STOP 2

DINOSAUR FOOTPRINTS FROM THE GLEN ROSE FORMATION (PALUXY RIVER, DINOSAUR VALLEY STATE PARK, SOMERVELL COUNTY, TEXAS)

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INTRODUCTION

Dinosaur footprints are found in the Glen Rose Formation and other Lower Cretaceous stratigraphic units over much of central Texas (Pittman, 1989; Rogers, 2002; Farlow et al., 2006). Dinosaur tracks were discovered in the rocky bed of the Paluxy River, near the town of Glen Rose, Texas, early in the 20th Century (Jasinski, 2008; Farlow et al., 2012b). Ellis W. Shuler of Southern Methodist University did pioneering studies on the dinosaur tracks (Shuler 1917, 1935, 1937), and Langston (1974) summarized much of the early literature.

What really put the dinosaur footprints of the Paluxy River on the map, though, were the herculean efforts that Roland T. Bird of the American Museum of Natural History made to secure trackway slabs for display at that institution and at the Texas Memorial Museum in Austin (Bird, 1985; Jasinski, 2008). In 1970 Dinosaur Valley State Park was created to protect the dinosaur footprints.

This guidebook briefly summarizes earlier work, and also serves as an interim report of research of our group still in progress, concerned with identifying the makers of the Paluxy River footprints, and determining what those animals were up to as they made their tracks. We will offer some comparisons of the dinosaur tracks of the Glen Rose Formation with those from other ichnofaunas around the world. The last quarter-century has seen an explosive increase in the technical literature dealing with dinosaur footprints, and we cannot possibly cite all of the relevant studies. For the sake of brevity we will emphasize publications from the present century, and summary papers and books, as much as possible. Even with this restriction, however, the literature is so vast that the literature-cited "tail" of this report starts to wag the "dog" of the text.

GEOGRAPHIC AND STRATIGRAPHIC OCCURRENCE OF TRACKSITES

As the Paluxy River flows eastward across Somervell County, Texas toward its eventual junction with the larger Brazos River, it makes a northerly and then a southerly loop west of the town of Glen Rose (Fig. 1A). Much of the northern loop is within the boundaries of Dinosaur Valley State Park. The river has cut into rocks of the Trinity Group, and the main track occurrences are in the lower member of the Glen Rose Formation (Fig. 1B; within the town of Glen Rose itself, well away from the river, there is an interesting dinosaur tracksite much higher in the section [Blair et al., 2012a, b]).

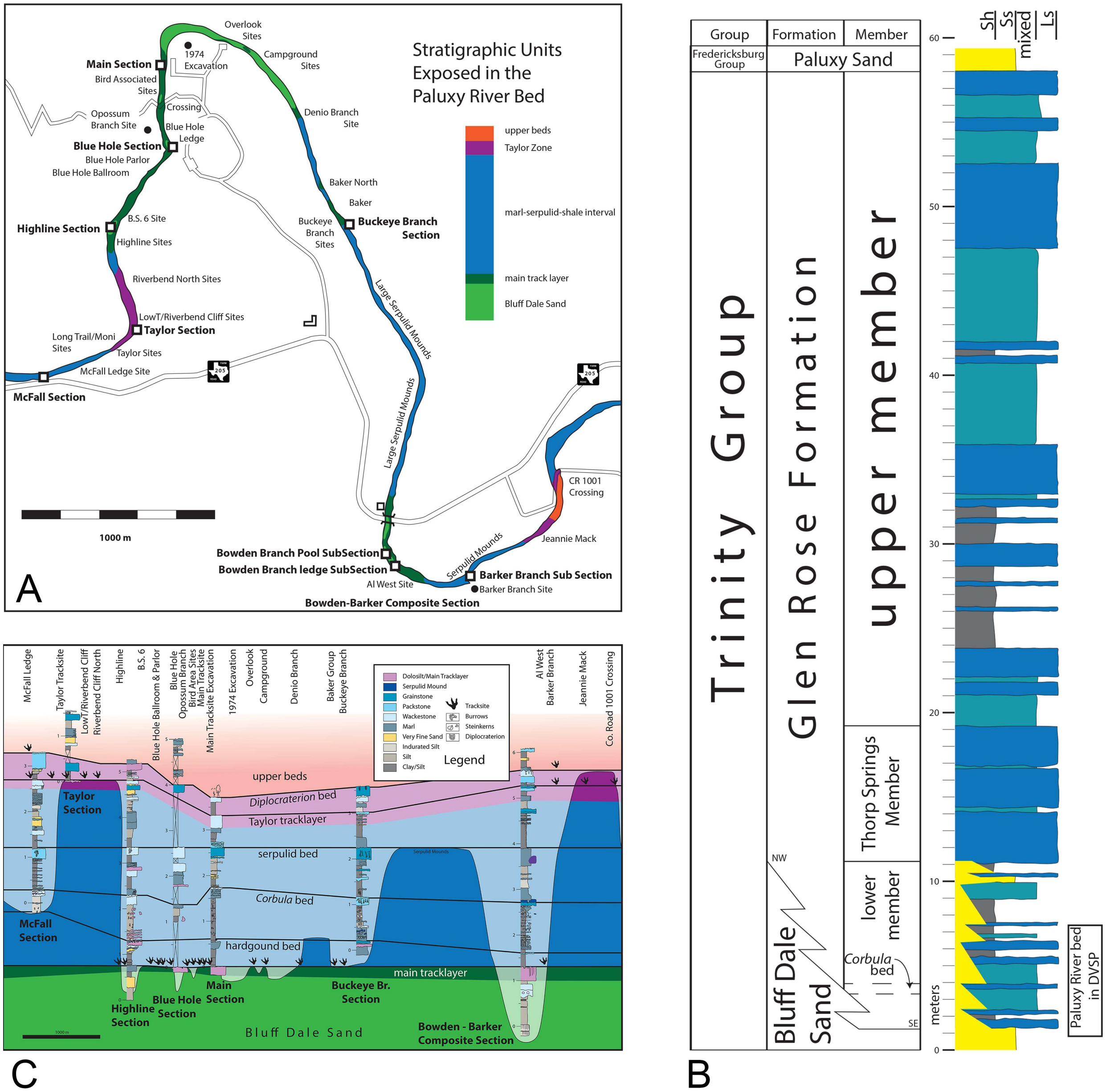


FIGURE 1. Location and stratigraphic occurrence of major Paluxy River dinosaur tracksites and other significant sites (Dattilo et al., 2014); **A**, the river flows from right to left as shown here. Individual horizons exposed in the river bed coded by color. **B**, the Glen Rose Formation stratigraphic section in the Glen Rose region. The tracklayers in and around Dinosaur Valley State Park are in the lower member of the formation; **C**, correlation of the footprint-bearing and other layers; dinosaur tracks occur in the Main Tracklayer, the Taylor Tracklayer, and the *Diplocraterion* bed.

The stratigraphy and sedimentology of the local section has been described in considerable detail (Dattilo et al., 2014 and references therein), and so will receive only brief treatment here, emphasizing the dinosaur trace fossils. Dinosaur footprints have been found at three levels over a roughly 6-meter interval in the lower member of the Glen Rose Formation, separated by beds containing a diverse benthic marine paleobiota (Feldman et al., 2011; Dattilo et al., 2014; Martin et al., 2015). The track-bearing intervals are designated the Main Tracklayer, the Taylor Tracklayer, and the *Diplocraterion* bed. The units in the Paluxy River section are not perfectly flat, but gently undulate up and down along the length of the river (Fig. 1C).

Fieldwork on the Paluxy's tracksites is not without challenges. During rainy weather the tracksites may be underwater for days or weeks on end, and at times the river flow may be so deep and fast as to be dangerous. Measuring and photographing footprints underwater can be tricky. During the summer, if water levels are high enough to cover the tracks, as temperatures warm in the afternoon, breezes begin to blow, creating ripples on the water through which the footprints are difficult to see. During dry spells the river may break up into a series of isolated pools. Wading around the prints at such times will kick up sediment that takes several minutes to settle out, and the rock surfaces underwater are very slippery. At those times when the river is almost or completely dry, air temperatures may shoot above the century (Fahrenheit) mark. Snakes are common in the river, and some of them are venomous, but this merely adds to the fun.

DISTINCTIVE FEATURES OF PALUXY RIVER TRACKSITES

Main Tracklayer (Figs. 2, 3A-G)—This unit is a 10-30 cm thick, homogeneous, sandy dolomitic wackestone (Dattilo et al., 2014). The surface of the unit is thickly dotted with small, U-shaped *Arenicolites* burrows, presumably made by benthic crustaceans or polychaetes (Figs. 2H, 3E, 5B, F, 6). R. T. Bird's trackway quarry was in this unit (Figs. 2A-E), and all of the unambiguous sauropod trackways occur in the Main Tracklayer (Figs. 2-4). Particularly impressive tracksites (Fig. 1A) occur in a stretch of river between the Main Tracksite and a rough road crossing to the south of Bird's quarry site (most of which is shown in Fig. 2A), at the Blue Hole, the Blue Hole Ballroom, and at the mouth of Denio Branch. However, many of these sites are often underwater or covered by coarse river sediment, and the Denio site is being actively eroded by the river.

