CONSTRUCTING AND TESTING HYPOTHESES OF DINOSAUR FOOT MOTIONS FROM FOSSIL TRACKS USING DIGITIZATION AND SIMULATION

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Abstract: Whilst bones present a static view of extinct animals, fossil footprints are a direct record of the activity and motion of the track maker. Deep footprints are a particularly good record of foot motion. Such footprints rarely look like the feet that made them; the sediment being heavily disturbed by the foot motion. Because of this, such tracks are often overlooked or dismissed in preference for more foot-like impressions. However, the deeper the foot penetrates the substrate, the more motion is captured in the sediment volume. We have used deep, penetrative, Jurassic dinosaur tracks which have been naturally split into layers, to reconstruct foot motions of animals living over 200 million years ago. We consider these reconstructions to be hypotheses of motion. To test these hypotheses, we use the Discrete Element Method, in which individual particles of substrate are simulated in response to a penetrating foot model. Simulations that produce virtual tracks morphologically similar to the fossils lend support to the motion being plausible, while simulations that result in very different final tracks serve to reject the hypothesis of motion and help generate a new hypothesis.

Key words: footprint, ichnology, simulation, dinosaur, locomotion, biomechanics.

A TRACK is a three-dimensional structure resulting from the interaction between an animal's foot and a compliant substrate. Though often observed only as surfaces with relief (either concave or convex), the deformation of surface layers necessitates subsurface movement of sediment, making tracks volumetric structures that extend beneath the surface upon which the animal trod (Allen 1989; Manning 2004; Milàn & Bromley 2006; Falkingham & Gatesy 2014). The 3D morphology of the resultant track volume is determined by the anatomy of the foot, the motions and forces of the limb, and the properties of the substrate (Padian & Olsen 1984; Minter *et al.* 2007; Falkingham 2014). Being able to interpret tracks confidently can therefore provide information about skeletal and soft-tissue anatomy, palaeoenvironment, and locomotor mechanics. It is the latter of these, locomotor mechanics, that is the focus of this paper.

Vertebrate ichnology can trace its roots to the early and mid-1800s (Duncan 1831; Kaup 1835; Hitchcock 1836, 1848, 1858; Cunningham 1838). It was Edward Hitchcock's pioneering work that formalized ichnology as a science. Hitchcock's impressive collection of fossil tracks is housed today in the Beneski Museum of Natural History, Amherst, USA. Hitchcock attributed many of the dinosaur tracks from the Connecticut Valley to large, extinct birds (Hitchcock 1836). Of course, we now know birds evolved from theropods, and so while Hitchcock was not strictly correct, his interpretation of dinosaur fossils was perhaps more accurate than other reconstructions at the time, which were based on osteological material. Unique to Hitchcock's historically and scientifically important collection is that many of the tracks were collected as multi-slab specimens, often affixed to each other by metal hinges or wires, exhibiting the volumetric nature of tracks. These tracks have often been figured as examples of 'undertracks' (e.g. Lockley 1991, fig 3.3; Seilacher 2007, pl. 2; Manning 2008, fig 12.10).

Hitchcock and his contemporaries were limited in the ways in which they could report and discuss the morphology of tracks, both as single and nested surfaces. Illustration and lithography (and later, photography) reproduced on paper, were the only means of communicating the form of footprints. This remained the case for a hundred years, and the vast majority of the ichnological

literature prior to the turn of the millennium is dominated by hand-drawn outlines, sketches, lithographs, and later black and white photographs.

Of course, the same can be said for any other fossils described during the nineteenth and early twentieth centuries, but bones can be drawn from multiple angles to communicate their shape. Images of, for instance, a femur in anterior, lateral and dorsal view can adequately convey the spatial relationships between features. Tracks and traces, conversely, are generally limited in the orientations that can be figured and used to observe topography, particularly with large museum specimens or tracksites, essentially making them '2.5D' (Falkingham 2016). Such tracks can be figured in a top-down plan view, or at some oblique angle that may be hard for readers to orient. Confounding this, the direction of light (and hence shadows) can confuse a reader as to whether the track is convex or concave, and therefore where features are relative to one another (Gatesy *et al.* 2005).

For questions focused on trackmaker identity, this is not necessarily a major barrier. Metrics such as track length, digit length and width, and interdigital angle can all be measured and displayed in two dimensions (Leonardi 1987; Thulborn 1990; Lockley 1991; Farlow *et al.* 2012). Similarly, trackway-scale measures such as stride, pace angulation and track rotation can also be measured from top-down plan views. We note, however, that as discussed elsewhere, these metrics measured directly from the tracks are not always homologous to the same measures of the trackmaker's foot (Falkingham & Gatesy 2014; Gatesy & Falkingham 2017; Farlow 2018) and cannot always be defined simply (Falkingham 2016; Lallensack 2019).

Other lines of scientific enquiry, particularly regarding the detailed kinematics of the foot and how the animal moved, rely much more on the three-dimensional morphology of track surfaces and volumes. Raised areas and depressions can inform as to how the foot interacted with the sediment, indicating which part of the foot hit the substrate first, or potentially where the greatest pressure was exerted (Bates *et al.* 2013; Hatala *et al.* 2013; Milàn *et al.* 2004), for example.

Attempts to discern the movements of the foot from fossil tracks are almost as old as the field of vertebrate ichnology itself. In his seminal work, Edward Hitchcock provided a sketch of a dinosaur foot (or, as he assumed, that of a large extinct bird) oriented above a volume of layered sediment (Hitchcock 1858, pl. 6, fig. 2), as a means of explaining the multiple surfaces observed in many of the tracks now held in the Beneski Museum (Fig. 1A). It is not clear if Hitchcock intended this figure to illustrate penetration of the volume (and the passing of the foot), transmission of displacement across sediment
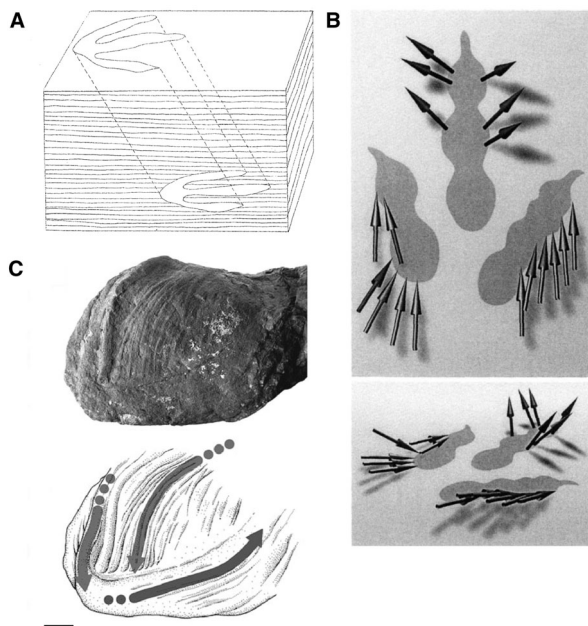

FIG. 1. Examples of communicating motion derived from tracks. A, Hitchcock (1858, pl. 6, fig. 2). B, Gatesy (2001, fig. 6). C, Avanzini *et al.* (2012, fig. 6).

layers, or some combination of both (Gatesy & Falkingham in press).

In recent years there have been a number of studies that have attempted to reconstruct dinosaur foot motions from fossilized footprints, often through detailed examination of striations left on the walls of the impression, but also through larger scale structures such as raised rims (Thulborn & Wade 1984; Gatesy *et al.* 1999; Gatesy 2001; Milàn *et al.* 2006; Avanzini *et al.* 2012; Cobos *et al.* 2016; Fig. 1B, C). In all cases, conveying complex 3D movements has been made difficult by the predominant 2D form of communication.

