Thunder Lizard Handstands: Manus-Only Sauropod Trackways from the Glen Rose Formation (Lower Cretaceous, Kendall County, Texas)

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Keywords: sauropods, ichnology, manus-only trackways, Glen Rose Formation

Running Head: Manus-only sauropod trackways, Texas

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Abstract: Three parallel, manus-only sauropod trackways from the Coffee Hollow A-Male tracksite (Glen Rose Formation, Kendall County, Texas) were studied separately by researchers from the Heritage Museum of the Texas Hill Country and the Houston Museum of Natural Sciences. Footprint and trackway measurements generally show good agreement between the two groups' data sets. Footprints appear to be shallowly impressed true tracks rather than undertracks. One of the Coffee Hollow trackways shows marked asymmetry in the lengths of paces that begin with the left as opposed to the right forefoot, and two of the Coffee Hollow trackways are unusually broad. The Coffee Hollow trackways differ enough from the manus portions of other Glen Rose Formation sauropod trackways to suggest that they were made by a different kind of sauropod. Greater differential pressure exerted on the substrate by the forefeet than the hindfeet probably explains the Coffee Hollow trackways, like other manus-only sauropod trackways, but the possibility that they indicate unusual locomotion cannot at present be ruled out.

INTRODUCTION

In early 1940, while searching for a suitable sauropod trackway to display behind the American Museum of Natural History's *Apatosaurus* mount, fossil collector Roland T. Bird briefly visited southern Texas. Late in 1938 Bird had found spectacular sauropod tracks in the bed of the Paluxy River further north (Bird, 1939, 1941, 1985), but he now hoped to avoid having to deal with the Paluxy's frequent floods (Bird, 1985). Although Bird did find some remarkable sauropod ichnites in southern Texas (Bird, 1944, 1954), he ultimately had to deal with the temperamental Paluxy to get the specimens he sought (Bird, 1941, 1944, 1954). But while he was in southern Texas, Bird discovered a kind of sauropod trackway whose interpretation remains contentious.

Reported "elephant tracks" on the Mayan Ranch in Bandera County turned out to constitute an unusual sauropod trail (Fig. 1): "I saw them while we were still 100 feet away. A double row of large, round circular prints. Without a doubt made by a sauropod, but as I interpret them, made by an individual while swimming. They were all typical forefeet impressions as if the animal had just been barely kicking bottom" (letter from Bird to Barnum Brown, 8 February 1940).

Bird's interpretation that Mayan Ranch sauropod trackway had been made by a "swimming" dinosaur (Bird, 1944, 1954) was uncontroversial at a time when sauropods were thought to have been mainly aquatic animals (Colbert, 1951). A generation later, however, the skeletal anatomy of sauropods was shown to be more like that of fully terrestrial than amphibious amniotes (Bakker, 1971; Coombs, 1975). Bird's interpretation of the Mayan Ranch sauropod trail was now called into question, and an alternative hypothesis offered: that manus-only or manus-dominated sauropod trackways instead are due to differential impression of the forefeet and hindfeet during normal quadrupedal locomotion, with manus and not pes prints being registered in sediment layers beneath the one on which the dinosaur actually walked (Lockley and Rice, 1990). Various authors have supported either the swimming or the under-tracking hypothesis, but most authors have favored the latter explanation (cf. Ishigaki, 1988, 1989; Lockley and Santos, 1993; Santos et al., 1994; Lee and Huh, 2002; Henderson, 2004; Vila et al., 2005; Lee and Lee, 2006; Hwang et al. 2008; Marty 2008; Ishigaki and Matsumoto, 2009; Milner and Lockley, 2016; Xing et al., 2016b). Computer simulation studies have also demonstrated that due to differential underfoot pressures, this effect may even occur on the tracking surface, and not just in undertracks (Falkingham et al., 2011a, 2012).

Vila et al. (2005) and Ishigaki and Matsumoto (2009) presented a new approach to interpreting the origin of manus-only sauropod trackways: If the trackway pattern of manus prints in manus-only sauropod trackways does not differ from the arrangement of manus prints in “standard” (manus plus pes print) trackways, the null hypothesis should be that manus-only trackways were not made by dinosaurs moving in any unusual manner—that is, that the absence of pes prints is a formational or preservational artifact. In contrast, if the arrangement of manus prints in manus-only trackways differs substantially from that in typical trackways, then perhaps the trackmakers were indeed doing something out of the ordinary when making the trackways.

In early 2007, the late Wann Langston of the University of Texas received a telephone call from Ms. Gail Flach, who owned property between Comfort and Sisterdale in Kendall County, Texas. Ms. Flach operated a limestone quarry (Coffee Hollow Limestone) on her property, selling rock slabs to local builders and contractors. She described the discovery of a series of what she thought were dinosaur tracks, and asked if Langston would be interested in coming to look at them. Langston contacted the Heritage Museum of the Texas Hill Country (HMTHC), whose volunteers agreed to work on the site.

At the same time, Ms. Flach also contacted Bakker at the Houston Museum of Natural Science (HMNS), asking if his institution would be interested in her discovery. As a result, two groups independently worked at the Coffee Hollow A-Male tracksite (the second part of the site name honoring an award-winning purebred Mammoth Donkey at the ranch on which the quarry is located), each unaware of the other's activities. Realization that they were each working on the same locality came when Bakker contacted Farlow, who had been advising the HMTHC, to see if Farlow wanted to join the HMNS effort. With that the two groups agreed to pool their efforts in a description of the site.

In October 2007, under commercial pressure to fill orders for her premium limestone, Ms. Flach had her workers break up the track layer to sell slabs to local builders. Fortunately, by this time the site had been documented.

The Coffee Hollow A-Male dinosaur tracksite preserves manus-only sauropod trackways like those discovered by R.T. Bird in Bandera County, and by other workers at other sauropod tracksites around the world. The Coffee Hollow A-Male tracksite therefore provides an opportunity to revisit the contentious issue of how manus-dominated sauropod trackways were made. Although we will not definitively answer the question of how the Coffee Hollow trackways were made, we will discuss the kinds of trackway evidence that would allow such a determination.

GEOLOGIC SETTING

The Coffee Hollow A-Male dinosaur tracksite consisted of three trackways in a level limestone layer exposed by quarrying operations (Figs. 2-5). Limestone from this layer is much in demand as a building stone, and decorative features such as fossils, ripple marks and animal burrows are also sought after. The track surface had been exposed by removing overburden of up to twenty feet of fossiliferous, marly limestone. It was bounded on the west by a natural slope, on the northeast by quarried area and fill, and on the southeast and south by unquarried overburden. The extent of the trackways to the southeast was not determined, and probably had not been reached.

The track layer (commercially known as the Sisterdale Cream Stone) lies about a meter below the base of the *Salenia texana* Zone (Whitney, 1952; Scott et al., 2007; Ward and Ward, 2007), and about 4 m below the *"Corbula"* Marker Bed at the top of the Lower Glen Rose Member of the Lower Cretaceous Glen Rose Formation. This is about the same stratigraphic position as very large sauropod tracks exposed in the bed of the Blanco River about three miles west of Blanco, Texas (Pittman, 1989; Scott et al., 2007; Ward and Ward, 2007). The Sisterdale Cream Stone is a wackestone-packstone containing burrows and ostracodes (Fig. 5). In addition, some distinctive vertebrate skeletal fossils were found during quarrying operations, including fishes and a small crocodyliform (now in the collection of the Heritage Museum of the Texas Hill Country, Canyon Lake, Texas). The exact stratigraphic position at which these vertebrate fossils were found is uncertain, but may have been just above the tracklayer, close to the *Salenia texana* zone. A distinctive joint pattern was oriented N20°W; one major joint extended through the central portion of the site (cutting across print A83 of the Right trackway), and minor joints spread throughout.

METHODS

Because both HMTHC and HMNS field crews independently worked the Coffee Hollow A-Male tracksite, a description of the procedures followed by both groups is necessary.

