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DICYNODONT TRACKWAYS FROM THE HOLBROOK MEMBER OF THE MOENKOPI FORMATION (MIDDLE TRIASSIC: ANISIAN), ARIZONA, USA

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ABSTRACT: *Therapsipus cumminsi* gen. et sp. nov. is a dicynodont trackway from the Holbrook Member of the Moenkopi Formation (early Anisian) in northeastern Arizona. The trackmaker was a wide-bodied animal with blunt digits that walked with a primitive alternate gait.

INTRODUCTION

The Triassic Moenkopi Formation of northeastern Arizona and southeastern Utah has yielded a diverse ichnofauna which consists of 22 taxa of vertebrate, and 5 invertebrate, tracks (Morales, 1987, table 1). The vertebrate ichnofauna, which was monographed by Peabody (1948), is dominated by species of *Chirotherium, Isochirotherium* and *Synaptichnium* (Haubold, 1971, 1984). Smaller vertebrate ichnotaxa include *Rhynchosauroides, Rotodactylus* and *Capitosauroides* (Morales, 1987). Here we describe an addition to this diverse ichnofauna, a new, large vertebrate ichnotaxon from the upper Moenkopi Formation of the Holbrook area, Navajo County, Arizona.

STRATIGRAPHY

In northeastern Arizona, the Moenkopi Formation consists of three members which are in ascending order the Wupatki, Moqui and Holbrook Members. Both the Wupatki (middle Spathian) and Holbrook (early Anisian) Members yield vertebrate ichnofossils in Arizona (Table 1). The ichnofossils described below are from the area of the town of Holbrook in the upper part of the formation. Unfortunately, there is no type or lectotype section for the Holbrook Member whose type area is the town of Holbrook. As a result, two lower boundaries have been used for the Holbrook Member (Morales, 1988). The first contact is drawn at the top of the highest bed of gypsum in the Moqui Member (McKee, 1954) and the second is at the base of the lowest persistent, ledge-forming sandstone above the gypsum. In the vicinity of the new ichnites these boundaries apparently coincide (Fig. 1). We measured a thickness of 16.6 m for the Holbrook Member (Fig. 1, 2A) at the tracksite which compares with 13.8 m (45 ft) which McKee (1954, table 4) measured at the town of Holbrook and 14.2 m (46.5 ft) that Welles (1947, table 1) measured west of town. The Holbrook Member is considered to be early Anisian in age on the basis of the presence of the benthosuchid *Eocyclotosaurus* (Morales, 1987).

SYSTEMATIC PALEONTOLOGY

Therapsipus ichnogen. nov.

Type species: *Therapsipus cumminsi* .

Included species: Known only from the type species.

Etymology: From Therapsida to note the postulated trackmaker.

Distribution: Triassic of North America.

Diagnosis: Therapsipus differs from other tracks of quadrupedal tetrapods in having a pentadactyl pes and a pentadactyl manus (in which digit I is poorly impressed) of large size with concave posterior margins and a pace angulation of about 85o.

Discussion: This trackway obviously represents a large, wide-bodied quadruped with blunt digits (Figs. 2B, 3-4). This suggests that the trackmaker was a herbivore. In the Middle Triassic the most common large herbivores were dicynodonts and rhynchosaurs. Rhynchosaurs can be eliminated as a possible trackmaker because of their very asymmetrically lengthened digits (e. g., Benton, 1990, figs. 18c, 20a). Therefore, it seems likely that the trackmaker was a dicynodont. The number of digits, relative size of the manus and pes and wide gait are consistent with this interpretation (King, 1988, 1990). Also the small digit I impression in the manus print would be consistent with a dicynodont interpretation (King, 1988, fig. 40e). Furthermore, there are no other large, wide-gaited tetrapods known from the Anisian which could be potential trackmakers.

Therapsipus cumminsi ichnosp. nov.

Holotype: Trackway illustrated in Fig. 2B (upper trackway and Fig 3 (trackway on right). A partial latex mold of this trackway is housed at the University of Colorado at Denver.

Type locality: Holbrook, Arizona (exact locality on file at the University of Colorado at Denver).

Type horizon: Holbrook Member of Moenkopi Formation (early Anisian).

Distribution: As for genus.

Left Pes Width/Length	Left Manus Width/Length	Right Pes Width/Length	Right Manus Width/Length
Trackway I			
	237/212	256/247	212/222
	234/217	232/248	235/202
			193/159
Trackway II			
236/247	253/221	227/257	214/174
224/205	236/175	222/241	204/220
	225/247	174/226	

TABLE 1. Width and length measurements of the tracks of *Therapsipus cumminsi* gen. et sp. nov.(in mm).

