMATIC PALEONTOLOGY

ARCHOSAURIA COPE, 1869
SUCHIA KREBS, 1974 SENSU BENTON AND CLARK, 1988
SHUVOSAURIDAE CHATTERJEE, 1993
EFFIGIA OKEEFFEAE NESBITT AND NORELL, 2006

HOLOTYPE: AMNH FR 30587—nearly complete skull, much of the cervical dorsal and sacral vertebrae, and the first two caudal vertebrae, right pes, left and right femur, left and right tibia, left and right fibula, right and fragments of the left scapula, left and right coracoids, right humerus, right ulna, right radius, right manus, left and right ilium, left and right ischia, right pubis, gastralia, and dorsal ribs.

REFERRED SPECIMENS: AMNH FR 30588—femur, ilium, ischium, pubis, sacrum, nearly complete caudal series; AMNH FR 30589—partial skull and cervicals, AMNH FR 30590—proximal femur.

TYPE LOCALITY AND STRATUM: The type specimen is from the Ghost Ranch *Coelophysis* Quarry (AMNH FR 30587) within the "siltstone member" of the Chinle Formation (Stewart et al., 1972).

DIAGNOSIS: A suchian archosaur distinguished from all other suchians except *Shuvosaurus* by the presence of an edentulous premaxilla, maxilla, and dentary, a posteriorly long anterodorsal process of the premaxilla, a long preacetabular process of the ilium that connects to the posterior process by a large thin flange, and a pubic boot that is 33% the length of the pubic shaft. Distinguished from *Shuvosaurus* by the presence of both a dorsal and posterior process of the maxilla, relatively shorter dentary, the absence of posterior process of the squamosal, a small fossa on the posterolateral side of the squamosal, and the presence of a large pit on the posterior side of the lacrimal.

DESCRIPTION AND COMPARISONS

SKULL: *Effigia* is represented by two skulls. AMNH FR 30587 (figs. 2–5) is a nearly complete skull missing both quadratojugals, the right splenial, and portions of the braincase. AMNH FR 30589 is an incomplete skull missing the right side and the posterior half. AMNH FR 30587 was obliquely crushed in a dorsoventral direction with a slight mediolateral component of shear during fossilization. On the other hand, AMNH FR 30589 (fig. 6) was compressed in a mediolateral direction with a slight dorsoventral component of shear during fossilization. The difference in crushing of the two skulls allows evaluation of certain elements in different planes and identification of possible distortions and cracks.

AMNH FR 30587 exhibits fine details of the surfaces of the elements and the articulations among most of the elements. Fragments of the sclerotic ring remain in the orbit. The small oval-shaped plates have a slight midline keel. The mandibular elements are tightly appressed to the ventral surface of the palate. As a result, some details of the palate, braincase, and mandibular elements cannot be observed in AMNH FR 30587. The palatal bones are somewhat disarticulated. Additionally, the occipital condyle was found adjacent to the orbit and the prootics whereas other closely related elements of the braincase were not recovered. The mandibular elements of AMNH FR30589 were removed from the rest of the skull.

The measurements presented below are estimates because of the dorsolateral crushing of the skull. The left side of AMNH FR 30587 is the least crushed and best represents the true sizes of the skull openings in life. The lightly built skull has a midline length of 170 mm (measured from the tip of the premaxilla to the posterior extent of the parietals). The antorbital fenestra is triangular as in most archosaurs. However, the anterior point of the triangle is not nearly as sharp as in *Postosuchus* (TTUP 9002), *Batrachotomus* (SMNS 52970), and *Teratosaurus* (BMNH 38646). The antorbital fenestra measures about 30 mm anteroposteriorly (maximum) and about 23 mm dorsoventrally (maximum) in AMNH FR 30587 and about 32 mm anteroposteriorly (maximum) and about 19 mm dorsoventrally (maximum) in AMNH FR 30589. The antorbital fossa is also triangle shaped, but is slightly longer at about 40 mm (maximum). The external naris is oval, elongated in anteroposterior direction, and anterodorsal to the antorbital fenestra. It measures about 37 mm (maxi-

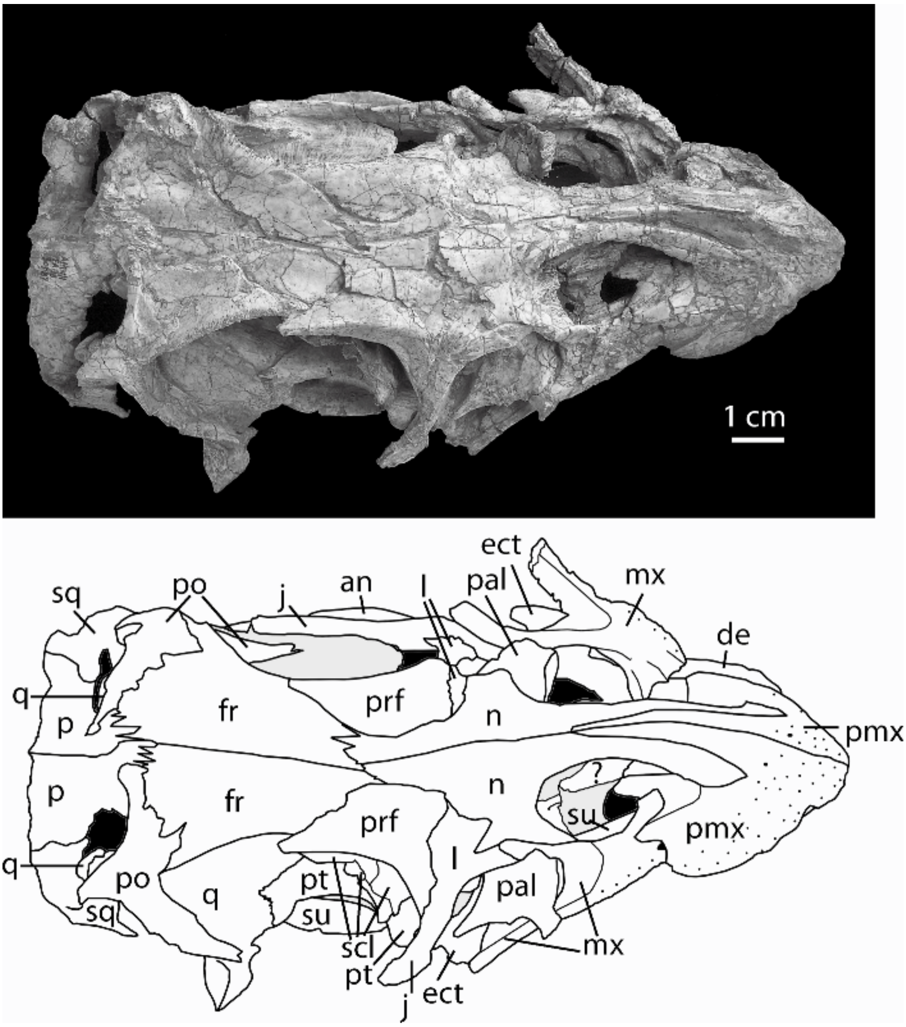


Fig. 2. Dorsal view of the skull of *Effigia okeeffeae* (AMNH FR 30587). Photo (above), drawing of specimen (below). Abbreviations are spelled out in appendix 3.

mum) anteroposteriorly and about 24 mm (maximum) dorsoventrally. The orbit is elliptical, measuring 56 mm anteroposteriorly (maximum) and 29 mm dorsoventrally (maximum). Both upper temporal fenestrae are crushed, and the lower temporal fenestrae are incomplete; thus, they could not be measured. An anteroposteriorly elongated mandibular fenestra measures 74 mm anteroposteriorly (maximum) and 15 mm dorsoventrally (maximum).

Chatterjee (1993) noted in his original skull description of the holotype of *Shuvosaurus* (TTUP 9280) that the skull was found articulated, although incompletely preserved. The now disarticulated holotype skull of *Shuvosaurus* has the following elements preserved: the right and left premaxilla, the left maxilla, the right ectopterygoid, portions of the right pterygoid, a partial braincase, the left lacrimal, left and right frontal, the left and right prefrontal, portions of the left and right postorbital, the left quadratojugal, the left squamosal, the left quadrate, the left and right dentary, and the left articular region including parts of the angular, articular, and surangular. The nasal and jugal are not now recognizable. The bone originally described

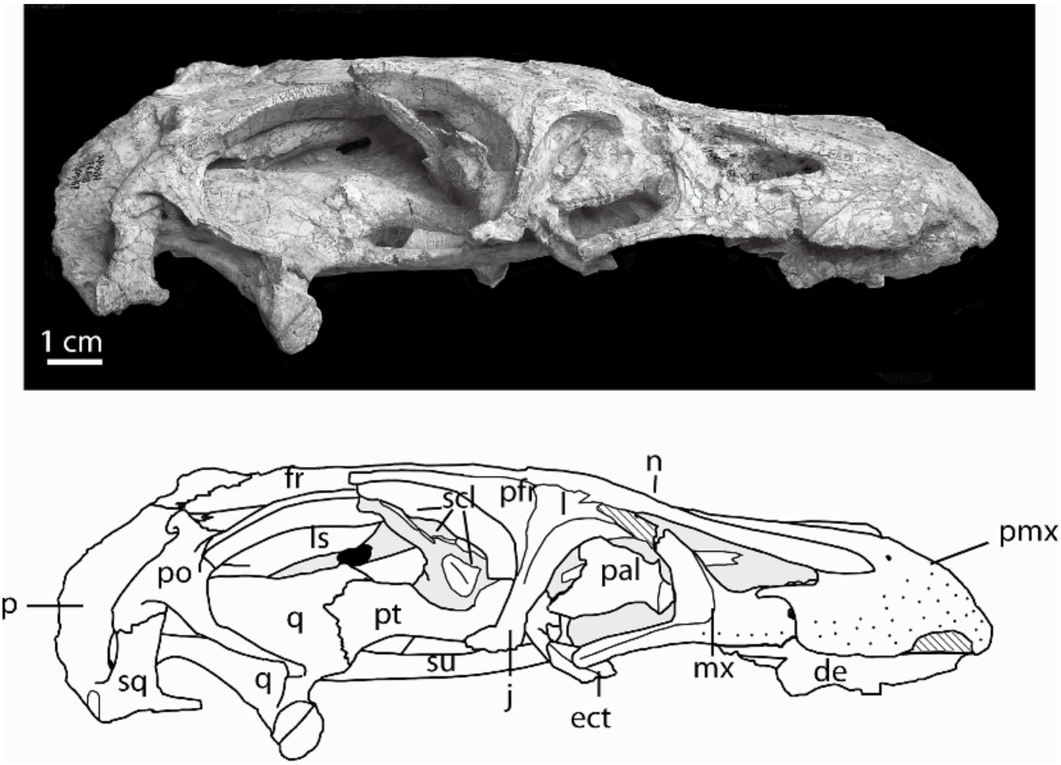


Fig. 3. Right lateral view of the skull of *Effigia okeeffeae* (AMNH FR 30587). Photo (above), drawing of specimen (below). The quadratojugal is unknown. Abbreviations are spelled out in appendix 3.

as the palatine by Chatterjee (1993) is actually the ectopterygoid, and the bone described by Chatterjee (1993) and Rauhut (1997) as the ectopterygoid is actually portions of the pterygoid.

PREMAXILLA: The premaxilla (AMNH FR 30587) is known from both sides of the skull. The right side is better preserved than the left. The premaxilla is edentulous, robust, and about the same length as the dentary. The main body is covered with small nutrient foramina, which extend to the base of the anterodorsal process. A similar system of foramina among birds, turtles, and other edentulous taxa (portions of the nasal and jugal of *Gallimimus*, GI DPS 1000/11; *Citipati*, IGM 100/978), taxa with a rhamphotheca, suggest that *Effigia* had a rhamphotheca. A large foramen is located just anterior to the ventral border of the external naris. The ventral edge of the premaxilla is mediolaterally narrow, sharp, and nearly horizontal between the articulation with the maxilla and the articulation with the other premaxilla. CT data indicate that a ventral shelf forms between the articulation of the left and right premaxillae. This shelf is clearly present in the three-dimensionally prepared premaxilla of *Shuvosaurus* (TTUP 9280). Additionally, CT data reveal a large anteroposteriorly directed fenestra formed between the premaxillae (fig. 7).

The anterodorsal process of the premaxilla is slightly longer than the anteroposterior length of the ventral edge of the premaxilla; *Shuvosaurus* (TTUP 9280) is the only other basal archosaur with such a long anterodorsal process of the premaxilla. It tapers to a point 1 cm anterior to the posterior edge of the external naris. The entire medial side of the process contacts the anterodorsal process of the other premaxilla. The dorsolateral side is bordered by the nasal. Here, the articulation between the nasal and the anterodorsal process forms a small groove along the entire length of the contact.

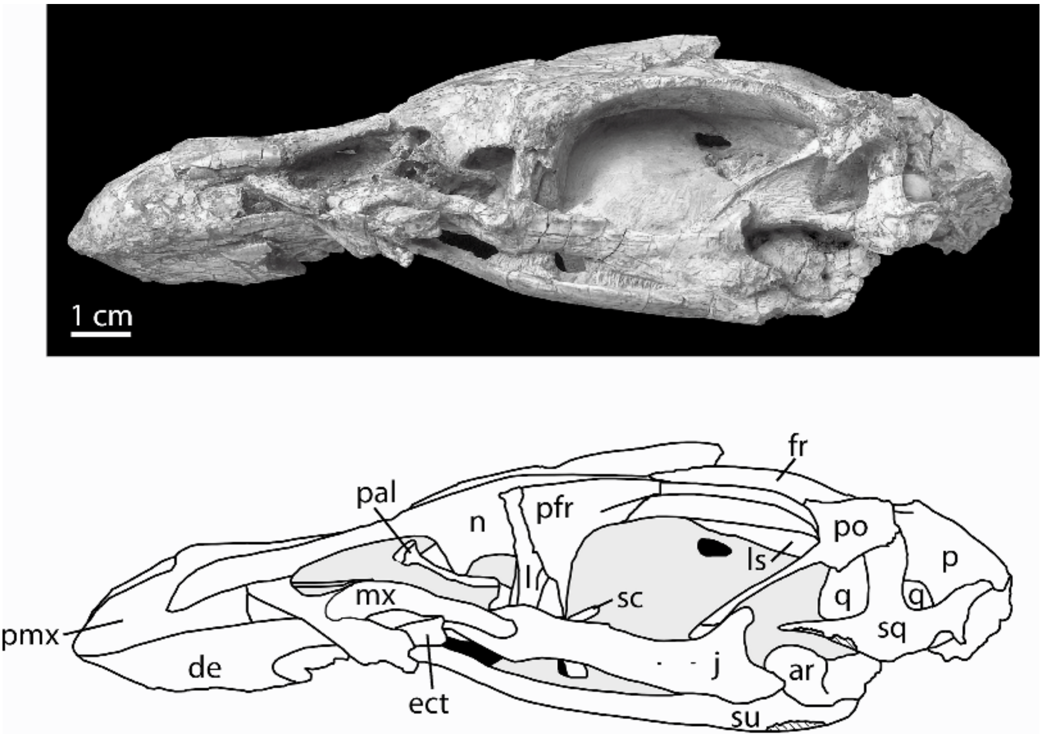


Fig. 4. Right lateral view of the skull of *Effigia okeeffeae* (AMNH FR 30587). Photo (above), drawing of specimen (below). Abbreviations are spelled out in appendix 3.

The nasal fits into a slot between the anterodorsal process and the main body of the premaxilla. Just ventral to this articulation, the premaxilla forms part of the anterior portion and half of the ventral border of the antorbital fenestra. The premaxilla laterally overlies the maxilla in a lap joint at the junction of the maxilla and the premaxilla. A small posteriorly projecting tonguelike process of the premaxilla lies on the dorsal part of the premaxilla–maxilla articulation. Ventral to this small process, the posterior margin of the premaxilla is concave.

The premaxillae of *Effigia* and *Shuvosaurus* (TTUP 9280) share some important characteristics. For example, both are edentulous, have a long anterodorsal process, and are larger, more robust than the maxilla. Both share a long posterior process than extends posteriorly to contact the nasal and has a small ventral posterior process. Only *Effigia* bears a posteriorly projecting tonguelike process of the premaxilla that lies on the dorsal part of the premaxilla–maxilla articulation. CT data confirm that *Effigia* shares a ventral shelf formed between the articulation of the left and right premaxillae with *Shuvosaurus* (TTUP 9280; fig. 7).

MAXILLA: Both maxillae of AMNH FR 30587 and the left maxilla of AMNH FR 30589 are preserved. The triradiate maxilla consists of an anterior portion, the posterior process, and the dorsal process. The entire anterolateral margin of the maxilla articulates with the medial side of the premaxilla. Each maxilla bears a small foramen formed by the anterior maxilla and the posterior edge of the premaxilla (fig. 8). The medial, dorsal, and ventral borders of the foramen are formed by the maxilla, whereas the lateral border is roofed by the premaxilla. The maxillary portion is concave and directed anteromedially medial to the premaxilla. CT data indicate that the foramen is not channeled on the medial surface of the premaxilla. A foramen created by the artic-

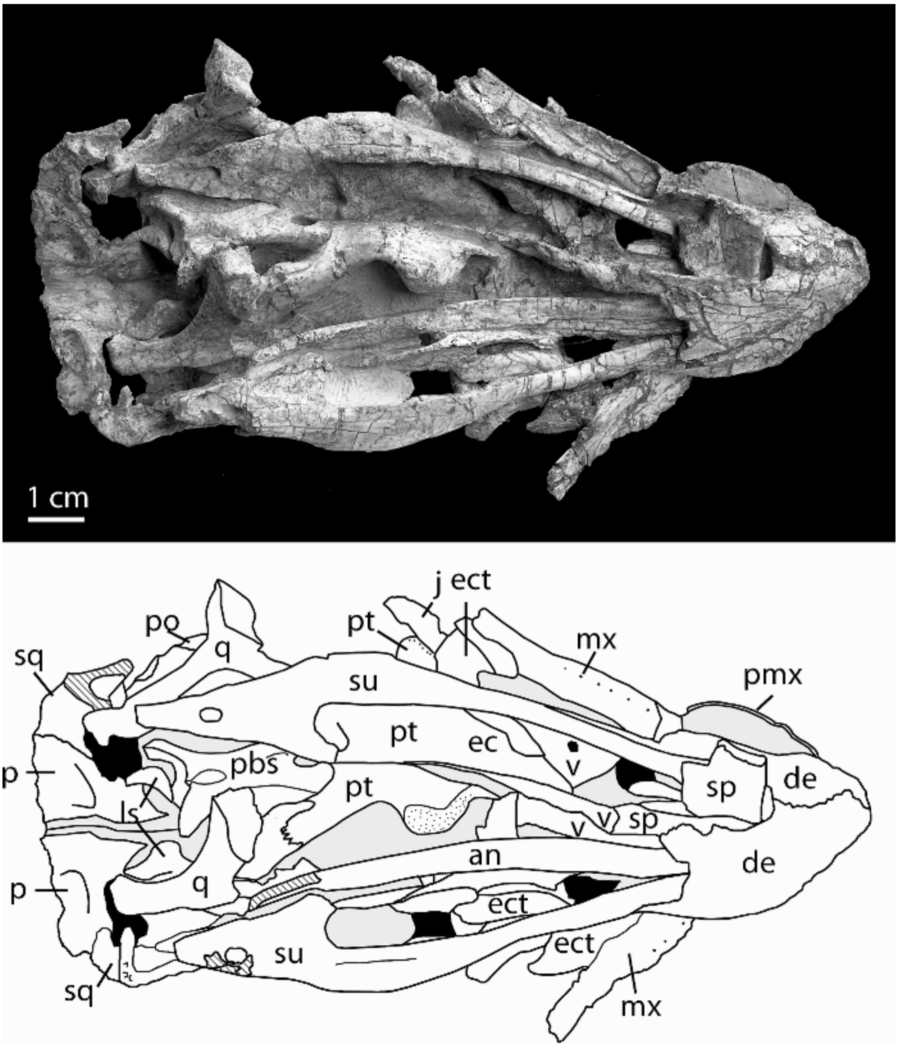


Fig. 5. Ventral view of the skull of *Effigia okeeffeae* (AMNH FR 30587). Photo (above), drawing of specimen (below). Abbreviations are spelled out in appendix 3.

ulation of the maxilla and the premaxilla appears in many "rauisuchian" taxa (*Batrachotomus* [SMNS 52970], *Postosuchus* [TTUP 9002]) and even in *Herrerasaurus* (PVSJ 407) and other unrelated taxa (Gower, 2000). However, in all of the taxa mentioned by Gower (2000), the foramen is observable on the maxilla and the premaxilla even if not in articulation. This is not the case in *Effigia*; there is no evidence for the presence of the foramen on the premaxilla if it is not articulated with the maxilla. The differences in the morphology of *Effigia* and *Postosuchus*, *Batrachotomus*, and other "rauisuchians" suggest that the two conditions are not necessarily homologous.

The palatal process of the maxilla lies medial to the small posterior process of the premaxilla. As in *Postosuchus* (TTUP 9002), *Batrachotomus* (SMNS 52970), crocodylomorphs, and *Euparkeria* (Gow, 1970), the palatal process extends anteriorly past the anterior extent of the body of the maxilla to articulate with the premaxilla. However, the palatal process does not contact the palatal process of the other maxilla. Instead of lying

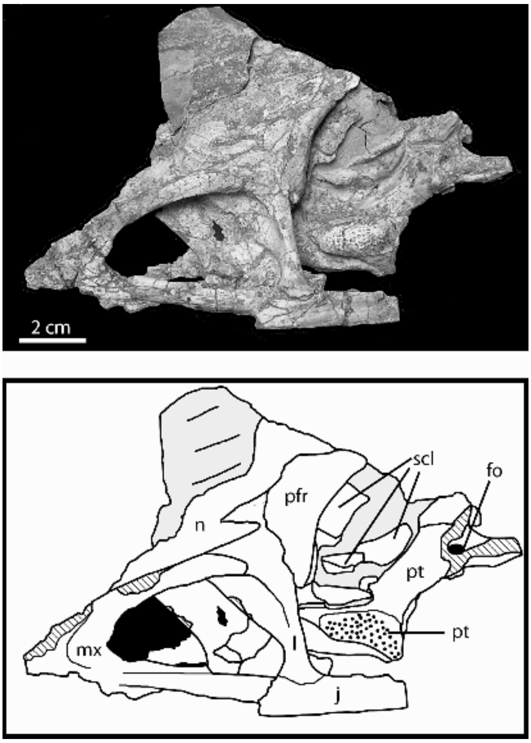


Fig. 6. Left lateral view of *Effigia okeeffeae* (AMNH FR 30589). The skull has been crushed dorsolaterally. Abbreviations are spelled out in appendix 3.

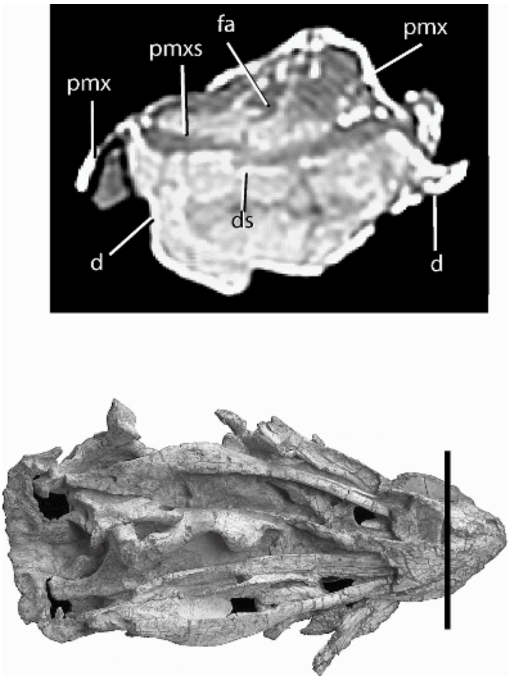


Fig. 7. CT data of *Effigia okeeffeae* (AMNH FR 30587; slice 53 of 543) highlighting the dorsal shelf of the dentaries and the ventral shelf created by the premaxillae. A small foramen (fa) is present between the articulation of the left and right premaxillae. The ventral view of the skull indicates where the CT slice was taken. Abbreviations are spelled out in appendix 3.

ventral to the premaxilla as in *Euparkeria* (TTUP 9002), *Batrachotomus* (SMNS 52970), and crocodylomorphs, the palatal process lies in an excavation on the dorsal surface of the posteromedial portion of the premaxilla in *Shuvosaurus* (TTUP 9280) and *Effigia* (AMNH FR 30587). The anterior portion of the maxilla has a shallow fossa on the entire lateral surface anterior to the edge of the antorbital fossa (figs. 3, 6, 8).

The anterodorsal side of the dorsal (ascending) process is thicker than the posteroventral side, similar to the state in *Arizonasaurus* (MSM 4590), *Batrachotomus* (SMNS 52870), and some stagonolepidids, and creates part of the posterior border of the external naris. The anterior side of the dorsal process is slightly convex, a condition elsewhere found only in *Arizonasaurus* (MSM 4590), *Batrachotomus* (SMNS 52870), and some stagonolepidids (e.g., *Desmatosuchus haplocerus*, TTUP 9024). The base of the dorsal process becomes concave ventrally where it meets the main body of the maxilla. The posterior side of the dorsal process forms the anterior margin and half of the dorsal margin of the antorbital fenestra. Most of the surface, except the dorsal edge, of the dorsal process is incorporated into the antorbital fossa. Disarticulation of the lacrimal and dorsal process of the maxilla indicates that most of the posteriormost portion of the dorsal process lies on top of the lacrimal and slightly overlaps the dorsal surface of the nasal. The medial edge of the dorsal process also articulates with the nasal.

The shape of the main body of the maxilla is complicated. An arcing, small ridge running dorsoventrally divides the main body into two portions. The area posterior to this ridge forms the anterior margin of the antorbital fossa. The body thins posteriorly

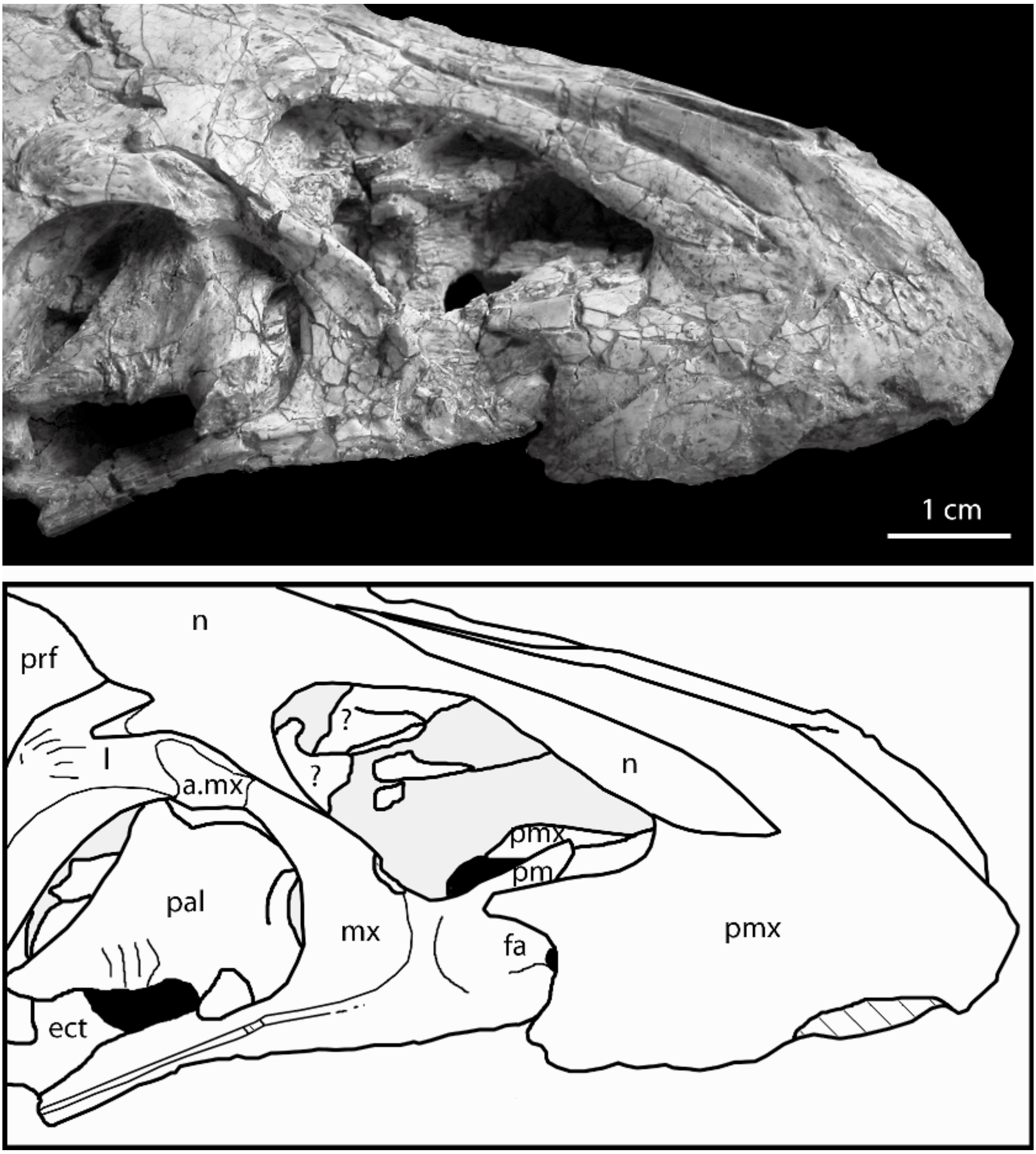


Fig. 8. The right premaxilla, maxilla, and nasal of *Effigia okeeffeae* (AMNH FR 30587). A small foramen lies between the premaxilla and the maxilla. Abbreviations are spelled out in appendix 3.

within the antorbital fossa. A small fossa lies anterior to the ridge and posterior to the maxilla–premaxilla articulation. This same small ridge gradually curves posteroventrally until it is subparallel with the ventral margin of the maxilla. This ridge also serves to separate the antorbital fossa and the rest of the maxilla. A similar ridge is found in a variety of taxa, including the theropod dinosaur *Coelophysis* and *Postosuchus*. In *Postosuchus* (TTUP 9002), the ridge is much more rounded and robust (Chatterjee, 1985). Similar to the ventral margin of the premaxilla, the ventral edge of the maxilla thins into a blade. A single row of foramina lies parallel to the ventral edge in the anterior

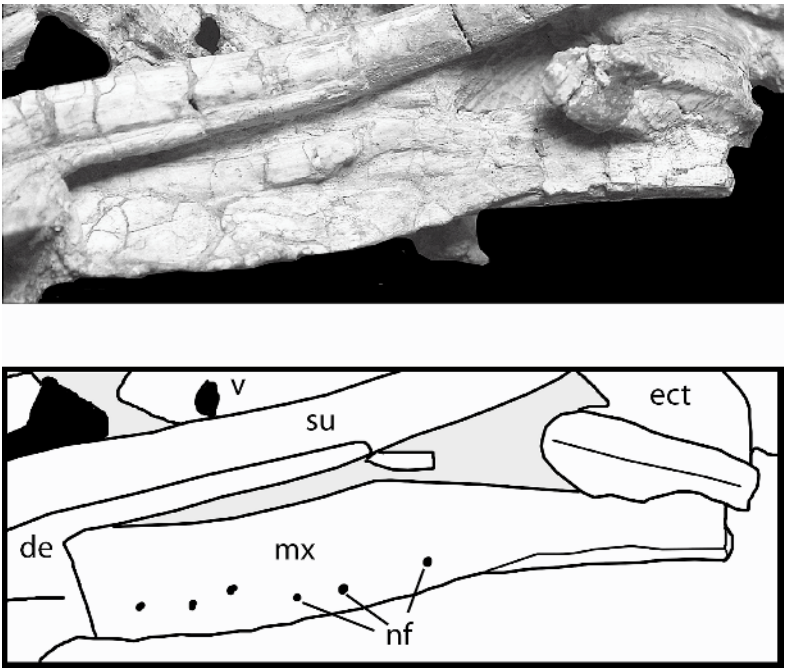


Fig. 9. The ventral view of the right maxilla of *Effigia okeeffeae* (AMNH FR 30587). The nutrient foramina pass through the lateral side to the ventral side. This figure illustrates the long posterior process of the dentary. Abbreviations are spelled out in appendix 3.

part, but is not present on the maxilla posterior to the anterior extent of the antorbital fenestra. Likewise, the sharp ventral edge flattens posterior to the anterior extent of the antorbital fenestra. Another small foramen (fig. 6) opens posteriorly and originates at the base of the posterior side of the dorsal process. This foramen also occurs in stagonolepidids (*Desmatosuchus haplocerus* TTUP 9024, *Longosuchus*) and it may be homologous to the posterior exiting foramen interpreted by Witmer (1995, 1997) as transmitting the maxillary nerve and maxillary vessels on the dorsal edge of the maxillae of *Arizonasaurus* (MSM 4590; Nesbitt, 2005a), *Batrachotomus* (SMNS 52970; Gower, 1999), and *Silesaurus* (ZPAL Ab III/361/26; Dzik, 2003).

The posterior process of the maxilla forms the ventral border of the antorbital fenestra and does not contact the lacrimal. The same small ridge that separates the main body of the maxilla becomes the entire posterior process beneath the antorbital fenestra. The posterior process becomes L-shaped in cross section posteriorly where the bottom of the L represents the lateral side and the flat side represents the ventral surface. The articulation between the jugal and the posterior process is difficult to distinguish, but it appears that the posterior process tapers ventral to the anterior portion of the jugal.

In ventral view, the ventral edge of the maxilla is 1 cm across (mediolaterally) for most of its length, and the posterior process slightly tapers posteriorly in ventral view. As stated previously, the anterior half of the ventral edge of the maxilla is a sharp edge whereas the posterior half is flat. The medially expanded ventral shelf is slightly concave and fits the dentary and the surangular during occlusion (fig. 9). Small fenestrae lie in the middle of the concave region in a line that parallels the ventral margin. These fenestrae have a one-to-one ratio with the nutrient foramina on the ventral edge of the lateral side of the maxilla.

The maxilla of *Effigia* appears to differ considerably from that of *Shuvosaurus* (TTUP 9280). However, the poor preservation and incompleteness of the maxilla of *Shuvosaurus* hinders comparisons. *Shuvosaurus* has no posterior or dorsal processes of the maxilla. Also, the extent of the antorbital fossa in *Shuvosaurus* approaches the premaxilla–maxilla contact. The medial side of the maxilla of *Shuvosaurus* bears an anterior and posterior pocket that is not present in *Effigia*. Additionally, the medial edge of the maxilla of *Shuvosaurus* seems to form a ‘‘secondary palate’’ where the medial processes of the maxillae meet at the midline and expand posteriorly.

NASAL: Both nasals are well preserved in AMNH FR 30587 (figs. 2, 3). The nasals are thin, large elements that form the anterior half of the skull table. Anteriorly, the nasal fits into a slot in the premaxilla. The anterior portion expands slightly anterior to the external naris and then rapidly tapers to a point that inserts into the body of the premaxilla. The dorsal edge of the anterior process is bordered by the anterodorsal process of the premaxilla until the anterodorsal process of the premaxilla tapers dorsal to the posterior extent of the external naris. Here, the left and right nasal contact each other at the midline. The ventral edge of the anterior portion of the nasal forms the dorsal edge of the external naris, and the main body of the nasal forms the posterior border of the external naris. The nasal thins at the edge of the external naris.

The ventrolateral margin of the nasal is divided into distinct anterior and posterior processes. The ventral edge between these two small processes borders the dorsal process of the maxilla. The anterior ventrolateral process, or descending process, terminates in a point that lies between the dorsal process of the maxilla and the external naris. Rauhut's (1997) interpretation of *Shuvosaurus* notes this small process, but it was not described in Chatterjee's (1993) original work. The descending process of the nasal is common to most basal archosaurs, including *Postosuchus* (TTUP 9002), *Batrachotomus* (SMNS 52970), stagonolepidids, and ornithodirans, but it is absent in all crocodylomorphs. The posterior ventrolateral process invades the dorsal portion of the lacrimal. It is not clear if the posterior ventrolateral process sits on the surface of the lacrimal or sits in a groove.

Posterior to the posterior ventrolateral process, the main body of the nasal borders the dorsal margin of the lacrimal and the dorsal border of the prefrontal. The posterior process of the nasal meets the frontal just dorsal to the anterior extent of the orbit. Here, the suture between the frontal and nasal interdigitates. The entire surface of the nasal is smooth and lacks the large, rugose ridge that is present on the nasal of *Postosuchus* (TTUP 9002) and *Batrachotomus* (SMNS 52970).

LACRIMAL: The right lacrimal of AMNH FR 30587 (figs. 3, 4) and the left lacrimal of AMNH FR 30589 (fig. 6) are well preserved. The lacrimal lies on the lateral surface of the jugal in AMNH FR 30589. In lateral view, the lacrimal is robust and the lateral surface is rounded. At the contact with the jugal, the lacrimal flares in both anterior and posterior directions. The exact configuration of the articulation between the two elements is not clear. The anterior edge of the lacrimal forms the posterior border of the antorbital fenestra. The dorsal part of the anterior border of the lacrimal splits into lateral and medial ridges separated by a deep fossa. Both the lateral and medial ridges are sharp. The lateral ridge continues ventrally and turns into a slightly rugose ridge that terminates before the jugal contact. The fossa created between the two ridges is part of the posterodorsal portion of the antorbital fossa. Both ridges terminate anterodorsally at the contact between the dorsal process of the maxilla. The shaft of the lacrimal is round in cross section at midshaft and dorsally it expands anteroposteriorly and becomes mediolaterally compressed.