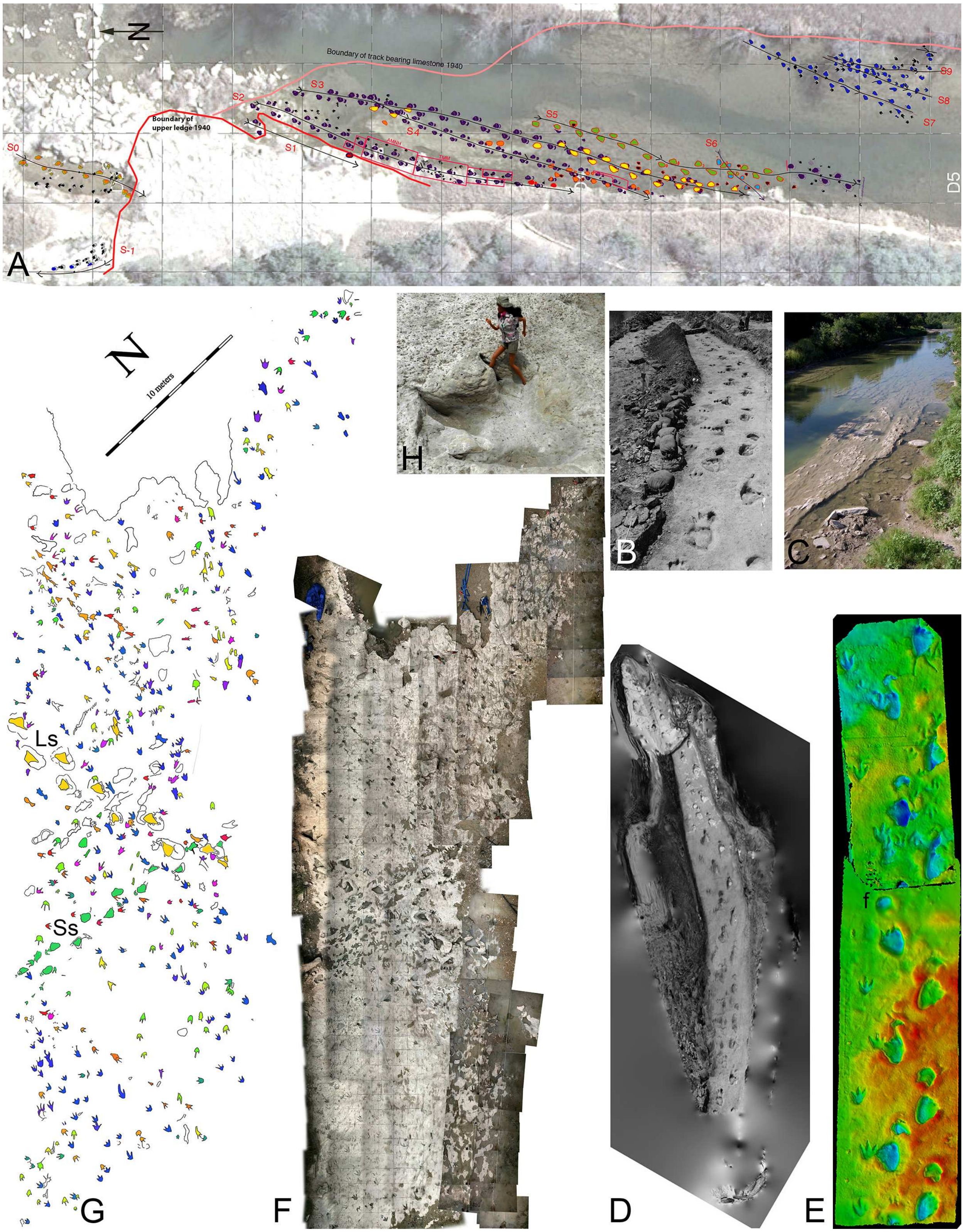
Dinosaur footprints in the Main Tracklayer are often quite deep (up to c. 25-30 cm), and some tracks pass through the layer to the underlying Bluff Dale Sand. The trackmakers had themselves to have been carrying most or all of their body weight, without being buoyed up by water, in order to make such deep footprints.

However, there are some intriguing prints that suggest that their makers were floating or swimming. One of these is a set of two parallel slash marks in the rock at the west bank portion of the Main Tracksite (Fig. 3E, F). These are claw marks only, and decrease dramatically in depth from one end to the other. Footprints attributed to swimming (or possibly swimming) bipedal dinosaurs have been described from a number of tracksites around the world (Whyte and Romano, 2001; Farlow and Galton, 2003; Moreno et al., 2004; Milner et al., 2006a, b; Ezquerra et al., 2007; Xing et al. 2011b, 2013a; Fujita et al., 2012; Romilio et al., 2013; Lockley and Tempel, 2014; Lockley et al., 2014b), and some of these are very similar to the prints described here. A second interesting set of traces consists of a discontinuous series of arcuate slash marks at one end of part of the Main Tracksite (Fig. 3A, G), also possibly made by a swimming animal.

If the Main Tracklayer contains footprints of both floating and walking dinosaurs, then water depth fluctuated (by a few meters?) over the interval during which it recorded footprints. Small but densely populated U-shaped burrows (*Arenicolites*) on the top surface of the Main Tracklayer also indicate a subaqueous environment, as these likely belong to suspension feeders. These burrows must have preceded the dinosaurs, though, as they are compressed within or otherwise deformed by the tracks.

Another interesting feature of the Main Tracklayer is a common mode of preservation of tridactyl prints in which the toe marks penetrate the rock further forward beneath the surface of the rock layer than at the surface, forming "toe tunnels" (Fig. 3D), suggesting a rather plastic consistency of the sediment at the time the tracks were made; Farlow has found it entertaining to watch little fishes swimming in and out of such tunnels, but he is of course very easily amused. Footprints of this kind may indicate something about the kinematics of the foot-substrate interaction of mud-slogging bipedal dinosaurs (cf. Platt and Meyer, 1991; Avanzini et al., 2012; Huerta et al., 2012; Falkingham and Gatesy, 2014). In some tridactyl footprints from the Main Tracklayer there was backflow of sediment into footprints, and even complete collapse of footprints,

FIGURE 2 (next page). Distinctive features of the Paluxy River Main Tracklayer; **A**, View of the Main Tracksite area (left: GPS 32.25324, -97.81883), the Bird Site (middle: 32.25260, -97.81869), and the East Bank (Ozark) Site (32.25221, -97.81856), with R. T. Bird's Rye Chart (Farlow et al., 1989) and other trackway maps superimposed (modified from Farlow et al., 2012). Individual sauropod trackways labeled S0 – S9. Much of the track-bearing bed in the river channel has been destroyed by erosion since 1940; **B – E**, R. T. Bird's sauropod-theropod "chase sequence"; **B**, 1940 Bird photograph of the two trackways; **C**, location of Bird's quarry along the west bank of the river; **D**, digital reconstruction of the two trackways in plan view created from Bird's photographs (Falkingham et al., 2014); **E**, digital model of a portion of the two trackways, created by LiDAR scanning of the American Museum slab (bottom, below seam) and the Texas Memorial Museum slab (above seam). The final sauropod manus print in the American Museum slab (f) is a fabrication; the actual manus is seen immediately above the seam in the Texas Memorial Museum slab; **F**, **G**, photomosaic and interpretive map of the Blue Hole Ballroom (32.24777, -97.81913). Note prints of a large sauropod (Ls) moving diagonally from left to right as illustrated here, and a small sauropod (Ss) moving diagonally from right to left; **H,** large theropod footprint showing distinct claw marks. Note numerous *Arenicolites* burrows. Paleontologist Dr. Barbara Mattel is about 30 cm tall.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after the footprint was lifted from the substrate. Very commonly, but not always, there is a linear gash at the rock surface indicating where the mud squeezed together after a toe was withdrawn from the sediment. The surface expression of roofed over and collapsed footprints can give the misleading impression of toe marks that are short, broad, and blunt, which has led to misidentification of theropod footprints as those of ornithopods.

Taylor Tracklayer (Figs. 3H-J, 5G-M)—This grainstone is about 6 meters stratigraphically above the Main Tracklayer. It crops out in the river bed at and above the upstream end of Dinosaur Valley State Park, and again downstream of the Main Tracklayer exposures, beyond the park boundaries (fig. 1A). In places it consists of a series of very thin beds. Mudcracks and/or microripples are present, but the huge *Arenicolites* aggregations so typical of the Main Tracklayer are absent.

