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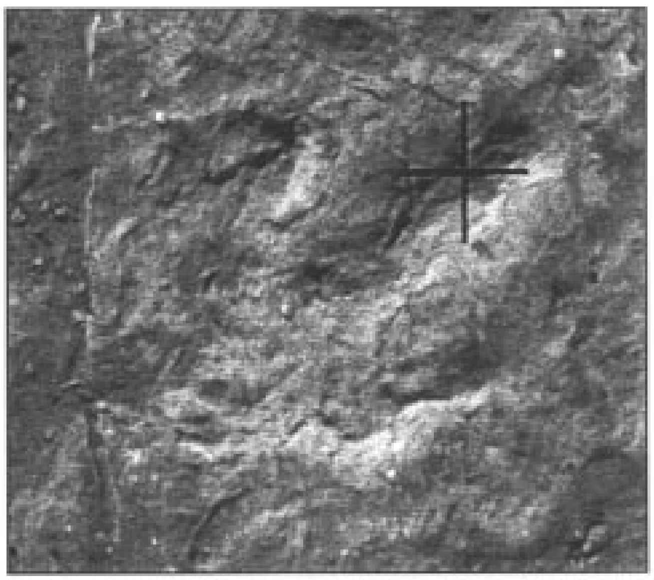

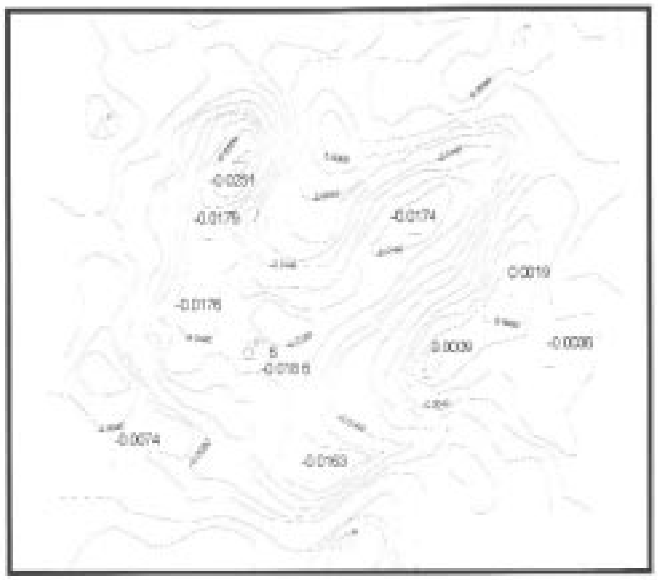

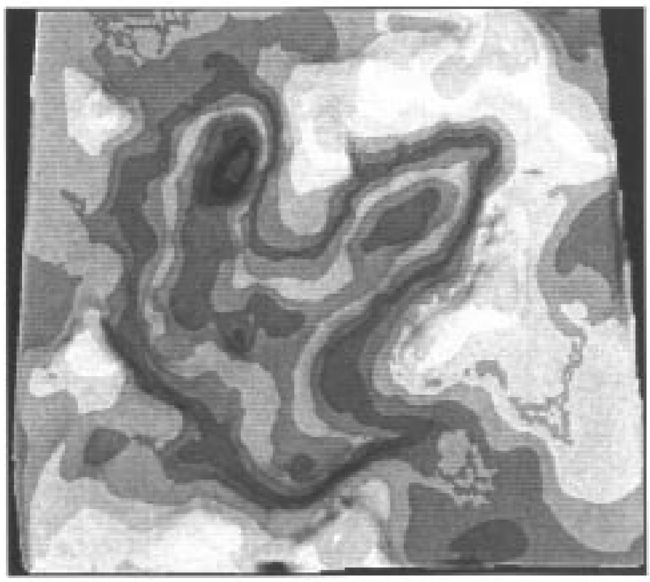

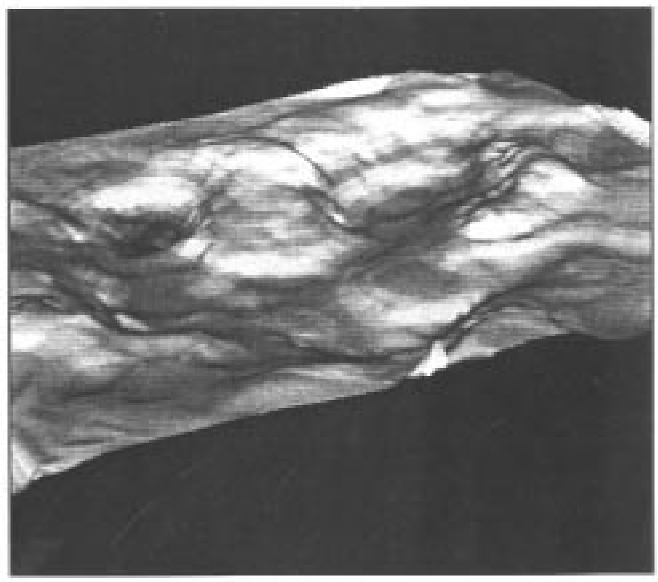

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Cover Illustration
Photo of Red Gulch Dinosaur Tracksite footprint (upper left); digital contour of track (upper right); Digital Terrain Model of track, planar view (lower left); and Digital Terrain Model of track, oblique view (lower right).

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AN UNUSUAL TETRAPOD TRACK MORPHOLOGY FROM THE PERMIAN COCONINO SANDSTONE, GRAND CANYON NATIONAL PARK, ARIZONA

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ABSTRACT—The Permian Coconino Sandstone at Grand Canyon National Park has yielded an important vertebrate ichnofauna. Currently all specimens from the Coconino Sandstone are assigned to species of *Chelichnus*. A morphologically distinct trackway has been discovered along the Hermit Trail and in Marble Canyon that differs from *Chelichnus* in: (1) possession of tail drag; (2) disparity in size between manus and pes impressions; (3) pace angulation greater than 90°; and (4) L-shaped manus impression. This represents a previously unrecognized morphology for Permian eolianites.

INTRODUCTION

Paleozoic tetrapod ichnofaunas from Grand Canyon National Park are among the most significant in North America (Hunt and Santucci, 1998a). The majority of specimens were collected by Charles Gilmore of the United States National Museum (Smithsonian) and described by him in a series of classic works (Gilmore, 1926b, 1927b, 1928a). Santucci and Wall (1995) conducted a preliminary reconnaissance of the Coconino Sandstone in the area of the Hermit Trail in Grand Canyon National Park (Fig. 1). The purpose of this paper is to describe an unusual track morphology from that location that is distinct from those previously reported within the Coconino Sandstone.