HMTHC Protocols

The three sauropod trackways were labeled Trails A, B, and C, going from north to south across the site (Figs. 2-4); the trackways are essentially parallel, with all three dinosaurs moving in a northwesterly direction, animal A being the rightmost of the three, and animal C the leftmost. Because the direction of travel of the trackmakers was toward a naturally occurring slope, and additional tracks were still being uncovered by quarrying operations further "up-trail" (in the direction from which the dinosaur had come) in the three trackways, footprints were numbered arbitrarily, starting with footprint 100 at the outcrop and numbered sequentially backward (up-trail). For each of the trackways, footprints of the right side were assigned odd numbers, and prints of the left side even numbers.

Trimble Business Center software was used to link GPS equipment (VRS) to a Trimble 5600 robotic total station enabling rapid acquisition of targets with near-centimeter accuracy. These points are referenced to the North American Datum of 1983 (NAD 83) as the horizontal control datum for the United States, and the North American Vertical Datum of 1988 (NAVD 88) as the vertical control datum of optometric height established for vertical surveying in the U.S. With this system, points were acquired around the perimeter of each mapped footprint with a maximum of a few centimeters between each point. At least 10 such points were taken for each print; for many prints there were 30 or more. In addition to the footprint perimeters, the boundary of the track surface (bluff edge, quarried edge and unexcavated boundary) was mapped, as well as several of the major joints, giving the orientation of these features. Back in the office, digital photographs were oriented, scaled and superimposed over the mapped track perimeters, confirming the accuracy of the mapping.

Prints 72 through 99 of the A trackway were mapped, as were prints 87-97 of the B trackway, and prints 74-99 of the C trackways. Other footprints were seen, but were broken up before they could be mapped: prints 58-71 of the A trackway, prints 78-86 of the B trackway, and prints 68-73 of the C trackway. In addition, tracks A73, A98, B85, B86, C75 and C77, though within the mapped portions of the trails, were either too poorly preserved or poorly exposed to map. Other footprints were reported to have been uncovered after the HMTHC crew had finished its work, such that there may have been more than 100 individual footprints at the site.

Measurements of individual footprints and of trackways were directly made with a tape measure in inches and feet (later converted to metric units). Footprint lengths and widths were measured (to the nearest half-inch)**.** Oblique paces and strides were measured (to the nearest inch) from the most anterior location along the front margin of each print, as was done by Farlow et al. (1989) for other Glen Rose Formation sauropod trackways. For comparison, oblique pace lengths were later made from footprint centers using the site map. Measurements of inner and outer trackway width were made at the positions of each print along the length of the trackway, as defined by the innermost and outermost edge, respectively, of the print. Pace angulations were not measured directly, but calculated from pace and stride measurements using the law of cosines; the width of the angulation pattern (Marty, 2008) was calculated from paces, strides, and the pace angulation using the law of sines (Farlow et al., 1989).

Footprint rotations (positive values indicate outward rotation with respect to the trackmaker's direction of travel, and negative values inward rotation) were not measured in the field, but a few estimates were later made from the trackway map (Fig. 2). A line was run through the middle of each of trackways A and C, and the angle formed between the anteroposterior axes of some of the better-registered footprints in each trackway and the line through the middle of the trackway measured.

Numerous digital photographs of trackways and individual footprints were taken, from a variety of angles, during all stages of field work. Photographs of individual footprints were taken from a stepladder at a height of about 7 ½ feet (2.3 meters) above the ground, with an American yardstick marked off in inches to indicate the scale. These photographs were taken from as nearly directly overhead as possible, but most of them were a bit oblique. The brightness and contrast of photographs were altered to make the prints stand out from the surrounding rock. Many of the trackway and tracksite photographs were later processed using COLMAP (Schönberger and Frahm, 2016; Schönberger et al., 2016) to build a post-hoc photogrammetric digital model (Falkingham, 2012; Falkingham et al., 2014) of the tracksite (Fig. 3A). Because the photographs were not originally taken with photogrammetry in mind, overlap was inconsistent, and objects such as scale bars and equipment moved around between images. This meant that 3D detail and resolution of the tracksite model was relatively low, and useful primarily as a 2D map (Fig. 4A).

HMNS Protocols

The three trackways were identified in terms of their position, compared with the direction of the dinosaurs' trackway. The HMNS Left Trackway is HMTHC trackway C, the HMNS middle trackway is HMTHC trackway B, and the HMNS Right Trackway is HMTHC trackway A.

Footprint width was measured directly on each print to the nearest millimeter. A reference line was run through the trackway along its overall direction of travel, and marked at four-foot intervals. Each of these four-foot increments was marked on graph paper (Fig. 6), and the position of each footprint drawn on the paper. The perpendicular distance from the innermost rear edge of the footprint to the reference line was measured, as was the angle formed by a line segment running across the back margin of the footprint with the reference line.

Oblique paces and strides were measured indirectly, from the trackway diagrams. To make these data as comparable to the HMTHC data as possible, paces and strides were measured from the anterior edges of the footprints as drawn on the trackway diagrams. Measurements made on the trackway diagram were converted to real world values by comparison with the distance on the diagram corresponding to the four-foot reference line increment marks. Pace angulations were measured on the trackway diagrams.

Two measurements of inner trackway width were made, the first of these a direct measurement. The distance from the inner rear edge of one footprint to the reference line was added to the distance from the inner rear edge of the immediately preceding contralateral footprint to the reference line, and this sum was taken to indicate the inner trackway width at the position of the more down-trail (in the direction toward which the dinosaur was moving) footprint.

Inner trackway widths were also measured from the trackway diagrams by drawing line segments connecting the innermost edges of two successive ipsilateral footprints, and then measuring the perpendicular distance from that line segment to the innermost edge of the intervening contralateral footprint, and finally converting this measurement to its real world value. Thus there could be two fewer measurements of inner trackway width than the number of footprints in alternating left-right sequence along the length of the trackway. Outer trackway width was measured in an analogous manner, except that, of course, it was measured using the outer rather than the inner edges of footprints.

Footprint rotation with respect to the dinosaur’s direction of travel was calculated in a two-step operation. The compass bearing of a footprint is perpendicular to the angle formed by the line segment running across the back margin of the footprint and the reference line indicating the dinosaur’s travel direction (Fig. 6). For left footprints, this bearing is calculated as: direction of travel (in degrees) + angle formed by the line segment running across the back margin of the footprint, minus 90°. For left footprint C78 (Fig. 6), this angle will be 287° + 73° minus 90°, or 270°. This bearing is 17° less than the dinosaur’s overall direction of travel, and so this footprint is rotated outward (away from the overall direction of travel) by 17°. For right footprints, the individual print bearing is calculated as direction of travel minus angle formed by the line segment running across the back margin of the footprint + 90°.

Overlapping photographs of the tracksite taken from overhead, using a drone, were combined to create a composite tracksite photograph that can be compared with the HMTHC tracksite digital model (Fig. 4B).

Negative latex copies (casts) of some of the prints were made. These were made after cleaning out loose sediment covering the prints, but without any attempt to remove any solidly adhering possible footprint fill material. These latex peels were later photographed by Farlow with photogrammetry in mind, and because of this the digital models created from the photographs by Falkingham have much greater resolution than the models for the full site, and contain reliable information in all three dimensions.

Track Layer and Track Fill Sampling

The HMTHC team collected rock samples associated with three of the footprints. Footprint A99 from the Right trackway (Fig. 2) was at the broken edge of the track exposure, making it possible to collect a section across the print (Fig. 7A-C). Rock material filling footprints was collected from print A97 or a nearby print (Figs. 7D) and from a print in the C (Left) trackway, print C83 or nearby (Figs. 7E-F). We have little direct information about the material comprising footprints in the B (Middle) Trackway. Cut surfaces across prints and/or fill were polished to facilitate interpretation of gross features, and thin sections cut for petrological analysis of microscopic features (Figs. 8, 9).