The Taylor layer contains numerous trails of elongate tracks with metatarsal impressions, many of which are largely infilled with a bluish-grey secondary sediment, which oxidizes to rusty-brown upon exposure (Kuban, 1989a, b). The infillings reduce the topographic relief of these tracks (Fig. 3H-J), sometimes leaving indistinct oblong depressions, which under some viewing conditions can resemble human tracks (Fig. 3I), an illusion often mistaken as real by creationists. However, when well cleaned, and especially clean and wet, the contrasting color and texture of the infilling material clearly demarcates the original track shapes and tridactyl digit patterns (Fig. 3H, J, 5K, L). Cores taken at the margin of the infillings show that the original tracks were several cm deep before the infilling episode. Some of the well oxidized infillings have become harder than the surrounding rock, causing the limestone to erode around them, creating “raised” relief (Fig. 5K).

As with the Main Tracklayer, tridactyl footprints of bipedal dinosaurs are most common, and possibly include ornithopod (Fig. 3J) as well as the usual theropod footprints. Sauropod footprints are at best rare. Tridactyl footprints sometimes occur in very long trackways (e.g. Fig. 5H), and relatively small tridactyl prints (Fig. 5I, J) are prominent at some sites.

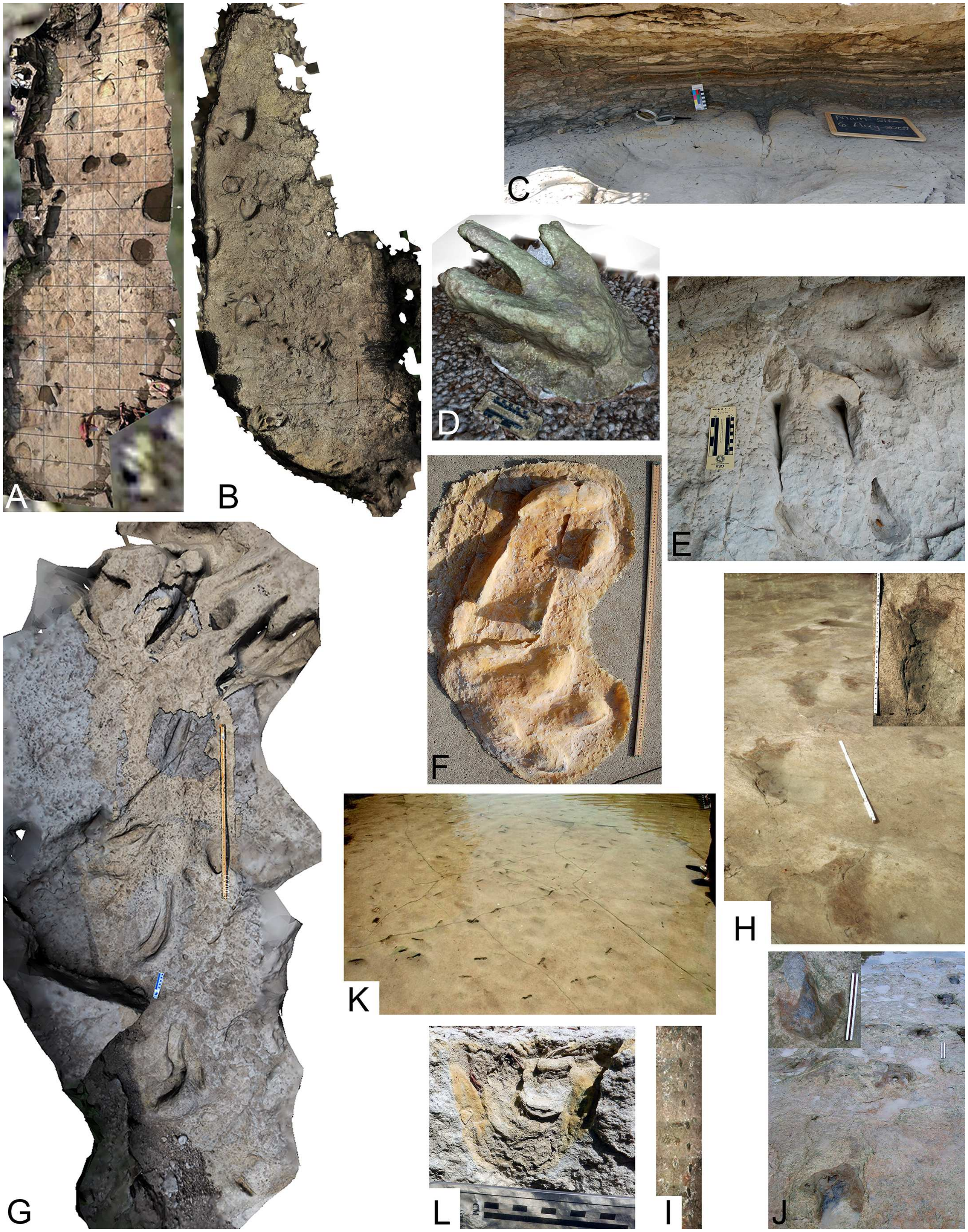
***Diplocraterion* Bed** (Fig. 3K, L, 5N)—Immediately above the Taylor Trackway is one of the most fascinating units of the local section, a resistant packstone dominated by large, U-shaped *Diplocraterion* burrows (Martin et al., 2015). Like the smaller *Arenicolites* of the Main Tracklayer, the *Diplocraterion* traces were probably made by benthic worms or crustaceans (Martin, 2013; Martin et al., 2015), but whether by larger individuals of the same species as the *Arenicolites*-maker, or a different form, is unknown. Only one dinosaur trackway is presently known from this unit, a series of morphologically nondescript tridactyls at the McFall Ledge Site (Figs. 1, 5N).

TRACKS AND TRACKMAKERS

Sauropods (Figs. 2, 3A, B, 4)—These are, of course, what caught R. T. Bird’s attention (Bird 1985 and references therein), and made the Paluxy River tracksites famous. Sauropod trackways are abundant in the Main Tracklayer, although even in that unit there are many more trackways of tridactyl dinosaurs.

Well-preserved manus prints have a double-U or horseshoe shape (Fig. 4F), and are deepest around the medial, anterior, and lateral rim, and shallowest at the center of the back part of the print. Bird made the

FIGURE 3 (next page). Distinctive features of the Paluxy River exposures. **A – G**, additional features of the Main Tracklayer. **A**, photomosaic of the portion of the Main Tracksite containing sauropod trackway S0 (Fig. 2, panel A) with 1-meter grid; south toward the top. A set of interesting arcuate traces (panel G) are seen at the top end of the image; **B**, digital model of the west bank portion of the Main Tracksite, with north toward the top of the image. The footprints shown in panels D – F are located toward the bottom of the model as shown here. Note unusual trackway of a northbound sauropod (animal [S-1], Fig. 2A); **C**, tridactyl footprint emerging from beneath overlying beds at the west bank portion of the Main Tracksite; **D**, digital model of a negative copy (cast) of a large tridactyl print (scale faintly visible at bottom of image) from near the south end of the west bank portion of the Main Tracksite. The toe marks punch deeply forward as tunnels into the rock; **E, F**, possible print of a swimming dinosaur (?) at the south end of the west bank portion of the Main Tracksite; **E**, the print in situ, shown as two parallel slashes in the rock to the right of the scale. Also note numerous *Arenicolites* traces (small dots in the rock surface); **F**, negative copy (cast) of the track and associated features. Note the triangular shadows associated with the slash marks, indicating that the trackmaker’s toes poked deep into the substrate before being pulled progressively more shallowly backward; **G,** digital model of discontinuous arcuate traces near the south edge of a portion of the Main Tracksite (near sauropod trackway S0 at the top of panel A). Meter stick provides scale; **H – I**, sequences of elongate footprints of bipedal dinosaurs, Taylor Tracklayer, Taylor Site (32.23842, -97.82181); **H**, particularly nice trackway; inset is overhead view of one of the prints; **I**, photomosaic of the classic “man track” trackway of creationists (Kuban 1989a, b) at a time when the color distinctions marking the toes were not distinct (cf. Fig. 5L for the same trackway viewed under ideal conditions); **J**, possible ornithopod trackway from the Taylor Site (inset is overhead view of single footprint); **K – L**, *Diplocraterion* traces, *Diplocraterion* bed. **K**, traces in surface view upstream (32.24237, -97.82119) from the Low T/Riverbend Cliff Site; **L**, vertical section through burrow at the Buckeye Branch Site (32.24433, -97.80690).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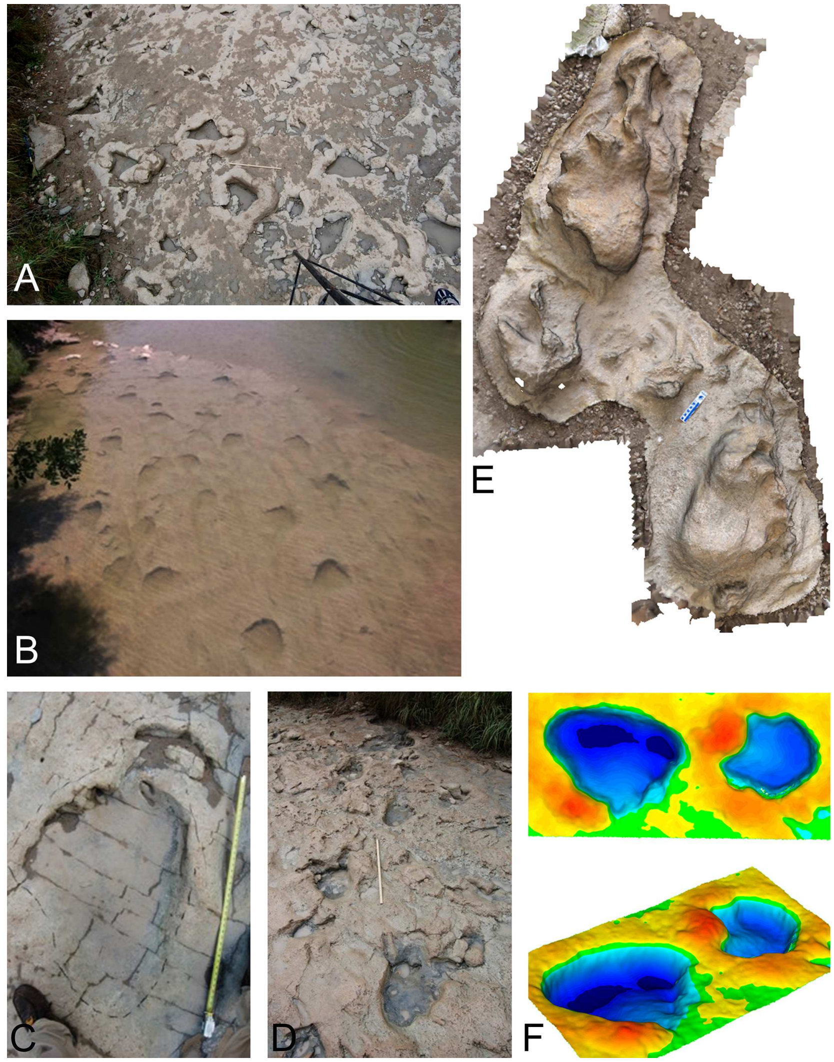