The posterior edge of the lacrimal borders the anterior margin of the orbit. A small dorsoventral fossa is located on the posterior side of the lacrimal just ventral to the articulation with the prefrontal (fig. 10). This feature represents a possible autapomorphy of *Effigia*. The dorsal half of the posterior side of the lacrimal articulates with the prefrontal. The posterior ventrolateral process of the nasal invades the anterodorsal portion, effectively dividing the dorsal portion of the lacrimal into anterodorsal and dorsal portions. The dorsal portion articulates with the nasal and the anterodorsal part

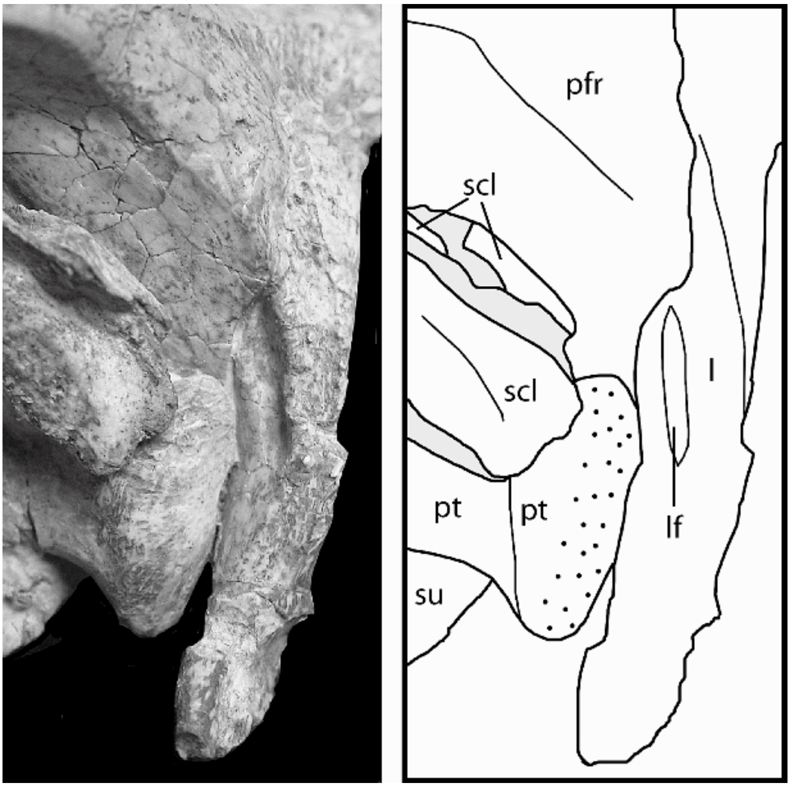


Fig. 10. Posterior view of the lacrimal of *Effigia okeeffeae* (AMNH FR 30587) emphasizing a large posterior fossa. Abbreviations are spelled out in appendix 3.

articulates with the posterior end of the dorsal process of the maxilla. Disarticulation of the anterodorsal part of the right lacrimal and dorsal process of the right maxilla of AMNH FR 30587 shows that the dorsal process of the maxilla lies on the surface of the lacrimal in a small depression. Both the dorsal process of the maxilla and the anterodorsal part of the lacrimal exclude the nasal from participating in the antorbital fenestra. The lacrimal is excluded from contact with the frontal by the prefrontal. A small patch of rugose surface lies between the posterior ventrolateral process of the nasal and the prefrontal.

The preserved portions of the lacrimal of *Shuvosaurus* (TTUP 9280) differ from those of *Effigia*. Even though the preservation of the lacrimal of *Shuvosaurus* is poor, the element lacks the posterior fossa and is much more mediolaterally compressed than that of *Effigia*.

FRONTAL: The frontal (fig. 11) forms the posterior half of the skull table and is the largest element of the skull. The dorsal surface is smooth like that of *Arizonasaurus* (MSM 4590). In contrast, crocodylomorphs, stagonolepidids, parasuchians, *Postosuchus* (TTUP 9002), and *Batrachotomus* (SMNS 52970) have frontals that are ornamented with ridges, dorsal sculpture, and/or fossae. Anteriorly, the frontal meets the nasal in an interdigitating suture and posteriorly, the frontal meets the parietal in an interdigitating suture. The frontal becomes sandwiched between the left and right prefrontals where it meets the nasal. The articulation with the postorbital is complex; posteriorly it is an interdigitating suture whereas the anterior portion of the postorbital overlaps the frontal. The frontal is not incorporated into the upper temporal fenestra and it does not participate in the upper temporal fossa as it does in dinosaurs (Langer, 2004; Langer and

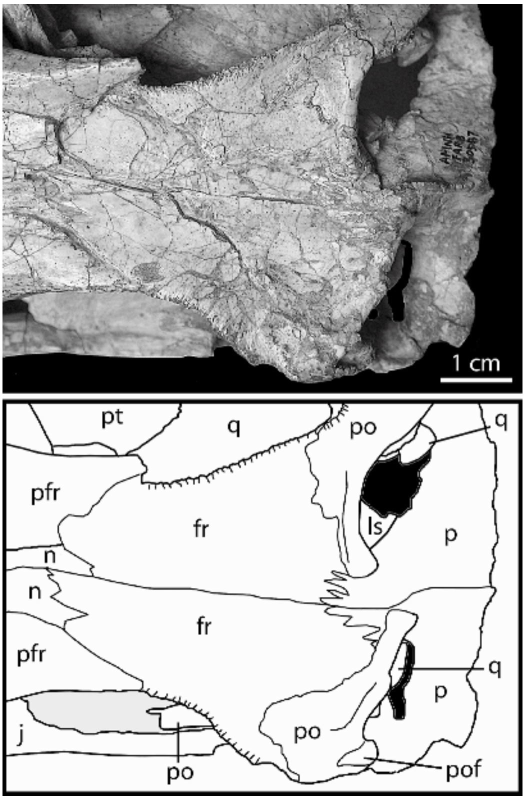


Fig. 11. A dorsal view of the frontals, parietals, and postorbitals of *Effigia okeeffeae* (AMNH FR 30587) emphasizing the relative size, position, and sutures among the elements. Abbreviations are spelled out in appendix 3.

Benton, in press). The orbital margin is slightly medially concave in dorsal view. In lateral view, the posterior orbital margin is rugose and uniformly thick. The same pattern of rugose bone continues on to the postorbital posteriorly. This pattern occurs in *Arizonasaurus* (MSM 4590), but a rugosity is absent in *Shuvosaurus* (TTUP 9280).

Ventrally, the frontal bears a large optic fossa that slopes dorsolaterally and stretches the entire length of the element. Small grooves (fig. 12) trend parallel to the slope of the optic fossa. The medial border of the optic fossa is the thickest part of the frontal.

PREFRONTAL: The prefrontal is well represented in AMNH FR 30587 (figs. 2, 3). It is triangular in dorsal view and is the thickest and most robust element in the skull. The prefrontal forms the anterodorsal border of the orbit. Here, it is much thicker than the frontal and extends medially. The frontal articulates with the frontal posteriorly, the nasal medially, and the lacrimal anteriorly. A low, rugose ridge originates at the orbital rim of the frontal and proceeds anteriorly through the center of the element connecting with the slightly rugose posterior region of the lacrimal. A shallow fossa lies anteroventrally to this ridge.

POSTFRONTAL: The postfrontal is absent in *Effigia*.

PARIETAL: Both parietals of AMNH FR 30587 (fig. 11) are nearly complete, but both lack the posterodorsal edge. The left and right parietals create a sagittal crest at the midline as with ornithomimid theropods. A thin piece of matrix lies between the left and right parietals at the midline, suggesting the individual had not finished growing and that the skull may belong to a subadult. The parietals meet the frontals at an interdigitating suture at the dorsally flat surface that characterizes the skull table formed by the frontals, prefrontal, and the nasal. Just lateral to the interdigitating suture with the frontal, the parietals contact the postorbital. Here, the medial process of the postorbital abuts the anteromedial portion of the parietal (fig. 13). The parietal is nearly vertical near the formation of the sagittal crest. From the midline, the parietals diverge and become more dorsoventrally oriented laterally. At first glance, the parietals seem to be dorsoventrally crushed in AMNH 30587, but the articulations with the squamosal, frontal, and postorbital indicate little crushing occurred during fossilization. The articulation pattern between the parietal and squamosal is not clear. A thickened ventral finger directed laterally overlaps the squamosal at the border of the upper temporal fenestra whereas the rest of the suture is difficult to interpret. The parietals thin posteriorly. The ventral side bears a boomerang-shaped ridge (fig. 13) located at the center of the element. A small fossa is located on the inside of the elbow of the boomerang. This ridge may have served as the attachment area for the supraoccipital.

POSTORBITAL: Both postorbitals of AMNH FR 30587 (figs. 2, 3, 11) are complete, but the left postorbital is crushed and distorted. The postorbital is described in three parts,

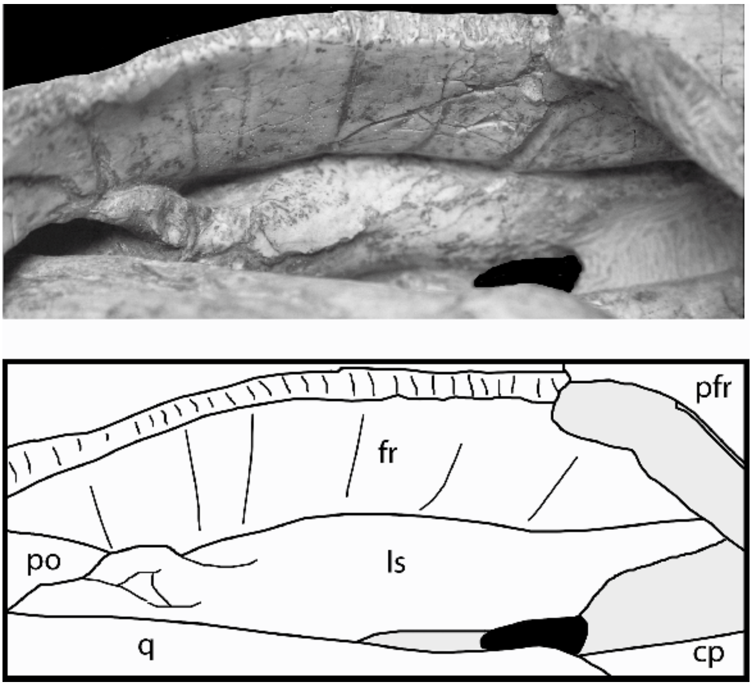


Fig. 12. The right lateralsphenoid of *Effigia okeeffeae* (AMNH FR 30587). Abbreviations are spelled out in appendix 3.

the body and posterior process, the medial process, and the ventral process.

The medial process dorsally overlaps the surface of the frontal. The anterior portion thins anteriorly. Here, the postorbital is slightly concave where it articulates with the frontal. The posterior portion of the anteromedial process bears a rounded raised ridge that outlines the upper temporal fenestra. This raised ridge is also present in *Shuvosaurus* (TTUP 9280). The anteromedial process of the postorbital excludes the frontal from participating in the upper temporal fenestra as in *Arizonasaurus* (MSM 4590; Nesbitt, 2005a). The medial extent of the anteromedial process ends in an expanded club-shaped process that contacts the anteromedial portion of the parietal.

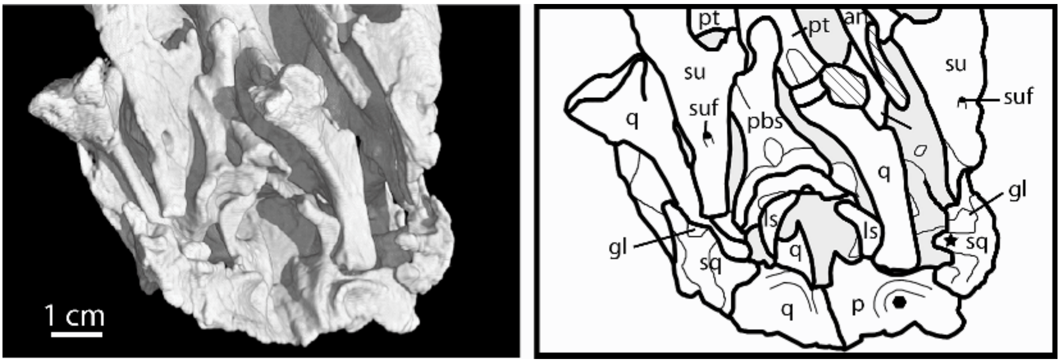


Fig. 13. The posterior portion of the skull of *Effigia okeeffeae* (AMNH 30587) in ventral view. The star indicates a small medially projecting process of the squamosal that is absent in *Shuvosaurus*. Abbreviations are spelled out in appendix 3.

The main body of the postorbital connects the anteromedial, ventral, and posterior processes. The rugose lateral edge of the frontal continues onto the anterior body of the postorbital, but does not continue far ventrally (fig. 3). The posterior process thins posteriorly and appears to dorsally overlap the squamosal. However, the exact configuration is not clear. A fossa ventral to the posterior process is similar to that of *Batrachotomus* (SMNS 52970) and *Arizonasaurus* (MSM 4590).

The ventral process forms nearly all the posterior border of the orbit. The process is anteroposteriorly thin in lateral view, but expands mediolaterally nearly 10 times its anteroposterior height. *Shuvosaurus* (TTUP 9280) has the same expansion of the ventral process. The ventral process tapers mediolaterally ventrally at the jugal contact. This contact is very limited, the ventralmost part of the ventral process fits into a small recessed area on the lateral surface of the dorsal process of the jugal. There is no apparent kink of the ventral process as in *Batrachotomus* (SMNS 52970), *Heptasuchus* (UW 11562), and *Postosuchus* (TTUP 9002).

SQUAMOSAL: Both squamosals (fig. 14) are nearly complete and in articulation in AMNH FR 30587, but both are slightly displaced ventrally. The life position is more similar to the right squamosal because articulation with the quadrate would not be possible in life if the anterior process was anteroposteriorly horizontal.

The squamosal is a complex bone that is separated into the body and five processes; anterior, posteromedial, ventral, posterior, and medial.

The body is formed by the convergence of all of the processes. A small, well-defined depression is located on the posterior portion of the body. This depression opens ventrally and is surrounded by a small rim of bone (fig. 14A,B). The squamosal of *Shuvosaurus* (TTUP 9280) (fig. 14C) lacks this well-defined depression. The head of the quadrate articulates with a depression on the ventral side of the body. This articulation between the quadrate and the squamosal is limited and is strictly confined by bone on the posterior and lateral sides. A small medially projecting process is located at the medial edge of the fossa where the head of the quadrate articulates. This small process is also absent in the squamosal of *Shuvosaurus* (TTUP 9280).

The anterior process articulates with the postorbital, but the exact configuration cannot be determined. The parallel dorsal

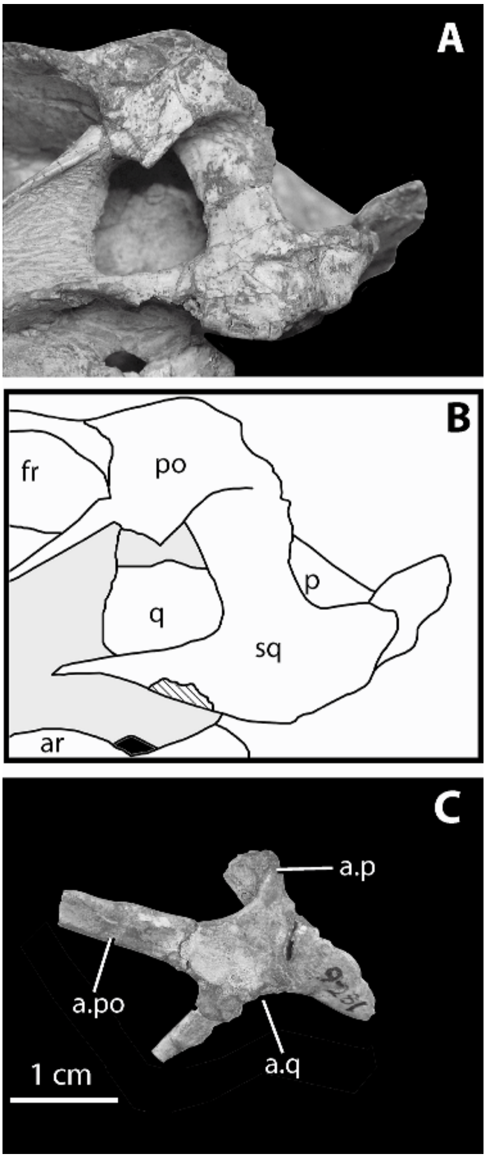


Fig. 14. Lateral view (**A, B**) of the squamosal of *Effigia okeeffeae* (AMNH FR 30587) compared with a lateral view of the squamosal of *Shuvosaurus* (**C**). Abbreviations are spelled out in appendix 3.

and ventral edges of the anterior process create a rectangular shape in lateral view (fig. 14A,B). Both the dorsal and the ventral edges are slightly rounded, whereas the anterior process is mediolaterally compressed. Compared to the anterior process of the squamosal of *Shuvosaurus* (TTUP 9280), the anterior process of *Effigia* is dorsoventrally much wider and anteroposteriorly much shorter. The lateral surface of the anterior process is smooth and bears no rugose ridges like in *Batrachotomus* (SMNS 80260) and *Postosuchus* (TTUP 9002).

The posteromedial process bends medially, becomes dorsoventrally compressed, and meets the squamosal in a complicated articulation. A small finger from the parietal overlaps the squamosal on the edge of the border of the upper temporal fenestra.

The prominent posterior process of the squamosal of *Shuvosaurus* (TTUP 9280) is completely absent in *Effigia*. The smooth, unbroken posterior edge of the posterior process is parallel to the ventral process. The posterior process of the squamosal of *Shuvosaurus* (TTUP 9280) is large and represents a key difference between the two taxa (fig. 14).

The thin ventral process tapers ventrally. The actual orientation of the ventral process is not clear; however the ventral process cannot be directed completely ventrally because the quadrate would not be able to articulate to the squamosal. The actual orientation must be between a strictly ventral position and the more anteriorly projecting preserved position. This process covers the articulation between the squamosal and the quadrate head laterally. The articulation with the quadratojugal is not preserved.

JUGAL: The left jugal is complete and most of the right jugal is missing in AMNH FR 30587 (figs. 4, 6). The posterior end of the jugal bifurcates into posterodorsal and posterior processes. The posterodorsal process is short and weakly contacts the ventral process of the postorbital. Here, there is a slight depression on the anterior side that articulates with the ventral process of the postorbital. The posterior process of the jugal is also short and appears to end in a rounded point. The manner of articulation with the quadratojugal cannot be determined in any of the specimens. Just anterior to the bifurcation of the two posterior processes, the bone is concave. Two small fenestrae, one exiting posteriorly and one exiting anteriorly, pierce the concave region (fig. 15). The ventral border of the orbit is formed by the main body of the jugal. The jugal is oval shaped in cross section, where the long axis is oriented dorsoventrally.

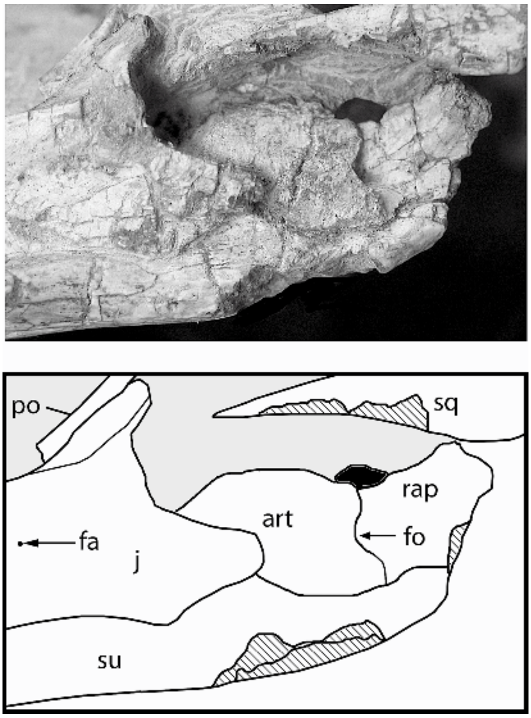


Fig. 15. The left articular, posterior jugal, and surangular of *Effigia okeeffeae* (AMNH FR 30587) in lateral view. The posterior mandible is slightly rotated dorsolaterally. Abbreviations are spelled out in appendix 3.

The anterior region of the jugal is crushed, but still can be interpreted. The lacrimal lies on the dorsal surface of the jugal as with nearly all archosaurs. It is not clear if the jugal had an anterodorsal process. If it had an anterodorsal process, it would be small and hidden behind the lacrimal in lateral view. The anterior process of the jugal proceeds anteriorly to the lacrimal and overlaps the posterior process of the maxilla. The articulation between the jugal and the maxilla is not clear. The anterior process forms part of the ventral antorbital fenestra border.

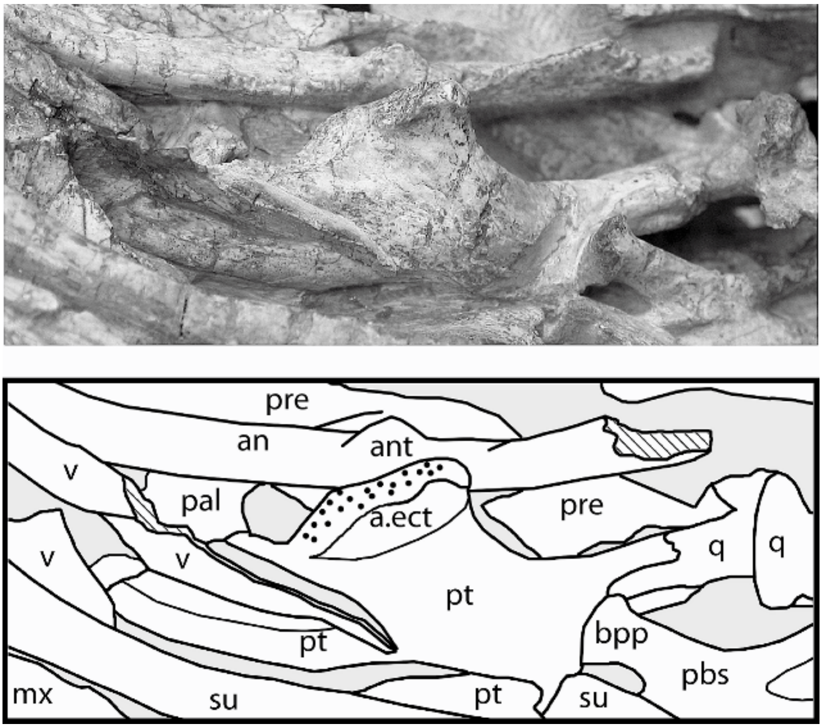


Fig. 16. A close-up of the pterygoid region of the skull of *Effigia okeeffeae* (AMNH 30587) in ventral view. The palatines have been displaced. Abbreviations are spelled out in appendix 3.

ECTOPTERYGOID: Both ectopterygoids are preserved in AMNH FR 30587 (figs. 5, 8, 9) out of articulation and the left ectopterygoid is preserved in articulation with the pterygoid in AMNH FR 30589. The main body of the ectopterygoid projects medially from the articulation with the jugal and then sharply curves posteriorly. The long posterior process is thick on its lateral side and thins medially. In AMNH FR 30589, the posterior process lies on the ventral surface of the ventrolateral edge of the pterygoid. The disarticulated pterygoid and ectopterygoid of AMNH FR 30587 reveal a depression on the ventral surface of the lateral flange of the pterygoid in which the ectopterygoid fits (fig. 16).

The ectopterygoid of *Effigia* is generally similar in form to that of *Postosuchus* (TTUP 9002), *Batrachotomus* (SMNS 80260), *Arizonasaurus* (MSM 4590), and *Sphenosuchus* (SAM 3014). However, it is most similar to that of *Sphenosuchus* in that both share an anteroposteriorly elongated ventral "head". The bone originally interpreted as the palatine of *Shuvosaurus* (TTUP 9280; Chatterjee, 1993) is actually the ectopterygoid (pers. obs.). The ectopterygoid of *Shuvosaurus* is like that of *Effigia* in having an anteroposteriorly elongated lateral "head". The bone originally identified as the ectopterygoid by Chatterjee (1993) and Rauhut (2003) is actually part of the pterygoid. Thus, the characters state, "deep ectopterygoid excavation" used by Chatterjee (1993) to ally *Shuvosaurus* with theropods is not supported with this new interpretation.

QUADRATE: The left (fig. 17) and right quadrates of AMNH FR 30587 are complete, but displaced anteriorly and laterally. Disarticulation of the dorsal process or "head" from the squamosal reveals that the articular surface is rounded, convex, and mediolaterally compressed. Two blade-thin flanges of bone originate just ventral to the articular face. One flange is located on the medial side and the other flange is located on the anterodorsal side. The medial blade is short

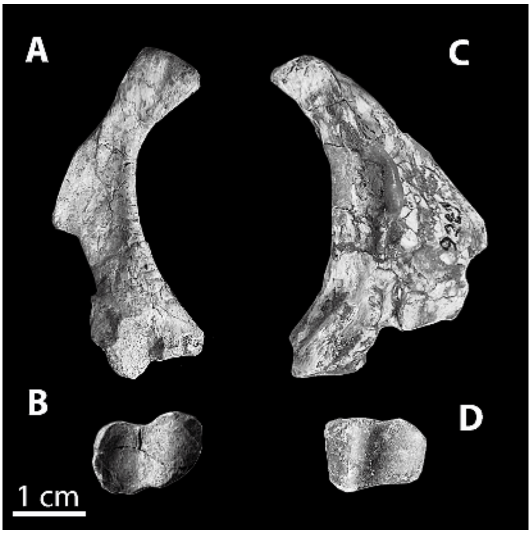


Fig. 17. The left quadrate of *Effigia okeeffeae* (AMNH FR 30587) in lateral (**A**) and distal (**B**) views compared to the right quadrate of *Shuvosaurus* (TTUP 9281) in lateral (**C**) and distal (**D**) views.

and ends halfway down the quadrate. The anterodorsal flange gradually expands anteriorly in the ventral direction. About halfway down the quadrate, the anterodorsal flange rounds off, and proceeds ventrally to join the main body of the quadrate. Walker (1990) observed the same flange in *Sphenosuchus* and homologized it with the anterodorsal process of the quadrate of crocodylians. He hypothesized that this flange served as a "protraction-stop". The position and size of this flange in *Effigia* suggest it is homologous to the same feature as crocodylians.

The posterior edge is slightly rounded and strongly bowed anteriorly. The distal end bears an anteriorly projecting process that serves to articulate with quadratojugal. No quadrate foramen or notch is present, similar to *Shuvosaurus*. It ends in a rounded point on the anteroventral edge. The body of the quadrate and the anterodistal flange create a fossa. In *Sphenosuchus*, the anterodistal flange and the anterodorsal process are nearly continuous; however, in *Effigia*, *Batrachotomus* (SMNS 52970), and *Arizonasaurus*, the anterodistal flange and the anterodorsal process are clearly separated. The distal end of the quadrate of *Effigia* lacks the well-defined groove located on the posteromedial side, present on the quadrates of *Arizonasaurus* (MSM 4590) and *Batrachotomus* (SMNS 52970). The posterior surface has a shallow furrow that is oriented dorsoventrally.

The condylar surfaces of the quadrate of *Shuvosaurus* (TTUP 9280) and *Effigia* are distinctive within Suchia. Both are square in distal view. Additionally, a small rim of bone located around the lateral edges surrounds the articular surfaces. The articular surface is mostly concave except that the extreme lateral side is slightly convex. The concave surface corresponds to a convex articular surface of the surangular and articular. Stagonolepidids, *Sphenosuchus*, and all specimens of *Arizonasaurus*, *Euparkeria*, *Batrachotomus*, *Postosuchus*, and *Saurosuchus*, instead, possess two distinct convex articular surfaces.

The quadrates must be anteroventrally orientated to properly articulate with the squamosal and the articular. This is clear given that the mandible is shorter with respect to the length of the premaxilla to the articulation between the squamosal and the quadrate. In comparison, nearly all basal archosaurs have quadrates that are anterodorsally oriented. Within Archosauria, only spinosaurids, theropods and, ornithomimid theropods have a similarly oriented quadrate (Rauhut, 2003).

Both quadrates remain articulated with the pterygoids, but not with the squamosals. The pterygoid ramus splits into two processes, a large dorsal process and a small, ventral, fingerlike process (figs. 16, 19). These two processes were reported by Walker (1990) for *Sphenosuchus*, but at the time, Walker was not certain that the more ventral process was distinct or was split off the orbital process during preservation. The two distinct processes found in *Effigia* indicate that Walker was correct in his assignment. Here, I use Walker's (1974, 1990) original terminology; the dorsal process is referred to the orbital process and the ventral process is referred to the pterygoid process. The orbital process is concave medially and convex laterally. Anteriorly, it joins the pterygoid at a suture. Here, the pterygoid is thicker than the orbital process and slightly overlaps the orbital process on both the medial and lateral sides. Thus, the orbital process may sit in a depression or a flattened surface at the pterygoid suture. Moreover, a broken margin at the orbital process–pterygoid suture of AMNH FR 30589 indicates a slight groove at the articular end of the pterygoid. Additionally, the same broken area reveals an anteriorly directed foramen (fig. 6) that is present near the orbital process–pterygoid suture that when the two elements are in articulation is not visible. The pterygoid process lies directly on the pterygoid just posterior to a thickened region on the ventrolateral edge of the lateral process of the pterygoid.

The quadrates of *Shuvosaurus* and *Effigia* are nearly identical (fig. 17). Both share the following characters: same square-shaped articular surface in ventral view, the presences of a posterior fossa near the distal articular surface, a short optic flange that articulates with the pterygoid, and absence of a quadrate foramen. The orientation of the quadrate in *Shuvosaurus* is not clear despite the reconstructions of Chatterjee (1993); nevertheless, the orientation was apparently similar to *Effigia* based on the nearly identical morphology of the quadrates and the general similarity between the squamosals.

PTERYGOID: Both pterygoids are complete and in articulation in AMNH FR 30587 (figs. 5, 16) and parts of the left pterygoid are preserved in AMNH FR 30589 (fig. 6). The articulated pterygoids are shifted laterally from the midline. The pterygoids contact the vomers medially, the palatines and the ectopterygoids laterally, and the quadrate posteriorly. The pterygoids articulate with each other deep within the skull and meet the cultriform process of the parabasisphenoid at their dorsal extent.

CT data indicate that the pterygoids together form a W in cross section anteriorly. Moving posteriorly, the middle "hump" of the W increases in height (dorsal) and the lateral parts of the W shorten. The vomers sit in a groove lateral to the edge of the W (fig. 18). Medial to the lateral processes the posterior shape of the articulated pterygoids is V-shaped and the most dorsally expanded. Posteriorly the V decreases in height.

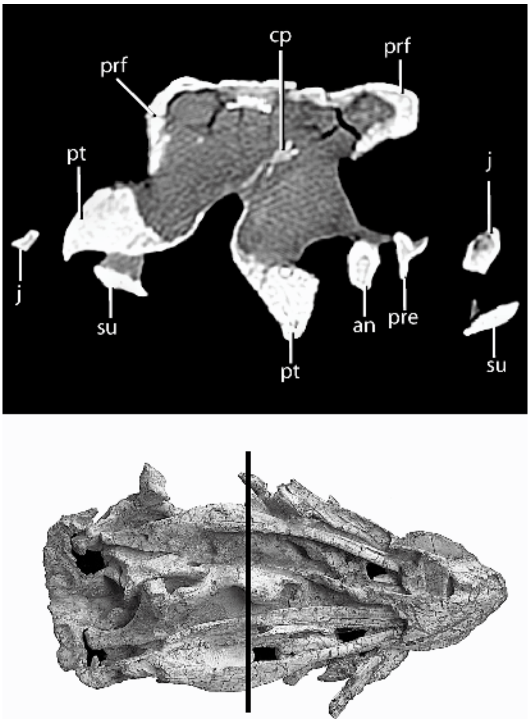


Fig. 18. CT data of the lateral processes and ventral extent of the pterygoid of *Effigia okeeffeae* (AMNH FR 30587; slice 296 of 543). The cultriform process of the parabasisphenoid is present between the pterygoids. The ventral view of the skull indicates where the CT slice was taken. Abbreviations are spelled out in appendix 3.

The anterior portion thins anteriorly. The thick lateral processes articulate with the ectopterygoid on the ventral side. A slight depression outlines the articulation (fig. 16). The lateral extent of the process arcs dorsally to form a slight cup on the dorsal side. The lateral edge is rounded and covered in small foramina, indicating that a cartilage cap was present in life. The posterior portion of the pterygoid articulates with the quadrate. The contact is dorsoventrally expanded, and the suture between the two elements is difficult to discern. A small process, the pterygoid process of the quadrate, overlaps the gently rounded ventral surface of the pterygoid. The articulation with the basipterygoid process of the parabasisphenoid remains obscured by the right mandible and the right pterygoid.

PALATINE: Both palatines (figs. 2, 3, 4) of AMNH FR 30587 have been disarticulated and rotated through the antorbital fenestra. Only the posteroventral side of the palatine is visible on the ventral surface of AMNH FR 30587. The left palatine is displaced laterally and the anterior side is rotated dorsally so that the element slants posteriorly. The left palatine is dorsoventrally flipped and the anterior end projects laterally.

The palatines are mostly hidden by other elements or matrix and CT data do not provide more information. However, the observable morphology indicates a close similarity to the palatine of *Batrachotomus* (SMNS 80260; Gower, 1999). The articular surface of the palatine that articulates with the maxilla is heavily striated and dorsoventrally thickened. The articular surface is thickest anteriorly and thins posteriorly. The pila postchoanalis projects laterally through the right antorbital fenestra; however, when rotated back to life position, the pila postchoanalis projects anteriorly. Moreover, the shape of the edge medial to the pila postchoanalis indicates that the choana is reduced relative to that of *Batrachotomus* (SMNS 80260).

VOMER: Possible nearly complete left and a partial right vomers (fig. 5) are present in AMNH FR 30587. The right vomer is still articulated with the pterygoid and the left is rotated ventrally and laterally. The vomer is a thin bone (>1 mm) that is anteroposteriorly elongated. The posterior end articulates to the medial surface of the pterygoid, just medial to the lateral flange. In *Sphenosuchus* (SAM 3014) and in Walker's (1961) reconstruction of *Stagonolepis*, the vomer is much shorter and does not reach the lateral process of the pterygoid. The vomers are located medial to the pterygoid and sit in a small groove as demonstrated by CT data. The anterior extent is much more difficult to observe because the mandible covers much of the anterior portion. The vomer does, however, taper anteriorly. Most of the ventral edge is broken, and the preserved edge shows no ventral expansion. The contact with the palatine is not clear because the elements are disarticulated.

BRAINCASE

PARABASISPHENOID: The parabasisphenoid (figs. 19, 20, 21) is slightly disarticulated from life position in AMNH FR 30587. It is clearly oriented horizontally, where the basal tubera are in a near horizontal plane with the basipterygoid processes. A horizontally oriented parabasisphenoid occurs in ornithodirans and *Arizonasaurus* (Gower and Nesbitt, 2006) in contrast with the more vertical orientation of the parabasiphenoids of, for example, *Postosuchus* and *Batrachotomus* (Gower, 2002). Moreover, the parabasisphenoid of *Effigia* is extremely elongated anteroposteriorly. The lateral margins between the basipterygoid processes and the basal tubera are laterally waisted (fig. 19). A large rounded, blind depression lies anterior to the basal tubera of the parabasisphenoid and the articulation with the basioccipital—the median pharyngeal recess (e.g., Witmer 1997; Gower 2002). The median pharyngeal recess is not subdivided (figs. 19, 20, 21). There is no obvious thin, low crest between the basal tubera, closely resembling the intertuberal plate in some non-crown-group archosauromorphs (e.g., Gower and Sennikov, 1996; Gower, 1997; Gower and Weber, 1998) and *Arizonasaurus* (Gower and Nesbitt, 2006). However, it may be difficult to compare archosauriforms that have verticalized parabasiphenoids with an intertuberal plate with the horizontally oriented parabasisphenoid of *Effigia* (Gower and Sennikov, 1996). *Effigia* does have a thin lamina of bone that separates the median pharyngeal recess from the basioccipital recess. It is unclear if the thin lamina in *Effigia* is homologous with that of the intertuberal plate in some non-crown-group archosauromorphs.

Foramina for the entrance of the cerebral branches of the internal carotid arteries are not located posteromedial to the base of the basipterygoid processes on the ventral surface of the parabasisphenoid as in *Arizonasaurus* (Gower and Nesbitt, 2006) and non-archosaur archosauromorphs (Benton, 1983; Evans, 1986; Parrish, 1993; Gower and Sennikov, 1996; Gower and Weber, 1998; Gower, 2002). Instead, there are distinct foramina on the lateral surface of the parabasisphenoid for the entrance of the

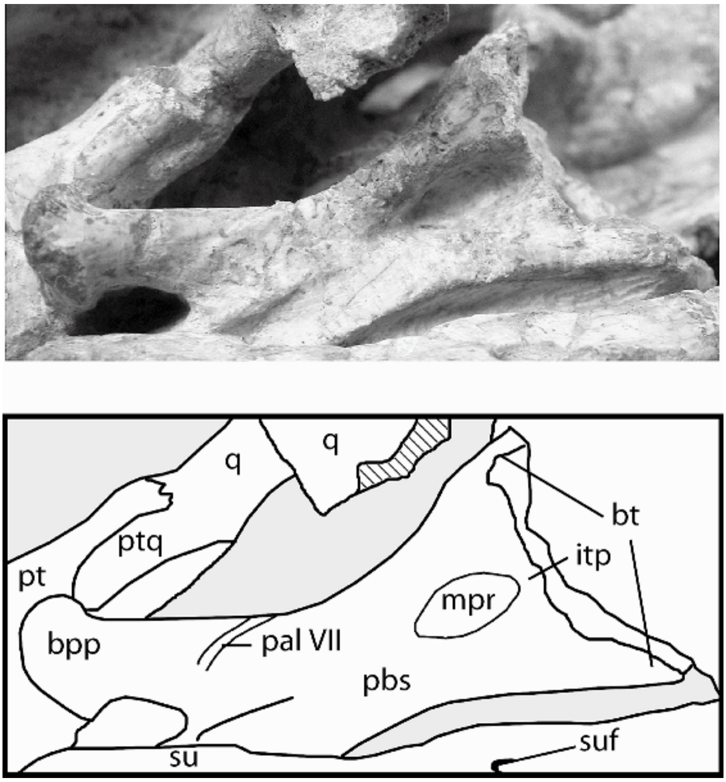


Fig. 19. The parabasisphenoid of *Effigia okeeffeae* (AMNH FR 30587) in ventral view. The small pterygoid process of the quadrate lies on the ventral surface of the pterygoid. Abbreviations are spelled out in appendix 3.

cerebral branches of the internal carotid arteries as in other suchian archosaurs (Parrish, 1993; Gower, 2002). As with *Batrachotomus* (Gower 2002), each foramen lies in a shallow groove that arcs from, presumably, the crista prootica (the prootic is disarticulated) to the posterodorsal edge of the basipterygoid process. However, the groove seems to bifurcate away from the foramina; one groove follows the ventral edge of the parabasisphenoid and the other is oriented posterolaterally toward the basipterygoid processes and the median pharyngeal recess. This division suggests that VII and the palatine branch of the facial nerve may have split here as inferred by Walker (1990) for *Sphenosuchus*.

