



The microvertebrate fauna of the Upper Triassic (Revueltian) Snyder Quarry, north-central New Mexico

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THE MICROVERTEBRATE FAUNA OF THE UPPER TRIASSIC (REVUELTIAN) SNYDER QUARRY, NORTH-CENTRAL NEW MEXICO

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ABSTRACT.—The Snyder quarry is a well-documented assemblage of Late Triassic invertebrates and vertebrates from the Painted Desert Member of the Upper Triassic Petrified Forest Formation in the Chama Basin, north-central New Mexico. The presence of Revueltian index taxa, including the aetosaurs *Typothorax coccinarum* and *Desmatosuchus chamaensis* and the phytosaur *Pseudopalatus buceros*, demonstrate that the Snyder quarry is of Revueltian (early-mid Norian) age. Screenwashing matrix from the primary bonebed at the Snyder quarry yielded a moderately diverse assemblage of microvertebrates, some of which were not represented in the macrovertebrate fauna. Microvertebrate fossils from the Snyder quarry are mostly scales and bone fragments—complete teeth are unusually rare. New records include a tooth of the hybodontoid shark *Lonchidion* and numerous scales of a palaeoniscid fish tentatively assigned to aff. *Turseodus*. The microvertebrate assemblage differs somewhat from the known macrovertebrate assemblage, and includes many more osteichthyan fossils. Osteichthyans dominate the microvertebrate fauna, and include semionotids, redfieldiids, palaeoniscoids, and indeterminate sarcopterygians. Osteichthyans are largely represented by scales, with the exception of the indeterminate sarcopterygians and actinopterygians, represented by fragments of dentigerous toothplates, fossils previously assigned to “colobodontids.” The microvertebrate tetrapod fauna represented by teeth includes metoposaurid amphibians, juvenile (?) phytosaurs (?), probable dinosaurs, aetosaurs and other diverse, unidentified archosauromorphs. Many of the vertebrae appear to pertain to small archosauromorphs. The microvertebrate assemblage is unusual in that recovered vertebrae and other non-cranial elements greatly outnumber intact teeth, which normally dominate Chinle microvertebrate assemblages. We interpret this as additional support for the hypothesis of a catastrophic origin for the Snyder quarry vertebrate assemblage, as more typical Chinle Group microvertebrate assemblages are attritional deposits in which teeth greatly outnumber vertebrae.

INTRODUCTION

The Snyder quarry (NMMNH locality 3845) is an exceptionally rich Upper Triassic fossil assemblage from the Painted Desert Member of the Petrified Forest Formation in north central New Mexico that has been the focus of much recent study (Heckert et al., 2000, 2004; Zeigler et al., 2002a,b,c; Heckert and Zeigler, 2003; Heckert et al., 2003a,b; Hurlburt et al., 2003; Lucas et al., 2003a,b; Rinehart et al., 2003; Tanner et al., 2003; Zeigler, 2003; Zeigler et al., 2003a,b,c,d,e) (Fig. 1). Macrofossil vertebrates, principally the bones and teeth of the archosaurian phytosaurs, aetosaurs, dinosaurs, and rauisuchians, dominate the assemblage. However, in 1999 one of us (ABH), with the help of the New Mexico Friends of Paleontology, collected ~3000 lbs (~1400 kg) of screenwash matrix from the principal bone-bearing interval of the site. Furthermore, ever since the initial preparation of Snyder quarry jackets in 1998, matrix from those jackets has been kept and screenwashed as well, and the junior author conducted an undergraduate thesis and related studies based on this material (Heckert et al., 2004; Jenkins, 2004; Jenkins and Heckert, 2004a,b). Here, we describe the microvertebrate fauna from the Snyder quarry, some of which was briefly mentioned in the annotated faunal list presented by Zeigler et al. (2003b). The nomenclature and taxonomy we use for this paper follows that developed by Heckert (2001, 2004) for Chinle microvertebrates from older strata in Texas, New Mexico, and Arizona, and complete references for the taxa listed in the systematic paleontology section are provided there. Unless otherwise noted, all specimens were recovered from screenwash concentrate, although a few

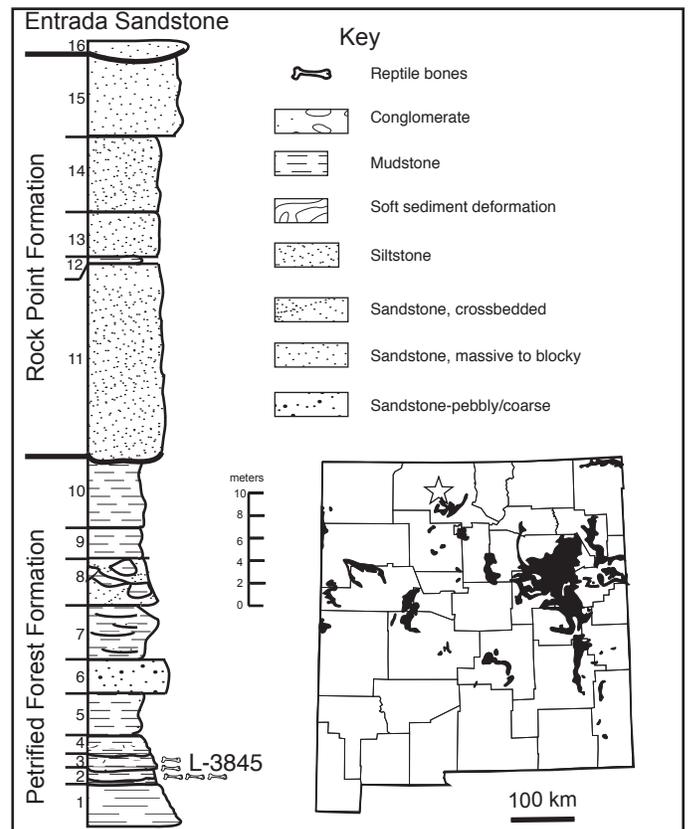


FIGURE 1. Index map and stratigraphic section showing the geographic location and stratigraphic position of the Snyder quarry (after Heckert et al., 2000a).

of the more diagnostic fossils were actually recovered by crew members during excavation for macrovertebrates.

STRATIGRAPHY AND AGE

The Snyder quarry is in the Painted Desert Member of the Petrified Forest Formation, 28.5 m below the contact with the overlying Rock Point Formation (Fig. 1). This stratigraphic position is approximately equivalent to the Canjilon quarry 4 km to the east and, probably, the Hayden quarry approximately 6 km to the south and east. The Snyder quarry is also at nearly the same stratigraphic horizon as the type locality of *Eucoelophysis baldwini* Sullivan and Lucas near Orphan Mesa and several other localities in the general vicinity (Lucas and Hunt, 1992; Hunt and Lucas, 1993a; Sullivan et al., 1996; Sullivan and Lucas, 1999; Lucas et al., 2002, 2003). All of these localities are much lower stratigraphically than the famous Whitaker (*Coelophysis*) quarry at Ghost Ranch, which is at least 50 m above the aforementioned theropod localities and in an entirely different stratigraphic unit, the Rock Point Formation (Sullivan et al., 1996; Lucas et al., 2002, 2003a).

The presence of the phytosaur *Pseudopalatus* and the aetosaur *Typhothorax coccinarum* Cope indicates a Revueltian (early-mid Norian) age for the Snyder quarry. This age assignment also confirms that the Snyder quarry fauna is older than the *Coelophysis* quarry at Ghost Ranch, as the latter includes the phytosaur *Redondasaurus*, and thus is of Apachean (late Norian-Rhaetian) age (Lucas, 1998; Lucas et al., 2003).

The Painted Desert Member in north-central New Mexico (Petrified Forest Formation undivided of older usage; see Lucas et al., 2003a, this volume) is stratigraphically equivalent to the Painted Desert Member of the Petrified Forest Formation in west-central New Mexico and northern Arizona. This is also the same stratigraphic interval as the Bull Canyon Formation in east-central New Mexico and West Texas (Lucas, 1993, 1997; Lucas et al., 2002, 2003). Thus, the Snyder quarry is broadly correlative to the upper faunas of the Petrified Forest National Park (e.g., Long and Padian, 1986; Murry and Long, 1989; Hunt and Lucas, 1995; Long and Murry, 1995; Heckert and Lucas, 2002a), as well as Bull Canyon Formation faunas in eastern New Mexico (Hunt, 1994, 2001) and West Texas, including the Post quarry (Small, 1989; Long and Murry, 1995). All specimens described and/or illustrated in this paper are deposited at the New Mexico Museum of Natural History and Science (NMMNH) in Albuquerque, New Mexico.

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley, 1880
ELASMOBRANCHII Bonaparte, 1838
EUSELACHII Hay, 1902
XENACANTHIFORMES Berg, 1955
XENACANTHIDAE Fritsch, 1889
Xenacanthus Beyrich, 1848
"Xenacanthus" moorei Woodward, 1889

The Snyder quarry has thus far yielded a single incomplete xenacanth tooth (Zeigler et al., 2003b). The specimen (NMMNH P-33112) is readily identifiable, possessing the unique bifid geometry and extended lateral cusps characteristic of xenacanth teeth (Fig. 2A-B). Only one lateral cusp remains on this specimen, however, the orientation of the lateral and central cusps with the base of the tooth is also diagnostic. The anterior lateral cusp and lateral cutting edge are present together with a small central cusp (Fig. 2A-B). The central and lateral cusps both align along the labial edge of the tooth. The specimen has a sub-ovoid base with a low root, and is referred to as "*Xenacanthus*" *moorei* in this study.

