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Adrian P. Hunt, Spencer G. Lucas, and Phillip Huber

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EARLY PERMIAN FOOTPRINT FAUNA FROM THE SANGRE DE CRISTO FORMATION OF NORTHEASTERN NEW MEXICO

ADRIAN P. HUNT, SPENCER G. LUCAS and PHILLIP HUBER
New Mexico Museum of Natural History, P.O. Box 7010, Albuquerque, New Mexico 87194-7010

Abstract—We describe an Early Permian ichnofauna from the upper part of the Sangre de Cristo Formation of San Miguel County, New Mexico. The ichnofauna includes the amphibian tracks *Anthichnium* sp., *Limnopus vagus*, cf. *Nanopus* sp. and cf. *Stenichnus* sp. Reptile tracks are *Dromopus lacertoides*, *Dromopus* sp., *Anomalopus supaiensis*, *Gilmoreichnus* sp. and *Dimetropus* sp. Invertebrate ichnotaxa include *Aenigmichnus multiformis* and *Paleohelcura tridactyla*, and the conifer *Walchia piniformis* is common. This locality is of Wolfcampian (Early Permian) age and represents an area of intermittent moisture (?pond margin) in a region of continual, unconfined flood-events. This locality contains the most diverse Early Permian ichnofauna reported from New Mexico and is one of the most diverse ichnofaunas of its age known from the Southwest.

INTRODUCTION

Footprints of fossil vertebrates are not uncommon in Early Permian red beds of the American Southwest, although localities like the one described here are rare. However, although these footprints attracted considerable interest during the first 30 years of the century (Lull, 1918; Gilmore, 1925, 1927, 1928; Moodie, 1929, 1930), essentially no work has been done on these footprint faunas since the Second World War, with a few notable exceptions (Baird, 1952, 1965a, b; Sarjeant, 1971). This is especially surprising given the recent renaissance in the study of Mesozoic footprints, particularly of dinosuars (Gillette and Lockley, 1989).

The situation in Europe has been very different. Several workers, notably Haubold and Gand, have published extensively on Late Paleozoic ichnofaunas. One thrust of this research has been to use vertebrate footprints in biochronology (Haubold, 1971, 1973, 1984; Gand and Haubold, 1988). We thus hope that this study and others like it will eventually allow fossil footprints to be utilized for intercontinental correlation of the Upper Paleozoic red beds of the Southwest.

However, before this goal can be reached, many basic data need to be gathered. As Baird (1965a) pointed out, much of the early work on Paleozoic footprints in North America was of poor quality. Many taxa were poorly diagnosed and illustrated, and most Late Paleozoic ichnotaxa from North America need taxonomic revision of the sort done by Baird (1952). There are also problems of paleoecology. Baird (1965a) concluded that there are two main footprint associations in the Late Paleozoic of the Southwest. One is the ichnofauna of the fluvial red beds, like the Abo and Sangre de Cristo Formations, and the other is the ichnofauna of eolian strata like the Coconino Formation of northeastern Arizona. There is also a problem of stratigraphy. Unfortunately, much of the older literature gives imprecise stratigraphic data. If a useful biochronology is to be based on footprints from the red beds of the Southwest, we must not only have valid taxonomy and attention to environment but we must also know the precise stratigraphic distribution of taxa.

Although footprints are common in Early Permian red beds in New Mexico, most published references refer only to their presence with no description of the prints or any details of location (e.g., Meyer, 1966). Indeed, there is only one published identification of a Permian footprint from New Mexico (Baird, 1965b). In this article, we describe a new and diverse ichnofauna from the Sangre de Cristo Formation in northeastern New Mexico and review the record of other Permian footprint localities in New Mexico. This ichnofauna is the most diverse described from New Mexico and is one of the most diverse known from the Early Permian of the Southwest. NMMNH refers to New Mexico Museum of Natural History.

STRATIGRAPHIC CONTEXT

NMMNH locality 1339 is in the NE1/4 SW1/4 SW1/4 sec. 21, T13N, R14W, San Miguel County, New Mexico (Fig. 1). The locality is in a flagstone quarry at the top of a small, flat-topped hill just north of Arroyo del Pueblo (Fig. 1).

The Sangre de Cristo Formation is a thick (up to 1700 m) unit composed mostly of nonmarine conglomerate, sandstone, siltstone and mudstone (Brown, 1984). It crops out widely in parts of northeastern New Mexico and southeastern Colorado. In the vicinity of NMMNH locality 1339, on the Pecos shelf, the Sangre de Cristo Formation reaches a thickness of 220–350 m (Read et al., 1944). The exact stratigraphic position of NMMNH locality 1339 cannot be readily determined as it lies on the crest of a hill a considerable distance from outcrops of the overlying Yeso Formation. However, field observations and the geologic mapping of Johnson (1970) suggest that it lies in the upper third of the Sangre de Cristo Formation, about 60–70 m below the contact with the overlying Yeso Formation. Lithologies near the locality are dominated by fine-grained grayish red (10 R 4/2) to light greenish gray (5 G 8/1) sandstone and siltstone. The tracks occur in a fine- to very-fine grained, subarkose (see Appendix).

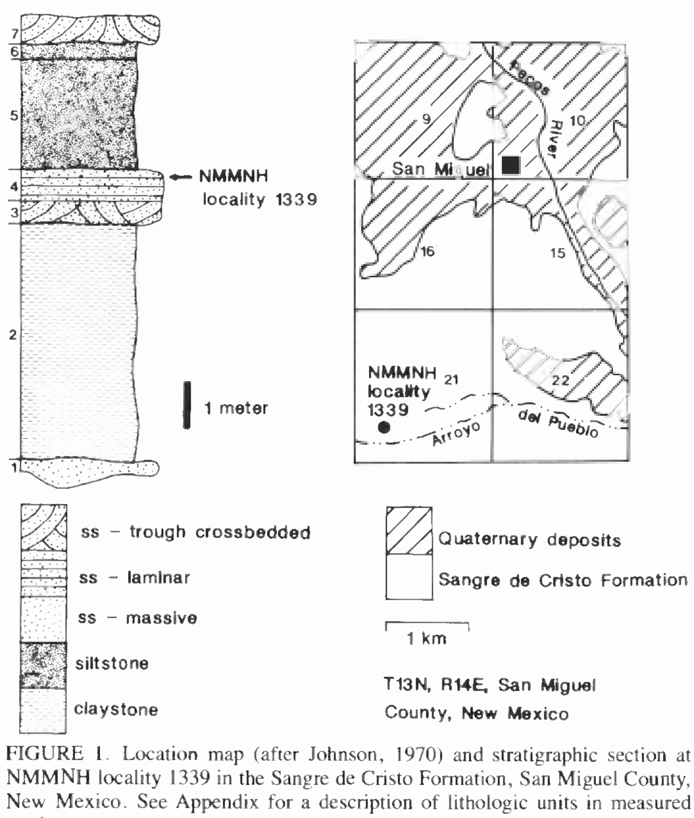

FIGURE 1. Location map (after Johnson, 1970) and stratigraphic section at NMMNH locality 1339 in the Sangre de Cristo Formation, San Miguel County, New Mexico. See Appendix for a description of lithologic units in measured section.

The Sangre de Cristo Formation is generally of alluvial and fluvial origin (Casey, 1980a, b; Brown, 1984; Soegaard and Caldwell, 1990) and represents red beds contiguous with units arbitrarily called Abo Formation in southern New Mexico, Cutler Formation in northwestern New Mexico and Earp Formation in southwestern New Mexico. NMMNH locality 1339 is in the "interbedded mudstone and tabular sandstone facies" of the upper part of the Sangre de Cristo Formation of Soegaard and Caldwell (1990). They interpret the abundance of mudstone in this facies to be indicative of prolonged vertical accretion on well-established floodplains (Soegaard and Caldwell, 1990). The laminar and ripple-laminar, tabular sandstones, such as at NMMNH locality 1339, represent unconfined sheetfloods under upper-flow regime conditions (Soegaard and Caldwell, 1990). These subenvironments are part of a larger scale, mud-rich alluvial fan complex (Soegaard and Caldwell, 1990).

The Sangre de Cristo Formation is a broadly diachronous unit (Brill, 1952). It ranges in age from Missourian (Pennsylvanian), north of Las Vegas, to Leonardian (Permian) in the southern Raton basin (Baltz, 1965). However, in the area of NMMNH locality 1339, the Sangre de Cristo overlies strata of Virgilian (Late Pennsylvanian) age and underlies rocks of Leonardian (late-Early Permian) age, and thus is Wolfcampian (early-Early Permian) in age.

The Sangre de Cristo Formation in the region of the track site has yielded a fairly large, but mainly undescribed, body-fossil fauna which includes the amphibian *Diplocaulus* (Langston, 1953; Olson and Vaughn, 1970; Berman and Reisz, 1980). This fauna is of middle to late Wolfcampian age (Berman and Reisz, 1980). Vaughn (1964) has also described probable *Gnathorhiza* (lungfish) burrows from the Sangre de Cristo Formation in northeastern New Mexico, and Berman (1976) reports body fossils of this taxon in San Miguel County. Vaughn (1969a) described Pennsylvanian vertebrates from the Sangre de Cristo in Colorado.

METHODOLOGY

Several terms used in the description of the tracks in this article need clarification (Fig. 2). The length and width of individual tracks refer to the maximum dimensions measured parallel and perpendicular to the long axis of the print. Digit divarication is the angle of splay of the digits measured from the outside of the first digit to the outside of the last digit. Stride is the distance between the posterior margin of two successive prints of the pes on the same side of the body in the direction of travel. Pace is the distance between the posterior margin of two successive prints of the pes on opposite sides of the body measured in the direction of travel. Pace angulation is the angle between a line drawn from the posterior margin of one pes to an equivalent point on the next pes print of the opposite side, and a subsequent line drawn to the equivalent point on the next pes print of the same side as the first. If a line is drawn between the posterior edges of a right and left pair of pes prints and the posterior edges of the associated manus prints, the glenoacetabular length is the distance in the direction of travel between the points where these two lines cross the midline of the track.

