Abstract—A recently discovered tracksite in the Abo Formation in the Quebradas region of Socorro County is distinguished by unusually high ichnodiversity and exceptional preservation. This site, NMMNH (New Mexico Museum of Natural History) locality 12617, is north of Tinajas Arroyo in the Cañon de Espinoso Member of the Abo Formation, about 5 meters below the base of the overlying Yeso Group. The fossil-bearing stratum is a 0.7-1.5 m thick interval of thin-bedded, ripple-laminated, very fine sandstone with extensive mudcracks. At locality 12617, many surfaces with trace fossils have microbially induced sedimentary structures (MISS), and microbial mediation of preservation likely caused some of the exceptional ichnofossil preservation at this site. The invertebrate trace (ribbon trail) *Olivellites (= Psammichnites)* is reported here from the Abo Formation for the first time. Tetrapod ichnogenera from locality 12617 are *Amphisauropus*, *Batrachichnus*, *Dromopus*, *Dimetropus*, *Limnopus* and *Varanopus*. Plant specimens consist of the conifer *Walchia*, the peltasperm *Supaia*, and the calliperid *Autunia conferta*. *Walchia* and *Supaia* are typical of the Abo Formation throughout its extent; most Abo fossil plant sites are dominated by conifer remains of several types, but some fewer by *Supaia*. Mixed assemblages are uncommon. *Autunia conferta*, of the small-pinnule type, is common only in the upper Abo Formation (Cañon de Espinoso Member). The ichnofaunal composition at NMMNH locality 12617, which is dominated by anamniote, parareptile/eureptile and synapsid tracks, is very different from that of the *Erpetopus* biochron just above it. This is consistent with data from North America and Europe that identify a substantial change in the composition of footprint ichnoassemblages at the beginning of the *Erpetopus* biochron (close to the beginning of the Leonardian) due to the diversification of sauropod reptiles, likely driven by climate changes (drying) across much of Pangaea. Indeed, paleoenvironmental changes across the Abo-Yeso transition—regional marine transgression and a trend towards drier climates—are well reflected in the changes in trace fossil and floral composition during the early Leonardian.

INTRODUCTION

Early reviews of the lower Permian tetrapod footprint record in the American Southwest identified relatively uniform assemblages of ichnotaxa in red-bed facies, which constituted most of the *Dromopus* biochron of Lucas (2007). However, extensive work in the upper Abo-lower Yeso strata of central New Mexico, especially by Sebastian Voigt (e. g., Voigt and Lucas, 2017), and by one of us (SGL) in Texas (Haubold and Lucas, 2001, 2003; Lucas et al., 2011), indicated that a substantial change in the tetrapod footprint assemblages took place close to the beginning of Leonardian time. This change became the basis of the *Erpetopus* biochron, which succeeds the *Dromopus* biochron and extends well into middle Permian time (e. g., Voigt and Lucas, 2018; Marchetti et al., 2022). Relatively recently, the change in footprint assemblages has been tied to a change in climate that likely followed the final collapse of the ice sheets in Permian Gondwana (Marchetti et al., 2022).

Here we document a trace fossil assemblage and an associated fossil plant assemblage that sit right on the boundary between the *Dromopus* and *Erpetopus* biochrons. These assemblages are part of a regional change in the biota that was at least in part driven by paleoenvironmental changes across the Abo-Yeso transition. In this paper, NMMNH refers to the New Mexico Museum of Natural History, Albuquerque.

STRATIGRAPHY

The fossils reported here are from a site, NMMNH locality 12617, that is north of Tinajas Arroyo in the Cañon de Espinoso Member of the Abo Formation, about 5 meters below the base of the overlying Yeso Group (Fig. 1). The fossil-bearing stratum is a 0.7-1.5 m thick interval of thin-bedded, ripple-laminated, very fine sandstone with extensive mudcracks. This stratum is part of the upper part of the Cañon de Espinoso Member of the Abo Formation, a stratigraphic interval characterized by red-bed mudrock intercalated with laminar and ripple-laminar, sandstone sheets and a few calcrite ledges. The contact is straight to slightly wavy parallel striae that have a beaded surface structure and are clumped so that they are associated with (and often radiate outward from) small, semicircular, mound-like structures. These mound-like structures could be gas domes or raindrop impressions. The striaions bear some resemblance to *Monomorphichnus*.
VERTEBRATE FOOTPRINTS