Recording and communicating 3D track data

Fortunately, the past two decades have seen significant advances in techniques capable of recording and communicating in three dimensions. Methods including laser scanning (Bates *et al.* 2008; Adams *et al.* 2010), structured light scanning or photogrammetry (Matthews *et al.* 2016) have all become more affordable and widespread, and enable the recording of 3D morphology either in the field or in the museum, of entire sites, or individual specimens.

These methods have had a significant and positive impact on palaeontology as a whole (Davies *et al.* 2017) and specifically on the field of ichnology, where 3D track morphology can now be recorded, disseminated and

presented as standard (Falkingham *et al.* 2018). Digitization techniques are now widely available, particularly photogrammetry, which can be carried out with little more than a compact camera, laptop and free software (Breithaupt & Matthews 2001; Matthews *et al.* 2006; Falkingham 2012; Mallison & Wings 2014; Matthews *et al.* 2016). Those data can then be included as supplemental to publications, as well as presented within papers in ways that communicate the 3D topography clearly, such as with contour lines or height mapping (Falkingham *et al.* 2018, fig. 2). Not only can digital tracks be used to enhance and visualize surface features but they can, in ideal circumstances, offer new insights into volumetric features. This may be from volumetric data derived from CT scans or simulations, or it may be through the alignment of multiple exposed surfaces in 3D space.

Even with these modern digitization techniques, attempts to reconstruct foot motions of dinosaurs and other extinct animals have generally lacked an important aspect of the scientific process: validation and testing. Using the detailed morphology of a track to reconstruct the kinematics of the foot that made it is all well and good, but how confident can we be in the reconstructions?

Comparative data from extant taxa

Use of living animals and physical modelling have provided comparative data for testing formational processes. Emu, turkeys, crocodiles and elephants have all served as modern track-making analogues for theropods, sauropods and other extinct animals (Gatesy *et al.* 1999; Milàn 2006; Milàn & Bromley 2006, 2008; Milàn & Hedegaard 2010; Platt *et al.* 2012; Farlow *et al.* 2013; Schanz *et al.* 2013; Milàn & Falkingham 2016; Farlow *et al.* 2017; Farlow 2018) though most of this research has been focused on the mechanisms of track formation broadly and have, for the most part, been concerned with relatively shallow, surficial tracks and the transmitted undertracks that may be associated with them. The data collected and analysed by these studies (and many others) has been invaluable to the study of fossil tracks, providing comparative data that allows us to recognize features of tracks that may be related to specific motions of the foot.

Our previous work has focused on deep tracks made by birds traversing extremely compliant substrates (Falkingham & Gatesy 2014, in press; Gatesy & Falkingham 2017, in press; Turner *et al.* 2020). By employing X-ray Reconstruction of Moving Morphology, or XROMM (Brainerd *et al.* 2010; Gatesy *et al.* 2010), we combined bi-planar x-ray and CT scanning to capture the motions of guineafowl feet *beneath* the sediment surface during the formation of the track. This has been combined with

sediment simulations to observe how the foot and sediment interact, at and below the sediment surface, and throughout the track formation process.

Penetrative tracks

Deep tracks necessarily record more of the motion of the foot, because the foot is in contact with and actively deforming the sediment over a greater distance than in shallower tracks. This makes deeper tracks a rich source of kinematic data. In cases where the sediment is relatively plastic, a deep track may manifest a large hole with sloped ends where the foot has entered and exited. In cases where the substrate can flow or collapse, it will seal up behind the descending foot, and again when the foot is withdrawn. Such tracks are termed penetrative, because they penetrate through surface and sub-surface sediment layers (Boutakiout *et al.* 2006; Falkingham & Gatesy in press; Gatesy & Falkingham in press).

Penetrative tracks are ideal for exploring foot motions of their track makers, if they can be identified as penetrative in nature, because they record passage of the foot throughout the sediment volume beneath the originally exposed surface on which the animal walked. Fortunately, Hitchcock's collection at the Beneski Museum of Natural History, Amherst contains dozens of specimens that are undoubtedly penetrative in nature.

We have used a multi-part penetrative track from this collection to reconstruct the foot motions of a small dinosaur walking over soft mud ~200 million years ago. Having reconstructed the motions of the foot, we then tested the validity of our reconstruction using computer simulations of sediment response to such motions.

MATERIAL AND METHOD

We digitized four specimens from the Beneski Museum of Natural History, Amherst: specimens ACM-ICH 31/51, 31/57, 31/58 and 31/59 (Fig. 2). These specimens display tracks of differing morphologies on upper and lower surfaces, from a tridactyl impression with a long posterior mark on the upper surface of 31/57 to three parallel scratches on the upper surface of 31/51. The specimens are attributed to the Early Jurassic age Portland Formation, Wethersfield (Wethersfield Cove), Connecticut, and were first described by Hitchcock (1848, pl. 15 figs 10–13; 1858, pl. 19 figs 6–9).

The tracks on the surface of each slab are so different that each has a unique specimen number, not all of which are sequential. The specimens were clearly originally collected together and all bear an earlier specimen number '175' carved into their surfaces. Clearly, these fossils show
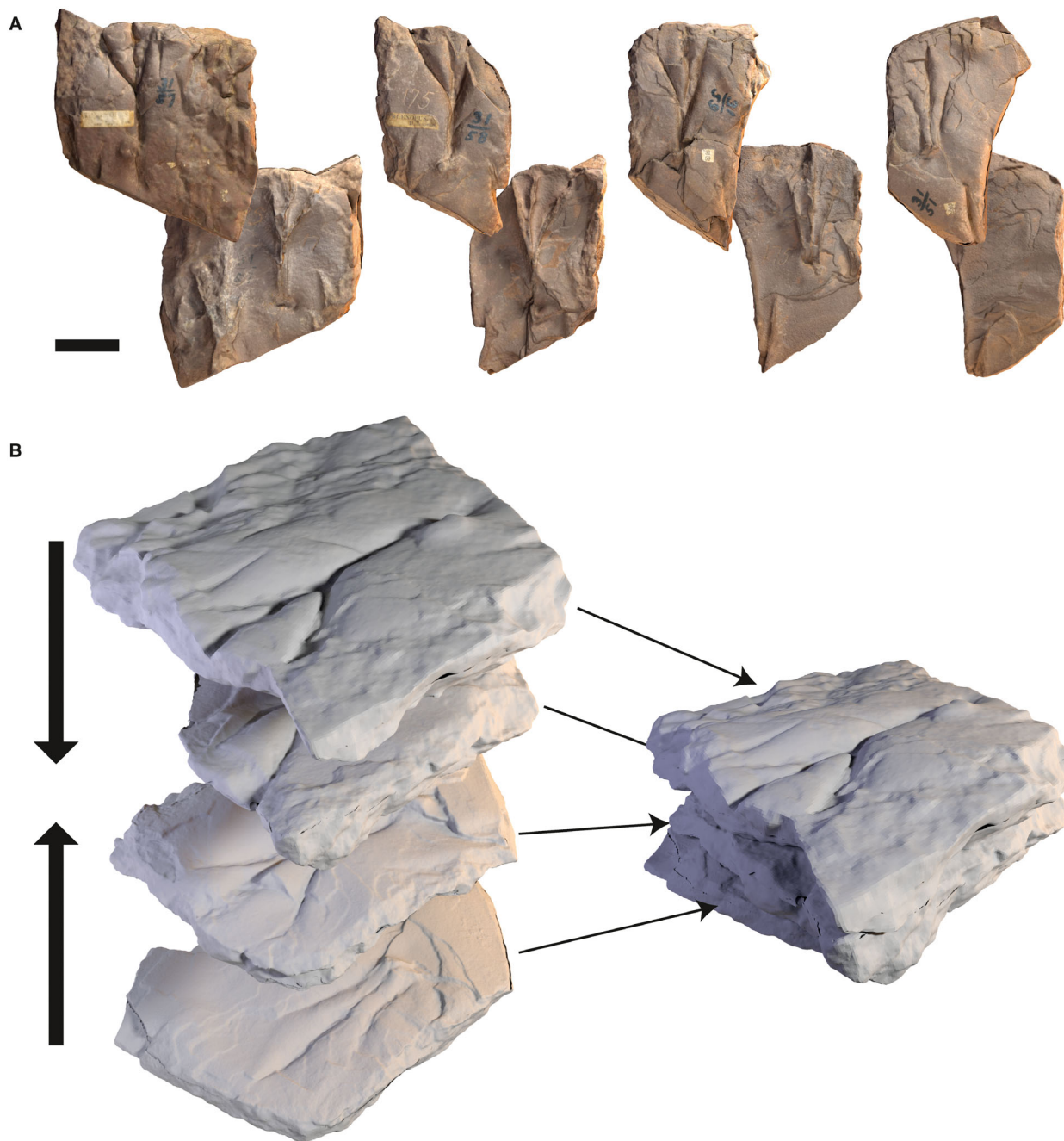
FIG. 2. Track volume exposed as four individual slabs, each with their own specimen numbers. A, from left to right, textured photogrammetric models of ACM-ICH 31/57, 31/58, 31/59, and 31/51, showing upper (concave) and lower (convex) surfaces of each specimen. Note the drastically different morphologies exposed on the upper surfaces, particularly 31/57 and 31/51. B, the four slabs rendered without texture, indicating how they fit together. In all images, major light source is from the upper-right. Scale bar represents 5 cm. Colour online.