DESCRIPTION OF ICHNOFOSSILS

Amphibians

Anthichnium sp.

A short, broad footprint with the wide digit impressions is represented by several examples on slab NMMNH P-14004 (Fig. 3A). The pes has five digits, a width of 22 mm, a length of 14 mm and a digit divarication of 110°. The digits are broad (3 mm). Digit V diverges from the other digits and is the shortest. Digit IV is the longest, and the other digits through I are of decreasing length. Digits IV and III are curved toward the midline. These tracks are similar to *Erpetopus willistoni* (Moodie, 1929, fig. 4) and *Limnopus vagus* (Gilmore, 1926, fig. 8). The digits of the New Mexico taxon are more curved than in *Limnopus* species (Baird, 1952, 1965a), although they are similar in having short feet with broad, rounded digits. NMMNH P-14004 footprints are also simialr to *Amphisauropus latus* (Haubold, 1973, fig. 14, 1971, fig. 14.8–10) and *A. imminutus* (Haubold, 1971, fig. 14.5–7). However, in gross morphology and particularly in the configuration of the four-toed manus, NMMNH P-14004 footprints are most similar to *Anthichnium* (Haubold, 1971, fig. 10.1–3). Thus, we tentatively assign NMMNH P-14004 to *Anthichnium* sp., which represents an edopoid and is known from the Pennsylvanian and Lower Permian of North America and Europe (Haubold, 1971, 1984).

Limnopus vagus

One of the most common footprints at this locality is represented on many slabs, including NMMNH P-14083, P-14052, P-14005 and P-14010 (Figs. 3B, 4F). Unfortunately, this track morphology is not well preserved in any of our specimens. It consists of a pes with five digits and a manus with four. The whole-digit impression, if preserved, are narrow to wide (2–6 mm), but often only the round pads at the ends of digits are represented. Both pes and manus are short and wide. A typical pes has a width of 31 mm and a length of 31 mm with digit divarication of about 75°. A typical manus has a length of 18 mm, a width of 25 mm and a digit divarication of 65°. On both the manus and the pes, digit V diverges more than the other digits. NMMNH P-14005 includes a trackway of this taxon with a pace of 49 mm, a stride of 145 mm, a glenoacetabular length of 46 mm and a pace angulation of 70°. These footprints are reminiscent of *Limnopus* species (Baird, 1952, figs. 1–4, 1965, fig. 14A–C). The New Mexico tracks are very similar in size to *L. vagus* (Baird, 1954, table 1), and we assign the

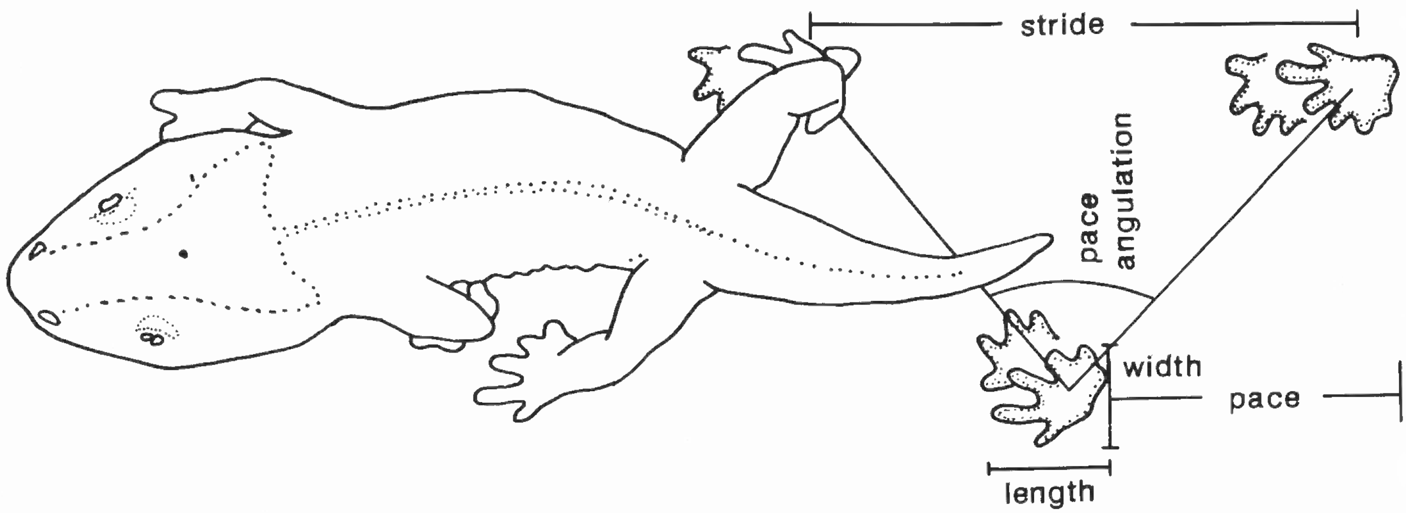

FIGURE 2. Explanation of some of the measurements of trackways utilized in this article (after Baird, 1965a).

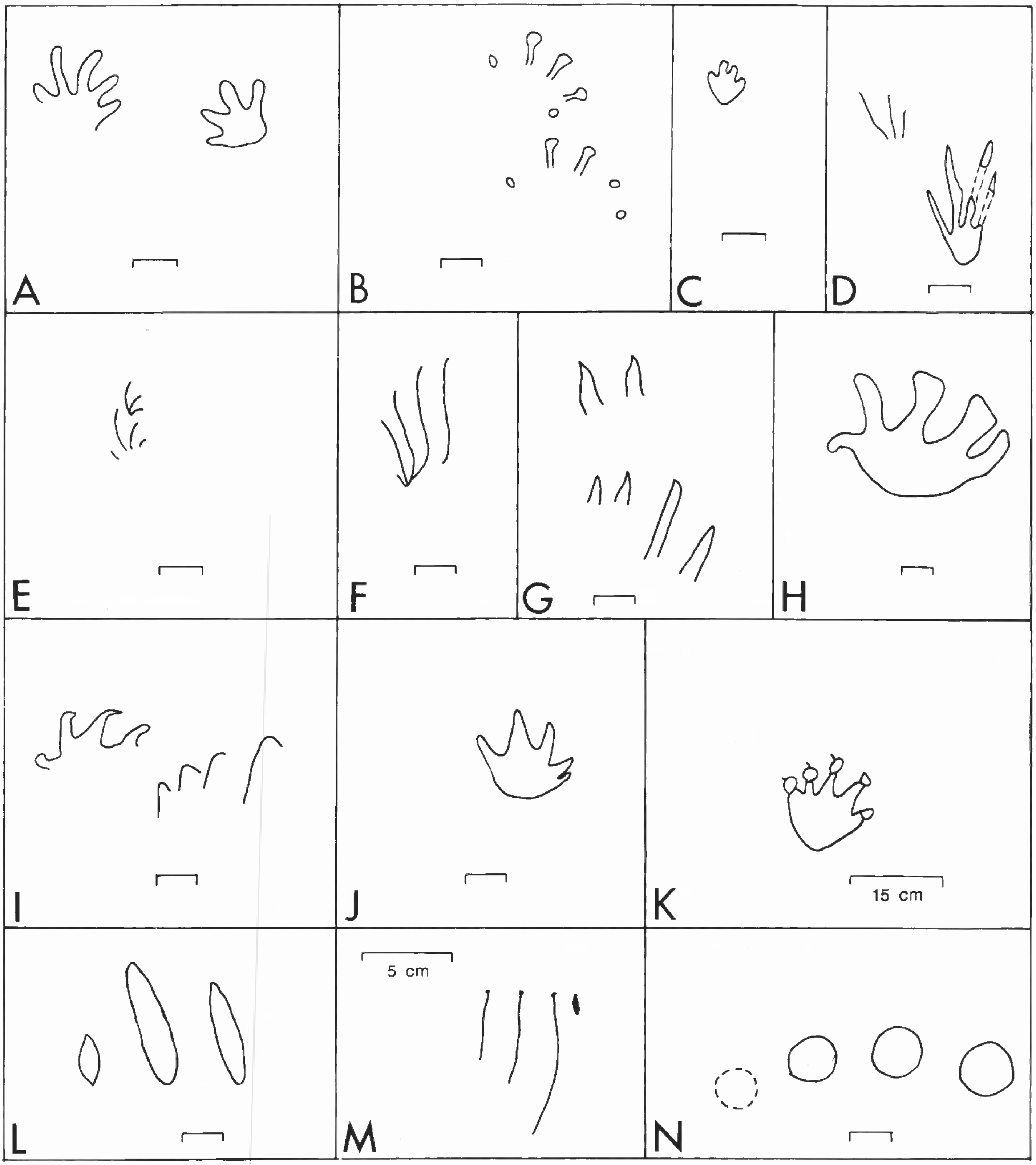

FIGURE 3. Outlines of footprints from Sangre de Cristo Formation (NMMNH locality 1339): A, NMMNH P-14004, *Anthichnium* sp.; B, NMMNH P-14083, *Limnopus vagus;* C, NMMNH P-14009, cf. *Nanopus* sp.; D, NMMNH P-14024, cf. *Stenichnus* sp.; E, NMMNH P-14094, *Dromopus lacertoides;* F, NMMNH P-14139, *Dromopus* swimming trace; G, NMMNH P-14061, indeterminate reptile I; H, NMMNH P-14013, *Anomalopus supaiensis;* I, NMMNH P-14143, indeterminate reptile III. J, NMMNH P-14139, *Gilmoreichnus* sp.; K, NMMNH P-14138, *Dimetropus* sp.; L, NMMNH P-14049, indeterminate reptile II; M, NMMNH P-14063, reptile swimming trace; N, NMMNH P-14071, ?reptile. All scale bars are 1 cm unless otherwise indicated.

