

## 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 (Lamyian) 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 For-

est 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<sup>2</sup> 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

plains, primarily fluvial in origin, but with some restricted ponds and tidal flats, that were developed during late Early (Spathian) and early Middle Triassic (Anisian) time.

Upper Triassic strata exposed in Arizona are dominantly nonmarine siliciclastic red beds assigned to the Chinle Group (Fig. 1). These strata are as much as 550 m thick and represent an array of fluvial, lacustrine and eolian depositional systems that covered northern Arizona during the late Carnian, Norian, and Rhaetian, about 228 to 200 Ma. Lucas (1993a, 1997) used a combination of lithostratigraphy and biostratigraphy to demonstrate the unity of all nonmarine Upper Triassic strata in the American West, and in so doing placed all of those strata into the Chinle Group. Riggs et al. (1996) lent further credence to this stratigraphic hypothesis by correlating deposits based on inferred source areas, determined primarily by U-Pb ages of detrital zircons. Lower Chinle Group strata are dominantly siliciclastics, principally mudstone and sandstone with minor siltstone and conglomerate. These strata represent the deposits of a large (Mississippi-scale) river system with paleoflow generally trending from southeast to northwest. Corresponding offshore deposits are the similarly aged upper Star Peak and Auld Lang Syne groups of Nevada (Lupe and Siberling, 1985; Lucas and Huber, 1994). The comparatively rare carbonate deposits in the Chinle Group represent cumulative pedons or areally restricted lakes.

Chinle Group strata exposed in northern Arizona contain one of the world's outstanding Late Triassic nonmarine fossil records. This record includes both trace- and body fossils. Trace fossils include coprolites and tetrapod footprints, and the body fossil record includes fossils of palynomorphs, charophytes, leaves and wood, ostracods, conchostracans, decapod crustaceans, gastropods, unionid bivalves, fishes and tetrapod vertebrates (e.g., Stewart et al., 1972b; Lucas, 1993a, 1997). This article organizes the rich Triassic vertebrate record of Arizona stratigraphically and biochronologically.

### HISTORY OF COLLECTION

The first Triassic vertebrate fossils from Arizona reported in the scientific literature were fragmentary amphibian and dicyodont bones described by F. A. Lucas (1904) from "Ward's Terrace" in north-central Arizona. These included the holotype humerus of the dicyodont *Placerias hesterunus*, the first Triassic vertebrate taxon named from Arizona. Arizona was thus relatively late to yield fossils during settlement in the American West, and indeed in the late 19<sup>th</sup> century the Triassic record of Arizona was overshadowed by those of New Mexico and Texas, principally due to the work of Cope (e.g., Cope, 1875, 1881, 1892). Still, even early in the 20<sup>th</sup> century Arizona's Triassic fossil record remained less important than that of other western states, for example Wyoming (Williston, 1905; Mehl, 1913).

This changed dramatically in the 1920s when Annie Alexander and companion Annie Kellogg invited Charles Camp, fresh out of graduate school at Columbia University, to the Petrified Forest area to collect fossil vertebrates for the UCMP. This would begin a "golden age" of collecting vertebrates from Upper Triassic strata for the UCMP that would last through the mid-1930s, spurring additional trips by the USNM and AMNH in the 1940s.

Beginning in the 1940s, the UCMP's focus moved down section to the Moenkopi Formation, resulting in extensive body fossil collections documented initially by Welles (1947) and trace fossils first described by Peabody (1948). These remain the foremost collection of Middle Triassic nonmarine vertebrates in North America. The 1950s and 1960s were relatively quiet, with few collectors operating, although this marks the beginning of the MNA's collections of Triassic vertebrates (Brady, 1954, 1958). The MNA would then initiate the next serious round of collecting with

TABLE 1. Triassic vertebrate types from Arizona (Body fossils only)

#### Moenkopi Formation

##### Osteichthyes

*Moenkopia wellsi*

*Taphrognathus bradyi*

##### Amphibians

*Haddockosaurus bradyi* Welles and Estes

*Virgilius wellsi* Warren and Marsicano

*Eocyclosaurus wellsi* Schoch

*Quasicyclosaurus wellsi* Schoch

*Wellesaurus peabodyi* Welles and Cosgriff

=*Stanocephalosaurus birdi* Brown

*Cosgriffius campi* Welles

##### Reptilia incertae sedis

*Anisodontosaurus greeri* Welles

##### Archosauromorpha

*Ammorhynchus navajoi* Nesbitt and Whatley

*Arizonasaurus babbitti* Welles

*Rhadalognathus boweni* Welles

#### Chinle Group

##### Chondrichthyes

*Reticulodus synergus* Murry and Kirby

##### Amphibia

*Kalamoikelor pinkleyi* Branson and Mehl, 1929

*Metoposaurus fraasi* Lucas, 1904

##### Synapsida

*Placerias hesternus* Lucas, 1904

*Placerias gigas* Camp and Welles, 1956

##### Reptilia incertae sedis

*Vanclavea campi* Long and Murry, 1995

*Acallosuchus rectori* Long and Murry, 1995

*Uatchitodon kroehleri* Sues, 1996

##### Trilophosauridae

*Trilophosaurus jacobsi* Murry, 1987

##### Phytosaurs

*Machaeroprotopus validus* Mehl, 1922

*Machaeroprotopus adamanensis* Camp, 1930

*Machaeroprotopus zunii* Camp, 1930

*Machaeroprotopus lithodendrorum* Camp, 1930

*Machaeroprotopus gregorii* Camp, 1930

*Machaeroprotopus tenuis* Camp, 1930

*Pseudopalatus pristinus* Mehl, 1928

*Pseudopalatus mccauleyi* Ballew, 1989

##### Sphenosuchians

*Hesperosuchus agilis* Colbert, 1952

*Parrishia mcreai* Long and Murry, 1995

##### Aetosaurs

*Acaenasuchus geoffreyi* Long and Murry, 1995

##### Dinosaurs

*Chindesaurus bryansmalli* Long and Murry, 1995

*Camposaurus arizonensis* Hunt et al., 1998

major efforts directed at the *Placerias* quarry (Jacobs and Murry, 1980) and the PFNP during the late 1970s and early 1980s, which is also when the UCMP returned to eastern Arizona.

The 1990s saw the NMMNH expand its focus from Texas and New Mexico westward into Arizona, and currently the PFNP itself is also engaged in collecting its own fossil vertebrates (see Parker and Irmis, 2005). Much more detailed histories of Triassic vertebrate paleontology in Arizona were compiled by Long et al. (1989), Murry and Long (1989) and Long and Murry (1995). Welles (1972) published a brief pictorial history rich in photographs of early 20<sup>th</sup> century workers and sites, and Parker (2002) provides a summary of different museum collecting localities in the PFNP.

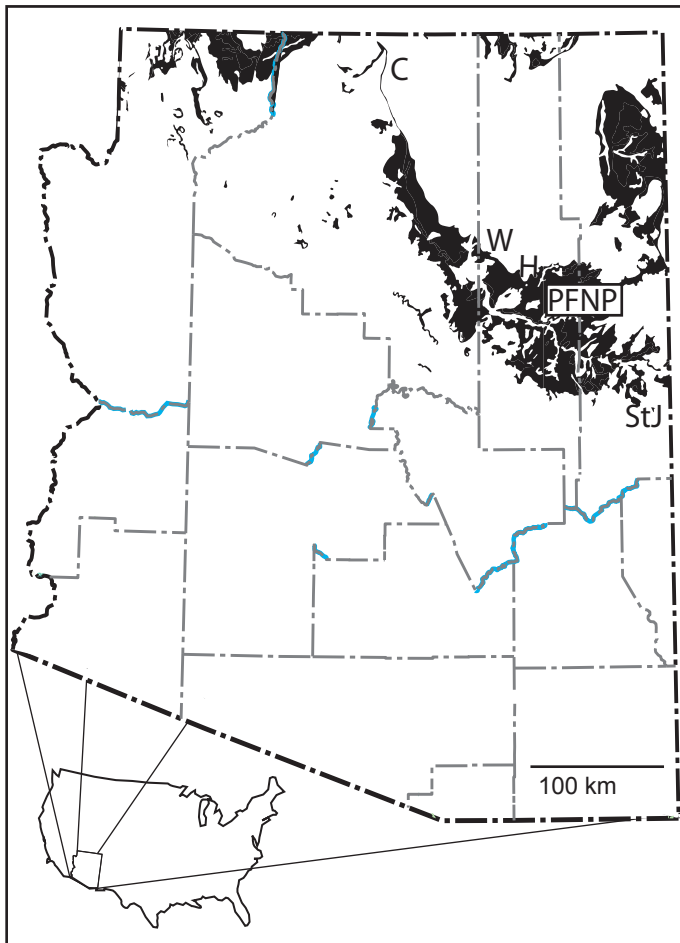


FIGURE 1. Index map showing the outcrop pattern of Triassic strata in northern Arizona. C = Cameron, H = Holbrook, W, = Winslow, PFNP = Petrified Forest National Park, StJ = St. Johns.

## EARLY-MIDDLE TRIASSIC VERTEBRATES IN ARIZONA

### Early-Middle Triassic Stratigraphy in Arizona

All Early-Middle Triassic strata in Arizona are assigned to the Moenkopi Formation, named by Ward (1901) for Moenkopi Wash in the north-central part of the state. Moenkopi Formation strata in Arizona are restricted to the northern portion of the state and divided into (in ascending order) the Wupatki, Moqui, and Holbrook members (McKee, 1954) (Fig. 2). This section is relatively thin (maximum thickness of ~150 m) and essentially entirely nonmarine, but is otherwise homotaxial with, and traceable into, the thicker intertongued marine/nonmarine Moenkopi Formation sections of southern Utah (McKee, 1951a,b, 1954; McKee et al., 1957; Stewart et al., 1972a; Blakey, 1989; Blakey et al., 1993). Essentially, the Wupatki Member, which is the stratigraphically lowest Moenkopi unit in Arizona, is equivalent to the "middle red member" in Utah. The overlying Moqui Member is the landward equivalent of these and younger strata, and the Holbrook Member is a terrestrial equivalent of the "upper red member." Complicating these correlations somewhat is the relatively poorly defined type sections and thus the criteria by which the members are distinguished (see critiques by Morales [1987] and Lucas [1993b]). It is clear, however, that the Holbrook Member in Arizona is stratigraphically equivalent to the Anton Chico Member of the Moenkopi Formation in New Mexico (Lucas and Hunt, 1987; Morales, 1987). Regardless of the niceties of published type sections (or the lack thereof), it is clear that the vast majority of

Moenkopi Formation	Member	Age	LVF	Faunas	Schematic Lithology
		Holbrook Member	Anisian	Perovkan	Geronimo Holbrook area Joseph City Radar Mesa
Moqui Member					
Wupatki Member	Spathian	Nonesian		Meteor Crater	

FIGURE 2. Generalized stratigraphic column of the Moenkopi Formation in Arizona; Perovkan faunas are listed alphabetically; no superposition of Perovkan faunas is implied.

Moenkopi Formation vertebrate occurrences are in the Holbrook Member. The most significant Wupatki Member faunas are those reported from the vicinity of Meteor Crater (Brown, 1933; Welles, 1947, 1993; Welles and Cosgriff, 1965; Morales, 1993a). Essentially all other records of vertebrates from the Moenkopi Formation in Arizona are derived from the Holbrook Member (Welles, 1947; Morales, 1987, 1993a; Cuny et al., 1999; Hunt et al., 2000; Nesbitt, 2000, 2001, 2003; Schoch, 2000; Lucas and Schoch, 2000; Nesbitt and Angielczyk, 2002; Nesbitt and Whatley, 2004).

Regional stratigraphic relationships indicate that the Wupatki Member correlates to Moenkopi strata in southeast Utah immediately above the *Tirolites*-bearing Virgin Limestone (McKee, 1954; Stewart et al., 1972a; Blakey, 1989; Blakey et al., 1993). This suggests a Spathian age for the Wupatki Member, which yields a limited assemblage of fossil tetrapods, apparently of Nonesian age (*sensu* Lucas, 1998), which are Arizona's oldest Triassic vertebrates. The overlying Moqui Member has not yielded any tetrapod fossils, although clastic sediments from these strata would seem likely to bear tetrapod body fossils.

Above the barren Moqui Member, the Holbrook Member yields the vast majority of tetrapod fossils from the Moenkopi Formation in Arizona. Productive Holbrook localities were first described by Welles (1947) and are primarily known from a series of localities near historic US Route 66 and modern-day Interstate 40. Morales (1987) and Lucas and Schoch (2002) provided the most recent reviews of Holbrook Member faunas, although the ongoing work of Nesbitt (2000, 2001, 2003; Nesbitt and Angielczyk, 2002; Nesbitt and Whatley, 2004) has added greatly to our understanding of the vertebrate record of the Holbrook Member. Holbrook Member faunas are of Perovkan (early Anisian) age (Lucas, 1998; Lucas and Schoch, 2002 and references therein).

### Early-Middle Triassic Faunas

Only the Wupatki and Holbrook members of the Moenkopi Formation have yielded identifiable vertebrate fossils, and the

majority of sites and taxa are known from the Holbrook Member (Table 1). Wupatki localities are limited to the immediate vicinity of Meteor Crater (Welles, 1947; Morales, 1993a). Holbrook Member localities are much more common and include the type section, the area around Geronimo, Radar Mesa, Joseph City, and other localities in the vicinity of Holbrook (Welles, 1947, 1967, 1993; Welles and Cosgriff, 1965; Welles and Estes, 1969; Morales, 1987, 1993a; Cuny et al., 1999; Hunt et al., 2000; Nesbitt, 2000, 2001, 2003; Nesbitt and Angielczyk, 2002; Nesbitt and Whatley, 2004).

### Wupatki Member

Published vertebrate records from the Wupatki Member include the capitosauroid temnospondyl *Wellesaurus* (“*Parotosuchus*”) *peabodyi*, which includes as a junior subjective synonym *Stanocephalosaurus birdi* Brown, 1933 (Lucas and Schoch, 2002) (Table 2). Welles (1993) described the trematosaur *Cosgriffius campi* from the Wupatki Member at Meteor Crater quarry. Unpublished material is present in the Wupatki Member at various localities (Morales, 1987). Putative unpublished tanystropheid specimens from the Wupatki Member in the UCMP collection (cf. Welles, 1969) are actually an unusual diapsid of uncertain affinities, but most likely an archosauromorph (Nesbitt and Thiessen, 2004). Tetrapod footprints from the Wupatki Member encompass the chirothere-dominated assemblage from near Meteor Crater documented by Peabody (1948, 1956). The Wupatki Member is not particularly fossiliferous, but did yield the first named tetrapod from the Moenkopi Formation, the holotype of *Stanocephalosaurus birdi* Brown (1933), recovered “six and six-tenths miles southwest of Winslow, Arizona, near the road to Pine and Payson...” (Bird, 1933, p. 1). By far the best Wupatki Member faunas are known from quarries in the vicinity of Meteor Crater. Welles and Estes (1965, also Welles, 1969, 1993) reported a fauna consisting of ganoid fish, a lungfish, and as many as 50 labyrinthodont skulls, including the holotypes of *Parotosuchus peabodyi* Welles and Cosgriff (1965) and *Cosgriffius campi* Welles (1993). Morales (1993) noted that the ichnofauna associated with the Wupatki Member in this area includes *Synaptichnium diabloense*, *Isochirotherium cotteri*, and *Rotodactylus cursorius*, following Peabody (1948).