a diversity of track forms that could quite easily be attributed to a diversity of track makers and foot morphologies. However, with close study it becomes apparent that these specimens are in fact all from the same track volume, made by the same foot. The underside of each slab matches perfectly the upper surface of the next. The sharply incised impressions, smooth surface, and broken extremities on undersides all indicate this track is penetrative in nature, the foot having passed through the upper slabs.

Each specimen was digitized using photogrammetry (Falkingham 2012), using photos taken with a Sony Nex-6 camera (16mp) and processed with AliceVision Meshroom (Jancosek & Pajdla 2011; Moulon *et al.* 2012). To capture the specimens completely, upper and lower surfaces were digitized separately, then aligned manually in Autodesk Maya using the sides of each slab as common reference. Individual slabs were then manually aligned to each other in 3D world space such that they fit together as closely as possible without intersecting. Traces are visible on every surface within the combined volume, giving the track a total depth of ~7 cm, with surfaces visible at approximately 0, 2, 3, 4.5 and 7 cm.

Six landmarks placed on the upper and lower surfaces of each specimen were used to define the passage of the foot through the track volume. These landmarks included the tips of each digit impression (I–IV), the point where the three digit impressions converged (the hypex), and a rounded feature at the rear of the track that we interpreted as a collapsed exit trace left by the withdrawing foot. Not all landmarks were present on all surfaces; for instance, the exit trace, hypex and hallux (DI) impression were not present on deeper surfaces, while the tip of the digit III impression was not present on the uppermost surface due to breakage. We do not consider these landmarks to necessarily be homologous to parts of the foot; sediment movement during and after foot penetration may shift features during track formation, particularly during foot withdrawal (Falkingham & Gatesy 2014). However, these features are consistently identifiable on multiple surfaces despite changing track morphology.

Each landmark was then connected to the corresponding landmark on the next surface with a straight line, that is, the landmark identifying the tip of digit IV on the uppermost surface of ACM-ICH 31/57, was connected to the same landmark on the underside of 31/57, which in turn was connected to the digit III landmark on the upper surface of 31/58. Repeating this process for each landmark provides a set of paths that can be used to constrain the motion of the foot that made the track.

To visualize the foot, a basic tridactyl morphology was constructed using cylinders for each toe, and a fifth cylinder in place of the metatarsals. The length of each digit was constrained by the distance in 3D space between the hypex and the connected tips of that digit. While the real foot that made the track may have been larger than this, it could not have been any smaller.

We then used Autodesk Maya to animate the foot model such that it enters and exits the volume while anatomical parts of the foot maintain contact as closely as possible with the paths created by the track-based landmarks. We note here that the temporal component is entirely arbitrary. Contrary to previous assertions that tracks are '4-dimensional' (Cobos *et al.* 2016), there is no measurable time component preserved along with the morphology. We seek to constrain a potential sequence of poses for which we can only guess at the approximate timing based on our previous studies of similarly sized extant taxa moving over similarly deep, soft substrates (Falkingham & Gatesy 2014; Gatesy & Falkingham 2017) in which such steps typically take ~1 s. Our reconstruction of foot motion takes 1.2 s from first contact with the substrate to complete foot withdrawal.

We term the resultant animation a 'hypothesis of motion,' a prediction of how the foot moved based on volumetric track morphology. Like any hypothesis, this pattern of movement can be tested, and either supported or rejected.

To test our hypothesis of motion, we used the Discrete Element Method (DEM) to simulate the formation of a track resulting from foot anatomy and motion as reconstructed from the Hitchcock specimen. As in previous work (Falkingham & Gatesy 2014) we used the open source software LIGGGHTS (https://www.cfdem.com; Kloss & Goniva 2010, 2011) to simulate individual grains of sediment, this time adding cohesion among particles. The foot model and motions were transferred from Maya into the LIGGGHTS simulation via custom Maya scripts (https://github.com/pfalkingham/MayaToLiggghts). Simulations were visualized using Ovito (https://www.ovito.org; Stukowski 2010).

The simulation recreated a sediment tray filled with particles, through which the foot moved. The simulated sediment used individual particle sizes of 0.2 mm radius, filling a volume of $17 \times 6 \times 8$ cm (15 656 372 particles). Particles were assigned properties such that the bulk response of the substrate represented a soft, wet mud; able to flow whilst retaining cohesion between particles (cohesion energy density, 75 000 Jm^{-3}; coefficient of friction, 0.8; Young's modulus, 5×10^7 Pa; density, 1200 kgm^{-3}; Poisson ratio, 0.4). The properties were arrived at through physical validation against real-world substrates as was the case in Falkingham & Gatesy (2014). Our simulation relies on displacement control; the movement of the foot is prescribed and is not affected by resistance from the substrate.

If the simulated track matches the fossil specimen closely, it provides support for our hypothesis of motion. If the simulation produces a track quite unlike the fossil, we can reject our hypothesis of motion. There is an element of unavoidable circularity to our process, relying as it does on validating our hypothesis against the input for our reconstructed motions. However, because the dynamic flow of sediment alters the final track morphology, it is not a foregone certainty that the simulated track will closely match the fossil specimen. In particular, the topography of areas of each surface not directly contacted

by the foot model can offer clues to similar sediment flow around the toes.

