Taphonomic analysis of a fire-related Upper Triassic vertebrate fossil assemblage from north-central New Mexico

Kate E. Zeigler, Andrew B. Heckert, and Spencer G. Lucas

2005, pp. 341-354. https://doi.org/10.56577/FFC-56.341

in:

Geology of the Chama Basin, Lucas, Spencer G.; Zeigler, Kate E.; Lueth, Virgil W.; Owen, Donald E.; [eds.], New Mexico Geological Society 56th Annual Fall Field Conference Guidebook, 456 p. https://doi.org/10.56577/FFC-56

This page is intentionally left blank to maintain order of facing pages.

TAPHONOMIC ANALYSIS OF A FIRE-RELATED UPPER TRIASSIC VERTEBRATE FOSSIL ASSEMBLAGE FROM NORTH-CENTRAL NEW MEXICO

KATE E. ZEIGLER[1], ANDREW B. HECKERT[2] AND SPENCER G. LUCAS[2]
[1]Dept. of Earth & Planetary Science, University of New Mexico, Albuquerque, NM 87131
[2]New Mexico Museum of Natural History, 1801 Mountain Rd. NW, Albuquerque, NM 87104

Abstract.—The Snyder quarry is an Upper Triassic bonebed located in north-central New Mexico. The locality is stratigraphically high in the Petrified Forest Formation of the Chinle Group, and tetrapod biostratigraphy places it in the Revueltian land-vertebrate faunachron (mid-Norian in age: 210-215 Ma). This site has yielded the remains of a wide variety of organisms, ranging from terrestrial and aquatic vertebrates to aquatic invertebrates, as well as a substantial volume of charcoalified wood. A taphonomic analysis of both the biological material and the associated sediments indicates that the bonebed is the result of a catastrophic mass mortality event. The sediments of the bonebed contain rip-up clasts from the surrounding floodplain, a significant portion of the bone and wood is aligned, there is a high density of bones over a large area, and a moderate degree of hydraulic sorting of the skeletal material, indicating brief transport and rapid deposition of the bonebed. There is no evidence of abrasion on the bones, indicating that transport was minimal. The skeletal material is associated, with no evidence of substantial weathering or vertebrate scavenging, reflecting a rapid burial of partially dissociated carcasses. A survivorship curve constructed for the phytosaurs, the dominant taxonomic group, shows a thanatocoenosis that matches the biocoenosis for a reptile population. Scanning electron microscopy of the charcoalified wood reveals that the internal structure of the cell walls has been homogenized, and the reflectance of the charcoal is significantly higher than that of other forms of plant fossil preservation. These two pieces of data are evidence that the wood was burned in a moderate temperature (300-450°C) ground fire. Thus, both the sedimentological and biological data from the Snyder quarry best fit the scenario of a catastrophic, Late Triassic wildfire.

INTRODUCTION

The Snyder quarry is an exceptionally productive and diverse Upper Triassic bonebed located in north-central New Mexico, in the Chama River basin, near the town of Abiquiu (Fig. 1) (Heckert et al., 1999a, b). The locality was discovered in 1998 by an amateur fossil hunter, Mark Snyder, and was extensively excavated from then through the summer of 2001 by crews from the New Mexico Museum of Natural History (NMMNH). The Snyder quarry has produced a rich array of fossil remains. Archosaurs dominate the bonebed, and include coelophysoid dinosaurs, two genera of aetosaurs, rauisuchians, and phytosaurs. Rarer taxa include a possible procolophonid, metoposaurid amphibians, semionotid fish, a decapod, a conchostracan, and unionid bivalves. There is also a significant quantity of charcoalified wood, which is an unusual occurrence in nonmarine Upper Triassic strata. The geologic and biological data retrieved from excavations of the Snyder quarry provide evidence of a catastrophic event. The presence of the charcoal, when combined with the other data, indicates that a wildfire or series of wildfires occurred. Abbreviations: NMMNH = New Mexico Museum of Natural History, Albuquerque; UCMP = University of California Museum of Paleontology, Berkeley.

STRATIGRAPHY AND AGE

The Snyder quarry is stratigraphically high in the Painted Desert Member of the Petrified Forest Formation of the Upper Triassic Chinle Group (Fig. 1). The designation of Chinle Group is used here following Lucas (1993) and Lucas et al. (1997), wherein the Chinle Formation was raised to group status in order to unify the lithostratigraphic nomenclature of nonmarine Upper Triassic strata in the western United States. The quarry is approximately 60 m below the base of the Middle Jurassic Entrada Sandstone. This horizon is approximately stratigraphically equivalent to the famous Canjilon phytosaur quarry, 4 km to the east, which was excavated by Charles Camp for the UCMP in 1930 and 1933. Based on the presence of the phytosaur *Pseudopalatus* and the aetosaur *Typothorax coccinarum*, the Snyder quarry is late Revueltian (mid-Norian) in age (Lucas, 1998, 1999) and thus is approximately 210-215 million years old.

LITHOSTRATIGRAPHY

The main bone-bearing horizon of the Snyder quarry (Level 1) is less than 30 cm thick and consists of a greenish-gray, intraformational, mud-clast conglomerate that becomes finer-grained upward and grades into a greenish silty mudstone (Fig. 2). The conglomerate is dominantly a sandy mudstone that is yellowish gray (5Y 7/2), with approximately 20% clasts. This conglomerate has a sharp, erosional contact with the underlying unit and has locally scoured the lower unit away completely.

A second conglomerate (Level 2) lies approximately 60 cm above the mudstone. This conglomerate is not as well defined as the underlying main horizon, and interfingers with silty mudstones. This conglomerate also fines upward into a pebbly to silty mudstone that is locally laminated and in places shows evidence of soft-sediment deformation in the form of disrupted laminae and pockets of pebbles. Overlying the laminated mudstones is a third conglomerate (Level 3) that is almost one meter thick, with

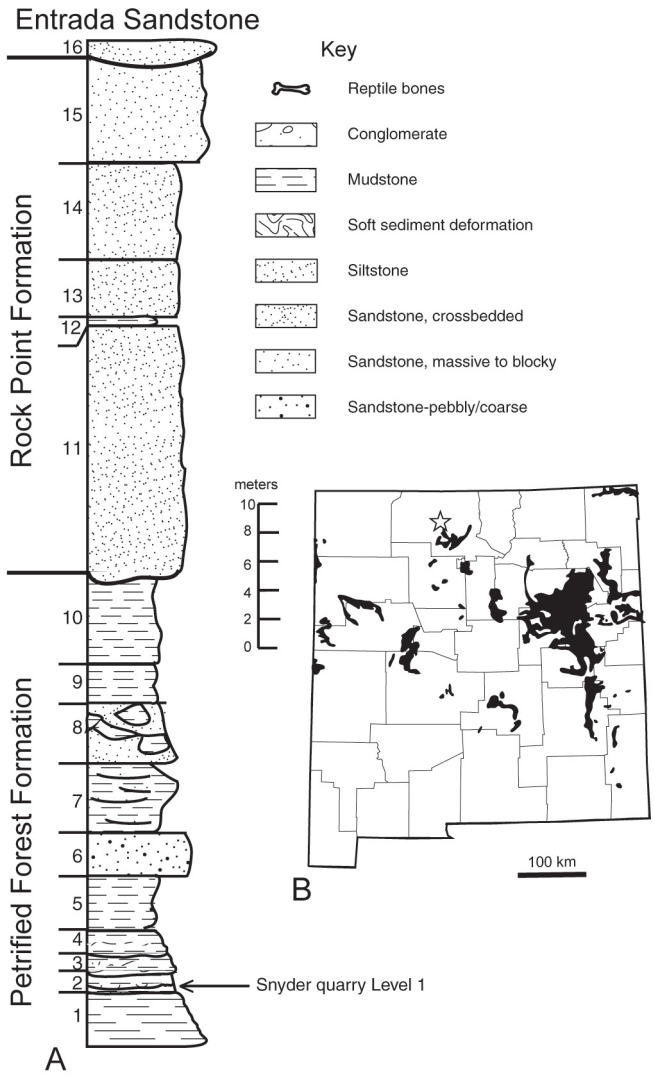

FIGURE 1: Location and stratigraphy of the Upper Triassic Snyder quarry. A. Stratigraphic column of the Upper Chinle Group in the Chama basin, showing the stratigraphic position of the Snyder quarry main level. B. Distribution of Triassic strata in New Mexico (star denotes the location of the Snyder quarry, NMMNH L-3845) (after Heckert et al.,

sharply defined upper and lower contacts. Very faint crossbed sets are evident in the northwestern face of this unit, and they dip between 10 and 20° to the northeast.

