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ON A DIVERSE TETRAPOD ICHNOFAUNA FROM EARLY PERMIAN RED BEDS IN SAN MIGUEL COUNTY, NORTH-CENTRAL NEW MEXICO

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ABSTRACT—Late Paleozoic red beds of the Sangre de Cristo Formation and overlying Yeso Group in San Miguel County in north-central New Mexico are locally rich in fossil tetrapod footprints. The largest public collection houses about 200 specimens with tetrapod footprints from 16 different localities within the study area. The assemblage includes tracks of *Batrachichnus* (Woodworth, 1900), *Limnopus* (Marsh, 1894), *Ichniotherium* (Pohlig, 1892), *Tambachichnium* (Müller, 1954), *Dimetropus* (Romer and Price, 1940), and *Dromopus* (Marsh, 1894). Less well recorded are tracks that are compared with *Matthewichnus* (Haubold, 1970), *Notalacerta* (Butts, 1891), and *Hyloidichnus* (Gilmore, 1927). This diverse ichnofauna is referred to as microsaur, temnospondyl, diadectomorph, eupelycosaur, non-diapsid eureptile ('captorhinomorph') and parareptile or diapsid eureptile trackmakers. In most cases, the track-trackmaker correlation is well supported by tetrapod body fossil remains from closely associated beds of the Sangre de Cristo Formation. Based on vertebrate tracks, the upper part of the Sangre de Cristo Formation in the study area is suggested to be of late Early Permian (late Artinskian/late Wolfcampian) age.

INTRODUCTION

Fossil tetrapod footprints from Paleozoic red beds of the southwestern part of San Miguel County, north-central New Mexico, have been known for over 25 years (Hunt et al., 1990). Sporadic collection of fossil footprints in this area was done by various scientists and non-professional geologists for almost two decades, before the authors started a more systematic fossil exploration in this part of the Sangre de Cristo Formation and the overlying Yeso Group a few years ago. This activity significantly augmented the amount of tetrapod footprint material and the number of track localities in the study area.

Though the Sangre de Cristo Formation of north-central New Mexico has long been known for its interesting vertebrate ichnofauna, the occurrence received relatively little attention in the literature. A first report (and for a long time only report) on the most productive footprint site in the upper part of the Sangre de Cristo Formation (Hunt et al., 1990) stimulated ichnological research in many other areas with Paleozoic footprints of New Mexico (Lucas and Heckert, 1995), but, unfortunately, did not sustain interest for the same kind of research in northern New Mexico. During the last almost 30 years, the tetrapod ichnofauna of the study area experienced only a single (but uncommented) update to its taxonomic composition (Minter and Braddy, 2009).

The recent interest in the topic has arisen from a comprehensive review of the Paleozoic tetrapod ichnofauna of New Mexico commenced by the authors in 2010 (Lucas et al., 2011, 2012, 2013a-c, 2014; Voigt and Lucas, 2012, 2013; Voigt et al., 2013a, b). The first results of this project cover a wide range of issues of vertebrate ichnology, including taxonomy, the faunistic interpretation of ichnofaunas, and the evolutionary ecology of early tetrapods, as well as the biostratigraphy and chronostratigraphy. Therefore, the purpose of this paper is at least twofold: We intend to present a revision of the Paleozoic footprint record of north-central New Mexico on the one hand and, on the other hand, to testify to the validity of some recently advanced concepts in Paleozoic vertebrate ichnology.

Geology

All tetrapod footprints described herein come from Early Permian red beds of the Sangre de Cristo Formation in San Miguel County, north-central New Mexico (Figs. 1, 2). The Sangre de Cristo Formation, up to 1700 m thick, is a succession of mainly siliciclastic deposits that accumulated in an active foreland basin (Rowe-Mora basin, or Taos trough) in response to various tectonic pulses of the ancestral Rocky Mountains (e.g., Brown, 1984; Soegaard and Caldwell, 1990). It consists of a lower, coarse-grained megasequence (mainly conglomerates) deposited on a high gradient braided alluvial plain, and an

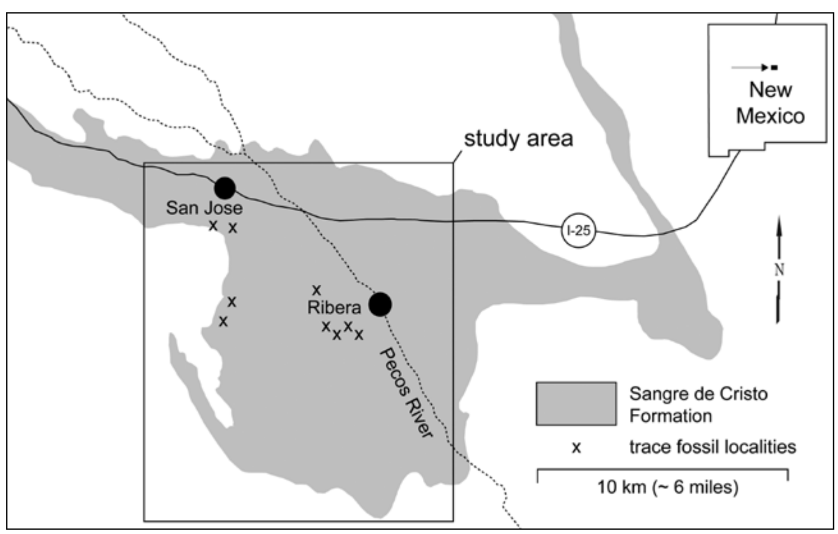

FIGURE 1. Geographic position of the study area in north-central New Mexico and generalized locations of the Permian tetrapod footprint localities.

upper, fine-grained megasequence (interbedded sandstone and mudstone) deposited on a broad, low gradient, mud-rich alluvial fan (Caldwell, 1987; Soegaard and Caldwell, 1990). Maximum thickness of the formation decreases from today's northern part of the basin towards the south and, consequently, the base of the succession is most likely diachronous.

The maximum age of the formation is constrained by invertebrate macrofossils, fusulinids and conodonts from underlying mid-Pennsylvanian (Desmoinesian) marine carbonates (Sutherland, 1963; Sutherland and Harlow, 1973; Baltz and Myers, 1999; Krainer et al., 2004; Lucas et al., 2015). Whereas most of the Sangre de Cristo Formation was previously thought to be of Middle to Late Pennsylvanian age (Soegaard and Caldwell, 1990), more recent studies on tectonostratigraphy and vertebrate paleontology suggest a mostly to entirely Early Permian age of the formation and a significant stratigraphic gap to the underlying mid-Pennsylvanian strata (Baltz and Myers, 1999; Berman et al., 2013; Lucas et al., 2015). At present, fossils are only known from the southernmost outcrops of the Sangre de Cristo Formation and include remains of plants, lungfish, xenacanth sharks, and tetrapods, as well as invertebrate traces and tetrapod footprints (Hunt et al., 1990; Berman, 1993; Berman et al., 2013; Rinehart et al., 2015). As far as these fossils being stratigraphically significant, they all indicate an Early Permian (Wolfcampian) age of the fossil-bearing deposits (Berman, 1993; Berman et al., 2013). The Sangre de Cristo Formation is conformably overlain by shallow-marine siliclastics and evaporite sediments of the late Early Permian (Leonardian) Yeso Group, which provides a minimum age for the strata discussed here.

All tetrapod footprints from the Sangre de Cristo Formation were collected from sites that occur in the upper reaches of the Pecos River drainage area between San Jose and Villanueva south of Interstate 25 (Fig. 1). In this part of the Taos trough, the formation reaches a thickness of 200–350 m (Read et al., 1944; Berman et al., 2013) and can be divided into two mudstone-dominated lithostratigraphic units (Soegaard and Caldwell, 1990; Lucas et al., 2015). The lower unit is characterized by thick, channel form sandstone and conglomerate, whereas laterally persistent sheet sandstone with intercalations of mudstone dominate the upper unit. Vertebrate body fossils have been mainly found in the lower unit (Berman, 1993; Berman et al., 2013); plants and trace fossils, however, are found exclusively in the upper unit (Hunt et al., 1990; Lucas et al., 2015; Rinehart et al., 2015). At the time of deposition of the Sangre de Cristo red beds, the study area represented an intermontane inland environment surrounded by the Uncompahgre, Pedernal, Sierra Grande and Cimarron uplifts and was situated at least 160 km away from the nearest marine shoreline (Soegaard and Caldwell, 1990; Kues and Giles, 2004). Paleobotanical and sedimentological evidence suggests a hot, seasonally arid climate. Tracksites in the upper part of the Sangre de Cristo Formation (Fig. 2) occur in sandstone beds that represent broad shallow channels, sheet flood deposits and local crevasse splays (Lucas et al., 2015).

