Simulating sauropod manus-only trackway formation using finite-element analysis

P. L. Falkingham^{1,*}, K. T. Bates², L. Margetts^{1,3}
and P. L. Manning^{1,4}

¹School of Earth, Atmospheric and Environmental Science, University of Manchester, Williamson Building, Oxford Road, Manchester M13 9PL, UK

²Adaptive Organismal Research Group, Faculty of Life Sciences, University of Manchester, Stopford Building, Manchester M13 9PL, UK

³Research Computing Services, University of Manchester, Kilburn Building, Oxford Road, Manchester M13 9PL, UK

⁴Department of Earth and Environmental Science, University of Pennsylvania, 254-b Hayden Hall, 240 South 33rd Street, Philadelphia, PA 19104-6316, USA

*Author for correspondence (peter.falkingham@manchester.ac.uk).

The occurrence of sauropod manus-only trackways in the fossil record is poorly understood, limiting their potential for understanding locomotor mechanics and behaviour. To elucidate possible causative mechanisms for these traces, finite-element analyses were conducted to model the indentation of substrate by the feet of *Diplodocus* and *Brachiosaurus*. Loading was accomplished by applying mass, centre of mass and foot surface area predictions to a range of substrates to model track formation. Experimental results show that when pressure differs between manus and pes, as determined by the distribution of weight and size of respective autopodia, there is a range of substrate shear strengths for which only the manus (or pes) produce enough pressure to deform the substrate, generating a track. If existing reconstructions of sauropod feet and mass distributions are correct, then different taxa will produce either manus- or pes-only trackways in specific substrates. As a result of this work, it is predicted that the occurrence of manus- or pes-only trackways may show geo-temporal correlation with the occurrence of body fossils of specific taxa.

Keywords: dinosaur; track; finite-element analysis; centre of mass

1. INTRODUCTION

Palaeobiologists strive to understand the behaviour of extinct animals, but are frustrated by the redundancy of vestigial body fossil evidence. Trace fossils present us with direct evidence of how past animals interacted with their surrounding biota and environment, significantly furthering understanding of organism behaviour and functional evolution in the fossil record [1,2]. Interpretation of manus-only sauropod trackways as swimming traces infers a degree of otherwise unknown aquatic ability in these giant animals. Some authors

have suggested the sauropod trackmaker was buoyed up by water and ‘punted’ off the bottom with their forefeet [3–5]. However, others have challenged this idea in favour of a preservational bias towards manus prints, attributing the occurrence of trackways to substrate conditions and undertrack phenomena [6].

These studies have presented evidence against a swimming origin for manus-only trackways, but as yet no causative mechanism relating to track formation or preservation has been proposed. To what extent are manus-only trackways linked to the specific aspects of trackmaker biology and locomotor mechanics? Alternatively, can prevailing sedimentological conditions at the time of track formation fully account for their occurrence, or do they represent an unknown taphonomic artefact of the rock record? Understanding of this phenomenon is important, not only for understanding sauropod behaviour and ecology, but fundamentally for interpretations of the trackway record of all quadrupedal tetrapods. Interpretations of the habitual locomotor mode in groups with uncertain and potentially diverse gaits will be misinformed if systematic bias leads to consistent loss of manus or pes prints in the fossil record. For example, prosauropod and hadrosaurian dinosaurs have been reconstructed as bipedal, quadrupedal or as capable of both forms of locomotion by different workers based on interpretation of skeletons (see [7,8] for reviews). Pes-only trackways assigned to these groups may not represent evidence for a bipedal gait, if instead there is simply a bias against manus preservation.

This paper presents the first attempt to investigate the mechanisms underpinning the formation of manus-only sauropod trackways by combining computer simulation with geotechnical theory.

