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REVIEW

Formation, preservation, and interpretation of dinosaur tracks

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Abstract: The fossilized tracks of dinosaurs were first reported in the scientific literature in 1836, not long after Buckland's discovery of *Megalosaurus*. Tracks record aspects of dinosaur locomotion, diversity, and ecology. To recover this information from a track requires an understanding of the track forming process. The interaction between foot anatomy, motion, and substrate means that diversity in track shape can indicate different trackmakers, but may also come from the *same* trackmaker moving across different environments, or in different ways. Being volumetric phenomena, diversity can also arise from how a track is exposed. Layers of sediment beneath the original sediment–air interface, that may or may not have directly interacted with the foot, can vary dramatically within a single track volume. Here, we describe the track forming process in detail, using examples from previous work with computer simulation and extant taxa, with a particular emphasis on how this can lead to an apparent increase in taxonomic diversity. We also present a novel advanced simulation of dinosaur foot motion derived from a fossil track, that builds on previous work. Motions previously determined from surface features are improved using CT scanning of internal track geometry. This reconstructed motion is then used to animate a virtual foot complete with phalangeal joints, claws, and textured skin, and the motion is tested against sediment simulations. Differences in morphology between fossil and simulation emphasize the complexities of track formation, and highlight that further work is required to fully understand the foot–sediment interaction.

Key words: dinosaur, footprint, ichnology, preservation, simulation, discrete element method (DEM).

EDWARD Hitchcock began documenting the many kinds of fossil tracks from the Connecticut Valley in 1835 (Fig. 1), and continued to name and describe tracks for nearly three decades until his death (Hitchcock 1836, 1848, 1858, 1865). The many distinct forms among the Connecticut Valley tracks have, over the past century and a half, been assigned a range of ichnotaxonomic names reflecting their diversity. Hitchcock himself named nearly a hundred ichnogenera and over two hundred ichnospecies (Rainforth 2005).

But does this ichnotaxonomic diversity represent a real biological diversity of trackmakers? It would be tempting to think that such diverse forms of footprints might be representative of an equally diverse fauna of trackmakers. Certainly, Hitchcock frequently referred to the diversity of the tracks in the same breath as the diversity of animals that made them, envisioning a rich fauna composed of dozens of different thick-toed and thin-toed bipeds and quadrupeds. In 1848 he went so far as to argue that the genus and species names he was applying were to the animals, not the tracks themselves (Hitchcock 1848). This practice has fallen out of favour, and ichnologists quite strictly apply ichnotaxonomic names, including those defined by Hitchcock, only to the tracks themselves, and not to the trackmakers.

As we shall discuss, a variety of tracks does not lend itself to a 1–1 mapping with diversity of trackmakers. Here, we will describe recent work exploring the mechanisms involved in track formation, with examples from Hitchcock's Connecticut Valley dinosaur tracks, but with applicability to fossil tracks found globally, and throughout the stratigraphic record. We will demonstrate that although many tracks look quite unlike the feet that made them, they still retain a wealth of information about how dinosaurs moved some 200 million years ago.

SOURCES OF VARIATION

Modern ichnologists are well aware of the difficulties in correlating types of footprints with trackmakers: that a single foot may leave many different tracks, and, conversely, that different animals may have such similar feet as to leave indistinguishably similar footprints. Three factors are involved in the final shape of a track: the form of the foot (anatomy), the motions of the foot (dynamics), and

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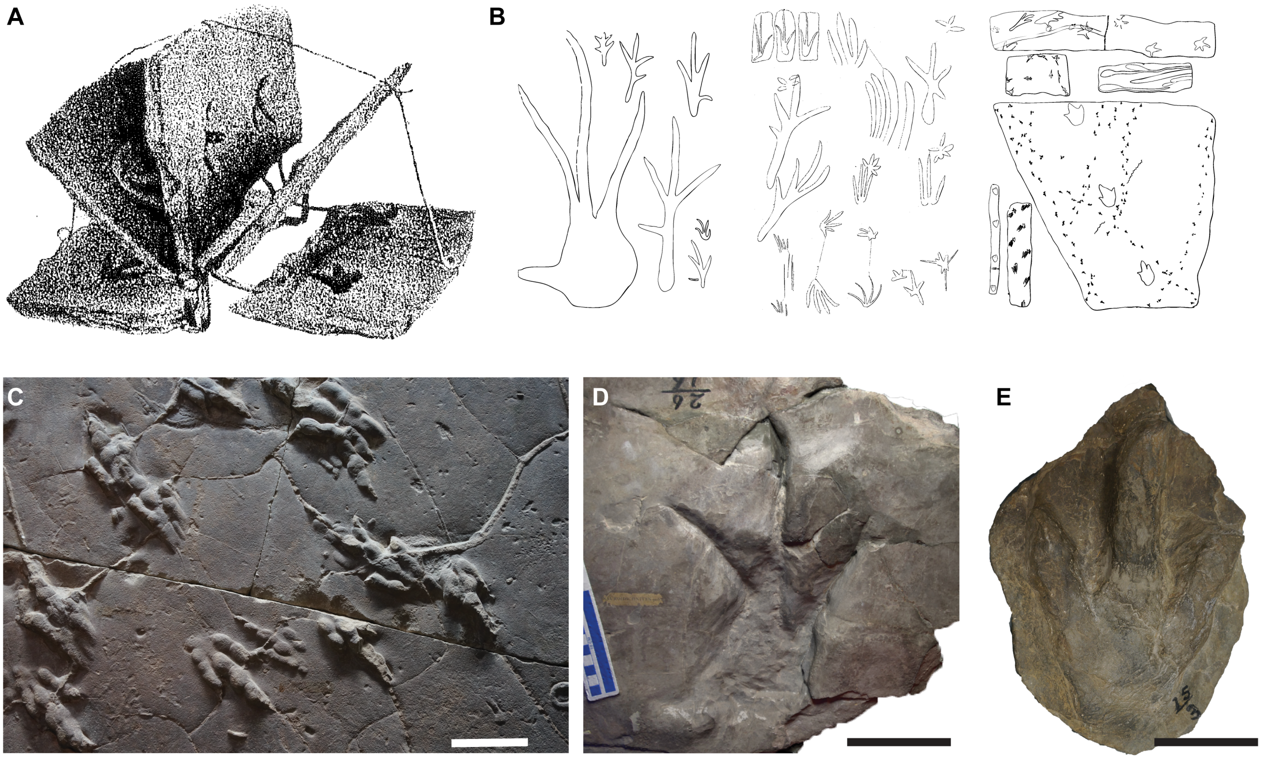

FIG. 1. Various Connecticut Valley dinosaur tracks from the collections of the Beneski Museum of Natural History, Amherst College, presented as 19th century drawings and modern photographs. A, specimen ACH-ICH 27/4, the 'Stoney Volume', as figured by Hitchcock (1858, pl. 52, fig. 6). B, outline drawings of tracks by Hitchcock (1858, pls 18, 20, 37). C, specimen ACH-ICH 9/14, slab with multiple high-definition tracks with pad and scale impressions. D, a large 'thin-toed' track, specimen ACH-ICH 26/16. E, specimen ACH-ICH 15/3, type specimen of *Eubrontes*. Scale bars represent 10 cm (C–E).

the deformability of the sediment (substrate) (Padian & Olsen 1984; Minter *et al.* 2007; Falkingham 2014).

To illustrate this point, consider walking across a sandy beach. The footprints you might leave in the dry sand would be large, featureless depressions, the sand collapsing into vague ovoid shapes. But as you walk toward the water, the substrate begins to take on a firmer consistency, grains held together by the moisture. Your footprints become shallower, but more defined; impressions of individual toes become clear and (should the sand be fine enough) even the skin texture of the underside of your foot might be recorded. Finally, as you reach the water, the sand becomes oversaturated and unable to retain its form. Your footprints once again collapse as you withdraw your foot, more completely even than in the dry sand. Despite your walking motions remaining the same (or at least similar), and your foot (hopefully) remaining unchanged in its anatomy, the footprints you would leave behind on your walk across the beach would be drastically different.

Now consider walking along the beach, parallel to the water, such that the moisture content, and therefore deformability, of the sediment remains relatively constant. Starting slowly, you increase your speed first to a jog, and then to a run, and finally to a sprint, before slowing down to a stop. Even though your foot has remained unchanged, and the sediment behaves consistently along your path, your footprints differ along your trackway. Those left as you walked slowly might be most like moulds of your foot, but the footprints left behind as you sprinted over the sand would look very different, expanded forward and backward by the motion of your foot striking then pushing off. Footprints near the start of our imaginary trackway will have proportionally deeper toes, where you have accelerated, while footprints near the end might have deeper heels where you have tried to slow down.

What if such variable footprints were made by an enigmatic long-extinct animal with unknown foot morphology, and each type (dry, firm and wet sand; walking and running) were found in isolation? We might assume that such tracks were made by multiple animals, and without a connection between them, each track might be different enough to warrant its own ichnotaxonomic assignation.

In other words, a single animal may leave many different forms of footprint (Thulborn 1990; Milàn 2006; Minter *et al.* 2007; Gatesy & Falkingham 2017; Farlow 2018).

Conversely, animals that have similar feet can leave similar footprints. We might, for the sake of a contrived example, imagine that we have been running on the beach to escape two species of big cat, perhaps a tiger and a lion. Their footprints will be very similar to each other, because their feet (and their motions) are similar. The same is true for many theropod, and some ornithopod, dinosaurs, who shared conservative three-toed foot morphologies (Wright 2004). A biologically diverse faunal assemblage may therefore leave behind a low diversity ichno-assemblage (Farlow *et al.* 2013).

We can clearly see from our analogy above then, that track diversity stems from the three factors that define the foot–sediment interaction: foot morphology, foot motion and substrate properties. This is compounded in ancient specimens (as we shall discuss) by additional variation resulting from the ways in which tracks become part of the fossil record and are later exposed; in other words, how they are preserved (Gatesy & Falkingham 2017; Falkingham & Gatesy 2020).

TRACK FORMATION

Simple motions & continuous substrates

The simplest concept of track formation is that of a foot pushing vertically down into a soft but competent substrate, leaving behind a mould of said foot when vertically withdrawn (Fig. 2A). Such a stamping mechanism is