PALEOZOIC TETRAPOD TRACKS FROM THE GRAND CANYON

Schuchert (1918) is credited as the first collector of tetrapod tracks in Paleozoic strata on the South Rim of the Grand Canyon. Lull (1918) utilized the portion of the collection from the Permian Coconino Sandstone to publish the first scientific description of Paleozoic tetrapod tracks from Arizona. In 1924, the National Park Service invited Charles Gilmore to visit Schuchert's locality and to prepare an *in situ* exhibit on a now abandoned portion of the Hermit Trail (Spamer, 1984). Gilmore (1926b) described this new collection of Coconino ichnofossils and was later funded, by the Marsh Fund Committee of the National Academy of Sciences (1926) and the Grand Canyon Exhibit Committee of the National Academy of Sciences (1927), to make additional collections and exhibits (Spamer, 1984). In addition to the new trace fossil collections from the Coconino, Gilmore collected vertebrate tracks from the Hermit Shale (Permian) and Wescogame Formation of the Supai Group (Pennsylvanian). Gilmore described this new material in additional monographs (Gilmore, 1927b, 1928a) and a short paper on the first tracks from the North Rim (Gilmore and Sturdevant, 1928). Gilmore also wrote three more popular papers describing his collecting efforts in the Grand Canyon (Gilmore, 1926a, 1927a, 1928b).

For the next 70 years there was little reevaluation of Gilmore's work except by Don Baird of Princeton (Baird, 1952, Baird in Spamer, 1984). A renaissance in Paleozoic track studies took place during the mid-1990's. The Rosetta Stone for a new re-evalualtion of Permian tracks was provided by studies of the extensive ichnofaunas from the redbeds of southern New Mexico (Haubold et al., 1995a, b; Hunt et al., 1995). The New Mexico tracksites provided large sample sizes of all the most significant Permian ichnotaxa and included a broad range of preservational variants. These samples provided a new perspective on the plethora of

