Heckert, A.B., and Lucas, S.G., eds., 2005, Vertebrate Paleontology in Arizona. New Mexico Museum of Natural History and Science Bulletin No. 29.

TRIASSIC VERTEBRATE FOSSILS IN ARIZONA

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Abstract—The Triassic System in Arizona has yielded numerous world-class fossil specimens, including numerous type specimens. The oldest Triassic vertebrates from Arizona are footprints and (largely) temnospondyl bones from the Nonesian (Early Triassic: Spathian) Wupatki Member of the Moenkopi Formation. The Perovkan (early Anisian) faunas of the Holbrook Member of the Moenkopi Formation are exceptional in that they yield both body- and trace fossils of Middle Triassic vertebrates and are almost certainly the best-known faunas of this age in the Americas. Vertebrate fossils of Late Triassic age in Arizona are overwhelmingly body fossils of temnospondyl amphibians and archosaurian reptiles, with trace fossils largely restricted to coprolites. Late Triassic faunas in Arizona include rich assemblages of Adamanian (Carnian) and Revueltian (early-mid Norian) age, with less noteworthy older (Otischalkian) assemblages. The Adamanian records of Arizona are spectacular, and include the "type" Adamanian assemblage in the Petrified Forest National Park, the world's most diverse Late Triassic vertebrate fauna (that of the *Placerias*/Downs' quarries), and other world-class records such as at Ward's Terrace, the Blue Hills, and Stinking Springs Mountain. The late Adamanian (Lamyan) assemblage of the Sonsela Member promises to yield new and important information on the Adamanian-Revueltian transition. Revueltian records are nearly as impressive as those of the Adamanian, including extensive exposures in the vicinity of the Petrified Forest National Park and the best-known tetrapod assemblages from the Owl Rock Formation. The combination of an exceptionally rich record and outstanding exposures of sedimentary sections that allow the correlation of tetrapod faunas means that Arizona will remain a hotbed of research on Middle and Late Triassic vertebrates for the foreseeable future.

Keywords: Triassic, Chinle Group, Moenkopi Formation, Perovkan, Adamanian, Revueltian

INTRODUCTION

The Triassic System in Arizona is known worldwide for its vertebrate fossils. The record of Middle Triassic vertebrates from the Holbrook Member of the Moenkopi Formation is one of the best of its age (Perovkan—Anisian, see Lucas, 1998; Lucas and Schoch, 2002) anywhere in North America. The Moenkopi Formation also yields a substantial vertebrate ichnofauna (Peabody, 1948). Still, the Middle Triassic vertebrates of Arizona pale in comparison to the rich, diverse, and storied collections of its Upper Triassic vertebrates. Highlights of the Upper Triassic of Arizona include the most diverse Upper Triassic vertebrate locality in the world (the *Placerias* quarry), the type fauna of the Adamanian (late-latest Carnian) land vertebrate faunachron (lvf), and the single best "laboratory" for studying Upper Triassic vertebrate evolution in stratigraphic and biostratigraphic context (Petrified Forest National Park). Both the Middle and Upper Triassic series are also important because of the large number of type specimens, particularly of Middle Triassic temnospondyls and Upper Triassic archosaurs (especially phytosaurs) from these strata (Table 1). This record is even more remarkable considering that the vast majority of it was gleaned from a few outcrop belts between the edge of the Colorado Plateau to the south and the Navajo and Hopi nations to the north. Thus, while the Moenkopi and Chinle have already yielded rich, diverse, and in some cases, magnificent collections, the possibility for even greater growth in the future is enormous.

Abbreviations: Throughout this article **AMNH** = American Museum of Natural History, New York; **FMNH** = Field Museum of Natural History, Chicago; **MCZ** = Museum of Comparative Zoology, Harvard University, Cambridge; **MNA** = Museum of Northern Arizona, Flagstaff; **NMMNH** = New Mexico Museum of Natural History and Science, Albuquerque; **PFNP** = Petrified Forest National Park (and **PEFO** to its collections); **SMU** = Southern Methodist University, Dallas; **UCMP** = University of California Museum of Paleontology, Berkeley; and **USNM** = United States National Museum of Natural History, Washington, D.C.