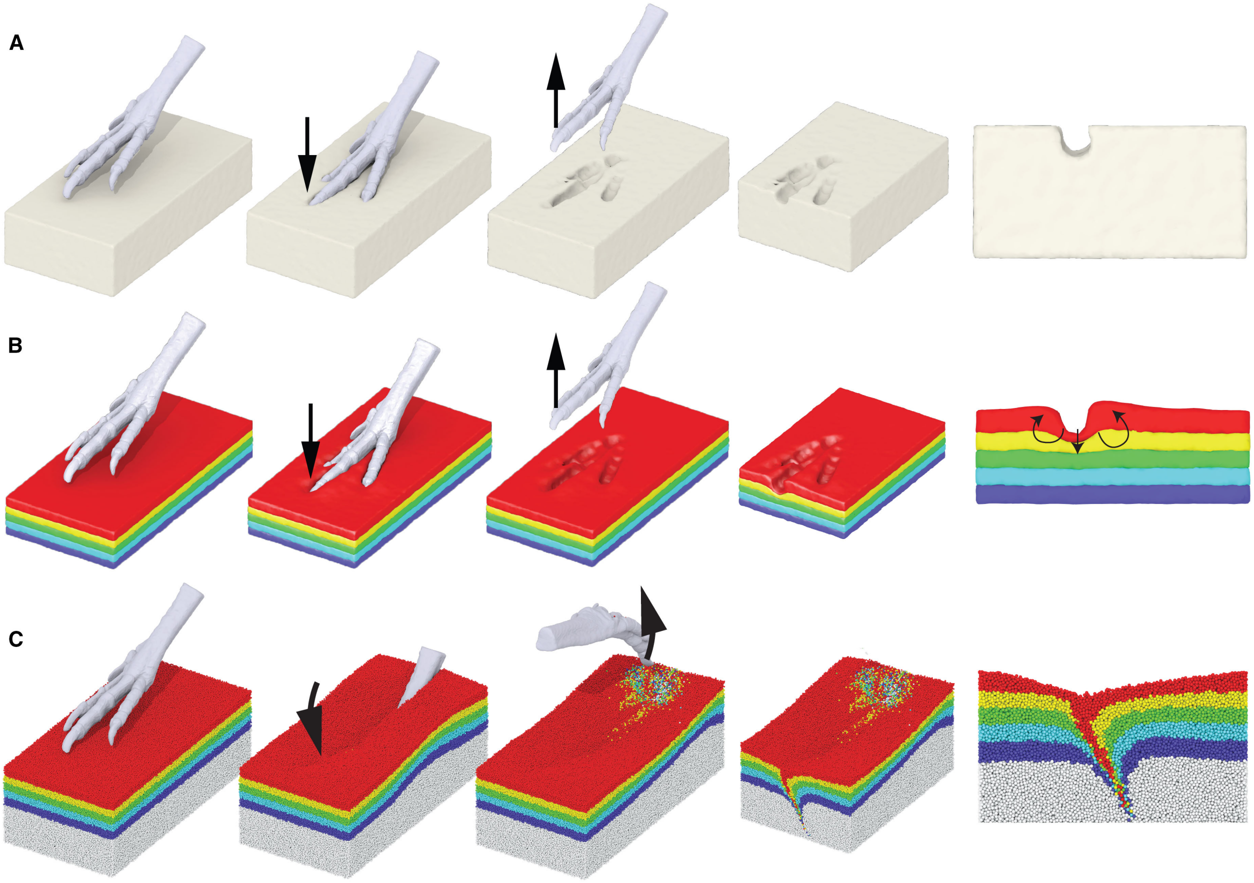

FIG. 2. Mechanistic concepts of track formation. A, simple mould concept; the foot indents the substrate vertically and pushes sediment down only, leaving a perfect mould of the foot; this is more simplistic than occurs in reality. B, the 'transmitted undertracks' mechanism acknowledges that sediment must go somewhere; sediment that is pushed down transmits forces and displacements to subsequent layers, producing impressions on sub-surface layers; however, distance of transmission is severely limited; in this case, if the yellow layer were exposed, a poorly defined impression would be visible, yet the green layer would show no track. C, the 'penetrative' mechanism, in which the foot passes through surface layers of sediment with a complex motion, penetrating multiple layers of sediment; if any sub-surface layer were fully exposed, narrow furrows would be visible over the full depth that the foot sank to. B and C are the result of discrete element simulations, presented as continuous and discrete surfaces respectively.

convenient, as it implies a direct relationship, a structural homology, between the foot and the track. Thus, measuring the overall length of the track is the same as directly measuring from the rearmost portion of the foot to the tip of the longest toe. Other metrics such as digit width, or interdigital angle (the spread of the toes) can similarly be measured from the track with the same confidence as if measured directly from the animal itself. Of course, such a mechanism for producing a track is, as we will demonstrate, grossly simplistic.

At large scales, the substrate might be considered to behave as a single continuous entity that deforms in response to the loading and movement of the foot, similar to a soft plastic. Indeed, the highly influential work carried out by J.R. Allen in the 1980s and 90s, used plasticine (modelling clay) as a proxy for sediment in his indenter experiments (Allen 1989, 1997).

Most track-bearing sediments are only partially (if at all) compressible. If the volume remains constant, the sediment moved by the foot must be displaced somewhere else. In other words, the sediment pushed down does not simply disappear. In constrained sediments, for instance when a soft, shallow layer is underlain by a stiff, deeper layer, the displaced sediment is forced outwards and upwards, leaving raised areas (displacement rims) around the indentation. If the sediment is not constrained beneath, however, sediment is able to move downwards to a greater extent. Sediment pushed down at the surface in turn pushes down the sediment below it, transmitting the forces and displacements below foot level. The logical result of such sub-surface motions, as observed first by Hitchcock (1841, 1858), and demonstrated later by Allen's (1989, 1997) and more recent experiments (Manning 2004; Milàn *et al.* 2004; Milàn & Bromley 2006; Jackson *et al.* 2009, 2010; Milàn & Falkingham 2016), is that layers of sediment *beneath* the surface on which the animal walks can be deformed, producing shallower, less defined tracks (Fig. 2B). Because the borders between layers of sediment may form weaknesses; it is not uncommon for a fossil track to break along such a boundary. The result is an exposed surface that may look like a typical footprint, but in fact was formed some distance below the foot–sediment interface. These types of tracks have commonly been referred to by several names, including 'undertracks', 'transmitted prints' and 'underprints' (Haubold 1971; Thulborn 1990; Lockley 1991; Marty *et al.* 2016). We have previously attempted to clarify this terminology, describing such features as *transmitted undertracks*, because they occur *under* the original surface as a result of *transmitted* displacements (Gatesy & Falkingham 2020). Taking this sub-surface deformation into account, a track can no longer be considered as just a deformed surface but is instead a 'track volume' extending below the foot–sediment interface.

Hitchcock's tracks are particularly notable for including specimens which have split along laminations, exposing tracks at multiple surfaces. Tracks preserved and exposed in this manner formed a major part of Hitchcock's understanding and organization of his collections, housed at the time in the Appleton Ichnological Cabinet, Amherst College. In many cases, the surfaces were articulated with metal hinges or wires, allowing an observer to view each surface in the context of layers above and below it. Hitchcock (1858, 1865) referred to one cabinet as a 'stony library' comprised of track 'books'.

Key among these track books is specimen ACM-ICH 27/4, frequently referred to as the 'Stoney Volume' (Fig. 1A). The specimen presents two small tracks exposed on eight surfaces of five slabs (tracks are unclear on the uppermost surface and not present on the lowermost) totalling *c.* 100 mm thickness. The slabs still retain the metal strap hinges that were fitted to allow the series to be displayed like a fanned book shortly after the specimen's acquisition in 1853. This specimen in particular has been used frequently since its first description in 1858, as an example of tracks forming below the sediment surface upon which the animal walked. The relatively flat bases to each track, and their striking similarity of form throughout the volume have led previous authors to champion the specimen as an example of transmitted undertracks (Thulborn 1990; Lockley 1991; Seilacher 2007). However, as we shall see later, the appearance of the tracks on this specimen is deceiving. Indeed, Nadon (2001) described the specimen as 'impossible' and did not offer any explanation as to its formation.

Complex motions & sediment as a granular medium

At a micro-level, any substrate is not in fact a continuum, but instead is comprised of small particles (grains) which themselves may be surrounded to varying degrees by water. It is the reorganization of the grains within a sediment, by the moving foot, that produce the final structure we term a 'track' (Gatesy 2003; Falkingham & Gatesy 2014; Gatesy & Ellis 2016).

When we consider track formation from a granular perspective, deformation of the substrate becomes far more complex, involving not only sediment 'flow' and reorganization, but discontinuities and blending of layers that are not possible in our simplified continuous plastically deforming concept above. Whilst we might usefully consider a sediment to be continuous and plastic for simple foot motions, more complex or deeper foot–sediment interactions require a particle-based way of thinking (Fig. 2C).

It would be an extremely rare and unusual event for a foot to indent into a sediment purely vertically like a

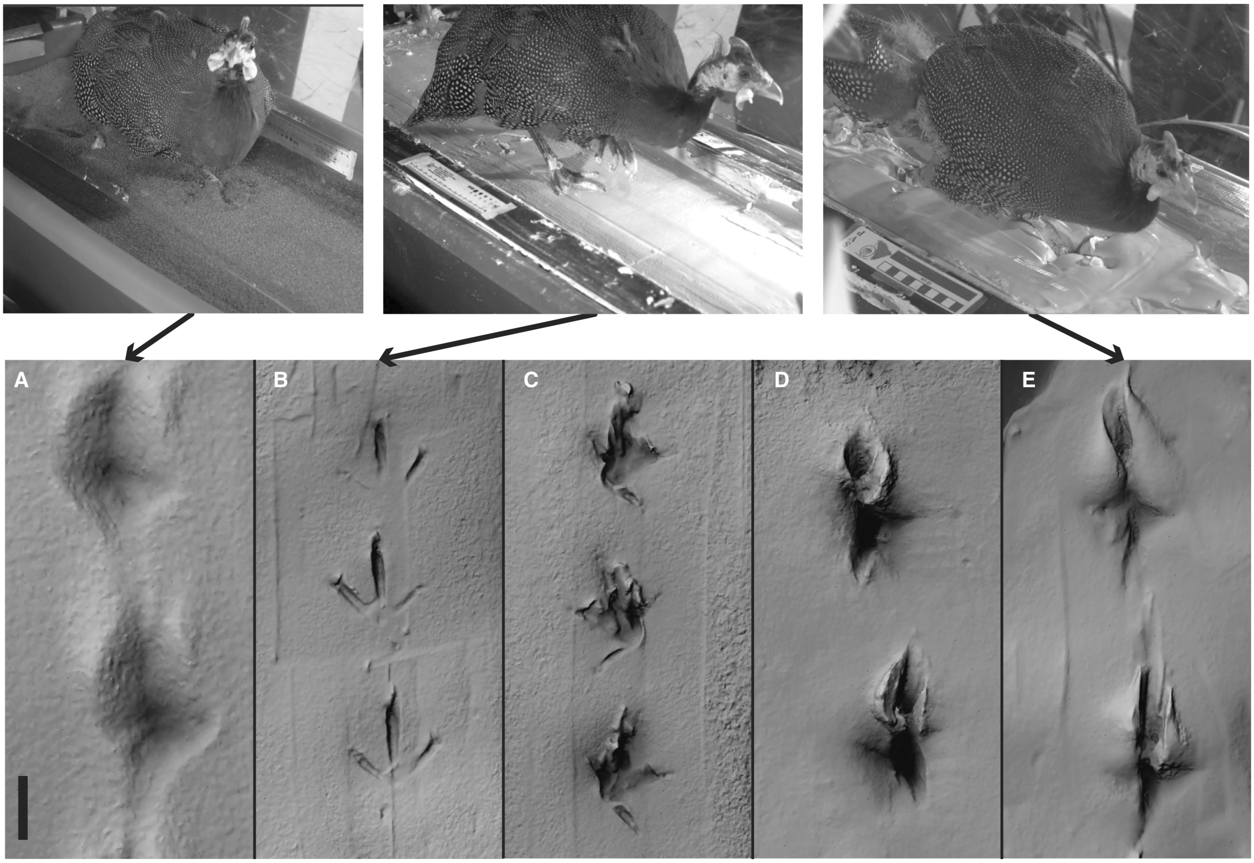

FIG. 3. Footprints left by a helmeted guineafowl (*Numida meleagris*) in a range of substrates, digitized via photogrammetry. A, dry granular material (poppy seeds). B–E, mud mixture of progressively increasing hydration. Scale bar represents 5 cm.

stamp or punch, and to withdraw in the same manner, during forward locomotion (though see Milàn *et al.* 2005). Instead, feet need to exert forces in the horizontal plane in order to slow and re-accelerate the body with each step. The most intuitive example of this is to think of our own feet, striking the ground first with our heel, then rolling forwards to support our weight on the entire foot, before finally kicking off with the toes. It is for this reason that our footprints left on a beach might be much deeper beneath the toes and heels, irrespective of our foot's arch (Hatala *et al.* 2021).

That tracks can record foot movements is one of their biggest appeals to palaeontologists. Tracks are fossilized motions, and can be used to tell us how extinct animals once moved in a way that simply is not possible from the bones alone (Gatesy *et al.* 1999; Gatesy 2001; Milàn *et al.* 2005; Milàn 2006; Graversen *et al.* 2007; Huerta *et al.* 2012; Cobos *et al.* 2016; Falkingham *et al.* 2020a). If we take our thought experiment away from the beach where we have been making shallow tracks on the surface of the sand, and instead go to a very deep, soft, mud, we will produce very different tracks. More than just the soles of our feet (no doubt in Wellington boots at this point) will contact the substrate. As we sink deeper, the heel, ankle, shin (perhaps even the knee) will be involved in the track-forming process (Campos-Soto *et al.* 2025). As we withdraw our foot (we shall assume the welly comes with us and does not get stuck in the mud), our body continues to move ahead before the foot leaves the mud entirely. The deeper a foot penetrates into the sediment, the more motion is recorded by the reorganization of the sediment's constituent grains. Deep tracks therefore record more of the motion, and more of the anatomy, than a simple shallow print can.

However, in recording more of the motion, the track will necessarily look less like a simple mould of the foot. Motions and foot configurations occurring later in the step overwrite and combine with deformations produced earlier. Deep tracks, especially those made by birds and small dinosaurs, are likely to involve the mud sealing up behind the relatively thin toes. We have experimentally recorded this phenomenon for birds traversing dry granular substrates through to very soft, wet muds (Fig. 3) (Falkingham & Gatesy 2014; Gatesy & Falkingham 2017, 2020; Turner *et al.* 2020). The track forming process can continue a short while after the foot has been removed from the sediment via slumping or collapse; we consider the track forming process to continue until the energy imparted by the foot ceases to move sediment. Additionally, deep and cohesive substrates may link motions between tracks, as the act of withdrawing one's foot adds additional motions and stresses to the next step (Turner *et al.* 2022).

