View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by Bournemouth University Research Online

Soft-sediment deformation below mammoth tracks at White Sands National Monument (New Mexico) with implications for biomechanical inferences from tracks

Matthew R. Bennett[1], *David Bustos*[2], *Matteo Belvedere*[1], *Patrick Martinez*[2], *Sally C. Reynolds*[1], *Tommy Urban*[4]

[1] Institute for Studies in Landscapes and Human Evolution, Bournemouth University, Poole, BH12 5BB, UK.
[2] National Park Service, White Sands National Monument, P.O. Box 1086, Holloman AFB, NM 88330, USA.
[4] Department of Classics, Tree-ring Laboratory, Cornell University, Ithaca, NY 14853-3201, USA.

*Correspondence to: Matthew R. Bennett [mbennett@bournemouth.ac.uk]

Abstract

Implicit in any biomechanical analysis of tracks (footprints), whatever the animal, is the assumption that depth distribution within the track reflects the applied plantar pressure in some way. Here we describe sub-track deformation structures produced by Proboscidea (probably *Mammuthus columbi*) at White Sands National Monument (WHSA) in New Mexico. Patterns of sub-surface deformation are consistent with the plantar pressure data for modern Proboscidea, but do not reflect track morphology. Our work cautions against over interpreting track topology of any large animal, including extinct animals such as sauropods, in terms of their biomechanics unless the subsurface stratigraphy and associated variation in shear strength is known.

Key words: ichnology, mammoths, footprints, Proboscidea, sub-track deformation.

Highlights:

- Proboscidean tracks show sub-track deformation structures.
- Deformation structures map onto the plantar pressure records of modern elephants.
- Indicate total strain response to trackmaker.
- Observations relevant to biomechanical inferences.
- Relevant to biomechanics of other large vertebrates, such as sauropods.

1. Introduction

As the foot of any large animal makes contact with a deformable substrate and the yield stress of that substrate is exceeded, strain will result both via material compression and displacement. The result is a depression (footprint or track) that will remain once the foot is removed, assuming the elastic limit of the substrate is exceeded and the material strength is sufficient to hold the track walls. The track provides a record, unless destroyed by subsequent taphonmic processes, overprinting or erosion, of the animal's presence, foot anatomy/size, behavioural biology and potentially biomechanics. Fundamental in any biomechanical interpretation of a track is the assumption that spatial variation in depth of the plantar contact-surface, equates in some form to patterns of applied plantar pressure. Bates et al. (2013) showed for human footprints that this only holds for shallow tracks. Deformation below the true track (or interface between sediment and foot) may accommodate strain, complicating this fundamental assumption (Graversen et al., 2007) and so called 'transmitted pressure' has been explored in a number of dinosaur track studies (e.g., Milàn and Loope, 2007; Lüthje et al., 2010; Thulborn, 2012,). Documenting different styles of deformation below a track in relation to plantar pressure therefore has the potential to contribute data to the biomechanical interpretation of tracks. However such data are rarely well-exposed on lithified ichno-surfaces and consequently such descriptions associated with large animals are comparatively rare in the literature (Graversen et al., 2007; Marty, 2008). Here we report sub-surface deformation structures below unlithified mammoth tracks at White Sands National Monument (WHSA, New Mexico) thereby contributing data to help understand this type of latent deformation. We relate this deformation to plantar pressure observations made for modern elephants (Panagiotopoulou et al., 2012, 2016).

2. Study site and methods: White Sands National Monument

Ichnofossils of extinct Rancholabrean fauna at White Sands National Monument (WHSA) in New Mexico comprise one of the largest concentrations of Cenozoic vertebrate tracks in North America (Fig. 1; Lucas et al., 2007). The tracks are visible only under specific moisture conditions (Bustos et al., 2018; Fig. 2A), although latent mammoth and giant ground sloth tracks have been successfully imaged via geophysics at WHSA (Urban et al., 2018). Tracks and trackways of humans, mammoth (Proboscidea), ground sloth (Folivora), canid and felid (Carnivora), and both bovids and camelid (Artiodactyla) are present (Fig. 1A). The tracks occur close to the surface of a playa (Alkali Flat) and are impressed into thinly bedded gypsiferous and siliciclastic muds and sands. These sediments were deposited along the margins of Pleistocene paleo Lake Otero (Allen et al., 2009), located in the north-south trending Tularosa Basin. Wind erosion of the former lake floor excavated lacustrine and lake-margin deposits to the level of the current playa and supplied sand to adjacent gypsum dunes.

This work is based on three localities. On the western shore of the playa the distal reaches of alluvial fans, originating in the San Andres Mountains, cut through sediments associated with high lake stands of Lake Otero and grade out over gypsiferous lake sediments that form the current playa floor (Fig. 1B). At a number of locations these fans contain large oval-shaped tracks (Fig. 2A, B and C) that link to form trackways interpreted elsewhere in the basin (Lucas et al., 2007; Pasenko, 2017) as being formed the passage of proboscideans, probably Columbian mammoth (*Mammuthus columbi*), although mastodon fossils are also known from the basin (Morgan and Lucas, 2005). In the distal reaches the fan sediments consist of horizontally stratified sand and silts with multiple shallow troughs/scours, and are between 500 and 200 mm thick, with longitudinal gradients of as little as 1 or 3 degrees. These fans are still active and receive occasional sheet wash during extreme rainfall events. However most of the discharge is confined to troughs 1 to 5 m wide and 20 to 30 mm deep which cut the fan surface.

