

Three-Dimensional Elasto-Plastic Soil Modelling and Analysis of Sauropod Tracks

Authors: Sanz, Eugenio, Arcos, Antonio, Pascual, Carlos, and Pidal, Ignacio Menendez

Source: Acta Palaeontologica Polonica, 61(2) : 387-402

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.00098.2014>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Three-dimensional elasto-plastic soil modelling and analysis of sauropod tracks

EUGENIO SANZ, ANTONIO ARCOS, CARLOS PASCUAL, and IGNACIO MENENDEZ PIDAL



Sanz, E., Arcos, A., Pascual, C., and Pidal, I.M. 2016. Three-dimensional elasto-plastic soil modelling and analysis of sauropod tracks. *Acta Palaeontologica Polonica* 61 (2): 387–402.

This paper reports the use of FEA (Finite Element Analysis) to model dinosaur tracks. Satisfactory reproductions of sauropod ichnites were simulated using 3D numerical models of the elasto-plastic behaviour of soils. Though the modelling was done of ichnites in situ at the Miraflores I tracksite (Soria, Spain), the methodology could be applied to other tracksites to improve their ichnological interpretation and better understand how the type and state of the trodden sediment at the moment the track is created is a fundamental determinant of the morphology of the ichnite. The results obtained explain why the initial and commonly adopted hypothesis—that soft sediments become progressively more rigid and resistant at depth—is not appropriate at this tracksite. We explain why it is essential to consider a more rigid superficial layer (caused by desiccation) overlying a softer layer that is extruded to form a displacement rim. Adult sauropods left trackways behind them. These tracks could be filled up with water due to phreatic level was close to the ground surface. The simulation provides us with a means to explain the differences between similar tracks (of different depths; with or without displacement rims) in the various stratigraphic layers of the tracksite and to explain why temporary and variable conditions of humidity lead to these differences in the tracks. The simulations also demonstrate that track depth alone is insufficient to differentiate true tracks from undertracks and that other discrimination criteria need to be taken into account. The scarcity of baby sauropod tracks is explained because they are shallow and easily eroded.

Key words: Sauropoda, ichnology, 3D, mathematical simulation, elasto-plastic model, soil mechanics, Spain, Miraflores tracksite.

Eugenio Sanz [esanz@caminos.upm.es], Antonio Arcos [antonio.arcos@caminos.upm.es], Carlos Pascual [CAPAS-CUAL-1@telefonica.net], Ignacio Menendez Pidal [ignacio.menendezpidal@upm.es] (corresponding author), Escuela de Caminos, Universidad Politécnica de Madrid, Campus Ciudad Universitaria C/Profesor Aranguren 3, 28040 Madrid, Spain.

Received 17 June 2014, accepted 17 June 2015, available online 6 July 2015.

Copyright © 2016 E. Sanz et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see <http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Footprints or tracks are the result of the interaction between a living being and the substrate it traverses (Baird 1957). Whether and how the track is preserved depends on the characteristics of the substrate (Milan and Bromley 2006; Lockley 2007) and on taphonomic processes (Marty et al. 2009). As tracks are created, the mechanical and elastic response of the substrate (such as the Goldilocks effect; Falkingham et al. 2011a, b) determine the form and size of the track. If the animal making the track is large (like a sauropod) the pressure exerted by its autopods on the sediment can be easily transmitted to underlying layers, forming “ghost tracks” or “undertracks”. If tracks are covered by new sediment before they are eroded, they are preserved and can yield information about the morphology of the autopods that created them, the dynamics of the animal at that moment

and the characteristics of the sediment being trodden. More commonly, however, tracks suffer environmental weathering before they are preserved and so the amount of information they can provide is significantly reduced. Understanding the mechanism of track preservation is especially important when studying ichnite fossils. It is essential to consider the factors that contribute to preservation if we want to understand the bias that exists against preservation of true tracks and small ichnites. This knowledge would allow us to determine whether differences between ichnites are true or whether they are the result of an imperfect preservation.

In general, the best-preserved tracks—and the ones that provide the most detail about the anatomy of the autopods that formed them—are those made in plastic sediments comprising very fine particles (clayey, sandy, and carbonaceous silt). The sediment must be moist, in order that the pressure of the autopod deforms the substrate and forms an

imprint that faithfully reproduces its anatomy and maintains its structure until it is covered by new mud. Excessive or deficient moisture content leads to tracks that are not faithful moulds of the autopod: either they collapse or hardly reveal their actual morphology.

Knowledge of the process that creates these dinosaur tracks was initially based on comparing present-day tracks left by mammals, reptiles and birds in their natural surroundings. Later experiments involved animals being made to traverse a variety of substrates under very specific conditions. Analysis of the tracks laid down allowed various aspects of track formation and the dynamics of the track-makers to be elucidated (Milàn et al. 2004; Milàn 2006; Milàn and Bromley 2006, 2008).

In both cases, an objective description of autopod footprints and their disposition on the trackpath is fundamental. In this respect, graphical representations (drawings or photos) supply valuable data. Nevertheless, the subjectivity of drawings and the conditions under which photos are taken are drawbacks that affect the validity of the conclusions drawn. In an attempt to overcome these problems, modern three-dimensional photography and 3D laser scanners are beginning to prove as being quite effective (Breithaupt and Matthews 2001; Breithaupt et al. 2001, 2004; Matthews et al. 2005, 2006; Bates et al. 2008a, b, 2009a, b; Falkingham 2012; Vila et al. 2013; Razzolini et al. 2014). These techniques not only provide a more objective interpretation of the tracks, but also yield information about the dynamics of the trackmakers.

More recently, application of FEA (Finite Element Analysis) to the study of ichnites has allowed certain aspects of their formation and their creators to be clarified. FEA is a computer simulation technique that uses a numerical method (FEM, Finite Element Method) to approximate the solutions to complex partial differential equations. FEA was first applied in many fields of engineering and physics. Its modern application has gone beyond these fields and, nowadays, FEA is used in comparative biomechanics (McHenry et al. 2006; Oldfield et al. 2012; Walmsley et al. 2013), biology (Madzvamuse et al. 2003), medicine (Kraft 2012), anthropology (Panagiotopoulou 2009) and geology (Bellian et al. 2005). In the field of paleontology, it is used both for bone remains and ichnology (Moreno et al. 2007; Arbour et al. 2009; Manning et al. 2009; Xing et al. 2009; Falkingham 2010).

This advance was made possible by the development of powerful computers with a large capacity for numerical modelling at a reasonable cost. In ichnology, FEA offers a series of advantages, including: (i) experiments can be rapidly adapted to test new hypotheses, simply by changing the boundary conditions and the load; (ii) experiment times are considerably reduced; (iii) as simulations are digital, many tests can be done without destroying the true track; (iv) even so, this potent facility does have certain limitations (Rayfield 2007). The biggest drawback with FEA is the lack of experimental data (laboratory tests) to define the parameters involved in the model. For this reason, assumptions and simplifications have to be adopted in many cases (McHenry et al. 2006).

The earliest studies on animal tracks were in the 1950s: Margetts et al. (2005, 2006) applied FEA to model dinosaur tracks, comparing the results to tracks held by the Amherst College Museum of Natural History. These authors pointed out that FEA can differentiate between dynamic and static loads, which is important in the case of dinosaur tracks, where not only the weight of the animal is important but also the dynamics of the displacement. In the same decade, Henderson (2006) simulated dinosaur footprints and obtained versions of their undertracks by applying certain erosion conditions to the tracks. This allowed the two to be compared, drawing conclusions that are useful in distinguishing true tracks from undertracks. However, these were artificial tracks: the undertracks were generated as a function of what was expected. For this reason, modelling began to be applied in terms of the characteristics of the substrate. The bases of this new line of investigation were studies of interactions between soil and an overlying object (Nakashima and Wong 1993; Abo-Elnor et al. 2004; Fervers 2004; Nakashima and Oida 2004; Mulungye et al. 2007).

An additional issue to be considered when simulating the process of track formation is any substrate itself that the dinosaurs or other reptiles trod. In general, the substrate was not uniform and was sometimes saturated with water. In this respect, the research by Popescu et al. (2005, 2006) is of interest.

Knowledge of all the parameters required for a good model simulation permits new interpretations of certain tracks, as in the case of the tracks studied by Falkingham et al. (2009). These authors analysed bird trackpaths using a high-resolution laser scanner and reconstructed them using a finite element simulator. This study indicated that simulations of trackpaths for webbed and non-webbed birds' feet were similar. In addition, the authors experimented by varying sediment conditions and the interdigital angles; they found that a webbed track only occurs under a very narrow set of sediment conditions. This raises doubt about whether certain tracks always show interdigital membranes; given the approximate nature of the results offered by this method, however, opinion is divided about their validity: Anfinson et al. (2009) and Lockley et al. (2009) do not accept the results, whilst others, such as Sellers et al. (2009), support them.

Falkingham (2010) showed that three factors are involved in the formation of animal tracks, namely: the force applied (weight of the animal), the substrate (its type and state) and the anatomy of the autopod (silhouette and base). The analysis also found that an underlying stiff layer is required in order that sufficiently deep prints are made. The conditions have to be "just right" if a print is to be produced—an effect dubbed the Goldilocks effect, that defines how the "correct" conditions fall within a narrow band between the margins of possible variation). Applied to a homogeneous substrate, the Goldilocks effect indicates that the loading conditions (i.e., the size of the animal, its locomotion and the morphology of the feet) have to be "just right" if the animal traversing the sediment is to produce a track. This has wide-ranging impli-

cations for interpretation about paleodiversity and paleoecology, based on the set of vertebrate tracks that are preserved.

Applying FEA to human footprints, Bates et al. (2013), observed how consolidation of the substrate affects how the footprint penetrates it. However, this interaction is only one of many possible factors that allow the sediment to resist deformation when subject to the loading associated with the locomotion of an animal. The authors admit that, in making physical and computational models of track formation, there is a need to study the vertical profile of the soil's mechanical characteristics.

Abbreviations.—FEA, Finite Element Analysis; FEM, Finite Element Method.

Objectives

The research reported in this paper is based on the application of a 3D numerical model to simulate the elasto-plastic behaviour of soil. This type of model is frequently used in geotechnical engineering; for example, to determine the deformation due to shallow building foundations, such as footings. This model, which was previously applied in 2D for the same ichnological tracksite, together with formulae of radial extrusion (Arcos et al. 2006), approximately reproduced the sections of a number of representative tracks. The Miraflores I tracksite (Fuentes de Magaña, Spain) is one of the most important sauropod tracksites in the Cameros Basin for studying sediment deformations produced by the passage of large dinosaurs. The disposition of the layers, dipping counterslope and forming a “V”, which points upstream in the Miraflores streambed, means that in the faces of the strata on the right bank, one can see a number of complete vertical sections of deformations produced by the tread of these large dinosaurs. In addition, the ground surface of the tracksite presents many good outcrops of the same stratification planes, where the morphology and other characteristics of the ichnites can be recognized. The variety and abundance of sauropod ichnites at this tracksite means it can be used to establish a typology of deformations for each particular stratigraphy, as a function of the weight of the dinosaur. Accordingly, one can differentiate increasingly pronounced prints, ranging from a simple compression of the layers to the extrusion of the sediment with the formation of a displacement rim (Arcos et al. 2006).

