

# MICRO- AND SMALL VERTEBRATE BIOSTRATIGRAPHY AND BIOCHRONOLOGY OF THE UPPER TRIASSIC CHINLE GROUP, SOUTHWESTERN USA

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**Abstract**—A long-term goal of vertebrate biostratigraphers is to construct a microvertebrate biostratigraphy for lower Mesozoic rocks that complements and extends the mammal-based biostratigraphy in place for Upper Cretaceous–Recent deposits. Here we report substantial progress toward achieving this goal based on the distribution of microvertebrate fossils in the Upper Triassic Chinle Group of the western USA. This biostratigraphic hypothesis independently corroborates the existing macrovertebrate biostratigraphy, recognizing four temporally successive assemblages—the Otischalkian, Adamanian, Revueltian, and Apachean, with subdivisions of the Adamanian (St. Johnsian and Lamyan) and Revueltian (Barrancan and Lucianoan). Many microvertebrate taxa, unfortunately, have long stratigraphic ranges and thus, while widespread and easily recognized, are not reliable index fossils. These taxa include the chondrichthyans *Lissodus* and *Reticulodus synergus*, most lepidosauromorphs (including sphenodontians), and various microvertebrate archosauromorphs. However, other taxa have relatively short stratigraphic ranges and occur in multiple localities and thus have some utility as index taxa. Adamanian index taxa include the procolophonid(?) *Cognathus obscurus* and the putative ornithischians *Tecovasaurus murreyi*, *Crosbysaurus harrisae* and *Krzyzanowskisaurus hunti*. Revueltian index taxa include the chondrichthyan *Reticulodus synergus*, the crurotarsan *Revueltosaurus callenderi* and the cynodont *Pseudotriciconodon chatterjeei*. Sphenodontian taxa appear to have relatively little utility as biostratigraphic markers at this time scale, although similar forms co-occur at the *Placerias* quarry in Arizona and correlative strata in the Tecovas Formation of West Texas. The best candidates for index taxa are those that, like therian mammals, have complex teeth and thus are identifiable to the genus or species level based on isolated teeth or tooth fragments. Many of these taxa are rare in the macrovertebrate record but common in some microvertebrate assemblages.

## INTRODUCTION

Ongoing work on microvertebrates from the Upper Triassic Chinle Group in the southwestern USA has made it possible to accurately plot stratigraphic ranges of many taxa, especially chondrichthyans and reptiles, for the first time. These stratigraphic ranges have diverse biostratigraphic and biochronological implications, including serving as a test of the existing (macro-) vertebrate biostratigraphy, refining the nonmarine Triassic timescale, and documenting evolutionary tempo among small vertebrates. While certain aspects of the microvertebrate record support the previous hypotheses, it is not surprising that there is also some incongruence between the macro- and microvertebrate biostratigraphic records.

There is a long tradition of using micro- and small vertebrates, principally mammals, for biostratigraphic purposes in nonmarine rocks of latest Cretaceous and younger age (e.g., papers in Woodburne, 2004). These techniques have not been utilized to the same extent in older rocks for a variety of reasons, including a lack of generically identifiable elements in the small size range, a general rarity (or absence) of mammals, and even a simple lack of fossiliferous sites. Consequently, vertebrate-based biostratigraphic hypotheses in these older strata tend to be based on the occurrence of larger vertebrates. In the case of the Chinle Group, the principal index taxa used are phytosaurs and aetosaurs, both of which include taxa that reached body lengths in excess of 5 m. Here we review the stratigraphic record of micro- and small vertebrates in the Chinle Group (Fig. 1) as a means of testing the macrovertebrate-based biostratigraphic hypotheses of Lucas and Hunt (1993; see also Lucas, 1998; Hunt, 2001; Hunt et al., 2005).

In this paper, the term “microvertebrate” is generally used to indicate fossil scales, bones, and teeth obtained by screenwashing—these fossils are typically no more than 1 cm maximum dimension and often much smaller. “Small vertebrates” refers to specimens that are

slightly larger (1–5 cm maximum dimension for individual elements). These specimens typically are recovered by surface collecting, but are still much smaller than the typical “macrovertebrate fauna” of phytosaurs, aetosaurs, rauisuchians, and large metoposaurid amphibians that is typical of many Chinle sites (e.g., Long and Murry, 1995). In this paper, FAD = first appearance datum (a biochronological event), HO = highest occurrence (a biostratigraphic datum), LAD = last appearance datum (a biochronological event) and LO = lowest occurrence (a biostratigraphic datum). NMMNH = New Mexico Museum of Natural History and Science, Albuquerque.

## PREVIOUS STUDIES

Initial collectors throughout the American West typically identified all nonmarine Upper Triassic strata as “Triassic” in age, although their comparisons to the German Keuper tend to suggest that they understood that the beds in question were likely of Late Triassic age (e.g., Cope, 1877). The similarity of fossiliferous sequences on and off the Colorado Plateau was recognized as early as the 1920s (Case, 1928a), and Camp (1930) first recognized superposed faunas of phytosaurs, although his work was largely stratophenetic in nature. Still, it was not until the 1950s that Colbert and Gregory (1957) first recognized superposed vertebrate fossil assemblages (faunas), thereby erecting a biostratigraphic hypothesis that divided Chinle faunas into an older, possibly Carnian fauna and a younger, possibly Norian fauna. The lithostratigraphic framework underpinning Colbert and Gregory’s biostratigraphy is essentially that of McKee et al. (1957). This biostratigraphic hypothesis was based largely on phytosaurs, and effectively an extension of Camp’s (1930) work as understood by Colbert and Gregory (e.g., Gregory, 1962a, b). Later workers would effectively follow Colbert and Gregory (1957), recognizing an older, Carnian fauna and a younger, Norian fauna from the Chinle, including the “Dockum” of Texas (e.g.,