RESULTS

The foot reconstruction is functionally tridactyl, with three forward facing digits and a smaller hallux (DI) pointing medially and located higher on the metatarsals. The position of the hallux indicates it was a left foot that made the impression. Our reconstructed digits lengths are 2, 4, 6, and 4.4 cm for digits I–IV respectively, though these are based on simple cylinders and do not account for substantial flexion/extension of the phalangeal joints. The metatarsals were represented with a single cylinder 6 cm long, though this was entirely arbitrary because there is no evidence of the ankle within the track volume. We also note that unlike extant birds, Jurassic dinosaurs had separate metatarsals rather than a fused tarsometatarsus, and this portion of the foot would have been wider than we have reconstructed here. All cylinders were given an arbitrary diameter of 1 cm, approximately in-line with modern bird feet of a similar size.

It is immediately obvious that the foot/toe dimensions required to keep contact between toe-tip impressions and the position of the hallux within the volume are substantially different from the apparent toe lengths recorded on any given surface. For instance, measuring the digit III impression directly on each surface yields lengths of 5.5, 5.5, 5.7, 7.1, 7, 10.4, 9.2, 1.7 cm (from the uppermost surface of 31/57 to the lower most surface of 31/51 respectively).

The reconstructed foot motion indicates a significant backward sweeping motion, with the foot exiting well behind the location where it entered (Fig. 3; Falkingham *et al.* 2020, movie S1). There is also a lateral, outward component to the foot motion as it descends. This would imply an extremely soft substrate at the time of track formation.

As the foot descends, the toes remain wide (interdigital angle ~60°) during most of the down and back motion (5 cm deep, 6 cm back), before converging together as the foot withdraws vertically through the raised features on each surface.

Our simulated track volume is generally similar to the fossil track from which the motion was constructed, offering support for our general hypothesis of motion (Fig. 4; Falkingham *et al.* 2020, movies S2, S3). The virtual nature of the simulation means that we can define layers within the volume based on starting positions of each particle; essentially creating virtual laminations. We are then able to separate layers and view the newly exposed track at any depth beneath the original surface. Virtually exposing simulated surfaces at depths corresponding to the relative positions of the fossil track surfaces allows us to make direct comparisons.

Subsurface layers indicate a very close match with the fossil specimens (Fig. 4), but the sediment–air interface is substantially different, lacking definition in the simulation. The indistinct topography is caused by the particles flowing around and over the descending foot. At sub-surface levels, particle-particle contacts prevent complete collapse. As the foot penetrates through the sediment, particles fill the path behind the descending toes. When surfaces are digitally exposed post-formation, the revealed impressions are narrow and slit-like. Removing just 1 mm of original surface particles reveals track morphology similar to the surface of ACM-ICH 31/57. If the paths of the digits are exposed in cross section (see below), they appear as sharp, nested Vs, characteristic of penetrative tracks (Gatesy & Falkingham in press).

DISCUSSION

The reconstructed foot and foot motions indicate a functionally tridactyl trackmaker moving over an incredibly soft substrate. But how confident can we be that our motion is representative of the real track forming process?

The DEM simulated track volume exhibits very similar features to the fossil specimens, supporting our hypothesized motions. Despite the foot model being highly abstracted (made from cylinders) and the motion being simplified accordingly (some interpenetration of cylinders during withdrawal, no bending of the digits) the simulated track volume bears striking similarity to the fossil on which the motion was based, at least beneath the sediment–air interface.

Interpreting the reconstructed motions

The large backward sweeping motion indicates that the animal was traversing deep, soft substrate when it made the track. It is unlikely therefore that this foot motion represents the normal locomotor kinematics of small dinosaurs when walking on firm ground, but presents insight into locomotion over highly compliant ground.

We have previously collected, using XROMM (Brainerd *et al.* 2010; Gatesy *et al.* 2010), kinematic data from guineafowl traversing a range of substrates from dry granular materials to deep, saturated soft muds (Falkingham & Gatesy 2014; Gatesy & Falkingham 2017, in press). In compliant substrates, the guineafowl exhibit a looping motion of the foot (Turner *et al.* 2020) where toe tips initially sink into the sediment before being pulled backward as the foot withdraws (Fig. 5).
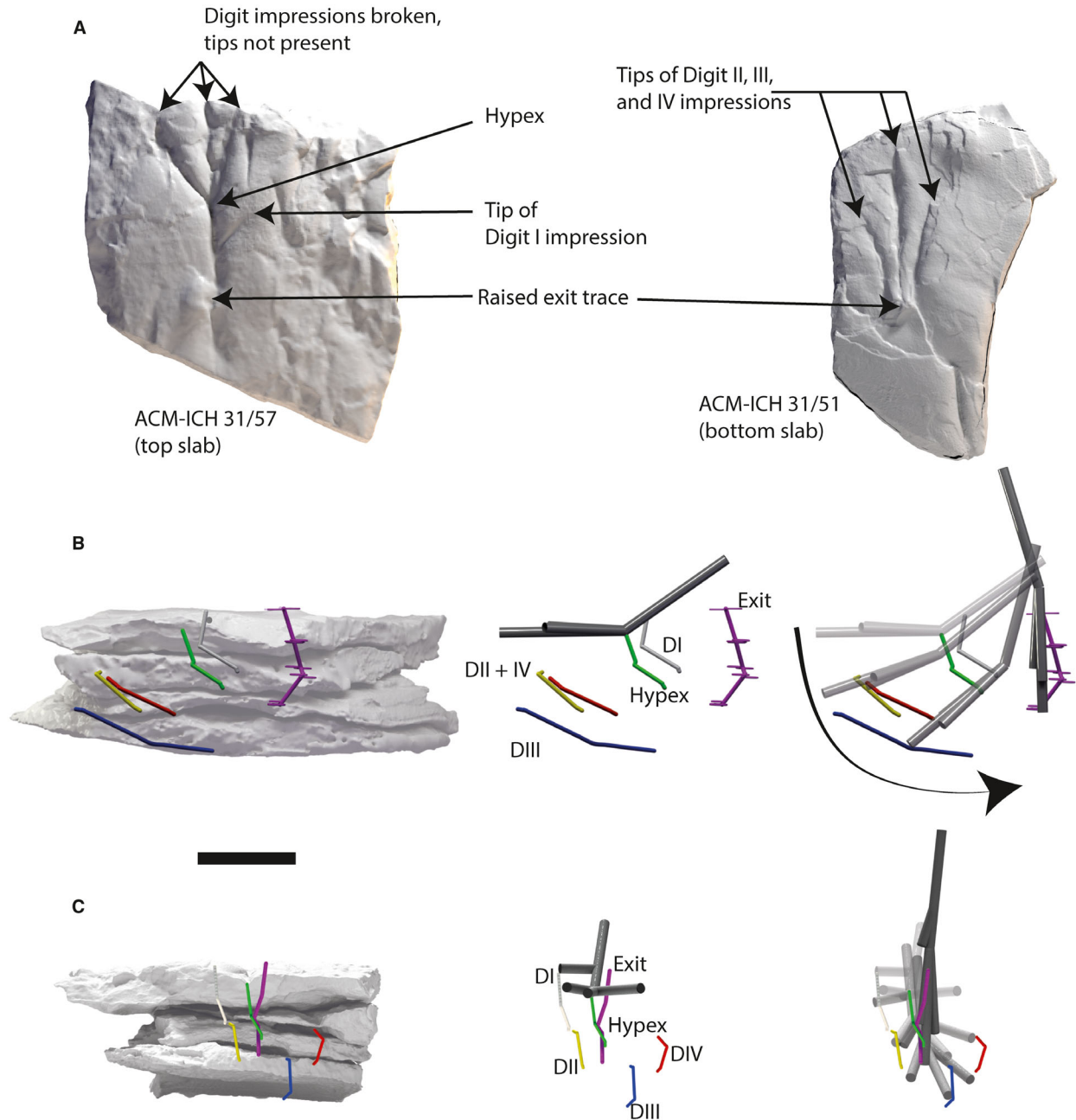
FIG. 3. Reconstructing motion of the track maker's foot. A, representative surfaces from ACM-ICH 31/57 and 31/51 (top and bottom slabs respectively) indicating features marked on upper and lower surfaces of each slab; not all features are visible on all surfaces, e.g. the upper surface is broken and does not preserve the tips of the impressions of digits II–IV, whilst on the lowest upper surface the toes do not converge, so no hypex mark is present. B–C, connected landmarks and reconstructed foot motion in: B, lateral; C, anterior view. Scale bar represents 5 cm.