The main bonebed conglomerate-mudstone package is interpreted as a channelized flow (conglomerate) grading into overbank deposits (fine-grained strata) (Blakey and Gubitosa, 1984; Kraus and Middleton, 1987; Dubiel, 1989). This unit is overlain by two more sequences of coupled conglomerate and mudstone. The laminated mudstone in the second sequence is interpreted as a small lake or pond deposit based upon the presence of the laminae, the soft-sediment deformation seen in these laminae as well as the presence of conchostracans, which live in standing water. The uppermost of the three conglomeratic beds is most likely a channel deposit as indicated primarily by the presence of the crossbeds. Early in the excavation of the quarry, it was evident that there was substantial depositional dip and topographic irregularity associated with levels 1 and 2, so that both are truncated to the east by the more nearly horizontal level 3.

TAPHONOMY

Sedimentological evidence

Lithology

The sediments of the main bonebed are an intraformational, mud-pebble conglomerate with abundant calcareous mudstone rip-up clasts; the bed has a sharp, irregular (erosional) base. There are areas within the conglomerate where there is a higher concentration of clasts, leading to a clast-supported fabric. These rip-up clasts range in size from 1 to 3 cm in diameter and are well rounded. Some of the rip-up clasts are nearly spherical, whereas others are elongate or flattened. These elongate clasts are pieces of fine-grained limey mudstone that are similar in texture and composition to the floodplain sediments of surrounding Chinle strata. The rip-up clasts thus were probably scoured up from the underlying mudstone unit and incorporated into the bonebed deposit. The presence of rounded clasts of floodplain material are evidence of a strong current of water crossing the floodplain, scouring out pieces of the underlying sediments, and transporting these rip-ups into a topographic low (Kraus and Middleton, 1987). The matrix of this conglomerate is a mix of illitic clays and detritial quartz. Both the presence of the mud rip-up clasts and the coarseness of the matrix indicate a powerful current that was carrying a very wide range of grain sizes (Voorhies, 1969).

The three intraformational conglomerates are the only remnants of paleochannels in the area, and little fossil material has been recovered outside of the conglomerates. Alluvial stratigraphy models (e.g., Allen, 1978; Leeder, 1978; Bridge and Leeder, 1979; and Friend et al., 1979) show that rapid sedimentation, coupled with limited reworking of sediments, reduces the density and connectedness of channel sandstones, which favors simple ribbon sandstone and abundant mudstone deposits. Rapid sedimentation rates would also inhibit paleosol development and favor low bone densities in floodplain deposits (Aslan and Behrensmeyer, 1996).

Bone abrasion

The deposit of bones and wood at the Snyder quarry can be examined from a sedimentological standpoint, treating the bones and wood as clasts affected by transport processes. Whereas the mud rip-up clasts are well rounded, indicating some degree of transport, the bones show no signs of abrasion (stage 0-1 of Cook, 1995; see also Fiorillo, 1988). Small, delicate processes are still present on many bones, and on those where they have been broken off, the fracture joint is not rounded down or worn smooth. The vast majority of the bones in the deposit thus are in excellent preservational condition (Fig. 3). If these bones had been acting as clasts in a flow of water for a long period of time, or over a

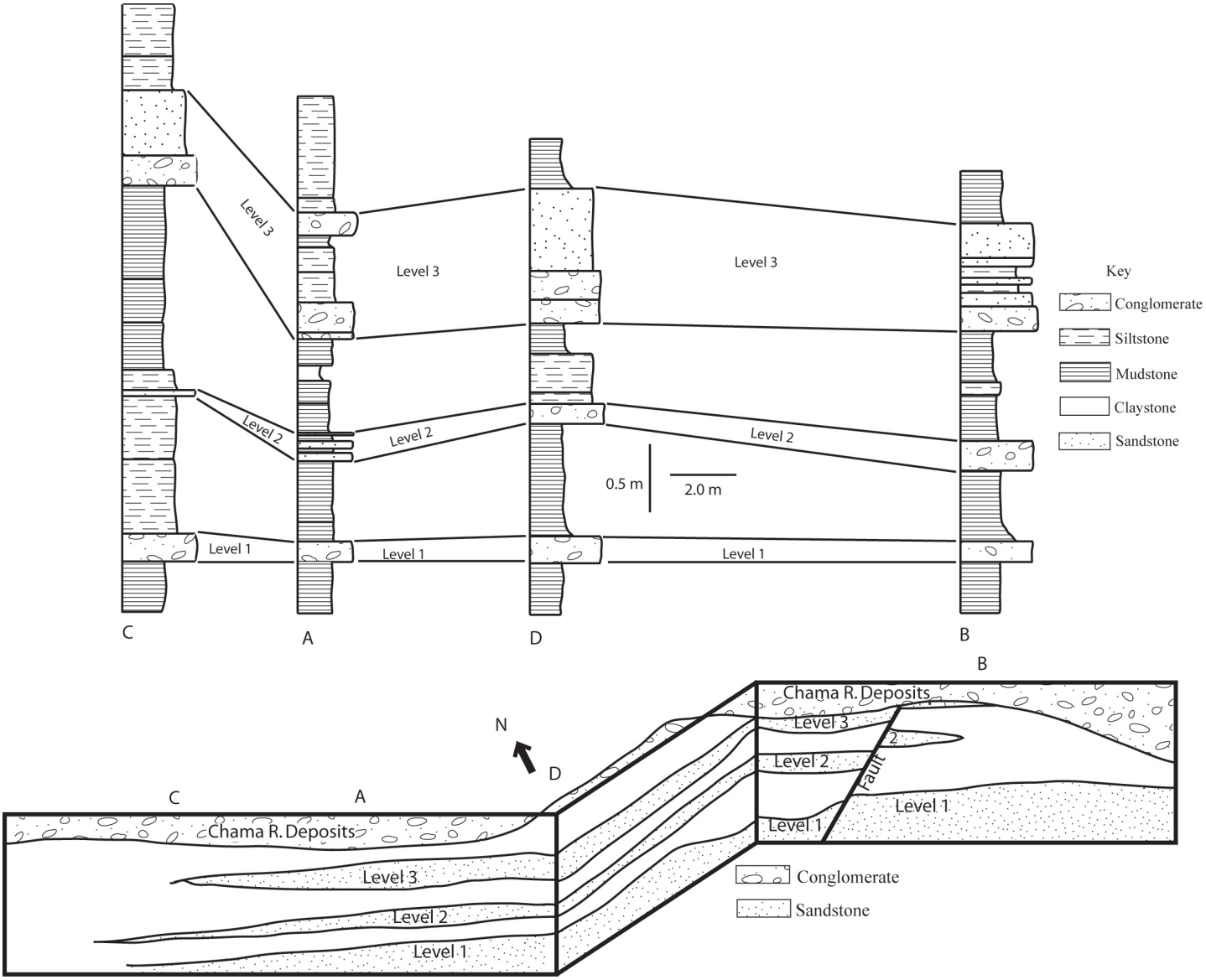

FIGURE 2: Detailed stratigraphy of the Snyder quarry. A. Microstratigraphic columns for the Snyder quarry. B. Block diagram of the quarry walls, showing relationships of three bone-bearing levels. Positions of microstratigraphic columns are marked along the top of the quarry wall.

long distance (km), the surfaces of the bones would be pitted, and delicate bone structures would be broken off or rounded down (Behrensmeyer, 1975; Shipman, 1981; Fiorillo, 1991).