Locality-2 is also situated on the western side of the current playa where extensive areas of interbedded peat and gypsum-rich silts outcrop at the surface. These appear to be linked to shallow canyons cut into the fans and relict deposits of Lake Otero; the peats date from between 22 and 33 kyr B.P. (Bustos et al., 2018). The third locality (Locality-3) is located on the eastern side of the playa in gypsiferous silts. Precise geochronology for these tracks at WHSA is not available, although a Terminal Pleistocene age is indicated by the co-existences of tracks of both humans and mega-fauna (Bustos et al., 2018). Sediments of the highest lake stands of Lake Otero have been dated to 15.56 kyr B.P. at two sites and represent an approximate age for the commencement of deflation of Lake Otero to the height of the current playa (Alkali Flat). Organic matter below the playa surface gives age ranges of 20 to 33 kyr B.P. and sediments from eroded lake remnants forming marginal escarpments have age ranges of 33 kyr to 10 kyr B.P. (Bustos et al., 2018). The most parsimonious interpretation of these data is that the tracks were made sometime before 10 kyr B.P. and after 15.56 kyr B.P. when the palaeo Lake Otero lake bed began to erode (Fig. 1B).

Tracks were identified in the field and mapped using a total station. Cross-sectional trenches were hand dug along the long axis of selected tracks, and the sections were photographed and described in the field using the facies codes of Miall. (1977). A second field site on the eastern side of Alkali Flat was also examined. Where tracks have been excavated they are documented individually using photogrammetry (DigTrace, www.digtrace.co.uk; Bennett and Budka, 2018) and orthorectified mosaics were constructed using Agisoft PhotoScan Pro (Version.1.4.4, www.Agisoft.com). Matthews et al. (2016) provides a review of close quarter photogrammetry.

3. Locality-1

This site consists of an east-west transect down the maximum gradient of a shallow alluvial fan extending over underlying gypsiferous silts on which a series of tracks and trackways were visible (Figs 2C and 3A). Surface definition of the tracks is poor, but, despite this, a series of tracks can be mapped and several tracks linked into trackways (Fig. 3A). The tracks are oval to circular in shape with axial-lengths between 300 and 550 mm based on surface expression, which probably exaggerates the true dimensions (Fig. 2B). The tracks are similar to mammoth tracks described previously at WHSA (Lucas et al., 2007) and ascribed to the ichnospecies *Proboscipeda panfamilia* as defined by McNeil et al. (2007). The ichnogenus *Proboscipeda* was erected by Panin and Avram (1962, *Proboscipeda enigmatica*) who defined it with respect to proboscidean tracks from the Miocene of Romania. Scrivner and Bottjer (1986) and Reynolds (1999) used *Proboscipeda* sp. more generally and it is preferred to the ichnogenus *Stegomastodonichum* (Aramayo and Bianco 1987, Remeika, 2001) or *Mammuthichnum* (Remeika, 2006) as discussed by Lucas et al. (2007). Late Pleistocene age mammoth body fossils have been recovered from the Otero Formation (Morgan and Lucas, 2005) and on this basis Lucas et al. (2007) ascribes the tracks at WHSA to mammoths. They have similar morphology to modern elephant tracks (Fig. 3B and C) and to other fossil elephant tracks such as those described by Kinahan et al. (1991) south of Walvis Bay in Namibia.

In a range of mammoth track studies in North America (e.g., McNeil et al., 2005; Retallack et al., 2018) modern elephant ontological and body-mass data (Western et al., 1983: Lee and Moss, 1995; Pasenko, 2017) has been used to provide age and size estimates from fossil tracks. This is based on a similarity in patterns of maturation and growth across a range of proboscideans (Roth, 1984) despite some variation (Marchenko, 2003) and was validated by McNeil et al. (2005, 2007), who plotted data from frozen mammoth carcases (e.g., Vereshchagin and Tikhonobv, 1999) on the growth data of Lee and Moss (1995). In the case of the WHSA tracks reported here this would equate to a shoulder height of between 1.8 and 3.3 m and suggests that the tracks were probably made by mature adults. Directional indicators in the tracks, such as digit nails, are indistinct, but from the long axis of the tracks they appear to suggest that the mammoths were walking down fan, presumably towards standing water on the playa.