However, even in the very softest substrates in our trials, the guineafowl did not produce backward motions to this extent, where the toes exit the substrate behind where the rear of the foot entered. Given that the size (at least in terms of toe length) of the reconstructed dinosaur foot is very close to that of the guineafowl, this difference in kinematics is interesting.

It may be that the fossil track was originally formed in extremely compliant substrate that failed to support the animal, meaning that this is more of a swimming trace, rather than that of walking. Certainly, the upper surface of the lowest slab (ACM-ICH 31/51), which exhibits three almost parallel scratches, is not dissimilar to tracks attributed to swimming theropods (Coombs 1980; Ezquerra
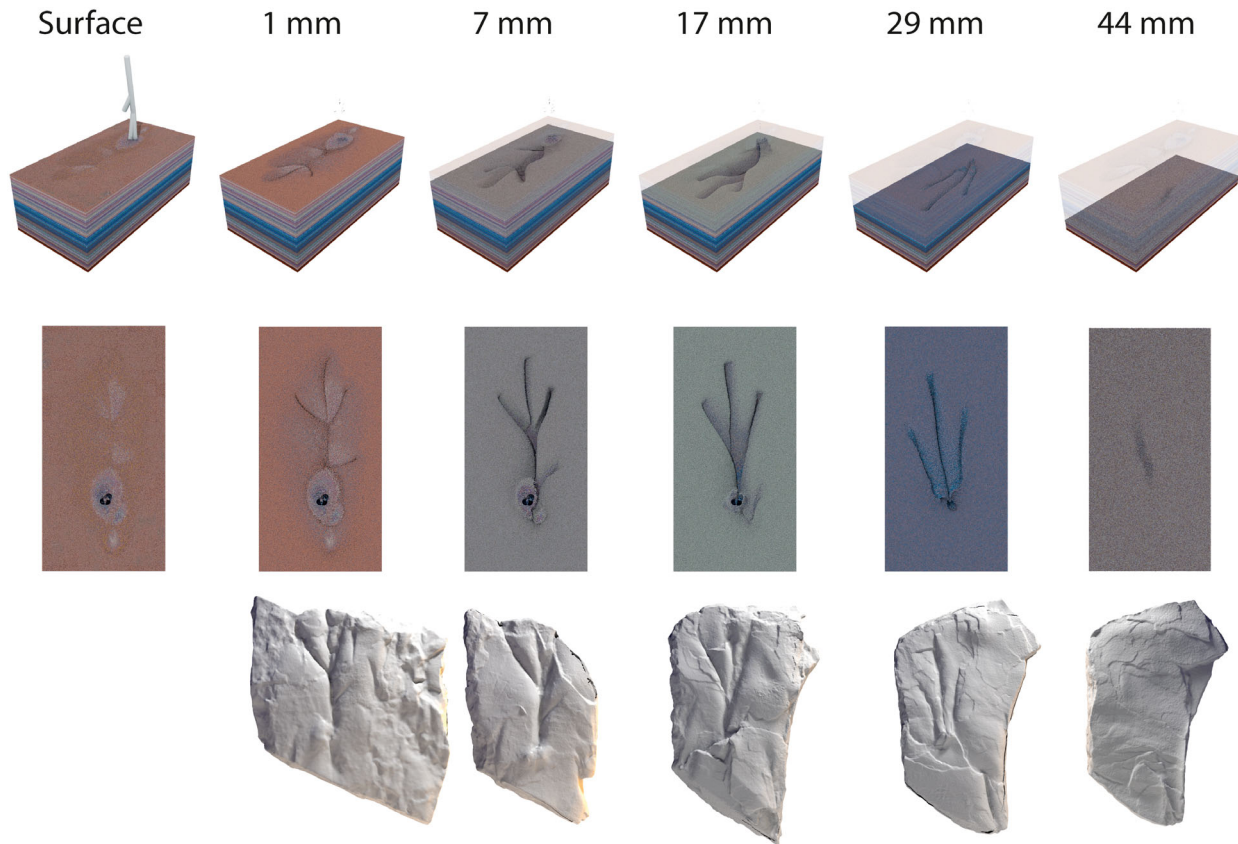
FIG. 4. Discrete Element Method simulation of the reconstructed foot motions. The sediment volume has been coloured randomly according to particle starting depth, creating visual laminations. The simulated track volume has been exposed at multiple depths corresponding to the position of the upper surface of each slab from the fossil specimen. Although the surface track lacks any anatomical details, removal of the uppermost 1 mm of sediment exposes clearly defined impressions similar to the surface of ACM-ICH 31/57. The lowest exposed simulated surface corresponds to the underside of ACM-ICH 31/51 (note that the image of the fossil has been horizontally mirrored to aid comparison).
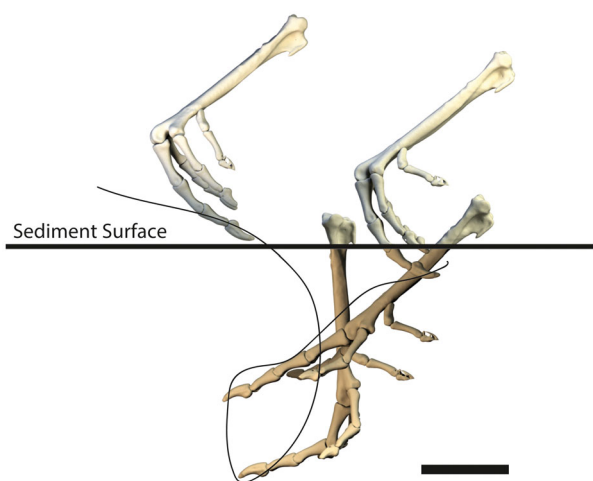

FIG. 5. Looping motion of a guineafowl foot traversing soft mud. Line indicates the path taken by the tip of digit III as the foot sinks and then exits the substrate. Scale bar represents 5 cm. Colour online.

et al. 2007; Milner & Lockley 2016). The seemingly clear distinction between 'walking' and 'swimming' becomes blurred on soft sediments that only partially resist the motion of the foot, and only partially support the animal (with the remainder of support coming from buoyancy).

Another explanation is that the exaggerated backward motion of the dinosaur foot may be related to the differing limb proportions (shorter metatarsals; longer, more vertical femur) and body shape (long muscular tail; more posterior centre of mass) and may therefore be evidence of kinematic differences between extant birds and bipedal Jurassic dinosaurs.

One further alternative is that this is simply an unusual step, that does not form part of a regularly alternating sequence. The isolated nature of the specimen means we cannot see the track in the context of a trackway.