The morphology of this specimen is representative of the xenacanth teeth found in other parts of the Chinle Group (Murry, 1982, 1986; Heckert, 2001, 2004). However, much debate has occurred over the taxonomy of these Upper Triassic xenacanthiformes (Heckert, 2001, 2004). Johnson (1980) first identified *Xenacanthus moorei* from the lower Kalgary locality in Texas. However, Schneider (1996) argued that the name "*Xenacanthus*" should not be applied to Triassic xenacanths because they are generically distinct from xenacanths of the Paleozoic. The closest alternate genus, *Pleuracanthus*, is based on a specimen whose teeth are so poorly preserved it makes little sense to use this taxon (Johnson, 1980; Heckert, 2004). Therefore, the generic name "*Xenacanthus*" is used here. Recently Johnson (pers. comm. to ABH, 2004) stated that "*Triodus*" is the proper generic name, but we have not been able to verify this.

It should be noted, however, that xenacanths are not present elsewhere in the Chinle basin during the Revueltian (Huber et al., 1993). The specimen belonging to the Snyder quarry microvertebrate assemblage is the only xenacanth found in the Chinle during this time period and may therefore be a contaminant from another locality (Zeigler et al., 2003b). The screenwashing facilities used at NMMNH to wash the Snyder quarry matrix were previously used to wash matrix from several other localities of slightly older (Adamanian) age. These Adamanian localities yielded numerous xenacanth shark teeth and may have contaminated the Snyder quarry assemblage (Zeigler et al., 2003b). Additionally, most workers that have described xenacanths in the Chinle Group have reported numerous specimens from each locality (Johnson, 1980; Murry, 1982, 1986, 1989a,b; Murry and Long, 1989; Heckert, 2001, 2004), so the fact that there is only one tooth from the Snyder quarry makes the record suspicious.

HYBODONTOIDEA Zangerl, 1981

HYBODONTOIDEA Zangerl, 1981

POLYACRODONTIDAE Glückman, 1964

Lonchidion Estes, 1964

Lonchidion humblei Murry, 1981

A single hybodont tooth found in the Snyder quarry assemblage (NMMNH P-41820—Fig. 2C) is 1 mm long and has an elongated crown that is wider than the tooth is tall and possesses a low, poorly defined cusp and a distinct labial protuberance (or "peg"). The tooth is rounded on both the lingual and labial sides, and faint texture on these faces appears almost as pitting

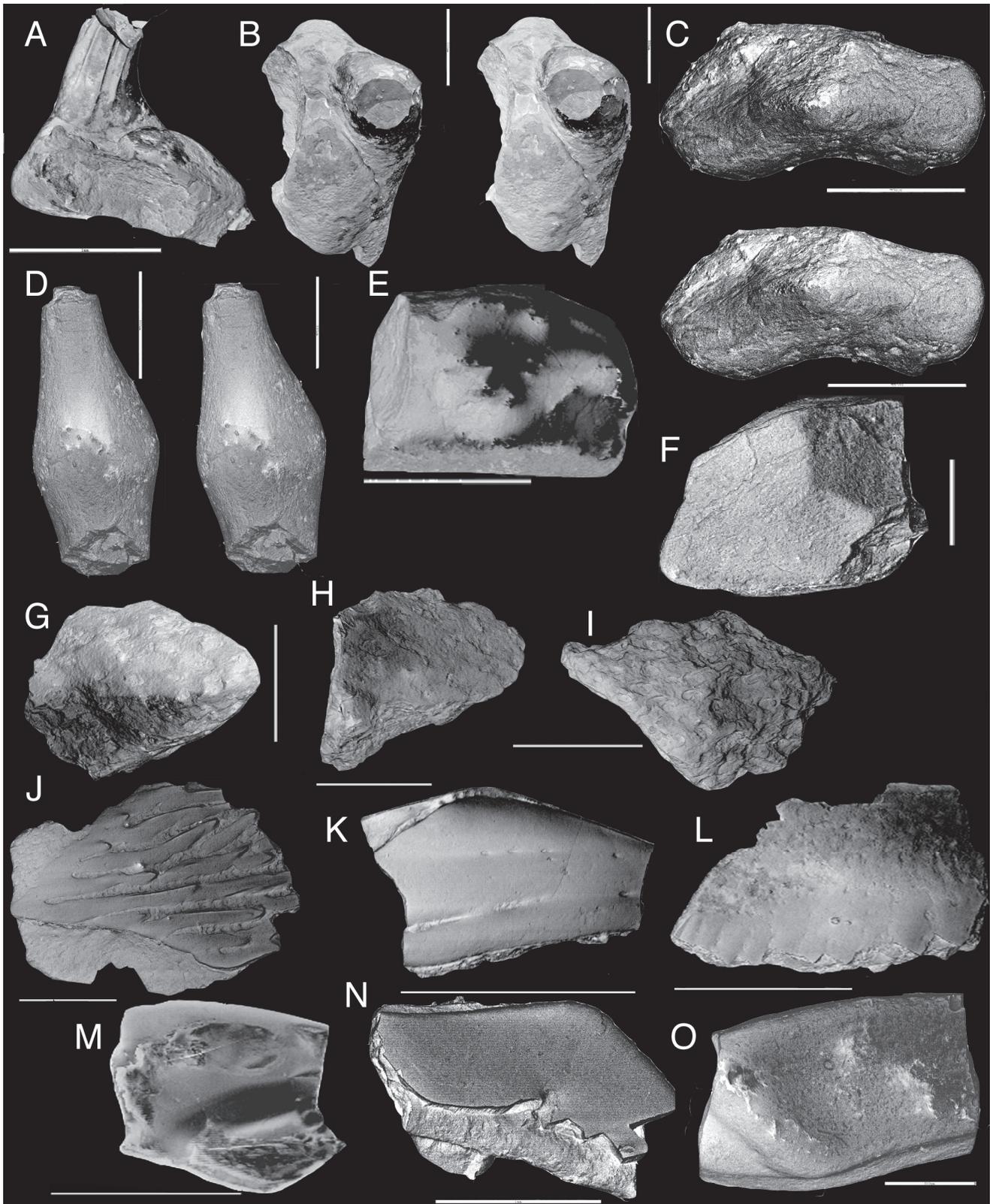


FIGURE 2. Scanning electron micrographs of chondrichthyans (A-C) probable chondrichthyans (D-I) and osteichthyans (J-O) from the Snyder quarry (NMMNH locality 3845). A-B. Xenacanth tooth (P-33112) in A. side view; B. stereo occlusal view; C. *Lonchidion* tooth (P-41820) in stereo labial view; D. chondrichthyan(?) dermal denticle(?) (P-43573) in side(?) view; E. chondrichthyan(?) tooth(?) (P-41819) in external(?) view; F. ctenacanth(?) tooth (P-40350) in side(?) view; G-I. chondrichthyan fin spine(?) (P-40345) in G. dorsal(?), H. anterior(?) and I. lateral(?) views; J-K. palaeoniscid scales (aff. *Turseodus*) in external view, J. 40283, K. P-40279. L-O. redfieldiid scales in external view, L. P-40270, M. P-40301, N. P-41804, O. P-41807. Scales = 0.5 mm (A-D) and 1 mm (E-O).

in some places (Fig. 2C). The tooth is extremely small (1 mm) yet is characteristic of Upper Triassic specimens of *Lonchidion* (= *Lissodus*) (Duffin, 1985; Rees and Underwood, 2002; Heckert, 2001, 2004).

Duffin (1985) synonymized *Lonchidion* and *Lissodus* based on similarities in tooth morphology, specifically the labial peg. However, Rees and Underwood (2002) suggested this feature is retained in both genera for functional reasons, specifically for interlocking teeth from adjacent tooth rows in the tooth whorl, and is therefore not a good systematic feature. They instead suggested several distinctions between *Lissodus* and *Lonchidion*. *Lonchidion* teeth possess larger roots than *Lissodus* and well-demarcated cusps but lack folds or other ornamentation on the crown, whereas weak folds ornament the crown of *Lissodus* (Rees and Underwood, 2002). Although the differences between *Lonchidion* and *Lissodus* appear minute, they represent distinct features that are readily diagnostic of the two genera. Because of the lack of fold ornamentation and the presence of a large root (inferred from the depression at the crown base), the tooth detailed in this study is identified as *Lonchidion*. Indeed, according to Rees and Underwood (2002), all Chinle specimens of “*Lissodus*” are in fact records of *Lonchidion*, specifically *Lonchidion humblei*.

Chondrichthyes indet.