Jurassic		Apachean		L-325 (Sloan Canyon Fm) Whitaker ( <i>Coelophysis</i> ) quarry	Apache Canyon Shark tooth hill Red Peak
		Revueltian		Owl Rock Fm microvertebrates L-110 (type Bull Canyon) (includes <i>Pseudotriciconodon chatterjeei</i> )	<i>Dolabrosaurus aquatilis</i> Snyder quarry
Late Triassic		Barrancan		L-1 (Type Revueltian)	Post quarry <i>Rileymillerus cosgriffi</i> <i>Pachygenelus milleri</i>
		Lucianoan			
Adamanian		Lamyman		Crystal Forest Lamy amphibian quarry	
		St. Johnisian		Crocodile Hill Dying Grounds L-2739 (Sixmile Springs) <i>Placerias-Downs'</i> quarries L-354 (Ojo Huelos)	Stinking Springs Mountain Blue Hills L-4127 Camp's "meal pots" L-1171 (Lamy) Rotten Hill L-1430 (Upper Kalgary) L-1312 (Lower Kalgary) Sunday Canyon
Otischalkian				<i>Trilophosaurus</i> quarries, incl. <i>Latiscopis disjunctus</i> & Schaeffer Fish quarry	

FIGURE 1. Stratigraphic distribution of screen-washed microvertebrate localities reported by Murry (1981, 1982, 1986, 1989a, b, c), Tannenbaum (1983), Kirby (1989a, b, c), Hunt and Lucas (1993), Kaye and Padian (1994), Heckert (1997, 2001, 2004) Hunt (2001) and Heckert and Jenkins (2005), as well as some other vertebrate occurrences.

Murry, 1982, 1986, 1990; Chatterjee, 1986; Long and Padian, 1986). Lucas and Hunt (1993) were able to subdivide each of these faunas, and therefore recognized a four-fold subdivision of the Chinle into (in ascending order) the Otischalkian, Adamanian, Revueltian, and Apachean land-vertebrate faunachrons (lvf). This subdivision was possible in large part because of the revised Upper Triassic stratigraphy of nonmarine strata in the American West presented by Lucas (1993), and was tied to other biostratigraphic schemes (e.g., megafossil plants, palynology) by Lucas (1997). Lucas (1998) formally defined the first appearance datum (FAD) for each of the faunachrons and provided additional stratigraphic evidence tying nonmarine Triassic lvfs to the global time scale. Subsequently, Hunt (2001) attempted to subdivide the Revueltian into three sub-lvfs (the Rainbowforestan, Barrancan, and Lucianoan, from oldest to youngest), and Hunt et al. (2005) subdivided the Adamanian into an older (St. Johnisian) and a younger (Lamyman) sub-lvf. We utilize these works, as well as much of the systematic literature published since Lucas and Hunt (1993), to present our current understanding of Upper Triassic macrovertebrate biostratigraphy of the Chinle Group in Figure 2.

Historically, the Otischalkian and Adamanian have been considered late and latest Carnian, respectively, whereas the Revueltian has been considered early-mid Norian and the Apachean late Norian or Rhaetian (Lucas and Hunt, 1993; Lucas, 1998). Although there are several tie-ins between selected taxa and the global stratigraphic timescale based on marine occurrences of nonmarine tetrapods (Lucas, 1998), we

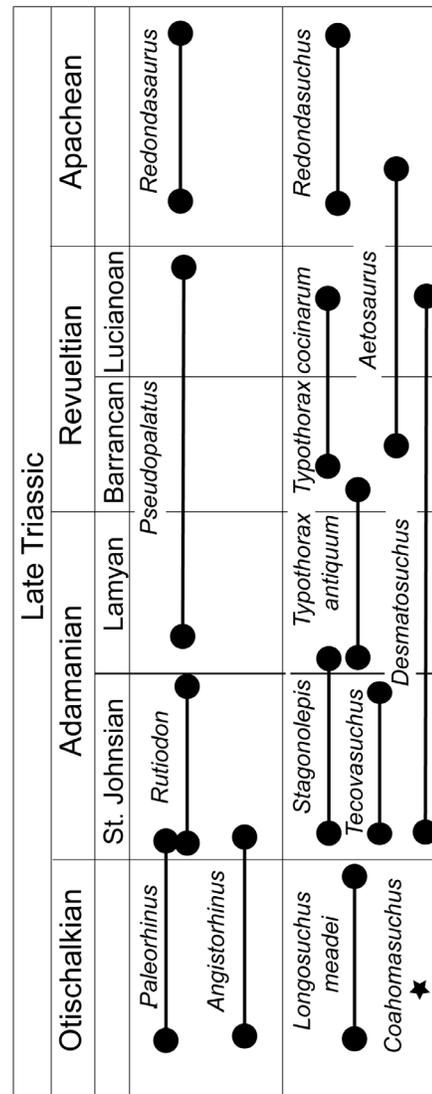


FIGURE 2. Biochronologic framework of Lucas and Hunt (1993; see also Hunt et al., 2005), modified to reflect our current understanding of tetrapod occurrences, distribution, and taxonomy.

refrain from utilizing those here because there is no reason to expect that the cross correlation corresponds exactly to the marine timescale, and we, like Lucas (1998), emphasize the nonmarine nature of this timescale.