FIGURE 4. Sauropod trackways; **A**, pes-only footprints of a large sauropod with conspicuous pressure ridges (Fig. 2F, G), and numerous associated tridactyl prints, Blue Hole Ballroom; **B**, three sauropod trackways (moving away from the viewer), East Bank (Ozark) Site. The trackway on the right is pes-only; **C**, Left manus-pes set, Bird Site (1 meter of tape is exposed). The manus is rather poorly preserved; **D, E**, portion of the trackway of a small sauropod, Blue Hole Ballroom (Fig. 2F, G); **D**, the trackway in situ; **E**, digital model of a negative copy (cast) of part of the trackway, with an associated tridactyl print. Note distinct claw or nail marks along the front and lateral margins of the pes prints; **F**, digital model showing depth distribution of very well-preserved right manus-pes set from the American Museum slab. The manus print is deepest along its front and its medial and lateral margins. The pes is deepest along its inner margin, and is as deep or deeper than the manus print.

reasonable suggestion that digits II-IV of the forefoot were bound together by soft tissue, and offset from digits I and V. There is no suggestion of a claw mark on digit I. Commonly, however, manus prints were distorted during emplacement of the hindfoot. Sometimes the sediment squashed the manus print from the rear, causing it to be little more than a semicircular mark or depression (Figs. 4B, C), and sometimes the pes overprinted and obliterated the manus print (Figs. 4A, B).

The hindfoot print is larger (as much as a meter or more in length) than the forefoot print, and is roughly triangular in shape. In well-preserved pes prints, there are three or four laterally-directed claw marks, and a nubbin mark corresponding to digit V (cf. Tschopp et al., 2015). Pes prints are deepest on the inner side of the print, particularly near the base of the mark for digit I and at the heel of the print (Fig. 4F), and pes prints are always as deep as, or deeper than, manus prints. There are often conspicuous displacement rims (pressure ridges) around the edge of pes prints (Figs. 4A, C, 5F). The outer edge of the pes print defines the outer edge of Paluxy sauropod trackways, and usually the inner edge of pes prints does not intersect the trackway midline (Figs. 2E, G, 4A, B, D, E).

R. T. Bird had hoped to describe his sauropod footprints under the name *Brontopodus*, but did not live to do so, and so Farlow et al. (1989) named these trace fossils *Brontopodus birdi* in his honor. Being a railroad enthusiast, Farlow (1992) characterized *Brontopodus* trackways as wide-gauge, in contrast with some other sauropod trace fossils (e.g. *Breviparopus*) that were dubbed narrow-gauge, but noted that the difference was more degree than kind. The distinction was further developed by Lockley et al. (1994), who suggested that narrow-gauge and wide-gauge sauropod trackways differ in relative size of manus and pes prints as well as in relative trackway width. Wilson and Carrano (1999) proposed that wide-gauge sauropod trackways could be interpreted as having been made by titanosaurs and their

