

# VERTEBRATE TRACKWAYS AMONG A STAND OF *SUPAIA* WHITE PLANTS ON AN EARLY PERMIAN FLOODPLAIN, NEW MEXICO

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**ABSTRACT**—Little is known about the habit and spatial distribution of Early Permian tropical vegetation, a sharp contrast with the Pennsylvanian from which many in-situ “T<sup>0</sup>” assemblages are known. Even less is known about the potential interaction of plants and vertebrates. Here we report the discovery of a small stand of 34 probable *Supaia* White plants from the Abo Formation of New Mexico. The plants were growing on a mudflat, subject to periodic flooding and exposure. The same mudflat hosts trackways of vertebrates that appear to have walked around or between the *Supaia* plants. The stems are preserved as molds, and vary from 20 mm to 70 mm in diameter, averaging 42.4 mm, indicating heights of approximately 2.5–4 m. The plants, which may be described as small trees given their estimated height, are as close as 110 mm to their nearest neighbor and average nearly 300 mm apart. A series of lines or filled fissures, which we interpret as roots, radiates from the base of each stem. Leaves of *Supaia thinfeldioides* White are the only foliage found in association with these stems, on bedding planes above and at the base of the lowest expression of the stem molds. Associated vertebrate trackways either congregate around some of the stems or wend their way between the stems and include those of a single large temnospondyl amphibian (*Limnopus* Marsh) and many of small predatory parareptiles (*Dromopus* Marsh). This study demonstrates that *S. thinfeldioides* were small-statured, weedy, opportunistic plants. It also shows that contemporaneous vertebrates prowled such environments, presumably either for food, shelter, or both given detectable pace and path.

## INTRODUCTION

**R**EAL-TIME OR so-called T<sup>0</sup> data (Johnson, 2007; DiMichele and Falcon-Lang, 2011) are among the most sought after in the fossil record. Under ideal circumstances they may reveal spatial patterns, growth conditions, behaviors of animals, and interactions among organisms comparable to those attainable from certain kinds of modern ecological studies. The most celebrated data of this type are trackway assemblages of vertebrates and invertebrates, which reveal aspects of behavior difficult to ascertain from most body fossils (e.g., Haubold, 1984; Buatois et al., 1998; Buatois and Mángano, 2007). For plants, the closest example to the trackway record is that of vegetation buried in situ by ash falls (Wing et al., 1993; Pfefferkorn and Wang, 2007; Opluštil et al., 2009), floods (Gastaldo et al., 2004; DiMichele et al., 2009; Falcon-Lang et al., 2011), or by other catastrophic means (e.g., DiMichele and Falcon-Lang, 2011 for summary of Paleozoic data), which allow determination of plant density and spacing, inferences about size, and habitats of growth. A combination of plant and vertebrate in situ records has the power to reveal trophic interactions, even if only by inference, but still one based on clear behavioral data; there are very few such examples known from the fossil record (e.g., Parker and Balsley, 1989; Carpenter, 1992).

Reported here is a stand of Early Permian tropical plants of slight stature, preserved on a mud flat in a seasonal environment, subject to periodic flooding and drying. The plants are likely *Supaia thinfeldioides* White (1929) based on the monotypic associated foliage litter. Alone this would be a singular discovery because so little is known about the growth habits and physical distribution of Early Permian tropical plants; many kinds of foliage are well known, but the habit of the plants to which such foliage was attached remains virtually unknown for broadleaved forms. In addition to the plants, however, this deposit contains trackways of at least two kinds of vertebrates, a large temnospondyl amphibian and small, predatory parareptiles.

*Supaia* White (1929) was erected to encompass a number of kinds of small forked fronds bearing pinnately compound foliage of xeromorphic aspect, from the earliest Permian of the Grand Canyon of Arizona. Originally thought to be confined to Early Permian age rocks of the western United States (Read and Mamay, 1964), *Supaia* has subsequently been described from the Permian of China (Wang, 1997; Deng et al., 2009), Europe (Gand et al., 1997; Galtier and Broutin, 2008) and possibly Sumatra (Booi et al., 2009), and thus appears to have been distributed across the Pangean low latitudes. Wang (1997) suggested an association with *Autunia*-type fructifications, which would support a peltaspermalean affinity, a conclusion supported by DiMichele et al. (2005). From its earliest description, the plant has been associated with environmental conditions indicative of seasonal dryness, with some indication of tolerance of severe moisture stress (White, 1929; Gand et al., 1997; DiMichele et al., 2007). Such suppositions, however strongly supported they may be by sedimentological and foliar morphological evidence, are uninformed by any knowledge of the stature of the *Supaia* plant or its population structure—common problems for many-to-most fossil plant species. Essentially, it is not known if this plant was tree, shrub, vine or ground-cover. These deposits suggest it was a small, upright, tree-like plant, several meters in height at most.

The vertebrate footprint ichnotaxa reported here are characteristic of red-bed ichnoassemblages across a wide part of the Early Permian Pangean tropics (Hunt and Lucas, 2006). They represent well known temnospondyl and parareptile trackmakers. However, their direct association with in situ Permian ‘trees’ is very unusual, perhaps unique in the Early Permian track record.

## GEOLOGICAL SETTING

**Location.**—The fossil assemblage documented here was discovered in an outcrop of the lower part of the Abo Formation exposed along Cuchillo Negro Creek on the US

