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THE BRAINCASE OF *ARIZONASAURUS BABBITTI*—FURTHER EVIDENCE FOR THE NON-MONOPHYLY OF 'RAUISUCHIAN' ARCHOSAURS

DAVID J. GOWER[1] and STERLING J. NESBITT[2]
[1]Department of Zoology, The Natural History Museum, London SW7 5BD, UK, d.gower@nhm.ac.uk;
[2]Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York 10964, nesbitt@ldeo.columbia.edu

ABSTRACT—The braincase of the rauisuchian pseudosuchian archosaur *Arizonasaurus babbitti*, from the Middle Triassic of the western United States, is described from two specimens. There are no obvious braincase autapomorphies and most of the other braincase features of *A. babbitti* are plesiomorphic for pseudosuchians/crurotarsans. The results of phylogenetic analyses of archosaurian braincase characters indicate that *A. babbitti* is not especially closely related to other rauisuchians for which braincase anatomy is known (*Batrachotomus kupferzellensis, Saurosuchus galilei, Postosuchus kirkpatricki, Tikisuchus romeri*). Given that *A. babbitti* is a member of a clade that includes *Poposaurus* and chatterjeeids to the exclusion of most other rauisuchians, braincase data suggest that Rauisuchia are not monophyletic. This is in accordance with a recent appraisal of non-braincase data but, in contrast, our analyses suggest that *Poposaurus* and its closest allies are more distantly related to Crocodylomorpha than are other rauisuchians.

INTRODUCTION

Archosauria comprises the extant birds and crocodilians and a diversity of extinct Mesozoic clades including the dinosaurs, pterosaurs, aetosaurs, phytosaurs, and 'rauisuchians' (sensu Gower, 2000). The archosaur crown group (= Archosauria of Gauthier, 1986; Avesuchia of Benton, 1999) is understood to comprise two major clades: crocodile-line (pseudosuchian/crurotarsan) and bird-line (ornithodiran) archosaurs (e.g., Gower and Wilkinson, 1996). Ornithodira (birds, dinosaurs, pterosaurs, and close relatives) have attracted much attention, and the origin of birds from within theropod dinosaurs has been a major focus of detailed evolutionary studies (e.g., Gauthier and Gall, 2001). In contrast, pseudosuchians (including phytosaurs, ornithosuchians, aetosaurs, 'rauisuchians,' and crocodylomorphs) have received comparatively little attention. The relatively poor understanding of pseudosuchian relationships has hindered attempts to address bigger evolutionary questions, such as the origin of the highly distinctive anatomy and biology of crocodilians. Recent insights into braincase anatomy of Triassic archosaurs (Gower and Weber, 1998; Gower, 2002; Gower and Walker, 2002) have shown some promise in clarifying both pseudosuchian phylogeny and the origin of the complex crocodilian ear and braincase region. Many more data, however, are required to test these preliminary results (Gower, 2002).

Currently, it seems that the anatomy and relationships of rauisuchians (sensu Gower, 2000) are key to further understanding of crocodile-line archosaurs because this large, diverse group of Triassic archosaurs is possibly para- or even polyphyletic, with some members possibly closely related to Crocodylomorpha (Parrish, 1993; Gower, 2000). Rauisuchian biology is poorly known and more basic information is required, particularly on anatomy and systematics (Gower, 1999, 2000). One possible monophyletic group ('clade X' of Nesbitt, 2005; see also Nesbitt, 2003) within Rauisuchia comprises taxa hypothesized to be closely related to *Poposaurus gracilis* and chatterjeeids (*Chatterjeea elegans, Sillosuchus longicervix*). The anatomy of the Middle Triassic *Arizonasaurus babbitti* indicates that it is possibly a member of this clade (Nesbitt, 2003, 2005). If so, *A. babbitti* assumes great importance as the only member of 'clade X' for which cranial elements, including the braincase, are currently known.

In this paper, we describe the braincase anatomy of *A. babbitti*, add this taxon into an existing character matrix of braincase data (Gower, 2002), and present the results of a phylogenetic analysis.

MATERIALS AND METHODS

The following description is based on two specimens. The best braincase material is part of the most complete specimen of *A. babbitti* found to date (see Nesbitt, 2003, 2005) Mesa Southwest Museum (MSM) P4590 (Figs. 1, 3–5). Additional information was obtained from MSM P4647 (Fig. 2). The braincase of MSM P4590 consists of the largely complete posterior and central parts. The laterosphenoids, and any other possible anterior ossifications, were not found with this material. As preserved, the braincase is in three pieces. The first, ventral piece (Figs. 1, 3) comprises the basioccipital and parabasisphenoid in articulation. These elements are essentially complete. They have undergone some shearing, so that the left side has moved anteriorly relative to the right. There has also been some lateral crushing, although this is less apparent or even absent in the thicker central portions of these elements.

The dorsal part of the braincase of MSM P4590 (Figs. 4, 5) is in two pieces. The right dorsolateral piece (Fig. 5) comprises the largely complete right exoccipital (lacking its anteroventral tip), opisthotic, and prootic, as well as one third of the supraoccipital. This part of the braincase is slightly flattened in the major plane of the paroccipital process. There is some minor damage to the more delicate regions, including the crista prootica. The final, left dorsolateral piece of the braincase (Fig. 4) includes a little more than half the supraoccipital, a reasonably complete left prootic (lacking a small piece of the crista prootica) and left exoccipital, the left opisthotic lacking the distal end of the paroccipital process, and the anteroventral tip of the right exoccipital. A small posteromedial piece of supraoccipital is seen to be missing when the two dorsolateral pieces of the braincases are placed together (Fig. 4). The two dorsolateral pieces were found in contact. As with the ventral piece, the left side is sheared anteriorly. The three pieces of the braincase do not now fit together in their exact original relationships. Overall, the position and course of sutures are difficult to determine. The surface preservation is slightly cracked and crushed, but many details are observable.