Here, we revisit the issue in an attempt to simulate the tracks in 3D, in order to explain the precise mechanism that causes deformation. We also comment on the following issues. (i) One of the more serious confusions relating to dinosaur ichnites is the inability to distinguish undertracks from true tracks; because of the enormous weight of these dinosaurs, the undertracks are sometimes very deep and can be mistaken for true tracks. (ii) In terms of the size of sauropod tracks, small footprints are scarce; mathematical modelling may be able to shed light on whether small prints could be left in the trackway under study. (iii) Another aspect of in-

terest is the influence that soil water content might have on the track as it is made; the saturation conditions of any soil type depend on its particle size distribution, the evaporation rate and the location of the phreatic level. Accordingly, track formation is dependent on how close to the shore the tracks were made, and whether the water level was falling—which is when the best tracks are preserved.

The specific objectives of this study are: (i) To reproduce tracks and undertracks using the finite element technique, simulating the stress and strain changes on the ground caused by sauropod footsteps. (ii) To understand the impact of footprint pressure through a vertical soil section, studying and quantifying how the following parameters act as determinants at the moment a footprint is formed: soil nature, thickness, presence of mechanically different soil horizons and their distribution over the soil column, moisture content of the layers in the tread zone. (iii) Based on the aforementioned conditions and parameters used to model the sauropod tracks, to reproduce small tracks of the same type in order to compare them with existing ichnites in this tracksite and discuss their frequency.

Geological setting

The tracks to be modelled occur in the Miraflores I tracksite (Pascual et al. 2005; Latorre et al. 2006), close to the village of Fuentes de Magaña (Soria Province, Spain) (Fig. 1).

This tracksite is composed of a series of sandy siltstone (mostly grey in colour, occurring in layers about 15 cm thick), carbonaceous sandy siltstone, and very thin layers of ochre and grey sandy siltstone. Their composition includes occasional pyrite cubes and mica laminae. Many of the layers contain tracks of dinosaurs and other reptiles. In particular, in one 14 m thick sequence, there are 13 layers containing ichnites (Latorre et al. 2006; Fig. 2).

These layers belong to the Huérteles Formation (Guiraud and Seguret 1985; Quijada et al. 2013) of the Oncala Group (Tischer 1966) of the Cameros Basin. They were deposited on a deltaic plain influenced by tides (Quijada et al. 2013). Using the sparse fossil content (ostracods and charophytes) and the stratigraphic sequence, we conclude that the sediments amassed during the Berriasian (Early Cretaceous) (Martín-Closas and Alonso 1998; Mas et al. 2004, 2011; Schudack and Schudack 2009; Clemente 2010).

Material and methods

Ichnites used for modelling.—Of the numerous tracks at the Miraflores I tracksite, described by Latorre et al. (2006) and Arcos et al. (2006), we chose two sauropod tracks and undertracks for study and modelling. These two are representative and well-preserved and their three dimensional geometry can be recognized. They appear in layer VIII-B, labelled as numbers 86 and 95 (Fig. 3). One of the tracks is

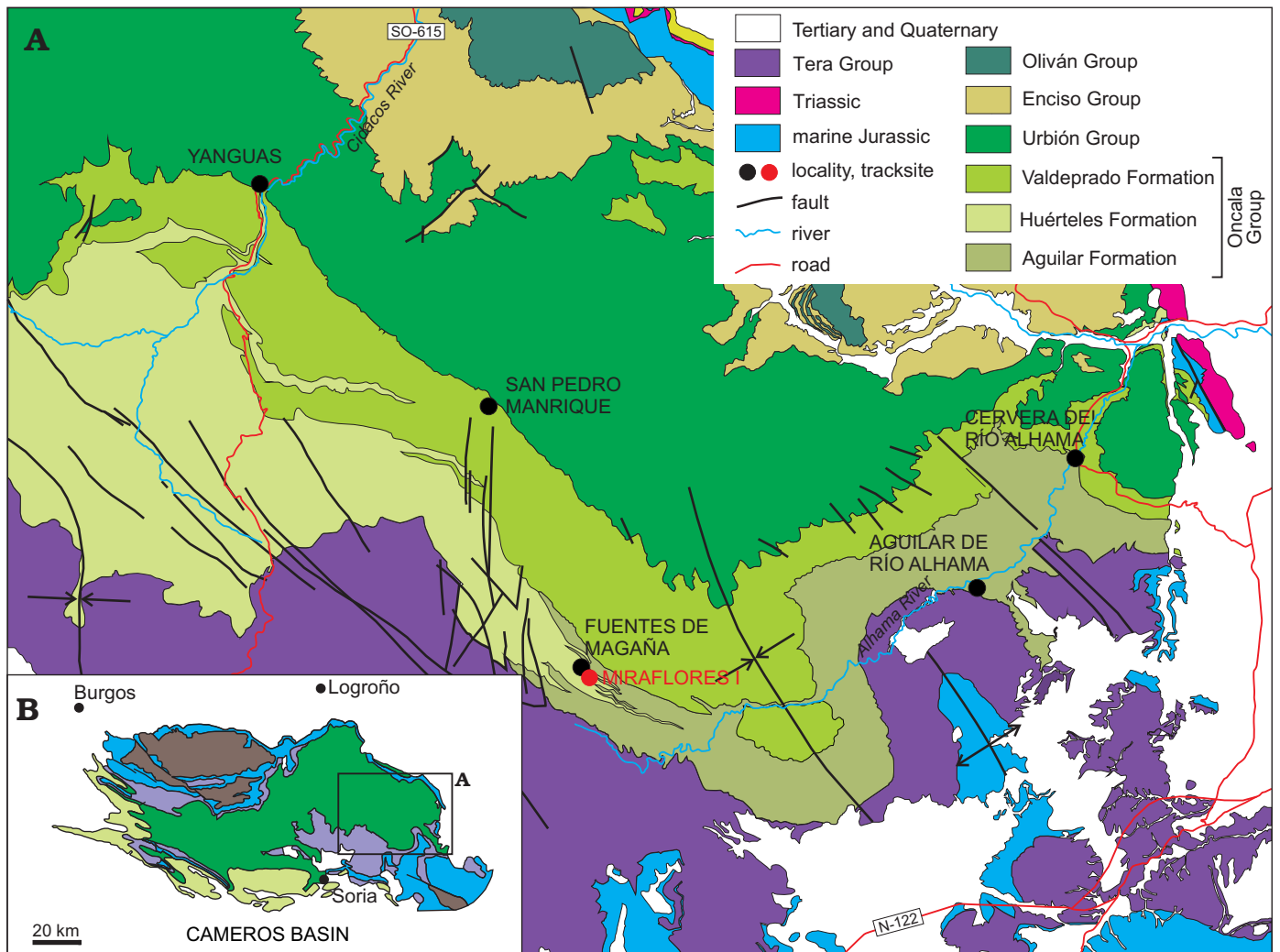


Fig. 1. Location of study area within Cameros Basin, Fuentes de Magaña, Soria, Spain (B) and geology of Miraflores I tracksite (A). Modified from Quijada et al. (2013).

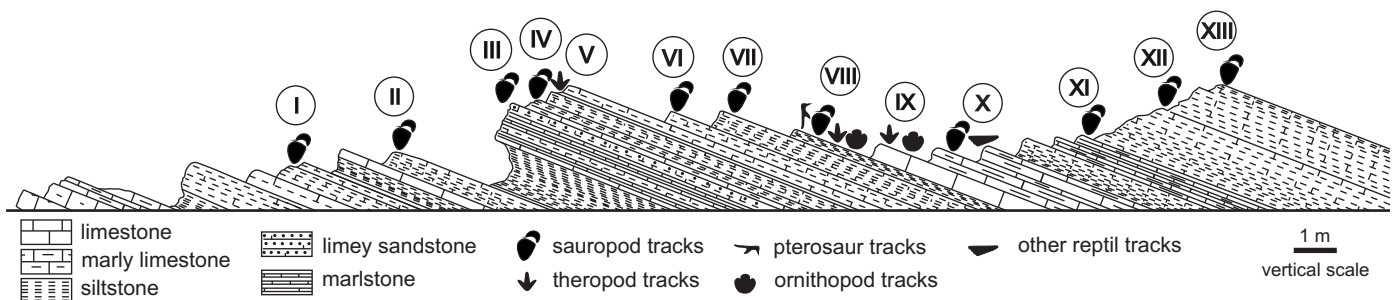


Fig. 2. Stratigraphic column of the Miraflores I tracksite, showing the layers containing dinosaur tracks (Roman numerals).

complete, but the other is missing its posterior part. They are oval in form, longer than wide (ca. length 86 cm, width 62 cm). The anterior part (toe end) is wider than the posterior and the heel is large and round. There are no toe marks to be seen, since these have been infilled by sediment.

In the sediment where these study tracks are visible, three layers of sediment are differentiated underlying the sauropod track, and one overlying layer that was deposited afterwards, infilling the track (Fig. 4B). Of the three un-

derlying layers, the upper one (layer 1; some 13 cm thick) comprises a number of very fine laminae on which the reptiles' autopods were placed directly—at the edges of the tracks these thin laminae are distorted upwards. Due to its plasticity, layer 2, lying directly below layer 1, was also deformed by the passage of the sauropod. The third and lowest layer was unaffected by the pressure of the animal (layer 3). Layer 2 is 15–16 cm thick. As it was trodden, some sediment was extruded some 10 cm above the rest of this layer (form-

ing a so-called displacement rim); in contrast, the centre of the footprint in layer 2 is depressed by about 7 cm. This created an undertrack at about 17 cm depth relative to the top of the displacement rim. The displacement rims are large and can exceed 20 cm in width. Thus, the original thicknesses of the three layers are: layer 1, 13 cm; layer 2, 16 cm; layer 3, undefined but sufficiently deep.

Modelling of the ichnites using finite elements.—This section describes how we used the finite element technique to reproduce the stress deformations caused by sauropod footsteps in the soil. Analysis using finite elements is based on discretizing the medium by dividing it into geometric forms (tetrahedrons in our case), denominated elements (15-node wedge elements in our case). In this way, each element shares its vertices or “nodes” with adjacent elements. The software used to simulate the sauropod tracks using FEM is Plaxis 3D Foundation V2.2. This software is intended for 3-dimensional geotechnical analysis of deformation and stability of soil structures, as well as for geo-engineering applications such as excavation, foundations and embankments.

The calculation process first requires the definition of a number of functions to determine the field of movement, based on nodal displacements. These functions, together with the stress-strain relationship assigned to the sediment, allow a stiffness matrix to be compiled. In turn, two equilibrium equations are established for each node, which express the nodal forces in terms of nodal displacements and stiffness. Once all the nodal displacements are known, calculation of the deformations and stresses for each element can proceed.

The stress-strain relationship assigned to the materials in this case is purely elasto-plastic, i.e., there is a linear relationship between stresses and deformations (strains), which is truncated if the yield condition is reached. In this case, the relationship is defined by the Mohr-Coulomb yield (failure) criterion (the criterion most commonly used in soil mechanics). During the incremental and iterative process of applying the stresses, the deformation (strain) becomes irreversible once an element reaches the yield condition.