Several microvertebrate elements appear to represent chondrichthyans but are not otherwise diagnostic. One of these is a fin spine (NMMNH P-40435) that is approximately 2 mm long and heavily pitted (Fig. 2G-I). The fragment is wide at the base and narrows toward the tip of the spine. Conical in shape, the fragment shows deep pits on all sides of the spine. This appears to represent a fin spine fragment of a chondrichthyan, possibly a hybodont, but is not otherwise diagnostic. A similar specimen (NMMNH P-40345) is illustrated in Figure 2D.

The assemblage also includes two partial teeth that may have belonged to ctenacanth sharks. The first of these specimens (NMMNH P-41819) is a rounded tooth with one large cusp and a wide base (Fig. 2E). The tooth is concave along one lateral edge and is approximately 2 mm long. Faint textural markings along the lateral face of the tooth may represent foramina or pores. The second specimen (NMMNH P-40350) is a partial tooth containing a distinct pointed cusp and blunt lateral features (Fig. 2F). The tooth has a narrow base and a fairly uniform width, the tooth narrowing just at the top of the cusp. Faint ridges zig-zag across the lateral face of the tooth, and some texture is visible.

OSTEICHTHYES Huxley, 1880

ACTINOPTERYGII Klein, 1885

PALAEONISCIFORMES

PALAEONISCIDAE Vogt, 1852

Palaeoniscidae indet. aff. *Turseodus*

The Snyder quarry contains multiple identifiable palaeoniscid scales that are tentatively referred to as aff. *Turseodus*, and we describe and illustrate several of these scales here. The first

identified scale (P-40283—Fig. 2J) possesses the thick ridges of enamel typical of many palaeoniscids. The ridges are densely packed and deep, running parallel to the long axis of the scale. The scale surface is glossy and shows the ganoin layer quite distinctly. The dentin is also visible in the groove surfaces along the scale. There are many woven canals in the dentin layer which are faintly visible in the ridges of the scale. Although partially complete, the specimen is identifiable as aff. *Turseodus*.

The second specimen (P-40279—Fig. 2K) is also identified as a palaeoniscid, however, this scale does not have the characteristic ridged appearance of aff. *Turseodus* scales. Instead the ganoin surface is dotted with several circular indentations that form a line along the long axis of the scale. These indentations outline a faint ridge running along the scale. Another ridge is visible just beneath these indentations, forming a narrow groove in the scale. Although this specimen does not possess deep ridges that reveal the dentin layer, it does show grooves that make it identifiable as aff. *Turseodus*. According to Schaeffer (1952), scale ornamentation is weakest at the opercular and subopercular of the palaeoniscid fish. It is therefore quite likely that this specimen is from one of these regions on the skull.

The scales of palaeoniscid fish are oriented in an anterodorsal-posteroventral direction (Schaeffer, 1952). Genus-level identification of some palaeoniscid fish is possible because of their highly varied scale ornamentation. In general, palaeoniscid scales along the dorsal and anal fins are highly ridged. These scales are rhomboidal in shape with branching ridges on their surfaces. Ridges run parallel to the ventral and dorsal margins of the scale. Individual scales are thick and partly overlap on articulated specimens. In some palaeoniscids, scales contain thickly crowded ridges of enamel, whereas in others, ridges are scarce.

Three layers are commonly present on palaeoniscid scales (Stamberg, 1998). The first, outermost layer is a ganoin, enamel-like layer containing ridges or tubercles (Fig. 2J). The second layer is made of cosmin or dentin and has many interwoven canals running along it. These canals are often visible if the top enamel layer has been worn away during fossilization. The innermost layer is made of isopedin and is formed of stratified bone (Stamberg, 1998). The lateral surface of the scale typically contains ridges, although the number of ridges varies. The medial surface, on the other hand, is always smooth, often housing a socket for the peg and socket articulation of the scale. These peg and socket facets weave the scales together along the body of the fish. The cosmin layer is typically much reduced and often absent in *Turseodus*, allowing for a smooth surface if the enamel layer has been worn away (Schaeffer, 1952; Murry, 1982).

Although the scales of *Turseodus* have detailed ornamentation, this alone is not necessarily diagnostic of the genus. The only palaeoniscid fish identified from complete material in the Chinle Group is the palaeoniscid *Turseodus* (Schaeffer, 1967; Murry 1982). However, Murry (1982, 1986) observed the presence of diverse palaeoniscid morphotypes in the lower Kalgary locality, (Tecovas Formation, Chinle Group), including the genus *Turseodus* (Heckert, 2001, 2004). Heckert (2001, 2004) identified palaeoniscid scales from various localities in the Chinle Group as having an affinity (aff.) to *Turseodus*, and this nomenclature

is adopted here. The palaeoniscid scales of the Snyder quarry microfauna are thus conservatively referred to as aff. *Turseodus*.

REDFIELDIFORMES Berg, 1940
REDFIELDIIDAE Berg, 1940
Redfieldiidae indet.

Many scales of the family Redfieldiidae are present in the Snyder quarry microvertebrate fauna, and four are illustrated here (Fig. 2L-O). Redfieldiid scales have little ornamentation, often only a glossy ganoin surface with faint interwoven canals. These canals are present on the ganoin surface and do not penetrate to the dentin layer. The scales we describe and illustrate are rhomboidal in shape and punctate, usually displaying the glossy ganoin exterior (Fig. 2L-M). Scales near the head of the fish often show a bumpy, rough texture along the scale. These scales also possess faint interwoven grooves oriented parallel to one another on the scale surface (Fig. 2L-O). Redfieldiid scales found in this faunal assemblage range in size from 1 to 2 mm maximum dimension. Although the scales are moderately diverse in appearance, they all possess a rhomboidal shape and glossy ganoin surfaces.

Several fragments of redfieldiid skull bones were also found in the assemblage (Fig. 3A-C). These skull bones are flat enameloid surfaces with embedded ossifications. The ossifications are either elongated bumps projecting off the face of the bone (P-40267—Fig. 3C) or flat, rounded nubs (P-33113—Fig. 3B). They are commonly ovoid in shape and closely spaced. They can be randomly distributed or oriented along an axis. The bumps vary in size, being small and close to the enameloid surface, or long, branching off the dermal bone. However, the skull fragments are all enameloid with 0.5-1 mm long embedded ossifications. This kind of dermal texture occurs on the parietals and frontals of redfieldiid skulls (Schaeffer, 1967) so these specimens are identified as skull bones of indeterminate redfieldiids following Heckert (2001, 2004).

Redfieldiids are classified as actinopterygians and are identified by their elongate, rhomboid ganoin scales, often with peg and socket articulations. Murry (1982) and Heckert (2001, 2004) identified glossy rhomboid scales from several localities in the Chinle Group as redfieldiids. Disarticulated skull bone fragments are more difficult to identify as redfieldiid, however, the redfieldiids *Cionichthyes* and *Lasalichthyes* have a distinct dermal texture (Schaeffer, 1967). Kaye and Padian (1994) identified fish with this distinct skull bone texture as redfieldiids as well. Ornamented skull bone fragments are therefore referred to as Redfieldiidae indeterminate (indet.) in this study. Redfieldiid scales possess the ganoin layer, with prominent interwoven canals. The scales are rhomboidal in shape, punctate, and have a quadrangular outline (Schaeffer, 1984). Distinct peg and socket articulations are present, with a second peg present on some scales. Up to 70% of the surface of the scale is composed of the ganoin layer (Schaeffer, 1984). The line where the ganoin layer meets the enamel is typically straight and smooth. The dermal bones of the skull are sinuous and broad, possessing close parallel ridges. These bones can sometimes be used to typify the group, as they often bear large, rounded circular nodules and shallow rounded pits (Schaeffer, 1967).

HALECOSTOMI Regan, 1923
SEMIONOTIFORMES Arambourg and Bertin, 1958
SEMIONOTIDAE Woodward, 1890
Semionotidae indet.

Several semionotid scales are preserved in the Snyder quarry fauna (Fig. 3D-E). Both scales illustrated here possess a diamond shape that suggests they were located posteriorly on the body (McCune et al., 1984) (Fig. 3D-E). The ganoin is clear and glossy along the face of the scale. Four faint pits ornament the surface of one of the scales (Fig. 3D). These indentations are the only ornamentation on the scale. The surface is not textured, and no interweaving layers are present.

Semionotiformes are identified by their diamond to faintly rhomboid shaped scales, often with concavo-convex peg and socket articulations (as opposed to the simple, straight-edge peg-and-socket articulations of redfieldiids). The scales we illustrate here (P-40274, P-41808—Figs. 3D,E) are typical. The scales of semionotid fish are unornamented, slender, and composed of ganoin (Brito and Gallo, 2002). The anterior scales are often larger and strongly imbricated. The posterior scales are diamond shaped, and the caudal scales are much shorter than those on other parts of the body (Brito and Gallo, 2002). The scales of semionotids are not cosmoid, as they do not have two bony layers of dentine and enamel. They instead possess one layer of ganoin which does not form grooves along the surface of the scale.

Zeigler et al. (2003b) also illustrated an incomplete semionotid skeleton found above the main bonebed level during the second excavation of 1998. This specimen, even though ~50% complete and articulated, lacks most of the head and thus is not diagnostic below the family level (e.g., McCune et al., 1984).

