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VERTEBRATE TRACE FOSSILS FROM ARIZONA WITH SPECIAL REFERENCE TO TRACKS PRESERVED IN NATIONAL PARK SERVICE UNITS AND NOTES ON THE PHANEROZOIC DISTRIBUTION OF FOSSIL FOOTPRINTS

ADRIAN P. HUNT[1], VINCENT L. SANTUCCI[2] and SPENCER G. LUCAS[1]

[1]New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104-1375;
[2]National Park Service, McLean, VA 22101

Abstract—Arizona has significant tetrapod ichnofaunas, many of which are from National Park Service units, including traces from the Pennsylvanian Wescogame Formation, Permian Coconino and DeChelly sandstones and Hermit Formation, Triassic Moenkopi Formation and Blue Mesa and Sonsela Members of the Petrified Forest Formation, Jurassic Navajo Sandstone, Cretaceous Toreva Formation, Miocene Bidahochi Formation and the Pliocene Verde Formation. Arizona ichnofaunas are significant for several reasons as they include the first large Paleozoic ichnofaunas described, westernmost Pennsylvanian tetrapod tracks in North America, largest collected and described sample sizes of trace fossils from eolianites, the most significant Early-Middle Triassic tetrapod ichnofaunas in the New World, and a Cretaceous dinosaur tracksite with multiple tail drags. Other vertebrate trace fossils from Arizona include coprolites from the Moenkopi Formation and Chinle Group and late Cenozoic cave deposits, putative nests from the Chinle Group and numerous middens from the late Pleistocene. There are four temporal phases in the taphonomy of tetrapod tracks: Devonian, Carboniferous-Triassic, Jurassic-Cretaceous and Cenozoic.
Keywords: track, trace fossil, coprolite, Arizona, Permian, Triassic, Jurassic, Neogene, Pleistocene

INTRODUCTION

Arizona preserves a rich record of fossil tetrapod tracks and other vertebrate trace fossils, and many specimens are preserved in areas administered by the National Park Service (NPS)(Fig. 1). The Arizona record of tracks is broadly reflective of Phanerozoic preservation trends. The purpose of this paper is to review prominent records of tetrapod tracks and other trace fossils from Arizona and to discuss those from National Park Service units in detail and to briefly discuss temporal trends in track preservation. Santucci et al. (1998) provided a review of vertebrate tracks from NPS units throughout the United States. They noted occurrences at 19 NPS units, and we are now aware of an additional 10 records. Other papers in this volume review aspects of the Arizona trace fossil record by time period (Elliott and Blakey, 2005; Heckert et al, 2005; Hunt et al., 2005; Lucas et al., 2005; Lucas and Heckert, 2005; Morgan and White, 2005). USNM refers to the United States National Museum (Smithsonian) in Washington; MNA refers to the Museum of Northern Arizona in Flagstaff; NMMNH refers to the New Mexico Museum of Natural History and Science in Albuquerque.

PENNSYLVANIAN TRACKS

Grand Canyon National Park

In the course of his work on the Paleozoic ichnofaunas of the Grand Canyon, Charles Gilmore (1926, 1927, 1928) described a low diversity assemblage of tetrapod tracks from the Pennsylvanian Wescogame Formation (Supai Group). Santucci et al. (1998) recognized only two valid ichnotaxa from the Wescogame: *Batrachichnus delicatulus* (= *Stenichnus yakiensis*) and *Limnopus* sp. (= *Ammobatrachus turbatans*, *Tridentichnus supaiensis* and *Anomalopus sturdevanti*).

Tracks from Outside NPS Areas

There are no Pennsylvanian tetrapod tracks known from outside Grand Canyon National Park in Arizona.

PERMIAN TRACKS

Grand Canyon National Park

Hermit Formation (Wolfcampian)

The Hermit Formation tetrapod tracks occur in redbeds, in contrast to the eolian strata of the Coconino Sandstone. The ichnotaxonmically-revised tracks of the Hermit Formation (Hunt and Santucci, 1998a,b) include the nearly ubiquitous Permian redbed temnospondyl track *Batrachichnus delicatulus*. Reptile tracks include *Parabaropus coloradensis* and *Hyloidichnus bifurcatus* (seymouriamorph or diadectid tracks) and the small pelycosaur track *Gilmoreichnus hermitanus*. Two other more problematical ichnotaxa are *Ichniotherium gilmorei* (Haubold, 1971b) and *Limnopus* sp. (*Parabaropus coloradensis* of Gilmore).