NMMNH (New Mexico Museum of Natural History and Science) locality 1339 south of Ribera is one of the most diverse late Paleozoic tetrapod footprint assemblages of New Mexico.

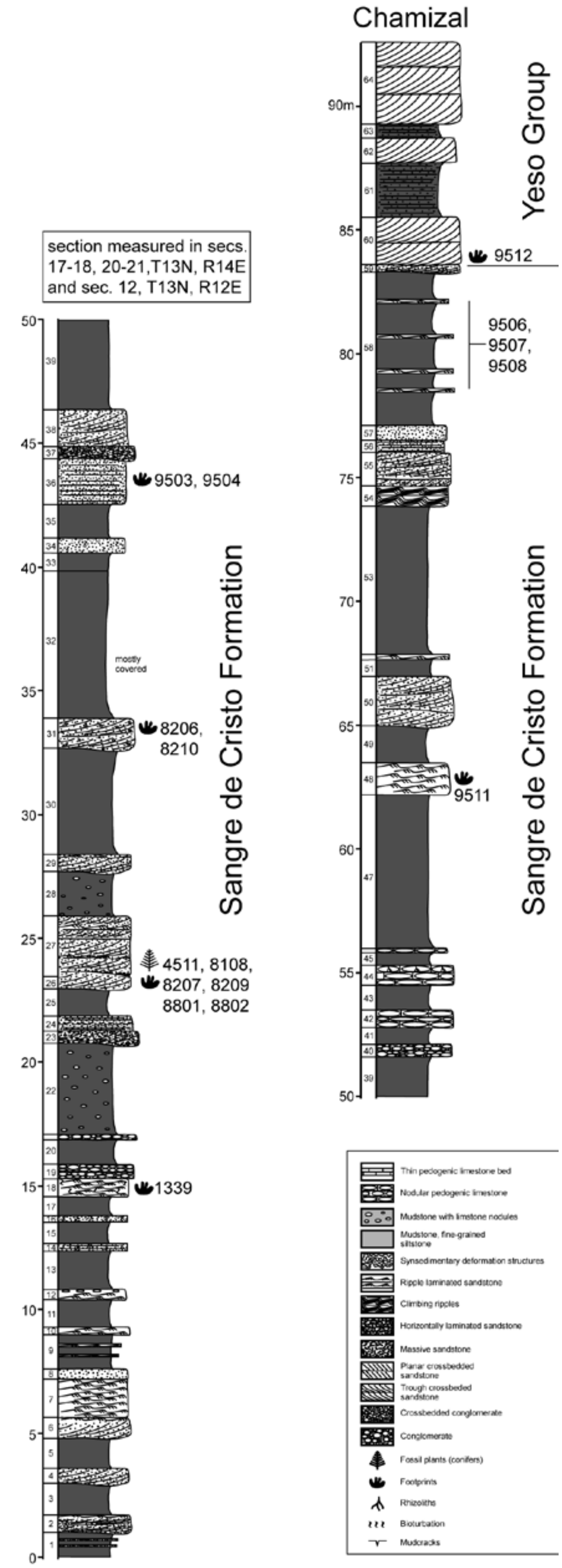

FIGURE 2. Reference section for the Sangre de Cristo Formation and basal Yeso Group in southwestern san Miguel County, north-central New Mexico (after Lucas et al., 2015), and the stratigraphic distribution of tetrapod footprint localities. Localities in this section are 1339, 4511, 8108, 8207, 8209, 8801, 8802, 9511 and 9512. The other localities have been projected into the section from other nearby, correlatable levels.

Vertebrate tracks are common and often well preserved, though true trackways are rather rare among the NMMNH material. The abundance and relatively high quality of footprints from NMMNH locality 1339 can be explained by the depositional environment that favored the preservation of traces. The track-bearing strata consist of evenly to unevenly parallel, mm-to-cm-thick, laminated, fine-grained sandstone separated by clayey to silty, mm-thick, laminated mudstone. Apart from tetrapod tracks and invertebrate traces (e.g., *Diplichnites, Lithographus, Stiallia, Tonganoxichnus*), the surfaces show tool marks, mud-cracks, mm- to cm-sized circular impressions (rain-drop or hail impressions), and microbially induced sedimentary structures (Hunt et al., 1990; Minter and Braddy, 2009; Lucas et al., 2015). Ripples are uncommon, and except for tool marks there is no other evidence of rapidly flowing water. Plant remains are not abundant and are almost exclusively represented by muddy impressions of walchian conifer branches and shoots. Root traces, however, are ubiquitous and preserved on more than half of all slabs from NMMNH locality 1339. Altogether, the lithological and paleontological content of the site suggests that the track-bearing red beds originated on a vegetated, episodically and shallowly inundated floodplain.

The sedimentology of the sites with Permian tetrapod footprints other than NMMNH locality 1339 in the study area is less well studied, but all of the localities are clearly in fluvial deposits. At these other localities, footprints are less abundant and less well-preserved than at locality 1339, probably due to hydrodynamically higher energy deposition and the resulting coarser grain size and higher lateral variability of depositional conditions.

Material and methods

About 200 specimens with Permian tetrapod footprints from the study area are preserved at NMMNH. They have been collected over the last 30 years by different parties of the museum, whereby collections were made mainly in three periods: before 1990, between 2000 and 2005, and between 2010 to 2013. The material comes from 16 different localities that are all situated in the upper half of the Sangre de Cristo Formation or in the most basal part of the overlying red beds of the local Yeso Group (Figs. 1, 2; Table 1). There is a remarkable imbalance of fossil footprint data through space and time in the study area, inasmuch as more than three-quarters of the tracks come from a single locality (NMMNH L-1339; Fig. 2, Table 1). NMMNH locality 1339 yields six to nine different tetrapod footprint taxa, the most diverse ichnoassemblage of the studied Permian track sites in north-central New Mexico. Almost all other localities with Permian tetrapod footprints yielded tracks assignable to only two ichnotaxa (Table 1).

Each NMMNH specimen with Permian tetrapod footprints from the study area was described in detail and photographed for the purpose of this work. Outline drawings were made of the better preserved tracks and true trackways in order to quantify parameters of the imprint morphology and trackway pattern or to facilitate comparison to material from other Permian footprint sites. Quantitative analyses were carried out according to standard procedures in vertebrate ichnology (Haubold, 1971; Leonardi, 1987; Voigt and Haubold, 2000). Our ichnotaxonomic concept is based on anatomically-controlled features of the imprint morphology and trackway pattern (Haubold, 1996). This study benefits from a comparative analysis conducted in 2010 to 2012 of all of the NMMNH Paleozoic tetrapod footprints. Map coordinates of all fossil localities mentioned in the text are on file at NMMNH.

PALEOICHNOLOGY

The fossil footprints described here can be assigned to six well-known and widely distributed Late Paleozoic tetrapod ichnotaxa. These are *Batrachichnus* (Woodworth, 1900), *Limnopus* (Marsh, 1894), *Ichniotherium* (Pohlig, 1892), *Dimetropus* (Romer and Price, 1940), *Tambachichnium* (Müller, 1954), and *Dromopus*

TABLE 1. Tetrapod ichnodiversity of the Sangre de Cristo Formation (NMMNH locality 1339 to NMMNH locality 9508) and overlying Yeso Group (NMMNH localities 9511 and 9512) in north-central New Mexico. A record in brackets refers to material that is only compared to the ichnotaxon.