SARCOPTERYGII Romer, 1955
COELACANTHIFORMES Berg, 1937
COELACANTHIDAE Agassiz, 1843
Coelacanthidae indet.

Several toothplates identified from the Snyder quarry consist of flat dermal plates with multiple small bulbous teeth dotting the surface (P-40323; Fig. 3F). These teeth are often oriented in parallel lines along the plate (P-40322; Fig. 3I). The teeth are blunt with faint striations winnowing into a point at the tip of the tooth. These teeth are about 0.1 mm in size and can sometimes join together to form a tooth row, several teeth appearing as an elongate block (P-40273—Fig. 3G). Wear facets can be seen on some tooth surfaces where the striations have been worn down (Fig. 3H). A rough texture is present surrounding the teeth on the dermal surface. Specimen NMMNH P-40273 (Fig. 3G) shows both the toothplate and the dermal bone of a coelacanth jaw. The jaw bone possesses faint ridges along the enamel. The toothplate begins abruptly forming a line of blunt teeth that run almost perpendicular to the ridges of the jaw bone.

Coelacanthidae toothplates from the Chinle Group have previously been referred to as Colobodontidae or Perleididae, extinct groups of actinopterygians similar to the palaeoniscids (Murry, 1982; Huber et al., 1993; Heckert, 2001). Colobodontids are per-

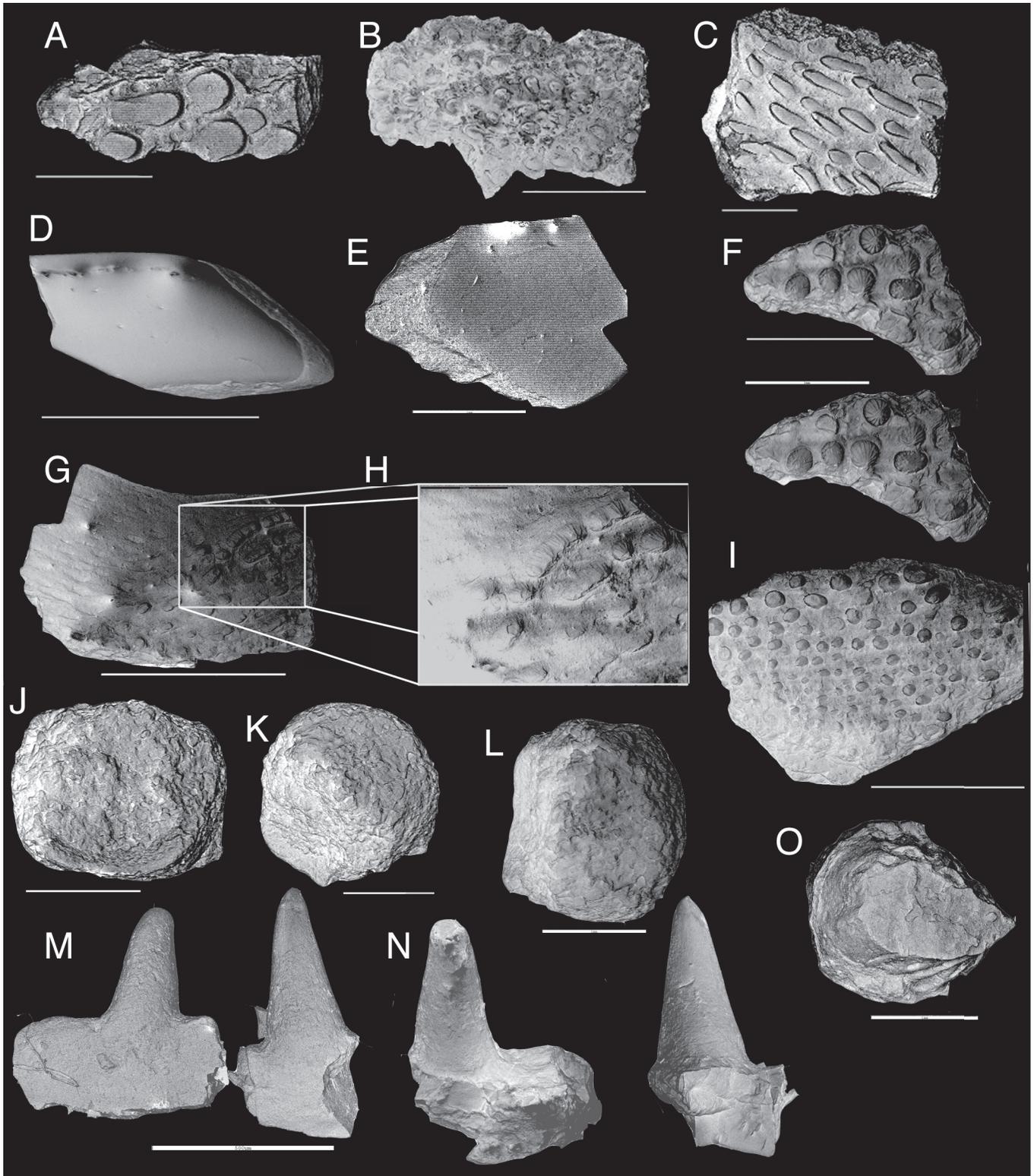


FIGURE 3. Scanning electron micrographs of osteichthyans from the Snyder quarry (NMMNH locality 3845). **A-C**, redfieldiid skull bones in external view; **A**, P-41802, **B**, P-33113, and **C**, P-40267. **D-E**, semionotid scale fragments in external view; **D**, P-40274, **E**, P-41808. (**F-I**) Coelacanth(?) toothplate fragments in occlusal view, **F**, P-40323 in stereo occlusal view; **G**, P-40273. **H**, enlarged view of wear facets on toothplate P-40273, **I**, P-40322. **J-L**, osteichthyan vertebra (P-40330) in **J**, articular, **K**, dorsal, and **L**, lateral views. **M-N**, osteichthyan tooth-bearing jaw fragments (P-41578) in **M**, labial and **N**, lingual views. **O**, osteichthyan(?) fin spine(?) fragment (P-43572) in dorsal(?) view. All scale bars = 1mm except H, M-N = 500 microns.

leidiformes that commonly show highly distinctive toothplates of conical or striated bumps (Heckert, 2001). This toothplate morphology is also typical of the coelacanth. Mutter (2002) described colobodontids as having durophagous or shell crushing dentition, however, and is certain that the Chinle Group toothplate specimens are not colobodontids (Mutter, pers. comm., 2002). The toothplates we describe and illustrate here are therefore identified as coelacanth because of their superficial similarities to coelacanth toothplates. Additionally, no colobodontid scales have been found in the Chinle Group, but coelacanth scales and skulls have been identified (Schaeffer, 1967; Elliott, 1987; Huber et al., 1993; Heckert, 2001, 2004). This suggests that the toothplate fragments are more likely coelacanthid and are therefore referred to as Coelacanthidae indeterminate in this study.

Osteichthyes indet.

There are multiple osteichthyan vertebrae and fin spines in the Snyder quarry assemblage. The smallest specimens are clearly osteichthyan, but due to poor preservation and general features cannot be more specifically identified. The osteichthyan vertebrae are round with pitted surfaces (e.g., NMMNH P-40330—Fig. 3J-L). They are small, ranging from 2 to 3 mm in size. They are ovate on the dorsal face with a round indentation comprising the entire surface. Incomplete zygapophyses are also visible (Fig. 3K). Osteichthyan fin spine fragments are also present in the assemblage (NMMNH P-43572; Fig. 3O). These spines range from 1 to 2 mm in size and are highly textured. The surfaces are often pitted with rounded indentations. Other indeterminate osteichthyan elements include a tiny jaw fragment bearing two tall, but relatively blunt, teeth (NMMNH P-40578—Fig. 3M-N). A much larger notochordal vertebra (NMMNH P-31652—Fig. 5A-C) is clearly that of an osteichthyan but is not identifiable to lower taxonomic levels.

AMPHIBIA Linnaeus, 1758 **TEMNOSPONDYLI Zittel, 1888** **Temnospondyli indet.**

Although temnospondyl amphibians were relatively abundant during the Late Triassic Period, few amphibian microvertebrate fossils have been identified at the Snyder quarry. One tooth (NMMNH P-41824—Fig. 4A) recovered from the Snyder quarry is identified as temnospondyl based on the striations along the outer enamel. Temnospondyls can also be identified based on the infolding (labyrinthodont) of dentine in their teeth. The antero-posteriorly oriented striations on this partially complete tooth suggest an amphibian affinity (Fig. 4A). These striations run parallel along the length of the tooth. The specimen is approximately 1 mm long and moderately rounded. It shows a slight bulge on the lingual (?) side, which may be evidence of recurvature. Due to poor preservation and the lack of other diagnostic features, however, this specimen cannot be identified below Labyrinthodontia indet.

Temnospondyli(?) indet.

Another possible temnospondyl fossil consists of an incomplete vertebral centrum with two transverse processes (NMMNH P-40359; Fig. 4B-C). The centrum is open across the dorsal surface and generally resembles that of an amphibian, particularly a temnospondyl, than any known Upper Triassic reptile.