Coconino Sandstone (Leonardian)

The most famous ichnofauna from Arizona is from the eolian Coconino Sandstone, first described in detail by Gilmore (Lull, 1918; Gilmore, 1926, 1927, 1928). The Coconino tracks pertain to the ichnogenus *Chelichnus* (McKeever and Haubold, 1996)(Fig. 2). The three valid species of *Chelichnus* are distinguished on the basis of size alone, and are presumed to be the tracks of a caseid-like animal (e.g., Haubold, 1971b). *Chelichnus bucklandi* has pedal impression lengths of 10-25 mm, *C. duncani* of 25-75 mm and *C. gigas* of 75-125 mm (McKeever and Haubold, 1996). Thus, all Gilmore's (and Lull's) named ichnotaxa from the Coconino Sandstone of the Grand Canyon can be placed in one of these three ichnospecies. Hunt and Santucci (1998a, b; 2001) reviewed the Grand Canyon tracks and also recognized a new (unnamed) morphotype.

Tracks from Outside NPS Areas

An area south of the Grand Canyon and north of Interstate 40 near Seligman in Yavapai County yields extensive ichnofaunas from the Coconino Sandstone. These specimens pertain to *Chelichnus bucklandi* and *C. duncani* and include parallel trackways (Kramer et al., 1995; Lockley and Hunt, 1995, figs. 2.11; Hunt et al., 2005).

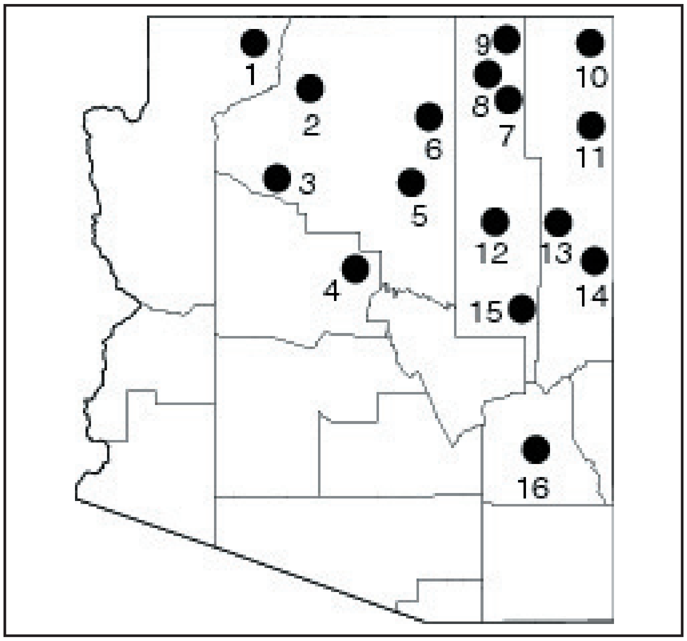

FIGURE 1. Distribution of vertebrate trace fossils in Arizona: 1. Pipe Springs National Monument: Jurassic tracks (Navajo Sandstone). 2. Grand Canyon National Park: Pennsylvanian-Permian tracks (Wescogame, Hermit and Coconino formations); Pleistocene dung and middens. 3. Seligman-Ashfork area: Permian tracks (Coconino Sandstone). 4. Montezuma Castle National Monument area: Tertiary tracks (Verde Formation). 5. Wupatki National Monument area: Triassic tracks (Moenkopi Formation). 6. Ward's Terrace area: Jurassic tracks (Moenave, Kayenta and Navajo formations). 7. Black Mesa: Cretaceous tracks (Toreva Formation). 8. Navajo National Monument area: Jurassic tracks (Navajo Sandstone). 9. Monument Valley Navajo Tribal Park area: Permian tracks (DeChelly Sandstone). 10. Teec Nos Pos area: Jurassic tracks (Summerville and Bluff formations). 11. Canyon DeChelly National Monument area: Permian tracks (DeChelly Sandstone). 12. Holbrook-Winslow area: Triassic tracks and coprolites (Moenkopi Formation); Tertiary tracks (Bidahochi Formation). 13. Petrified Forest National Park: Triassic tracks, coprolites and putative nests (Petrified Forest Formation). 14. St. Johns area (including *Placerias* quarry and Screaming Neotoma Cave): Triassic coprolites (Bluewater Creek Formation); Pleistocene middens and dung (cave). 15. Show Low area: Permian tracks (Schnebly Hill Formation). 16. Graham County (Southeastern Arizona): Tertiary tracks (Verde Formation).

The DeChelly Sandstone yields tracks that are very similar to those from the Coconino Sandstone near Canyon DeChelly National Monument in Apache County, northeastern Arizona, near the New Mexico border, and also from the area of Monument Valley Navajo Tribal Park (McKee, 1934; Brady, 1947; Vaughn, 1963; Morales and Haubold, 1995; Lockley et al., 1995). The ichnofauna of the eolian DeChelly Sandstone is broadly similar to that of the Coconino Sandstone in being dominated by *Chelichnus* (*C. bucklandi* and *C. duncani*)(Hunt et al., 2005). The DeChelly is unusual among Permian eolianites in yielding a specimen of the lacertoid track *Dromopus* cf. *D. agilis* (Haubold et al., 1995b).