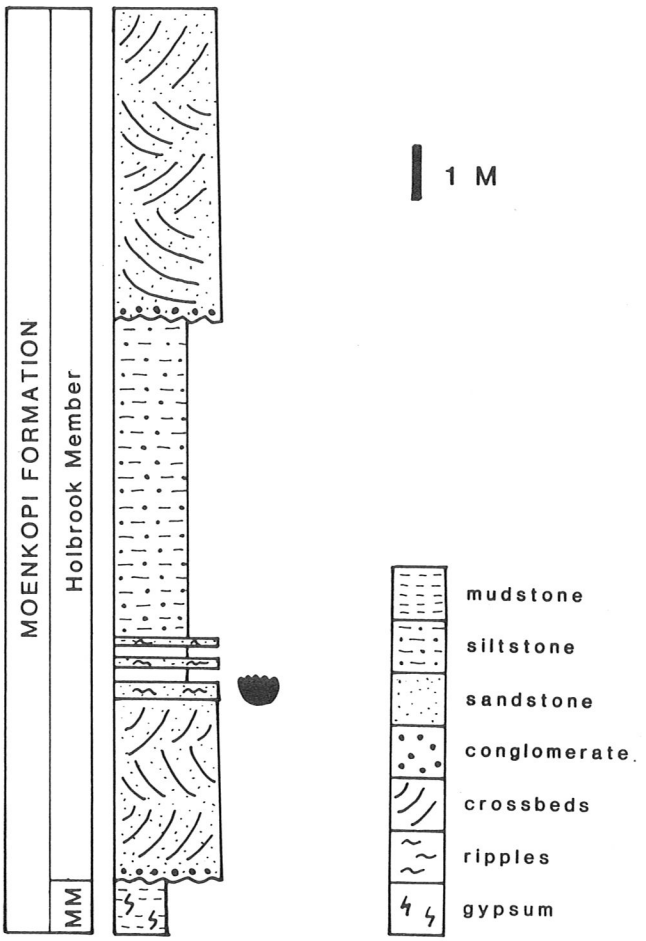

FIGURE 1. Stratigraphic section of the upper Moenkopi Formation, Holbrook, Arizona (USA) showing the stratigraphic level of *Therapsipus cumminsi*, gen. et sp. nov. MM is Moqui Member.

Referred specimens: None.

Etymology: For Gary S. Cummins, Assistant Superintendent of Grand Canyon National Park and former Superintendent of Petrified Forest National Park, for his support of paleontological research in the National Park Service.

Diagnosis: As for genus.

Description: Two trackways head north and northeast respectively (Figs. 2B, 3). The northerly track (trackway I) starts with a right manus print and a left manus print. The northeasterly holotype trackway (trackway II) starts with a right pes print and a left manus print.

Pes impressions are slightly longer than wide whereas manus prints are slightly wider than long. Pes impressions average 224 mm in width and 250 mm in length (n = 7) and manus prints average 224 mm in width and 214 mm in length (n = 10) (Table 1). The pes prints has 5 digit impressions with digit III being the longest and the other digits decreasing in size away from it.

In the manus prints, digit I leaves only a small impression if any. Impressions of digits II and IV are the longest and are subequal in length. The impressions of digits II and V are shorter and subequal in length.

The pes prints diverge from the midline of the trackway at about 45o whereas the manus prints diverge at about 60o. Pace angulations average 84o degrees (n = 3) for trackway I measured from manus prints.

Discussion: This species can easily be distinguished from the common chirotheres of the Holbrook Member by several features: (1) low pace angulation; (2) large size of manus imprints relative to pes imprints; and (3) lack of divergent digit V impression on manus print.

There are no Triassic trackways from Europe that are very similar to *Dicynodontipus*. The only reasonably well known ichnogenus that has been assigned a therapsid origin is *Dicynodontipus* (see Haubold, 1984 for summary). This ichnogenus represents a much smaller trackmaker (foot l

