THE RAUISUCHIAN ARCHOSAUR SAUROSUCHUS FROM THE UPPER TRIASSIC CHINLE GROUP, SOUTHWESTERN U.S.A., AND ITS BIOCHRONOLOGICAL SIGNIFICANCE

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Abstract—We document the first occurrence of the rauisuchian archosaur *Saurosuchus* from the Upper Triassic Chinle Group in the southwestern United States. The fossiliferous horizon is low in the Blue Mesa Member of the Petrified Forest Formation in the Blue Hills of east-central Arizona and yields fragmentary, but highly distinct, skull bones and teeth of *Saurosuchus* sp. In the Blue Hills and elsewhere in Arizona and New Mexico, the Blue Mesa Member yields a tetrapod fauna of Adamanian (latest Carnian) age. Therefore, the occurrence of *Saurosuchus* facilitates correlation of the Blue Mesa Member with the Upper Triassic Ischigualasto Formation in Argentina, the type and only other locality to yield fossils of *Saurosuchus*. This strengthens previous Chinle-Ischigualasto correlations based on the shared presence of the aetosaur *Stagonolepis* (=*Aetosauroides*) and the kannemeyeriid dicynodont *Ischigualastia*. The shared presence of *Stagonolepis* and the rhynchosaur *Hyperodapedon* (=*Scaphonyx*) further correlate the Ischigualasto to the upper portion of the Santa Maria Formation in Brazil, indicating an Adamanian age for the dinosaurs in that unit as well.

Keywords: rauisuchian, Adamanian, Petrified Forest Formation, Ischigualasto Formation

INTRODUCTION

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Nonmarine Upper Triassic red-bed strata exposed in the vicinity of St. Johns, Arizona, have long yielded abundant vertebrate fossils, principally of metoposaurid amphibians, phytosaurs, aetosaurs, and other archosaurian reptiles (Camp, 1930; Camp and Welles, 1956; Jacobs and Murry, 1980; Long and Ballew, 1985; Lucas et al., 1997). Rauisuchian-grade archosaurs, however, are rare components of the fauna, and fragmentary rauisuchian fossils have been referred to *Poposaurus* or *Parrishea* (Long and Murry, 1995). Here, we describe new rauisuchian fossils discovered by one of us (SEK) and discuss their biochronological significance. In this paper, NMMNH refers to the New Mexico Museum of Natural History, Albuquerque.

STRATIGRAPHY AND AGE

Low-lying badlands exposures of the Chinle Group near St. Johns, Arizona, are assigned to the Bluewater Creek and overlying Petrified Forest formations (Fig. 1). The Petrified Forest Formation consists of, in ascending order, the Blue Mesa, Sonsela, and Painted Desert members. The principal fossiliferous horizons are high in the Bluewater Creek Formation and low in the Blue Mesa Member (Fig. 1, see also Lucas et al., 1997). NMMNH locality 3763 occurs in a coarse lithic sandstone approximately 8 m above the base of the Blue Mesa Member and 9 m below the Sonsela Member. The associated fauna from this stratigraphic interval includes the dipnoan Arganodus, the metoposaurid temnospondyl Buettneria pefecta Case, the phytosaurs Rutiodon spp. (sensu Ballew, 1989, and including the type of Machaeroprosopus zunii Camp), the aetosaurs Stagonolepis wellesi (Long and Ballew), and Desmatosuchus haplocerus (Cope), (=Acaenasuchus geoffreyi Long and Murry), indeterminate derived archosaurs, and ornithischian dinosaurs referred to Revueltosaurus (Long and Murry, 1995; Lucas et al., 1997). We note here that records of Poposaurus and Parrishea are based on a proximal femur and cervical centrum, respectively (Long and Murry, 1995), and we doubt that either element is generically determinate.

The fauna of the Blue Mesa Member in the Blue Hills is thus very similar to the fauna from the same unit in the Petrified Forest National Park, which yields the type assemblage of the



FIGURE 1. Measured stratigraphic section and index map of the St. Johns area showing the position of NMMNH locality 3763.