REPTILIA Linnaeus, 1758 **Reptilia indet.**

There are multiple miscellaneous limb bone elements, scute fragments, and vertebrae that are found in the Snyder quarry matrix. The specimens are clearly reptilian but due to poor preservation and general features, they cannot be more specifically identified. One reptilian scute (P-40378; Fig. 4D-E) with a partial spine has numerous elongated pits along the dermal surface that appear to be oriented along the length of the specimen (Fig. 4D). The spine is conical in shape and projects off of the surface of the scute at a slight angle (Fig. 4E). Two metapodial fragments were identified including the distal end of a phalanx, or finger bone (P-40375; Fig. 4F-G). This phalanx has a large head that tapers into the narrow shaft. The surface of the specimen is dotted with sections of matrix that obscure the bone surface slightly. One reptilian limb bone appears to be the distal end of a small (4 mm) femur (P-40372; Fig. 4H-I, 5F-H). There are two rounded condyles on the apparent distal end of this slender bone. The condyles are not well-developed, and there is little other morphological detail. A similar, but somewhat larger element (NMMNH P-33140—Fig. 5D-E) is noteworthy in that it is extremely elongate, with a distal(?) end with condyles of unequal length, the medial(?) condyle being shorter than the lateral(?) one. Another reptilian limb element appears to be the distal(?) end of a small metapodial (P-40374; Fig. 4J-K). A similar bone (NMMNH P-36066; Fig. 4L-M) appears to represent a second small metapodial. It is laterally compressed and has a relatively flat articular surface that extends farther ventrally than dorsally, but the element is incomplete.

Multiple reptilian vertebrae and vertebral fragments were also found in the Snyder quarry assemblage. One specimen (P-40352) is a vertebral centrum with incomplete neural arches (Fig. 4N-O). The centrum is deeply concave (coelous). No processes are visible on this vertebra. The vertebra clearly pertains to a reptile, as it consists of a centrum and complicated neural arch. Heckert (2004, fig. 97a-c) described a similar, more complete sacral vertebra from the Adamanian Bluewater Creek Formation in west-central New Mexico. A larger sacral centrum (NMMNH P-35979—Fig. 5I-K) is relatively compressed dorso-ventrally, with extensive articulations for sacral ribs.

SYNAPSIDA Osborn, 1903 **CYNODONTIA Owen, 1861**

The one synapsid specimen from the Snyder quarry is the distal end of a left humerus (P-29044—Fig. 5L-M) and is approx-



FIGURE 4. Scanning electron micrographs of amphibians (A-C) and reptiles (D-O) from the Snyder quarry (NMMNH locality 3845). A. Labyrinthodont tooth (P-41824) in occlusal view; B-C, amphibian centrum (P-40359) in B. articular and C. dorsal views; D-E, reptilian osteoderm and partial spine (P-40378) in D. dorsal(?) and E. lateral (?) views; F-G, distal phalanx (P-40375) in F. ventral, and G. lateral view; H-I distal end of a femur (P-40372) in H. lateral, and I. medial views; J-K, distal metapodial(?) (P-40374) in J. lateral and K. ventral views; L-M, distal metapodial(?) (P-36066) in J. dorsal, and K. ventral views; N-O, vertebra (P-40352) in N. articular view; O, lateral views. Scales = 1 mm (A-C, N-O) or 2 mm (D-M).

imately 15 mm in length, recovered during the very first excavation in 1998 and described at length by Zeigler et al. (2003b, fig. 6). The shaft of the humerus is circular with thin walls and the cavity is filled with crystalline matrix inside the shaft. The distal end of the humerus is broad and complex, showing multiple condyles and one foramen. Two condyles are present on the distal end; the ectepicondyle on the lateral side and entepicondyle on the medial side (Fig. 5L). The ectepicondyle is round and thin, projects medially and is concave on the dorsal side of the specimen (Fig. 5L). The entepicondyle has a foramen located just above the condyle surface. The trochlea, a small facet to which the ulna attaches, is well developed and strongly convex. Zeigler et al. (2003b) tentatively identified this specimen as a tritylodont based on its similarity to *Oligokyphus*, first described by Kuhne (1956). There are no synapomorphies of tritylodontids identifiable in the humerus.

DIAPSIDA Osborn, 1903
LEPIDOSAUFORMA Benton, 1983
LEPIDOSAURIA Haeckel, 1866
Lepidosauria indet.

The only lepidosaur specimen present in the Snyder quarry microvertebrate assemblage is a small jaw fragment (P-35971—Fig. 5N-O), approximately 7 mm long, recovered during excavation of macrovertebrates in May, 1999 and described in preliminary fashion by Zeigler et al. (2003b, fig. 9). This particular jaw fragment is encased in matrix which cannot be prepared out without damage to the specimen. The jaw is long and narrow with small rod-like teeth that run perpendicular to the length of the jaw. The teeth are slightly recurved, cylindrical in shape, and moderately closely spaced (0.1 mm) in a groove. The teeth do not appear rooted to the jaw bone as in thecodonts, but are attached to the side of the jaw in pleurodont fashion (Fig. 5O). Sixteen teeth are preserved in this jaw. Although it is a fragmentary specimen, this jaw is referred to a lepidosauromorph, based on its simple cylindrical recurved teeth, long slender jaw bone, and pleurodont implantation (Zeigler et al., 2003b).

ARCHOSAUFORMA Huene, 1946
ARCHOSAURIFORMES Gauthier, 1984

Archosauriformes are the most common reptiles represented in the Snyder quarry assemblage. Multiple archosaur teeth, limb bones, and vertebrae were found including specimens from the clades Parasuchidae, Sphenosuchidae, and Stagonolepididae as well as less determinate remains we here assign to Archosauriformes indet. Heckert (2004) codified a variety of morphotypes for archosauriform teeth from the lower Chinle Group and we use that taxonomic nomenclature to describe teeth here. Godefroit and Cuny (1997) identified several tooth synapomorphies that characterize Archosauriformes, with the caveat that these features are paralleled in numerous non-archosauriform taxa and subject to modification and reversal within the Archosauriformes (Godefroit and Cuny, 1997, p. 5-6). In effect, archosauriform (=Archosauria of Romer, 1956) teeth are thecodont, conical and pointed

medio-laterally, possess anterior and posterior keels and are frequently serrated or, in more derived groups, denticled. Therefore, we identify many morphotypes of reptilian teeth exhibiting these characters as archosauriform.

Several indeterminate archosauriform teeth were discovered in the Snyder quarry microvertebrate assemblage (Fig. 6A-I). The serrated edge and tapered length suggest these teeth are archosauriform. Figure 6A-B shows an incomplete tooth (NMMNH P-40347) with one serrated tooth edge. Approximately 2.5 mm tall (basal-apically), this tooth conical to somewhat recurved. The tooth tapers toward the tip and narrows into an edge along the serration. The tooth bears a rough texture of ripple marks, and these marks are oriented along the labial faces of the tooth and oriented along the long axis. These marks are likely remnants of enameloid present on the tooth outer surface. Following Heckert (2004), this is an archosauriform morphotype G tooth, which Heckert (2004) also reported from both Kalgary microvertebrate localities in the Tecovas Formation of West Texas as well as the Krzyzanowski bonebed from the Blue Mesa Member of eastern Arizona.

ARCHOSAURIA Cope, 1869
CROCODYLOTARSI Benton and Clark, 1988
PHYTOSAURIDAE Jaeger, 1828

Phytosaurs are the most commonly recovered vertebrate fossils from the Snyder quarry, but most phytosaur fossils are in the macrovertebrate size range. A morphotype I phytosaurid tooth is present in the microvertebrate assemblage of the Snyder quarry (NMMNH P-41836—Fig. 6C-D). Morphotype I, as defined by Hunt (1994) and used by Heckert (2001, 2004) is a tall, weakly recurved tooth with extremely fine serrations. The phytosaurid tooth from the Snyder quarry is long and cylindrical in shape, with faint serrations on both lateral edges. The serrations are extremely fine and appear to have wear facets. This tooth probably pertains to a juvenile phytosaur, but is small enough that it may represent a small archosauriform of uncertain affinities, not necessarily a phytosaur.

AETOSAURIA Nicholson and Lydekker, 1889
STAGONOLEPIDIDAE Lydekker, 1887
Stagonolepididae? indet.

Zeigler et al. (2003b, fig. 5) identified a single tooth (NMMNH P-36067; Fig. 6E-F) as a procolophonid from the Snyder quarry. We revise this assignment, as the tooth in question is relatively simple and proportionately tall for a procolophonid. Furthermore, it possesses denticles along the mesial face, a feature more characteristic of archosauriforms than anapsids. The tooth is relatively low, blunt, and bulbous compared to most Triassic archosauriforms, but actually compares well with teeth of aetosaurs, especially those of *Desmatosuchus* (Small, 1985, 1989, 2002). Therefore, we consider this tooth a likely stagonolepidiid, not a procolophonid.