The alignment of bones and the disarticulation of skeletons at the Snyder quarry strongly suggests some fluvial transport of the bones. However, the lack of clear signs of abrasion on the bones indicates that they were not transported a long distance, but probably only a few tens of meters. Indeed, most broken elements are found with their counterparts nearby. However, it should be noted that in a series of experiments in the East Fork River of Wyoming, Aslan and Behrensmeyer (1996) found that when bones were introduced into an active channel, long transport distances did not necessarily result in more abrasion than did short transport distances.

Bone deposition

The bones and wood are themselves a single depositional layer that is less than 30 cm thick, on average, and that rests directly above or within the top of a conglomerate (Figs. 2, 5). Bone distribution densities range from 1 bone/m^2 to 67 bones/m^2, with a mean bone density of 16 bones/m^2 (only elements >5 cm long were counted, and all counts were based on field measurements). The bones do not appear to be interlayered with other sediment layers in any part of the quarry, though there is a topography to the bone bed. The high average bone density, coupled with the lack of interlayered sediments, indicates that the bones and wood accumulated during a single depositional event that most likely

FIGURE 3: Selected vertebrate fossils from the Snyder quarry showing the excellent preservation of the Snyder quarry material. A. *Eucoelophysis* skull (NMMNH P-30852) and left tibia (NMMNH P-29046). B. Archosaur radius (NMMNH P-34750) and phytosaur metapodial (NMMNH P-34728). C. *Desmatosuchus chamaensis* paramedian scute (NMMNH P-32795). D. *Pseudopalatus buceros* skull (NMMNH P-31292). Scale bars for A, B, and C = 2 cm, D = 10 cm.

took place during a very short time interval. Also, the difference in size ranges between the sedimentary particles of the deposit (i.e. the mud clasts) and the skeletal elements implies that the bones were not transported far from the site of death (Fiorillo et al., 2000). Many of the bones in the deposit are associated, and partially articulated pieces of carcasses would be too large to be stream bedload, implying that these skeletal segments could not have been transported over significant distances.

Bone alignment

Strike measurements of 79 bones and 30 pieces of wood in the quarry (taken with a Brunton compass) indicate a preferential alignment to the north-northeast/south-southwest (Fig. 4), which is also evident from the quarry map (Fig. 5). This alignment does not appear to be related to the size of the object, as large pieces of wood as well as small fragments of bone are aligned similarly. Objects such as skulls and scutes do not appear to have any strong alignment, but this is due to the weight and size of the skulls and the hydrodynamic properties of the scutes, which act as large, flat sheets (see below). The alignment of material is evidence for interaction of the organic debris with a strong unidirectional flow of water. Voorhies (1969), in a series of experiments, showed that linear skeletal elements will tend to align parallel to the current if they are submerged. This is not necessarily evidence of a significant amount of transport, but merely supports the presence of a strong current to orient these objects (Voorhies, 1969; Sander, 1987; Behrensmeyer, 1988; Fiorillo, 1991). A random orientation of bones should signal a sudden end to transport before hydraulic equilibrium could be reached, or could be dues to current velocities

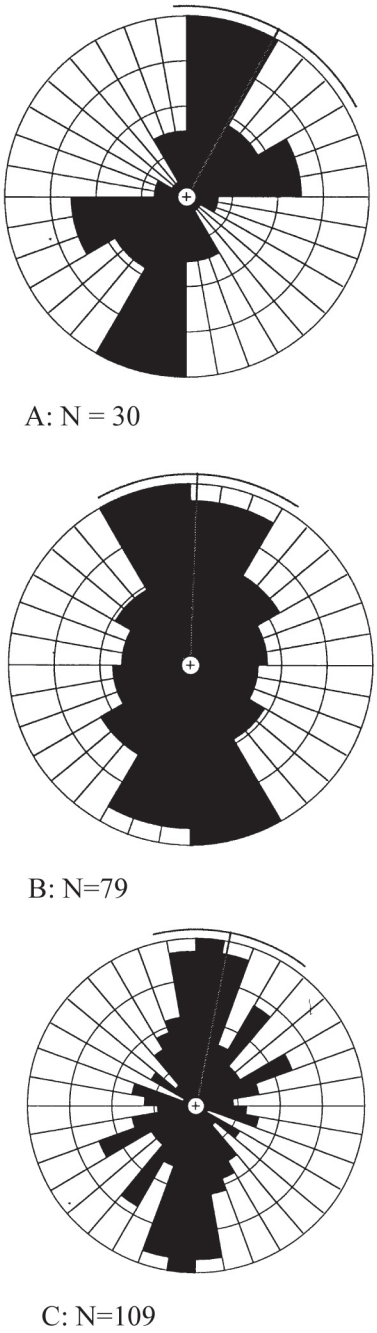

FIGURE 4: Rose diagrams indicating paleocurrent directions from the Snyder quarry. A: bone measurements, B: wood measurements, C: combined bone and wood data.

that were not strong enough to orient material (Fiorillo, 1991).

Hydrodynamics

In the quarry, all shapes and sizes of bones are present, from large phytosaur skulls (>1 m) to very small, delicate theropod bones (<10 mm) (Fig. 3). The range in sizes and surface areas of the bones thus varies widely throughout the quarry. Voorhies (1969) defined three classes of modern mammalian bones based upon surface area to volume ratios (SA:V). Group I bones are those with high SA:V ratios, including vertebrae, ribs and toe bones. Group II bones have an intermediate SA:V ratio and include femora, tibiae, ulnas, radii and metatarsals. Group III bones are those with low SA:V ratios and include skulls and mandibles. These different groupings are related to the hydrodynamic properties of the bones within each class. For example, it takes a more powerful current to move a large, heavy object versus a small, light object. Group I bones are removed by low velocity currents, whereas Group III bones are removed by high velocity currents.

While Voorhies' classification scheme was developed using sheep and bovid bones and will not apply to all animals equally (e.g., Blob, 1997), it can be used as a first order estimation of hydraulic transport for the Triassic bones in the Snyder quarry as they are, in shape and size, well within the range of bones studied by Voorhies (1969). For the Triassic animals, scutes and girdle elements (including interclavicles) were added to the elements in Group I, and most limb elements to Group II.

All three Voorhies Groups are present in the Snyder quarry (Table 1). Though Group I bones dominate the assemblage, the other groups are also significant. There is a strong bias in the quarry towards scutes, which is due, in part, to the large number (several hundred) of these bones that are part of the dermal armor of a single animal, such as phytosaurs and aetosaurs (Long and Murry, 1995). Even if this is taken into account, Group I still dominates the assemblage.

This is evidence for a low velocity current transporting the bones, though this does not rule out a much stronger current acting on the bones and wood prior to the current slowing enough for this material to be deposited. The presence of the smaller bones could also be interpreted as evidence of a sudden slowing of the current to the point where the carrying capacity of the water was low enough to allow the smaller elements to settle out among the larger ones. In experiments in the East Fork River, heavy and light bones separated within 1-2 years of being placed in the channel

TABLE 1: Voorhies Groups (Voorhies, 1969) for the Snyder quarry, with the minimum number of recovered elements for each skeletal element counted from the quarry maps compiled during the 2000 field season.

VOORHIES GROUP	ELEMENT	MINIMUM NUMBER RECOVERED SUMMER 2000 (From maps)
I	Ribs, Gastralia	98
	Vertebrae	61
	Hip bones	4 (3 Ilia)
	Metapodials, phalanges	10
	Scutes	276
II	Femora	5
	Tibiae	3
	Ulnae, Radii	8
	Ankle bones	10 (Astragali)
III	Lower jaws	6
	Skulls	12


Map A: Eastern half
of Snyder quarry
N
1 meter

FIGURE 5: Snyder quarry field maps. A: Eastern quarry. B: Western quarry.