Ichnotaxa

Amphisauropus kablikae

Footprints from NMMNH locality 12617 that we assign to *Amphisauropus* are well represented by NMMNH P-83700 (Fig. 3B) and P-83740 (Fig. 3C). P-83740 shows diagnostic features of *Amphisauropus* that include pentadactyl manus and pes; short digits; short manus “palm” imprint; and manus strongly rotated inward and pes imprints rotated outward. In P-83780 the manus imprint is 30 mm long and 55 m wide. In P-83740 the manus is 28 mm long and 55 mm wide, whereas the pes is 55 mm long and 60 mm wide. P-83700 only preserves four-digit imprints in the manus, which opens up the possibility it belongs to *Limnopus*, but we assign it to *Amphisauropus* largely because of its short “palm” imprint, so that the footprint is much wider than long (compare the dimensions to P-83740). Voigt and Lucas (2018) regarded *Amphisauropus* as monospecific, so *A. kablikae* is the ichnospecies assignment. The most likely trackmakers are anamniote reptilomorphs, especially Seymouriamorpha (Voigt and Lucas, 2015, 2017, 2018).

Batrachichnus salamandroides

NMMNH P-83742 (Fig. 3A) is an excellent example of *Batrachichnus* from locality 12617. It preserves about 18 footprints in concave epirelief that have a pentadactyl pes and tetradactyl manus. Manus lengths are 9-10 mm, and widths are 8-10 mm. Pes lengths are 12-15 mm, and widths are 10-12 mm. Other characteristic features of *Batrachichnus* include distally rounded, straight digits; manus imprints are as long as wide; manus digits are short, with III the longest, and IV shorter than II; pes imprints are longer than wide; and pes digit length increases from I to IV, with digit V shorter than digit II. Tracks of this ichnogenus were mostly made by small anamniote tetrapods, especially temnospondyls, though some *Batrachichnus* may have been made by “microrosaurs” (Stimson et al., 2012; Voigt and Lucas, 2015, 2017, 2018; Allen et al., 2022). *Batrachichnus* is monospecific (Voigt and Lucas, 2015), so the material from locality 12617 is assigned to *B. salamandroides*.

Dimetropus leisneranus

Only one specimen from locality 12617 can definitely be assigned to *Dimetropus*, NMMNH P-83697 (Fig. 4). This is a single pes track with a long, bean-shaped sole, a very long digit IV and much shorter and closely spaced digits II and III. Digit lengths are acute. Length is 90 mm and width is 28 mm, so this footprint is relatively small for a *Dimetropus* footprint. It closely resembles a pes impression of *Dimetropus* from the lower Permian Dunkard Group in Pennsylvania illustrated by
FIGURE 2. MISS and invertebrate trace fossils from NMMNH locality 12617. A, C, MISS in convex hyporelief, NMMNH P-83697A (A) and 83697B (C). B, *Olivellites*, NMMNH P-83737, in convex hyporelief.
Lucas et al. (2016, fig. 4). The size, digit proportions and long and ovoid sole impression are diagnostic of *Dimetropus*. We regard *Dimetropus* as monospecific (see Voigt and Lucas, 2017) and thus assign our material to *D. leisneranus*. *Dimetropus* is the track of most eupelycosaurs except for varanopids and derived caseids (Voigt and Lucas, 2015, 2017, 2018).

**Dromopus lacertoides**

The most common footprint ichnotaxon at locality 12617 is *Dromopus* (Fig. 5A-C). These are lacertoid tracks with a very slender, curved and acuminate digit impressions and an elongate digit IV. As is characteristic of *Dromopus*, the pentadactyl manus and pes imprints have a palm/sole that is short, and the digits are long, slender, and distally tapered. Digit length increases from I to IV. Digit IV is highly elongated. Our specimens fall into two size groups, those with pes impressions ~ 30 mm long and those with pes impressions ~ 50 mm long (Fig. 5). *Dromopus* is the track of various lizard-like Permian parareptiles and eureptiles such as bolosaurids and araeoscelids (Voigt and Lucas, 2015, 2017, 2018). The ichnogenus is monospecific, so we refer our specimens to *D. lacertoides* (Voigt and Lucas, 2015).