NMMNH locality	*Matthewichnus*	*Batrachichnus*	*Limnopus*	*Ichniotherium*	*Tambachichnium*	*Dimetropus*	*Notalacerta*	*Hyloidichnus*	*Dromopus*	Specimens indet.	Total NMMNH specimens
L-1339	(+)	+	+	+	+	+	(+)	(+)	+	+	152
L-4511	-	-	-	-	-	-	-	-	+	-	2
L-8108	-	-	-	-	-	-	-	-	+	-	2
L-8206	-	-	+	-	-	-	-	-	+	+	9
L-8207	-	+	-	+	-	-	-	(+)	+	+	12
L-8209	-	-	-	-	-	+	-	-	-	-	1
L-8210	-	+	-	-	-	-	-	-	-	+	2
L-8801	-	-	-	+	-	-	-	-	-	-	3
L-8802	-	-	-	-	-	-	-	-	+	-	0
L-9503	-	+	-	-	-	-	-	-	+	-	1
L-9504	-	-	-	-	-	-	-	-	-	+	1
L-9506	-	-	-	-	-	-	-	-	-	+	1
L-9507	-	+	-	-	-	-	-	-	-	-	1
L-9508	-	-	-	-	-	-	-	-	+	+	2
L-9511	-	-	-	-	-	-	-	-	-	+	1
L-9512	-	+	-	-	-	-	-	-	+	+	8
localities	(+)	+	+	+	+	+	(+)	(+)	+	+	198

(Marsh, 1894). A detailed and amended characterization of these ichnotaxa is given in Voigt (2005). In order to avoid redundancy, we will focus in this paper solely on the most important and diagnostic features of the ichnotaxa.

Batrachichnus (Woodworth, 1900) (Figs. 3, 9A)

Referred specimens: NMMNH P-13994, isolated manus-pes couple, concave epirelief; NMMNH P-14005, faint trackway of 11 tracks, convex hyporelief; NMMNH P-14083, isolated manus-pes couple, convex hyporelief; NMMNH P-45922, three manus-pes couples of faint trackway, concave epirelief; NMMNH P-45935, two more distinctly preserved manus-pes couples of the same trackway, concave epirelief; NMMNH P-45951, faint trackway of four manus-pes couples, concave epirelief; NMMNH P-61989, incomplete trackway, part and counterpart (all from NMMNH locality 1339).

Description and discussion: This ichnotaxon is characterized by the tetradactyl manus imprint, small tracks that do not exceed 40 mm in total length, and a trackway pattern of usually regularly alternating manus-pes couples. *Limnopus* has larger tracks, and *Matthewichnus* a much more irregular trackway pattern. Besides *Dromopus*, *Batrachichnus* is the most common tetrapod track at NMMNH locality 1339 and is known from five other localities within the study area.

Limnopus (Marsh, 1894) (Figs. 4, 9B)

Referred specimens: NMMNH P-61936, isolated manus imprint, convex hyporelief; NMMNH P-61941, three imprints of the same trackway, convex hyporelief; NMMNH P-61943, six imprints of two trackways, convex hyporelief; NMMNH P-61945, isolated large manus-pes couple, convex hyporelief (all from NMMNH locality 8206).

Description and discussion: Tracks of quadrupedal tetrapods with tetradactyl manus imprints. Tracks are identical to *Batrachichnus* except for the fourth digit of the manual track that seems to be about as long as digit II in *Limnopus*, but about as long as digit I in *Batrachichnus* (Voigt, 2005). This feature, however, is only reliable for large tracks (>40 mm total length). Smaller tracks often demonstrate a remarkable variability in the relative length of the manual digit IV impression. Variability within tracks of the same trackway (and hence the same animal) indicates extramorphology as a major reason for apparently extended digit IV impressions. An even larger problem is the more or less continuous range of digit IV impression lengths of small tracks, making replicatable assignments difficult. Unambiguously, *Batrachichnus* and *Limnopus* are tracks of at least two different biotaxa with significantly different ranges of body size.

Ichniotherium (Pohlig, 1892) (Figs. 5, 9C)

Referred specimens: NMMNH P-14138, three tracks of the same trackway with faint tail/body trace, convex hyporelief; NMMNH P-45910, isolated pes imprint, convex hyporelief; NMMNH P-45911, pes imprint and proximal part of manus imprint, concave epirelief; NMMNH P-45943, fragmentary manus imprint, convex hyporelief (all from NMMNH locality 1339); NMMNH P-70773, sequence of three pes imprints, concave epirelief (from NMMNH locality 8207).

Description and discussion: Tracks of this ichnotaxon are easy to recognize by size and shape. All pes imprints of *Ichniotherium* from the Sangre de Cristo Formation well exceed 10 cm in length and show a distinct circular heel impression. Digits are, in most pes imprints, reduced to faint impressions of the distal parts of digit III and IV, whereas the digit tips are usually preserved as deep, oval- to circular-shaped impressions. A complete, well-preserved *Ichniotherium* manus imprint has not yet been recovered from the Sangre de Cristo Formation. *Ichniotherium* is common especially at NMMNH locality 1339, taking numerous specimens with mainly digit tip impressions (e.g., NMMNH P-14009, -14011, -14049, -14050, -14071, -14074, -14076, -14080, -14091, -14100, -14107, -14117, -14135, -24614, -45922, -45925, -45929, -45952,

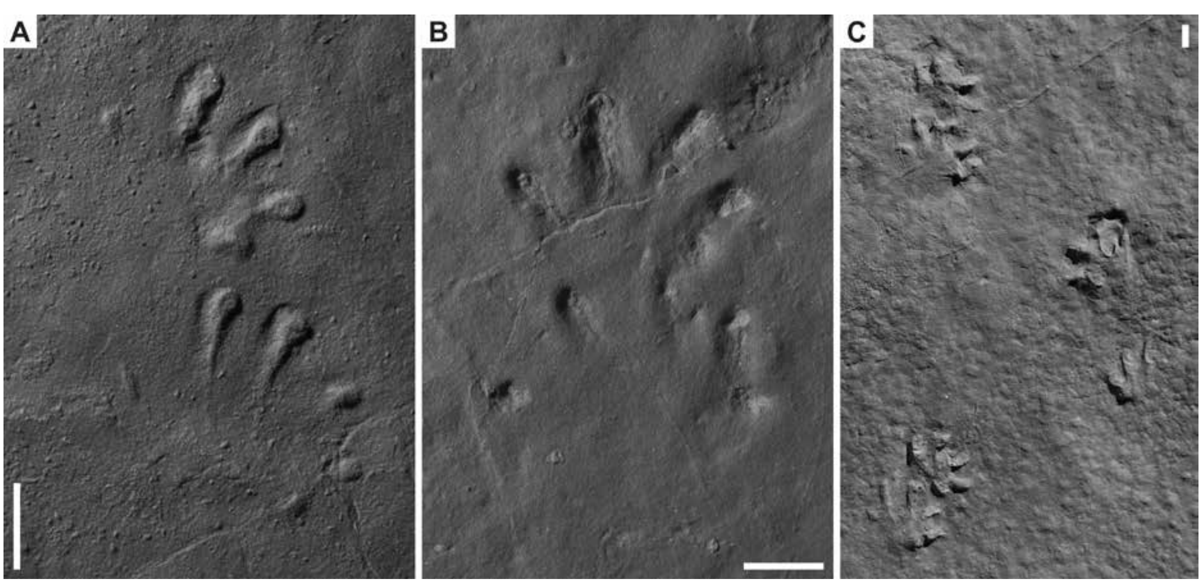

FIGURE 3. *Batrachichnus* (Woodworth, 1900). Representative specimens from the Sangre de Cristo Formation of north-central New Mexico. Material: A. NMMNH P-14083; B. NMMNH P-13994; C. private collection of Henri Ortiz, Pueblo, San Miguel County, New Mexico. Scale bars: 1 cm.

-66606, -66607) into account that most likely belong to the ichnotaxon. Remarkable is NMMNH P-14138 (Hunt et al., 1990: fig. 5F), because it is one of only three specimens with a tail or body trace in the global record of *Ichniotherium*. The other specimens come from the Early Permian Tambach Formation of Thuringia, central Germany (Voigt, 2002: pl. I, fig. 2; Dalman et al., 2013: fig. 1).