If the foot penetrates the surface layer of a substrate, it may go on to pass through subsequent sub-surface layers until it can find enough resistance to support the animal's weight. Much as for the transmitted undertracks described above, should the rock be broken open at a subsurface layer we will see a track produced below the surface of the sediment on which the animal walked. We have termed such tracks *penetrative undertracks* (Gatesy & Falkingham 2020), because they are formed *under* the original sediment surface, not by transmission of force and displacement, but by direct contact with the foot as it *penetrates* the layer. If exposed at the original surface, such tracks might be termed simply *penetrative tracks*.

Key to this concept is that transmitted undertracks are formed indirectly (Gatesy 2003), never touching the foot and decreasing in definition with depth. Penetrative undertracks, conversely, are all formed through direct sediment–foot interactions and can appear quite different with depth, but are generally crisp and well-defined wherever they occur.

If the animal walks upon a very soft mud, and the foot sinks to a deeper level, we must be clear what 'surface' we refer to. We would argue that the surface on which the animal walked, the 'tracking surface' (Fornos *et al.* 2002; Marty *et al.* 2016; Lallensack *et al.* 2025), is the sediment–air interface, or if submerged in shallow water the interface between sediment and water. Where the foot stops sinking remains a sub-surface level.

In both the transmitted and penetrative scenarios, tracks do not occur as a single deformed surface, but as a volume. In the transmitted-track mechanism above, the track volume extends primarily below the foot–sediment interface. However, when discussing penetrative formation, the track volume extends somewhat below, but primarily *above*, the foot's deepest intrusion all the way back up to the original tracking surface.

Among the dinosaur tracks held at the Beneski Museum of Natural History, Amherst College, are many examples of penetrative tracks. Most are exposed as surfaces on slabs, but partial specimens can often be seen in cross-section along slab edges (Fig. 4). Such tracks are generally characterized by narrow, almost slit-like digit impressions and are often elongate or distended (Figs 1B, D, 4A–E). Over multiple surfaces within a single track volume, the form of the impression can change quite considerably due to the angle and motion of the foot as it interacted with the sediment at that depth.

It is this combination of foot motion and surface depth that we think is responsible for a large portion of the variation among penetrative tracks. We have previously described such changes in morphology with depth as intra-volumetric variation (Gatesy & Falkingham 2017). There is great utility in understanding the formational processes involved in feet making penetrative tracks, both in recognizing a source of diversity de-coupled from organismal taxonomic diversity, and in ultimately using these tracks to reverse-engineer the limb motions of long-extinct animals. But first it will be useful to demonstrate and observe penetrative track formation directly.

Simulating track formation mechanisms

One of the fundamental difficulties in attempting to study foot–substrate interactions is that both components (sediment and foot) are opaque. If we are interested in the movement of sediment and foot *below* the surface, we must somehow find a way to see the un-seeable. Allen (1989, 1997) used plasticine as a substrate, which could be stabilized with wax and then sectioned. But penetrative tracks are likely to form in very soft sediments (soft enough for a small foot to easily sink into), which makes them difficult to work with. Milàn & Bromley (2006, 2008) used dyed cement, which hardened and could be serially sectioned or broken apart as layers. Others have used sand and plaster of Paris (Manning 2004; Jackson *et al.* 2009, 2010) with a similar effect. In all of these cases, sediment deformation entails laboriously constructing layered substrates, only to use them once before physically exposing their internal structure as a lossy sequence of cross sections or surfaces. Such methods only permit tracks to be observed *after* formation, and then solely at a coarse vertical or horizontal resolution.

To fully observe the track forming process temporally and spatially, we have turned to computer simulations (Falkingham & Gatesy 2014; Falkingham *et al.* 2020a). A computational approach known as the discrete element method (DEM) can be used to simulate large numbers of individual particles, their response to motion being governed by parameters such as cohesion, elasticity, and compressibility. We used this approach via the open-source software LIGGGHTS (www.cfdem.com) (Kloss *et al.* 2011).

In describing the penetrative mechanism above, we have wandered far from the simplistic hypothetical examples we started with. Attempting to understand penetrative track formation in a very complex world of multi-jointed feet making complex motions as they interact with a sediment is too large a leap for the moment.

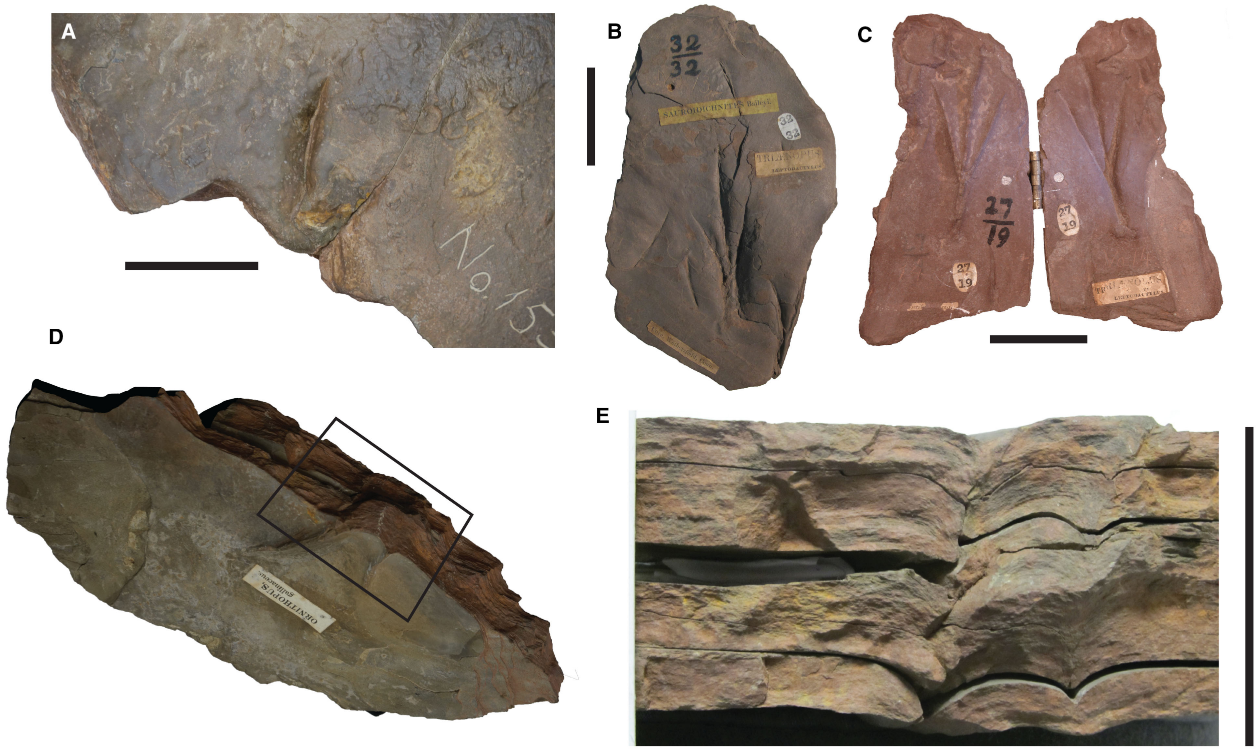

FIG. 4. Samples of penetrative tracks from the Beneski Museum of Natural History, Amherst College, exposed on surfaces and in cross section. A, ACH-ICH 32/28, exposed on four surfaces of two slabs, and broken along impression of digit IV. B, ACH-ICH 32/32 a 'thin-toed' track volume, one surface shown from a set of three slabs. C, specimen ACH-ICH 27/19, a 'thin-toed' specimen presented on four surfaces of two slabs connected by a metal hinge. D, ACH-ICH 41/4 the lowermost positive relief impression of a track exposed on multiple surfaces and as cross section through the middle digit, displaying downturned laminations. E, close-up of the cross section highlighted in D. Scale bars represent 5 cm.

For now, let's make things simpler again, and look at the formation of a penetrative track in an abstract sense, taking just a single cylinder indenting vertically (Fig. 5). We might consider this cylinder to be analogous to the middle toe of a bird or theropod dinosaur. We shall keep the motion simple too, prescribing a slow vertical downward motion to the cylinder. We will also not worry yet about getting the cylinder out of the sediment and look only at the deformation during entry. For the purposes of the following simulations, our virtual sediment approximated a cohesive fine sand, though our experience of many more of these simulations tells us that the general patterns we shall describe are quite resistant to changes in the substrate properties.

Whilst our simulation computes the motion of each individual grain in the sediment, we need a means of visualizing the deformation in a way that relates to the fossil tracks. To this end, we apply a colour to each particle, based on its starting depth. Essentially, we are creating laminations within our virtual sediment, much like the laminations found in the fossil track specimens (Fig. 5).

Indenting the cylinder into the sediment just a little way represents our simplest description of track formation – the cylinder indents and pushes sediment out to the sides and upwards, producing displacement rims (Fig. 5B, C). There is some transmission of motion beneath the cylinder, a kind of sedimentary bow-wave, but it is quite limited in extent. Removing the cylinder at this stage would leave behind an impression that closely matches the form of the indenter.

If our sediment is deep and soft, the cylinder is able to continue moving downwards, penetrating through the upper surface, and into the sub-surface laminations (Fig. 5D, E). As the cylinder continues to penetrate deeper, incised layers above collapse into the gap behind it, sealing the entry. Above the cylinder, we are left with V-shaped structures, which form as each layer is distended by the moving cylinder, then reseal in its wake. These V-shapes are nested within each other, all pointing in the direction of the cylinder's motion. As we let our cylinder come to rest near the bottom of the sediment volume, we can see that the resultant track volume

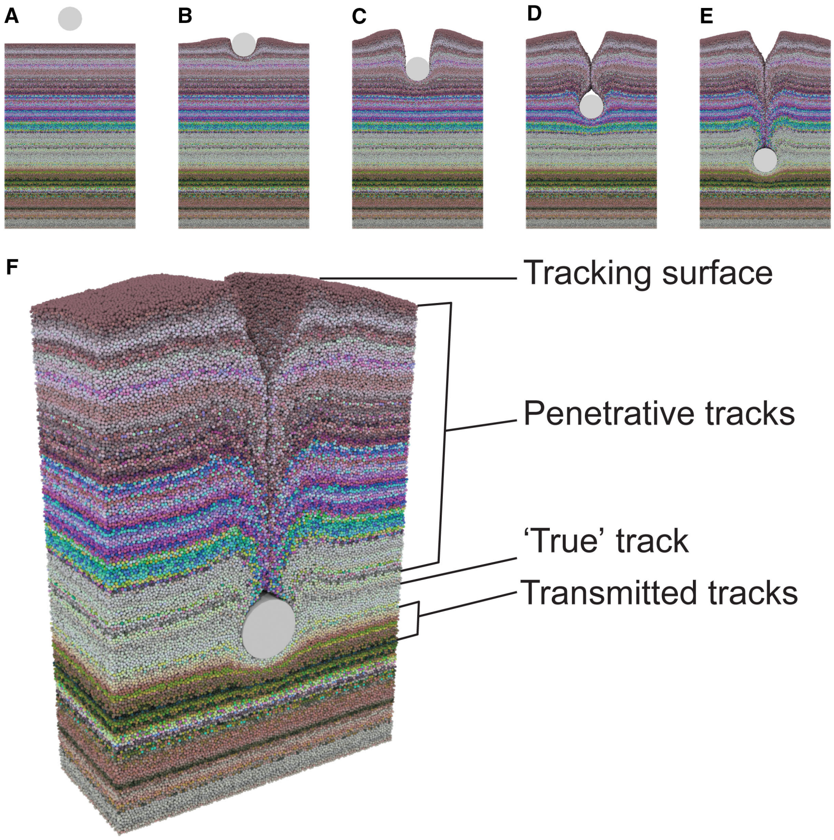

FIG. 5. Formation and composition of a penetrative track. A–E, progressively deeper penetration of the substrate by a cylinder; as cylinder sinks to a shallow level (B), we see the traditional mould-based mechanism of track formation, but as the cylinder sinks deeper (D, E), it penetrates sediment layers; at no point is deformation transmitted more than a short distance below the advancing cylinder. F, the composition of a penetrative track volume.

extends above the indenter all the way to the sediment surface, and just a little way below the indenter.