MSM P4647 is a partial braincase (Fig. 2). The parts preserved are approximately 40% larger than those of the braincase of MSM P4590. The braincase is in three pieces, the supraoccipital

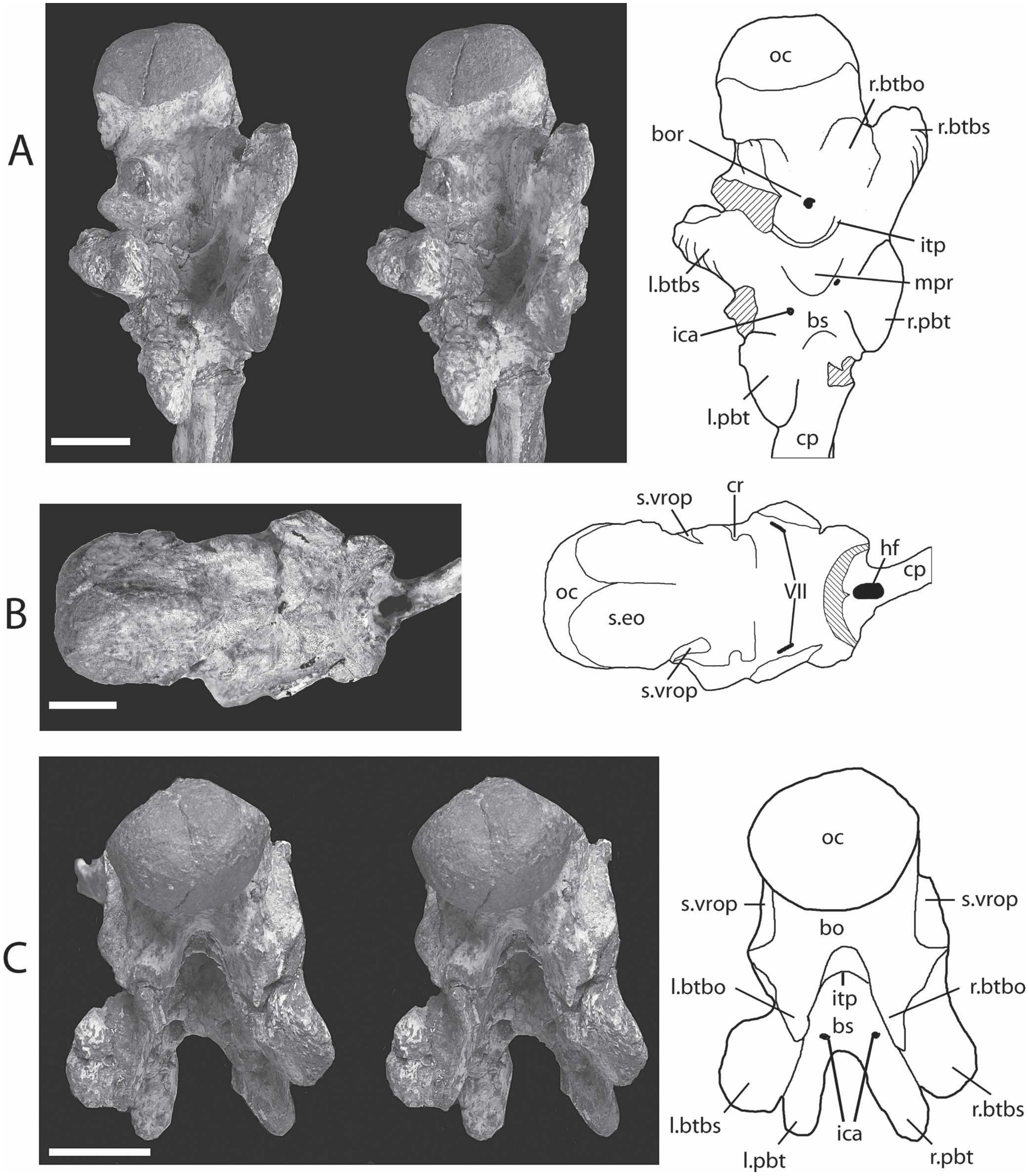

FIGURE 1. The braincase of *Arizonasaurus babbitti*, showing the basioccipital region of the smaller specimen MSM P4590 in ventral (**A**), dorsal (**B**), and posterior (**C**) views. Scale equals 1 cm.

region including the prootic (dorsal), the basioccipital region (ventral), and an internal cast of the hindbrain. As with the braincase of MSM P4590, the more delicate regions are not preserved. Both paraoccipital processes, the posterior portion of the occipital condyle, the cultriform process of the parasphenoid, and the basipterygoid processes are missing and most outer surfaces are abraded. The internal surface of the dorsal part is well preserved and fine details can be observed. Although the dorsal