Four trenches were excavated at this locality positioned along the central axis of a track, heel (proximal) to toes (distal) and in all cases the distal side is shown on the right. Trenches 2 to 4 were cut in tracks along the same trackway (Mammoth-1), that is made by the same animal (Fig. 4). In Trench-1 (Fig. 5) the base of the true track (plantar-contact surface) forms a shallow basin with a maximum depth of 98 mm, 513 mm wide and is infilled conformably by stratified medium-grained sand and silt. Below the plantar contact surface distally stratified sands and silts show a series of tight chevron folds which verge downwards in a proximal direction toward the centre of the track. A short slip-plane is visible on the distal side of these folds. The deformation-front cuts outs the silts and sands and rests on the sub-base of grey gypsiferous silts. The silts and sands emerge proximally as a series of displaced, lozenge-shaped boudins truncated above by a listric-parting or localised thrust fault. The gypsiferous silts and clays at the base of the section are injected into this melange on the proximal side below the listric fault. The observed structures are consistent with a maximum distal loading via the foot causing the distal wall to be compressed and dragged downwards with the rotation of the foot in the latter part of stance. Pressure release in the proximal region leads to injection of fluidised gypsiferous silts. There are three phase of continuous deformation: (1) distal compression below the track-maker’s toes (d1); (2) rotation below the plantar surface (d2); and (3) diapiric injection as the plantar load is released proximally (d3).

In Trench-2 (Fig. 6A) the surface basin is 123 mm deep, 71 mm wide and is infilled conformably with stratified sands inter-bedded with fine sand, coarse sand scours and silt partings with occasional mass sand units. The plantar surface is probably the composite of two tracks, a partial impression of a pes overstepping the proximal part of a manus. Below this basin massive sands with occasional silt stringers overlie grey gypsiferous silts. These beds have been slightly domed beyond the distal end of the track and the contact with the grey silts shows ball-and-pillow load structures. These structures appear to have been deformed by a second phase of deformation which is also associated with a large, irregular, tight isoclinal fold that hinges proximally. The upper boundary of these folded surfaces forms a sharp truncated contact with the overlying beds in the form a local thrust fault or parting. Three phases of deformation (d1, d2 and d3) are visible in this case with overprinting of D1 by D2 and also of note is the broad and domed distal uplift.

In Trench-3 (Fig. 6B) the section is transverse to the long axis of two tracks with a hindleg foot catching the heel of the foreleg track. The main track is 348 mm wide and 68 mm deep and it again in filled by conformable horizontally stratified sands and gravels with coarse grained sands concentrated at the base of small scours. There is some evidence for trough bedding associated with asymmetrical infill in part of the track. The interface between the underlying sands and the grey gypsiferous silts is again loaded in this case with a slight distal vector. This is over cut by a marked listric fault at the distal end of the track. At the proximal base of this fault there is a small fold of fine sand and silt. Proximal to this there is a diapiric structure which rises sub-vertically toward the suture of the two superimposed tracks. There are three phases of deformation (d1, d2 and d3) which are visible in which d1 is not necessarily vertical but has a slight forward or distally directed component. The D3 component seems to be less proximally directed and more vertically driven.

Finally, Trench-4 (Fig. 6C) is the deepest and most deformed of all the sections examined at this site. There appears to be a single track 342 mm wide and 100 mm deep again infilled conformably by stratified sands and silts. On the distal side there is prominent wedge shaped fold structure of silts and fine sands pushed in both a vertical and distal direction into the underlying gypsiferous silts. On the proximal side there is a structure which is best described as a roll of massive sand with multiple stringers and rip-up clasts of grey silt. The outer contact of this structure is cross cuts surrounding beds and the upper surface is bounded by an irregular shear zone. Together both the distal and proximal structures look like the roots on a tooth. Fluid deformation of the grey silts is visible and they include one large floating clast of bedded sand and silt. ***Interpretation***: The initial phase of deformation appears to consist of a vector with both a downward and distal component associated with partial fluidisation of the gypsiferous silts. A second rotational phase creates a shear zone, which ends in a ‘rolled’ mass of sand and silt which erodes surrounding beds. Fluid release is also visible during and after this phase of deformation.

The four trenches examined at Locality-1 show a similar sequence of deformation associated with the loading of saturated gypsiferous silts below a more competent sand horizons. Rapid loading by the foot would provide insufficient opportunity, due to the low permeability, for the underlying sediments to drain causing rapid rise in pore water pressures and consequently deformation. Loading below the forefoot is evidence by listric faults and/or chevron folds in the footwall. Shear, during toe-off, displaced material in a posterior direction in broad shear zone between more competent indurated beds at depth and the track base. A component of fluid release and hydro-fracturing appears to be part of this process as pressure was released first at the heel. In all cases the morphology of the mammoth track is a simple basin shape when excavated, and the morphology appears independent of the scale of sub-track deformation.

4. Locality-2

At this locality the surface is horizontal and tracks are visible only as ‘ghost tracks’ on the surface picked out by peculiar moisture and salt conditions. Careful trowelling-back of the surface to a depth of 30 to 50 mm reveals a series of tracks in planform (Fig. 7A and B) revealed by the outcrop pattern of gypsum-rich silts, fine sands and organic-rich sands in a broader outcrop of peat (organic dominated silts). The true track is infilled by grey, massive gypsum silts which are interpreted as a settling deposit within the track-base following passage of the trackmaker. These are in turn overlain by cross-bedded sands and silts forming the main track infill. Around the periphery of this core fill circular and lenticular sand and silt units outcrop. These units are extremely compressed with visible changes in elevation indicated small fault scarps with surface throws of a few millimetres. Some of the lenticular sand outcrops are separated from the main track by surrounding areas of organic-rich sediments which verge and merge with the surround peat. Small salt filled desiccation cracks occur across the surface and are both cross-cut by, and are in turn cross-cut, the tracks. A second set of tracks in the form of small circular impressions are visible and resemble the tracks of camels found elsewhere at WHSA (Lucas et al., 2007).

