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” 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 thinfeldiioides 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 (Limnopterus Marsh) and many of small predatory parareptiles (Dromopus Marsh). This study demonstrates that S. thinfeldiioides 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

REAL-TIME OR so-called T° 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 White, 1993; Gand et al., 1997; DiMichele et al., 2007). Such reconstructions, 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.

GEOL OGY SETT I NG

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
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 Chuchillo 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.
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...
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 thinnfeldoides*, 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
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.
(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.

Instead, 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*...
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 thimfeldioides*. 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 parataxonomous to allochthonous assemblages, subject to degrees of transport that are difficult to determine. These 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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