Another probable aetosaur tooth is present in the Snyder quarry (Fig. 6G-H). The tooth is fragmentary, however, one

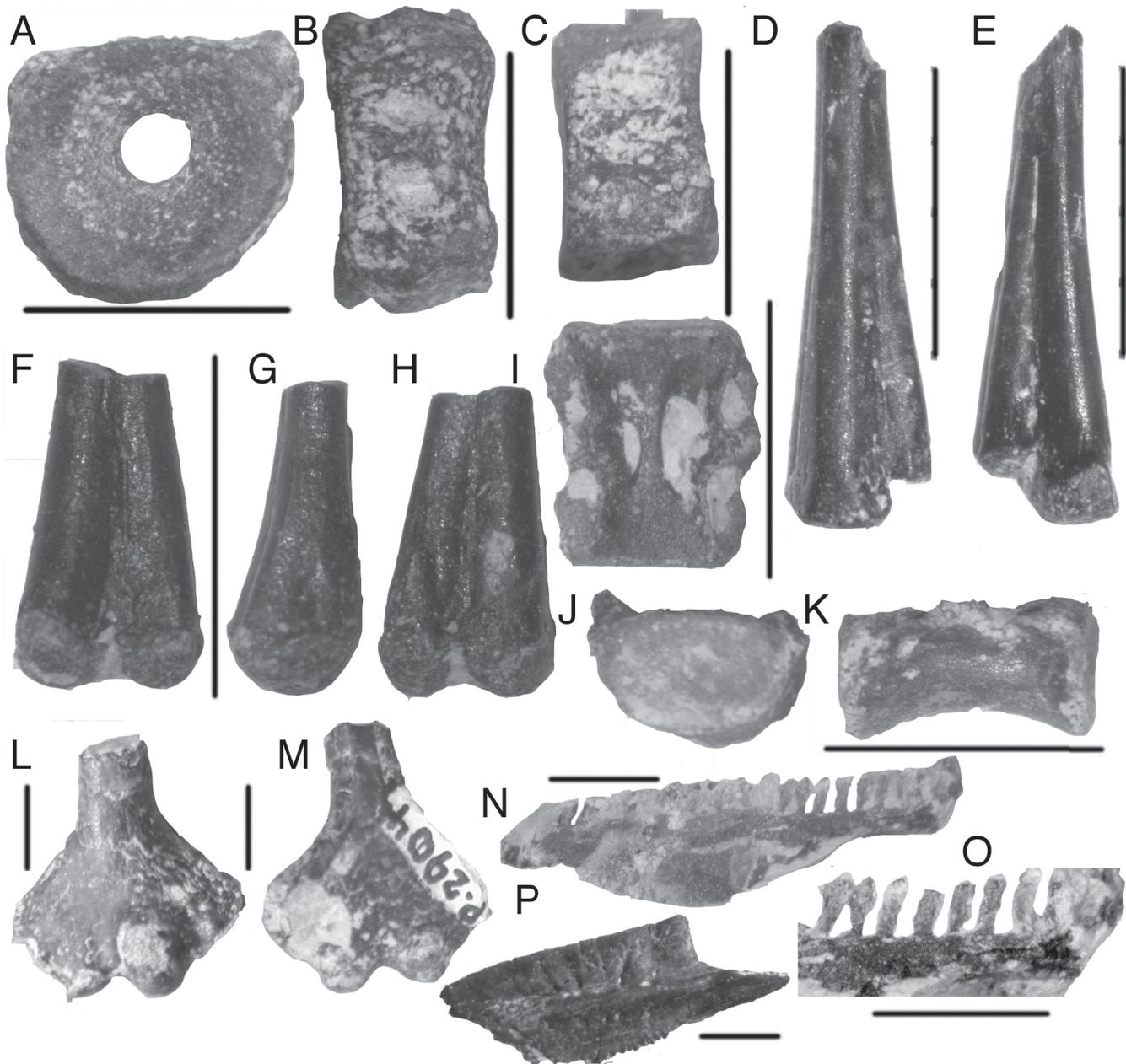


FIGURE 5. Digital photographs of amniotes from the Snyder quarry. **A-C**, Osteichthyan centrum (P-31652) in **A**. articular, **B**. dorsal, and **C**. lateral views; **D-E**, reptilian distal femur(?) (P-33140) in **D**. anterior(?) and **E**. posterior(?) views; **F-H**, reptilian distal femur(?) (P-40372) in **F**. anterior, **G**. lateral, and **H**. posterior views; **I-K**, reptilian sacral centrum (P-35979) in **I**. dorsal, **J**. articular, and **K**. lateral views; **L-M**, cynodont left distal humerus (P-29044) in **L**. dorsal view, and **M**. ventral view; **N-O**, lepidosauromorph jaw fragment (P-35971) in **N**. labial(?) view **N**. overview, and **O**. close-up of dentition; **P**. sphenosuchian scute (P-30772) in dorsal view. All scales equal 5 mm except N-O = 2 mm.

serrated edge is present (NMMNH P-40348—Fig. 6G-H). The tooth itself is conical (very slightly backswept) and serrated. This serrated edge shows multiple wear facets (Fig. 6H). The tooth retains the enameloid outer edge and has long ridges which run parallel along the length of the tooth. Some of these ridges curve upward toward the serrations toward the base of the tooth. Serrations (denticles) are unusual in aetosaurs, but are known in some taxa (Walker, 1961; Heckert and Lucas, 2000; Small, 2002). The partial tooth is roughly triangular in shape, with a bulbous base

that tapers toward the tip of the tooth. This specimen is referred to Stagonolepididae based on the worn, serrated edge, tapered shape, and ridges of enamel. One of the more intriguing aspects of this tooth is the apparent wear facet along its serrated edge (Fig. 6H). The wear facet lies along the ridge of the serration creating a small cavity in the serration row.

Aetosaurs possess a remarkably reduced dentition consisting primarily of simple conical weakly recurved teeth (Walker, 1961; Heckert and Lucas, 2000). Because aetosaurs have such

reduced and simplistic dentitions, their teeth are relatively rare, and seldom identified in Upper Triassic microvertebrate collections, but they are present in the fauna from the Snyder quarry.

Sphenosuchidae?

A relatively large (22 mm) sphenosuchian scute (NMMNH P-30772—Fig. 5P) was found at the Snyder quarry and described and illustrated by Zeigler et al. (2003b, fig. 11). This scute contains a distinctive ridge projecting off of the dorsal face (Fig. 5P). The ridge is oriented along the long axis of the scute and extends from the center of the prong to the anterior end of the scute. There are two rows of round pits that run along each side of the ridge. The straight, pointed, cylindrical prong projects off the posterior edge of the scute. Multiple grooves radiate out from the ridge and run parallel to one another along the face of the scute. The narrow, elongate shape and distinctive posterior prong identify this scute as sphenosuchian instead of a phytosaur or aetosaur (Parrish, 1994; Zeigler et al., 2003b).

“MISSING” TAXA AND THE BIOCHRONOLOGY OF THE SNYDER QUARRY

In spite of extensive collecting efforts, several taxa that are otherwise typical of Revueltian faunas in the Chinle Group have not been recovered from the Snyder quarry. Characteristic Revueltian taxa “missing” from the Snyder quarry assemblage include the dipnoan *Arganodus*, the metoposaur *Apachesaurus*, the aetosaur *Aetosaurus* and the putative ornithischian *Revueltosaurus callenderi*. Most of these taxa are probably absent because of taphonomic and/or ecological effects, but there may be some stratigraphic, and therefore biochronological implications to the absence of *Revueltosaurus callenderi*.

Taphonomic bias almost certainly accounts for the absence of *Arganodus*, as the depositional environment of the Snyder quarry (topographic low or pond in a fluvial system; e.g., Tanner et al., 2003; Zeigler, 2002, 2003) may simply have been wetter than the intermittently dry facies that typically yield lungfish fossils.

Apachesaurus is the most commonly recovered Revueltian metoposaur, yet all the temnospondyl fossils recovered from the Snyder quarry, including the labyrinthodont tooth documented here, are too large to pertain to *Apachesaurus* and instead appear to pertain to *Buettneria*. Indeed, of more than 1,182 specimens recovered and catalogued from the Snyder quarry, not one is definitely referable to *Apachesaurus*, nor are any known *Apachesaurus* specimens in the hundreds of bones that have been tentatively identified and are currently awaiting preparation. This absence is puzzling, as *Apachesaurus* often co-occurs with other typical Revueltian microvertebrates (Long and Murry, 1995; Hunt, 2001) and its stratigraphic range extends into the Apachean (Hunt, 1993). Locally, such as at Dinosaur Hill in the Petrified Forest National Park, *Apachesaurus* even dominates some Revueltian tetrapod assemblages (ABH, pers. obs.), so its absence at the Snyder quarry is difficult to explain.

