Arizonasaurus and its implications for archosaur divergence

Sterling J. Nesbitt

University of California Museum of Paleontology,
1101 Valley Life Science Building, Berkeley, CA 94720-4780, USA
(snesbitt@uclink.berkeley.edu)

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The Moenkopi Formation has yielded partial and isolated remains of important archosaurs including raiisuchian skull fragments and isolated poposaur centra and pelvic girdle elements. A recently discovered skeleton referable to *Arizonasaurus babbitti* shows that most of these archosaurian remains belong to one taxon. Characteristics of the skeleton of *Arizonasaurus* show that it belongs to a poorly known group of Middle Triassic (240–230 Myr ago) archosaurs called the ctenosauriscids, and that ctenosauriscids are or are closely related to poposaurs. Furthermore, many characteristics of *Arizonasaurus* provide evidence that poposaurids and ctenosauriscids are derived raiisuchians. The presence of a poposaurid in the early Middle Triassic suggests that the divergence of birds and crocodiles occurred earlier than previously thought. Middle Triassic ctenosauriscids also allow the correlation of Triassic faunas in Europe, Asia, North America and Africa. The Moenkopi Formation fauna represents a transitional fauna between Early and Late Triassic faunas.

Keywords: *Arizonasaurus*; poposaur; raiisuchian; Moenkopi Formation; Middle Triassic; archosaur

1. INTRODUCTION

The Triassic Period (245–208 Myr ago) was an important time in archosaur evolution. Recent phylogenies of basal archosaur relationships (Gauthier 1986; Benton & Clark 1988; Sereno 1991) have shown that the crocodile–bird split occurred during or by the Middle Triassic. However, the extensive footprint evidence from the Lower and Middle Triassic of Europe and the western United States suggests that the crocodile–bird split occurred in the Early Triassic (Haubold 1969; Demathieu & Haubold 1978). The lack of archosaurian body fossils in the Lower and Middle Triassic has led to much speculation. A new pseudosuchian from the early Middle Triassic Moenkopi Formation helps to clarify some basal archosaur relationships and gives a new minimum for the crocodile–bird split.

Recent expeditions to the upper Moenkopi Formation (early Middle Triassic) of northern Arizona have recovered archosauromorph reptiles including prolacertiforms, ‘chatterjeeids’, basal raiisuchians, rhynchosaurs and additional material of *Arizonasaurus* (Nesbitt 2001). The species *Arizonasaurus babbitti* was erected solely on a nearly complete left maxilla from the Middle Triassic

strata of the Moenkopi Formation (Welles 1947). The holotype is so incomplete that the taxon has been considered to be a dinosaur, a trilophosaurid, a stagonolepid, a poposaur, a proterosuchian, a raiisuchian, nomen dubium and most currently an erythrosuchid (Hunt 1993). New evidence from a partial skull and skeleton suggests that *Arizonasaurus* is a poposaurid.

2. SPECIES DESCRIPTION

Archosauria: Pseudosuchia: Poposauria: *Arizonasaurus babbitti* Welles, 1947.

(a) *Holotype*

University of California Museum of Paleontology (UCMP) 36232, partial left maxilla.

(b) *Other material*

Mesa Southwest Museum (MSM) P4590, a partial skeleton consisting of a partial skull including fragmentary left maxilla, left frontal, left dentary, left and right articular and partial surangular, right prearticular, braincase, left quadrate, left jugal, right squamosal, and pterygoid, cervical vertebrae, dorsal vertebrae, sacral vertebrae, and nearly complete pectoral and pelvic girdles.

(c) *Horizon and locality*

The holotype came from the Upper Moenkopi Formation (Holbrook Member) near Holbrook, Arizona, USA. The partial skeleton, discovered by Dylan Rust in 2002, was found in an equivalent horizon in the Upper Moenkopi Formation, 33 km from the type locality.

(d) *Age*

The Upper Moenkopi Formation has been dated to the early Anisian (240 Myr ago; early Middle Triassic) by the presence of the temnospondyl *Eocyclotosaurus* (Lucas & Schoch 2002) and by magnetostratigraphy (Steiner *et al.* 1993). The lowermost Chinle Formation (Carnian) lies unconformably on top of the Moenkopi Formation (Stewart *et al.* 1972).

(e) *Diagnosis*

The species differs from all other pseudosuchians in that the ascending process of the maxilla is triangular and has a long, deep fossa that runs dorsoventrally along the posterior border.