Several well-preserved pes imprints (NMMNH P-45910, -45911, -70773) clearly suggest that *Ichniotherium* tracks from the Sangre de Cristo Formation show a relatively short pedal digit V. This feature is known from two Pennsylvanian-Permian *Ichniotherium* ichnospecies: (1) *Ichniotherium willsi* (Haubold and Sarjeant, 1973), which is here considered to be a junior subjective synonym of *Ichniotherium* (= *Baropus*) *hainesi* (Carman, 1927); and (2) the much more common and widely distributed *Ichniotherium cottae* (Pohlig, 1885) (Voigt et al., 2005, 2007, 2012). *I. hainesi* and *I. cottae* are only differentiated

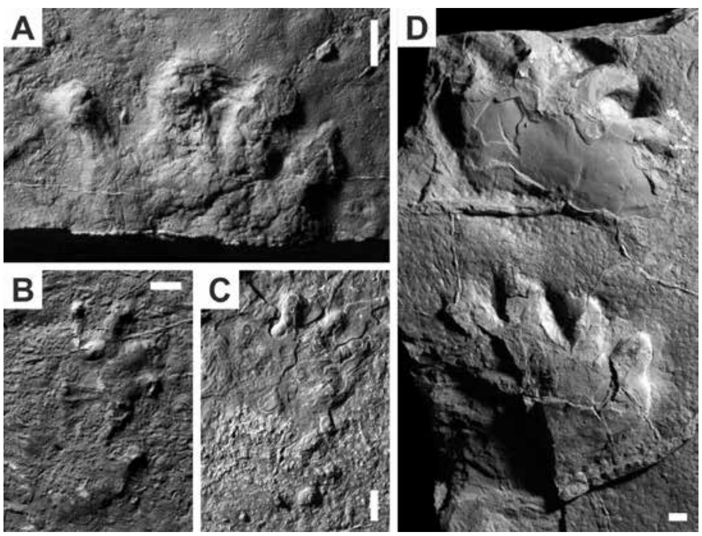

FIGURE 4. *Limnopus* (Marsh, 1894). Representative specimens from the Sangre de Cristo Formation of north-central New Mexico. Material: A. NMMNH P-61938; B. NMMNH P-61941; C. NMMNH P-61943; D. NMMNH P-61945. Scale bars: 1 cm.

by the trackway pattern, considering that pes imprints of the former ichnospecies are directed outward from the hypothetical trackway midline and parallel or slightly rotated inward in the latter ichnospecies. NMMNH P-70773 (Fig. 9C) shows pes imprints in which the orientation clearly matches the trackway pattern of *I. cottae*.

Tambachichnium (Müller, 1954) (Figs. 6, 9D)

Referred specimens: NMMNH P-45913, isolated pes or manus imprint, convex hyporelief; NMMNH P-61922, isolated pes or manus imprint, concave epirelief (from NMMNH locality 1339).

Description and discussion: Tracks of this ichnotaxon are characterized by long and slender digits with distinct digit tip impressions that most likely were produced by sturdy claws of the trackmaker. Manus and pes imprints of *Tambachichnium* differ only in size (Voigt, 2005). Because all specimens of the ichnotaxon from the study area are isolated tracks, it is impossible to assign them to the manus or pes. There is an undeniable similarity of the imprint morphology to *Dromopus*. Both ichnotaxa, however, clearly differ by the maximum imprint length (≥10 cm in *Tambachichnium*; ≤8 cm in *Dromopus*) and, more importantly, the digit proportions. *Dromopus* shows a relatively longer digit IV impression, with a disproportionate increase of digit length from II to IV. In *Tambachichnium* the total length of the impressions of the middle digits increases proportionally, which is expressed by the fact that the tips of digit II to IV are in the same line.

For a long time, *Tambachichnium* was only known from its stratum typicum, the Early Permian Tambach Formation in Thuringia, central Germany (Müller, 1954; Haubold, 1998). During the last 10–15 years, we obtained knowledge of the same kind of tracks from several other strata such as the Rabejac Formation of southern France (author, personal observation, 2004), the Goldlauter, Rotterode and Oberhof Formations of central Germany (Voigt, 2005), the Maroon Formation of central Colorado (Voigt et al., 2005), the Abo Formation of New Mexico (Lucas et al., 2013c), and the Bleichenbach Formation of central

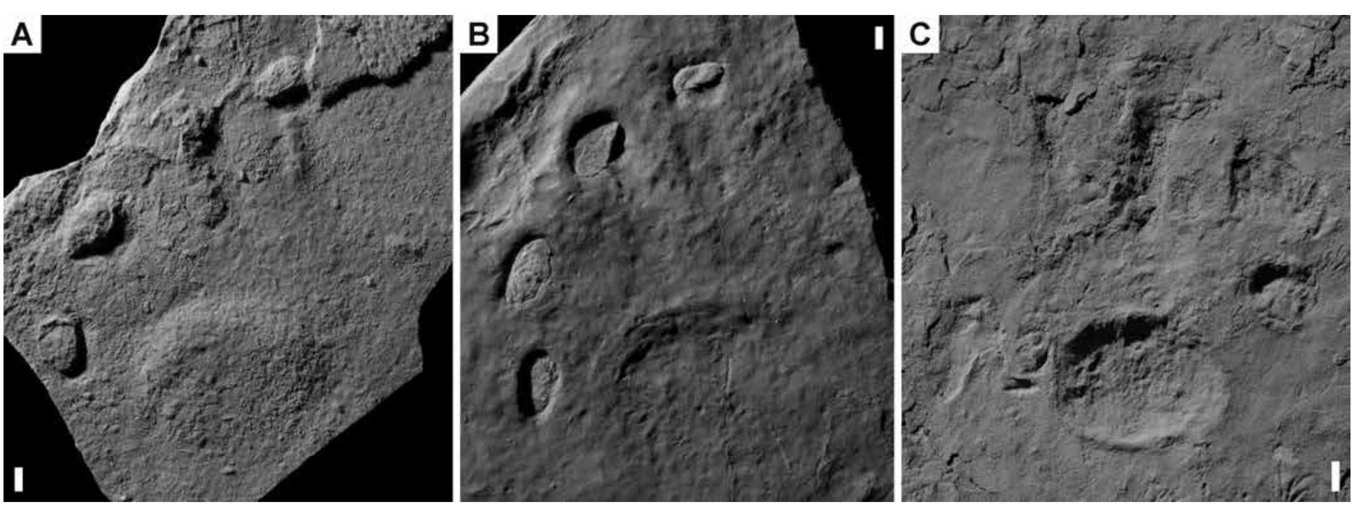

FIGURE 5. *Ichniotherium* (Pohlig, 1892). Representative specimens from the Sangre de Cristo Formation of north-central New Mexico. Material: A. NMMNH P-45910; B. NMMNH P-45911; C. NMMNH P-70773. Scale bars: 1 cm.

Germany (author, personal observation, 2014). Including the occurrence from the study area, *Tambachichnium* is known from eight formations and four locales in North America and Europe. Most, if not all, of the relevant strata are of Early Permian age. Thus, *Tambachichnium* has advanced to the rank of a principal morph of Early Permian tetrapod footprints.

Dimetropus (Romer and Price, 1940) (Figs. 7, 9E)

Referred specimens: NMMNH P-45926, one more complete track and several tracks showing nail impressions only, convex hyporelief (from NMMNH locality 1339); NMMNH P-70771, incomplete manus-pes couple, convex hyporelief (from NMMNH locality 8207); NMMNH P-61948, isolated manus-pes couple, convex hyporelief (from NMMNH locality 8209).

Description and discussion: This kind of track varies much in shape, depending on the depth of the impression (Fig. 7). Shallow imprints made on a relatively dry substrate show a more or less oval-shaped heel and up to five, often isolated digit tip impressions that are arranged on a virtual circular arc (Fig. 7A). Deep impressions made on a relatively wet substrate show a proximo-laterally extended heel connected to up to five slender, parallel to slightly radially positioned digit impressions (Fig. 7B). It may be due to the heavy body and a comparatively small sole and palm that *Dimetropus* tracks demonstrate an enormous range of preservation, resulting in numerous synonyms (Voigt, 2005). The ichnotaxon is not exceedingly common within the study area, but a few unambiguous specimens come from at least three different localities. The local record is dominated by shallow to very shallow, near-surface tracks. Some imprints (e.g., NMMNH P-14003, -14084, -14100, -14101) that most likely can be assigned to *Dimetropus* are reduced to tiny nail impressions arranged on the typical circular arc.