The excavated cross-section (Fig. 7C) lies transverse to the direction of travel. Below the base of the track infill there are a series of lenticular units of silt and sands, cut vertically into each other vertically. These have unconformable bases formed by slip surfaces whose long-axis parallels the direction of travel. The outcrop patterns are consistent with a series of small thrust faults (see in transverse section in Figure 7C) similar to that documented by Graversen et al. (2007) below Middle Jurassic theropod tracks. We suggest that decollement occurred along the interface between firmer gysiferous silts at depth and the overlying peat-rich sediment and displaced sand/silt unit moved both in an anterior and posterior direction relative to the trackmaker's foot. This creates the observed 'halo' of displaced sediment around the true track. While the horizontal surface appears to be truncated we do not believe that erosion has been significant due to the small desiccation cracks and their relationship to the tracks and the surrounding halo of displaced blocks. Some of the blocks cropping out at the surface may also represent diapiric structures. A second trench (Fig. 7D) located to the southwest shows this. Here there is a mammoth track overstepped by a human track. A complex and diapiric structure lies anterior to the direction of mammoth travel and the track itself is underlain by a complex melange of deformed sand and silt blocks. Note that the track infill contains a number of irregular sediment clasts presumably derived from the surface outcrop of diapiric, probably syn-imprinting. This diapiric structure also creates a visible 'halo' around the track in outcrop and is again concentrated primarily to the anterior of the trackmaker's foot. This deformation is cumulative associated with both the initial (and dominant) mammoth track and the later (minor) human footfall.

5. Locality-3

This locality lies on the eastern side of the playa. The main set of mammoth tracks recorded consists of a combination of manus and pes tracks, in association with two human trackways (Fig. 8). The manus track is more circular than the pes, which is common in proboscidean footprints (Fig. 3) and reflects the subtle anatomic differences (pes foot skeletal is more digitigrade than the manus) and the fact that around 60% of the weight of extant proboscidean is supported by the forelimbs (Pasenko, 2017). Compared to the coeval Proboscidea track record, the tracks are large (400 to 650 mm) suggesting the possibility that they were made by a mature bull. Mammoth tracks were left after the southward human trail, as they cut across the human trackway. Placement of the manus by the mammoth caused deformation of the adjacent human tracks some 1.5 to 2.2 metres away. Subsequently, a human overstepped the mammoth tracks (Fig. 8). Again there is no visible surface expression of the anterior sediment displacement in the form of a rim structure. Moreover the morphology of the excavated manus track while modified by the subsequent human track placement appears independent of the anterior deformation.

In the vicinity of this location another mammoth track was sectioned (Fig. 9A). This track is underlain by increasingly indurated gypsiferous silts at depth. Deformation consists of compressed beds below the track and a small diapiric structure to the anterior side of the trackmaker's foot which does not break the surface. This is a common type of deformation structure at WHSA associated with localities where gypsiferous silts and sands become more indurated at depth. This represents a classic expulsion rim structure, although significantly at WHSA this is rarely visible as a surface bulge. This may either be due to subsequent erosion or more likely syn-imprinting surface flow. At other locations Proscibedean tracks can leave substantial expulsion rims, normally higher on the anterior side of the footmaker's foot. Figure 9B shows an example excavated by the senior author below Holocene fossil elephant track from Walvis Bay, Namibia (Kinehan et al. 1991; Morse et al., 2013; Fig. 2C). Here there is both an anterior and posterior rim structure, although the anterior rim is more peaked such that the laminated silts outcrop and have been eroded by syn-imprinting slumping.

6. Discussion

The localities described here from WHSA provide a range of different deformation responses to loading below the feet of Proboscidea and these are summarised in Figure 10. At Locality-1 the substrate decreases in strength below a firmer surface layer, before increasing in strength again at depth. This creates a shear zone in which deformation occurs below the plantar surface of the foot and the base of the true track. Fluid escape of pressurised pore water is a feature of the observed deformation structures (Fig. 10A). Rotational movement of sediment blocks beneath Palaeocene tracks ascribed to mammal pantodont *Titanoides* has been described by Lüthje et al. (2010). Where a firmer substrate occurs at depth relative to a thick, but weak surface layer deformation occurs differently. This is true at the sites where peat outcrops at the surface. Here decollement and slip at the interface between the peat and firmer silts at depth causes blocks of sediment to rise around the margins of the track to form a halo of deformation. This is very similar, although perhaps less regimented, to the deformation structures described by Graversen et al. (2007) for biped theropod tracks. Deformation occurs both in an anterior and posterior fashion although it seems to be primarily directed posteriorly (Fig. 10B). The third style of deformation involves diapiric displacement in front of the track or to its rear (Fig. 10C). This may be visible at the surface or removed either by subsequent erosion or just as likely by surface sediment flow (see: Milàn and Loope, 2007).