Comparative Trackway Data (Supplementary Online Material Table 1)

We scoured the dinosaur trackway literature for measurements of the manus portion of sauropod trackways, including “standard” trackways composed of both manus and pes prints, trackways that were explicitly characterized by the authors as “manus-dominant” (manus and pes prints both present, but manus prints more deeply or clearly impressed than pes prints), and manus print-only trackways. We admit that the distinction between “standard” and “manus dominant” trackways is somewhat arbitrary. Some of what we characterize as standard trackways may well have been manus-dominant, but unless the authors of the studies so designated them, they are not labeled as manus-dominant by us. We will distinguish between standard and explicitly identified manus-dominant trackways in many of our graphs, but for many data analyses we will group the two trackway categories together.

Data are variably reported in the literature. Measurements of manus width are commonly reported (and will be used as the chief proxy for trackmaker size in this study), as are pace lengths and stride lengths, and pace angulations, but the details of how measurements were made are seldom reported, and may vary among studies. For example, Farlow et al. (1989) measured manus and pace lengths of the classic Glen Rose Formation *Brontopodus* trackways using as reference points the front margins of the manus prints, rather than the print centers, because in some Paluxy River trackways manus prints are squashed from the rear by sediment squeezed forward during impression of the pes. In most published measurements of sauropod manus step lengths, however, print centers were probably used as the reference points. Trackway widths may be expressed as inner or outer trackway widths, and/or the width of the angulation pattern (cf. Marty, 2008).

For comparisons among trackways, we used the means of published values of parameters for each trackway, if more than one measurement of the parameter was reported by the authors; if only a single measurement was available, this was the value employed. In many cases values of one or more parameters were not reported, but could be estimated from the author's trackway diagrams. We will make quantitative comparisons of sauropod trackways using all of these kinds of data extracted from the literature, but our results should be taken with caution due to the limitations of those data. Some trackway parameters are geometrically related (cf. Farlow et al., 2018b for crocodile trackways), such that values that authors did publish can serve as proxies for parameters that were not reported.

Forelimb Length vs. Manus Size in Sauropods

To estimate the water depth necessary to float a sauropod while its forefeet maintained contact with the bottom, and assuming that water would have reached the animal's shoulder, we compared the manus width and forelimb length of mounted sauropod skeletons. Manus width and forelimb length were measured from digital models collected during a previous study (Bates et al., 2016) via laser scanning or photogrammetry. Measurements were made using Autodesk Maya 2017. Forelimb length was measured as the combined segment lengths of humerus, radius, and manus; this undoubtedly underestimates the actual length. Manus width was measured as the maximum distance across the manus in a medial-lateral direction. Measuring forelimb length as summed segment lengths makes the result resistant to pose. However, manus width is more dependent on the way in which the skeleton (manus) is reconstructed. Compounding this issue, distal portions of the autopodia were generally captured least well by both laser scanning and photogrammetry, and often contained extensive reconstructions of missing autopodial elements. These data therefore represent rough approximations.

RESULTS

Track Layer and Overtrack Fill Lithology

In cross section (Fig. 7A-C) the manus prints are a few centimeters deep, with at least some prints showing an elevated displacement rim (Marty et al., 2016) around the print margin. Because the upper surface of the layer in which the tracks are observed shows greater vertical deformation associated with the prints (Figs. 7B, 7C, 8A) than the material overlying it (Figs. 7D, 8C), we interpret the manus prints as true tracks rather than undertracks (Marty et al., 2016; cf. Sanz et al., 2016). Furthermore, the fill layer overlying some prints shows ripple marks (Fig. 7G), which would have been squashed had the fill layer itself been the one on which the dinosaur trod.

What we therefore interpret as the track layer (Figs. 7C, 8A, 9A-C) consists of four fairly similar, repetitive sedimentary units, each of which fines upward from fine-grained packstone to mudstone. Most of the grains are ostracodes, dasyclads, and foraminiferan tests. Scattered through the track layer are sparse, subangular to subrounded quartz sand grains whose diameters range 0.3-0.8 mm, with a concentration of diameters at 0.4-0.5 mm. Diagenetic mud clots of 0.2-0.4 mm diameter are distributed through the layer, along with birdseye structures of comparable size. In addition to the fossils already listed, there are small (0.5-3 mm across) gastropods and also small (up to 7 mm across), thin (0.05-0.1 mm thick) fragments of possible crustacean or limulid carapace; the abundance and diversity of body fossils decreases vertically across the layer. The layer is marked by thin (< 1 cm) burrows and occasional (reworked?) worm (?) tubes. The uppermost portion of the track layer (unit 4) is markedly deformed by the dinosaur footprint, being squashed beneath the track and pushed up away from it.

The overall environmental interpretation of the track layer is of a subaqueous (indicated by the graded beds), shallow-water situation, very close to shore (source of the sand grains), with a low-diversity, sparse (stressed?) benthic fauna. The clotted structures and birdseyes suggest algal or microbial growth; the presence of dasyclads suggests a closed lagoon (C. Meyer, personal communication).

The material filling footprints has a more complicated microstructure than the material of the track layer (Figs. 7D, 8C and D, 9D). The basal sublayer (unit 1) may have preceded higher sublayers by a prolonged interval of time, because those upper layers show onlap over it. The very base of unit 1 is a foraminiferan/ostracode packstone, the forams of which are similar to those of the track layer. The remainder of unit 1 is a mudstone or wackestone with vertical birdseye structures separating possible microstromatolitic columns 2-3 mm across.

Fossils are rare or absent in the track fill laminae above unit 1. Unit 2 shows faint microlaminations (0.1-0.2 mm thick) composed of angular, discrete mudstone fragments or lithoclasts. There are scattered, equant fenestrae (0.2-0.5 mm) at a uniform depth along the upper surface of the unit. Unit 3 consists of thin lamellae like those of unit 2, with fenestrae of 0.1-0.5 mm diameter lined up along the base of the unit. The remaining units (4-7) appear to be traction deposits of micro-lithoclasts. These are monomictic, well-rounded, nearly spherical (length/width ratio up to 1.5) bits of lime mud of 0.1-0.3 mm diameter in a packstone or grainstone matrix. Unit 6 shows moldic porosity, with nearly spherical, well-rounded voids that are 0.1-0.5 mm across. There is no bioturbation of the overtrack fill.

The surface of the fill material of some prints shows a wrinkled texture suggestive of a microbial mat (Figs. 10A, 11A), or ripple marks (Fig. 7G). Overall the track fill material suggests deposition on a tidal flat, or even a supratidal situation that was only occasionally flooded, in either case probably with an algal mat cover (cf. Kvale et al., 2001; Paik et al., 2001; Marty et al., 2009; Diedrich, 2012; Carvalho et al., 2013; Alcalá et al., 2014; Cariou et al., 2014; Dai et al., 2015; Campos-Soto et al., 2017; Cónsole-Gonella et al., 2017). Similar overtrack fills are known from tridactyl footprints from the Glen Rose Formation of southern Texas (Farlow et al., 2006).

Because we have no information about the material underlying trackway B, our inferences about whether the Coffee Hollow trackways are true tracks as opposed to undertracks apply mainly to trackways A and C. Indeed, the footprints in trackway B are particularly faint, so of the three trackways this one is the best candidate for being composed of underprints, but we have no other reason for thinking this to be the case. The wrinkled texture of the surface of some trackway B prints (Fig. 10A), as already noted, suggests the presence of a fill layer covering true tracks.

Footprint Morphology and Preservation

As with many other sauropod trackways, manus prints of the three Coffee Hollow A-Male trackways present as sub-circular, elliptical, crescent-shaped, or hoof-shaped depressions (Figs. 7A, F, G, 10-13). Like manus prints of the Mayan Ranch trackway (Fig. 1), they are shallowly impressed (only a few to several cm maximum depth), but in some cases the shallowness is probably due in part to fill covering the footprint. Print outlines are particularly faint in the Middle (B) trackway (Fig. 10).

If the size of the prints as preserved is a true indication of the size of the manus, these three dinosaurs were among the bigger sauropod trackmakers known, both from the Glen Rose

Formation and from dinosaur tracksites more generally (Figs. 14-16). The Left (C) and Right (A) trackways are similar in manus print width, and about 25-35 % larger than manus prints of the Middle (B) trackway. If the prints as preserved were undertracks, it is possible that their dimensions could exaggerate the sizes of the autopodia that made them (cf. Farlow et al., 2006; Milàn and Bromley, 2006; Marty, 2008; Jackson et al., 2009, Castanera et al., 2012a; Thulborn, 2012; Xing et al., 2015a; Brusatte et al., 2016). As already discussed, however, the preservation of the prints, particularly of trackways A and C, suggests that they are true tracks rather than undertracks.