GEOLOGIC SETTING

During Triassic time, Arizona lay at or near the western margin of equatorial Pangea. Southern Arizona appears to have been relatively high, and rivers drained north and west across the northern part of the state. Moenkopi strata in Arizona were deposited near the southern margin of a mixed marine-nonmarine basin centered in Utah (McKee, 1951a,b; McKee et al., 1957; Stewart et al., 1972a). Overlying Chinle Group strata are part of a vast depositional basin that, during Late Triassic time, spanned as much as 2.3 million km^2 along the western equatorial margin of the supercontinent of Pangea (Lucas, 1993a, 1997; Lawton, 1994). Early paleomagnetic evidence suggests that the strata encompassing the localities studied here were deposited at a paleolatitude of approximately 15-18° N (e.g., Dubois, 1964; Smith et al., 1981). However, more recent paleogeographic reconstructions place these localities at a more equatorial latitude, perhaps as low as 5-10°N (Golonka et al., 1994) and no more than 15° north latitude by the beginning of the Jurassic (Golonka et al., 1996).

During Middle Triassic time, northern Arizona lay near a Cordilleran seaway that encroached deep into present-day Utah (McKee et al., 1957; Stewart et al., 1972a; Carr and Paull, 1983; Blakey et al., 1993). Lower-Middle Triassic strata in Arizona are relatively thin (30-150 m maximum thickness) and are assigned to the Moenkopi Formation. Moenkopi Formation strata are principally nonmarine siliciclastic redbeds, but also include bedded evaporites (principally gypsum), especially in the medial Moqui Member. These strata represent lowland deposits and arid coastal

TABLE 4. Vertebrate faunas of the Petrified Forest National Park and vicinity broken down by stratigraphic unit

Blue Mesa Member, PFNP	
Chondrichthyes:	*"Xenacanthus" moorei*
	Lissodus humblei
	"Acrodus" sp.
Osteichthyes:	Redfieldiid indet.
	Palaeoniscidae indet. aff. *Turseodus*
	Actinopterygii indet.
	Arganodus dorotheae
Amphibia:	*Buettneria perfecta*
	Apachesaurus gregorii
	Metoposauridae indet.
Reptilia *incertae sedis*	*Colognathus obscuris*
	Acallosuchus rectori Long and Murry
	Vancleavea campi Long and Murry
Synapsida:	*Placerias* sp.
Lepidosauromorpha:	Possible sphenodont
Archosauromorpha:	*Trilophosaurus buettneri*
Archosauriformes:	Morphotypes D?, G, K, L
Phytosaurs:	*Rutiodon* spp.
Aetosaurs:	*Stagonolepis wellesi*
	Desmatosuchus haplocerus
Rauisuchians:	Rauisuchia indet.
	Poposauridae indet
Sphenosuchia	cf. *Hesperosuchus*
	Parrishia mccraei Long and Murry
Theropoda:	at least one taxon
Ornithischia:	*Crosbysaurus harrisae*
	Ornithischia indet.
Trace fossils:	Vertebrate coprolites
	Grallator sp.
	Reptilia indet.
Sonsela Member, PFNP and vicinity	
Amphibia:	*Buettneria perfecta*
	Apachesaurus gregorii
	Metoposauridae indet.
Phytosaurs:	
	Rutiodon sp.
	Pseudopalatus mccauleyi Ballew
	Pseudopalatus spp.
Aetosaurs:	*Stagonolepis wellesi*
	Paratypothorax sp.
	Typothorax coccinarum
Rauisuchians:	*"Postosuchus"* sp.
	Chatterjeeidae indet.
Painted Desert Member, PFNP	
Chondrichthyes:	*Reticulodus synergus*
Osteichthyes:	Redfieldidae indet.
	Palaeoniscidae indet. aff. *Turseodus*
	Semionotidae indet.
	Arganodus dorotheae
Amphibia:	*Apachesaurus gregorii*
	Metoposauridae indet.:
Phytosaurs:	*Pseudopalatus* spp.
	Pseudopalatus buceros
Aetosaurs:	*Typothorax coccinarum*
	Desmatosuchus chamaensis
	Paratypothorax?
Rauisuchians:	*"Postosuchus"* sp.
	hatterjeeidae indet.
Sphenosuchidae	Sphenosuchidae indet.
Crurotarsi	*Revueltosaurus callenderi*
Theropoda:	*Chindesaurus bryansmalli* Long and Murry
	Ceratosauria aff. *Coelophysis*
Trace fossils:	Vertebrate coprolites

