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Reinterpretation of palmate and semi-palmate (webbed) fossil tracks; insights from finite element modelling

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ABSTRACT

A track from the Late Cretaceous previously described as being generated by a semi-palmate bird was studied with the aid of high resolution laser scanning. Substrate conditions at the time of track formation were diagnosed (fine-grained, soft, waterlogged sediment) and used to constrain a finite element track simulator. The indentation of a non-webbed virtual tridactyl foot in such conditions created a resultant track with features analogous to 'webbing' between digits. This 'webbing' was a function of sediment deformation and subsequent failure in 3D, specific to rheology. Variation of substrate conditions and interdigital angle was incrementally stepped. Apparent webbing impressions were clearly developed only within a limited range of sediment conditions and pedal geometry.
The implications of this work are that descriptions of 'webbed' tracks should account for the possibility that webbing was indirectly formed through sediment failure and not necessarily the direct impression of a webbed foot. Additionally, dating the earliest occurrence of webbed feet in the fossil record, and potentially extending phylogenetic ranges, should be treated with caution when based upon evidence from tracks.

1. Introduction

Fossil vertebrate tracks are a source of information on the size, speed, limb kinematics and even behaviours of the animals that made them (Day et al., 2004; Manning, 2004 and references therein). In many cases, the fossil tracks provide information that is not preserved in skeletal remains. The record of palmate and semi-palmate (webbed) Cretaceous birds, for instance, is almost exclusively ichnological (Yang et al., 1995; Lockley and Rainforth, 2002; Lockley et al., 2004), with only a single web-footed specimen described to date (You et al., 2006).

Records of webbed bird tracks extend into the Early Cretaceous (Lim et al., 2000; Kim et al., 2006), and thereafter are not uncommon (e.g. Yang et al., 1995; Lockley and Rainforth, 2002; Lockley et al., 2004). The appearance of webbed bird tracks at this time has been interpreted as evidence of a considerable diversification of shore birds.

Sarjeant (1967) described a number of tracks from the Middle Triassic of Mapperly Park, Nottingham (UK) and described *Swinnertonichnus* as a small theropod track that displayed webbing, a feature not currently reported in body fossils of dinosaurs. These tracks were reinterpreted by King and Benton (1996) who observed no such evidence of webbing, noting that if substrate conditions were good enough to preserve interdigital webbing, claw impressions should also be present.

Track morphology is dependant upon a number of interacting factors, including limb kinematics, limb morphology and substrate properties. Once exposed, a track is subjected to the effects of weathering and erosion, which may further modify the geometry (Bates, 2006; Henderson, 2006; Bates et al., 2008). In order to recover information regarding the trackmaker, the interaction of these factors must be taken into account. These controlling factors will vary with sediment particle size and distribution, density, along with the air and/or water occupying the pore spaces between the particles. A clear example of this is demonstrated when water content is increased, reducing the amount of air filling the voids, resulting in the sediment volume becoming less compressible. The bulk density of the sediment increases, as does the shear strength, until the critical saturation point is reached, water then begins to push the particles apart, and the sediment fails (Karafiath and Nowatzki, 1978). In terms of track formation, a waterlogged sediment would prove soft, and easily deformed, but the incompressibility would lead to sediment being forced upwards around the foot to form displacement rims (Manning, 2004).

The effects of the limb–sediment interaction impact heavily upon the *volume* of sediment, and not just the surface in contact with the foot (Allen, 1989, 1997; Manning, 1999, 2004; Milàn et al., 2004; Milàn, 2006; Milàn and Bromley, 2006, 2008; Manning et al., in review). The

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consequence of this is that a track must be treated as a full three-dimensional volume, and not simply a surface feature representing the two-dimensional outline of the trackmaker's foot. Force will not only be transmitted downwards below the foot, but also out and up as sediment moves along the path of least resistance, according to Rankine's theory of shear (Craig, 1997; Manning, 2004).

The primary implications of complex deformation generated by a dynamic load are that tracks may appear substantially different to the morphology of the trackmaker's foot, depending on such conditions as those listed above, as well as which track surface within the volume is exposed. The fossil track collection at the Amherst College Museum of Natural History contains numerous examples where this is the case, with single trackways containing traces with varying numbers of digits, or individual tracks preserved as 'books' where several layers of rock have been peeled apart to reveal subsurface features. Each 'page' of the book may have a considerably different morphology to the last (Margetts et al., 2006; Manning et al., in review).

The 3D nature of tracks has been the focus of analogue modelling by track workers over the past decade (Allen, 1989, 1997; Manning, 1999, 2004; Milàn et al., 2004; Milàn, 2006; Milàn and Bromley, 2006; Manning, 2008; Milàn and Bromley, 2008). Such work has provided a quantitative approach to investigating the effects of substrate properties on track morphology, at the surface and within the sediment volume. Such physical modelling, however, is time consuming and in many cases requires physical sectioning and extraction of subsurface layers within the volume. This extraction process is destructive, disrupting the relative position of track surfaces within the volume.