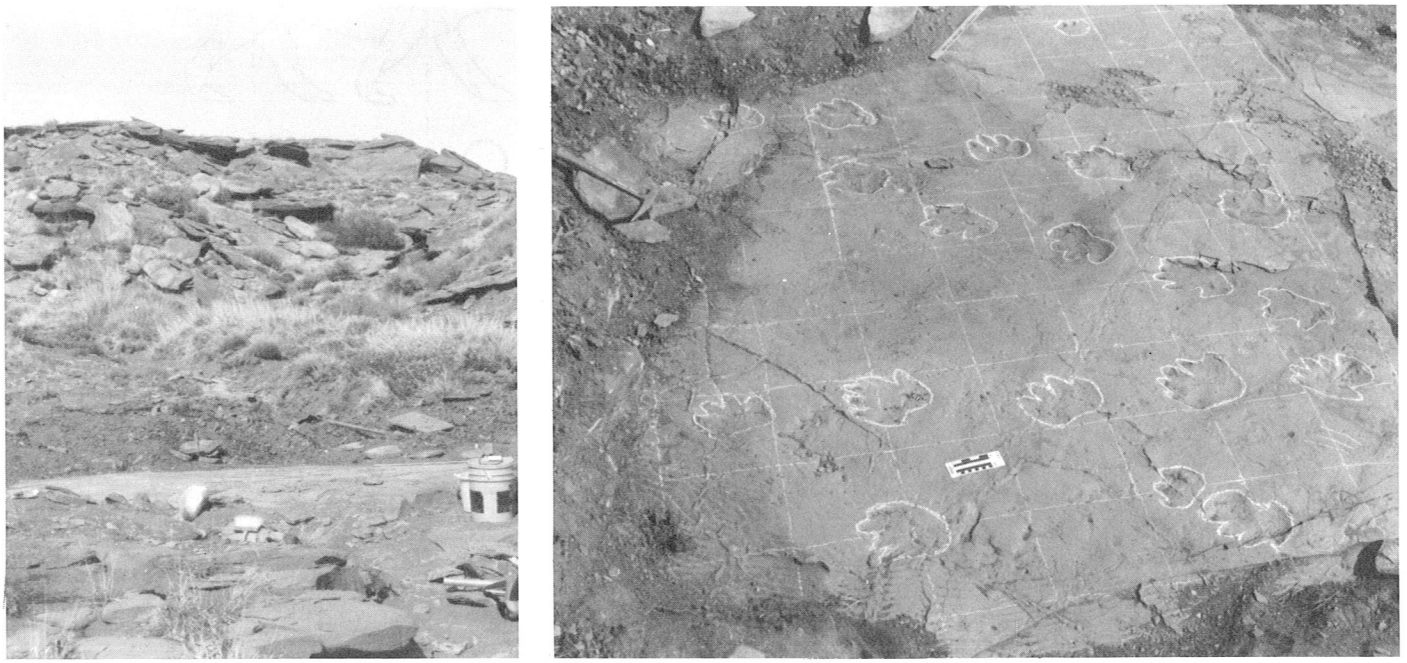

FIGURE 2. Type locality of *Tharapsipus cumminsi* gen. et sp. nov. at Holbrrok, Arizona. A, Overview of type locality. Trackway is on flat surface about a third of the way up frame to left of buckets. The hillside behind the locality is composed of the upper Holbrrok Member of the Moenkopi Formation. B, Overview of trackway surface. Grid squares are in ft.