2. MATERIAL AND METHODS

Finite-element analysis (FEA) was used to model the response of a homogeneous, cohesive substrate to the calculated load from a sauropod manus and pes. For each analysis, an indenter or ‘virtual foot’ was generated atop a meshed volume of soil, composed of 20-node hexahedral elements. The indenters were generated and scaled to represent sauropod autopodia. Two sauropods were used; *Diplodocus* and *Brachiosaurus* because they represent distinct sauropod groups, and have been suggested as having considerably different centre of mass (CM) positions [9]. Indenter morphology was based on predicted track outlines for the two taxa by [10], fig. 9.3 and scaled according to the specimens used in calculating mass by [9] (figure 1). The indenters were given material properties to make them rigid in comparison with the substrate, consistent with interpretations of the sauropod manus as a functionally rigid, block-like structure [11].

Fossil trackways suggest that the manus and pes were planted in a predominantly vertical manner in sauropods as opposed to having any considerable horizontal component [12]. The walking velocities and limb kinematics of sauropods are unknown, so to avoid unfounded assumptions, loads equal to the animal’s weight (mass multiplied by gravity) were used throughout this study. Load was distributed over the ‘foot’ surface in a vertical manner and apportioned to fore and hind limbs according to the gleno-acetabular position of the CM [9]. This force was distributed between a single fore- and hind-foot to represent a quadrupedal limb cycle during walking, essentially treating the animal as two linked bipeds [13]. This is a simplification of the true force vectors and underfoot pressures of sauropods, but is sufficient for the purposes of this initial analysis, and can be elaborated upon in future studies. The mass and CM position for the two dinosaurs used are shown in table 1. After initial loading, providing the substrate had not failed, the load was removed and the substrate allowed to recover the elastic portion of deformation.

For each experiment, the shear strength of the soil (C_u) was lowered until the substrate could no longer support the applied load (see electronic supplementary material). The elastic modulus (E) was

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Figure 1. Pes and manus outlines used to create indenters. (a) *Diplodocus* and (b) *Brachiosaurus*. Scale bar, 0.2 m. Redrawn from [10], fig. 9.3.

altered accordingly to be $1000 \times Cu$ [14], and Poisson's ratio (ν) was set at 0.3. While plastic deformation does occur prior to failure, the extent of this deformation is relatively minor on the scale of an animal's foot, and only occurs close to the bearing capacity. In order to produce a track deeper than a centimetre or so (very shallow when the pes of the animal may be up to a metre in length), a cohesive substrate must fail. Having found the value of Cu corresponding to failure, it may be generally considered that substrates with greater Cu will not deform sufficiently to produce a track, while weaker substrates will not support the foot and a track will be formed. FEA simulations were undertaken using PARAFEM (www.parafem.org.uk), as in Falkingham and co-workers [15,16].

3. RESULTS

FEA results suggest that, if there is a difference in pressures between manus and pes, resulting from weight distribution and/or foot surface area, then there is a range of substrates in which only the manus or pes can create tracks. Using hypothesized pes and manus morphology [10] combined with CM and mass estimates [9], *Diplodocus* cannot produce manus-only trackways, but would be expected to produce pes-only trackways when $Cu = 13\text{--}45 \text{ kN m}^{-2}$ and *Brachiosaurus* would be expected to produce manus-only trackways between $Cu = 65$ and 110 kN m^{-2} . If the simulated tracks are visualized, and failure is halted at a 5 cm depth to represent a firmer subsurface layer, virtual trackways are generated as in figure 2. It can be seen for *Brachiosaurus* that, at low values of Cu , both manus and pes indent and create obvious tracks, complete with raised displacement rims. As Cu increases, the pes impressions fail to indent to any significant depth, leaving only manus impressions until Cu becomes so high that neither manus nor pes can significantly indent the substrate (figure 2).