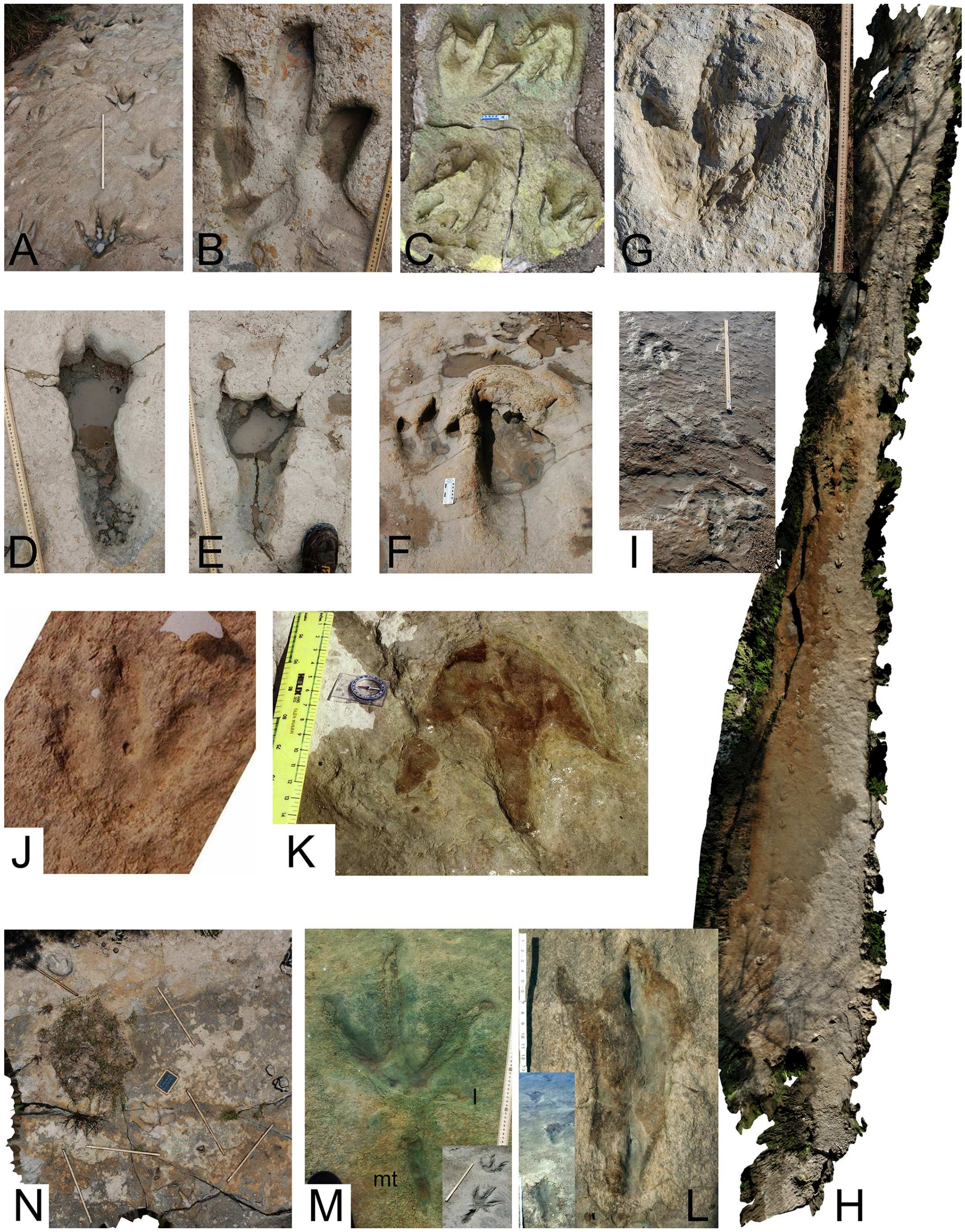


FIGURE 5. Tridactyl footprints. Meter stick (or portions thereof) provides scale in most images; **A – F**, footprints in the Main Tracklayer; **A**, well-preserved theropod prints near the south end of the Blue Hole Ballroom (Fig. 2F, G); **B**, large theropod footprint, Blue Hole. Note the many dot-like indentations in the rock surface (*Arenicolites* traces), a characteristic feature of the Main Tracklayer; **C**, digital model of negative copy of four well-preserved theropod prints, Opossum Branch Site; **D – E**, elongate tracks, Blue Hole Ballroom. Note suggestion of three toe marks at the ends of the prints, and the lack of any suggestion of a digit I mark; **F**, large theropod print associated with sauropod pes print, Bird Site; **G – M**, footprints in the Taylor Tracklayer; **G**, positive copy of single footprint of large theropod, part of the long trackway illustrated in panel H; **H,** digital model of the McFall Ledge site (32.23733, -97.82449), showing a long trackway of a large theropod; **I**, sequence of footprints of a small bipedal dinosaur, Dattilo Station 754 (32.24230, -97.82122); **J**, individual small (length 25 cm) tridactyl print, Low T/Riverbend Cliff Site (32.23990, -97.82023); **K - L**, color-delimited tridactyls, Taylor Site; **L**, footprint from the classic "man track" sequence under ideal viewing conditions, showing tridactyl nature (Fig. 3H); inset shows portion of the trackway; **M**, very large elongate print with metatarsal (mt) and digit I (I) impressions, Low T/Riverbend Cliff; inset shows oblique view of the same print and another nearby large tridactyl; **N**, digital model of medium-sized tridactyl dinosaur trackway, *Diplocraterion* bed, McFall Ledge site. The animal marches diagonally from lower right to upper left across the image. A rectangular gap marks where a single footprint was removed from the trackway by a person unknown.

close relatives. Trackway gauge continues to be reported in descriptions of sauropod ichnites, albeit with modifications, reservations, and recognition that the differences between narrow- and wide-gauge trackways are not hard and fast (Dalla Vecchia et al., 2000; Lockley and Meyer, 2000; Lockley et al., 2002a, b, 2004, 2006b, 2008, 2014e; Marty et al., 2003, 2006; 2010, 2013; Romano and Whyte, 2003; Meijide Fuentes et al., 2004; Moreno and Benton, 2005; Pascual Arribas et al., 2005; Wright, 2005; Le Lœuff et al., 2006; Zhang et al., 2006; Mezga et al., 2007; Romano et al., 2007; Bessedik et al., 2008; González Riga and Calvo, 2009; Moratalla, 2009; Pieńkowski et al., 2009; Santisteban et al., 2009; Santos et al., 2009, 2015; Xing et al., 2010, 2011a, 2013c, 2014a, 2015a, b, d, e, 2016; Castanera et al., 2011, 2012; Diedrich, 2011; Kim and Lockley, 2012; Masrour et al., 2013; Schumacher and Lockley, 2014; Fernández-Baldor et al., 2015; González Riga et al., 2015; Mesa and Perea, 2015; Pérez-Lorente, 2015; Tschopp et al., 2015); de Valais et al. 2015; Xing 2015c, f).

Identifying the kind(s) of sauropod responsible for Paluxy River *Brontopodus* has turned out to be more challenging than first thought. The trackmaker was initially—and without any great enthusiasm--interpreted as *Pleurocoelus* (Langston, 1974; Gallup, 1989; Farlow et al., 1989; Pittman, 1989; Farlow, 1992). Over the following years, a greater diversity of sauropod candidates for the Paluxy trackmaker turned up. *Sauroposeidon* was described by Wedel et al. (2000a, b), and then the Texan formerly known as *Pleurocoelus* was given the splendid name *Paluxysaurus* (Rose, 2007), only to have that name turn out (bummer!) to be a likely junior synonym of *Sauroposeidon* (D'Emic and Foreman, 2012; D'Emic, 2013). By latest tabulation, there may be as many as three distinct sauropod taxa in the Trinity Group and correlative units in the region, with the genera *Astrophocaudia* and *Cedarosaurus* as well as *Sauroposeidon* (D'Emic, 2013). So which of these skeletal taxa (if any) was the *Brontopodus*-maker, or whether more than one of them was responsible for such trackways in the Glen Rose Formation, remains to be determined (if it can be). However, it is worth noting that the pes of *Cedarosaurus* (Gallup, 1989, D'Emic, 2013) seems to match the morphology of the Paluxy River sauropod hindfoot prints. The phalangeal skeleton of *Sauroposeidon* and *Astrophocaudia* is unknown.

The Paluxy River sauropod footprints may have implications for interpreting some distinctive sauropod trace fossils from other sites. R. T. Bird (1985 and references therein) saw a sauropod trackway from the Glen Rose Formation on the Mayan Ranch in South Texas that consisted mainly of manus prints. He concluded that the trackmaker had been half-floating, pulling itself along by its forefeet, its hindquarters supported by the water. Lockley and Rice (1990) proposed an alternative hypothesis: that manus-only and manus-dominated sauropod trackways are artifacts of undertrack formation. Walking sauropods are interpreted as having carried a greater concentration of weight per unit surface area on the sole of the manus than on the pes, such that deformation of sediment layers beneath that on which the dinosaurs trod was effected only by impression of the manus. Most (Vila et al., 2005; Lockley 2014c, e; Falkingham et al., 2011, 2012), but not all (Ishigaki and Matsumoto, 2009) workers have supported the undertrack hypothesis, and for most sauropod manus-dominated trackways the present authors also find it compelling.

But perhaps not for sauropod trackways from the Glen Rose Formation. In sauropod trackways from the Paluxy River and elsewhere in Texas that preserve both manus and pes prints, hindfoot prints are always as deeply impressed, or more deeply impressed, than manus prints (Fig. 4F), an observation inconsistent with differential autopodial pressure as the sole explanation for manus-dominated trackways (Farlow et al., 2012a). Conceivably such trackways were in fact made by wading or punting sauropods (Wilson and Fisher, 2003; Henderson, 2004).

Bipedal dinosaurs—Even in the Main Tracklayer, but especially in the Taylor Tracklayer, tridactyl footprints of bipedal dinosaurs numerically dominate the Paluxy River ichnofauna (Figs. 2F, G, 5, 6). Well-preserved large (c. 45-55 cm long) tridactyls (Fig. 5A-C, F-H, 6) have long, narrow toe marks, often with indications of sharp claw tips (Fig. 2H). The digit III impression sometimes shows a slight sigmoidal curvature along its length (Fig. 6). These footprints sometimes preserve indications of digital pads, but not often. Compared with skeletal taxa, these trackmakers would have been comparable in size to large allosaurs and medium-sized tyrannosaurs (Fig. 7C).

In addition to the large tridactyls, there seems to be a second concentration of smaller footprints (c. 25-40 cm long) that is particularly evident in the Taylor Tracklayer (fig. 5I, J) and the *Diplocraterion* bed (Fig. 5N). If their makers were theropods, they would have been roughly the size of *Dilophosaurus*, *Aucasaurus*, *Allosaurus*, and large ornithomimids (Fig. 7C).

For trackmakers from the Glen Rose Formation and other Early Cretaceous formations from Texas more generally, there seems to be a trimodal distribution of trackmaker sizes, with peaks at roughly 25, 35-40, and 45-50 cm (Fig. 7D). Intriguingly, for a worldwide sample of trackways attributed to theropods, a footprint length of 30 cm is the most common size class, at least for putative theropod trackways of Cretaceous age, with the suggestion of a much smaller secondary mode at footprint lengths of about 50 cm. So the Paluxy River bipedal dinosaur footprint assemblage, if dominated by theropods, seems roughly consistent with what is seen

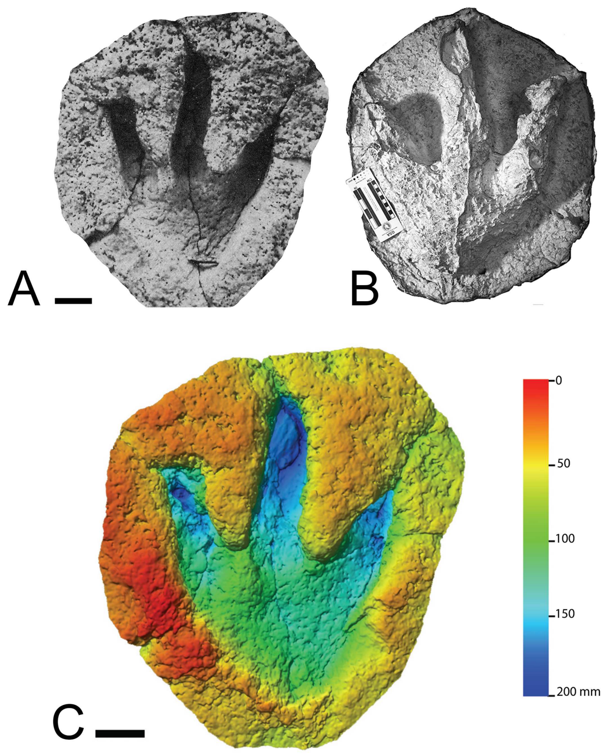


FIGURE 6. The Glen Rose bandstand footprint (Shuler, 1935), the type of *Eubrontes (?) glenrosensis*. **A**, Shuler's photograph of the print, from Adams et al. (2010); **B**, negative copy (cast) of the print; **C**, digital depth-coded image of the print (Adams et al., 2010).

elsewhere.