Penetrative tracks 'produce' diversity with depth

Our simple simulation serves to demonstrate the formation of tracks above and below the foot–sediment interface throughout the track forming process. A key observation from this simple simulated scenario is that the penetrative formation mechanism results in a track volume that begins with a penetrative surface track, continues through a sequence of penetrative undertracks, before we reach the 'true track' or foot–sediment interface, which is finally underlain by a minimal thickness of transmitted undertracks. Even with this extremely simple indenter, motion, and substrate, we can see the origin of diverse track morphologies depending on where the track is exposed.

One of the big advantages of our virtual footprint is that it can be sliced and separated however we wish. If we were to randomly split the track volume along one of our laminations, the chance that the newly exposed surfaces would present a penetrative undertrack is clearly far greater than a transmitted undertrack or surface track. Separating layers in 3D can produce a virtual analogue to the 'pages' of Hitchcock's 'Stoney Volume' ACM-ICH 27/4 (Figs 6–8). Doing so exposes deep, narrow, slit-like furrows, far thinner than the indenting cylinder (Fig. 6A). Undersides of layers possess positive impressions consisting of steep, sharp ridges (Fig. 6A). Alternatively, we might compare our simulation with that of penetrative tracks that have broken in cross-section, where we can see clear similarities in the downturned laminations (Figs 4D, 5).

Diversity from preparation & exposure

Our simulation enables us to separate layers perfectly, incorporating every particle or grain that belonged to a specific starting layer, no matter how far it may have been

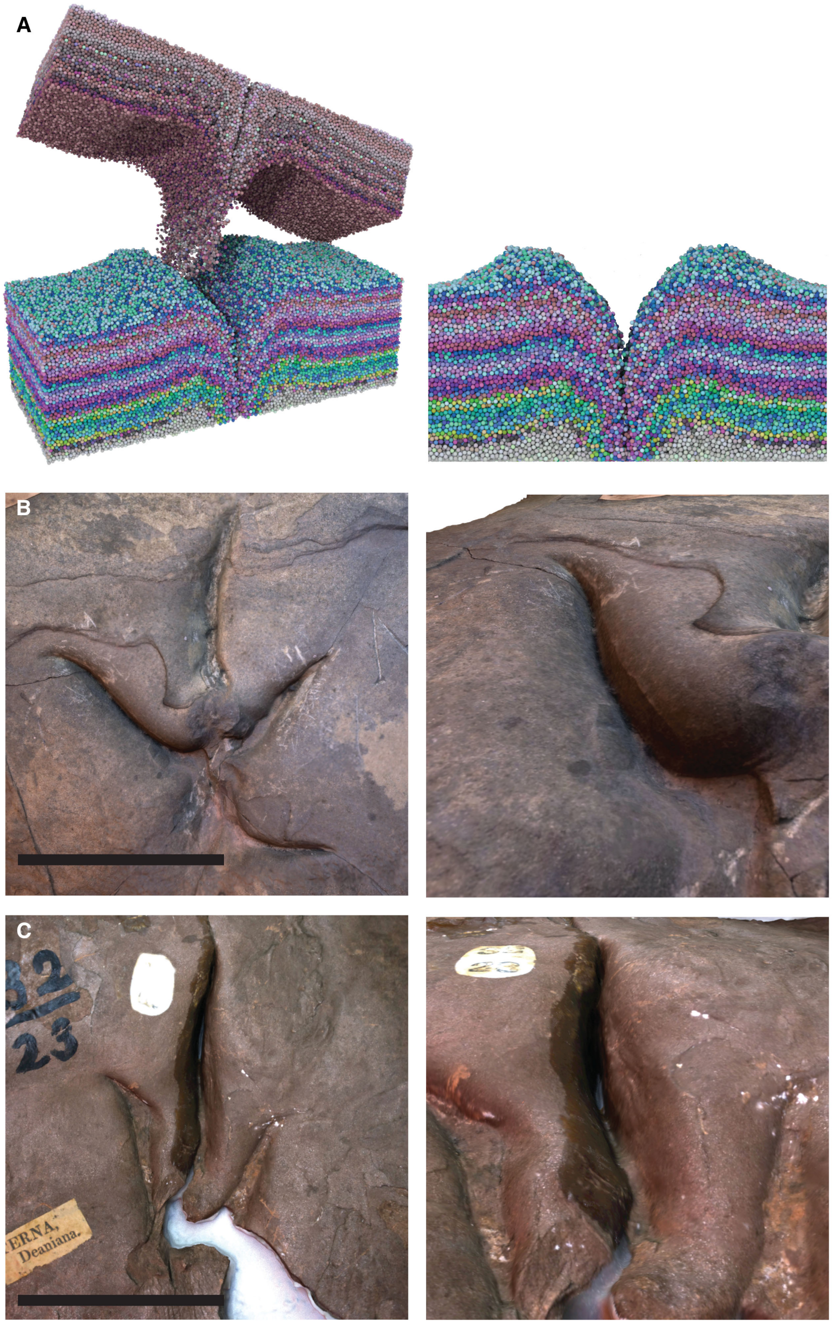

FIG. 6. Complete and clean separation of penetrative layers in simulation and digitized fossil specimens. A, our penetrative simulation is separated cleanly along an originally horizontal layer, exposing a narrow furrow. B, ACH-ICH 32/28, a thin-toed specimen mostly cleared of overlying sediment layers, resulting in the narrow furrow of a penetrative track; note that the central digit III impression has not been fully cleared. C, similarly, ACH-ICH 32/23 presents a fully prepared middle digit impression, but only partially cleared impressions of digit II and digit IV (innermost and outermost of the three main toes, respectively). Scale bars represent 5 cm.

displaced. But real fossil tracks cannot be broken so perfectly. Inevitably when separating penetrative tracks, some rock from the layers above will remain in the tightly pinched furrows on the layer below.

When such fill is minimal, or when the preparator fully excavates the overlying layers, the result is a penetrative undertrack with toe impressions much narrower and sharper than the toes that made it (Fig. 6). From his earliest works, Hitchcock (1836) categorized such tracks as leptodactylous, or ‘thin-toed’, believing them to have been made by trackmakers with particularly narrow digits. We have demonstrated here and elsewhere (Gatesy & Falkingham 2020) that the narrow digit impressions of these tracks are the result of sediment sealing and are not the result of thin-toed feet. The diversity among these forms is therefore not representative of the diversity of trackmakers, but instead a range of foot motions and sediment responses.

Overlying material typically remains within the penetrative furrows because breaks, whether natural or man-made, are unable to follow the sharply deflected laminations. Fractures instead ‘jump’ across from one furrowed wall to the other, leaving a more or less flat base, usually of rock identical in colour and texture. In such cases, the partially filled furrow might easily be interpreted as a shallow impression instead of a penetrative one. If occurring over multiple surfaces, it would be easy to attribute a transmitted track formation mechanism (Figs 7, 8).

We have previously demonstrated (Gatesy & Falkingham 2020) that many of the tracks in Hitchcock’s collections formerly interpreted as transmitted undertracks are, in fact, penetrative undertracks; including the ‘Stoney Volume’ ACM-ICH 27/4 (Fig. 8). Despite this track being used for several decades as an example of transmitted vertebrate tracks, there is strong evidence that in fact the feet passed *through* all of the visible surfaces. While we have detailed our findings previously for this and other specimens (Gatesy & Falkingham 2020), we will summarize our reasoning here:

1. Our simulations have shown that it is impossible to transmit detailed displacement over the distances seen in the specimen, at least for animals with bird like feet and long digits, as is the case here. Our simple cylinder was unable to transmit morphologically accurate displacement to any significant depth beyond its deepest penetration.
2. The flat base of each track, steeply dipping track walls, and abrupt intersection between the two, are consistent with the laminae separation described above, in which the break ‘jumps’ from one wall to the other following the path of least resistance.
3. The base of each track shows faint striations running along the length of each digit (Fig. 8C). We interpret these as resulting from the break crossing multiple down-turned laminae.

On top of our diversity from depth, a second layer of diversity therefore arises from the way in which penetrative specimens break or are prepared. This is post-formational variation (Gatesy & Falkingham 2017), not associated with either the track maker or the sediment conditions when the track was made. This form of diversity is a confounding factor in the study of fossil tracks.

OBSERVING PENETRATIVE TRACK FORMATION IN LIVING BIRDS

Our simple cylinder simulation described above offers a means of observing and understanding the sediment motions and mechanisms involved in penetrative track formation. But of course the feet of animals, including our dinosaur track makers, are not simple cylinders indenting vertically. They are complex structures, consisting of multiple segments all moving relative to each other. There is also the not insignificant matter of foot removal, which is something we have deftly avoided up to now in both our hypothetical descriptions and our simulations. So how to go about documenting the track formation process for a real case?

The dinosaurs that made the Connecticut Valley tracks in the Early Jurassic are long extinct, but their descendants are still very much alive. Extant birds, particularly ground-dwelling birds, possess tridactyl feet very similar to those of theropod dinosaurs. Hitchcock himself originally ascribed the fossil tracks he studied to some long extinct birds (Hitchcock 1836). And so we turn to living birds as models for footprint formation.

As for our simulated cases, sediment opacity makes the task of observing foot motions somewhat difficult, a difficulty that is now compounded by the relatively short time in which a step can occur when an animal is moving moderately quickly. Simply observing a bird run over a soft substrate, even in slow motion, will tell you very little about the foot and substrate beneath the visible sediment–air interface.

In order to overcome this, we employed highspeed biplanar x-ray cinematography via a technique known as XROMM (x-ray reconstruction of moving morphology; Brainerd *et al.* 2010; Gatesy *et al.* 2010; Falkingham & Gatesy 2014). This technique involves aligning two x-ray emitters such that their beams cross at a right angle. High-speed video cameras record the images produced by the x-ray systems. Calibrating the camera positions relative to each other means that the 3D coordinates of any given point appearing in both images can be calculated. By matching digital models of the animals’ bones (acquired via CT scanning) to the shadows in the x-ray images, the bones can be animated to visualize their motions. The x-ray cameras are supplemented by standard high-speed light video cameras, which are also calibrated in 3D space. In the centre of this set-up was a 3.75 m long alley, the central 1.25 m of which consisted of a 20 cm deep tub that could be filled with different sediments (Fig. 9).

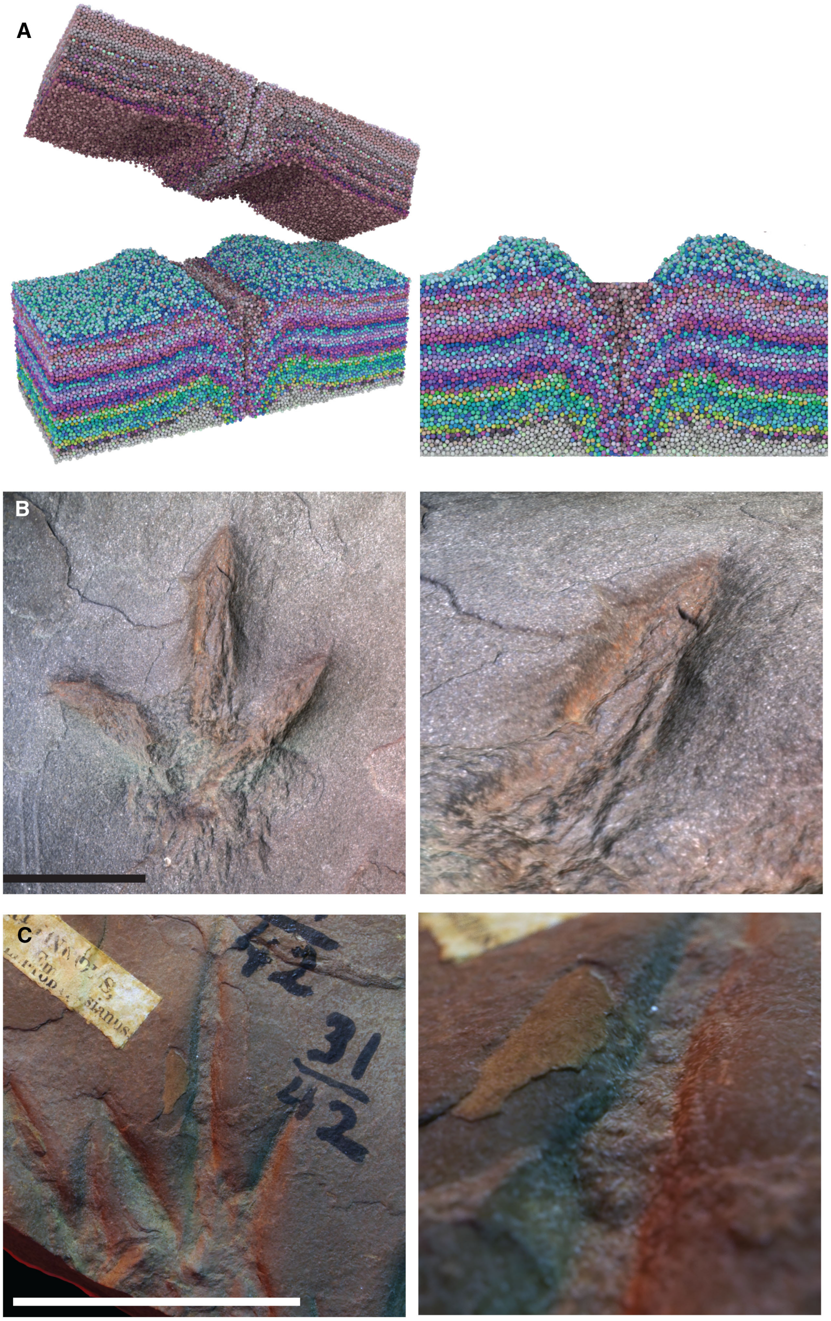

FIG. 7. Partially prepared or exposed penetrative track layers demonstrated in a particle simulation and photogrammetric digital models of track specimens. A, the simulated layers are separated based on original laminations, but the break is allowed to 'jump' across the central furrow, leaving an apparently flattened base to the track formed from highly dipping overlying layers. B–C, ACH-ICH 18/2 (B) and ACH-ICH 31/42 (C) demonstrate this effect in fossil tracks; in B, the down-turned laminations in the 'false bottom' of the toe impression have produced longitudinal wrinkle-like ridges, while in C the overlying layers were more homogenous and did not leave striations; however, the sharp transition from flat base to steep walls of the impression, combined with associated impressions on the underside of the slab, indicate the penetrative nature of the specimen. Scale bars represent 5 cm.