In well-registered sauropod manus or pes prints the sole shows impressions or wrinkles indicative of sole pads (cf. Farlow et al., 1989; Dalla Vecchia and Tarlao, 2000; Milàn et al., 2005; Platt and Hasiotis, 2006; Mateus and Milàn, 2010; Huh et al., 2003; Romano and Whyte, 2012; Castanera et al., 2016b; Hall et al., 2016). Occasionally the skin texture of the sole is recorded as an abutting polygonal pattern (Lockley et al., 1998, 2008; Currie et al., 2003; Platt and Hasiotis, 2006; Kim et al., 2010; Mateus and Milàn, 2010; Navarette et al., 2014; Piñuela Suarez, 2015; Castanera et al., 2016a; Fondevilla et al., 2017; Paik et al., 2017).

There is no indication of such sole scalation in the Coffee Hollow manus prints as preserved (Figs. 10-13). At a larger scale, however, the surface of the latex peels of some of the better prints (Fig. 13) shows a rough texture reminiscent of that which occurs on the sole of the hands and feet of elephants (cf. Hall et al., 2016), and/or as “pull-up” features created by suction as the foot is withdrawn from the sediment (Kvale et al., 2001). However, to the extent that the molded footprints had firmly adhering overtrack fill, the texture of the peels reflects the surface of the fill material rather than the soles of the trackmakers' forefeet.

If the Coffee Hollow footprints are true tracks, then the absence of pes prints cannot be due to differential preservation of manus and pes prints as undertracks. However, differential pressure might result in manus-only prints even if the tracks were true tracks, if there was more pressure loading on the forefoot than on the hindfoot (Falkingham et al., 2011a). A potential problem with the hypothesis of differential loading as a factor in creating Glen Rose Formation sauropod manus-only or manus-dominant trackways, however, is that to date wherever else sauropod trackways showing both forefoot and hindfoot impressions occur in this unit, the pes prints are always as deeply impressed as, or more deeply impressed than, manus prints (Fig. 17; also see Farlow et al., 1989, 2015; Farlow, 1992: figs. 10, 11).

On the other hand, support for the differential pressure hypothesis comes from the CertainTeed Gypsum mine (previously known as the Briar Site, Nashville, Arkansas), in the De Queen Formation, a sedimentary unit correlative to the Glen Rose Formation. Long sauropod trackways were first reported from this locality by Pittman and Gillette (1989). More recently, Platt et al. (2018) described theropod trackways and sauropod footprints from a different part of the same quarry. Dinosaur footprints at this site were interpreted as true tracks. In most sauropod trackways from the Briar site, manus and pes are about equally deeply impressed, but at one portion of the site, where the substrate at the time of track formation is thought to have been firm (Platt et al., 2018), manus prints are slightly deeper than associated pes prints (B.F. Platt, personal communication). Furthermore, there are manus prints in the same area of the quarry that are unaccompanied by pes prints (Platt et al., 2018). The sauropod prints from the Briar Site are morphologically similar to those from the Glen Rose Formation (Farlow et al., 1989; Pittman and Gillette, 1989). Consequently differential pressure cannot be excluded as a possible explanation for manus-only sauropod trackways in the Glen Rose Formation (Falkingham et al., 2011a).

Consistency of Measurements

Summary measurements for the three sauropod trackways are presented in Table 1, and internal correlations between different measurements of the same parameter within the HMTHC or HMNS data sets, and between the HMTHC and HMNS data sets, are presented in Table 2 and Figures 18 and 19. Some individual measurements differ markedly between the two data sets, due to differences in measurement protocols between the two teams, difficulties in measuring these sometimes faint prints, or both. Most mean and median values of footprint and trackway parameters, however, are gratifyingly very close (within a few centimeters of linear measurements, and a few degrees of angular measurements) between HMNS and HMTHC values of the same measurement; exceptions include some measures of trackway inner and outer width, paces, strides, and pace angulations. It should be noted, however, that the calculated means and medians are generally not based on the same number of measurements for the HMNS and HMTHC data sets, which may account for some of the differences in average values between the two data sets. Correlations between HMTHC and HMNS measurements of the same parameter (Table 2; Fig. 18) are generally good (Pearson's r at least 0.65, with $p <$

0.001); the lowest correlations are between measurements of trackway outer width (r = 0.559, p = 0.003), and between measurements of footprint rotation (which correlation is not statistically significant; r = 0.225; p = 0.532, but is based on a small sample size [N = only 10]).

HMTHC measurements of paces and strides using different reference points (print front margin vs. print center) have mean values (Table 1) that differ by less than 10 %, with step lengths measured from the front edges of the prints being longer than those measured from the print centers. The two different ways of measuring trackway inner width using the HMNS data set yield mean values that differ by 20-30 %, with the direct method yielding larger mean values than the estimate based on trackway diagrams. Not too much should be made of this discrepancy, however, because the two sets of measurements were made very differently. This highlights a warning for comparisons of trackway measurements among studies: before concluding that values differ between trackways described by different authors, one should be sure that the measurements were made the same way (Falkingham, 2016). In any case, the different ways of measuring paces in the HMTHC data set, and trackway inner width in the HMNS data set, are both highly correlated (Table 2).

Inter-relationships among Trackway Parameters

Some of the trackway parameters are geometrically related (Fig. 19). After removing the effects of trackmaker size (with manus print width serving as the size proxy), all of the measures of trackway width (inner, outer, and WAP) are unsurprisingly correlated with each other, and more interestingly, with pace length (Table 3), but either less strongly, or not at all, with stride length. Because pace as measured here is oblique to the trackmaker's direction of travel, this step length parameter is partly related to the trackway width to an extent that the stride is not.

Comparisons with Other Sauropod Trackways (Supplementary Table 1)

Unsurprisingly, the length of the step (measured either as the oblique pace or the stride) increases with increasing sauropod size (Fig. 14). Most manus-only trackways (including Bird's Mayan Ranch trackway) and manus-dominant trackways do not differ from those of standard trackways (those with manus and pes prints, other than those explicitly identified as manus-dominant trackways) in relative stride or oblique pace length. Coffee Hollow trackways A and C fall within the scatter of standard sauropod trackway points for both oblique pace and stride, and trackway B is on the edge of scatter for stride. Trackway B is different, however, in showing an unusually long oblique pace for the size of its manus prints.

All measures of trackway width also unsurprisingly increase with trackmaker size (Fig. 15), although the relationship between inner trackway width and manus width shows a great deal of scatter. It is tempting to attribute this scatter to the existence of wide-, medium-, and narrow-gauge trackways (Farlow, 1992; Lockley et al., 1994; Romano et al., 2007; Marty, 2008; Marty et al., 2010). However, for standard plus manus-dominant trackways, analyses of covariance of trackway width against trackway gauge (with manus print width as the covariate) show only one statistically significant difference between narrow-gauge trackways on the one hand, and medium- to wide-gauge trackways, on the other: that involving outer trackway width

(F = 8.059, p = 0.005, N = 70 narrow-gauge trackways and 80 medium-wide gauge trackways), and even that comparison shows very little difference, and considerable overlap, between the two groups (Fig. 15C). As with step lengths, most manus-only and manus-dominant trackways, including the Mayan Ranch trackway and Coffee Hollow A-Male trackway C, plot among points for standard sauropod trackways. Trackway A looks relatively a bit broader than usual in some comparisons, and Trackway B is especially wide in all comparisons—not surprising, given that trackway width is closely related to oblique pace length in sauropodomorph trackways (Table 3). However, trackway B is not unique in its breadth. A standard trackway from the Late Cretaceous of the southern Pyrenees, attributed to a titanosaur (Vila et al., 2013: Fig. 3B), is also quite broad (Fig. 15A).

