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PERMIAN TETRAPOD FOOTPRINTS FROM THE LUCERO UPLIFT, CENTRAL NEW MEXICO

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Abstract—Red beds of the Early Permian Abo Formation and overlying DeChelly Sandstone (Yeso Group) in the Lucero uplift of central New Mexico are locally rich in fossil tetrapod footprints. The New Mexico Museum of Natural History and Science in Albuquerque, New Mexico, houses 30 specimens with tetrapod footprints from 18 different localities within the study area. The assemblage includes tracks of *Amphisauropus* Haubold, 1970, *Ichniotherium* Pohlig, 1892, *Hyloidichnus* Gilmore, 1927, and *Dromopus* Marsh, 1894, that are referred to seymouriamorph, diadectomorph, captorhinid and parareptile or diapsid eureptile trackmakers. The relative abundance of *Amphisauropus* tracks seems to be a characteristic feature of Early Permian tetrapod footprint assemblages in central New Mexico that are intermediate between coastal plain and inland to upland paleoenvironments. Based on vertebrate tracks, the upper part of the Abo Formation in the study area is suggested to be of late Early Permian (~Artinskian/late Wolfcampian to early Leonardian) age.

INTRODUCTION

Tetrapod footprints from Early Permian red beds in New Mexico provide a global standard for understanding the Early Permian footprint record (e.g., Lucas and Heckert, 1995; Lucas et al., 1998, 2011; Haubold, 1996, 2000; Haubold and Lucas, 2001a; Voigt and Lucas, 2015a, b). The New Mexican tracksites extend across nearly the entire state in a north-south direction, but the most extensively collected and studied sites are in the Robledo and Doña Ana Mountains of southern New Mexico (Hunt et al., 1995, 2005; Lucas et al., 1995; Voigt and Lucas, 2015b). Here, we revise the Early Permian track record of the Lucero uplift in central New Mexico (Fig. 1) and place it into broader context in terms of ichnofacies and biostratigraphy.

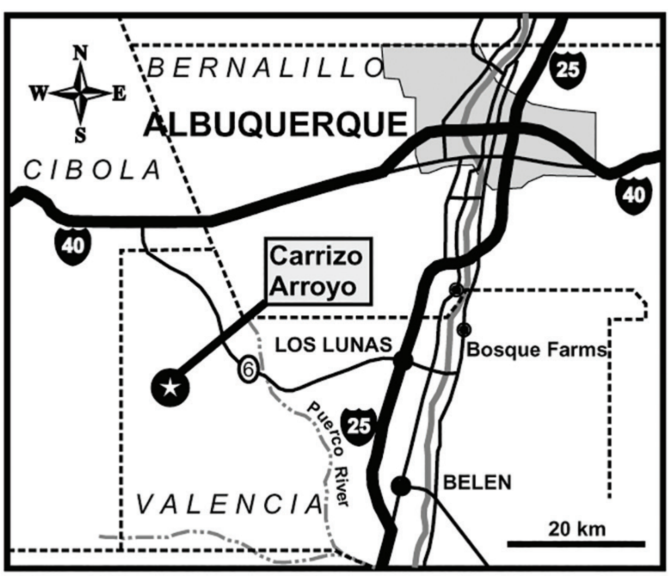

FIGURE 1. Geographic position of the study area in central New Mexico.

MATERIALS AND METHODS

Fossil footprints have been collected sporadically from the Early Permian strata in the Lucero uplift since 2000. All footprints collected are stored at the New Mexico Museum of Natural History and Science (NMMNH) in Albuquerque, New Mexico. The trace fossil sites have been given NMMNH locality numbers. Localities 4513, 5123, 5395, 5414, 5415, 5416, 7754, 7759, 7760, 7763, 7764, 8799, 10200, 10201, 10202, 10203 and 10204 are in the Abo Formation, and localities 6140 and 6141 are in the DeChelly Sandstone of the Yeso Group. Some tracks were left in the field because they could not be readily collected, and have been documented photographically (Lucas et al., 2004, 2005). All the tracksites have been placed into a detailed lithostratigraphic framework based primarily on Lucas and Zeigler (2004; Fig. 2).

GEOLOGY

There are 18 known localities with Early Permian tetrapod footprints in the Lucero uplift, most on the high mesas above Carrizo Arroyo (Fig. 1, Table 1). They occur in two Early Permian lithostratigraphic units, the Cañon de Espinoso Member of the Abo Formation and the DeChelly Sandstone of the Yeso Group. Lucas et al. (2004) documented some of the Abo tracks from the Lucero uplift. These tracks, in the Cañon de Espinoso Member, are in relatively thin beds (typically less than 0.5 m thick) of laterally extensive sandstone (Fig. 2). These are thin, tabular sandstone beds that have sharp contacts with underlying siltstone and overlying mudstone. They lack rip-up clasts, and their dominant bedform is ripple lamination. This bedform and the geometry of the beds suggest they represent non-channelized surface overbank flow of sand that formed a sandflat on the floodplain (Voigt et al., 2013a; Lucas et al., 2013c, d).