We previously applied XROMM to helmeted guineafowl (*Numida meleagris*) walking on solid surfaces, and over compliant substrates (Falkingham & Gatesy 2014; Turner *et al.* 2020). We have recorded sub-surface foot motions of birds walking over a dry sand-like substrate, and over muds at varying degrees of hydration. Unfortunately, the relatively high density of sand and clay makes it difficult to clearly see through them with x-rays. To

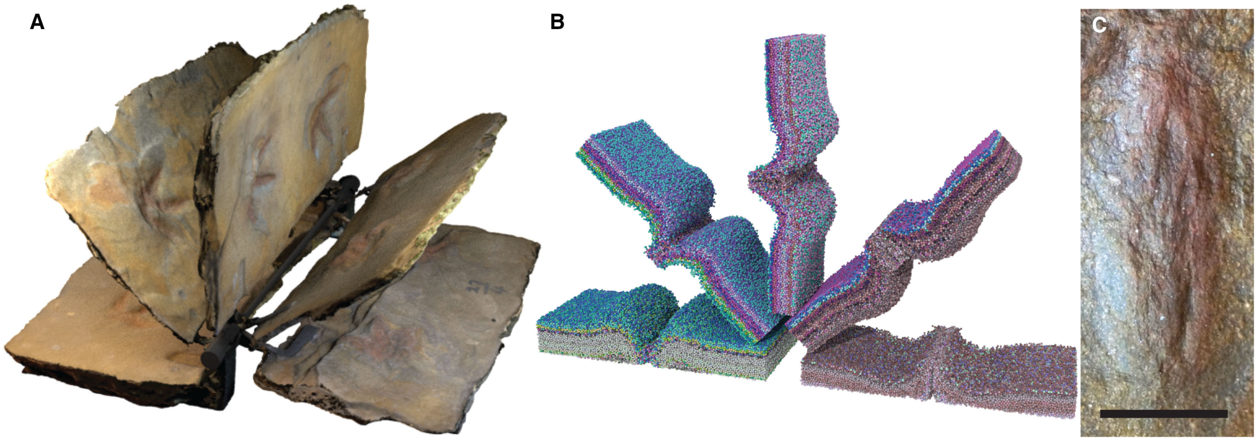

FIG. 8. A, Hitchcock's 'Stoney Volume' (ACH-ICH 27/4) presented as a photogrammetric digital model. B, our simple cylinder simulation exposed in the same way. Truncated penetrative layers give the illusion that the track on each surface is shallow, leading to the long-held interpretation that this specimen is an example of transmitted undertrack formation. However, longitudinal striations along the base of the impressions (C), along with the depth at which tracks retain detail, informs us that this specimen was in fact formed by the foot penetrating each surface, and the sediment closing behind it. Scale bar in C represents 1 cm.

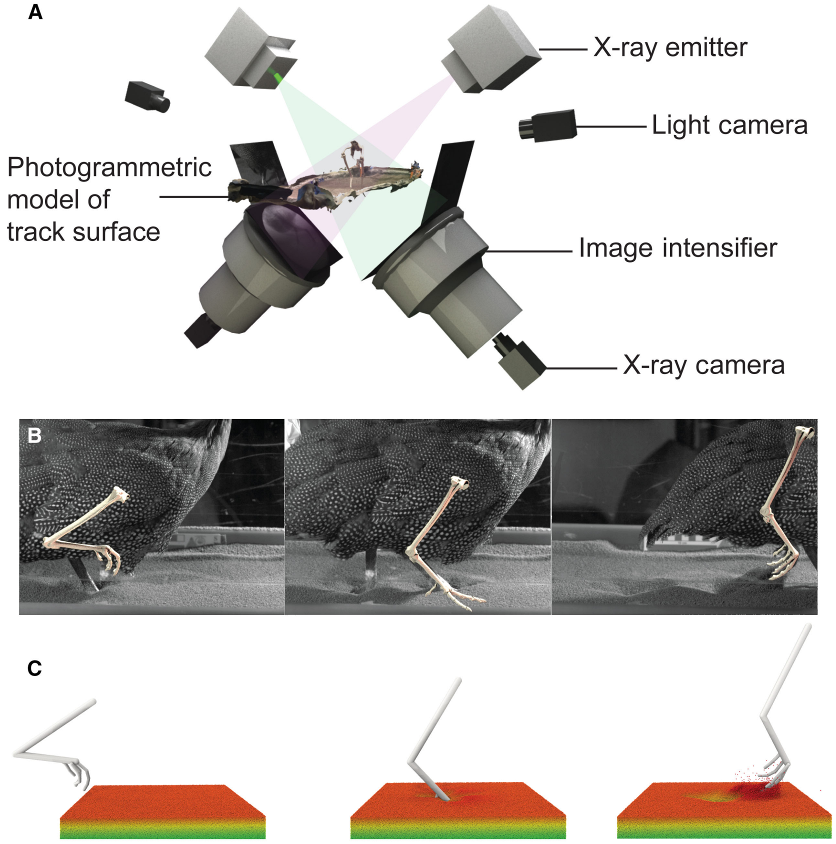

FIG. 9. XROMM data and associated DEM simulation. A, experimental XROMM set-up represented in 3D space together with photogrammetric model of track surface, and aligned CT models of the pelvis and hindlimbs. B, a sequence from a single footstep on poppy seeds, with foot and lower limb reconstructed. C, the same motions transferred to the discrete element simulation, producing a virtual footprint; see Falkingham & Gatesy (2014).

account for this, we instead used poppyseeds as our dry granular material, and a clay/glass-bubble mix for our mud. These artificial substrates behaved similarly to their natural counterparts, but could be seen through with x-rays without requiring extremely high energies.

After the birds had walked over the substrates, between the x-ray beams, we digitized the resultant tracks using photogrammetry (Falkingham 2012; Falkingham *et al.* 2018), producing a 3D model of the substrate surface. This was then incorporated into the virtual scene containing cameras and bone motions (Fig. 9).

Motion of the foot on compliant substrates

We have collected data and observations from four birds walking on (or through) dry, moist, saturated and over-saturated sediments across nearly 200 trials, and in almost all sediment conditions the foot penetrated the surface of the sediment. Only the firm mud was able to support the foot sufficiently to keep the top of the toes visible throughout the formation of a shallow print. In all other cases, the toes sank beneath the sediment–air interface, whether on poppy seeds (our sand substitute) or mud. Put another way, penetration of the substrate was the norm, not the exception.

As might be expected, the more water that was added to our mud mixture, the softer it became, and the deeper the animal's foot sank. On our softest, wettest, substrates, the birds would sink almost to the knee, leaving at the sediment surface large elongate tracks (Fig. 3) created not only by the foot, but much of the lower leg too.

Perhaps less obvious was the depth to which the toes sank on dry grains (poppy seeds). Even though the bird's overall motion was consistent and seemed relatively unperturbed by the compliant substrate, our XROMM data indicated that the tips of the toes sank to *c.* 5 cm depth. To put that in context, the hip height of the bird was *c.* 21 cm, meaning the tips of the digits were penetrating nearly a quarter of hip height. The non-cohesive nature of the grains ensured collapse when the foot was removed, leaving only a vague diamond-shaped impression at the surface (Fig. 3).

Sub-surface sediment motion

The moving foot is only part of the track forming system; movement of the sediment, the reorganization of its constituent grains into the final track form, is equally important.

We used the DEM simulation to model the response of the substrate to the guineafowl's foot, transferring the 3D motions from the XROMM dataset into the DEM simulation (Falkingham & Gatesy 2014). Being a much larger sediment volume than our simple cylinder cases above, the simulation required many more particles; over 10 million. Simulations of this size, especially combined with the complex motions of a multi-jointed foot, cannot be run in any reasonable length of time on a normal desktop computer, and so we took advantage of major supercomputer resources in the UK and USA.

Surface tracks in the simulation satisfyingly matched the real tracks left by the guineafowl (Fig. 10), and combined with our validation tests lent confidence to simulated observations beneath the sediment surface. As with the cylinder simulations, the virtual substrate could be sliced, or virtual layers could be pulled apart, to present penetrative tracks at any depth within the track volume. This meant that tracks could be watched while they formed, at any level at or below the sediment surface, from any angle. We have previously described this process as 'track ontogeny'; in the same way that an organism might develop from embryo to adult, so might a track develop from the first interaction of the foot until the point at which all imparted energy has ceased to move the sediment (Falkingham & Gatesy 2014; Lallensack *et al.* 2025).

Separating the layers (Fig. 10) and being able to view the guineafowl tracks in the same way that Hitchcock's tracks can be observed has offered an incredible insight into diversity caused by variations in foot movements at multiple depths. It has enabled us to link morphological features within the track volume with specific motions of the foot.

Perhaps the best example of this is a small tridactyl track, ACM-ICH 37/24, which displays a bulbous disturbance approximately halfway along the S-shaped impression left by digit III. If one were to assume this track were a simple surficial footprint, the logical interpretation would be some kind of anatomical correlate, perhaps pathology. But knowing that the track is penetrative, and observing it beside the simulated guineafowl track exposed a few mm beneath the surface, it becomes clear that this feature is actually the exit trace of the foot. Having passed through the collected layer, the toes converged, as bird toes do, and were withdrawn through the entry trace of the foot (Fig. 11; Falkingham & Gatesy 2014).

PRESERVING WHAT HAS FORMED

Having dealt with the formation of a footprint, we now turn to the matter of preserving it. As for bones, teeth and shells, the process of fossilization requires burial, lithification, exposure, and finally discovery and preparation.