(Aslan and Behrensmeyer, 1996). Given the mix of bones sizes and shapes in the Snyder quarry deposit, it can be assumed that the deposit took less than a year to form and was not subjected to extensive fluvial action (Behrensmeyer, 1988). However, bone transport is not only determined by size, density and shape of the element, but also by the environment of transport and the nature of the fluid flow (Behrensmeyer, 1975). If the density of the fluid is increased by the presence of a large suspended load, bones will be transported more easily and sorting will be less likely to occur (Behrensmeyer, 1975).

A third possibility is that the assemblage was not, in fact, transported far, and instead winnowing by biological processes modified the assemblage. Nevertheless, strong preferential alignment of the bones and virtual lack of evidence of scavenging make biological winnowing of the assemblage an unlikely process.

Biological evidence

Association of skeletal elements

Within the deposit, the bones are not fully articulated and there are only two instances of partial articulation in the Snyder quarry material. The first is a skull of the theropod dinosaur *Eucoelophysis* with three articulated cervical vertebrae. The second is a *Eucoelophysis* pubis with articulated femur and tibia. However, the bones of various animals are closely associated. Fiorillo (1991) defined associations of skeletal elements based on the proximity of specimens and the similarity in relative sizes of individual elements. In the eastern portion of the quarry, more than 2 m^2 of the bone horizon consist of the scutes of *Typothorax coccinarum* arranged in a mass that suggests they represent a single individual (Figs. 5, 6). To the east of this group of scutes is a massive phytosaur skull with 12 large phytosaur vertebrae encircling it (Fig. 5).

These and other close associations of skeletal elements of a single taxon are interpreted as the remains of a single individual. Had the carcasses been fully decayed, the bones, with no tissues to bind them together, would have been easily scattered (Hill, 1979). In fact, the associated skeletal units can be interpreted as remains of carcasses that were transported and rapidly buried before further disarticulation could take place (Holz and Barberena, 1994). Catastrophic mortality events usually result in a higher percentage of preserved skeletons because the death event affects an entire community at once (Loomis, 1912; Voorhies, 1969; Smith, 1980; Wood et al., 1988). However, the lack of complete articulation is evidence that the carcasses were not whole when they were buried, but were in some intermediate stage of decay or had been scavenged (Behrensmeyer, 1975; Holz and Barberena, 1994). Some minor degree of transport probably finished disassociating those bones that cannot be definitively associated with other bones of the same taxon.

Bone weathering

In addition to showing no signs of abrasion, the bones do not show a significant degree of subaerial weathering (Fig. 3). Bones that are exposed to subaerial processes go through distinct stages of weathering (Behrensmeyer, 1978). The Snyder quarry material shows Stage 0 weathering, with smooth surfaces and no cracks, other than those associated with post-depositional and post-fossilization stresses. None of the bones exhibit splintering or longitudinal cracking that would be associated with long-term exposure to the elements. Based on modern analogues, this effectively limits the duration of bone exposure to a maximum of about 3 years (Behrensmeyer, 1978). Thus, it is likely that these bones were subaerially exposed for much less time, perhaps only a few weeks or months. Behrensmeyer (1975) noted that bone does not survive for long in surface environments, but must be quickly buried if it is to appear unweathered when fossilized. The narrow range of bone weathering stages, as well as the low degree of weathering are evidence for both rapid burial and for a mass death event, wherein all of the skeletons were effectively exposed to physical and chemical degradation at the same time (Fiorillo et al., 2000).

FIGURE 6: Photograph of *in situ* mass of associated *Typothorax coccinarum* scutes from the Snyder quarry (photograph by P.S. Zeigler, 6/2000).

Scavenging

As discussed earlier, the bones themselves are in excellent condition. There is only one bone that shows puncture marks or scratches that would be associated with scavenging of the carcasses by other animals. This is a scute of the aetosaur *Desmatosuchus chamaensis* (NMMNH P-32797) that has two puncture marks that penetrate halfway through the body of the scute, and are approximately 4 cm apart (Fig. 7). However, predators and scavengers are the greatest initial influence on the disassociation of a carcass (Behrensmeyer, 1975). It is possible that the lack of damage to the bones is evidence that the carcasses were buried quickly, before vertebrate scavengers could attack them to any significant degree. Alternatively, the disarticulation of the carcasses may be the primary sign of vertebrate scavenger activity,

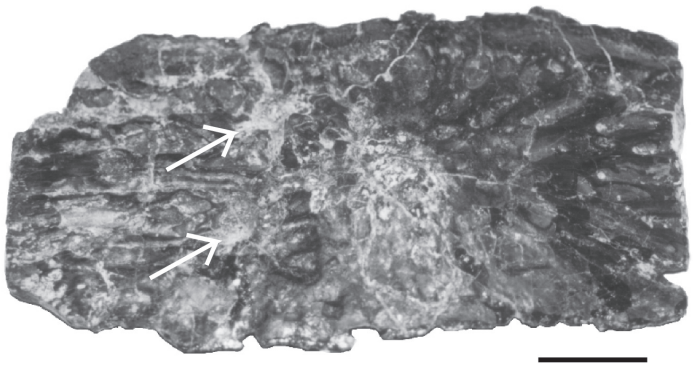

FIGURE 7: *Desmatosuchus chamaensis* scute (NMMNH P-32797) with puncture marks (phytosaur tooth marks?) marked with arrows.

rather than marks left on bone surfaces. Another consideration is that mass death situations can create so much food for local scavengers that many skeletons may be left more or less intact, or if the carcasses dry quickly and mummify, they become unattractive to scavengers (Behrensmeyer, 1975).

Bone fracture

While most of the bones are in excellent condition as far as the bone surface itself is concerned, all of the bones are fractured at least once and usually in multiple places. These fractures are perpendicular to the long axis of the bones, and the break surfaces are smooth. In fresh bones, break surfaces are usually ragged, and the most common type of break is a spiral fracture (Myers et al., 1980; Shipman, 1981; Fiorillo et al., 2000). The perpendicular fracturing of the Snyder quarry bones points to post-burial and post-fossilization damage, not damage to fresh bone structure since the compaction of sediments can crush and distort buried bone (Behrensmeyer, 1975). Also, clay-rich units, such as the Petrified Forest Formation, will go through considerable volumetric expansion and contraction with the addition of water and with desiccation (Dodson, 1971). This change in volume will cause breakage of enclosed bones, though the broken pieces may themselves end up being quite well-preserved (Dodson, 1971; Behrensmeyer, 1975). This is further evidence of a relatively rapid burial of fresh, untouched bones. Most of the bones with obvious pre- or syndepositional fractures are relatively delicate elements such as phytosaur skulls.

Minimum Number of Individuals

Calculations of the minimum number of individuals (MNI) for the different taxa represented in the Snyder quarry are still approximate, because only a portion of the material removed from the quarry has been prepared. MNIs of the Snyder quarry fossils were taken using all the material that had been prepared and catalogued, as well as the known phytosaur skulls. MNIs are calculated by taking the maximum number of a sided bone found in a deposit (Badgley, 1986). Based on the number of skulls recovered from the main horizon, the phytosaur MNI is 10. The aetosaur MNI is divided between the two genera represented in the quarry and is based on the two associated clusters of scutes for *Typothorax coccinarum* and on the presence of widely scattered scutes of *Desmatosuchus chamaensis*. Thus, the *T. coccinarum* MNI is 2, and the *D. chamaensis* MNI is 1. The rauisuchian MNI is 2, based on one large complete femur and one small distal femur.