### INDEX FOSSILS

In order to use fossils in correlation, there must be a stratigraphically superposed suite of fossils, the most useful of which are termed index fossils. An index fossil is classically recognized as one that has a short stratigraphic range (and therefore brief temporal career), a widespread distribution, is easily recognized, and locally abundant. In the Chinle Group, first phytosaurs (e.g., Camp, 1930; Colbert and Gregory, 1957) and then aetosaurs (Lucas and Hunt, 1993; Lucas and Heckert, 1996) were used as index fossils. Representatives of both taxa are nearly ubiquitous throughout the Chinle, although accurately identifying a phytosaur requires a nearly complete skull, and phytosaur taxonomy remains an unresolved morass, with multiple schemes in use (Ballew, 1989; Long and Murry, 1995; Hungerbühler, 2002). Consequently, aetosaurs, many of which are identifiable to genus or even species-level from isolated osteoderms, are the preferred macrovertebrate index taxa of the Chinle (e.g., Lucas and Heckert, 1996; Heckert and Lucas, 2000). One of the

goals of this paper is to introduce an additional suite of possible index fossils, namely the micro- and small vertebrates of the Chinle Group.

To identify a fossil taxon as an index fossil, its relatively short stratigraphic range must be identified. Some workers have recently claimed that it is necessary to understand the phylogenetic position of a fossil taxon in order to use it as an index fossil, as more primitive taxa are likely to have longer stratigraphic ranges (e.g., ghost lineages) than are contemporaneous, more derived taxa. However, we contend that phylogenetic position is essentially meaningless in biostratigraphy. Sound biostratigraphy simply requires an independently testable lithostratigraphic framework and documented occurrences of fossils of extremely similar, if not identical, morphology (“morphospecies”). Phylogenetic systematists insist that taxa be defined by the presence of shared, derived characters, but that argument simply overlies an additional suite of hypotheses (e.g., character polarity, outgroup selection, etc.) on the basic premise that identical morphology reflects identical taxonomic position.

Indeed, as the long-standing and successful biostratigraphic utility of conodonts makes clear, it is not even necessary to know precisely where in the tree of life a taxon “fits” phylogenetically to have biostratigraphic significance. The relatively recent identification of the conodont animal as a chordate did essentially nothing to alter the existing conodont-based biostratigraphy, other than to indicate that some co-occurring “taxa” were simply individual P, S and M elements of a single species (e.g., Sweet and Donoghue, 2001). We highlight this argument here because there are many Triassic microvertebrate taxa (including many of the following) whose phylogenetic positions are uncertain, yet these taxa are biostratigraphically useful and thus are biochronologically important.

#### STRATIGRAPHIC DISTRIBUTION OF CHINLE MICROVERTEBRATES

Many of the publications on Chinle microvertebrates have focused on a single locality (or even taxon), and thus it is important to understand the actual stratigraphic distribution of known Chinle sites. Useful reviews of microvertebrates have been published by Murry and Long (1989) and Murry (1989b) for the Petrified Forest National Park, Murry (1989a) for Texas and eastern New Mexico, Hunt and Lucas (1993) for New Mexico, and Heckert (2004) for the Chinle basin generally. General faunal reviews are too numerous to cite here, and many have been called out already, but other recent papers focusing on Arizona faunas. In Figure 1, we update Heckert’s (2004, fig. 6) assessment to better reflect our current stratigraphic and biostratigraphic understanding, especially given the recent biostratigraphic hypothesis of Hunt et al. (2005).

##### Otischalkian

To date, Otischalkian sites are largely restricted to the type faunas associated with the *Trilophosaurus* quarries and the Schaeffer fish quarry, which comprise most of the type assemblage of the Otischalkian lvf as originally defined by Lucas and Hunt (1993; Fig. 1). All of these localities are low in the Colorado City Formation. Some (e.g., Lehman and Chatterjee, 2005) have argued that this unit is, in fact, correlative with younger strata, but their hypothesis does not address the criticisms of Lehman (1994) leveled by Lucas et al. (1994), and we reject the correlation of the Otis Chalk vertebrate localities advocated by Lehman and Chatterjee (2005). Heckert (2004) argued that the lower Kalgary locality may be as old as Otischalkian, but we consider it Adamanian (St. Johnian) instead.

##### Adamanian

Strata of Adamanian age are the most extensively sampled for microvertebrates in the Chinle Group. We follow Hunt et al. (2005) and subdivide this record into older, St. Johnian and a younger, Lamyian fauna, and in the following paragraphs we explicate the assignment of

Adamanian faunas to these two sub-lvfs as illustrated in Figure 3.

##### Adamanian (St. Johnian) fauna

Adamanian microvertebrate localities are known in Texas, New Mexico, and Arizona, and many of these are of St. Johnian age. Adamanian (St. Johnian) localities in Texas are all in the Tecovas Formation of West Texas (Murry, 1982, 1986, 1989a; Heckert, 2004) and, in addition to the Kalgary localities, include diverse localities in Crosby County (Case, 1928a, b; Long and Murry, 1995), Palo Duro Canyon (Case, 1932; Murry, 1982, 1986, 1989a), Rotten Hill (Murry, 1989a), and Sunday Canyon (Murry, 1989a). New Mexican microvertebrate localities of Adamanian age include the Los Esteros Member of the Santa Rosa Formation (Heckert and Lucas, 2001), the Ojo Huelos Bed of the San Pedro Arroyo Formation (Heckert and Lucas, 2002b; Heckert, 2004), and the basal Bluewater Creek Formation (Heckert, 1997, 2001, 2004). Microvertebrate localities of Adamanian (St. Johnian) age in Arizona include the *Placerias*-Downs Quarry in the Bluewater Creek Formation (Tannenbaum, 1983; Murry, 1987; Murry and Long, 1989; Kaye and Padian, 1994; Lucas et al., 1997), several localities in the Blue Mesa Member of the Blue Hills, including Camp’s (1930) “meal pots” localities and other small vertebrate assemblages (Heckert et al., 1999; Heckert, 2002, 2004; Zanno et al., 2002), microvertebrate localities in the Blue Mesa Member in the vicinity of Stinking Springs Mountain (Polcyn et al., 1998, 2002), and in the type section of the Blue Mesa Member in the Petrified Forest National Park (e.g., Murry and Long, 1989; Murry, 1989b, 1990; Long and Murry, 1995; Heckert, 2004). Presently, there is no reliable way to stratigraphically organize localities from different outcrop belts, but all of these quarries either yield or are closely associated with localities that yield St. Johnian index fossils such as *Stagonolepis wellesi*, *Rutiodon*-grade phytosaurs, and/or *Krzyzanowskisaurus hunti*.