Chatterjee (1993) reported a lateral position of the foramina for the entrance for the internal carotids on the dorsolateral side of the parabasisphenoid for *Shuvosaurus* (TTUP 9282). The large "pneumatic" openings on the left side of the parabasisphenoid described and illustrated by Chatterjee (1993) are not present on the left side of the same specimen (TTUP 9282). These "pneumatic" features seem to be the result of crushing, preparation, or bone abnormalities. However, AMNH FR 30587 and *Shuvosaurus* (TTUP 9282) share the same system of two grooves on the parabasisphenoid that lead to the foramen that transmitted the cerebral branches of the internal carotid arteries. In lateral view, the basipterygoid processes are the same size as the basal tubera.

A sharp ventral keel of bone separates the left and right basipterygoid processes. The ridge increases in prominence anteriorly. Mandibular bones obscure most of the lateral margins of the parabasisphenoid. The exposure of the left lateral side shows that the parabasisphenoid is rather deep and concave. The basipterygoid processes are anteriorly elongated and smoothly convex at their articular surfaces.

CT data indicate the posterior lateral wall of the parabasisphenoid is extremely thin (figs. 20, 21) and thickens anteriorly. A pair of fossae divided by a thin lamina at the midline is located at the anterior margin of the main body of the parabasisphenoid (fig. 20) just anterior to the base of the basipterygoid processes and dorsal to the small midline projection of the parabasisphenoid. The fossae are external, open anteriorly, and are divided by a thin lamina of bone projecting from the ventral margin of the cultriform process to the anteroventral margin of the parabasisphenoid. The fossae are blind and seem to be nonpneumatic. These fossae are known only in *Shuvosaurus* (TTUP 9282) and *Effigia*; however, CT data are not available for many basal archosaur taxa. Chatterjee (1993) considered these to be pneumatic cavities in his description of the parabasisphenoid of *Shuvosaurus* but did not provide any justification.

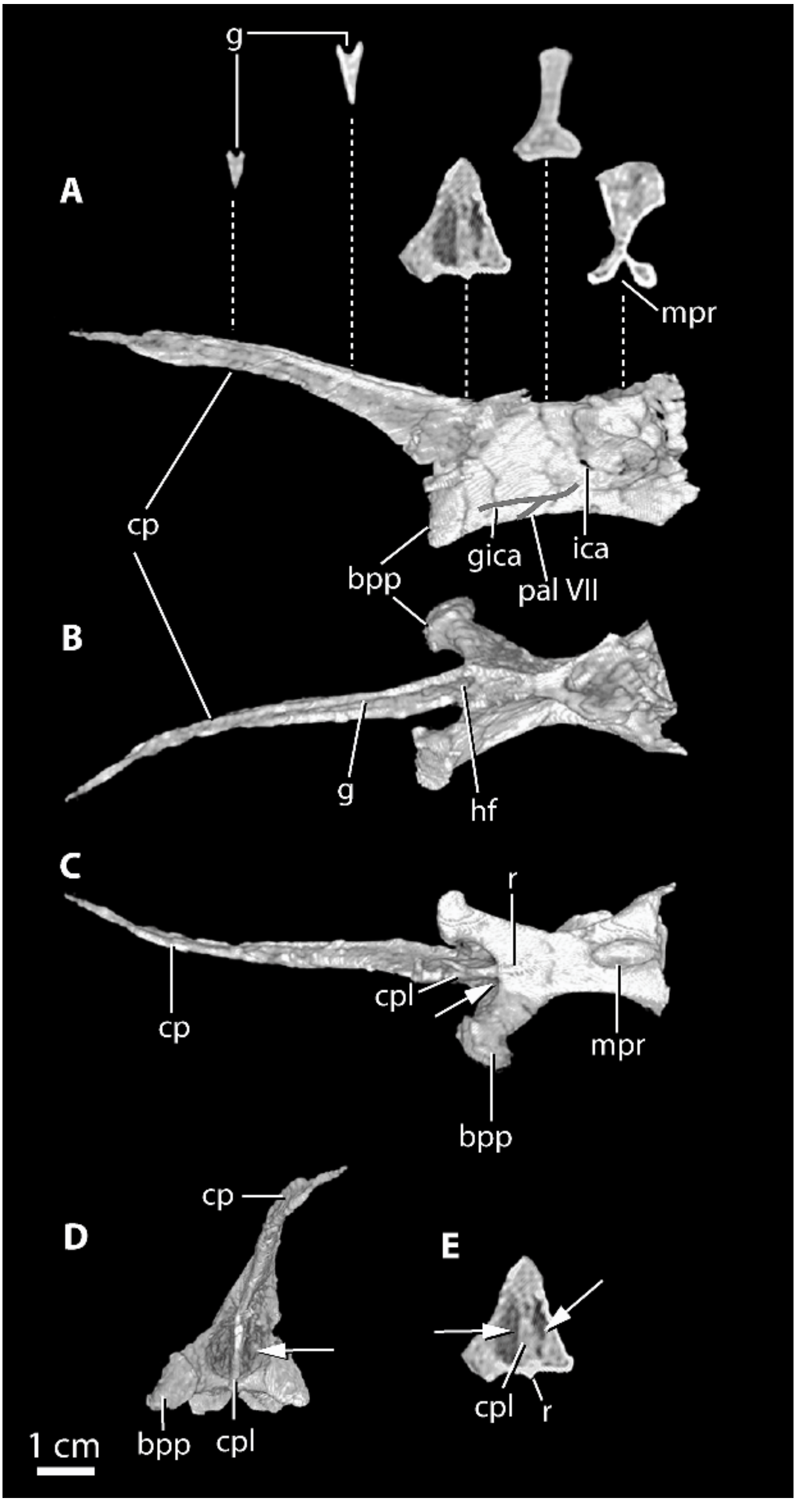
The cultriform process of the parabasisphenoid is completely preserved in AMNH FR 30587 (fig. 20). It is long, slender, and pointed and is tallest about one-third of the length from the base. CT data indicate that the tip of the cultriform process reaches a point level with the posterior extent of the antorbital fenestra. The dorsal surface bears an anteroposteriorly directed groove along its entire length. A small ventrally deep fossa, the hypophyseal (pituitary) fossa, lies at the posterior extent of the groove where the cultriform process meets the body of the parabasisphenoid. The lateral surfaces of the base of the cultriform process carry no clear grooves that might have carried the palatine branch of the facial nerve similarly to *Arizonasaurus* (Gower and Nesbitt, 2006). Both *Batrachotomus* and *Postosuchus* have grooves on the lateral surfaces of the base of the cultriform process (Gower, 2002).

BASIOCCIPITAL: The basioccipital (fig. 22) was discovered dorsal to the left orbit, disarticulated from the rest of the braincase. The occipital condyle is crescent shaped in posterior view. The region between articulations with the exoccipitals is concave in two directions, anteroposteriorly and mediolaterally. The mediolateral concave region indicates that the foramen magnum was large and that, ventrally, the exoccipitals did not meet along the midline. The exoccipitals meet in the following early archosaurian taxa: *Postosuchus*, *Batrachotomus*, *Arizonasaurus*, *Tikisuchus*, *Saurosuchus* (“rauisuchians”), *Euparkeria* (archosauriform), *Desmatosuchus haplocerus* (TTUP 9024) and *Stagonolepis* (stagonolepidids), and *Silesaurus* (ornithodiran). The exoccipitals are separated in crocodylomorphs (Walker, 1990; Clark et al., 2000) and theropods. The ventral extent of the foramen magnum opens into a basin anteriorly divided by a thin midline lamina. This basin was hypothesized by Chatterjee (1993) to hold the pons Varolii. Lateral to the basin, two well-defined pockets lie side by side (fig. 22). The more anterior pocket is interpreted as the cochlear recess and the more posterior pocket is interpreted as the metotic foramen.

The basal tubera of the basioccipital are weakly developed and lie directly anterior to a horizontal plane created by the occipital condyle. A deep fossa, the basioccipital recess, deepens anteriorly between the tubera and terminates in a deep pit at the anterior margin of the basioccipital. The area between the occipital condyle and the basal tubera is concave in the mediolateral direction.

The basioccipital sat on the larger parabasisphenoid so that the parabasisphenoid tubera surround the basal tubera of the basioccipital when in natural articulation. It appears that a small unossified gap may exist at this contact similar to *Shuvosaurus* (TTUP 9282), *Postosuchus* (TTUP 9002), and *Batrachotomus* (SMNS 80260). A ventrally directed lamina separates the fossa between the basitubera of the basioccipital and the median pharyngeal recess.

LATEROSPHENOID: Both laterosphenoids (fig. 12) are in articulation in AMNH FR 30587. CT data indicate the left laterosphenoid is slightly displaced medially, causing a “caving in” of the anterior portion of the braincase (fig. 21A). Additionally, CT data show that the right laterosphenoid is crushed dorsoventrally. As a result, the anteroposteriorly directed ridge is a result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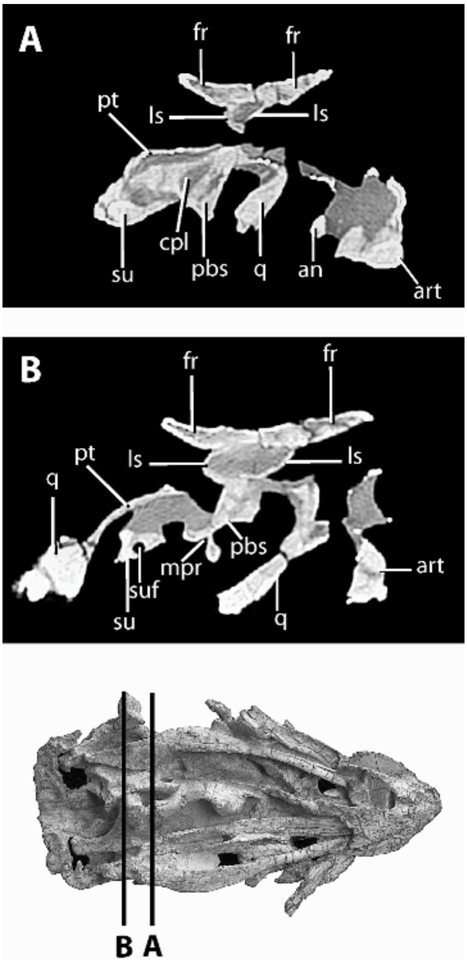

Fig. 21. CT data of *Effigia okeeffeae* (AMNH FR 30587) highlighting two fossae in the parabasisphenoid (**A**; slice 379 of 543) and the thin lamina between the left and right lateral surfaces of the parabasisphenoid (**B**; slice 417 of 543). The ventral view of the skull indicates where the CT slices were taken. Abbreviations are spelled out in appendix 3.

of crushing. The posterior portion of the laterosphenoid articulated with the postorbital in a manner similar to that of most archosaurs. The internal surface of the laterosphenoid is concave and the external surface is convex. The laterosphenoid lies at the medial edge of the ventral optic fossa of the frontal. The dorsal margin articulates with the parietal posteriorly and the frontal anteriorly. Apparently, the posteroventral end of the laterosphenoid is sandwiched between a medial and a lateral anterior process of the parietal. However, this associ-

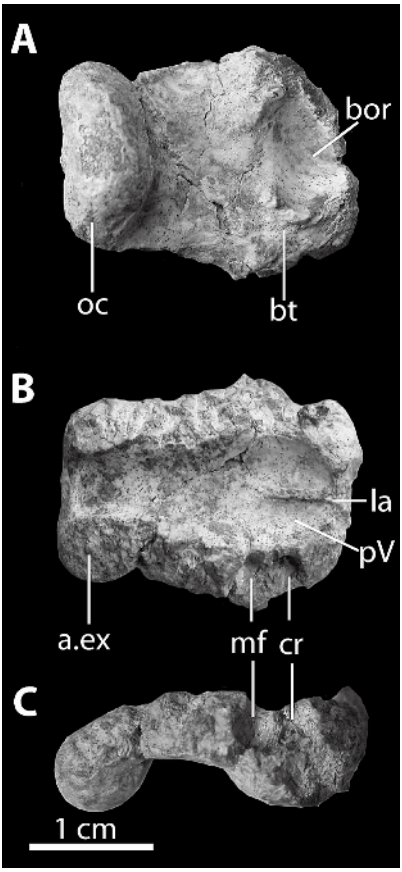

Fig. 22. The disarticulated basioccipital of *Effigia okeeffeae* (AMNH FR 30587) in ventral (**A**), dorsal (**B**), and left lateral (**C**) views. Abbreviations are spelled out in appendix 3.

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Fig. 20. The parabasisphenoid of *Effigia okeeffeae* (AMNH FR 30587) compiled from CT data in lateral (**A**), dorsal (**B**), ventral (**C**), and anterior (**D**) views and a slice through the anterior lamina separating two deep fossae (**E**). Individual slices and their position along the parabasisphenoid are shown above. The arrows indicate the large fossae at the anterior portion of the parabasisphenoid. Abbreviations are spelled out in appendix 3.

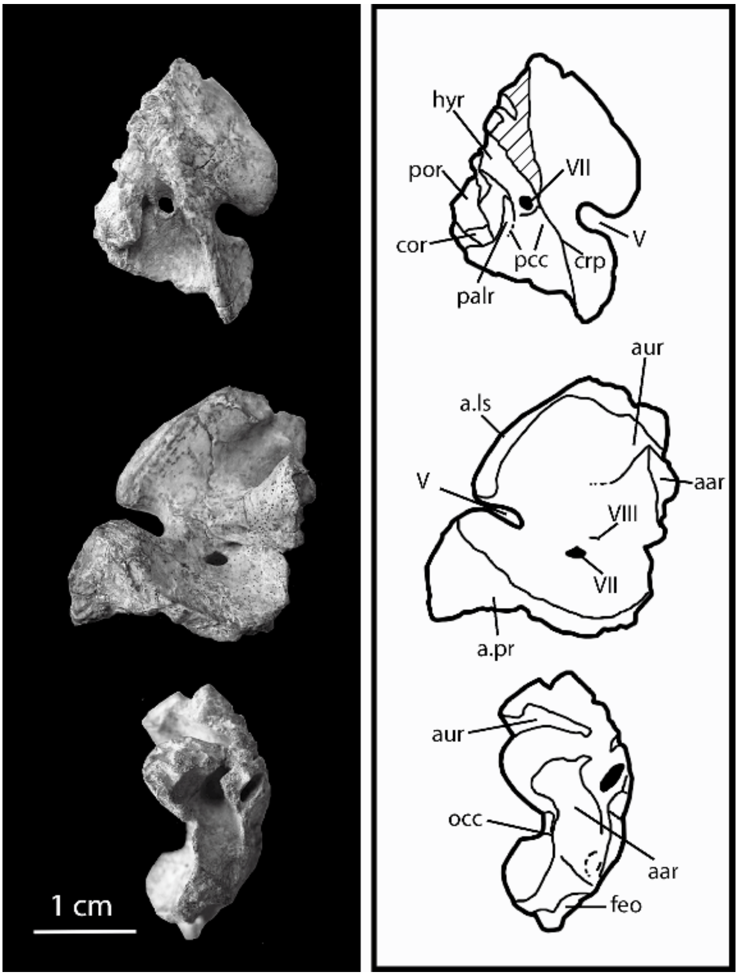

Fig. 23. The prootic of *Effigia okeeffeae* (AMNH FR 30587) in lateral (**A**), medial (**B**), and anterior (**C**) views. Abbreviations are spelled out in appendix 3.

ation may have been artificially caused by crushing. A lateral ridge located medial to the postorbital–squamosal bar possibly is homologous to the cotylar crest described for basal archosauriforms by Clark et al. (1993). The dorsal margin of the cotylar crest contacts the medial edge of the optic fossa of the frontal. A lateral foramen of the left laterosphenoid observed only in CT data is interpreted as the foramen for nerve IV because of the similar position to that of other archosaurs. The dorsoventral crushing of the right laterosphenoid artificially closed the foramen for nerve IV. The left and right laterosphenoid converge and taper anteriorly.

The flat bone that Chatterjee (1993) identifies as the laterosphenoid in *Shuvosaurus* is featureless and not as anteroposteriorly elongated. The large lateral processes originally illustrated by Chatterjee (1993; fig. 5G,H) for *Shuvosaurus* are missing or lost.

PROOTIC: Both prootics (fig. 23) of AMNH FR 30587 were recovered. The right prootic was lodged in the right orbit and the left prootic was between the distal ends of the quadrates. Here, I describe the external and internal surfaces separately.

A posterior projecting and tapering tongue of the prootic overlaps the opisthotic at the base of the paroccipital process, as in a wide range of diapsids. The posteriormost end would have formed a well-defined suture with the opisthotic as evidenced by the rough internal surface and the presence of well-defined suture between the prootic and the opisthotic of *Shuvosaurus* (TTUP 9282).

A distinct ventrolateral ridge bisects the prootic. This ridge, termed the crista prootica for a comparable feature in lizards (Versluys, 1898), is described by Walker (1990) as "the flange" for *Sphenosuchus*. Gower and Sennikov (1996) suggest that this is the area for attachment of the m. protractor pterygoidei. The posterior part of the crista prootica is incompletely preserved, but forms the anterior border of the fenestra ovalis. The posterior edge would have contacted the opisthotic. Moving ventrally along the border between the prootic and the opisthotic, a small posterior-facing concavity is interpreted as part of the cochlear recess. Here the prootic is at its thickest. This same part of the cochlear recess is present in the exact same position as in *Sphenosuchus* (SAM 3014; Walker, 1990). The portion of bone with part of the cochlear recess is directed ventrolaterally, similar to the crista prootica.

A deep convex triangular area created between these two (part of the cochlear recess and crista prootica) structures was termed the postcarotid recess by Walker (1990). At the dorsal tip of the triangle, a circular foramen is surrounded by a raised rim of bone. This foramen is interpreted as the opening for facial nerve (VII). The facial nerve is set in a prominent groove for the hyomandibular branch of this nerve. The well-defined groove proceeds dorsally and posteriorly over the fenestra ovalis, identical to the condition described for *Sphenosuchus* (SAM 3014; Walker, 1990). A small notch on the anterolateral edge of the rim surrounding the opening for the facial nerve (VII) allows the palatine branch of the facial nerve (VII) to pass anteroventrally. Thin laminae of bone surround the raised rim around the opening of the facial nerve (VII). These laminae form small fossae, the precochlear cavities, that were interpreted by Walker (1990) in *Sphenosuchus* to represent pneumatic features. It is not clear if the small shallow cavities in *Effigia* are homologous to those of *Sphenosuchus* or are even pneumatic features.

Openings for cranial nerves VII and VIII lie adjacent to each other on the internal surface of the prootic. Cranial nerve VIII projects dorsally to pass through the anterior ampullary recess and is much smaller than the opening for VII. Cranial nerve VII pierces the prootic and passes through into the postcarotid recess.

One-half of the auricular recess is formed by the prootic and the other, presumably, by the epiotic/supraoccipital. This is the case in *Shuvosaurus*, *Sphenosuchus* (Walker, 1990), and *Batrachotomus* (Gower, 2002), but possibly not in *Arizonasaurus* (Gower and Nesbitt, 2006). The trigeminal foramen forms a well-defined notch in the prootic, and it would have been completed by the laterosphenoid. It seems that there is only one large opening for the trigeminal and the passing blood vessels. It is unlike the division of the trigeminal foramen into two distinct openings (e.g., *Stagonolepis* Walker, 1990; Gower and Walker, 2002) or into two distinct but connected openings (e.g., *Sphenosuchus* Walker, 1990).

The articular surface with the laterosphenoid is oriented anterodorsally. This is the case in non-crown-group archosaurs as reported by Gower and Sennikov (1996) and with *Arizonasaurus* (Gower and Nesbitt, 2006), *Saurosuchus* (Alcober, 2000), *Sphenosuchus* (Walker, 1990), and *Batrachotomus* (Gower, 2002). The laterosphenoid–prootic contact of *Desmatosuchus haplocerus* (TTUP 9024) is oriented almost completely anteroposteriorly (Small, 2002). The prootic is thickest at its contact with the laterosphenoid.

In contrast with *Batrachotomus* and *Arizonasaurus*, the anterior ampullary recess lies entirely within the bone. The anterior temporal foramen present in *Sphenosuchus* is absent in *Effigia*. Also, there is no evidence that the quadrate contacted the prootic, a character used by Gower (2002) and others to unite crocodylomorphs.

In anterior view, the anterior ampullary recess and the semicircular canal are visible (fig. 23). The foramen for cranial nerve VI does not look like it pierces the prootic in the same location as in *Arizonasaurus* and *Batrachotomus*, but seems to pierce the parabasisphenoid as in crocodylomorphs and birds.

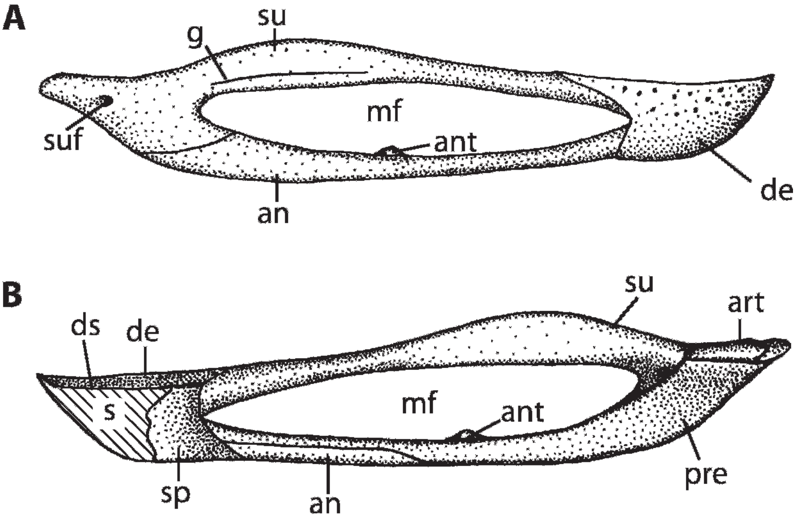

Fig. 24. Reconstructions of the mandible of *Effigia okeeffeae* in lateral (**A**) and medial (**B**) views. Abbreviations are spelled out in appendix 3.

Mandible: A lateral reconstruction (fig. 24) of the mandible shows that this structure in *Effigia* is strongly modified relative to other archosaurs. The surangular, angular, and prearticular are anteriorly elongated and the dentary is anteriorly foreshortened. The cutting surface of the mandible is restricted to the dentary. The extent of the splenial and coronoid is uncertain. Additionally, the articulation among the dentary and the surangular, angular, and prearticular is covered in all available specimens.

Dentary: The left and right dentaries (fig. 25) are present in AMNH FR 30587 and the right dentary is present in AMNH FR 30589. Both dentaries of AMNH FR 30587 are compressed dorsoventrally, so that the medial surface cannot be observed. The dentary is restricted to the anterior end of the mandible, representing approximately one-fourth of its total length. The posterior edge, half way between the dorsal and ventral edges, creates the anterior border of the mandibular fenestra. A thin, long process originating at the anterodorsal border lies on the lateral surface of the surangular for 3.5 cm. The anterior end is slightly rounded. The dorsal cutting surface is restricted to the areas that occlude with the premaxilla and the anterior half of the maxilla. There is no ventral expansion at the anterior end of the dentary as in large and small specimens of *Postosuchus* (TTUP 9002), *Batrachotomus* (SMNS 80260), and *Dromicosuchus* (UNC 15574). However, Gower (1999) notes that the ventral expansion is less apparent in the larger specimens of *Batrachotomus*. The dorsal occlusal edge is anteroposteriorly horizontal, just like the premaxilla and maxilla. The external surface is speckled with small fenestrae that open dorsally and/or anteriorly. As with the premaxilla, the external surface of the dentary indicates that it may have had a rhamphotheca covering them in life. CT data indicate a medial shelf is present between the left and right elements (fig. 7), similar to *Shuvosaurus* (TTUP 9280).

The joint between the left and right dentary is similar to that of crocodylians, *Shuvosaurus* (TTUP 9280), and possibly *Lotosaurus*. *Effigia*, *Shuvosaurus*, *Lotosaurus*, and *Alligator* share the posterior expansion of the suture between the left and right elements, and a strongly rugose articular surface as evidenced by AMNH FR 30589. The dentaries of *Postosuchus*, *Batrachotomus*, *Saurosuchus*, *Arizonasaurus*, *Hesperosuchus*, and *Dromicosuchus* do not have anteroposteriorly expanded articulations between the

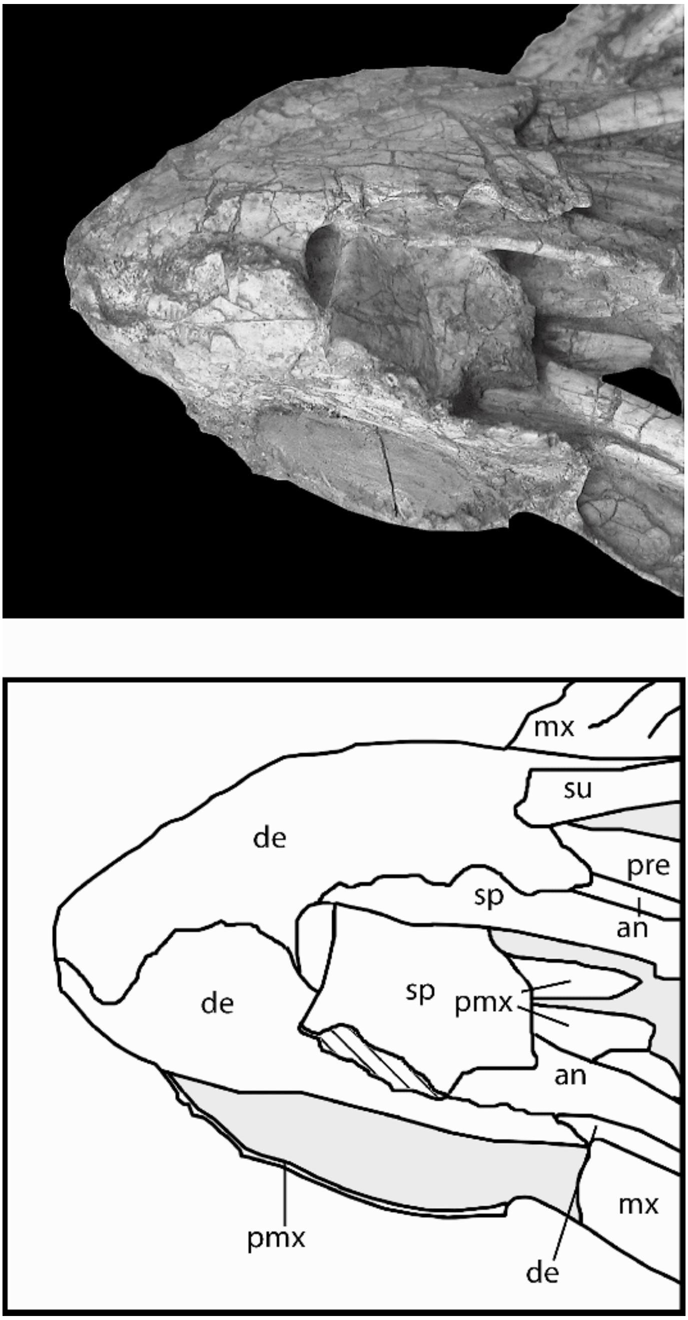

Fig. 25. The dentary, in ventral view, of *Effigia okeeffeae* (AMNH FR30587) in articulation with the mandibular elements. Abbreviations are spelled out in appendix 3.

left and right dentaries. *Effigia* has a small groove at the posterior side of the shelf formed by the left and right dentaries.

The foreshortening of the dentary does not occur in any basal archosaur other than *Shuvosaurus* (TTUP 9280). Moreover, an edentulous dentary is only known in one other basal archosaur, *Lotosaurus*. The dentary of *Shuvosaurus* (TTUP 9280) is slightly longer than that of *Effigia*.

PREARTICULAR: The prearticular (fig. 26) is out of articulation in AMNH FR 30587 and in articulation in AMNH FR 30589. The posterior portion expands dorsoventrally and terminates as a cradle for the articular on the medial side. Here the bone is thinnest. Moving anteriorly just ventral to the anteriormost extent of the angular surangular suture, the prearticular forms both the ventral edge of the mandible and the ventral edge of the mandibular fenestra. Anterior to that, the prearticular twists and becomes compressed dorsoventrally, but is still closely appressed with the angular. The anterior portion gradually thins anteriorly and possibly does not reach the dentary. The anterior-most tip is unknown in all specimens. The general morphology reflects that of *Batrachotomus*, *Postosuchus*, and *Arizonasaurus* except that the anterior portion is much more elongated in *Effigia*.

SURANGULAR: Both surangulars (figs. 5, 15, 26) are preserved articulated in AMNH FR 30587 and a three-dimensionally prepared left surangular is present in AMNH FR 30589. As with the angular and prearticular, the surangular is much elongated, stretching from the articular to the dentary. The surangular forms the entire dorsal border of the mandibular fenestra, where the edge of the surangular is sharp. In lateral view, dorsal to the mandibular fenestra, the surangular is dorsoventrally expanded posteriorly relative to the anterior portion. Consequently, the posterior portion is more platelike in cross section than the more rounded anterior portion. The lateral surface bears a longitudinal groove located dorsal to the mandibular fenestra that may have held either blood vessels or nerves or both. *Effigia* differs from *Batrachotomus*, *Postosuchus*, and *Arizonasaurus* in lacking a thick ridge running parallel to the dorsal margin. Anteriorly, a small posterior process of the dentary covers the lateral surface of the surangular.

Posterior to the mandibular fenestra, the surangular is platelike and forms the posterior border of the mandibular fenestra. A small process of the surangular narrowly contributes to the ventral border of the mandibular fenestra, just dorsal to the contact with the angular. In AMNH FR 30587, separation between the angular and surangular indicates that the angular forms only a small portion of the lateral surface of the posterior mandible. In AMNH FR 30589, the angular and surangular are firmly appressed together with a visible suture.

The surangular expands medially to form a small shelf between the mandibular fenestra and the contact with the articular surface of the articular. The surangular contributes to the mandibular glenoid adjacent to the portion formed by the articular. The surangular portion is concave in contrast with the fully convex articular. The large contribution of the surangular to the mandible also occurs in *Sphenosuchus* (SAM 3014; Walker, 1990) and, to a much lesser extent, in *Batrachotomus* (SMNS 80260; Gower, 1999). An anteroposteriorly directed suture is formed between the articular and the surangular in the glenoid. Additionally, the lateral edge is raised and rounded relative to the articular region of the surangular. The surangular terminates in a gently rounded, thickened process. AMNH FR 30589 shows that this process fits into a groove in the articular (fig. 26).

A large surangular foramen is located on the lateral surface ventral to the articulation with the quadrate. The foramen projects anteromedially/posterolaterally. The other opening of the foramen is located on the medial side of the surangular posterior to the mandibular fenestra (fig. 26). This foramen occurs in *Shuvosaurus* (TTUP 9280), but is absent in *Postosuchus*, *Batrachotomus*, *Saurosuchus*, parasuchians, or crocodylomorphs. It is uncertain whether *Arizonasaurus* has a surangular foramen (Nesbitt, 2005a). The foramen is present in at least two stagonolepidids (*Longosuchus* and *Desmatosuchus haplocerus*, TTUP 9024), *Revueltosaurus*, *Euparkeria*, *Herrerasaurus*, and all theropods.

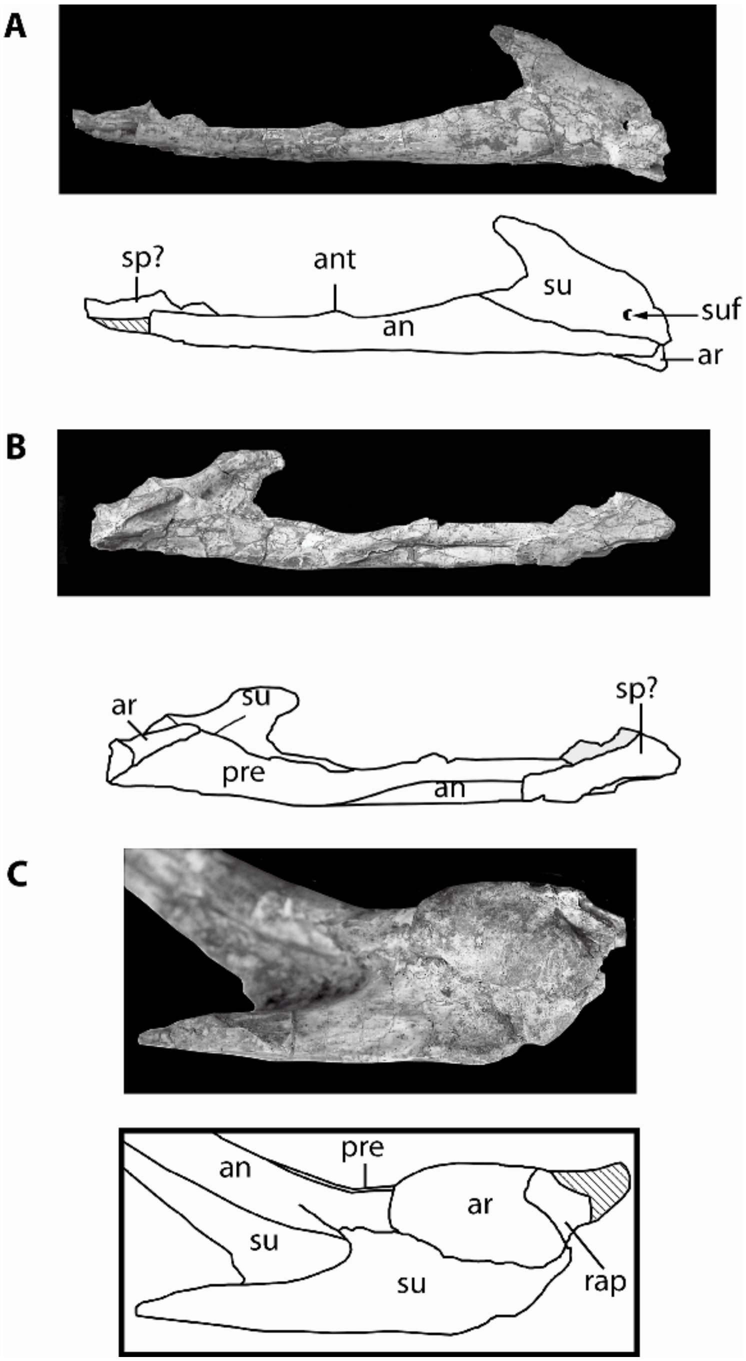

Fig. 26. Three-dimensionally prepared mandible of *Effigia okeeffeae* (AMNH FR 30589). (**A**) lateral view. (**B**) medial view. (**C**) dorsal view of the articular. Abbreviations are spelled out in appendix 3.

ANGULAR: The left angulars are preserved in AMNH FR 30587 (fig. 5) and AMNH FR 30589 (fig. 26). The angular and prearticular form the ventral border of the mandibular fenestra. The posterior portion expands mediolaterally and meets the surangular at a suture. A small splint of the angular proceeds toward the posterior end of the mandible. In cross section, the shaft of the angular is D-shaped, where the flat side faces dorsally. The anterior end is covered by the dentary. A thickened knob (fig. 26: ant) is present on the dorsal surface one-third of the length of the element from the posterior edge of the mandibular fenestra. This knob may be autapomorphic for *Effigia*; however, the area is not preserved in any specimen of *Shuvosaurus*.

CORONOID: An anteroposteriorly elongate bone abutting the medial surface of the right surangular of AMNH FR 30587 may be the coronoid. If so, the coronoid stretches from the dentary to the midpoint of the mandibular fenestra. The posterior portion suggests that the coronoid was elongated like that of *Sphenosuchus* and other crocodylomorphs.

SPLENIAL: Both splenials (fig. 25) are known from AMNH FR 30587. The left splenial is in articulation and the right is disarticulated from the mandible. The platelike splenial is as deep dorsoventrally as the dentary and is about half the anteroposterior length as the dentary. The dorsal shelf created by the articulation of the left and right dentaries excludes the splenial from the anterior part of the mandible. The ventral edge is rounded and tapers anteriorly.

ARTICULAR: Both articulars (figs. 15, 26) are known in AMNH FR 30587 and AMNH FR 30589. The articular is sandwiched between the surangular and the prearticular. The surangular excludes the articular from participating in the lateral surface of the mandible, and the prearticular excludes most of the articular from participating in the medial surface. The articulation with the surangular follows the extent of the convex articular surface in dorsal view. The surangular sits in a lateral groove of the articular.

The dorsal articular surface is completely convex and corresponds to the concave articular surface of the quadrate. This differs from all other archosaurs except *Shuvosaurus*. The crux of the concave articular surface is directed anteromedially. A deep fossa lies under the posterior edge of the articular surface. The fossa opens posteriorly to a concave dorsal margin of the retroarticular process. The termination of the retroarticular process arcs slightly dorsally and medially. This morphology is similar to the retroarticular process of *Arizonasaurus* (MSM 4590; Nesbitt, 2005a). The ventral surface of the articular is flat.

The morphology of the articular is generally simplified compared to other archosaurs. The articulars of *Revueltosaurus*, *Batrachotomus*, *Postosuchus*, *Arizonasaurus*, *Tikisuchus*, and *Rauisuchus* all share the presence of a medial process with a piercing foramen. The articular of *Effigia* and *Shuvosaurus* (TTUP 9280) is more similar to that of stagonolepidids, as evidenced by the reduced retroarticular process and the absence of a medial process. However, the convex articular surface for the quadrate is completely convex, a character only present in *Effigia* and *Shuvosaurus* (TTUP 9280).

POSTCRANIAL SKELETON

AXIAL: I use Wilson's (1999) vertebral laminae terminology to described the cervical and dorsal vertebrae of crocodile-line archosaurs following suggestions from Wilson (1999) for "rauisuchians" and Parker (2003) for other basal archosaurs (i.e., stagonolepidids) and Nesbitt (2005a) for the pseudosuchian *Arizonasaurus*.

