

## New evidence of large dicynodonts in the upper Moenkopi Formation (Middle Triassic) of northern Arizona

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Large dicynodont tracks and bones have been discovered in the Perovkan age (= Early Anisian) upper Moenkopi Formation of northern Arizona, representing the earliest appearance of this group in North America. Dicynodont fossils are found throughout the stratigraphic section of the Holbrook Member and include a worn tusk, a cervical vertebra, two isolated footprints, and a trackway. The tusk was discovered in the uppermost sandstone of the Holbrook Member, making it the highest known occurrence of a vertebrate in the Moenkopi Formation sequence. The cervical vertebra was discovered in a conglomerate channel midway through the stratigraphic sequence of the Holbrook Member. The trackway was published as the holotype of the ichnospecies *Therapsipus cummingsi*, and the isolated footprints also can be referred to this taxon. One of the isolated footprints was found at nearly the same stratigraphic level as the vertebra, whereas the other was discovered in the lowermost sandstone of the Holbrook Member and represents the lowest occurrence of dicynodonts in the formation.

The Moenkopi dicynodont bones show similarities to the Triassic Kannemeyeriiformes. In particular, the large size of the tusk and its surface texture compare well to those of other kannemeyeriiforms. The cervical vertebra shows similarities to the Late Triassic *Placerias gigas*, but lacks a strongly amphicoelous centrum. Kannemeyeriiforms include the largest dicynodonts of the Early and Middle Triassic, and our material supports the presence of this group in the Middle Triassic of North America.

### INTRODUCTION

The fauna of the Holbrook Member of the Moenkopi Formation has long been thought to be dominated by temnospondyl amphibians, but recent collecting has revealed a previously unrecognized diversity of amniotes (Nesbitt 2000). Most of the known amniotes are carnivores including poposaurs and other basal archosaurs, but herbivores including rhynchosaurs also are present, though rare. New localities have produced fragmentary synapsid remains that can be referred to the Dicynodontia.

Although dicynodonts have a rich fossil record ranging in age from the Late Permian to Late Triassic, relatively little is known about the North American dicynodont fauna. No Permian dicynodont remains have been discovered in North America, but this fact more likely reflects the lack of fossiliferous Late Permian terrestrial sediments in North America than the true absence of the group. The Triassic record of North American dicynodonts is somewhat better. The first North American material referred to the Dicynodontia consisted of several large teeth collected near the Phoenixville railroad tunnel in Pennsylvania that were described by Cope (1870). The identification of these specimens as dicynodonts has been questioned (e.g., Huene, 1926), and remains unconfirmed. The next report of a North American dicynodont was made by Lucas (1904), who erected the taxon *Placerias besternus* based on a single fragmentary humerus collected in the Adamanian-age (= latest Carnian; Lucas, 1998a) Blue Mesa Member of the Petrified Forest Formation of Arizona. Lucas (1904) expressed un-

certainty about the affinities of *Placerias*, suggesting that it might be a pariasaur, but Williston (1904) confirmed its dicynodont nature. Williston (1904) also described two additional dicynodonts, *Eubrachiosaurus browni* and *Brachybrachium brevipes*, based on fragmentary postcranial remains collected in the Otischalkian-age (= Carnian; Lucas, 1998a) Popo Agie Formation of Wyoming. Subsequent authors have debated whether *Eubrachiosaurus* and *Brachybrachium* are truly distinct from *Placerias*. Camp and Welles (1956) considered *Eubrachiosaurus* to be a distinct taxon that was closely related to *Placerias*, and King (1988) treated both *Eubrachiosaurus* and *Brachybrachium* as valid taxa. Lucas and Hunt (1993) noted that *Brachybrachium* is a *nomen dubium* because the holotype has been lost, and considered *Eubrachiosaurus* to be synonymous with *Placerias* (a view echoed by Lucas, 1998b). However, Long and Murry (1995) suggested that *Eubrachiosaurus* was more similar to *Ischigualastia*. Given the nature of the material in question, we suspect that a definitive resolution of the systematic position of *Eubrachiosaurus* will be difficult to achieve.