Aetosaurus is not common in North America, even though it has been documented at several sites (Heckert and Lucas, 1998;

Small, 1998), and its small, delicate scutes may be absent due to the taphonomy of transport, burial, and subsequent excavation. Hunt (2001) considered the absence of *Aetosaurus* in stratigraphically higher exposures of the Bull Canyon Formation biostratigraphically significant. However, the *Aetosaurus* specimens described by Small (1998) appear to come from an interval roughly equivalent to that of the Snyder quarry in the upper Painted Desert Member of the Petrified Forest Formation in Colorado. Given the taphonomic and stratigraphic variables, it is difficult to ascribe biostratigraphic significance to the absence of *Aetosaurus* in the Painted Desert Member of the Chama Basin.

The putative ornithischian dinosaur *Revueltosaurus callenderi* is readily identifiable from isolated teeth and is known from diverse localities of Revueltian age in the American Southwest (Hunt, 1989, 2001; Padian, 1990; Long and Murry, 1995; Heckert, 2002). Indeed, it appears to be an index taxon of the Revueltian (Hunt and Lucas, 1994; Lucas, 1998; Heckert, 2002), although Parker et al. (pers. comm.; in review) have identified additional material that suggests that *R. callenderi* is actually a crurotarsan, not a dinosaur. Like *Apachesaurus*, *Revueltosaurus* often co-occurs with diverse other Revueltian taxa. However, unlike *Apachesaurus*, *Revueltosaurus* does not occur in younger (Apachean) strata. It is therefore possible that the Snyder quarry is a deposit in strata somewhat younger than the last appearance of *R. callenderi*. This hypothesis is, admittedly, based on the lack of age-diagnostic taxa, and thus weaker than a hypothesis based on the presence of an index taxon. We note the complete lack of *Revueltosaurus* fossils in this otherwise extremely fossiliferous interval of the Painted Desert Member in the Chama Basin.

Indeed, Hunt (2001) proposed subdividing the Revueltian lvf into an older, Barrancan (R1) interval and a younger, Lucianoan (R2) interval (a thought first documented in Lucas and Hunt, 1993 and Lucas, 1997). If this is valid, the Snyder quarry and other localities at this stratigraphic level in the Chama Basin may represent the equivalent of Hunt's (2001) Lucianoan sub-lvf of the Revueltian. Hunt (2001) indicated that he thought the Canjilon quarry was in this stratigraphic interval, as were Kirby's (1989, 1991, 1993) Owl Rock localities. Although we have not found any of Hunt's (2001) putative Lucianoan index taxa (principally *Lucianosaurus wildi* and *Pseudotriciconodon chatterjeei*, both microvertebrates only known from their type locality), the fauna of this interval is similar to that predicted by Hunt's hypothesis. That is, the Chama Basin Painted Desert Member lacks typical Barrancan taxa such as *Revueltosaurus*, *Aetosaurus*, and the rauisuchian(?) *Shuvosaurus*. However, we note that if the Chama Basin fauna is indeed Lucianoan in age, then *Desmotosuchus*, specifically *D. chamaensis* is now known from both the Barrancan (R1) and Lucianoan (R2) sub-lvfs.

TAPHONOMY

Zeigler (2002, 2003; see also Tanner et al., 2003) studied the taphonomy of the macrovertebrates found in the Snyder quarry and concluded that the macrovertebrate fossils were deposited locally and rapidly buried as part of one fauna. Furthermore, based on analysis of abundant fossilized charcoal throughout the

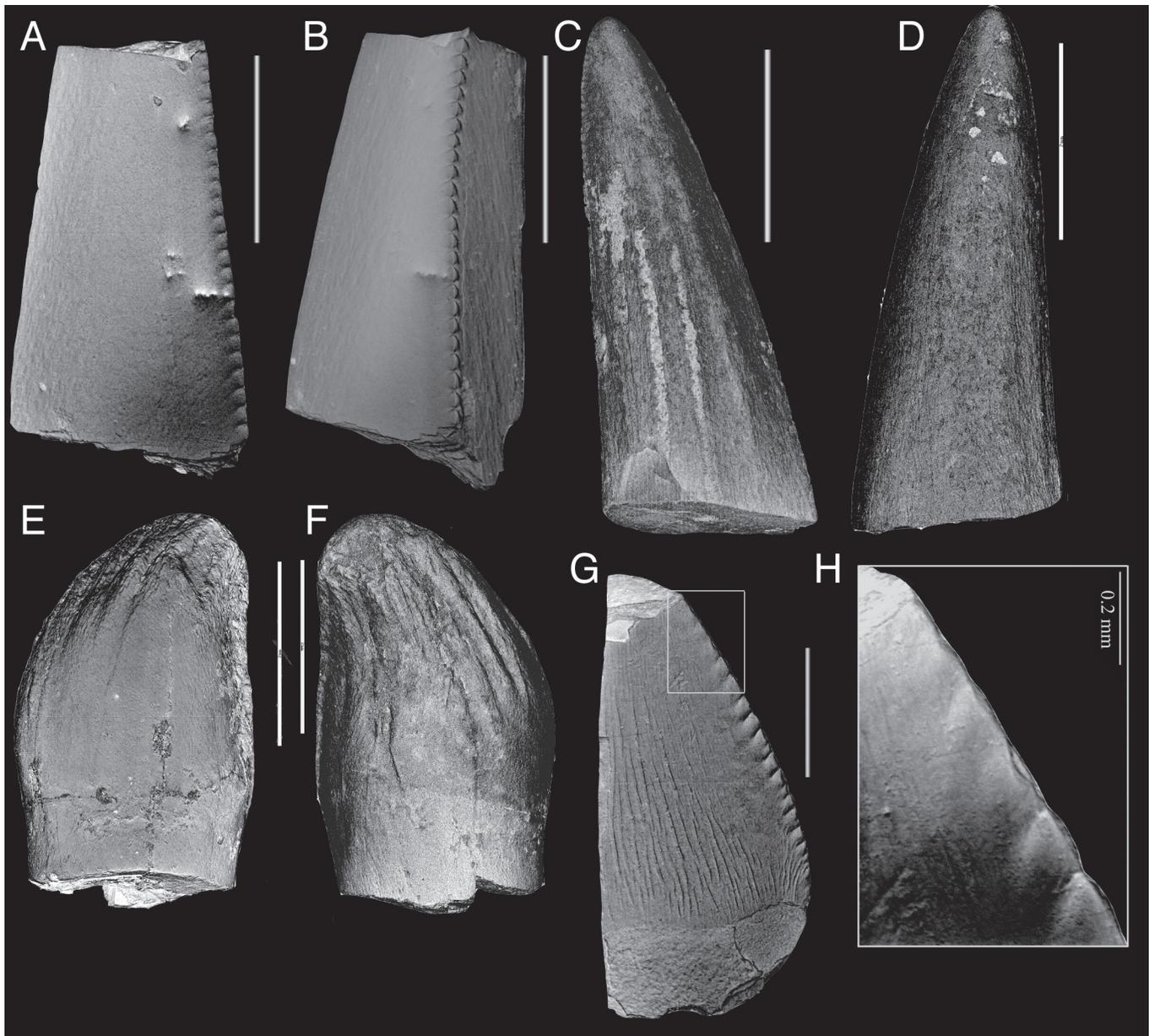


FIGURE 6. Scanning electron micrographs of archosauromorphs from the Snyder quarry (NMMNH locality 3845). **A-B**, indeterminate archosauriform tooth (P-40347) in **A**. labial and **B**. mesio-distal views; **C-D**, phytosaur type I tooth (P-41836) in **C**. mesio-distal, and **D**. labial views; **E-F**, aetosaur tooth (P-36067) in **E**. labial and **F**. lingual views; **G-H**, aetosaur tooth (P-40348) in **G**. labial, and **H**. close-up views. All scales = 2 mm except H = 200 microns.

bonebed and surrounding area at the same stratigraphic level, Zeigler (2003) suggested that the assemblage documents a catastrophic wildfire. During our studies we compiled observations on the microvertebrates, including the elements preserved and their condition. We note here that the microvertebrate assemblage, which consists principally of vertebrate fossils less than 1 cm in maximum dimension, is part of the same “fauna,” in that the microvertebrates are found in the same deposit as the macrovertebrates. However, micro- and macrovertebrate assemblages from the same locality do not necessarily share the same taphonomic history. For example, some microvertebrate assemblages clearly represent attritional deposits that developed over a rela-

tively long period of time (e.g., the “Dying Grounds” in Petrified Forest National Park—Murry and Long, 1989; Heckert, 2004) that may or may not coincide with the deposition of the associated macrovertebrate fauna. Furthermore, because it is relatively easy to rework microvertebrates, it is important to document their taphonomy to test the hypothesis that the macro- and microvertebrates do in fact represent a single assemblage in geological time and space. Here, we consider the preservation, including condition, completeness, weathering, and composition of the microvertebrate elements from the Snyder quarry and compare these characteristics to the taphonomic analysis of Zeigler (2002, 2003) and depositional model of Tanner et al. (2003).