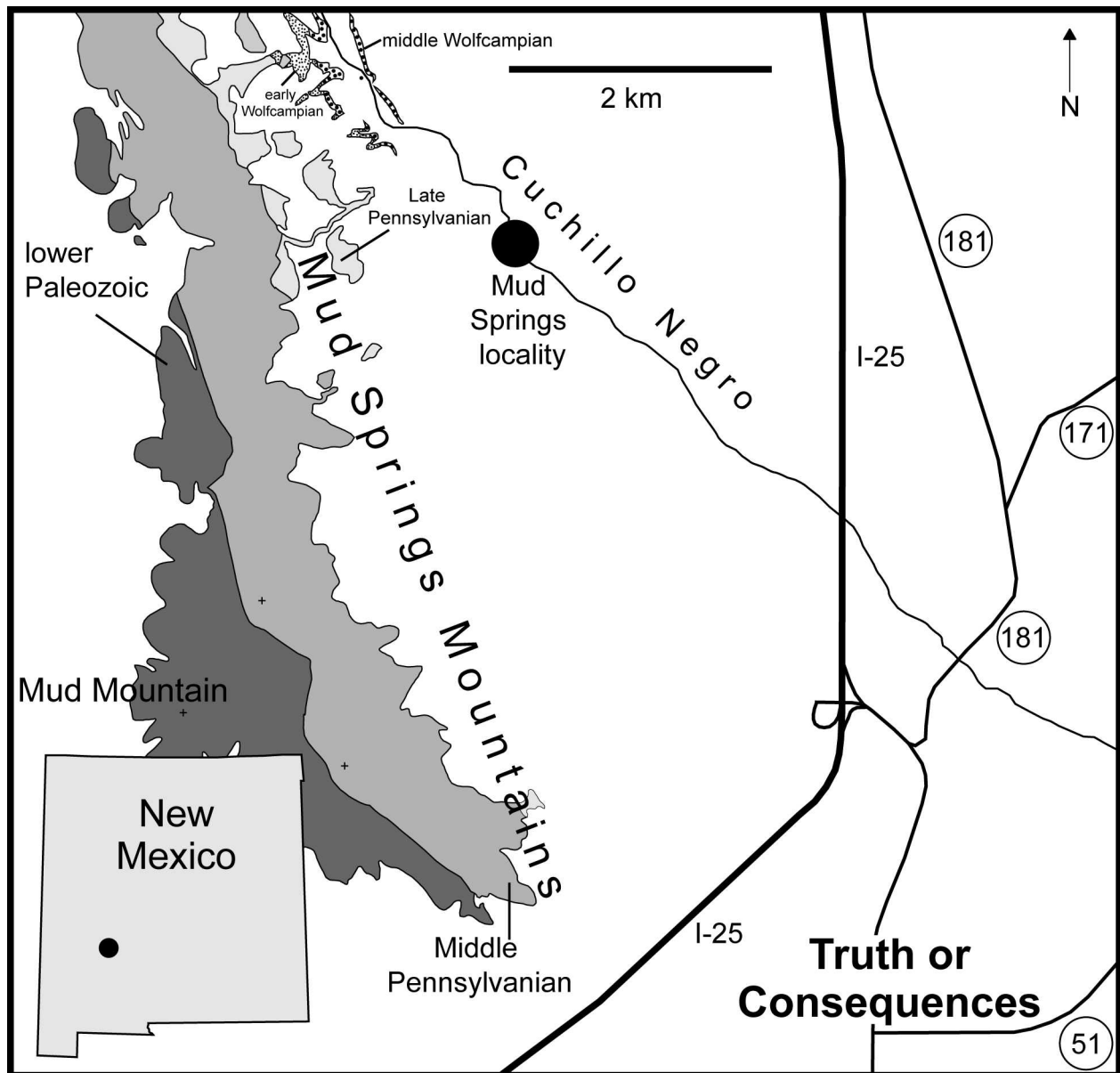


FIGURE 1—Location of study site (black dot) on Cuchillo Negro Creek, east of the Mud Springs Mountains and northwest of the town of Truth or Consequences in southern New Mexico.

Geological Survey Cuchillo, New Mexico 7½' Quadrangle to the northwest of the town of Truth or Consequences (Fig. 1). The map coordinates are in the locality database of the New Mexico Museum of Natural History (NMMNH) as locality 8376.

*Physical geology and age.*—The thickness of the Abo Formation outcrop exposed along the Cuchillo Negro Creek is 21 m (Fig. 2). The exposed Abo red beds are mostly siltstone-mudstone (comprising 60% of the section) with two intercalated sandstone units (comprising 40% of the section) (Figs. 2, 3.1). The siltstone to mudstone is commonly finely laminated (lithofacies Fl) or appears massive (lithofacies Fm) (lithofacies codes after Miall, 1996). Pedogenic carbonate nodules and lenses (lithofacies P) are present in the siltstone-mudstone at the base of the lower sandstone unit. In the siltstone-mudstone succession between the two sandstone units, pedogenic carbonate nodules float in the fine-grained sediments and two nodular, lenticular, calcareous pedogenic

horizons (lithofacies P) are present. The upper pedogenic horizon contains poorly-developed rhizoliths.

The lower sandstone unit is 3.1 m thick, composed of fine-grained sandstone displaying trough cross-bedding (lithofacies St), low-angle cross-bedding (lithofacies Sl) and fine-grained sandstone with horizontal lamination (lithofacies Sh). The lower contact is erosional and grain-size and bed thickness decrease upward. In the horizontally laminated upper part, desiccation cracks occur in several layers. Intercalated in the fine-grained sandstone are two thin siltstone-mudstone beds that are 0.2 and 0.6 m thick. The footprints and fossil plants documented here are in the upper part of this unit (Fig. 2, Bed 4; Fig. 3.2).

The upper sandstone (Fig. 2, units 11–17, Fig. 3.1) unit is 6.5 m thick and is composed of individual sandstone beds displaying trough cross-bedding (lithofacies St), low-angle cross-bedding (lithofacies Sl), horizontal lamination (lithofacies Sh) and rare ripple cross lamination (lithofacies Sr). The