CERVICAL VERTEBRAE: The cervical vertebrae are represented by parts of the atlas (fig. 27), an anterior cervical (fig. 28C,D), a mid- to posterior cervical (fig. 28A, D), and two cervicodorsal vertebrae (fig. 29) in articulation with the anterior dorsal vertebrae from AMNH FR 30587 and three anterior to midcervical vertebrae from AMNH FR 30589. The atlas is represented by the intercentrum and both neutral arches. The intercentrum is saddle shaped in anterior or posterior view. The raised dorsolateral surfaces articulated with the ventral articulation surface of the neural arch. The ventral surface bears a groove running mediolateral

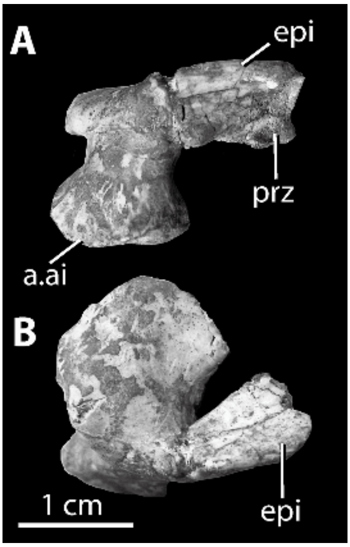

Fig. 27. The left neural arch of the atlas of *Effigia okeeffeae* (AMNH FR 30587) in lateral (**A**) and dorsal (**B**) views. Abbreviations are spelled out in appendix 3.

across the length of the element. A small, deep fossa is located at the midline, just anterior to the groove; it opens posteriorly. The ventral surface anterior to the groove is gently rounded anteriorly.

The right and left neural arches of the atlas (fig. 27) were found next to the skull of AMNH FR 30587. The ventral articular surface is divided in two, an anterior part and a posterior part. The anterior part slants in the anterodorsal/posteroventral direction. The posterior part is anteroposteriorly flat. The mediodorsal process is circular in dorsal view. Anteriorly, there is a depression between the anteroventral articulation surface and the mediodorsal process. The ventral surface of the mediodorsal process is concave. Furthermore, the medial edge of the mediodorsal process thins and there is no rugose suture area between the two halves of the neural arches. The posterior process is essentially a postzygapophysis with a large epipophysis on the dorsal surface. The ventral surface is flat and the edges taper into a blade.

The anterior cervical vertebra is well preserved (fig. 28C, D). Both the anterior and posterior articular ends are deeply concave. The neurocentral suture is visible in lateral view. The diapophysis is large and the articular surface is circular. The diapophysis articular surface is much smaller than the parapophysis articular surface. The parapophysis is located on the anteroventral surface of the centrum and grades anteriorly into the face of the centrum. The articular surface of the parapophysis is concave. The centrum is flat on the ventral surface where the parapophyses originate. The posterior portion of the centrum is rounded. Overall, the centrum is more dorsoventrally compressed than the posterior cervical and dorsal vertebrae, but remains the same length. The ventral surface bears a weak midline keel.

Additionally, one of the anterior cervicals from AMNH FR 30589 bears pleurocoel-like depressions on the posterolateral portion of the centrum. The pleurocoel-like feature is a fossa with a distinct rim of bone surrounding it, which complies with Britt's (1992) definition of a true pleurocoel. However, the distinct rim of bone does not enclose a pocket, so the presence of a true pleurocoel is ambiguous. A cervical vertebra with a pleurocoel was also found isolated among *Coelophysis* material. Many *Shuvosaurus* cervical vertebrae also have the same pleurocoel-like feature. Additionally, *Sillosuchus* has very similar features in all of the cervical vertebrae (Alcober and Parrish, 1997). However, the pleurocoels in *Sillosuchus* are better defined than in *Effigia* and *Shuvosaurus*, and nearly all of the pleurocoels are surrounded by a rim of bone enclosing a pocket. The pleurocoel-like features present in *Effigia* and *Shuvosaurus* are very similar to those on the posterior portion of anterior cervical centra of coelophysoids (Rauhut, 2003) and cannot be differentiated; the pleurocoels in *Sillosuchus* are much more like sauropods (Wedel et al., 2000) and more derived theropods.

The morphology of the anterior vertebra indicates that the neck was elongated more like that of a theropod than that of *Postosuchus* or *Batrachotomus*. The neck of *Effigia* is not like the progressively anteriorly elongated neck of *Arizonasaurus* (Nesbitt, 2003, 2005a); all of the cervical vertebrae, though elongated relative to those of *Postosuchus* and *Batrachotomus*, are about the same length.

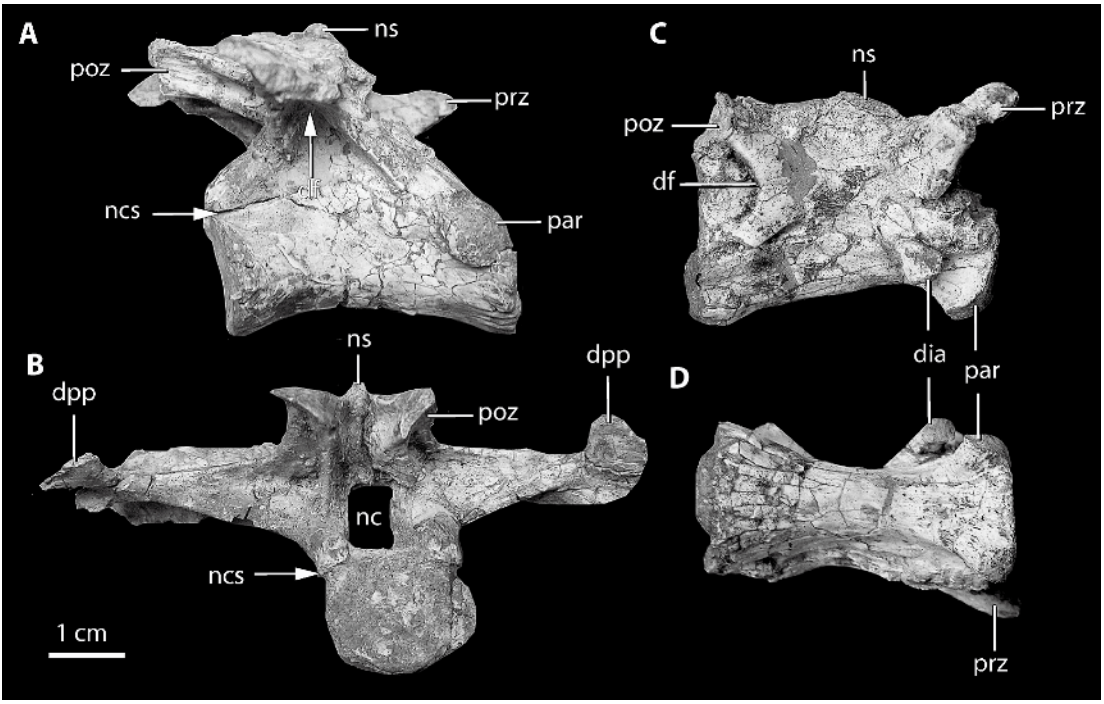

Fig. 28. Cervical vertebrae of *Effigia okeeffeae* (AMNH FR 30587) including a posterior cervical vertebra in lateral (**A**) and posterior (**B**) views and an anterior cervical vertebra in lateral (**C**) and ventral (**D**) views. The posterior cervical vertebra does not have pleurocoels and the anterior cervical vertebra has a small depression on the posterior portion of centrum. However, this depression is not a true pleurocoel. *Effigia* and *Shuvosaurus* have pleurocoels only on the midanterior cervical vertebrae. Abbreviations are spelled out in appendix 3.

The only apparent difference between the cervical vertebrae of *Shuvosaurus* and *Effigia* is that the *Shuvosaurus* cervicals have a much better defined ventral midline keel on the centrum. However, this may result from individual variation, because not all of the *Shuvosaurus* vertebrae have the well-pronounced ventral keels.

The mid- to posterior cervical of AMNH FR 30587 (fig. 28A, B) was prepared three dimensionally like the anterior cervical. The centrum is rounded and lacks a ventral keel. The parapophyses are gently raised from the surface of the centrum, project laterally, and are separated from the articular surface of the centrum. The articular surfaces of the diapophyses are not preserved. Each diapophysis is connected to the centrum by four laminae: (1) the prezygadiapophyseal lamina connects to the prezygapophysis; (2) the postzygadiapophyseal lamina connects to the postzygapophysis; (3) the posterior centrodiapophyseal lamina connects to the posterior end of the centrum; (4) the paradiapophyseal lamina connects to the parapophysis. These laminae define three deep fossae. All of the fossae meet in the center of the vertebra beneath the neural arch and a small shallow fossa at the base of the neural arch. All of the deep fossae and thin laminae create a weak point here. The neural spine is very short. This configuration of the four laminae is also present in *Arizonasaurus* (MSM 4590), *Poposaurus* (CFMNH UR357), *Postosuchus* (TTUP 9002), and *Fasolasuchus* (PVL 3850). The neural spine is very short.

The postzygapophyses and prezygapophyses are slightly concave. The neural arch is short and is located over the center of the centrum. The diapophysis is incomplete, but the preserved portion indicates that it was

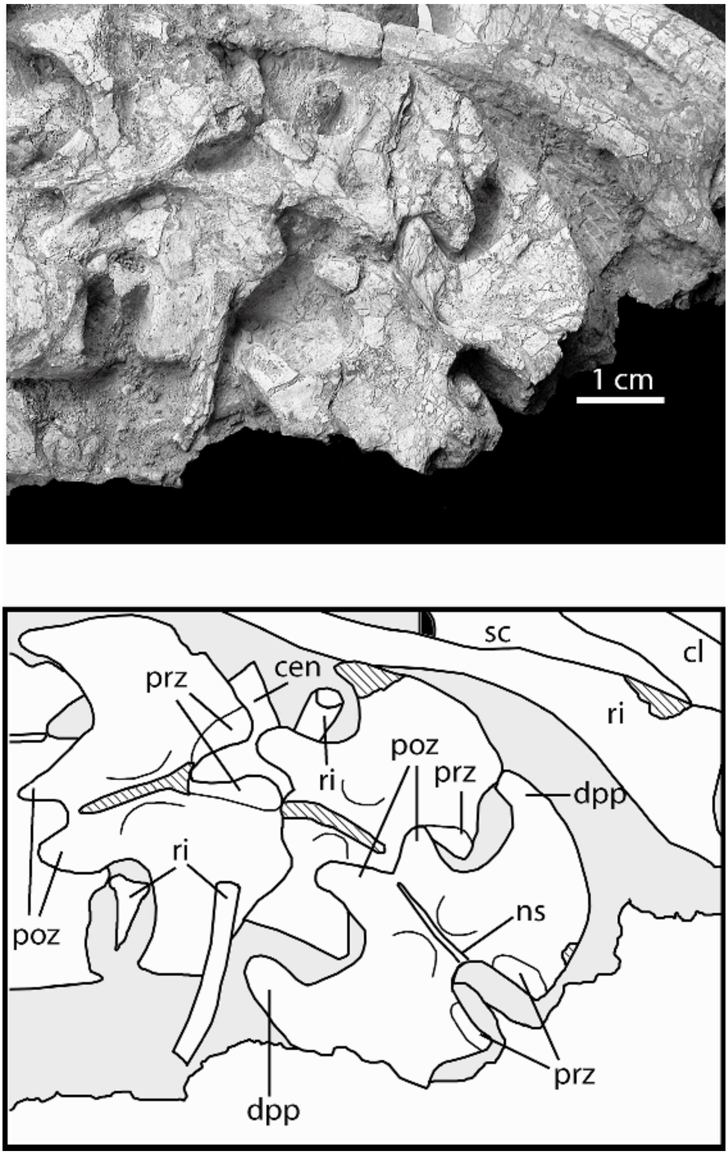

Fig. 29. Articulated dorso-cervical series (AMNH FR 30587) in dorsal view. The scapula is located on the backside of the articulated dorso-cervicals. A possible fragment of a left clavicle is present in the upper left corner. Abbreviations are spelled out in appendix 3.

anteroposteriorly expanded like that of the posterior-most cervicals. Small posteriorly directed diapophyses are present (fig. 29).

The posterior cervicals are in articulation with the anterior-most dorsal vertebrae. Unfortunately, only a dorsal view of the posterior cervicals is available (fig. 29). The transverse processes of the anterior dorsal vertebrae expand posterolaterally (fig. 29). The transverse processes bear a posteriorly directed process on the posterolateral margin. The prezygapophyses lie directly on the transverse process. The postzygapophyses are shorter than those of the anterior cervical.

The short neural spines are located over the center of the centrum like that of the posterior dorsal vertebrae.

DORSAL VERTEBRAE: A series of articulated anterior dorsal vertebrae of AMNH FR 30587 (fig. 29) indicates the transverse processes change posteriorly along the dorsal series. Like the posterior cervical vertebrae, the anterior dorsal transverse processes expand posterolaterally (fig. 29). Furthermore, both the anterior dorsal vertebrae and the posterior cervical vertebrae share a posteriorly directed process on the posterolateral edge on the transverse process and the neural spines are also short, like that of the posterior dorsal vertebrae.

Although the dorsal vertebrae of *Shuvosaurus* are known only from centra, they do share some characteristics with *Effigia*, including dorsoventrally compressed centra, pronounced centrum rims, a radiating pattern of small ridges directed from the edge of the centrum rim toward the center of the centrum, amphicoelous centra, and shallow fossae between the body of the centra and the neurocentral canal. The poorly preserved dorsal vertebrae of *Sillosuchus* exhibit the same characters as *Shuvosaurus* and *Effigia*, but appear to have true pleurocoels in the centrum (see Britt, 1993; Wedel, 2000).

Effigia and *Shuvosaurus* isolated centra cannot be differentiated from those of early theropod dinosaurs (Nesbitt et al., in press). This similarity has led some authors (e.g., Hunt et al., 1998) to assume all of these “theropod” vertebrae represent only theropods and that theropod dinosaurs were rather common in the Late Triassic of North America (see Nesbitt et al., in review).

Four articulated dorsal vertebrae and associated ribs from the midregion of AMNH FR 30587 were recovered that are believed to have articulated with the dorsal vertebrae articulated with the sacrum (fig. 30). The articulated state of all the other remains of AMNH FR 30587 suggest that the connecting dorsal vertebrae between the four articulated and the last two dorsal vertebrae were lost during excavation in 1947. Therefore, the exact position of the four dorsal vertebrae cannot be determined. All four centra have been separated from their respective neural arches. However, the neural arches remain in a state of quasi-articulation. The centra are much more dorsoventrally compressed than the last two dorsal vertebrae. The centra faces are oval, with the long axis running mediolaterally. Still, the centra are markedly amphicoelous, have centra rims that are pronounced, and have the same radiating pattern of small ridges directed from the edge of the centrum rim toward the center of the centrum as the posterior-most dorsal vertebrae. The fossa between the centra body and the neurocentral suture is similar in depth to that of the last two dorsal vertebrae. None of these centra have ventral keels.

The dorsal neural arches are well preserved, but disarticulated from the centra. Like the posteriormost dorsal vertebrae, the same four major laminae—(1) the thin posterior centroparapophyseal lamina (pcpl; connects posterior portion of the centrum to the parapophysis), (2) the paradiapophyseal lamina (ppdl; connects the diapophysis with the parapophysis), (3) the postzygadiapophyseal lamina (podl; connects the diapophysis with the prezygapophysis), and (4) the prezygadiapophyseal lamina (prdl; connects the prezygapophysis with the diapophysis)—define the same three deep, converging fossae described above. An additional fossa that lies above the transverse process at the base of the neural arch makes the neural arch thinner at the base. The transverse processes are directed laterally, contain both the diapophysis and the parapophysis at the lateral edge, and are rectangular in dorsal view. The diapophysis is offset from the parapophysis in the anterior-most dorsal. The diapophysis and parapophysis combine to form one continuous facet in the last dorsal in this series.

The neural arches are much shorter (× 2/3) than the sacral neural spines. Moreover, the anterior and posterior tips of the neural arch are pointed; in lateral view, the neural spine is widest at the apex (fig. 30). Like the posterior dorsal neural spines, the middorsal neural spines are concave on both the anterior and posterior edges. The prezygapophyses and postzygapophyses are widely spaced and there are apparent hyposphene–hypantrum articulations between the vertebrae. Hyposphene–hypantrum articulations are also

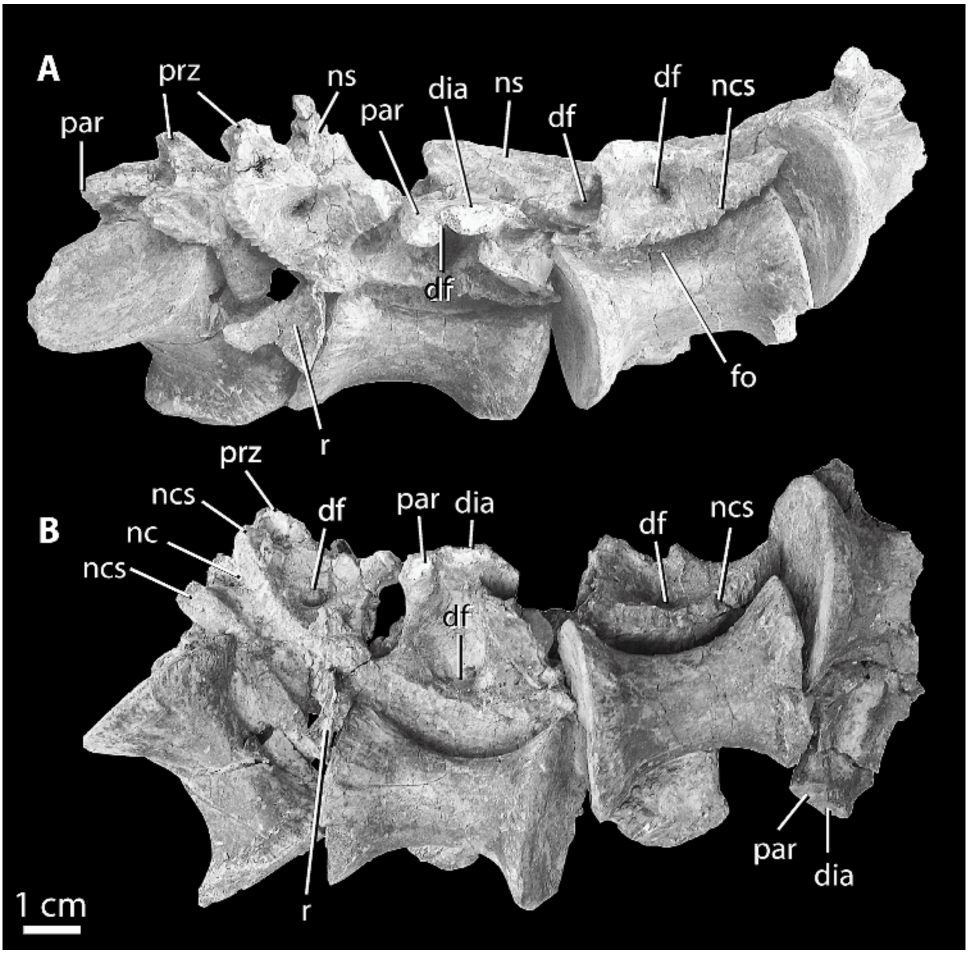

Fig. 30. Four semi-articulated dorsal vertebrae (AMNH FR 30587) in lateral (**A**) and ventral (**B**) views. Abbreviations are spelled out in appendix 3.

present in *Arizonasaurus* (MSM 4590; Nesbitt, 2005) and in many theropods. A small fossa is located on the medial wall of the neural canal just below the prezygapophysis.

The last two dorsal vertebrae of AMNH FR 30587 (fig. 31) were found in articulation with the sacral vertebrae. The centra are heavily waisted between the two centra faces and have shallow fossae between the centra body and the neurocentral suture. In cross section, the centra are nearly circular, just like the anterior and posterior centrum faces. The centra are amphicoelous, have pronounced rims, and have small striations radiating from the centra rim toward the middle of the centrum. There is no ventral keel.

Although the transverse processes are broken off, thin laminae are evident on the last two dorsal vertebrae. Both have thin pcpl, ppdl, podl, and prdl. A very deep fossa that is directed mediodorsally forms under the union of the ppdl and the pcpl. This deep fossa is also present in the dorsal vertebrae of *Arizonasaurus*, *Postosuchus*, *Batrachotomus*, *Bromsgroveia*, and *Poposaurus* and may be a synapomorphy of this group. Additionally, two more deep fossae are present, one directed posteriorly between the ppdl and prdl and another directed anteriorly between

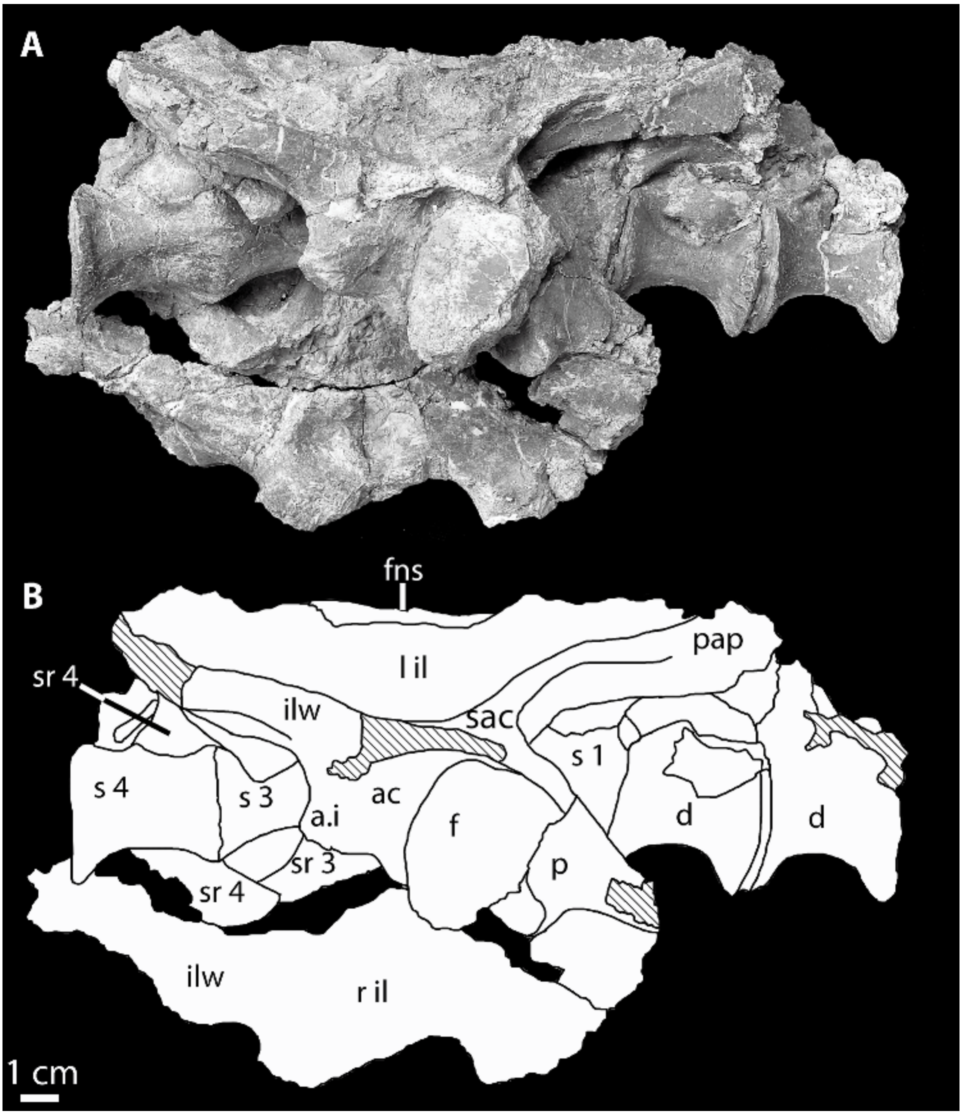

Fig. 31. The pelvis of *Effigia okeeffeae* (AMNH FR 30587) in a semilateral view. The right ilium is poorly preserved and fragmentary. Abbreviations are spelled out in appendix 3.

the pcpl and the podl. All three fossae converge in the center of the processes just under the neural spine. The transverse processes of the last dorsal articulates with the preacetabular process of the ilium.

The neural spines are centrally located over the body of the centrum. No spine tables are present at the apices of the neural spines. A small anteriorly pointing process is present on the last dorsal vertebra. Both the anterior and posterior sides are concave; the edges of the neural spine are very thin. These thin edges proceed ventrally to form either the prezygapophyses or the postzygapophyses. Hyposphene–hypantrum articulations are present in the posterior dorsal vertebrae.

Only the heads of the ribs are preserved with the dorsal vertebrae, and all are out of articulation. The capitulum and tuberculum are offset, rounded in cross section, and separated by a thin web of bone. A thin web of bone between the capitulum and tubercu-

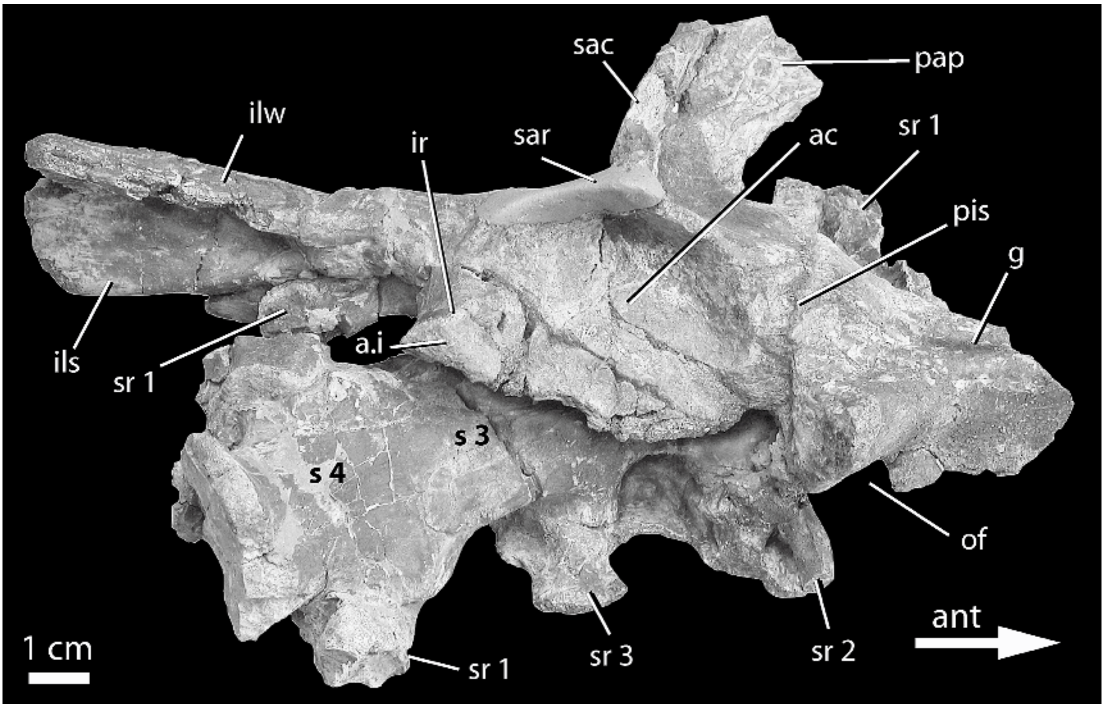

Fig. 32. The right ilium and pubis of *Effigia okeeffeae* (AMNH FR 30588) in lateral view. The sacrals were rotated into ventral view during crushing, but are still in articulation with the ilium. Abbreviations are spelled out in appendix 3.

lum is found in other suchians (e.g., *Arizonasaurus*) and not restricted to theropods (*contra* Carpenter, 1997).

SACRAL VERTEBRAE: Both AMNH FR 30587 (fig. 31) and AMNH FR 30588 (fig. 32) preserve a complete series of sacral vertebrae. The sacrum consists of four completely fused vertebrae with the last being the biggest. Sacrals two and three are slightly more gracile than the first and last sacral. All of the sacral vertebrae are dorsoventrally compressed even more so than the middorsal vertebrae. The centrum rims are pronounced on both the anterior and posterior parts of the sacrum, but poorly developed within the sacral series. A shallow ventral groove lies on the centrum of the fourth sacral. Sacrals one, two, and three have a fossa in between the body of the centrum and the neurocentral suture. The neural spines of all four sacral vertebrae are fused together. The neural arches of AMNH FR 30587 are slightly expanded dorsally and have a rugose surface pattern. In comparison, the neural arches of AMNH FR 30588 are smooth and do not expand dorsally. In both specimens, the prezygapophyses and postzygapophyses are completely fused.

The sacral ribs are solid, yet lightly constructed. The sacral bridges between the ilium and the sacrals are anteroposteriorly waisted and unlike the anteroposterior expanded sacral ribs of *Postosuchus* (TTUP 9002). The first and the fourth sacral ribs are located in the center of the centrum. Sacral rib two is shared by sacrals one and two and sacral rib three is shared by sacrals two and three. In comparison, the sacrum of *Sillosuchus* contains at least five sacral vertebrae (Alcober and Parrish, 1997), but the same pattern of attachment (i.e., the sacral vertebrae in the middle of the sacrum share sacral ribs) of the sacral ribs to the centrum.

Sacral ribs one and two articulate only to the preacetabular crest of the ilium. Sacral rib three articulates with the thin flange between the iliac blade and the preacetabular process directly above the ischiadic process. Sacral

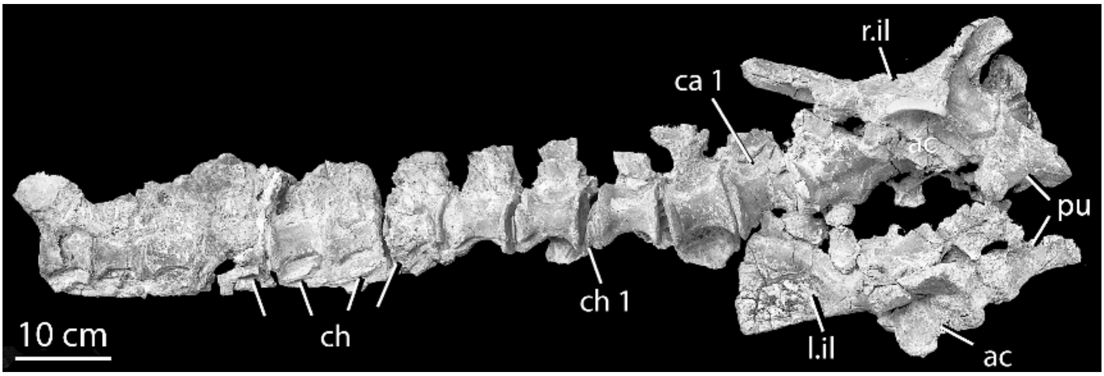

Fig. 33. Articulation of AMNH FR 30588. The specimen was slightly dorsoventrally crushed; the 12 caudal vertebrae are in lateral view, the right ilium is in lateral view, the sacral vertebrae are in ventral view, and the left ilium is in ventral view. Abbreviations are spelled out in appendix 3.

rib four is the largest and is anteroposterior longer than any of the other sacral ribs. The anterior end articulates into a socket on the iliac wing near the posterior edge of sacral rib three. The rest of sacral rib four articulates with the thin iliac flange just above the dorsal ridge on the medial side of the iliac wing.

The derived features of the sacrum of *Effigia* can also be found in other closely related taxa. *Effigia* and *Shuvosaurus* share the following characters: sacral four the largest, extreme dorsoventral compression of the sacral centra, and a similar sacral rib configuration. Additionally, *Effigia*, *Shuvosaurus*, and *Sillosuchus* share neural arch fusion and the absence of the centra rims within the sacrum. The presence of four or more sacral vertebrae is rare among archosaurs, especially the crocodile-line archosaurs. *Effigia*, *Shuvosaurus*, *Poposaurus*, and *Sillosuchus* (five sacrals) all share the presence of at least four fused sacral vertebrae. Furthermore, *Effigia*, *Shuvosaurus*, *Poposaurus*, *Sillosuchus*, *Arizonasaurus*, *Bromsgroveia*, and *Poposaurus* share the fusion of the prezygapophyses and postzygapophyses, similar sacral rib morphology (gracile sacral rib bridges), and the first sacral rib articulates extensively with the preacetabular process of the ilium.

CAUDAL VERTEBRAE: The first 29 caudal vertebrae are preserved in articulation with the pelvis in AMNH FR 30588. The first three caudal vertebrae (fig. 33) are the largest and are about the same size as the last sacral vertebra. Like the dorsal vertebrae, the centrum rims are pronounced, have a radiating pattern of small ridges directed to the center of the centrum, and are amphicoelous. A small ventral groove is present on the first sacral and becomes more pronounced on successive caudal vertebrae. The transverse processes are as long as the centrum in the anterior caudal vertebrae. Most of the distal edges of the neural arches and transverse processes are broken. One completely preserved neural arch possesses a small anterior processes on the most dorsal part and a larger posterior process. As with the dorsal neural arches, the anterior and posterior edges are concave. The prezygapophyses and postzygapophyses are much smaller and more closely packed in comparison with the dorsal vertebrae. The caudal vertebrae become more mediolaterally compressed posteriorly.

The morphology of the caudal vertebrae gradually becomes more slender posteriorly. The transition occurs at caudal vertebrae 19, 20, and 21. The more slender form has a longer centrum, with smaller articular faces. Additionally, the neural spine becomes smaller where the anterior and posterior ends still project dorsally, but the area between the two ends is flat. The transverse processes disappear at the transition. The prezygapophyses become more elongated posteriorly whereas the postzygapophyses remain the same size. The prezygapophyses overlap about one-fourth of the previous caudal vertebra (fig. 34). The anterior end of the prezygapophyses terminates in a point. The prezygapophyses and postzygapophyses ar-

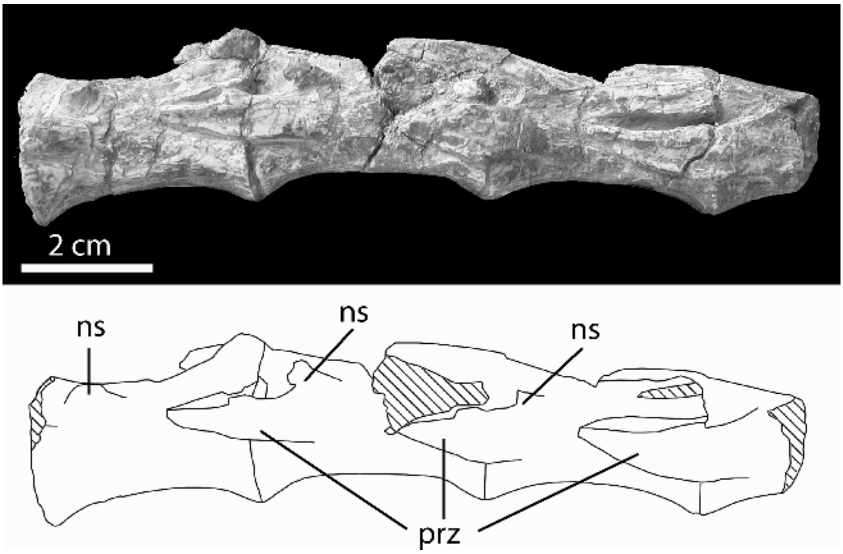

Fig. 34. Four articulated distal caudal vertebrae of *Effigia okeeffeae* (AMNH FR 30588). Note the reduced neural arch and the anteriorly elongated prezygapophyses. Anterior is to the left of the figure. Abbreviations are spelled out in appendix 3.

ticular surfaces articulate just below the anterior part of the neural spine. Much of the elongated prezygapophyses that overlap the proceeding caudal do not articulate with the articular surface of the postzygapophyses. The neural arches are short and it is not clear whether small accessory processes are present on the anterior portion of the neural spine of the midcaudal vertebrae as with *Rauisuchus* and *Batrachotomus*.

Chevron facets on the posterior end of the caudal vertebrae first appear between the third and fourth caudal vertebrae. The chevrons (fig. 33) are gracile with two rounded heads, mediolaterally compressed shafts, and slightly arc posteriorly. The shaft of the chevron is elongated and does not expand anteroposteriorly at its distal end. A shallow groove lies on the anteroventral side.

RIBS AND GASTRALIA: Fragments of dorsal ribs and gastralia were found associated with the dorsal vertebrae. The dorsal rib fragments are mediolaterally compressed and their anterior and posterior sides are blade-like. The gastralia are thin, oval in cross section, and taper laterally. The gastralia become more tightly packed posteriorly. An elbow is formed at the contact between the left and right gastralium. Here, the gastralia become more dorsoventrally flattened. A short series from the midline indicates that the elbows were imbricated or very closely spaced. Not all of the gastralia meet at the midline.