Dromopus (Marsh, 1894) (Figs. 8, 9F)

Referred specimens: NMMNH P-14094, about 30 tracks of at least five, but not traceable trackways, convex hyporelief; NMMNH P-14144, numerous tracks of several, not traceable trackways, convex hyporelief; NMMNH P-32648, numerous tracks of several, not traceable trackways on both sides of slab; NMMNH P-32650 and NMMNH P-32651, mass occurrences of small tracks, no traceable trackways, convex hyporelief; NMMNH P-32657 and NMMNH P-32660, numerous tracks of several, not

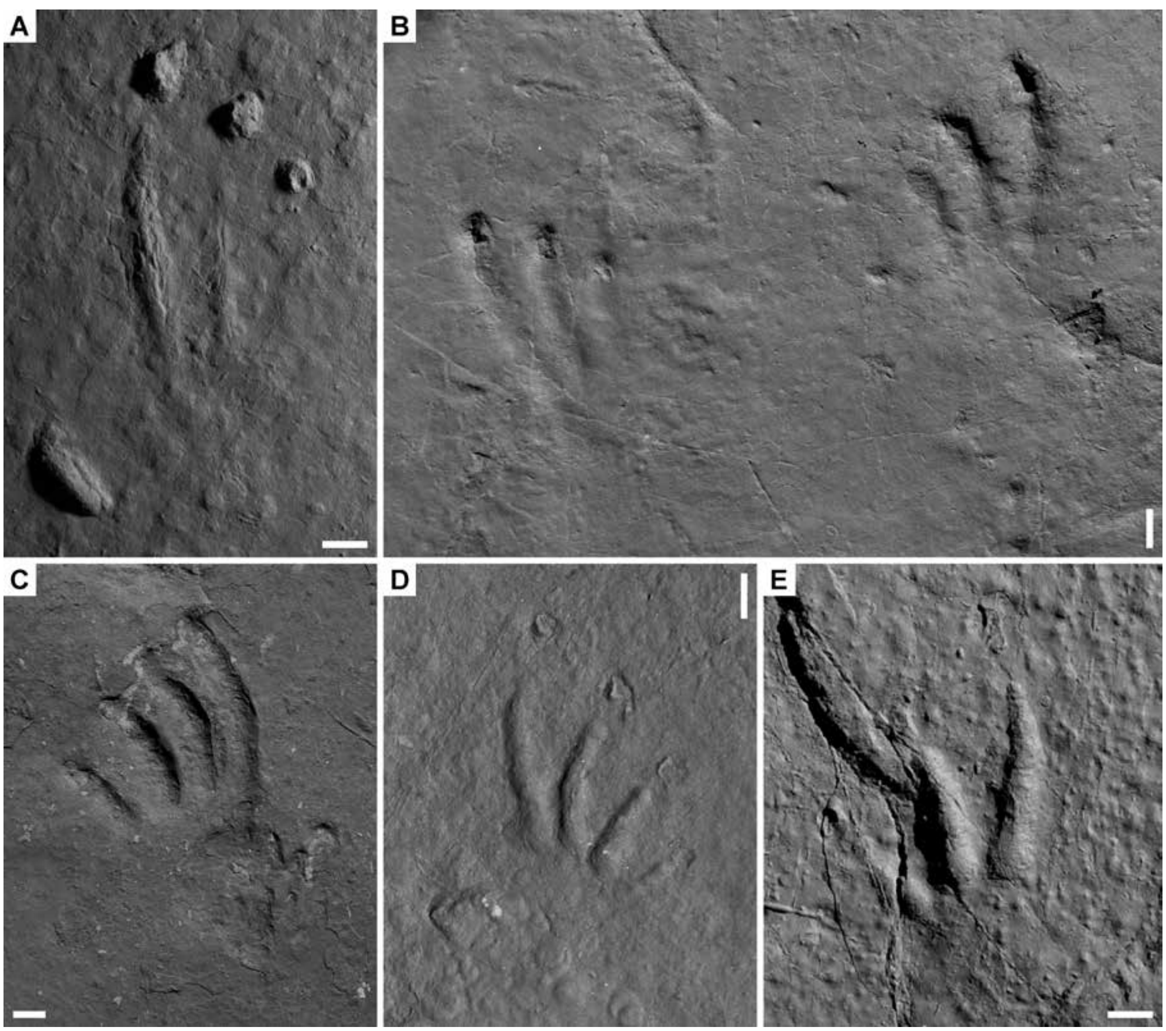

FIGURE 6. *Tambachichnium* (Müller, 1954). Representative specimens from the Sangre de Cristo Formation of north-central New Mexico. Material: A. NMMNH P-45913; B-E. private collection of Henri Ortiz, Pueblo, San Miguel County, New Mexico. Scale bars: 1 cm.

traceable trackways, concave epirelief; NMMNH P-32662, mass occurrences of small tracks, no traceable trackways, concave epirelief; NMMNH P-45930 and NMMNH P-45931, numerous tracks of several, not traceable trackways, convex hyporelief (all from NMMNH locality 1339); NMMNH P-37622, numerous tracks of several, partially traceable trackways, convex hyporelief (from NMMNH locality 4511); NMMNH P-61946, numerous tracks of several, not traceable trackways, convex hyporelief (from NMMNH locality 8108); NMMNH P-61936, numerous tracks of three or more trackways, convex hyporelief; NMMNH P-61939, mass occurrence of small tracks, no traceable trackway, convex hyporelief (from NMMNH locality 8206).

Description and discussion: Dromopus is the most common and most widely distributed type of Pennsylvanian-Permian tetrapod footprints (e. g., Haubold, 1971, 2000; Gand, 1988; Lucas and Heckert, 1995; Voigt, 2005; Marchetti, 2014). The tracks are characterized by long and slender digits with acute tips. The fourth digit of manus and pes imprints is disproportionately extended with respect to the remaining digits. There is a tendency to digitigrade preservation, especially of the manus imprint. *Dromopus* tracks are known from more than half of all Permian tetrapod footprint localities of the study area. Trampled surfaces with a projected hundreds to thousands of such tracks per square meter are remarkably abundant. True trackways are a major exception for the material from the study area, not only on surfaces with *Dromopus* mass occurrences. The total imprint length of *Dromopus* tracks from the Sangre de Cristo Formation ranges from about 1–6 cm.

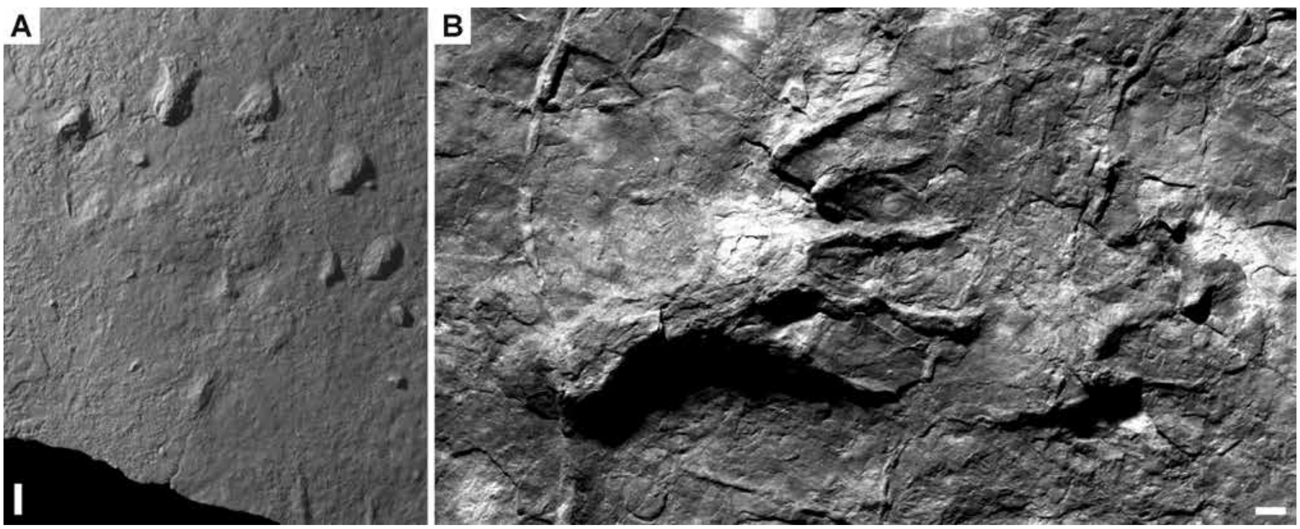

FIGURE 7. *Dimetropus* (Romer and Price, 1940). Representative specimens from the Sangre de Cristo Formation of north-central New Mexico. Material: A. NMMNH P-45926; B. NMMNH P-61948. Scale bars: 1 cm.