In standard plus manus-dominant sauropodomorph trackways, the pace angulation shows a weak negative correlation with manus width (r = -0.160, p = 0.022, N = 206; Fig. 16A), with no difference between narrow-gauge and medium- to wide-gauge trackways (Fig. 16B). Manus-only and manus-dominant trackways, including those from Coffee Hollow, plot among the points for standard trackways, albeit among trackways with pace angulations on the low side, indicating a less linear, more zig-zagged, trackway pattern. The Coffee Hollow and Mayan Ranch trackways have lower pace angulations than typical sauropod trackways from the Glen Rose Formation.

Manus rotation (positive values = outward rotation, negative values inward rotation) also weakly decreases with increasing manus width in standard plus manus-dominant trackways (r = -0.198, p = 0.036, N = 113; Fig. 16C), again with no difference between narrowand medium- to wide-gauge trackways (Fig. 16D). Lallensack et al. (2018) also found trackways of small sauropods to have surprisingly large manus rotations (supination angles in their usage). Once again there is no difference between manus-only and standard trackways in this comparison. Manus rotation of trackway B regrettably could not be measured due to the poor preservation of the individual prints.

The pace angulation, relative trackway width (expressed as the ratio of trackway width/manus print width), and the stride/oblique pace ratio are inter-related (Fig. 19). For standard plus manus-dominant sauropod trackways, there is a strong positive correlation between pace angulation and the stride/oblique pace ratio (Kendall's tau-b = 0.784, Spearman's rho = 0.912, p for both statistics < 0.001, N = 201; Fig. 19B); both parameters are an expression of how linear as opposed to zig-zagged a trackway pattern is. Manus-only and manus-dominant trackways plot among points for standard trackways, with Coffee Hollow trackway A (Right trackway) falling among points at the low end of both variables (Fig. 19B); all three Coffee Hollow trackways (and less convincingly the Mayan Ranch trackway) plot well below points for typical Glen Rose Formation sauropod trackways. For standard plus manus-dominant trackways, relative trackway width is at least weakly negatively correlated with the stride/oblique pace ratio (inner trackway width/manus width: Kendall's tau-b = -0.396, Spearman's rho =-0.557, N = 117; outer trackway width/manus width: Kendall's tau-b = -0.336, Spearman's rho = -0.481, N = 153; width of angulation pattern/manus width: Kendall's tau-b = -0.381, Spearman's rho = -0.522, N = 81; p for all statistics < 0.001). Unsurprisingly, the more linear a trackway is, the relatively narrower it is. Manus-only and manus-dominant trackways again plot among standard trackways, but Coffee Hollow trackway B once again shows a particularly broad trackway (but not uniquely so) for its (rather low) values of the stride/pace ratio Fig. 19D).

Most standard sauropodomorph trackways show oblique paces that step off from the left manus to be about as long as oblique paces that begin with the right manus (Fig. 20). There is a slight suggestion, albeit one that is not quite statistically significant, that smaller sauropodomorphs stepped off with longer paces beginning with the left forefoot, while bigger sauropods had longer paces beginning with the right forefoot (standard plus manus-dominant trackways: Kendall's tau-b = -0.123, p = 0.073; Spearman's rho = -0.187, p = 0.063; N = 99 trackways). Most manus-dominant and manus-only trackways plot among standard trackways in this relationship. However, some manus-only sauropod trackways, including Coffee Hollow trackway A and some trackways from North Africa (Ishigaki and Matsumoto, 2009) show marked left vs. right stepping off asymmetry.

Forelimb Length vs. Manus Size in Sauropods

There is a great deal of scatter in the limited data presently available for the relationship between manus width and forelimb length in sauropods (Fig. 21). Furthermore, both the width of the intact manus, and the length of the forearm, would have been somewhat larger in the living animals, due to the presence of cartilage and other soft tissues, than in skeletal mounts (cf. Bonnan et al., 2010; Holliday et al., 2010; Tsai et al., 2018). In any case, the data suggest that the Coffee Hollow sauropod trackmakers could have had forelimbs as much as 4 or 5 m in length.

DISCUSSION

Explanations for manus-only sauropod trackways fall into two categories: preservational or formational artifacts in prints created during normal walking (differential pressure exerted by the manus and pes on the substrate) or unusual behavior ("swimming"). In the spirit of multiple working hypotheses, we now consider the pros and cons of each of these interpretations as applied to the Coffee Hollow A-Male manus-only sauropod trackways.

Preservation Artifact (and Perhaps More than One Kind of Trackmaker?)

Because differential autopodial pressure plausibly accounts for most sauropod manus-only trackways (cf. Lockley and Rice, 1990; Vila and Galobart, 2005; Falkingham et al., 2011a; cf. Falkingham et al., 2010, 2011b), this hypothesis must be considered a potential explanation for the manus-only nature of the Coffee Hollow trackways. Although preservation as undertracks probably does not apply to the Coffee Hollow prints, their very shallowness elicits suspicion that the absence of pes prints in these trackways might be due to a formational/preservational artifact, with relatively greater pressure exerted on the substrate by the forefeet than by the hindfeet. As already noted, in presently known sauropod trackways from the Glen Rose Formation that consist of both manus and pes prints, whether faintly/shallowly registered or deeply impressed, the manus prints are not more deeply impressed than pes prints (Fig. 17). The Briar Site in Arkansas, on the other hand, preserves associated sauropod manus-pes sets similar to those from Texas, in a few of which forefoot prints are deeper than the hindfoot prints; isolated manus tracks occur nearby. Consequently unusual depth distributions of manus and pes prints in sauropod trackways from the Cretaceous of the U.S. Gulf Coast region could well be responsible for the unusual occurrence of manus-only trackways in the Glen Rose Formation. If the Arkansas trackmakers were all the same kind of sauropod, this would indicate that under different circumstances a given sauropod was capable of making trackways with very different manus vs. pes depth distributions.

Another possibility is that the Coffee Hollow and Mayan Ranch trackmakers were made by a different kind of sauropod, with a different location of the animal's center of mass, and different pressure loading on the forefeet and hindfeet, than the makers of most other Glen Rose Formation sauropod trackways. At present, three sauropod genera are known from the Trinity Group of Texas (D'Emic, 2013; cf. Gallup, 1989; Tidwell et al., 1999; Wedel et al. 2000a, b; Rose, 2007; D'Emic and Foreman, 2012; Britt et al., 2017): the somphospondylians *Sauroposeidon* and *Astrophocaudia*, and the brachiosaurid *Cedarosaurus*. Of these three taxa, the pes is known only for *Cedarosaurus*, and the manus of all three is unknown. Farlow et al. (1989) assigned the name *Brontopodus birdi* to sauropod tracks from the Glen Rose Formation of Texas, with a trackway from R.T. Bird's Paluxy River track quarry serving as the type specimen. Although the morphology of the pes of *Cedarosaurus* is consistent with that of hindfoot prints of *Brontopodus* as displayed at the Paluxy River sites (Farlow et al., 1989), the same could well have been true of the pedes of one or both of the other two Trinity sauropods. On the basis of present knowledge, it is impossible to say which, if any, of the known Trinity sauropods was the *Brontopodus*-maker, and whether *Brontopodus* was made by only one sauropod taxon.

Although morphological details of the manus prints of the three Coffee Hollow A-Male sauropod trackmakers are not particularly clear, their shape seems consistent with *Brontopodus*. The manus prints of Coffee Hollow sauropods A and C are comparable in size and preservation to the manus prints of the Blanco River sauropods (Fig. 17D), and occur at the same stratigraphic level, suggesting that they were produced by the same kind of trackmaker. Pes prints of the Blanco River trackways, however, are perhaps different enough in appearance from their Paluxy River counterparts that the big south Texas prints might eventually be assigned to a different ichnospecies than *B. birdi* (contra Farlow et al., 1989). Perhaps one of the Texas sauropods did have a pedal structure different than that of *Cedarosaurus*.

The classic Paluxy River *Brontopodus* are unquestionably true tracks. If the Coffee Hollow and Blanco River prints also are true tracks, or close to being true tracks, their makers were likely bigger animals than most of their north Texas counterparts, which might further support the conclusion that the south Texas dinosaurs were a different kind of sauropod.