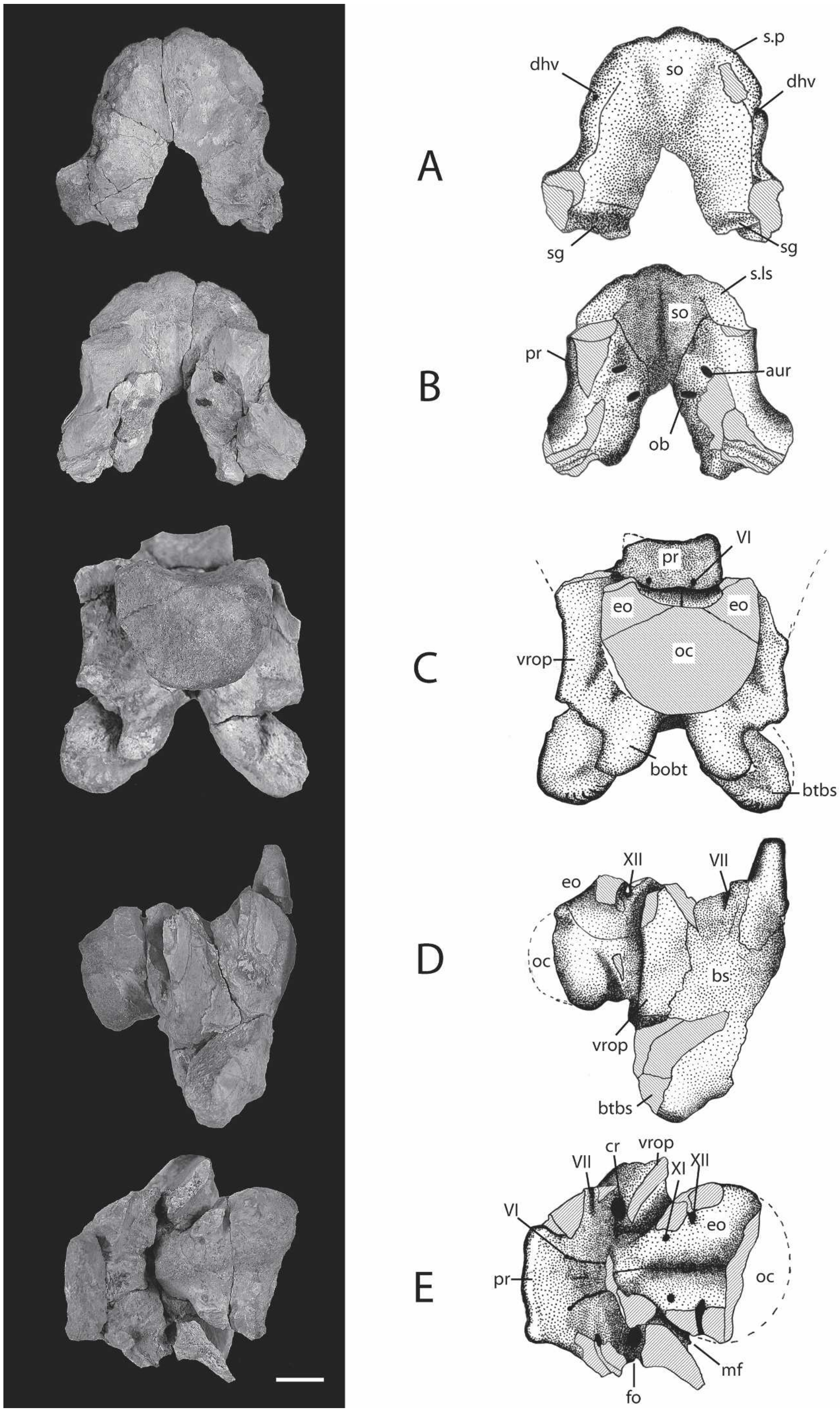

FIGURE 2. The braincase of *Arizonasaurus babbitti*. The supraoccipital region of the larger specimen MSM P4647 in posterior (**A**) and anterior (**B**) views. The basioccipital region of MSM P4647 in posterior (**C**), right lateral (**D**), and dorsal (**E**) views. Scale equals 2 cm.

and ventral parts were not found in articulation, the natural endocast links these parts and can be used to rearticulate the braincase. Together, the dorsal and ventral parts are uncrushed and preserve the original three-dimensional form. Comparative material is as reported by Gower (2002:50).

Abbreviations

The following abbreviations are used in Figures 1–5: **aar**, anterior ampullary recess (external and anterior vertical semicircular canals open into this concavity); **aur**, auricular recess; **bo**, basioccipital; **bor**, basioccipital recess; **bpt**, basipterygoid process; **bptf**, basipterygoid facet; **bs**, parabasisphenoid; **btbo**, basal tuber of basioccipital; **btbs**, basal tuber of parabasisphenoid; **cp**, cultriform process of bs; **cpbs**, clinoid process of bs; **cr**, cohlear/lagenar recess; **dhv**, foramen possibly for dorsal head vein (and position of associated sinus on internal surface of endocranial cavity); **dv**, dorsal part of vestibule; **hf**, hypophyseal (pituitary) fossa; **ica**, foramen for cerebral branch of the internal carotid artery; **itp**, intertuberal plate sensu Gower and Sennikov (1996); **eo**, exoccipital; **f**, fossa; **fo**, fenestra ovalis; **fm**, foramen magnum; **g.pVII**, groove probably for palatine ramus of facial nerve; **l.**, left; **mf**, metotic foramen (see Gower and Weber, 1998); **mpr**, median pharyngeal recess; **ob**, otic bulla (formed by medial wall of vestibule of otic capsule); **oc**, occipital condyle; **op**, opisthotic; **pit**, pit; **plf**, possible lateral margin of perilymphatic foramen; **pp**, paroccipital process; **pr**, prootic; **r.**, right; **rb**, fossa for attachment of retractor bulbi eye muscle; **sg**, stapedial groove; **s.bo**, surface for articulation with basioccipital; **s.eo**, surface for articulation with exoccipital; **s.ls**, surface for articulation with laterosphenoid; **s.p**, surface for articulation with parietal; **s.vrop**, surface for articulation with vrop; **so**, supraoccipital; **soppr**, suture between opisthotic and prootic; **V**, foramen for trigeminal nerve; **VI**, foramen for abducens nerve; **VII**, position of passage of facial nerve; **XII**, foramen for hypoglossal nerve; **vrop**, ventral ramus of the opisthotic.

