Hitchcock's Leptodactyli, penetrative tracks, and dinosaur footprint diversity

STEPHEN M. GATESY[*,1] and PETER L. FALKINGHAM[2]

[1]Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912 U.S.A., stephen_gatesy@brown.edu;

[2]School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, U.K., p.l.falkingham@ljmu.ac.uk

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*Corresponding author

ABSTRACT—Starting with his first report on fossil footprints from the Connecticut Valley over 180 years ago, Edward Hitchcock described what he interpreted as a burgeoning ancient fauna founded on ever-increasing nominal track diversity. For three decades, Hitchcock made countless contributions to ichnology, but his inference of thin-toed animals (Leptodactyli) from thin-toed tracks is flawed by modern criteria. Leptodactylous tracks are now recognized as variants made by thick-toed feet penetrating into soft, collapsing substrates. Herein, we take a closer look at the creation of such penetrative tracks using computer simulations of particle flow. Classic specimens are used to demonstrate how different modes of surface presentation make penetrative tracks challenging to recognize and interpret. Evaluation of 266 specimens from 43 leptodactylous ichnotaxa reveals that ~90% are penetrative. We propose that a reliance on a single formation mechanism confounded Hitchcock's ability to reliably recognize different trackmakers. This is not an old problem applicable only to fossils collected long ago; domination of a transmission-based model continues to bias the field today. Most texts and many publications either omit collapsed penetrative tracks or fail to recognize them as a significant source of variation. Without proper regard for subsurface toe movement and sediment flow, inferences of foot shape from track shape can, as for Hitchcock, be led far astray. The misidentifcation and misunderstanding of penetrative tracks impact our conception of the diversity of life in the Early Jurassic, as well as in other ichnofaunas worldwide.

INTRODUCTION

Throughout the mid 19th century, Edward Hitchcock assembled a massive collection of Early Jurassic footprints from the Deerfield and Hartford basins of the Connecticut Valley. He described and interpreted these fossils in landmark publications (Hitchcock, 1836, 1841, 1848, 1858, 1865) that continue to be cited in modern works, and mark the beginning of vertebrate ichnology as an intellectual field. Morphological diversity among tracks was so high that Hitchcock named almost 100 ichnogenera and over 200 ichnospecies (Rainforth, 2005). This classic reference material, now the Hitchcock Ichnology Collection in the Beneski Museum of Natural History at Amherst College, is both scientifically and historically significant.

From the outset, Hitchcock (1836) separated tracks that he presumed to have been made by birds (*Ornithichnites*) into two divisions: Pachydactyli (thick-toed) and Leptodactyli (thin-toed) (Fig. 1). From 1845 onward he applied these group terms, as well as an ever-changing nomenclature, to the trackmakers rather than the tracks themselves (Hitchcock, 1845). Pachydactylous animals were thought to have left tracks that “show moulds or casts of toes wide in proportion to their length, with distinct claw and phalangeal impressions.” By contrast, “leptodactylous feet and tracks are narrow and rarely show phalanges or claws...” (Hitchcock, 1858:30). Understanding the mechanisms of pachydactylous and leptodactylous track formation is key to explaining the morphological diversity among tetrapod tracks in the Connecticut Valley and other ichnofaunas.

Researchers generally agree that pachydactylous prints formed in relatively firm ground (Deane in Silliman, 1843; Nadon and Issler, 1997; Gatesy et al., 1999; Rainforth, 2005; Milàn, 2006). Sediments receptive to thick-toed track formation were sufficiently deformable to retain an impression, but resistant enough to prevent the foot from sinking too deeply (Falkingham et al., 2011a, 2014). Specimens bearing detailed impressions (of digital pads, claws, and even skin) are our most reliable evidence of pedal structure. Given such anatomical fidelity, pachydactylous tracks have received the majority of attention from modern ichnologists for Connecticut Valley taxonomy, faunal analysis, biostratigraphy, and trackmaker identification (e.g. Olsen and Padian, 1986; Olsen et al., 1998; Olsen and Rainforth, 2003; Rainforth, 2003).

By contrast, the source of leptodactylous tracks has been more controversial. Throughout his 29-year publication span, Hitchcock maintained that most thin-toed tracks were created by thin-toed animals (Hitchcock, 1848). However as early as 1844, doubts about this interpretation were being raised (Deane, 1844; Marsh, 1848). Deane offered an alternative: “If the foot was planted upon the stratum while yet too soft to retain its form… the distinctive marks of organization disappear, each toe being simply represented by a linear depression, that has sometimes been mistaken for the impress of a slender toe” (Deane, 1861:29). Rather than reflecting anatomical disparity, both pachydactylous and leptodactylous tracks might have been created by thick-toed feet.