FIGURE 2. Photographs of NMMNH P-34225, *Saurosuchus* sp., from NMMNH locality 3763. **A-B**, Maxilla fragment in **A**, lateral and **B**, medial views; **C-D**, Right maxilla fragment in **C**, lateral and **D**, medial views; **E-F**, Anterior left maxilla fragment in **E**, lateral and **F**, medial views; **G-H**, Isolated tooth in **G**, labial and **H**, mesial views; **I-J**, Isolated tooth in **I**, labial and **H**, mesial views. All scale bars = 2 cm.

Adamanian land-vertebrate faunachron (lvf) of Lucas and Hunt (1993a) (Lucas, 1993, 1997, 1998; Long and Murry, 1995; Lucas et al., 1997). Particularly significant are the co-occurrence of the phytosaur *Rutiodon* and the aetosaur *Stagonolepis*, both of which are index taxa of the Adamanian lvf (Lucas and Hunt, 1993a; Lucas, 1997, 1998). These taxa indicate a latest Carnian (Tuvalian) age and facilitate correlations to Triassic strata in eastern North America, Brazil, Argentina, and Scotland (Lucas, 1998, 2000).

DESCRIPTION

NMMNH P-34225 from NMMNH locality 3763 consists of numerous fragmentary bones and teeth surface collected from a relatively small area (~10 m²) in the lower Blue Mesa Member of the Blue Hills. All of the elements are associated, of similar preservation, and approximately the same size, and isolated teeth and tooth fragments well match teeth found in bone fragments. Thus, all of the fossils described here appear to represent a single taxon and individual (Fig. 2).

All of the bone fragments we illustrate are tooth bearing (Figs 2A-E, 3), and are deep and laterally compressed, typically measuring 40-50 mm tall dorso-ventrally but only 10-15 mm medio-laterally. Although many of the erupted tooth crowns were

broken off, bone weathering and breakage permit examination of replacement teeth (Figs. 2A-D, 3). The external surface of these bones exhibits sculpturing consisting of subparallel elongate grooves and ridges (Figs. 2A,C,E, 3A-C). These are not the typical nutrient foramina associated with the tooth row of numerous reptiles, which are considerably smaller, more circular, and located closer to the tooth row (Figs. 2E, 3C). Instead, the sculpturing is extensive ornamentation of the bone surface. Comparison with the medial surface (Figs. 2B,E,F, 3D) demonstrates that this is not a preservational artifact, as the medial surface is smooth in all of these bones.

The dorsal margin of some maxillary bones is rounded posteriorly but bears a longitudinal ridge or crista that forms the ventral border of the antorbital fossa (Figs. 2C, 3B). One fragment with an incomplete dorsal margin does bear a slight lateral depression (Fig. 2E, 3C). This is probably the anterior border of the antorbital fossa, although it could be the anterior border of the narial fossa, in which case the bone is a fragment of the premaxilla, not the maxilla.

The associated teeth, including visible replacement teeth, are moderately large (20-40 mm crown height), straight (conical) in lateral or medial view, laterally compressed, and bear anterior and posterior serrations. The serrations are somewhat fine (3/



FIGURE 3. Interpretative sketches of NMMNH P-34225, *Saurosuchus* sp., from NMMNH locality 3763. **A**, Maxilla fragment in lateral view; **B**, Right maxilla fragment in lateral view; **C-D**, Anterior left maxilla fragment in **C**, lateral and **D**, medial views. All scale bars = 2 cm. Abbreviations: aofo = antorbital fossa; idp = interdental plates; nf = nutrient foramen; t = tooth.

mm). Most appear symmetrical antero-posteriorly and are nearly so labial-lingually. Some appear slightly more bulbous labially. Tooth crowns are generally approximately 2-3 times taller than antero-posteriorly long. Teeth still in place, including replacement teeth, are deeply set in tooth sockets separated by interdental plates. These plates are pentagonal in occlusal view, with the apices set laterally and the bases lingually.