Most Tecovas Formation localities occur low in the unit, although the upper and lower Kalgary localities are clearly superposed (Fig. 3). The microvertebrate fauna of the Los Esteros microvertebrate site (NMMNH locality 1171, type locality of *Krzyzanowskisaurus hunti*) is associated with a typical Adamanian assemblage. The Sixmile Canyon microvertebrate assemblage in the Bluewater Creek Formation is also associated with occurrences of *Stagonolepis*. This is also obviously the case with the most diverse Chinle locality and type St. Johnian fauna, the *Placerias* Quarry (Lucas et al., 1997; Hunt et al., 2005) as well as the micro- and small vertebrate localities in the Blue Hills. The type Adamanian assemblages, including the microvertebrate assemblages from “Dying Grounds” and “Crocodile Hill,” are by definition Adamanian (Lucas and Hunt, 1993; Lucas, 1998) and are St. Johnian in age (Hunt et al., 2005).

##### Adamanian (Lamyian)

With the recent recognition of the Lamyian sub-lvf as a discrete interval of Adamanian time (Hunt et al., 2005), several localities assigned to either Adamanian or Revueltian age in the past are, in fact, Lamyian. This includes, of course, the classic Lamyian amphibian quarry in the Garita Creek Formation of central New Mexico, which yields a small microvertebrate assemblage (Rinehart et al., 2001), as well as the Crystal Forest microvertebrate locality (Murry, 1989b) in the Jim Camp Wash Bed of the Sonsela Member of the Petrified Forest National Park in Arizona.

##### Revueltian

Presently the FAD of the aetosaur *Typhothorax coccinarum* marks the onset of Revueltian time (Lucas, 1998; Hunt et al., 2005). Hunt (2001) advocated a three-fold subdivision of the Revueltian into Rainbowforestan, Barrancan, and Lucianoan sub-lvfs. The Rainbowforestan of Hunt (2001) is, for all intents and purposes, equivalent to the Lamyian of Hunt et al. (2005), and we have chosen to use the latter term so as to avoid confusion with the Rainbow Forest Bed of Heckert and Lucas (2002a). We follow Hunt (2001) in recognizing an

older (Barrancan) and a younger, (Lucianoan) sub-lvf, although we follow others in noting that the Lucianoan is recognized primarily by the absence of some typical Barrancan taxa (e.g., *Revueltosaurus callenderi*) and the presence of taxa thus far known solely from their type specimens (e.g., *Lucianosaurus*, *Pseudotriconodon*).

#### Revueltian (Barrancan)

Chinle Group localities low in the Bull Canyon Formation include, and are correlative to, the type Barrancan fauna of Hunt (2001). These faunas include the vertebrate assemblages, including small- and microvertebrates, from the Barranca and Revuelto badlands in eastern New Mexico (Hunt, 1994, 2001) and the Post and Miller quarries in West Texas (Chatterjee, 1983, 1984, 1985, 1986, 1991, 1993; Small, 1989; Lehman and Chatterjee, 2005). All localities in the Painted Desert Member of the Petrified Forest National Park are of Revueltian age (Lucas and Hunt, 1993; Hunt and Lucas, 1995; Heckert and Lucas, 2002a; Parker and Irmis, 2005). We suspect that most, if not all, are Barrancan, especially those below the Black Forest Bed.

#### Revueltian (Lucianoan)

We loosely associate stratigraphically higher localities of Revueltian age as Lucianoan, following Hunt (2001). The type Lucianoan fauna comes from high in the Bull Canyon Formation near Luciano Mesa (Hunt, 2001) and includes the type locality of *Pseudotriconodon chatterjeei* Lucas and Oakes (1988) and *Lucianosaurus wildi* Hunt and Lucas (1994). Other stratigraphically high small- and microvertebrate localities of Revueltian age that we tentatively identify as Lucianoan include the Snyder quarry, which is very high in the Painted Desert Member of the Petrified Forest Formation of northern New Mexico (Heckert and Jenkins, 2005), as well as the Owl Rock Formation localities described by Kirby (1989, 1991, 1993; Murry and Kirby, 2002) in northern Arizona.

#### Apachean

The Apachean lvf is defined by the FAD of the phytosaur *Redondasaurus* and also includes the aetosaur *Redondasuchus* as an index taxon (Lucas and Hunt, 1993; Lucas, 1998). There are several small- and microvertebrate assemblages associated with the type Apachean fauna, such as those of Gregory's quarry, and others in the Redonda Formation include the faunas of Shark Tooth Hill and Red Peak (Murry, 1989a; Lucas et al., 1999a; Heckert et al., 2005). The microvertebrate assemblages of the Sloan Canyon Formation in northeastern New Mexico are also of Apachean age (Lucas et al., 1997; Hunt and Lucas, 1993; Heckert et al., 2002).