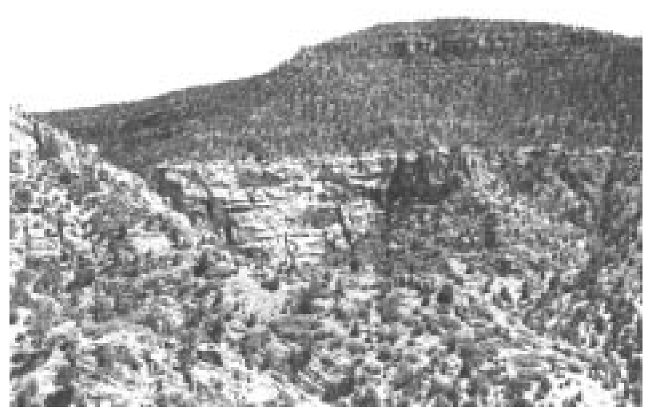

FIGURE 1. Cross section view of the Permian stratigraphy near the Hermit Trail at Grand Canyon National Park. The Coconino Sandstone is overlain by the Kaibaba Limestone.

ichnotaxonomic names of tetrapod tracks from Permian redbeds, most of which had been described on the basis of small sample sizes. During the same timeframe there was a major reevaluation of the equally confused ichnotaxonomy of tetrapod tracks from Permian eolianites (Morales and Haubold, 1995; Haubold et al., 1995a, b; McKeever and Haubold, 1996; Haubold, 1996; Hunt and Santucci, 1998a,b). Hunt and Santucci (1998a) presented a reassessment of the ichnotaxonomy of the Coconino tracks from Grand Canyon National Park on the basis of this new synthesis (Table 1).

TETRAPOD ICHNOLOGY OF THE COCONINO SANDSTONE

The first fossil footprints to be described in the scientific literature came from Permian eolianites of Scotland (Grierson, 1828). Subsequently, paleontologists described important ichnofaunas from eolian strata of Germany (Cornberger Sandstein), Colorado (Lyons Sandstone), and Arizona (Coconino Sandstone, DeChelly Sandstone), as well as additional specimens from Scotland (Hopeman, Corncockle and Locharbriggs Sandstone formations). An extensive literature describes many ichnotaxa from these formations. However, recent work spearheaded by Hartmut Haubold has demonstrated that virtually all tetrapod tracks from Permian eolianites represent three ichnospecies of one ichnogenus, with only the rarest exceptions (Haubold et al., 1995b; McKeever and Haubold, 1996; Haubold, 1996). All of the Coconino vertebrate tracks apparently fall within three species of *Chelichnus* (McKeever and Haubold, 1996). *Chelichnus* is characterized by rounded manual and pedal impressions that are of nearly equal size and that exhibit five short, rounded toe impressions (though fewer than five may be preserved). Trackways have a pace angulation of about 90°, and the manual and pedal impressions are close together (McKeever and Haubold, 1996). 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 (Haubold, 1971). *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 of Gilmore's and Lull's named ichnotaxa from the Coconino Sandstone of the Grand Canyon can be placed in one of these three species. Gilmore (1927b) was aware of the similarity between some of his specimens from the Grand Canyon and those from Scotland, but he persisted with his (and Lull's) distinct ichnotaxonomy (Gilmore, 1928a).

Singularly, size is not the ideal criterion with which to distinguish between ichnospecies, however, the revised ichnotaxonomy presented here represents the current consensus (Table 1). The low ichnotaxonomic diversity of the Coconino is in keeping with the low animal diversity that would be expected in an arid dunefield.

Gilmore was aware that the Coconino Sandstone and Hermit Shale were deposited in different sedimentary environments, however, Baird (1965) was the first to emphasize that the differences between the Permian ichnofaunas of the redbeds of the American West and those of eolianites might be a result of facies differences. There has been a long tradition of recognizing ichnofacies in invertebrate traces, but the concept has only recently been applied to vertebrate tracks (Lockley et al., 1994). Tetrapod ichnofacies have been defined as "multiple ichnocoenoses that are similar in ichnotaxonomic composition and show recurrent association in particular environments (Lockley et al., 1994, p. 242). Lockley and others (1994), Hunt and others (1995), Haubold (1996) and Hunt and Lucas (1998a) have all discussed Permian tetrapod ichnofacies.

The low-diversity tetrapod ichnofauna of the Coconino Sandstone has been interpreted to represent the *Chelichnus* ichnofacies (= *Laoporus* ichnofacies of Lockley et al., 1994) that is known from the DeChelly and Coconino sandstones of Arizona, the Lyons Sandstone of Colorado, the Hopeman, Corncockle and Locharbriggs Sandstone formations of Scotland, the Cornberger Sandstein of Germany and the Los Reyunos Formation of Argentina (Hunt and Lucas, 1998a, b; Hunt and Santucci, 1998a).