Besides the initial specimen from Arizona and the possible records from Wyoming, *Placerias* also has been reported from other Carnian-age localities in the Blue Mesa Member in Arizona, the Bluewater Creek Formation in Arizona and New Mexico, and the Pekin Formation (Newark Supergroup) of North Carolina (see review in Lucas, 1998b). The vast majority of this material is from the *Placerias* Quarry, in the Bluewater Creek Formation, and was described by Camp and Welles (1956). Camp and Welles considered the speci-

mens from the *Placerias* quarry to represent a new species, *P. gigas*, although Lucas and Hunt (1993) and Lucas (1998B) have considered *P. gigas* to be a synonym of *P. hesternus*.

Lucas and Hunt (1993) also described some fragmentary dicynodont postcranial remains from the Adamanian-age (=latest Carnian; Lucas, 1998a) Los Esteros Member of the Santa Rosa Formation of New Mexico, which they referred to cf. *Ischigualastia*. Long and Murry (1995) also considered these specimens, and although they agreed with Lucas and Hunt that they were not *Placerias*, they did not consider them to be referable to *Ischigualastia* either. Instead, they considered the femur in particular to show similarities to *Stableckeria* and *Dinodontosaurus*. A specimen referred to *Ischigualastia* also has been discovered in the Revueltian-age (=Norian; Lucas, 1998a) Cooper Creek Formation (Dockum Group) of Texas (Edler, 2000). However, this specimen is poorly preserved and there is some question regarding its dicynodont affinities (A. Hungerbühler, personal communication, 2002). Finally, dicynodonts have been reported from the Otischalkian-aged (=Carnian; Lucas, 1998a) Wolfville Formation (Newark Supergroup) of Nova Scotia by Baird and Olsen (1983). Baird and Olsen do not elaborate on the nature of the material or its affinities beyond 'dicynodont therapsid,' but Lucas and Hunt (1993) cited a personal communication from D. Baird stating that it consists of weathered fragments of the occiput and braincase.

The new material described here consists of an isolated tusk and cervical vertebra, and footprints referable to the ichnotaxon *Therapsipus cummingsi*. The tusk and cervical vertebra were collected at MSM locality 00-103 and UCMP locality V4119, respectively. Site information pertaining to the ichnofossils attributed to the dicynodont is housed at the MSM. All of the specimens are of Perovkan age (=early Anisian; Lucas, 1998a), making them the oldest known dicynodont fossils from North America.

Institutional abbreviations: **MSM**: Mesa Southwest Museum, Mesa, AZ, USA; **UCMP**: University of California Museum of Paleontology, Berkeley, CA, USA.

## GEOLOGY AND OCCURRENCE

The Middle Triassic Moenkopi Formation is part of a thick sequence of marine and continental redbeds that typify the lower Mesozoic sedimentary rocks of western North America (Stewart et. al 1972; Morales 1987). The Moenkopi Formation unconformably overlies the Permian marine Kaibab Formation, and is overlain unconformably by the Late Triassic Chinle Formation (Stewart et. al 1972; Cook 1989). Easily recognized by its sandstone benches and brightly colored strata (McKee 1954; Nesbitt 2000), the Moenkopi extends over northern Arizona, New Mexico, Utah, Nevada, and western Colorado (Cook 1989). It is thinnest in the east, and gradually thickens as it extends west and north into southern Utah (Stewart et. al 1972).

In northern Arizona, the Moenkopi Formation is divided into three accepted members, the Wupatki, Moqui, and Holbrook (McKee 1954). All three are separated by widespread gypsum layers (Welles 1947). Occurring below the lowermost gypsum layer, the Wupatki Member is the oldest of the three and has been assigned a Spathian age by Welles and Cosgriff (1965) and Morales (1987). Lucas (1998a) assigned the Wupatki Member to his Nonesian Land-vertebrate Faunachron, which he correlated with the Olenikian marine stage. It contains a diverse ichnofauna (Peabody 1948), as well as two main vertebrate quarries that have produced a fauna dominated by temnospondyls and semionotiform fishes (Morales 1987). The Moqui Member lies between the lowermost and uppermost gypsum layers, and has been assigned a Late Spathian age (Morales 1987). No vertebrate fossils have been reported from the Moqui Member, but it has received relatively little scientific scrutiny and has not been systematically prospected. The Holbrook Member is the youngest member of the Moenkopi Formation, and has produced the largest assemblage of fossil vertebrates. The Holbrook Member is underlain by the uppermost gypsum layer and is overlain by the unconformity that separates the Moenkopi Formation from the Chinle Formation. Lucas (1998a) assigned the Holbrook Member to his Perovkan Land-vertebrate Faunachron, which he considered to likely be of Anisian age.