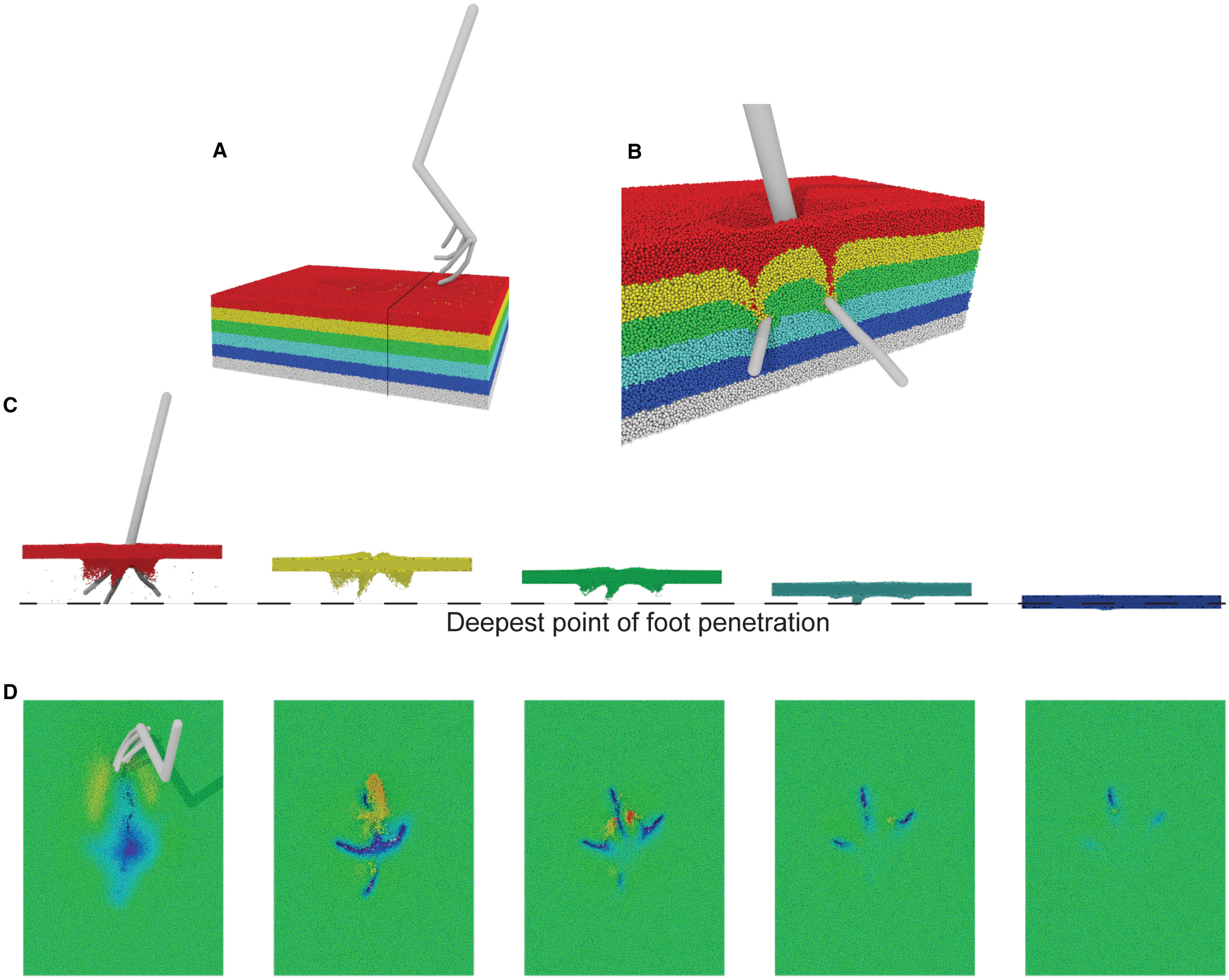

FIG. 10. Simulated guineafowl track. A, final simulation, particles coloured according to starting depth. B, a slice through the track volume at mid-stance, as located in A, demonstrating the penetrative nature of the track (digit II is behind the plane of the slice at this time). C, anterior view of separated layers at mid-stance; the tip of digit III reached the blue layer, penetrating through all layers above. D, each surface coloured according to local height (red–blue = 2 cm). See Falkingham & Gatesy (2014) for full sequence over time and depth.

Footprints are dealt an additional hurdle in the journey towards becoming a museum specimen, in that they are not distinct entities, but sediment deformations. In order for a track to form at all, a sediment must be soft enough that a foot can easily deform it and leave a trace, but firm enough to retain the impression (Nadon 2001; Falkingham *et al.* 2011, 2014). The sediment must then be (or become, through drying out) strong enough that subsequent burial does not obliterate or overly distort the impression. In this regard the fossilization of a footprint at the surface might be considered more like the preservation of some soft-bodied organism, rather than a skeleton. Undertracks, either transmitted or penetrative, have the advantage that they are 'pre-buried', and are consequently more resilient to surface processes occurring prior to lithification (weathering, erosion, etc.) This further increases the likelihood that a penetrative track will be exposed and collected at a surface below that on which the animal originally walked.

One place tracks and body fossils deviate is in how they have traditionally been described as well, or poorly, preserved. In the case of body fossils, 'well preserved' is clear in its meaning; the fossil retains the majority of the morphology (and even chemistry) possessed by the organism during life. Conversely, 'poorly preserved' implies parts are missing or distorted, and that this loss of fidelity has occurred post mortem.

The term 'well preserved', when applied to fossil tracks, has traditionally been reserved for those tracks that look most like feet, and possess crisp, well-defined boundaries.

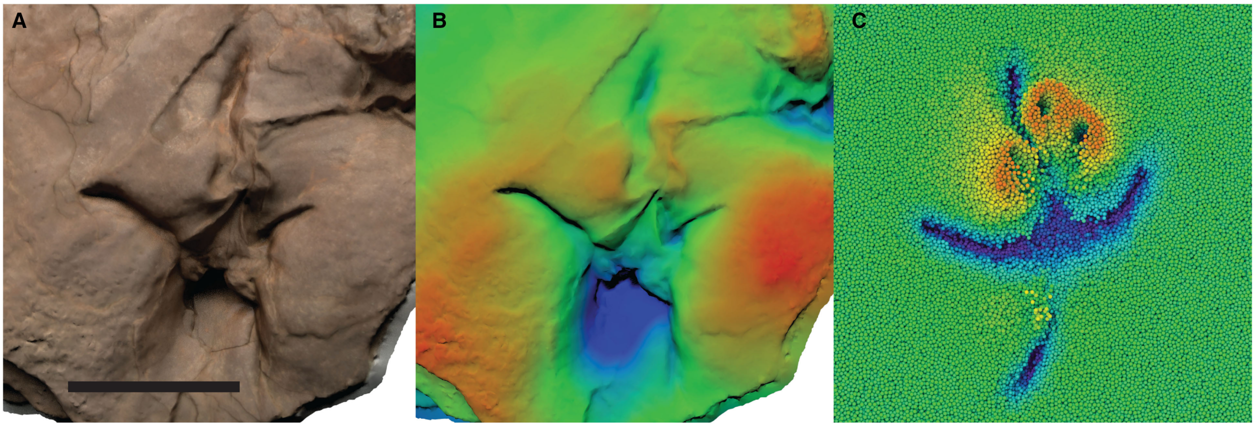

FIG. 11. Fossil dinosaur track and simulated guineafowl track showing exit structures. A–B, ACH-ICH 37/24: A, photo-textured photogrammetric model; B, height-mapped digital model. C, simulated guineafowl track showing similar structures in a similar anatomical location. The raised areas are caused by the toes converging below the visible surface and exiting toward the front of the track, indicating that specimen ACH-ICH 37/24 is a penetrative track (Falkingham & Gatesy 2014). Scale bar represents 5 cm.

Clear anatomical moulds such as pad impressions or skin textures would typically warrant the label 'well preserved' or 'elite'. This may stem from an innate desire to identify the trackmaker, albeit less explicitly than Hitchcock assigning binomial names to trackmakers from tracks alone. This bias is common in the literature, and you will rarely find the words 'well-preserved' beside an image of a deep, penetrative track such as those seen throughout Hitchcock's collections. Consider Marty *et al.*'s comment about modern tracks made on a beach: 'on the same surface shorebirds left well preserved tracks because their feet did not penetrate through the mat' (Marty *et al.* 2009, p. 134), clearly this implies that if the birds feet had penetrated the surface, the tracks would no longer be well-preserved *even though they have just been formed*.

This is not an uncommon view. Belvedere & Farlow (2016) described in detail a numerical scale for quantifying the 'quality of preservation' of vertebrate tracks, 'reflecting progressively better preservation of morphological details'. Tracks scoring 0 on this scale would show 'no morphological details' though could be 'organized in a trackway'. At the other end of the scale, 'well-preserved' tracks score a 3 if digit impressions are 'sharp and clear' and distinct digital pads are present, among other morphological features. Following this scale, the guineafowl tracks left behind in dry poppy seeds (Fig. 3A) would undoubtedly score a 0.

To us, this is counterintuitive; the guineafowl tracks in poppy seeds may lack morphological detail at the surface, but not a single grain has moved between the end of the track forming event, and their capture through photogrammetry. It seems absurd then to call these fresh tracks 'poorly preserved' (Falkingham & Gatesy 2020). Nevertheless, other authors (e.g. Marchetti *et al.* 2019) have continued to make the case that only 'well-preserved' tracks, those that retain clear morphological features, should be used as a basis for ichnotaxonomy. If this is the case, then ichnotaxonomy ceases to be a means of communicating track morphology, and is instead given some implied biological meaning. In some ways, this is more closely aligned with Hitchcock's original aim of naming the trackmakers, than it is with the more descriptive, ethological approach of invertebrate ichnotaxonomy (Minter *et al.* 2007).

The semantics of the word 'preservation' may seem tangential to our discussion about diversity and formation so far but, as we have seen, the tracks that contain the most information about motion often do not look like the feet that made them. It is imperative that we do not as a field ignore such tracks simply because they are not 'elite' enough to identify the shape of the scales under the toes. It is also important that we acknowledge the diversity among tracks that does not stem from a diversity of trackmaker foot anatomies. We advocate using the word 'preservation' to denote variations and modifications occurring only *after* the track has formed (Gatesy & Falkingham 2017; Falkingham & Gatesy 2020; Lallensack *et al.* 2025) when all energy imparted by movement of the foot has ceased to move sediment particles.

RECOVERING MOTION

Now that we understand the formational processes of the track, and that deep messy tracks are not second-class, 'poorly-preserved', specimens, we can focus on what these kinds of tracks can reveal about their trackmakers. Specifically, the deeper a foot sinks, the more motion contributes to the final track morphology. In principle, this means more motion can be recovered from such a track than for a shallow print.

We have previously demonstrated a workflow for reconstructing foot motions and basic anatomy from penetrative tracks, using the fossils to generate 'hypotheses of motion', and then subsequently testing those hypotheses with simulation (Falkingham *et al.* 2020a). The process is as follows: we digitize the surfaces of the fossil track and reconstruct the exposed parts of the track volume relative to each other in 3D. At each exposed surface (the top and bottom of individual slabs), we mark analogous points (e.g. digit tips and the hypex), and then connect them in 3D space providing 3D trajectories along which parts of the foot are likely to have moved. We can then animate the foot such that all of its parts follow their respective trajectories. Note that at this stage, there is no temporal component, whether the foot took half a second or three seconds cannot be directly ascertained. Given the size of the trackmaker for this specimen is similar to the guineafowl we used in our earlier experiments, we apply a similar stance period as a starting point.

Reconstructing the basic proportions of the foot is not trivial, because no one surface is a 'print' of the foot (Fig. 10). Measuring digit lengths directly from any of the surfaces does not yield a 'foot-like' anatomy, as we previously showed with our guineafowl (Falkingham & Gatesy 2014). Instead, we must measure in three dimensions; using the reconstructed trajectories, we find the maximum distance between the hypex and the toe-tip trajectories, which gives us a minimum length the toes must be (if the toes are shorter than this, they cannot reach from the hypex to the tip).

The reconstructed motions are first verified visually against the fossil, animating the foot in the same 3D environment as the digitized tracks, to ensure that the motion passes through the points we expect it to. At this point, we have what we refer to as a 'hypothesis of motion'.

To test our hypothesized motion, we use the animated foot as an indenter in a discrete element simulation. Initial parameters for the substrate are a 'best guess' based on the morphology of the tracks, though as noted earlier sub-surface tracks appear to be quite robust to changes in substrate parameters. If our simulated tracks fail to match the morphology of the fossils, we can reject our hypothesis of motion. If our simulations produce comparable morphologies, we can consider our reconstructed foot motion to be supported.

Our application of this method has so far been focused on a single track volume from Hitchcock's collections at the Beneski Museum, comprised of four slabs (Falkingham *et al.* 2020a, 2020b) with the individual specimen numbers ACM-ICH 31/57, 31/58, 31/59, and 31/51 (Fig. 12A). For that reconstruction, we used an extremely simplified foot. Each digit was represented by a single smooth, rigid cylinder, not unlike our cylinder simulations above. The metatarsals were also represented by a single rigid cylinder. Despite this oversimplification, the simulated tracks matched the fossils in their morphology, providing support for our hypothesis of motion.

However, the simplification raises questions: Would jointed toes behaving more realistically change the morphology of the tracks? Would pointed claws, expanded digital pads, and a more realistic skin texture affect the way in which sediment particles are drawn down around the foot? To explore these questions, we created a more complex, realistic foot and repeated the simulation.