APPENDICULAR

SCAPULA: A nearly complete right scapula (fig. 35) and a partial left scapula are present in AMNH FR 30587. The size of the scapula is remarkable given the relative size of the forelimb, measuring 18 cm (maximum) dorsoventrally and 11 cm (maximum) anteroposteriorly. Most of the scapular blade is 1 mm thick. The articular end can be divided up into three sections, a posterior portion that makes up the glenoid fossa, an anterior portion that articulates with the coracoid, and a small lateral fossa that lies between the posterior portion and the anterior portion. The anterior portion is triangular and corresponds with the articular surface of the coracoid. The thin flange anterior to the articulation with the coracoid is straight and thin. The posteroventral edge of the scapula is the thickest and thins into a blade in both the anterior and dorsal directions. Additionally, a small groove is present in the middle of the posteroventral edge. This same groove is present in *Arizonasaurus* (MSM 4590) and

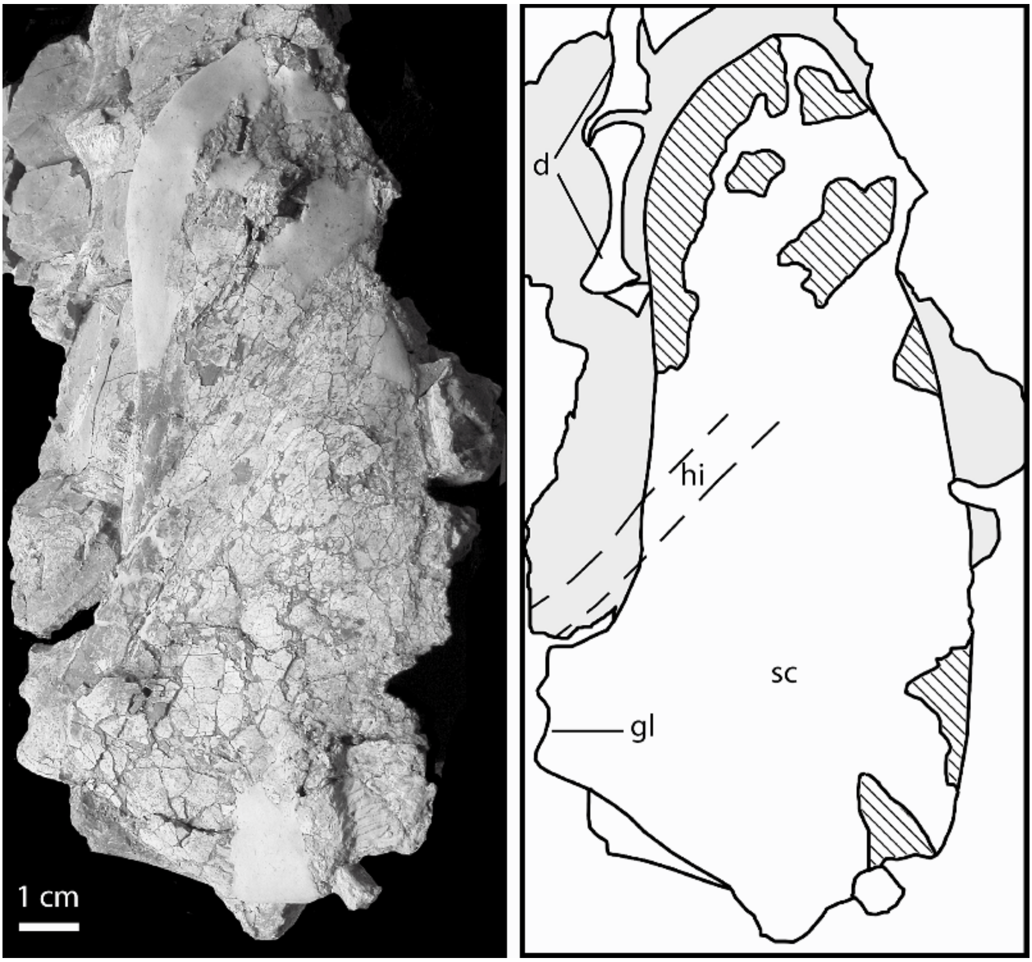

Fig. 35. The right scapula of *Effigia okeeffeae* (AMNH FR 30587) in lateral view. The impression of the humerus that was articulated with the glenoid is highlighted. Abbreviations are spelled out in appendix 3.

parasuchians, but is absent in *Hesperosuchus* (AMNH FR 6758).

The right humerus was found articulated with the glenoid. The angle of the articulated humerus with the complete glenoid indicates that the glenoid was directed posteroventrally. If the glenoid is pointed posteroventrally, then the scapular blade would be oriented posterodorsally.

CORACOID: Both coracoids (fig. 36) were recovered from AMNH FR 30587. As with the scapula, the coracoids are large relative to the forelimb and hindlimb. The coracoid measures ~14 cm anteroposteriorly. The glenoid fossa, located one-third of the way from the posterior edge, faces dorsally. The articular surface is nearly flat and slopes slightly posteriorly. The edge of the articular surface creates a lip that overhangs the "neck" of the glenoid fossa. In dorsal view, the glenoid fossa is circular. The articulation with the scapula is triangular, rugose, and located just anterior to the glenoid fossa. The thin dorsal edge of the coracoid is horizontal and articulates with the scapula along the length of the element. Here, the bone is 1 mm thick. Posterior to the glenoid fossa, the bone is much thicker than the anterior portion. A small fossa that opens dorsally sits between two rounded ridges that converge posteriorly

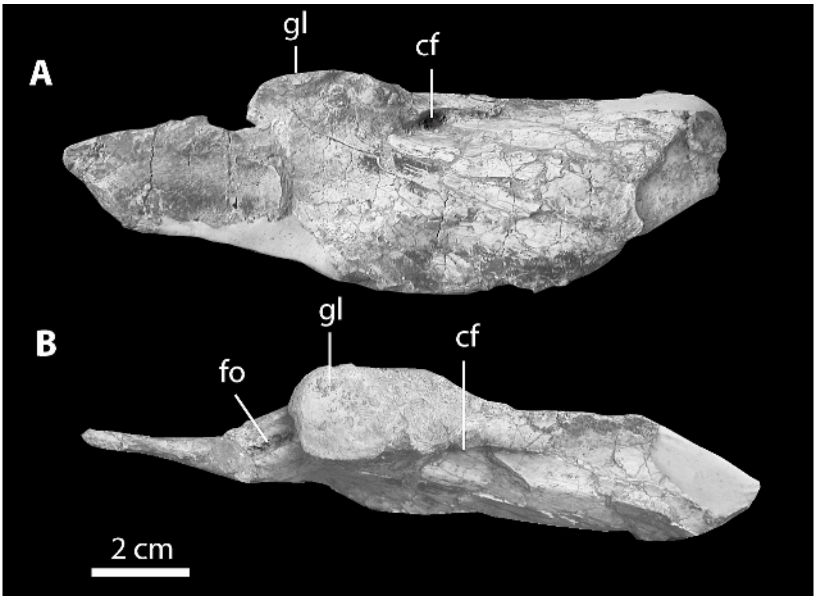

Fig. 36. The right coracoid of *Effigia okeeffeae* (AMNH FR 30587) in lateral (**A**) and dorsal (**B**) views. Abbreviations are spelled out in appendix 3.

on the dorsal margin posterior to the glenoid fossa. This fossa is also present in *Sillosuchus* and *Shuvosaurus*. The coracoid thins where the two dorsal ridges converge.

The ventral edge thins to a blade and is slightly dorsoventrally expanded anteriorly relative to the posterior end. A small rugose thickening occurs on the posteroventral surface. There is no groove on the ventral margin for the left or right interclavicle. The circular coracoid foramen is positioned anterior to the glenoid fossa and 1 cm ventral to the dorsal border.

The coracoid of *Effigia* is similar to that of *Shuvosaurus*. However, the coracoid foramen of *Effigia* is much smaller. The coracoid of *Postosuchus* is also similar in size and shape. Yet, the coracoid of *Postosuchus* bears a ventral groove in which the interclavicle lies. Similar to *Effigia*, the coracoid of *Arizonasaurus* lacks the ventral groove found in *Postosuchus*.

CLAVICLE: A small segment of bone located near the scapula and the coracoids possibly represents a left clavicle (fig. 29). The segment is rectangular in cross section and bears a groove on the dorsal surface. The clavicle of *Effigia* is much larger proportionally (relative to body size) than the clavicles of *Batrachotomus*.

HUMERUS: The right humerus (fig. 37) was found articulated with the scapula at the proximal end and with the ulna and radius at the distal end; however, only the proximal head and the distal end were recovered. Fortunately, an internal and external mold of the complete shaft indicates that the midshaft is hollow, about 1.5 cm mediolaterally wide, and the overall length of the humerus is about 15 cm. The mold also indicates that the humerus is relatively straight, but that the distal condyles are twisted 20° relative to the proximal anterior surface. The proximal anterior articular surface is composed of a symmetrical, rounded protuberance in the center of the anterior face. In posterior view, the articular surface is rounded, but asymmetrical, with the lateral protuberance being much larger than the medial protrusion. In proximal view, the articular surface is D-shaped where the straight edge of the D is mediolaterally oriented. Only the top part of the deltopectoral crest is preserved, but it demonstrates that the area between the deltopectoral crest and the proximal articular surface is concave.

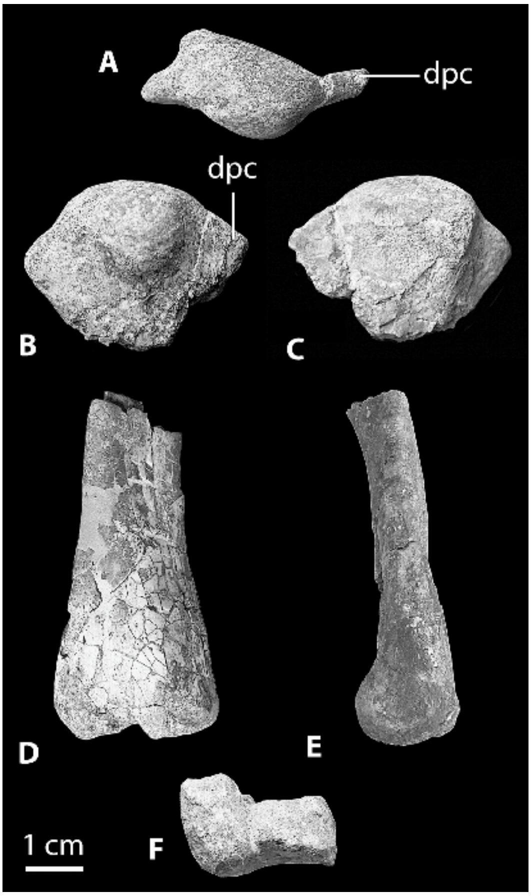

Fig. 37. The right humerus of *Effigia okeeffeae* (AMNH FR 30587). The proximal portion of the humerus in proximal (**A**), posterior (**B**), and anterior (**C**) views and the distal portion in anterior (**D**), right lateral (**E**), and distal (**F**) views.

A small triangular projection is located lateral to the proximal articular surface. The projection thins laterally.

In distal view, the humerus is parallelogram shaped. The distal end bears two condyles, a medial and a radial condyle. The medial condyle is slightly more robust and is expanded more in the anterior and posterior directions. A weakly developed groove occurs on the posterior side of the medial condyle. The lateral condyle is expanded in the mediolateral direction relative to the medial condyle. A fossa is present in between the two condyles on the anterior side and a fossa surrounded by a rim of bone is present on the posterior side between the two condyles. The anterolateral ridge leading to the radial condyle is sharp. No ectepicondylar groove is present.

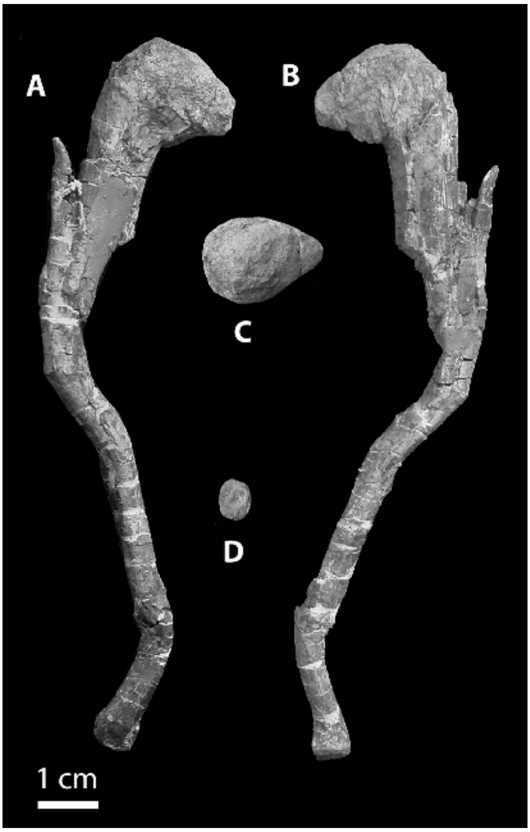

Fig. 38. The right ulna of *Effigia okeeffeae* (AMNH FR 30587) in right lateral (**A**), left lateral (**B**), proximal (**C**), and distal (**D**) views.

The humerus of *Effigia* is reduced in size and length relative to other crocodile-line archosaurs, yet it is similar in proportions. The proximal part of the humerus of *Postosuchus* (TTUP 9002) is similar to that of *Effigia*; however, the proximal portion of the deltopectoral crest projects more laterally than in *Postosuchus*. In *Postosuchus*, the proximal portion of the deltopectoral crest projects more ventrolaterally. *Postosuchus* and *Effigia* share the similarly developed groove that occurs on the posterior side of the medial condyle. *Effigia* and *Shuvosaurus* both lack an ectepicondylar foramen and groove.

ULNA: The right ulna (fig. 38) was broken and twisted before fossilization, but

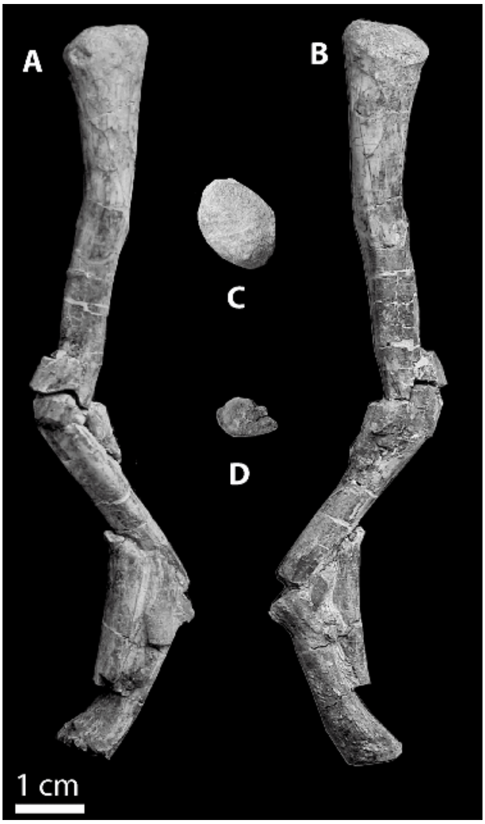

Fig. 39. The right radius of *Effigia okeeffeae* (AMNH FR 30587) in right lateral (**A**), left lateral (**B**), proximal (**C**), and distal (**D**) views.

remains whole. The length of the element is estimated at 14 cm, roughly equal to the length of the humerus. The proximal head measures 1.5 cm mediolaterally and 2.5 cm anteroposteriorly. It is expanded posteriorly and the articular surface is rounded, but lacks an olecranon process. The posterior surface of the proximal end is concave. The diameter tapers ventrally. The distal end is no wider than the shaft just dorsal to it. The distal articular surface is slightly rounded and is 7 mm in diameter.

RADIUS: The right radius was also broken and twisted before fossilization, but remains whole (fig. 39). The length of the element is estimated at 14 cm, roughly equal to the length of the humerus. The proximal end is expanded in all directions, rounded in proximal view, and the proximal articular surface is flat in the middle and rounded around the edges. In cross section, the shaft is D-shaped, where the flat side is on the lateral side. Unlike the ulna shaft, the shaft of the radius is about the same diameter for the length of the element. The distal end is weakly expanded, American football shaped, and has a sharp posterior ridge connecting the shaft to the distal articular surface. The distal end measures 11 mm anteroposteriorly by 7 mm mediolaterally. The distal end of the radius is comparatively more robust than that of the ulna.

Fig. 40. The partial right manus of *Effigia okeeffeae* (AMNH FR 30587) in anterior view. Abbreviations are spelled out in appendix 3.

MANUS: Portions of the right manus (fig. 40) were recovered somewhat articulated with both the radius and the ulna. Metacarpals III, IV, and V were found articulated together and a potential metacarpal I and the carpals were found together nearby. Unfortunately, the identity of the two carpals cannot be determined with certainty. The proposed metacarpal I proximal portion is broken, shifted ventrally, and appressed against the shaft. Metacarpal I is estimated to have been 12 mm long and 5.5 mm wide. It has a dorsoventrally compressed shaft and the distal end is asymmetrical; only the medial side bears a rounded articular surface; the lateral side tapers to a sharp edge. The morphology is strongly reminiscent of metacarpal I of *Coelophysis* and other theropods. Metacarpal II was not preserved. Metacarpal III is the most robust and measures 20 mm. The proximal head is wide (7.5 mm) and bears a dorsolateral projection. In posteroventral view, the proximal end is separated into two halves down the midline. Both halves have a similarly sized rounded articular surface. A small fossa is located underneath the lateral articular surface. In proximal view, the articular surface is D-shaped with a small notch in the middle of the flat side of the D; the flat side is the posterior surface. The lateral edge of the shaft is sharper and located more anterodorsally than the rounded medial edge. The articular surface is the widest of metacarpals III, IV, and V. Metacarpal IV is more gracile than metacarpal III and is 18 mm long. The proximal end thickens dorsally. A small shelf is present from the proximal articular surface to midshaft on the medial side. A tiny, yet distinct groove occurs on the proximolateral surface. A small rugose ridge located on the proximal half of the posterior surface trends from the medial side to the lateral side. The shaft is nearly circular in cross section. In proximal view, the articular surface is triangular. Metacarpal V is the most gracile metacarpal and is 12 mm long. The proximal surface is mediolaterally compressed. Both the lateral and medial edges of the shaft are sharp. A small phalanx was articulated with the end of metacarpal V. The phalanx is strongly reduced with no distinct features. It measures 5 mm. A much more robust phalanx is also present and may belong with either metacarpal III or metacarpal I. This phalanx indicates that at least one of the digits was not as reduced as much as digit I.

ILIUM: The ilium (figs. 31, 32, 33) of *Effigia* closely resembles that of *Shuvosaurus*. None of the ilia are complete in AMNH FR 30587 or AMNH FR 30588, yet, between the four, almost all portions of the ilium can be described. The supra-acetabular rim is well developed and caps the entire dorsal portion of the of the acetabulum. Unfortunately, the supra-acetabular rim is plastically deformed, so it is impossible to tell whether the acetabular rim projects slightly ventrally at its lateralmost edge as in *Shuvosaurus* (TTUP 9001). The supra-acetabular crest originates on the lateral-most extent of the acetabular rim and projects dorsally and anteriorly. The supra-acetabular crest is thin and slightly rugose, like in *Poposaurus* (CFMNH UR357) and *Shuvosaurus*. Furthermore, the supra-acetabular projects anteriorly only, unlike the supra-acetabular crests of *Postosuchus*, *Arizonasaurus*, *Bromsgroveia*, and *Batrachotomus*, where the supra-acetabular projects anteriorly and posteriorly at the medial margin of the ilium. The supra-acetabular crest in *Effigia* also arcs anteriorly, creating a fossa just anterior to the crest. *Poposaurus*, *Shuvosaurus*, the Moenkopi "chatterjeeid" (Nesbitt, 2005b) and possibly *Sillosuchus* (PVSJ 85) all share this fossa. As the supra-acetabular crest arcs anteriorly along the preacetabular process, it becomes less pronounced. The anterior-most end of the preacetabular process is not preserved. The ribs of the first and second sacral vertebrae articulate with the preacetabular process only. The last dorsal vertebra also has a modified transverse process that articulates with the anterior portion of the preacetabular process.

The postacetabular process of the iliac blade projects posteriorly and is thickest just posterior to the acetabulum. Ventrally, the thickest part of the iliac blade splits into two ridges, a ventral ridge and a dorsal ridge, that continue until the posterior extent of the iliac blade. A shallow fossa lies between the two ridges. The ventral ridge creates the ventral edge of the iliac blade. The dorsal ridge is equivalent to the ridge on the medial side of other archosaur ilia that is close to the sacral articulation. The sacral ribs articulate completely dorsal to the ridge in *Effigia*. As in *Shuvosaurus*, the iliac blade and the preacetabular process are connected by a thin flange of bone. The region between the preacetabular process and the iliac blade creates a shallow fossa. The dorsal extent of the thin flange is unknown.

The ventral border bears an emargination between the pubic and ischiadic processes. *Poposaurus*, *Shuvosaurus*, *Arizonasaurus*, and *Bromsgroveia* also have an emarginated ventral acetabular margin. The convex ischiadic process corresponds with the concave pit of the ischium. A small ridge separates the iliac blade from the ischiadic process. The small ridge disappears as it grades anterodorsally into the acetabulum. Dorsal to the ridge, a slightly concave shelf is present. In bird-line archosaurs (e.g., *Silesaurus* and birds) the same shelf is present and is called the antitrochanter. The "antitrochanter" in *Effigia* possibly functioned similar to bird-line archosaurs (i.e., it articulates with a sloping posterior portion of the proximal femur), yet the orientations of the femora of bird-line archosaurs (femoral head generally directed medially) and the femora of *Effigia* (femoral head directed anteriorly) are much different.

The anterior acetabulum wall was formed only by the pubis. Without the pubis articulated, the acetabulum is unbordered anteriorly. The ilium is most robust where the pubis articulates. The large space between the ischiadic process and the pubic process separated the pubis and ischium in life.

PUBIS: Both ilia in AMNH FR 30588 and the right ilium in AMNH FR 30587 remain in articulation with their respective pubes (figs. 31, 32, 33). In proximal view, the pubis is divided into two portions, the dorsal portion that articulates with the ilium and the ventral portion that forms the anterior border of the acetabulum. The part that makes up the acetabulum slants slightly anteroventrally. There is no shelf that is part of the medial margin of the acetabulum on the pubis like in crocodylomorphs (e.g., *Hesperosuchus* UCMP 129740). A dorsal groove is present on the lateral side of the proximal pubis (fig. 41). This groove is also present in *Arizonasaurus* (MAM 4590) and *Postosuchus* (TTUP 9002). The obturator foramen is oval and located just medial to the proximal end of the pubis. The posterior edge of the obturator foramen is equal with that of the most proximal portion of the pubis. The left and right pubes articulate medial to the obturator foramen. The right pubis of AMNH FR 30587 shows a thickened area of articulation to the left pubis 1 cm anterior to the obturator foramen. The articular surface is oval and rugose. A similarly thickened articulation is present in *Arizonasaurus* (Nesbitt, 2005a).

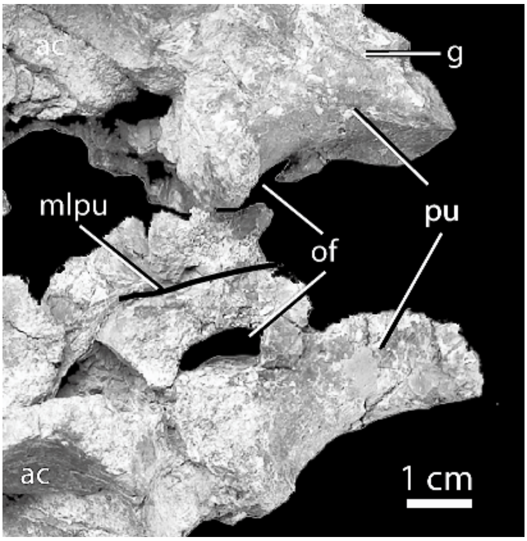

Fig. 41. A close-up of the pubes of *Effigia okeeffeae* AMNH FR 30587 (fig. 42) in articulation in a semiventral view. The pubes meet at their midlines for the entire length of the elements. Abbreviations are spelled out in appendix 3.

AMNH FR 30587 preserves most of the right shaft and boot of the pubis (fig. 42) and fragments of the left boot. The proximal shaft of the pubis is L-shaped in cross section where the shorter part of the L is lateral and the thickest and the longer part of the L makes up the pubic apron. Distally, the pubic apron disappears and a large well-defined ridge running parallel to the pelvic shaft develops. The same sharp ridge is present in *Shuvosaurus*. The pubic boot is large, dorsolaterally compressed, and similar in proportions to the pubic boot of *Shuvosaurus*. The ventral border of the boot is rounded. The distal end of the boot is broken, but possibly ended in a sharp point as it does in *Shuvosaurus*. The left and right pubic boot contact each other along their entire length.

ISCHIUM: Both the left and right ischia (fig. 43) of AMNH FR 30587 and AMNH FR 30588 were found in articulation with their respective ilia. The ischia are identical to *Shuvosaurus* and are similar to those of

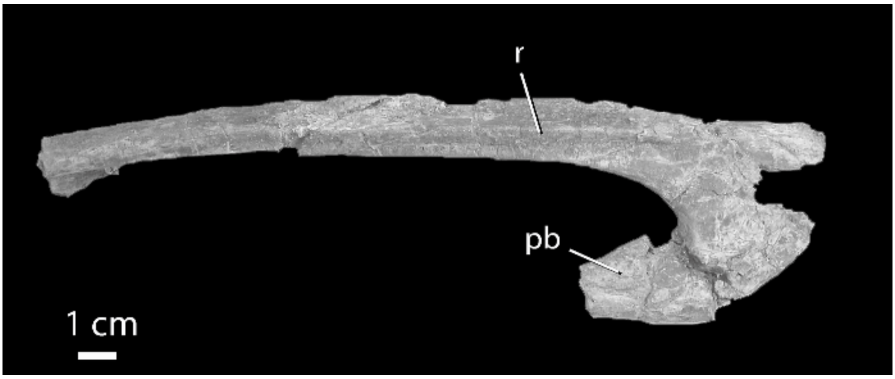

Fig. 42. The pubis of *Effigia okeeffeae* (AMNH FR 30587) in lateral view. Abbreviations are spelled out in appendix 3.

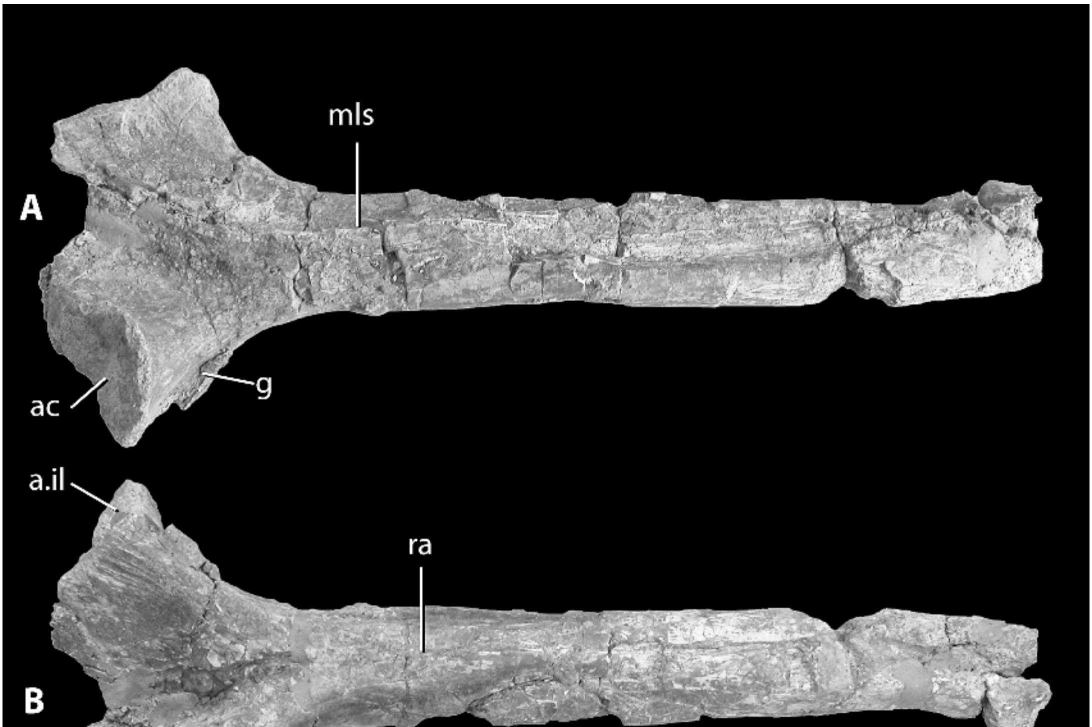

Fig. 43. The ischium of *Effigia okeeffeae* (AMNH FR 30587) in ventral (**A**) and dorsal (**B**) views. Abbreviations are spelled out in appendix 3.

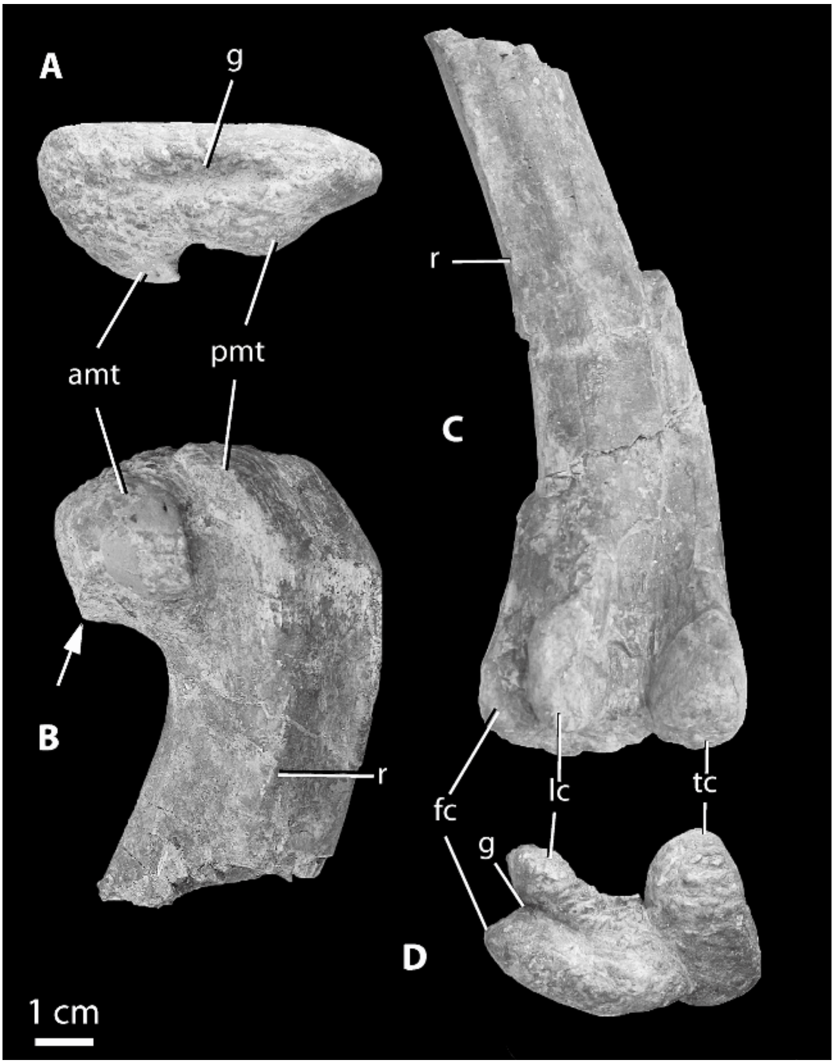

Fig. 44. The left proximal femur of *Effigia okeeffeae* (AMNH FR 30588) in proximal (**A**) and medial (**B**) views and the distal femur of *Effigia okeeffeae* (AMNH FR 30587) in posterior (**C**) and distal (**D**) views. The arrow highlights the abrupt change in angle at the proximal head of the femur. Abbreviations are spelled out in appendix 3.

Arizonasaurus, *Postosuchus*, *Saurosuchus*, and *Batrachotomus*. The left and right ischia in both specimens are completely fused (no suture visible) for the entire length of both elements. A raised sharp ridge is present on the ventral side where the two ischia meet. A raised area is present where the ischia meet on the dorsal side. This raised area is only present in *Effigia*, *Shuvosaurus*, and *Sillosuchus*. A deep valley between the two proximal heads shallows posteriorly. The proximal end of the ischium has two articular surfaces, a concave articulation to the ilium and another making up part of the acetabulum. The acetabular part of the ischium is delimited by a large ridge. The shaft of the ischium is D-shaped in cross section. The distal end of the ischia slightly expand dorsally and ventrally.

FEMORA: The proximal femora (fig. 44) are represented by the extreme proximal head of the right femur in AMNH FR 30587 and the proximal portion of AMNH FR 30588. The proximal head is robust in both the anteroposterior and mediolateral planes. In proximal view, the femur bears two medial tubera, one anterior and one more posterior. The anterior tuber projects posteriorly at its apex, producing a hook (fig. 44). A distinct groove separates the anterior and posterior tubera. The region posterior to the posterior tuber slopes in a dorsolateral/ventromedial direction that is slightly deflected posteriorly. This region articulates with the "antitrochanter" region of the ischiadic process of the ilium. There is no anterolateral tuber like in the femora of *Poposaurus* (CFMNH UR357), *Postosuchus* (TTUP 9002), stagonolepidids, or parasuchians. The proximal surface of the femur has a rugose texture made up of small bumps and grooves with no particular orientation. Additionally, the proximal surface also has a groove that runs anteriorly and posteriorly.

The right femur of AMNH FR 30588 preserves more of the proximal shaft. In lateral view, the anterior edge arcs anteriorly and then abruptly dorsally at the head of the femur (fig. 44). This morphology has been termed the distal "corner" of the femoral head by Novas (1996), and creates a well-defined anterior edge that is also present in *Poposaurus*, *Alligator*, and dinosauriforms (Novas, 1996). A small rugose region on the lateral side of the femur is interpreted as the proximal dorsal tuberosity present in *Alligator* because of the similar position and shape. The posterior edge is narrow dorsally and becomes more rounded ventrally. In medial view, the anterior medial tuber is restricted to the head of the femur whereas the posterior medial condyle runs further ventrally. A small gap (1 cm) separates the posterior medial condyle from a poorly developed ridge that runs parallel with the anterior and posterior edges of the femur.

Both proximal portions of the femora were found articulated in the acetabulum of the respective ilia. In both cases, the "head" of the femur was articulated in the anterior portion of the acetabulum. Consequently, the anteromedial condyle articulated with the acetabulum. The acetabular rim and the pubis restrict movement laterally and anteriorly, respectively. The exact orientation of the distal condyles to the "head" cannot be determined because of the slight plastic deformation described above. However, the distal condyles must be nearly 150° apart from the "head" in order for this animal to be able to move it legs in the anteroposterior plane. Furthermore, the femur of *Shuvosaurus* articulates with the ilium in the same way as this taxon and the "head" and the distal condyles are nearly 150° apart.

Both the distal portions of the femora of AMNH FR 30587 are preserved. The posterolateral edge of the shaft is sharp and the anteromedial edge is rounded. The distal ends of the femora expand medially and laterally and have three condyles. The tibial condyle is the most robust and a small fossa parallels its medioposterior edge. The lateral condyle ends in a sharp point and is the smallest among the three condyles. The fibular condyle is separated from the lateral condyle by a sulcus, which is also present in *Coelophysis* (Colbert, 1989), other coelophysoids (Rowe and Gauthier, 1990), and *Dromicosuchus* (Sues et al., 2003). Like the proximal surface of the femur, the distal surface is also rugose, with a system of bumps and grooves with no particular orientation.

The femora are thin walled, hollow, and are laterally compressed. Breaks close to midshaft show that the bone is thicker at the anterior and posterior edges of the femur compared to the medial and lateral sides.

TIBIA: The left tibia (fig. 45) is nearly complete except for a broken midsection, and the right tibia is only represented by the proximal and distal extremities. The tibia is more robust than the fibula and is nearly round in cross section over the length of the element. The tibia is hollow. The proximal end expands equally in the anterior and posterior directions. In proximal view, the tibia is D-shaped, where the rounded part is medially orientated. The lateral margin bears a low, wide, and U-shaped depression that deepens posteriorly. The U-shaped depression is manifested in posterior view. This depression possibly articulates with the lateral condyle of the femur. The ridge on the lateral side of the U-shaped groove may correspond to the depression, crista tibiofibularis, between the fibular condyle and the

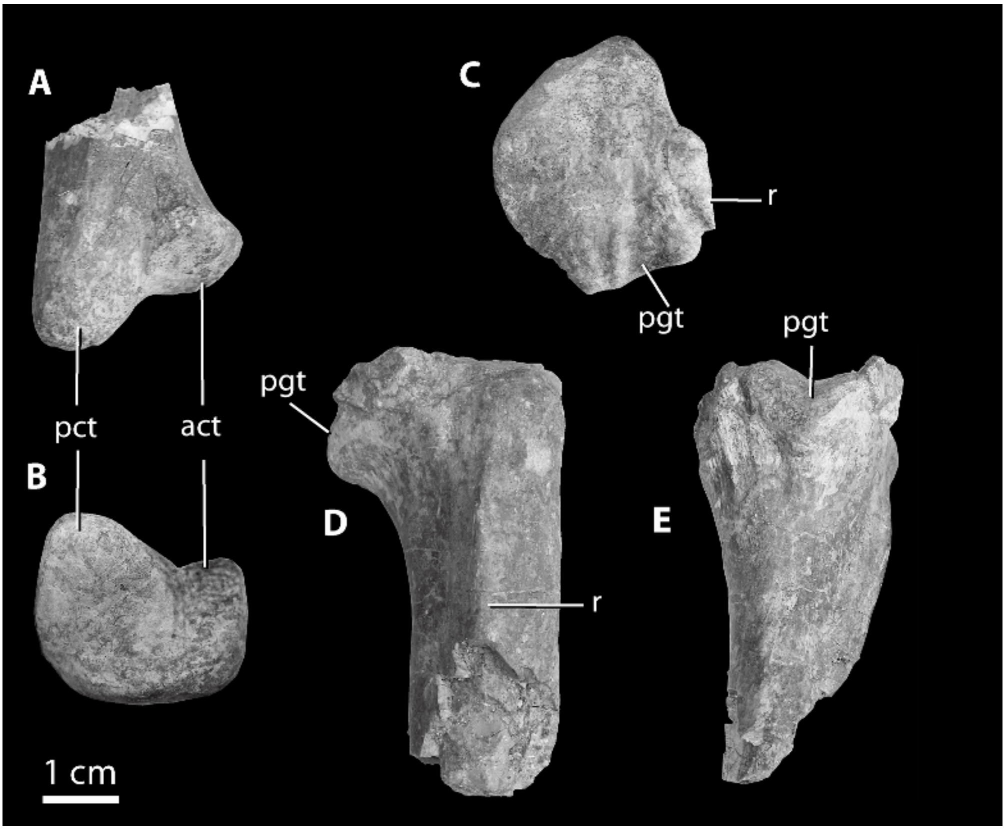

Fig. 45. Distal right tibia of *Effigia okeeffeae* (AMNH FR 30587) in lateral (**A**) and distal (**B**) views. Proximal right tibia (AMNH FR 30587) in proximal (**C**), lateral (**D**), and posterior (**E**) views. Abbreviations are spelled out in appendix 3.

lateral condyle of the femur. The U-shaped groove is present in *Postosuchus*, *Batrachotomus*, *Shuvosaurus*, and in the crocodylomorphs *Sphenosuchus* (Walker, 1990) and *Dromicosuchus* (Sues et al., 2003). A vertical distinct ridge (3 cm long) is located just below the proximal surface on the lateral surface. Other than *Shuvosaurus*, no other crocodile-line archosaurs have this feature. In contrast, some dinosauromorphs also have this tibial crest, including *Silesaurus* (Dzik, 2003) and members of the Theropoda (Rauhut, 2003). The distal end slightly expands anteriorly and posteriorly and bears two connected facets that articulate with the astragalus. The anterolateral distal facet is slanted dorsomedially and the posteromedial distal facet slants dorsolaterally. This condition is similar to the distal tibia of *Postosuchus*, *Shuvosaurus*, stagonolepidids, and crocodylomorphs. The anterior facet also has a small "lip" on the anterior side of the tibia.