All of the localities that have produced dicynodont ichnofossils and body fossils are located in the Holbrook Member, near the town of Holbrook, Arizona (Fig. 1). The lowest occurrence is represented by a single isolated pes print that is stratigraphically just above the uppermost gypsum bed of the Moqui Member (Fig. 2). The next evidence of dicynodonts in the Holbrook Member is two semi-parallel trackways made by wide-bodied quadrupeds (Fig. 2B). These trackways were described by Hunt et al. (1993) as the holotype of *Therapsipus cummingsi*. Further up the column, just below the conglomerate in which most vertebrate fossils have been collected in the Moenkopi Formation, another isolated pes print was discovered by Tom Olson (Fig. 2C). Although larger than the holotype, this track also can be assigned to *T. cummingsi*. Detailed locality information for the new prints is housed at the MSM. The isolated cervical vertebra (UCMP 158811, Fig. 3) was collected from the conglomerate layer itself by Sam Welles at a locality just east of Holbrook, Arizona (UCMP V4119). Finally, the isolated tusk (MSM 3310, Fig. 4) marks the uppermost occurrence of dicynodonts in the Moenkopi Formation. It was found by Tom Olson in a coarse sandstone deposit (MSM 00-103), an unusual depositional setting for Moenkopi vertebrates.

## DESCRIPTION

The caniniform tusk (Fig. 2) is 54 mm long and 28 mm wide at its widest point, and shows the absence of enamel that is characteristic of dicynodont tusks (Camp and Welles



Fig. 1. The location of the fossil localities, near the town of Holbrook. The outlined area shows the extent of the Moenkopi Formation. Modified from Morales (1987).

1956; Poole 1956). Although it is weathered and incomplete, the tooth appears to show signs of predepositional wear on its tip. It is not clear if the wear is due to use or weathering. In cross section, the tusk shows several concentric growth features, suggesting a typical cone-in-cone structure found in dicynodont tusks as well as many other teeth (Camp and Welles 1956; Thackeray 1991). As preserved, the tusk is round in cross section near its tip, but is more oval proximally. However, the oval shape near its base may be the result of post-mortem crushing, and similar deformation can be observed in other isolated dicynodont tusks (Fig 5). Small patches of the outer surface possess a wrinkled texture. The tusks of some other Triassic dicynodonts (e.g., *Placerias*, *Kannemeyeria*) also possess a wrinkled or corrugated outer surface (Camp and Welles 1956).

Only the centrum and the base of the neural arch of the cervical vertebra are preserved (Fig. 3). As preserved, the vertebra is twice as tall as wide. The cranial face of the centrum is slightly concave, whereas the caudal face of the centrum is more strongly concave. Each face of the centrum is nearly circular and measures 61 mm tall by 55 mm wide. The body of the centrum is somewhat waisted, and pos-