### Holbrook Member

In contrast to the unfossiliferous Moqui Member and the relatively unfossiliferous Wupatki Member, the Holbrook Member of the Moenkopi Formation in Arizona yields numerous vertebrates, principally tetrapods (Welles, 1947; Table 2). This record is developed from a variety of sites, including the type section near Radar Mesa (Benz, 1980; Lucas and Hunt, 1993; Cuny et al., 1999), the Geronimo quarry (Welles, 1947, 1954, 1967; Welles and Estes, 1969), as well as other, more isolated occurrences (Cuny et al., 1999; Hunt et al., 2000; Warren and Marsicano, 2000), particularly in the vicinity of Holbrook (Nesbitt, 2000, 2001, 2003; Nesbitt and Angielczyk, 2002; Nesbitt and Whatley, 2004).

The Geronimo quarry was excavated by UCMP parties in the 1930s and 1940s, and the fauna of this quarry formed the basis of Welles’ (1947) classic work. The fauna includes indeterminate chondrichthyans, palaeoniscids, the brachyopid *Haddockosaurus bradyi*, Welles, the cyclotosaurid *Cyclotosaurus randalli* Welles, *Rhadalaognathus boweni* Welles, the archosaur *Arizonasaurus babbitti* Welles, and the enigmatic reptile *Anisodontosaurus greeri* Welles (Welles, 1947, 1954, 1967; Welles and Estes, 1969; Hunt et al., 1998c). The vertebrate fauna of Radar Mesa consists of the brachyopid *Haddockosaurus bradyi*, the cyclotosaurid *Cyclotosaurus randalli*, an indeterminate cynodont and the problematic reptile *Anisodontosaurus greeri* (Benz, 1980; Lucas and Hunt, 1993; Hunt et al., 1998c; Cuny et al., 1999), although we agree with Lucas and Hunt (1993) that some of these identifications (from Benz,

TABLE 2. Moenkopi Formation Vertebrates from Arizona

### Wupatki Member

*Osteichthyes* indet. (ganoid scales)  
 Dipnoi indet.  
*Wellesaurus peabodyi* (Welles)  
 = *Stanocephalosaurus birdii* (Brown)  
*Cosgriffius campi* Welles  
*Diapsida incertae sedis*

### Trace fossils:

*Capitosauroides bernburganis* Haubold  
*Chirotherium* spp.  
*Isochirotherium* spp.  
*Synaptichnium diabloense* Peabody  
*Isochirotherium cotteri* Peabody  
*Rotodactylus cursorius* Peabody

### Holbrook Member Fauna

?*Boreosomus* sp.  
*Moenkopia wellesi*  
 Dipnoi indet.  
*Taphrognathus bradyi* Welles  
*Vigilius wellesi* Warren and Marsicano  
*Haddockosaurus bradyi* Welles and Estes  
*Cyclotosaurus randalli*  
*Rhadalaognathus boweni*  
*Anisodontosaurus greeri*  
*Eocyclotosaurus wellesi* Schoch  
*Quasicyclotosaurus wellesi* Schoch  
*Ammorhynchus navajoi* Nesbitt and Whatley  
*Anisodontosaurus greeri* Welles  
*Arizonasaurus babbitti* Welles

### Trace fossils:

*Synaptichnium cameronense* Peabody  
*Synaptichnium* sp.  
*Isochirotherium marshalli* Peabody  
*Isochirotherium* sp.  
*Rotodactylus mckeei* Peabody  
*Rotodactylus bradyi* Peabody  
*Therapsipus cumminsi* Hunt et al.  
 coprolites

\*Complete binomen including author = Type specimen

1980) are probably more specific than can be verified from the preserved material.

Recently Warren and Marsicano (2000) and Schoch (2000) have reevaluated the taxonomy of many Moenkopi temnospondyls. Warren and Marsicano (2000) restricted the binomen *Haddockosaurus bradyi* to the type specimen, and named *Vigilius wellesi* based on a skull referred to that taxon by Welles and Estes (1969). Schoch (2000) considered both *Cyclotosaurus randalli* and *Rhadalaognathus boweni nomenia dubia*. Schoch also erected the new taxa *Eocyclotosaurus wellesi* and *Quasicyclotosaurus wellesi*.

Similarly, over the last decade Nesbitt has re-examined the classic localities in the Holbrook Member of the Moenkopi Formation, and he and those working with him have discovered numerous new localities. These localities are typically in the general area of Holbrook, but extend to the east and west along Interstate 40 and to the southeast well past Woodruff. We highlight some of the most significant localities here.

A locality near Joseph City west of Holbrook yields a remarkably well-preserved ichnofauna including fossils of *Chirotherium* that preserve pedal skin impressions (Nesbitt, 1999). This general area is also the home to one of Nesbitt’s (2000, 2001)



FIGURE 3. Skull of *Eocyclotossaurus* sp. (UCMP4924/42841) from the Holbrook Member of the Moenkopi Formation near Hunt, Arizona, in **A**, dorsal, and **B**, ventral views. Scale bars = 2 cm.

Holbrook Member body fossil faunas, which includes hybodont fish spines, temnospondyls, a putative dicynodont (Nesbitt and Angielczyk, 2002), and the archosaur *Arizonasaurus*. Nesbitt (2000) also documented a microvertebrate site near Holbrook that yields chondrichthyan teeth and osteichthyan scales as well as fragmentary labyrinthodont amphibians, archosauriform teeth, and fragmentary reptile remains. Nesbitt (2003) also noted the widespread occurrence of *Arizonasaurus*, and Nesbitt and Whatley (2004) documented the new rhynchosaur *Ammorhynchus navajoi* from numerous sites extending from north of Winslow to the south and east of Woodruff, between Holbrook and St. Johns.

Moenkopi strata in Arizona extend much farther south than the classic collecting localities along modern-day Interstate 40, and indeed good fossils have been collected as far south as Hunt. Indeed, such strata are locally productive, and the UCMP holds unpublished records of temnospondyls from this area, including a skull of the Perovkan index taxon *Eocyclotossaurus* illustrated here (Fig. 3).

#### Early-Middle Triassic Vertebrate Traces

The Moenkopi Formation has yielded the most significant Early-Middle Triassic tetrapod ichnofauna in the Western Hemisphere. It has two distinct ichnofaunas, one from the late Spathian Wupatki Member and the other from the early Anisian Holbrook Member (Peabody, 1948, 1956). Coprolites have also been reported from both the Wupatki and the Holbrook members (e.g., Benz, 1980; Hunt et al., 2005b).

The Wupatki ichnofauna includes the amphibian track *Capitosauroides bernburgensis* the small reptile tracks *Rhynchosauroides* sp. and *Rotodactylus cursorius*, the small-manus chirothere *Isochirotherium coltoni* and the large manus chirotheres *Chirotherium minus*, *C. barthii*, *C. moquinense* and *Synaptichnium diabloense* as well as possible therapsid tracks (Peabody, 1948, 1956; Haubold, 1971a,b). Peabody (1956) reported swimming traces from the Wupatki Member near Meteor Crater, and he mentioned that they were common in many places in the Little Colorado River valley. Kirby (1987) reported swimming traces from Wupatki National Monument.

The Holbrook ichnofauna includes the small reptile tracks *Rhynchosauroides schochardti*, *R. moenkopiensis* and *Rotodactylous bradyi*, the small-manus chirothere *Isochirotherium marshalli*, the

large manus chirotheres *Chirotherium rex* and *Synaptichnium cameroneense* and the dicynodont track *Therasipus cumminsii* (Peabody, 1948, 1956; Haubold, 1971a, b; Hunt et al., 1993).

Benz (1980) reported coprolites from the Moqui and Holbrook members of the Moenkopi Formation. Benz (1980, pl. 7) illustrated some indeterminate coprolites and noted that coprolites were locally abundant. Many coprolites contain temnospondyl bones, including intercentra (Morales, 1987). Coprolites are present at other Moenkopi localities, but they have not been described.

#### UPPER TRIASSIC STRATIGRAPHY IN ARIZONA

Gregory (1917) was the first to present a unified stratigraphy of the Upper Triassic Series in Arizona, coining the term Chinle Formation and subdividing it into four informal members, A, B, C, and D, (in descending order). Units B (Owl Rock Member) and C (Petrified Forest Member) were later formalized by Gregory himself (Gregory, 1950), and additional USGS work on the Colorado Plateau, during the uranium boom of the 1950s formalized other terms, such as Sonsela Sandstone Bed in the middle of the Petrified Forest Member (Akers et al., 1958) and Rock Point Member (Church Rock Member in northern Arizona) (Stewart et al., 1972b). Indeed, the uranium boom spurred several important syntheses (Harshbarger et al., 1957; Reeside et al. 1957; Stewart et al., 1972b) and complimentary large-scale maps (Cooley et al., 1969; Repenning et al., 1969). These workers essentially established the Upper Triassic stratigraphic framework used by most workers in Arizona. We note here that careful reading of Stewart et al. (1972b) reveals that the USGS had developed a sound lithostratigraphic framework for Upper Triassic strata on the Colorado Plateau. The next major step was Lucas' (1993a) effort to raise the Chinle from formation to group status. By raising the Chinle from formation to group rank, Lucas essentially simplified the nomenclature in use by ceasing to rely on informal members (e.g., Blue Mesa Member for "lower" Petrified Forest Member, Painted Desert for "upper" Petrified Forest Member) and other mappable units. An example of the latter is the "sandstone and siltstone member" (Cameron Formation) informally used by Stewart et al. (1972b). Lucas (1993a) also abandoned the term "Church Rock" to describe strata otherwise known as "Rock Point," noting the rather arbitrary nature of the distinction as explained by Stewart et al. (1972b). Formalizing these stratigraphic relationships and units also encompassed explicit definitions and detailed descriptions of type sections for these units. It is also important that Lucas (1993a) was the first synthetic study to definitively address the relationship of the Chinle on the Colorado Plateau to Upper Triassic strata off of the Plateau, and that we follow his decision to unite all nonmarine Upper Triassic strata in the American West as part of the Chinle Group.

Since 1993 we at the NMMNH have made diverse contributions to documenting the stratigraphic relationships of Upper Triassic fossils and strata across Arizona (e.g., Hunt and Lucas, 1995; Lucas, 1995; Lucas and Heckert, 1996a,b; Heckert and Lucas, 1997, 1998a,b, 2001, 2002a,b, 2003a). Key among these were Lucas and Heckert's (1996a) biostratigraphic breakdown of Upper Triassic vertebrate fossils from Arizona and Heckert and Lucas' (2002a) revision of the Upper Triassic stratigraphy of the PFNP. We build upon the latter to describe the succession of Upper Triassic strata of Arizona.

Critical to developing a robust tetrapod biochronology is identifying an independent method by which to stratigraphically organize vertebrate fossil localities. Detailed lithostratigraphy and regional lithostratigraphic correlation provide such a method. Since the original description of the Chinle (Gregory, 1917, 1950), detailed lithostratigraphic studies of Chinle Group strata in Arizona include those of Cooley (1957, 1958, 1959), Akers et al. (1958),

Repenning et al. (1969), Stewart et al. (1972b), Billingsley (1985a,b), Ash (1987, 1992), Dubiel (1989a), Lucas (1993a, 1997), Heckert and Lucas (1996b, 1997, 1998a,b, 2002a,b, 2003a) and Lucas et al. (1996). Chinle Group lithostratigraphic units in Arizona (Fig. 4) can be organized into eight, temporally successive lithosomes:

1. Zuni Mountains Formation (“mottled strata” of previous authors)/Shinarump Formation—The base of the Chinle Group in Arizona is a profound disconformity, the Tr-3 unconformity of Pipiringos and O’Sullivan (1978). The unconformity separates upper Carnian (Tuvalian) strata of the basal Chinle Group from underlying Perovkan (lower Anisian) strata of the Holbrook Member of the Moenkopi Formation (Morales, 1987; Steiner et al., 1993) or older strata (e.g., Permian DeChelly Sandstone). The basal Chinle Group strata are assigned to the Zuni Mountains Formation (formerly “mottled strata,” see Heckert and Lucas, 2003b) or the Shinarump Formation. Where the two units co-occur, the Zuni Mountains Formation strata are typically stratigraphically below the Shinarump Formation (Lucas et al., 1997c), although we have seen the two units interfinger, especially in the Chinle Valley.

Stewart et al. (1972b) introduced the term “mottled strata” to refer to color-mottled siltstone, mudstone, and sandstone at the base of the Chinle Group. Heckert and Lucas (2003b) formalized this stratigraphic unit, coining the term “Zuni Mountains Formation.” These strata, as much as 10 m thick in Arizona, represent a cumulative pedon and locally contain extensive rhizoliths (=crayfish bioturbation of Hasiotis and Mitchell, 1993). No vertebrate fossils are known from this unit.

The Shinarump Formation locally overlies the Zuni Mountains Formation or rests directly on the Moenkopi Formation or older strata, such as the Permian DeChelly Sandstone at Canyon DeChelly. Shinarump strata in Arizona are as much as 30 m of quartzose sandstones and siliceous conglomerates (most clasts are extrabasinal quartzite, chert and jasper, with additional Paleozoic limestone cobbles) that are typically trough- or planar-crossbedded. Shinarump strata represent large, north- to northwestward-flowing rivers at the onset of Chinle Group deposition. Confirmed Shinarump vertebrate occurrences in Arizona are nonexistent, although some of the fossils Heckert et al. (2002) documented from the type area of the Cameron Formation may be from the Shinarump Formation. Palynomorphs (Litwin et al., 1991) and megafossil plants of the *Eogingkoites* florachron of Ash (1980) indicate a late Carnian (Tuvalian) age for these strata and the faunas they yield.

2. Bluewater Creek, Mesa Redondo and Cameron formations—lower Chinle Group strata in Arizona that conformably overlie the Zuni Mountains or Shinarump formations comprise three distinct lithofacies to which three formation names are applied. The Bluewater Creek Formation of Lucas and Hayden (1989) is as much as 65 m thick in Arizona and consists of red-bed bentonitic mudstones, siltstones and minor trough-crossbedded and ripple-laminated micaceous sandstone. It is exposed from the PFNP eastward, particularly in the vicinity of St. Johns and the Beautiful Mountain area of the Navajo Nation. Arizona’s oldest Late Triassic vertebrate assemblage comes from the basal Bluewater Creek Formation at the *Placerias* quarry near St. Johns (Camp and Welles, 1956; Jacobs and Murry, 1980; Kaye and Padian, 1994; Lucas and Heckert, 1996a; Lucas et al., 1997a) and the Cameron Formation near its type section (Heckert et al., 2002).