The patterns of deformation summarised in Figure 10 all result from a peak anterior load across the trackmaker's foot and are consistent with the available plantar pressure data for modern African (Fig. 11) and Asian elephants which show peak pressures in the distal reaches and a slight shift in the

Centre of Pressure from heel toward the lateral digits (digits III-V; Panagiotopoulou et al., 2012, 2016). In shallow loose soil elephants often leave a lateral nail divot during the later phases of stance as noted by Pasenko (2017) and shown in Figure 2E. Elephants have a large elastic pad at the heel which acts to cushion and distribute pressure (Weissengruber et al., 2006; Hutchinson et al., 2011). It is common to both African and Asian elephants and there is nothing in the skeletal or soft-tissue analysis of mammoths preserved in permafrost (Fisher et al, 2014; Boeskorov et al., 2014) to suggest that other proboscidean had different foot structures although this heel cushion evolved through time as described by Hutchinson et al. (2011) as the Proboscidea feet became increasingly subunguligrade. The subsurface deformation reported here involves anterior loading followed by posterior shear during toe-off and finally pressure release via hydrofracturing and/or diapiric rise in areas of the foot unloaded first. Deformation as a result of heel loading is not a feature of sub-surface observed.

The observations reported here provide insight into the scale of deformation beneath mammoth tracks or for that matter any Proboscidea noting that fossil elephant tracks are part of the African Plio-Pleistocene record (Leakey and Harris, 1987; Kinhan et al., 1991; Roberts et al., 2008). It is worth a word caution here however. White Sands has a unique gypsiferous substrate whose properties could lead to patterns of deformation which are not found at non-gypsiferous localities. While possible, and something which needs to be tested at other sites by future research, we note that similar patterns of deformation are found beneath Proboscidea at Walvis Bay (Kinhan et al., 1991) and beneath the tracks of other large vertebrates (Graversen et al., 2007; Milàn and Loope, 2007; Lüthje et al., 2010; Thulborn, 2012) with more conventional clastic sedimentary facies. We believe therefore that the observations made here reinforce the work of Bates et al. (2013) which suggests that the link between pressure and depth may only hold for shallow and therefore relative firm substrates. Notwithstanding potential substrate differences we would also suggest that the work has implications for the biomechanical analysis of other large quadruped vertebrates in the fossil record, most notably sauropods. Rim based deformation structures have been observed by Thulborn (2012) below sauropod tracks and modelled by Sanz et al. (2015). Sauropods may have had plantar pressure characteristics broadly similar to that of Proboscidea, with extensive heel pads especially on their pedes (e.g., Bonnan 2005). The digit and associated claw impressions are more prominent however. Our point is that further insight into sauropod, or other large vertebrates, may be derived from a more detailed analysis of subsurface deformation where it is exposed. In addition some of the track-based models for sauropod tracks (e.g., Falkingham et al., 2010; Sanz et al., 2015) could usefully include variations in plantar pressure potentially drawn from those of Proboscidea. In addition, the possibility to study and compare the deformation structures provides data to define the impression window for different trackways, therefore delivering additional data to support or discard gregarious behaviour hypotheses of an extinct animal.

7. Conclusions

We have described for the first time the scale and range of deformation that occurs below mammoth tracks in Pleistocene playa sediments. The style of deformation is a function of the near-surface stratigraphy and variations in associated shear strength with depth. Classic diapiric structures around the track-margins are common where strength increase with depth and there is a near-surface zone of more deformation material. Where more competent sand units overlying saturated silts occur, the deformation structures appear to be dominated by a wider shear zone and fluid escape structures. In other situations where softer sediment overlies more competent units with a sharp unit boundary listric-faults and other brittle deformation styles are typical. The patterns of deformation are consistent with distribution of plantar pressure beneath the feet of modern elephants. In conclusion the data presented here adds to our understanding of deformation below large vertebrates including dinosaurs such as sauropods.

Acknowledgements

The fieldwork was conceived and undertaken by MRB, DB, and TMU. Others contributed data, insight, specific analytical procedures and contributed to the write-up. Views and conclusions are those of the authors and do not necessarily reflect policies of the National Park Service (NPS). MRB acknowledges Natural Environment Research Council grants (NE/H004246/1 and NE/M021459/1). The authors would like to extend their sincere thanks to Olga Panagiotopoulou for providing access to the African elephant plantar pressure data. The 3D data in Figure 2E was collected on behalf of MRB by Katy Thompson. The assistance of Vince Santucci and Daniel Odess at Locality-3 is gratefully acknowledged. A large number of people have worked on the White Sands animal tracks over the years, including Neffra Matthews, Tom Noble, Vince Santucci, Jackson Jakeway, P. Willey and Cyrus Green. The 3D footprint models associated with this paper are available at: http://footprints.bournemouth.ac.uk/

References

Allen, B., Love, D.W., Myers, R. G., 2009. Evidence for late Pleistocene hydrologic and climatic change from Lake Otero, Tularosa Basin, south-central New Mexico. New Mexico Geol. 31, 9–25.

Aramayo, S.A., Bianco, T.M., 1987. Hallazgo de una icnofauna continental (Pleistoceno tardio) en la localidad de Pehuen-Co (Partido de Coronel Rosales) Provincia de Buenos Aires, Argentina. Parte I: Edentata, Litopterna, Proboscidea. Parte II: Carnivora, Artiodactyla y Aves. IV Congreso Latinoamericano de Paleontologia. Bolivia. Actas, 1, 516–547.