The Schnebly Hill Formation has yielded a single pedal impression of *Dimetropus* sp. from a roadcut of the Schnebly Hill Formation in east-central Arizona near Show Low in Navajo County (MNA V 3392)(Haubold et al., 1995a).

TRIASSIC TRACKS

Wupatki National Monument

Wupatki National Monument preserves extensive outcrops of the Early-Middle Triasic Moenkopi Formation. There is a single *in situ* site that preserves a trackway of *Chirotherium* sp. There are also trackways on sandstone blocks lying on a talus slope beneath this site. These specimens are in need of study. Kirby (1987) reported swimming traces from Wupatki that he attributed to amphibians.

Petrified Forest National Park

Tetrapod tracks are found in three locations at Petrified Forest National Park in different units of the Petrified Forest Formation of the Chinle Group (upper Carnian-Norian). The first locality is a sandstone in the Teepees area in the upper Carnian Blue Mesa Member *sensu* Heckert and Lucas (2002)(Adamanian land vertebrate faunchron; St. Johnsian sub-land vertebrate faunachron), not the Monitor Butte Member as reported by Martin and Hasiotis (1998). These specimens include several pedal impressions of *Rhynchosauroides* sp., indeterminate swimming traces which could have been produced by phytosaurs and an indeterminate large trackway (Santucci and Hunt, 1993; Santucci et al., 1995: Martin and Hasiotis, 1998). Martin and Hasiotis (1998, fig. 5, left image) illustrate a dinosaurian track that we identify as a right pes impression of *Grallator* sp.

The second locality is in the Agate Bridge Bed of the upper Carnian Sonsela Member of Heckert and Lucas (2002)(Adamanian land vertebrate faunchron; Lamyan sub-land vertebrate faunachron) (= Petrified Forest Member of Martin and Hasiotis, 1998) near the Rainbow Forest. This ichnofauna includes *Rhynchosauroides* sp. and specimens that we identify as cf. *Grallator* and cf. *Brachychirotherium* sp. (Martin and Hasiotis, 1998).

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

Tracks from Outside NPS Areas

The Moenkopi Formation has yielded the most significant Early-Middle Triassic tetrapod ichnofauna in the Western Hemisphere. It has two distinct ichnofaunas, one from the Nonesian (late Spathian) Wupatki Member and the other from the Perovkan (early Anisian) Holbrook Member (Peabody, 1948).

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

The Holbrook ichnofauna includes the small reptile tracks *Rhynchosauroides schochardti*, *R. moenkopiensis* and *Rotodactylus bradyi*, the small-manus chirothere *Isochirotherium marshalli*, the large manus chirotheres *Chirotherium rex* and *Synaptichnium cameronense* and the dicynodont track *Therasipus cumminsi* (Peabody, 1948, 1956; Haubold, 1971a, b; Hunt et al., 1993). Some Moenkopi tracks preserve skin impressions (e. g., Nesbitt, 1999).

There are no Late Triassic tetrapod tracks known from Arizona outside Petrified Forest National Park.

JURASSIC TRACKS

Navajo National Monument

There are two tridactyl tetrapod tracks at Navajo National Monument from the Navajo Sandstone. Santucci et al. (1998) reported that the tracks were found in 1933, about a mile from Keet