UNUSUAL TRACKS

In 1993, we noted a morphologically enigmatic trackway near the present Hermit Trail and have subsequently reexamined this trackway and others in the same area. The trackway is distinct from most Coconino *Chelichnus* tracks in five characteristics (Fig. 2 and 3): (1) the trackway proceeds directly up the dune face, whereas most trackways traverse at an oblique angle; (2) the tracks are much larger than average for the Coconino; (3) there is a prominent, sinuous tail drag; (4)

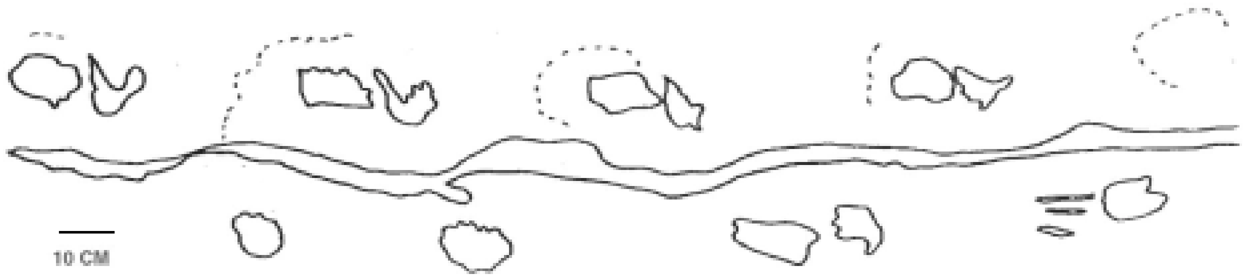

FIGURE 2. Map of trackway exhibiting unusual morphology from the Permian Coconino Sandstone near the Hermit Trail, Grand Canyon National Park, Arizona.

FIGURE 3. Overview of tracksite looking up the dune face. A small *Chelichnus duncani* trackway (left arrows) zigzags up the dune face to the right ofo the large enigmatic trackway (right arrows).

the manus print is smaller than the pes: and, (5) the manus track is L-shaped. Subsequently, a second trackway of similar morphology was discovered near the first trackway. We later noted that Price (1998, p. 21) illustrated a similar trackway from the Coconino near Buck Farm Canyon, a side canyon of Marble Canyon within Grand Canyon National Park. Price's (1998, p. 21) specimen also has a sinuous tail-drag and L-shaped manus tracks (note first manus print on the left side of trackway in foreground of photograph).

The first Hermit Trail trackway is preserved *in situ* on a bedding plane that dips 55^{o}. The left portion of the trackway is more distinct than the right. The pes tracks are ovoid with no distinct digital impressions. The tracks are oriented with the long axis in the direction of travel. The pes tracks average 10 cm in length and exhibit a stride between 55 and 58 cm. The manus tracks average 8 cm in antero-posterior length. These tracks are variable in morphology. Several are L-shaped with one axis directed antero-lateral to the direction of travel and the other lateral to slightly postero-lateral. The tail drag is continuous and sinuous, however, it is variable in width with a maximum of 5 cm. The pace angulation varies from between 90^{o} to 120^{o}.

These trackways do not conform to any of the trackway morphologies described by Gilmore. Furthermore, they differ from *Chelichnus* (*sensu* McKeever and Haubold, 1995) in: (1) possession of tail drag; (2) disparity in size between manus and pes impressions; (3) pace angulation greater than 90^{o}; and (4) L-shaped manus impression. The only other tracktypes identified in Permian eolianites are lacertoid in morphology (Haubold et al., 1995). These tracks do have larger pace angulations, disparity in size between manus and pes impressions, and tail drag marks. However, lacertoid tracks are smaller and possess small sole pads.

In conclusion, the new trackway appears to represent a new component of the Coconino ichnofauna. Further study is needed to confirm whether this represents a new ichnotaxon. It is highly unlikely, but still possible that this track morphology represents an extreme extramorphological variant of *Chelichnus*.

TABLE 1. Tetrapod ichnofauna of the Coconino Sandstone

Chelichnus duncani (Owen, 1842) (=*Baropezia arizonae, Allopus? arizonae, Baropezia eakini, Agostopus matheri, Agostopus medius, Palaeopus regularis, Barypodus tridactylus, Barypodus metszeri, Nanopus maximus, Laoporus noblei*, in part of Gilmore, 1926b)

Chelichnus gigas (Jardine, 1850) (=*Barypodus palmatus, Amblyopus pachypodus, Baropus cocninoensis*)

Chelichnus bucklandi (Jardine, 1850) (=*Dolichopodus tetradactylus, Laoporus schucherti, Laoporus coloradensis, Nanopus merriami, Laoporus noblei*, of Lull, 1918)

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