Invertebrate trace fossils associated with this kind of sediments are mostly horizontal walking and grazing traces as well

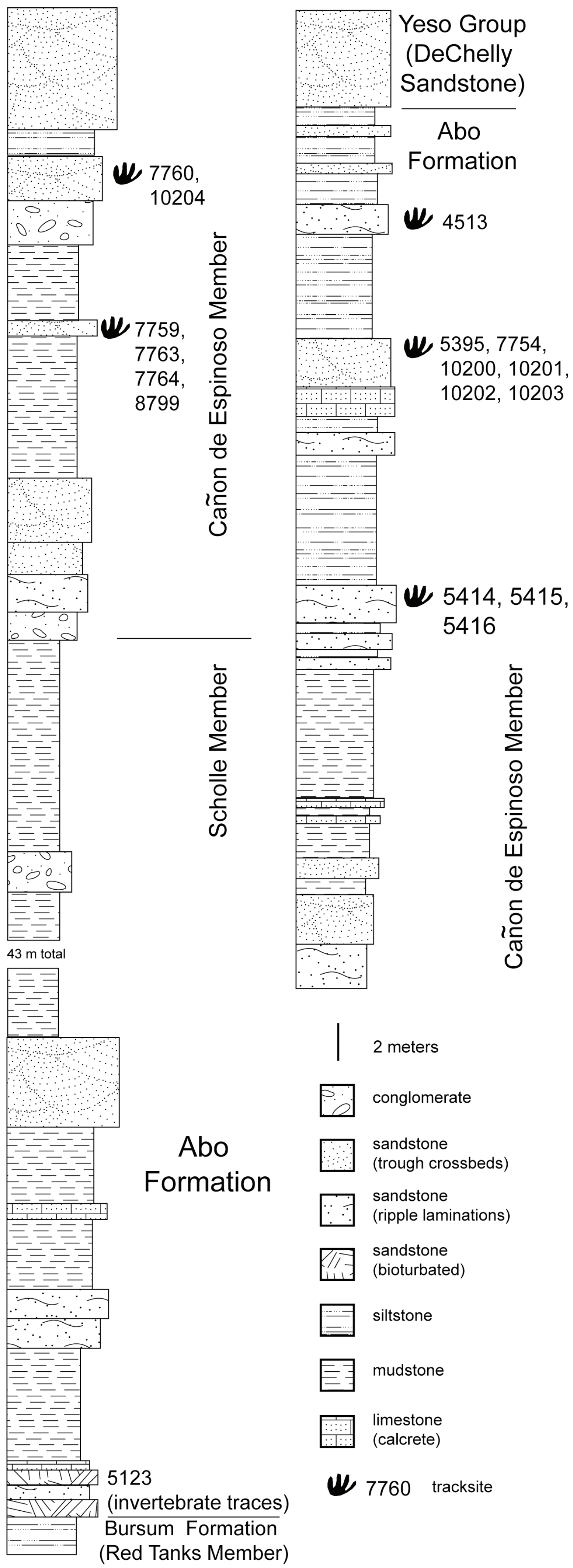

FIGURE 2. Measured stratigraphic section of the Abo Formation and basal Yeso Group in the Lucero uplift of central New Mexico and the stratigraphic distribution of Abo tetrapod footprint localities (modified from Lucas and Zeigler, 2004 and Lucas et al., 2004).

as feeding burrows (*Diplopodichnus*, *Palaeophycus*, *Protovirgularia*, *Scoyenia*). Indeed, at Carrizo Arroyo near the base of the Abo Formation there is an extensive assemblage of such invertebrate traces (Lucas and Lerner, 2004). At some of the Abo tetrapod tracksites (localities 4513, 5395, 7759, 7760, 7763, 8799), walchian conifer (NMMNH P-38764, -40495) and *Supaia* (NMMNH P-66584) plant impressions, as well as root traces (NMMNH P-38763/40496, -40197, -40487 to -40490, -58688), are associated with the tracks. NMMNH locality 4513 yielded a single specimen (NMMNH P-66583) of the characteristic invertebrate trace *Sphaerapus* (Lucas et al., 2013b).

In the Lucero uplift, Yeso Group tracks are much less common and not well preserved when compared to those from the Abo Formation (Lucas et al., 2005). Tracks occur at two levels in the DeChelly Sandstone, one ~3.8 m above the base of the unit and the other ~22 m below the top of the unit. The DeChelly Sandstone is ~70 m thick at Carrizo Arroyo (Lucas and Zeigler, 2004). Tracks in the DeChelly Sandstone at Carrizo Arroyo are present in laminated/ripple-laminated and wind-rippled sandstone of fluvial and eolian origin, respectively. Associated invertebrate traces were assigned to *Skolithos* and *Diplopodichnus* by Lucas et al. (2005). They assigned the Yeso tetrapod tracks to *Limnopus*, *Amphisauropus* and *Dimetropus*, but according to the present revision, these tracks are too poorly preserved to justify any ichnotaxonomic assignment.

PALEOICHNOLOGY

The fossil footprints from the Abo Formation of the Lucero uplift can be assigned to four well-known and widely distributed Late Paleozoic tetrapod ichnotaxa. These are *Amphisauropus* Haubold, 1970, *Ichniotherium* Pohlig, 1892, cf. *Hyloidichnus* Gilmore, 1927, and *Dromopus* Marsh, 1894. A detailed and amended characterization of these ichnotaxa is given in Voigt (2005) and Marchetti (2014). In order to avoid redundancy, we will focus this paper solely on the most important and diagnostic features of the ichnotaxa.