#### MICRO- AND SMALL VERTEBRATE BIOSTRATIGRAPHY

Figure 3 depicts our present understanding of the micro- and small-vertebrate biostratigraphy of the Chinle Group as it relates to the lvf system erected by Lucas and Hunt (1993) and subsequently modified. We note that the underlying lithostratigraphic framework is essentially that of Lucas (1993, 1997) with some subsequent modification (e.g., Heckert and Lucas, 2002a). Because of the extensive literature on Chinle macrovertebrate biostratigraphy (e.g., Lucas and Hunt, 1993; Long and Murry, 1995; Lucas, 1997; Lucas et al., 1997; Hunt, 2001; Hunt et al., 2005), we choose not to provide a detailed overview of the reasons for assigning microvertebrate occurrences a specific age. In most cases, the age assignments are based on the occurrence of biostratigraphically significant macrovertebrate taxa within the same unit. This is justified because most vertebrate fossil assemblages on which the biostratigraphic framework is based occur more or less throughout the stratigraphic units in question, and indeed, many microvertebrate faunas were collected from known macrovertebrate sites (e.g., Murry, 1982, 1986, 1989a, b, c; Murry and Long, 1989; Kaye and Padian, 1994; Heckert, 2004). This still provides a test of the existing macrovertebrate-

based biostratigraphy, because the ranges of microvertebrate taxa can be compared directly to those of the macrovertebrates.

To review all of the micro- and small vertebrates known from the Chinle greatly exceeds the scope of this paper. Rather, we choose to highlight the records we consider the most biostratigraphically significant as well as some taxa with great biostratigraphic potential that has yet to be realized.

In the following paragraphs, we review the micro- and small vertebrate occurrences that support the biostratigraphy and biochronologic hypotheses advanced here. We do this in systematic order for convenience, following the systematic paleontology utilized by Heckert (2004), to which we refer the reader for taxon references.

#### Chondrichthyes Huxley

#### Elasmobranchii Bonaparte

#### Xenacanthiformes Berg

#### Xenacanthidae Fritsch

#### *Triodus* Jordan

#### *"Triodus" moorei* (Woodward)

Xenacanth sharks very nearly fail to cross the Permo-Triassic boundary, and the surviving species in the Chinle is remarkably small and only identified from microvertebrate fossils recovered during screenwashing (e.g., Johnson, 1980; Murry, 1982, 1986, 1989a, b; Heckert, 2001, 2004). Presently, Hampe and Schneider are revising the Triassic xenacanth, and although Schneider (1996) used *"Xenacanthus" moorei* to describe these teeth, *"Triodus" moorei* may be a better binomial (Hampe, 2003; pers. commun.). All such occurrences are stratigraphically low in the Chinle Group, and typically associated with faunas of Adamanian (St. Johnsian) age (Heckert, 2004). It thus appears likely that *"Triodus" moorei* is an index taxon of Adamanian (St. Johnsian) time.

#### Hybodontidae Zangerl

#### Hybodontidae Owen

#### Polyacrodontidae Glückman

#### *Lissodus* Brough

#### *Lissodus humblei* Murry

Since Murry (1981) first identified *Lissodus* from the Chinle Group in Texas, its occurrences have greatly expanded, and it is now the most long-lived and widespread chondrichthyan in the Chinle Group (e.g., Murry, 1981, 1986; Huber et al., 1993; Heckert, 2004). The possibility exists that there are multiple species of *Lissodus* (Huber et al., 1993), and that *L. humblei* might therefore have a more limited stratigraphic range. We are currently restudying *Lissodus* specimens from the Sloan Canyon Formation in northeastern New Mexico identified as a possible new species of *Lissodus* by Huber et al. (1993). We also note that, as used here, *Lissodus* = *Lonchidion* of Rees and Underwood (2002) and others, including Heckert (2004).

#### *Diplolonchidion murryi* Heckert

Heckert (2004) recognized several hybodont teeth similar to *Lissodus* from the Upper Kalgary microvertebrate locality in the Tecovas Formation of West Texas. To date, the type locality is the only known occurrence of this taxon, so it has no current biostratigraphic utility.

#### Hybodontidae Owen

#### Acrodontinae Maisey

#### *Reticulodus synergus* Murry and Kirby

Murry and Kirby (2002) erected the new genus and species *Reticulodus synergus* for a small shark known from isolated teeth in localities of Revueltian age in Arizona, Utah, and New Mexico. *Reticulodus* occurs in the Sonsela and Painted Desert members of the Petrified Forest Formation and the Owl Rock Formation in Arizona, an interval equiva-

lent to the Rock Point Formation in Utah, and the Bull Canyon Formation in New Mexico (Murry and Kirby, 2002).

**Osteichthyes** Huxley  
**Actinopterygii** Klein

The Chinle Group has a rich and diverse assemblage of osteichthyans, principally various actinopterygian taxa (Schaeffer, 1967; Huber et al., 1993; Johnson et al., 2002), but much of it is either long-lived (Huber et al., 1993) or known from fragmentary material recovered from screenwashing (Murry, 1982; Heckert, 2004). Accordingly, osteichthyan fish are among the least biostratigraphically useful fossils in the Chinle Group. Among osteichthyans, only lungfish have much potential for serving as index taxa (see below), although there is some hope that Chinle fish faunas may ultimately correlate to those of the Newark Supergroup.

**Sarcopterygii** Romer  
**Actinistia** Cope  
**Dipnoi** Müller  
**Ceratodontidae** Gill  
**Arganodus dorotheae** (Case)

Lungfish teeth are among the few fragmentary osteichthyan fossils from the Chinle Group that are readily identifiable to genus. Presently all Chinle Group lungfish are assigned to the genus *Arganodus*, and those identified to the species level are *Arganodus dorotheae*. Lungfish teeth occur throughout the stratigraphic section (e.g., Murry and Long, 1989; Huber et al., 1993), and their occurrences, obviously, are facies-controlled. However, lungfish “acme zones” appear to occur at or near the base of the Chinle Group (e.g., Murry and Long, 1989; Polcyn et al., 1998; Zeigler et al., 2001) as well as within the Painted Desert Member within the Petrified Forest National Park (Murry, 1989c). This same genus occurs in broadly coeval strata in Morocco, albeit at much larger size (Martin, 1981a, b).