The theropod MNI is 4 based on three left tibiae and a right that is significantly larger than the other three. At least one metoposaurid amphibian is represented by a single vertebra and three teeth, and at least one procolophonid reptile by a single tooth. Based on a nearly complete body and thousands of scales found in the deposit, of which there are two different varieties (redfieldiid and semionotid), the minimum number of fish found is at least two, though this is clearly a gross underestimation.

These MNIs suggest a strong predominance among the tetrapods of the large, semi-aquatic predators, the phytosaurs (Ballew, 1986, 1989). The other tetrapod taxa that are represented by smaller MNIs are mostly those animals that are terrestrial, including *Eucoelophysis* and the aetosaurs *Typothorax* and *Desmatosuchus* (Colbert, 1989; Heckert and Lucas, 1999, 2000). This grouping of animals is representative of the animals that would typically be in and around a channel or other water source.

Age profile

The 10 phytosaur skulls that have been recovered from the quarry (Fig. 8) are not fully prepared. In fact, only three skulls have been completely prepared, and three others are in different stages of preparation. However, as they were excavated, the lengths of most of the skulls were measured in the field. The sizes of the phytosaur skulls range from one that is approximately 30 cm long to one that is more than a meter in length. If one assumes that overall length of a phytosaur skull reflects approximate ontogenetic age (Camp, 1930; Gregory, 1962; Holz and Barberena,

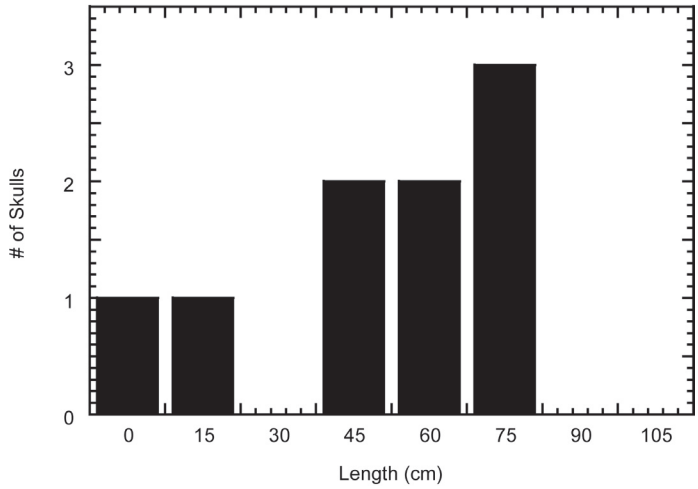

FIGURE 8: Age distribution histogram for the phytosaurs of the Snyder quarry.

1994), then the Snyder quarry skulls may be considered to represent an ontogenetic series, from juvenile to adult (with adult skulls being considered as those longer than 100 cm). The majority of the skulls (6) are of intermediate size (70 to 100 cm in length) and probably correspond to subadult or young adult individuals. A frequency of smaller sizes (= juveniles) that is relatively low with an increasing number of larger sizes corresponds to a normal population of reptiles (Holz and Barberena, 1994). Thus, in this case, the thanatocoenosis is the same as the biocoenosis in terms of population structure and is evidence for a mortality event that was catastrophic for the population (Weigelt, 1927; Voorhies, 1969; Wilson, 1988; Holz and Barberena, 1994; Therrien and Fastovsky, 2000).

Fossil wood

Fossil wood was analyzed not just from the Snyder quarry, but from the same horizon over an area approximately 400 meters in radius around the quarry. This wood is very unusual in its preservation as well as in microscopic features. It is not silicified, as is typical for wood from the Petrified Forest Formation (e.g., Ash, 1989; Heckert and Lucas, 1998; Ash and Creber, 2000). Rather, the wood from the Snyder quarry is mostly charcoalified; it is black, crumbly and only partially silicified in places.

Large portions of the long pieces of wood are composed of a black, shiny, low density material that is fractured into cubes that are typically less than 1 cm^3. Some large pieces of wood strongly resemble charcoal, with a deep black color and a silky, fibrous texture. The charcoal-like material was examined with the SEM, and microphotographs reveal cell walls that are completely homogenous (Fig. 9). Rather than the lamellar, flaky structure seen in living plant tissue, the cell walls of the Snyder quarry wood are completely smooth, with no signs of internal structure.

This material is fusain, or fossil charcoal. Fusain is commonly defined as patches of a black, fibrous or silky, opaque material that retains three dimensional cellular structure, is brittle, is chemically inert and has a relatively high reflectance value when compared with other coal macerals (Scott, 1989, 2000; Jones and Chaloner, 1991; Scott and Jones, 1991; Jones et al., 1991, 1993). In experiments conducted on blocks of pine wood, cell walls that are normally composed of the primary and secondary walls with middle lamellae become homogenized into a single structure between 280° and 320°C (Cope, 1980, 1981; Jones and Chaloner, 1991; Scott, 2000).

Comparison of the wood from the Snyder quarry with the experimental wood and other samples shows that the wood has homogenized cell walls (Fig. 9), indicating that this material is, indeed, fossil charcoal. Reflectance microscopy work carried about by Dr. A.C. Scott and Dr. I. Glasspool further supports this interpretation and indicates that the plant material was burned in a moderate temperature ground fire (A.C. Scott, pers. comm., Dec. 2001). The average reflectance value obtained from 100 analyses of charcoal fragments is 1.56% (with a range of 1.20% to 2.33%), which corresponds to an approximate pyrolysis temperature of 400°C (Jones et al., 1991).

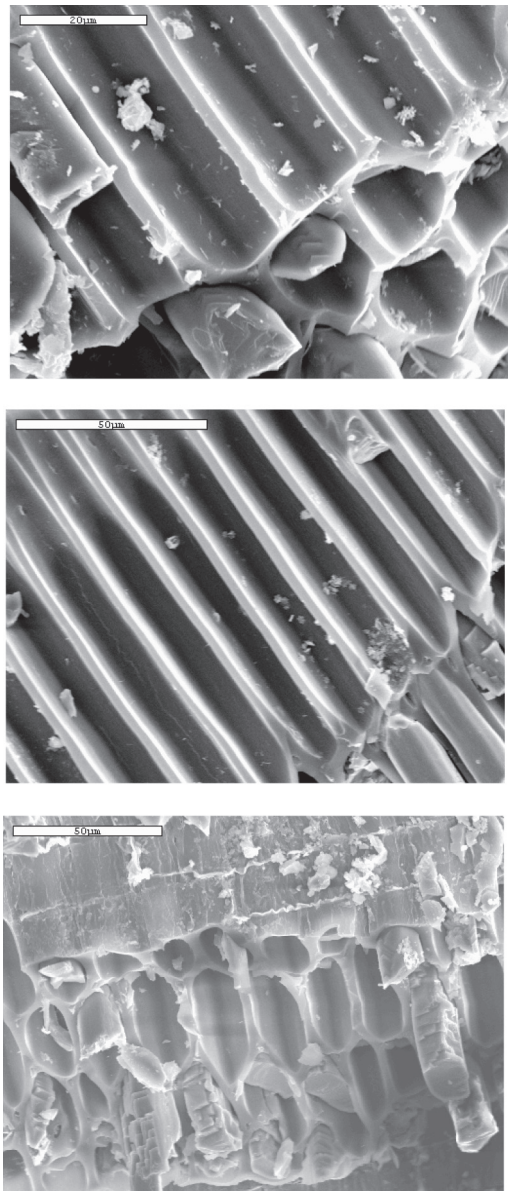

FIGURE 9: Scanning electron microphotographs of charcoal (NMMNH P-34885) from the Snyder quarry, showing completely homogenized cell walls.