Calculations were calibrated using the geometry of the fossilized deformations, both on the surface and at depth, thanks to the availability of the vertical sections in the field (Fig. 5). The values that really serve to calibrate the model are the deformation values. Since the program offers values for displacements, it was necessary to transform the measurements of depth/thickness shown in Fig. 4B and express them instead as displacements. Thickness measurements and displacements are both shown in Fig. 4B. These calculated displacements are important in terms of the mathematical model employed. For problems of large deformations, more advanced finite element models are being developed; however, these are not yet implemented in the software—at least not in the 3D software we are using here. The calibration stage of this process is and deeply described in the SOM (Supplementary Online Material available at http://app.pan.pl/SOM/app61-Sanz_et_al_SOM.pdf) and has been devel-

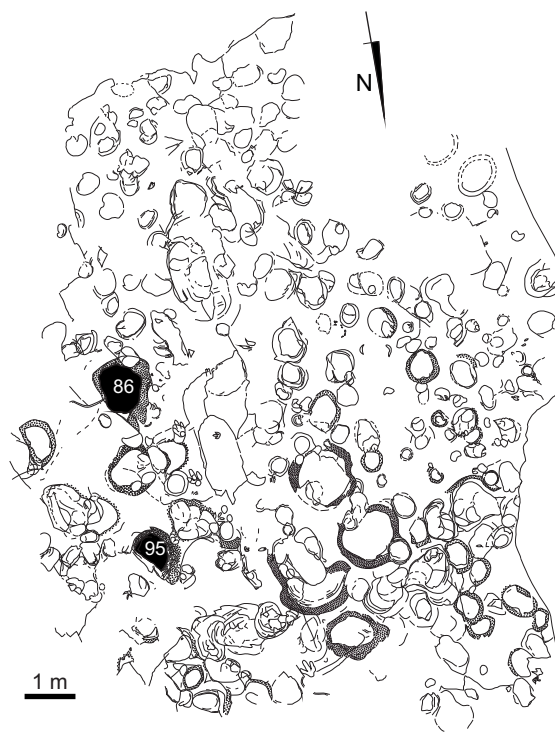


Fig. 3. Scheme showing traces from layer VIII-B of Miraflores I tracksite and view of the tracks 86 and 95.

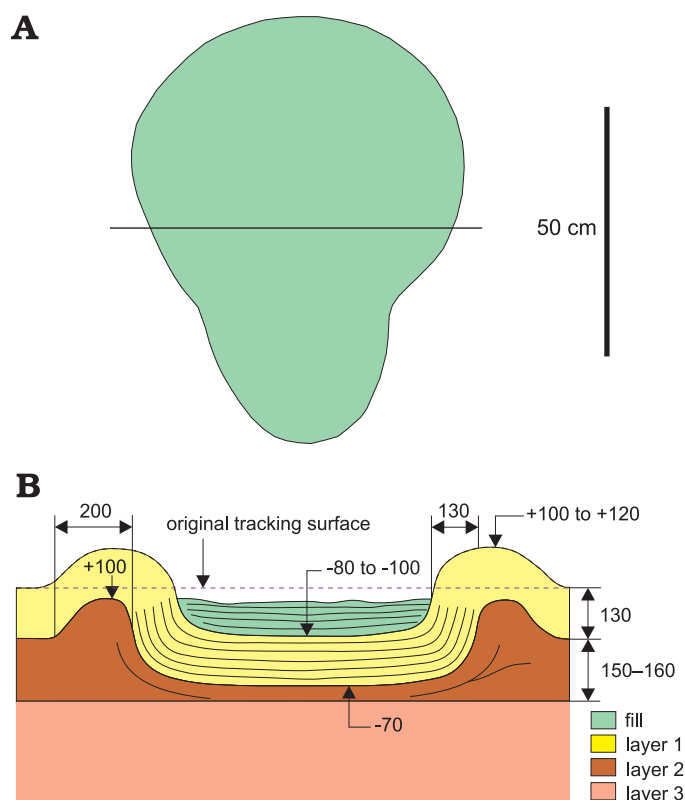


Fig. 4. Tracks 86 and 95 in the Miraflores I tracksite. **A.** Plan view of the autopod, without toe marks, that formed tracks 86 and 95; horizontal line indicates the zone where the section was made. **B.** Section of the track/footprint to be reproduced, with mean values of the vertical displacements and measurements of thickness, both in mm.

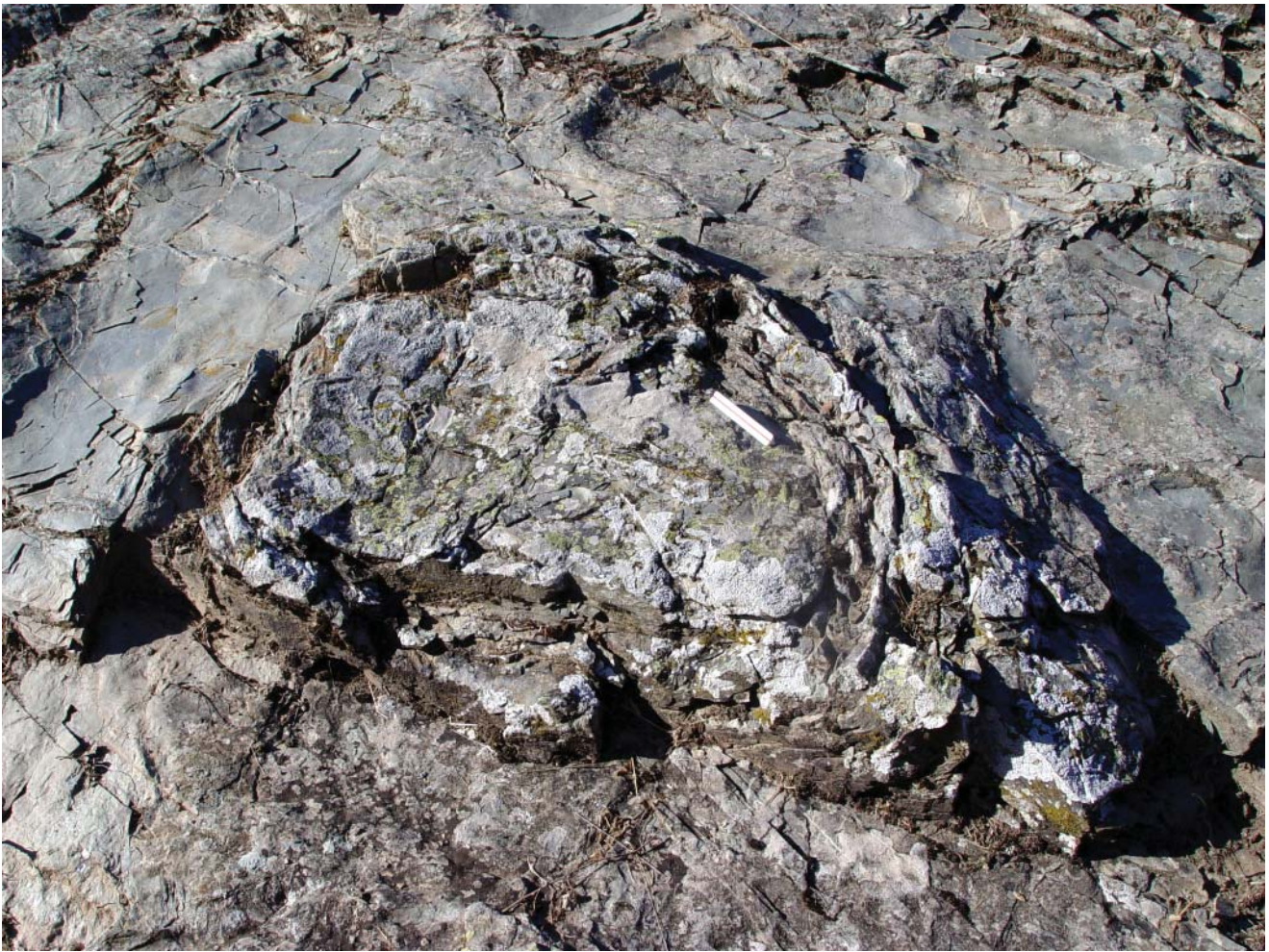


Fig. 5. Track 95 in layer VIII-B of the Miraflores I tracksite, Berriasian (Early Cretaceous), Soria, Spain, showing footprint section. Scale 120 mm.

oped for long time by using additional methodologies in the first 2D models. Results were adjusted within 3D model, checking the coherence between them.

Another problem when simulating the formation of traces concerns the substrate on which the dinosaurs and other reptiles trod on. Often, the substrate was not uniform and sometimes may have been waterlogged. Interesting research on this subject has been carried out by Popescu et al. (2005, 2006) and Falkingham et al. (2014).

According to the microscopic petrography of samples of the outcrop, we can infer that the ground originally trodden was mostly silty mud, with a small proportion of very fine sand. In all probability, the soil would have been totally saturated, since we are dealing with a waterlogged area; at least, this is the assumption made in the model.

Given these conditions and bearing in mind that the footfall is a dynamic action, we believe it is appropriate to consider the load applied as a rapid or “short term” load. For the given soil conditions, this track is correctly reproduced by an elasto-plastic model under undrained conditions. According to the current state of knowledge of these techniques, it is precisely this model that is recommended for the loading processes where there is neither consolidation

nor drainage—this is due to the reduced permeability of the soil associated with the short-lived application of the loads. Given the various possibilities for modelling undrained soil behaviour, we opted for doing an effective stress analysis using effective strength parameters.

Nevertheless, even though these animals were walking very slowly, a tangential force must have been applied on the ground immediately beneath the foot to cause the animal to move forward. Sauropods are estimated to have walked at a speed of around 4 km/h (Alexander 1976). The figure for theropods is three times faster—around 11 or 12 km/h (Alexander 1976). However, the tangential force has not been taken into account. Given the great weight of the dinosaurs, the central symmetry of the displacement rim that surrounds the footfall, as well as the rest of the deformations and the horizontal ground surface, it is valid to simplify the action and consider the footfall as a purely vertical pressure. In any case, the applied loads that would result from this calculation are greater than if we consider a tangential force. Alexander (1989) estimated that the force could be double for small, fast dinosaurs running at full speed.

The toe pads at the end of these animals’ limbs would have acted as buffers to reduce the dynamic effect, although

we are unable able to say to what degree. In any case, in the end, the dinosaur’s load was fully transmitted to the ground, so that the buffering effect of the pads does not influence the results of the finite elements model.

The elements that served to define the model and assess the results are summarised in Fig. 4 (a plan view of the sole, Fig. 4A; a section through the footprint, indicating the dimensions of the deformations and thicknesses of each of the layers described above, Fig. 4B).

Figure 4A yields the perimeter inside of which a uniform pressure is applied. The form represented encloses an area of 0.377 m², equivalent to a radius (of a circular space) of 0.35 m. Figure 6 shows the calculation model, with two layers of silt—13 and 16 cm thick—overlying a more rigid layer that is thicker but, for our purposes, of undefined depth. In the initial simulation, the phreatic layer was considered to lie at the ground surface.