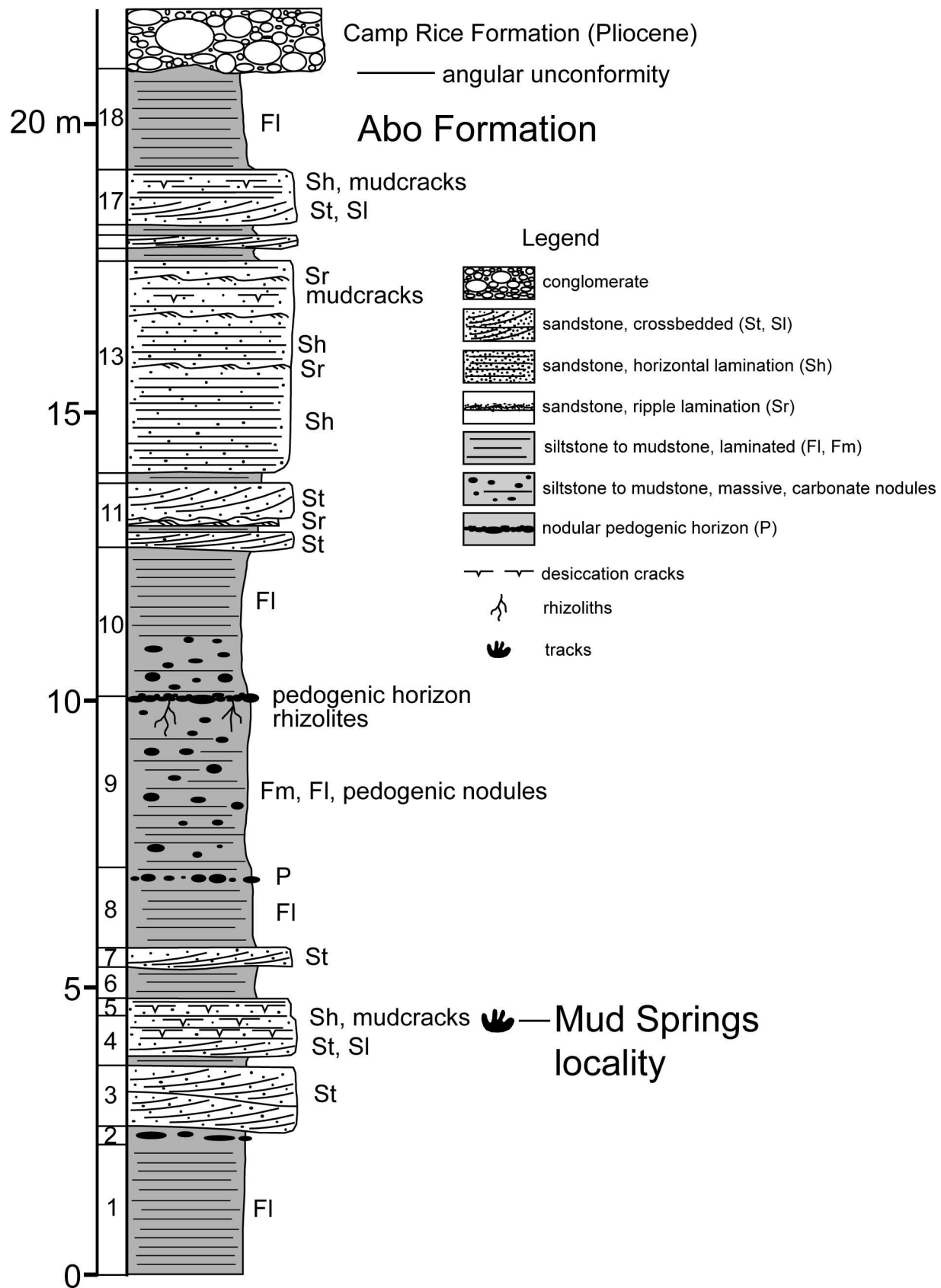


FIGURE 2—Lithologic log of the Abo Formation at the study site on Cuchillo Negro Creek. Plant stems and vertebrate trackways studied occur in Bed 4.





FIGURE 3—Outcrop on Cuchillo Negro Creek. 1, exposure of Early Permian Abo Formation overlain by Pleistocene Palomas Formation; plant fossils and vertebrate trackways occur on the bedding surface exposed at the bottom of the outcrop to the left of the person standing at the outcrop base; 2, bedding surface on which stem casts and trackways are preserved; the *Limnopus* trackway can be seen to the right of the Jacob's Staff.

lower contact is erosional. Several thin siltstone-mudstone layers are intercalated. Mudcracks occur in the upper part of the sandstone unit within horizontally laminated sandstone.

Sandstone units in the Abo Formation commonly occur as sandstone sheets, which can be traced laterally over long distances (e.g., Krainer and Lucas, 2010; Lucas et al., 2005a). Sandstone sheets correspond to the architectural element CH (channel) of Miall (1996). We suggest that at

Cuchillo Negro the sandstone units form such sandstone sheets, although the limited local exposure does not allow tracing them laterally.

Sandstone sheets were deposited in broad, shallow channels of a probable low sinuosity river system. The sandstone units are similar to the sandstone sheets described from the Abo Formation at Jemez River in northern New Mexico and at the type locality near Abo Pass in central New Mexico (Eberth

and Miall, 1991; Lucas et al., 2005a; Krainer and Lucas, 2010), but finer-grained than farther north.

The siltstone-mudstone (lithofacies Fl, Fm) is assigned to the element FF (floodplain fines) of Miall (1996), representing mainly floodplain deposits that formed by the settling of fine-grained sediment from sheetfloods on extensive floodplains. The presence of fine lamination (lithofacies Fl) indicates that the sediments were deposited from suspension.

Compared to the Abo Formation at Jemez River or near Abo Pass, the Abo Formation at Cuchillo Negro Creek is developed in a more distal facies with fine-grained sandstone being the coarsest sediment. The main sources of the sediments of the Abo Formation were the Uncompahgre and Zuni uplifts to the north and the Pederal uplift to the east of the current location of the Mud Springs Mountains (e.g., Kues and Giles, 2004, fig. 11). Towards the south, grain-size decreased continuously, and the non-marine red beds of the Abo Formation interfinger with the shallow marine carbonates of the Hueco Group about 25–75 km to the south of the Mud Springs Mountains in the southern Caballo, Doña Ana and Robledo Mountains.

Although the Abo Formation in this area has not been definitively dated either biostratigraphically or chronostratigraphically, the Abo Formation regionally is known to be of middle-late Wolfcampian (approximately Sakmarian-Artinskian) age. This is based primarily on the fact that in northern and central New Mexico it disconformably overlies the mixed marine-nonmarine lower Wolfcampian Bursum Formation (e.g., Lucas and Krainer, 2004; Krainer and Lucas, 2010), and in southern New Mexico the Abo Formation laterally interfingers with middle-late Wolfcampian marine strata of the Hueco Group (e.g., Lucas et al., 1995, 1998, 2011). The Mud Springs track and plant locality is in the lower part of the Abo Formation, so it is almost certainly of middle Wolfcampian age.