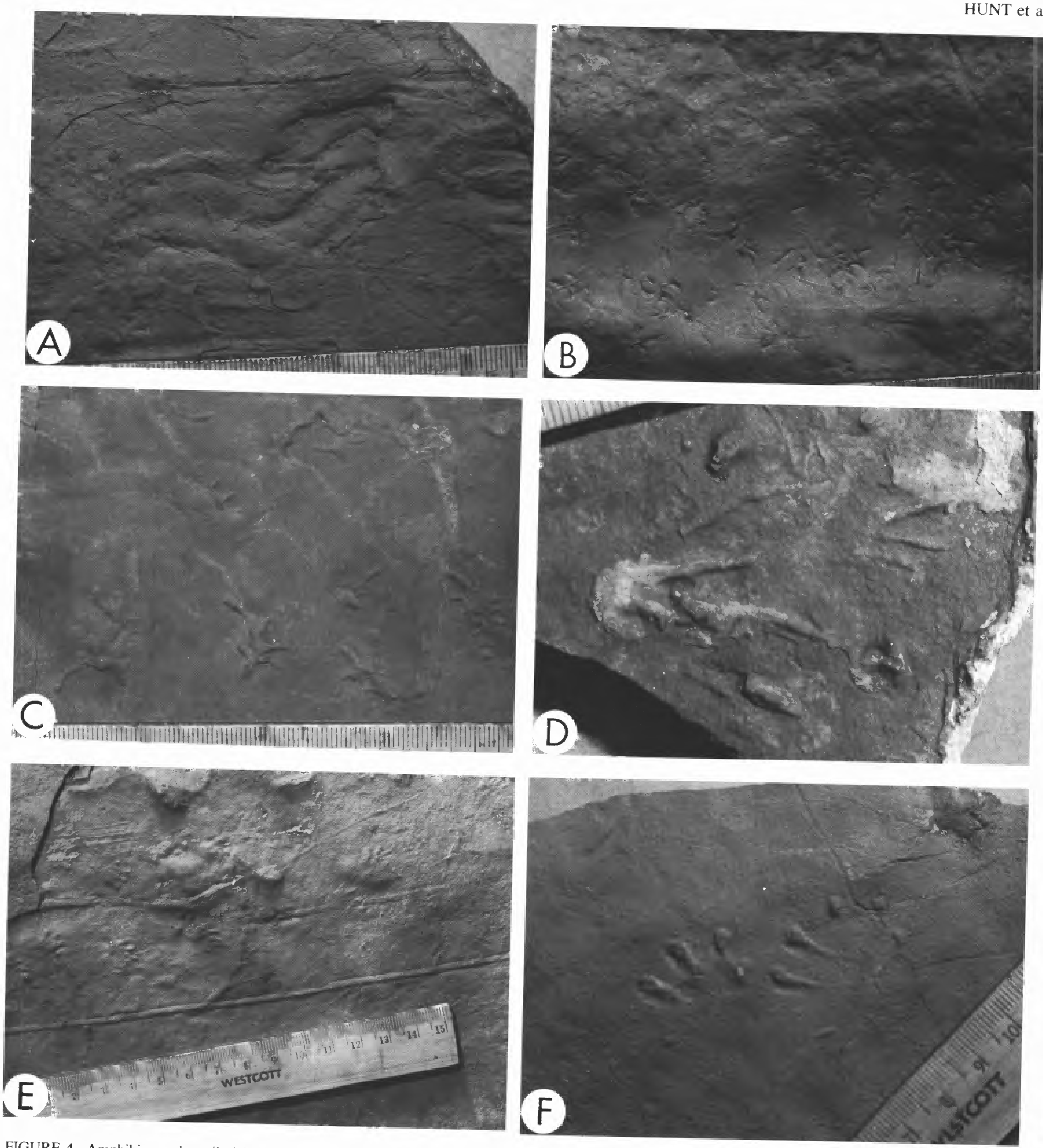

FIGURE 4. Amphibian and reptile ichnofossils from the Sangre de Cristo Formation (NMMNH locality 1339). Scales in mm. A, NMMNH P-14127, *Dromopus* swimming trace. B, NMMNH P-14115, *Dromopus lacertoides*. C, NMMNH P-14075, *Dromopus lacertoides*. D, NMMNH P-14024, c. *Stenichnus* sp. E, NMMNH P-14009, cf. *Nanopus* sp. F, NMMNH P-14083, *Limnopus vagus*.

Sangre de Cristo tracks to this taxon. *Limnopus vagus* is also known from the Utopia Limestone Member of the Howard Formation in Texas, which is of Upper Pennsylvanian (Virgilian) age (Baird, 1952). Different species of the ichnogenus *Limnopus* are known from the Lower Permian of North America (Haubold, 1971). It represents an eryopoid labyrinthodont (Haubold, 1971).

cf. *Nanopus* sp.

Only one trackway in our collection has a well-developed tail drag (Figs. 3C, 4E). This trackway (NMMNH P-14009) is fairly poorly preserved and becomes increasingly indistinct across the slab. The pes has four digits, a length of 13 mm, a width of 11 mm and a digit divarication of 80°. The digits increase in length from I to IV, and V is shorter. The digits coalesce posteriorly into a rounded heel impression. The manus apparently has three or possibly four digits with a length of 7 mm and a width of 8 mm. The heel of the manus is angled to the tail drag at about 60°. The tail drag has a width of 3 mm and becomes less distinct, together with the footprints, across the slab. The trackway has a stride of 39 mm and a pace of 17.5 mm. These prints are poorly preserved, but are broadly similar, though smaller than, "*Nanopus quadratus*" (Gilmore, 1927, fig. 4), which represents an eryopoid labyrinthodont (Haubold, 1971). Gilmore (1927, fig. 3) erroneously illustrated a supposed manus and pes of *Nanopus obtusus* ("*obtusis*" sic). This illustration shows two peds, and his illustrations of *Nanopus quadratus* are actually those of *N. obtusus* (Baird, written commun., 1990). These errors are due to a misreading of plate captions in Matthew (1905; Baird, pers. commun., 1990). Haubold (1971) places Matthew's (1905) species of *Nanopus* in the genus *Anthichnium*, but Baird (written commun., 1990) reserves judgment pending restudy of Matthew's holotypes and the genoholotype of *Nanopus* (Marsh, 1894). Spamer (1984) transferred *Nanopus merriami* (Gilmore, 1927) to *Laoporus* and *N. maximus* to *Barypodus metzeii* on the advice of Baird (Baird, pers. commun., 1990). NMMNH P-14009 is also similar to *Anthichnium*, and *Anthichnium* and *Nanopus* should be revised to deemphasize apparent regional differences in nomenclature (Haubold, written commun., 1990). We tentatively refer NMMNH P-14009 to cf. *Nanopus* sp. pending revision of this taxon and of *Anthichnium*. If the manus of NMMNH P-14009 is tridactyl, then it probably represents a microsaur rather than *Nanopus* (Baird, written commun., 1990).

cf. *Stenichnus* sp.

NMMNH P-14024 is a slab preserving one manus and pes pair (Figs. 3D, 4D). The pes impression has four digits, two of which are very poorly preserved. The pes has a length of 29 mm and a width of 18 mm with a digit divarication of 48°. The digits are long and slender and coalesce into a rounded heel in the posterior 55 mm of the track. The posterior margin of the manus lies at a bearing of 34° and a distance of 33 mm from the posterior margin of the pes. Apparently, only three digits are preserved in the manus impression. The manus has a width of 12 mm, a length of 15 mm and a digit divarication of 40°. The three slender digits coalesce into an indistinct heel print for the posterior 6 mm of the print. Both the manus and pes have wide, U-shaped heels. NMMNH P-14024 is assigned to the genus cf. *Stenichnus* sp. because of its similarity to *S. yakiensis* (Gilmore, 1927, pl. 19.2). NMMNH P-14024 differs from the holotype of *S. yakiensis* in being about twice the size and in having relatively smaller heel impressions (Gilmore, 1927). *Stenichnus* is known from the Lower Permian Supai Formation of the Grand Canyon in Arizona (Gilmore, 1927) and probably represents a microsaur (Haubold, 1971). *Stenichnus*, like most Late Paleozoic footprint ichnotaxa, in need of restudy (Baird, written commun., 1990). For example, in both NMMNH P-14024 and Gilmore's specimens (Gilmore, 1927, pl. 19.2), it is difficult to distinguish between the toe impressions and toe drags (Baird, written commun., 1990).

Reptiles

Dromopus lacertoides

A number of poorly preserved tracks of one animal are preserved on NMMNH P-14094 and NMMNH P-14075 (Figs. 3E, 4B–C). Two of the better preserved manus/pes pairs allow a reconstruction of this footprint type. The pes consists of five narrow, curving digits with the longest overlapping a horizontal plane through the heel of the manus. The manus consists of three shorter digits of similar morphology. The digits of the pes all curve inward, with V being very short, IV being very long and the remaining digits decreasing in size towards I. The length of the pes is 13 mm with a width of 9 mm and a digit divarication of 82°. The manus is 6.5 mm wide and 9 mm long. Smaller tracks of similar morphology (e.g., pes length less than 5 mm) are preserved on NMMNH P-14115.

These tracks are very similar to *Dromopus agilis* (Gilmore, 1926, fig. 3), although much smaller. They are closest to *D. lacertoides* (Patterson, 1971; Haubold, 1973, figs. 29–32, 1984, fig. 56), and we assign the New Mexico footprints to this taxon. Similar tracks are known from the Rotliegend of Germany (Pabst, 1908, pl. 23.1), and from the Abo Formation of the Robledo Mountains in southern New Mexico (Bowlds, 1989a, p. 14). *Dromopus lacertoides* is known from the Late Pennsylvanian and Early Permian of Europe, and other species have a similar range in North America (Haubold, 1971). *Dromopus* probably represents an araeoscelid (Haubold, 1971).