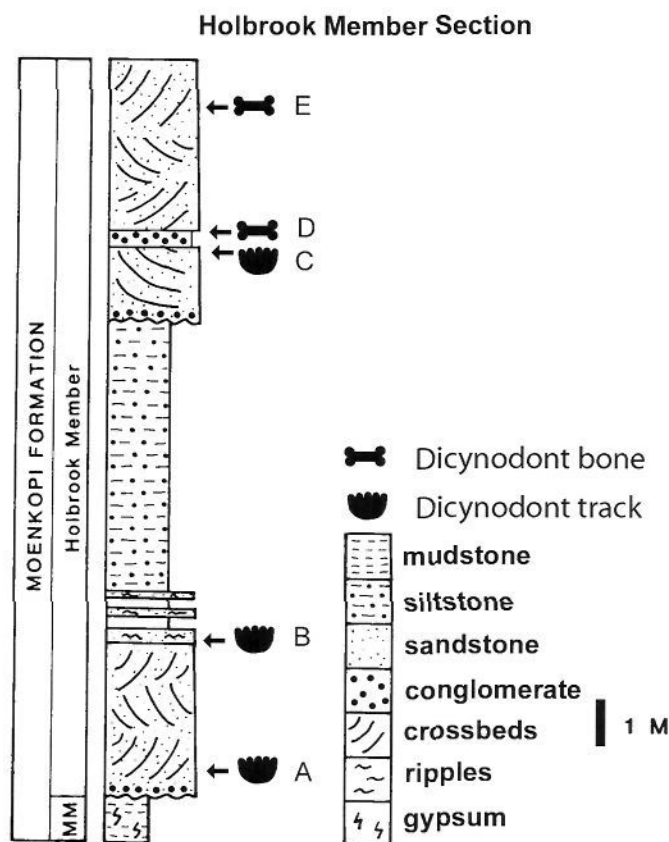


Fig. 2. Stratigraphic column of the Moenkopi Formation near Holbrook, Arizona. A. Lowermost occurrence of *Therapsipus cumminsi*. B. Holotype trackway of *Therapsipus cumminsi*. C. Uppermost occurrence of *Therapsipus cumminsi*. D. Position where the cervical vertebra was discovered by Sam Welles in 1938. E. Position where the tusk was discovered by Tom Olsen in 1999. Stratigraphic section modified from Hunt 1993. MM=Moqui Member.

sesses a median groove on its ventral surface. The parapophyses are well-developed, expanded mediolaterally, and are contiguous with the cranial face of the centrum. The preserved lower portion of the diapophyses suggests that they expanded dorsoventrally. The neural canal is nearly circular and measures 23 mm in diameter.

All of the manus and pes prints in the Holbrook Member can be assigned to *Therapsipus cumminsi* (Fig. 6). In their description of this ichnotaxon, Hunt et al. (1993) noted that it can be recognized by a low pace angulation, similar size of the manus and pes, and the small or poorly impressed digit I on the manus impression. Furthermore, all of the impressions possess a single large pad impression and relatively blunt digits. No scales or claw markings are preserved on any of the tracks. The overall size of the tracks and number of digits on the pes fit well with reconstructions of the dicynodont manus and pes and hypotheses regarding the locomotion of this group (e.g., King 1990).





Fig. 3. The Holbrook Member dicynodont cervical vertebra (UCMP V4119/158811) in caudal (left) and lateral (right) views. The scale bar equals one centimeter.

The impressions also are similar to other tracks attributed to dicynodonts from Australia (Retallack 1996) and Schweinfurthia (Karl 1995). Hunt et al. (1993) identified the tracks as those of a dicynodont because they are the only large, wide-bodied herbivores known from the Anisian. Although rhynchosaurs also are common herbivores at this time, Hunt et al. (1993) did not consider them as possible trackmakers because of their asymmetrically lengthened digits.

#### DISCUSSION

The material presented here is too fragmentary to allow a precise taxonomic identification. However, we feel that a dicynodont identification for both the trace and body fossils is justified for several reasons. As noted above, Hunt et al. (1993) considered *Therapsipus cumminsi* to be dicynodont tracks. This attribution is based mainly on the fact that the tracks were made by a large, wide-bodied animal with a sprawling gait that was probably herbivorous. The Holbrook Member of the Moenkopi Formation preserves a diverse ichnofauna described by Peabody (1948), but the majority of these ichnotaxa are much smaller than *T. cumminsi*. Among the larger members of the ichnofauna reptilian tracks, particularly *Chirotherium*, are the most abundant. *Chirotherium* spp. are characterized by a relatively narrow, quadrupedal trackways, a small manus print directly in front of the pes print, and the similarity of the pes to a reversed human hand (i.e., with the "thumb" on the opposite side; Peabody 1948). The digits of *Chirotherium* spp. are much longer than *T. cumminsi* digits, and *T. cumminsi* does not have the reversed "thumb" observed in all *Chirotherium* ichnotaxa. Without a reversed "thumb" on any of *T. cumminsi* impressions, it is possible to rule out the makers of all *Chirotherium* tracks as the maker of *T. cumminsi*. Given that dicynodonts are the only large, wide-bodied animals