4. DISCUSSION

Computer analysis allows specific control over experimental inputs, and by modifying input parameters related to soil properties and loading conditions

(reflecting trackmaker biology) it is possible to demonstrate the factors responsible for producing manus-only trackways. These results demonstrate that formation of a track in a cohesive substrate relies upon having a Cu sufficiently low at the surface that the applied load cannot be supported. In homogeneous substrates, the deformation prior to failure is relatively small until the bearing capacity is reached, at which point failure occurs. Based on current predictions of CM position [9] and sauropod foot shape and size [10], there were potentially large disparities between the pressures exerted by the manus and pes in different sauropod dinosaurs. These different pressures mean that the range of substrates (based on Cu value) capable of recording both manus and pes impressions varies considerably for sauropod taxa. In *Brachiosaurus*, where CM is positioned relatively anteriorly, the range of substrates in which only the manus will produce tracks may be large, resulting in a higher likelihood of manus-only trackway formation.

Manus-only trackways with irregular footfall patterns (e.g. [17]) may suggest modified locomotor behaviour and perhaps swimming/punting, but to date supportive experimental evidence is lacking. The mechanism described here clearly reduces the need to invoke elaborate mechanisms for manus-only trackway formation such as swimming (or punting) sauropods. Therefore, a manus-only trackway may not necessarily be evidence of a very soft, submerged substrate, but instead of a substrate sufficiently firm as to prevent track formation by the pes of these large animals, having significant consequences for palaeoenvironmental interpretations. Undertrack preservational bias is secondary to the mechanism described here, as notable undertracks will only form in substrates in which the surface track has made a significant impression. In complex heterogeneous substrates, undertrack formation will probably become important, although we hypothesize that the mechanism described here of differing pressures between manus and pes will still be primary. The novel methods presented, provide a means to explore this.

The difference observed in predicted pressures of manus and pes in sauropods is not consistent with such distribution in extant elephants, where CM position and manus/pes area ratio are approximately equal [9]. Future research may show a relationship between CM and foot surface area in extant taxa, and it may be possible that such a relationship could be used to validate or constrain CM estimates of extinct taxa, though we acknowledge the reconstruction of pedal soft tissue morphology from only osteological material, particularly of larger animals, is not straightforward.

That manus- or pes-only trackways can be formed by obligate quadrupeds highlights the need for caution when interpreting locomotor mode from trackways. The presence of a bipedal trackway may not be evidence of bipedalism. Such confounding information supports the need for further gait reconstructions based on osteology, and then supported by trackway evidence, particularly where locomotor mode is

Table 1. Values used to simulate track generation by manus and pes of *Diplodocus* and *Brachiosaurus*. Mass and CM values from [9].

	mass (kg)	CM (% gleno-acetabular distance)	weight applied to foot (kN)	foot surface area (m ²)	pressure (kN m ⁻²)
<i>Brachiosaurus manus</i>	25 922	37.4	95.1	0.144	662.3
<i>Brachiosaurus pes</i>		62.6	159.2	0.401	396.58
<i>Diplodocus manus</i>	11 449	11.5	12.9	0.158	81.93
<i>Diplodocus pes</i>		88.5	99.4	0.345	288.36

Figure 2. (a) Required shear strength (C_u) to support manus and pes of *Diplodocus* and *Brachiosaurus*. Foot morphology and mass/CM estimates used predict that *Diplodocus* would leave pes-only trackways in substrates with $13 < C_u < 45 \text{ kN m}^{-2}$ and *Brachiosaurus* would leave manus-only trackways when $65 < C_u < 110 \text{ kN m}^{-2}$. (b) Composite trackways generated from FEA results of separate *Brachiosaurus* manus and pes simulations. Deformation was artificially stopped at 5 cm to prevent complete failure and to represent a firmer subsurface layer. White bars, manus; black bars, pes.

disputed or potentially variable (e.g. hadrosaurs, prosauropods).

This work highlights the need for confident mass estimates, CM predictions and soft tissue morphology reconstructions of extinct animals in order to understand their palaeobiology and evolution, not only through body fossils, but also from tracks and trackways. Future research in this area will focus on determining if there is a geo-temporal relationship between manus-only trackways and sauropod phylogeny, given that a phylogenetic shift in CM position has been posited by some authors [9].

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