The Mesa Redondo Formation of Cooley (1958) is exposed west of St. Johns near Hunt. It is as much as 36 m of interbedded sandstones and mudstones with a significant conglomerate component. No vertebrate fossils have been reported from the Mesa Redondo Formation. We suspect that Mesa Redondo Formation strata are simply a particularly coarse-grained facies of the Bluewater Creek Formation, probably an essentially condensed section

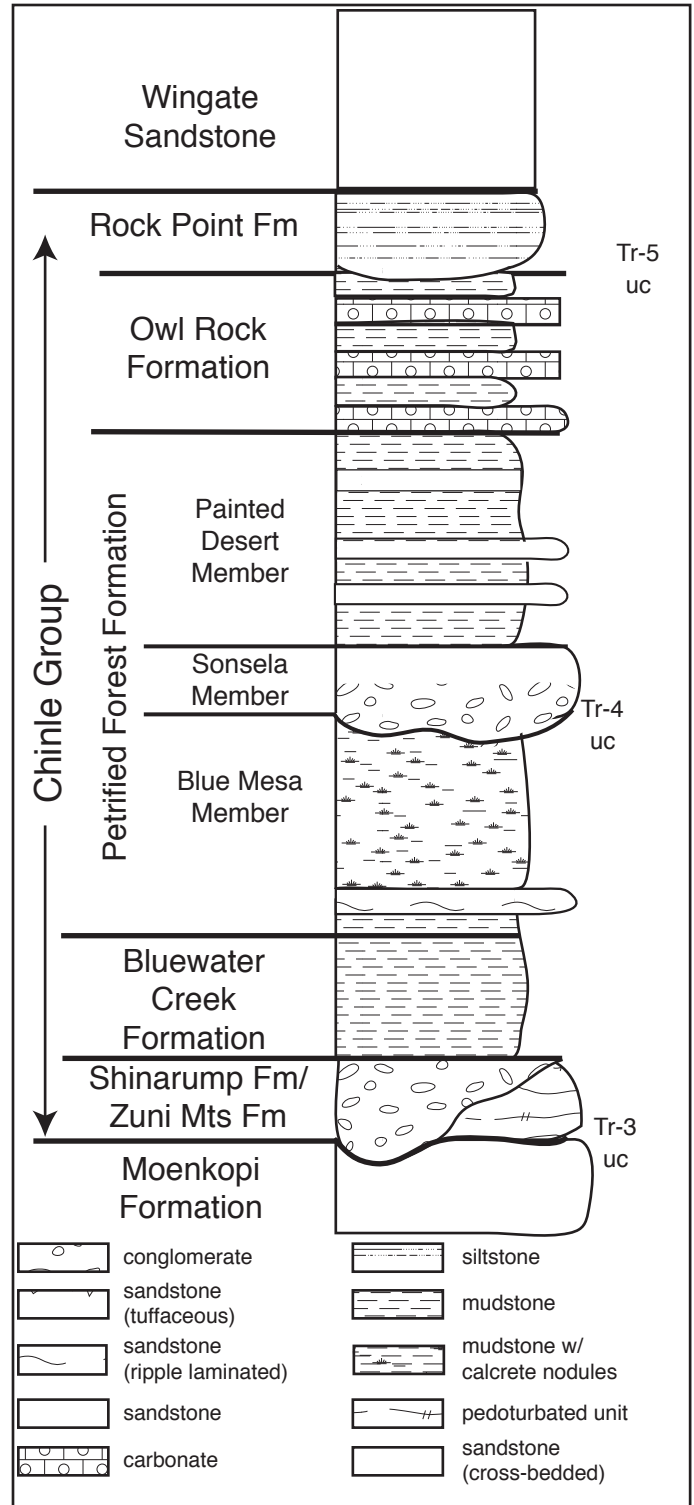


FIGURE 4. Generalized stratigraphy of the Chinle Group in northeastern Arizona. uc = unconformity

near the southern margin of the Chinle basin.

The Cameron Formation of Lucas (1993a) was formerly termed the “sandstone and siltstone member” (Repenning et al., 1969) or “sandstone and mudstone member” (Stewart et al., 1972b) of the Chinle. It is as much as 85 m of mostly laminar and ripple laminar sandstone interbedded with minor mudstone beds. The Cameron Formation is exposed from the vicinity of Cameron northward to the northern rim of the Grand Canyon at Lee’s Ferry.

Heckert et al. (2002) described a small assemblage of vertebrates, principally metoposaurid amphibians and indeterminate pelycosaurs, from the Cameron Formation and, possibly, the underlying Shinarump Formation. Curiously, this fauna had escaped the attention of previous workers, including Long and Murry (1995) and Lucas and Heckert (1996a). Together with the *Placerias* quarry fauna, this is the oldest Late Triassic vertebrate fauna in Arizona. Cameron Formation strata are more axial than the homotaxial Bluewater Creek and Mesa Redondo formations, hence their greater thickness and predominantly sandy composition, as they probably represent deposits of the Chinle trunk drainage and its immediate tributaries in northeastern Arizona.

3. Blue Mesa Member of the Petrified Forest Formation—The Petrified Forest Formation consists of three members (ascending): Blue Mesa, Sonsela, and Painted Desert (Lucas, 1993a). At its type section the Blue Mesa Member is as much as 77.7 m of mostly variegated (purple, green, gray, red) bentonitic mudstone with minor siltstone and micaceous sandstone (Lucas, 1993a; Heckert and Lucas, 2002a). Numerous fossil vertebrate localities are present in the Blue Mesa Member across its outcrop belt. The most extensive are those in the Teepees-Camp Mesa area of the PFNP (e.g., Camp, 1930; Long and Murry, 1995; Heckert and Lucas, 2002a; Parker, 2002). These localities produced the type vertebrate fossil assemblage of the Adamanian lvf of Lucas and Hunt (1993; Lucas, 1998, 2000).

4. Sonsela Member of the Petrified Forest Formation—The base of the Sonsela Member is a basin-wide unconformity, the Tr-4 unconformity of Lucas (1993a; also see Heckert and Lucas, 1996a, 2002a,b). The Sonsela Member is as much as 40 m thick in Arizona (Deacon, 1990), and divided into three formal bed level units, the Rainbow Forest, Jim Camp Wash, and Agate Bridge beds, in ascending order (Heckert and Lucas, 2002a). Both the Rainbow Forest and Agate Bridge beds of the Sonsela consist primarily of quartzose and feldspathic conglomeratic sandstones and conglomerates. Beds at the base of the Rainbow Forest Bed are dominated by coarse-grained sandstone and pebble- to cobble-conglomerates dominated by extrabasinal chert pebbles but also including substantial rip-up clasts of underlying Blue Mesa Member strata. Conversely, in the Agate Bridge Bed, conglomerate clasts are dominantly intraformational rip-ups of mudstone and calcrete pebbles derived either from the underlying Blue Mesa Member or Jim Camp Wash Bed, with occasional chert- and quartzite- dominated beds. Jim Camp Wash beds tend to be less well-indurated sandstones interbedded with bentonitic mudstones, and form many of the prominent purple-and-white striped outcrops in the PFNP. Deacon (1990) explored the geology of the Sonsela Member in detail, but the unit was long thought to be only sparsely fossiliferous. With the relatively recent recognition of a thicker, more complex Sonsela interval (Heckert and Lucas, 2002a; confirmed independently by Woody, 2003), the actual stratigraphic distribution of vertebrate occurrences in the park requires some revision (see Parker and Irmis, 2005; Hunt et al., 2005a). Painted Desert Member occurrences are essentially unchanged, but many localities thought to be in the Blue Mesa Member are now properly placed in the Jim Camp Wash Bed in the middle of the Sonsela. Consequently, the vertebrate fauna of the Sonsela, which was long thought to be exceedingly sparse (e.g., Hunt et al., 2001, 2002b) is in fact rather rich. It is important to note, however, that the basic composition of the underlying Blue Mesa Member fauna is essentially unchanged, as the richest localities (e.g., “Dying Grounds/Crocodile Hill/Phytosaur Basin,” see Parker, 2002) are all still within the Blue Mesa Member (Heckert and Lucas, 2002a).

5. Painted Desert Member of Petrified Forest Formation—the Painted Desert Member is as much as 300 m of mostly red-bed,

bentonitic mudstone with some persistent ledges of micaceous sandstone. In the PFNP, the lower part of the Painted Desert Member contains numerous vertebrate fossil localities of early Revueltian age, principally in the type area in the Painted Desert, but also in the southern portion of the park in the vicinity of the Flattops.

Historically, many workers have noted informal bed-level units in the Painted Desert Member (e.g., Cooley, 1957; Roadifer, 1966; Ash, 1985, 1987, 1992; Billingsley, 1985a,b; Murry, 1990). Many of these have informal names associated with them, although the stratigraphic relationships are somewhat difficult to discern (e.g., contradictions between Painted Desert sandstones of Billingsley, 1985a,b). Ash (1992) formalized one of these units, the Black Forest Bed (“Black Forest Tuff” of previous workers) and Riggs et al. (2003) published an isotopic date of  $213 \pm 1.7$  Ma for this bed. This is an important date because it provides a minimum age for the bulk of the known fauna of the Painted Desert Member in the park, as almost all vertebrate records from the park are stratigraphically below this bed (Heckert and Lucas, 2002a). Heckert and Lucas (2002a) strove to standardize the bed-level nomenclature of the Painted Desert Member in the PFNP, coining the terms Lithodendron Wash and Kachina Point beds for persistent sandstone units in the northern portion of the park and Flattops beds 2-4 for similar units cropping out in the southern portion of the park.

6. Owl Rock Formation—as much as 120 m thick, the Owl Rock Formation is characterized by persistent limestone ledges interbedded with variegated siltstones, mudstones and minor sandstones. Long interpreted as a lacustrine deposit (e.g., Blakey and Gubitosa, 1984; Dubiel, 1989a,b,c, 1993), a restudy of Owl Rock limestones reveals that they are principally calcretes that represent relatively dry, stable landscapes subjected to paleosol development (Lucas and Anderson, 1993; Tanner, 2000, 2003). Fossil vertebrate localities are found in the Owl Rock Formation on Ward’s Terrace north of Cameron (Kirby, 1989, 1990, 1991, 1993). These localities are of late Revueltian age.

7. Rock Point Formation—The youngest Chinle Group strata in Arizona belong to the Rock Point Formation, and are as much as 160 m of repetitively-bedded red-bed sandstone, siltstone and non-bentonitic mudstone. To our knowledge, no vertebrate fossils have been reported from the Rock Point Formation in Arizona, but nearby in northern New Mexico and southeast Utah pelycosaurs and other Apachean-age vertebrates are known from the unit (Harshbarger et al, 1957; Hunt and Lucas, 1993a; Sullivan et al., 1996).

8. The Wingate Sandstone (Lukachukai Member of the Wingate of older usage) conformably overlies the Rock Point Formation, where the latter is present in northern Arizona. Furthermore, evidence is mounting that the unconformity at the base of the Wingate where the Rock Point is absent is actually the same surface where the Rock Point Formation disconformably overlies the Owl Rock Formation across northern Arizona; this is the Tr-5 unconformity of Lucas (1993a). Jurassic units of the Glen Canyon or San Rafael groups overlie the Rock Point Formation with supposed unconformity throughout this region—the J-0 (supposed base of the Wingate Sandstone and therefore the base of Glen Canyon Group) or J-2 (base of San Rafael Group) unconformities of Pippingos and O’Sullivan (1978). However, recent lithostratigraphic studies (also see Marzolf, 1994) indicate that the Dinosaur Canyon Member of the Moenave Formation and at least part of the Wingate Sandstone are laterally equivalent to the Rock Point Formation (Lucas et al., 1997a,b; Lucas et al., 2005). This means the J-0 and Tr-5 unconformities represent a single surface (Fig. 4). Fossils at the base of the Wingate Formation in Utah indicate a Triassic age (e.g., Morales and Ash, 1993; Lucas et al., 1997b,c).

Some fossils from the Dinosaur Canyon Member indicate an Early Jurassic age, which suggests a relatively continuous Triassic-Jurassic transition on the Colorado Plateau (e.g., Lucas and Heckert, 2001b; Lucas et al., 2005), not the abrupt Triassic-Jurassic hiatus long envisioned.

### UPPER TRIASSIC VERTEBRATES IN ARIZONA

In the following sections we review the stratigraphic and geographic distribution of Upper Triassic vertebrates in Arizona. There are hundreds of vertebrate localities in Chinle Group strata in Arizona, principally in strata of the Bluewater Creek, Petrified Forest, and Owl Rock formations. Most of these localities are concentrated in a few areas, namely Cameron, Ward's Terrace, the Petrified Forest National Park, Stinking Springs Mountain, the *Placerias* quarry, and the greater St. Johns area, especially the Blue Hills. In this paper we dedicate separate sections to each of these collecting areas. We also present a final section to list of some of the other, less well known localities.

#### Cameron

The vertebrate fossil record in the Cameron area exclusive of Ward's Terrace (see below) is relatively scanty, although a small fauna of "typical" Chinle vertebrates is known from the immediate vicinity of Cameron (Heckert et al., 2002), and this is also the area of Mehl's (1922) type specimen of the phytosaur *Machaeroprotopus validus* (Table 3). A relatively thin but complete section of the Chinle Group is exposed in this area, including the Shinarump, Cameron, Petrified Forest, Owl Rock, and Rock Point formations (Cooley et al., 1969; Stewart et al., 1972b; Lucas, 1993a). Ash (1980) described some fossil plants from the Shinarump Formation in this area and Heckert et al. (2002) deduced that most vertebrate fossils from this area, were either from the Shinarump Formation or else from a stratigraphically low interval of the Cameron Formation (Fig. 5). This is especially true of fossils from the vicinity of "Tanner's Crossing" now housed at the MNA. The type of Mehl's (1922) *Machaeroprotopus validus* is now lost, but based on his description of the fossiliferous locality, it is probably higher in the section, most likely in the Painted Desert Member (see the Revueltian Ward's Terrace section). The fauna described by Heckert et al. (2002) includes the metoposaurus *Buettneria perfecta*, indeterminate phytosaurs, and tetrapod coprolites. Lithostratigraphic correlations and the presence of abundant large metoposaurs, specifically *Buettneria*, are consistent with an Otischalkian or Adamanian age, especially when the stratigraphic distribution of metoposaurs in Arizona is considered (Hunt and Lucas, 1993). Lithostratigraphic correlation of the Shinarump Formation and other lower Chinle units (Cameron and Bluewater Creek formations) also suggests an Otischalkian to Adamanian age for the Cameron vertebrate assemblages (Lucas and Heckert, 1996a; Heckert et al., 2002).