DESCRIPTION

External Surface

Basioccipital—The basioccipital in *Arizonasaurus babbitti* forms most of the occipital condyle (Figs. 1–3). The condylar 'stalk' is relatively a little longer than in *Batrachotomus kupferzellensis*. Each basal tuber projects ventrally, with a broad rounded notch in its ventrolateral end. This notch represents the basioccipital border of a probably partly unossified gap (see Gower, 2002, and references therein) between the tubera of the basioccipital and parabasisphenoid and the ventral end of the ventral ramus of the opisthotic. Ventromedially, each tuber extends downwards as a thin process tightly in contact with the basal tuber of the parabasisphenoid. The tubera of the basioccipital are separated medially by a broad, rounded notch, anteroventral to which lies a shallow, midline basioccipital recess. The suture with the parabasisphenoid is generally clear except posteromedially, just anterior to the basioccipital recess. The lateral edge of the posterior surface of each basioccipital tuber bears a large posterior groove that receives the ventral ramus of the opisthotic. The lateral surface of the basioccipital bears no indication of a subvertical ridge or crest, such as is present in *B. kupferzellensis* (Gower, 2002).

Exoccipital—A suture between exoccipital and opisthotic is not apparent. The ventral parts of the exoccipitals meet in the midline (Figs. 1, 2), to exclude the basioccipital from the foramen magnum and the posteroventral floor of the endocranial cavity. Each exoccipital bears a pair of foramina for the passage of the hypoglossal nerve. The more posterior foramen is larger and passes through the exoccipital transversely. The smaller passage for the anterior branch of the nerve passes through the braincase in an anteromedial–posterolateral orientation, so that the two external foramina lie closer together than the internal pair of each exoccipital. As with the basioccipital, the lateral surface of the exoccipital lacks a subvertical crest, so that the ventral end of the metotic foramen is open instead of being partly closed off laterally. The lateral surface is gently convex, with the hypoglossal foramina situated on the anterolateral surface, within the larger embayment that represents the external opening of the metotic foramen. The embryonic metotic fissure is retained as an apparently undivided (sensu Gower and Weber, 1998) metotic foramen.

Supraoccipital—Posterodorsally, the supraoccipital appears as a subsemicircular element (Figs. 2, 4). Participation in the border of the foramen magnum seems unlikely, but sutures with the exoccipitals are not entirely apparent, and this requires verification. The external dorsal surface bears a faint midline ridge. Laterally, the areas for articulation with the parietals are not represented as clearly defined facets. The dorsolateral part of the supraoccipital is pierced by a foramen, probably for the passage of the dorsal head vein. This lies further anterodorsally than the interpreted position of potentially the same foramen in *B. kupferzellensis* (Gower, 2002).

Epiotic—Nowhere is an unequivocal epiotic–supraoccipital suture apparent. It is not known, therefore, whether a separate epiotic ossification was present.

Opisthotic—The opisthotic forms the majority of the paroccipital process. This has a subtriangular distal end, with the ventral edge extending farther than the posterior edge. The form of the posttemporal fenestra is unclear. Proximally, the posteroven-

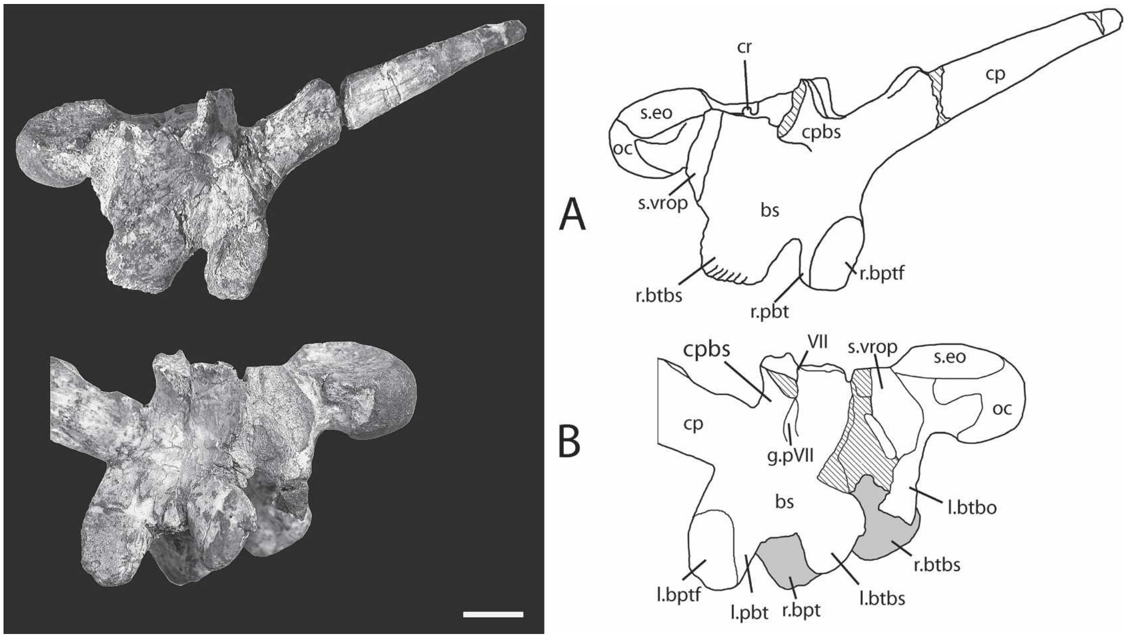

FIGURE 3. The braincase of *Arizonasaurus babbitti*, showing the basioccipital region of the smaller specimen MSM P4590 in right lateral (**A**) and left lateral (**B**) views. Scale equals 1 cm.