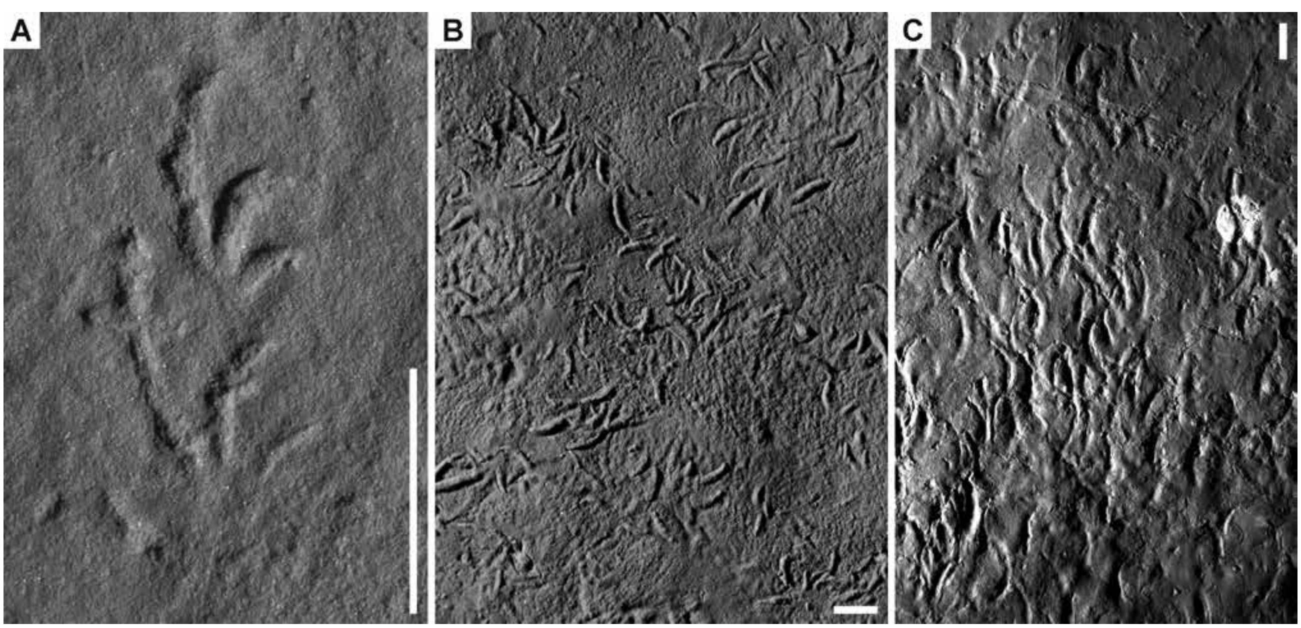

FIGURE 8. *Dromopus* (Marsh, 1894). Representative specimens from the Sangre de Cristo Formation of north-central New Mexico. Material: A. NMMNH P-14094; B. NMMNH P-32651; C. NMMNH P-32662. Scale bars: 1 cm.

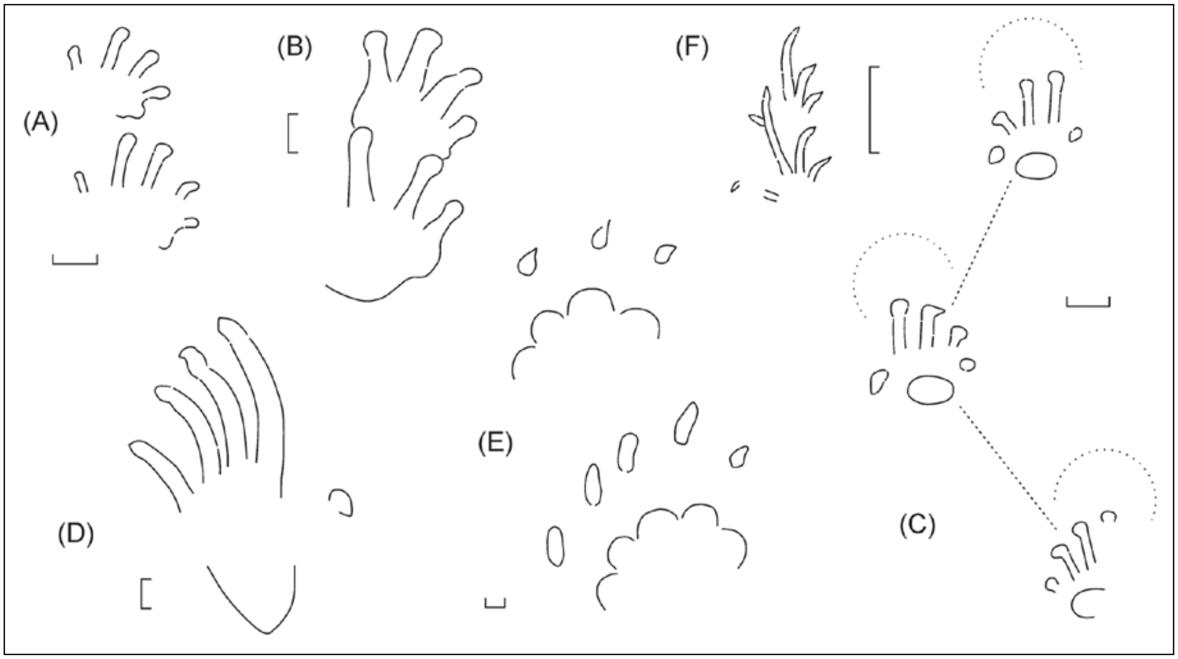

FIGURE 9. Outline drawings of representative tracks of the dominating tetrapod ichnotaxa from the Sangre de Cristo Formation of north-central New Mexico: A. *Batrachichnus*, left manus-pes couple, NMMNH P-14083; B. *Limnopus*, left manus-pes couple, NMMNH P-61941; C. *Ichniotherium*, incomplete trackway showing pes imprints only, NMMNH P-70773; D. *Tambachichnium*, right manus or pes imprint, cf. Figure 6C; E. *Dimetropus*, right manus-pes couple, NMMNH P-70771; F. *Dromopus*, left manus-pes couple, NMMNH P-14094.

Other Tetrapod Tracks (Fig. 10)

Apart from the aforementioned six tetrapod ichnotaxa, the Sangre de Cristo Formation gives evidence of at least three more types of fossil tetrapod tracks. We keep the latter separate because the material is sparse and rather poorly preserved, so that its ichnotaxonomic assignment has to be considered provisional.

cf. *Matthewichnus* (Haubold, 1970)

Referred specimens: NMMNH P-32644, about 40 indistinct tracks of the same trackway showing a continuous tail/body trace, convex hyporelief; NMMNH P-32649, 30 to 40 indistinct tracks of the same trackway have a continuous tail/body trace, concave epirelief; all from NMMNH locality 1339.