FIBULA: The fibula (fig. 46) is best represented (AMNH FR 30587) by a nearly complete left fibula, broken about two-thirds of the way down and shifted a centimeter anteriorly, and missing the distal extremity. The right tibia is represented by the proximal and distal ends. The fibula is slender and compressed mediolaterally over its entire length. From midshaft, the fibula expands posteriorly proximally. This expansion culminates in a slight "head" on the posterior edge in proximal view. In proximal view, the fibula is comma shaped, whereas the posterior "head" is larger than the anterior side. The lateral side of the fibula preserves a long, poorly developed iliofibularis trochanter that starts on the anterior edge about one-third of the way down from the proximal edge and

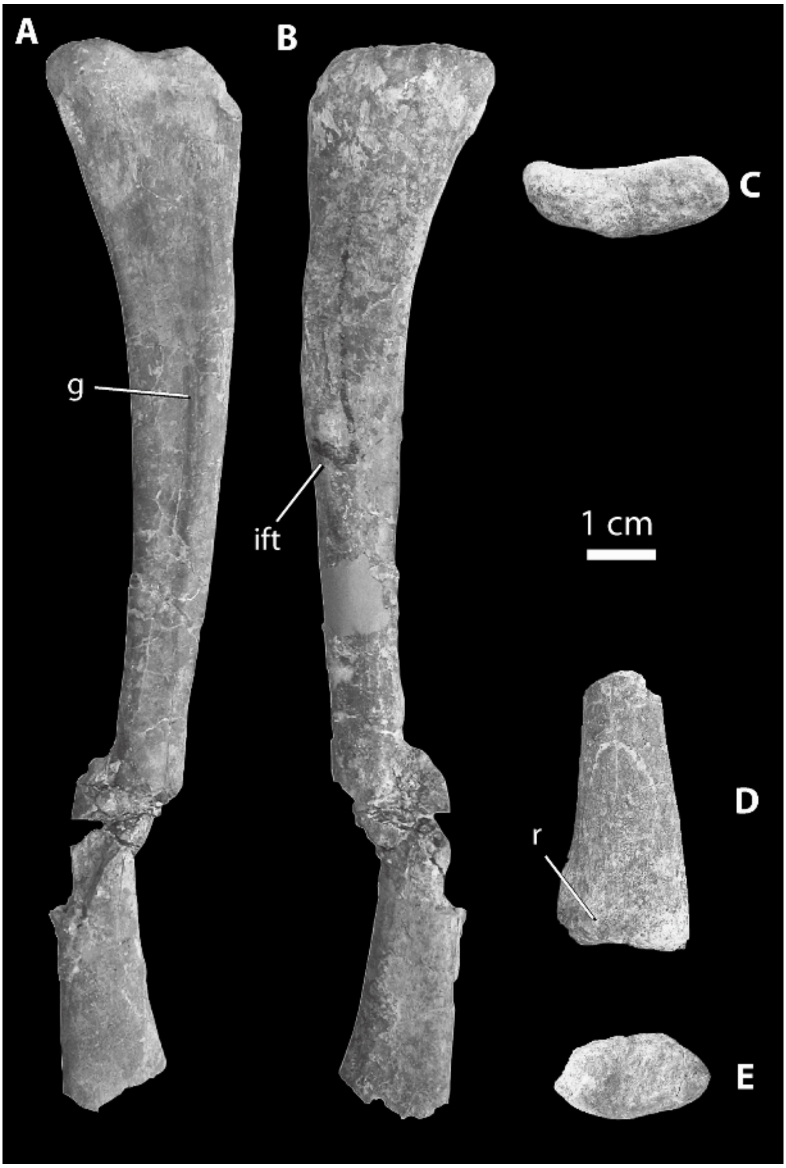

Fig. 46. The left fibula of *Effigia okeeffeae* (AMNH FR 30587) in medial (**A**), lateral (**B**), and proximal (**C**) views. The distal right femur of *Effigia okeeffeae* (AMNH FR 30587) in lateral (**D**) and distal (**E**) views. Abbreviations are spelled out in appendix 3.

moves posteriorly across the shaft to merge with the posterior edge. The iliofibularis trochanter disappears about two-thirds of the way down the shaft from the proximal end. The medial surface bears a groove running dorsoventrally about one-third of the way down from the proximal end for 3 cm distally. A similar groove on the fibula of *Alligator* serves as the origin of attachment for the M. tibialis. The distal end expands anteriorly and posteriorly. The medial surface expands medially to form a lip. All of these features of the fibula are also present in *Shuvosaurus* (*contra* Long and Murry, 1995).

PES: A semiarticulated, incomplete right pes (AMNH FR 30587; fig. 47) was discov-

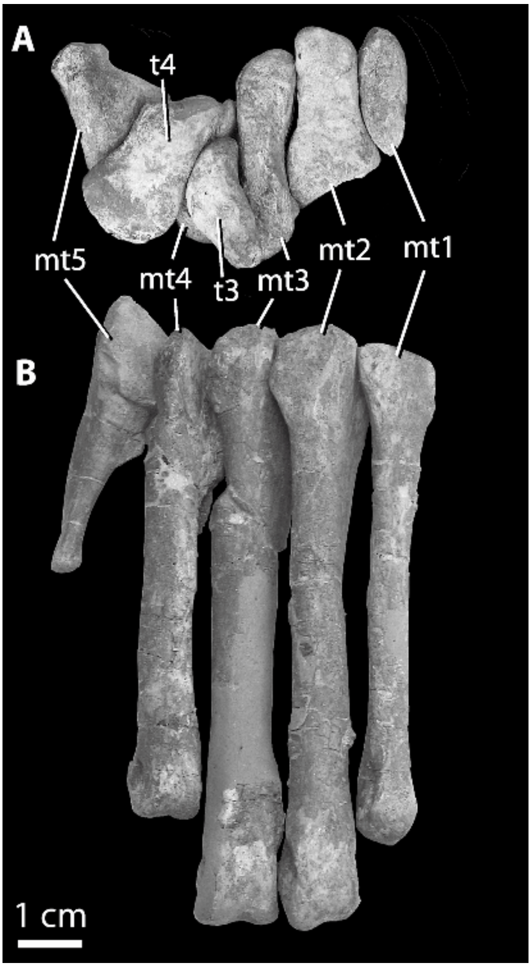

Fig. 47. The right pes of *Effigia okeeffeae* (AMNH FR 30587) in proximal (**A**) view with tarsals and in anterior (**B**) view without tarsals. Abbreviations are spelled out in appendix 3.

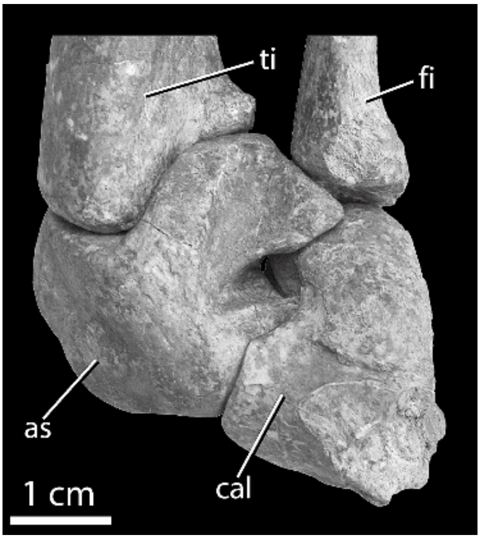

Fig. 48. The right ''crocodile-normal ankle'' of *Effigia okeeffeae* (AMNH FR 30587) articulated with the tibia and fibula in posterior view. The posteriorly direct calcaneum tuber is broken. Abbreviations are spelled out in appendix 3.

ered next to the sacrum, abutting against the right ilium. The recovered elements of the pes consist of the following elements: astragalus, calcaneum, two tarsals, five metatarsals, six phalanges, and one ungual. The ankle is clearly crocodile-normal, where rotation occurs between the calcaneum and astragalus (fig. 48).

The astragalus (fig. 49D–F) is complete and well preserved. The morphology of the astragalus closely matches that of *Alligator* with a few exceptions. In particular, the *Effigia* astragalar fossa accepts the posteromedial distal facet of the tibia. In *Alligator*, the tibia does not articulate here. A ridge of bone (ar in fig. 49) separates this fossa in *Effigia* from the rest of the astragalus. Even though the tibia of *Alligator* does not articulate with the astragalar fossa, the depression where the posteromedial distal facet of the tibia of *Effigia* fits is possibly homologous to the astragalar fossa of *Alligator*. Unfortunately, this character state in basal crocodylomorphs is unknown. Additionally, the fibular facet of the astragalus is half-moon shaped in *Shuvosaurus*, whereas it is more square in *Alligator*. The anterior hollow area in *Shuvosaurus* is reduced in comparison with *Alligator*.

The astragalus ''peg'' is well developed and fits into the trough-shaped facet of the calcaneum snugly. Rotation between the calcaneum and astragalus was limited; the peg and socket configuration allows a maximum of only 20° of rotation. The articulation between the tibia and the astragalus is also very tight with little room for soft tissue. Like in all other taxa with crocodile-normal ankles, the tibia only articulates with the astragalus. On the other hand, the fibula articulates with both the astragalus and the calcaneum (see fig. 49). The fibula does not

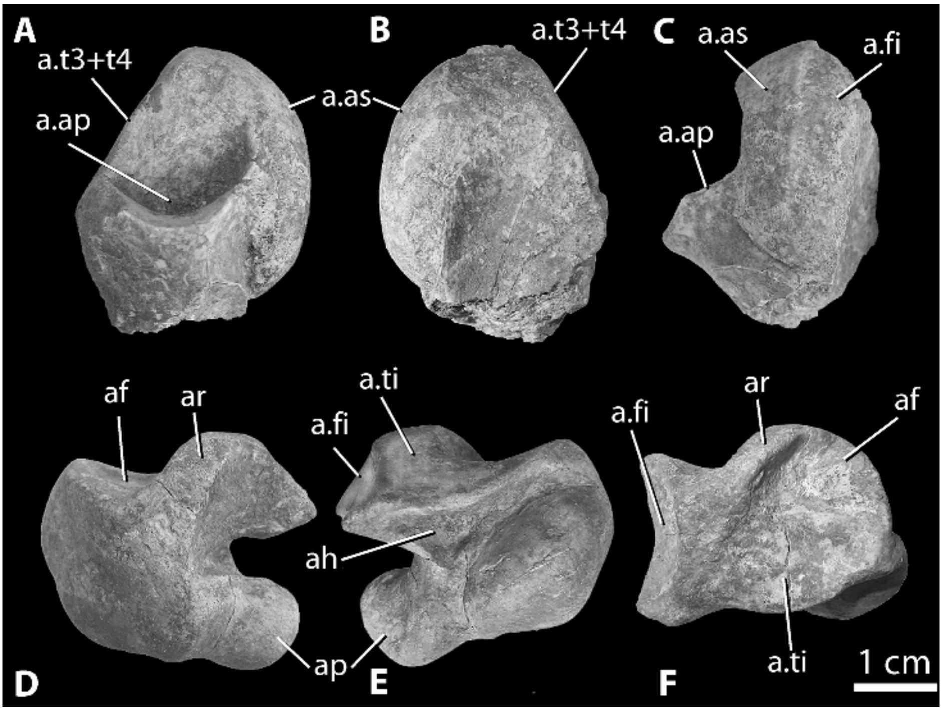

Fig. 49. The calcaneum of *Effigia okeeffeae* (AMNH FR 30587) in medial (**A**), lateral (**B**), and dorsal (**C**) views and the astragalus (AMNH FR 30587) in anterior (**D**), posterior (**E**), and dorsal (**F**) views. Abbreviations are spelled out in appendix 3.

fit as closely with the calcaneum and the astragalus as does the tibia does with the astragalus.

The calcaneal tuber (fig. 49A–C) is not preserved in AMNH FR 30587. The holotype calcaneal tuber of *Shuvosaurus* (TTUP 9001) preserves a very large expansion projecting dorsally, but does not have a ventral expansion (Long and Murry, 1995); crocodylomorphs and rauisuchians such as *Postosuchus* all have calcaneal tubera that expand equally dorsally and ventrally. Additionally, the tuber in the holotype of *Shuvosaurus* (TTUP 9001) does not have a dorsoventral groove (Long and Murry, 1995). The trough-shaped facet for the astragalar peg is deep both laterally and posteriorly relative to *Alligator*. A small hump running dorsoventrally within the trough-shaped facet for the astragalar peg corresponds to a concave area on the astragalus peg. The facet for the astragalar trochlea articulates with the astragalus, and the facet for the fibula share the same amount of surface area. This differs from *Alligator*, in which the facet for the fibula takes up two-thirds or more of the articular surface of the calcaneum. The area just lateral to the facet for the fibula is slightly concave.

The two tarsals (fig. 50) were found more or less articulated to the pes. Tarsal 4, the larger of the two, bears a large ventral process that abuts against the posterolateral side and also in part lies on top of metatarsal IV (fig. 50). Because the metatarsals were slightly displaced from articulation, there are two options for the articulation of metatarsal V and tarsal 4. Metatarsal V could articulate to the anterolateral surface or the posterolateral surface of tarsal 4. Comparisons of the articulation between tarsal four and metatarsal V with *Alligator* and *Protosuchus* (AMNH FR 3024) suggests that metatarsal V articulated with the posterolateral surface. Additionally, the convex proximal head of metatarsal V fits well with the concave posterolateral surface of tarsal 4. The concave anteromedial edge of tarsal 4 in dorsal

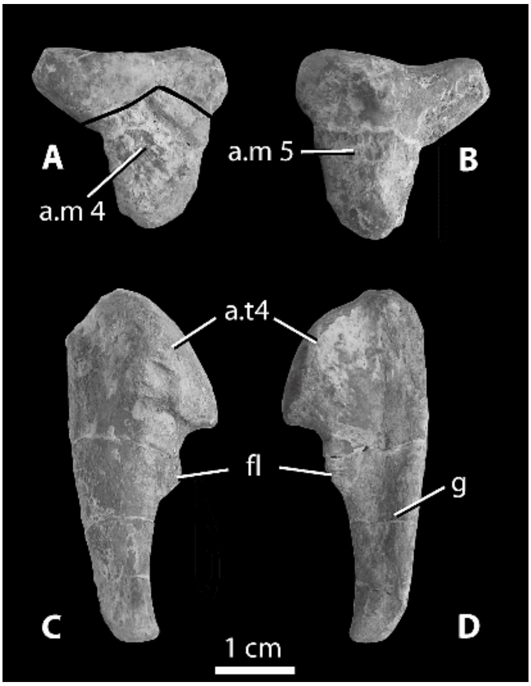

Fig. 50. Tarsal 4 of *Effigia okeeffeae* (AMNH FR 30587) in anteromedial (**A**) and posterolateral (**B**) views. The black line in **A** outlines the dorsal extent of the articulation with metatarsal four. The fifth metatarsal in lateral (**C**) and medial (**D**) views. Abbreviations are spelled out in appendix 3.

view fits the convex posterolateral edge of tarsal 3. Tarsal 3 thickens posteriorly. A sharp ridge on the ventral surface divides the ventral surface in roughly equal sides, curves form a anteroposterior direction anteriorly to a medial direction posteriorly, and possibly fits between 3 and 4.

The five metatarsals are well preserved (fig. 47), but some outer layers of bone were lost during excavation and proximal portions of metatarsals III and IV are shifted posteriorly 2 mm. Metatarsal I measures 74 mm, about the same length as metatarsal IV. Furthermore, metatarsal I is the most gracile and has no anterior pit like that of metatarsals II, III, and IV on the anterior surface near the distal end. The proximal head expands medially and laterally. Metatarsal II measures 90 mm and is nearly the same length as metatarsal III. The proximal portion expands and bears a concave anteromedial margin for articulation with the convex proximal portion of metatarsal I and a sigmoidal posterolateral side that corresponds to the inverse sigmoidal edge of the metatarsal III. Metatarsal III measures 89 mm and has the largest proximal expansion in the anteromedial/posterolateral direction. In proximal view, the proximal end is dumbbell shaped. Metatarsal IV measures 73 mm. The anteromedial edge, in proximal view, is concave and articulates with the most anterior dumbbell of metatarsal III. Metatarsal V is the shortest of the five and measures 47 mm. The proximal "head" articular surface is directed medially. The anterior surface is convex along most of its length, and the posterior surface is correspondingly concave over its length. A small, sharp flange of bone originates on the medial side about halfway down the metatarsal and is medially directed. The distal end terminates in an articular surface. No phalanges were found at the end of metatarsal V; however, the other phalanges were not completely articulated to the other metatarsals and the small phalanges that are usually articulated with the fifth metatarsal could have easily been washed away.

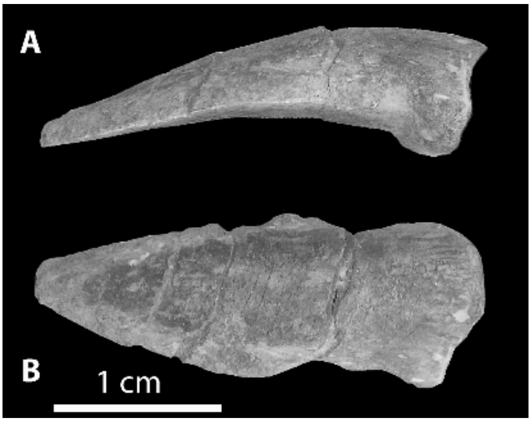

Fig. 51. An ungual of *Effigia okeeffeae* (AMNH FR 30587) in lateral (**A**) and dorsal (**B**) views.

The phalanges are unspecialized and cannot be put back in articulation with any certainty. The one ungual (fig. 51) recovered is dorsoventrally compressed and is slightly bowed ventrally. Most of the unguals of the holotype of *Shuvosaurus* are mediolaterally compressed except for the dorsoventrally

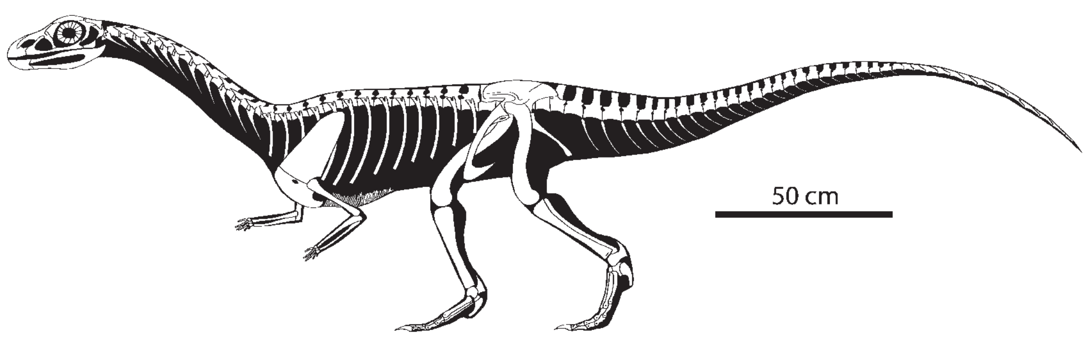

Fig. 52. Reconstruction of *Effigia okeeffeae* from all of the available specimens. Details of the distal tail, the number of vertebrae, and the proportions of the femur are uncertain (from Nesbitt and Norell, 2006).

compressed ungual of digit I. Therefore, the ungual recovered from *Effigia* is possibly from digit I.

A skeletal reconstruction of *Effigia okeeffeae* is presented in figure 52. This reconstruction is based on AMNH FR 30587, 30588, and 30589. Only the distal portion of the tail, parts of the manus, and part of the cervical vertebrae series are missing in all three AMNH specimens. The estimated length of the entire skeleton is 2 m long.

HISTOLOGY

Histological sections reveal growth rates and bone tissues and, in turn, may lead to hypotheses about growth and life strategies (Chinsamy, 1993, 1994; Reid, 1997a, 1997b; Curry, 1999; Horner et al., 2000; Sander, 2000; Ricqlès et al., 2003). In the following section I describe the thin sections of *Effigia* and then hypothesize about the growth strategy of *Effigia*.

The femur of AMNH FR 30589 was sectioned (fig. 53A–E) approximately between the midshaft and the fourth trochanter. However, the orientation of the fragment is not clear. The cross section is oval, but asymmetrical. Small cracks and the collapse of one of the sides into the marrow cavity occurred after death. The marrow cavity contains no cancellous tissue and is rather large. The bone has thin walls, reminiscent of theropod dinosaurs (Ricqlès et al., 2003).

Large erosion rooms speckle the inner perimedullar region (fig. 53D). Haversian tissue deposition thickness varies in the perimedullar region (fig. 53A–C). One side of the bone has a few scattered Haversian systems whereas the other side has Haversian tissue dense enough to completely eliminate all evidence of early growth stages (fig. 53C,E). Additionally, some of the heavily remodeled areas have been cross-cut by primary bone deposition as evidenced by Haversian systems cross-cut by primary bone (see arrows in fig. 53E). This heavy remodeling, as pointed out by Ricqlès et al. (2003), suggests sequential relocation of the marrow cavity through development.

The inner cortex is mostly composed of strongly vascularized fibro-lamellar bone (see areas between arrows in fig. 53B). In polarized light, a longitudinal section indicates that fibro-lamellar bone reached halfway between the inner and outer cortex (fig. 53D). The primary osteons are oriented longitudinally in the inner cortex. The oldest preserved line of arrested growth (LAG) occurs at the lateral extent of the Haversian systems in figure 53A. The primary osteons are oriented longitudinally, the bone is strongly vascularized, and the bone appears to be constructed out of a fibro-lamellar matrix in between each LAG in the inner cortex. The total thickness of the zones between the LAGs decreases toward the external surface of the bone. There appear to be at least four well-defined LAGs throughout the cortex and maybe two more in the outermost external cortex (fig. 53B). The outer part of the external cortex is composed of lamellar-zonal tissue. There, the primary osteons, though still strongly

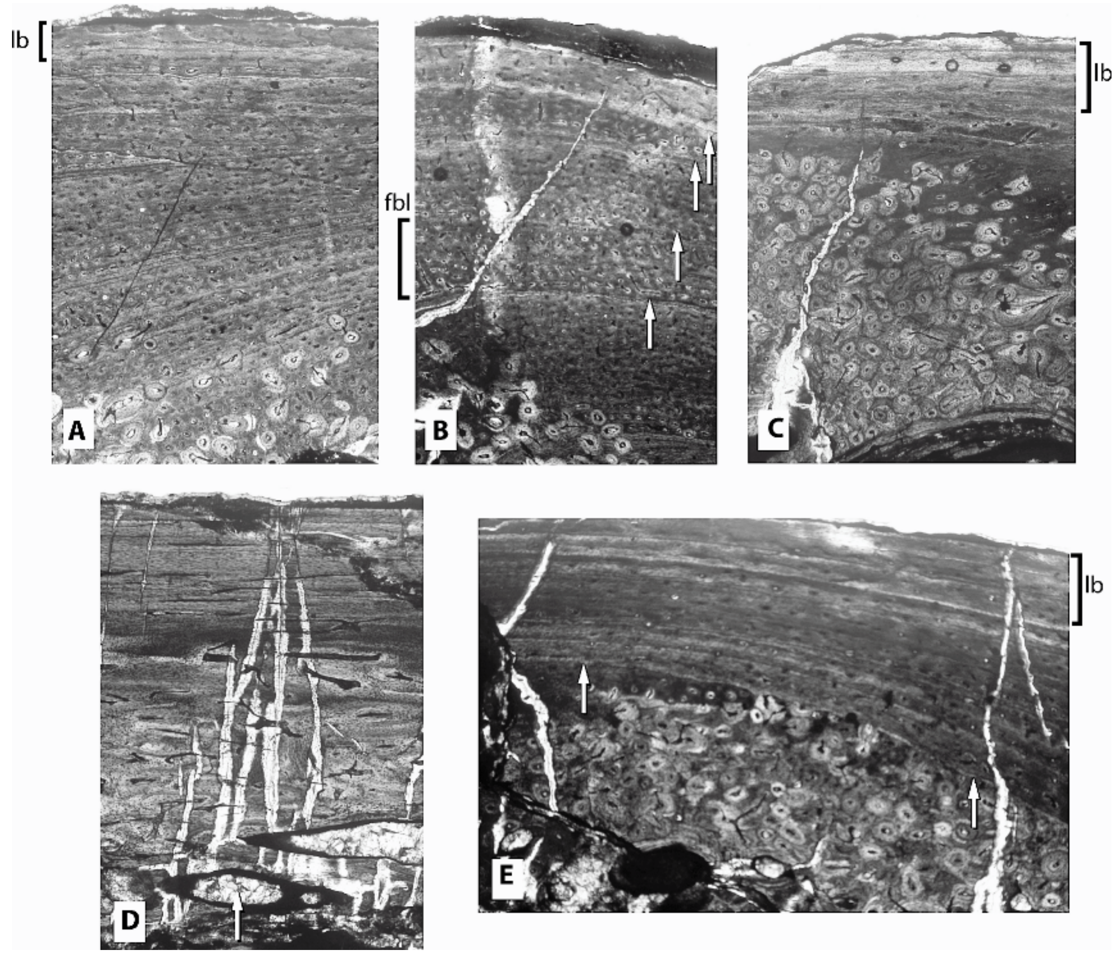

Fig. 53. Comparisons of histological sections taken near the midshaft of the right femur of AMNH FR 30589. **A–C, E** are transverse sections and **D** is a longitudinal section. The arrows indicate LAGs in **A**–**C**. The arrow in **D** indicates one of the large reabsorption pits near the middle of the bone. The arrows in E indicate where secondarily modified bone is cross-cut by primary bone. Note the extensive remodeling in all the sections in the inner portions of the sections. **B** shows an example of fibro-lamellar bone (= fbl) and **A**, **C**, and **D** show examples of lamellar-zonal bone (= lb) located on the edges of the bone.

vascularized, become circular and have short anastomoses. No Haversian systems are located in the outer cortex. However, a densely packed cluster of Haversian systems lies adjacent against the lamellar-zonal tissue on one side of the bone (fig. 53C). The histology sections of the femur indicate that the midshaft of the femur had experienced extensive remodeling.

The inner cortex and parts of the inner external cortex compare well with that of *Terrestrisuchus*, a basal crocodylomorph. Both share the presence of longitudinal primary osteons surrounded by a matrix of fibro-lamellar bone (Ricqlès et al., 2003). However, Ricqlès et al. (2003) note that other crocodile-line archosaurs, parasuchians, stagonolepidids, and *Postosuchus* also have fibro-lamellar bone; it is restricted to the inner cortex. Additionally, Ricqlès et al. (2003) argue that *Postosuchus* has zones of fibro-lamellar bone between each LAG through the majority of inner cortex and some of the inner external cortex. The fibrolamellar zones of *Effigia* between the LAGs are much wider and much more similar to that of *Terrestrisuchus*. The thick zones of fibro-lamellar bone in the humerus of *Terrestrisuchus* and the thinner fibro-lamellar zones of *Postosuchus* led Ricqlès et al. (2003) to suggest that *Terrestrisuchus* and *Postosuchus* grew at elevated rates compared to the other crocodile-line archosaurs. *Effigia* possibly grew at rates comparable to both *Terrestrisuchus* and *Postosuchus*.

The femur of *Effigia* grew rapidly early in life as evidenced by the fibro-lamellar bone combined with few LAGs. The innermost cortex is made up of woven fibro-lamellar bone that is typical of dinosaur and pterosaur bone structure (Ricqlès et al., 2003; Padian et al., 2004). The femur of *Effigia* continued to grow at fast rates through the outer inner cortex and the inner external cortex, but left LAGs. Only in the external cortex did the femur of *Effigia* start to slow down and deposit the lamellar-zonal bone typical of crocodile-line archosaurs. Here, the orientation of the primary osteons switches from longitudinal to more circular.

In sum, *Effigia* grew more like a crocodylian than a dinosaur; however, it grew at higher rates than most typical crocodile-line archosaurs except basal crocodylomorphs (e.g., *Terrestrisuchus*).

The probable higher rates of growth of *Effigia* relative to *Alligator* and other crocodylians raises the question, is the holotype a juvenile or an adult? Tetrapods grow relatively more quickly while young. Crocodile-line archosaurs have a much shorter period of rapid growth and a much longer period of slow growth as they near maturity (Padian and Horner, 2004). In contrast, most dinosaurs and pterosaurs grow rapidly through life and then slow down their growth only later in life (Chinsamy, 1995; Chinsamy and Dodson, 1995). The presence of at least four LAGs, with the possibility of two more, and extensive remolding in the femur of *Effigia* suggest that AMNH FR 30587 had been growing for a minimum of 4 years, assuming each LAG represents 1 year. However, the number of LAGs is not a good indicator of maturity alone; other skeletal elements must be evaluated independently (Horner et al., 1999, 2000).

The dissociation of elements of the braincase and the presence of the well-defined interdigitating sutures among the postorbital, frontal, and parietals suggest that the animal was a juvenile. Furthermore, the neurocentral sutures of the presacral vertebrae had not closed by the time of death. In modern crocodylians, the neurocentral suture of the cervical vertebrae closes at maturity (Brochu, 1996). The rough texture of the proximal and distal ends of the limb bones also suggest that AMNH FR 30578 had not matured.

AMNH FR 30587 is immature as evidenced by the combination of the immature skull, postcrania, and histology sections of the femur. Moreover, the holotype is the biggest specimen known. Therefore, all of the known specimens of *Effigia*, all from the Ghost Ranch *Coelophysis* Quarry, are immature.

DISCUSSION

RELATIONSHIPS

A modified version of Benton's (1999) phylogenetic analysis of basal archosaurs was used to test the relationships of *Effigia*, *Shuvosaurus*, and *Chatterjeea* (Nesbitt and Norell, 2006). The phylogenetic analysis presented in Nesbitt and Norell (2006) had three specific goals: (1) to give a basic understanding of the relationships of *Effigia*, (2) to test if similar characters between theropods and *Effigia* are convergences or homologues, and (3) to test Long and Murry's (1995) hypothesis that the skull of *Shuvosaurus* belongs to the postcrania of *Chatterjeea*. Benton's (1999) basal archosaur matrix provides a synthesis of most basal archosaur phylogenies (Benton and Clark, 1988; Sereno, 1991; Juul, 1994) appropriate to testing the three goals listed above. Here, I use the matrix of Nesbitt and Norell (2006) and add *Sillosuchus longicervix* and two additional characters (numbers 82 and 83; see appendix 4 and 5 for character list and scorings) as a preliminary attempt at examining the relationships of *Effigia* and close relatives (see Group X and Group Y below). This phylogeny is not, however, utilized to give the exact position of *Effigia* and close relatives within Suchia because many more "rauisuchian," stagonolepidid, and crocodylomorph were excluded and a revised character matrix is required for the groups. A large, thorough analysis is currently being prepared by a group of basal archosaur workers.

A unique tree was recovered with 158 steps (21 taxa, 83 characters, characters weighted equally, unordered, consistency index [CI] 0.5949, retention index [RI] 0.8363). Relative to Nesbitt and Norell (2006), Bremer support values changed at the *Effigia* + *Shuvosaurus* node with the addition of *Sillosuchus*.

Effigia is well supported within Suchia (fig. 54). The fully developed crocodile-normal ankle, crocodylomorph-like pes, and other unambiguous synapomorphies within Suchia clearly place *Effigia* more closely related to crocodiles than to birds. Therefore, most of the theropod-like characters that *Effigia* exhibits are convergent with dinosaurs, theropods, and other clades within Theropoda (see below). The placement of *Effigia* within Dinosauria as a basal theropod requires the addition of 27 steps and its placement as sister to ornithomimids requires an additional 30 steps.

The intensely debated affinities of *Shuvosaurus* were evaluated in the same phylogenetic analysis with new information from *Effigia* (Nesbitt and Norell, 2006). In 1993, Chatterjee assigned an enigmatic archosaur skull, *Shuvosaurus*, from the Late Triassic Miller (Post) Quarry to an ornithomimid dinosaur based on the edentulous jaws, braincase, and overall similarity. Chatterjee's controversial interpretation implied ornithomimids were present in the Late Triassic and, thus, most theropod clades had diverged by the Late Triassic. Long and Murry (1995) described *Chatterjeea* based on abundant postcranial associated skeletons also from the Miller Quarry. They suggested that *Chatterjeea* is a pseudosuchian closely related to "poposaurs" and *Postosuchus* and named the family Chatterjeeidae. Long and Murry (1995) did not recognize skull material for *Chatterjeea*, but suggested that the skull of *Shuvosaurus* belonged to the body of *Chatterjeea* based on the following five reasons: (1) close association between *Chatterjeea* disarticulated postcrania and the cranium of *Shuvosaurus*, (2) similar size of *Chatterjeea* and *Shuvosaurus*, (3) the lack of any other ornithomimid remains in the Post Quarry, (4) the failure of Chatterjee (1993) to present a clear case for the ornithomimid affinities of the skull of *Shuvosaurus*, and (5) the similar stratigraphic ranges of both *Shuvosaurus* and *Chatterjeea*. More recently, Rauhut (1997, 2003) disagreed with Long and Murry (1995) and argued that *Shuvosaurus* was a basal theropod.

The phylogenetic analysis of Nesbitt and Norell (2006) demonstrates that *Shuvosaurus* and *Effigia* are closely related and strongly supports the hypothesis that the skull of *Shuvosaurus* belongs to the postcrania of "*Chatterjeea*." Additionally, "*Chatterjeea*" and *Shuvosaurus* were scored independently and incorporated in the matrix of Nesbitt and Norell (2006). As a result, *Effigia*, *Shuvosaurus*, and "*Chatterjeea*" formed a polytomy. For the analysis here and Nesbitt and Norell (2006), the scorings for *Shuvosaurus* and "*Chatterjeea*" were combined. *Shuvosaurus* has priority over *Chatterjeea*, so *Chatterjeea* is a subjective junior synonym of *Shuvosaurus* and, thus, Shuvosauridae has priority over Chatterjeeidae. Shuvosauridae is not defined phylogenetically here because it is premature to assign Shuvosauridae to a particular node.

Relationships with Other Rauisuchians

The phylogenetic analysis presented in Nesbitt and Norell (2006) indicates a close relationship among *Effigia* and other rauisuchians. Here, this relationship will be more completely examined. This part of the discussion will highlight similar character states and possible relationships among *Effigia*, *Postosuchus* (TTUP 9002), *Batrachotomus* (SMNS 80260), *Saurosuchus* (PVL 2198, PVSJ 32), and Nesbitt's (2005a) Group X containing the following taxa: *Arizonasaurus* (MSM 4590), *Lotosaurus*, *Bromsgroveia* (WM G3), *Poposaurus* (CFMNH UR357), *Sillosuchus* (PVSJ 85), and *Shuvosaurus* (TTUP 9280).

The strongly derived skull of *Effigia* shares few characters that are thought to be apomorphies with the skulls *Postosuchus*, *Batrachotomus*, and *Saurosuchus*. *Effigia* shares the presence of a small foramen between the maxilla and premaxilla with *Postosuchus* and *Batrachotomus*, but not with

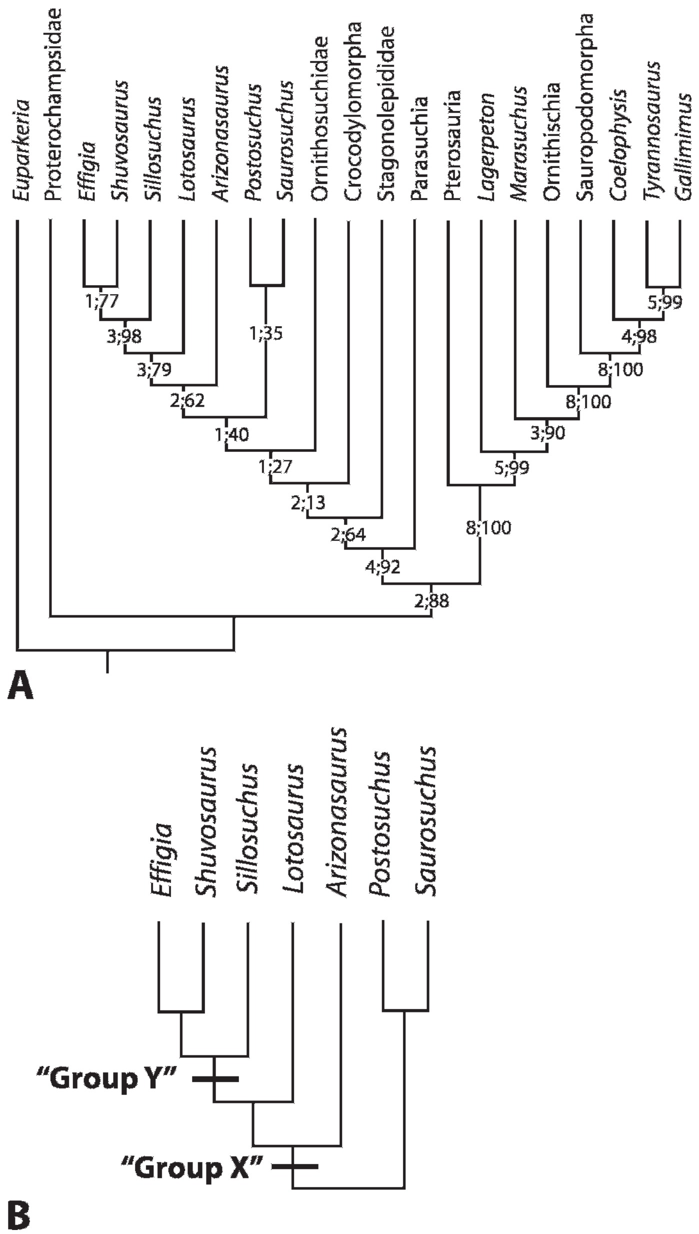

Fig. 54. The relationships of *Effigia okeeffeae* among basal archosaurs (**A**) (21 taxa, 83 characters, characters weighted equally, unordered, Tree Length = 158, consistency index [CI] 0.5949, retention index [RI] 0.8363). Support values (left, decay; right, bootstrap) are listed at each node. (**B**) *Effigia*, Group X, and Group Y enlarged from **A**. Group X contains *Arizonasaurus*, *Lotosaurus*, *Sillosuchus*, *Effigia*, and *Shuvosaurus* and Group Y contains *Sillosuchus*, *Effigia*, and *Shuvosaurus*.