Calculations were made assuming different characteristics for the material and different autopod pressures, until the deformations obtained were considered sufficiently close in both form and dimension.

Soil parameters were made to vary, though only within the range that characterizes the type of material to which they belong. In addition, the calibration process aimed not only to adjust the depth of the tread: it was also necessary to reproduce the perimeter rims and their dimensions of both width and height.

A soil behaviour model was used, which takes into account that the load is applied rapidly and over a short period. This is commonly known as a “short term” load situation, a definition that aims to indicate that the process of loading is shorter than the drainage time for the substrate. The model is refined in this way, since it is not enough to use the classic strength parameters to characterize this situation in an approximate way. Rather, we consider the variation in pore pressure that occurs when a load is applied over low permeability materials. This implies that effective calculation parameters can be used to define the behaviour, but it requires additional parameters to be defined, such as permeability.

Results

Reproduction of the large ichnites.—*True tracks:* In order to obtain a model similar to that observed in situ, a number of calibration simulations were done, varying the parameters of soil and applied load. The best results obtained for the parameters is presented in Table 1 for each of the three soil layers.

We looked for the force transmitted by the foot, using increments of 5 kN. When the results approximated to reality, we continued with increments of 1 kN in each calculation. These results were obtained for a force of 57 kN which, taking into account the area of the footprint, is equivalent to a uniform surface load of around 150 kN/m².

Figure 7A is a global scheme of the results to reproduce the track of the sauropod footfall, while Fig. 7B is a maxi-

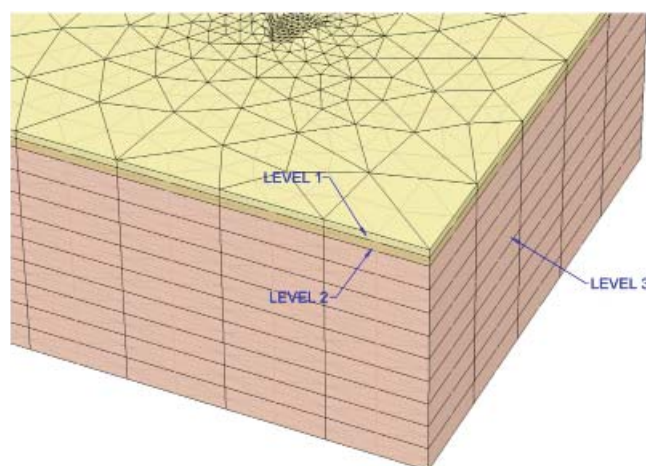


Fig. 6. Detail of the calculation model: layer III of Miraflores I tracksite.

mum-detail graphic that the model creates of the deformations of the surface of layer 1 after the footfall, which is very similar to the ichnite photographed in Fig. 5. The results are an approximate reproduction of the deformations produced in the field, particularly those observed in layer 2.

Given that the phreatic level is situated on the surface, water flows into the hollow of the track, leaving its elevated perimeter dry. Figure 7C shows a detail of the phreatic water flooding the interior of the footprint.

The soil parameters used in the simulation, which are assumed to be valid, are given in the Table 1.

Figure 7D allows these deformations to be quantified and compared with those in Fig. 4B. It shows the vertical displacements on the surface of layer 1 after the footfall. As we can see from the diagrams of the simulations—even though it is barely appreciable in the field—there is a small variation in the depth of the track (this is smaller than it appears because the vertical scales are exaggerated). In the discussion section of this paper, we offer an explanation for this observation.

Table 1. Parameters for the various soil layers used in the ichnite modelling (γ_{unsat} unsaturated unit weight of the soil). γ_{sat} , saturated unit weight of the soil; k , isotropic permeability; ν , Poisson’s ratio; E_{ref} , Young’s modulus; c_{ref} , cohesion; ϕ (°), friction angle; E_{incr} , increase of stiffness with depth; c_{incr} , increase of cohesion with depth.

	Layer 1	Layer 2	Layer 3
Name	I (sandy silty mud)	II (plastic sandy silt)	III (marly silt)
Type	undrained	undrained	undrained
γ_{unsat} [kN/m ³]	14	16	18
γ_{sat} [kN/m ³]	16	18	20
k [m/day]	8.64E-02	8.64E-04	8.64E-05
ν [-]	0.30	0.33	0.30
E_{ref} [kN/m ²]	10000	2000	30000
c_{ref} [kN/m ²]	10	10	40
ϕ [°]	27	28	28
E_{incr} [kN/m ²]	0	0	1955
c_{incr} [kN/m ³]	0	0	10

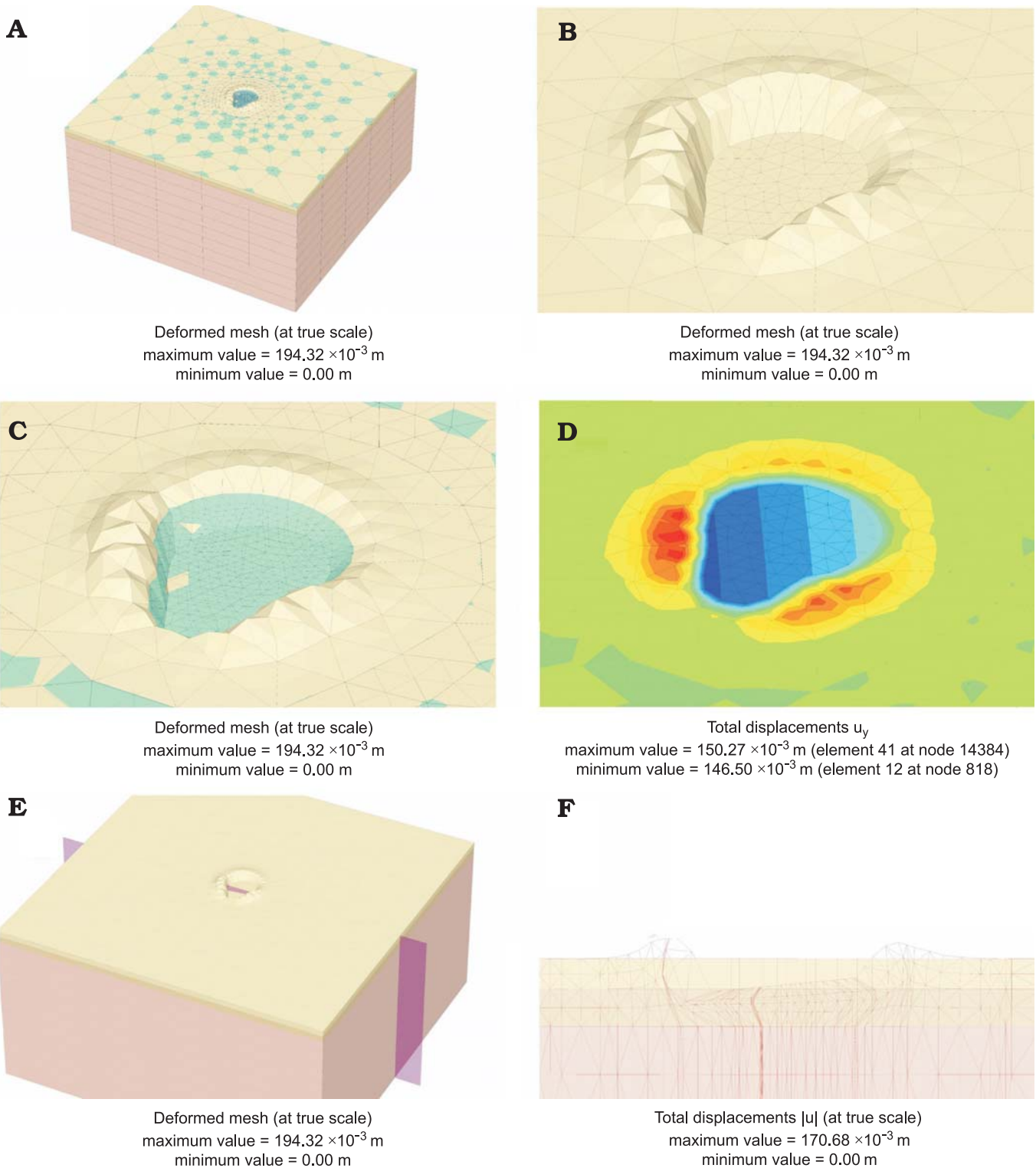


Fig. 7. Results of the calculation model. **A.** Calculation model for big footprint after the footfall. **B.** Deformed mesh (at true scale) after the footfall (surface of layer 1). **C.** Detail of simulation model with phreatic level. **D.** Vertical displacement after the footfall (surface of layer 1); scale in mm. **E.** Position of the vertical section. **F.** Vertical displacements of the section shown in E.

Figure 7E gives the position of the vertical section through the model which appears in Fig. 7F and shows the original and deformed mesh. The figure reveals the reduction in thickness below the track and the formation of a displacement rim by extrusion of the material from beneath

the footfall. The extrusion phenomenon is affected by the limitation of the model to reproduce large deformations.

Figure 8 represents how the ichnites would be if layer 1 were softer and more plastic than layer 2. This situation would correspond to the initial state of the outcrop/tracksite

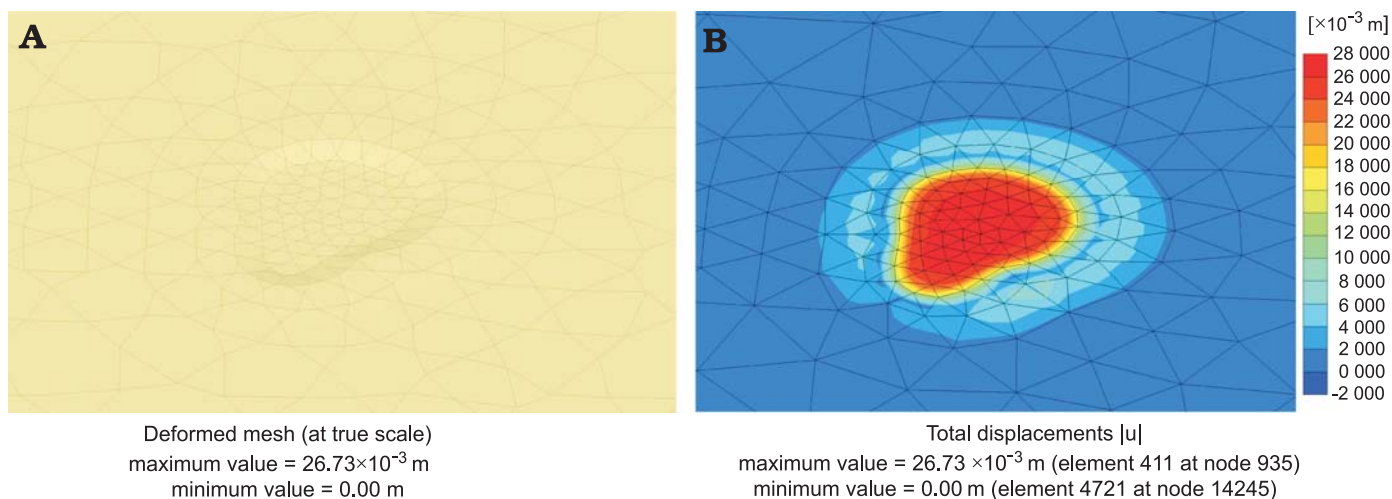


Fig. 8. Deformed mesh and vertical displacement in layer 1. **A.** Deformed mesh after a footfall in a plastic layer 1; at true scale. **B.** Vertical displacement after the footfall (surface of the plastic layer 1); scale in mm.