*Fossiliferous deposit.*—The plant stems (Fig. 4.1, 4.2) occur at the base of, and project through, a 7-cm-thick interval of siltstone and claystone beds; approximately seven such beds comprise the total thickness of the exposed interval (Fig. 2, Bed 4; Fig. 3.1, at base of exposure; Fig. 3.2). Immediately below the stem- and footprint-bearing layer is a dark claystone surface covered with mudcracks. Neither the stems nor their presumed roots were identifiable at that level. In the sedimentary layers comprising the 7-cm zone of silt-clay lamination above the base of the deposit, there is at least one surface with raindrop imprints, indicating subaerial exposure. Beds at the top of this interval contain isolated specimens of *Supaia thimfeldioides* foliage (Fig. 4.3). The *S. thimfeldioides* specimens, isolated leaves only, were identified by the following features: Once compound leaf architecture, the rachis wide, composed both of the vascular strand and thin flanking lamina created by the confluence of adjacent pinnules. Pinnules elongate, 4 to 5 times longer than wide, decurrent and narrowly confluent, slightly constricted at the base, widely spaced/clearly distinct. The only clearly visible pinnule venation, the pinnule midvein, is decurrent, strong, and extends nearly to the tip of the pinnule. As described by White (1929) and in other studies of large populations (e.g., DiMichele et al., 2007), there is considerable morphological and size variation in *Supaia*. This variation is demonstrated by the many species described by White (1929) and by the variation in some of these, especially *S. thimfeldioides*, the most common form, within the scope of which the Cuchillo Negro specimens fall.

The plants and trackways are exposed on an irregularly shaped surface with maximum dimensions of 3 by 5 m. Most of the tree molds are found in an area of 3 by 2 m. Approximately one half of the total surface area represented by the maximum extent of the exposed, stem-mold bearing beds, was missing from the outcrop due to erosion and local mining of flagstone. These beds dip gently to the north (Figs. 3, 4.4) and are buried by alluvium.

We interpret this deposit to have originated in periodic floods of sediment-bearing water into a shallow depression. This depression may represent a small, largely abandoned shallow channel or channel margin. The depositional environment was regularly and perhaps mostly exposed following periodic flooding and was close enough to more permanently exposed areas that tetrapods of various sizes could cross its surface shortly after floodwaters subsided.

#### PLANT AND ANIMAL REMAINS

*Fossil plants.*—Thirty-four stem molds were identified on the exposed bedding surfaces. These molds are nearly circular in cross-sectional aspect and average 42.4 mm in diameter, ranging from 20 mm to 70 mm (Fig. 4.1, 4.2). They are filled with dark brown or black siltstone that contrasts with the reddish-brown bedding plane surface on which they are exposed. The stem molds were inferred to be at least 70 mm in height, based on two specimens that were exposed on a bedding surface 70 mm above the large bedding plane on which the majority of the specimens were identified (Figs. 3, 4.4). Although these specimens were not exposed in longitudinal section, they appear to project upward from below; given the rarity of this kind of preservation, it seems reasonable to assume that these specimens are not a second stand of stems originating at a different level in the sediment.

Radiating concentrically from each mold are several thin, crack-like lines filled with the darker matrix material. These cracks probably mark the course of roots. Some could be traced as far as 50 cm from the stem mold. They usually followed a sinuous course through the siltstone matrix (Fig. 4.1, 4.2). If these cracks represent the former courses of roots, their presence around the two specimens buried in later deposited sediment suggests that they may have formed adventitiously from the stems and that the plants were shallowly, but broadly rooted.

Foliage of *Supaia thimfeldioides*, inferred to have been produced by the stems, was identified on several different bedding surfaces in this deposit. The best-preserved specimens (Fig. 4.3) were found between the basal and the upper-most bed in which the stem molds appear. We interpret this foliage to have been shed from the stems. Based on studies of *Supaia* foliage from other places (e.g., White, 1929; Wang, 1997), these leaves were likely to have remained attached to the parent plant for multiple seasons. Although relatively small, most being 20 cm or less from base to apex, the compound, forked *Supaia* leaf appears to have had a woody petiole and thick lamina, requiring considerable metabolic investment.

The distance to nearest neighboring stem averaged 296.2 mm, and ranged from 110 mm to 800 mm. Edge effects and the irregular surface area introduce biases, particularly for stems with few others in close proximity, which ought to skew the results slightly towards greater inter-stem distances. If the outlying measurements of 750 and 800 mm are eliminated, the average distance between stems is reduced slightly to 266.2 mm.

The heights of these plants are estimated to fall between 2.5 and 4.5 m. This was determined from the model of Niklas and Spatz (2004), which was derived from the empirical study of