Saurosuchus (PVSJ 32). However, the foramen of *Effigia* is channeled on the lateral surface of the maxilla, a feature not present in *Batrachotomus* and *Postosuchus*. Thus, this character may not be homologous among these taxa and other archosaurs (see Gower, 2000). The presence of a kinked postorbital, thought to be a character uniting *Postosuchus*, *Batrachotomus*, and *Saurosuchus*, is not present in *Effigia*. *Effigia* shares no other characters that are unambiguously found in *Postosuchus*, *Batrachotomus*, and *Saurosuchus*.

Most of the character states shared among *Effigia*, *Postosuchus*, *Batrachotomus*, and *Saurosuchus* occur in the postcranium, particularly the pelvis. All of these taxa share the presence of a morphologically similar posteriorly directed pubic boot. Although pubic boots occur in neotheropods, *Herrerasaurus*, and *Staurikosaurus*, the presence of a pubic boot may be a synapomorphy for a clade of crocodile-line archosaurs. Moreover, the pubic shafts of *Effigia*, *Postosuchus*, *Batrachotomus*, and *Saurosuchus* are ventrally elongated. Ornithodirans also have elongated pubes (Benton and Clark, 1988), yet the presence of this feature within a group of crocodile-line archosaur suggests it may be apomorphic for these taxa. *Effigia*, *Postosuchus*, *Batrachotomus*, and *Saurosuchus* all share the presence of a supra-acetabular crest dorsal to the supra-acetabular rim. In *Postosuchus*, *Batrachotomus*, and *Saurosuchus*, the crest is more massive than in *Effigia* and does not arc anteriorly as it does in *Effigia*. The presence of a supra-acetabular crest has repeatedly been used as a phylogenetic character to unite a subset of "rauisuchians" (Benton and Clark, 1988; Parrish, 1993). Gower (2000) suggests that the crests may not be homologous, but it has yet to be explicitly tested. The similar ischium morphology uniting *Effigia*, *Postosuchus*, *Batrachotomus*, and *Saurosuchus* is also found in *Lotosaurus*, *Arizonasaurus*, and *Poposaurus*.

RELATIONSHIPS WITH GROUP X

Effigia possesses all of the characters presented in Nesbitt (2005a) for Group X containing *Arizonasaurus*, *Bromsgroveia*, *Poposaurus*, *Shuvosaurus*, and *Sillosuchus*. Additionally, a clade containing *Arizonasaurus*, *Sillosuchus*, *Effigia*, and *Shuvosaurus* is supported by the preliminary phylogenetic analysis presented here. Group X is united by the following character states (not all used in the phylogenetic analysis):

1. Loss of osteoderms. The articulated dorsal and cervical region of *Effigia* clearly lacks osteoderms.
2. Long, thin mediolateral supra-acetabular crest on ilium. In *Effigia*, the crest is oriented dorsoventrally and arcs anteriorly.
3. Waisted area of the ilium between pubic and ischiadic processes. This is equivalent to Galton and Walker's (1996) and Benton and Clark's (1988) perforated acetabulum character and is clearly present in *Effigia*.
4. First sacral rib articulates extensively with the anteriorly pointing crest of the ilium. The first sacral rib articulates completely with the anteriorly pointing crest in *Effigia*.
5. Sacral rib bridges between the sacral vertebrae and the ilia are anteroposteriorly narrow.
6. No spine tables or distally expanded neural spines.
7. Sacral vertebrae fully fused: the prezygapophyses and postzygapophyses fuse together and the distal neural arches fuse.

Other potential characters uniting Group X as listed by Nesbitt (2005a):

1. Posterior cervical vertebrae have divided parapophyses: This character cannot be confirmed in any of the *Effigia* specimens.
2. Thin ischiadic boot: This character is present in *Effigia*. However, the boot is not as well developed as in *Poposaurus* and *Arizonasaurus*.
3. Dorsolaterally thin pubic boot: The pubic boot of *Effigia* is extremely posteriorly elongated and dorsolaterally compressed. A small, thin posteriorly directed pubis boot is present in *Sillosuchus* (*contra* Alcober and Parrish, 1997).

For the first time, the skulls of three members of Group X, *Effigia*, *Shuvosaurus*, and *Arizonasaurus*, can be compared. The skulls of *Arizonasaurus*, *Shuvosaurus* and *Effigia* share the following features:

1. Smooth frontal and nasal: The frontals and nasals of parasuchians, stagonolepidids, crocodylomorphs, *Postosuchus*, *Batrachotomus*, and *Saurosuchus* are ornamented with grooves, bumps, and ridges. The frontals and nasals of *Effigia*, *Shuvosaurus*, and *Arizonasaurus* all are smooth. Proterochampsids have sculptured nasals and frontals. Other archosaurs also have smooth frontals and nasals (e.g., theropods, *Silesaurus*).
2. Similar textured orbital margin of frontal: The orbital rim of the frontal is rugose and lightly striated dorsoventrally in *Arizonasaurus*, *Shuvosaurus*, and *Effigia*. Taxa such as *Postosuchus*, *Saurosuchus*, and *Batracho-*

tomus lack this type of sculpturing at the orbital margin.

3. External nasal margin created by dorsal process of maxilla: The posterior border of the external nasal is formed by the dorsal process of the maxilla in all three taxa. *Batrachotomus* (a taxon that is not a member of Group X) and some stagonolepidids (*Desmatosuchus haplocerus* [TTUP 9024], *Longosuchus*, but not *Aetosauroides*) also have a condition similar to that of *Effigia* and *Arizonasaurus*. In *Postosuchus*, *Saurosuchus*, and crocodylomorphs, a posterior process of the premaxilla fits between the external naris and the dorsal process of the maxilla, thus excluding the maxilla from the external naris. The external nasal margin is not preserved in the skull of *Shuvosaurus*.
4. Anteroposteriorly expanded lateral process ("head" that articulates with the jugal) of the ectopterygoid: This character state is present in Group X and in *Sphenosuchus*. An anteroposteriorly expanded lateral process of the ectopterygoid is present in proterochampsids (*Charanesuchus*, *Gualosuchus*, and *Tropidosuchus*). However, in proterochampsids, the anterior portion articulates with the maxilla as well as the jugal. In *Arizonasaurus*, *Effigia*, and *Shuvosaurus*, the ectopterygoid only articulates with the jugal.
5. Slightly anteriorly elongated and horizontally oriented parabasisphenoid: The parabasisphenoid of *Arizonasaurus* is oriented more like that of ornithodirans than that of other crocodile-line archosaurs (see Gower, 2002). The ventral margins of the parabasisphenoid pterygoid processes lie in a horizontal line with the ventral margin of the basitubera in *Arizonasaurus* (Gower and Nesbitt, 2006). In addition, the parabasisphenoid of *Arizonasaurus* is slightly anteriorly elongated. *Shuvosaurus* and *Effigia* both have horizontally oriented parabasiphenoids and an anteriorly elongated parabasisphenoid. In other crocodile-line archosaurs and in non-crown-group archosaur archosauriforms such as *Euparkeria*, the parabasisphenoid pterygoid processes lie well below the basitubera Some crocodile-line archosaurs, such as *Sphenosuchus*, also elongate the parabasisphenoid; however, *Sphenosuchus* elongated the parabasisphenoid in an anteroventral direction.
6. Absence of a quadrate foramen: The quadrates of *Arizonasaurus*, *Effigia*, and *Shuvosaurus* all lack a quadrate foramen. The quadrate foramen is present in archosaurs plesiomorphically (proterochampsids and *Euparkeria*) and nearly all clades of crocodile-line archosaurs (parasuchians, *Riojasuchus*, *Postosuchus*, *Batrachotomus*, stagonolepidids) except basal crocodylomorphs (*Hesperosuchus*, *Dromicosuchus*, and *Sphenosuchus*).

RELATIONSHIPS WITH GROUP Y

Arizonasaurus, *Shuvosaurus*, and *Effigia* share many character states to the exclusion of all other crocodile-line archosaurs. However, no distinct pair of foramina for the entrance of the cerebral branches of the internal carotid arteries is located posteromedial to the base of the basipterygoid processes on the ventral surface of the parabasisphenoid as in *Arizonasaurus* (Gower and Nesbitt, 2006) and other non-crown-group archosaur archosauromorphs (Benton, 1983; Evans, 1986; Parrish, 1993; Gower and Sennikov, 1996; Gower and Weber, 1998; Gower, 2002). Instead, there are distinct foramina on the lateral surface of the parabasisphenoid for the entrance of the cerebral branches of the internal carotid arteries in *Effigia* and *Shuvosaurus* and as in other suchian archosaurs (Parrish, 1993; Gower, 2002).

The similarities of *Effigia*, *Shuvosaurus*, and *Sillosuchus* within Group X suggest a close relationship. A full phylogenetic analysis of Group X is premature at this time for reasons discussed in Nesbitt (2005a). Instead of providing a diagnosis and definition of the clade containing these three taxa, I propose Group Y that unites *Effigia*, *Shuvosaurus*, and *Sillosuchus* based solely on shared derived character states. The results from the preliminary phylogenetic analysis presented above support a group containing *Sillosuchus*, *Effigia*, and *Shuvosaurus*. The following shared character states were not used in the preliminary phylogenetic but serve as an exploration of new character states that may be later used in a more complete phylogenetic analysis. *Effigia*, *Shuvosaurus*, and *Sillosuchus*, or Group Y, share the following postcranial characters:

1. Sacral vertebrae neural arches completely fused together. Convergent with theropod dinosaurs.
2. Loss of the centra rims within the sacrum. The centra rims within the sacrum are only

slightly expanded; the entire sacrum is nearly cylinder shaped. Convergent in theropod dinosaurs (e.g., *Coelophysis*, Aves).

3. Presence of four or more sacral vertebrae. *Sillosuchus* has at least five sacral vertebrae, whereas *Shuvosaurus* and *Effigia* have four. Convergent in dinosaurs.
4. A thin lamina of bone connects the posterior iliac wing with the preacetabular process of the ilium. This thin lamina expands dorsally higher than both the posterior iliac wing with the preacetabular process. Convergent in theropod dinosaurs.
5. Short, strongly fused ischia wherein the individual ischial shafts are rounded in cross section. The ischia of *Arizonasaurus*, *Poposaurus*, *Batrachotomus*, *Saurosuchus*, and *Postosuchus*, although usually strongly fused, are all strongly mediolaterally compressed and posteriorly elongated.
6. Posterior faces of the centra of the cervical vertebrae compressed dorsoventrally. The posterior centrum face is oval whereas the long axis is oriented mediolaterally.
7. Strongly amphicoelous cervical vertebrae. The vertebrae of *Effigia*, *Shuvosaurus*, and *Sillosuchus* have distinct centra rims that surround the articular faces of the centra. The sharp rim creates a bowllike structure that is strongly amphicoelous.
8. "Pleurocoels" (see description of cervical vertebrae above) located on the posterior portion of the centra of anterior cervical vertebrae. Convergent in coelophysoid dinosaurs (Rauhut, 2003).
9. Parapophysis laterally expanded and the ventralmost portion of the parapophysis is on the same plane as the ventral surface of the centrum. Here, the ventral surface of the centrum is nearly anteroposteriorly flat.
10. The preacetabular process of the ilium is nearly the same length or longer than the postacetabular process of the ilium in *Effigia*, *Shuvosaurus*, and *Sillosuchus*. Most basal archosaurs have a short preacetabular process and a long postacetabular process. *Poposaurus* also has a preacetabular process of the ilium that is nearly the same length or longer than the postacetabular process of the ilium.
11. Absence of a distinct ridge of bone for the attachment of the m. caudusfemoralis (= fourth trochanter). Both *Shuvosaurus* and *Sillosuchus* lack this feature. The character state is unknown in *Effigia*.

Effigia and *Shuvosaurus* are more completely preserved than *Sillosuchus*. It is possible that some of the following character states may be present also in *Sillosuchus*; however, until more material of this taxon is found, these character states cannot be confirmed or denied. *Effigia* and *Shuvosaurus* share the follow character states:

1. Femur lacking lateral proximal tuber. Basal crocodylomorphs, stagonolepidids, parasuchians, and *Euparkeria* all have two medial proximal tubera and one lateral tuber. Some members of Group X (*Arizonasaurus* and *Poposaurus*), *Postosuchus*, and *Batrachotomus* also have all three tubera. This character cannot be evaluated in the poorly preserved and crushed femora of *Sillosuchus*.
2. Anteromedial femoral tuber larger than all other crocodile-line archosaurs and expands or "hooks" posteriorly (see fig. 44). The much larger anteromedial tuber relative to the posteromedial tuber hooks posteriorly. A sulcus separates the two medial tubera. The anteromedial tuber is similar to the "offset femoral head" of a dinosaur femur. However, the "offset femoral head" of a dinosaur femur articulates into the acetabulum medially whereas the "offset head" of *Effigia* and *Shuvosaurus* articulate with the acetabulum anteriorly.
3. Groove between the fibular condyle and the lateral condyle of the distal portion of the femur in distal view: This is convergent in basal crocodylomorphs (e.g., *Dromicosuchus*) and basal theropods (e.g., *Coelophysis*).
4. Pubis with large mediolaterally compressed pubic boot greater than 33% of the length of the shaft of the pubis. *Sillosuchus* does have a small pubic boot. The small size of the pubic boot in *Sillosuchus* may be autapomorphic for the taxon because other potentially related taxa, *Poposaurus*, *Arizonasaurus*, *Postosuchus*, and *Batrachotomus*, all have relatively larger pubic boots. On the other hand, the presence of a large pubic boot may be apomorphic for a clade containing *Shuvosaurus* and *Effigia*.
5. Long distinct ridge oriented parallel on the lateral side of the shaft of the pubis (see fig. 42). This distinct, sharp ridge runs from the anterodorsal edge to the posteroventral edge across the pubic shaft. The presence of this feature may be apomorphic for a clade containing *Shuvosaurus* and *Effigia*.
6. Dorsoventrally compressed unguals. The unguals of *Shuvosaurus* are enlarged and have a system of well-defined grooves for blood vessels. The one recovered dorsoventrally compressed ungual from *Effigia* is identical

to the ungual of digit I of *Shuvosaurus* (TTUP 9001).

7. Anteriorly elongated caudal prezygapophyses. Convergent with many theropod clades (Rauhut, 2003).
8. Fibular crest on the lateral side of the proximal portion of the tibia. This feature is present in nearly all basal dinosaurs and close relatives (e.g., *Silesaurus*).
9. Proximal portion of the humerus expanded less than twice the width of the midshaft of the humerus. The proximal portion of the humerus of most crocodile-line archosaurs is at least twice the width of the midshaft. The proportions of the proximal end, shaft, and the distal end of the humerus of *Effigia* and *Shuvosaurus* is similar to that of ornithodiran taxa (Fraser et al., 2002), but rather different than other crocodile-line archosaurs.

The strongly derived skulls of *Effigia* and *Shuvosaurus* share the following characters:

1. Elongated parabasisphenoid: Rauhut (2003) used the elongation of the parabasisphenoid (Rauhut, 2003; character 56) to support a clade containing *Shuvosaurus*, *Coelophysis bauri*, and *Coelophysis rhodesiensis*. Thus, the elongation of the parabasisphenoid must be convergent among the clade containing *Effigia* and *Shuvosaurus* and the clade containing *Coelophysis bauri* and *Coelophysis rhodesiensis*.
2. The presence of two grooves leading to the foramen for the internal carotid arteries located on the lateral and ventrolateral sides of the parabasisphenoid (see description of the parabasisphenoid above): Presence of this condition in both *Effigia* and *Shuvosaurus* may indicate a synapomorphy for the clade containing the two.
3. Exoccipitals separated by a gap: Crocodylomorphs and theropods also possess this character.
4. Deep parabasisphenoid recess (character 76 in the phylogenetic analysis of Nesbitt and Norell, 2006): Cited by Rauhut (1997) as a potential link between theropods and *Shuvosaurus*, the presence of a deep parabasisphenoid recess is convergent among *Effigia*, *Shuvosaurus*, and theropods. Rauhut (2003) notes the presence of a similar recess in the basal crocodylomorph *Dibothrosuchus*. In theropods, the parabasisphenoid recess is subdivided posteriorly by a thin midline lamina; a subdivision of the parabasisphenoid recess does not occur in *Effigia* and *Shuvosaurus*.
5. Edentulous premaxilla (character 74 in the phylogenetic analysis of Nesbitt and Norell, 2006): An edentulous premaxilla is common to a number of ornithodiran archosaurian groups (e.g., therizinosaurids, ornithomimids, pterosaurs), but rare among crocodile-line archosaurs with the exception of the stagonolepidid *Desmatosuchus haplocerus* (TTUP 9024; Small, 2002) and *Lotosaurus*. *Effigia*, *Shuvosaurus*, and *Lotosaurus* are unusual in this respect.
6. Anterodorsal process of the premaxilla longer than the length of the anteroposterior length of the premaxilla (character 75 in the phylogenetic analysis of Nesbitt and Norell, 2006).
7. Ventral premaxillary shelf formed by the articulation between the right and left premaxillae: This character evolved in several groups with edentulous premaxillae (e.g., oviraptorids, ornithomimids), but seems to be rare among crocodile-line archosaurs.
8. Edentulous maxilla (character 74 in the phylogenetic analysis of Nesbitt and Norell, 2006). This widely distributed character evolved in many archosaurian groups (e.g., ornithomimids, birds) and non-archosaurian groups (e.g., testudines). However, the limited distribution within crocodile-line archosaurs suggest that it represents a potential synapomorphy of the clade containing *Effigia* and *Shuvosaurus* and possibly *Lotosaurus*.
9. Mandibular fenestra greater than half the length of the mandible (character 77 in the phylogenetic analysis of Nesbitt and Norell, 2006): This unique character represents a potential synapomorphy of *Effigia* + *Shuvosaurus*.
10. Large surangular foramen: A surangular foramen is present in *Euparkeria* (Ewer, 1965), *Revueltosaurus*, some stagonolepidids (*Desmatosuchus haplocerus* [TTUP 9024], *Longosuchus*), *Herrerasaurus*, and nearly all theropods.
11. Absence of anteroposteriorly oriented surangular ridge: A distinct anteroposteriorly oriented surangular ridge is present in *Arizonasaurus*, *Postosuchus*, *Saurosuchus*, *Batrachotomus*, *Herrerasaurus*, and some theropods.
12. Anteroposteriorly expanded suture between the dentaries: The weak contact of the dentaries of *Arizonasaurus*, *Postosuchus*, *Saurosuchus*, *Batrachotomus*, and basal crocodylomorphs (*Hesperosuchus*, *Sphenosuchus*) differs from the anteroposteriorly expanded suture between the dentaries of *Effigia* and *Shuvosaurus*. Only in later crocodyliforms

does the suture between the dentaries expand anteroposteriorly.

13. Largely concave distal articular margin of the quadrate and corresponding convex articular surface of the articular: In contrast, the quadrates of all crocodile-line archosaurs and most other archosaurs have a convex articular facet of the quadrate and a corresponding concave articular facet of the articular.
14. Elongated ventral process of the postorbital forms part of the ventral margin of the orbit. Common to archosaurs with an enlarged orbit (e.g., ornithomimids), but not present within the crocodile-line archosaur clade.
15. Orbit greater than 25% of the length of the skull. Even though the skull of *Shuvosaurus* is not complete, the length of the orbit can be estimated from the distance between the lacrimal and the postfrontal, both which are still articulated to the frontal. Again, this is common to archosaurs with an enlarged orbit (e.g., ornithomimids), but not present within the crocodile-line archosaur clade.
16. Postfrontal absent: Crocodylomorphs and dinosaurs also lack the postfrontal (Benton and Clark, 1988; Sereno, 1991).
17. Anteroventrally angled quadrates: Nearly all basal archosaurs have anterodorsally/posteroventrally angled quadrates. Spinosaurids and ornithomimids have a similar orientation of the quadrate as *Effigia* and *Shuvosaurus*.

Group Y has yet to be tested phylogenetically in a rigorous analysis and to do so at present would be premature. However, the list of character states presented above is only known in *Effigia*, *Shuvosaurus*, and *Sillosuchus* (except where noted) among crocodile-line archosaurs, but not among all archosaurs. This potential group containing *Effigia*, *Shuvosaurus*, and *Sillosuchus* will remain unnamed to avoid confusion in the future until it can be both diagnosed and defined in a phylogenetic analysis. Shuvosauridae would be an appropriate name for Group Y containing *Effigia*, *Shuvosaurus*, and *Sillosuchus*.

HOW DOES *LOTOSAURUS* RELATE TO GROUP Y?

Lotosaurus is known from a nearly complete articulated skeleton, including a skull (Zhang, 1975). However, the skeleton has never been fully described. I have not examined the holotype firsthand, but I have examined casts and photographs of the holotype and can use information coded and illustrated by Parrish (1993) to compare it to *Effigia*. It is not clear how much of the skeleton has been restored, so the following comparisons are tentative.

Lotosaurus was found to clade with members of Group X and found to be the sister taxon to all members of Group Y in the preliminary analysis presented here. *Lotosaurus* has a "crocodile-normal ankle" according to Parrish (1993), which place *Lotosaurus* among various "rauisuchians" in his phylogenetic analysis. The pelvis of *Lotosaurus* shares similar character states with *Effigia* and *Shuvosaurus*. The ilium has a thin distinct supra-acetabular crest that is anteriorly directed, a well-pronounced supra-acetabular rim, a waisted region between the pubic and ischiadic processes, and a thin flange connects the short preacetabular process with the posterior iliac wing. The pubis is longer than the ischium, but lacks a pubic boot. Additionally, *Lotosaurus* has at least three sacral vertebrae and a fused "rauisuchian-like" ischium. Based on the preceding pelvic characters, *Lotosaurus* is hypothesized to be more closely related to *Effigia* and *Shuvosaurus* than to stagonolepidids, parasuchians, and crocodylomorphs.

The skulls of *Effigia*, *Shuvosaurus*, and *Lotosaurus* share the presence of edentulous jaws, but are these features homologous? Unfortunately, the uncertainties concerning the sutures between the premaxilla and the nasal and the nasal and maxilla prohibit comparisons with the character states of *Shuvosaurus* + *Effigia*. However, the edentulous premaxilla and maxilla exhibit similar proportions to those of *Shuvosaurus* and *Effigia*. It appears that *Lotosaurus* also shares the distinct medial premaxillary shelf with *Effigia* and *Shuvosaurus*. The body of the maxilla of *Lotosaurus* is reduced in size with long dorsal and posterior processes similarly to *Effigia*. The mandible shares derived character states with *Effigia*. The mandibular fenestra is large and anteriorly shifted. This is similar to *Effigia* and *Shuvosaurus*, but the dentary is longer than in *Lotosaurus* and the surangular and angular are proportionally shorter. Additionally, *Lotosaurus* also shares a medial distinct shelf of the dentaries with *Effigia* and *Shuvosaurus*. The much smaller size of the orbit and the large size of the lower temporal fenestra of *Lotosaurus* differ from the proportions present in *Shuvosaurus* and *Effigia*. According to Parrish (1993), *Lotosaurus* has a postfrontal and postorbital–quadratojugal contact; *Shuvosaurus* and *Effigia* have neither. However, these character states cannot be confirmed.

Nevertheless, the differences between *Lotosaurus* and *Effigia* and *Shuvosaurus* represent plesiomorphic states within the Archosauria according to previous phylogenetic hypotheses (Benton and Clark, 1988; Sereno, 1991; Parrish, 1993; Juul, 1994; Benton, 1999). For instance, the presence of a postfrontal, the size of the orbit, and length of the dentary of *Lotosaurus* is more similar to forms such as *Euparkeria*, most "rauisuchian" taxa, and most ornithodirans, thus, plesiomorphic for Archosauria. Yet, *Lotosaurus* bears edentulous jaws (character states that unite Lotosaurus + *Effigia* + *Shuvosaurus* in the preliminary analysis presented here) and other potential synapomorphies with *Effigia* + *Shuvosaurus*. Even though not listed by Nesbitt (2005a) as a member of Group X because of unconfirmed characters states, it is clear that *Lotosaurus* belongs to this group based on this discussion and discussions in Nesbitt (2005a). Therefore, as indicated by the early Middle Triassic age (Zhang, 1975), *Lotosaurus* is closely related to Group Y and may be preserving character transformations between basal members of Group X and Group Y.

If *Lotosaurus* is more closely related to *Shuvosaurus* and *Effigia* than to *Arizonasaurus*, the ctenosauriscids (as proposed by Nesbitt 2005a) would be paraphyletic. Until a full description of *Lotosaurus* appears and it is known which parts of the skeleton are a composite or reconstructed, the phylogenetic position of *Lotosaurus* is tentative.

CONVERGENCES

In this section, I examine the characters that *Effigia* and close relatives have that are convergent with ornithodirans, dinosaurs, coelurosaurs, Ornithomimosauria, and the edentulous clade of ornithomimids (*Garudimimus* + Ornithomimidae of Kobayashi and Lü 2003; Kobayashi and Barsbold 2005). This section explains each character state and comments whether the character present in *Effigia* and close relatives and a clade within the Ornithodira are actually the same character state or just convergent/analogous. For example, the presence of a posteriorly directed process on the posterolateral portion of the transverse processes of the posterior cervical vertebrae of *Effigia* and a probable clade containing *Gallimimus* and *Archeornithomimus* cannot be homologous, yet the character is identical (the process in the same position, off the same bone, etc.) in both taxa. Other characters described are generally similar, but are actually different after a close inspection. The discussion of these convergences will help clarify characters for use in basal archosaur phylogenetic analyses.

CONVERGENCES WITH ORNITHODIRANS

1. Osteoderms absent. The presence of osteoderms in the outgroups to Archosauria (*Euparkeria*, proterosuchians; Parrish, 1993; Benton, 1999) indicates that the presence of osteoderms is plesiomorphic for Archosauria. Furthermore, the absence of osteoderms has been used as a character to unite the Ornithodira in multiple analyses (Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Juul, 1994; Benton, 1999). Nearly all of the crocodile-line archosaurs groups, stagonolepidids, crocodylomorphs, parasuchians, ornithosuchians, and some of the "rauisuchians" have dorsal osteoderms. Though the arrangement of the osteoderms differ among and within archosaur groups, all have at least one parasagittal row of dorsal osteoderms. *Effigia* and *Shuvosaurus* certainly did not have dorsal osteoderms, as evidenced by articulated dorsal regions without osteoderms and the lack of a single osteoderm clearly associated with any of the specimens. Nesbitt (2005a) utilized the absence of osteoderms along with six other characters to support a clade (= Group X of Nesbitt, 2005a) including *Arizonasaurus*, *Ctenosauriscus*, *Lotosaurus*, *Poposaurus*, and *Shuvosaurus*. The close relationship between *Shuvosaurus* and *Effigia* suggests all of these taxa are related, and the absence of osteoderms may support a clade within the crocodile-line archosaurs.

2. Atlas epipophyses. The atlas neural arches of *Effigia* and *Shuvosaurus* bear epipophyses identical to those of neotheropods, *Eoraptor* (Sereno et al., 1993), and *Herrerasaurus*. The distribution of epipophyses on the atlas neural arch is poorly sampled because of the absence of preserved atlas regions in many basal archosaurs. In fact, *Sillosuchus* does not have epipophyses, and the features labeled as such by Alcober and Parrish (1997), but not describe in their text, are actually broken laminae stretching from the postzygapophyses to the neural spine.
3. Ventral deflection of the paraoccipital processes. Although the paraoccipital processes were not recovered for *Effigia*, the paroccipital processes of *Shuvosaurus* are ventrally deflected. Therefore, Rauhut (1997) interpreted the ventral deflection of the paraoccipital processes in *Shuvosaurus* as homologous to the theropod condition.
4. Fibular crest of the tibia. A fibular crest of the tibia is present in *Effigia*, *Shuvosaurus*, and dinosauromorphs, including *Silesaurus* and Theropoda. The crest is located on the anterior portion of the tibia on the lateral side.
5. Elongated prezygapophyses in distal caudal vertebrae. Anteriorly elongated prezygapophyses are present in the distal caudal vertebrae in *Herrerasaurus*, *Staurikosaurus*, *Eoraptor* (Langer, 2004), and *Coelophysis* (contra Rauhut, 2003) and in many coelurosaurians (e.g., tyrannosaurids and ornithomimids). Elongated prezygapophyses are absent in *Allosaurus*, *Dilophosaurus*, oviraptorsaurids, and therizinosauroids (Rauhut, 2003).

CONVERGENCES WITH DINOSAURIA

1. Reduction of forelimb/hindlimb ratio. The length of the forelimb and hindlimb of *Effigia* is similar to that of theropod dinosaurs and not that of crocodile-line archosaurs. Most crocodile-line archosaurs have a nearly one-to-one ratio between forelimb and hindlimb lengths.
2. Postfrontal absent. Originally described as a potential synapomorphy by Benton (1984) for Dinosauria, the absence of a postfrontal is now understood to be independently lost by multiple archosaurian clades (Sereno and Novas, 1993; Novas, 1996). This includes *Shuvosaurus* + *Effigia*, Crocodylomorpha (Gauthier, 1986), and possibly Dinosauria (Langer and Benton, in press).
3. Offset femoral head. The offset femoral head is one of the characters that diagnoses the Dinosauria (Langer and Benton, in press). The proximal femurs of *Effigia* and *Shuvosaurus* have a morphology that resembles an offset femoral head of a dinosaur. However, a closer examination reveals differences between a dinosaurian offset femoral head and the offset femoral head of *Effigia* and *Shuvosaurus*. The offset femoral head articulates with the acetabulum medially in dinosaurs whereas the offset femoral head of *Effigia* and *Shuvosaurus* articulates anteriorly. Additionally, the anteromedial condyle of *Effigia* and *Shuvosaurus*, though hooklike and similar to the dinosaurian offset femoral head, is located further posteriorly and is more anteroposteriorly elongated. Even though *Effigia* and *Shuvosaurus* share a similar proximal femora morphology with dinosaurs, the femora of *Effigia* and *Shuvosaurus* and dinosaurs function in different ways.
4. Brevis fossa. Novas (1996) used the presence of a brevis fossa as a synapomorphy of the Dinosauria. Romer (1927) and Novas (1996) consider the brevis fossa to be associated with the m. caudifemoralis brevis. Novas (1992) defines the brevis fossa as "a distinct and prominent shelf on the posterolateral margin of the iliac blade, placed externally to the posteroventral iliac margin, which runs from the ischiadic peduncle to the posterior end of the blade." This definition restricts the presence of the brevis shelf to Dinosauria. The key to Novas's (1992) definition implies that the lateral margin of the brevis fossa must not be the posteroventral margin of the ilium, but a separate ridge that originates on the lateral surface near the ischiadic peduncle (see Novas, 1996: fig. 8).

   Under the strict definition of Novas (1992), *Effigia* (AMNH FR 30589) and *Shuvosaurus* do not have a brevis fossa. However, the posteroventral edge and a medial ridge for the articulation of the sacral ribs create a large ventrally directed pocket reminiscent of the brevis shelf present in dinosaurs. In *Poposaurus*, the ventrally directed pocket is even more dramatic. This pocket in *Poposaurus*, *Shuvosaurus*, and *Effigia* possibly also represents the attachment for the M. caudifemoralis brevis.
5. Ischium with slender shaft and "ventral" keel restricted to the proximal third of the bone. Also used by Novas (1996) to diagnose the Dinosauria. Novas (1996) utilizes this character to differentiate the plesiomorphic condition present in *Euparkeria*, stagonolepidids, *Lager-*

peton, and *Marasuchus*, where a ventral "keel" of the ischium is located along most of the length of the ischium and articulates with a thin ventral keel of the pubis. Dinosaurs restrict the ventral "keel" to the upper third of the ischium, and the ischium shaft is slender and more rodlike.

The ventral "keel" of the ischium is restricted to the proximal third of the bone in both Group X and dinosaurs. In *Postosuchus*, *Batrachotomus*, *Saurosuchus*, and in basal members of Group X, the ischium has a short ventral keel, but the ischia are mediolaterally compressed. In members of Group Y or derived members of Group Y, the ischium has a short ventral keel that is restricted to the proximal third of the element and the ischia are slender and rodlike in cross section.

6. Elongated parabasisphenoid. Previously discussed in character 1 uniting the skulls of *Shuvosaurus* and *Effigia*.

CONVERGENCES WITH NEOTHEROPODA

1. Incorporation of additional sacral vertebrae. Archosaurs have two sacral vertebrae plesiomorphically (Sereno and Arcucci, 1993, 1994). In crocodile-line archosaurs, the addition of sacral vertebrae is rare; *Desmatosuchus haplocerus* has three (Parker, 2003) and all the members of Group X have at least three (Nesbitt, 2005a). Both *Shuvosaurus* and *Effigia* have four fused sacral vertebrae and two additional vertebrae that articulate with the ilium. Basal theropods have at least five sacral vertebrae and progressively incorporate more vertebrae into the sacrum in later taxa.
2. Thin-walled limb bones. Theropods, pterosaurs, and some suchians (*Postosuchus*, *Poposaurus*, *Arizonasaurus*, crocodylomorpha) have thin walled bones with nearly hollow cavities as illustrated by the histological sections of *Effigia* (fig. 53). As a result, bones of members of Group Y are commonly mistaken for theropod bones from the Late Triassic (e.g., Kirby, 1989; Hunt et al., 1998).
3. Antitrochanter, present on the ilium. An antitrochanter is a raised area dorsal to the region articulating with the ischium that articulates with the proximal head of the femur. Considered by many authors (Novas, 1992; Sereno and Arcucci, 1994) to represent a synapomorphy of the dinosauriformes, the antitrochanter is now known to be present in the crocodylomorphs *Terrestrisuchus* and *Caiman* (Fraser et al., 2002) and *Effigia* and *Shuvosaurus*. Because dinosaurs, crocodylomorphs, and *Effigia* + *Shuvosaurus* share no direct relationship and clades between them have no antitrochanter, the presence of an antitrochanter must be a homoplastic character. The presence of an antitrochanter may have something to do with similar complexes of locomotary adaptations (i.e., bipedalism; Hutchinson, 2001). Novas (1996), followed by Fraser et al. (2002), also point out that the presence of an "antitrochanter" is variable within a single taxon (e.g., *Herrerasaurus*).

   The wide distribution of this character suggests that the evolution of the antitrochanter is complex and the presence or absence of the character may be plastic. Nonetheless, Fraser et al. (2002) argued that a kidney-shaped antitrochanter possibly represents a synapomorphy of a clade close to Dinosauria. However, the plesiomorphic state in Theropoda is to have the antitrochanter on the ischium and not a separate antitrochanter on the ilium. Only in more derived theropods (e.g., tetanurans) does the antitrochanter migrate back to the ilium.
4. Fusion of sacral vertebrae into rigid rod. Theropods, *Effigia*, and *Shuvosaurus* fuse their sacral vertebrae into a ridged rod. As the sacral vertebrae become more rigid, the loss of distinct centrum rims located at the articular surfaces becomes apparent until each vertebra is nearly impossible to pick out individually without the help of sacral ribs.
5. Pleurocoels in the cervical vertebra. *Effigia* and *Shuvosaurus* have structures that satisfy the requirements of Britt (1993) to be called true pleurocoels located on the posterior half of the anterior cervical centra. An identical pleurocoel-like feature in coelophysoid theropods has been used by Rauhut (2003) to unite a clade of coelophysoids.

CONVERGENCES WITH COELUROSAURIA

1. Expanded pubic boot. The pubes of *Effigia* and *Shuvosaurus* bear extremely posteriorly elongated boots as with some basal coelurosaurs.
2. Enlargement of the preacetabular process of the ilium. Although no *Effigia* ilia are completely preserved, the very similar ilia of *Shuvosaurus* are complete. The long preacetabular process is about the same length as the long posterior iliac wing. An elongated preacetabular process is absent in all other

crocodile-line archosaurs outside of Group X. Rauhut (2003; character 169) used the relationship of the preacetabular process relative to the posterior iliac wing to separate coelurosaurs from other theropods. Coelurosaurs, with a few exceptions, have a preacetabular process equal or greater in length than the posterior iliac wing.

3. Preacetabular fossa. An excavated fossa anterior to the supra-acetabular crest and dorsal to the supra-acetabular rim is present in *Effigia* and other closely related taxa. Hutchinson (2001) identifies this fossa as the ''cuppedicus'' fossa in coelurosaurs and some carnosaurs. The position, deepness, and morphology of the ''cuppedicus'' fossa in *Effigia* is most similar to ornithomimids even though present in most coelurosaurs outside Aves.

CONVERGENCES WITH ORNITHOMIMOSAURIA

1. Enlargement of the orbit relative to the length of the skull. *Effigia* and ornithomimids have a similarly high proportion of orbital length relative to length of the skull. The length of the orbit of *Effigia* is about one-third the length of the skull.
2. Posteroventral rotation of the squamosal. The orientation of the squamosal in *Effigia* and *Shuvosaurus* is similar to that of ornithomimids. In both, the squamosal is oriented posteroventrally. Other than some stagonolepidids, crocodile-line archosaurs have squamosals that are oriented anteroposteriorly.
3. Anteroventrally angled quadrate. This character state is also present in baryonychid theropods (such as *Suchomimus* and *Baryonyx*; Rauhut, 2003) as evidenced by their shorter jaws. Used as a character by Rauhut (2003: character 51), this character state seems to be correlated with a posteroventral rotation of the squamosal.
4. Lacrimal–frontal contact absent. Plesiomorphically for the Archosauria, the prefrontal completely separates the lacrimal from the frontal. Ornithomimids revert to the plesiomorphic condition as indicated by Rauhut (2003: character 35).

CONVERGENCES WITH THE EDENTULOUS CLADE OF ORNITHOMIMIDS

1. Posteriorly directed process on each diapophysis of the posterior cervical vertebrae. The presence of posterior directed process on each diapophysis is known only in *Archeornithomimus*, *Gallimimus*, and *Effigia*.
2. Edentulous jaws. Edentulism occurs in a number of theropod clades (e.g., oviraptosaurids) and non-archosaurian taxa (e.g., turtles).