The advance of computer power, combined with software design that takes advantage of multiple processors simultaneously, means that complex simulations such as the deformation of a substrate volume under dynamic loading conditions can be run to completion in feasible time frames. Such a simulation has many advantages over physical modelling, including precise and independent control of variables, and complete freedom to view a structure in three (or even four) dimensions non-destructively.

With this in mind we aim to test the hypothesis that web-like features may be formed as a function of sediment, and not automatically assumed to be of semi-palmate/palmate origin. A comparison of fossil tracks and finite element modelling (FEA) of substrate under dynamic loading is used herein to test this hypothesis.

1.1. The finite element method

Finite element analysis (FEA) is a numerical analysis technique common in engineering for exploring the mechanics of continuous media, though the method is applicable to a broad variety of mathematical problems that arise in almost all areas of science (Burnet, 1987; Smith and Griffiths, 2004). In simple terms, the method approximates the governing equations of a continuous system by dividing the continuum into 'finite elements.'

Many palaeontologists will primarily associate FEA with its use in testing load and subsequent stress within bones (Rayfield et al., 2001; Rayfield, 2004, 2005). Rayfield (2007) provides a review of the uses of FEA in palaeontology and also of the method itself.

A volume of sediment is composed of individual grains (of varying size and form), as well as water and air in pore spaces. However, a given volume of sediment, sufficiently large in relation to its constituent grains, can be considered as a single entity. This entity will have properties that define its behaviour under load (assuming homogeneity, heterogeneous volumes can be treated as 'blocks' of differing homogeneous volumes). As such, a volume of sediment can be treated as a continuum, and studied using FEA. This has been the case in the engineering fields for several decades, and the use of FEA for solving problems involving soils and sediments is now common place; for example, soil settlement (Scheiner et al., 2006), tire–soil interaction (Nakashima and Wong, 1993; Shoop, 2001; Fervers, 2004; Nakashima and Oida, 2004; Shoop et al., 2006) and building foundation problems (Johnson et al., 2006). A framework is therefore in place for defining and solving problems of soil deformation under load. This framework can be used to study vertebrate track formation.

2. Materials and methods

2.1. Fossil track

The specimen used as an example of a semi-palmate track was a cast of *Sarjeantopodus semipalmatus* (Lockley et al., 2004). The original fossil is held in the collections of the University of Colorado Dinosaur Tracks Museum (specimen no: CU-MWC224.4). The original locality was in eastern Wyoming, (U.S.A.), though was located on private land so exact locality data is withheld (Lockley et al., 2004). Found in the Late Cretaceous Lance Formation, the track horizon was located as casts on the underside of a 0.1 m thick, fine-grained sand/mud layer, situated a few centimetres above a major dinosaur track layer (Lockley and Rainforth, 2002; Lockley et al., 2004). The track horizon where CU-MWC224.4 was located also preserved raindrop impressions and small ripples.

In addition to the specimen (cast), a hand held laser scanner was used to generate a 3D digital surface of the track. The scanner used was a Polhemus FastScan Cobra capable of achieving >0.1 mm resolution. This allowed virtual manipulation of the track, including viewing the surface as an impression rather than a cast, and also allowing profile sections to be taken non-destructively. A digital representation of the track was directly compared with a surface generated by the FEA.

2.2. Finite element simulations

The software used herein was developed in-house, being a modified version of a three-dimensional finite element program in Smith and Griffiths (2004). The program uses a von Mises elasto-plasticity model to represent the plastic behaviour of the sediment.

A relatively simple cuboid mesh was created from hexahedral elements, each defined by eight nodes. To increase efficiency and decrease run time whilst maintaining a high resolution output, a scaling factor produced larger elements away from the source of loading (the 'foot'), and smaller elements beneath the load where deformation would be most intense and complex. The simulation was run at the meter scale for ease of use, though the results are directly scalable. The mesh measured 2 m×2 m at the surface, and was 1 m deep. This large size prevented any boundary effects caused by fixed nodes at the edges of the soil volume. Whilst the elements were arranged in 1 cm layers, these layers were given uniform properties creating a homogeneous sediment.

Loading was achieved through the direct displacement of surface nodes defining a track outline. The outline represents a generic tridactyl foot measuring 0.6 m in length (Fig. 1).

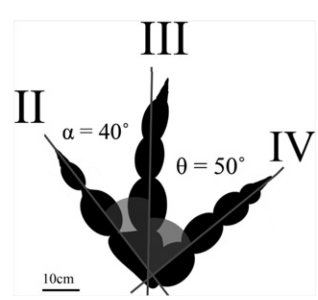

Fig. 1. Outline used to represent tridactyl foot. Interdigital angle (IDA) between Digits II and III — 40°, IDA between Digits III and IV — 50°. Foot length = 60 cm.