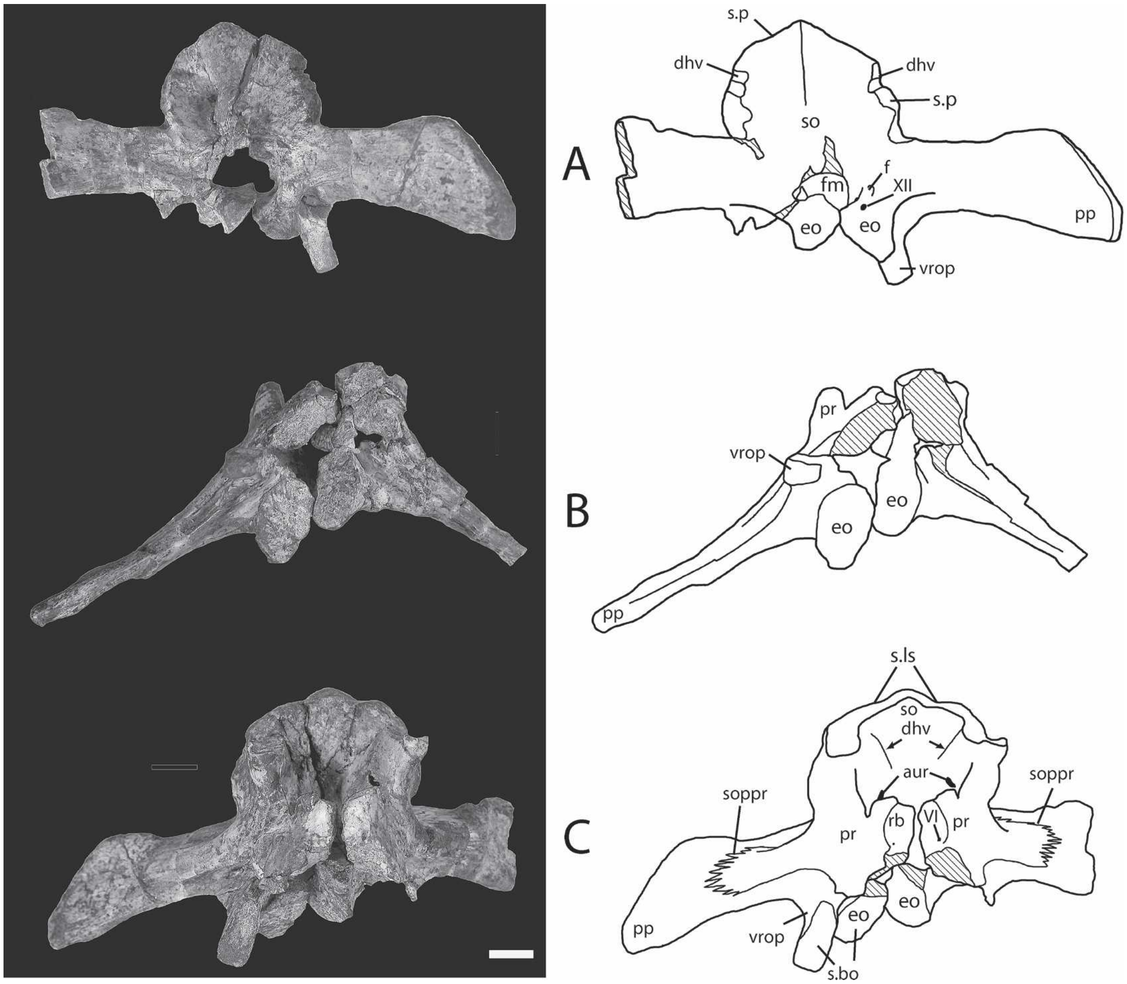

FIGURE 4. The braincase of *Arizonasaurus babbitti*, showing the supraoccipital region of the smaller specimen MSM P4590 in posterior (**A**), ventral (**B**), and anterior (**C**) views. Scale equals 1 cm.

tral surface of the paroccipital process forms the upper end of the metotic foramen and fenestra ovalis, separated by the dorsal end of the ventral ramus of the opisthotic. The ventral ramus is very well developed. It is mostly blade-like, with a thinner medial edge, but the ventral end is somewhat expanded. In the smaller MSM P4590, the ventral ramus is disarticulated from its contact with the basal tubera of the basioccipital and parabasisphenoid (Figs. 3, 5), whereas the contact is preserved as a partly interdigitating suture in the larger MSM P4647 (Fig. 2). In both specimens it resembles the ventral ramus of non-crown-group archosaurs (Gower and Senninkov, 1996; Gower and Weber, 1998) in being large, standing proud, and being clearly visible in lateral and posterior views.

Inner Ear—The ossified part of the inner ear (Figs. 2, 4, 5) is not especially well preserved in either specimen, but several details can be described. There is no indication of an external cochlear prominence (Walker, 1990; Gower, 2002), with the cochlear recess lying medial to a fairly thick region of undifferentiated bone. The cochlear recess appears to have been fairly long and straight. Its posteromedial border is interpreted as being represented by a groove in the anterolateral surface of the basioccipital (Figs. 1–3), about 4 to 5 mm long in MSM P4590. Its anteromedial border is formed by the prootic and ventrally it perhaps sits in the parabasisphenoid. The juncture between the cochlear and vestibular regions of the inner ear are not well preserved, but there is no indication that the two parts were partially separated by a crest (see Gower, 2002).

The vestibular part of the inner ear generally resembles that in other diapsids. The medial wall is not entirely closed, but is apparently more completely ossified (more complete otic bulla) in the larger MSM 4647. The regions holding the ampullary recesses are incompletely prepared, but there is nothing to indicate that the morphology of this region is unusual. The anterior and posterior ampullae were held by the prootic and opisthotic, respectively, while the dorsal ampulla apparently lay in the lower end of the supraoccipital (or possibly epiotic, if present), close to the estimated dorsal border of the prootic. On the proximal end of the ventral ramus of the opisthotic, at the juncture between the thicker dorsal vestibular part and the thinner ramus proper, there is a small, posteromedially open pit, visible on both sides of MSM P4590 (Fig. 5).