#### Ward's Bonebed

The first vertebrate fossils from the Upper Triassic of Arizona to receive scientific description were found at Ward's Terrace in north-central Arizona (Lucas, 1904). Here a complete Chinle section consists of the Shinarump, Cameron, Petrified Forest, Owl Rock and Rock Point formations (Cooley et al., 1969). Lucas' (1904) fossils include the types of the temnospondyls *Metoposaurus fraasi* (now recognized as *Buettneria perfecta*: Hunt, 1993) and the dicynodont *Placerias hesternus*. This locality is widely known as "Ward's bonebed," after discoverer Lester Ward (Welles, 1972) and is in the Blue Mesa Member of the Petrified Forest Formation. Mehl (1922, 1928) collected phytosaurs, including the type specimen of *Machaeroprotopus validus* Mehl from a higher stratigraphic interval, but these specimens are now lost. In the 1940s the AMNH returned to

TABLE 3. The vertebrate fauna of the Chinle Group in the vicinity of Cameron (exclusive of the Owl Rock Formation)

#### Cameron Formation, type area

Taxa:	
Amphibia:	<i>Buettneria perfecta</i>
Phytosaurs:	Phytosauridae indet.
Trace fossils:	Vertebrate coprolites

#### Blue Mesa Member, Ward's Terrace

Taxa:	
Osteichthyes:	<i>Arganodus dorotheae</i>
Amphibia:	<i>Buettneria perfecta</i> <i>Apachesaurus gregorii</i> Metoposauridae indet.
Synapsida:	<i>Placerias hesternus</i> Lucas
Phytosaurs:	<i>Rutiodon</i> spp. <i>Smilosuchus gregorii</i> <i>Stagonolepis wellsi</i>
Aetosaurs:	<i>Desmatosuchus haplocerus</i>
Rauisuchians:	" <i>Postosuchus</i> " sp.
Sphenosuchidae	<i>Hesperosuchus agilis</i> Colbert
Trace fossils:	Vertebrate coprolites

Ward's bonebed and extracted a gigantic phytosaur skull identified as *Machaeroprotopus gregorii* by Colbert (1952). Colbert (1952) also named the early sphenosuchian *Hesperosuchus agilis* for a partial skeleton recovered from the area. Long and Murry's (1995) faunal list for Ward's bonebed includes the metoposaurs *Buettneria perfecta* and *Apachesaurus gregorii*, *Rutiodon*-grade phytosaurs (= *Leptosuchus* and *Smilosuchus*), the aetosaurs *Stagonolepis wellsi* and *Desmatosuchus haplocerus* and the rauisuchian *Postosuchus kirkpatricki* in addition to the type specimens just listed (Table 3). Lucas and Heckert (2002) described a topotype skull of *Placerias* from this, the type locality of *Placerias hesternus* Lucas. *Rutiodon*-grade phytosaurs and the aetosaurs *Stagonolepis* and *D. haplocerus* are index taxa of the Adamanian lvf and therefore demonstrate an Adamanian age for the fauna at Ward's bonebed.

#### Petrified Forest National Park

The Petrified Forest National Park (PFNP; PEFO is the National Park Service acronym) is the singlemost important laboratory for the study of Upper Triassic vertebrate evolution in North America. No other area possesses the stratigraphically superposed quantity and diversity of vertebrate fossils, long history of vertebrate fossil collecting, detailed stratigraphic framework, and potential for numerical age calibration. Obviously, we can only review this wealth of information in the most cursory manner, so here we attempt to highlight what we consider the most important aspects of the vertebrate record of the PFNP and provide a reasonably comprehensive bibliography of its scientific literature. Figure 6 shows the evolution of stratigraphic nomenclature for the park relevant to our discussion, and Figure 7 shows the general stratigraphic position and age of the PFNP faunas. Elsewhere in this volume Parker and Irmis (2005) provide insight into the newest discoveries at the park.

The Upper Triassic record of the PFNP is, therefore, unmatched, because:

- (1) C.L. Camp began his research on Triassic vertebrates here, excavating localities first identified by Annie Alexander and Anne Kellogg. Their initial success essentially created his position at the UCMP and thus spurred arguably the greatest 15 years of vertebrate collection in the Chinle (Camp, 1930; Welles, 1972; Long et al., 1989; Long and Murry, 1995).



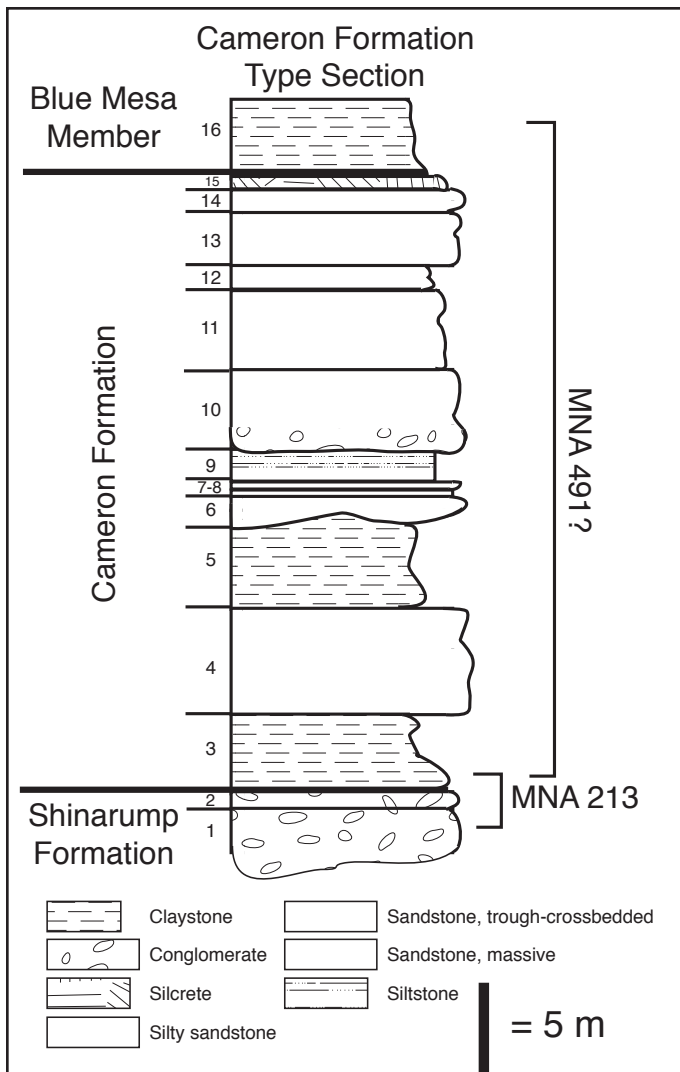


FIGURE 5. Generalized stratigraphy of lower Chinle Group strata in the vicinity of Cameron, Arizona, showing the probable stratigraphic distribution of tetrapods from MNA localities 213 and 491.

(2) The “Dying Grounds,” “Crocodile Hill” and “Phytosaur basin” areas, first excavated by Camp, are phenomenally rich (Long and Murry, 1995; Parker, 2002), and the faunas collected from these localities serve as the type assemblage of the Adamanian lvf (Lucas and Hunt, 1993). These tetrapods, especially the index taxon *Stagonolepis*, are now known to occur throughout a similar stratigraphic interval, not only in the American Southwest (e.g., Lucas and Hunt, 1993; Lucas, 1997), but also across much of Pangea, including Brazil and Argentina (Lucas, 1998; Lucas and Heckert, 2001a; Heckert and Lucas, 2002c).

(3) The outstanding exposures of the PFNP allow numerous vertebrate localities to be correlated stratigraphically, demonstrating not just that Revueltian faunas occur in strata stratigraphically higher than Adamanian faunas, but facilitating detailed resolution of vertebrate stratigraphic ranges (Lucas and Hunt, 1995; Heckert and Lucas, 2002a; Parker and Irmis, 2005; Hunt et al., 2005a). Essentially, it is now clear that the vertebrate faunas from the Petrified Forest National Park come not just from the Blue Mesa Member

(lower Petrified Forest Member of some workers) and the Painted Desert Member (upper Petrified Forest Member), but also the Sonsela Member as well (Heckert and Lucas, 2002a; Woody, 2003) (Fig. 7). In fact, it appears likely now that many of the localities outside of the classic “Dying Grounds” and “Crocodile Hill” localities in the immediate vicinity of Blue Mesa itself are not in the Blue Mesa Member, but are instead in the Jim Camp Wash Bed of the Sonsela Member, so in the next few years researchers can expect the fauna of the Sonsela Member to go from rare occurrences (e.g., the phytosaur from the Agate Bridge Bed documented by Hunt et al., 2002a) to a well-known and described fauna consisting of metoposaurs, phytosaurs, aetosaurs, and other typical Chinle taxa. Indeed, ongoing work suggests that Hunt’s (2001) “Rainbowforestan” sub-lvf of the Revueltian may indeed be discernable within the PFNP (Stocker and Parker, 2004; Woody and Parker, 2004), but is probably better termed the Lamyian sub-lvf of the Adamanian; Hunt et al., 2005a). All of this is despite the fact that a detailed lithostratigraphic framework for the park, including numerous correlated measured sections and vertebrate localities, was only published quite recently (Heckert and Lucas, 2002a). Regardless, biostratigraphic hypotheses of the superposed tetrapod faunas include Long and Padian (1986), Murry and Long (1989), Murry (1990), Lucas and Hunt (1993, 1995), Long and Murry (1995), Lucas and Heckert (1996a) and Heckert and Lucas, (2002a), and Hunt et al. (2005a), but see commentary by Parker and Irmis (2005).

(4) The sheer volume of vertebrate collecting activity in the park and its immediate environs necessarily resulted in the collection of numerous type specimens (Table 4). Some of these remain valid and in use today (*Chindesaurus bryansmalli* Long and Murry) or are so unusual that they remain valid if somewhat enigmatic (*Acallosuchus rectori* Long and Murry, *Vancleavea campi*, Long and Murry, *Parrishia mcreai*, Long and Murry). Others have succumbed to the unending synonymies of previously named archosaurs (e.g., the phytosaurs, including *Pseudopalatus pristinus* Mehl, *Machaeropsopus lithodendrorum* Camp and *M. adamanensis* Camp).

Important systematic vertebrate fossil collections from the PFNP include microvertebrates, temnospondyl amphibians, numerous problematic archosauromorphs, phytosaurs, aetosaurs, “rauisuchians,” “sphenosuchians,” and dinosaurs. Microvertebrate collections from the park have been reported by Murry and Long (1989), Murry (1989a, 1990), Heckert (2001, 2004), and Murry and Kirby (2002). The richest such assemblage is that of the Dying Grounds locality excavated by Murry (1989a) and Heckert (2001, 2004), although this locality has only just been tapped, and much work remains at all of the known sites, not to mention the as-yet-undiscovered ones. The vast majority of what we know of Chinle sharks and bony fish in Arizona comes from these microvertebrate sites. Important selachian records from the park include referred specimens of *Reticulodus synergus* (Murry and Kirby, 2002) from the Painted Desert Member as well as abundant specimens of “*Xenacanthus*” *moorei* from the Blue Mesa Member (Murry, 1989a; Heckert, 2001, 2004, 2005).

Metoposaurs are a common component of the PEFO fauna, but are relatively understudied in the park. PFNP specimens figure prominently, however, in various reviews (e.g., Colbert and



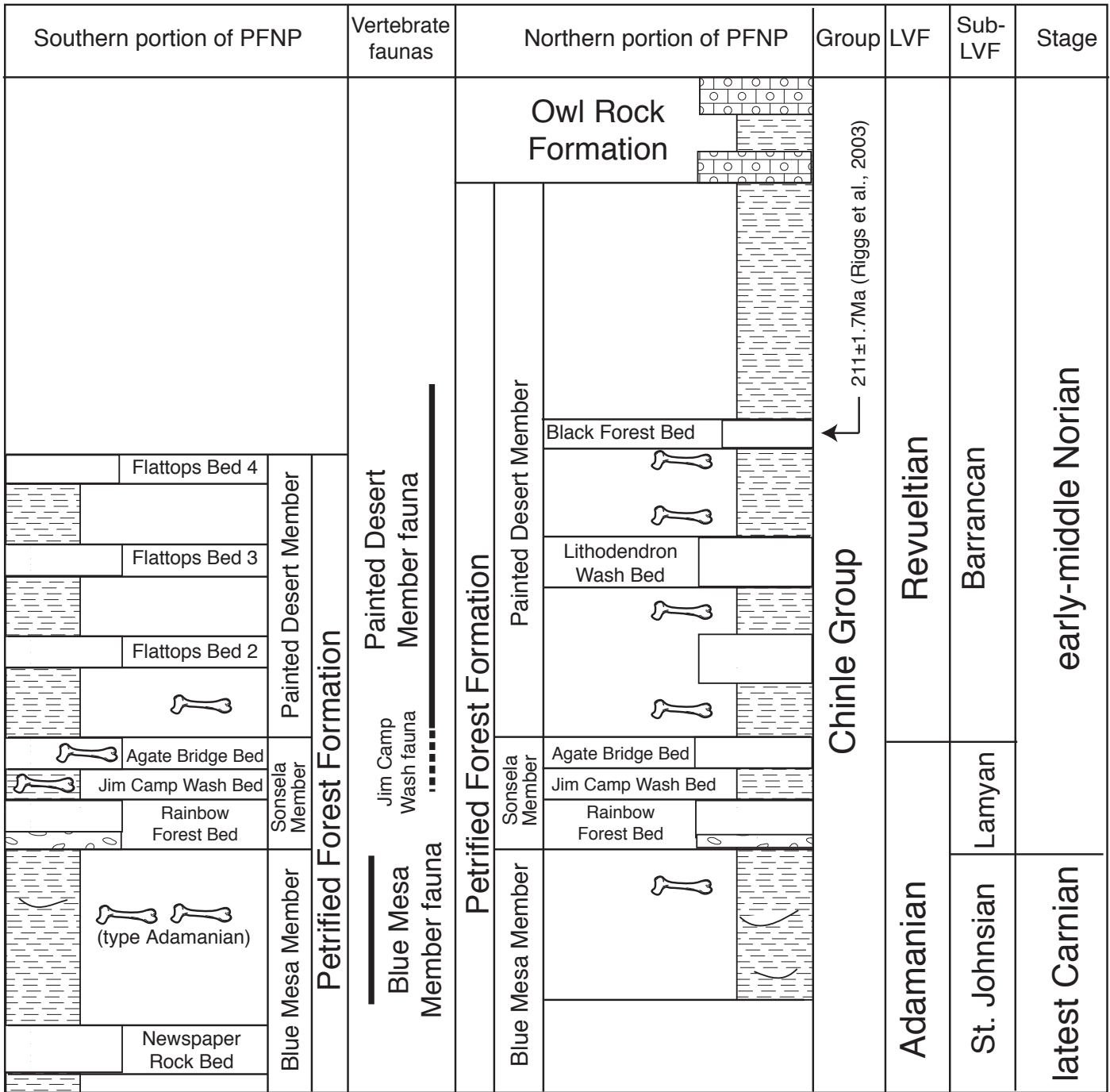


FIGURE 7. Chart showing the general stratigraphic distribution and age of Upper Triassic vertebrate faunas in the Petrified Forest National Park. Biostratigraphy follows Heckert and Lucas (2002a) with modifications based on Hunt et al. (2005a) and Parker and Irmis (2005).

Imbrie, 1956; Gregory, 1980; Davidow-Henry, 1989; Hunt, 1989a, 1993a; Long and Murry, 1995) as well as some studies on the distribution of such specimens in the park (Hunt and Lucas, 1993b). Hunt and Lucas (1993) utilized the stratigraphic and geographic distribution of metoposaurs in the park to demonstrate that large metoposaurs (*Buettneria*) are abundant in the lower stratigraphic units and rare in stratigraphically higher intervals. Conversely, small metoposaurs (*Apachesaurus*) are rare in the lower part of the section and much more common in the Painted Desert Member. The “Dinosaur Hill” area in the Painted Desert Member is especially rich with records of *Apachesaurus*, including associated skeletons. This pattern appears to hold true throughout the Chinle generally, and probably has paleoenvironmental and, possibly,

paleobiogeographic, significance.