**Amphibia** Linnaeus

In the Triassic, amphibians generally make poor index fossils because individual taxa are long-ranging, and often a nearly complete skull is required to make a generic or specific identification (e.g., Hunt, 1993; Lucas and Schoch, 2002). The most common Chinle amphibians are metoposaurids; among members of this group, the diminutive *Apachesaurus* is readily recognized by its elongate centra, but it has a long stratigraphic range and, like many larger metoposaurids, indicates little but a Late Triassic age (Hunt, 1993). There are other, smaller temnospondyls in the Chinle Group (*Laticopsis disjunctus* Wilson, 1948 and *Rileymillerus cosgriffi* Bolt and Chatterjee, 2000), but these are presently known solely from their type specimens and thus, as yet, are not of biostratigraphic significance.

**Parareptilia** Olson  
**Procolophonidae** Seeley

Procolophonids are ideal candidates for microvertebrate index fossils because they possess complex dentitions that are easily recognized from isolated fragments. Unfortunately, they are rare in the Chinle Group, and none of the occurrences are referable to a taxon that occurs at more than one location, so at present there are no procolophonid-based correlations in the Chinle (assuming that *Colognathus* is not a procolophonid; see below). Still, we briefly review the record of procolophonids from the Chinle Group here in the hopes that it will spur additional collecting and description to facilitate future correlations, particularly with the Newark Supergroup in eastern North America, which has a diverse assemblage of procolophonids and procolophonid-like taxa (Gilmore, 1928; Colbert, 1946; Sues and Olsen, 1993; Sues and Baird, 1998; Sues et al., 2000).

Presently there are the following reports of procolophonids from the Chinle Group: (1) indeterminate putative procolophonid microvertebrates from the *Placerias* quarry in the Bluewater Creek Formation of Arizona (Tannenbaum, 1983; Kaye and Padian, 1994); (2) the type and only known specimen of *Libognathus sheddi* Small (1997) from the Bull Canyon Formation of West Texas; (3) undescribed procolophonids, including a leptopleurine, from the Owl Rock Formation in Arizona (Sues and Olsen, 1993); (4) a leptopleurine from the Owl Rock Formation in Utah distinct from the Arizona specimen (Fraser et al., 2005); and (5) unidentified probable procolophonids from the lower Kalgary site in the Tecovas Formation in West Texas (Heckert, 2004).

**Reptilia** Linnaeus  
**Synapsida** Osborn  
**Cynodontia** Owen

Cynodonts (including their descendants, the mammals) are the only small-bodied, biostratigraphically useful synapsid taxa in the Chinle Group. They are generally rare in the Chinle Group, and tiny, with the exception of an unnamed taxon from the Redonda Formation (Lucas et al., 1999a). There are numerous localities that yield isolated cynodont teeth, including the *Placerias* quarry, the Kalgary localities, and one or more localities in the Bull Canyon Formation in east-central New Mexico (Tannenbaum, 1983; Hunt, 1994, 2001; Kaye and Padian, 1994; Heckert, 2001, 2004). The handful of diagnostic, named cynodonts include the tritheledont *Pachygenelus milleri* Chatterjee (1983), the triconodont *Pseudotriconodon chatterjeei* Lucas and Oakes (1988), and the early mammal *Adelobasileus cromptoni* Lucas and Hunt (1990). To date, most of these taxa remain endemic to their type localities, but a few records of potential biostratigraphic utility are highlighted in the following paragraphs.

***Pseudotriconodon chatterjeei*** Lucas and Oakes

*Pseudotriconodon chatterjeei* is known solely from the holotype specimen, so it would appear that its biostratigraphic utility is limited, although Hunt (2001) suggested it was an index taxon of his Lucianoan lfv. However, the genus occurs in several localities outside the Chinle basin, including occurrences in Belgium, Luxembourg, France, and England (Hahn et al., 1987; Cuny et al., 1995; Godefroit and Battail, 1997; Cuny, 2004). It therefore may be useful as it is one of the few Chinle microvertebrates that, at the genus level, is not endemic to the Chinle basin. All *Pseudotriconodon* occurrences are of Revueltian to Apachean age.

***Rewaconodon tikiensis*** Datta et al.

Only a single specimen that may represent *Rewaconodon* is known from the Chinle (aff. *Rewaconodon* of Heckert, 2004). We include it here because again, it is known from outside the basin (Datta et al., 2004), providing a possible correlation between Adamanian strata in North America and the Tiki Formation of India.

**Diapsida** Osborn  
**Lepidosauromorpha** Benton  
**Sphenodontia** Williston  
**Sphenodontidae** Cope

Numerous workers have reported sphenodontians from the Chinle Group, principally from Arizona (Murry, 1987a; Kaye and Padian, 1994) and Texas (Heckert, 2001, 2004). Although sphenodontians are often recognizable from dentulous fragments, they tend to make poor index fossils because individual genera, and even species, have long stratigraphic ranges (Fraser, 1988a). Sphenodontian taxa therefore appear to have relatively little utility as biostratigraphic markers at this time scale, although similar forms co-occur at the *Placerias* quarry in Arizona and

correlative strata in the Tecovas Formation of West Texas (Heckert, 2004). Presently, sphenodont-based correlations, within the group as well as between basins, are at a much coarser level of resolution than that offered by other vertebrates. This is summarized briefly for several taxa.

***Planocephalosaurus* Fraser**

***Planocephalosaurus lucasi* Heckert**

Heckert (2004) identified the new species *P. lucasi* from the lower Tecovas Formation (lower Kalgary microvertebrate site) in Crosby County, Texas. The holotype remains the only known specimen of the taxon, but the genus is known from Triassic-Jurassic strata in fissure fills in Great Britain (Fraser, 1994). Unlike Heckert (2004), we consider the lower Tecovas Formation to be Adamanian, not Otischalkian, in age, although it probably represents earliest Adamanian time.