Subsequent workers have dealt with thin-toed tracks in various ways. Hay (1902) and Haubold (1971, 1986) appear to have taken Hitchcock’s forms at face value. Lull noted that some tracks were “undoubtedly so altered by the nature of the sediment… that one cannot even visualize the form of the foot itself” (1953:146), yet included Hitchcock’s leptodactylous ichnospecies in his monographs (1915, 1953). More recent authors (Olsen, 2002; Rainforth, 2005), bolstered by experimental data (Gatesy et. al., 1999; Manning, 2004), have subscribed to Deane’s interpretation (1844, 1861). The majority of thin-toed tracks from the Connecticut Valley are now considered formational (among-step) and intravolumetric (among-depth) variants

(Gatesy and Falkingham, 2017) of thick-toed tetrapods. Most are considered to be so “dominated by substrate and kinematic factors” (Rainforth, 2005:290) as to preclude inference of all but the most basic pedal features. Yet leptodactylous tracks offer a unique source of functional data, which inform and constrain reconstructions of pedal kinematics (Gatesy et al., 1999; Avanzini et al., 2012; Cobos et al., 2016).

Dismissing thin-toed tracks as poorly preserved (Gatesy and Falkingham, 2017) or as only relevant to locomotor analyses is imprudent. Herein, we address three reasons why thin-toed tracks deserve a closer look. First, the processes involved in their formation are not yet fully resolved. We describe the underlying mechanisms of pachydactylous and leptodactylous track formation based on computer simulations of sediment movement. Second, leptodactylous tracks can be deceptively challenging to recognize and interpret (Getty et al., 2017:29-36). We present examples from the Connecticut Valley for which surface topography can be misleading. Finally, leptodactylous track formation has been a major driver of morphological diversity (Rainforth, 2005; Gatesy et al., 1999; Gatesy and Falkingham, 2017). We survey the types and named examples of Hitchcock’s thin-toed taxa to assess their formation mechanism. By integrating leptodactylous tracks into a more complete picture of footprint variation, we hope to shed new light on Hitchcock’s seminal work, clear up misperceptions, and offset the pachydactylous bias that pervades the field.

METHODS

Simulating Track Formation Mechanisms

We carried out discrete element method (DEM) computer simulations to explore substrate displacement during track formation in cohesive substrates. The DEM (Kloss et al., 2012) represents media as individual particles that interact with one another, polygonal indenting objects, and gravity. Rather than simulate the actual movements of a live animal's entire foot (Falkingham and Gatesy, 2014), we modeled just one toe as a 13 mm diameter horizontal cylinder descending vertically at ~70 mm/s. By reducing variables to such an extent, we sought to visualize the fundamental reorganization of sediment caused by an indenting digit.

The simulated substrate was composed of 0.3 mm diameter particles and parameterized to behave at a gross level like a soft mud or fine sand. Particle properties were consistent throughout the volume, which acted as infinite along the cylinder axis through use of periodic boundaries, and was sufficiently large in other dimensions to avoid edge effects. Simulations and particle trajectories were visualized as transverse slices using Ovito (http://ovito.org; Stukowski, 2010). Particles were colored based on initial starting depth, enabling visualization of packets analogous to sedimentary layers or laminae.

We compared our deep simulation results to several actual cross sections. A Connecticut Valley specimen from the Yale Peabody Museum of Natural History (YPM VP.057950) was cut serially on a diamond rock saw, polished, coated with glycerin, and imaged on a flatbed scanner. Colored laminae were accentuated by manipulating brightness/contrast in Adobe Photoshop (www.adobe.com). Comparison of our virtual laminar pattern was also made with published images of a drill core from the Portland Formation, Hartford, Connecticut showing what has been interpreted as leptodacylous tracks in cross section (Olsen, 2002). Finally, the surface edges and internal laminar boundaries visible on a naturally fractured section through one multi-slab specimen (ACM-ICH 41/4) were traced on a digital photograph in Photoshop.