Amphisauropus Haubold, 1970 (Fig. 3)

Referred specimens: NMMNH P-58686 (Fig. 3A), 32 imprints of two parallel trackways preserved in convex hyporelief from NMMNH locality 7763; NMMNH P-58687 (Fig. 3B), two manus-pes couples of the same trackway preserved in convex hyporelief from NMMNH locality 7759; NMMNH P-58688, three imprints of the same trackway preserved in convex hyporelief from NMMNH locality 7763; NMMNH P-58689 (Fig. 3C), 12 imprints with digit dragging traces of a single trackway preserved in concave epirelief from NMMNH locality 7763; NMMNH P-58690, isolated manus-pes couple

TABLE 1. Tetrapod ichnodiversity of the Early Permian Abo Formation (NMMNH locality 4513 to NMMNH locality 10204) and overlying Yeso Group (NMMNH localities 6140 and 6141) of the Lucero uplift in central New Mexico. A record in brackets refers to material that is only compared to the ichnotaxon. Abbreviations: CEM - Cañon de Espinoso Member of the upper Abo Formation; DS - DeChelly Sandstone of the overlying Yeso Group.

NMMNH locality	Lithostratigraphy	*Amphisauropus*	*Ichniotherium*	*Hyloidichnus*	*Dromopus*	Specimens indet.	Total NMMNH specimens
L-4513	Abo Fm. (CEM)	—	—	(+)	+	+	6
L-5395	Abo Fm. (CEM)	—	—	—	—	+	1
L-5414	Abo Fm. (CEM)	—	—	—	+	—	3
L-5415	Abo Fm. (CEM)	—	—	—	—	+	3
L-5416	Abo Fm. (CEM)	—	—	—	—	+	1
L-6140	Yeso Group (DS)	—	—	—	—	+	no collection
L-6141	Yeso Group (DS)	—	—	—	—	+	2
L-7754	Abo Fm. (CEM)	—	—	—	—	+	no collection
L-7759	Abo Fm. (CEM)	+	+	+	—	—	4
L-7760	Abo Fm. (CEM)	+	—	(+)	+	—	4
L-7763	Abo Fm. (CEM)	+	—	—	+	—	5
L-7764	Abo Fm. (CEM)	—	—	—	+	+	no collection
L-8799	Abo Fm. (CEM)	—	—	—	—	—	1
L-10200	Abo Fm. (CEM)	—	—	—	+	+	no collection
L-10201	Abo Fm. (CEM)	+	—	—	—	+	no collection
L-10202	Abo Fm. (CEM)	—	—	—	—	+	no collection
L-10203	Abo Fm. (CEM)	+	—	—	+	+	no collection
L-10204	Abo Fm. (CEM)	—	—	—	—	+	no collection
NMMNH locality	Lithostratigraphy	+	+	(+)	+	+	**30**

preserved in convex hyporelief from NMMNH locality 7759; NMMNH P-58691 (Fig. 3D), 15 small imprints of a single trackway preserved in convex hyporelief from NMMNH locality 7763; NMMNH P-58692, isolated manus-pes couple preserved in concave epirelief from NMMNH locality 7759; NMMNH P-58693 (Fig. 3E), isolated manus-pes couple preserved in convex hyporelief from NMMNH locality 7760; NMMNH P-58695, two manus-pes couples of the same trackway preserved in concave epirelief from NMMNH locality 7763; NMMNH P-58696, isolated manus-pes couple preserved in concave epirelief from NMMNH locality 7760; NMMNH P-66585, three manus-pes couples of a single trackway preserved in convex hyporelief from NMMNH locality 8799.

Description: Trackway of quadrupedal tetrapod with pentadactyl manus and pes imprints ranging from 10 to 70 mm in length. Manus about one fourth shorter than pes imprints and distinctly wider than long. Manual digits short; digit length increases from I to IV, digit V is a little bit longer than I; palm more than half as long as imprint length. Pes imprint about as long as wide, with longest digit IV and V slightly longer than II. Manus and pes imprints show distinct pads at the base of digit I (Fig. 3B). Trackways usually with a manus that is strongly rotated inward and pes imprints rotated outward. Some of the material has curved digit dragging traces (Fig. 3C).

Discussion: Based on the shape, proportions and orientation of manus and pes imprints, the described tracks are readily assigned to the ichnogenus *Amphisauropus* (Haubold, 1970, 1971; Voigt, 2005, 2012; Marchetti, 2014; Marchetti et al., 2015). The Lucero uplift actually yields one of the most abundant records of *Amphisauropus* tracks in the world. It is one of just a few localities at which ichnofossil material covers the entire size range of *Amphisauropus* tracks (cf. Voigt, 2005). Regarding the imprint morphology and the trackway pattern, there is no difference from European records of Amphisauropus (Voigt, 2005; Voigt et al., 2012; Marchetti et al., 2015). Potential trackmakers of *Amphisauropus* are anamniote reptiliomorphs, notably Seymouriamorpha (Haubold, 2000; Voigt, 2005).