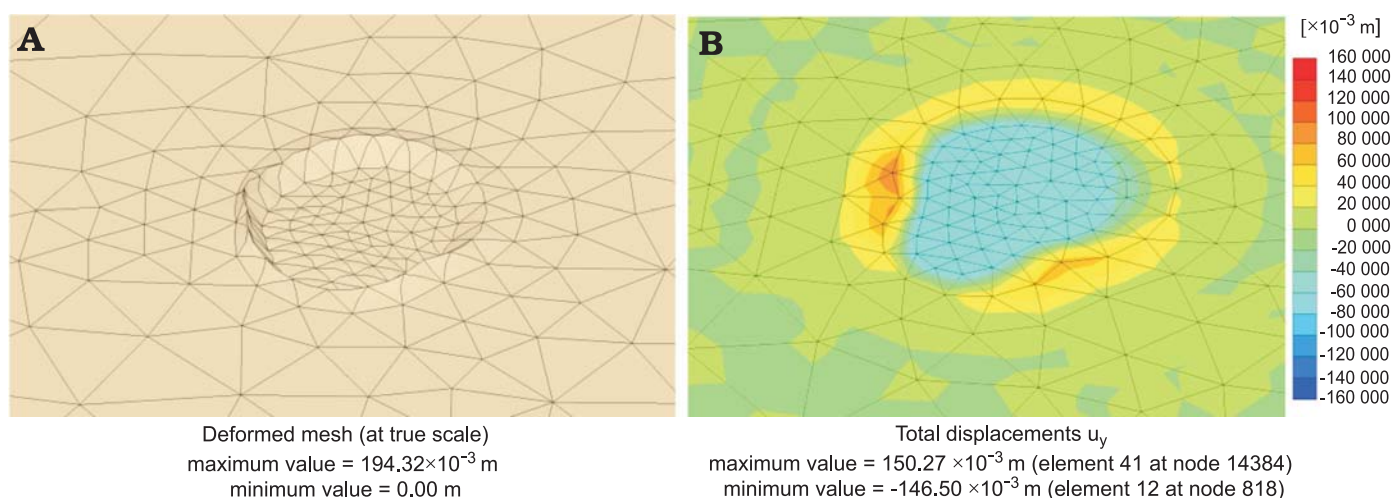


Fig. 9. Deformed mesh and vertical displacement in layer 2. **A.** Deformed big footprint, mesh after footfall (surface of layer 2); at true scale. **B.** Vertical displacements after the footfall (surface of layer 2); scale in mm.

when the moisture in the surface layer has not yet been lost, i.e., before it hardens through desiccation. One can see how the footfall makes a track of maximal depth with a flat base within the silhouette of the footfall. The figure also shows a shallow peripheral zone that sinks towards the centre, with no formation of a displacement rim. This type of simulation resembles the undertrack (whose simulation is described in the following section), although it is deeper and lacks a displacement rim.

The undertracks: The software employed allows any of the layers to be eliminated from the visualization, as indicated in Fig. 9A, which shows the deformation of the upper surface of layer 2 after the footfall. The figure closely approximates to the deformations observed in the field. In fact, this figure reflects what an undertrack would look like if all the fill material were removed. As we can see, the base of the undertrack is flat and horizontal.

In this case, it is even more interesting to determine the dimensions of these deformations, since the field data for

layer 2 are more reliable because they have not been affected by erosion (whereas in layer 1, erosion has eliminated the crest of the displacement rim). The layer 2 simulation is represented in Fig. 9B, which shows the vertical displacements in layer 2 after the footfall.

Reproduction of small tracks.—The tracksite contains a number of small tracks that have the same form as the large ones. In order to simulate these smaller tracks, we repeated the calculation used for large tracks, applying progressively smaller forces on layer 1 (which is 13 cm thick, and overlies layer 2, 16 cm thick). For a footfall force of less than 0.4 t, the model produces a track some 4 mm deep, with no displacement rim (Fig. 10B). This is the most frequent type of small track observed in the field; the small tracks are shallow—only a few millimetres—and they lack displacement rims. If we examine the undertrack in layer 2, its depth is 2.5 mm (Fig. 10C). Figure 10A magnifies the deformations in layer 1 (track) by 20, while Fig. 10B, C (track and un-

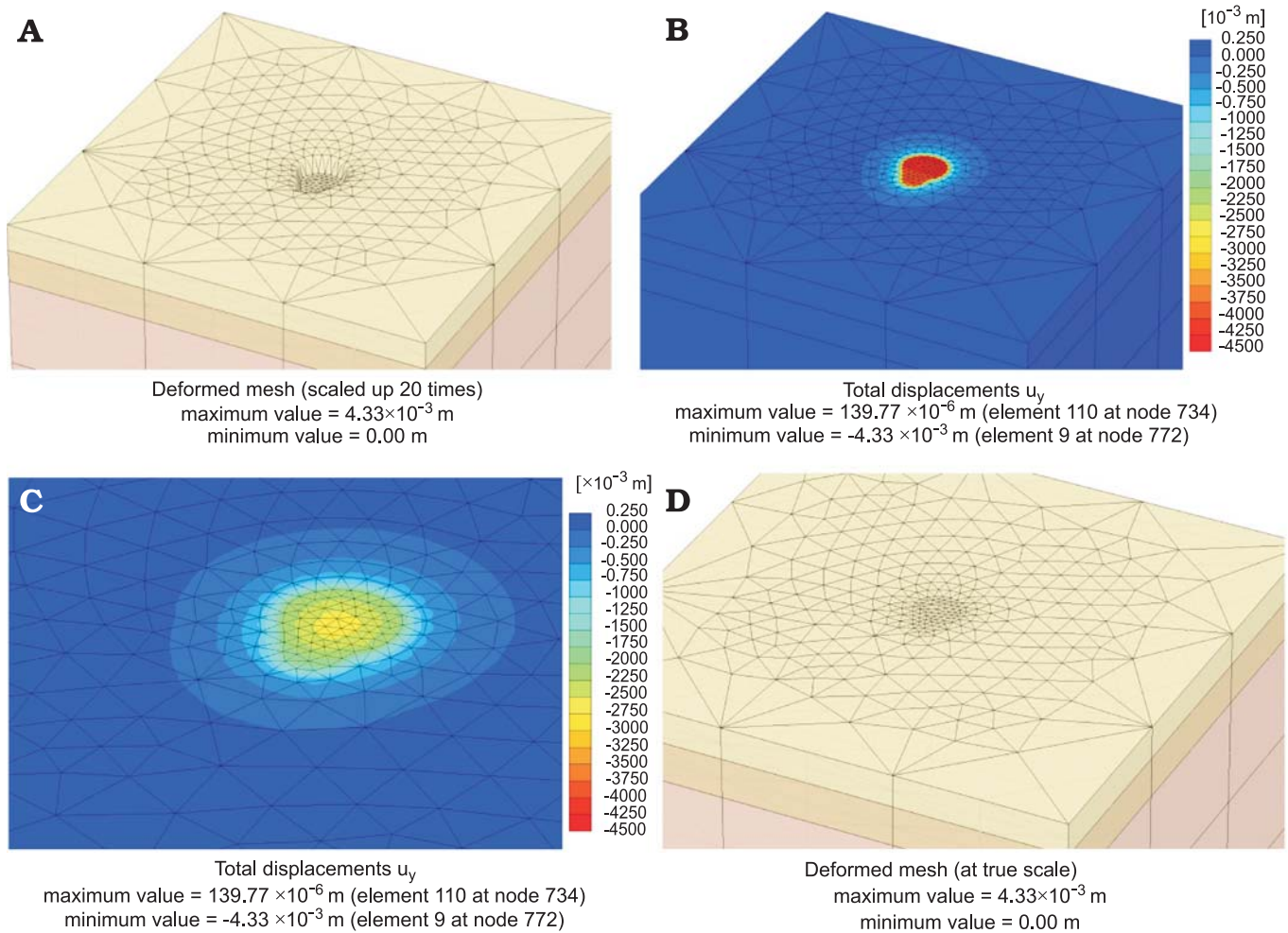


Fig. 10. Deformed mesh and vertical displacement in layer 1, scaled 20 times. **A.** Deformed small footprint, mesh after footfall (surface of layer 1); scaled up 20 times. **B.** Vertical displacements after footfall (surface of layer 1); scale in mm. **C.** Vertical displacements after footfall (surface of layer 2); scale in mm. **D.** Deformed mesh after the footfall (surface of layer 1); at true scale.

dertrack, respectively) show the vertical displacement on a scale that is adjusted to the minimum and maximum displacements obtained in this calculation (0 mm to a little more than 4 mm).

Figure 10D and E represents the deformations and displacements, respectively, after a small footprint is made in layer 1. This matches the representation for the initial calculation of a large footprint (deformations are not amplified and displacement is shown on a scale with a range of ± 160 mm). The deformations are so small compared to the previous ones that they are not represented with any precision.

Discussion

The primary result is the satisfactory reproduction of the large track (coinciding the “in situ” tracks in layer VIII-B of the Miraflores I tracksite), which was obtained using a distributed load of just over 150 kN/m^2 ; this is equivalent to a force of 6 tonnes applied by the limb. These results are similar to those obtained previously using simple analytical

models and 2D modelling, which reproduced the extrusion in layer 2 (Arcos et al. 2006), and which accord with the expected weight range for these dinosaurs.

In the simulation of the undertrack, its depth is similar to that of the true track. In the field, it could be easily confused for a true track, if the covering layer of sediment had been eroded away. This raises the question of whether deep sauropod tracks should be designated as true tracks if there is no additional evidence (as is commonly the case), such as of clear impressions of the toes.

Soil moisture conditions not only vary in space but also through time and this phenomenon can have important consequences for the form of the track generated by a particular species of dinosaur in a particular place.

All this occurs in accordance with the alternating sequence of saturation and desiccation in the paleoenvironment that affects the surface layer of sediment. For a given soil granulometry, the model conditions can be changed so that, instead of assuming hardening of layer 1 through desiccation and evaporation, we can consider the top layer to be completely saturated like the remainder of the soil profile.

In this case, the mathematical model generates a shallower track with no displacement rim, even though the soil is softer. In this way, modelling of the tracks under various substrate conditions allows us to apply the results to true tracks that have a similar appearance but different depths.

For the small tracks, the chosen force exerted by the limbs was 0.4 t, which accords with the expected weight of the young dinosaurs.