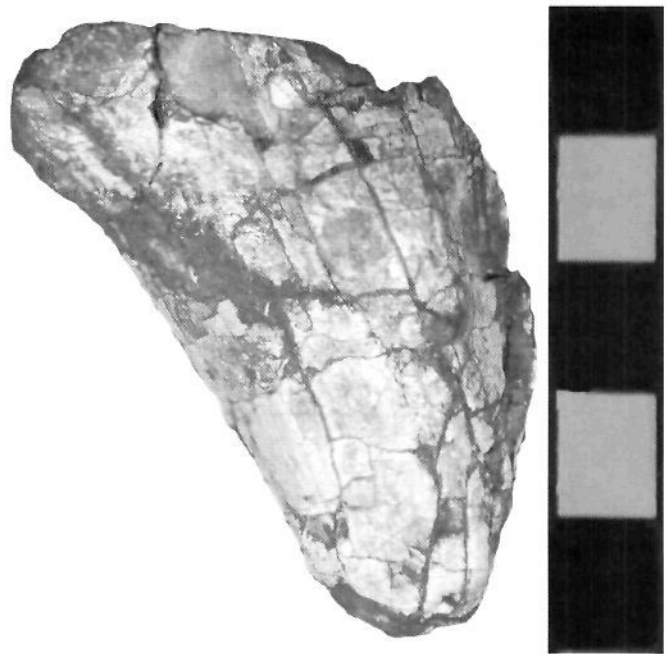


Fig. 4. The Holbrook Member dicynodont tusk in lateral view (MSM 00-103/3310). The scale bar equals five centimeters.

present in the Anisian, and the similarities of *T. cumminsi* both to other dicynodont tracks and to the dicynodont manual and pedal skeletons, we agree with Hunt et al. (1993) that this ichnotaxon most likely was made by large dicynodonts.

Based on the size, morphology, and apparent growth pattern of the tusk, we consider that it can be assigned to the Dicynodontia. The amphicoelous centrum, strong neural arch pedicels, and well developed parapophyses of the

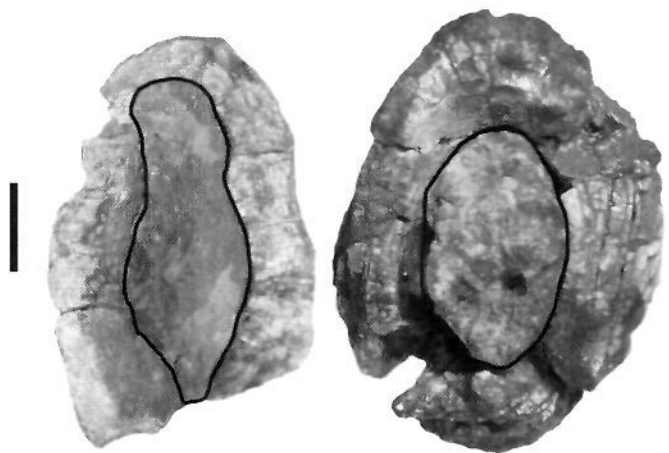


Fig. 5. The base of an isolated tusk from *Kannemeyeria* sp. (UCMP V4747/42874) (left) from the Middle Triassic of South Africa compared to the base of MSM 00-103/3310 (right). Notice that the base of each tusk is deformed and not circular in cross-section. The scale bar equals one centimeter.

cervical vertebra suggest that it is also referable to the Dicynodontia. This identification is corroborated by a comparison of the proposed dicynodont body fossils to the relatively diverse assemblage of Moenkopi tetrapods known from body fossils. Temnospondyl amphibians can be eliminated because of their small size and lack of a fully ossified centrum. Most amniotes from the Moenkopi Formation such as a questionable cynodont (Cuny et al. 1999), rhynchosaurs, and the primitive lepidosauromorph *Anisodontosaurus greeri* (Hunt et al. 1998) also can be eliminated because of their small size. A prolacertiform is present in the Moenkopi Formation (Nesbitt in press), but its cervical vertebrae are expanded craniocaudally and the maximum size of the animal is much smaller than the proposed dicynodont material would

allow. Larger reptiles such as erythrosuchids (Hunt 1993) and raiisuchids (Morales 1987; Nesbitt 2000) are also present in the upper Moenkopi. Both have large teeth, but their teeth are always laterally compressed and do not grow to the size of the tusk. The cervical vertebrae of raiisuchids tend to be longer than they are tall, which is not the case in our vertebra. Erythrosuchid cervical vertebrae are stouter than raiisuchian cervicals, but they are still longer than the proposed dicynodont vertebra. Moreover, the position of the parapophyses on erythrosuchid and raiisuchid cervical vertebrae is more caudal than the in MSM 3310. Erythrosuchid and raiisuchid parapophyses also are not contiguous with the face of the centrum, unlike the dicynodont vertebra.