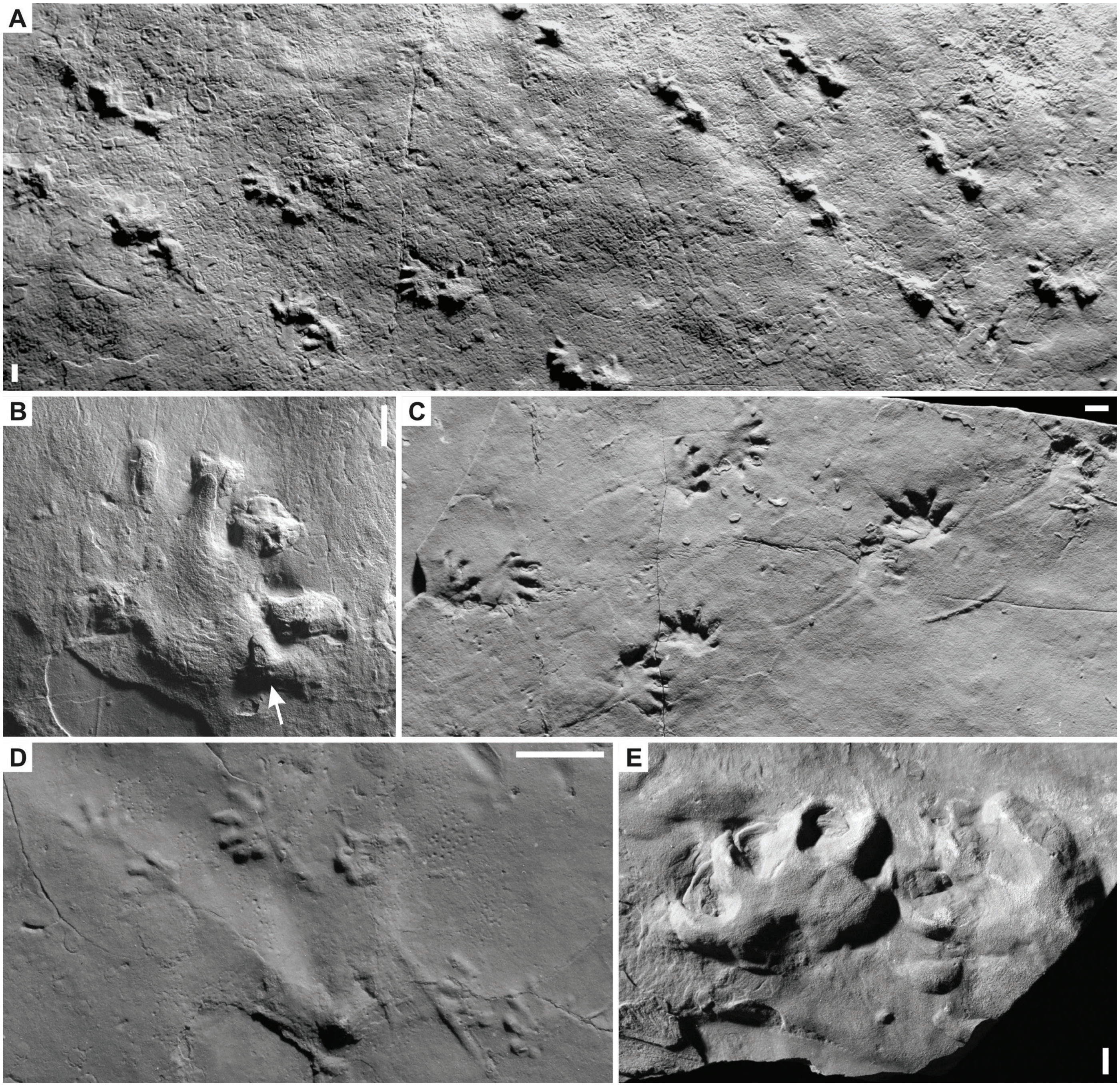

FIGURE 3. *Amphisauropus* Haubold, 1970. Representative specimens from the Abo Formation of the Lucero uplift in central New Mexico. Material: **A**) NMMNH P-58686, two parallel trackways; **B**) NMMNH P-58687, isolated left pes imprint showing a distinct pad at the base of digit I (arrow); **C**) NMMNH P-58689, trackway with digit dragging traces; **D**) NMMNH P-58691, small tracks of a longer trackway; **E**) NMMNH P-58693, isolated left manus-pes couple. Scale bars: 1 cm.

Ichniotherium **Pohlig, 1892 (Fig. 4)**

Referred specimen: NMMNH P-58692, isolated pes imprint preserved in convex hyporelief from NMMNH locality 7759.

Description: Nine-centimeter-long pentadactyl track with enlarged, blunt digit tips. Imprint about as long as wide, sole characterized by large, short, oval-shaped pad. Digit length increases from I to IV, and V about as long as II.

Discussion: NMMNH P-58692 is interpreted to represent an undertrack of the ichnogenus *Ichniotherium*. It is the only specimen of this typical element of Late Carboniferous-Early Permian tetrapod ichnoassemblages from the study area. The ichnogeneric assignment is based on the shape and proportions of the digits as well as the characteristic oval-shaped heel impression (Voigt and Haubold, 2000; Voigt, 2005, 2012; Voigt and Lucas, 2015b). The relatively short fifth digit of the described track is in accordance with two ichnospecies, *Ichniotherium cottae* (Pohlig, 1887) and *Ichniotherium hainesi* (Carman, 1927), that can only be separated by trackway parameters (Voigt, 2005; Voigt et al., 2007; Voigt and Lucas,

FIGURE 4. *Ichniotherium* Pohlig, 1892. Isolated left pes imprint and only known specimen of the ichnotaxon from the Abo Formation of the Lucero uplift in central New Mexico. Material: NMMNH P-58692. Scale bar: 1 cm.