DISCUSSION

There are several possible taphonomic processes that could produce a fossil assemblage like the Snyder quarry. These include attritional and catastrophic flood events, drought, disease, predator traps or fire. Of these various processes, the attritional flood and drought events can be immediately ruled out. The skeletal material in the bonebed is in excellent condition and does not show the range of weathering stages and abrasion that would be expected in material deposited in a series of flood events (Behrensmeyer, 1978). An example of attritional remains accumulated in channels is a pair of Upper Triassic quarries from Howard County, Texas (Elder, 1987). These two quarries, Quarry 3 and Quarry 3a, are part of a series of quarries that produced assem-

blages dominated by *Trilophosaurus* that are found in the Chinle Group. In Quarry 3 a mixture of heavy, worn bones and delicate, well preserved bones occur with occasional association or articulation. Rare coprolites and broken unionid shells are also found in the deposit. Some of the bones have boring marks interpreted as being from gastropods and indicating subaqueous exposure of the bones. This assemblage is seen as a series of fresh carcasses joining a bedload of older, more transported material. Quarry 3a has a very high percentage of worn bones with a few semi-articulated aetosaur fragments present. There are no coprolites present, and this quarry is interpreted as also being an attritional assemblage with a few individuals being added to an existing deposit.

In the Snyder quarry deposit, there is also no repeated interlayering of sediments and bones that would indicate a series of floods occurring over time over a broad area. The assemblage cannot be due to drought conditions either, as is thought to be the case with the famous *Coelophysis* quarry (Schwartz and Gillette, 1994). This deposit lies in the Rock Point Formation and is considered the largest Late Triassic assemblage of dinosaurs ever found (Hunt and Lucas, 1993), with thousands of individuals preserved (Colbert, 1989; Schwartz and Gillette, 1994). In this deposit, the skeletons are concentrated in a localized channelized deposit, interpreted as a crevasse splay, and covered with fine-grained paleosol sediment (Schwartz and Gillette, 1994). The age distribution of the skeletons shows the age profile of a living population with high numbers of adults in their prime. All of the skeletons have uniform preservation, show few signs of long distance transport (Therrien and Fastovsky, 2000), are fully or partially articulated and many have been found in distorted positions interpreted as due to desiccation of the corpse (heads and tails arched over the back as nuchal ligaments and tendons dried and tightened). In the Snyder quarry, the sedimentological evidence does not include mudcracks or laminations that would be produced by a drying slackwater deposit. There is also no evidence of trampling or scavenging of the corpses. In a drought-produced assemblage, the corpses themselves would be expected to be fully to partially articulated, and would be found in distorted positions with their heads and tails arched over the back (Weigalt, 1927).

A catastrophic flood hypothesis, such as that described for the Upper Cretaceous Careless Creek Quarry (Fiorillo, 1991), best fits the sedimentological evidence from the Snyder quarry: bones and wood are aligned, the elements show a moderate degree of hydrodynamic sorting, mud rip-up clasts are present, and there is no weathering or abrasion of the material. This scenario also fits moderately well with the biological evidence in that the survivorship curve of the phytosaurs is consistent with a catastrophic event. However, the lack of articulation of the material and the mix of terrestrial, semi-aquatic and aquatic vertebrates do not fit as well with a catastrophic flood event. If the flood itself was the primary cause of catastrophic death, then the corpses should be either fully or partially articulated, and the faunal assemblage should be more monospecific (as with the Careless Creek Quarry assemblage).

The catastrophic survivorship curve and the mix of articulation states at the Snyder quarry are similar to those of a south Brazilian Triassic reptile-dominated assemblage described by Holz and Barberena (1994). The assemblage is from the Middle to Upper Triassic Santa Maria and Caturrita formations. The skeletons, including those of rhynchosaurs, dicynodonts, cynodonts and thecodonts, are distorted, and there is a mix of partially articulated and non-articulated material. The deposit is moderately sorted, with a strong component of lag deposition. The age profile of the animals is similar to that of a normal, living population and, in conjunction with the other data, the locality was interpreted as a series of catastrophic flood events that deposited the articulated corpses, while the disarticulated elements represent those animals that were killed, but not immediately buried.

The scenario that best fits all of the data from the Snyder quarry is a paleowildfire. The biological evidence is consistent with this hypothesis: a catastrophic age profile, a mix of vertebrate groups, and the presence of abundant charcoal. The additional geological evidence for a strong flow of water, including the presence of rip-up clasts, orientation of material, hydrodynamic sorting and evidence of a rapid burial (lack of weathering and scavenging) could represent the aftermath of a fire on a landscape, with increased run-off and erosion. However, although this scenario best fits all of the data from the quarry itself, there is no direct evidence that links the deaths of the animals in the quarry to a forest fire. In fact, the fire may have occurred upstream and prior to the deaths of the animals, so that the charcoal was washed into the deposit later on.

We are not the first to invoke the paleowildfire hypothesis to explain a bonebed. Sander (1987) proposed a similar sequence of events for a Lower Permian assemblage of tetrapods from Archer County, Texas, including *Archeria*, *Eryops*, *Edaphosaurus*, and *Dimetrodon*. The fossil material ranges from fully articulated to completely disarticulated, and the fossils rest on a layer of plant debris that includes several logs. There is a strong degree of preferred orientation to the skeletons and logs. Sander attributed the orientation to moderate transport of the material by moving water, with the corpses of the animals lining up along a shoreline. Sander argued that these animals were trapped along the edge of a lake by a wildfire, and the reptiles either suffocated or drowned in an attempt to escape the fire. Lake currents then transported the skeletons and plant debris from the fire to the far edge of the lake where they were deposited. The plant and log debris appear to be charcoalified and were taken as evidence for burning of the floral material, though Sander never demonstrated that the material had, in fact, been burned.

With this caveat in mind, it is worthwhile to consider briefly the stratigraphically equivalent Canjilon quarry, which lies approximately 4 km to the east of the Snyder quarry and is the single richest deposit of phytosaurs yet found (Long et al., 1989; Hunt and Lucas, 1993). Like the Snyder quarry, the Canjilon quarry is dominated by phytosaurs, with at least 11 individuals represented by skulls, and an age profile that is very similar to that of the Snyder quarry, with young adults predominating (Zeigler et al., 2002).

An initial taphonomic evaluation of the material from the quarry (undertaken in the Spring of 2001, also see Hunt and Downs, 2002; Martz, 2002) reveals a mix of articulated and asso-

ciated skeletal material. There is a vague sense of orientation of the elements on the quarry maps drawn by Charles Camp during excavations in the late 1920s and early 1930s (Long et al., 1989; Hunt and Lucas, 1993). The presence of two fully articulated phytosaur skeletons, together with numerous clusters of associated material, provide evidence for a lack of significant fluvial transport. The sediments encasing the material are bentonitic mudstones that are typical of Chinle floodplain deposits. The occurrence of the fossil material in these sediments further suggests little or no postmortem transport. The fossil material itself is in excellent condition, with no evidence of weathering, abrasion, trampling, or vertebrate scavenging.

Taphonomically, the floodplain is usually host to attritional assemblages of disarticulated vertebrate remains, in contrast to channel and channel margin sediments, which hold either thick accumulations of attritionally derived material or catastrophic assemblages (Behrensmeyer, 1982). The abundance of material found at the Canjilon quarry, together with the excellent preservation of the fossils, does not support an attritional taphonomic process. Instead, this quarry is also most likely a catastrophic assemblage. Initial surveys of the quarry itself did not turn up the same friable charcoalified wood fragments similar to those found at the Snyder quarry, but small pieces of apparently silicified wood were discovered. Upon closer examination under a microscope, small cubes of what appears to be pyrofusinite, which is a fire byproduct, were identified. It is possible that the difference in the preservation of the wood is due to a different groundwater chemistry in the Canjilon quarry that replaced portions of the semi-charred wood with silica, creating this mixture of silicified and carbonized wood.

When the Snyder quarry, the Canjilon quarry, and the distribution of charcoal around the Snyder quarry are considered together, it becomes much more realistic to invoke the paleowildfire hypothesis to explain the taphonomy of both localities, as well as the presence of abundant charcoal throughout the area. It is now possible to consider the extent of such a fire. The temperatures suggested by the SEM images (280-320°C) and the reflectance microscopy data (400°C) are maximum temperature estimates. However, the amount of biomass, both in terms of animal remains and plant material, in both quarries suggests a very widespread high-temperature fire that potentially burned at higher temperatures.