Bates, K.T., Savage, R., Pataky, T.C., Morse, S.A., Webster, E., Falkingham, P.L., Ren, L., Qian, Z., Collins, D., Bennett, M.R., McClymont, J., 2013. Does footprint depth correlate with foot motion and pressure? J. Royal Soc. Interface , 10, p.20130009.

Bennett, M.R., Budka M., 2018. Digital Technology for Forensic Footwear Analysis and Vertebrate Ichnology. Springer International Publishing.

Boeskorov, G.G., Potapova, O.R., Mashchenko, E.N., Protopopov, A.V., Kuznetsova, T.V., Agenbroad, L. and Tikhonov, A.N., 2014. Preliminary analyses of the frozen mummies of mammoth (*Mammuthus primigenius*), bison (*Bison priscus*) and horse (*Equus* sp.) from the Yana-Indigirka Lowland, Yakutia, Russia. Integrative zoology, 9, 471–480.

Bonnan, M.F., 2005. Pes anatomy in sauropod dinosaurs: implications for functional morphology, evolution, and phylogeny. Thunder-Lizards: The Sauropodomorph Dinosaurs. Indiana University Press, Bloomington, pp.346-380.

Bustos, D., Jakeway, J., Urban, T.M., Holliday, V.T., Fenerty, B., Raichlen, D.A., Budka, M., Reynolds, S.C., Allen, B.D., Love, D.W., Santucci, V.L., Odess, D., Willey, P., McDonald, H.G. and Bennett M.R., 2018. Footprints preserve terminal Pleistocene hunt? Human-sloth interactions in North America. Science advances, 4, p.eaar7621.

Falkingham, P.L., Bates, K.T., Margetts, L., Manning, P.L., 2010. Simulating sauropod manus-only trackway formation using finite-element analysis. Biol. Lett., 7, 142–145.

Fisher, D.C., Shirley, E.A., Whalen, C.D., Calamari, Z.T., Rountrey, A.N., Tikhonov, A.N., Buigues, B., Lacombat, F., Grigoriev, S., Lazarev, P.A., 2014. X-ray computed tomography of two mammoth calf mummies X-Ray CT of Mammoth Calves. J. Paleontol, 88, 664–675.

Graversen O., Milàn J., Loope D.B., 2007. Dinosaur tectonics: a structural analysis of theropod undertracks with a reconstruction of theropod walking dynamics. J. Geol, 115, 641–654.

Hutchinson, J.R., Delmer, C., Miller, C.E., Hildebrandt, T., Pitsillides, A.A., Boyde, A., 2011. From flat foot to fat foot: structure, ontogeny, function, and evolution of elephant “sixth toes”. Science, 334(6063), 1699–1703.

Kinahan, J., Pallet, J., Vogel, J., Ward, J., Lindique, M., 1991. The occurrence and dating of elephant tracks in the silt deposits of the lower !Khuiseb River, Namibia. Cimbebasia, 13, 37–-43.

Leakey, M.D., Harris, J.M., 1987. Laetoli: A Pliocene Site in Northern Tanzania. Clarendon Press.

Lee, P.C., Moss, C.J., 1995. Statural growth in known-age African elephants (*Loxodonta africana*). J. Zool., 236, 29–41.

Lucas, S.G., Allen, B.D., Morgan, G.S., Myers, R.G., Love, D.W., Bustos, D., 2007. Mammoth footprints from the upper Pleistocene of the Tularosa Basin, Doña Ana County, New Mexico. Bull. N. M. Mus. Nat. Hist. Sci. 42, 149–154.

Lüthje, C.J., Milàn, J., Jørn H Hurum, J.H. 2010. Paleocene tracks of the mammal pantodont genus Titanoides in coal-bearing strata, Svalbard, Arctic Norway. J Vert Palaeont. 30, 521-527

Marchenko, E., 2003. Individual development and biology of the woolly mammoth (*Mammuthus primigenius* Blumenbach, 1799). Third International Mammoth Conference, May 2003, Dawson City, Yukon, Canada.

Marty, D., 2008. Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez-Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology.. GeoFocus, 21, 1–278.

Matthews, N.A., Noble, T.A., Breithaupt, B.H., 2016. Close-range photogrammetry for 3D ichnology: the basics of photogrammetric ichnology; pp.29-55 in P. Falkingham, D. Marty, A. Richter (eds.), Dinosaur Tracks: The Next Steps. Indiana University Press, Bloomington, Indiana, 520 pp.

McNeil, P., Hills, L.V., Kooyman, B., Tolman, S.M., 2005. Mammoth tracks indicate a declining Late Pleistocene population in southwestern Alberta, Canada. Quat. Sci. Rev., 24, 1253–1259.

McNeil, P., Hills, L.V., Tolman, S.M., Kooyman, B., 2007. Significance of latest Pleistocene tracks, trackways and trample grounds from southern Alberta, Canada. Bull. N. M. Mus. Nat. Hist. Sci., 42, 209–224

Miall, A.D., 1977. Lithofacies types and vertical profile models in braided river deposits: a summary. In: Miall, A.D., Ed., Fluvial Sedimentology, Geological Survey of Canada, 597–604.