If the Coffee Hollow trackmakers were different forms than the Paluxy River trackmakers, the depth distribution of manus and pes prints seen in the Paluxy River tracks (Fig. 17A) might not also have characterized the Coffee Hollow sauropods. If the Coffee Hollow trackways had been made by the brachiosaurid *Cedarosaurus*, it would be entirely expected that the forelimbs exerted more pressure on the ground than the hindlimbs, potentially resulting in manus-only trackways (Henderson, 2006; Falkingham et al., 2011a). However, keep in mind that the pes of *Cedarosaurus* is a good match for the morphology of the Paluxy River pes prints, which are consistently as deep as or deeper than manus prints. The same is true for sauropod trackways at other sites in the Glen Rose Formation (Fig. 17B-D), including the big Blanco River prints.

The differential pressure hypothesis for the creation of Glen Rose Formation manus-only sauropod trackways might receive considerable support from discovery of more complete fossils of the three sauropod taxa known from the skeletal fauna. If it were established that one of the sauropod taxa had the morphology and relative sizes of the manus and pes, and a position of the animal's center of mass, consistent with the production of pes prints as deep or deeper than manus prints (as at the Paluxy River tracksites), while another sauropod from the Glen Rose Formation had the autopodial and body proportions consistent with the production of manus-dominant trackways, this would tip the scales toward interpreting Glen Rose Formation manus-only sauropod trackways as being formational or preservational artifacts.

Even more compelling support for this hypothesis would be discovery of manus-dominant sauropod trackways somewhere in the Glen Rose Formation, with manus prints more deeply impressed than pes prints, as at the Briar Site in Arkansas. This would indicate either that a single species of sauropod was capable of altering its walking to create standard and manus-dominant trackways as it adjusted to different substrate conditions, or that there was more than one kind of footprint-making sauropod in Texas during the Early Cretaceous, with differences in the location of the center of mass and/or the relative sizes of the front and rear autopodia, between/among the different trackmakers (Henderson, 2006; Falkingham et al., 2011a).

As previously noted, Coffee Hollow sauropod trackways A and B are unusually broad for the size of their makers (Fig. 15), but not uniquely so. Vila et al. (2013: Fig. 3B) illustrated a standard sauropod trackway from the southern Pyrenees that is similarly broad across both the manus and pes portions of the trackways. If such a trackway were to be found in the Glen Rose Formation, and especially if its manus prints were deeper than its pes prints, this would provide the strongest possible support for interpreting the Glen Rose manus-only sauropod trackways as artifacts of differential autopodial pressure on the substrate. Equally or more interestingly, given the differences in overall size, pace length and trackway width (relative to manus width), and relative depth distribution of manus and pes prints between most Glen Rose Formation sauropod trackways (Fig. 17) and this hypothetical trackway, it would strongly suggest the representation of more than one kind of track-making sauropod in the ichnofauna, consistent with the skeletal fauna.

Unusual Behavior

Until such a hypothetical trackway is found in the Glen Rose Formation, though, an alternative hypothesis for the Coffee Hollow manus-only trackways must be considered. For at least trackways A (Right) and especially B (Middle), the trackway pattern differs enough from what is routinely seen in Glen Rose Formation sauropod trackways to suggest that these animals might have been doing something out of the ordinary. Sauropod B took unusually long oblique paces (Fig. 14) and made an unusually broad trackway (Fig. 15) for its size. Sauropod A similarly had a rather broad trackway (Fig. 15), and also showed very marked asymmetry between steps that began with the left as opposed to the right forefoot (Fig. 20A).

Note that if the three Coffee Hollow trackways, contrary to our interpretation, were in fact undertracks, the likely increase in footprint dimensions of undertracks relative to true tracks might exacerbate the hermeneutic problem of the unusual breadth of trackways A and B, because their makers could have been smaller animals than their footprint dimensions would otherwise indicate. Furthermore, any increase in apparent manus print size due to preservation as undertracks would also be expected to cause the trackway to appear narrower than in a corresponding “true” trackway.

Although hypothesized unusual behavior would not necessarily involve “swimming,” it is worth considering the possibility that R.T. Bird might have been correct in thinking that (at least some?) Glen Rose Formation manus-only sauropod trackways were made by dinosaurs that were wading in water deep enough for their makers to punt, pulling themselves along by their forefeet, while their hind legs floated above the bottom. Some analyses of the location of the center of buoyancy relative to the center of mass in certain sauropods (forms related to camarasaurs and brachiosaurs: Wilson and Fisher, 2003; Henderson, 2004) suggest that this would cause the hindquarters of a wading dinosaur to lift off the bottom while the forefeet were still pushing against the substrate. Such a punting sauropod might then be able to glide with its body supported by the water, thereby taking longer oblique paces and creating a wider trackway than would be possible for the same animal’s unsupported body. If much of the dinosaur’s weight was buoyed up by the water, this might also result in shallowly impressed manus prints.

On the other hand, any buoyancy/punting hypothesis for the Coffee Hollow manus-only trackways would require the same center of mass interpretation that would result in manus-dominated trackways that include impressions of both forefeet and hindfeet. One would expect that a sauropod “back-heavy” enough to be making deeper pes than manus prints during routine walking would likely punt with its hindfeet rather than its forefeet. In contrast, it would be a “front-heavy” walker of the kind likely to produce manus-dominant trackways that would be the expected candidate to be a forelimb-punter. On the face of it, this makes it hard to imagine that the sauropods responsible for the Paluxy River footprints would have been manus-only punters.

Ironically, then, it might be that discovery of manus-dominant sauropod trackways in the Glen Rose Formation would not only make a differential pressure explanation for manus-only sauropod trackways more plausible, but also be a prerequisite for supporting the hypothesis that manus-only trackways could have been made by punting sauropods! The best evidence for forefoot-supported punting sauropods would therefore be discovery of trackways in which pes prints were absent, but the manus prints were fairly deeply impressed, indicating a soft substrate in which pes prints would likely have registered, had the dinosaurs actually been normally walking rather than punting. This is not true of the shallowly impressed Coffee Hollow A-Male trackways.

Other than being manus-only, there is nothing unusual in the pattern of trackway C (Left trackway), and the same is true of R.T. Bird's manus-dominated Mayan Ranch trackway. However, if trackway C was made at the same time as trackways A and B, and if the latter two trackways were in fact made by punters, it would not be unreasonable to think that the same was true of trackway C.

Although aquatic animals that engage in underwater pedestrianism may do so while completely submerged (cf. Zug, 1971; Brand, 1979; Martinez, 1996; Martinez et al., 1998; Coughlin and Fish, 2009; Grigg and Kirshner, 2015; Farlow et al., 2018a, b), the likely pneumaticity of their bodies makes it unlikely that sauropods could have done the same (Henderson, 2004). This in turn sets an upper limit to how deep the water through which hypothetical punting sauropods moved could have been: probably no more than a few to several meters (Figs. 21, 22).

Conclusions

The presently available evidence does not decisively rule out either the differential pressure or the unusual behavior hypothesis for the origin of the Coffee Hollow A-Male manus-only sauropod trackways. On balance, however, comparison of these trackways with sauropod trackways from other ichnofaunas provides stronger support for the differential pressure hypothesis, with the especially interesting, possible corollary hypothesis that more than one kind of sauropod is represented in the Glen Rose Formation ichnofauna. We have described the kinds of trackway evidence that would allow an unambiguous verdict in favor of each of the two hypotheses. Now we can hope for future discoveries in the field to deliver that evidence.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of R.T. Bird and Wann Langston. We commend Ms. Gail Flach and her associates for their recognition of the importance of the site, and for interrupting quarry work while study proceeded. Numerous volunteers assisted in cleaning and documenting the tracksite. For two days, 21 members of the Heritage Museum of the Texas Hill Country volunteered to clean, measure, photograph, trace, and map the tracksite. We thank Matt Bonnan, Don Henderson, Christian Meyer, Jens Lallensack, and Brian Platt for useful discussions or unpublished data, and Brian Platt (again) and the University of Arkansas Center for Advanced Spatial Technologies for providing the LIDAR image of a portion of the Briar Site (CertainTeed Gypsum mine). Hendrik Klein and John Foster made several helpful comments on the manuscript. Jim Whitcraft assisted in the production of illustrations. This research was supported by a grant from the National Geographic Society to Farlow. The Department of Library Services of the American Museum of Natural History kindly granted permission to reproduce some of R.T. Bird's images of the Mayan Ranch site.