The shallow displacements of both simulated tracks and undertracks produced by young animals explains why small tracks would not be impressed very sharply when the upper sediment layer had a particular consistency (as in the Miraflores I tracksite). It also explains that even slight erosion would erase the tracks. These reasons may be behind the lower frequency of small tracks at this tracksite, even though the presence of small handprints clearly indicates that the number of baby sauropods at this site was much higher than the number of footprints would suggest. The greater pressure exerted by the hands on the sediment meant that the handprints were imprinted more deeply and/or persisted in the face of subsequent erosion.

The pressure exerted to create this type of track means that they were not prone to flooding once the load was released because they were not sufficiently deep to intercept the phreatic level. If ponding did occur, the water would rapidly dry up.

The undertrack produced by small tracks is so shallow as to be practically non-existent. In this case, therefore, the way to distinguish an undertrack “in situ” would be by observing extremely shallow prints, in which case its edges would be very difficult to identify. A very shallow angle light is required to be able to distinguish the undertracks and, even then, differentiation is poor.

Leaving aside the qualities of the sediments assumed in the modelling, it is known (Currie 1983) that when dinosaurs walked along a shoreline, the underwater tracks created while wading through water are deeper than those created in sediments exposed to the air.

If the draining of water from the waterlogged zones was rapid (regression phase), the naturally clayey soils would retain much of their moisture (more time would be required for them to drain completely). This phenomenon is observed in reservoir draw offs. Under these conditions, the sediment would maintain a residual plasticity and be easily mouldable by autopods. If the ichnites were produced over a day or a number of weeks whilst the substrate was drying out (and becoming firmer), the ichnites produced at the beginning would be deeper than later ones (Thulborn 1990). Prints made by the largest and heaviest animals would have a greater chance of persisting than ones made by juveniles. Once the substrate had completely dried out, the passing sauropods would not leave any impressions in it at all.

Modelling of these footprints (ichnites) has served to demonstrate how the type and state of the trodden sediment is a basic conditioning factor for track formation. The most important observation, from the point of view of soil mechan-

ics, is that the initial—and commonly adopted—hypothesis of soft sediments that become firmer and more resistant with depth (Terzaghi 1943) (i.e., layer 1 is softer and more easily deformed than layer 2) did not yield satisfactory results in the initial model runs. In the field (Fig. 4), the deformation suggests extrusion of layer 2 towards the outer edge of the footprint, whilst layer 1 adapts to the deformation, possibly breaking the perimeter line of the track. To reproduce this using the model, it was necessary that layer 2 was the softest and most easily deformed of the three layers, possessing considerable plasticity and capable of being extruded to form the displacement rim that is observed in the fossil tracks.

The initial hypotheses seem to be appropriate for sediments deposited very shortly before being trodden, where hardly any moisture has been lost. In this case, the morphology of the track is different. The simulation required a rigid layer of sediment beneath layer 2 to cause extrusion of layer 2. This firmness of the underlayer (layer 3) is confirmed in the field—this layer is not deformed. Although sediment in layer 3 has a similar composition to the other layers, it is much stiffer; this is explained by a sediment layer that was already partly consolidated.

The lithology and granulometry of layers 1 and 2 are similar, though layer 1 is slightly sandier. The phreatic level would have been very close to the surface and the alternating wet and dry periods experienced under the paleoclimate prevailing at that time would have meant that the most superficial layer (layer 1) was subject to alternating conditions of saturation and desiccation. Evaporation led to desiccation of the soil surface, which caused it to harden and transforming its mechanical properties. This would have favoured the creation of a crust on the surface through the effect of cementation and/or suction, giving rise to a material that was more brittle—with greater rigidity but less resistance.

Another aspect to consider is the soil compaction that would have occurred due to the load of the dinosaurs walking over barely consolidated sediments (similar to the compaction caused by bulldozers in the construction of earth embankments). The maximum consolidation of a particular type of soil occurs at a particular moisture content (as exploited in the Proctor compaction test in soil engineering). Although there may have been excess moisture in the medium where the ichnites were created, consolidation would have been greater than if the ground had been dry. The direct consequence of consolidation is an increase in the resistance to erosion of the treadmark, increasing the chances that the track would be preserved—in other words the formation of a track conferred a degree of self-preservation. This is the reason why ichnites are often found in relief at the Miraflores I tracksite (Fig. 5).

Another important issue brought to light by the model simulations is that where the phreatic level is close to the surface (the most common situation given that moist, plastic soils tend to occur close to the shoreline of waterlogged areas), water floods the large tracks (Fig. 7C), flowing into

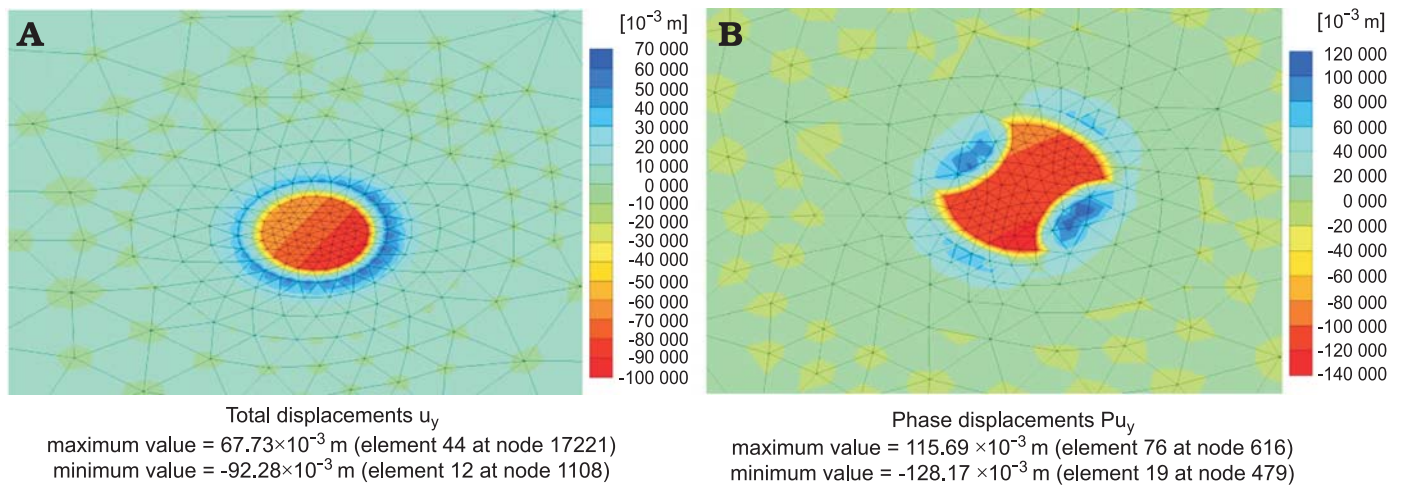


Fig. 11. Vertical displacement after circular and pressure-shaped curvilinear quadrilateral. **A.** Vertical displacement after a circular pressure. **B.** Vertical displacement after a pressure-shaped curvilinear quadrilateral with concave and convex alternate sides.

the hollow formed by the footprint. This leaves the ground around its elevated perimeter dry.

Under these conditions, sauropods would leave behind them a surface spangled with small puddles of water that could be quite long-lasting, since the water contained in the footprints would be connected to the phreatic water and so would not easily evaporate. Meanwhile, the juveniles, whose footsteps would not be capable of making puddles, would be trying to dodge around the puddles, given that it would be more trouble to walk on sediment already puddled by adults. The intensity of the footprint or dinoturbation would be directly related to the wetted surface and could give rise to formation of true mudflats, where the resistance of the soils was residual due to the continuous kneading effect of the footsteps. The turbidity created by tramping through the water would mean that clay would settle in the puddles themselves. This could explain why, at other track-sites, some tracks—and even retraction cracks—contain a thin layer of clay infill. Such clay infill is not observed at the Miraflores I tracksite, either because it was never produced or because it was subsequently eroded.

During a transgressive phase, these puddles would act, on one hand, as a buffer against erosion and, on the other hand, as preferential sedimentation pools. For this reason, one can sometimes find infill sediments of a different type from the strata that bear the tracks. In the baby tracks, this infill does not occur because these tracks did not flood with water which, additionally, made them more vulnerable to erosion.

Since these puddles were isolated, they must have created a particular ecological environment containing an abundance of organic matter from a proliferation of algae and other microorganisms.

Another important issue raised by the simulations undertaken relates to the formation of displacement rims and the fact that the base of the simulated track is not completely horizontal. Leaving aside the anatomical and dynamic factors of sauropods, the model indicates not only that soil mechanics but also the geometry or shape of the footfall

were influential in the formation of the displacement rims. For a displacement rim to be produced, the first and most essential condition is the existence of several soil levels in the vertical profile—each possessing the particular mechanical characteristics favouring rim formation. Yet, once this condition is met, the distribution and geometry of the displacement rim on the periphery of the track depends on the form of the silhouette of the footprint. In effect, although the force is applied vertically (as if the animal did not have to pull the foot forwards) onto a level and horizontal soil surface, even if the pressure was constant over the entire surface, the base of the track would not be completely level but slightly deeper at the front. This feature would not occur in the undertracks, nor in true tracks formed on a soft layer 1. In other words, the deeper front edge only appears along with a displacement rim. We should point out that this greater depth, though minimal, has not been observed in the field, so the explanation we give here applies only to the model simulations.

To clarify this question, we did additional calculations using different geometrical figures but maintaining the same area as the large track. The hypothesis posed is that the extrusion could also be the cause of the variation in depth observed in the base of the track, even though these variations are very small. We also hypothesize that the extrusion depends on the shape of the track. Indeed, it is logical to think that the material extruded from beneath the foot travels over a minimum distance until it emerges beyond the print as a displacement rim—and this depends on the form that the silhouette of the track takes. This would lead to differences in the volumes evacuated and cause the variable depth of the base of the track. This question raises the specific need to study the effect that concavities or convexities of the track's perimeter produce in the displacement rims, and in the deformations of the base of the track.

The pressure applied was the same as for the study track, i.e., 150 kN/m^2 ; since the area of the simulated track was kept constant, this means the same total force of 57 kN.

We studied two forms—one a circle, and the other a shape with two axes of symmetry formed by circumferential arcs (Falkingham et al. 2010). The vertical displacements for both cases are given in the following figure (Fig. 11). As we can see, these displacements are in the same order of magnitude as those obtained for the simulated track.

Figure 11B corresponds to the circumference, which is greater in the second figure. In the second figure, we can see how the concave perimeter causes displacement rims that are higher than in the convex zones, and how the rim disappears at the corners. In the circular form, there are no such differences, due to the lack of inflection points in the fully convex form.

The circumstances outlined above suggest that concavities affect an area that is greater than the perimeter. On the other hand, the smaller dimensions of the figure in the direction of the concavities facilitates the extrusion phenomenon.

In any case, both figures show how the surface inside the perimeter is not completely horizontal, a feature that coincides with the results of the track analysis. It is quite possible that this effect does not represent any physical phenomenon but is due to the discretization of the medium that the software performs automatically, and which does not respect all the symmetries of the figures represented.