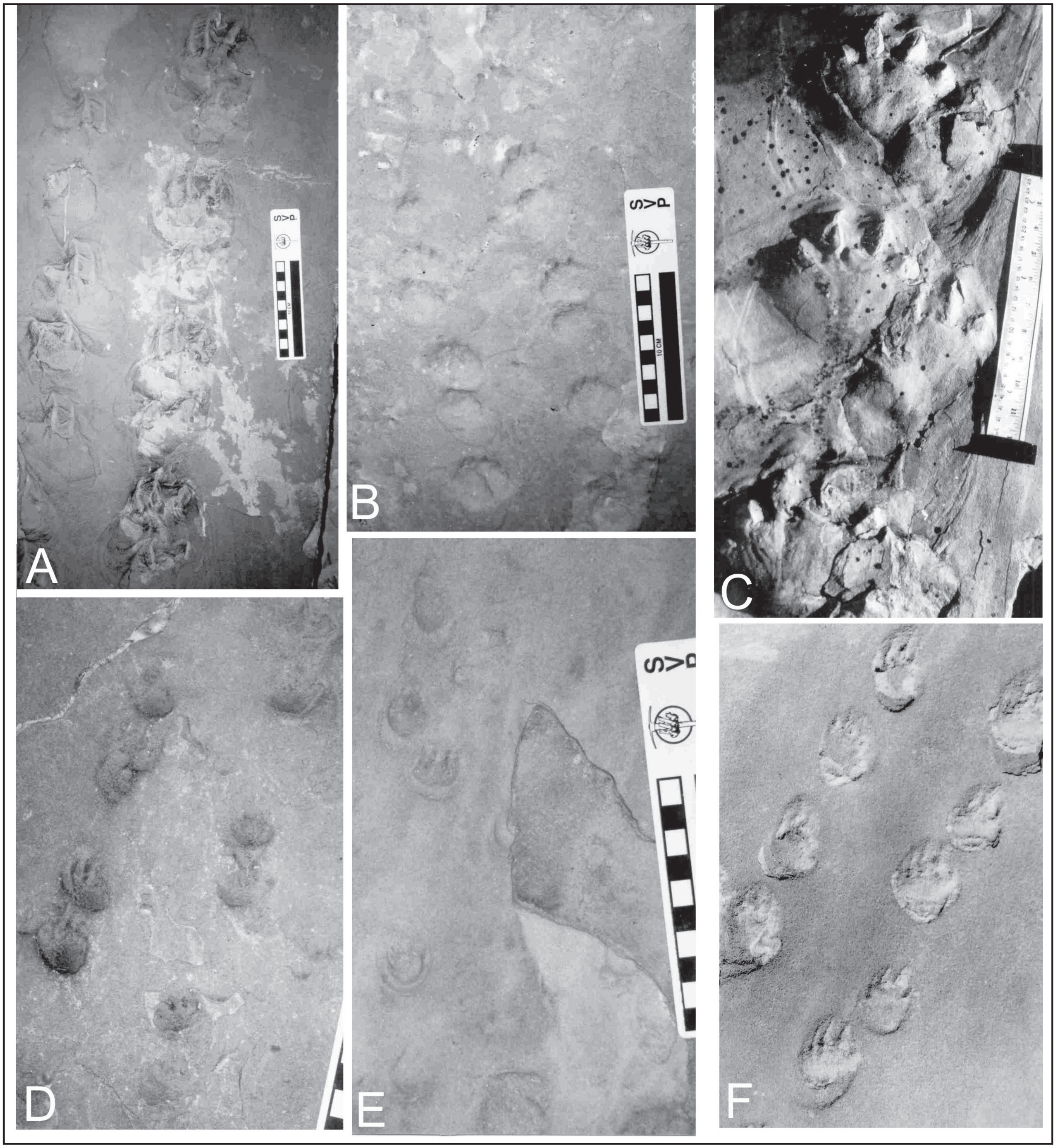

FIGURE 2. *Chelichnus* trackways from the Coconino Sandstone (Early Permian), Grand Canyon National Park, Arizona. **A**, *Chelichnus gigas*; **B**, *Chelichnus duncani*; **C**, *Chelichnus gigas*; **D**, *Chelichnus bucklandi*; **E**, *Chelichnus bucklandi*; **F**, *Chelichnus duncani*. Scale bars are in cm.

Seel archeological site. Mellberg (pers. comm., to VLS, 2005) indicated that the tracks originated about 10 miles outside the monument boundary near Tall Mountain. He reported that the 360-acre monument property does not preserve any tetrapod tracks.

The two tracks from near Navajo National Monument represent two morphotypes (Fig. 3). The first morphotype is a tridactyl, longer than wide, with a relatively long medial digit impression and narrow digit impressions (Fig. 3B). This track clearly pertains to a theropod dinosaur and we assign it to *Eubrontes* sp. The second morphotype is tridactyl, wider than long with relatively wide digit impressions and a shot medial digit impression (Fig. 3A). This track represents an ornithischian and is similar to *Dinepodus*.

Pipe Spring National Monument

Cuffey et al. (1998) described and illustrated three tracks *in situ* in the basal Navajo Sandstone from the Pipe Spring National