It is impossible to write even the most general review of phytosaurs without referring to the PFNP and its specimens. The phytosaurs from PFNP figure prominently in the literature (Camp, 1930; Anderson, 1936; Colbert, 1947; Gregory, 1962a,b, 1969; Ballew, 1986, 1989; Hunt, 1989b, 1993b, 1994; Long and Murry, 1995; Hungerbühler, 2002), and phytosaurs collected in the park are continually re-evaluated, redescribed, and re-illustrated. Camp (1930) named two species (*Machaeropsopus lithodendrorum* and *M. adamanensis*) from exposures within the current boundaries of the park, and Mehl’s (1928) holotype of *Pseudopalatus pristinus* was collected from within the present-day boundaries of the park. It should be noted that the holotype of *Pseudopalatus macauleyi* Ballew

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

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

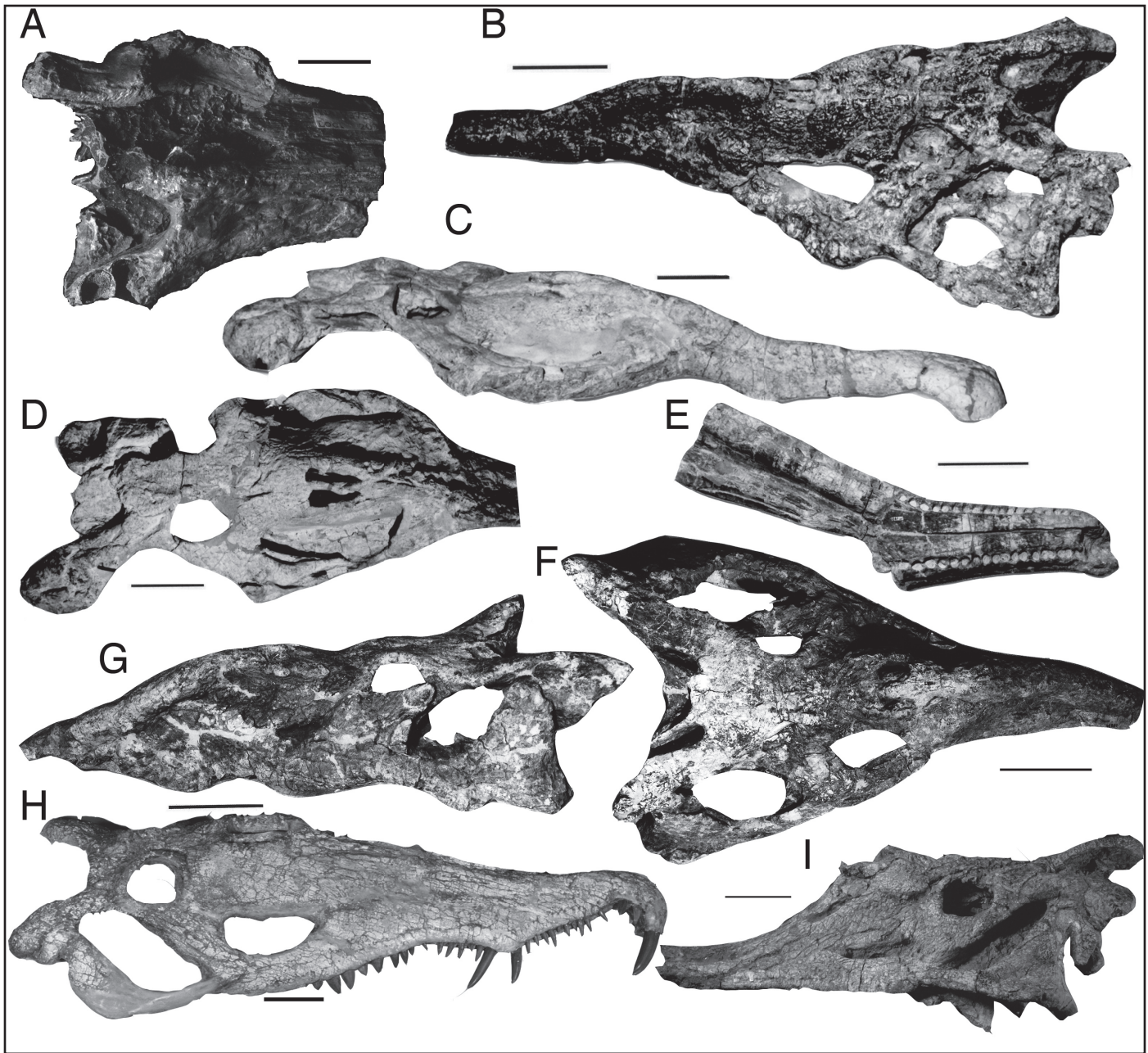


FIGURE 8. Biostratigraphically significant phytosaur fossils from Chinle Group strata in Arizona. **A**, Fragmentary skull of a juvenile *Parasuchus* (= *Paleorhinus*) (MNA 2698) from the *Placerias* quarry; **B**, *Rutiodon* sp. (USNM 15841) from Point of Bluff, **C-E**, *Rutiodon* sp. (USNM 17098) from the Bluewater Creek Formation near Picket House Draw, including (**C-D**), skull in **C**, dorsal, and **D**, right lateral views and **E**, lower jaw in dorsal view; **F-G**, incomplete skull of *Pseudopalatus* sp. (USNM 15831) from the Billings Gap area in **F**, left lateral and **G**, dorsal views; **H**, skull of male *Pseudopalatus buceros* (MNA V3478) from MNA locality 214 in the Owl Rock Formation in lateral view as exhibited at the MNA; **I**, skull of female *Pseudopalatus buceros* (MNA V3495) in lateral view. Scale bars = 2 cm (A) and 10 cm (B-I).

Southwest generally. Still, several important specimens are known from this area, and more will doubtless come to light as workers concentrate on more terrestrial facies (paleosols and distal floodplains; e.g. Hunt et al., 1996). These include records of "rauisuchians," "sphenosuchians," and *Revueltosaurus*, among others. Long and Murry (1995) documented several "rauisuchians" *sensu lato* from throughout the fossiliferous section at the PFNP. Many of these are fragmentary (and probably not identifiable to genus and species, *contra* Long and Murry), but include records of larger taxa ("*Postosuchus*") as well as more gracile smaller poposaurs ("*Chatterjeea*") (Long and Murry, 1995; see also Parker and Irmis, 2005). Sphenosuchians from the park include possible records of

*Hesperosuchus* and *Parrishia* (Parrish, 1991; Long and Murry, 1995; Clark et al., 2000; Parker and Irmis, 2005). The other important crurotarsan from the PFNP is the enigmatic taxon *Revueltosaurus callenderi*. Long thought to be an ornithischian dinosaur based on its highly convergent tooth morphology newly discovered cranial and postcranial fossils now demonstrate that this taxon is actually an unusual crurotarsan (Parker et al., 2005).

Fossils of dinosaurs and/or closely related taxa remain relatively rare at the PFNP, although focusing collecting efforts on more terrestrial strata definitely increases the probability of finding such taxa (Hunt et al., 1996; Hunt, 1998). With the removal of *Revueltosaurus* from the Ornithischia (Parker et al., 2005;

see above), the only unquestionably dinosaurian material from the PFP consists of various fossils assigned to the Theropoda, principally Coelophysidae (Padian, 1986; Hunt et al., 1996; Hunt, 1998; Hunt and Wright, 1999; Parker and Irmis, 2005). Most of these fossils come from a narrow stratigraphic interval in and around “Dinosaur Hill” in the Painted Desert Member of the Petrified Forest Formation in the northern portion of the park (Heckert and Lucas, 2002a; Parker, 2002). The type locality of the probable herrerasaurid *Chindesaurus bryansmalli* Long and Murry (1995) also lies in the Painted Desert Member near this horizon. The sole exceptions to this are Blue Mesa Member localities yielding a coelophysoid theropod (Hunt et al., 1996) and the possible ornithischian *Crosbysaurus* (Heckert, 2001, 2004).

Finally, it should be noted that many institutions have collected from the park, and thus fossils from the park are distributed far and wide across the North American continent. Parker (2002) reviews the disposition of these collections, and is an essential guide to researchers interested in the vertebrate paleontology of the park.

### Stinking Springs Mountain

Recently Polcyn et al. (2002) documented a rich new microvertebrate assemblage and several other vertebrate localities in the vicinity of North Stinking Springs Mountain and Richey Tank, approximately halfway between the Petrified Forest National Park and other, classic collecting localities in the vicinity of St. Johns (Fig. 9). These localities are therefore important in helping to solidify correlations between these two areas, and the microvertebrate locality described by Polcyn et al. (2002) is remarkably diverse and will probably eventually yield one of the most diverse Chinle Group faunas known (Table 5).

Polcyn et al. (2002) were unwilling to definitively correlate their localities to a larger-scale stratigraphy, instead indicating that they believed that SMU localities 252, 253, and 255 (252 is the microvertebrate locality) were low in the lower Petrified Forest Member (Blue Mesa Member of our usage), and that SMU 251 and 254 (North Stinking Springs Mountain and SMU 254 (Richey Tank) were at or near the lower Petrified Forest Member-upper Petrified Forest Member transition.

In that same volume, Heckert and Lucas (2002a) re-evaluated the lithostratigraphy of the Petrified Forest National Park. There, they demonstrated that the Sonsela Member, rather being a single, thin (< 10 m thick) sandstone, as traditionally believed, is in fact a tripartite unit consisting of thin basal and upper sandstone- and conglomerate-dominated units (Rainbow Forest and Agate Bridge beds, respectively) that form cliffs above and below a thick (~30 m), more slope-forming sandstone and mudstone interval (Jim Camp Wash Bed). Based on this observation, our studies of the stratigraphy of the Chinle Group in this area, and Polcyn et al.’s (2002) published descriptions of their sections, we propose here that most of their upper localities are, in fact, in the Sonsela Member, quite possibly in the Jim Camp Wash Beds (Fig. 10). Polcyn et al.’s (2002) stratigraphically lowest localities are, we believe correctly placed low in the Blue Mesa Member (lower Petrified Forest Member of their usage). The phytosaur skulls they document (Polcyn et al., 2002, fig. 4) independently support this assessment, as the skull of *Pseudopalatus* is the stratigraphically highest skull (from SMU 254), and skulls of *Rutiodon*-grade phytosaurs were found at SUM localities 254 and 251, in intervals known to produce similar skulls (see also Parker and Irmis, 2005). The faunas of the Stinking Springs area thus support existing biostratigraphic correlations of Chinle Group strata in Arizona (Lucas and Heckert, 1996; Heckert and Lucas, 1997, 2002a). Further study of these localities should therefore result in additional biostratigraphic insights.

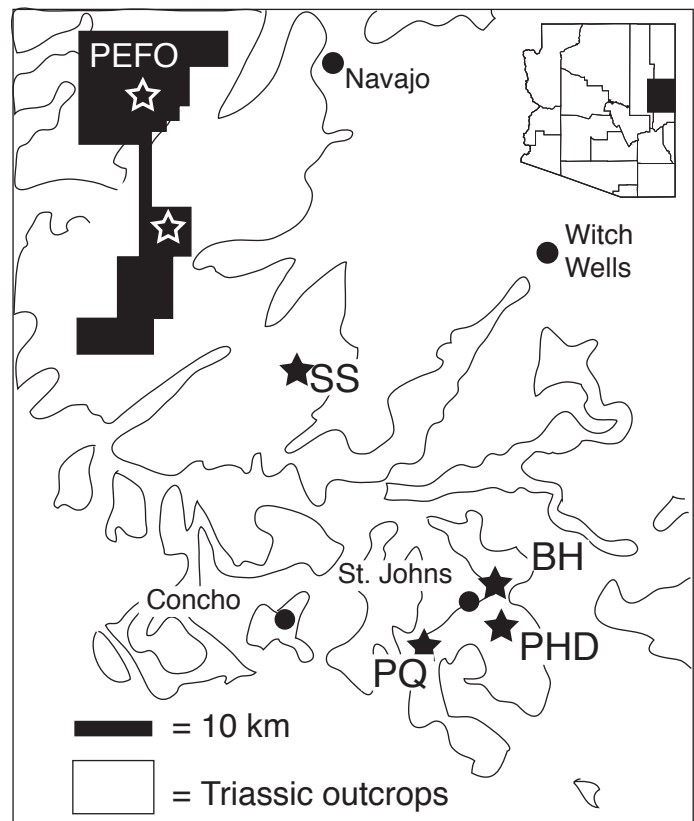


FIGURE 9. Index map showing the distribution of Chinle Group strata in east-central Arizona and the general location of localities discussed here. BH = Blue Hills; PEFO = Petrified Forest National Park; PHD = Picket House Draw; PQ = *Placerias* quarry, SS = Stinking Springs Mountain

### Placerias Quarry

Located 10.4 km to the south and west of St. Johns, the *Placerias* quarry yields the most diverse Upper Triassic fauna in the world (Fig. 9; Table 6). Although located in a primarily covered area with few discrete outcrops, the *Placerias* quarry preserves an incredibly rich fauna, including dicynodonts (*Placerias*—37+ individuals), phytosaurs, aetosaurs, dinosaurs, and a host of microvertebrates. Long and Murry (1995) and, to a lesser extent, [Tannenbaum-] Kaye and Padian (1994) provide the best reviews of the history of excavation. The *Placerias* quarry was long thought to lie in the Blue Mesa Member of the Petrified Forest Formation, but Lucas et al. (1997c) convincingly demonstrated that the quarry is actually near the base of the Chinle in the Bluewater Creek Formation. This exceptionally rich deposit yielded hundreds of bones, some associated, during UCMP excavations in 1930-1932 (Camp and Welles, 1956; Long and Murry, 1995) and MNA excavations in 1978 and 1979 that included screenwashing (Jacobs and Murry, 1980; Tannenbaum, 1983; Kaye and Padian, 1994).

The most unusual aspect of this quarry is the abundance of dicynodonts, a minimum of 37 individuals of the genus *Placerias*, from which the locality derives its name (Camp and Welles, 1956; including Camp, 1956). Although the *Placerias* quarry yields an enormous number of specimens, few, if any, are articulated, including the skulls of *Placerias*, which are almost completely disarticulated. Still, it is clear that many of the specimens of macrovertebrates were at least associated, and it is quite likely that careful comparison of Camp’s notes and field numbers will turn the UCMP collection of thousands of isolated bones into associated partial skeletons of several individuals (Parker, pers. comm.; Martz, pers. comm.). Although Camp and the UCMP

TABLE 5. The vertebrate fauna of Stinking Springs Mountain (after Polcyn et al., 2002).

Chondrichthyes  
 Xenacanthidae: *"Xenacanthus" moorei*  
 Hybodontidae: *Lissodus (Lonchidion) humblei*  
 Hybodontidae: *Acrodus* sp.

Osteichthyes  
 Redfieldiidae  
 Palaeoniscidae  
 cf. *Turseodus* sp.  
 cf. *Australosomus* sp.  
 "Colobodontidae"  
 Semionotidae  
 Sarcopterygii  
 Dipnoi: Ceratodontidae  
 Crossopterygii: Coelacanthidae  
 cf. *Chinlea* sp.