CONCLUSION

The Snyder quarry is a particularly rich Upper Triassic bonebed that appears to have a relatively unique combination of sedimentological and taphonomic data. Perhaps the simplest explanation for the data from the Snyder quarry might be a catastrophic flood event that swept a group of animals into a topographic low. However, the unusual state of preservation of the wood ties this assemblage to a very different sequence of events:

1) Abundant charcoal and partially charred wood indicates that a forest fire, or series of fires, swept through the region.

2) Terrestrial animals may have sought shelter in a source of water and were trapped, or may have asphyxiated on the shores nearby. The semi-aquatic phytosaurs probably also succumbed to temperature and asphyxiation.

3) Once the fire passed, leaving behind a devastated landscape, the carcasses of these animals began to decay without being disturbed by scavengers.

4) Sometime later, precipitation on the ash-laden (and now hydrophobic) soil caused elevated run-off and erosion rates. The floodwaters generated by this higher run-off were powerful enough to move partially decayed corpses and downed tree limbs.

5) All of the organisms' remains as well as tree limbs and logs were transported and oriented, then deposited in a topographic low or a channel meander bend. The actual transport distance was apparently short, possibly because the fluvial system was overloaded with sediment.

6) The increased erosion rates and subsequent precipitation events filled the deposit with sediments, rapidly burying the corpses and wood, before further weathering, abrasion or scavenging could occur.

Thus, the Snyder quarry is the first bonebed that can be linked to a forest fire and as such, it is also the first direct evidence of a paleowildfire to be reported from Upper Triassic Chinle sediments.

ACKNOWLEDGMENTS

We extend our thanks to the NMMNH Friends of Paleontology, Ghost Ranch and A. Downs for their aid in excavations. Funding for this project was provided by the University of New Mexico RPT grant, the New Mexico Geological Society Grant-in-Aid, and the Society of Vertebrate Paleontology Patterson Award. We also thank Dr. Raymond Rogers, Dr. Timothy Jones, Dr. A. Scott, Dr. A. Fiorillo and an anonymous reviewer for their thorough, critical reviews.

REFERENCES

Allen, J.R.L., 1978, Studies in fluviatile sedimentation: an exploratory quantitative model for the architecture of avulsion-controlled alluvial sites: Sedimentary Geology, v. 21, p. 129-147.

Ash, S.R., 1989, A catalog of Upper Triassic plant megafossils of the western United States through 1988: *in* Lucas, S.G. and Hunt, A.P., Dawn of the Age of the Dinosaurs in the American Southwest, p. 189-222.

Ash, S.R. and Creber, G.T., The Late Triassic *Aurucarioxylon arizonicum* trees of the Petrified Forest National Park, Arizona, USA: Palaeontology, v. 43, p. 15-28.

Aslan, A. and Behrensmeyer, A.K., 1996, Taphonomy and time resolution of bone assemblages in a contemporary fluvial system: the East Fork river, Wyoming: Palaios, v. 11, p. 411-421.

Badgley, C., 1986, Counting individuals in mammalian fossil assemblages from fluvial environments: Palaios, v. 1, p. 328-338.

Ballew, K.L., 1986, A phylogenetic analysis of Phytosauria (Reptilia: Archosauria) from the Late Triassic of the western United States: Masters Thesis, University of California, Berkeley, CA, 75 p.

Ballew, K.L., 1989, A phylogenetic analysis of Phytosauria from the Late Triassic of the western United States: *in* Lucas, S.G. and Hunt, A.P. eds., Dawn of the Age of the Dinosaurs in the American Southwest, p. 309-339.

Behrensmeyer, A.K., 1975, The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolph, Kenya: Bulletin of the Museum of Comparative Zoology, v. 146, p. 473-578.

Behrensmeyer, A.K., 1978, Taphonomic and ecologic information from bone

weathering: Paleobiology, v. 4, p. 150-162.

Behrensmeyer, A.K., 1982, Time resolution in fluvial vertebrate assemblages: Paleobiology, v. 4, p. 150-162.

Behrensmeyer, A.K., 1988, Vertebrate preservation in fluvial channels: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 63, p. 183-199.

Blakey, R.C. and Gubitosa, R., 1984, Controls of sandstone body geometry and architecture in the Chinle Formation (Upper Triassic) Colorado Plateau: Sedimentary Geology, v. 38, p. 51-86.

Blob, R.W., 1997, Relative hydrodynamic dispersal potentials of soft-shelled turtle elements: Implications for interpreting skeletal sorting of non-mammalian terrestrial vertebrates: Palaios, v. 12, p. 151-164.

Bridge, J.S. and Leeder, M.R., 1979, A simulation model of alluvial stratigraphy: Sedimentology, v. 26, p. 617-644.

Camp, C. L., 1930, A study of the phytosaurs with description of new material from western North America: University of California Press, Berkeley, 174 p.

Colbert, E.H., 1989, The Triassic dinosaur *Coelophysis*: Museum of Northern Arizona Bulletin 57, 160 p.

Cope, M.J., 1980, Physical and chemical properties of coalified and charcoalified phytoclasts from some British Mesozoic sediments: an organic geochemical approach to palaeobotany: *in* Douglas, A.G. and Maxwell, J.R., eds., Advances in Organic Geochemistry, p. 663-677.

Cope, M.J., 1981, Products of natural burning as a component of the dispersed organic matter of sedimentary rocks: *in* Brooks, J., ed., Organic Maturation Studies and Fossil Fuel Exploration, p. 89-109.

Cook, E., 1995, Taphonomy of two non-marine Lower Cretaceous bone accumulations from southeastern England: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 116, p. 263-270.

Dodson, P., 1971, Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 10, p. 21-74.

Dodson, P., 1974, The significance of small bones in paleoecological interpretation: Contributions to Geology, University of Wyoming Special Paper no. 2.

Dubiel, R.F., 1989, Depositional environments of the Upper Triassic Chinle Formation in the eastern San Juan basin and vicinity, New Mexico, U.S.: Geological Survey Bulletin 1801-B, 22 p.

Elder, R.L., 1987, Taphonomy and paleoecology of the Dockum Group, Howard County, Texas: Journal of the Arizona-Nevada Academy of Science, v. 22, p. 85-94.

Fiorillo, A.R., 1988, Taphonomy of Hazard Homestead Quarry (Ogallala Group), Hitchcock County, Nebraska: Contributions to Geology, University of Wyoming, v. 26, p. 57-97.

Fiorillo, A.R., 1991, Taphonomy and depositional setting of Careless Creek quarry (Judith River Formation), Wheatland County, Montana, U.S.A.: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 81, pp. 281-311.

Fiorillo, A.R., Padian, K. and Musikasinthorn, C., 2000, Taphonomy and depositional setting of the *Placerias* quarry (Chinle Formation: Late Triassic, Arizona): Palaios, v. 15, p. 373-386.

Friend, P.F., Slater, M.J. and Willams, R.C., 1979, Vertical and lateral building of river sandstone bodies, Ebro Basin, Spain: Journal of the Geological Society of London, v. 136, p. 39-46.

Gregory, J.T., 1962, The genera of phytosaurs: American Journal of Science, v. 260, p. 652-690.

Heckert, A.B. and Lucas, S.G., 1998, Stratigraphic distribution of petrified wood in the Petrified Forest National Park and vicinity, Arizona: *in* Santucci, V. and McClelland, L., eds., National Park Service Paleontological Research vol. 3, National Park Service Geologic Resources Division Technical Report, p. 125-129.

Heckert, A.B. and Lucas, S.G., 1999, A new aetosaur (Reptilia: Archosauria) from the Upper Triassic of Texas and the phylogeny of aetosaurs: Journal of Vertebrate Paleontology, v. 19, p. 50-68.