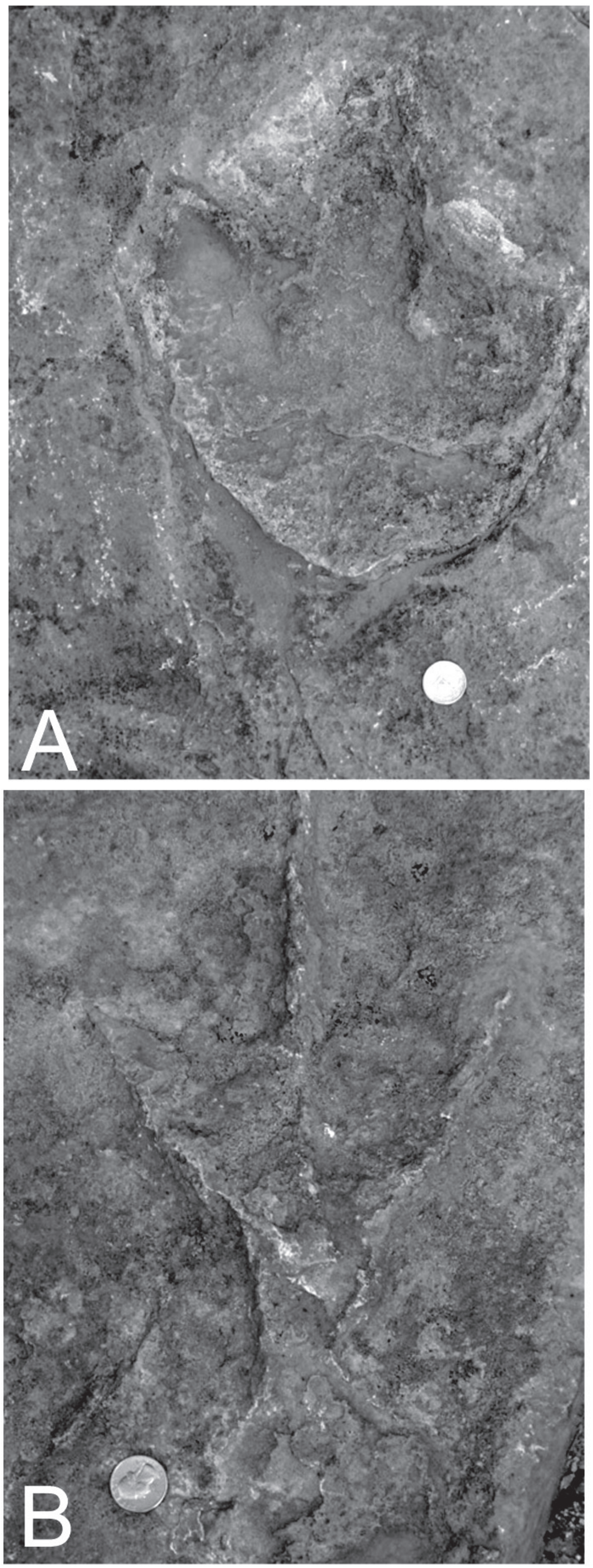

FIGURE 3. Jurassic dinosaur tracks from the Navajo Sandstone, Tall Mountain area, Arizona. **A**, Ornithischian track. **B**, Theropod track (*Eubrontes* sp.).

Monument (also see Cuffey et al., 1997 and Santucci et al., 1998, p. 112, fig. 2F). These tridactyl tracks are unusual in that the medial digit impression is not appreciably longer than the lateral digit impressions (Cuffey et al., 1998, fig. 3). Cuffey et al. (1998) identified the tracks as questionably *Eubrontes* sp. This identification is consistent with the size of the tracks, but not with the length of the middle digit impression. Additional tracks first reported by Stokes (1988) and studied by Cuffey (Cuffey et al., 1997; Cuffey et al., 1998) resemble Late Triassic tracks that have been assigned (probably incorrectly) to *Pseudotetrasauropus* in the relative length of the digit impressions (e. g., Lockley et al., 1993, fig. 2b). "*Pseudotetrasauropus*" is tetradactyl but is often preserved as a tridactyl undertrack.

Tracks from Outside NPS areas

The Dinosaur Canyon Member of the Moenave Formation on Ward's Terrace (Navajo Nation) has a sparse tetrapod footprint record (Lucas et al., 2005a,b). Tetrapod footprints are assigned to *Eubrontes* sp. and *Batrachopus deweyi* (Olsen and Padian, 1986; Irby, 1993a, b, 1995, 1996a,b). These records are stratigraphically high in the Moenave Formation (Lucas et al., 2005).

The Kayenta Formation on Ward's Terrace yields tetrapod footprints that are mostly assigned to the theropod ichnogenera *Eubrontes* sp. and *Grallator* sp. (Lockley and Hunt, 1995). Particularly significant is the relatively thin (< 5 m thick) footprint-bearing interval at the top of the Springdale Member of the Kayenta. This narrow interval yields tracks (mostly of *Eubrontes*) from St. George Utah to Tuba City, Arizona, which Lucas et al. (2005) refer to it as the Springdale megatracksite.

The Navajo Sandstone yields an extensive record of tetrapod footprints that includes theropod dinosaurs (*Grallator* sp., *Eubrontes* sp.), prosauropod dinosaurs (*Otozoum* sp.), ornithopod dinosaurs (*Anomoepus* sp.) and cynodonts (*Brasilichnium* sp.) (e.g., Baird, 1980; Cuffey et al., 1997; Lockley and Hunt, 1995; Rainforth and Lockley, 1996; Santucci et al., 1998). There is a strong need for ichnotaxonomic study of the Jurassic tetrapod tracks of the western United States to establish a ichnospecies-level taxonomy. Currently, ichnogenera that were established for the Liassic of the northeastern United States are utilized in the West and Southwest with scant regard to ichnospecies-level ichnotaxonomy.