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Figure 1. R. T. Bird's Mayan Ranch "swimming" sauropod trackway. **A - B**. Photograph and map of the trackway as seen in 1940. Most of the footprints were made by the left and right forefeet of the dinosaur; the single pes print noted by Bird is labeled. **C**. Cast (negative copy) of a right manus print from the trackway made by Farlow. Note the hoof-like shape of the print; anterior to the top. Maximum print width = 62 cm. **D**. Bird's cartoon of how he interpreted the progression of the trackmaker. Panels A, B, and D from Bird (1944), and reproduced courtesy of the American Museum of Natural History.

Figure 2. Coffee Hollow A-Male tracksite map. Inset shows location of the site in the state of Texas.

Figure 3. Ground-level views of the three Coffee Hollow A-Male trackways. **A**. The HMTHC field crew at work, cleaning and documenting the site. Individual footprints are labeled following HMTHC naming conventions. **B**. Detail of trackway A (Right trackway of HMNS). **C**. Detail of trackway C (Left trackway of HMNS).

Figure 4. Overall tracksite images. **A.** Digital model of the tracksite created from digital photographs taken by the HMTHC field crew. Color and contrast are artificially altered to enhance the distinctiveness of the footprints. Some footprints have a ghostly "double-strike" configuration due to imperfections in the model. **B.** Image of the tracksite made from

photographs taken by the HMNS field crew using a drone; scale bar in figure applies specifically to this panel. In both images footprints are labeled using HMTHC naming conventions.

Figure 5. Stratigraphic section of the Glen Rose Formation as exposed at the Coffee Hollow A-Male tracksite.

Figure 6. Diagram (redrawn from field notes) illustrating how HMNS footprint and trackway measurements were made. To facilitate comparisons, the HMTHC labels for footprints are added to the diagram. Numbers along the left margin (32 – 56) indicate some of the four-foot increments marked off on the field diagram. Individual footprint widths are indicated (in mm) above each print; thus the width of print C78 is 630 mm. A line is run through the trackway along its direction of travel, and its orientation relative to magnetic north indicated (bottom of figure; in this case the direction of travel is 287°. The measured distance from the inner rear edge of the footprint to the reference line is indicated above a short line segment running from the edge of the print to the reference line; for footprint C81, this distance is 615 mm. A line segment running across the rear margin of the print forms an angle with the reference line, and is drawn on the diagram next to the footprint; for print C78, the angle is 73°. The bearing of the footprint relative to the dinosaur's direction of travel will be perpendicular to the line running across the print's rear margin.

Figure 7. Cross-sections and fill associated with footprints. **A – C**. Manus print A99 (Right trackway). **A**. The broken footprint in situ. **B.** Oblique view of the footprint, seen from the top left of the print as displayed in panel A, showing part of a section across the footprint. Note slight displacement rim that slopes down into the bowl-shaped depression of the footprint proper. **C**. Pieces of the cross-section across the footprint. **D**. Two facing sides of a polished section through a rock piece interpreted as overtrack fill of A97 or a nearby print. The lower view is printed with left and right reversed, so that its face is directly comparable with that of its counterpart in the upper view. This piece sat atop the material interpreted as the track layer; if this interpretation of the track layer is correct, the base of the fill would be at the bottom of the two sections illustrated here. **E - F**. Fill of manus print (either C83 or a nearby print in the Left trackway). **E**. Cut piece through the fill (the label on the slab identifying this piece as coming from print C70 is incorrect). The bottom of the piece as illustrated here sat atop the footprint as exposed in the quarry. **F.** View of the underside of the fill piece, showing the location of the cut piece from panel E. **G.** Broken fill piece partially covering print A86, with ripples atop the fill.

Figure 8. Thin sections through pieces of the track layer and overtrack fill. Scale bars = 1 cm. **A – B**. Several sections (labeled with red letters) through the left portion of the slab cut across manus print A99 shown in Figure 7C; the sections were cut through the underside of the footprint as illustrated in Figure 7C. **A.** The base of the footprint occurs along the marginal edge of section A3, and the top edges of sections B2 and B4. Details of portions of the columns

labeled 1 - 3 appear in Figure 9. **B**. Interpretive drawing showing the four microstratigraphic layer units observed vertically across the sections. Note especially the compression of unit 4, relative to underlying layers, beneath the footprint floor as opposed to outside the print (column 1 vs. columns 2 and 3 in panel A); also see Fig. 9A-C. **C – D**. Thin sections (**C**) and interpretive drawing (**D**) of the seven microstratigraphic units observed vertically across the sections through the overtrack fill of manus print A97 (or a nearby print in the trackway); compare with Fig. 7D, which shows the two opposing faces of the same surface. An enlarged image of a portion of the column labeled “Detail” is shown in Figure 9.

Figure 9. Details of thin sections through cross sections of a footprint and fill. Scale bars = 2 cm. **A – C**. Portions of columns 1 (beneath the footprint), 2 (through and beneath the displacement rim), and 3 (outside the footprint), respectively, from Figure 8A. Numbers along the margins of the slices label four sequential layer units (Fig. 8B), with tic marks indicating boundaries between the units. **D**. Portion of the section through footprint fill labeled “Detail” in Figure 8C. Numbers along the margin of the slice label the seven sequential layer units through the fill (Fig. 8D), with tic marks indicating boundaries between the units.

Figure 10. HMTHC B (HMNS Middle) trackway footprints. The brightness and contrast of photographs have been manipulated to increase the clarity of print outlines. Prints with an odd number are rights, and prints with an even number are lefts. See Figure 2 for locations of prints in the trackway. **A**. B88. **B**. B89. **C**. B90. **D**. B93. **E.** B94. **F**. B96 overlapping print C97.

Figure 11. HMTHC C (HMNS Left) trackway footprints. The brightness and contrast of photographs have been manipulated to increase the clarity of print outlines. Prints with an odd number are rights, and prints with an even number are lefts. See Figure 2 for locations of prints in the trackway. **A**. C84. **B**. C85. **C**. C86. **D**. C87. **E**. C88. **F**. 89. **G**. C90. **H**. C91. **I**. C93. **J**. C94. **K**. C96. **L**. C98. **M**. C99.

Figure 12. HMTHC A (HMNS Right) trackway footprints. The brightness and contrast of photographs have been manipulated to increase the clarity of print outlines. Prints with an odd number are rights, and prints with an even number are lefts. See Figure 2 for locations of prints in the trackway. **A**. A75. **B**. A76. **C**. A77. **D**. A78. **E**. A79. **F**. A80. **G**. A81. **H**. A82. **I - J**. A83. **I.** Footprint in situ. **J**. Latex negative copy (cast) of the print; note large joint and solution feature cutting across the print. **K**. A84. **L**. A85. **M**. A87. **N**. A88. **O**. A89. **P**. A97.

Figure 13. Negative copies (casts) of Coffee Hollow A-Male sauropod footprints. Note the irregular texture of what is either the print sole or the surface of footprint fill. **A - B.** Prints from one of the large sauropods (probably [Right] trackway A). **A**. Maximum diameter across the print = 67 cm; maximum relief = 7 cm. **B**. Maximum diameter = 61 cm; maximum relief = 3-4 cm. **C - D**. Footprint from the middle (B) trackway. **C**. Photograph of the print; maximum diameter = 48 cm. **D**. Digital model of track relief; the images are rotated clockwise to the view

in panel C. Scale bar = 10 cm. Top row = plan view, bottom row = oblique view. Warm colors in the heat maps indicate deeper parts of the footprint.