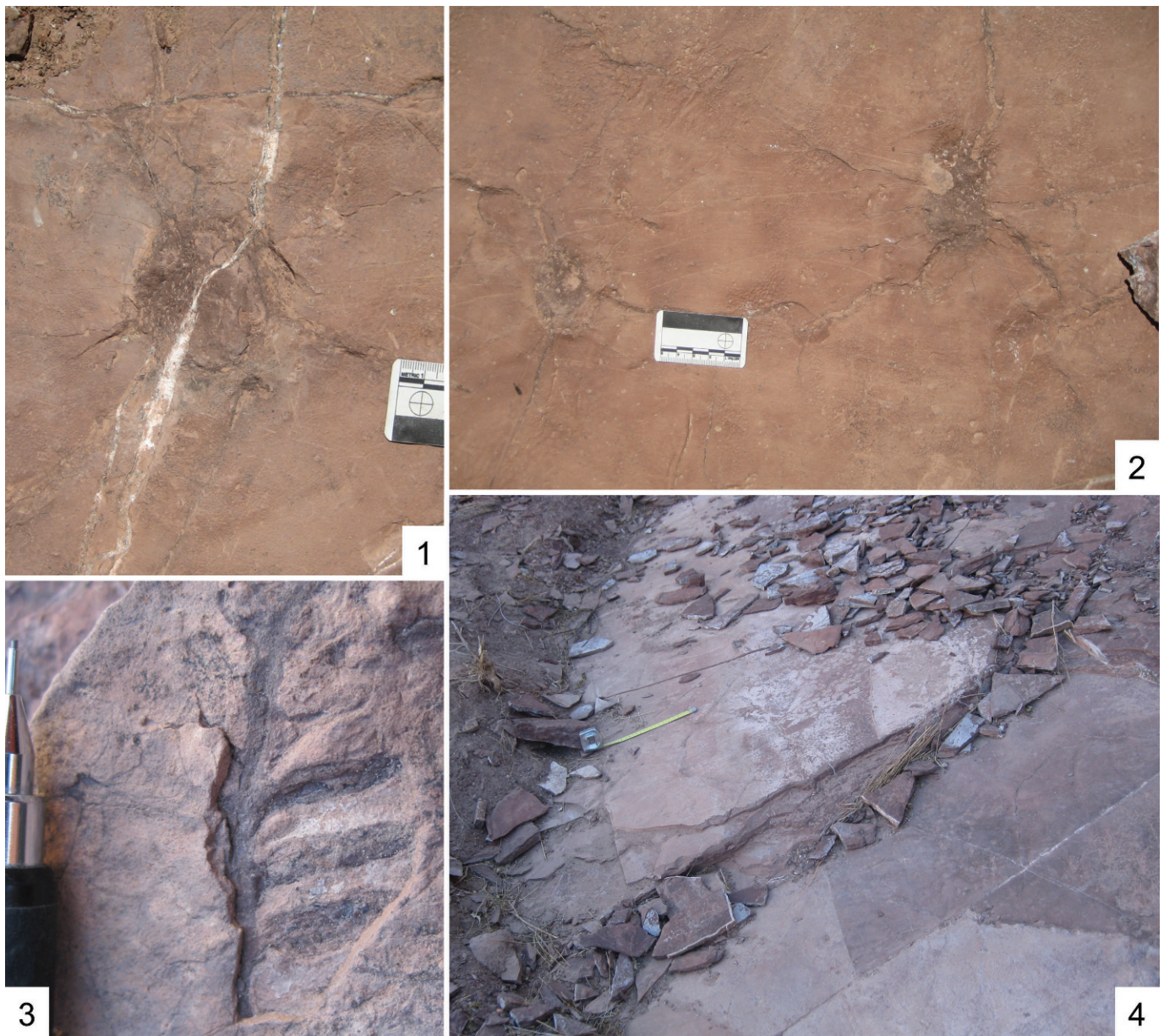


FIGURE 4—Plant fossils and the fossiliferous layer. 1, fossil stem cast with radiating sediment-filled cracks, inferred to be the remains of adventitious roots, scale in centimeters (black and white bars); 2, a pair of fossil stem casts with radiating sediment-filled cracks inferred to be roots, scale=5 cm; 3, foliage of *Supaia thinnfeldtioides* found on the lower bedding surface of the interval bearing the fossil stem casts, tip of mechanical pencil=1 mm; 4, fossiliferous layer; stem casts originate on the lowermost layer and project through several layers of siltstone and claystone. Scale is 25 cm (yellow tape).

extant woody, tree-sized plants, supplemented with data from self-supporting herbaceous plants and juvenile woody trees. The critical constants in this model were estimated empirically, which is not possible for the extinct pteridosperms, particularly the peltasperms, for which few whole plants are known on which such determinations could be based. The *Supaia* stems are large enough to fall within the linear, two-thirds slope portion of the Niklas and Spatz (2004) log-log curve of stem height versus stem diameter. *Supaia* may have been physically constructed quite differently from woody trees and self-supporting herbs, however, possibly having a pteridosperm-type vine-like, vascular architecture consisting of multiple vascular bundles (e.g., Stidd, 1981). Thus, these estimates should be treated with caution, and allowance must be made for the plants to have been somewhat smaller than these projections, given the growth architectures illustrated by

such studies as that of Pfefferkorn et al. (1984) or Falcon-Lang (2009).

*Vertebrate trackways.*—Two very different kinds of tetrapod footprints are preserved in concave epirelief at the Mud Springs tracksite (NMMNH Locality 8376, Fig. 5.1–5.4, 6). Most common are footprints that display diagnostic features of the ichnogenus *Dromopus* Marsh (1894), which mostly consist of 2 to 4 nearly parallel digit marks that are long, thin, slightly curved and have pointed tips. The best-preserved specimens (e.g., Fig. 5.4) show an evident increase in digit length from digits I through IV. These lacertoid tracks are up to 30 mm long, lack sole imprints and do not form organized trackways. Because of this and their generally incomplete preservation, manus tracks cannot be distinguished confidently from pes tracks.

*Dromopus* is one of the most common kinds of tetrapod footprints found in the Abo Formation across New Mexico