Baird (written commun., 1990) notes that the closest occurrence of *Dromopus* to this locality is at Castle Peak, Texas where *Dromopus (Varanopus) palmatus* (Baird, ms; new combination) occurs. Subjective junior synonyms of this taxon, according to Baird (written commun., 1990) are *V. impressus, V. elrodi* and *V. didactylus* (Moodie, 1930) and *V. langstoni* (Sarjeant, 1971). Haubold (written commun., 1990) concurs with the latter designation. Sarjeant (1971) proposed a new genus for "*V.*" *didactylus*, but this taxon is probably produced by the *Dromopus palmatus* trackmaker running on two toes (Baird, written commun., 1990).

Dromopus sp. swimming trace

A common footprint morphology at NMMNH locality 1339 consists of four thin (1 mm in width) parallel and sigmoidal digit impressions (Figs. 3F, 4a, 5A). This ichnotaxon is present on NMMNH P-14139 and P-14142. A typical pes is 14 mm wide and 27 mm long. On NMMNH P-14139, this morphology appears to change into a *Dromopus*-like morphology (Haubold, 1971, fig. 18.1–5). Thus, this track morphology probably represents the swimming trace of *Dromopus;* its claws are just scratching the substrate. *Dromopus* is an araeoscelid (Haubold, 1971).

Anomalopus supaiensis

NMMNH P-14013 is a slab with a single print of a large vertebrate (Figs. 3H, 5c). This ?pes has a width of 83 mm, a length of 73 mm and a digit divarication of 55°. Digit impressions are more deeply incised at their tips, which are acute. The track shows a resemblance to *?Megapezia coloradensis* (Lull, 1918, fig. 3, pl. 3) and to the Late Permian taxon *Herpetichnus loxodactylus* (Haubold, 1971, fig. 58.5). However, NMMNH P-14013 is identical to *Anomalopus (Tridentichnus) supaiensis* (Gilmore, 1927, pl. 21, fig. 37) from the Wescogame Formation (Supai Group) of the Grand Canyon. Baird (written commun., 1990) suggests that *Ammobatrachus turbatans* (Gilmore, 1928) is a subjective junior synonym of this taxon. *Anomalopus* represents a captorhinid trackway that is known from the Early Permian of North America (Haubold, 1971). The genus also extends into the Pennsylvanian of North America and Europe (Haubold, 1971).

We note that in the literature on ichnofossils, the name Supai Formation is used for track-bearing strata in the Grand Canyon (e.g., Haubold, 1971). However, the Supai is now a Group (McKee, 1982). Most of the ichnofossils described by earlier workers (e.g., Gilmore, 1926, 1927, 1928) are from the Wescogame Formation, of probable Virgilian (Late Pennsylvanian) age (McKee, 1982). Gilmore (1926) described one problematic ichnofossil from the Esplanade Sandstone which is Wolfcampian-?Leonardian (Early Permian) in age (McKee, 1982).

Gilmoreichnus sp.

A common, five-toed track (Figs. 3J, 5E) is represented on several slabs (NMMNH P-14142, P-14139). None of these tracks are well

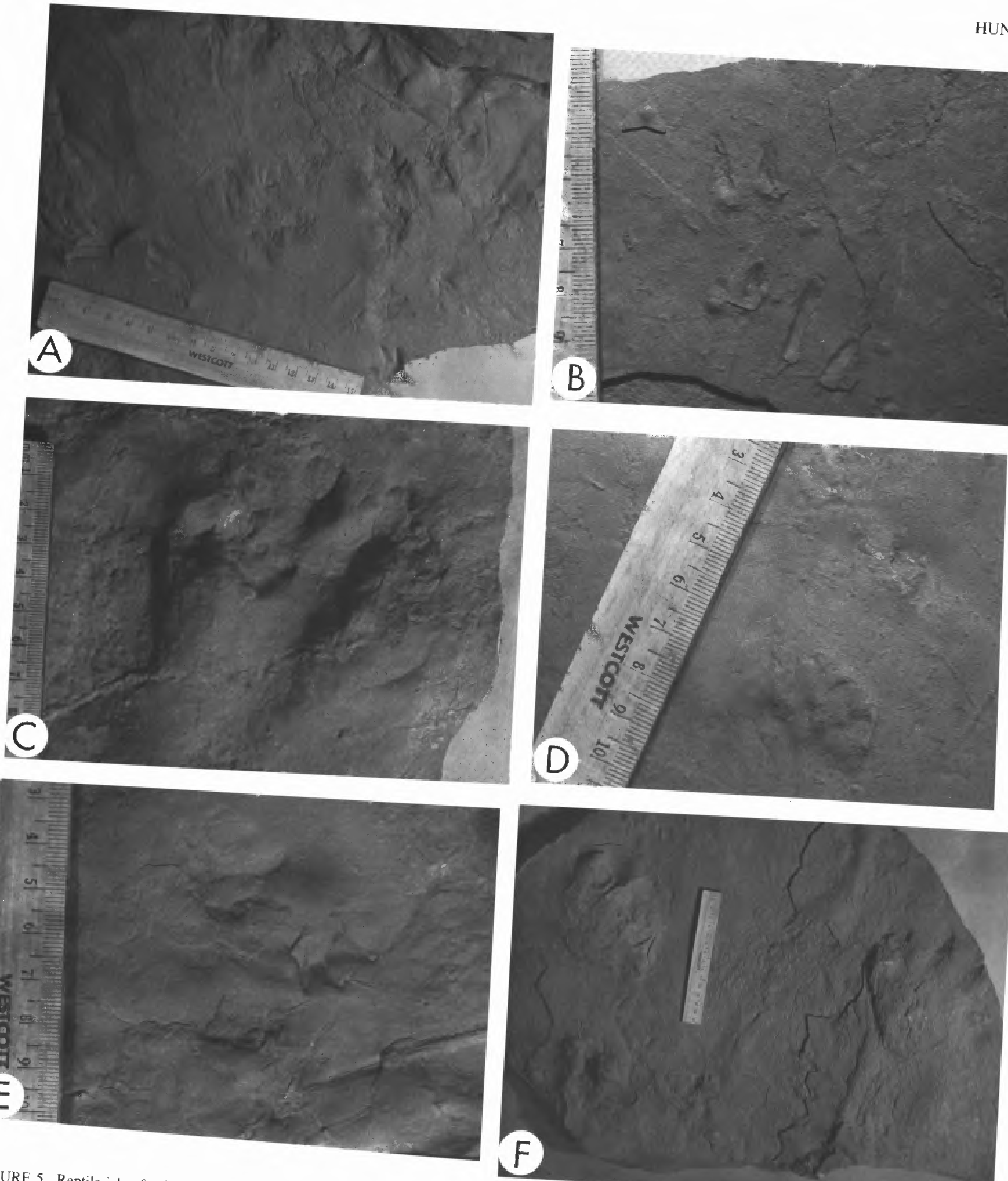

FIGURE 5. Reptile ichnofossils from the Sangre de Cristo Formation (NMMNH locality 1339). Scales in mm. A, NMMNH P-14139, *Dromopus* swimming trace in bottom left and *Gilmoreichnus* sp. in center right. B, NMMNH P-14061, cf. indeterminate reptile I. C, NMMNH P-14013, *Anomalopus supaiensis*. D, NMMNH P-14026, indeterminate reptile III. E, NMMNH P-14139, *Gilmoreichnus* sp. F, NMMNH P-14038, *Dimetropus* sp.

preserved. A typical pes has a length of 12 mm, a width of 20 mm and a digit divarication of 55°. The narrow digits sometimes curve toward the midline. The manus prints appear similar in morphology and size to those of the pes. These tracks show similarities to *Erpetopus willistoni* (Moodie, 1929, fig. 4; Sarjeant, 1971, fig. 4). They are also similar, but smaller than, *Gilmoreichnus kablikae* (Haubold, 1984, fig. 63) and *G. hermitanus* (Gilmore, 1927, fig. 21, pl. 15). We assign the smaller New Mexico specimens to *Gilmoreichnus* sp. *Gilmoreichnus* is an ophiacodont trackway that is known from the Pennsylvanian and Early Permian of Europe and North America (Haubold, 1971).

Dimetropus sp.

NMMNH P-14138 is a slab containing three positive prints of the largest vertebrate track preserved at this locality. (Figs. 3K, 5F). These tracks are a right pes and a left manus and pes. The right pes is better preserved and has five digits and a tapering heel impression. The length and width of the pes are 170 mm and 150 mm, respectively, with a digit divarication of 75°. Digits I through IV are of increasing length, with V being shorter. The heel impression is deepest on the inner and posterior margin. Each digit has an expansion near its tip, with the distal end tapering to a point. The left manus has ?four digits with a maximum width of 135 mm and a length of 118 mm. The digit divarication is 97°. The heel has a more even depth on the manus than on the pes. Digit IV has an expanded area near its tip, but this feature is not visible on the other digits due to poor preservation. Digit I has a backward curving claw impression. The pace of the track is estimated at 300 mm. In the relative length of the digits and the expanded pads proximal to the claw impressions, NMMNH P-14138 is very similar to the holotype of *Dimetropus* (= *Dimetrodon* [as used as an ichnotaxon by Tilton, 1931]) *berea* (Tilton, 1931, fig. 1A; Haubold, 1971, fig. 20.3). However, because of poor preservation, we only assign NMMNH P-14138 to *Dimetropus* sp. *Dimetropus* is a widespread Early Permian (also known from the Pennsylvanian) ichnotaxon that represents a sphenacodont (Haubold, 1971).