Skeletal data (Farlow et al., 2006, 2012a, 2014; cf. Fanti et al., 2013) show a clear difference between theropods and bipedal or potentially bipedal ornithischians in relative width of digits (Fig. 7A), with theropods having relatively skinnier toes, especially at large sizes. The large Paluxy tridactyls are clearly theropod-like in this feature, and are longer than broad, which is usually interpreted as a theropod feature in tridactyl footprints. A good candidate for the maker of the big tridactyls is the allosaur *Acrocanthosaurus* (Langston, 1974; Pittman, 1989; Currie and Carpenter, 2000; Farlow, 2001).

The smaller Paluxy tridactyls are also longer than broad, and sometimes preserve digital pad impressions. They have a theropod-like appearance, but the morphological differences between the feet and footprints of theropods and ornithopods become blurred at smaller sizes (Castanera et al., 2013a, b; Escaso et al., 2014; Farlow et al., 2014). Consequently, although we suspect that most or all of these prints were also made by theropods, we cannot be certain of this.

A striking feature of some tridactyl trackways in both the Main Tracklayer and the Taylor Tracklayer is the presence of an elongate depression behind the digital portion of the footprint (Kuban, 1989a; Figs. 3H, 5D, E, L, M). Such elongate prints have been reported from numerous other dinosaur tracksites around the world (Leonardi, 1979; Calvo, 1991; Kvale et al., 2001; Dalla Vecchia et al., 2002; Lockley et al., 2003, 2006a, 2013, 2014a, b, d; Milner et al., 2006a; Rodríguez-de la Rosa et al., 2004; Conti et al., 2005; Gand et al., 2007; Nicosia et al., 2007; Petti et al., 2008a; Rubilar-Rogers et al., 2008; Gierliński et al., 2009; Ishigaki et al., 2009; Ishigaki, 2010; Li et al., 2010; Xing et al., 2011c, 2014e, 2015c, g; Boutakiout et al., 2012; Moreno et al., 2012; Lockwood et al., 2014; McCrea et al., 2014b; Citton et al., 2015; Pérez-Lorente, 2015). Some of these prints may be slip or skid marks, but most of them (including those from the Paluxy River) record the impression of the metatarsal region of the foot in the substrate. Footprints with metatarsal impressions could be made when the trackmaker was sitting, of course, but many trackways composed of such elongate prints show forward locomotion of the animal, and—very strangely—the step length of the dinosaur seems not much to have been affected by this unusual mode of progression. Whether the creation of such "elongate", "metatarsal", or "semiplantigrade" footprints reflects deliberate foraging behavior on the part of crouching animals (Kuban, 1989a), or merely an adjustment to substrate conditions (e.g., Pérez-Lorente, 2015), is uncertain.

In any case, registry of the metatarsal region in some Paluxy River footprints provides additional clues to the trackmakers (Farlow et al., 2013). In those ornithischians that retain a digit I, this toe is generally longer, relative to the length of digit III, than in theropods (Fig. 7B). Consequently the presence of a very short digit I impression in a large tridactyl footprint from the Taylor Tracklayer (Fig. 5M) supports the interpretation that the trackmaker was a big theropod; similar footprints have been reported elsewhere (e.g. Nicosia et al., 2007). In contrast, the absence of a digit I impression in some of the elongate footprints from both the Main and Taylor Tracklayers (Fig. 5D, E) suggests that the maker of such prints was a form that had lost this toe, perhaps an ornithomimosaur (cf. Lockley et al., 2006a; Petti et al. 2008a). Hunt (2003) described a probable theropod foot skeleton from the Early Cretaceous Trinity Group of Arkansas, the exact affinities of which are uncertain, but whose erstwhile owner might be a candidate for the maker of many of the Paluxy elongate tracks that lack a digit I impression. More speculatively, we might consider a bipedal ornithischian with a foot like that of the dryosaurid *Eousdryosaurus* (Ecaso et al., 2014), although bigger—should such a dinosaur ever turn up.

Some of the elongate tracks made by smaller dinosaurs from the Taylor Tracklayer do show a hallux impression, however, and so there may have been more than one kind of trackmaker responsible for the elongate prints. The same may be true for the smaller Paluxy bipedal dinosaurs more generally; they may have included adults of relatively small-bodied species, but also smaller, immature individuals of the large theropod species.

Trackways with elongate footprints from the Taylor Tracklayer have become (in)famous as having been interpreted as made by giant humans that supposedly coexisted with dinosaurs (Hastings, 1987; Kuban, 1989a, b; Farlow et al., 2012b). One of the more renowned such trackways (Figs. 3I, 5L) consists of footprints that sometimes have a humanoid appearance (Fig. 3I), but even these show shallow but definite indications of a tridactyl configuration at the front end of the footprint, and under the best viewing conditions color differences (due to differences between the material that filled in the tracks vs. the surrounding rock) display three distinct toe marks (Fig. 5L). Just as the Paluxy River sauropod footprints were first identified by locals as elephant tracks (Farlow et al., 1989), and typical tridactyl dinosaur footprints from around the world are commonly first interpreted as bird prints (cf. Shuler, 1917), the Paluxy River "man track" story seems to have begun as a case of folk natural history, but one that metastasized.

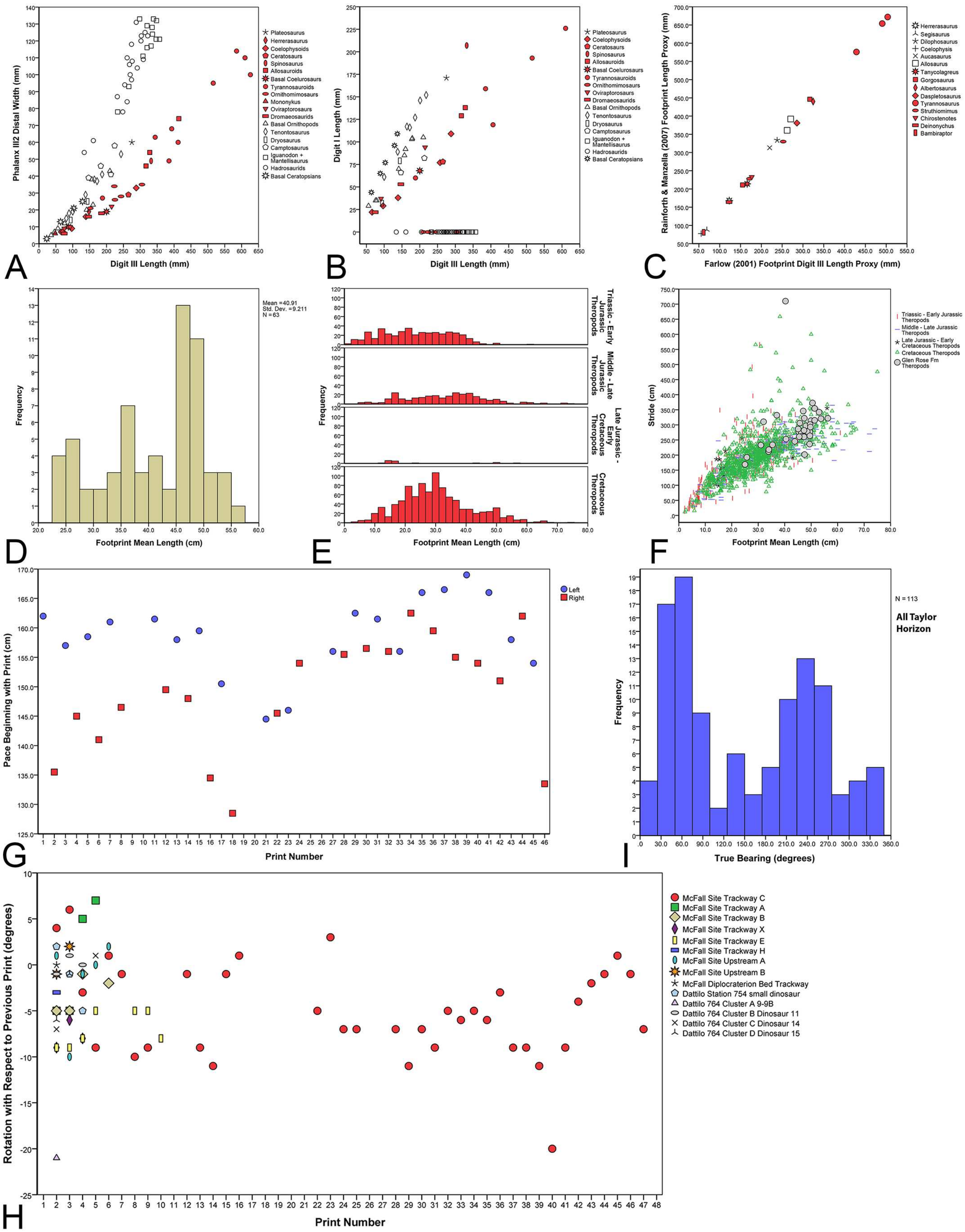
Weirdness of the elongate tracks notwithstanding, the bipedal trackmakers of the Paluxy River and other sites in the Glen Rose Formation seem to have been very similar to other bipedal dinosaurs in their typical locomotion. The stride length of Glen Rose bipeds, relative to footprint length, is very similar to that of trackways attributed to theropods from the entire Mesozoic of the whole world (Fig. 7F). There is a "main sequence" of trackways in which stride length increases with increasing trackmaker size, but starts to level off among the biggest trackmakers. This presumably defines the normal stride length: footprint length relationship of dinosaurs going about their business in no particular hurry. Above the main sequence are scattered points that presumably correspond to running dinosaurs, with the maximum stride length seen among animals with a footprint length of about 40 cm.