These explanations are not mutually exclusive, of course. We are probably seeing contrasts between dinosaur and bird due to both biomechanical and environmental factors.

Confidence in the reconstruction and simulation

There are a number of assumptions, simplifications, and unknowns that we shall address.

Sediment and track volume. Our simulation used particle properties that approximated, on a bulk scale, a sediment that flows relatively easily, but maintains cohesion between particles, akin to a soft mud. Our particle size was much larger than the grain size of the sediment in which the dinosaur walked, but this was a limitation of available computational resources and, more importantly, the ability to visualize and process the data.

We cannot know the exact substrate properties at the time of track formation, because water content is not recorded in the lithified substrate. We therefore chose sediment parameters that produced a virtual substrate which behaved qualitatively like soft, saturated mud.

Fortunately, sensitivity testing of virtual sediment parameters indicates that subsurface track morphology is relatively robust to substrate consistency, though the track at the sediment–air interface varies considerably as particle properties are changed. To test the effects of sediment conditions on the final track morphology, we ran the simulation with more and less cohesion. In each case, tracks exposed on subsurface layers remained consistent between parameters. Only the uppermost layers near the surface are be able to move freely and respond differently depending on input properties. The sediment–air interface shows more variation depending on substrate parameters. In both simulated tracks, and real tracks produced by guineafowl, we have not observed deep tracks that retain this level of definition at the surface; sediments soft enough to allow the foot to penetrate deeply will tend to flow or collapse into the open track at the surface, unconstrained by surrounding sediment.

Assuming the animal was moving forward, we can infer that the foot must have ultimately moved forward relative to where it entered the substrate, and that this has not been recorded in the four-piece track presented here. In our guineafowl data, we can see many cases where the foot rises relatively vertically, before moving forwards through the very top layers of the substrate, reworking entirely the surface impression made on foot entry.

The well-defined surface of the uppermost slab in our specimen (ACM-ICH 31/57), in combination with the above, leads us to conclude that this is not the true surface on which the animal walked, and that the track volume is therefore missing the uppermost portion of the foot–sediment interaction. This is not unreasonable; the track volume must have been exposed at some level in order to be discovered in the first place, and given our observations of real and simulated tracks, the real

sediment–air interface would almost certainly be unrecognizable as a track. In our previous experimental work with guineafowl (Falkingham & Gatesy 2014; Gatesy & Falkingham 2017) we have observed that tracks made in extremely soft substrates lack almost all anatomical information at the sediment–air interface (Fig. 6A). There are instances within the Hitchcock collection, such as ACM-ICH 39/8 (Fig. 6B), that exhibit similar features on the upper most surface, but sharper, more anatomically complete tracks on a lower surface. It seems highly likely therefore that ACM-ICH 31/59 is not the original surface on which the animal trod, though whether we are missing a sediment–air interface or a sediment–water interface (i.e. whether or not the surface of the sediment was submerged when the track was formed) is not clear.

We have taken the fossil track at face value and assumed that it is a 1:1 record of the original track volume at the time it was formed. How confident can we be that this is the case, and that the track has not undergone significant deformation during preservation (i.e. post formational modification *sensu* Gatesy & Falkingham 2017)? The most likely form of deformation that would affect our reconstruction is compaction; that the fossil volume has been compressed during burial and subsequent lithification.

There are two reasons for making the case that the fossil is not appreciably deformed from the original. Firstly, the depth of the track is already extreme, with the toe tips sinking deeper than the foot is long. If the track volume were expanded vertically, it would become difficult to find a foot anatomy that could consistently connect landmarks on surfaces. Secondly, the already steep sided furrows on each surface, and tall raised area around the exit trace would become unreasonably extended, and unlike any comparable features seen in real or simulated tracks.

Reconstructed foot. Our reconstructed foot is deliberately simplified and abstracted, relying on simple cylinders to represent digits and the foot. The lack of joints means that the virtual toes are unable to flex or extend. Our reasons for this are two-fold: to reduce complexity of the simulated model, and because there are currently no direct correlates for individual phalanges (e.g. toe-pad impressions) visible on the fossil from which to reconstruct these subtly motions. The virtual foot also lacks phalangeal pads, tuberosities or scales, and claws. Again, this is predominantly a practical limitation to simplify the computational demands, and reduce the input assumptions, of the simulation.

That the abstracted foot is still able to produce simulated tracks closely matching the fossil specimen is interesting, but not entirely unsurprising. The phalanges of bird and tridactyl dinosaur feet are limited primarily to
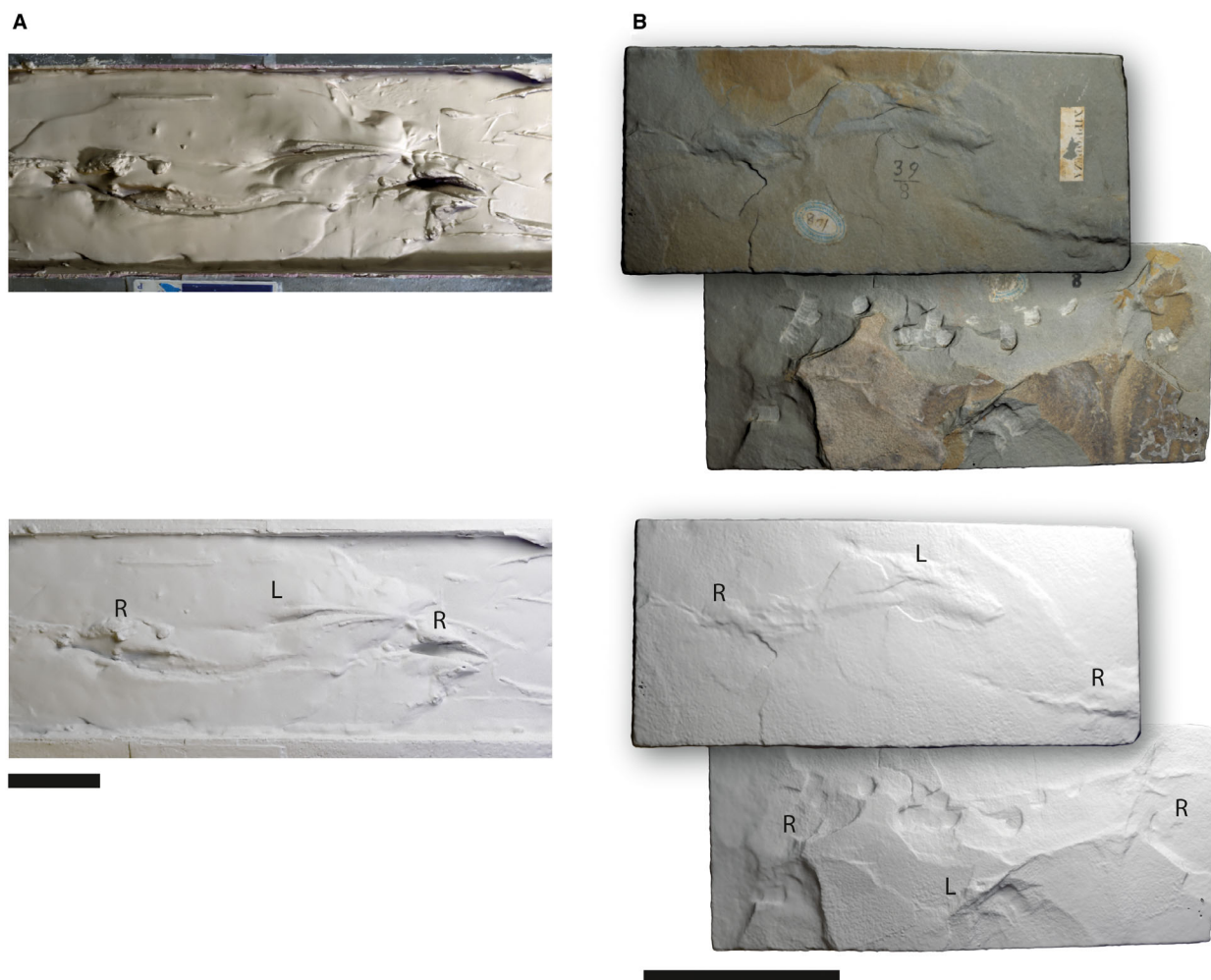
A