Indeterminate reptile I

NMMNH P-14061 is a slab with the impression of a ?four-toed pes and a two-fingered manus (Figs. 3G, 5B). These negative prints are smooth impressions suggesting scratch marks, rather than the flat imprint of a foot and hand. The pes is 33 mm wide and 29 mm long with no heel impression and a digit divarication of 20°. The digits are wide (3–4 mm), and, where well preserved, they exhibit acute tips. The left two digits are very close together (4 mm), whereas the right two digits, which extend further posteriorly, are more widely separated. The manus impression consists of two digit impressions which are at an angle of 33° to the long axis of the pes. The length and width of the manus are both 13 mm. The manus digits are also widely separated and apparently have sharp points at their anterior ends. The tracks are similar to large *Laoporus* species (Lull, 1918, fig. 2; Gilmore, 1928, fig. 1–2), an ichnotaxon that represents a caseasaur (Haubold, 1971). Caseasaurs are restricted to Leonardian strata, and all Early Permian vertebrates from New Mexico are of Wolfcampian age (Berman and Reisz, 1980).

Indeterminate reptile II

NMMNH P-14049 is a single tridactyl print with three broad and parallel digit impressions (Figs. 3L, 6A). The track has a width of 32 mm and a length of 29 mm. The central digit is the longest, the right digit is about two-thirds of its length, and the left digit is about a third the length of the right. There is no heel impression, and the digits extend further posteriorly from left to right. The left digit apparently preserves one pad and comes to a fairly acute point. The middle digit apparently preserves two pads, and the right digit is too poorly preserved to detect pads. This print shows similarities to *Ichniotherium cottae* (Grand and Haubold, 1988, fig. 3.B15), but is too poorly preserved for positive identification.

Indeterminate reptile III

NMMNH P-14143 includes a very poorly preserved trackway of an animal with a very short and wide pes (Figs. 3I, 5D). The pes is 30 mm wide and 16 mm long with four narrow digits (2.5 mm). The digits divaricate at 130°. Behind the digits is a wide, shallow heel impression. The posterior margin of the print is inclined inwards toward the midline at an angle of 60°. NMMNH P-14126 preserves the same track morphology with a better preserved manus. The manus has three digits with a length of 11 mm, a width of 12 mm and a digit divarication of 70°. The digits are narrow, and the posterior margin of the manus appears to be at an angle of 60° to the midline. The pes digits have their distal ends deflected about 90° from the long axes of the remainder of the digits. NMMNH P-14143 and P-14126 may represent a poorly preserved specimen of *V. curvidactylus* (Sarjeant, 1971, figs. 5, 3h–i). The deflected tips of the digits are particularly suggestive of this relationship. *Varanopus* represents a captorhinomorph (Haubold, 1971), but could also represent a small pelycosaur (Baird, written commun., 1990).

These specimens are also similar to *"V." langstoni* (Sarjeant, 1971, pl. 6, figs. 3a–b, 6). This species actually represents *Dromopus*, because the fourth digit is the longest, and Sarjeant (1971, pl. 6, figs. 3, 6b) illustrates an overstep of two pes or manus impressions by a pes impression (Haubold, written commun., 1990). Baird (written commun., 1990) notes that NMMNH P-14126 lacks the elongation and length disparity of pedal digit impressions that characterize *Dromopus*. *Dromopus* may be a subjective junior synonym of *Notalacerta* (Baird, written commun., 1990).

Indeterminate reptile swimming traces

A number of specimens (NMMNH P-14057, P-14026, P-14017, P-14063) have longitudinal grooves produced by claws dragging on the substrate while swimming. The largest is NMMNH P-14063 (Fig. 3M), which has four longitudinal grooves over a width of 55 mm. Each drag mark ends in a distinct pit. Size alone suggests that NMMNH P-14063 was produced by a pelycosaur. The other claw drags preserve three or four grooves and exhibit no diagnostic morphology. Other specimens (NMMNH P-14012) have marks made by dragging claws that end in a poorly preserved footprint (Fig. 6B).

?Reptile

NMMNH P-14071 is a poorly preserved positive print of a large ?reptile (Figs. 3N, 6C). This print consists of three deep, round toe impressions with diameters averaging 12 mm. A fourth faint toe impression is visible in oblique light. From the left, the first three impressions are of increasing depth, and the fourth is more shallow. This track shows similarities to *Baropezia sydnensis* (Gilmore, 1926, fig. 12), *Baropus cocconinoensis* (Gilmore, 1927, pl. 7), *Brachydactylus fontis* (Toepelman and Rodeck, 1936, fig. 2) and *Gilmoreichnus brachydactylus* (Gand and Haubold, 1988, fig. 3.A5). However, NMMNH P-14071 is too incomplete to allow precise identification.

Invertebrate traces

Paleohelcura tridactyla

NMMNH P-14141 preserves an invertebrate track which is 90 mm wide and consists of a median tail drag (1 mm in width) flanked by tiny footprints (2 by 0.5 mm) which are in clumps of three (Fig. 6D). The distance between the groups of footprints is 2–3 mm in the direction of travel. The footprints are sometimes arranged in a line, but are usually staggered. This trackway is similar to a specimen that Brady (1947, pl. 67, fig. 1) attributed to *Paleohelcura tridactyla*.

However, both the holotype of *P. tridactyla* (Gilmore, 1926, pl. 12.1; Brady, 1947, pl. 66.1) and the referred specimen (Brady, 1947, pl. 67.1) are about three times the size of NMMNH P-14141. Both Gilmore (1926, p. 34) and Brady (1947, fig. 1) indicate that this taxon is very variable. NMMNH P-14141 differs from the holotype in having more closely spaced feet in the direction of travel and in not having the pes impressions arranged in en-echelon rows, relative to the tail drag. In conclusion, we tentatively assign NMMNH P-14141 to *Paleohelcura tridactyla*. *?Paleohelcura lyonsensis* Toepelman and Rodeck, 1936 is a junior subjective synonym of *Paleohelcura tridactyla*. Brady (1947) argued that this ichnotaxon was produced by a scorpion, although it is

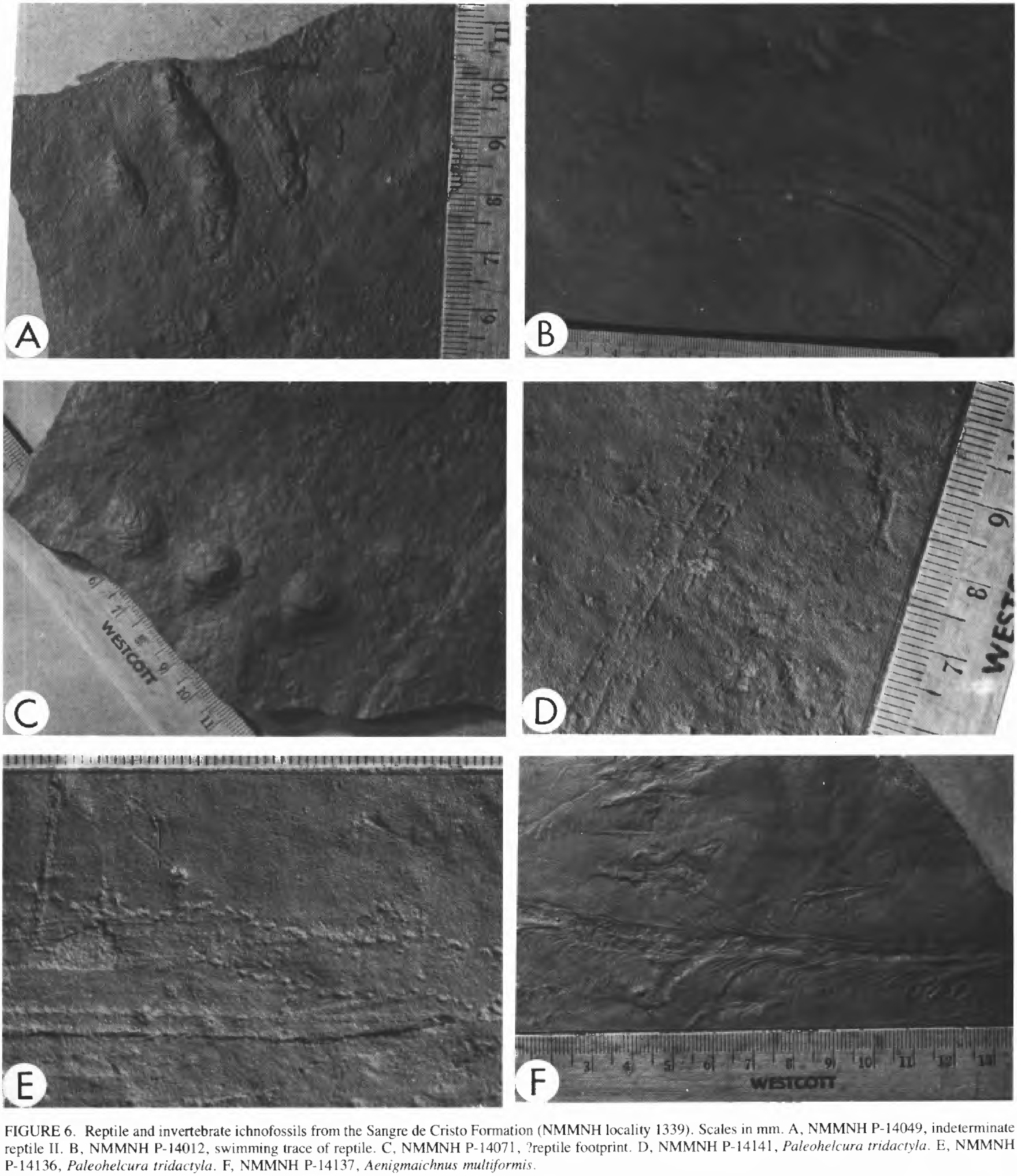

FIGURE 6. Reptile and invertebrate ichnofossils from the Sangre de Cristo Formation (NMMNH locality 1339). Scales in mm. A, NMMNH P-14049, indeterminate reptile II. B, NMMNH P-14012, swimming trace of reptile. C, NMMNH P-14071, ?reptile footprint. D, NMMNH P-14141, *Paleohelcura tridactyla*. E, NMMNH P-14136, *Paleohelcura tridactyla*. F, NMMNH P-14137, *Aenigmaichnus multiformis*.

similar to isopod (Brady, 1947, pl. 68.4) and spider (Alf, 1968, fig. 3) tracks. Similar tracks were attributed to a millipede by Moodie (1929). Savage (1970) illustrated similar trackways which he suggested were formed by crustaceans. Kietzke (oral commun., 1990) suggested that these tracks may represent notostracans or isopods, and we note that MacDonald (1989) attributes similar trackways to a silverfish. Obviously, more work needs to be done to assess the relationships of this ichnotaxon.