2015b). Tracks of *Ichniotherium* are referred to diadectomorph anamniotes (Voigt, 2005; Voigt, et al. 2007).

cf. *Hyloidichnus* Gilmore, 1927 (Fig. 5)

Referred specimens: NMMNH P-32488 (Fig. 5A), isolated manus-pes couple preserved in concave epirelief from NMMNH locality 4513; NMMNH P-58694 (Fig. 5B), isolated manus-pes couple preserved in convex hyporelief from NMMNH locality 7760. Several other tracks preserved in concave epirelief at NMMNH locality 4513 could not be readily collected, so they were left in place (Fig. 5C; cf. Lucas et al., 2004: fig. 3A).

Description: Tracks of quadrupedal tetrapods with pentadactyl imprints up to 60 mm in length. Manus imprints more complete than pes imprints, and the latter also show a significant mediolateral decrease in relief. Both imprints about as long as wide, with long, straight and slender digits. Digits of manus imprint increase in size from I to IV, and V about as long as I. Digits have tapering tips that are straight forward to curved inward in digits I to IV, but rotated outward in digit V. Digit tip impressions may be bifurcated. Remarkably short and indistinct palm/sole impression.

Discussion: This kind of tetrapod footprint is relatively common in the study area but only known from isolated manus and pes imprints and imprint couples, respectively. The tracks are compared with *Hyloidichnus* because of their similarity to the holotype of the ichnogenus from the Hermit Formation of the Grand Canyon (Gilmore, 1927). The tracks from the study area are most similar to *Hyloidichnus* regarding the shape and proportions of the digits, the tapering digit tips, as well as the short palm/sole impression. Unfortunately, all three specimens

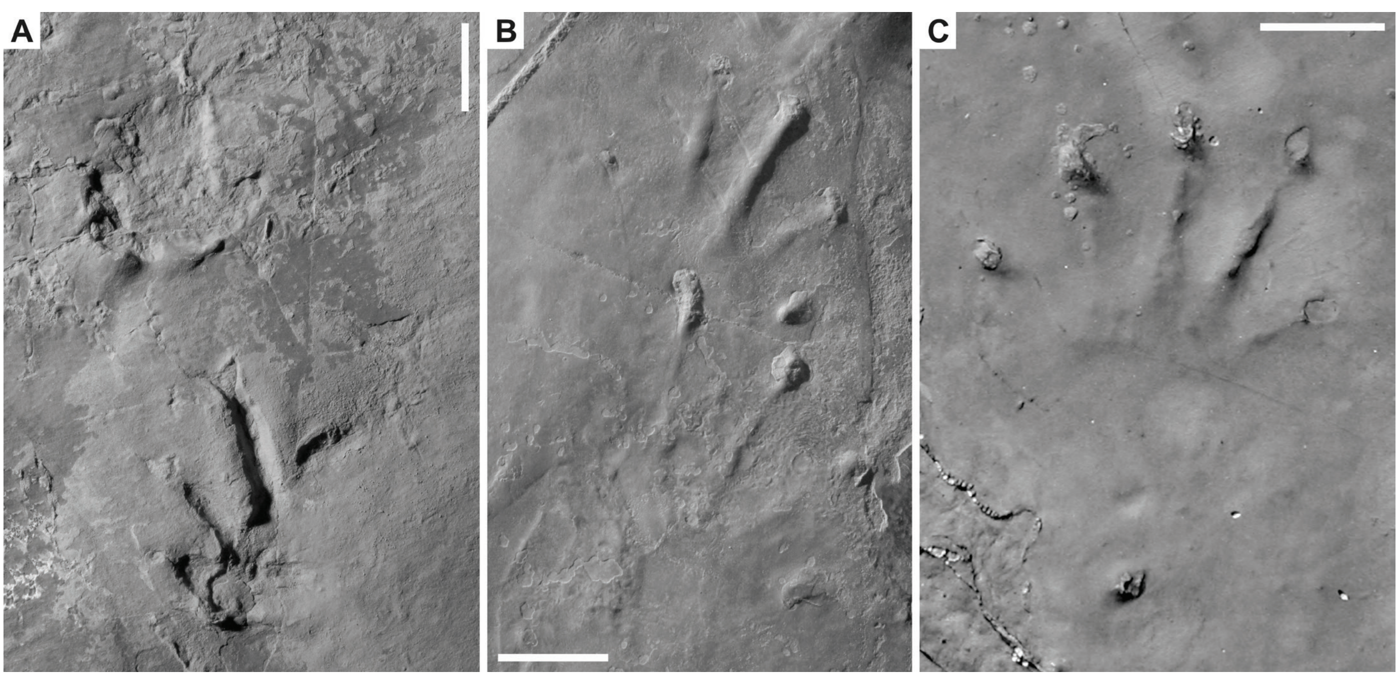

FIGURE 5. Cf. *Hyloidichnus* Gilmore, 1927. Representative specimens from the Abo Formation of the Lucero uplift in central New Mexico. Material: **A**) NMMNH P-32488, left manus-pes couple; **B**) NMMNH P-58694, right manus-pes couple; **C**) field specimen, left manus (cf. Lucas et al., 2004: fig. 3A). Scale bars: 2 cm.

from the Lucero uplift lack the impression of the fifth digit of the pes imprint, so the material cannot ultimately be separated from similar tracks of the ichnogenus *Varanopus* Moodie, 1929. Hitherto known *Varanopus* tracks usually show more flexible digits and do not exceed 45 mm in length (Voigt, 2005, 2012), and we assign the Lucero tracks to cf. *Hyloidichnus*. Tracks of *Hyloidichnus* are referred to captorhinids (Haubold, 1971; Gand, 1988; Gand and Durand, 2006) or, even more specifically, to moradisaurine capthorinids (Voigt et al., 2009, 2010).