Amphibia: Temnospondyli  
*Buettneria* sp.  
*Apachesaurus* sp.  
 Incertae sedis: Type A,B,C

Amniota  
 Synapsida: Therapsida  
 Cynodontia  
 Reptilia: Parareptilia: Procolophonidae  
 Reptilia: Diapsida  
 Lepidosauromorpha  
 Sphenodontidae  
 ?Lepidosauromorpha incertae sedis  
 Archosauromorpha  
 Archosauromorpha incertae sedis *Vanleavea* sp.  
 Trilophosauridae: *Trilophosaurus jacobsi*

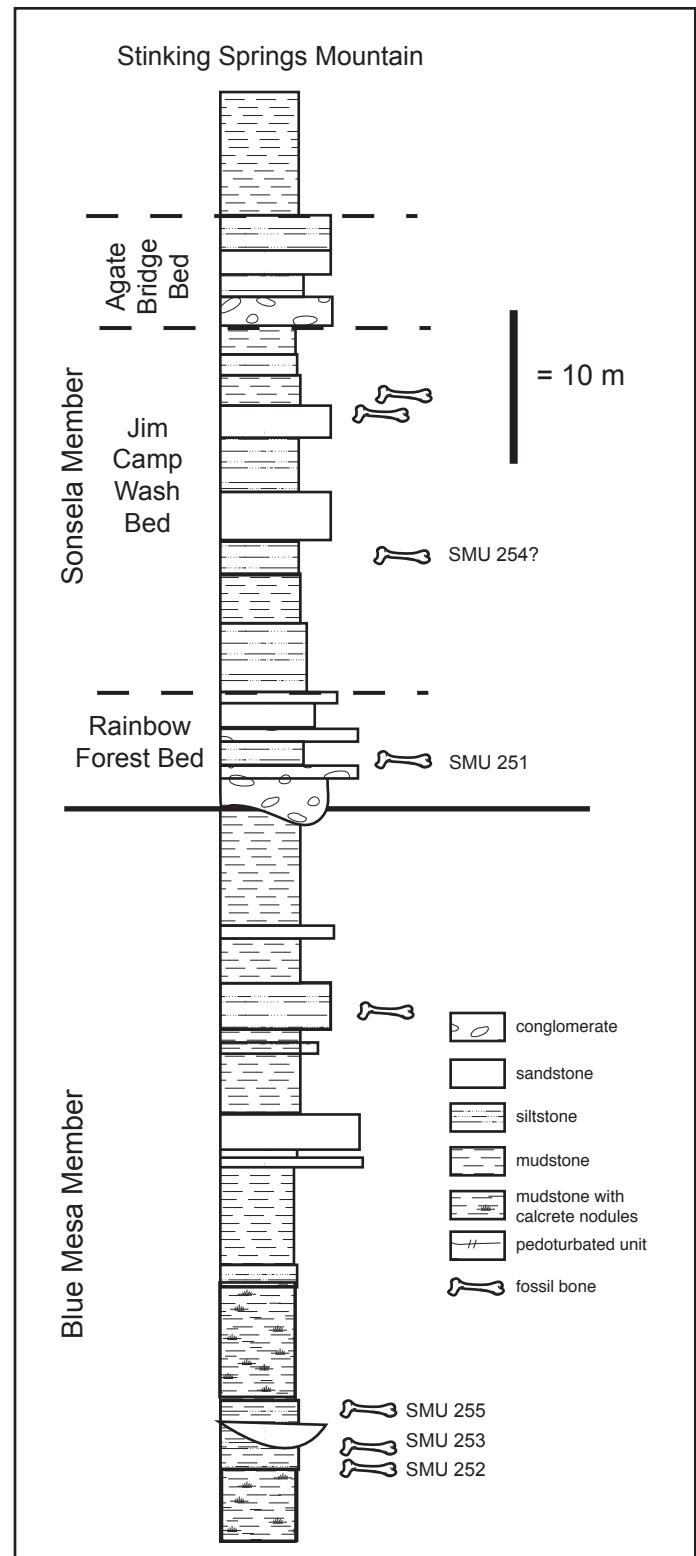
Crurotarsi:  
 Archosauria: Pseudosuchia  
 Phytosauridae:  
*Smilosuchus* sp.

Stagonolepididae  
*Stagonolepis wellsi*  
*Desmatosuchus (Acaenasuchus geoffreyi)*

Rauisuchidae:  
*Postosuchus kirkpatricki*  
*Poposaurus gracilis*  
*Chatterjeea elegans*  
 Ornithischia: *Revueltosaurus callenderi*

Crocodylomorpha:  
 cf. *Parrishia*  
*Hesperosuchus agilis*

Archosauria: Dinosauria  
 Ornithischia incertae sedis  
 Saurischia  
 Theropoda: Ceratosauridae  
 Archosauria: incertae sedis  
 Other Reptilia indet.  
 Neodiapsid indet.  
 Trace fossils: Vertebrate coprolites



crews exerted themselves mightily, their only publication on the fauna was Camp and Welles' (1956) monograph on *Placerias* itself. Camp and Welles' (1956) study of the dicynodonts remains the definitive monographic treatment of *Placerias*, but we note here that we agree with others that Cox's (1965) reconstruction of the skull of *Placerias* is the most accurate available.

The fauna as a whole has been reviewed several times, including by Camp and Welles (1956), Jacobs and Murry (1980), Tannenbaum (1983; Kaye and Padian, 1994), Long et al. (1989), Long and Murry (1995) and Lucas et al. (1997c). Jacobs and Murry (1980) were also the first to report on the fauna of the "Downs' quarry," an assemblage 60 m east of the *Placerias* quarry and slightly (<2 m)

FIGURE 10. Stratigraphic column showing our interpretation of the stratigraphic relationships described by Polcyn et al. (2002) for fossil vertebrate localities in the vicinity of Stinking Springs Mountain. Base of column is approximately ~10-20 m above the base of the Bluewater Creek (=Mesa Redonda) Formation locally.

higher stratigraphically. Long and Murry (1995) provided identifications of the catalogued UCMP and MNA collections. Lucas et al. (1992) published an article on theropod dinosaurs from the quarry that, while fragmentary, represent some of the oldest known in

TABLE 6. The vertebrate fauna from the *Placerias* quarry\*

Chondrichthyes:  
 Ctenacanthidae: *Phoebodus* sp.  
 enacanthidae: "*Xenacanthus*" *moorei*  
 Hybodontidae: *Lissodus* (*Lonchidion*) *humblei*  
 Hybodontidae: *Acrodus* sp.  
 Osteichthyes:  
 Redfieldiidae  
*Cionichthys* sp.  
*Lasalichthys* sp. / *Synorichthys* sp.  
 Palaeoniscidae  
*Gyrolepis* sp.  
 cf. *Turseodus* sp.  
 cf. *Australosomus* sp.  
 "Colobodontidae"  
 Semionotidae  
 Sarcopterygii: Dipnoi: Ceratodontidae  
 Crossopterygii: Coelacanthidae cf. *Chinlea* sp.  
 Amphibia: Temnospondyli  
*Buettneria* sp.  
*Apachesaurus* sp.  
*Incertae sedis*: (at least 4 types)  
 Amniota  
 Synapsida: Therapsida  
 Cynodontia  
 Dicotylodonta  
*Placerias hesternus*  
 Reptilia: Parareptilia: Procolophonidae indet.  
 Reptilia: Diapsida  
 Lepidosauromorpha  
 ?Kuehneosauridae  
 Sphenodontidae  
 ?Lepidosauromorpha *incertae sedis*  
 Archosauromorpha  
 Prolacertiformes: *Tanytrachelos* sp.  
 Trilophosauridae: *Trilophosaurus jacobsi* Murry  
*Trilophosaurus* sp.  
 ?Proterochampsid  
 Archosauria: Pseudosuchia  
 Phytosauridae:  
*Rutiodon* sp.  
*Paleorhinus* sp.  
 Stagonolepididae  
*Stagonolepis wellesi*  
*Desmatosuchus haplocerus*  
*D. haplocerus* (= *Acaenasuchus geoffreyi*)  
 Podosauridae:  
*Postosuchus kirkpatricki*  
*Poposaurus gracilis*  
*Chatterjeea elegans*  
 Sphenosuchia  
*Parrishia mcraei*\*  
*Hesperosuchus agilis*  
 Large sphenosuchian  
 Archosauria: Dinosauria: Ornithischia *incertae sedis*  
 Saurischia  
 Herrerasauridae indet.  
 Theropoda: *Camposaurus arizonensis* Hunt et al.  
 Archosauria: *incertae sedis*:  
 Reptilia *incertae sedis*:  
*Utahitodon kroehleri* Sues  
 Other Reptilia indet.  
 Trace fossils: Vertebrate coprolites

\*After diverse sources, including Kaye and Padian (1994), later publications that modified the faunal list (e.g., Sues, 1996; Heckert, 1996; Heckert et al., 2004) and our own examinations of the collections.

North America, and Hunt et al. (1998a) named the theropod *Camposaurus arizonensis*. Fiorillo and Padian (1993) and Fiorillo et al. (2000) reviewed the taphonomy of the site, concluding that it represented a wet floodplain assemblage with a high water table that was intermittently flooded, but not a bog or pond as some previous authors had suggested. Fiorillo et al. (2000) implicated a drought event(s) in the mortality of the vertebrate fauna. We note here that the microvertebrate fauna, particularly the aquatic component of that fauna, hints at a more complicated taphonomic scenario, probably involving crevasse-splay deposition of aquatic vertebrates as well. Interestingly, several other important localities in the Chinle, especially parts of the "Dying Grounds/Crocodile Hill" area in the PFNP appear to preserve similar environments, yet are depauperate in dicynodonts.

Aside from dicynodonts and the dinosaurs, the macrovertebrate fauna remains little studied, although Lucas et al. (1997a) addressed in detail the problematic nature of the phytosaur *Parasuchus* (= *Paleorhinus*) from the Downs quarry, first discussed by Padian (1994) and re-illustrated here (Fig. 8A). Otherwise, the principal studies of macrovertebrates from the *Placerias* quarry are restricted to Camp and Welles (1956) and Long and Murry (1995), the latter of which rely extensively on *Placerias* quarry material for illustrations of Chinle archosaurs, particularly of specimens of the aetosaurs *Stagonolepis* and *Desmatosuchus* and the "rauisuchians" *Postosuchus* and *Poposaurus*. Long and Murry (1995) also utilized these fossils for much of their text descriptions and diagnoses of these taxa, although we are extremely skeptical of their species-level identifications, particularly regarding *Postosuchus kirkpatricki* and *Poposaurus gracilis*.

The microvertebrate fauna is at least equal in importance to the macrovertebrate fauna. Jacobs and Murry's (1980) original assessment doubled the known diversity of Chinle vertebrates from the Colorado Plateau, and Tannenbaum (1983; Kaye and Padian, 1994) illustrated much of that fauna. Murry (1987) named the second known species of the archosauromorph *Trilophosaurus*, *T. jacobsi* from a series of dentulous jaw fragments from this assemblage. Sues and Olsen (1993) considered this specimen to be a procolophonid and proposed the name *Chinleogomphius* for the taxon, but our recent work (Heckert et al., 2004a, 2006) demonstrates that *T. jacobsi* is a valid species that is indeed congeneric with *Trilophosaurus buettneri*, and that the type material likely represents hatchling individuals. Sues (1991) documented the presence of venom-conducting teeth from this fauna, and this taxon was later named *Utahitodon kroehleri* by Sues (1996). We are still studying much of the microvertebrate fauna, which includes rich and important records of cynodonts and sphenodonts, among others.

The macrovertebrate fauna of the *Placerias* quarry is, effectively, identical to that of the type Adamanian fauna of Lucas and Hunt (1993; Lucas and Heckert, 1996a; Lucas et al., 1997a; Lucas, 1998) from Dying Grounds in the PFNP. Shared age-diagnostic macrovertebrate taxa include the phytosaur *Rutiodon*, and the aetosaurs *Desmatosuchus haplocerus* and *Stagonolepis wellesi*, all index taxa of the Adamanian.

A phytosaur from the adjacent Downs' quarry appears to represent the highest stratigraphic occurrence of the phytosaur *Parasuchus* (Padian, 1994; Lucas et al., 1997c) (Fig. 8A). *Parasuchus* is an index taxon of the Otischalkian lvf, while the rest of the quarry yields a tetrapod fauna typical of the Adamanian lvf. However, as Lucas et al. (1997c) and Lucas (1998) note, the lvfs are defined by the first appearance datum (FAD), operationalized by the stratigraphically lowest occurrence of the index taxa, so the occurrences of the Adamanian index taxa *Stagonolepis* and *Rutiodon* at the *Placerias* quarry define the assemblage as Adamanian in age. The presence of *Parasuchus* is thus most parsimoniously



explained as a relatively rare holdover (Lucas et al., 1997c). The aetosaurs of the *Placerias* quarry have not been treated separately from those of other Upper Triassic faunas, but do figure prominently in reviews by Long and Ballew (1985) and Long and Murry (1995) and less so in Heckert and Lucas (2000). It is important to note that specimens of *Desmatosuchus* from the *Placerias* quarry (at least as identified by Long and Murry, 1995) were used to create the composite casts in the UCMP and NMMNH collections and on display at the PFNP. The *Placerias* quarry also yields many of the known juvenile specimens of *Desmatosuchus* (= *Acaenasuchus*) (Heckert and Lucas, 2002b).

Collections from the *Placerias* quarry are housed primarily at the UCMP, although the vast majority of the microvertebrates and a representative macrovertebrate collection are housed at the MNA. The FMNH collected screenwash from this site, but the resulting concentrate remains largely unpicked. The NMMNH is also home to a small collection of fragmentary vertebrates and many coprolites from the site. A handful of *Placerias* quarry specimens are housed in the paleontological collections of the University of Tübingen, apparently as the result of an exchange between Camp and F. von Huene.

### St. Johns

The *Placerias* quarry is only the most productive locality in the vicinity of St. Johns. To the north and east of St. Johns lie the Blue Hills (Fig. 9), a strip of badlands developed in the lower Chinle Group, with numerous localities most extensively worked by the UCMP in the 1920s and again in the 1980s. More recently, we at the NMMNH have initiated extensive collecting projects there since 1997, largely as a result of the successful prospecting work of Stan Krzyzanowski. There are several other, less-well-known localities in the area that have also produced important vertebrate collections, including Big Hollow Wash, Pickett House Draw, Conchas, and Hunt (e.g., Long and Murry, 1995; Heckert and Lucas, 2001, 2003a) (Fig. 9).

Camp's field parties collected numerous vertebrates from the Blue Hills, which yields a "typical" assemblage of larger metoposaurs, phytosaurs (including the type specimen of *Mach-aeroprotopus zunii*), aetosaurs, and other large vertebrates (Table 7). More interestingly, perhaps, are his collections of small vertebrates from the Blue Hills, many of which come from unusual localities he termed "meal pots," as they occur in a "mealy shale" immediately underlying the principal bone-bearing horizons. Many of these vertebrates remain unstudied and largely undescribed, but the tiny skull of the Krzyzanowski amphibian (Morales, 1993b; Zanno et al., 2002) may have been derived from a geologically similar, albeit stratigraphically higher, site. One of us (ABH) is currently washing matrix from this site (NMMNH locality 4127). "Meal pots" localities have yielded the *Reueltosaurus hunti* specimens known from Arizona (Heckert, 2002, 2005). These sites are especially noteworthy because they preserve abundant fossils that, while small, are larger than most screenwashed microvertebrate faunas, and therefore should lend insight into the skeletal anatomy of vertebrates too large to recover from screenwashing and yet too small to be typical macrovertebrates.