(f) *Description*

Until now, only a left maxilla was known (Welles 1947). About 50% of the skeleton of *Arizonasaurus* is known from the new occurrence (MSM P4590; figure 1). The concentration of disarticulated bones and unrepeatable elements of MSM P4590 suggest that the remains represent a single individual. The closure of vertebral sutures indicates that the animal was at least a sub-adult. The limbs and the tail were not found.

The holotype (UCMP 36232) and the maxilla of MSM P4590 are nearly identical (figure 2). *Arizonasaurus* has a posterodorsally pointing ascending process on the maxilla. It is concave on the posterior side, forming the anterior boundary of the antorbital fenestra. Its convex anterior margin borders either a large naris or a cranial opening posterior to the naris. The anterior maxilla bears a palatal process that forms an interlocking premaxilla–maxilla

Figure 1. Skeletal anatomy of *Arizonasaurus babbitti*. Illustrated bones are based on MSM P4590 and the outline of the skeleton is based on *Postosuchus kirkpatricki*. (a) Partial maxilla in lateral view (dashed lines indicate reconstructed outline of the element); (b) third cervical vertebra with broken neural spine in lateral view; (c) anterior dorsal vertebra in lateral view; (d) left ilium in lateral view; (e) fused left and right ischia in lateral view; (f) left pubis in lateral view; (g) incomplete left scapula with articulated coracoid in lateral view; and (h) complete left dentary in lateral view. Scale bars of individual elements represent 5 cm. Skeletal scale bar represents 0.5 m. Abbreviations: ap, ascending process; epi, epipophysis; cen, centrum; cor, coracoid; ns, neural spine; pb, pubic boot; piw, posterior iliac wing; pop, parapophysis; pz, postzygopophysis; sac, supraacetabular crest; sca, scapula.

joint. Seven alveoli are preserved in the more complete UCMP 36232, but MSM P4590 fragments suggest that at least 10 alveoli could have been situated in the elongate, gracile maxilla. A single tooth present in the jaw indicates that the teeth were serrated along both edges, slightly recurved and laterally compressed. The dentary is long and gracile and has an overall structure similar to those of other carnivorous pseudosuchians. The reduction in size and increase in length of other elements of the skull such as the jugal and squamosal suggest that *Arizonasaurus* had an extremely gracile skull.

The anterior cervical vertebrae are elongate and become progressively shorter posteriorly. The cervical neural arches are nearly three times the height of the centra and are slightly curved posteriorly. The anterior dorsal vertebrae have elongated neural spines roughly five to 10 times the height of the centra. Each neural spine has small grooves that run longitudinally up the neural spine. Neural spines that are articulated to the centra gradually curve anteriorly or posteriorly to varying degrees depending on the position along the vertebral column. Most of the neural spines recovered were disarticulated, so their exact configuration along the vertebral column cannot be determined, but it is probable that the anterior neural spines curve anteriorly, whereas the posterior neural spines curve posteriorly.

A complete but disarticulated pelvic girdle is preserved. The pubes are long and gracile, and end in a small boot; they articulate medially to form a thin apron. The pronounced acetabular rim allows anterior–posterior motion of the femur and buttresses the leg in the hip socket, like other rauisuchids (Bonaparte 1984). A distinct mediolateral supraacetabular crest curves posteriorly to join the posterior iliac wing to the crest and curves anteriorly on the medial portion of the ilium, culminating in a point. The ischia are fused together along their lengths; the proximal ends create a ‘T’ shape in dorsal view and articulate with the posteroventral part of the ilia.

3. PHYLOGENETIC ANALYSIS

Phylogenetic analysis of *Arizonasaurus* can help to resolve the poorly understood relationships among rauisuchians, crocodyliforms, aetosaurs, poposaurids and the nearly unknown ctenosauriscids. *Arizonasaurus* can be diagnosed as a rauisuchian on the basis of a combination of the following characteristics: interlocking premaxilla–maxilla articulation, a supraacetabular ‘swelling’ on the ilium (Parrish 1993), a well-developed acetabular rim and laterally compressed, slightly recurved teeth. *Arizonasaurus* also shares several characteristics with the poposaurids, including the lack of osteoderms, completely fused ischia and a supraacetabular crest on the ilium. The extremely tall neural

Figure 2. (a) Partial maxilla of MSM P4590 compared with the holotype maxilla (b) (UCMP 36232: photograph courtesy of UCMP). Both share a small palatal process that articulates with the premaxilla, a deep fossa that runs dorsoventrally along the posterior border, and a similar ascending process. Scale bars, 1 cm.