*Complete binomen including author = Type specimen known from that area

(1989) was collected outside of the park, but from strata contiguous with exposures in the PFNP and within recently proposed boundary expansions. This phytosaur was recovered from the Jim Camp Wash beds in Dry Wash just east of the present park boundary. New specimens continue to come to light as well (e.g., Hunt et al., 2002a), and the stratigraphic distribution of these and other specimens from the park are integral to the study of the evolution, distribution, and biostratigraphy of phytosaurs.

Along these lines, we illustrate here two little-known phytosaur specimens (Fig. 8B, F-G) mentioned by Lucas and Heckert (2000) and collected from just outside of current park boundaries, but well within the proposed expansion. George Pearce collected one of these specimens, USNM 15841, 6.4 km southwest of Adamana at or near Point of Bluff in 1937 for the Smithsonian. The stratigraphic horizon is probably the Blue Mesa Member of the Petrified Forest Formation, which crops out extensively in the lower badlands of this area, but it might be in the lower Jim Camp Wash beds, which are exposed above the base. We assign this specimen to *Rutiodon* sp. based on the presence of supratemporal fenestrae that are exposed in dorsal view and at the level of the skull roof (Fig. 8B) (Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002). This is another occurrence of an Adamanian index taxon (*Rutiodon*) in strata of the upper Blue Mesa Member, correlative to Dying Grounds and thus the type Adamanian assemblage.

The second one of these skulls (USNM 15831—Fig. 8F-G) was collected in the general vicinity of Billings Gap, also in 1937, but by G. F. Sternberg. Strata exposed at Billings Gap are almost exclusively interbedded sandstones and mudstones of the Jim Camp Wash Bed, and this specimen almost certainly was collected low in this interval, where vertebrate fossils are abundant (ABH, pers. obs). This is also the approximate horizon, but somewhat to the north of, the type locality of *Pseudopalatus macauleyi* (Ballew, 1989). We assign this specimen to *Pseudopalatus* sp. based on the presence of supratemporal fenestrae that are exposed in dorsal view but are narrow, slit-like, and depressed below the level of the skull roof (Fig. 8G) (e.g., Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002), but, pending more detailed examination of the relationships of pseudopalatines, we refrain from making a species-level identification. (see also Parker and Irmis, 2005)

Once thought to be exceedingly rare, we now know that aetosaur fossils are actually common within the park. Long and Ballew (1985) were the first to demonstrate this by identifying isolated osteoderms (scutes) to genus, and indeed the whole concept of aetosaur biostratigraphy and biochronology (e.g., Lucas and Hunt, 1993; Lucas and Heckert, 1996b; Lucas, 1997, 1998; Heckert and Lucas, 2000a, 2002c) was developed largely as a result of this work. Since Long and Ballew's (1985) study, aetosaurs from the PFNP are featured in both faunal reviews (Murry and Long, 1989; Long et al., 1989; Long and Murry, 1995; Lucas and Hunt, 1995; Lucas and Heckert, 1996; Heckert and Lucas, 2000a) and descriptions of particular records (e.g., Hunt and Lucas, 1992; Heckert and Lucas, 2002c,d; Parker and Irmis, 2005).