Nevertheless, there are differing opinions as regards anatomy. For example, in biped tracks, the medial part is the deepest because the feet are directed towards the centre of the trace, creating more pressure in this area. In sauropods, the feet would normally be directed towards the edge of the track (even if only slightly) or to the front, so one would expect the tracks to be deeper on the opposite side, or not at all.

Thus, whilst we have not been able to clarify this question fully, doing this additional simulation has demonstrated that the geometry of the track strongly influences the form and volume of the displacement rim.

Conclusions

Though the model simulations done refer to the specific case of the Miraflores I tracksite, and assuming particular soil conditions at the moment the footsteps were imprinted, the methodology and some of the conclusions drawn from this study go beyond the local geography and may be worth considering at other similar outcrops of dinosaur ichnites.

Modelling of fossil ichnites of sauropod dinosaurs, using 3D mathematical models traditionally employed to study soil mechanics, is possible—even if the initial data about soil characteristics are incomplete. These soil characteristics can be inferred and, in any case, missing data obliges more effort to be spent in calibrating the model. This has been demonstrated in previous studies by Margetts et al. (2005, 2006), Falkingham et al. (2009, 2010, 2011a, b), and Schanz et al. (2013). The present study is different because it focusses on the sedimentological aspects.

The results obtained can be judged to be satisfactory because they reproduce the geometry of the tracks with relative accuracy, as well as the soil conditions prevailing at the moment the footprint was made. The modelled tracks possess the same characteristics as those found “in situ”, being a direct consequence both of the animal that created them and the conditions at the moment the soil was trodden. The forces exerted that were assumed in the model are coherent with the weights expected for these sauropods. This was possible because we were able to rely on a conceptual model of the track that was very well-defined in three dimensions, thanks to the natural outcrops of sections in the field.

Having successfully simulated the track(s) at the Miraflores I tracksite, the model was applied to explore other suppositions, such as the reproduction of undertracks, baby tracks, and the formation of displacement rims. We do not consider that we have exhausted all the possibilities with this model and will continue new lines of investigation. What we have discovered is a field of application with great possibilities that could be used to improve ichnite interpretation at dinosaur tracksites.

Modelling of the ichnites has served to confirm how the type and state of the trodden sediment is a fundamental determining factor at the moment a track is created. The most significant observation, from the point of view of soil mechanics, is that the initial and commonly posed hypothesis—of soft layers of sediment that increase in rigidity and resistance with depth (i.e., a top layer 1 that is softer and less resistant than layer 2 beneath)—does not produce a satisfactory result in the initial modelling simulations. Rather, it was necessary to consider layer 2 as the softest and most deformable of the three layers. The upper layer (layer 1) is not exactly a firm or strong layer. It is rigid but not very resistant (low strength properties). Therefore, the layer is brittle and prone to fracture. The lower layer (layer 2) overlies a stiffer, more resistant layer (layer 3) and so it can only be deformed radially by means of a radial extrusion mechanism. Thus, the vertical pressure functions to overcome the horizontal resistance that limits the extrusion. The greater rigidity of the surface layer can be ascribed to the evaporation and desiccation to which it would be subject.

In term of the formation of displacement rims, it was found essential to consider the properties of the various soil layers to explain their appearance. In our case, the requirement was for the trodden layer to be somewhat more rigid than the layer extruded beneath it). The form of the displacement rim depends partly on the geometry of the footprint—as we demonstrated in additional simulations using tracks with pure geometries. We suspect that the small differences in the depth of the base of the simulated tracks are due to the discretization of the medium that is performed automatically by the software, since the examples of tracks in the field have flat, horizontal bases.

The results indicate that the discretization used in the model is good enough to reproduce the shape of the displacement rims with sufficient accuracy in the majority of cases,

though it is possible that the precision is insufficient for small prints. We intend to refine the model as part of future studies.

It is known that dinosaurs of different weight (with respect to the size of their feet) and moving at different velocities can affect the depth of the print. At the Miraflores I tracksite, it was also demonstrated that changing soil moisture conditions were the reason for the presence of tracks that are similar, but of different depths and both with or without displacement rims, just as we confirmed with the series of model simulations in which the moisture content of the upper layer (layer 1) was varied, i.e., considering it to be either saturated with water or desiccation.

Modelling of the undertracks demonstrated that the criterion of depth is not sufficient in itself to distinguish true tracks from undertracks, since they can be very similar in depth. Therefore, it is necessary to take other discriminatory elements into account to differentiate the true tracks, which might be very shallow in some cases. This brings into question the designation of deep sauropod tracks (which are very frequently found) and suggests they should only be designated as true tracks if there is some additional feature as well.

Another important conclusion from an ecological and sedimentological standpoint is that when the phreatic level is close to the surface—which is most commonly the case—the model simulations show that water fills the large tracks but not the smallest ones (which don't penetrate as far as the water level). Due to dilatancy, the elevated rim of the track is left dry. Large sauropods left behind them a surface spangled with small puddles that could be quite persistent, since the ponded water was connected to the phreatic level and would not have been easily evaporated.

As Falkingham (2011a, b) demonstrated, simulation of small sauropod prints showed their depth was shallow enough that they would be easily eroded and, as a result, their frequency at tracksites would be far lower than adult prints. This is much less the case for handprints, whose greater pressure increases the depth of the print and so its resistance to erosion, as can be observed in the tracksite under study.

Acknowledgements

We would like to thank to Grzegorz Niedźwiedzki (Department of Organismal Biology, Uppsala University) and anonymous reviewer for every suggestion and observation which have improved the work.

References

- Abo-Elnor, M., Hamilton, R., and Boyle, J.T. 2004. Simulation of soil-blade interaction for sandy soil using advanced 3D finite element analysis. *Soil and Tillage Research* 75 (1): 61–73.
- Alexander, R.M. 1976. Estimates of speeds of dinosaurs. *Nature* 261: 129–130.
- Alexander, R.M. 1989. *Dynamics of Dinosaurs and Other Extinct Giants*. 167 pp. Columbia University Press, New York.
- Anfinson, O.A., Lockley, M.G., Kim, S.H., Kim, K.S., and Kim, J.Y. 2009. First report of the small bird track *Koreanaornis* from the Cretaceous of North America: implications for avian ichnotaxonomy and paleoecology. *Cretaceous Research* 30: 885–894.
- Arbour, V.M. and Slevely, E. 2009. Finite element analyses of ankylosaurid dinosaur tail club impacts. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology* 292: 1412–1426.
- Arcos, A., Sanz, E., Pascual, C., Uriel, S., Latorre, P., and Hernández, N. 2006. Las deformaciones producidas en los sedimentos por el paso de grandes dinosaurios: el caso del yacimiento de saurópodos de Miraflores I, Fuentes de Magaña (Soria, España). In: Colectivo Arqueológico-Paleontológico Salense (ed.), *Actas de las III Jornadas sobre Dinosaurios y su Entorno*, 193–222. Salas de los Infantes, Burgos.
- Baird, D. 1957. Triassic reptile footprint faunules from Milford, New Jersey. *Bulletin of the Museum of Comparative Zoology* 117: 449–520.
- Bates, K.T., Falkingham, P.L., Hodgetts, D., Farlow, J.O., Breithaupt, B.H., O'Brien, M., Matthews, N., Sellers, W.I., and Manning, P.L. 2009a. Digital imaging and public engagement in palaeontology. *Geology Today* 25: 95–100.
- Bates, K.T., Manning, P.L., Hodgetts, D., and Sellers, W.I. 2009b. Estimating mass properties of dinosaurs using laser imaging and 3D computer modelling. *PLoS ONE* 4 (2): e4532.
- Bates, K.T., Manning, P.L., Vila, B., and Hodgetts, D. 2008a. Three dimensional modelling and analysis of dinosaur trackways. *Palaeontology* 51: 999–1010.
- Bates, K.T., Rarity, F., Manning, P.L., Hodgetts, D., Vila, B., Oms, O., Galobart, À., and Gawthorpe, R. 2008b. High-resolution LiDAR and photogrammetric survey of the Fumanya dinosaur tracksites (Catalonia): Implications for the conservation and interpretation of geological heritage sites. *Journal of the Geological Society, London* 165: 115–127.
- 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., and Crompton, R.H. 2013. Does footprint depth correlate with foot motion and pressure? *Journal of the Royal Society Interface* 10: 20130009.
- Bellian, J.A., Kerans, C., and Jennette, D.C. 2005. Digital outcrop models: applications of terrestrial scanning LIDAR technology in stratigraphic modelling. *Journal of Sedimentary Research* 75: 166–176.
- Breithaupt, B.H. and Matthews, N.A. 2001. Preserving paleontological resources using photogrammetry and geographic information systems. In: D. Harmon (ed.), *Crossing Boundaries in Park Management. Proceedings of the 11th Conference on Research and Resource Management in Parks and Public Lands*, 62–70. The George Wright Society, Inc., Hancock.
- Breithaupt, B.H., Matthews, N., and Noble, T. 2004. An integrated approach to three-dimensional data collection at dinosaur tracksites in the Rocky Mountain West. *Ichnos* 11: 11–26.
- Breithaupt, B.H., Southwell, E.H., Adams, T., and Matthews, N.A. 2001. Innovative documentation methodologies in the study of the most extensive dinosaur tracksite in Wyoming. In: V.L. Santucci and L. McClelland (eds.), *6th Fossil Research Conference Proceedings Volume*, 113–122. Geologic Resources Division, Lakewood.
- Clemente, P. 2010. Review of the Upper Jurassic–Lower Cretaceous stratigraphy in Western Cameros Basin, Northern Spain. *Revista de las Sociedades Geológicas de España* 23: 101–143.
- Currie, P.J. 1983. Hadrosaur trackways from the Lower Cretaceous of Canada. *Acta Paleontologica Polonica* 28: 63–73.
- Falkingham, P.L. 2010. *Computer Simulation of Dinosaur Tracks*. 201 pp. Unpublished Ph.D. Thesis, University of Manchester, Manchester.
- Falkingham, P.L. 2012. Acquisition of high resolution 3D models using free, open-source, photogrammetric software. *Palaeontologia Electronica* 15 (1): 15.1.1T. <http://palaeo-electronica.org/content/issue1-2012/technical-articles/92-3d-photogrammetry>
- Falkingham, P.L., Bates, K.T., Margetts, L., and Manning, P.L. 2011a. Simulating sauropod manus-only trackway formation using finite-element analysis. *Biology Letters* 7: 142–145.
- Falkingham, P.L., Bates, K.T., Margetts, L., and Manning, P.L. 2011b. The