Description and discussion: Tracks assigned to cf. *Matthewichnus* are small (total imprint length is usually around 10 mm or less) and show tetradactyl manus imprints, a continuous tail/body trace and a strikingly irregular trackway pattern (Fig. 10A). The imprint morphology is similar to *Batrachichnus*, but both ichnotaxa are significantly different in the arrangement of the tracks (Voigt and Lucas, 2015). There are only two specimens among the studied material that show tracks comparable to *Matthewichnus*, and both come from NMMNH locality 1339.

cf. *Notalacerta* (Butts, 1891)

Referred specimens: NMMNH P-14014, three pieces of the same trackway, but pieces do not fit, and two of them show six tracks each, the third one shows two or three tracks only, and all trackway segments have sharp and continuous tail/body trace, all tracks preserved in convex hyporelief, from NMMNH locality 1339.

Description and discussion: Tracks compared to *Notalacerta* are represented by a single specimen, which is striking in its extremely sharp and straight tail/body trace (Fig. 10B). The long and slender digits and their proportions are superficially similar to *Dromopus*, but they differ by the much shorter fourth digit and, moreover, *Dromopus* has never been observed with such a continuous and deep tail/body trace. We compare the tracks of NMMNH P-14014 with the usually Pennsylvanian ichnogenus *Notalacerta*. Supposed Early Permian records of this ichnotaxon come from Canada (Calder et al., 2004) and southern New Mexico (Voigt and Lucas, 2015).

cf. *Hyloidichnus* (Gilmore, 1927)

Referred specimens: NMMNH P-32664/32665, isolated manus-pes couple with faint tail/body trace, part and counterpart (NMMNH locality 1339); NMMNH P-70772, isolated manus or pes imprint, concave epirelief (NMMNH locality 8207).

Description and discussion: Medium-sized, semiplantigrade to semidigitigrade tracks with long and slender digits and acute digit tip (Fig. 10C). These tracks show the typical morphology of advanced "captorhinomorph" footprints, usually assigned to *Varanopus* (Moodie, 1929) and *Hyloidichnus* (Gilmore, 1927). Both ichnotaxa essentially differ in the relative length of the fifth digit of the pes imprint and the maximum imprint size (Voigt et al., 2009, 2013b). The fifth digit of the only known pes imprint from the study area (NMMNH P-32664/32665) is, unfortunately, not preserved. *Varanopus* is a small track measuring up to about 40 mm in total length (Voigt, 2005; Marchetti, 2014). The discussed tracks from the Sangre de Cristo Formation are 42 to 70 mm in length and, thus, are more likely assigned to *Hyloidichnus*.

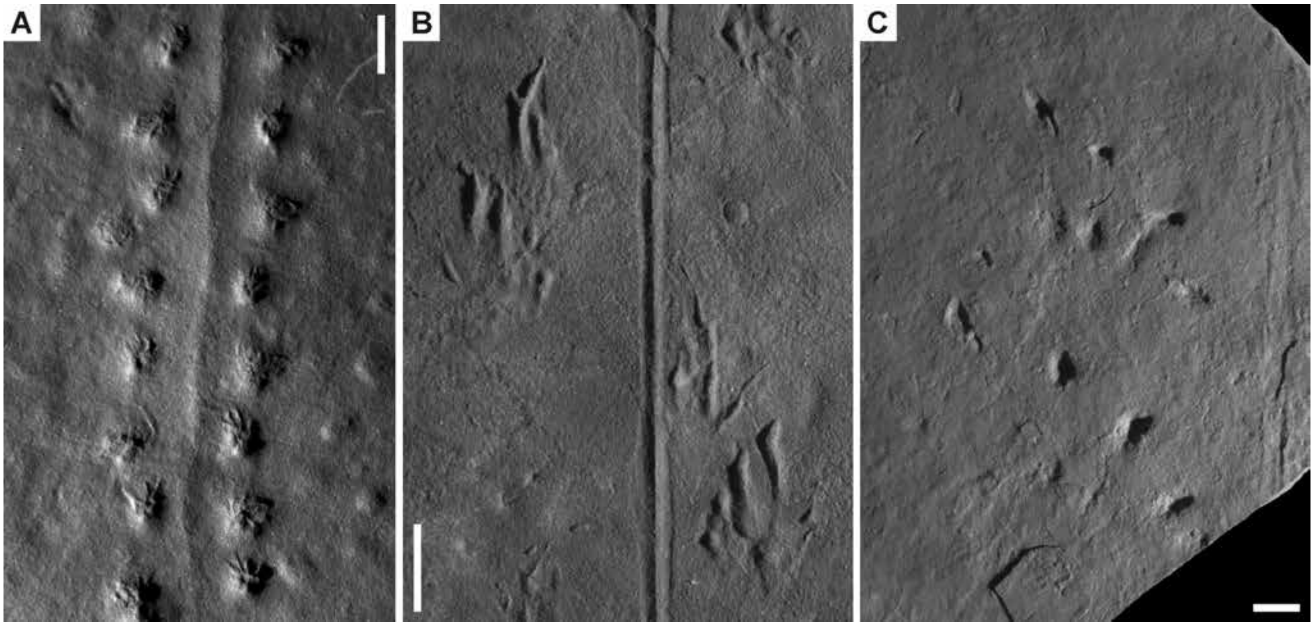

FIGURE 10. Rare and insufficiently preserved types of tetrapod footprints from the Sangre de Cristo Formation of north-central New Mexico: A. cf. *Matthewichnus* (Haubold, 1970); B. cf. *Notalacerta* (Butts, 1891); C. cf. *Hyloidichnus* (Gilmore, 1927). Material: A. NMMNH P-32644; B. NMMNH P-14014; C. NMMNH P-32664/32665. Scale bars: 1 cm.

FAUNISTIC INTERPRETATION

At least on the level of families and orders, there is a viable concept of the faunistic interpretation of Permian tetrapod footprints (Haubold, 2000; Voigt, 2005, 2012). According to this, *Matthewichnus* is usually referred to microsaurian lepospondyls, *Batrachichnus* to small and medium-sized semiaquatic to terrestrial temnospondyls, *Limnopus* to large, eryopid-like temnospondyls, *Ichniotherium* to diadectomorph reptiliomorphs, *Tambachichnium* and *Dimetrodon* to varanopid and sphenacodontid Eupelycosauria, respectively, *Notalacerta* and *Hyloidichnus* to protorothyrid and captorhinid non-diapsid eureptiles, and *Dromopus* to araeoscelid Diapsida or similarly sized sauropsids with a lacertoid foot pattern.

The Sangre de Cristo Formation yields not only vertebrate tracks but also a relatively diverse assemblage of tetrapod body fossils (Berman, 1993; Berman et al., 2014; Lucas et al., 2015). As these fossil bones and the discussed tetrapod ichnofossils come from the same formation and more or less the same area, it is interesting to compare both records, especially with regard to the validity of conventional track-trackmaker correlations. The faunistic interpretation of Early Permian tetrapod footprints seems to be quite advanced considering that the majority of tetrapod ichnotaxa from the study area is well represented by skeletal remains of the expected potential trackmakers from the same place (Table 2). However, there are still some gaps in knowledge regarding body fossils of microsaurs, varanopid eupelycosaurs, protorothyridid “captorhinomorphs,” and potential trackmakers of *Dromopus*. The latter increases awareness about the quite different taphonomy of tracks and bones if the most common type of footprint is not represented by a single bone of the potential trackmaker. On the other hand, it is remarkable that there is no evidence of seymouriamorphs from the study area, either from the body fossil or the ichnofossil record. The co-occurrence of *Ichniotherium cottae* and *Diadectes* supports the track-trackmaker correlation gained from the Early Permian Bromacker assemblage in central Germany (Voigt et al., 2007).

BIOSTRATIGRAPHIC IMPLICATIONS

The tetrapod footprint assemblage of the upper unit of the Sangre de Cristo Formation is sufficiently abundant and diverse enough in order to evaluate its potential biostratigraphic significance (Fig. 11). Five of six reliably identified tetrapod ichnotaxa from these beds, i.e. *Batrachichnus*, *Limnopus*, *Ichniotherium*, *Dimetropus* and *Dromopus*, are known from Pennsylvanian as well as Permian strata (Voigt, 2005). It is quite possible that the stratigraphic range of the remaining *Tambachichnium* also starts in the Pennsylvanian, taking into consideration a record of uncertain Pennsylvanian-Permian age (Voigt et al., 2005), and the Late Pennsylvanian first occurrence of varanopid eureptiles (Campione and Reisz, 2010) as the most likely trackmakers.