**Limnopus heterodactylus**

*Limnopus* is the tracks that are larger than but otherwise nearly identical to *Batrachichnus* except for the fourth digit of the manus imprint, which is about as long as digit II in *Limnopus*, but about as long as digit I in *Batrachichnus*. In addition, the digits are relatively shorter in *Limnopus*. At locality 12617, *Limnopus* is best represented by NMMNH P-83692 (Fig. 6), a trackway preserved in convex hyporelief with 3 pes and 2 manus tracks. Dimensions are pes length = 58 mm, width = 46 mm, and manus length = 43 mm and width = 49 mm. Thus, the manus is of nearly equal length and width, whereas the pes is distinctly longer than wide. Digits are short with rounded tips, and the manus is tetradactyl. This specimen bears comparison to *Ichniotherium*, but the tetradactyl manus supports assignment to *Limnopus*. *Limnopus* is monospecific, so we assign our specimens to *L. heterodactylus* (Voigt and Lucas, 2015). Potential trackmakers are large-size temnospondyls such as eryopids (Voigt and Lucas, 2015, 2017, 2018).

**Varanopus isp.**

*Varanopus* (Fig. 5D) is tracks of quadrupedal tetrapods with pentadactyl manus and pes imprints up to 45 mm long. The manus imprint is slightly wider than long, and the pes imprint is as long as wide and about one-fifth longer than the manus imprint. Digit length increases from I to IV, and in the pes imprint digit V is as long as II or III, but shorter than II in the manus imprint. All digits have acute distal ends (distinct claw impressions), and the palm/sole imprint is very short, about one-fifth of total imprint.
A small collection of plant fossils was obtained from locality 12617, and a single specimen from locality 12615, which is at the same stratigraphic level as 12617 and nearby. In combination, these plant-fossil assemblages are unusual, when considered in light of the many assemblages known from the Abo Formation across New Mexico (e.g., Hunt, 1983; DiMichele et al., 2007, 2013, 2015). Most Abo plant-fossil assemblages are dominated by walchian conifers, sometimes to the exclusion of other types of plants. *Supaia*, particularly *S. thinnfeldioides*, is of secondary abundance, and generally is found in different assemblages from the conifers and, where exposures reveal, in stream-side settings subject to periodic flooding and burial (DiMichele et al., 2012). However, in the Arroyo de Alamillo Formation and the upper Abo Formation, it is not unusual to encounter other kinds of plants, including callipterids.

The only specimen found at Locality 12615 is *Walchia* sp. (Fig. 7A). In contrast, Locality 12617 contains a more diverse assemblage, including three, and perhaps four, unusual, rarely encountered taxa, although none are well enough preserved for definitive identifications. These include a specimen that in gross morphology resembles *Yuania* or *Plagiozamites* (Fig. 7B), *Walchia* sp. (Fig. 7C - the specimen is partially obscured by sediment), small pinnuled pinnae that are possibly *Autunia conferta* (Fig. 7D-E), and a specimen that may be a marattialean fern or a callipterid (Fig. 7F). Among the specimens also is one of unusual morphology that appears to be a cluster of pinnae, perhaps at the end of an immature frond, which, under close examination, appears to be similar to the *Autunia conferta* specimens; this specimen is partially obscured by fine sediment, making identification difficult (Fig. 8).

**Paleobotanical Details**

The “typical” paleobotanical element identified in the two assemblages is *Walchia*, a conifer (Fig. 7A, C). Walchian conifers are characterized by leaves of various, but generally narrow, widths that are of sigmoidal shape (see Looy and Duijnste, 2013). The leaves were borne on plagiotropic branches that were regularly shed from the main stems, creating a great deal of branch litter (Looy, 2013), which is how the plant remains are generally preserved.

The single specimen illustrated in Figure 7B is morphologically ambiguous. Initially, we identified this specimen as most likely to be *Supaia* sp. Re-examination leads us to question this identification. The pinnules/leaves lack visible venation; however, there is no indication of a midvein, which, even without visible lateral veins, would be expected in *Supaia*, at least on some of the pinnules, due to its sunken character. In addition, the pinnules/leaves are straight sided throughout, showing tapering in the upper 1/4 to a bluntly pointed apex (Fig. 7B, arrow). Furthermore, the pinnules/leaves are attached close to right angles to the axis on which they are inserted. These are characteristics of noeggerathialeans, leading to the possibility that this specimen may be *Yuania* (e.g., Wang and Chaney, 2010), or some other form of noeggerathialean. The apex of the one pinnule on which it is preserved is similar to that of *Plagiozamites*, which is long studied and occurs widely geographically and stratigraphically (e.g., Bassler, 1916; Němejc, 1931; Feng et al., 2017). However, the venation in *Plagiozamites* terminates successively at the margin of the leaf; there is no such indication in this specimen.