NMMNH P-14136 contains several trackways of *Paleohelcura tridactyla* and a similar trackway that differs in not having a tail drag (Fig. 6E). Given the variabilty in the presence of the tail drag in this taxon (Brady, 1947, fig. 1), we assign all these tracks to *Paleohelcura tridactyla*. MacDonald (1989) attributes similar tracks to a springtail.

Aenigmichnus multiformis

An enigmatic series of trails is preserved on slab NMMNH P-14137 (Fig. 6F). The best preserved is up to 35 mm wide. The trails are irregularly lengthened arcuate lines, arranged en echelon and sometimes have a central groove. Moodie (1930, fig. 1) illustrated an identical track which he attributed to *Aenigmichnus multiformis*. Hitchcock thought that this ichnotaxon was produced by an annelid worm, but Moodie (1930, fig. 1 caption) thought that it was a rill mark produced by a "slow-drizzle run-off." The arcuate nature of one trail on NMMNH P-14137 on an apparently originally horizontal bedding plane and the several directions of trails on this slab indicate that this feature is not a rill mark. However, this trail is broadly similar to chevron marks illustrated by Pettijohn and Potter (1964, pl. 62). Nevertheless, the Permian ichnotaxon differs from the chevron marks in not being associated with other parallel grooves and in having oblique lines that are irregular in length and narrow. These tracks are similar to supposed trilobite trails illustrated by Gilmore (1928, pl. 5.1), and we suggest that the New Mexico trackway was produced by an arthropod. Bowlds (1989a, p. 14) illustrates identical tracks from the Abo Formation of the Robledo Mountains in southern New Mexico.

Hitchcock's (1865) concept of *Aenigmichnus* is very broad and includes specimens similar to NMMNH P-14137 (Hitchcock, 1865, pl. 12, figs. 2–4) and others which are of totally different morphology (Hitchcock, 1865, pl. 1, figs. 4–5). Haentzschel (1975) suggests that Moodie (1930) may have been wrong in his taxonomic assignment. Pending much needed revision of the ichnogenus, we tentatively assign NMMNH P-14137 to *Aenigmichnus multiformis*.

Invertebrate(?) trace

A common type of ichnofossil at NMMNH locality 1339 is an elliptical depression with longitudinal striations (Fig. 7). These traces are up to 16 mm long and 7 mm wide. The striations and irregular distribution of these traces indicate that they are not stray toe marks; they may represent fecal pellets. However, in one instance there is a faint impression of a ?claw next to one of these marks (Fig. 7), suggesting that they may represent isolated toe marks. Alternatively, these traces may represent invertebrate (?crustacean) burrowing traces (Kietzke, oral commun., 1990).

PLANT FOSSILS

Plant fossils are common at NMMNH locality 1339 (NMMNH P-P-14022, P-14023 and P-14029). All specimens represent one species of conifer (Fig. 8). Rigid branchlets up to 200 mm long and 3 mm wide bear twigs at angles averaging 60°. The twigs are up to 35 mm long, 1 mm wide and are sheathed in small, falcate, needle-like leaves. These specimens are referable to *Walchia piniformis* (White, 1929, pl. 41 figs. 1–5, pl. 42 figs. 1–5, pl. 47). *Walchia* is a common element in Early Permian floras in New Mexico (Hunt, 1983).

Ray and Smith (1941) reported *Walchia piniformis* from the Magdalena Formation in the Moreno Valley of northern New Mexico. However, they did not differentiate either the Sangre de Cristo Formation or Triassic strata from the Magdalena Formation. We think it probable that the *Walchia* specimens they reported are from the Sangre de Cristo Formation.

FIGURE 7. ?Invertebrate traces (NMMNH P-14098) from the Sangre de Cristo Formation (NMMNH locality 1339). Note that to the right of the trace in the center-right of the picture is a claw-like impression. Scale in mm.

ICHNOFAUNA COMPARED TO THE BODY-FOSSIL RECORD

NMMNH locality 1339 preserves a record of a very diverse fauna including at least three invertebrates, four amphibians and six reptiles (Fig. 9). Early Permian red beds in New Mexico have also produced a diverse body-fossil fauna (e.g., Case et al., 1913; Berman and Reisz, 1980). It is important to combine knowledge gleaned from ichnofaunas with that from body-fossil faunas to get a complete picture of the Early Permian bestiary in New Mexico. Thus, we briefly review the probable trackmakers of NMMNH locality 1339, compared with selected records of these animals from body fossils in New Mexico. Late Paleozoic footprints are generally not well preserved, and therefore pedal morphology is hard to reconstruct. Thus, the following comments on probable trackmakers should be considered tentative. Baird (written commun., 1990) believes that some authors have gone beyond the limits of the data in assigning probable trackmakers to Late Paleozoic ichnotaxa.

Amphibian trackways are very common at NMMNH locality 1339. *Limnopus vagus* and cf. *Nanopus* sp. are trackways of eryopoids (Haubold, 1971), which are known from the Cutler Formation of northwestern New Mexico (Langston, 1953). Cf. *Stenichnus* sp. probably represents a microsaur (Haubold, 1971), a group also known from the Cutler in northwestern New Mexico (Eberth and Berman, 1983). Baird (written commun., 1990) believes that *Stenichnus* may represent some

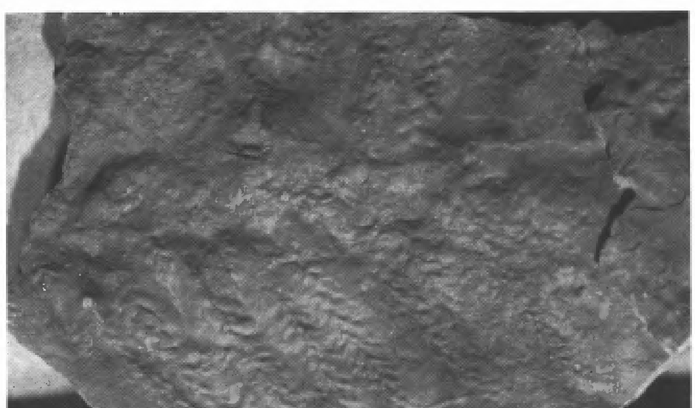

FIGURE 8. The conifer *Walchia piniformis* (NMMNH P-14029) from the Sangre de Cristo Formation (NMMNH locality 1339). Scale in mm.

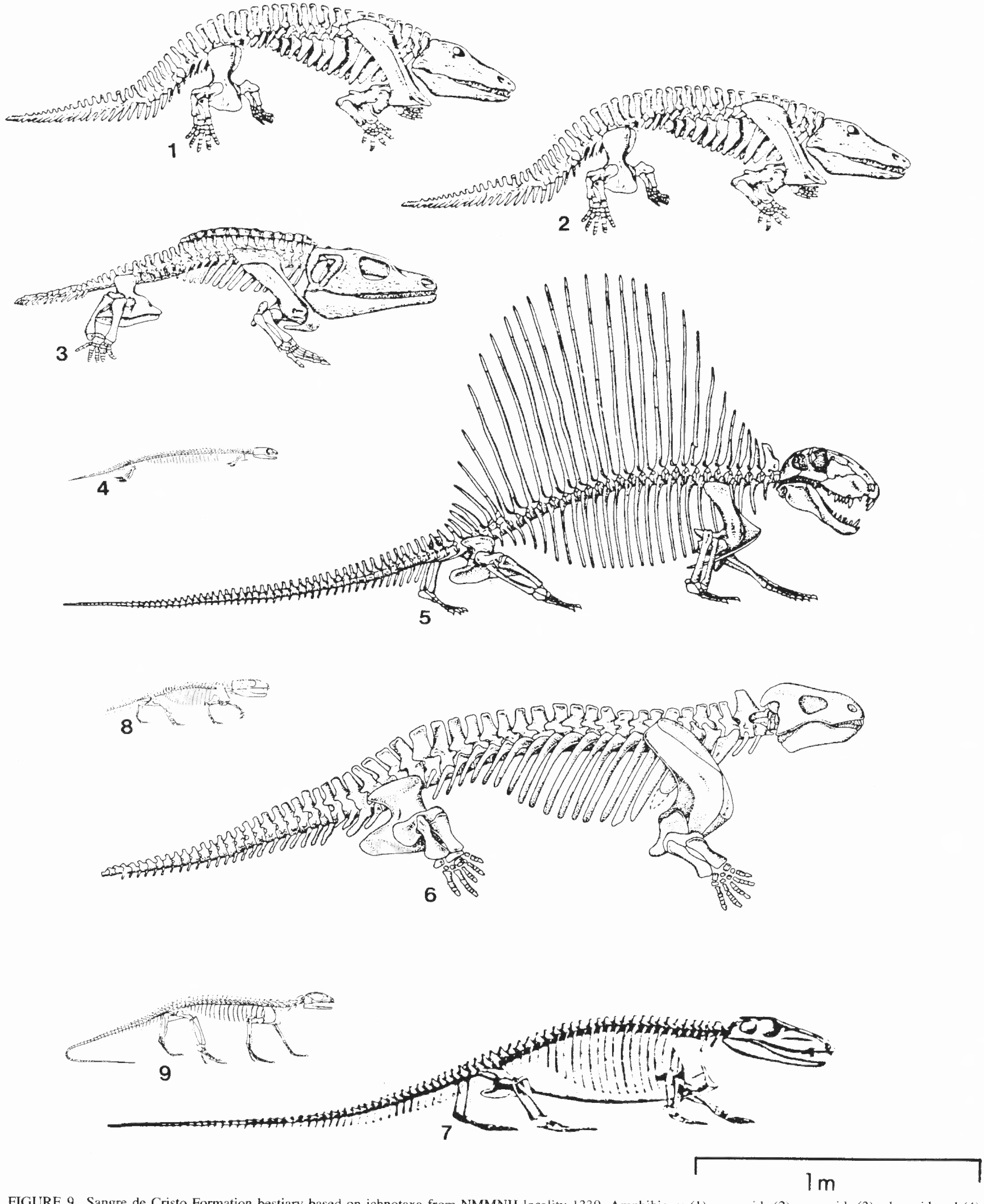

FIGURE 9. Sangre de Cristo Formation bestiary based on ichnotaxa from NMMNH locality 1339. Amphibians: (1) eryopoid, (2) eryopoid, (3) edopsoid and (4) microsaur. Reptiles: (5) sphenacodont, (6) captorhinomorph, (7) ophiacondont, (8) captorhinid and (9) araeoscelid. Skeletal reconstructions representing possible trackmakers are from Carroll (1988) and Romer (1966). Scale is 1 m.