Still more important is the Krzyzanowski bonebed (NMMNH locality 3764), located well to the north (~1-2 km) of most UCMP localities. The Krzyzanowski bonebed is highly unusual in the Chinle generally and Arizona in particular in that it preserves abundant small vertebrates, including several not previously reported from the Blue Hills. Aside from a few fragments of large metoposaur elements and occasional phytosaur teeth, all of the fossils come from animals with limbs less than 20 cm long. The fauna recovered from the Krzyzanowski bonebed thus far includes extremely fragmentary metoposaurid amphib-

TABLE 7. The vertebrate fauna of the St. Johns area exclusive of the *Placerias* quarry.

### Uppermost Bluewater Creek Formation/Blue Mesa Member Blue Hills

Osteichthyes:	Actinopterygii indet., <i>Arganodus</i> sp.
Amphibia:	<i>Buettneria perfecta</i> <i>Apachesaurus</i> sp.
Reptilia indet.	Multiple taxa
Synapsida:	<i>Placerias</i> sp.
Archosauromorpha:	Multiple taxa
Archosauriformes:	Type H?*, L teeth*
Phytosaurs:	<i>Rutiodon</i> spp.
Aetosaurs:	<i>Stagonolepis</i> sp. <i>Desmatosuchus</i> sp.
Rauisuchians:	<i>Rauisuchia</i> indet. <i>Saurosuchus</i> sp. <i>Poposaurus gracilis</i>
Sphenosuchians:	<i>Sphenosuchia</i> indet. <i>Parrishia</i> (derived archosaur)
Theropoda:	at least one taxon
Ornithischia:	<i>Ornithischia</i> indet.* <i>Reueltosaurus hunti</i>
Trace fossils:	Vertebrate coprolites

### Lower Chinle Group, Big Hollow Wash

Osteichthyes:	<i>Arganodus dorotheae</i> (N)
Amphibia:	<i>Buettneria perfecta</i>
Phytosaurs:	<i>Rutiodon</i> spp.
Aetosaurs:	<i>Stagonolepis wellesi</i> <i>Desmatosuchus haplocerus</i> (S)
Rauisuchians:	" <i>Postosuchus</i> " sp.(S)

(N)=Big Hollow Wash N only; (S) = Big Hollow Wash S only

ians, isolated phytosaurs, at least one sphenosuchian, several fish, probable theropods, and a possible ornithischian. Among the most intriguing of these are a fish with an elongate, edentulous rostrum, and a tiny tetrapod dentary bearing teeth that closely resemble those traditionally assigned to Triassic ornithischians (Heckert et al., 2004b). Microvertebrates include hybodont chondrichthyans, actinopterygian fish, at least two archosauriforms, postcrania of *Trilophosaurus*, probable theropods, the ornithischian *Crosbysaurus*, and a possible prosauropod dinosaur (Heckert et al., 2004b).

There are two particularly important aspects the Krzyzanowski bonebed—(1) the extreme richness of the deposit; and (2) its preservation of relatively complete small vertebrate elements, some of which were previously known only from fragmentary microvertebrate remains. The richness of this deposit cannot be overstated—we estimate bone density to range from 100 to 5,000/m<sup>2</sup>. The macrovertebrate fauna includes diverse taxa that possess teeth and other elements previously known only from screenwashing. The bonebed therefore is potentially a "Rosetta Stone" where isolated teeth from microvertebrate faunas can be matched to more readily identifiable skulls and lower jaws. Thus, the bonebed not only provides a glimpse into a Late Triassic ecosystem, but could lend insight into ecosystems represented by more fragmentary faunas elsewhere.

All vertebrate localities in the Blue Hills are from high in the Bluewater Creek Formation or very low in the Blue Mesa Member of the Petrified Forest Formation (Fig. 11). This is important, because the tetrapod fauna is extremely similar to the type Adamanian assemblage of the PFNP, including the Adamanian index taxa *Rutiodon* and *Stagonolepis*. This demonstrates that Adamanian time encompasses this stratigraphic interval (e.g., Lucas and Heckert, 1996a; Heckert and Lucas, 1997, 2001, 2003a).

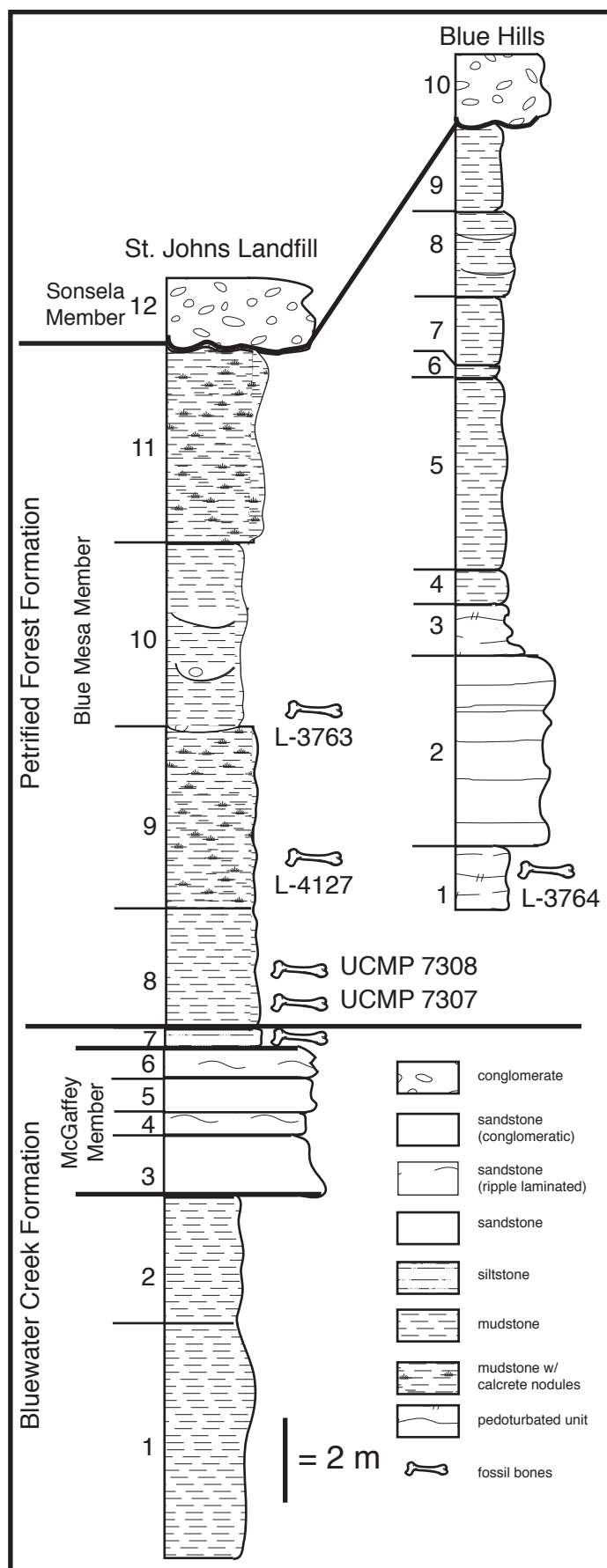


FIGURE 11. Stratigraphy of vertebrate fossil occurrences in the Blue Hills of east-central Arizona.

In addition to the Blue Hills, there are several other productive, albeit less well-studied, localities in the vicinity of St. Johns, including sites near Concho and Hunt. Here we illustrate an isolated phytosaur skull (USNM 17098—Fig. 8C-E) from immediately east of St. Johns in Picket House Draw. This skull was collected by G.E. Hazen for the USNM in 1946 5 km east of St. Johns. Importantly, the stratigraphic information on file at the USNM indicates that the specimen was collected less than 15 m above the Chinle Group base. In the vicinity of St. Johns, strata this low in the Chinle Group almost certainly pertain to the Bluewater Creek Formation (Heckert and Lucas, 1997, 2001, 2003a), so this is a relatively rare occurrence of a well-preserved phytosaur in that unit. We assign this phytosaur to the genus *Rutiodon* based on the presence of supratemporal fenestrae that, while incompletely preserved, are clearly at the level of the skull roof and exposed in dorsal view and elongate, deep squamosals that are knob-like in lateral view (Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002). This fossil thus helps solidify the Adamanian age of the Bluewater Creek Formation.

#### Owl Rock Formation Localities

Until recently, the only vertebrate fossils known from the Owl Rock Formation were recovered from that unit in Arizona, largely as a result of the work of Kirby (1989, 1990, 1991, 1993; Murry and Kirby, 2002), although there is a significant volume of unpublished material in the collections of the MCZ, as well. Owl Rock Formation localities in Arizona are known from Moenkopi Wash, Landmark Wash, Tloi Eechii, and Salt Seeps Wash (Table 8). Of these, Moenkopi Wash, Landmark Wash and Tloi Eechii are the most important, as they yield by far the most material.

Kirby (1993) reported a fauna consisting of indeterminate redfieldiids, possible semionotids, the coelacanth *Chinlea sorenseni*, indeterminate metoposaurs, the aetosaur *Typhorax coccinarum*, the phytosaur *Pseudopalatus*, and the rauisuchian *Postosuchus* from MNA locality 214 in Moenkopi Wash. Landmark Wash is even richer, and yields the chondrichthyan *Reticulodus synergus*, indeterminate redfieldiids, palaeoniscids, and semionotids, the metoposaurids *Apachesaurus gregorii* and other, indeterminate metoposaurids, a sphenodont, *Pseudopalatus*, *Typhorax coccinarum*, "*Postosuchus*," a chatterjeiid, a sphenosuchid, possible ceratosaurs, problematic teeth that might represent herbivorous dinosaurs, and abundant coprolites (Kirby, 1991, 1993; Heckert, 2001; Murry and Kirby, 2002). This same basic fauna is known from Tloi Eechii, which is home to the "Billingsley bonebed" (MNA locality 36) and other localities, with the addition of numerous undescribed leptoleurine procolophonids in the collection of the MCZ (Schaff, pers. comm.). The Owl Rock Formation procolophonid in Arizona differs from the one recently reported from Utah by Fraser et al. (2005).

We illustrate here two phytosaur skulls from the Owl Rock Formation because they both pertain to *Pseudopalatus* and reinforce the Revueltain age of the unit (Fig. 8H-I). Both skulls can be assigned to *Pseudopalatus* with confidence because they have narrow, slit-like supratemporal fenestrae that are depressed below the level of the skull roof but are still visible in dorsal view and because they possess elongate, knob-like squamosals (Ballew, 1989; Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002). Most previous authors (e.g., Kirby, 1993; Hunt, 1994; Long and Murry, 1995; Hungerbühler, 2002) have, either explicitly or implicitly, assigned the more robust specimen (MNA V3478) to one taxon (*P. buceros*) and the other (MNA V3495) to another (*P. pristinus*). However, we follow Zeigler et al. (2002a, 2003) and consider the robust skull a likely male morph and the gracile skull a likely female morph, both of a taxon properly recognized as *Pseudopalatus buceros* (Lucas et al., 2002).

TABLE 8. The vertebrate fauna of the Chinle Group in the Navajo Nation of northeastern Arizona.

<b>Owl Rock Formation, Moenkopi Wash</b>	
Osteichthyes:	Redfieldiid indet. Semionotidae(?) indet. Coelacanthidae indet.
Amphibia:	Metoposauridae indet.
Phytosaurs:	<i>Pseudopalatus</i> sp.
Aetosaurs:	<i>Typothorax coccinarum</i>
Rauisuchians:	" <i>Postosuchus</i> " sp.
Trace fossils:	Vertebrate coprolites
<b>Owl Rock Formation, Landmark Wash</b>	
Chondrichthyes:	<i>Reticulodus synergus</i> Murry & Kirby
Osteichthyes:	Redfieldiid indet. Palaeoniscidae indet. aff. <i>Turseodus</i> Semionotidae indet.
Amphibia:	<i>Apachesaurus gregorii</i> Metoposauridae indet.
Lepidosauromorpha:	Sphenodontidae indet
Phytosaurs:	<i>Pseudopalatus</i> spp.
Aetosaurs:	<i>Typothorax coccinarum</i>
Rauisuchians:	" <i>Postosuchus</i> " sp. Chatterjeeidae indet.
Sphenosuchidae	Sphenosuchidae indet.
Theropoda:	Ceratosauria indet.
Ornithischia:	Ornithischia(?) indet.
Trace fossils:	Vertebrate coprolites
<b>Owl Rock Formation, Tohachi Wash</b>	
Chondrichthyes:	<i>Reticulodus synergus</i>
Osteichthyes:	Redfieldiid indet. Palaeoniscidae indet. aff. <i>Turseodus</i> Semionotidae indet.
Amphibia:	<i>Apachesaurus gregorii</i> Metoposauridae indet.
Procolophonidae:	Leptopleurinae indet.
Lepidosauromorpha:	Sphenodontidae indet <i>Tricuspisaurus</i> (?)
Phytosaurs:	<i>Pseudopalatus</i> spp.
Aetosaurs:	<i>Typothorax coccinarum</i>
Rauisuchians:	" <i>Postosuchus</i> " sp. Chatterjeeidae indet.
Sphenosuchidae	Sphenosuchidae indet.
Theropoda:	Ceratosauria indet.
Ornithischia:	Ornithischia(?) indet.
Trace fossils:	Vertebrate coprolites
<b>Lower Chinle Group, Little Round Rock</b>	
Amphibia:	<i>Buettneria perfecta</i>
Phytosaurs:	<i>Pseudopalatus</i> spp. <i>Pseudopalatus tenuis</i> Camp <i>Machaeroprotopus gregorii</i> Camp

\*Complete binomen including author = Type specimen from area

### Miscellaneous Arizona Localities

In addition to the major collecting areas documented in the previous pages, there are many more isolated occurrences of vertebrates from the Chinle Group of Arizona. These include both published and unpublished records, many from the Navajo Nation. These occurrences include vertebrates found in the vicinity of Winslow, Little Round Rock, Chinle valley/Many Farms, and Allentown. In the following paragraphs we briefly review these occurrences, and comment on their significance.

Brady (1954, 1958) published two occurrences of the aetosaur *Desmatosuchus haplocerus* from Triassic strata in Arizona.

The first of these was "8 miles west of Lupton" (Brady, 1954, p. 19) and the second "near St. Michaels" (Brady, 1958, p. 61). Bedrock in the vicinity of Lupton and Many Farms consists principally of strata of the lower Chinle Group, strata we would refer to either the Bluewater Creek Formation or the overlying Blue Mesa Member of the Petrified Forest Formation. Long and Murry (1995) noted the co-occurrence of *Buettneria perfecta*, *Stagonolepis welliesi*, and *Poposaurus gracilis* with the *Desmatosuchus* specimens from St. Michaels. Parker (2003) reviewed occurrences and thought that both of Brady's specimens were derived from the Blue Mesa Member. From reading Brady (1954), it is clear that E.H. Colbert provided the identification of *Desmatosuchus* for Brady's material. Ironically, Camp and Welles (1956) did not cite this identification, nor did they subsequently identify aetosaurs from the *Placerias* quarry as *Desmatosuchus*, even though they had made significant collections of *Desmatosuchus* postcrania from the site.