A few tetrapod footprints, assigned to theropod dinosaurs (*Megalosauripus* sp.), sauropod dinosaurs and pterosaurs (*Pteraichnus* sp.), are known from the Middle-Upper Jurassic Summerville Formation and Bluff Sandstone in northeastern Arizona (e.g., Lockley et al., 1996; Lockley and Mickelson, 1997).

CRETACEOUS TRACKS

Tracks from Outside NPS Areas

There is only one tetrapod tracksite reported from the Cretaceous of Arizona. Irby and Albright (2002) described a tracksite in the Toreva Formation (middle Coniacian) of the Black Mesa Basin that preserves over 100 footprints and rare tail-drag marks. Irby and Albright (2002) describe both ornithopod and theropod tracks, although we are not convinced that theropod tracks are present (e. g., Irby and Albright, 2002, fig. 7b). Unfortunately, no tracks can be associated with the putative tail-drag marks.

CENOZOIC TRACKS

Montezuma Castle National Monument

"Elephant Hill" is a proboscidean tracksite at Montezuma Castle National Monument. (Santucci et al., 1998, fig. 3G)(Fig. 4). Tracks occur in a limestone unit of the Pliocene Verde Formation. The proboscidean tracks are 40-45 cm in diameter with a stride of

FIGURE 4. Proboscidean track from the Pliocene Verde Formation, Montezuma Castle National Monument.

about 2 m. The tracks are overstepped with superimposed manual and pedal impressions (Brady and Seff, 1959). There are at least two track localities in the area around the monument that yielded specimens reposited at the American Museum of Natural History (Santucci et al., 1998).

Tracks from Outside NPS Areas

The Miocene Bidahochi Formaion preserves tracks of two types of birds and a camel (Breed, 1973; Lockley and Hunt, 1995; MNA collection). Breed (1973) reported tracks of two different types of birds from the Coliseum Diatreme about 60 km north of Holbrook in Navajo County. One morphotype of bird track resembles traces of the modern Canada Goose (*Branta*), and the other represents a large heron-like wader.

Czaplewski (1990) mentioned the presence of mammal tracks in the Pliocene Verde Formation, including cat, tapir, camel, and proboscidean traces. These tracks were briefly described by McGeorge and Schur (1994), who also mentioned "antelope-like" tracks. Thompson et al. (2002) describe tracks from the Pliocene Bear Springs fauna. They mention camel, horse and mastodon tracks from Bear Springs.

SIGNIFICANCE OF THE ARIZONA TETRAPOD TRACK RECORD

The record of tetrapod tracks in Arizona is extensive and important. Some of the most significant aspects of these ichnofaunas are:

1. The first large Paleozoic ichnofaunas were described from Grand Canyon National Park.

2. The westernmost Pennsylvanian tetrapod tracks in North America (Wescogame Formation at Grand Canyon National Park).

3. The largest collected and described sample sizes of trace fossils from eolianites (Coconino and DeChelly sandstones)

4. Significant late Early Permian (Leonardian) tetrapod ichnofaunas – other notable Leonardian tracks are limited to Texas and Oklahoma (Haubold and Lucas, 2001, 2003; Lucas and Hunt, 2005).

5. The Moenkopi tracks represent the most significant Early-Middle tetrapod ichnofaunas in the New World.

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

OTHER TETRAPOD TRACE FOSSILS

The majority of the tetrapod trace fossils from Arizona are tracks. However, there are other trace fossils known from the state, notably of coprolites and nests. We briefly review this record, which warrants more detailed study. There are no records of eggs or skin impressions from Arizona (exclusive of tracks with skin impressions: e.g., Nesbitt, 1999).

Coprolites

In Arizona, vertebrate coprolites have been described from the Moenkopi Formation, Chinle Group, Moenave Formation, Fort Crittenden Formation and unnamed late Cenozoic cave deposits. Vertebrate coprolites have an acme zone in the Permo-Triassic (Hunt and Lucas, 2005), so it is not surprising that the fossiliferous Triassic red beds in Arizona yield abundant vertebrate coprolites.

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

Vertebrate coprolites are locally common in strata of the Upper Triassic Chinle Group. Hunt et al. (1998) described *Dicynodontocopros maximus* from the Bluewater Creek Formation at the *Placerias* quarry near St. Johns. They also noted that *Heteropolacopros texaniensis* occurs in the Blue Mesa Member of northeastern Arizona. This occurrence is actually at Petrified Forest National Park (Hunt and Santucci, 1994). Heckert (2001, 2004) and Murry (1989) noted the occurrence of coprolites, some of which contain fish scales, teeth and plant debris, from the Blue Mesa Member at the "Dying Grounds" locality in Petrified Forest National Park. Undescribed coprolites occur in the Blue Mesa and Painted Desert members of the Petrified Forest Formation at Petrified Forest National Park. Wahl et al. (1998) described coprophagy in coprolites from the Blue Mesa Member at Petrified Forest National Park.