CONVERGENCE CONCLUSIONS

The many convergences between *Effigia* and ornithomimids suggest that a ''theropod-like body plan'' developed in a group of crocodile-line archosaurs before it evolved in later theropod dinosaurs. In the Late Triassic of North America, all of the theropods, such as *Coelophysis bauri*, had simple unspecialized bodies that contrast strongly with the diversity of coeval crocodile-line archosaurs. An iterative pattern of morphological evolution suggests that some of the Late Triassic suchians may have occupied similar adaptive zones as subsequent clades of dinosaurs. The presence of a dinosaur-like suchian is not just an anomaly. Other Triassic archosaurs also converge on later Cretaceous dinosaurian forms. For example, other Triassic archosaurs that resemble later dinosaurs includes the carnosaur-like suchians such as *Postosuchus* (Chatterjee, 1985) and ankylosaur-like suchians such as aetosaurs. *Effigia* was part of an entire fauna that was convergent with later Cretaceous dinosaurian faunas. This repetitive evolution suggests that only in the Jurassic after most clades of crocodile-line archosaurs became extinct, did dinosaurs begin to explore new adaptive opportunities.

The character states of members of Group Y that are shared with contemporaneously early theropods makes identification of ''dinosaurian-like'' isolated elements and even partial skeletons difficult. The presence of three or more sacral vertebrae, hollow vertebrae and limb bones, the presence of an enlarged pubic boot, and an elongated parabasisphenoid were once thought of as dinosaur synapomorphies and useful in dinosaur identification, but are all present in members of Group Y. Isolated vertebrae, teeth, limb bones, and most tooth-bearing elements cannot be unambiguously assigned to the Dinosauria or Group Y. Moreover, in many cases, isolated archosaur bones cannot be assigned to specific clades of the Archosauria because of the high number of plesiomorphic features in basal archosaurs, convergences between different clades (e.g., *Shuvosaurus* and theropods), and the absence of diagnostic characters in certain anatomical regions (e.g., dorsal vertebrae; Nesbitt et al., in press). Dinosaurs are more recognizable from isolated elements only after the extinction of "rauisuchians," parasuchians, aetosaurs, and basal ornithodirans outside Dinosauria and Pterosauria at the end of the Triassic.

DISTRIBUTION OF GROUP Y

"*Chatterjeea elegans*" was first described by Long and Murry (1995) from the Cooper Canyon Formation of the Dockum Group. In their description, Long and Murry listed localities containing "*Chatterjeea*" -like remains. Long and Murry included undiagnositic material including centra and metatarsal fragments. Description of the more complete material from *Effigia* and a reexamination of *Shuvosaurus* permit a new recognition of other members of Group Y in North America from isolated remains. Here, I include only diagnostic materials referable to Group Y (see appendix 2). The diagnostic elements include femora, ilia, ischia, calcania, astragali, sacra, and skull fragments.

The following paragraphs describe the temporal distributions of members of Group Y. It is unknown if each occurrence is a different taxon because the diagnostic characters used to identify the material are characters that are possibly plesiomorphic for a clade containing *Sillosuchus*, *Shuvosaurus*, and *Effigia* (see discussion above).

Temporally, members of Group Y are distributed throughout the Triassic sediments of the western United States in the Moenkopi Formation, Chinle Formation, and Dockum Group (fig. 55). Recently, Nesbitt (2005b) reported an unnamed "*Chatterjeea*-like" taxon, or "chatterjeeid," from the Anisian Moenkopi Formation of northern Arizona. The extension of this group into the early Middle Triassic indicates that members of Group Y were present by the early Middle Triassic. The first occurrence of members of Group Y in the Late Triassic is found at the bottom of the Chinle Formation at the base of the Mesa Redonda Member of the Chinle Formation at the *Placerias* Quarry. This material consists of a nicely preserved proximal femur (MNA 3743). The *Placerias* Quarry taxon is 40% larger than both *Shuvosaurus* and *Effigia*. Moreover, an isolated proximal femur from the Garita Creek Formation of the Dockum Group, an equivalent to the Bluewater Creek Member of the Chinle Formation, is also larger than younger members of Group Y. The femur and tibia from the Mesa Redonda Member of the Chinle Formation and the femur from the Garita Creek Formation of the Dockum Group are the only occurrences of members of Group Y from these units. A questionable isolated distal femur with a sulcus between the lateral and fibular condyles from the Pekin Formation (AMNH FR 34421) of the Newark Supergroup suggests that members of Group Y were present on the east coast of North America. Crocodylomorphs and theropod dinosaurs also have the same sulcus; however, the large size or the distal femur suggests it belongs to a member of Group Y. No other confirmed occurrences have been found in the Newark Supergroup. The material from the Tecovas Formation of the Dockum Group consists of sacral vertebrae, ischia, and femora that share character states with members of Group Y.

The upper units (Petrified Forest Member of the Chinle Formation and Bull Canyon Formation of the Dockum Group) contain abundant remains of members of Group Y. Many limb bones, ilia, and vertebrae of members of Group Y have been mistaken for dinosaurian remains (= theropods of Kirby, 1989; see Nesbitt et al., in press). The holotype of "*Chatterjeea*" comes from the Miller (Post) Quarry within the Bull Canyon Formation and abundant isolated fragments belonging to members of Group Y occur at the base of the Petrified Forest Member of the Chinle Formation. The uppermost formations in the west also contain members of Group Y. The Owl Rock Member of the Chinle Formation material is fragmentary and the Rock Point Member material consists of complete skeletons from the Ghost Ranch *Coelophysis* Quarry described here.

Additionally, two more members of Group Y have been reported from the Late Triassic.

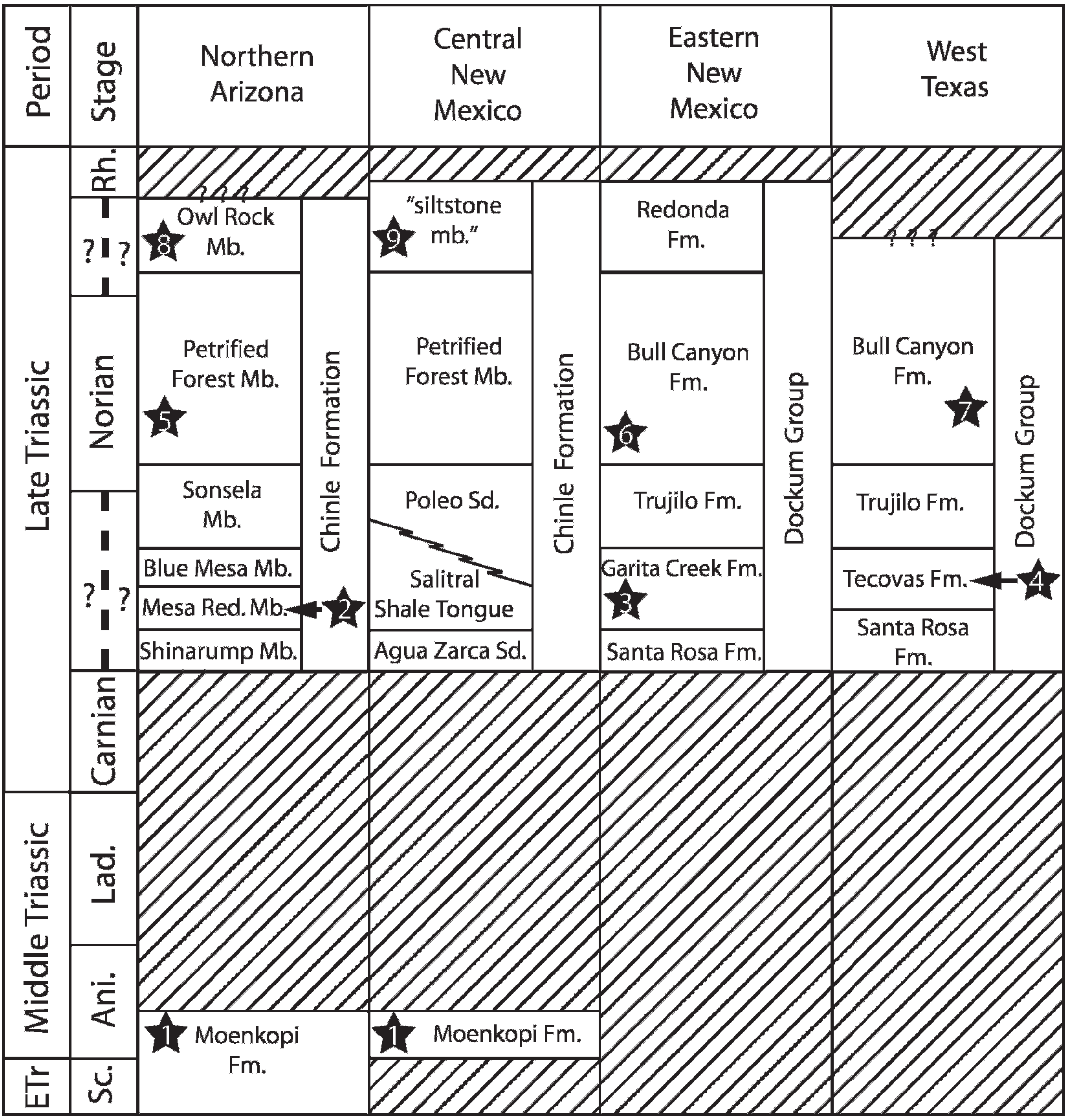

Fig. 55. The distribution of members of Group Y in North America during the Triassic. The first occurrence (1) of members of Group Y occurs in the Middle Triassic Moenkopi Formation. The holotype of *Shuvosaurus* is from the Bull Canyon Formation of the Dockum Group and the holotype of *Effigia* is from the "siltstone member" of the Chinle Formation. The numbers refer to specimens in appendix 2. Mesa Red. Mb. = Mesa Redondo Member.

Sedylmeyer and Small (1997) reported a new form from the Eagle Basin of Colorado. This specimen has not been published, but definitely represents a new taxon. *Sillosuchus*, a taxon from the Ischigualasto Formation of Argentina (Alcober and Parrish, 1997) shows that the members of Group Y had a large biogeographic range. The reorganization of isolated remains of members of Group Y indicates that they were widespread temporally and geographically in the North America.

CONCLUSION

Effigia is one of the most completely known early suchians in both its cranial and postcranial remains. The skull bears characteristics shared only by *Shuvosaurus* among crocodile-line archosaurs. In addition, the skull of *Shuvosaurus* shares some characters with *Arizonasaurus* and few characters with other "rauisuchians" such as *Postosuchus*, *Saurosuchus*, and *Batrachotomus*. The skull and skeleton strongly suggest that the holotype skull of *Shuvosaurus* belongs to the holotype postcrania of the "*Chatterjeea*." Moreover, *Effigia* demonstrates that *Shuvosaurus* is not a basal theropod as previously suggested. *Effigia* possesses all of the character states used to diagnose Group X. Group Y including *Sillosuchus*, *Shuvosaurus*, and *Effigia* may be supported by a minimum of nine characters and a maximum of 30 derived character states within the crocodile-line archosaurs. Many of the character states that *Effigia* and *Shuvosaurus* share are convergent with ornithodirans, dinosaurs, neotheropods, coelurosaurs, and ornithomimids. The convergences suggest that a "theropod dinosaur body plan" developed in a group of crocodile-line archosaurs before it appeared in theropod dinosaurs. Remains of possible close relatives or members of Group Y from the Middle Triassic through near the end of the Triassic in the southwestern United States suggests that members of Group Y were well established in North America and Argentina.

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APPENDIX 1

LIST OF SPECIMENS

Archosauriform

Euparkeria capensis (Ewer, 1965)
SAM 5867, skull and partial skeleton.

Pseudosuchia indet.

Gracilisuchus stipanicicorum (Romer, 1972)
PVL 4612, skull and skeleton; MCZ 4117 skull and skeleton.
Revueltosaurus callenderi (Parker et al., 2005)
PEFO 33787, partial skull and skeleton.

Stagonolepidids

Desmatosuchus haplocerus (Cope, 1892; Small, 2002; Parker 2003)
TTUP 9024, skull.

"Rauisuchians"

Postosuchus kirkpatricki (Chatterjee, 1985; Long and Murry, 1995; Weinbaum, 2002)
TTUP 9001, skull and skeleton; TTUP 9002, skull and skeleton.
Saurosuchus galilei (Sill, 1974; Alcober, 2000)
PVL 2198, postcranial skeleton; PVSJ 32, skull and partial skeleton.
Batrachotomus kuperferzellensis (Parrish, 1993, Gower, 1999)
SMNS 52970, skull and skeleton; SMNS 80260, skull and skeleton.
Teratosaurus suevicus (Benton 1986)
BMNH 38646, complete maxilla.
Teratosaurus silesiacus (Sulej, 2005)
ZPAL Ab III 563, partial skull and partial postcranium.
Fasolasuchus tenax (Bonaparte, 1981)
PVL 3850, partial skeleton; PVL 3851, partial skeleton.
Tikisuchus romeri (Chatterjee and Majumdar 1987)
ISI R 305, partial skull and fragmentary skeleton.
Lotosaurus adentus (Zhang, 1975; Parrish, 1993)
IVPP no number, full skeleton .
Bromsgroveia walkeri (Galton 1985; Galton and Walker, 1996; Benton and Gower, 1997)
WM G3, ilium.
Poposaurus gracilis (Mehl, 1915, Colbert, 1961)
CFMNH UR357, postcranial partial skeleton.
=*Lythrosuchus langstoni* (Weinbaum, 2002)
TMM 31025–12, partial postcranium.
Arizonasaurus babbitti (Welles 1947; Nesbitt 2003, 2005a)
UCMP 36232, maxilla; MSM 4590, skull and partial skeleton.
Shuvosaurus inexpectatus (Chatterjee, 1993; Rauhut, 1997)
TTUP 9280, skull; TTUP 9281, partial skull; TTUP 9282, braincase.
=*Chatterjeea elegans* (Long and Murry, 1995)
TTUP 9001, postcranium.
Sillosuchus longicervix (Alcober and Parrish, 1997)
PVSJ 85, postcranium.
Heptasuchus clarkei (Dawley et al., 1979; Wroblewski, 1997)
UW 11562, partial skull and fragmentary postcranium.
"*Prestosuchus chiniquensis*" (Barberena, 1978)
PVUFRGS, 0156 T, complete skull.

Crocodylomorphs

Sphenosuchus acutus (Haughton, 1915; Walker, 1990)
SAM 3014, complete skull and partially articulated postcranium.
Terrestrisuchus gracilis (Crush 1984)
BMNH P. 47, skull and skeleton.
Hesperosuchus agilis (Colbert, 1952; Parrish, 1991; Clark et al., 2000)
AMNH 6578, partial skull and skeleton; UCMP 129740, partial postcranium; CM 29894 articu lated skull and partial skeleton.
Dromicosuchus grallator (Sues et al., 2003)
UNC 15574, complete skull and articulated skeleton.

Dinosauriforms

Silesaurus opolensis (Dzik, 2003)
ZPAL Ab III/361, skull and skeleton.
Herrerasaurus ischigualastensis (Novas, 1993; Sereno, 1993; Sereno and Novas, 1993)
PVSJ 383, postcranial skeleton; PVSJ407, skull.
Coelophysis bauri (Colbert 1989)
AMNH 7224, skull and skeleton.

APPENDIX 2

SPECIMENS OF GROUP Y

See figure 53 for stratigraphic distribution.

1. Moenkopi Formation

MSM P3346; right femur missing the distal end.
MSM P3262; proximal portion of the femur.
MSM P3300; ilium fragment.
MSM P3260; pelvis (left and right ilium and three sacral vertebrae).
UCMP 37809; right femur missing the complete distal end.

2. Mesa Redondo Member of the Chinle Formation

MNA V3743; proximal portion of the femur.

3. Garita Creek Formation of the Dockum Group

NMMNH P17881; proximal portion of the femur.

4. Tecovas Formation of the Dockum Group

TMM 31100–495; sacral vertebra.
TMM 31100–353; ischia.
TMM 31100–512; ischia.
TMM 31100–210; femur.
TMM 31100–408; femur.

5. Petrified Forest Member of the Chinle Formation

PEFO 34038; proximal portion of the femur.
PEFO 33956; fragmentary right femur.
PEFO 33920; astragalus.
PEFO 33919; cervical centra fragments.

6. Bull Canyon Formation (New Mexico)

NMMNH P4095; complete femur.
NMMNH P7702; distal portion of the femur.

NMMNH P4693; astragalus.
NMMNH P4679; distal portion of the femur.
NMMNH P4678; distal portion of the tibia.
UCM 52081; premaxilla.
UCM 52080; ilium.

7. Bull Canyon Formation (Texas)

TTUP 9280; holotype of *Shuvosaurus*; nearly complete skull.
TTUP 9281; referred specimen of *Shuvosaurus*.
TTUP 9282; braincase of *Shuvosaurus*.
TTUP 9001; holotype of "*Chatterjeea*;" postcrania.
TTUP 9003–9011; partial skeletons of "*Chatterjeea*."

8. Owl Rock Member of the Chinle Formation

MNA L 853; incomplete cervical, dorsal, and caudal vertebrae, femora, tibiae, and metatarsal fragments.

9. "Siltstone member" of the Chinle Formation

AMNH FR 30587; holotype of *Effigia okeeffeae*; complete skull, most of the vertebrae except caudal vertebrae, pes, femur, tibia, fibula, scapula, coracoid, humerus, ulna, radius, manus, ilium, ischium, pubis, gastralia, ribs.
AMNH FR 30588; referred specimen; femur, ilium, ischium, pubis, sacrum, nearly complete caudal series.
AMNH FR 30589; referred specimen; partial skull and cervicals.
AMNH FR 30590; referred specimen; proximal portion of the femur.

APPENDIX 3

ANATOMICAL ABBREVIATIONS

V,	cranial nerve V
VII,	cranial nerve VII
VIII,	cranial nerve VIII
a.,	articulates with
aar,	anterior ampullary recess
ac,	acetabulum
act,	anterior condyle of the tibia
af,	astragalur fossa
ah,	anterior hollow of the astragalus
ai,	atlas intercentrum
amt,	anterior medial tuber
an,	angular
ant,	angular tuber
ap,	astragalar peg
ar,	astragalar ridge
art,	articular
as,	astragalus
aur,	auricular recess
bor,	basioccipital recess
bpp,	basipterygoid processes
bt,	basal tuber
ca,	carpal
cal,	calcaneum
cen,	centrum
cer,	cervical vertebra
cf,	coracoid foramen
ch,	cheveron
cl,	clavicle
co,	coracoid
cor,	cochlear recess
cp,	cultriform process
cpl,	cultriform process lamina
cr,	cohlear recess
crp,	crista prootica
d,	dorsal vertebra
de,	dentary
df,	deep fossa
dia,	diapophysis
dpc,	deltopectoral crest
dpp,	diapophysis posterior process
ds,	dentary shelf
ect,	ectopterygoid
epi,	epiphysis
ex,	exoccipital
f,	femur
fa,	foramen
fbl,	fibro–lamellar bone
fc,	fibular condyle
feo,	fenestra ovalis
fi,	fibula
fl,	flange
fns,	fused neural spines
fo,	fossa
fr,	frontal
g,	groove
ga,	gastralia
gica,	groove for internal carotid artery
gl,	glenoid
hf,	hypophyseal (pituitary) fossa
hi,	humerus impression
hyr,	hyomandibular branch of cranial nerve VII
i,	ischium
ica,	foramen for cerebral branch of the internal carotid artery
ift,	iliofibularis trochanter
il,	ilium
ils,	iliac shelf
ilw,	iliac blade
ir,	ischiadic process rim of the ilium
is,	ischium
itp,	intertuberal plate
j,	jugal
l,	lacrimal

la,	lamina
lb,	lamellar–zonal bone
lc,	lateral condyle
lf,	lacrimal fossa
ls,	laterosphenoid
m#,	metatarsal #
man,	manus
mls,	midline suture
mf,	metotic foramen
mlpu,	midline contact of the pubes
mpr,	median pharyngeal recess
mt,	metatarsal
mx,	maxilla
n,	nasal
nc,	neural canal
ncs,	neurocentral suture
nf,	nutrient fenestra
ns,	neural spine
oc,	occipital condyle
occ,	ossous common crus
of,	obtrator fenestra
p,	parietal
pal,	palatine
pal VII,	possible groove that held the palatal branch of cranial nerve VII
palr,	palatine ramus branch of cranial nerve VII
pap,	preacetabular process
par,	parapophysis
pb,	pubic boot
pbs,	parabasisphenoid
pcc,	precochlear cavities
pct,	posterior condyle of the tibia
pe,	pes
pgt,	proximal groove of the tibia
pis,	pubis–ilium suture
pm,	palatal process of the maxilla
pmt,	posterior medial tuber
pmx,	premaxilla
pmxs,	premaxilla shelf
po,	postorbital
pof,	postorbital fossa
por,	postcarotid recess
poz,	postzygopophysis
pr,	prootic
pre,	prearticular
prf,	prefrontal
prz,	prezygapophysis
pt,	pterygoid
ptq,	pterygoid process of the quadrate
pu,	pubis
pV,	pons Varolii
q,	quadrate
r,	ridge
ra,	raised region of the ischium
rap,	retroarticular process
ri,	rib
sar,	supra–acetabular rim
sac,	supra–acetabular crest
sc,	scapula
scl,	sclerotic ossicles
sp,	splenial
sq,	squamosal
sr #,	sacral rib #
s #,	sacral vertebra #
su,	surangular
suf,	surangular foramen
tc,	tibia condyle
ti,	tibia
t3,	tarsal 3
t4,	tarsal 4
v,	vomer

APPENDIX 4

CHARACTERS AND SCORINGS

1. Skull length: less (0) or more (1) than 50% of length of the presacral vertebral column (Sereno, 1991; Benton, 1999)
2. Subnarial fenestra or foramen between premaxilla and maxilla: absent (0), present (1) (Benton and Clark, 1988; Juul, 1994; Benton, 1999)
3. Jugal–lacrimal articular relation: lacrimal overlaps jugal (0), jugal overlaps lacrimal (1) (Sereno and Novas, 1993; Benton, 1999)
4. Jugal posterior process, shape: tapering (0), forked (1) (Sereno and Novas, 1993; Benton, 1999)
5. Postfrontal: present (0), absent (1) (Gauthier, 1986; Benton and Clark, 1988; Juul, 1994; Bennett, 1996; Benton, 1999)
6. Postorbital–jugal bar behind orbit: curved or straight. (0), "stepped" (1) (Benton and Clark, 1988; Juul, 1994; Benton, 1999)
7. Lower temporal fenestra shape: nontriangular (0), triangular and reduced in size (1) (Benton and Clark, 1988; Juul, 1994; Benton, 1999)
8. Squamosal overhanging quadrate and quadratojugal laterally: absent (0), present, and contacting the lower temporal fenestra dorsally (1), present, but excluded from the rim of the lower temporal fenestra by postorbital and quadratojugal (2) (Benton and Clark, 1988; Juul, 1994; Benton, 1999)

9. Quadrate head in lateral aspect: hidden by squamosal (0), exposed (1) (Sereno and Novas, 1992; Juul, 1994; Benton, 1999)
10. Pterygoid–ectopterygoid articular relation: ectopterygoid ventral (0), ectopterygoid dorsal (1) (Sereno and Novas, 1993; Benton, 1999)
11. Size of posttemporal opening: fenestra (0), foramen (1) (Sereno and Novas, 1993; Benton, 1999)
12. Parasphenoid rostrum: rodlike (0), a dorsoventrally expanded wedge (1) (Parrish, 1993; Juul, 1994; Benton, 1999)
13. Palatal teeth (pterygoid, palatine, vomer): present (0), absent (1) (Benton and Clark, 1988; Sereno, 1991; Juul, 1994; Benton, 1999)
14. Intramandibular joint: absent or poorly developed (0), well developed (1) (Sereno and Novas, 1993; Juul, 1994; Benton, 1999)
15. Centrum shape in presacrals 6–9 (or 10): subrectangular (0), parallelogram–shaped (1) (Gauthier, 1986; Sereno, 1991; Benton, 1999)
16. Length of presacral centrum 8 divided by length of presacral centrum 18: less (0) or more (1) than 1.0 (Gauthier, 1986; Juul 1994; Benton, 1999)
17. Cervical ribs: slender (0), short and stout (1) (Gauthier, 1986; Benton and Clark, 1988; Juul, 1994; Benton, 1999)
18. Hyposphene—hypantrum accessory intervertebral articulations in trunk vertebrae: absent (0), present (1) (Gauthier, 1986; Juul, 1994; Benton, 1999)
19. Number of sacral vertebrae: two (0), two plus an incipient third (1), three or more (2) (Gauthier, 1986; Juul, 1994; Benton, 1999)
20. Accessory neural spine on midcaudal vertebrae: absent (0), present (1) (Benton and Clark, 1988; Sereno, 1991; Juul, 1994; Benton, 1999)
21. Clavicle: present (0), rudimentary or absent (1) (Gauthier, 1986; Sereno, 1991; Benton, 1999)
22. Interclavicle: present (0), absent (1) (Gauthier, 1986; Juul, 1994; Benton, 1999)
23. Scapulocoracoid notch at anterior junction of scapula and coracoid: absent (0), present (1) (Parrish, 1993; Benton, 1999)
24. Forelimb–hindlimb length ratio: more than 0.55 (0), less than 0.55 (1) (Gauthier, 1986; Sereno, 1991; Juul, 1994; Benton, 1999)
25. Deltopectoral crest on humerus: rounded (0), subrectangular (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
26. Deltopectoral crest elongate and with apex situated at a point corresponding to less (0) or more (1) than 38% down the length of the humerus (Benton 1990; Juul 1994, character 59; Benton 1999)
27. Manual digit I (pollex—thumb): metacarpal I and ungual phalanx similar in size to those of manual digits II–V (0), metacarpal I robust and half or less the length of metacarpal II, first phalanx longer than metacarpal I or any other phalanx in the hand, lingual phalanx I much larger than other unguals (1) (Gauthier, 1986; Benton, 1990, 1999)
28. Manual digits I–III: comparatively short with relatively blunt unguals on at least digits II and III (0), long penultimate phalanx with trenchant unguals on digits I–III (Gauthier, 1986; Juul, 1994; Benton, 1999)
29. Metacarpal III and IV bases: lie more or less in the same plane as the inner metacarpals (0), lie on palmar surfaces of manual digits III and IV, respectively (1) (Gauthier, 1986; Juul, 1994; Benton, 1999)
30. Manual digit IV: five (0), four (1), fewer than four (2) phalanges (Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Benton, 1999)
31. Supra–acetabular crest on ilium: absent (0), present (1) (Gauthier, 1986; Juul, 1994; Benton, 1999)
32. Brevis shelf on ventral surface of postacetabular part of ilium: absent (0), present (1) (Gauthier, 1986; Juul, 1994; Benton, 1999)
33. Acetabulum: laterally orientated (0), ventrally deflected (1), open ventrally (2) (Benton and Clark, 1988; Juul, 1994; Benton, 1999)
34. Acetabulum: imperforate (0), semiperforated (1), extensively perforated (2) (Gauthier, 1986; Juul, 1994; Benton, 1999)
35. Acetabular antitrochantcr on ilium and ischium: absent (0) present (1) (Sereno and Arcucci, 1994a; Benton, 1999)
36. Pubis length: shorter than ischium (0), longer than ischium (1) (Benton and Clark, 1988; Juul, 1994; Benton, 1999)
37. Pubis length: less (0) or more (1) than three times width of acetabulum (Sereno, 1991; Juul, 1994; Benton, 1999)
38. Pubic acetabular margin, posterior portion: continuous with anterior portion (0), recessed (1) (Sereno, 1991; Benton, 1999)
39. Pubic foot: absent (0), present with only a posterior expansion (1) or present with both an anterior and posterior expansion (2) (Gauthier, 1986; Juul, 1994; Benton, 1999)
40. Tibia–femur ratio: less than 1.0 (0), more than 1.0 (1) (Gauthier, 1986; Sereno, 1991; Juul, 1994; Benton, 1999)
41. Femoral proximal head: rounded and not distinctly offset (0), subrectangular and distinctly offset (1) (Gauthier, 1986; Juul, 1994; Benton, 1999)
42. Femoral head articular surface: limited extent (0), extends under head (1) (Sereno and Arcucci, 1994a; Benton, 1999)
43. Fossa trochantcrica on femoral head: absent (0), present (1) (Novas, 1996; Benton, 1999)
44. Femoral fourth trochanter: absent (0), moundlike (1), sharp (aliform) ridge (2) (Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Juul, 1994; Bennett, 1996; Benton, 1999)
45. Femoral lesser (anterior) trochanter: absent (0), weakly developed (1), a spike or crest (2) (Gauthier, 1986; Novas, 1992; Juul, 1994; Benton, 1999)
46. Cnemial crest on tibia prominent: absent (0), present (1) (Benton and Clark, 1988; Juul, 1994; Benton, 1999)
47. Tibial distal end: unexpanded, or only slightly expanded, and rounded (0), transversely expand-

ed, with a subrectangular end (1) (Gauthier, 1986; Sereno, 1991; Benton, 1999)

48. Tibia with posterolateral flange, with receiving depression on dorsal aspect of astragalus: absent (0), present (1) (Novas, 1992; Juul, 1994; Benton, 1999)
49. Fibula and calcaneum shape: unreduced (0), fibula tapering and calcaneum reduced in size (1) (Gauthier, 1986; Juul, 1994; Benton, 1999)
50. Ventral astragalocalcaneal articular facet size: small (0), large (1) (Sereno, 1991; Benton, 1999)
51. Astragalar tibial facet: concave (0), flexed/convex (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
52. Ascending process of the astragalus on the anterior side of the tibia absent (0), height less than half the width of the astragalus (1), height more than half the width of the astragalus (2). (Benton, 1999)
53. Astragalar posterior groove: present (0), absent (1). (Sereno, 1991; Benton, 1999).
54. Astragalar anteromedial corner shape: obtuse (0), acute (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
55. Calcaneal proximal articular face: convex or flat (0), concave (1) (Novas, 1992; Juul, 1994; Benton, 1999)
56. Calcaneal distal articular face: transverse width more (0) or less (1) than 35% of that of the astragalus (Sereno, 1991; Juul, 1994; Benton, 1999)
57. Calcaneal tuber: prominent (0), rudimentary or absent (1) (Gauthier, 1986; Sereno, 1991; Juul, 1994; Benton, 1999)
58. Calcaneal tuber orientation: lateral (0), deflected more than 45° posterolaterally (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
59. Calcaneal tuber shaft proportions; taller than broad (0), broader than tall (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
60. Calcaneal tuber distal end: anteroposteriorly compressed (0), rounded (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
61. Calcaneal tuber distal end, with dorsoventrally aligned median depression: absent (0), present (1) (Parrish, 1993; Juul, 1994; Benton, 1999)
62. Articular surfaces for fibula and distal tarsal IV on calcaneum: separated by a nonarticular surface (0), continuous (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
63. Hemicylindrical calcaneal condyle: absent (0), present (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
64. Distal tarsal 4: transverse width broader (0) or subequal (1) to distal tarsal 3 (Sereno, 1991; Juul, 1994; Benton, 1999)
65. Distal tarsal 4, size of articular facet for metatarsal V: more (0) or less (1) than half of lateral surface of distal tarsal 4 (Sereno, 1991; Benton, 1999)
66. Metatarsus configuration: metatarsals diverging from ankle (0), compact metatarsus, with metatarsals I–IV tightly bunched (Benton and Clark, 1988; Sereno, 1991; Juul, 1994; Benton, 1999)
67. Metatarsal midshaft diameters: I and V subequal or greater than II–IV (0), I and V less than II–IV (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
68. Metatarsal I length, relative to length of metatarsal III: 50–75% (0), 85% or more (1) (Sereno, 1991; Benton, 1999)
69. Metatarsals II–IV: shorter (0) or longer (1) than 50% of tibial length (Sereno, 1991; Juul, 1994; Benton, 1999)
70. Metatarsal V, ‘‘hooked’’ proximal end: present (0), absent, and articular face for distal tarsal 4 subparallel to shaft axis (1) (Sereno, 1991; Juul, 1994; Benton, 1999)
71. Phalanges on pedal digit V: four (0), three (1), two (2), one (3), none (4) (Gauthier, 1986; Benton and Clark, 1988; Juul, 1994; Benton, 1999)
72. Dorsal body osteoderms: absent (0), present as a single median row (1), a paramedian pair per cervicodorsal vertebra (2), more than one paramedian pair per cervico–dorsal vertebra (3) (Gauthier, 1986; Benton and Clark, 1988; Sereno, 1991; Juul, 1994; Benton, 1999)
73. Edentulous premaxilla absent (0) or present (1) (Nesbitt and Norell, 2006)
74. Edentulous maxilla absent (0) or present (1) (Nesbitt and Norell, 2006)
75. Anterodorsal process of the premaxilla less than the length of the premaxilla (0) or greater than the length of the premaxilla (1) (Nesbitt and Norell, 2006)
76. Deep parabasisphenoid recess absent (0) or present (1) (Nesbitt and Norell, 2006)
77. Mandibular fenestra less than half the length of the mandible (0) or greater than half the length of the mandible (1) (Nesbitt and Norell, 2006)
78. Presence of maxillary fenestra absent (0) or present (1) (Gauthier, 1986)
79. Pleurocoels on cervical vertebrae absent (0), present as one pair (1) or present as two pairs (2) (Gauthier, 1986)
80. Distal scapula expanded (0) or straplike (1) (Gauthier, 1986)
81. Metacarpal IV present (0) or absent (1) (Gauthier, 1986)
82. Neural spines of sacral vertebrae separated at the dorsal margin (0) or fused together into a lamina of bone at the dorsal margin (1) (new)
83. Preacetabular process of the ilium much shorter than the postacetabular process of the ilium (0) or subequal or longer (1) (new)

APPENDIX 5
DATA MATRIX

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Euparkeria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Proterochampsidae	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0
Parasuchia	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ornithosuchidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	?	1	0	0	1	0	1	1	1	0	0	0	0
Stagonolepididae	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	?	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	1	0	0	1	0	1	0	0	0	0
Postosuchus	0	1	0	0	0	1	0	2	0	0	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0
Crocodylomorpha	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	0	?	0	0
Pterosauria	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2	0	1	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Lagerpeton	0	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	1	1	0
Marasuchus	0	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	0	0	?	?	?	1	1	0	?	?	?	?	1	0	0	1	1	1	0	0	0	1	0	1
Gallimimus	0	1	1	1	1	0	0	0	1	1	1	0	1	1	1	1	0	1	2	0	1	1	0	1	1	1	1	1	1	2	1	1	0	2	1	1	1	0	1	1	1	1
Sauropodomorpha	0	1	1	1	1	0	0	0	1	1	1	0	1	0	1	1	0	1	2	0	1	1	0	1	1	1	1	0	1	2	1	1	0	2	1	1	1	0	0	1	1	1
Ornithischia	0	0	0	0	1	0	0	0	1	1	1	0	1	0	1	1	0	0	2	0	1	1	0	1	1	1	0	0	0	2	1	1	0	2	1	1	1	0	0	1	1	1
Effigia	0	0	0	?	1	0	?	0	0	?	1	?	1	0	1	?	?	1	2	0	0	?	1	1	?	?	?	0	0	?	1	0	1	1	1	1	1	1	1	?	0	0
Arizonasaurus	0	?	0	0	?	1	?	0	0	?	?	0	0	0	1	?	?	0	2	?	0	0	1	?	?	?	?	?	?	?	1	0	1	1	0	1	1	1	1	?	0	0
Shuvosaurus	0	0	0	?	1	0	?	0	0	?	1	?	1	0	?	?	?	?	2	0	?	?	1	?	0	0	?	?	?	?	1	0	1	1	1	1	1	1	1	?	0	0
Tyrannosaurus	0	1	1	1	1	0	0	0	1	1	1	0	1	1	1	1	0	1	2	0	1	1	0	1	1	1	1	1	1	2	1	1	0	2	1	1	1	0	1	1	1	1
Coelophysis	0	1	1	1	1	0	0	0	1	1	1	0	1	1	1	1	0	1	2	0	1	1	0	1	1	1	1	1	1	2	1	1	0	2	1	1	1	0	1	1	1	1
Lotosaurus	0	?	0	0	0	1	0	0	0	?	0	0	1	0	1	0	1	?	2	0	0	0	?	0	0	0	?	0	?	1	1	0	1	1	0	1	1	1	0	0	0	0
Saurosuchus	0	1	0	0	0	1	0	0	0	0	0	0	1	0	0	?	1	1	0	0	0	0	1	0	0	0	0	0	0	?	1	0	1	0	0	1	1	1	1	0	0	0
Sillosuchus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	2	0	?	?	?	?	?	?	?	?	?	?	1	0	1	1	0	1	1	1	1	?	?	?

	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83
Euparkeria	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0
Proterochampsidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0	0	0	0	0	0
Parasuchia	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Ornithosuchidae	0	2	2	1	1	1	0	0	?	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0
Stagonolepididae	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	?	0	0	0	0	0	0
Postosuchus	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0
Crocodylomorpha	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0
Pterosauria	0	0	0	0	0	0	1	?	0	0	1	0	0	0	1	?	0	0	0	?	0	1	0	1	0	1	1	0	2	0	0	0	0	0	0	0	?	?	0	0	?
Lagerpeton	0	2	0	0	0	0	1	?	0	0	1	1	0	1	1	?	?	?	?	1	0	1	1	1	1	0	1	1	4	0	?	?	?	?	?	?	0	?	?	0	0
Marasuchus	1	2	1	0	0	0	1	?	0	0	1	1	0	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	4	0	?	?	?	?	?	?	0	?	?	0	0
Gallimimus	1	2	2	1	1	1	1	?	0	2	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	4	?	1	1	0	1	0	1	1	1	1	0	1
Sauropodomorpha	1	2	2	1	1	1	0	?	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	3	?	0	0	0	0	0	0	1	0	0	0	0
Ornithischia	1	2	2	1	1	1	1	?	0	1	1	1	0	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	4	?	0	0	0	0	0	0	0	0	?	0	1
Effigia	0	0	0	0	0	0	0	1	1	0	0	0	0	0	?	?	?	?	?	1	1	0	0	1	1	0	0	0	?	0	1	1	1	1	1	0	1	0	0	1	1
Arizonasaurus	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0	0	0	0	?	0	0
Shuvosaurus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	1	1	0	0	0	?	0	1	1	1	1	1	0	1	0	?	1	1
Tyrannosaurus	1	2	2	1	1	1	1	?	0	2	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	4	?	0	0	0	1	0	1	1	1	1	0	1
Coelophysis	1	2	2	1	1	1	1	?	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	4	?	0	0	0	1	0	0	2	0	0	0	0
Lotosaurus	0	2	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	1	?	?	0	0	0	0	0	?	0	1	1	?	?	1	0	0	0	0	0	0
Saurosuchus	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Sillosuchus	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	1	1