Crurotarsans more derived than phytosaurs and aetosaurs are decidedly uncommon in the PFNP, as they are in the American

and Lucas (2002c) consider the aetosaur *Acaenasuchus* to be a junior subjective synonym of *Desmatosuchus*, as the former appears to represent a juvenile of the latter, increasing the observed number of specimens of *Desmatosuchus* known from these quarries by as many as 30 additional osteoderms (Long and Murry, 1995). Even if *Acaenasuchus* is a valid taxon, it is only known from deposits of Adamanian age (Heckert and Lucas, 2002c), The Adamanian phytosaur *Rutiodon* (*Leptosuchus* of some authors) also occurs in the *Placerias*/Downs' quarries as several squamosals representing at least three individuals (Long and Murry, 1995). In contrast, *Parasuchus* is known from the same quarries by only a partial skull of a subadult phytosaur discussed previously.

These facts, when corroborated with the low stratigraphic position of the *Placerias*/Downs' quarry complex, suggest that these quarries were deposited very early in Adamanian time, shortly after the first occurrence of *Stagonolepis* and *Rutiodon*. These taxa, combined with abundant *Desmatosuchus*, are all hallmarks of the Adamanian (Lucas and Hunt, 1993; Lucas, 1997, 1998), and the occurrence of comparatively rare *Parasuchus* indicates holdover of that particular taxon into the earliest Adamanian.

Therefore, despite the presence of *Parasuchus* at the *Placerias*/Downs' quarries, we assign them an Adamanian age, as did Lucas (1993b), Lucas and Hunt (1993), Lucas and Heckert (1996a), Lucas et al. (1997c), and Heckert and Lucas (1997, 2001, 2003a). This means that (1) the Downs' quarry *Parasuchus* fossil is apparently younger than most other records of the genus (2) the lower Bluewater Creek Formation is Adamanian, and that Otischalkian time, if it is represented by Chinle Group strata in eastern Arizona, is only represented by the Zuni Mountains and Shinarump formations.

Other St. Johnsian Vertebrates from Arizona

As noted above, the fossil assemblage typical of the Adamanian lvf comes from the Blue Mesa Member of the Petrified Forest Formation in the PFNP. First collected and studied by Charles Camp, this is the best known Adamanian assemblage from the Chinle Group (e.g., Camp, 1930; Murry and Long, 1989; Murry, 1990; Hunt and Lucas, 1993, 1995; Long and Murry, 1995). The assemblage comes from a narrow stratigraphic interval 5-10 m thick in the upper part of the Blue Mesa Member (Lucas, 1993b; Heckert and Lucas, 2002).

Typical Adamanian vertebrates of this assemblage (Table 2) include the aetosaurs *Stagonolepis wellesi* and *Desmatosuchus haplocerus* and numerous specimens of the phytosaur *Rutiodon*, whose taxonomic status remains in flux (Ballew, 1989; Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002). The larger metoposaur *Buettneria* is considerably more common than its smaller counterpart *Apachesaurus* throughout Adamanian strata, particularly in the PFNP (Hunt and Lucas, 1993).

Smaller late Adamanian vertebrate assemblages are known from the upper Bluewater Creek Formation and Blue Mesa Member near St. Johns, including both the Blue Hills (Lucas and Heckert, 1996a; Heckert and Lucas, 1997, 2001, 2003) and Stinking Springs Mountain (Polcyn et al., 2002). The St. Johns assemblage is particularly important because it can easily be shown, on a lithostratigraphic basis, to be above the early Adamanian *Placerias*-Downs' quarry assemblage (Fig. 12). Thus, the stratigraphic superposition of the earliest and later Adamanian (St. Johnsian) vertebrate fossil assemblages can be demonstrated in the St. Johns area.