Nevertheless, the tetrapod footprint assemblage from the Sangre de Cristo Formation is here proposed to be of Early Permian age, which is essentially based on two reasons: (1) *Tambachichnium*, which is remarkably abundant in the study area, seems to be most common in Sakmarian and Artinskian red-beds (Voigt, 2005); and (2) large captorhinomorph tracks (total imprint length >40 mm) are only known from post-Sakmarian strata (Gand and Durand, 2006; Voigt et al., 2009, 2011). A minimum age of the Sangre de Cristo tetrapod ichnofauna is especially inferred from the lack of *Erpetopus*, a supposed captorhinomorph footprint that first appears in Kungurian (early Leonardian) beds (Voigt and Lucas, 2013; Lucas, 2014; Marchetti, 2014). All these

TABLE 2. Track-trackmaker correlation chart for the discussed tetrapod footprints. Data of body fossil remains from the Sangre de Cristo Formation of north-central New Mexico are based on Berman (1993), Berman et al., 2014; Lucas et al., 2015).

Ichnogenus	Potential Early Permian trackmaker	Correlated Sangre de Cristo Formation tetrapod body fossil remains
Matthewichnus	Anamniota: Lepospondylia: Microsauria	-
Batrachichnus	Anamniota: Temnospondylia: Dissorophoidea	Temnospondyls indet.; *Platyhystrix*
Limnopus	Anamniota: Temnospondylia: Eryopidae	*Eryops*
Ichniotherium	Anamniota/Amniota: Diadectomorpha: Diadectidae	*Diadectes*
Tambachichnium	Amniota: Eupelycosauria: Varanopidae	-
Dimetropus	Amniota: Eupelycosauria: Sphenacodontidae	Sphenacodontids indet.; *Sphenacodon*
Notalacerta	Amniota: Eureptilia: Protorothyrididae	-
Hyloidichnus	Amniota: Eureptilia: Captorhinidae	Captorhinids indet.
Dromopus	Amniota: Parareptilia / Eureptilia	-

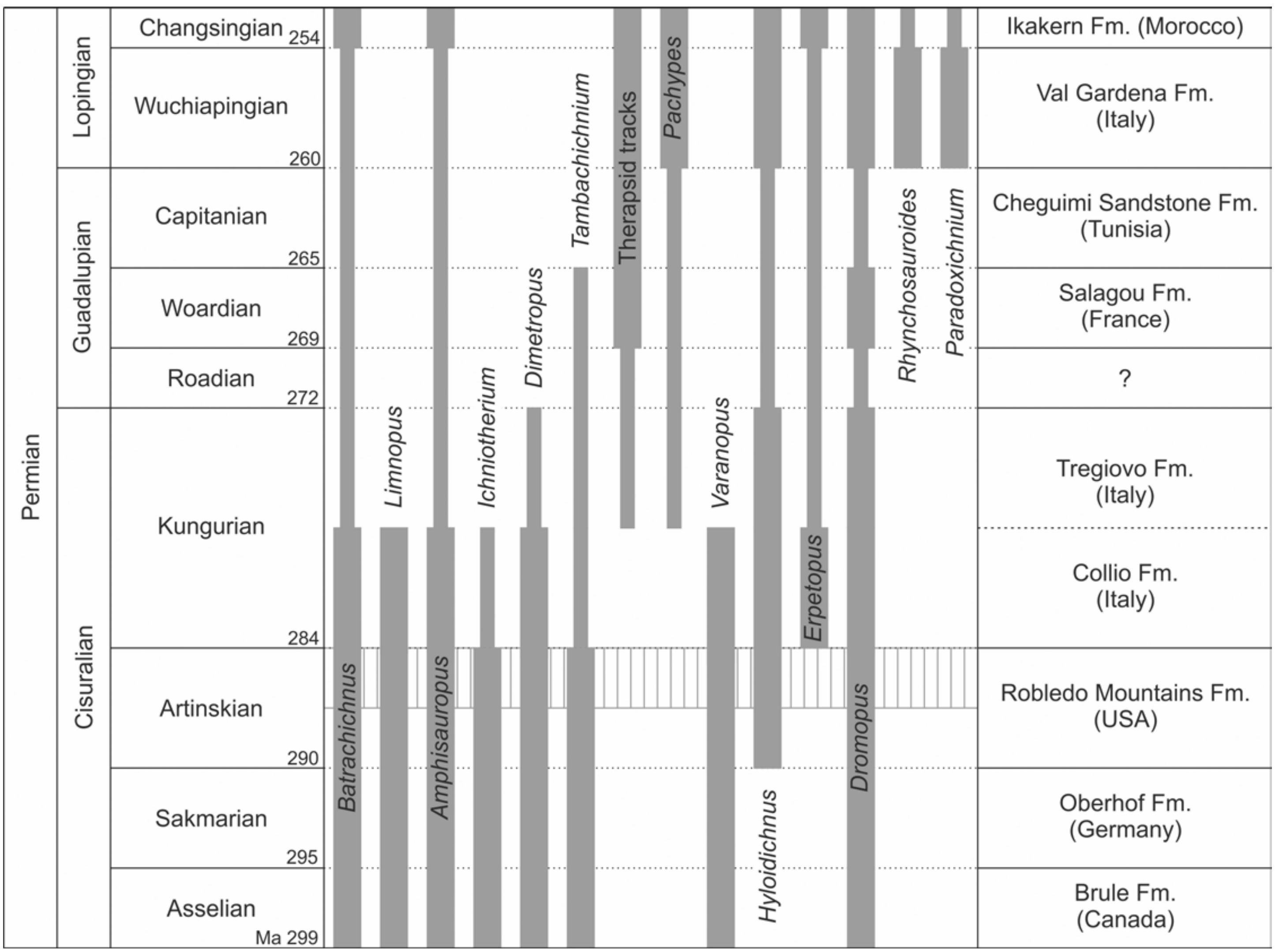

FIGURE 11. Stratigraphic range of common and well-known Permian tetrapod ichnotaxa (thick bar = fossil evidence; thin bar = distribution supposed) and proposed position of the tetrapod ichnoassemblage from the Sangre de Cristo Formation of north-central New Mexico (vertically hatched area). Formation 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), Lucas (2007), Voigt et al. (2010, 2013b), Hminna et al. (2012), and Marchetti (2014).

considerations restrict the age of the footprint-bearing strata of the Sangre de Cristo Formation to the Artinskian. As the tracks on NMMNH P-32664/32665 are unusually large for Early Permian "captorhinomorph" footprints (cf. *Hyloidichnus*), the discussed strata should be of the latest possible age before the onset of *Erpetopus* and, hence, the footprints suggest a late Artinskian (late Wolfcampian) age (Fig. 11).

CONCLUSIONS

1) Fossil tetrapod footprints are locally common and diverse in red-beds of the Sangre de Cristo Formation and lowermost Yeso Group of the southwestern part of San Miguel County, north-central New Mexico.
2) About 200 fossil tetrapod footprint specimens from 16 localities within the study area are housed at the New Mexico Museum of Natural History and Science, Albuquerque.
3) The vertebrate ichnofossil assemblage is dominated by tracks assigned to *Batrachichnus*, *Limnopus*, *Ichniotherium*, *Tambachichnium*, *Dimetropus*, and *Dromopus*.
4) Other tracks are compared to Matthewichnus, Notalacerta and Hyloidichnus, but the material is insufficient to confirm a genus-level assignment.
5) The vertebrate ichnofossil assemblage is interpreted to represent tracks of Microsauria, Temnospondyla, Diadectomorpha, Eupelycosauria, non-diapsid Eureptilia ("Captorhinomorpha"), and Parareptilia or Eureptilia with a lacertoid foot pattern. This interpretation is partially supported by the tetrapod body fossil record of the study area.
6) Based on the footprints there are strong arguments for a late Early Permian (late Artinskian/late Wolfcampian) age of the footprint-bearing strata of the Sangre de Cristo Formation in the southwestern part of San Miguel County, New Mexico.

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