***Clevosaurus latidens* Fraser**

Fraser (1993) was the first to report specimens of *Clevosaurus* from Upper Triassic strata in North America, including a specimen from the *Placerias* quarry he named *Clevosaurus latidens*. The *Placerias* quarry fauna is Adamanian (St. Johnsian) in age (Lucas et al., 1997; Hunt et al., 2005); the only other possible occurrence of *Clevosaurus latidens*, a specimen of aff. *C. latidens*, is from the Tecovas Formation of West Texas (Heckert, 2004), which is also of St. Johnsian age, suggesting that *C. latidens* may be an index taxon of St. Johnsian time. The genus *Clevosaurus* is widespread both geographically and stratigraphically, and is known from strata of Triassic and Jurassic age in North America, Great Britain, China, South America and South Africa (Fraser, 1988b; Wu, 1994; Sues and Reisz, 1995; Bonaparte and Sues, 2006; Jones, this volume).

***Paleollanosaurus fraseri* Heckert**

Presently *Paleollanosaurus* is only from the genoholotype specimen, from the lower Tecovas Formation (lower Kalgary microvertebrate site) in Crosby County, Texas. It therefore does not, as yet, have biostratigraphic utility, but is of Adamanian (St. Johnsian) age.

**Archosauromorpha Huene**

**Drepanosauridae Berman and Reisz**

One group of Triassic archosauromorphs that has great, yet currently unrealized, biostratigraphic potential is the drepanosaurs. Currently there are three unambiguously drepanosaurid specimens known from the Chinle Group: (1) *Dolabrosaurus aquitilis* from the Painted Desert Member of the Petrified Forest Formation (Berman and Reisz, 1992) in New Mexico; (2) a pectoral girdle of a generically undiagnostic drepanosaurid from the Rock Point Formation in New Mexico (Harris and Downs, 2002); and (3) at least some of the putative *Protoavis* material from the Post Quarry (Bull Canyon Formation) in West Texas (Harris, personal commun.). Because drepanosaurids are well known from marine strata in Italy (e.g., Pinna, 1980, 1984, 1986; Renesto, 2003) and fissure fills in Great Britain (Renesto and Fraser, 2003; Fraser and Renesto, 2004) and have highly distinctive postcrania (Pinna, 1984; Renesto, 2003), they have great potential to emerge as significant index fossils. However, a more extensive and identifiable record of drepanosaurids will be needed from the Chinle Group to realize this potential.

**Trilophosauridae Gregory**

***Trilophosaurus* Case**

Specimens of the unusual archosauromorph *Trilophosaurus* are only common at the *Trilophosaurus* quarries at Otis Chalk and Kahle's *Trilophosaurus* quarry in Borden County, both in Texas, but their total distribution is much wider and individual *Trilophosaurus* teeth are identifiable to the species-level, so they have a much wider biostratigraphic

utility. Heckert et al. (2006b) recently revised the genus and provided detailed stratigraphic ranges for the species *T. buettneri* and *T. jacobsi*. Nearly simultaneously, Mueller and Parker (2006) named a new species, *T. dornorum*, that appears to be very similar to (and may be synonymous with) *T. jacobsi*. *T. buettneri* is an index taxon of Otischalkian-Adamanian (St. Johnsian) age; *T. jacobsi* marks an interval of Adamanian (St. Johnsian-Lamyian) time and, if valid, *T. dornorum* is an index taxon of late Adamanian (Lamyian) to early Revueltian (Barrancan) time.

**Archosauriformes Gauthier**

**Archosauria Cope**

**Crocodylotarsi Benton and Clark**

***Revueltosaurus callenderi* Hunt**

*Revueltosaurus callenderi* was originally described as a possible ornithischian dinosaur (Hunt, 1989), although it is now clear that *Revueltosaurus* is actually a crurotarsan (Parker et al., 2005). However, none of the biostratigraphic correlations identified by previous workers (e.g., Padian, 1990; Hunt and Lucas, 1994; Heckert and Lucas, 1997; Heckert, 2002) are invalidated, and indeed the fact that Parker et al. (2005) and Hunt et al. (2005) have identified diagnostic postcrania and small skull bones only increases its biostratigraphic potential. To date, *Revueltosaurus* has only been found in rocks of Revueltian (Barrancan) age, including records from the Bull Canyon Formation in New Mexico and the Painted Desert Member in Arizona and, possibly, Utah (Heckert, 2002; Heckert et al., 2005, this volume).

**Stagonolepididae Lydekker**

Although much of the existing biostratigraphy of the Chinle Group is based on aetosaurs (e.g., Lucas and Hunt, 1993; Lucas and Heckert, 1996; Lucas, 1997, 1998), these hypotheses were largely developed using larger taxa. In the last decade, smaller aetosaurs, with osteoderms in the size range of small vertebrates described here, have been documented with increasing frequency in the Chinle Group. Chief among these are occurrences of *Aetosaurus* in the Bull Canyon Formation in New Mexico (Heckert and Lucas, 1998) and Rock Point Formation in Colorado (Small, 1998). *Aetosaurus* has typically been interpreted as a Revueltian index fossil (Lucas and Heckert, 1996; Heckert and Lucas, 2000), and the New Mexico occurrences are unambiguously Barrancan (Hunt, 2001). However, the Colorado occurrence is difficult to evaluate because of the less-well developed Upper Triassic stratigraphic framework in Colorado relative to New Mexico and Arizona, and other occurrences suggest an Apachean age for some records.