Near Ward's Terrace another small vertebrate assemblage in the Blue Mesa Member is of some importance to understanding regional litho- and biostratigraphy. These outcrops of the Blue Mesa Member contain a typical Adamanian fossil assemblage, including the highest occurrence of the dicynodont *Placerias*. This demonstrates the utility of the Adamanian lvf throughout the Bluewater Creek Formation-Blue Mesa Member lithostratigraphic section. Further, the Ward's Terrace localities are important to understanding Late Triassic tetrapod biochronology as they are clearly in the Blue Mesa Member and therefore also demonstrably above the *Placerias*-Downs' quarry fauna. The result of this combination of robust lithostratigraphy with accurate stratigraphic placement of fossil occurrences means that the stratigraphic position of the assemblages shown in Figure 12 are well-documented throughout the Upper Triassic section in Arizona.

Lamyan (late Adamanian) Vertebrates

It has long been thought that the Sonsela Member is depauperate in vertebrates (e.g., Long and Padian, 1986; Long and Murry, 1995; Hunt and Lucas, 1995), and as recently as 2002 any record form the unit was thought to be exceptionally rare (Hunt et al., 2002a). It is now apparent, with a better understanding of the Sonsela lithosome (Heckert and Lucas, 2002a; Woody, 2003), that tetrapods are actually a common component of the Sonsela, and that many localities long thought to be in either the Blue Mesa Member or the Painted Desert Member in fact lie in the Jim Camp Wash beds of the Sonsela Member (Heckert and Lucas, 2002a; Parker and Irmis, 2005). Hunt et al. (2005a) considered this fauna equivalent to the type Lamyan (late Adamanian) fauna, based on the shared occurrence of the phytosaur *Pseudopalatus* and the aetosaur *Typothorax antiquum*. Other tetrapods known from this interval include the aetosaur *Paratypothorax* (including the specimen described by Hunt and Lucas, 1992), and the holotype and some referred material of *Pseudopalatus mccauleyi*. Low in this interval the Adamanian index taxon *Stagonolepis* is known, and *Typothorax coccinarum* has also been recorded from the unit (Parker and Irmis, 2005).

Much work is underway by several parties to try to better delineate the actual stratigraphic ranges of individual vertebrate taxa (e.g., Heckert and Lucas, 2002a; Hunt et al., 2005a; Parker and Irmis, 2005). This is especially the case in the Sonsela Member of the Petrified Forest National Park and vicinity, as the obvious implication of numerous Sonsela localities is that the turnover from the type Adamanian assemblage to a Revueltian assemblage must occur somewhere within the Sonsela Member. It is extremely important to note that the type Adamanian assemblage, that is the classic collecting localities of "Dying Grounds," "Crocodile Hill," and "Phytosaur Basin," among others (Parker, 2002), are all still within the Blue Mesa Member. Therefore, the fauna of the Blue Mesa Member remains largely unchanged in spite of this stratigraphic revision. What does change dramatically is the vertebrate fauna of the Sonsela Member, which goes from being exceedingly sparse (e.g., Hunt et al., 2002a), to rather rich, including both Adamanian and Revueltian faunal elements (Heckert and Lucas, 2002a; Hunt et al., 2005a; Parker and Irmis, 2005).

Early Revueltian Vertebrates

An extensive vertebrate fossil assemblage of early Revueltian age is known from the lower part of the Painted Desert Member of the Petrified Forest Formation in the PFNP (e.g., Camp, 1930; Long and Padian, 1986; Padian, 1986, 1990; Murry and Long, 1989; Murry, 1990; Hunt and Lucas, 1993a, 1995; Long and Murry, 1995). The Painted Desert Member assemblage (Table 3) is significant in that the large metoposaurs are much less common, but the smaller genus *Apachesaurus* is considerably more abundant than in the Adamanian faunas. As documented by Hunt and Lucas (1995), other faunal elements include the phytosaurs *Pseudopalatus*, the aetosaurs *Typothorax coccinarum* and *Desmatosuchus chamaensis* (*"D." chamaensis* of Parker and Irmis, 2005), the rauisuchians *Postosuchus*, and *Chatterjeea elegans* (Long and Murry,