Clark and Fastovsky (1986) reported coprolites from the Whitmore Point Member of the Moenave Formation (Lower Jurassic: Hettangian) near Fredonia, Arizona. There are other unstudied specimens in the NMMNH collection. Heckert et al. (2003) described coprolites from the Fort Crittenden Formation (Upper Cretaceous: Campanian).

Arizona preserves extensive late Pleistocene dung, principally at Grand Canyon National Park, where almost 450 km of the canyon of the Colorado River is present. The famously deep incision of the river exposes extensive outcrops of Paleozoic strata, including limestone units. The Cambrian Muav Limestone of the Tonto Group and the Mississippian Redwall Limestone contain hundreds of caves within the national park. These caves yield extensive late Pleistocene-Holocene vertebrate faunas which include fossil dung as well as invertebrate and invertebrate fossils (e. g., Mead, 2005). Indeed, these caves provide a unique look at the late Pleistocene-early Holocene faunas and floras of the southwestern United States with vertebrates from fish to birds as well as plant and pollen remains. The preservation within these dry caves is exceptional and includes, for example, soft tissue of *Oreamus harringtoni* (hair, muscle, ligament) as well as keratinous horn sheaths and large quantities of dung (Mead et al., 1986; Santucci et al., 2001).

These superb paleontological deposits are the result of a unique set of circumstances: (1) long and deep canyon; (2) exposure of a sequence of marine limestones; (3) development of hundreds of caves in these limestones; (4) dry, hot climate, which provides exceptional conditions for preservation; and (5) inaccessible location of many of these caves (which has limited disturbance). In that the Grand Canyon caves provide exceptional preservation, an abundance of fossils and provide a unique window into an ancient world, they collectively constitute a Lagerstätte. The term Lagerstätten was introduced by Seilacher (1970) to refer to fossil localities that display exceptional preservation in quality, quantity and diversity, after the German word for "mother lode." Seilacher (1970, 1990) recognized two forms of Lagerstätten: (1) Konzentrat-Lagerstätten ("concentration mother lodes") contain large numbers of fossils that largely exclude the preservation of soft parts; and (2) Konservat-Lagerstätten ("conservation mother lodes"),which are distinguished by the preservation of soft parts and a diversity of taxa. Thus, Konzentrat-Lagerstätten are distinguished primarily by quantity, whereas Konservat-Lagerstätten are distinguished by the quality of preservation (Seilacher, 1990). Hunt et al. (2005) recently expanded the concept of Lagerstätten by designating an ichnological example. The Grand Canyon caves collectively comprise two forms of speleological Lagerstätte: a Konzentrat-Lagerstätte and a Konservat-Lagerstätte. This Lagerstätte gives a unique insight into the late Quaternary of the southwestern United States.

Many of the caves in Grand Canyon National Park preserve fossil dung, including Vulture Cave, Rampart Cave, Muav Caves, Stanton's Cave, Tse'an Bida Cave, Tse'an Kaetan Cave, Steven's Cave, Sandblast Cave, Shrine's Cave, Hummingbird Cave, Crescendo Cave, Rebound Cave, Left Eye Cave, Five Windows Cave, White Cave, Disappearing Cave, CC:5:1 cave, CC:5:3 cve, CC:5:4 cave and CC:5:6 cave (Santucci et al., 2001; Mead et al., 2003). These dung represent rodents (?*Peromyscus*), packrats (*Neotoma* spp.) carnivore (*Bassariscus astutus*), Shasta Ground Sloth (*Nothrotheriops shastensis*), Harrington's Mountain Goat (*Oreamus harringtoni*), Bighorn Sheep (*Ovis canadensis*) and raptors (Santucci et al., 2001; Mead et al., 2003). The dung occurs in a variety of contexts, from isolated pellets through matted dung to stratified dung deposits (Santucci et al., 2001). The most spectacular accumulation was in Rampart Cave, which preserved extensive Shasta Ground Sloth dung before a fire in 1976 (Santucci et al., 2001, figs. 9-12; McDonald, 2003, fig. 1.6: Fig. 5). Tetrapod dung occurs in other caves in Arizona such as Screaming *Neotoma* Cave south of St. Johns (Bell and Glennon, 2003).