***Dromopus* Marsh, 1894 (Fig. 6)**

Referred specimens: NMMNH P-38761, several tracks preserved in convex hyporelief from NMMNH locality 4513; NMMNH P-40487 to -40490, numerous undertracks preserved in convex hyporelief or as part and counterpart from NMMNH locality 5414; NMMNH P-58695, several tracks of two trackways preserved in concave epirelief from NMMNH locality 7763; NMMNH P-66586 (Fig. 6A), several small tracks preserved in convex hyporelief from NMMNH locality 7759; NMMNH P-66587 (Fig. 6B), several small tracks preserved in concave epirelief from NMMNH locality 7760.

Description: Preservationally didactyl manus and pes imprints ranging about 10 to 30 mm in length. Digits long, slender and distally tapered. Manus and pes imprints very similar in shape, but manus smaller than pes. All imprints only show digits III and IV that are slightly curved; digit IV is significantly longer than III. Primary marginal overstepping of the manus imprint by the pes is common.

Discussion: Dromopus is the most common and most widely distributed kind of Late Carboniferous-Early Permian tetrapod footprint and easy to recognize by its lacertoid imprints (Haubold, 1971, 1996; Gand, 1988; Haubold et al., 1995; Voigt, 2005, 2012; Voigt and Lucas, 2015a, b). The oldest named ichnospecies of *Dromopus* is *D. lacertoides* Geinitz, 1861. All collected specimens from the study area show didactyl preservation. This kind of preservation was previously considered to represent a separate ichnospecies, *D. palmatus* (Moodie, 1929) = *D. didactylus* Moodie, 1930 (Gand, 1988). An ichnospecies separation of *Dromopus*, however, has never been demonstrated to be justified by anatomically controlled features of the imprint morphology or trackway pattern (Haubold, 1996; Voigt, 2005, 2012; Marchetti, 2014; Marchetti et al., 2015). *Dromopus* is probably the track of lizard-like Permian parareptiles and eureptiles such as bolosaurids and araeoscelids (Haubold, 1971, 2000; Voigt, 2005, 2012).

ICHNOFACIES

Early Permian tetrapod footprints are widely distributed in New Mexico in a spectrum of paleoenvironments from coastal plain to inland alluvial fans (Hunt and Lucas, 1998, 2005, 2006; Voigt and Lucas, 2012; Voigt et al., 2013a). Early Permian ichnoassemblages of northern New Mexico are most similar to contemporaneous tracksites of central Europe, such as the Thuringian Forest Basin in central Germany (Voigt, 2005) or the Sudetic Basin in southern Poland (Voigt et al., 2012). These inland to upland ichnoassemblages are especially characterized by an abundance of *Ichniotherium* tracks (Hunt and Lucas, 1998, 2005, 2006; Voigt et al., 2005, 2007; Voigt and Lucas, 2015b), whereas *Ichniotherium* is absent in coastal lowland deposits of Early Permian age (Voigt and Lucas, 2012; Voigt et al., 2013a; Voigt and Lucas, 2015a). Between these two extremes, Early Permian ichnoassemblages that are remarkably rich in *Amphisauropus* tracks (Hunt and Lucas, 2005, 2006; Lucas et al., 2001, 2009, 2013c, d; Lerner et al., 2003) can be found almost exclusively in central New Mexico. In terms of Early Permian tetrapod ichnofacies, this is also the location of the tetrapod ichnoassemblage from the Cañon de Espinoso Member of the upper Abo Formation in the Lucero uplift (Fig. 7). On the basis of the relative abundance of *Am-*