Figure 3. A strict consensus of the two most parsimonious cladograms was created using PAUP v. 4.0 (Swofford 2001). Nine taxa and 24 characters were used in the analysis. A confidence interval of 0.72 and a retention index of 0.79 were obtained for the two most parsimonious trees. Bootstrap values, given in parentheses, are from 100 replications and the decay values are also given. (a) Archosauria (loss of palatal teeth); (b) Pseudosuchia (crocodile-normal ankle, ilium sub-horizontal/down turned, crocodylian femur); (c) Rauisuchia (interlocking premaxilla-maxilla articulation, a supraacetabular crest on the ilium (Parrish 1993), a well-developed acetabular rim); and (d) Poposauria (lack of osteoderms, completely fused ischia, three or more sacral vertebrae, sacral ribs that articulate with the anterior pointing flange of the ilium).

spines on the dorsal vertebrae and the lack of osteoderms demonstrate that *Arizonasaurus* is a ctenosauriscid, an enigmatic group that was previously known only from fragmentary remains. The cranial material of *Arizonasaurus* is important because it is the only cranial material known for any described poposaurid and is comparable to the skull material of *Lotosaurus*, another ctenosauriscid from the Middle Triassic of China (Zhang 1975). In addition, the new material from *Arizonasaurus* confirms the recent hypothesis that 'poposaurian' pelvis found in association with ctenosauriscids actually belong to ctenosauriscids (Ebel *et al.* 1998).

Figure 4. A phylogeny showing the relationships among pseudosuchian archosaurs in the Triassic. The stratigraphic position and relationships of *Arizonasaurus* show that the crocodile-bird split occurred during the Early Triassic.

With this new evidence, possible ctenosauriscids include *Arizonasaurus babbitti* (Arizona) (Welles 1947), *Ctenosauriscus koeneni* (Germany) (Krebs 1969), *Lotosaurus adentus* (China) (Zhang 1975), *Bromsgroveia walkeri* (England) (Galton 1985) and 'Hypselorhachis mirabilis' (Tanzania) (Krebs 1969). Determining interrelationships among these taxa was not attempted because the remains are only partly described, incomplete and non-comparable. Ctenosauriscids have a cosmopolitan distribution in the early Middle Triassic, and because they are not known to occur in the Late Triassic they may be useful in correlating Middle Triassic faunas.

A phylogenetic analysis of 24 characteristics (see electronic Appendix A available on The Royal Society's Publications Web site) used the best known rauisuchids (*Postosuchus*, *Saurosuchus*), poposaurs (*Poposaurus*, 'Chatterjeea'), aetosaurs (*Desmotosuchus*), crocodyliforms (*Terrestrisuchus*) and *Marasuchus* (bird-line archosaur) plus *Euparkeria* as the outgroup of Archosauria, to establish relationships of ctenosauriscids (*Arizonasaurus*). In two 38-step trees, two poposaurs (*Poposaurus*, 'Chatterjeea') and the ctenosauriscid (*Arizonasaurus*) fall together as a well-supported clade (figure 3). Although relationships among members of this clade are not resolved, the pelvis of *Arizonasaurus* is less derived than in *Poposaurus* and 'Chatterjeea'. The position of *Postosuchus* as the sister group to this clade is poorly supported but might be clarified with the addition of more complete material of lesser known taxa such as other rauisuchians. The poposaurids, ctenosauriscids and *Postosuchus* are

reconstructed as derived rauisuchians. The presence of *Arizonasaurus*, a derived rauisuchian, in the early Middle Triassic suggests that nearly all pseudosuchian archosaur groups had evolved and diversified by the Early Triassic (245–240 Myr ago). Furthermore, the stratigraphic position of *Arizonasaurus* reveals that the crocodile–bird split occurred in the Early Triassic (figure 4). This new information will put tighter constraints on molecular calibration dates for the crocodile–bird divergence.

Arizonasaurus was the dominant predator in a transitional early Middle Triassic fauna. The Moenkopi fauna represent a very important transition from an archaic assemblage dominated by giant amphibians and primitive amniotes to a more ‘modern’ fauna consisting of crocodiles, turtles, lizards, mammals, birds and dinosaurs. This faunal change has been recorded around the world (Lucas 1998), but the more complete Moenkopi fauna helps to link other faunas biogeographically. Moreover, the Moenkopi show that there is less of a faunal gap between the Lower Triassic and the Upper Triassic faunas than previously thought (Benton 1983).

4. SUPPLEMENTARY INFORMATION

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