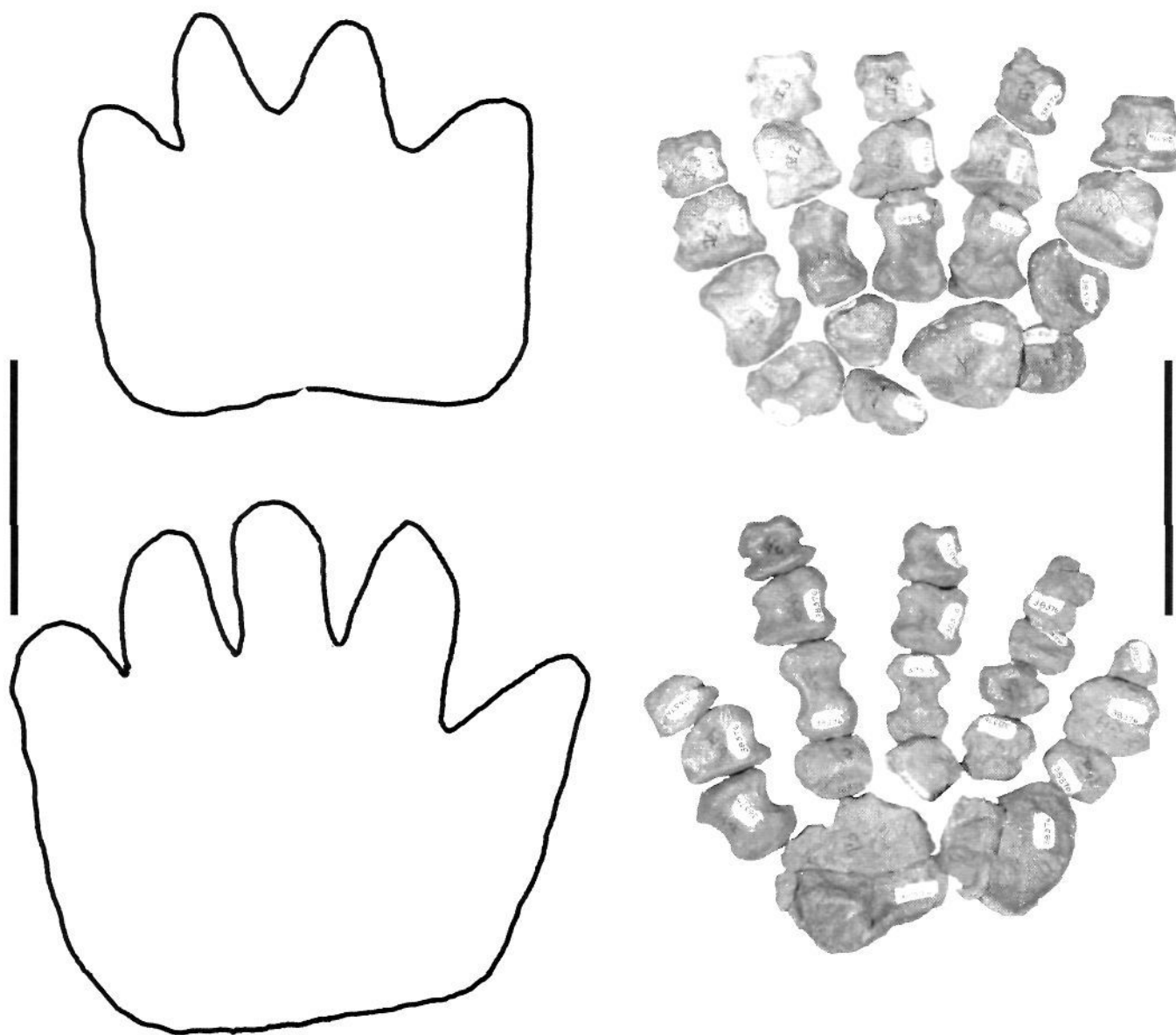


Fig. 6. A composite drawing of the manus (upper left) and pes (lower left) of *Therapsipus cummingsi* compared to the manus (upper right) and pes (lower right) of *Kannemeyeria* sp. from South Africa. Scale is equal to ten centimeters. Modified from Hunt 1993.