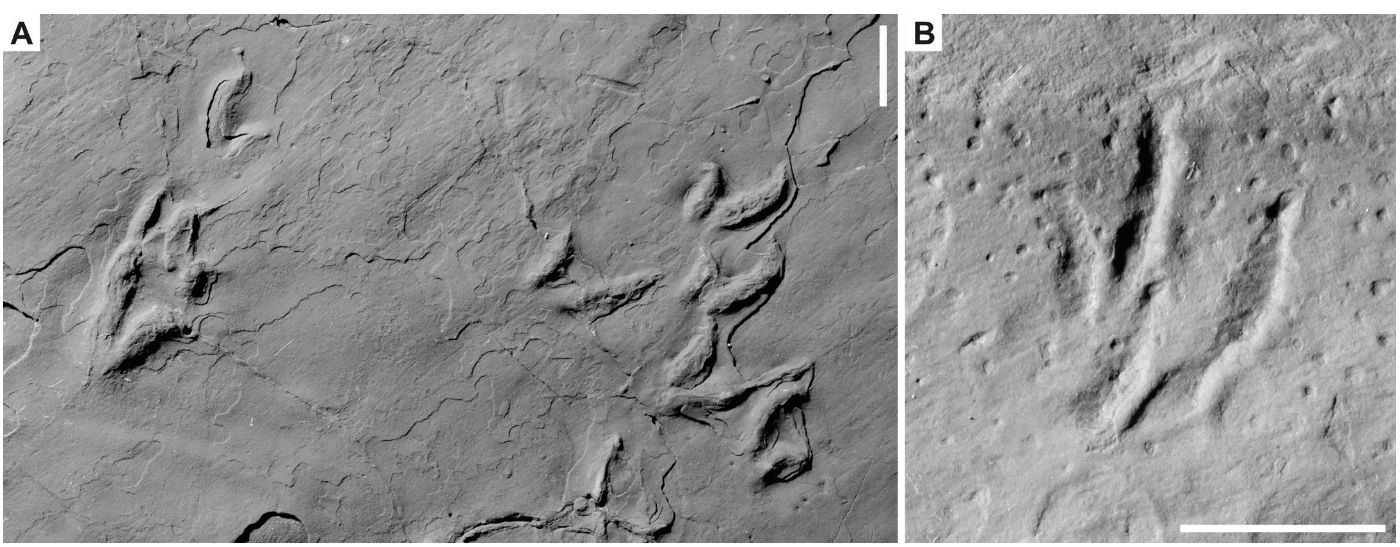

FIGURE 6. *Dromopus* Marsh, 1894. Representative specimens from the Abo Formation of the Lucero uplift in central New Mexico. Material: **A**) NMMNH P-66586; **B**) NMMNH P-66587. Scale bars: 1 cm.

phisauropus and its sparse record of *Ichniotherium*, the Early Permian tetrapod ichnoassemblage of the study area occupies an intermediate position between the typical coastal plain paleoenvironments of southern New Mexico and the inland alluvial fan paleoenvironments of northern New Mexico.

BIOSTRATIGRAPHY

The Abo Formation has long been regarded by most workers to be wholly of middle-late Wolfcampian age. However, in the Robledo Mountains of southern New Mexico, the Abo Formation interfingers with the marine Hueco Group. Microfossils (mostly foraminiferans) from the Hueco Group indicate that the interfingering Abo strata are of early Leonardian age (Lucas et al., 2015a). The interfingering Abo strata (recognized as the Robledo Mountains Formation of the Hueco Group: Lucas et al., 2015a) contain an extensive tetrapod footprint assemblage, characteristic of all but the highest Abo strata, where, most likely due to paleoecological differences, a somewhat different footprint assemblage is present. Furthermore, regional stratigraphic relationships indicate that the Robledo Mountains Formation is equivalent to only a portion of the upper part (within the Cañon de Espinoso Member) of the Abo Formation (Lucas et al., 2015b). Nevertheless, it is impossible with current data to determine the Leonardian base precisely in Abo sections that are wholly nonmarine, such as in the Lucero uplift. Given that the Abo footprints around Carrizo Arroyo are present throughout the Cañon de Espinoso Member (Fig. 2), they likely straddle the Wolfcampian-Leonardian boundary.

Solely based on the tetrapod footprints, the upper Abo Formation of the Lucero uplift in central New Mexico is here proposed to be of late Early Permian (~Artinskian) age. This interpretation takes into account the first occurrence of *Hyloidichnus*, about 22 m above the local base of the Cañon de Espinoso Member and the absence of *Erpetopus* tracks that seem to first appear in Kungurian strata (Fig. 8; Marchetti et al., 2015). On this assumption, the described tetrapod ichnoassemblage is about the same age as those from the Robledo Mountains (Voigt and Lucas, 2015a) and Sangre de Cristo formations (Voigt and Lucas, 2015b) of southern and northern New Mexico, respectively, but older than the tetrapod footprint assemblage of the Arroyo de Alamillo Formation of the Yeso Group in the Cerros de Amado area of central New Mexico (Fig. 8; Lucas et al., 2013a).

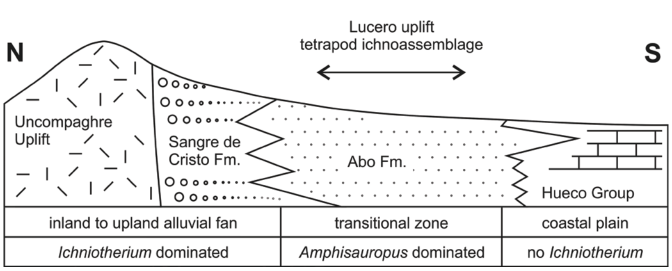

FIGURE 7. Schematic north-south cross-section of Early Permian strata in New Mexico showing spectrum of paleoenvironments represented by tetrapod tracksites (based on Hunt and Lucas, 1998, 2005, 2006).