B

FIG. 6. Tracks made in deep, soft substrates. A, modern guineafowl tracks recorded immediately after being made record little information about foot morphology at the surface. B, upper and lower surfaces of specimen ACM-ICH 39/8, displaying amorphous marks on the upper surface, but sharp tridactyl impressions on the underside (slab thickness ~1–2 cm). All presented as photo-textured and plain photogrammetric models. Main light source from the upper right, and animals in both cases traversed left to right. R and L indicate right and left footfalls respectively. Scale bars represent 10 cm. Colour Online.

flexion and extension. Any such bending of the toes would result in small changes to apparent length visible in the track (between the hypex and the digit tips) and the foot.

Utility of the simulation. The primary purpose of the simulation was to act as a test of the hypothesized motion and foot anatomy derived from the fossil track. In this regard, the simulation has served its purpose. The incongruence of the surface track in the fossil and simulation prove that the DEM simulation is not pre-determined to always produce an identical facsimile of the input, and indicates that the top of the fossil is probably not the top of the original track. But the similarity between simulated tracks and fossil surfaces

beneath the original surface provides support for our hypothesis of motion generally.

The simulated track also offers an ability to observe the internal geometry of the final track in ways not possible from the fossil, which exposes only eight roughly horizontal surfaces. Slicing the simulated track vertically in sagittal and transverse directions exposes deformed laminations where the foot has passed (Fig. 7). In transverse sections, normal to the orientation of the toes, laminations are drawn downwards producing tightly nested Vs characteristic of penetrative undertracks (Gatesy & Falkingham in press). Further back, where the foot exits, the structure becomes more chaotic as particles are pushed aside by the rising foot, then collapse back into the space left as the foot is withdrawn. Sagittally, folds and faults of
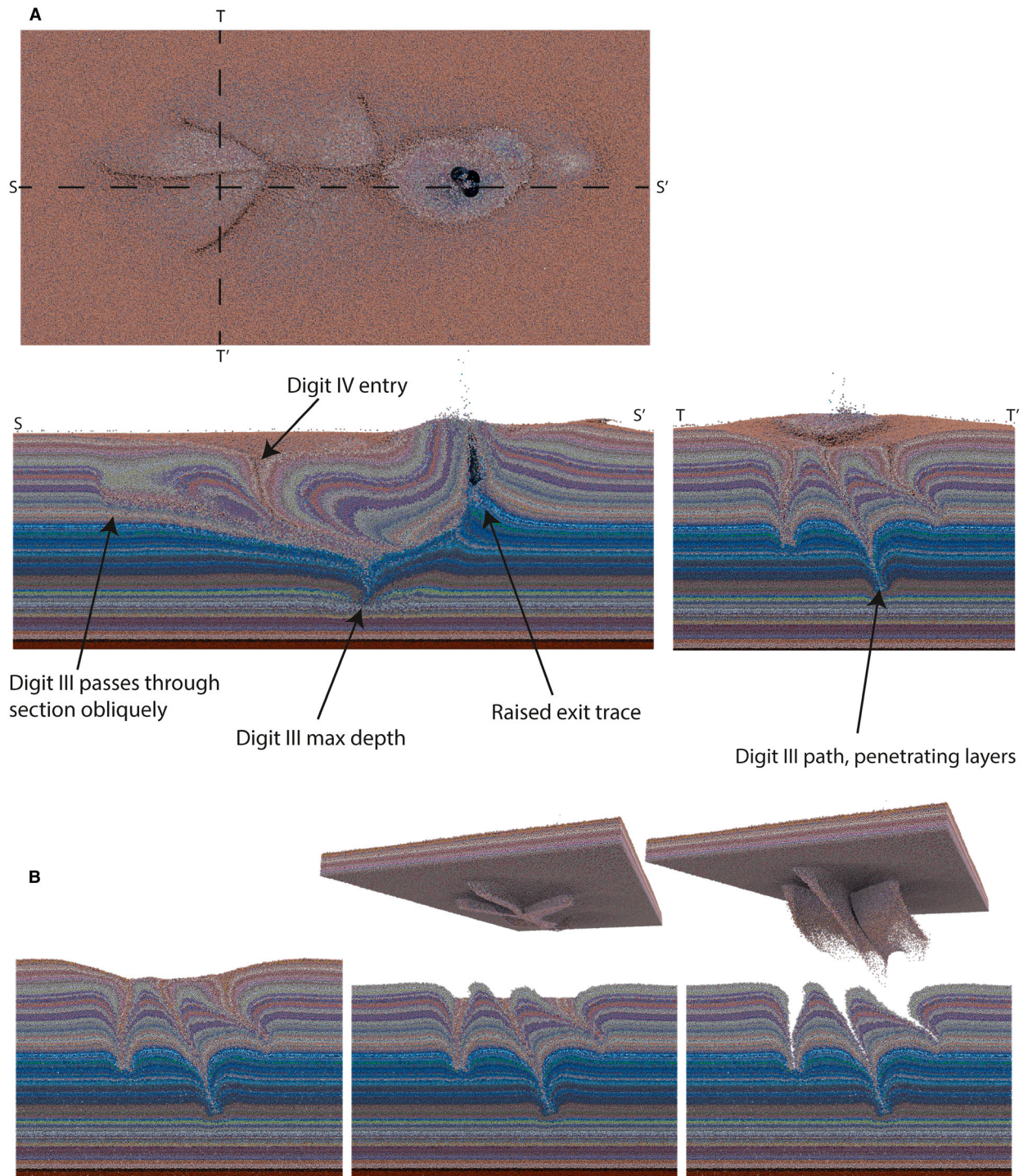
FIG. 7. Sectioned views of the simulated track volume. A, transverse (T) and sagittal (S) sections through the final simulation; random colouration based on starting depth of each particle enables visualization of laminations and deformation thereof; sections show highly complex structures beneath the original surface characteristic of penetrative tracks. B, a horizontal slice demonstrating the breaking of layers within the narrow furrows left by the digits; this breaking of upper laminations within the impression creates a flat 'false' bottom visible in many penetrative tracks.

interbedded laminations can be observed following the paths of the toes (Fig. 7). We note that in our simulations of this narrow-toed foot, transmitted undertracks barely occur.

Surfaces of fossil slabs are formed by breaks in the rock which imperfectly follow laminations and bedding planes, but the simulation can be separated perfectly between layers. Splitting of rock will generally follow laminations, but breaks tend to 'jump' across small gaps, such as lower portions of the narrow slits left by the digits. We have shown elsewhere (Gatesy & Falkingham in press) that this phenomenon has the potential to truncate deep penetrative tracks and make them appear like shallow surface tracks. The undersides of specimens ACM-ICH 31/58 and 31/59 both exhibit these truncated positive-relief tracks, and the simulation provides a way of viewing these surfaces as they would look if there were complete (Fig. 7). We refer readers to Gatesy & Falkingham (in press) for a full treatment of this topic.