Figure 14. Comparison of step lengths between Coffee Hollow A-Male sauropod trackways, and those of sauropods or basal sauropodomorphs from other localities. HMNS and HMTHC in the figure key refer to separate measurements made by the Houston Museum of Natural Science and by the Heritage Museum of the Texas Hill Country, respectively, but the names labeling the trackways in the key are HMTHC usage; HMTHC trackway A is the HMNS Right trackway, HMTHC trackway B is the HMNS Middle trackway, and HMTHC trackway C is the HMNS Left trackway. Other trackway data are from Supplementary Online Material Table 1; all data are either trackway means or single measurements (when only a single measurement could be made on a trackway). The Glen Rose Fm trackway label in the figure key is for trackways from that unit consisting of prints of both manus and pes. **A**. Oblique pace length of the manus portion of the trackway vs. manus print width (here and elsewhere, a proxy for trackmaker size). **B**. Stride length of the manus portion of the trackway vs. manus print width. Note that trackway B (Middle trackway) shows a fairly long pace for its size, but not so much its stride.

Figure 15. Measures of manus trackway width vs. manus width. Labeling conventions as in Fig. 14. All data are trackway means or single measurements. **A**. Inner trackway width. **B - C**. Outer trackway width. **B.** All trackways. **C**. Standard plus manus-dominant trackways, differentiated on the basis of trackway gauge (narrow-gauge vs. medium- to wide-gauge). **D**. Width of

angulation pattern. In some comparisons trackway A presents as relatively broad. Trackway B is unusually broad in all relevant comparisons.

Figure 16. Pace angulation and manus print rotation as a function of trackmaker size in sauropod and basal sauropodomorph trackways. **A - B**. Pace angulation vs. manus print width. **A**. All trackways. **B**. Standard plus manus-dominant trackways, differentiated on the basis of trackway gauge. **C - D**. Manus rotation vs. manus width. **C**. All trackways. **D**. Standard trackways. Some manus-dominant trackways plot within the scatter for standard trackways in the pace angulation vs. manus width comparison, but two manus-dominant trackways show large pace angulations for the size of their prints. (Data about manus rotation were unavailable for trackways identified as manus-dominant.) Manus-only trackways (including the Coffee Hollow trackways) plot within the scatter for standard trackways in both sets of comparisons; the Coffee Hollow trackways do show pace angulations on the low side, though.

Figure 17. Relative depth of impression of manus and pes prints in sauropod trackways from the Lower Cretaceous of the U.S. Gulf Coastal plain. **A - C.** Glen Rose Formation, Texas. In these trackways pes prints are impressed as deeply as, or more deeply than, manus prints. **A.** Digital model of a negative copy (cast) of a right manus-pes set from the Paluxy River, Dinosaur Valley State Park, Somervell County (Farlow et al., 2015). Cool colors indicate greater depth. **B - C**. Trackways in situ; meter stick provides the scale. Color and contrast have been manipulated to enhance distinctness of prints. **B**. Slightly oblique view of a right manus-pes set of a shallowly

registered trackway, South San Gabriel River, Williamson County. The dinosaur was moving away from the viewer, with the meter stick positioned along the trackway midline; pes print length 74 cm. **C**. Oblique view of a right manus-pes set of a very large sauropod, Blanco River, Blanco County. The manus print is 65-70 wide, and the pes print 110 cm long. **D**. LIDAR image of a portion of the Briar Site (De Queen Formation, CertainTeed Gypsum mine, Nashville, Arkansas). Ellipses surround two sauropod manus-pes sets; width of the manus in the upper set about 53 cm, and width of the manus in the lower set about 40 cm. The manus prints are slightly more deeply impressed than their associated pes prints (B.F. Platt, personal communication). Note the presence of several manus prints without associated pes prints. Other footprints are attributed to large theropods. Image courtesy of Platt and the Center for Advanced Spatial Technologies, University of Arkansas.

Figure 18. Comparisons between HMTHC and HMNS measurements. Data cases are individual measurements for the three trackways; the same legend applies to all panels. **A**. Manus width. **B**. Oblique pace. **C**. Pace angulation. **D**. Trackway inner width. **E**. Trackway outer width. **F**. Manus print rotation.

Figure 19. Interrelationships among trackway parameters. Panels A and C plot individual measurements for each of the three Coffee Hollow trackways, using HMTHC data; panels B and D plot trackway means or single measurements for the Coffee Hollow (both HMNS and HMTHC data) and other sauropod and basal sauropodomorph trackways. **A - B**. The pace angulation and

the stride/oblique pace ratio are positively correlated. **A**. Trackway A (Right trackway) shows lower values of both the pace angulation and the stride/pace ratio than the other two Coffee Hollow trackways. **B**. All three Coffee Hollow trackways plot at the low end of the pace angulation: stride/ oblique pace ratio relationship, but among points for standard sauropod trackways. Other manus-only, and also manus-dominant, trackways similarly plot among the trend defined for standard trackways. **C - D**. Trackway inner width/manus width ratio vs. stride/oblique pace ratio. **C**. Each of the three Coffee Hollow trackways plots in a different region of morphospace, with trackway B showing a particularly broad trackway relative to the stride/pace ratio. **D**. Across sauropod trackways more generally, relative trackway inner width decreases with increasing values of the stride/oblique pace ratio. Manus-only and manus-dominant trackways mostly plot among standard trackways. Coffee Hollow trackway B (Middle trackway) and a "standard" trackway of a small sauropod from the Early Cretaceous of China (Chabu 8D Trackway S4; Lockley et al., 2018) have unusually broad trackways in this comparison.

Figure 20. Asymmetry of manus oblique pace lengths in sauropod and basal sauropodomorph trackways. **A**. Ratio of the mean value of paces beginning with the left foot, to the mean value of paces beginning with the right foot. Different symbols are used for the Coffee Hollow trackways to denote values obtained using different reference points for measuring pace lengths. Most manus-only or manus-dominant trackways plot among data cases for standard trackways, but Coffee Hollow trackway A and manus-only trackways from North Africa (Ishigaki

and Matsumoto 2009b) show more extreme values. **B**. Frequency distribution of the pace asymmetry ratio in different manus trackway categories. Most trackways in all categories show fairly similar values of paces beginning with the left, as opposed to the right, manus, but some manus-only trackways show more extreme values.

Figure 21. Forelimb length vs. manus width in mounted sauropod skeletons. Some of these points should be viewed as very rough approximations due to extensive reconstruction of missing elements in the skeleton, particularly around the autopodia**.** Key to specimens: *Amargasaurus* (Museo Argentino de Cinencias Naturales 'Bernardino Rivadavia', Buenos Aires MACN N-15); *Apatosaurus* (Carnegie Museum of Natural History CM 3018); *Dicraeosaurus* (Berlin Museum für Naturkunde MfN MB.R composite mount, with majority of material from individual m, and remaining material from individual o [Heinrich 1999]); *Diplodocus* (Denver Museum of Natural Science DMNS 1494); *Dreadnoughtus* (Museo Padre Molino, Río Gallegos, Argentina MPM-PV 1156; 3D files from Lacovara et al 2014—this point is particularly problematic, because the manus is a total reconstruction); *Giraffatitan* (Berlin Museum für Naturkunde MfN MB.R mount, primarily based on MfN MB.R.2181); *Jobaria* (Australian Museum, Sydney MNN TIG mounted cast of several overlapping individuals, mainly MNN TIG 3); *Mamenchisaurus* (Institute for Vertebrate Paleontology and Paleoanthropology IVPP multiple specimens, primarily IVPP V456-458); *Patagosaurus* (cast based on Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires PVL 4170); *Rapetosaurus* (Field Museum of Natural History FMNH PR 2209); *Sauroposeidon* (*Paluxysaurus*) (Fort Worth Museum of Science and History FWMSH 93B-10).

Figure 22. A whimsical exploration of the punting hypothesis for manus-only sauropod trackways (cartoon by R.T. Bakker). The sauropods are interpreted as brachiosaurids, with longer forelimbs than hindlimbs, unlike R.T. Bird's interpretation (Fig. 1D). The difference in size between the two dinosaurs in the cartoon is probably greater than that between the two large and the smaller sauropod at Coffee Hollow (Table 1); it is unlikely that a punting sauropod could have been completely submerged, as the smaller dinosaur in the cartoon is depicted.