Long trackways provide especially useful information about trackmaker locomotion (Dalla Vecchia et al., 2001; Mossman et al., 2003; Day et al., 2004; Huh et al., 2006; Kim and Huh, 2010; Wings et al., 2012; Xing et al., 2015c). The long theropod trackway from the McFall Ledge site (Fig. 5H) shows an interesting pattern of step (pace) lengths (Fig. 7G): the animal generally took longer paces when stepping off from its left as opposed to its right foot. Disparity in pace lengths initiated with the left as opposed to the right foot is also seen in the longest tridactyl dinosaur trackway known from the Paluxy River (extending for more than 150 steps, making it one of the longest dinosaur trackways in North America), which also occurs in the Taylor Tracklayer. Dinosaur trackways with unequal step lengths have been reported from other ichnofaunas (e.g. Ishigaki and Matsumoto, 2009; Ishigaki and Lockley, 2010; Foster, 2015; McCrea et al., 2015). The usual interpretation for such trackways is the trackmaker had been injured and was limping, but McCrea et al. (2015) hypothesized that many such cases may have more to do with animal psychology than pathology, being examples of the more general phenomenon of laterality in tetrapods.

Most Paluxy River bipedal trackmakers walked with their footprints angling slightly inward with respect to their direction of travel (negative rotation; Fig. 7H).

A bewildering assortment of ichnotaxonomic names has been applied to tridactyl dinosaur footprints

FIGURE 7 (next page). Interpreting tridactyl dinosaur footprints. **A,** relative width of digit III of bipedal or potentially bipedal dinosaurs. At small sizes, there is little difference between ornithischians and theropods, but with increasing size ornithopods have relatively stout toes, and theropods relatively narrow toes; **B**, digit I length vs. digit III length. Most theropods have a relatively shorter digit I than do most ornithischians, but some members of both groups completely lose digit I (plotted as length of zero in this graph); **C**, comparison of two skeletal proxies of footprint size in theropods. For prints where the proximal end of the digit III impression is well-preserved, Farlow (2001) suggested that a skeletal proxy would be half the length of phalanx 1 plus the combined lengths of phalanges 2-4. Rainforth and Manzella (2007) suggested that a proxy for overall footprint length would be the total lengths of all the phalanges of digit III plus the difference in length between metatarsals III and IV. The two proxies are graphed to show how one proxy is related to the other in the same specimen; **D**, size frequency distribution of trackways of bipedal (mostly theropod?) dinosaurs from Lower Cretaceous sites in Texas. There seem to be three modes, at about 25-30, 35-40, and 45-50 cm footprint length. **E**, worldwide size-frequency distribution for trackways attributed to non-avian theropods from all intervals of the Mesozoic; data cases are trackways represented by at least one stride measurement. For the Cretaceous, the most common size class (length 30 cm) is close to one of the modes for the Texas size-frequency distribution; **F**, stride length as a function of footprint length in trackways attributed to non-avian theropods. The maximum stride length occurs at footprint lengths of about 40 cm; Glen Rose Formation trackways nicely match the pattern for all trackways; **G**, pace lengths along the long trackway from the McFall Ledge Site (Fig. 5H). The dinosaur generally took longer paces when stepping off from the left as opposed to the right foot; **H**, footprint rotation relative to the overall direction of travel of Taylor Tracklayer bipedal dinosaur trackways. For each print, rotation is measured by comparing the azimuth of the individual print with the average of that azimuth and that of the preceding print (the average indicating the overall direction of movement); negative rotation means that the footprint turns inward relative to the animal's movement direction; **I**, direction of travel of Taylor Horizon dinosaurs. Each data case is either the mean for a trackway, or the value for an isolated print.


A
Phalanx III2 Distal Width (mm)
Digit III Length (mm)
Plateosaurus
Herrerasaurus
Coelophysoids
Ceratosaurs
Spinosaurus
Allosauroids
Basal Coelurosaurs
Tyrannosauroids
Ornithomimosaurs
Mononykus
Oviraptorosaurs
Dromaeosaurids
Basal Ornithopods
Tenontosaurus
Dryosaurus
Camptosaurus
Iguanodon + Mantellisaurus
Hadrosaurids
Basal Ceratopsians
B
Digit I Length (mm)
Digit III Length (mm)
C
Rainforth & Manzella (2007) Footprint Length Proxy (mm)
Farlow (2001) Footprint Digit III Length Proxy (mm)
Herrerasaurus
Segisaurus
Dilophosaurus
Coelophysis
Aucasaurus
Allosaurus
Tanycolagreus
Gorgosaurus
Albertosaurus
Daspletosaurus
Tyrannosaurus
Struthiomimus
Chirostenotes
Deinonychus
Bambiraptor
D
Frequency
Footprint Mean Length (cm)
Mean =40.91
Std. Dev. =9.211
N =63
E
Frequency
Footprint Mean Length (cm)
Triassic - Early Jurassic Theropods
Middle - Late Jurassic Theropods
Late Jurassic - Early Cretaceous Theropods
Cretaceous Theropods
F
Stride (cm)
Footprint Mean Length (cm)
Triassic - Early Jurassic Theropods
Middle - Late Jurassic Theropods
Late Jurassic - Early Cretaceous Theropods
Cretaceous Theropods
Glen Rose Fm Theropods
G
Pace Beginning with Print (cm)
Print Number
Left
Right
I
Frequency
True Bearing (degrees)
N = 113
All Taylor Horizon
H
Rotation with Respect to Previous Print (degrees)
Print Number
McFall Site Trackway C
McFall Site Trackway A
McFall Site Trackway B
McFall Site Trackway X
McFall Site Trackway E
McFall Site Trackway H
McFall Site Upstream A
McFall Site Upstream B
McFall Diplocraterion Bed Trackway
Dattilo Station 754 small dinosaur
Dattilo 764 Cluster A 9-9B
Dattilo 764 Cluster B Dinosaur 11
Dattilo 764 Cluster C Dinosaur 14
Dattilo 764 Cluster D Dinosaur 15

from around the world (Calvo, 1991; Lockley and Meyer, 2000; Thulborn, 2001; Farlow and Galton, 2003; Calvo and Mazzetta, 2004; Clark et al., 2004; Day et al., 2004; Diedrich, 2004, 2011; Gangloff et al., 2004; Barco et al., 2005, 2006; Getty, 2005; Huh et al., 2006; Li et al., 2006; Lü et al., 2006; Lucas et al., 2006; Gand et al., 2007; Lockley et al., 2007, 2008, 2011, 2013; 2014a, c, e, 2015b, c; Rainforth, 2007; Wings et al., 2007; Bessedik et al., 2008; Fujita et al., 2008; Boutakiout et al., 2009; Sullivan et al., 2009; Belvedere et al., 2010; Li et al., 2010; Niedźwiedzki, 2011; Nouri et al., 2011; Xing et al., 2011b, c; 2013b, 2014a, b, c, d, e, f, h, 2015a, c, e, 2016; Moreau et al., 2012, 2014; Wagensommer et al., 2012; Fanti et al., 2013; Cobos et al., 2014; Fiorillo et al., 2014; McCrea and Pigeon, 2014; McCrea et al., 2014a, b; Foster, 2015; Li et al., 2015; Lallensack et al., 2015; Weems and Bachman, 2015). Criteria used to discriminate among these footprint taxa include relative toe lengths, angles between toes, the footprint width/length ratio, the extent to which the distal impression of digit III extends beyond the distal impressions of digits II and IV, the shape of a triangle defined by the tips of the marks of digits II-IV, and the configuration of the back of the footprint. Ichnotaxa are sometimes distinguished by bivariate characters, sometimes by multivariate analyses, sometimes by geometric morphometrics, and sometimes by the qualitative "gestalt" of the footprints.