Because the simulation is dynamic, it also provides insight into the formation, or ontogeny, of the track (Falkingham & Gatesy 2014). We present in Figure 8 an 'ontogenetic sequence' of the track at 25, 50, 75, and 100% of the foot motion, exposed at sub-surface layers equivalent to the positions of upper surfaces of each slab in the fossil specimen. The upper surface, just 1 mm below the original sediment–air interface exhibits relatively stable digit impressions, the toes having passed through this surface early in the track forming process. Over time, the metatarsal segment elongates backwards from the hypex, before the foot exits through the surface. This elongated metatarsal impression is not dissimilar to tracks described as being made by dinosaurs walking on their metatarsals in a plantigrade fashion (Kuban 1989), but as seen in our reconstructed motion, in this case the foot interacts with the sediment in a digitigrade manner. Below the upper surface, at intermediate depths, we see a similar sequence of formation; digit impressions first, followed by elongation of the metatarsal impression and appearance of the hallux impression, then finally an exiting of the foot reworking the sediment layer. The hallux appears more posterior with depth, and also changes orientation from being directed medially at the surface to anteriorly pointed at depth. At the deepest level, equivalent to the upper surface of the lowest slab ACM-ICH 31/51, the 'toe impressions' are created entirely by a dragging of the tips of the digits through the sediment surface. As such, they do not reflect the anatomy of the foot at all. The formation of the parallel toe marks on the upper surface of ACM-ICH 31/51 are interesting to observe ontogenetically, because the apparent interdigital angle changes throughout the track forming process, as do the relative lengths of each digit. Because these impressions are formed by only the tips of the digits, they do not
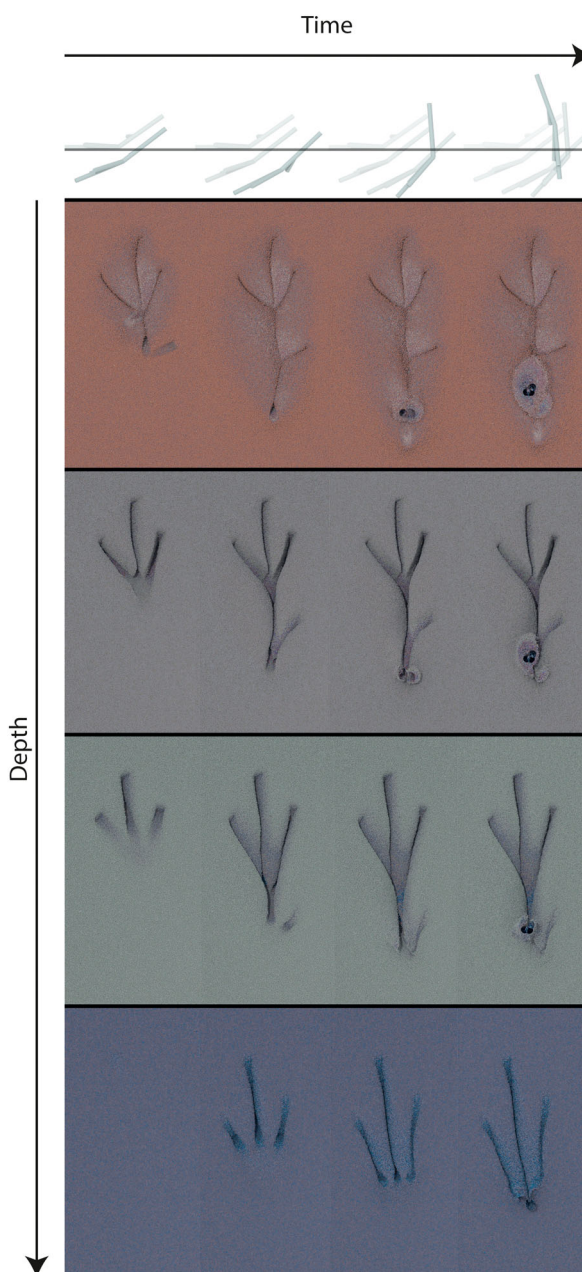

FIG. 8. Track ontogeny of the four-part fossil volume. Shown at 25, 50, 75, and 100% of the foot motion, exposed at surfaces corresponding to the depth of each slab.

record any aspect of the foot anatomy. At this depth, even the number of toes is not correctly recorded because the hallux fails to reach this layer.

As the foot is withdrawn, we can see the formation of the double-peak structure visible in the fossil on all of the layers. This distinctive feature occurs at the rear of the track, offset to the left (laterally) on the uppermost surface of ACM-ICH 31/57, but occurring more aligned with the metatarsal impression on deeper surfaces. The

simulated track allows us to observe how these peaks are produced by the converging toes as the foot withdraws.

CONCLUSIONS AND FURTHER WORK

Using a deep penetrative track, preserved and collected as multiple slabs from a single track volume, we were able to reconstruct foot proportions and foot motions of the trackmaker. The foot was functionally tridactyl, and approximately 6 cm long, probably belonging to a small bipedal dinosaur.

The reconstructed foot, even though very simplistic, indicated that foot and digit proportions are not directly measurable from any given surface. This highlights the importance of treating tracks as volumetric structures, rather than reading them as literal imprints of feet. The track is an excellent reminder that 'footprints are not feet' (Gatesy & Falkingham 2017).

The motions required for the foot to produce the fossil track were determined from identifiable landmarks on upper and lower surfaces of slabs from within the track volume. The resulting motion involved a large backward sweeping of the foot sinking deeply into the sediment, before being withdrawn behind the initial entry position. These motions indicate that the trackmaker was locomoting over (or through) extremely soft, possibly submerged sediment. The motions are distinct from experimental data collected from extant birds, though the extent to whether these differences are due to biomechanics and anatomy, or specific locomotor strategies over different substrates is unclear.

We were able to test our hypothesis of motion using computer simulation. By transferring the foot anatomy and motions into a particle simulation, we were able to test if the predicted motions and foot do indeed produce a track like the fossil specimen. Subsurface tracks matched the fossil closely, while the surface track failed to maintain definition after foot withdrawal. It is likely that the fossil specimen is missing the upper most portion of the foot–sediment interaction, and our hypothesis of motion is therefore incomplete.

The ability to *test* hypotheses of foot motion derived from fossil tracks brings, we hope, a key component of the scientific process to ichnology that has not previously been feasible in many cases. Although we have only used a very simplified, abstracted foot constructed with cylinders, future work will explore a more iterative process between fossil and simulation, in order to refine the hypotheses of motion and foot anatomy. By adding joints in the digits, soft tissue anatomy, and more complex motions, as well as varying virtual substrate parameters such as cohesion and particle size, we will be able to test systematically which motions and foot anatomies produce simulated tracks most like the fossil specimen.

Although we have presented this process using a particularly deep and exceptionally preserved fossil track in which major anatomical landmarks can be tracked throughout the volume, we see no reason why this method cannot also be applied to shallower tracks preserving skin impressions and striations from which foot motions may be discerned.

DATA ARCHIVING STATEMENT

Input files and final output frame of the simulated track, as well as photos and photogrammetric models of figured track specimens are available as supplemental data from figshare: https://doi.org/10.6084/m9.figshare.12251270

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