There is no clear indication of the perilymphatic foramen in the ventral ramus of the opisthotic. Even in the best-preserved example (the right side of MSM P4590), the thin medial edge of the ventral ramus is imperfectly preserved so that a perhaps slightly broken notch represents only the possible lateral border of the perilymphatic foramen (Fig. 5). However, it seems reasonable to interpret that a large foramen held entirely within the ramus can be ruled out. Instead, the foramen may have been small and/or positioned far medially, perhaps only notching the medial border of the ventral ramus of the opisthotic. This is speculative to a degree and requires verification from better preserved material. Whatever the form of the foramen, the orientation of the ventral ramus of the opisthotic strongly suggests

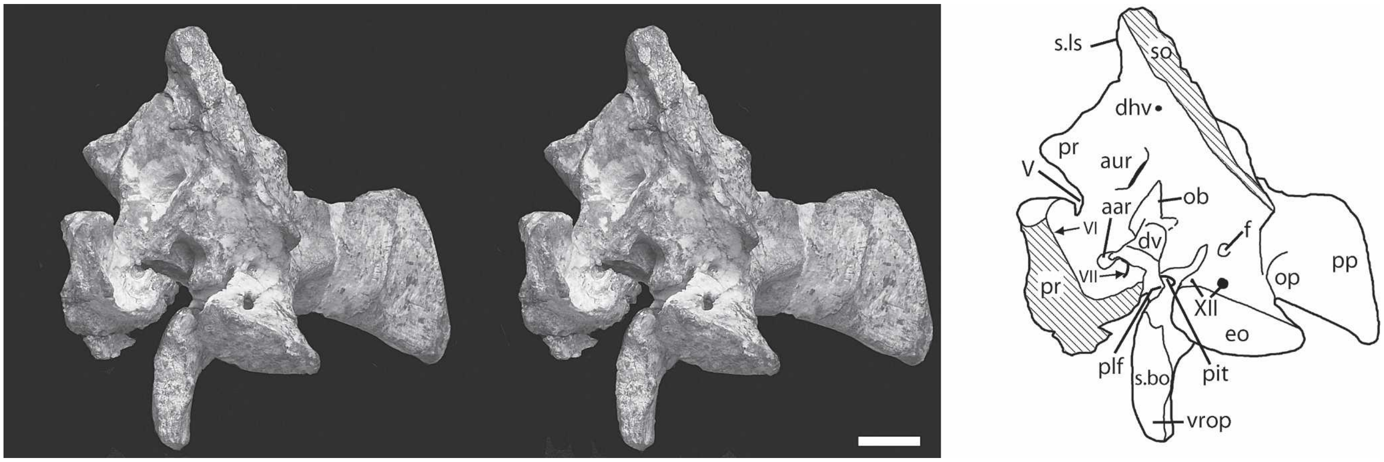

FIGURE 5. The braincase of *Arizonasaurus babbitti*, showing the internal surface of the right supraoccipital region of the smaller specimen MSM P4590. Scale equals 1 cm.

that the perilymphatic duct passed back from the inner ear in a posteromedial direction (or at least lay far medially, if not passing through a foramen in the opisthotic). In this respect, the situation in *A. babbitti* is similar to that in *Euparkeria capensis* and *Sphenodon* (Gower and Weber, 1998) and contrasts with that in the aetosaur *Stagonolepis* and crocodylomorphs (Gower and Walker, 2002).

Prootic—Posteriorly, a tapering tongue of the prootic overlaps the opisthotic at the base of the paroccipital process, as in a wide range of diapsids. Anteriorly, the prootic forms a substantial part of the opening for the passage of the trigeminal nerve and probably the middle cerebral vein. The notch in the anterior of the prootic is simple and lacks subdivision. The rest of the foramen would probably have been formed by the laterosphenoid, if ossified. There is no subhorizontal ridge on the lateral surface of the prootic below the trigeminal foramen, such as is present in some other Triassic archosaurs (e.g., Gower and Sennikov, 1996; Gower, 2002). The crista prootica is moderately developed. Its lateral edge bears an apparently single foramen for the facial nerve that lies in a groove for the extracranial passage of the hyomandibular and palatine branches of this nerve. Anteroventrally, the opposite prootics meet along the midline. Each is upturned, with a largely anteriorly directed concavity that is the probable site of attachment of the retractor bulbi musculature (Fig. 4). Towards the ventrolateral corner of the concavity, and entirely within the prootic, lies the external foramen for the abducens nerve. This foramen is very close to the prootic-parabasisphenoid suture in the larger MSM P4647.

Parabasisphenoid—The parabasisphenoid is marginally verticalized, with the basipterygoid processes lying a little below the level of the basal tubera (Fig. 1). Posteriorly, there is a narrow, 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). Anteroventral to this is a midline, blind parabasisphenoid recess (Fig. 1; probably equivalent to the median pharyngeal recess of Witmer, 1997). Immediately anterior to this, and posteromedial to the base of the basipterygoid processes, lies a pair of foramina probably for the passage of the cerebral branches of the internal carotid arteries. Except in *Turfanosuchus dabanensis* (Wu and Russell, 2001), these foramina are positioned on the lateral surface of the parabasisphenoid in pseudosuchian archosaurs. The posterior surfaces of the basal tubera of the parabasisphenoid are striated in both specimens. In lateral view, the basipterygoid processes are a little larger than the basal tubera. The slightly depressed facet for articulation with the pterygoid covers most of the anteroventral part of the lateral surface of the process (Fig. 3) and less than half of the medial surface.

Dorsolaterally, a narrow piece of the parabasisphenoid is seemingly sandwiched between the lower part of the ventral ramus of the opisthotic plus the basioccipital and the crista prootica. Here the parabasisphenoid possibly reaches the lower border of the fenestra ovalis. In front of this area, the parabasisphenoid bears a subvertical clinoid process with a clearly developed posterior groove (Fig. 3). This groove holds no foramen for the cerebral branch of the internal carotid artery, and instead may have carried only the palatine branch of the facial nerve for most of its course from the facial foramen to the notch between basipterygoid process and basal tuber.