Taken together, all of these features well-match descriptions of the rauisuchian *Saurosuchus galilei* (Reig, 1959, 1961; Sill, 1974; Alcober, 2000). Indeed, Alcober (2000, p. 303) diagnosed *Saurosuchus* from all other rauisuchians by, among other features, the presence of sculpturing on the skull roof and the maxilla. The only differences between this specimen and the type and referred material of *Saurosuchus* is that the teeth of NMMNH P-34225 are not as strongly recurved as the teeth illustrated by Sill (1974, pl. 1, p. 331). However, no one has ever studied tooth variation in rauisuchians in detail, and the dentition of the contemporaneous phytosaurian archosaurs often exhibit greater variation within a single jaw than that described here between South and North American *Saurosuchus* (Hunt, 1994; Hungerbühler, 2000). In all other details, NMMNH P-34225 closely conforms to published illustrations and descriptions of *Saurosuchus*, particularly those of Sill (1974, fig. 2) and Alcober (2000, figs. 1-2), including the apomorphic presence of deep grooves and ridges in the maxilla. Therefore, we identify NMMNH P-34225 as *Saurosuchus* sp.

SIGNIFICANCE

NMMNH P-34225 is significant for several reasons. First, it is a relatively rare record of a crurotarsan carnivore from the Blue Hills and the Chinle Group. Second, it is the first record of *Saurosuchus* from outside the type locality in the Ischigualasto Formation of Argentina, and only the third individual known from cranial material (Alcober, 2000). Third, the presence of *Saurosuchus* in the Blue Mesa Member of the lower Chinle strengthens previous correlations of the lower Chinle with the Ischigualasto Formation (Lucas et al., 1993; Lucas and Hunt, 1993b; Heckert and Lucas, 1996).

Terrestrial predatory archosaurs, particularly crurotarsans, are rare elements of the Chinle fauna. Previous Adamanian records of these groups, referred to as "poposaurs," "rauisuchians," and "sphenosuchians," include Hesperosuchus agilis Colbert, Poposaurus gracilis Mehl, Parrishea mccreai Long and Murry, Chatterjeea elegans Long and Murry, and Postosuchus kirkpatricki Chatterjee (Long and Murry, 1995; see also Gower, 2000 for commentary on rauisuchian systematics). The addition of Saurosuchus adds substantially to this record. We note, however, that the systematics of the taxa listed above are very poorly known, and most are identified from fragmentary fossils (Long and Murry, 1995). In particular we suspect that taxa with stratigraphic ranges spanning the Late Triassic (e.g., Postosuchus, Poposaurus, and Hesperosuchus) in fact each represent multiple species, if not genera. We note that, of the Chinle archosaurs, the derived crurotarsans and dinosaurs are the only taxa that show no appreciable evolutionary turnover during the Late Triassic, regardless of the taxonomic scheme selected (note Long and Murry, 1995, fig. 199). However, other archosaurs, including phytosaurs and aetosaurs, exhibit generic-level turnover two to three times during the same interval (e.g., Lucas and Hunt, 1993a; Long and Murry, 1995, fig. 199; Lucas, 1997, fig. 23.12, 1998).

The second point is that even in areas other than the Chinle basin, crurotarsans in general and rauisuchians in particular are rare. Previously, *Saurosuchus* was known only from the type and six referred specimens from the Ischigualasto Formation, including two incomplete skulls (Alcober, 2000). The Arizona specimen is thus only the eighth fossil referred to *Saurosuchus* and the third consisting of cranial material.

Finally, the presence of *Saurosuchus* in the Blue Mesa Member of the Chinle Group strengthens previous Chinle-Ischigualasto correlations. Lucas and Hunt (1993b) tentatively assigned an incomplete femur from the Adamanian-aged Los Esteros Member of the Santa Rosa Formation in eastern New Mexico to the kannemeyeriid dicynodont *Ischigualastia*, noting that *Ischigualastia* was previously only known from the Ischigualasto Formation. Similarly, we have long held that the aetosaur *Aetosauroides* from the Ischigualasto Formation is a subjective junior synonym of *Stagonolepis*, known from dozens of Adamanian localities in the Chinle (Heckert and Lucas, 1996, 1999, 2000). *Saurosuchus*, then, is the third taxon now known from both the Chinle and Ischigualasto basins.