INCREASING COMPLEXITY OF MOTION & ANATOMY

Adding phalangeal joints

Building on our previous model, we took a CT scan of a guineafowl foot and digitally deformed it to match the size and proportions of the dinosaur foot, as determined from the fossil slabs (Fig. 12). This new foot mesh was divided into segments based on the position of the phalangeal joints in the guineafowl. Each segment was capped with a rounded end that overlapped the rounded end of the next segment, so that as a given phalangeal segment rotated, the mesh remained a closed system (i.e. particles were prevented from entering the foot between segments). In order to keep the simulation manageable, the polygon count, or complexity, of the foot mesh had to remain low, and so while individual scales were not present on the mesh, it still had a roughness to it that was lacking in the smoother cylinder-based foot.

To animate the new jointed foot, we maintained positions of digit tips but added a curvature to the toes. Individual joint motions are not necessarily apparent from the four parts of the fossil track, only digit tips, hypex and exit. As such, the curvature of the digits was subjective, but grounded in our many x-ray observations of guineafowl feet in substrates (Turner *et al.* 2020).

In addition to the upper and lower surfaces of the track slabs, which were previously digitized through photogrammetry, we also used µCT data to more fully map toe paths between exposed surfaces, within slabs. The four slabs were scanned at the University of Texas High-Resolution X-ray CT Facility in Austin, Texas, USA. For each slab, the centres of the nested-V shapes, where the toes had passed, were manually segmented in slices oriented front-to-back and top-down. This tracing was

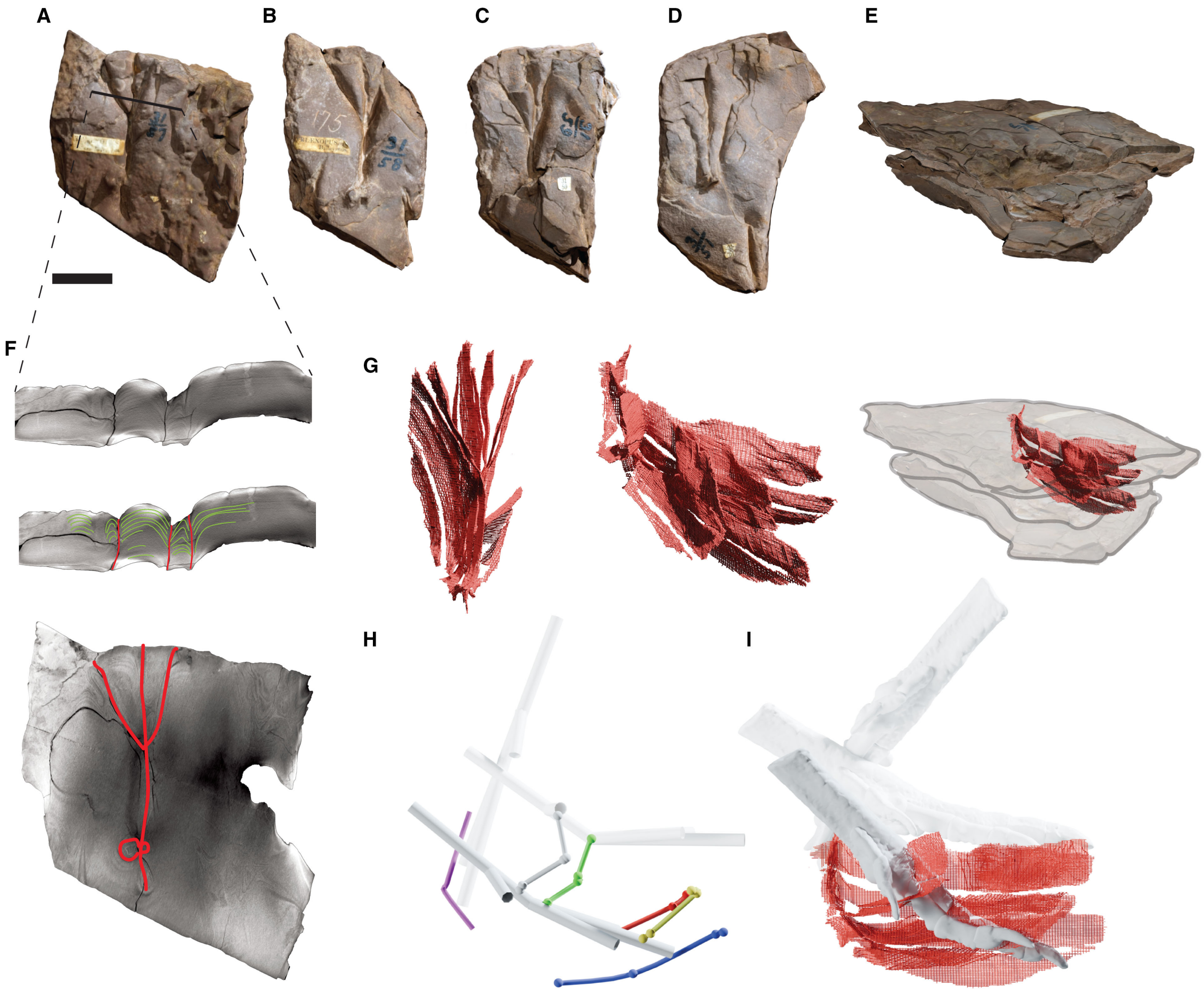

FIG. 12. Track comprised of specimens ACH-ICH 31/57, 31/58, 31/59 and 31/51, and reconstructed motions. A–D, presented in top-down view for each surface; E, the stacked collection; scale bar represents 5 cm. F, CT slices in transverse and planar orientation, with the centre of the nested Vs highlighted in red. G, the 3D structure resulting from transverse and planar tracings at regular spacing, in isolation and in the context of the track volume. H, our original cylinder foot, with motion prescribed by points on fossil surfaces connected by straight lines. I, our new jointed foot with flexible toes, animated using the 3D lattice.

done at regular intervals, rather than for every slice, resulting in a three-dimensional lattice that could be visualized in the same 3D space as the surface scans and simulations (Novotny *et al*. 2019) (Fig. 12F, G).

Once again, we found a good match between morphology of the fossil track slabs, and of the simulated track volume, exposed at equivalent positions, though with some notable differences this time (Fig. 13). The track at the sediment–air interface was quite different to the uppermost surface of the fossil, presenting a much smaller interdigital angle, and a greater anterior offset to digit II. This is attributed to the collapse of sediment at the surface, which is not constrained by particles above. We previously posited that the fossil track does not necessarily retain the original tracking surface, and that what was collected is probably missing an upper portion that may or may not have ever been preserved. It is therefore unsurprising that the simulation and the fossil differ at the very surface.

Sub-surface layers exposed in the simulation do tend to have a deeper bowl-like form than the surfaces of the fossil track, or the earlier cylinder-based simulation, and a more apparent displacement rim to the rear of the track, though the overall track morphology still matches the fossil surfaces and CT-derived lattice. That each simulated surface has this deep impression is attributed to the thicker digits of our foot model, which when adducted create a larger effective surface area moving down and backwards through the particles. This is exacerbated by our relatively large particle size.

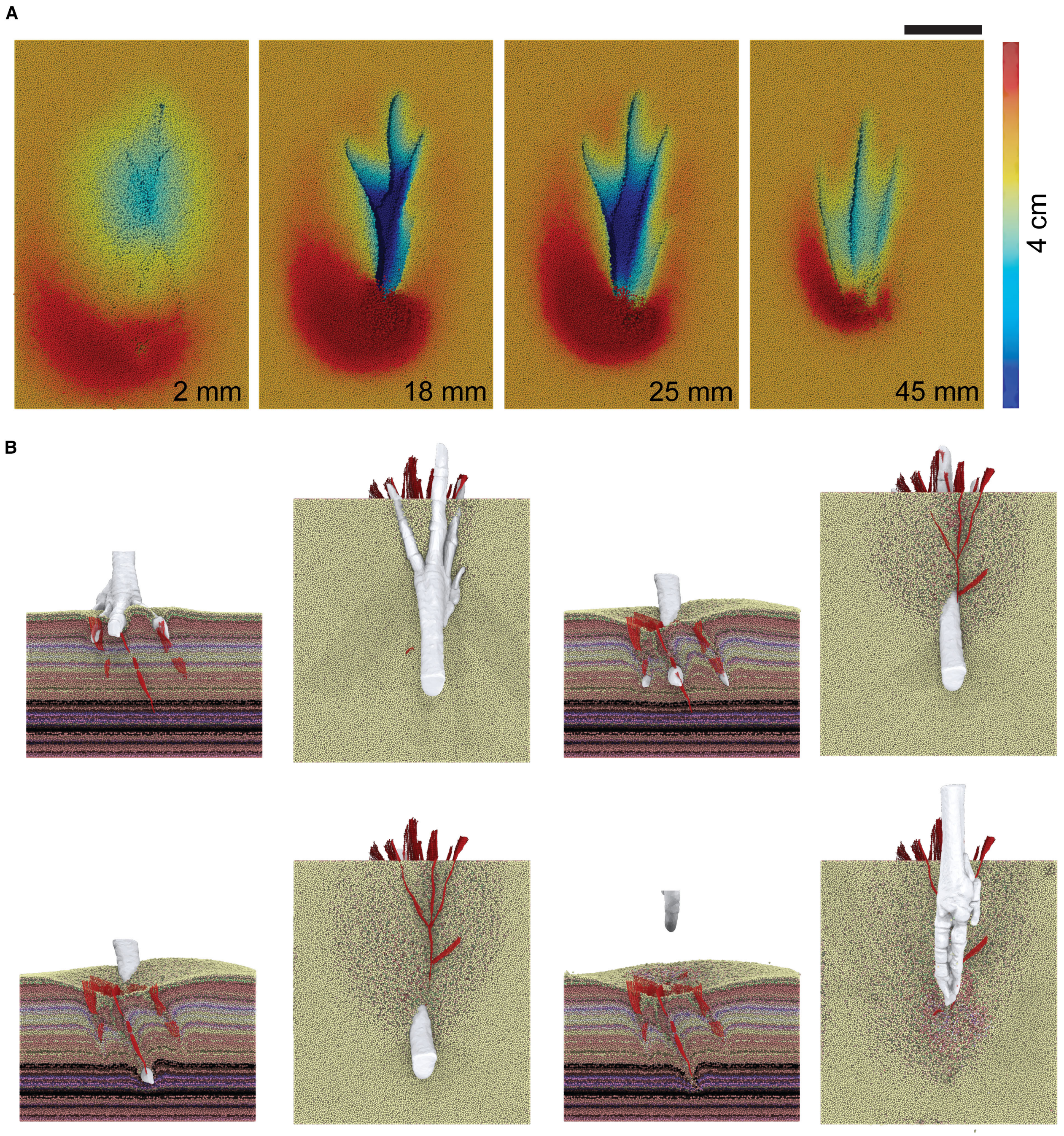

FIG. 13. Simulated track using a jointed foot. A, surfaces from within the simulated track volume corresponding to the position of upper surfaces of slabs comprising the fossil track volume (Fig. 12A–D); colour mapped according to relative height, red to blue is 4 cm, black scale bar is 5 cm; whilst track morphology is generally similar to the fossil, a major difference arises in how much sediment is scoured from within the track, and pushed backwards into a posterior displacement rim; this is attributed to the size of particles and the difficulty with which they can pass between the tightly adducted toes. B, a time series of track formation exposed as a transverse slice across the three digit traces near the front of the track; the 3D lattice is incorporated into the same world space and shows a good match with the simulated nested-Vs, though this match is better at depth, where the digit tips are further apart and particles can pass between toes.

The particles of our simulation are <1 mm in diameter and already push the limits of what is feasible to simulate and subsequently visualize, at this scale. Whilst they can behave at a macro level as a flowable substrate akin to mud, at the micro level they lack real-world complexities such as inter-particle fluids and pore pressures, and are too large to pass through small gaps between digits in the same way a fine mud can. Consequently, as the foot moves backwards with toes together, particles fill in from above and in front, rather than flowing around and between the toes. This can be seen in cross section (Fig. 13B), where the toes follow the paths of our CT lattice structure, as do the initial deformations of our simulated sediment. However, as the foot penetrates the upper layers, the gap between digits II and III restricts particle flow. To fill the void left behind, particles spill over from between digits III and IV, which are spread wider, and the result is that the nested-V shapes are offset from the path of the digits. At deeper levels, the deformation of our simulation more closely matches the lattice structure and the fossil track surfaces. That our simulated tracks differ from the fossils in these upper layers is encouraging evidence that our simulations are not 'doomed to succeed' in all cases, but the matching morphology at depth lends confidence to our broader hypothesis of motion.