other group of long-bodied vertebrate such as a nectridean. *Anthichnium* sp. represents a eropsoid (Haubold, 1971), and such amphibians are not known to occur in New Mexico (Romer, 1947).

Most of the reptile groups represented by tracks at NMMNH locality 1339 are also known from body fossils in New Mexico. Cf. *Varanopus*-like prints are probably the track of a captorhinomorph (Haubold, 1971, 1984). Several captorhinomorphs are present in Early Permian faunas in New Mexico (e.g., Langston, 1966). Baird (written commun., 1990) considers that *Gilmoreichnus* sp. represents a generalized eureptilian, but Haubold (1971) suggests that it represents an ophiacodont. Ophiacodonts are known from the Cutler Formation of northwestern New Mexico (Berman and Reisz, 1980). *Dimetropus* is the trackway of a sphenacodont, a group common in New Mexico (e.g., Berman, 1977). *Dromopus lacertoides* represents an araeoscelid (Haubold, 1971), a group also known from body fossils in New Mexico (Eberth and Berman, 1983).

Two reptile ichnotaxa represent animals that are not known from body fossils in New Mexico. *Herpetichnus* sp. represents an unknown reptile, and *Anomalopus supaiensis* represents a captorhinid (Haubold, 1971), a group that is not known to occur in New Mexico (Seltin, 1959). In general, the most common animals at NMMNH locality 1339 are small reptiles and amphibians.

There are no arthropod body fossils from the Early Permian of New Mexico to account for the trackways at NMMNH locality 1339. Nevertheless, the ichnofauna corresponds well to the body-fossil record in the Early Permian of New Mexico. The only exceptions are: (1) invertebrate tracks, because no invertebrate body fossils of Early Permian age are present in New Mexico; (2) araeoscelids, which are rare in the Early Permian; and (3) caseasaurs, whose presence is based on a very tentatively identified ichnofossil.

PERMIAN FOOTPRINT LOCALITIES IN NEW MEXICO

Meyer's (1966) reference to animal tracks being common in Wolfcampian strata of southeastern New Mexico is typical of most reports of vertebrate footprints in the Permian of New Mexico in that there is no description of ichnotaxa nor are there any locality data. There are only six footprint localities, other than the one described here, which we know the location of, either from the literature or from personal observation (Fig. 10).

Baird (1965b) published the only previous formal description of terrestrial footprints from the Permian of New Mexico. These specimens were collected by Zeller in the Earp Formation from near the mouth of Mine Canyon in the Big Hatchet Mountains (Zeller, 1965; Fig. 10). Baird recognized two trackways similar to *Varanopus curvidactylus*, which represents a captorhinomorph known from Wolfcampian and early Leonardian strata (Baird, 1965b). Another poorly preserved trackway was tentatively attributed to a lacertoid reptile and a third to a limulid xiphosauran.

Bowlds (1989a, b; MacDonald, 1989) reported on a very diverse footprint locality in the Abo Formation of the Robledo Mountains, west of Las Cruces (Fig. 10). Bowlds (1989a, b) claimed that 50 ichnotaxa are represented in this assemblage as well as the plants *Neuropteris*, *Pecopteris*, ?*Rhynia*-like plant and several new taxa. Several of the ichnotaxa in the Robledo assemblage are found at NMMNH locality 1339, as noted above. Fossils from this locality are reposited in the National Museum of Natural History, Los Angeles County Museum and Carnegie Museum. The New Mexico Museum of Natural History has a trackway, which came from the Robledo locality (NMMNH locality 1461; MacDonald, 1989). This specimen (NMMNH P-14162) is block of fine sandstone with negative impressions of part of a trackway. The tracks include the anterior portion of a left manus, most of a right manus, a complete left pes and the posterior portion of a second left manus. The left pes has a length of 130 mm, a width of 90 mm and a digit divarication of 75°. The pes has five thin digit impressions and a heel impression about 40 mm long. The left manus has at least four inwardly curving digits, an estimated length of 90 mm and a width of about 80 mm. Digit I of the manus has a recurved tip. The stride, estimated from the left manus impressions, is about 460 mm, and the pace, estimated from the anterior of the manus impressions, is about 250 mm. Based on general morphology and size we assign NMMNH P-14162 to *Dimetropus* sp.

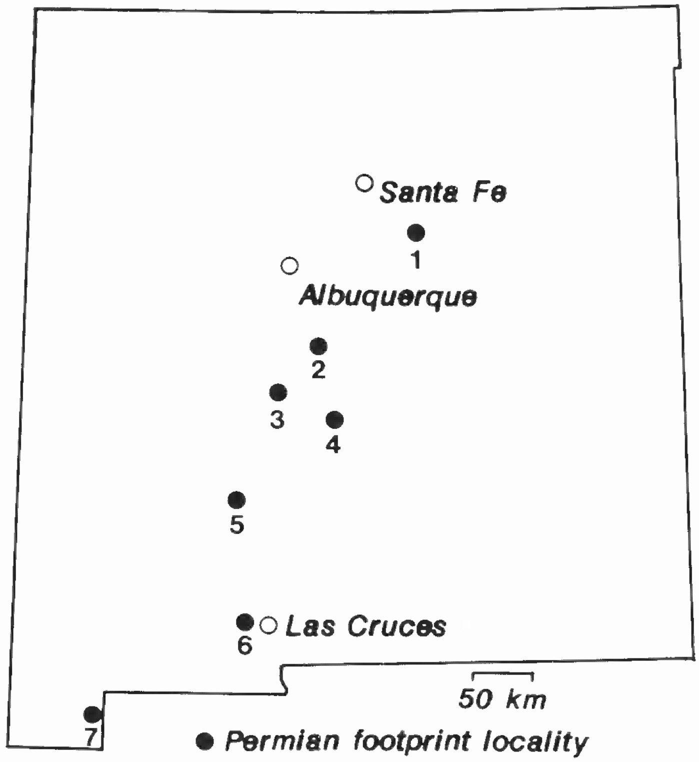

FIGURE 10. Location of Early Permian footprint localities in New Mexico. 1, San Miguel (this report); 2, Abo Pass (Hatchell et al., 1982); 3, East of Socorro (Cappa, 1975; Cappa and MacMillan, 1983); 4, Bingham (this report); 5, Fra Cristobal Mountains (this report); 6, Robledo Mountains (Bowlds, 1989a, b; MacDonald, 1989); 7, Big Hatchet Mountains (Baird, 1965b).

On the 1986 New Mexico Geological Society Field Conference, we noted, but did not collect, small footprints in the Abo Formation of the central Fra Cristobal Mountains (Fig. 10). One of us (SGL) also collected a small ichnofauna from the Abo Formation, east of Bingham, in Socorro County (Fig. 10). These footprints are in a ripple-laminar sandstone of the Abo Formation in the SW1/4 SW1/4 NE1/4 sec. 16, T5S, R6E on a ridge crest just south of NM Highway 380.

Cappa (1975; Cappa and MacMillan, 1983) noted vertebrate tracks in siltstones of the upper Abo Formation, in a 2.6 km^2 area centered in sec. 23, T2S, R1E east of Socorro (Fig. 10). One of us (APH) subsequently noted vertebrate footprints in this area.

Hatchell et al. (1982, fig. 7) illustrated a trackway, that we identify as *Dimetropus* sp., from the NE1/4 NW1/4 sec. 36, T3N, R5E in Valencia County, near the stratotype of the Abo Formation (Fig. 10). This trackway was preserved in a sandstone in the upper Abo Formation, 6 m from the contact with the overlying Meseta Blanca Member of the Yeso Formation (Hatchell et al., 1982). It has subsequently disappeared. Both Hatchell et al.'s (1982) and Cappa's (1975) localities are in the upper Abo Formation. Trackways apparently do not occur in the lower Abo in central New Mexico because this stratigraphic interval is dominated by coarse clastics (Hunt, 1983).

Branson and Branson (1946, p. 1181) stated that they collected "more than 100 slabs containing footprints from red siltstones of the Abo Formation [in New Mexico]." Subsequently, Carl C. Branson, the Director of the Oklahoma Geological Survey, wrote to D. Baird in 1954, suggesting that he study the specimens (Baird, written commun., 1990). On a recent visit to the University of Missouri, one of us (APH) was unable to locate this collection. Unfortunately, the published reference gave no locality information. Branson and Branson (1946) did note the ichnofauna was similar to that from the Coconino Formation of the Grand Canyon in Arizona.