The cultriform process of the parabasisphenoid is almost completely preserved in MSM P4590 (Fig. 3). It is long, slender, and pointed, being at its tallest about one third of the length from the base. 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 (see Gower, 2002). The upper end of the posterior wall of the hypophyseal fossa bears a low midline ridge. The narrower base of the fossa is imperfectly preserved and prepared in the available specimens. Prootic would have intervened between the parabasisphenoid and laterosphenoids in the region preformed by the pila antotica (see Gower, 2002: character 20).

Laterosphenoid—The laterosphenoid is not preserved in any known specimen.

Internal Surface

Basioccipital—Contact between the exoccipitals along the midline and between the exoccipitals and prootics prevents exposure of the basioccipital in the posterior part of the endocranial cavity. The basioccipital is exposed briefly anterolaterally, where it forms part of the lower end of the metotic foramen and the posteromedial wall of the cochlear recess.

Exoccipital—The exoccipitals met along the midline to form a flat to gently transversely concave floor to the posterior part of the endocranial cavity. The exoccipitals are anteriorly tapered, much as in *B. kupferzellensis* (Gower, 2002). Dorsally, in the region where the fused exoccipital-opisthotic boundary must lie, the upper end of the metotic foramen is not pinched off of to form a separate foramen for the possible passage of the posterior cerebral vein, such as is seen in *B. kupferzellensis* and *P. kirkpatricki* (Gower, 2002). However, the medial wall of the exoccipital pillar does hold a concavity (Fig. 5), possibly for a vascular sinus (see Gower, 2002:62).

Supraoccipital—There is no clear sutural demarcation between the supraoccipital and the epiotic (if present as a separate ossification). The supraoccipital probably formed the posterior part of the ceiling of the endocranial cavity, though perhaps not at the foramen magnum itself, where the exoccipitals may make midline contact. The suture with the prootics here is not unequivocally detectable, and it is unclear how much the supraoccipital/epiotic may have contributed to the upper part of the vestibule of the otic capsule. The supraoccipital may also not have contributed to the auricular recess. Anterodorsal to this recess, there is a clear pit that represents the internal foramen for the passage of the dorsal head vein and perhaps the position occupied by an associated sinus, which lies anterior to the level of the external foramen.

Opisthotic—The opistotic contributes to the inner ear, as described above. As in *B. kupferzellensis* (Gower, 2002:63), the contact between the ventral ramus of the opisthotic and the basioccipital is oblique.

Prootic—Although the supraoccipital-prootic suture is not clear, it seems possible that the prootic may have formed more of the dorsal end of the vestibule of the otic capsule than in, for example, *B. kupferzellensis* (Gower, 2002). The prootic also perhaps forms all of the auricular recess, the posterodorsal edge of which does not bear a clear groove for the expected passage of the middle cerebral vein to the trigeminal foramen.

Ventrally, the opposite prootics meet along the midline to form the floor of the endocranial cavity. Posteriorly the prootics contact the exoccipitals, and briefly (laterally) the basioccipital, toward the upper ends of the cochlear recesses. Posterior to the trigeminal foramen, the internal foramen for the passage of the facial nerve lies immediately anterior to a subvertical ridge that demarcates the anterior limit of the otic capsule (Fig. 5). The internal foramen for the facial nerve lies farther forward than the external opening on the crista prootica. Farther forward still, the anteroventral corner of the internal surface of the prootic holds the external foramen for the abducens nerve. This is positioned closer to the midline than the corresponding external foramen. The lower part of the prootic appears to hold the dorsal end of the cochlear part of the capsule.

Parabasisphenoid—The parabasisphenoid is not exposed on the walls or floor of the endocranial cavity.

PHYLOGENY

We scored *A. babbitti* for the 27 braincase characters presented by Gower (2002), resulting in the following additional row of data: 00000 00110 00001 100?0 00010 00. Three of our character scorings for *A. babbitti,* the incomplete ossification of the medial wall of the vestibular part of the otic capsule (character 7), the possible contribution of the supraoccipital to the foramen magnum (19), and the exact form of the perilymphatic foramen (21), are not clearcut based on the described specimens and must be reassessed if new material is found.

The data were analysed using branch-and-bound parsimony searches implemented in PAUP* 4.0b10 (Swofford, 1998). Trees were rooted with *Proterosuchus*. Separate analyses were carried out with characters 1 and 2 ordered and unordered (see Gower, 2002). Support for each node in the strict consensus trees was measured using the decay index (Bremer, 1988; Donoghue et al., 1992) and bootstrap proportions (Felsenstein, 1985), the latter based on 1000 replicates and a maximum of 100 trees held for each iteration. Parsimony matrix randomization permutation-tail probability tests (Faith and Cranston, 1991) on 100 permutations of the complete data set (heuristic searches with 10 random addition sequences and a maximum of 100 trees held in memory) resulted in a minimum possible score of 0.01, whether or not characters were unordered and the outgroup (*Proterosuchus*) was included. This allows rejection of the null hypothesis that the data are no more hierarchically structured than are comparable but random, phylogenetically uninformative data—a recommended minimum requirement of data to be used for phylogenetic inference (Faith and Cranston, 1991). With characters 1 and 2 ordered, 15 most-parsimonious trees (MPTs) were recovered. The strict consensus, with support values, of these MPTs is shown in Fig. 6A. With characters 1 and 2 unordered five MPTs were recovered, the strict consensus being shown in Fig. 6B.