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One of the specimens illustrated in Figure 7D-E resembles *Autunia conferta* of a small pinnuled variety (see variation illustrated in Kerp, 1988). The preservation of this specimen makes identification uncertain. However, the shape of the pinnules, broadly attached with decurrent bases and acuminate apices, suggests such an affinity.

The specimen illustrated in Figure 7F also may be a...
callipterid, possibly *Autunia conferta*. The pinnules are broadly attached and have well developed, sunken midveins, typical of this species. However, the pinnules have rounded apices and, to the degree visible, lateral venation that is not strongly ascendant (Fig. 7F, arrow). From another perspective, pinnule shape and venation are more like that found in marattialean ferns. This would be quite unexpected, based on what is known of the overall Abo Formation red-bed plant assemblages. Nonetheless, as noted above, the upper parts of the Abo Formation (and this continues into the lower parts of the Yeso Group) contain plant-fossil taxa that are atypical of the great majority of specimens encountered. Rare specimens from elsewhere in the Abo have been attributed to *Pecopteris* (an invalid name for marattialean foliage [Cleal, 2015] but, nonetheless, still widely in use for vegetative material), but even these specimens are of questionable identity.

One additional specimen was found in this collection that is of uncertain, possibly callipterid or tree-fern, affinity, illustrated in Figure 8A. Parts of this specimen are enlarged in Figures 8B and 8C. Partially covered with fine mud, the specimen is difficult to interpret. It appears to represent a palmate or closely inserted array of pinnae lined with small pinnules. The pinnules appear to be closely spaced, broadly attached, and with decurrent bases. They are straight sided and have truncated apices (assuming the apices are truly revealed and not downcurved into the sediment). A midvein appears to be present on many of the pinnules and it is deeply sunken, the pinnule laminae vaulted on either side of it. Lateral venation is not visible. As far as is possible to infer from this information, an affinity with the callipterids, possibly *Autunia conferta* seems more likely than with the marattialean ferns. In either case, the specimen may represent the terminal portion of a juvenile leaf that was not yet fully expanded.

**DISCUSSION**

Voigt and Lucas (2017) documented the turnover from the *Dromopus* biochron to the *Erpetopus* biochron in central New Mexico. Here, the stratigraphically lowest footprint assemblages of the *Erpetopus* biochron are in the uppermost
FIGURE 7. Plant specimens from NMMNH localities 12615 (A) and 12617 (B-F). 

A, Conifer Walchia sp. NMMNH P-83741. 

B, Unique specimen of uncertain affinity, possibly noeggerathalean. Arrow points to what is possibly a pinnule/leaf tip. NMMNH P-833701. 

C, Conifer, Walchia sp. Specimen is partially covered with fine sediment. NMMNH P-83693. 

D, Callipterid, cf Autunia conferta. Apical region enlarged in image E, NMMNH P83696. 

E, Specimen of uncertain affinity. Pinna with pinnules. Possibly A. conferta or a marattialean fern. Arrow points to region of the pinna where pinnule venation is vaguely visible. NMMNH P83694. 

Scale bars = 1 cm.
5 m of the Abo Formation. This is a point in earliest Leonardian time, likely latest Artinskian (Lucas et al., 2022). Footprint ichnoassemblages of the *Dromopus* biochron in central New Mexico are dominated by the footprints of temnospondyls (*Batrachichnus*, *Limnopus*), reptiliomorphs (*Amphisauropus*, *Ichniotherium*), pelycosaur-grade synapsids (*Dimetropus*, *Tambachichnium*), and parareptiles/eureptiles (*Dromopus*). Obviously, the locality 12617 footprint ichnoassemblage belongs to the *Dromopus* biochron. The footprint ichnoassemblages of the *Erpetopus* biochron are defined by the first appearance of *Erpetopus* and are dominated by eureptile tracks, especially *Varanopus* and *Erpetopus*.