Regarding condition, microvertebrate fossils from the Snyder quarry, like the macrovertebrates documented by Zeigler (2002, 2003), show no evidence of bone abrasion, and so were not transported for a long period of time or over a long distance (Shipman, 1981). Although the microvertebrates in the quarry are completely disarticulated, they do not appear worn or otherwise damaged. The teeth, vertebrae, and limb bone elements documented here still possess delicate serrations, processes, and articulation facets (Figs. 2-6). The broken surfaces of bones are not worn and rounded, and instead appear as sharp breaks in the bone, many of which are probably the result of matrix collection and screenwashing (e.g., Fig. 4H-I, L-M). The lack of abrasion on the microvertebrates suggests that they, like the macrovertebrate fossils, were only transported a short distance (10-100 meters) (Zeigler, 2003).

Furthermore, the microvertebrates in the Snyder quarry do not show evidence of cracking or flaking, suggesting they were not subaerially exposed for more than a few months or years. Indeed, given the small size of the specimens, their essentially unweathered condition suggests that they were deposited within days or weeks of death and disarticulation (e.g., Behrensmeyer, 1978). Because the specimens are all essentially unweathered, it suggests that they were deposited at the same time, as the main bone bed is clearly a relatively high-energy deposit. Furthermore, the elements documented here lack puncture marks or scratches, typically considered evidence of scavenging (Shipman, 1981). Indeed, the microvertebrates in the Snyder quarry assemblage appear pristine, showing no evidence of weathering or scavenging. Furthermore, they do not show any evidence of being digested, such as stripping of enamel from teeth or pitting of bone surfaces, both of which are indicative of passing through the digestive tract of carnivores (Fisher, 1981; Rensberger, 1987; Rensberger and Krentz, 1988).

The depositional horizon that contains the macrovertebrate assemblage is ~30 cm thick (Tanner et al., 2003), and this interval was sampled for microvertebrates both by screenwashing matrix from jackets as they were prepared and by collecting sediment for screenwashing at or near the bone layer during excavations in 1999. This narrow band of strata shows a high concentration of fossils (principally macrovertebrates) that abruptly ends as a new layer of mudstone begins. This thin layer containing a rich fossil assemblage is highly suggestive of instantaneous deposition rather than an attritional process. If the assemblage were an attritional deposit, the fossils would likely show varying degrees of abrasion, weathering, and depositional layering. Because the fossils show essentially no abrasion, weathering, or scavenging, and are deposited in a concentrated region, it is more likely that the bones were laid down in the same depositional event.

One of the most important aspects of the microvertebrate assemblage at the Snyder quarry is its rather unique composition. The two most commonly recovered identifiable elements in most Upper Triassic microvertebrate assemblages, particularly those in the Chinle Group, are fish scales and vertebrate teeth (Murry and Long, 1989; Hunt and Lucas, 1993; Kaye and Padian, 1994; Heckert, 2004). Typically, more aquatic localities yield more scales, while more terrestrial assemblages are dominated by rep-

tile teeth (Hunt and Lucas, 1993; Heckert, 2001, 2004). This is obviously at least in part a bias of the fossil record—a single disarticulated fish can yield several hundred scales, and most Triassic vertebrates continually shed teeth, also potentially contributing dozens, and in the case of phytosaurs, hundreds of teeth to the fossil record. Additionally, scales and teeth are relatively durable, and thus may survive in the environment longer than other elements. Therefore, although fish scales are a common component of the Snyder quarry microvertebrate assemblage, vertebrate teeth are surprisingly rare. Indeed, unlike the vast majority of Chinle microvertebrate sites, which yield many more identifiable teeth than bones (Heckert, 2001, 2004), the Snyder quarry microvertebrate assemblage actually yields more isolated bones than identifiable teeth. We ascribe this taphonomic difference to different modes of accumulation. Therefore, we hypothesize that the unusually high abundance of microvertebrate bones relative to teeth and scales is taphonomically significant at the Snyder quarry.

Zeigler (2002, 2003) and Tanner et al. (2003) well documented the rapid accumulation of the macrovertebrate assemblage of the Snyder quarry. As we noted previously, the microvertebrate elements share characteristics with the macrovertebrate elements (lack of weathering, abrasion, and evidence of scavenging) that suggest rapid deposition. We also hypothesize that the relative abundance of microvertebrate limbs and vertebrae and the corresponding paucity of teeth indicate a catastrophic origin for the microvertebrate assemblage. That is, we hypothesize that, like the macrovertebrate assemblage, the microvertebrates were caught up in the fire documented by Zeigler (2002, 2003; Tanner et al., 2003) or its immediate after effects. Consequently, the microvertebrate assemblage consists of the disarticulated remains of numerous skeletons from a single geological instant rather than the time-averaged, attritional deposition of isolated teeth that typifies roughly contemporaneous microvertebrate assemblages throughout the American Southwest. We note that this hypothesis explains both the preservation and composition of the microvertebrate assemblage in addition to supporting the paleowildfire hypothesis of Zeigler (2002, 2003; Tanner et al., 2003).

This distribution of microvertebrate elements does not depend on whether a site is solely a microvertebrate assemblage or a mixed microvertebrate and macrovertebrate assemblage. That is, in typical Upper Triassic microvertebrate assemblages in the American Southwest, teeth and scales outnumber identifiable bones regardless of whether macrovertebrates are present. Thus, in principally microvertebrate assemblages such as the Kalgary localities in Texas (Murry, 1982, 1986, 1989a; Heckert, 2001, 2004), the Ojo Huelos beds at Hubble Bench in central New Mexico (Heckert, 2001, 2004; Heckert and Lucas, 2002), Shark Tooth Hill in eastern New Mexico (Murry, 1989a; Hunt and Lucas, 1993b) and Stinking Springs, eastern Arizona (Polcyn, 2002), teeth and scales outnumber identifiable bones. The same is true of diverse macrovertebrate quarries later sampled for microvertebrates, including the *Trilophosaurus* quarries (Murry, 1982, 1986, 1989a; Heckert, 2001, 2004) and Rotten Hill (Murry, 1982, 1986, 1989a) in Texas and the *Placerias* quarry (Jacobs and Murry, 1980; Tannenbaum, 1983; Murry, 1987; Kaye and Padian,

1994) and “Dying Grounds” in Arizona (Murry, 1989b; Murry and Long, 1989; Heckert, 2001, 2004).

The taphonomy of the microvertebrate fossils in this assemblage thus yields similar trends to those discovered by Zeigler (2002, 2003) in her analysis of the macrovertebrate fauna of the Snyder quarry. Therefore, taphonomic analyses of both the macro- and microvertebrate fauna of the Snyder quarry suggest the fauna were part of one paleoenvironment and were deposited essentially instantaneously during an apparently catastrophic event.

SIGNIFICANCE

There are several key results of this study that we elaborate here. These include: (1) screenwashing even a well-studied vertebrate locality does indeed increase the known taxonomic diversity from the site; (2) the faunal assemblage from the Painted Desert Member in the Chama Basin may in fact represent a “Lucianoan,” or at least younger Revueltian assemblage than the type assemblage; and (3) microvertebrate assemblages, if properly analyzed, can lend additional insight into the taphonomy of known sites.

Regarding new records, both the palaeoniscid fish aff. *Turseudus* and the hybodont shark *Lonchidion*, represent two taxa not previously identified at the Snyder quarry. Amphibians are rare in the Snyder quarry microvertebrate assemblage and are represented by a few teeth and vertebral fragments, including one metoposaurid centrum, but another vertebra from the site may also represent a temnospondyl not known from the macrovertebrate assemblage. Reptiles dominate the terrestrial microvertebrate assemblage. As in the macrovertebrate assemblage, multiple phytosaur, aetosaur, and indeterminate archosauriform tooth fragments are present in the microvertebrate assemblage. Numerous reptilian limb bones and vertebrae were also discovered, and indeed these, while less diagnostic, outnumber the identifiable teeth from the assemblage. Many of these probably represent small amniotes not sampled in the macrofossil assemblage.

The biostratigraphy of the Snyder quarry and the numerous other localities at the same stratigraphic level is both simple and complex. At the simplest level, the macrovertebrate assemblage clearly indicates a Revueltian age, based on the presence of the phytosaur *Pseudopalatus buceros* and *Typhorax coccinarum*. More difficult to assess is whether it may pertain to Hunt’s (2001) Lucianoan sub-lvf. We tentatively suggest that it does. While Hunt (2001) listed some of the biases and other problems inherent in identifying the Lucianoan sub-lvf, we note that the long history of collecting in the Chama Basin effectively comprises a test of Hunt’s (2001) biostratigraphic hypothesis, and the absence of identifiable *Revueltosaurus* teeth from this stratigraphic interval, the upper Bull Canyon Formation and the Owl Rock Formation corroborates at least part of his biostratigraphic hypothesis.

Finally, the taphonomic data associated with the microvertebrate fauna of the Snyder quarry corroborates the macrovertebrate taphonomy particularly well. Thus, the microvertebrate assemblage corroborates Zeigler’s (2002, 2003; Tanner et al., 2003) hypothesis of a paleowildfire that resulted in catastrophic mortality and rapid deposition not only of the macrovertebrate

fauna, but the microvertebrate fauna as well. Thus, while it is not possible to unambiguously implicate the wildfire in the death burial of the vertebrate fauna, the wildfire, the death and disarticulation of the vertebrates, and the subsequent burial of burned wood and vertebrate remains are clearly closely linked in time.

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