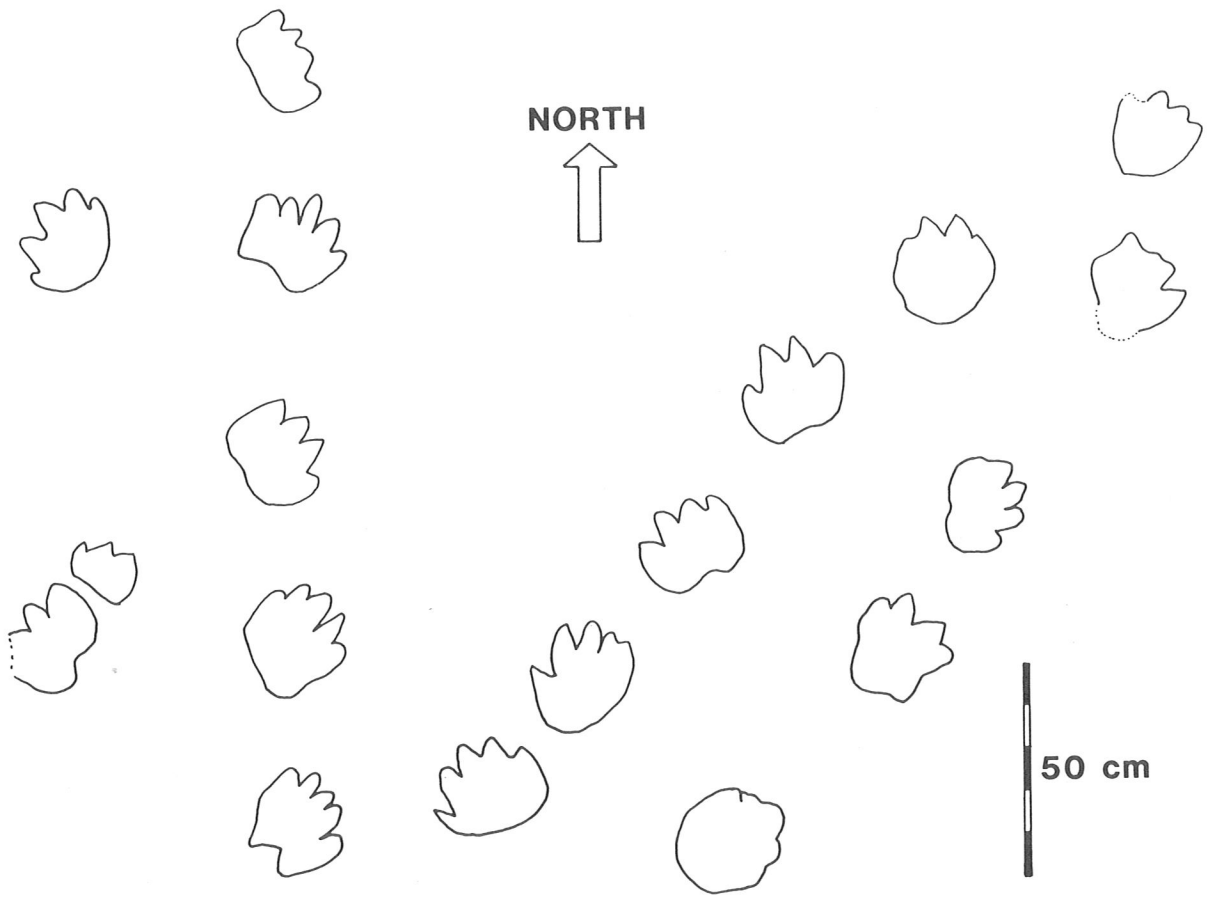

FIGURE 3. Map of the two trackways of *Therapsipus cumminsi,* gen. et sp. nov., Holbrook Member of the Moenkopi Formation, Holbrook, Arizona, USA. The holotype is the trackway on the right.

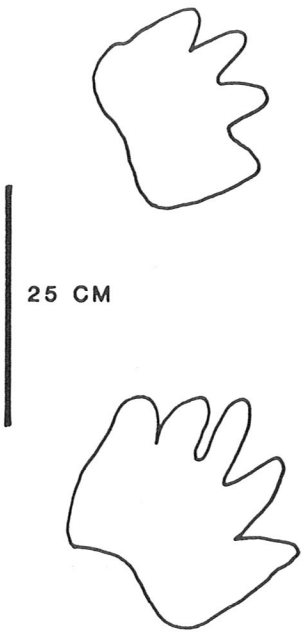

FIGURE 4. Manus-pes pair of *Therapsipus cumminsi* gen. et sp. nov. fromtrackway I, Holbrook Member of the Moenkopi Formation, Holbrook, Arizona, USA.

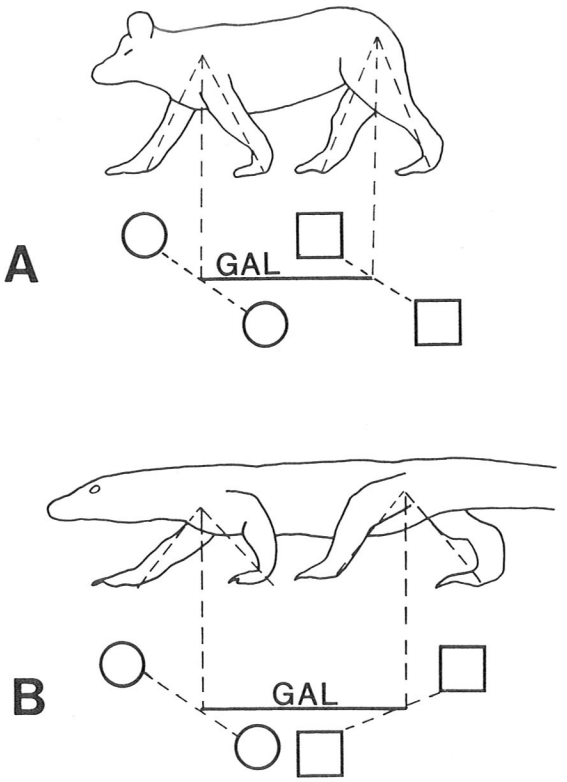

FIGURE 5. Different ways to calculate Gleno-Acetabular Length (GAL) depending on gait. A, GAL calculation for the mammalian amble. B. GAL calculation for the primitive alternate pace (after Leonardi, 1987).

length about 5 cm) with elongated manus and pes heel impressions and a narrow track width. Courel et al. (1968) described unnamed "theromorphoid" tracks from the Lower Triassic of France that more closely resemble *Therapsipus* in having short, blunt digit impressions and in being somewhat larger (foot length about 10-12 cm). However, the "theriomorphoid" is known only from isolated tracks (not trackways) and thus it is difficult to compare with the Moenkopi trackways.