Abo trace and plant fossil assemblages are of fairly consistent composition through most of the Abo Formation—footprints of the *Dromopus* biochron, invertebrate traces dominated by arthropod walking traces (*Diplichnites*, etc.) and floral assemblages dominated by walchian conifers and/or *Supaia* (e.g., DiMichele et al., 2007; Minter and Braddy, 2009; Voigt and Lucas, 2015, 2017). However, this changes in the uppermost Abo-lower Yeso stratigraphic interval. We posit that at least some of these changes reflect two regional paleoenvironmental changes that began late during Abo deposition: (1) a marine transgression from the seaways to the south; and (2) the onset of a drier climate (Mack and Dinterman, 2002; Mack, 2003; Lucas et al., 2013a, b) (Fig. 9). In the Cerros de Amado-Mesa del Yeso area of Socorro County, note the following:

1. The locality documented here, 12617, is the stratigraphically highest known *Dromopus* biochron footprint site, and it is very close to the same stratigraphic level as the oldest *Erpetopus* biochron sites, which are NMMNH localities 3037, 8176, and 8177, in the interval 3-5 m below the Yeso base (Voigt and Lucas, 2017, fig. 2).
2. There is a relatively high abundance of MISS in this interval, and MISS are generally most common in nearshore marine to shallow marine settings (Noffke, 2010). Notable is the MISS at locality 12617 as well as the occurrence of the pseudofossil Astropolithon, a biomat ruptured by a gas dome, 7 m below the Yeso base at NMMNH locality 8771 (Lerner and Lucas, 2017; Lucas and Lerner, 2017).
3. The trace fossil assemblage reported by Minter and Lucas (2009) is dominated by the traces *Cruziana* and *Rusophycus*, rarely seen stratigraphically lower in the Abo-Yeso section. Minter and Lucas (2009) considered this assemblage to be from the uppermost Abo Formation, but stratigraphic restudy places it at least 5 m above the Yeso Group base (Lucas and Krainer, 2017) (Fig. 9). Minter and Lucas (2009) suggested that this is a freshwater trace fossil assemblage, but the abundance of ribbon traces such as *Cruziana* may be suggestive of some marine influence. *Olivellites*, a characteristically marine trace, is present at locality 12617.
The plant remains found in red beds of the Abo Formation or its stratigraphic correlates are remarkably compositionally consistent, and of low diversity, throughout most of the state from areas in the south, near Alamogordo and Las Cruces, to northern exposures in the Zuni Mountains. The dominant elements are consistently walchian conifers of several kinds and the peltasperm Supaiata thinfeldioides. Deviations from this floral monitory are found in the upper red beds, near the transition to the Yeso Group. Locality 12617 from these upper red beds, epitomizes these later floras in the presence of a number of suspected rare elements, such as Autunia, which is found at a number of upper Abo locations, but also the plant remains with a possible noeggerathiallean affinity. The latter is consistent with other rare, unusual plant occurrences in these strata.

The upper Abo Formation gives no indication of major changes in landscape architecture, such as elevational heterogeneity. A large coastal plain of flat aspect appears to have persisted throughout Abo deposition. Given that plants, in particular, are sensitive indicators of physical conditions, the appearance in the upper Abo Formation and lower Yeso Group of new kinds of plants intermixed with conifers and supaioids, suggests changes of a regional nature involving climate, which is what plants would have perceived. The ultimate cause of such changes, as addressed above, may be a change in marine proximity, or reflect a more distant factor, such as a change in atmospheric circulation, brought on by northward drift of the region or tectonic factors affecting airflow patterns.

The Abo Formation in New Mexico is equivalent to strata to the east in Texas that record a much more diverse biota of plants and animals. The significant difference between these parts of western Pangea indicate major regional differences in physical conditions. Those elements of flora in New Mexico represent a subset of what is found in Texas. In New Mexico there is a greater representation of supaioids, a lower representation of peltaspermous plants such as gigantopterids and callipterids, and an almost total absence of such otherwise widespread plants such as pteridosperms, marattialean tree ferns, and calamitaleans, with a diversity of conifers found in both areas. Given that Texas appears to be the more humid of these two regions, the appearance in the upper Abo Formation of greater diversity, including plants found more commonly to the east, suggests a brief period of increase in regional humidity, within an overall drying trend.

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