Shuler (1917, 1935) applied two names to tridactyl footprints from the Glen Rose Formation in Somervell County. The first (1917) was the tongue-twisting *Eubrontes (?) titanopelopatidus*, for which no type specimen seems to have been secured. In 1935 Shuler applied the more euphonious name *Eubrontes (?) glenrosensis* to a splendid Main Tracklayer footprint which was installed in a bandstand on the town square in Glen Rose (Fig. 6), where it has remained ever since, but has regrettably undergone a certain amount of degradation (Adams et al., 2010) due to exposure to the elements. Langston (1974) suggested that the Paluxy large tridactyls might better fit under the moniker *Irenesauripus*, a name originally applied to footprints from the Early Cretaceous of British Columbia.

Our group has thus far deliberately refrained from discussing names for the Glen Rose Formation tridactyls, but will eventually offer an opinion on this matter. It is probably fair to say, however, that there is a diversity of opinion among us as to how meaningful such names are. Footprints are three-dimensional records of the interaction of a foot with a substrate. Apart from the issue of the extent to which the surface expression of footprint outlines, or linear measures and angles, can capture that complexity, there is the matter of whether or to what extent the vagaries of footprint emplacement, preservation, and modern erosion (Platt and Meyer, 1991; Kvale et al., 2001; Nadon, 2001; Gatesy, 2003; Manning, 2004, 2008; Henderson, 2006; Graverson et al., 2007; Milàn and Bromley, 2006, 2008; Falkingham et al., 2010; Jackson et al., 2009, 2010; Avanzini et al., 2012; Huerta et al., 2012; Thulborn, 2012; Santos et al., 2013; Razzolini et al., 2014; Carvalho et al., 2013; Alcalá et al., 2014; Cariou et al., 2014; Falkingham, 2014; Falkingham and Gatesy, 2014; Lockley and Xing, 2015; Pérez-Lorente, 2015) render the characters thought to be useful in defining different tridactyl footprint morphotypes and ichnotaxa unreliable. Even the more optimistic members of our group confess to a nagging worry that the ichnotaxonomy of tridactyl dinosaur footprints may be, to borrow the words of an ancient sage, "futile and pursuit of wind" (Ecclesiastes 1:14, Jewish Study Bible).

TRACKMAKER BEHAVIOR AND ECOLOGY

Behavior—What were the trackmakers doing? For the most part, it seems, nothing particularly interesting. In both the Main Tracklayer (Farlow et al., 2012b) and the Taylor Tracklayer (Fig. 7F), the bipedal dinosaurs were moving in roughly the same numbers either northward or southward, presumably walking along the local shoreline. This pattern provides no evidence for group behavior on the part of the carnivorous dinosaurs. Interestingly, theropod trackways in the Taylor Tracklayer are most commonly oriented northeast-southwest, similar to linear trends of *Diplocraterion* burrow tops in the overlying *Diplocraterion* bed (Martin et al., 2015). This coinciding of burrow trends and trackways may reflect the presence of a northeast-southwest shoreline that shifted laterally with a slight rise in relative sea level between deposition of Taylor Tracklayer and *Diplocraterion* bed sediments (Martin et al., 2015).

In contrast, tracksites which show a pronounced single direction of trackmaker travel are usually interpreted as showing animals moving together (Lingham-Soliar et al., 2003; Barco et al., 2006; McCrea et al., 2014; Moreno et al., 2012; García-Ortiz and Pérez-Lorente, 2014; Lockley et al., 2015b; but see Roach and Brinkman, 2007; Getty et al., 2015). In the Main Tracklayer, nearly all of the sauropods were traveling to the south (Fig. 2A), in contrast to the trackways attributed to theropods. Farlow et al. (2012b) therefore hypothesized that (most of?) the sauropods, unlike the theropods, were not routine occupants of the footprint sites, but rather a herd of animals passing through the area at one time.

The two trackway slabs collected by R. T. Bird for the American Museum and the Texas Memorial Museum may record a dramatic story. A large theropod stepped along the trackway of a large sauropod, repeatedly treading upon the big herbivore's footprints;

at one point both trackways bend to the left (Figs. 2B, D, E). Bird (1985) thought the meat-eater actually attacked the sauropod, but Farlow et al. (2012b) hypothesized the predator was only following the herbivore—at least over the preserved portions of the two trackways.

Ecology—The association of footprints of sauropods with those of large or small theropods is a recurrent theme in dinosaur footprint assemblages (Calvo, 1991; Dalla Vecchia et al., 2000, 2001; Lockley and Meyer, 2000; Moreno and Pino, 2002; Romano and Whyte, 2003; Ahmed et al., 2004; Calvo and Mazzetta, 2004; Day et al., 2004; Leonardi and dos Santos, 2004; Moreno et al., 2004; Hernández Medrano et al., 2005-2006; Foster and Lockley, 2006; Bessedik et al., 2008; Belvedere et al., 2010; Nicosia et al., 2007; Petti et al., 2008b; Ishigaki et al., 2009; Sacchi et al., 2009; Xing et al., 2010, 2013c, 2014a, f, 2015a, c, e, 2016; Diedrich, 2011; Hornung et al., 2012; Wagensommer et al., 2012; Bravo Cuevas, 2013; Cariou et al., 2014; Lockley et al., 2014b, 2015b; Schumacher and Lockley, 2014; González Riga et al,. 2015; Pérez-Lorente, 2015), and not terribly surprising, given the common co-occurrence of such animals in skeletal assemblages. Perhaps more interesting is the fact that the theropod-sauropod association is frequently seen in carbonate environments (Lockley, 2007). Given the huge size of the Paluxy River sauropods and theropods, it is unlikely that their habitat was limited to the carbonate mudflats in which their tracks were preserved, an inference supported by the occurrence of skeletal material of the presumed trackmakers in more inland clastic settings, as well as the apparently large geographic ranges of these animals (Wedel et al., 2000a, b; Rose, 2007; D'Emic et al., 2012, 2013; D'Emic and Foreman, 2012), and by the broader worldwide paleoenvironmental occurrences of related forms (Mannion and Upchurch, 2010).

The greater abundance of footprints and trackways attributed to theropods than of sauropods in the Glen Rose Formation, a seemingly unexpected situation given the usual relative abundance of large herbivores and carnivores (cf. Hatton et al., 2015), is also seen in many (Leonardi, 1989; Foster and Lockley, 2006; Lockley et al., 2015a; Pérez-Lorente, 2015) but not all (Weems and Bachman, 2015) other dinosaur track assemblages. Leonardi (1989) suggested that this reflected greater activity on the part of carnivorous than herbivorous dinosaurs, an interpretation endorsed by Farlow (2001) by analogy with the movement ecology of extant large mammals. *Acrocanthosaurus* was a huge meat-eater, with large adults possibly weighing as much as 5000-6000 kg (Henderson and Snively, 2004; Bates et al., 2009). Individual theropods that big might have had home ranges covering tens of thousands of square kilometers (Farlow, 2001), and patrolled long distances in a single day, giving them ample opportunity to make lots of footprints in suitable environments.

Some workers (e.g. Hunt and Lucas, 2007; Lockley, 2007 [and references therein]) have proposed recognition of tetrapod trace fossil ichnofacies analogous to the ichnofacies recognized by ichnologists working on traces of benthic invertebrates (cf. Martin, 2013 [and references therein]). The details of how such ichnofacies are to be defined differ, but in both schemes one of the ichnofacies was named after *Brontopodus*. Lockley (2007 [and earlier]) associated his *Brontopodus* ichnofacies with platform carbonate situations. Hunt and Lucas (2007: Table 2) went further, defining a *Brontopodus* "archetypal tetrapod ichnofacies" associated with "coastal plain, clastic or carbonate marine shoreline" environments, and characterized by footprint assemblages in which the "majority of tracks are terrestrial, quadrupedal herbivores with small quantity (generally > 10% of terrestrial carnivore tracks)". Lockley's *Brontopodus* ichnofacies was interpreted by Hunt and Lucas as one of the constituent ichnocoenoses within their more inclusive ichnofacies; as interpreted by Hunt and Lucas, their *Brontopodus* ichnocoenosis, like Lockley's ichnofacies of the same name, is associated with "carbonate marine shorelines" (Hunt and Lucas 2007:66). What made their *Brontopodus* ichnofacies "archetypal" is that it is not restricted to a particular time interval, and so ranges from the Late Jurassic through the Recent; *Brontopodus* itself, the ichnogenus after which the ichnofacies was named, therefore does not have to be present.

Which these concepts will catch on, if any, is still up in the air. Defining the *Brontopodus* archetypal ichnofacies as being characterized by a "small" number of predator trackways, which at the same time constitute > 10% of the trackway assemblage, seems rather odd. We would have thought that the "> 10%" was a typographical error that should have read "< 10%", except that the phrase appears more than once in Hunt and Lucas (2007). Be that as it may, if the *Brontopodus* ichnofacies is defined as having substantially fewer carnivore than herbivore trackways, this would seem to disqualify the Glen Rose Formation of Texas, the type formation for *Brontopodus*, from membership therein. Can't win them all.

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