- 'Goldilocks' effect: preservation bias in vertebrate track assemblages. *Journal of the Royal Society Interface* 8: 1142–1154.
- Falkingham P.L., Hage, J., and Bäker, M. 2014. Mitigating the Goldilocks effect: the effects of different substrate models on track formation potential. *Royal Society Open Science* 1 (3): 140225.
- Falkingham, P.L., Margetts, L., and Manning, P.L. 2010. Fossil vertebrate tracks as paleopenetrometers: Confounding effects of foot morphology. *Palaios* 25: 356–360.
- Falkingham, P.L., Margetts, L., Smith, I.M., and Manning, P.L. 2009. Re-interpretation of palmate and semi-palmate (webbed) fossil tracks; insights from finite element modelling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 271: 69–76.
- Fervers, C.W. 2004. Improved FEM simulation model for tire-soil interaction. *Journal of Terramechanics* 41: 87–100.
- Guiraud, M. and Seguret, M. 1985. A releasing solitary overstep model for the Late Jurassic–Early Cretaceous (Wealdian) Soria strike-slip basin (Northern Spain). In: N. Christie-Blick and K.T. Biddle (eds.), *Strike-Slip Deformation, Basin Formation, and Sedimentation. Society of Economic Paleontologists and Mineralogists Special Publication* 37: 159–175.
- Henderson, D.M. 2006. Simulated weathering of dinosaur tracks and the implications for their characterization. *Canadian Journal of Earth Sciences* 43: 691–704.
- Kraft, R.H., Mckee, P.J., Dagro, A.M., and Grafton, S.T. 2012. Combining the finite element method with structural connectome-based analysis for modeling neurotrauma: connectome neurotrauma mechanics. *PLoS Comput Biol* 8 (8): e1002619.
- Lockley, M.G. 2007. The morphodynamics of dinosaurs, other archosaurs, and their trackways: holistic insights into relationship between feet, limbs, and the whole body. In: *Sediments organism interactions: A multifunctional Ichnology. SEMP Special Publication* 88: 27–51.
- Lockley, M., Chin, K., Houck, K., Matsukawa, M., and Kukihara, R. 2009. New interpretations of *Ignotornis*, the first-reported Mesozoic avian footprints: implications for the paleoecology and behavior of an enigmatic Cretaceous bird. *Cretaceous Research* 30: 1041–1061.
- Latorre Macarrón, P., Pascual Arribas, C., Sanz Pérez, E., and Hernández Medrano, N. 2006. El yacimiento con huellas de Saurópodos de Miraflores I. Fuentes de Magaña. (Soria, España). In: *Colectivo Arqueológico-Paleontológico de Salas* (ed.), *Actas de las III Jornadas Internacionales sobre Paleontología de Dinosaurios y su entorno*, 235–252. Salas de los Infantes, Burgos.
- Madzvamuse, A., Wathen, A.J., and Maini, P.K. 2003. A moving grid finite element method applied to a model biological pattern generator. *Journal of Computational Physics* 190: 478–500.
- Manning, P.L., Margetts, L., Johnson, M.R., Withers, P.J., Sellers, W.I., Falkingham, P.L., Mummery, P.M., Barrett, P.M., and Raymont, D.R. 2009. Biomechanics of dromaeosaurid dinosaur claws: application of X-ray microtomography, nanoindentation, and finite element analysis. *The Anatomical Record: Advances in Integrative Anatomy and Evolutionary Biology* 292: 1397–1405.
- Margetts, L., Smith, I.M., and Leng, J. 2005. Simulating dinosaur track formation. In: E. Oñate and D.R.J. Owen (eds.), *VIII International Conference on Computational Plasticity (COMPLAS), Extended Abstracts*, 4. CIMNE, Barcelona.
- Margetts, L., Smith, I.M., Leng, J., and Manning, P.L. 2006. Parallel three-dimensional finite element analysis of dinosaur trackway formation. In: H.F. Schweiger (ed.), *Numerical Methods in Geotechnical Engineering*, 743–749. Taylor & Francis, London.
- Martín-Closas, C. and Alonso Millán, A. 1998. Estratigrafía y bioestratigrafía (Charophyta) del Cretácico Inferior en el sector occidental de la Cuenca de Cameros (Cordillera Ibérica). *Revista de la Sociedad Geológica de España* 11: 253–269.
- Marty, D., Strasser, A., and Meyer, C.A. 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: Implications for the study of fossil footprints. *Ichnos* 16: 127–142.
- Mas, R., Benito M.I., Arribas, J., Alonso, A., Arribas, M.E., Lohmann, K.C., González-Acebrón, L., Hernán, J., Quijada, E., Suárez, P., and Omodeo, S. 2011. Evolution of an intraplate rift basin: the Latest Jurassic–Early Cretaceous Cameros Basin (Northwest Iberian Ranges, North Spain). In: C. Arenas, L. Pomar, and F. Colombo (eds). *Post-Meeting Field Trips Guidebook, 28th IAS Meeting Zaragoza. Geo-Guías* 8: 117–154.
- Mas, R., García, A., Salas, R., Meléndez, A., Alonso, A., Aurell, M., Bádenas, B., Benito, M.I., Carenas, B., García-Hidalgo, J.F., Gil, J., and Segura, M. 2004. Segunda fase de rifting: Jurásico Superior–Cretácico inferior. In: J.A. Vera (ed.), *Geología de España*, 503–522. SGE-IGME, Madrid.
- Matthews, N.A., Breithaupt, B.H., Noble, T., Titus, A., and Smith, J. 2005. A geospatial look at the morphological variation of tracks at the Twentymile Wash dinosaur tracksite, Grand Staircase-Escalante National Monument, Utah. *Journal of Vertebrate Paleontology* 25: 90A.
- Matthews, N.A., Noble, T.A., and Breithaupt, B.H. 2006. The application of photogrammetry, remote sensing and geographic information systems (GIS) to fossil resource management. *Bulletin New Mexico Museum of Natural History and Science* 34: 119–131.
- McHenry, C.R., Clausen, P.D., Daniel, W.J.T., Meers, M.B., and Pendharkar, A. 2006. Biomechanics of the rostrum in crocodylians: a comparative analysis using finite-element modeling. *The Anatomical Record* 288A: 827–849.
- Milàn, J. 2006. Variations in the morphology of emu (*Dromaius novaehollandiae*) tracks reflecting differences in walking pattern and substrate consistency: ichnotaxonomic implications. *Palaeontology* 49: 405–420.
- Milàn, J. and Bromley, R.G. 2006. True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. *Palaeogeography, Palaeoclimatology, Palaeoecology* 231: 253–264.
- Milàn, J. and Bromley, R.G. 2008. The impact of sediment consistency on track and undertrack morphology: experiments with emu tracks in layered cement. *Ichnos* 15: 19–27.
- Milàn, J., Clemmensen, L.B., and Bonde, N. 2004. Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland) —undertracks and other subsurface deformation structures revealed. *Lethaia* 37: 285–296.
- Moreno, K., Carrano, M.T., and Snyder, R. 2007. Morphological changes in pedal phalanges through ornithomimid dinosaur evolution: A biomechanical approach. *Journal of Morphology* 268: 50–63.
- Mulungye, R.M., Owende, P.M.O., and Mellon, K. 2007. Finite element modelling of flexible pavements on soft soil subgrades. *Materials & Design* 28: 739–756.
- Nakashima, H. and Oida, A. 2004. Algorithm and implementation of soil-tire contact analysis code based on dynamic FE-DE method. *Journal of Terramechanics* 41: 127–137.
- Nakashima, H. and Wong, J.Y. 1993. A three-dimensional tire model by the finite element method. *Journal of Terramechanics* 30: 21–34.
- Oldfield, C.C., McHenry, C.R., Clausen, P.D., Chamoli, U., Parr, W.C., Stynder, D.D., and Wroe, S. 2012. Finite element analysis of ursid cranial mechanics and the prediction of feeding behaviour in the extinct giant *Agriotherium africanum*. *Journal of Zoology* 286: 171–171.
- Panagiotopoulou, O. 2009. Finite element analysis (FEA): applying an engineering method to functional morphology in anthropology and human biology. *Annals of Human Biology* 36: 609–623.
- Pascual Arribas, C., Latorre Macarrón, P., Hernández Medrano, N., and Sanz Pérez, E. 2005. Las huellas de dinosaurios de los yacimientos del arroyo Miraflores (Fuentes de Magaña-Cerbón-Magaña, Soria). *Celtiberia* 99: 413–442.
- Popescu, R., Prevost, J.H., and Deodatis, G. 2005. 3D Effects in Seismic Liquefaction of Stochastically Variable Soil Deposits. *Geotechnique* 55: 21–32.
- Popescu, R., Prevost, J.H., Deodatis, G., and Chakraborty, P. 2006. Dynamics of nonlinear porous media with applications to soil liquefaction. *Soil Dynamics and Earthquake Engineering* 26 (6–7): 648–665.
- Quijada, I.E., Suarez-Gonzalez, P., Benito, M.I., and Mas, R. 2013. New insights on stratigraphy and sedimentology of the Oncala Group (east-

- ern Cameros Basin): implications for the paleogeographic reconstruction of NE Iberia at Berriasian times. *Journal of Iberian Geology* 39: 313–334.
- Razzolini, N.L., Vila, B., Castanera, D., Falkingham, P.L., Barco, J.L., Canudo, J.I., Manning, P.L., and Galobart, A. 2014. Intra-trackway morphological variations due to substrate consistency: The El Frontal Dinosaur Tracksite (Lower Cretaceous, Spain). *PLoS ONE* 9 (4): e93708.
- Rayfield, E.J. 2007. Finite element analysis and understanding the biomechanics and evolution of living and fossil organisms. *Annual Review of Earth and Planetary Sciences* 35: 541–576.
- Schanz, T., Lins, Y., Viehhaus, H., Barciaga, T., Sashima, L., Preuchoft, H., Witzel, U., and Sander, P.M. 2013. Quantitative interpretation of tracks for determination of body mass. *PLoS ONE* 8 (10): e77606.
- Sellers, W.I., Manning, P.L., Lyson, T., Stevens, K., and Margetts, L. 2009. Virtual palaeontology: gait reconstruction of extinct vertebrates using high performance computing. *Palaeontologia Electronica* 12 (3): 12.3.13A. http://palaeo-electronica.org/2009_3/180/index.html
- Schudack, U. and Schudack, M. 2009. Ostracod biostratigraphy in the Lower Cretaceous of the Iberian Chain (eastern Spain). *Journal of Iberian Geology* 35: 141–168.
- Terzaghi, K. 1943. *Theoretical Soil Mechanics*. 538 pp. John Wiley and Sons, New York
- Thulborn, T. 1990. *Dinosaur Tracks*. 410 pp. Chapman & Hall, London.
- Tischer, G. 1966. Über die Wealden-Ablagerung und die Tektonik der östlichen Sierra de los Cameros in den nordwestlichen Iberischen Ketten (Spanien). *Beihefte zum Geologischen Jahrbuch* 44: 123–164.
- Vila, B., Oms, O., Galobart, A., Bates, K.T., and Egerton, V.M. 2013. Dynamic Similarity in Titanosaur Sauropods: Ichnological Evidence from the Fumanya Dinosaur Tracksite (Southern Pyrenees). *PLoS ONE* 8 (2): e57408.
- Walmsley, C.W., McCurry, M.R., Clausen, P.D., and McHenry, C.R. 2013. Beware the black box: investigating the sensitivity of FEA simulations to modelling factors in comparative biomechanics. *PeerJ* 1: e204.
- Xing, L., Yong, Y.E., Chunkang, S.H.U., Guangzhao, P., and Hailu, Y.O.U. 2009. Structure, orientation and finite element analysis of the tail club of *Mamenchisaurus hochuanensis*. *Acta Geologica Sinica* 83: 1031–1040.