The postcranial skeleton of several Triassic dicynodonts has been described and figured in some detail (e.g., Pearson 1924; von Huene 1935; Camp 1956; Sun 1963; Cox 1965, 1969; Cruickshank 1967, 1975; Bandyopadhyay 1988; Surkov 1998), but there appears to be no recognized synapomorphies that would allow MSM 3310 to be referred to a particular clade. Moreover, most recent reviewers of Triassic dicynodont taxonomy (e.g., Keyser and Cruickshank 1979; Cox and Li 1983; King 1988, 1990) have focused on skull characters and do not include postcranial characters in the diagnoses of their proposed groups. Maisch (2001) included postcranial characters in his review of Triassic dicynodont phylogeny and taxonomy, but did not discuss vertebral characters in particular. However, based on the large size of the preserved tracks and bones, and their early Middle Triassic age, we consider it likely that the Moenkopi dicynodont remains can be referred to the Kannemeyeriiformes sensu Maisch (2001).

We compared the tusk and cervical vertebra in detail to those of the Late Triassic dicynodont *Placerias gigas* housed in the collections of the UCMP. *Placerias* is the most complete kannemeyeriiform known from North America (e.g., Lucas 1904; Camp and Welles 1956; Cox 1965; Lucas and Hunt 1993; Lucas 1998b) and is represented by hundreds of disarticulated skeletal elements. The tusks of *Placerias* show little similarity to our specimen, because they are significantly reduced and do not appear to have extended much beyond the alveolus (Camp and Welles 1956). The cervical vertebrae of *Placerias* compare well to that recovered in the Holbrook Member. Both have well-developed parapophyses and amphicoelous centra that are round in cross-section. However, the Holbrook centrum differs from that of *Placerias* and most other Triassic dicynodonts because it is less strongly amphicoelous. In *Placerias*, the faces of the centra are strongly concave, and are separated by only a thin (5mm–10mm) section of bone. In contrast, the Holbrook centrum has only a slightly concave posterior face, and a nearly flat anterior face. These observations suggest that the Moenkopi dicynodont remains are not referable to *Placerias*.

The unusual morphology of the centrum raises the possibility that the Moenkopi dicynodont represents a new taxon. However, we have chosen not to erect a name or refer the material to a taxon lower than Kannemeyeriiformes because our specimens are very fragmentary and possess so few diagnostic features. The taxonomy of dicynodonts is littered with names based on fragmentary, poorly preserved, and undiagnostic specimens, and we do not wish to unnecessarily contribute to this confusion. Moreover, by referring our material to the Kannemeyeriiformes, we feel we are accurately portraying what can be said about the specimens. A narrower identification goes beyond the level of precision that our data permit, and raises the possibility that this material might inadvertently be used to form hypotheses about biodiversity, biogeography, and biochronology that

ultimately are not possible with the evidence at hand. An identification below the level of Kannemeyeriiformes will be appropriate only if more informative material comes to light and the phylogenetic affinities of the Moenkopi dicynodont can be rigorously examined.

Dicynodonts were most abundant and diverse during the Late Permian, and many clades became extinct at the end of the Permian (King 1990). However, by the end of the Early Triassic and the start of the Middle Triassic, the kannemeyeriiforms had begun a minor radiation that lasted until the middle of the Late Triassic (King 1990). The kannemeyeriiforms were generally larger than their Permian relatives and appear to have rapidly achieved a cosmopolitan distribution. The Moenkopi dicynodont remains are important because they represent the earliest known appearance of this group in North America, and establish a kannemeyeriiform presence on this continent in the early Middle Triassic. However, our material is too fragmentary to allow us to corroborate Camp's (1956) prediction that the ancestors of the Placeriinae or Stahleckeriinae should be found in Middle Triassic of North America, or Hunt et al.'s (1993) hypothesis that *Shansiodon*, an Anisian dicynodont, might be present in the Moenkopi. As the dicynodont fossil record of North America becomes better known, it will be important to synthesize this information with the emerging phylogenetic hypotheses (e.g., Angielczyk 2001; Maisch 2001) to elucidate the biogeographic history of the group.

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