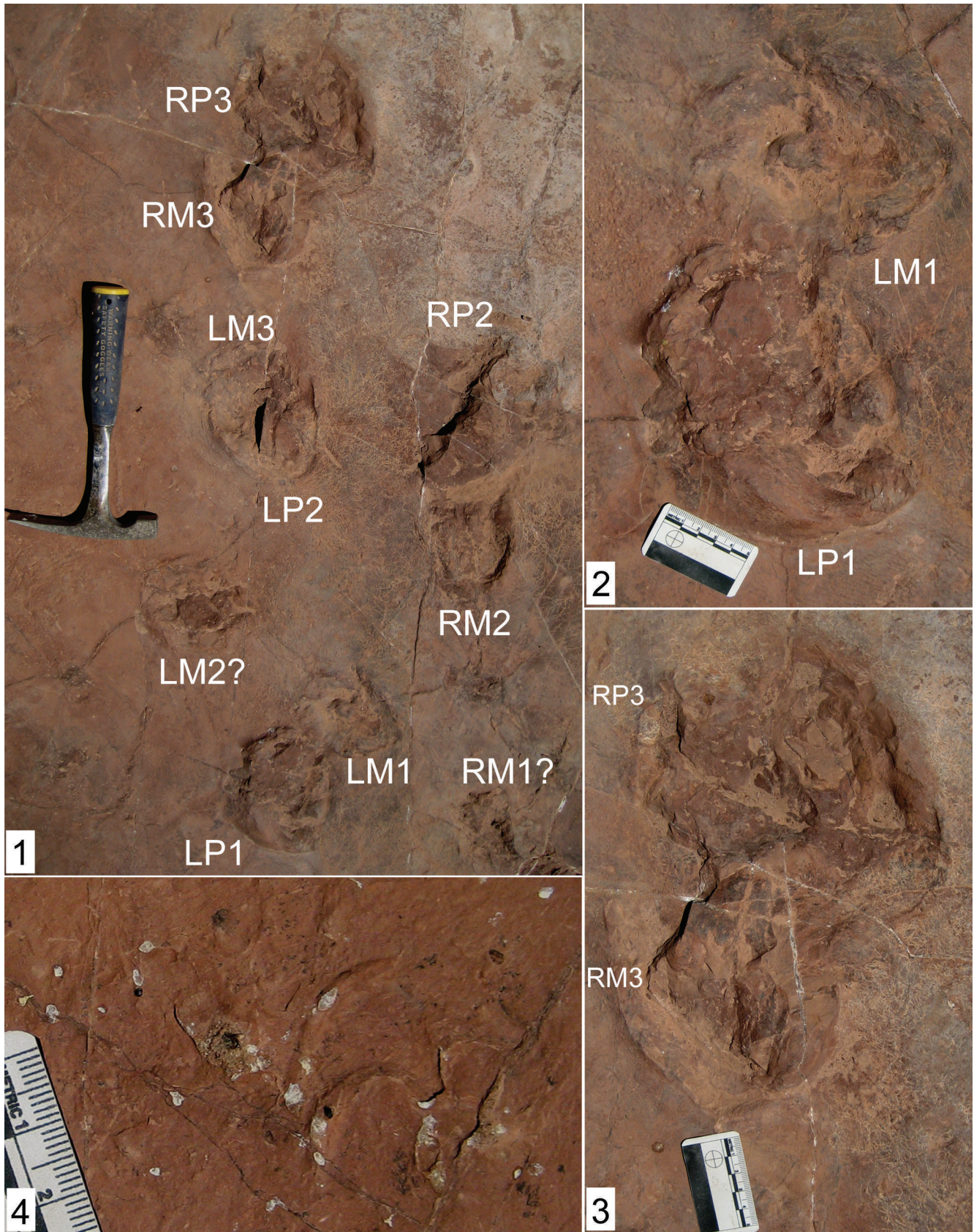


FIGURE 5—Selected tetrapod footprints at the Mud Springs locality. 1, overview of part of the temnospondyl trackway, *Limnopus* sp., geology hammer=28.5 cm in length; 2, 3, close-up views of selected *Limnopus* footprints, scale=5 cm; 4, parareptile (*Dromopus*) footprints, finest division of scale in millimeters. Trackway abbreviations: RP=right pes; RM=right manus; LM=left manus; LP=left pes; number refers to footprint sequence.



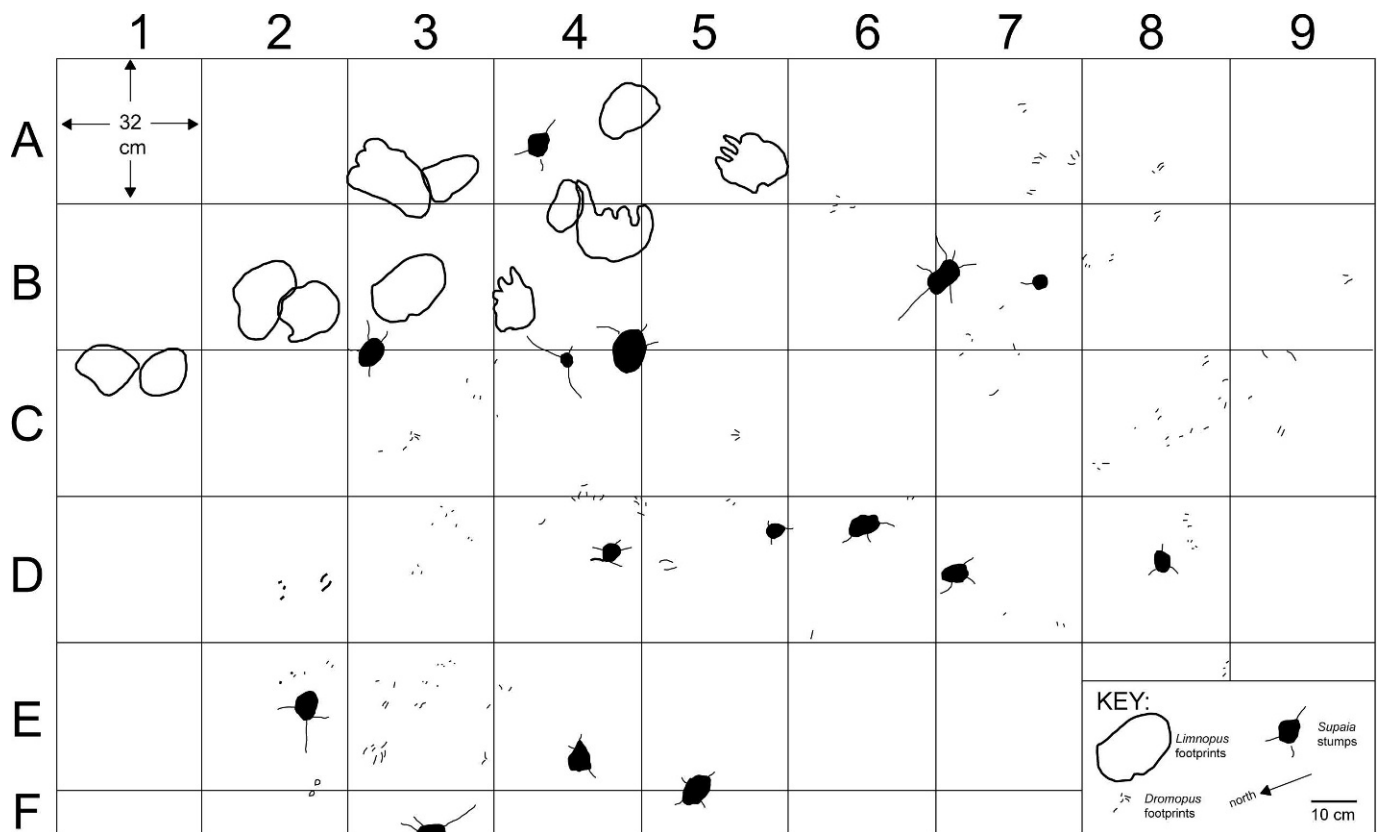


FIGURE 6—Map of a portion of the fossiliferous bedding surface where vertebrate trackways were exposed most prominently. One trackway of a large temnospondyl amphibian (*Limnopus*) indicates a single animal moving through the *Supaia* plants, the basal casts of which are shown as dark ovals. Numerous trackways of smaller parareptiles (*Dromopus*) can be seen.

(e.g., Haubold et al., 1995; Lucas et al., 2005b, 2005c; Hunt and Lucas, 2006; Minter and Braddy, 2009). It has long been identified as the footprint of a relatively small predatory parareptile, most likely an araeoscelid (e.g., Haubold, 1971, 1984). The ichnogenus *Dromopus* is widely distributed in Early Permian red bed ichnoassemblages, especially in the western United States, eastern Canada and western Europe (Hunt and Lucas, 2006). *Dromopus* occurrences like that at the Mud Springs tracksite, in which there are numerous poorly preserved footprints not organized into trackways, are characteristic occurrences in the Abo Formation. At the Mud Springs tracksite, the *Dromopus* tracks show no evident pattern, except they are more greatly concentrated in two areas—in quadrants D-E/2-4 and B-D/7-8 (Fig. 6).