Heckert, A.B. and Lucas, S.G., 2000, Taxonomy, phylogeny, biostratigraphy, biochronology, paleobiogeography, and evolution of the Late Triassic Aetosauria (Archosauria: Crurotarsi): Zentralblatt für Geologie und Paläontologie, Teil 1, p. 1539-1587.

Heckert, A.B., Rinehart, L.F., Lucas, S.G., Downs, A., Estep, J.W., Harris, J.D., Reser, P.K., Snyder, M., 1999a, A diverse new Triassic fossil assemblage from the Petrified Forest Formation (Revueltian: Early-Mid Norian) near Abiquiu, New Mexico: New Mexico Geology, v. 21, p. 42.

Heckert, A.B., Lucas, S.G. and Rinehart, L.F., 1999b, From decapods to dinosaurs: a diverse new fauna from a bonebed in the Upper Triassic (Norian) Petrified Forest Formation: Journal of Vertebrate Paleontology, v. 19, no. 3, p. 50A.

Heckert, A.B., Zeigler, K.E., Lucas, S.G., Rinehart, L.F. and Harris, J.D., 2000, Preliminary description of coelophysoids (Dinosauria: Theropoda) form the Upper Triassic (Revueltian: early-mid Norian) Snyder quarry, north-central New Mexico: New Mexico Museum of Natural History and Science, Bulletin 17, p. 27-31.

Hill, A., 1979, Disarticulation and scattering of mammal skeletons: Paleobiology, v. 5, p. 261-274.

Holz, M. and Barberena, M.C., 1994, Taphonomy of the south Brazilian Triassic paleoherpetofauna: pattern of death, transport and burial: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 107, p. 179-197.

Hunt, A.P. and Downs, A.D., 2002, Taphonomy of the Late Triassic Canjilon quarry (Petrified Forest Formation: Chinle Group), north-central New Mexico: Data from new excavations: New Mexico Museum of Natural History Bulletin 21, 291-296.

Hunt, A.P. and Lucas, S.G., 1993, Stratigraphy and vertebrate paleontology of the Chinle Group (Upper Triassic), Chama basin, north-central New Mexico: New Mexico Museum of Natural History Bulletin 2, p. 61-69.

Kraus, M.J. and Middleton, L., 1987, Dissected paleotopography and base-level changes in a Triassic fluvial sequence: Geology, v. 15, p. 18-21.

Jones, T.P. and Chaloner, W.G., 1991, Fossil charcoal, its recognition and palaeoatmospheric significance: Palaeogeography, Palaeoclimatology, Palaeoecology (Global and Planetary Change Section), v. 97, p. 39-50

Jones, T.P., Scott, A.C. and Cope, M., 1991, Reflectance measurements and the temperature of formation of modern charcoals and implications for studies of fusain: Bullétin de la Societé de Géologie France, v. 162, no. 2, p. 193-200.

Jones, T.P., Scott, A.C. and Mattey, D.P., 1993, Investigations of "fusain transition fossils" from the Lower Carboniferous: Comparisons with modern partially charred wood: International Journal of Coal Geology, v. 22, p. 37-59.

Jones, T.P., Ash, S. and Figueiral, I., 2002, Late Triassic charcoal from Petrified Forest National Park, Arizona, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 188, p. 127-139.

Leeder, M.R., 1978, A quantitative stratigraphic model for alluvium, with special reference to channel deposit density and interconnectedness: *in* Miall, A.D., ed., Fluvial Sedimentology: Canadian Society of Petroleum Geologists Memoir 5, p. 587-596.

Long, R.A. and Murry, P.A., 1995, Late Triassic (Carnian and Norian) tetrapods from the southwestern United States: New Mexico Museum of Natural History Bulletin 4, 254 p.

Long, R.A., Lucas, S.G., Hunt, A.P. and McCrea, R.T., 1989, Charles Camp: collecting Late Triassic vertebrates in the American Southwest during the 1920s and 1930s: *in* Lucas, S.G. and Hunt, A.P., eds., Dawn of the Age of the Dinosaurs in the American Southwest, p. 65-71.

Loomis, F.B., 1912, Osteology and affinities of the genus *Stenomylus*: American Journal of Science, v. 179, p. 297-323.

Lucas, S.G., 1993, The Chinle Group: Revised stratigraphy and biochronology of Upper Triassic strata in the western U.S.: Museum of Northern Arizona, Bulletin 59, p. 27-50.

Lucas, S.G., 1998, Global Triassic tetrapod biostratigraphy and biochronology: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 143, p. 347-384.

Lucas, S.G., 1999, Tetrapod-based correlation of the nonmarine Triassic: Zentrallblat für Geologie und Paläontologie, Teil 1, p. 497-521.

Lucas, S.G., Heckert, A.B., Estep, J.W. and Anderson, O.J., 1997, Stratigraphy of the Upper Triassic Chinle Group, Four Corners regions: New Mexico Geological Society, 48th Field Conference Guidebook, p. 81-108.

Martz, J.W., 2002, A new map for the Late Triassic Canjillon Quarry (Petrified Forest Member, Chinle Formation), and the ontogeny of *Typothorax coccinarum* (Archosauria, Stagonolepididae): Journal of Vertebrate Paleontology, v. 22, no. 3, p. 84A.

Myers, T., Voorhies, M.R., and Corner, R.G., 1980, Spiral fractures and bone pseudotools at paleontological sites: American Antiquity, v. 45, p. 483-489.

Sander, P.M., 1987, Taphonomy of the Lower Permian Geraldine bonebed in Archer County, Texas: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 61, p. 221-236.

Scott, A.C., 1989, Observations on the nature and origin of fusain: International Journal of Coal Geology, v. 12, p. 443-475.

Scott, A.C., 2000, The pre-Quaternary history of fire: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 164, p. 281-329.

Scott, A.C. and Jones, T.P., 1991, Fossil charcoal: a plant-fossil record preserved by fire: Geology Today, Nov-Dec, p. 214-216.

Schwartz, H.L. and Gillette, D.D., 1994, Geology and taphonomy of the *Coelophysis* quarry, Upper Triassic Chinle Formation, Ghost Ranch, New Mexico: Journal of Paleontology, v. 68, p. 1118-1130.

Shipman, P., 1981, Life History of a Fossil: An Introduction to Taphonomy and Paleoecology, Harvard University Press, Cambridge, 222 p.

Smith, R.M.H., 1980, The lithology, sedimentology and taphonomy of flood-plain deposits of the Lower Beaufort (Adelaide Subgroup) strata near Beaufort West: Transactions of the Geological Society of South Africa, v. 83, p. 399-413.

Therrien, F. and Fastovsky, D.E., 2000, Paleoenvironments of early theropods, Chinle Formation (Late Triassic), Petrified Forest National Park, Arizona: Palaios, v. 15, p. 194-211.

Voorhies, M.R., 1969, Taphonomy and population dynamics of an Early Pliocene vertebrate fauna, Knox County, Nebraska: University of Wyoming Contributions to Geology, Special Paper 1, 69 p.

Weigelt, J., 1927, Rezente Wirbeltierleichen und ihre Paläontologische Bedeutung. Max Weg, Leipzig, 227 pp.

Wilson, M.V.H., 1988, Taphonomic processes: information loss and information gain: Geoscience Canada, v. 15, p. 131-148.

Wood, J.M., Thomas, R.G. and Visser, J., 1988, Fluvial processes and vertebrate taphonomy: the Upper Cretaceous Judith River Formation, South Central Dinosaur Provincial Park, Alberta, Canada: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 66, p. 127-143.

Zeigler, K.E., Lucas, S.G. and Heckert, A.B., 2002, The Late Triassic Canjilon quarry (Upper Chinle Group, New Mexico) phytosaur skulls: Evidence of sexual dimorphism in phytosaurs, New Mexico Museum of Natural History Bulletin 21, p. 179-188.