Milàn, J., Loope, D.B. 2007. Preservation and erosion of theropod tracks in eolian deposits; examples from the Middle Jurassic Entrada Sandstone, Utah, USA. J. Geol 115, 375-386.

Morgan, G.S., and Lucas, S.G., 2005. Pleistocene vertebrate faunas in New Mexico from alluvial, fluvial, and lacustrine deposits. Bull. N. M. Mus. Nat. Hist. Sci., 28,185–248.

Morse, S.A., Bennett, M.R., Liutkus-Pierce, C., Thackeray, F., McClymont, J., Savage, R. & Crompton, R.H. (2013). Holocene footprints in Namibia: the influence of substrate on footprint variability. Am. J. Phys. Anthropol. 151, 265–279.

Panagiotopoulou, O., Pataky, T.C., Hill, Z., and Hutchinson, J,R. 2012. Statistical parametric mapping of the regional distribution and ontogenetic scaling of foot pressures during walking in Asian elephants (Elephas maximus). J. Exp. Biol. 215, 1584–1593. doi:10.1242/jeb.065862

Panagiotopoulou, O., Pataky, T.C., Day, M., Hensman, M.C., Hensman, S., Hutchinson, J.R., and Clemente, C.J., 2016. Foot pressure distributions during walking in African elephants (Loxodonta africana). Royal Soci. Open Sci., 3, p.160203.

Panin, N., Avram, E., 1962, Noe urme de vertebrate in Miocenul Subcarpatilor rominesti. Studii si Cercetari de Geologie, 7, 455–484.

Pasenko, M.R., 2017. Quantitative and qualitative data of footprints produced by Asian (Elephas maximus) and African (Loxodonta africana) elephants and with a discussion of significance towards fossilized proboscidean footprints. Quat. Int., 443, 221–227.

Remeika, P., 2006. Fossil footprints of Anza-Borrego; In: Jefferson, G. T. and Lindsay, L., (Eds.), Fossil treasures of the Anza-Borrego Desert: the last seven million years. Sunbelt Publications, 311–327.

Retallack, G.J., Martin, J.E., Broz, A.P., Breithaupt, B.H., Matthews, N.A., Walton, D.P., 2018. Late Pleistocene mammoth trackway from Fossil Lake, Oregon. Palaeogeogr. Palaeoclimatol. Palaeoecol., 496, pp.192–204.

Reynolds, R.E., 1999. Gomphothere tracks in southern California: San Bernardino County Museum Association Quarterly, 46, 31–32.

Roberts, D.L., Bateman, M.D., Murray-Wallace, C.V., Carr, A.S., Holmes, P.J., 2008. Last interglacial fossil elephant trackways dated by OSL/AAR in coastal aeolianites, Still Bay, South Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol., 257, 261–279.

Robertson, G.M., Sternberg, G.F., 1942. Fossil mammal tracks in Graham county, Kansas. Trans. Kans. Acad. Sci., 45, 258–261.

Roth, V.L., 1984. How elephants grow: heterochrony and the calibration of developmental stages in some living and fossil species. J. Vert. Paleontol., 4, 126–145

Sanz, E., Arcos, A., Pascual, C., Pidal, I.M., 2015. Three-dimensional elasto-plastic soil modelling and analysis of sauropod tracks. Acta Palaeontol. Pol., 61, 387–402.

Scrivner, P.J., Bottjer, D.J., 1986. Neogene avian and mammalian tracks from Death Valley National Monument, California: Their con-text, classification and preservation: Palaeogeogr. Palaeoclimatol. Palaeoecol., 57, 285–331.

Thulborn, T., 2012. Impact of sauropod dinosaurs on lagoonal substrates in the Broome Sandstone (Lower Cretaceous), Western Australia. PLoS One, 7(5), p.e36208.

Urban, T.M., Bustos, D., Jakeway, J., Manning, S.W., Bennett, M.R., 2018. Use of magnetometry for detecting and documenting multi-species Pleistocene megafauna tracks at White Sands National Monument, New Mexico, USA. Quat. Sci. Rev., 199, 206–213.

Vereshchagin, N.K., Tikhonov, A.N., 1999, Exterior of the mammoth. Cranium, 1, 1–93.

Weissengruber, G.E., Egger, G.F., Hutchinson, J.R., Groenewald, H.B., Elsasser, L., Famini, D., Forstenpointner, G., 2006. The structure of the cushions in the feet of African elephants (Loxodonta africana). J. Anat. 209, 781–792. doi:10.1111/j.1469-7580.2006.00648.x

Western, D., Moss, C., Georgiadis, N., 1983. Age estimation and population age structure of elephants from footprint dimensions. J. Wildl. Manag., 47, 1192–1197.

Figure Captions

Figure 1: White Sands National Monument (WHSA). **A.** Geological and locational context. All the study sites reported here are located on the western side of Alkali Flat. Note that the precise locations of the study sites are not indicated in accordance with National Park Service (NPS) protocol and US Law. Interested parties may apply to the NPS for further details if required. **B.** Sketch cross-section for Locality-1 with geochronological controls.