In both ordered and unordered analyses, the MPTs are congruent with the strict component consensus presented by Gower (2002), and the support values are largely the same. In the analysis with all characters unordered, *A. babbitti* is sister taxon to the clade comprising other ‘rauisuchians,’ aetosaurians and crocodylomorphs (Fig. 6). In the analysis with two ordered characters, the position of *A. babbitti* is unresolved relative to those of *Euparkeria capensis* and phytosaurs. Thus, parsimonious interpretation of braincase character data indicates that *A. babbitti* is not especially closely related to other ‘rauisuchians.’ This contradicts the results of a previous analysis of 24 non-braincase characters (Nesbitt, 2003), and is instead compatible with the hypothesis that ‘rauisuchians’ are a non-monophyletic assemblage (e.g. Parrish, 1993; see Gower, 2000). The shortest trees recovered when rauisuchian monophyly is enforced are substantially longer than the MPTs for both ordered (an additional five steps) and unordered (four steps) analyses. Templeton tests, however, do not allow us to reject the null hypothesis that these differences are explained by random sampling error for both ordered ($p = 0.29$) and unordered ($p = 0.13$) analyses.

DISCUSSION

There are no obvious braincase autapomorphies for *Arizonasaurus babbitti*. Although the tarsus is unknown, *A. babbitti* appears to be a pseudosuchian archosaur (Nesbitt, 2003; Nesbitt, 2005). The only braincase feature that may contradict this assumption is the posteroventral position of the entrance foramina for the cerebral branches of the internal carotid foramina. Laterally positioned foramina have been interpreted as a possible synapomorphy of crown-group archosaurs (Gower and Weber, 1998). The plesiomorphic condition, however, is present in *Turfanosuchus dabanensis* (Wu and Russell, 2001), which clearly has a crocodile-like ankle, and is thus probably a pseudosuchian/crurotarsan. Based on current knowledge (Gower, 2002), most other braincase features of *A. babbitti* are plesiomorphic for pseudosuchian archosaurs. For example, the ventral ramus of the opisthotic is prominent laterally, the perilymphatic duct apparently exited the otic capsule posteromedially through an incompletely ossified frame, middle ear pneumaticity is not apparent, and there is no contact between laterosphenoid and parabasisphenoid. The only notably derived feature relative to non-crown-group archosaurs is the apparently elongated cochlear recess.

Nesbitt (2003, 2005) presents evidence for the monophyly of a group of rauisuchians (“Poposauria” of Nesbitt, 2003; “clade X” of Nesbitt, 2005) comprising *A. babbitti*, poposaurids sensu Long and Murry (1995) and chatterjeeids sensu Long and Murry (1995). Given the reality of this clade, the present study indicates that rauisuchians are not monophyletic because *A. babbitti* does not group with the other included rauisuchians (*B. kupferzellensis, P. kirkpatricki, S. galilei, T. romeri*). Rauisuchian non-monophyly was also suggested by Parrish (1993), although character scorings for one of his key exemplar taxa, *P. kirkpatricki*, were based on composite material (Long and Murry, 1995). Contrary to Parrish (1993), our study indicates that the rauisuchians in Nesbitt’s ‘clade X’ are more distantly related to crocodylomorphs than are non-clade X rauisuchians. We stress

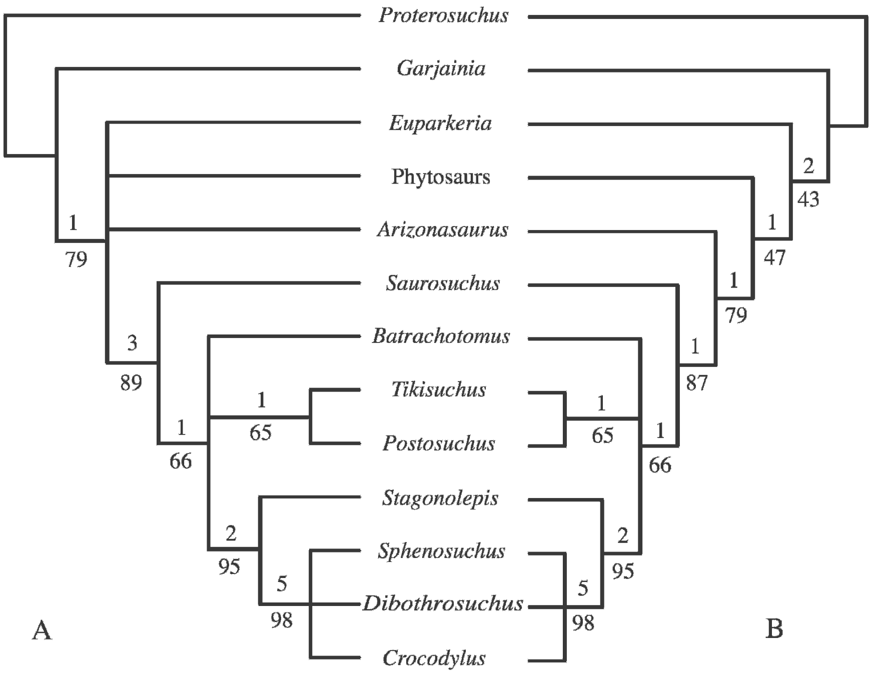

FIGURE 6. Strict consensus summaries of most-parsimonious trees (MPTs) retrieved by parsimony analysis of 27 braincase characters, showing decay indices (above nodes) and bootstrap proportions (below nodes). **A**, consensus of 15 MPTs (L = 40; CI = 0.77; RI = 0.86) from analysis with two characters ordered. **B**, consensus of five MPTs (L = 39; CI = 0.77; RI = 0.86) from analysis with all characters unordered.

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that rauisuchian phylogeny is still not robustly resolved, and further analyses incorporating a wider range of taxa and characters are required. A reappraisal of the cranial anatomy of *P. kirkpatricki* (J. Weinbaum, pers. comm.) will be an important contribution to this additional research. The uncertainty surrounding rauisuchian phylogeny is embedded within an incomplete understanding of pseudosuchian interrelationships. New studies of the signals and conflicts across braincase and non-braincase characters among pseudosuchians are now required.

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