The other kind of tetrapod footprint at locality 8376 is identified by us as *Limnopus* Marsh (1894). These form a trackway in the northeastern portion of the trackway surface that consists of at least six associated manus-pes sets and two less clear manus(?) tracks. These tracks are relatively large for Early Permian footprints—pes imprints are as much as 14 cm long and manus imprints are up to 11 cm long—though size appears to have been exaggerated by the spreading out of the trackway imprint in the substrate in which these undertracks are registered (Fig. 5.1–5.3). Manus imprints are directly in front of pes imprints or are overstepped, and the few digits discernable suggest some rotation of both manus and pes toward the trackway midline. Because the digits are not very well preserved, exact digit counts cannot be made for manus or pes (at minimum there are four) and the relative lengths of the digits cannot be determined. However, the preserved digits

are short, thick and have blunt tips. Most significant is that they are short relative to the large, nearly round and plantigrade sole imprints. Based on the length between manus and pes imprints on the same side of the body, in which there is no overstepping, the gleno-acetabular length is estimated at ~50 cm.

There are only two possible Early Permian ichnogenera to which this large trackway could be assigned—*Ichniotherium* Pohlig (1892) and *Limnopus*. *Ichniotherium* is unlikely on morphological grounds, primarily because the Mud Springs tracks lack any hint of the relatively long, dumbbell-shaped digit imprints characteristic of *Ichniotherium* and because the short digits of the Mud Springs tracks are only a small proportion of the entire footprint length, which is mostly the sole imprint. In *Ichniotherium* the digit imprints are longer than the sole imprint (e.g., Voigt and Haubold, 2000; Voigt et al., 2007). Also, in New Mexico and elsewhere *Ichniotherium* is known only from inland fluvial facies (e.g., Hunt and Lucas, 2006), so its occurrence at the Mud Springs locality in distal floodplain facies near the Hueco shoreline would be unusual.

Indeed, the large trackway at the Mud Springs locality can be assigned with confidence to *Limnopus* on morphological grounds, especially the short blunt toes and large plantigrade sole, which exemplify the ichnogenus (e.g., Haubold et al., 1995; Hunt et al., 1995). *Limnopus* has long been identified as the track of a relatively large temnospondyl amphibian (e.g., Haubold, 1971, 1984). It is a characteristic tetrapod footprint found in Early Permian red-bed ichnoassemblages in the western United States, eastern Canada and Western Europe (Hunt and Lucas, 2006). Indeed, the Mud Springs *Limnopus*



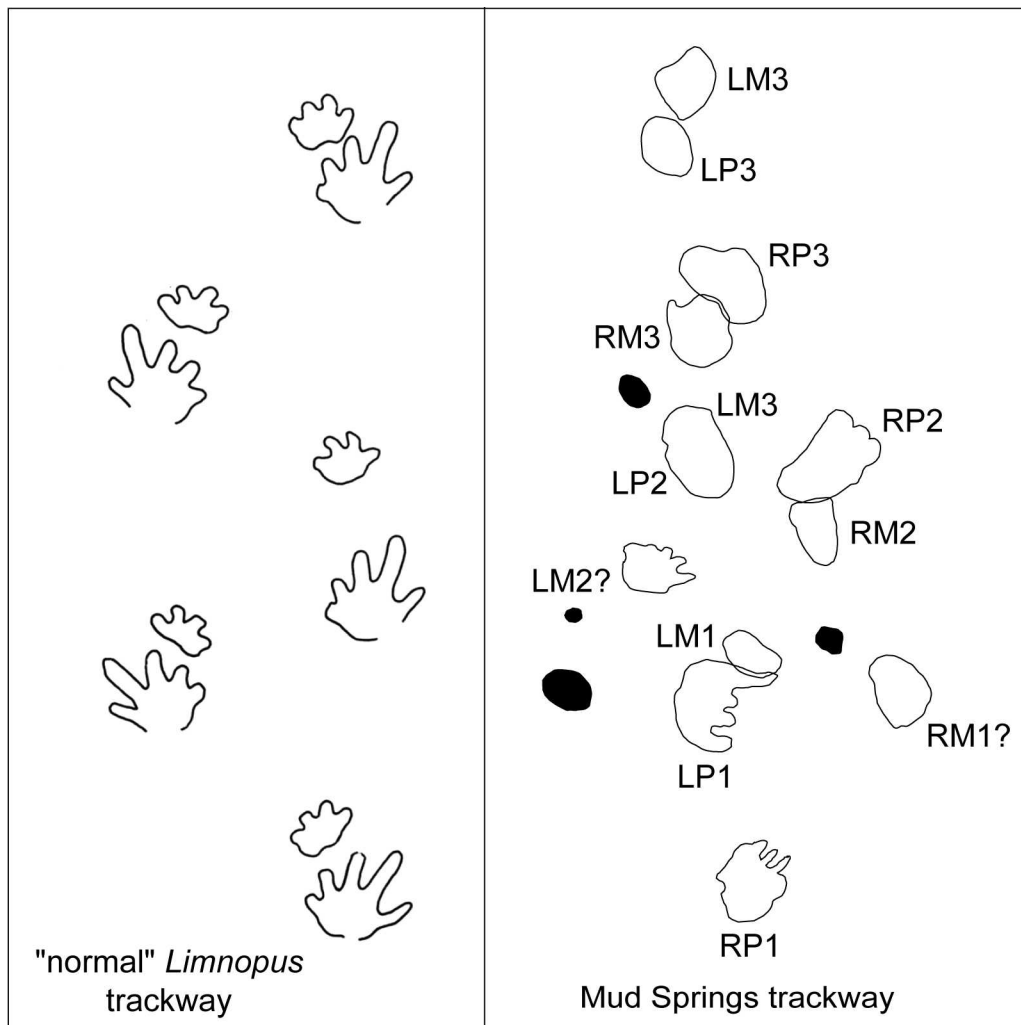


FIGURE 7—Comparison of characteristic *Limnopus* trackway (after Baird, 1965) and the *Limnopus* trackway at the Mud Springs locality. Trackway abbreviations: RP=right pes; RM=right manus; LM=left manus; LP=left pes; number refers to footprint sequence.

tracks are among the largest *Limnopus* tracks known from the Abo Formation (cf. Haubold et al., 1995; Hunt et al., 1995), although as noted above their size has arguably been exaggerated somewhat by the taphonomy of their preservation.