The most studied and scientifically significant dung relates to the Shasta Ground Sloth (*Nothrotheriops shastensis*)(Fig. 5), which yields more than 70 species of plants as well as insect and parasite remains (McDonald, 2003). Evidence from this dung has been important in the discussion of scenarios relating to the causation of late Pleistocene extinctions (McDonald, 2003). Shasta Ground Sloth dung is one of only a few instances where coprolites, in the absence of body fossils, has been utilized to infer the presence of a species (McDonald, 2003; cf. Hunt et al., 1998). Bat guano is also common in caves in Arizona (e. g., Santucci et al., 2001), but its distribution has not been well documented.

The application of an ichnotaxonomic methodology to tetrapod coprolites has been useful in the Paleozoic and Mesozoic (e. g., Hunt et al., 1998). We believe that there will be a utility in applying binomials to Late Cenozoic dung for several reasons: (1) it will draw attention to these significant trace fossils and they will be more consistently described and recorded resulting in the recognition of their independent utility in biostratigraphy and environmental analysis (e. g., Hunt et al., 1998); (2) it will introduce rigor into the identification of dung – assumptions are currently being made about attributions of dung based on unstated assumptions which may or may not be correct; and (3) data derived from (1) and (2) will allow study of their distribution, in both the presence and absence of the producer, which could have potential in taphonomic and paleoecological analyses.

FIGURE 5. Abundant dung of the Shasta Ground Sloth (*Nothrotheriops shastensis*) in Rampart Cave, Grand Canyon National Park, prior to the 1976 fire.

Tetrapod nests

Putative tetrapod nests have been described from the Agate Bridge Bed of the upper Carnian Sonsela Member (Adamanian land vertebrate faunchron; Lamyan sub-land vertebrate faunachron) (= Flattop sandstone #1 of Hasiotis et al., 2004) at Petrified Forest National Park. These putative nests (> 100) are closely spaced pits (average spacing 64 cm) with circular to elliptical openings 10-20 cm in diameter (Hasiotis et al., 2004). Unfortunately, Hasiotis et al. (2004) do not segregate description and interpretation and they do not establish clear criteria by which these structures can be evaluated as nests. Some potentially important data, such as parental body impressions, are not described. We do not accept that the structures that they interpret as shallow footprints (Hasiostis et al., 2004, fig. 3G) are tetrapod tracks, but instead we believe that they are erosional pits. These structures are in need of more detailed study before their interpretation as vertebrate nests can be validated.

Two types of nest-related trace fossils are common in the late Pleistocene-Holocene. Packrats (*Neotoma* spp.) periodically clean their dens and produce middens (piles) of discarded material. Middens can become cemented by repeated trampling and urination. Middens are common in late Pleistocene-Holocene caves and cliff overhangs. The ringtail procyonid *Bassariscus astutus* forms deposits that are also the result of nest-cleaning, and these are known as ringtail refuse deposits. Both middens and ringtail refuse deposits are numerous in caves at Grand Canyon National Park (Santucci et al., 2001), but there is no comprehensive study of their distribution in Arizona. However, middens are present in other caves in Arizona (e. g., Bell and Glennon, 2003) and we believe that they may be the most numerous vertebrate trace fossils in Arizona. There is evidence of other late Pleistocene vertebrate nests in Arizona such as raptors including the condor (*Gymnogyps*)(Mead et al., 2003; Mead, 2005).

PHANEROZOIC PRESERVATION OF TETRAPOD TRACKS

The temporal pattern of tetrapod track occurrences in Arizona is broadly similar to global trends. Thus, tracks are first common in the Carboniferous, Permian tracks are very abundant, Mesozoic tracks are common and Cenozoic tracks are much rarer than Mesozoic tracks. There are temporal trends in vertebrate taphonomy (e. g., Hunt, 1987), but there has been little discussion of causality related to tetrapod track taphonomy. We would expect that four fundamental factors should affect track preservation and abundance:

1. Tracks will only be common when terrestrial tetrapods are common.

2. Increasingly complex vegetation, increased terrestrial ground cover and increased sediment binding took place through the Phanerozoic.

3. Tetrapod tracks will be more common when ground cover is less extensive.

4. The preservation potential of tetrapod tracks increases with body size because of the increased depth of sediment penetration.

We thus identify four temporal phases in the taphonomy of tetrapod tracks.

1. Devonian – few tracks, because terrestrial tetrapods are rare and lack of plant ground cover resulted in frequent reworking of terrestrial surfaces.

2. Carboniferous-Triassic – many tracks because terrestrial tetrapods are common and increased ground cover reduced the reworking of terrestrial surfaces.

3. Jurassic-Cretaceous – tracks will be numerous and preserved in more diverse sedimentary environments because terrestrial animals are very large, even though ground cover is increased.

4. Cenozoic – increased ground cover, especially after the diversification of grasses, resulted in less unvegetated areas where tracks can be preserved (with a few notable exceptions such as lacustrine margins).

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