CONCLUSION

We have discussed the formation of dinosaur tracks, from a theoretical viewpoint, and with examples from those collected by Edward Hitchcock over 150 years ago. By studying these historically and scientifically important tracks, we have shown that track formation mechanisms can be complex, involving penetration of the foot through the surface and deep into the sediment. Long held views about track formation, such as transmission of deformation over substantial depths, do not stand up to scrutiny when applied to a mechanistic, granular perspective of the foot–sediment interaction. The incorporation of significant foot motion into the track forming process is a major source of diversity among the smaller tracks of the Connecticut Valley, and probably elsewhere (Gatesy & Falkingham 2020). Deep tracks, incorporating considerable motion from the foot and other limb elements, do not look like the feet that made them. But footprints are not feet (Gatesy & Falkingham 2017), they are a record of motion as much as, if not more than, they are of anatomy.

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Author contributions. PLF and SMG carried out all research and writing equally. PLF coordinated the drafting and editing of the manuscript.

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REFERENCES

Allen, J. R. L. 1989. Fossil vertebrate tracks and indenter mechanics. *Journal of the Geological Society*, **146**, 600–602.

Allen, J. R. L. 1997. Subfossil mammalian tracks (Flandrian) in the Severn Estuary, S. W. Britain: mechanics of formation, preservation and distribution. *Philosophical Transactions of the Royal Society B*, **352**, 481–518.

Belvedere, M. and Farlow, J. O. 2016. A numerical scale for quantifying the quality of preservation of vertebrate tracks. *In* Falkingham, P. L., Marty, D. and Richter, A. (eds) *Dinosaur tracks the next steps*. Indiana University Press.

Brainerd, E. L., Baier, D. B., Gatesy, S. M., Hedrick, T. L., Metzger, K. A., Gilbert, S. L. and Crisco, J. J. 2010. X-ray reconstruction of moving morphology (XROMM): precision, accuracy and applications in comparative biomechanics research. *Journal of Experimental Zoology. Part A, Ecological Genetics and Physiology*, **313**, 262–279.

Campos-Soto, S., Tessier, B., Mouazé, D., Benito, M. I., Quijada, I. E. and Suarez-Gonzalez, P. 2025. Formation and preservation of vertebrate tracks in semi-liquid sediments: insights from tidal flats and laboratory experiments. *Sedimentology*, **72**, 5–33.

Cobos, A., Gasco, F., Royo-Torres, R., Lockley, M. G. and Alcala, L. 2016. Dinosaur tracks as 'four-dimensional phenomena' reveal how different species moved. 245–255. *In* Falkingham, P. L., Marty, D. and Richter, A. (eds) *Dinosaur tracks: The next steps*. Indiana University Press.

Falkingham, P. L. 2012. Acquisition of high resolution three-dimensional models using free, open-source, photogrammetric software. *Palaeontologia Electronica*, **15** (1), 1T.

Falkingham, P. L. 2014. Interpreting ecology and behaviour from the vertebrate fossil track record. *Journal of Zoology*, **292**, 222–228.

Falkingham, P. L. and Gatesy, S. M. 2014. The birth of a dinosaur footprint: subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. *Proceedings of the National Academy of Sciences*, **111**, 18279–18284.

Falkingham, P. L. and Gatesy, S. M. 2020. Discussion: Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present by Lorenzo Marchetti et al. *Earth-Science Reviews*, **208**, 103320.

Falkingham, P. L., Bates, K. T., Margetts, L. and Manning, P. L. 2011. 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**, 140225.

Falkingham, P. L., Bates, K. T., Avanzini, M., Bennett, M., Bordy, E. M., Breithaupt, B. H., Castanera, D., Citton, P., Díaz-Martínez, I., Farlow, J. O., Fiorillo, A. R., Gatesy, S. M., Getty, P., Hatala, K. G., Hornung, J. J., Hyatt, J. A., Klein, H., Lallensack, J. N., Martin, A. J., Marty, D., Matthews, N. A., Meyer, C. A., Milàn, J., Minter, N. J., Razzolini, N. L., Romilio, A., Salisbury, S. W., Sciscio, L., Tanaka, I., Wiseman, A. L. A., Xing, L. D. and Belvedere, M. 2018. A standard protocol for documenting modern and fossil ichnological data. *Palaeontology*, **61**, 469–480.

Falkingham, P. L., Turner, M. L. and Gatesy, S. M. 2020a. Constructing and testing hypotheses of dinosaur foot motions from fossil tracks, using digitization and simulation. *Palaeontology*, **63**, 865–880.

Falkingham, P. L., Turner, M. and Gatesy, S. 2020b. Supplemental data to Falkingham et al. 'Constructing and testing hypotheses of dinosaur foot motions from fossil tracks, using digitization and simulation' [dataset]. Figshare. https://doi.org/10.6084/m9.figshare.12251270

Farlow, J. O. 2018. *Noah's ravens: Interpreting the makers of tridactyl dinosaur footprints*. Indiana University Press.

Farlow, J. O., Holtz, T. R. Jr, Worthy, T. H. and Chapman, R. E. 2013. Feet of the fierce (and not so fierce): pedal proportions in large theropods, other non-avian dinosaurs, and large ground birds. 88–132. *In* Parrish, J. M., Molnar, R. E., Currie, P. J. and Koppelhus, E. B. (eds) *Tyrannosaurid paleobiology*. Indiana University Press.

Fornos, J. J., Bromley, R. G., Clemmensen, L. B. and Rodriguez-Perea, A. 2002. Tracks and trackways of *Myotragus balearicus* Bate (Artiodactyla, Caprinae) in Pleistocene aeolianites from Mallorca (Balearic Islands, Western Mediterranean). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **180**, 277–313.

Gatesy, S. M. 2001. Skin impressions of Triassic theropods as records of foot movement. *Bulletin of the Museum of Comparative Zoology*, **156**, 137–149.

Gatesy, S. M. 2003. Direct and indirect track features: what sediment did a dinosaur touch? *Ichnos*, **10**, 91–98.

Gatesy, S. M. and Ellis, R. G. 2016. Beyond surfaces: a particle-based perspective on track formation. 82–91. *In* Falkingham, P. L., Marty, D. and Richter, A. (eds) *Dinosaur tracks: The next steps*. Indiana University Press.

Gatesy, S. M. and Falkingham, P. L. 2017. Neither bones nor feet: track morphological variation and 'preservation quality'. *Journal of Vertebrate Paleontology*, **37**, e1314298.

Gatesy, S. M. and Falkingham, P. L. 2020. Hitchcock's Leptodactyli, penetrative tracks, and dinosaur footprint diversity. *Journal of Vertebrate Paleontology*, **40**, e1781142.

Gatesy, S. M., Middleton, K. M., Jenkins, F. A. and Shubin, N. H. 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature*, **399**, 141–144.

Gatesy, S. M., Baier, D. B., Jenkins, F. A. and Dial, K. P. 2010. Scientific rotoscoping: a morphology-based method of 3-D motion analysis and visualization. *Journal of Experimental Zoology. Part A, Ecological Genetics and Physiology*, **313**, 244–261.

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

Hatala, K. G., Gatesy, S. M. and Falkingham, P. L. 2021. Integration of biplanar X-ray, three-dimensional animation and particle simulation reveals details of human 'track ontogeny'. *Interface Focus*, **11**, 20200075.

Haubold, H. 1971. *Ichnia amphibiorum et reptiliorum fossilium. Handbuch Der Paläoherpetologie. Part 18*. G. Fischer, Stuttgart.

Hitchcock, E. 1836. Ornithichnology – description of the foot marks of birds (Ornithichnites) on New Red Sandstone in Massachusetts. *American Journal of Science*, **29**, 307–340.

Hitchcock, E. 1841. *Final report on the geology of Massachusetts*. Adams & J. H. Butler, Amherst & Northampton.

Hitchcock, E. 1848. An attempt to discriminate and describe the animals that made the fossil footmarks of the United States, and especially of New England. *Memoirs of the American Academy of Arts and Science*, **3**, 1–256.

Hitchcock, E. 1858. *Ichnology of New England: A report on the sandstone of the Connecticut Valley, especially its fossil footmarks*. William White, Boston.

Hitchcock, E. 1865. *Supplement to the ichnology of New England*. Commonwealth of Massachusetts, 96 pp.

Huerta, P., Fernández-Baldor, F. T., Farlow, J. O. and Montero, D. 2012. Exceptional preservation processes of 3D dinosaur footprint casts in Costalomo (Lower Cretaceous, Cameros Basin, Spain). *Terra Nova*, **24**, 136–141.

Jackson, S. J., Whyte, M. A. and Romano, M. 2009. Laboratory-controlled simulations of dinosaur footprints in sand: a key to understanding vertebrate track formation and preservation. *Palaios*, **24**, 222–238.

Jackson, S. J., Whyte, M. A. and Romano, M. 2010. Range of experimental dinosaur (*Hypsilophodon foxii*) footprints due to variation in sand consistency: how wet was the track? *Ichnos*, **17**, 197–214.

Kloss, C., Goniva, C. and The Minerals, Metals & Materials Society (TMS). 2011. LIGGGHTS – Open source discrete element simulations of granular materials based on LAMMPS. 781–788. *In Supplemental proceedings: Materials fabrication, properties, characterization, and modeling, Vol. 2*. Wiley & Sons.

Lallensack, J. N., Leonardi, G. and Falkingham, P. L. 2025. Glossary of fossil tetrapod tracks. *Palaeontologia Electronica*, **28** (1), a8.

Lockley, M. G. 1991. *Tracking dinosaurs*. Cambridge University Press.

Manning, P. L. 2004. A new approach to the analysis and interpretation of tracks: examples from the Dinosauria. *Geological Society, London, Special Publications*, **228**, 93–123.

Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L., Feola, S., Melcho, R.N. and Farlow, J.O. 2019. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the palaeozoic to the present. *Earth-Science Reviews*, **193**, 109–145. https://doi.org/10.1016/j.earscirev.2019.04.008

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.

Marty, D., Falkingham, P. L. and Richter, A. 2016. Dinosaur track terminology: a glossary of terms. 399–402. *In* Falkingham, P. L., Marty, D. and Richter, A. (eds) *Dinosaur tracks: The next steps*. Indiana University Press.

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. and Falkingham, P. L. 2016. Experimental and comparative ichnology. 15–27. *In* Falkingham, P. L., Marty, D. and Richter, A. (eds) *Dinosaur tracks: The next steps*. Indiana University Press.

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.

Milàn, J., Christiansen, P. and Mateus, O. 2005. A three-dimensionally preserved sauropod manus impression from the Upper Jurassic of Portugal: implications for sauropod manus shape and locomotor mechanics. *Kaupia*, **14**, 47–52.

Minter, N. J., Braddy, S. J. and Davis, R. B. 2007. Between a rock and a hard place: arthropod trackways and ichnotaxonomy. *Lethaia*, **40**, 365–375.

Nadon, G. C. 2001. The impact of sedimentology on vertebrate track studies. 395–407. *In* Tanke, D. and Carpenter, K. (eds) *Mesozoic vertebrate life*. Indiana University Press.

Novotny, J., Tveite, J., Turner, M. L., Gatesy, S., Drury, F., Falkingham, P. and Laidlaw, D. H. 2019. Developing virtual reality visualizations for unsteady flow analysis of dinosaur track formation using scientific sketching. *IEEE Transactions on Visualization and Computer Graphics*, **25**, 2145–2154.

Padian, K. and Olsen, P. E. 1984. The fossil trackway *Pteraichnus*: not pterosaurian, but crocodilian. *Journal of Paleontology*, **58**, 178–184.

Rainforth, E. 2005. Ichnotaxonomy of the fossil footprints of the Connecticut Valley (Early Jurassic, Newark Supergroup, Connecticut and Massachusetts). PhD thesis. Columbia University, 1316 pp.

Seilacher, A. 2007. *Trace fossil analysis*. Springer.

Thulborn, R. A. 1990. *Dinosaur tracks*. Chapman & Hall.

Turner, M. L., Falkingham, P. L. and Gatesy, S. M. 2020. It's in the loop: shared sub-surface foot kinematics in birds and other dinosaurs shed light on a new dimension of fossil track diversity. *Biology Letters*, **16**, 20200309.

Turner, M. L., Falkingham, P. L. and Gatesy, S. M. 2022. What is stance phase on deformable substrates? *Integrative and Comparative Biology*, **62**, 1357–1368.

Wright, J. L. 2004. Bird-like features of dinosaur footprints. 167–181. *In* Currie, P. J. (ed.) *Feathered dragons: Studies on the transition from dinosaurs to birds*. Indiana University Press.