Parker's (2003) thesis was built on the description of a single enormous individual of *Desmatosuchus* collected from the uppermost Bluewater Creek Formation near Many Farms on the Navajo Nation in northeastern Arizona. Although Parker (2003) mentions an associated fauna, it appears that little of this fauna was collected and none has been described. Long and Murry (1995) listed several other lower Chinle Group occurrences, including Allentown, Nazlini, Window Rock, Lukachukai, Round Rock, and Rincon Basin E, northeast of Winslow. Like Lupton/St. Michaels, lower Chinle Group strata are the only rocks cropping out in the immediate vicinity of Allentown and Nazlini, so we concur that these occurrences are almost certainly in the Bluewater Creek Formation and/or Blue Mesa Member. Biostratigraphically noteworthy occurrences in these strata include *Desmatosuchus* from Allentown and *Stagonolepis*, "*Leptosuchus*" and "*Smilosuchus*" from near Nazlini (Long and Murry, 1995). All of these are Adamanian index fossils that occur in strata expected to be of Adamanian age.

Finally, it is worth noting that vast tracts of the Triassic System in Arizona remain essentially unexplored paleontologically. For example, extensive outcrops of the Chinle Group are exposed north of the Grand Canyon, in Painted Desert State Park (near Winslow), and on the Navajo Reservation. Additionally, the PFNP occupies only a thin sliver of the Triassic outcrop belt in the area. Thus, while Arizona's record of Triassic vertebrates is truly world class, it also demonstrates great potential to improve still further. Indeed, the recent work of Polcyn et al. (2002) demonstrates that new localities in heretofore under-explored areas can be hugely productive, and of course the Krzyzanowski bonebed is a reminder that, even in well-known areas, important new localities may await discovery.

### LATE TRIASSIC TRACE FOSSILS

Although we have mentioned some trace fossil records in the review of the Triassic vertebrate record, we feel it important to separate the trace fossil record from this discussion. In the following paragraphs we provide an overview of the stratigraphic occurrence of vertebrate trace fossils from the Chinle Group in Arizona. These traces consist of tetrapod tracks and vertebrate coprolites. Putative reptile "nests" from the PFNP are of questionable validity (Hunt et al., 2005b; see below).

Tetrapod tracks are found in three locations at Petrified Forest National Park in different units of the Petrified Forest Formation of the Chinle Group (upper Carnian-Norian). The first locality is a sandstone in the Teepees area in the upper Carnian Blue Mesa Member (Adamanian land vertebrate faunachron; Saintjohnsian sub-land vertebrate faunachron), not the Monitor Butte Member as reported by Martin and Hasiotis (1998). These specimens include several pedal impressions of *Rhynchosauroides*

sp., indeterminate swimming traces which could have been produced by phytosaurs and an indeterminate large trackway (Santucci and Hunt, 1993; Santucci et al., 1995; Martin and Hasiotis, 1998). Martin and Hasiotis (1998, fig. 5, left image) illustrate a dinosaurian track that Hunt et al. (2005b) identify as a right pedal impression of *Grallator* sp.

The second locality is in the Agate Bridge Bed of the upper Carnian Sonsela Member (Adamanian land vertebrate faunachron; Lamyian sub-land vertebrate faunachron) (= Petrified Forest Member of Martin and Hasiotis, 1998) near the Rainbow Forest. This ichnofauna includes *Rhynchosauroides* sp. and specimens that Hunt et al. (2005b) identify as cf. *Grallator* and cf. *Brachychirotherium* sp. (Martin and Hasiotis, 1998).

The locality in the Flatops area is in the Agate Bridge Bed of the upper Carnian Sonsela Member (Adamanian land vertebrate faunachron; Lamyian sub-land vertebrate faunachron) (= Flatop # 1 of Martin and Hasiotis, 1998). This locality yielded indeterminate, medium-sized reptile tracks (Martin and Hasiotis, 1998).

The vast majority of tetrapod tracks in the Late Triassic of western North America are from Apachean (late Norian or ?Rhaetian) strata and the Petrified Forest tracks are rare examples of Carnian tracks.

Vertebrate coprolites are locally common in strata of the Upper Triassic Chinle Group. Hunt et al. (1998b) described *Dicynodontocopros maximus* from the Blue Mesa Member of the Petrified Forest Formation at the *Placerias* quarry near St. Johns. They also noted that *Heteropolacropus texaniensis* occurs in the Blue Mesa Member of northeastern Arizona. This occurrence is actually at Petrified Forest National Park (Hunt and Santucci, 1994). Undescribed coprolites occur in the Blue Mesa and Painted Desert members of the Petrified Forest Formation at Petrified Forest National Park. Wahl et al. (1998) described coprophagy in coprolites from the Blue Mesa Member at Petrified Forest National Park.

Putative tetrapod nests have been described from the Agate Bridge Bed of the upper Carnian Sonsela Member (Adamanian land vertebrate faunachron; Lamyian sub-land vertebrate faunachron) (= Flatop sandstone #1 of Hasiotis et al., 2004) at Petrified Forest National Park. Hunt et al. (2005b) consider that these structures are in need of more detailed study before their interpretation as vertebrate nests can be validated.

## TRIASSIC TETRAPOD BIOCHRONOLOGY

Lucas (1998, 2000) presented a global biochronology based on the occurrence of tetrapods in Triassic strata across Pangea. Six of the land-vertebrate faunachrons (lvf) he recognized are relevant to discussion here—the Early Triassic Nonesian lvf, the Middle Triassic Perovkan lvf, and the Late Triassic Otischalkian, Adamanian, Revueltian, and Apachean lvfs (Figs. 2, 12).

The Nonesian record is of an extensive, chirothere-dominated ichnofauna and a largely undescribed body fossil fauna of fishes, amphibians (capitosaur and trematosaur) and, reptiles from the Spathian Wupatki Member. The record of Perovkan vertebrates from Moenkopi Formation is one of the best in the hemisphere, and the Chinle Group hosts the type Adamanian assemblage and numerous other exceptional Adamanian and Revueltian faunas, as well as sparse Otischalkian records. Trace fossil records from Arizona include well-preserved tetrapod footprints of Nonesian and Perovkan age and less spectacular Adamanian-Apachean records (Hunt et al., 2005b).

Lucas (1998) defined the Perovkan lvf as the interval of time from the first occurrence datum (FAD) of the dicynodont *Shansiodon* to the first occurrence of the temnospondyl *Mastodontosaurus*. Although neither are known from the Moenkopi Formation, the Perovkan index fossil *Eocyclotosaurus* is a relatively common component of Moenkopi Formation faunas in Arizona (Welles, 1947;

Morales, 1987, 1993a). Marine occurrences of this taxon indicate an Anisian age for these records (Lucas and Schoch, 2002). The diverse tetrapod faunas of the Holbrook Member of the Moenkopi Formation in Arizona thus comprise the single best-known Perovkan fauna known from the Americas (Lucas, 1998).

Arizona boasts one of the world's outstanding fossil records of Late Triassic vertebrates. Historically, much of what we know about Late Triassic vertebrate faunas and evolution, including early dinosaur evolution, has been built on this record (Gregory, 1957; Colbert, 1972, 1985; Padian, 1986, 1994; Murry, 1989b; Hunt, 1991; Lucas and Hunt, 1993; Long and Murry, 1995; Hunt et al., 1998a; Heckert and Lucas, 2000b; Heckert, 2001). Detailed lithostratigraphy and stratigraphic organization of Arizona's Late Triassic vertebrate fossil localities identifies a minimum of four temporally-successive vertebrate fossil assemblages. These are of early Adamanian (St. Johnsian), late Adamanian (Lamyian), early Revueltian (Rainbowforestan) and late Revueltian (Barrancan) age (Fig. 12). The Adamanian lvf has as its type assemblage the vertebrate fossils from the PFNP in Arizona. The fauna of the Sonsela Member in the PFNP promises to yield one of the best-known Lamyian faunas known, and early Revueltian vertebrates from the PFNP represent one of the best-known assemblages of that age. The Late Triassic vertebrate record of Arizona thus provides data fundamental to biochronological organization of the Late Triassic vertebrate record and therefore to understanding vertebrate evolution during the Late Triassic.

The Adamanian land-vertebrate faunachron (lvf) is based on the vertebrate fossil assemblage from the Blue Mesa Member of the Petrified Forest Formation in the Petrified Forest National Park near the defunct village of Adamana, Arizona (Lucas and Hunt, 1993; Lucas, 1998), and is of St. Johnsian age (Hunt et al., 2005a). The *Placerias* quarry fauna is the type assemblage of the St. Johnsian sub-lvf, and is also the best-such fauna, and the faunas of Stinking Springs Mountain and the Blue Hills, while not as rich, are also clearly of St. Johnsian age. The faunas of the Jim Camp Wash and Agate Bridge beds are the only Lamyian faunas known from Arizona at this time. The Revueltian lvf, defined for tetrapod collections made near Revuelto Creek, New Mexico, is well-represented by fossils from the Painted Desert Member of the Petrified Forest Formation in the Petrified Forest National Park and from the Owl Rock Formation at Ward's Terrace. Fossils found elsewhere in Arizona may represent the Otischalkian and Apachean faunachrons as well. In the following pages we describe the biostratigraphy and biochronology of Triassic vertebrate faunas in Arizona.

### Otischalkian Vertebrates

The oldest Late Triassic vertebrate assemblage from Arizona is the fauna from the vicinity of Tanner's Crossing near Cameron, Arizona. As Heckert et al. (2002) documented and we pointed out earlier, any vertebrates from the Shinarump Formation in this fauna (principally MNA locality 213) are likely of Otischalkian age, as the Shinarump is homotaxial with other basal Chinle deposits that yield tetrapod fossils of Otischalkian age (Lucas and Hunt, 1993, Lucas, 1997, 1998).

### St. Johnsian (early Adamanian) Vertebrates from the *Placerias* Quarry

The best unambiguously Late Triassic vertebrate assemblage from Arizona is of early Adamanian age and is known from the *Placerias* and Downs' quarries near St. Johns. Detailed lithostratigraphic studies indicate these quarries are near the base of the Bluewater Creek Formation (Lucas et al., 1997a). The only comparably old Late Triassic vertebrate faunas in Arizona are those from the base of the Cameron Formation in northern Arizona (Heckert et

Age		LVF	sub-LVF	Cameron/ Ward's T.	PFNP	St. Johns	Misc
<b>Late Triassic</b>	Rhaetian	Apachean					200 Ma
			no Apachean body fossil records in Arizona				
	Norian	Revueltian	Barrancan	Owl Rock fauna  <i>M. validus</i> (?)	211±1.7 Ma Painted Desert Fauna		
			Lamyman		Jim Camp Wash fauna		Billings Gap fauna
	Carnian	Adamanian	St. Johnsian	Ward's bonebed  Cameron	Dying Grounds	Blue Hills Fauna  <i>Placerias</i> quarry	Stinking Springs Mt. Little Round Rock Many Farms
			Otis.	MNA 213			228 Ma

FIGURE 12. Correlation chart showing the approximate stratigraphic distribution of the Upper Triassic body fossil faunas discussed here. Faunas of the same approximate age and stratigraphic position are shown at the same horizontal level. See Lucas et al. (2005, this volume) for a more detailed description of the Triassic-Jurassic transition in Arizona.

al., 2002). Biochronologically useful fossils known from the *Placerias* quarry include the phytosaurs *Parasuchus* and *Rutiodon* and the aetosaurs *Stagonolepis* and *Desmotosuchus*. Biochronologically useful fossils reported from the Bluewater Creek Formation in the Blue Hills include numerous specimens of the phytosaur *Rutiodon* and the aetosaur *Stagonolepis* (Long and Murry, 1995). Almost all of these fossils indicate an Adamanian (latest Carnian) age. The only discrepancy with this argument lies in the presence of *Parasuchus*, elsewhere known only from strata of Otischalkian (late Carnian) age. The biochronological debate thus rests on the significance of the single specimen of *Parasuchus*. Long and Murry (1995)

recognize literally hundreds of elements, principally osteoderms (scutes), of the aetosaur *Stagonolepis* from the *Placerias*/Downs' quarries. *Stagonolepis* is an index taxon of the Adamanian lvf (Lucas and Hunt, 1993; Hunt and Lucas, 1993a). Similarly, Long and Murry (1995) note that remains of *Desmotosuchus* also number in the hundreds. Recent work on *Desmotosuchus* suggest that *D. haplocerus*, to which the *Placerias* quarry specimens are assigned, is restricted to strata of Adamanian age (Zeigler et al., 2002b; Parker, 2003, 2005). Younger (Revueltian) records of *Desmotosuchus* instead pertain to *Desmotosuchus chamaensis* (Zeigler et al., 2002b) or the new taxon *Desmotosuchus smalli* (Parker, 2005). Further, Heckert

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 demon-

strates 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.

#### Lamyian (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 from 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 Lamyian (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 phytosaur *Pseudopalatus*, the aetosaurs *Typothorax coccinarum* and *Desmatosuchus chamaensis* ("*D.*" *chamaensis* of Parker and Irmis, 2005), the rauisuchians *Postosuchus*, and *Chatterjeea elegans* (Long and Murry,

1995). Problematic archosauromorphs include *Revueltosaurus calenderi* (Padian, 1990) and the enigmatic taxon *Vanccleavea* (*sensu* Hunt et al., 2002b). Dinosaurs include the herrerasaurid theropod *Chindesaurus* and an unnamed coelophysid (Padian, 1986; Long and Murry, 1995; Hunt et al., 1998a; Parker and Irmis, 2005).

### Late Revueltian Vertebrates

The Owl Rock Formation on Ward's Terrace north of Cameron has produced an extensive vertebrate fossil assemblage of late Revueltian age (Kirby, 1989, 1991, 1993), one of the few vertebrate assemblages known from the unit, as other records consist of isolated fossils in Utah (Fraser et al., 2005) and unpublished material in the collections of the MCZ (C.R. Schaff, pers. comm.; H.-D. Sues, pers. comm.). Characteristic taxa (Table 4) include the shark *Reticulodus synergus*, the phytosaur *Pseudopalatus*, the aetosaur *Typothorax*, and possible *Postosuchus*. Kirby (1991, p. iii) also noted the presence of rare metoposaurids and rare sphenodontid and kuhneosaurid lepidosauromorphs. This fauna is interesting in the absence of *Desmatosuchus*, indicating that the latest Revueltian is relatively depauperate in aetosaur taxa

### CONCLUSIONS

The Triassic System in Arizona has yielded numerous world-class specimens, including numerous type specimens. The Arizona tetrapods, carefully placed in a detailed lithostratigraphic framework, are a cornerstone of Triassic nonmarine tetrapod biostratigraphy and biochronology both in the American West (Lucas, 1997) and globally (Lucas, 1998, 2000). The Perovkan (early Anisian) faunas of the Moenkopi Formation are exceptional in that they yield both body- and trace fossils of Middle Triassic verte-

brates and are almost certainly the best-known faunas of this age in the New World. The Adamanian records of Arizona are equally spectacular, and include the "type" Adamanian assemblage in the PFNP, the world's most diverse Late Triassic fauna (that of the *Placerias/Downs'* quarries), and other world-class records such as at Ward's Terrace, the Blue Hills, and now Stinking Springs Mountain. The late Adamanian (Lamyian) assemblage of the Sonsela Member promises to yield new and important information on the Adamanian-Revueltian transition. Revueltian records are nearly as spectacular as those of the Adamanian, although most are confined to the exposures in the vicinity of the PFNP. 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.

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