CONCLUSIONS

Based on the above, we offer the following conclusions:

1. Red beds of the Early Permian Abo Formation and overlying DeChelly Sandstone (Yeso Group) in the Lucero uplift of central New Mexico are locally rich in fossil tetrapod footprints.
2. The New Mexico Museum of Natural History and Science houses 30 specimens with tetrapod footprints from 18 different localities in the Early Pemian strata of the Lucero uplift.
3. The assemblage includes tracks of *Amphisauropus* Haubold, 1970, *Ichniotherium* Pohlig, 1892, cf. *Hyloidichnus* Gilmore, 1927, and *Dromopus* Marsh, 1894 that are referred to seymouriamorph, diadectomorph, captorhinid and parareptile or diapsid eureptile trackmakers.
4. The relative abundance of *Amphisauropus* tracks characterizes Early Permian tetrapod footprint assemblages in central New Mexico that are intermediate between coastal plain and inland to upland paleoenvironments.
5. Based on vertebrate tracks, the upper part of the Abo Formation (Cañon de Espinoso Member) in the study area is of late Early Permian (~Artinskian/late Wolfcampian to early Leonardian) age.

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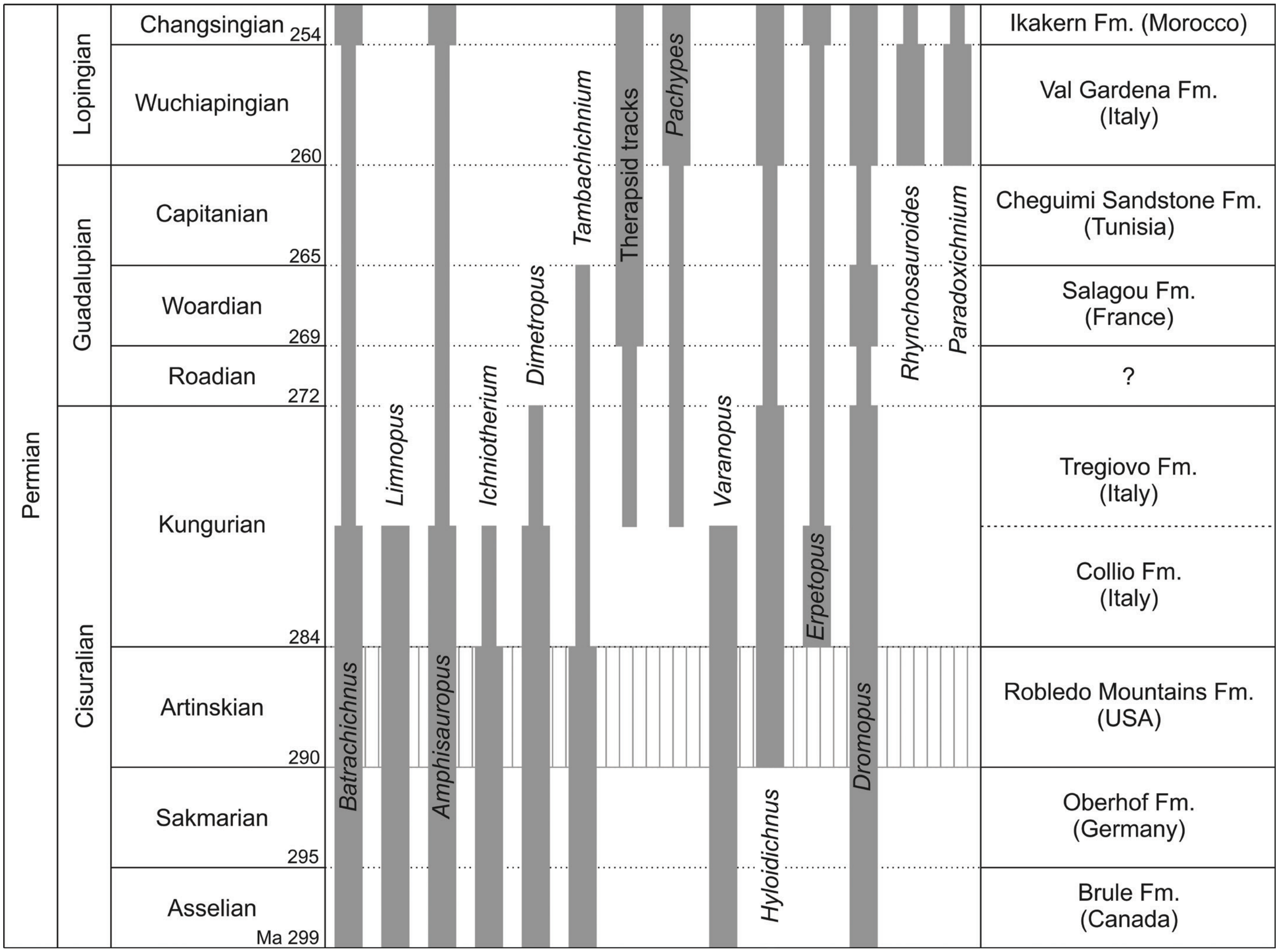

FIGURE 8. Stratigraphic range of common and well-known Permian tetrapod ichnotaxa (thick bar = fossil evidence; thin bar = distribution inferred) and proposed position of the tetrapod ichnoassemblage from the upper Abo Formation of the Lucero uplift in central New Mexico (vertically hatched area). Formation names in the right column exemplify footprint-bearing deposits of the respective time interval. Note that the total stratigraphic range of the formations may be longer or shorter than the referred intervals. Data are compiled from Haubold (2000), Van Allen et al. (2005), Voigt (2005), Gand and Durand (2006), Schneider et al. (2006, 2014), Lucas (2007), Voigt et al. (2010, 2013b), Hminna et al. (2012), and Marchetti (2014).

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Sand Canyon near Abo Pass. Photo courtesy of Bonnie Frey.