BIOCHRONOLOGY

Although there is no biochronologic framework for Early Permian vertebrate ichnotaxa in North America, a detailed biochronology has been worked out in Europe for the Rotliegend (Haubold, 1971, 1973, 1984, table 7; Gand and Haubold, 1988). The co-occurrence in the Sangre de Cristo Formation of *Dimetropus, Gilmoreichnus, Dromopus lacertoides* and a *Varanopus*-like footprint is similar to the fauna of the Rabejac of France (Gand and Haubold, 1988, fig. 3) and the Oberhoefer Schichten of Germany (Haubold, 1984, table 7). These units are of late Rotliegend age or Leonardian (Haubold, 1973, fig. 1). However, most of the ichnotaxa present at NMMNH locality 1339 are also known from Wolfcampian and Pennsylvania strata. Given the lack of a North American biochronology, and bearing in mind the inferred age of the Sangre de Cristo Formation in this area, we consider it most parsimonius to assign this locality a Wolfcampian age. This age is consistent with the abundance of *Walchia* at this locality, which elsewhere in New Mexico comprises 90% of some Wolfcampian floras (Hunt, 1983).

PALEOECOLOGY

The presence of abundant invertebrate and vertebrate trackways at NMMNH locality 1339, formed on a wet substrate, and the numerous swimming traces (and tracks without tail drags), formed in shallow water, suggest that this locality represents an environment of fluctuating, but persistent, moisture. The preservation of raindrop impressions also suggests fluctuating moisture conditions. Sedimentological context suggests that this was an area of persistent and unconfined flooding (Soegaard and Caldwell, 1990), possibly a pond margin.

On one slab (NMMNH P-14115), vertebrate tracks are in a small depression formed by a large ripple, and other topographically higher portions of the slab are covered with raindrop impressions. Since raindrop impressions do not obscure the tracks, it is likely that runoff from the shower that produced the tracks collected in the depression formed by the ripple. Vertebrate footprints were then preferentially preserved in the wet depression after the raindrop-pitted surface dried.

The abundance of *Walchia piniformis*, a xerophytic plant (White, 1929; Cridland and Morris, 1963), the presence of aestivating lungfish (Vaughn, 1964) and paleocalcretes (Brown, 1984) in the Sangre de Cristo Formation suggest that the environment was arid and seasonally dry (cf. Hunt, 1983).

In the last 20 years, there has been discussion about the distributional patterns of Early Permian vertebrates in the Southwest (Vaughn, 1966, 1969b, 1970; Berman and Reisz, 1980; Berman et al., 1987). Vaughn (1966, 1969b, 1970) recognized "truly deltaic" and "somewhat more upland" faunas. Berman and Reisz (1980) referred to the former as "coastal plain." Subsequently, Berman et al. (1987) cast serious doubt on the validity of Vaughn's hypothesis. Potentially, footprints could be used to discriminate between such faunas, if they are different, given that ichnotaxa are far more common in Early Permian red beds than body fossils. The ichnotaxa from NMMNH locality 1339 include *Dimetropus*, which was probably produced by *Dimetrodon*, one of Vaughn's "marker" taxa for the "truly deltaic/coastal plain" facies. This is in agreement with the presence of *Diplocaulus* in the Sangre de Cristo Formation (Berman and Reisz, 1980), as this is also a "marker" taxon for this facies.

Thus, NMMNH locality 1339 probably formed at a pond margin in an area of persistent and unconfined flood events. The environment was arid and seasonally dry.

ACKNOWLEDGMENTS

The locality described here was brought to our attention by Phil Bircheff, who recognized that a diverse ichnofauna was being excavated in a flagstone quarry. We are grateful to Tomas Romero of La Puebla, New Mexico for permission to collect these tracks, Kaye Toolson for assistance with field work and D. Baird, H. Haubold and K. Kietzke for their helpful reviews. We are particularly grateful to Dr. Haubold for sending us much literature on European Permian footprints and original photographs of specimens.

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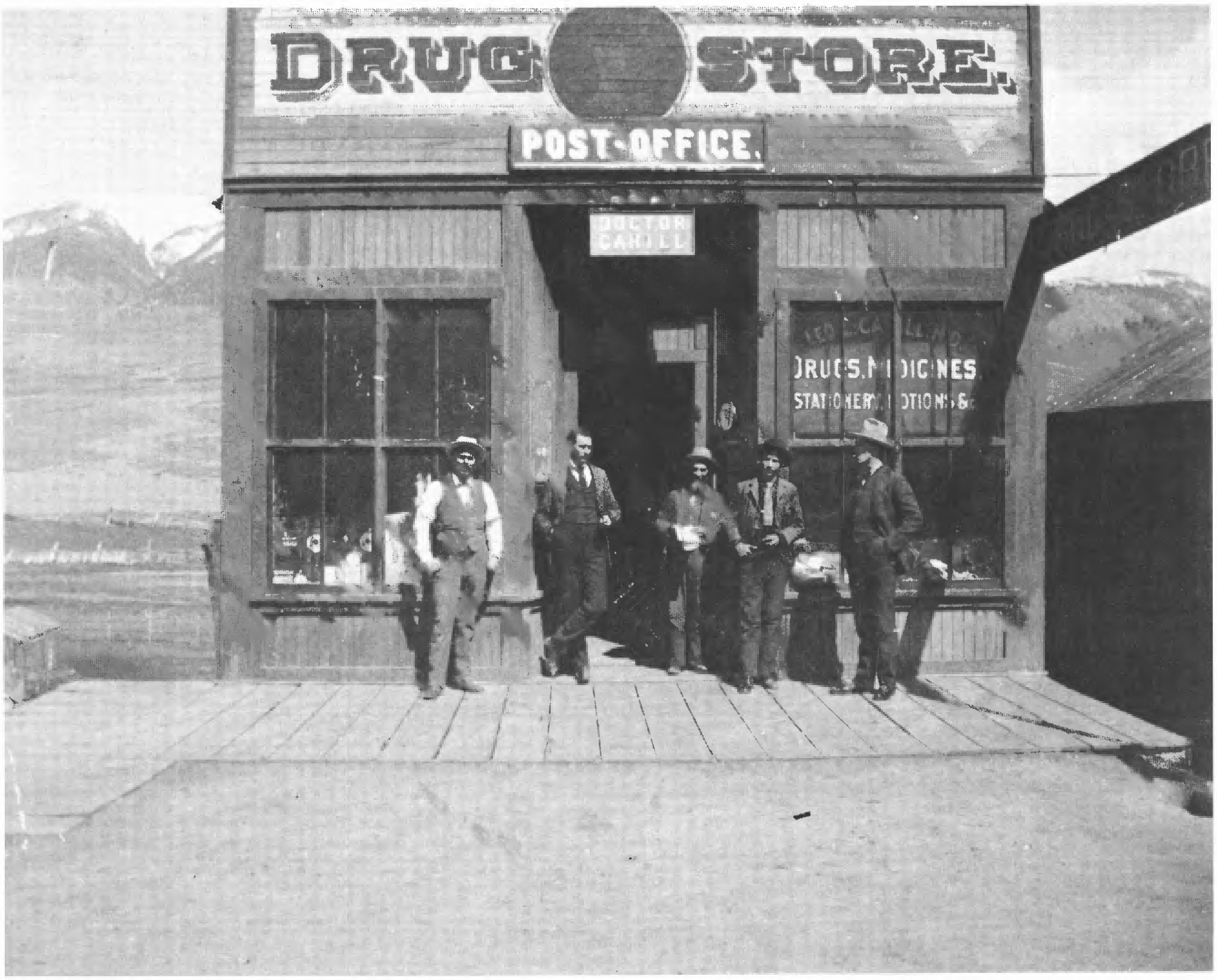
APPENDIX—STRATIGRAPHIC SECTION

The stratigraphic section in Figure 1 is described below. Strata are horizontal. Rock colors are those of Goddard et al. (1984).

unit	lithology	thickness (m)
	Sangre de Cristo Formation:	
7	Sandstone and clayey sandstone; sandstone is grayish red (10 R 4/2), very fine grained, subrounded to subangular, well sorted, subarkose, not calcareous and trough crossbedded; clayey sandstone is light greenish gray (5 G 8/1), very fine to fine grained, subangular, poorly sorted, quartzose and micaceous, not calcareous and trough crossbedded.	0.6
6	Sandy siltstone to sandstone, grayish red (10 R 4/2), very fine grained, subangular, poorly sorted, quartzose, not calcareous and bioturbated.	0.3
5	Sandy siltstone, grayish red (10 R 4/2), slightly calcareous, forms slope.	2.4
4	Clayey sandstone and sandstone; clayey sandstone is light greenish gray (5 G 8/1), very fine to fine grained, subangular, poorly sorted, quartzose and micaceous, not calcareous and laminar; sandstone (lower half of unit) is grayish red (10 R 4/2), subrounded to subangular, well sorted, subarkose, not calcareous and laminar; forms ledge; vertebrate and invertebrate tracks (NMMNH locality 1339) at top.	0.6
3	Clayey sandstone, light greenish gray (5 G 8/1), very fine to fine grained, subangular, poorly sorted, not calcareous, carbonaceous plant debris, trough crossbedded, soft sediment deformation structures.	0.5
2	Silty claystone, grayish red (10 R 4/2) with light greenish gray (5 GY 8/1) mottles, moderately calcareous.	5.2
1	Sandstone, grayish red (10 R 4/2), very fine grained, subrounded to subangular, well sorted, subarkose, common large mica crystals, not calcareous.	0.2



Dr. Leo L. Cahill poses with some friends (including Joseph W. Quick and Pete Perry) in the doorway of his Elizabethtown drug store in 1899. What wondrous nostrums, notions and nosegays confronted the weary traveler upon his arrival, one can only guess. And while one was browsing, the good doctor would post your letters and sell you some stamps—stamps for which the collector would gladly commit mayhem today! Photo courtesy of Museum of New Mexico, neg. no. 99869.