It is possible that *Therapsipus* is related to *Cynodontipus* from the Early-Middle Triassic of southern France (Ellenberger, 1976). The French track is about the same size (25 cm long), but a trackway is not known for this ichnogenus. Furthermore, only the outline of the impressions of digits II-IV are known. Digit impressions I and V were reconstructed based on comparisons with other ichnotaxa and therapsid skeletons. Moreover, Ellenberger (1976) claimed that *Cynodontipus* tracks revealed the impressions of hair on the feet of the trackmaker. We consider this interpretation to be suspect. In conclusion, we consider *Cynodontipus* to be a nomen dubium and that the affinities of its trackmaker are unclear.

GAIT

Some indication of the gait of *Therapsipus* cane be derived from consideration of the gleno-acetabular length. The gleno-acetabular length (GAL) of a quadrupedal vertebrate is the distance from the center of the glenoid cavity to the center of the acetabulum (Leonardi, 1987). There are different ways to calculate this distance based on the gait of the animal (Leonardi, 1987, pl. 8C-E). In case of the mammalian amble (Fig. 5A), the body length is the distance between the intersections with the midline of the line of the hands and of the line of the feet with both these lines being subparallel (Leonardi, 1987). Utilizing this methodology the GAL for trackway II is 38.5 cm. This is unreasonably short for an animal with such big feet and such a wide carriage. Alternatively, we can hypothesize that the trackmaker walked with the primitive alternate pace in which case all four limbs touch the ground at one point in the walking cycle. In this case the GAL is the segment that unites the intersection points of the line of the reference points of the hands (the segment that joins homologous points in two successive fore-footprints of the opposite side) and the line of reference points of the feet with the midline (Fig. 5B). Such a calculation yields a GAL of 80.5 cm for *Therapsipus* which is much more consistent with other evidence about the size of the trackmaker. In conclusion, calculation of the GAL indicates that the trackmaker of *Therapsipus* was walking with a primitive alternate pace.

PALEOECOLOGY

It is apparent that the ichnofauna of the Holbrook Member (Table 2) is sampling a very different ecosystem than the osseus fauna. The tracks are dominated by chirotheres which undoubtedly represent derived archosaurs. In contrast, the body-fossil record is dominated by temnospondyl amphibians (Morales, 1987). Lucas and Hunt (1993) noted that Early-Middle Triassic vertebrate faunas tend to be either temnospondyl- or dicynodont-dominated. However, Early-Middle Triassic ichnofaunas are often, like the Holbrook Member ichnofauna, dominated by

Wupatki Member	Holbrook Member
Rhynchosauridids	
Rhynchosauroides sp.	*Rhynchosauroides schochardti* *Rhynchosauroides moenkopiensis*
Large manus chirotheres	
Chirotherium minus *Chirotherium barthii* *Synaptichnium diabloense*	*Chirotherium rex* *Synaptichnium cameronense*
Small manus chirotheres	
Isochirotherium coltoni	*Isochirotherium marshalli*
Rotodactylids	
Rotodactylus cursorius	*Rotodactylus bradyi*

TABLE 2. Vertebrate ichnofaunas of the Wupatki (middle Spathian) and Holbrook (early Anisian) Members of the Moenkopi Formation in northeastern Arizona.

tracks of archosaurs. This suggests that there are in fact three main vertebrate communities represented in the fossil record: (1) dicynodont-dominated faunas represented by body fossils (e. g., most Early-Middle Triassic osseus faunas of South Africa, India, and China); (2) temnospondyl-dominated faunas represented by body fossils (e. g., most Early-Middle Triassic osseus faunas of Europe and the western United States); and (3) archosaur-dominated faunas represented by ichnofossils (e. g., most early-Middle Triassic ichnofaunas from Europe and North America).

The occurrence of *Therapsipus* in the Holbrook Member indicates that body fossils of dicynodonts should also be present. The most common early Anisian dicynodont is *Shansiodon* which is present in China, Russia, South Africa, Zambia, Tanzania and Argentina (Lucas, 1993). On the basis of the presence of *Therapsipus* in the Moenkopi Formation we predict that *Shansiodon* bones may be found in this unit.

ACKNOWLEDGMENTS

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