The Ischigualasto Formation and the upper Santa Maria Formation (Alemoa Member) in Brazil share several taxa. These include the aetosaur *Stagonolepis* (=*Aetosauroides*) (Heckert and Lucas, 1996, 2000) and the rhynchosaur *Hyperodapedon* (=*Scaphonyx*) (Langer and Schultz, 2000). The shared presence of *Stagonolepis* indicates an Adamanian age for the fauna of the Alemoa Member (Lucas, 1998) which also yields the early dinosaurs *Staurikosaurus pricei* Colbert, *Saturnalia tupiniquim* Langer et al., and *Guaibasaurus candelariensis* Bonaparte et al., and at least one unnamed prosauropod (Langer et al., 1999; Bonaparte et al., 1999; Galton, 2000)

Chronological implications of Chinle-Ischigualasto-upper Santa Maria correlations are: (1) a maximum age of approximately 228 Ma for the Ischigualasto fauna (Rogers et al., 1993) is thus also a maximum age for the Adamanian lvf (Heckert and Lucas, 1996); (2) dinosaurs from the Ischigualasto Formation are no older than Adamanian dinosaurs from the Chinle Group and other localities (Heckert and Lucas, 1996); (3) Otischalkian dinosaurs from the Chinle, Newark Supergroup, Morocco, and India are the oldest known dinosaurs.

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UPPER TRIASSIC DINOSAUR TRACK FROM FORT WINGATE, NEW MEXICO

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Abstract—We describe a probable theropod dinosaur footrint (cf. *Grallator* sp.) from the Upper Triassic Bluewater Creek Formation near Fort Wingate, west-central New Mexico. *Contra* previous assertions, this is not the track of a new ichnospecies, the oldest dinosaur from the Chinle, or an unexpected record. The Bluewater Creek Formation, and thus the track, is of Adamanian (latest Carnian) age, and probable trackmakers (small theropods) were diverse and locally abundant by Adamanian time. The oldest dinosaurs, including theropods, from the Chinle Group are from demonstrably older (Otischalkian) strata. Consequently, tracks of *Grallator* are not unexpected in the Chinle Group generally and the Bluewater Creek Formation in particular.

Keywords: Carnian, Grallator, Upper Triassic, theropod, footprint, Chinle Group

INTRODUCTION

Tetrapod footprints are known from Chinle Group strata in Wyoming, Utah, Colorado, Arizona and New Mexico. Most of these tracks are from the upper part of the Chinle Group in strata of the Rock Point Formation and its correlatives (Lucas, 1997). These strata are of Apachean (late Norian-Rhaetian) age. The tetrapod ichnofauna from these strata is characterized by *Rhynchosauroides* (rhynchocephalian tracks), *Brachychirotherium* (aetosaur tracks), *Grallator* (theropod dinosaur tracks), *Pseudotetrasauropus* (prosauropod dinosaur tracks) and *Tetrasauropus* (sauropod? dinosaur tracks) (e.g., Lockley and Hunt, 1995). Indeed, this ichnofauna represents the typical Late Triassic ichnofauna also found in eastern North America (e.g., Olsen, 1988), western Europe (Lockley and Meyer, 1995) and southern Africa (Olsen and Galton, 1984).

Tracks older than Apachean are relatively rare in the Chinle Group, which is clearly due to the abundance of favorable facies for track preservation in the younger portion of the Chinle than in pre-Apachean strata. One of the oldest and most interesting pre-Apachean records is an apparent dinosaur track from the lower part of the Chinle at Fort Wingate, New Mexico. Hasiotis et al. (1994) originally reported this track and concluded that it represents a pre-late Carnian dinosaur. Here, we describe this track and interpret its significance to the origin of dinosaurs.

PROVENANCE

The track described here is from MNA (Museum of Northern Arizona) locality 530, which is just south of Fort Wingate, New Mexico at UTM zone 12, 723130E, 3926140N (Fig. 1). MNA locality records state that it is in the "Monitor Butte Member" of the Chinle (also see Hasiotis et al., 1994). This means it is in strata of the lower part of the Bluewater Creek Formation of Lucas and Hayden (1989; also see Heckert and Lucas, 2002). Indeed, it is in one of the slumped sandstone beds that Ash (1978) documented as part of his "Ciniza Lake Beds."

AGE

Tetrapod fossils provide the best age control for the Bluewater Creek Formation, and megafossil plants corroborate the age assignment. Although studies of Chinle vertebrates in the Zuni Mountains date back to the early part of the 20th century (Mehl et al., 1916), most bones from the Bluewater Creek Formation are fragmentary and only identifiable as "phytosaur" or "aetosaur" and only indicative of a Late Triassic age. Heckert



FIGURE 1. Index map and stratigraphic section showing the location of MNA locality 530.