Perhaps most interesting about the *Limnopus* trackway at the Mud Springs site is its unusual gait and trackway pattern, which suggests an amphibian that walked very slowly, meandering through the *Supaia* stems (Figs. 6, 7). Comparison of the Mud Springs *Limnopus* trackway with characteristic ('normal') *Limnopus* trackways in the published literature (Fig. 7) indicates that the trackway pattern and gait of the Mud Springs *Limnopus* trackmaker (a temnospondyl amphibian) was unusual. Compared to 'normal' trackways, the Mud Springs *Limnopus* trackway is narrow, has a wide pace angulation and an irregular stride with overstepping of the manus by the pes in some manus-pes pairs.

If the larger imprints are identified as pes and smaller as manus (as is the case in *Limnopus*), then the trackway can be interpreted as two complete strides evidently affected by the trees along its borders. Thus, the imprint identified as the initial right pes track (RP1 in Fig. 7) strides forward to RP2 and to RP3, whereas the initial left manus/pes pair (LM1/LP1 in Fig. 7) strides forward to LM3/LP2 and LM3/LP3. This interpretation is supported by the stride lengths on both sides

of the body, which have a fairly consistent value of ~50 cm. If LM2 is interpreted as the second left manus imprint, then it indicates that the left manus was placed outside of the carriage as the temnospondyl pivoted on pes imprint LP1. Moving RP1 and RM1 to RM2/RP2, though, is difficult to interpret as it suggests that the right manus would either have had to be swung over the *Supaia* tree in quadrant A4 (Fig. 6), or moved to the left of it. The overstepping evident in RM2/RP2 and RM3/RP3 indicates deliberate flexure of the body and great extension of the hindlimb to place it anterior to the manus, which would have taken place in a slow gait.

Given the poor preservation of the *Limnopus* trackway at the Mud Springs site, other interpretations are possible, but clearly it differs substantially from a 'normal' *Limnopus* trackway (Fig. 7). These differences are readily understood as reflecting the temnospondyl trackmaker changing gait to accommodate the obstructions posed by the *Supaia* trees.

#### DISCUSSION

The small stand of plants described here appears to be a cohort that colonized a freshly exposed mudflat on a floodplain bordering a watercourse or within a braidplain, an environmentally heterogeneous setting, one that includes significant areas of disturbance (Naiman and Décamps, 1997).

The stand survived several subsequent floods and repeated influx of thin layers of sediment. Based on associated foliage, we believe these plants are most likely *Supaia thinnefeldioides*. Plant fossils occur in numerous exposures of Abo Formation (or equivalent) siltstone-sandstone sheet and channel-form deposits throughout central and southern New Mexico (Hunt, 1983; MacDonald, 1994; DiMichele et al., 2007). In almost all instances, the flora consists of either the conifer *Walchia* or the peltasperm *Supaia* in monotypic parautochthonous to allochthonous assemblages, subject to degrees of transport that are difficult to determine. This is, to our knowledge, the only in situ, autochthonous stand of plants reported from the Early Permian, not only from the Abo Formation but from anywhere in North America.

The plants show no evidence of deep rooting, instead appearing to have rooted adventitiously into the surrounding sediment, including new layers of sediment that were introduced in floods subsequent to initial plant-establishment. This kind of environment was subject to regular flooding disturbance of varying degrees of intensity, occasionally severe enough to kill local vegetation, as indicated by the truncation of the entire stand of *Supaia* stems by one of the flood layers. Height estimates of approximately 4.0 m, based on allometric calculations (Niklas and Spatz, 2004), suggest that these plants were little more than shrubs to small trees. The morphology of *Supaia* foliage, which is strongly xeromorphic (White, 1929), suggests multi-year leaf retention, consistent with growth in a habitat subject to extreme variations in moisture availability. These various lines of evidence suggest an opportunistic plant that colonized disturbed substrates, probably had a relatively short life span, and occurred in low diversity to monotypic stands. The channel-margin to braidplain setting provides ample opportunity for dispersal and colonization of flood-disturbed surfaces. What is perplexing is that more such stands of stems or stem molds of this type have not been seen—this may simply be a ‘search image’ matter, and more such discoveries might be expected.

As has been remarked on elsewhere (Hunt, 1983; DiMichele et al., 2007), the flora of the red-to-yellow Abo Formation siltstone-sandstone beds is of remarkably low diversity. The flora is best preserved in upward fining sheet siltstones, which are the main hosts for trace fossils and macrofossils, particularly where thin beds of siltstone are separated by clay partings or ‘drapes’. These clay-drape deposits are frequently mudcracked and bear raindrop imprints, strong evidence of alternating flooded and exposed conditions. The most commonly encountered fossils are branches and branch-fragments of conifers, most often *Walchia*, though *Ernestiodendron* also has been observed. These can occur as isolated specimens or as accumulations of multiple specimens, up to dense mats of material. *Supaia* foliage is more restricted in occurrence, but it too tends to occur in isolation of any other taxa, and vary from isolated leaves to dense accumulations. The uppermost Abo beds have revealed rare occurrences of other taxa such as callipterids and sphenopsids. These patterns of widespread monodominance appear to reflect the composition of the source vegetation and thus to have been drawn from low diversity assemblages. If most of the *Supaia thinnefeldioides* plants were colonists of disturbed streambanks or mudflats this may explain their patchy distribution, but it still fails to account for why they so rarely occur in mixed assemblages with conifers. Doubly perplexing are the seemingly identical depositional environments (as distinct from environments of growth), as far as we have been able to determine, of the deposits differentially dominated by conifers or *Supaia*. Based on the sizes of the conifer branches that have

been encountered, some nearly a meter in length, it appears that the conifers were considerably larger plants than the small, weedy *Supaia* plants reported here, which may be key to their generally distinct occurrences. *Supaia* may have preferred environments in periodically disturbed habitats, too consistently disturbed for conifers to survive to reproductive age.

The vertebrate trackmakers at the site are parareptiles and a relatively large temnospondyl amphibian. The aggregation of predatory parareptiles may reflect feeding on smaller animals such as arthropods, occurring among the *Supaia* trees. The amphibian clearly changed gait as it moved between trees. Thus, even though the vertebrates present were not herbivores, a case can be made for the presence of the *Supaia* trees affecting their behavior, and thus providing a rare ‘snapshot’ of a very localized setting of vertebrates and plants during the Early Permian.

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