**Dinosauria Owen**

**Ornithischia Seeley**

Although some, such as Parker et al. (2005), have cast doubt on the affinities of all Upper Triassic ornithischians known solely from fossil teeth (e.g., Hunt and Lucas, 1994; Heckert, 2004), a variety of these taxa are readily identifiable, almost certainly diagnostic, and occur at several localities in the Chinle Group. Thus, even if they prove to pertain to non-dinosaurian taxa (as did *Revueltosaurus callenderi*), they still have biostratigraphic significance, much like the case of the Late Cretaceous dromaeosaurid *Richardoestesia* (e.g., Currie et al., 1990; Sankey, 2002). Therefore, we present here an overview of the biostratigraphic significance of several basal ornithischians (or putative ornithischians), updating previous hypotheses of Heckert and Lucas (1996) and Heckert (2004).

***Protecovasaurus lucasi* Heckert**

The putative "carnivorous" ornithischian *Protecovasaurus* is known from localities of both Otischalkian (*Trilophosaurus* quarry 1) and Adamanian age (lower and upper Kalgary quarries). Because the Kalgary localities are of St. Johnsian age, the stratigraphic range of

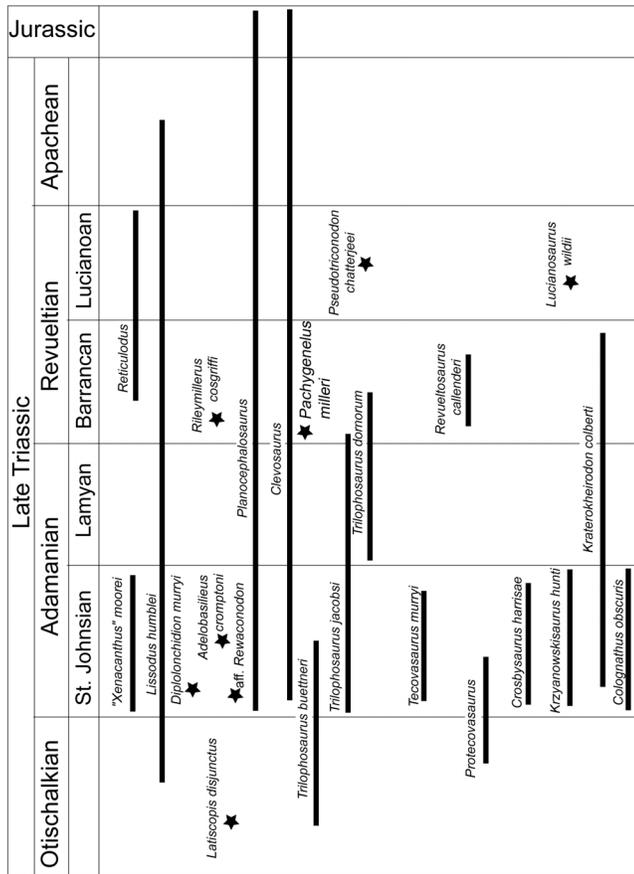


FIGURE 3. Temporal distribution of micro- and small vertebrate taxa from the Chinle Group. Taxa known from single occurrences marked with stars.

*Protecovasaurus* appears to encompass Otischalkian-Adamanian (St. Johnian) time.

***Tecovasaurus murryi* Hunt and Lucas**

*Tecovasaurus* occurs at the type locality and also at the *Placerias* quarry, both of Adamanian (St. Johnian) age (Hunt and Lucas, 1994; Heckert, 2001, 2004). Therefore, *Tecovasaurus* may be an index taxon of St. Johnian time. A *Tecovasaurus* sp. tooth illustrated by Heckert (2004, figs. 55d-e) is probably another occurrence of this taxon at the lower Kalgary locality, which is also of Adamanian (St. Johnian) age.

***Crosbysaurus harrisae* Heckert**

The extremely distinctive dentition of *Crosbysaurus* occurs in numerous deposits of Adamanian (St. Johnian) age. These include the type locality at lower Kalgary, the upper Kalgary locality, Sixmile Spring in western New Mexico, the *Placerias* quarry, and the “Dying Grounds” in the Petrified Forest National Park (Heckert, 2001, 2004). All but the Dying Grounds locality are very low in the Chinle Group, and all are of Adamanian (St. Johnian) age, so *Crosbysaurus* is clearly an index taxon of St. Johnian time.

***Krzyzanowskisaurus hunti* (Heckert)**

As documented by Heckert (2005), the re-appraisal of *Revuelto-saurus* as a crurotarsan required a new generic name for “*Revultosaurus*” *hunti* if it does indeed represent an ornithischian. Even if it proves to be a non-dinosaurian taxon closely related to *R. callenderi*, as thought by Parker and Irmis (2005), it likely represents a distinct taxon at the generic level. *Krzyzanowskisaurus* occurrences are all of Adamanian (St. Johnian) age, so it is an index taxon of that lvf.

***Vertebrata incertae sedis*  
*Colognathus obscurus* (Case)**

The enigmatic vertebrate *Colognathus obscurus* (Case) has vari-ously been considered a fish, a procolophonid, and a procolophonid relative (e.g., Case, 1928a, 1932; Murry, 1982, 1986). Regardless of its taxonomic affinities (which remain enigmatic), it is easily recognized, relatively abundant (15+ identified specimens in museum collections), and has a stratigraphic career restricted to strata of St. Johnian age (Heckert, 2006). Thus *Colognathus* is one of the best small vertebrate index taxa known from the Chinle.

***Kraterokheirodon colberti* Irmis and Parker**

Irmis and Parker (2005) recently named the enigmatic taxon *Kraterokheirodon*, which is one of the rarest, and strangest, small vertebrates in the Chinle. The two known specimens were derived from very different stratigraphic horizons, so even though it is exceedingly rare, it has a long stratigraphic range (Adamanian [St. Johnian]-Revueltian [Barrancan]).

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