Figure 2: Mammoth tracks at White Sands National Monument (WHSA, New Mexico). **A.** The tracks are colloquially referred to as 'ghost tracks' since they are only visible in specific ground moisture and salt states. As a rule of thumb true dimensions of the track are normally about 75% smaller than their surface expression. **B.** Mammoth tracks picked out by subtle salt blooms. **C.** When excavated or in the case illustrated wind deflates the tracks they are normally elliptical in the direction of travel and nail/toe impression can normally be seen as in this case at the bottom of the track. **D.** Trenches at Locality-1. **E.** A 3D oblique view of a modern elephant track (*Loxodonta africana*) from South Africa. Note the divot and nail grooves associated with toe-off.

Figure 3: Tracks of modern African elephants (*Loxodonta africana*). **A.** Shows a typical elephant track in fine sand taken by the senior author at Amboseli National Park Kenya in 2008. Note the surface texture and lateral push-ridges and prominent anterior nail impression. The posterior of the foot is to the top of the image. **B.** An elephant trackway from Amboseli National Park Kenya in 2008. **C.** Fossil elephant tracks south of Walvis Bay, Namibia. These tracks are probably between 0.5 and 1 K BP. Note how these fossil tracks are associated with more circular basin-like tracks.

Figure 4: Map of the tracks at Locality-1. **A.** Main mammoth tracks visible at the time of the survey. **B.** Track diameters, note these measurements are based on surface expression and may over-estimate the true size of some of the tracks.

Figure 5: Annotated sketch of the deformation structures below manus mammoth track, Trench-1. Facies codes are modified from Miall (1977): Pg=peat; Sm=massive sands; Sh-stratified sands; St=trough bedded sands; Fm=massive silts; Sm/Sh[m]=melange of sand and silt; PS=plantar surface. The codes d1 to d3 refer to observed phases of deformation.

Figure 6: Annotated sketches of the deformation structures in Trenches 1 to 4. See Figure 5 for key. Facies codes are modified from Miall (1977): Pg=peat; Sm=massive sands; Sh-stratified sands;

St=trough bedded sands; Fm=massive silts; Sm/Sh[m]=melange of sand and silt; PS=plantar surface. The codes d1 to d3 refer to observed phases of deformation. **A.** Trench-2. **B.** Trench-3. **C.** Trench-4.

Figure 7: Mammoth tracks at Locality-2. **A.** Orthomosaic of the study site which was revealed by simply trowelling back the top few centimetres of the surface. Note the desiccation cracks. Scale bars are 0.5 m. **B.** Interpretation of the orthomosica shown in A indicating the outcrop patterns and 'halos' around the tracks. **C.** Section through northern face of the trench shown in A and B. **D.** Mammoth track overstepped by a human track. This site is located a few metres to the west of that shown in A. Facies codes are modified from Miall (1977): Pg=peat; Sm=massive sands; Sh-stratified sands; St=trough bedded sands; Fm=massive silts; Sm/Sh[m]= melange of sand and silt; PS=plantar surface.

Figure 8: Interaction of a double human trackway and a set of mammoth tracks at Locality-3. **A.** The relative chronology of the two human trackways and the mammoth tracks. Note the deformation of the southbound trackway by the mammoth manus track. **B.** Orthorectified mosaic of the area shown in in (A). **C.** Depth rendered 3D models of the human trackway showing deformation of the tracks by the mammoth.

Figure 9: **A**. Cross section through a right manus mammoth track close to Locality-3 (WHSA) where the substrate increases in shear strength with depth. Note the diapiric structure on the anterior side. **B.** Three-dimensional model of fossil elephant track south of Walvis Bay Namibia. Track was captured using a Konica-Minolta VI900 optical laser scanner in 2010 by the senior author. N indicates the nails **C.** Cross section through the track reconstructed from outcrop patterns around the track. Facies codes are modified from Miall (1977): Pg=peat; Sm=massive sands; Sh-stratified sands; St=trough bedded sands; Fm=massive silts; Sm/Sh[m]=melange of sand and silt; PS=plantar surface. The codes d1 to d3 refer to observed phases of deformation.

Figure 10: Schematic models of deformation structures below Proboscidea tracks observed at WHSA. Schematic strength and strain profiles are provided below and indicate the likely stratigraphic conditions each type of deformation may be associated with. This summary is not necessarily exhaustive and other types of deformation may also occur, but is presented here as an indicative guide. **A.** Competent surface horizon overlying a more impermeable saturated layer increasing

with strength at depth. This causes a fluidised layer which shows evidence of shear and fluid escape of pressurised pore water. **B.** In this scenario we have softer surface sediments overlying more competent sands and silts. Decollement, shear and diapiric rise all occur around the main body of the track. **C1, C2.** Here with have a more uniform substrate that increases in shear strength with depth, diapiric displacement of sediment occurs. The two versions reflect whether the fore-bulge remains visible or not.

Figure 11: Means of the peak pressure patterns created from the peak pressure sample during the whole stance phase for African elephants. Peak pressure patterns shown here were smoothed (using a Gaussian blur) to interpolate between pressure grid points. Data courtesy of Panagiotopoulou et al. (2016)