(1997a,b) was the first to report more age-diagnostic tetrapod fossils from the Bluewater Creek Formation, including scutes of the aetosaur *Stagonolepis*, an index taxon of the Adamanian (latest Carnian: Tuvalian) land vertebrate faunachron (Lucas and Hunt, 1993; Lucas, 1997, 1998). Thus, Hasiotis et al.'s (1994) statement that the track is from the "early late Carnian" part of the Chinle is incorrect. The track is Adamanian, which is the latter part of the late Carnian.

DESCRIPTION AND IDENTIFICATION

Two tracks and a third impression (possible track) were collected at MNA locality 530. One slab catalogued as MNA V3303 is preserved in convex epirelief on a ripple-laminated, grayish yellow micaceous sandstone. It is a tetradactyl pes impression 70 mm long and 69 mm wide, with pointed digit tips. Poorly preserved, it may be assignable to *Brachychirotherium*, although *Brachychirotherium* typically has blunter digits (Lockley and Hunt, 1995). Hunt and Lucas (2001) documented an Adamanian record of *Brachychirotherium* in the Chinle Group of eastern New Mexico.

A second, much larger structure is also catalogued under MNA V3303. It too is preserved in convex epirelief on a grayish



FIGURE 2. Probable *Grallator* track (MNA V1581) from the Bluewater Creek Formation in west-central New Mexico. **A**, Photograph of convex impressions; **B**, Interpretive sketch of A. Abbreviations: u = ungual phalanx trace; II, III, IV = digits II, III, and IV. Scale bar for A in cm.

yellow micaceous sandstone. This structure appears to preserve four long (~100 mm) pointed, thin and widely separated digits. However, we are not certain that it is a footprint.

MNA V1581 (Fig. 2) is the single, tridactyl track described by Hasiotis et al. (1994). It, too, is preserved in convex epirelief, but the matrix is an olive-gray siltstone. The middle digit is 43 mm long, and is flanked by shorter digits that are 29 and 25 mm long. The digits are long and slender, and the tips are pointed. The digits converge posteriorly to a "heel" that appears to be rounded, although it may not be complete. Each digit appears to preserve phalangeal pads, in the formula 2-3-4.

Identification of a single track is problematic. As has been demonstrated, extramorphological variation can produce a wide range of track morphologies from a single trackmaker (e.g., Peabody, 1948; Haubold, 1996). On face value, MNA V1581 appears to be the tridactyl pes impression of a theropod dinosaur, usually referred to the ichnogenus Grallator (e.g., Olsen et al., 1998). This seems a reasonable identification of MNA V1581, especially given its relatively long middle toe (mesaxonic), which is characteristic of Grallator (Hunt et al., 2000; Lucas et al., 2001). However, given that MNA V1581 is a single track, we consider the identification tentative. Hasiotis et al.'s (1994) statement that MNA V1581 represents a "new ichnospecies allied to Coelurosaurichnus" is much more than can be concluded from a single track. Furthermore, Leonardi and Lockley (1995) presented convincing arguments to abandon the poorly conceived taxon Coelurosaurichnus Huene 1940 as a junior subjective synonym of Grallator Hitchcock 1858, so even if such an identification were possible, the track would be referred to the ichnogenus Grallator.

SIGNIFICANCE

If correctly identified, the *Grallator* track from the Bluewater Creek Formation at Fort Wingate represents the stratigraphically lowest dinosaur footprint from the Chinle Group. It does not, however, represent the oldest Chinle dinosaur record, as diverse bones and teeth of dinosaurs are known from both Otischalkian and Adamanian strata of the Chinle (Hunt et al., 1998). Indeed, these body fossils include many small theropods, the type of animal most likely to be the trackmaker of MNA V1581.

The Fort Wingate *Grallator* track is a relatively old dinosaur track, but equally old dinosaur tracks are known from a variety of localities, including South Africa and the German Keuper (e.g., Haubold, 1971, 1984). Therefore, the Fort Wingate *Grallator* track represents an entirely expected record, well within the temporal and morphological range of known early dinosaur tracks.

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Brain of Machaeroprosopus, x1. a. Dorsal view. b. ventral view (from Camp, 1930, fig. 47, p. 131).