Specimens, Photogrammetry, and Ichnotaxonomic Surveys

We analyzed and created 3-D models of fossil tracks housed in the Hitchcock Ichnology Collection (HIC) within the Beneski Museum of Natural History, Amherst College (Amherst, Massachusetts, USA). Our wording for referring to specific slabs and tracks warrants explanation. Each catalogued specimen consists of one or more slabs designated as "ACM-ICH" followed by a fraction (e.g. 27/4), which denotes its previous location within the former Appleton Cabinet (Hitchcock 1865). The catalogue number has traditionally been used to identify the entire slab as well as to specify the tracks it bears. This poses no problems for a single slab bearing just one track, but many specimens, particularly larger slabs, display tracks attributed to multiple ichnotaxa. In such cases, tracks from different ichnospecies can share the same catalog number to signify their association. Similarly, the term 'specimen' is flexibly applied to either the entire catalogued object (slab or slabs) or to examples of ichnotaxa (track or tracks) on that object. Finally, slabs frequently bear leptodactylous tracks on both sides, which we refer to as the upper and lower surfaces. Hitchcock split some specimens into multiple slabs (sometimes with different catalogue numbers), which we designate as top, middle, and bottom. For example, in a three-slab specimen, the lower surface of the top slab is the counterpart to the upper surface of the middle slab.

We digitized entire slabs or select tracks using close-range photogrammetry (Falkingham, 2012; Matthews et al., 2016), processed with either Agisoft Photoscan (www.agisoft.com) or

COLMAP (Schönberger and Frahm, 2016; Schönberger et al., 2016) and OpenMVS (http://cdcseacave.github.io/openMVS/). Resulting 3D models were visualized and rendered in Autodesk Maya (www.autodesk.com), both as photo-textured models and with a custom heightmap shader (Falkingham et al., 2018). White transect contours were produced by projecting a horizontal line vertically down onto 3D models and rendering from an oblique perspective. Digital cross sections were created in Maya by splitting the mesh models along projected surface curves. Sedimentary laminae were traced manually in Adobe Photoshop.

Based on criteria from our simulations, physical cross-sections, and observed modes of presentation, we examined hundreds of slabs within the HIC in order to evaluate the formation mechanisms responsible for thin-toed tracks. Leptodactylous ichnotaxa were sampled in two ways based on their classic description (Hitchcock, 1858) and a recent revision (Rainforth, 2005). First, we inspected the type specimens of Rainforth's (2005) revised ichnospecies that we considered most similar to Hitchcock's from 1858.

To survey Hitchcock's assemblage more broadly, we tallied the track specimens he listed as "In the Cabinet" for what we deemed leptodactylous taxa in his 1858 monograph (Table 1). After removing inadvertent duplicates and adding three that were figured but not yet acquired (Rainforth, 2005), the total came to 312 specimens. We were able to confidently locate 266 (85.3%) of these within the HIC. About half of the missing 46 were excluded because we were unable to definitively identify the specified ichnotaxon on its designated slab(s). The remainder can be attributed to loss or destruction over the last 160 years, physical inaccessibility (e.g. back side of wall mount), renumbering issues, typographical errors, and Hitchcock's assignment of single tracks to more than one taxon.

RESULTS AND DISCUSSION

Track Formation Mechanisms

Pachydactylous Track Formation and Transmitted Undertracks—A shallow simulation (Fig. 2) demonstrates the 'traditional' formation mechanism found in most texts (e.g. Thulborn, 1990; Lockley, 1991). Vertical intrusion a small distance into the virtual substrate deforms the initially planar layering (Fig. 2A). The former air-sediment boundary, representing a pachydactylous 'true' track if the cylinder were removed, is thrown into a deep U-shape (Fig. 2B). The toe model directly contacts the floor of the potential true track, which conforms to its circular profile. Sloping walls ascend to elevated marginal ridges. The uppermost dark grey layer undergoes thinning directly below the cylinder, but thickens somewhat laterally.

Changes in layer curvature and thickness can be explained by tracing the trajectories of individual particles (Fig. 2C; Allen, 1997; Ellis and Gatesy, 2013; Falkingham and Gatesy, 2014; Gatesy and Ellis, 2016). We visualized true track development by following 21 superficial particles. Upon cylinder contact, those directly below the model are driven downward and begin to diverge. Growing gaps between particles are filled by particles enlisted from within the thinning dark grey layer. Such spreading and recruitment are required to increase surface area as the developing true track transitions from a flat sheet into a highly contoured shape (Gatesy, 2003; Gatesy and Ellis, 2016). Peripheral particles rise and move outward to contribute to the upper walls and the thickening marginal rim. Those not starting directly beneath the cylinder are lifted up and out, with little inter-particle spreading.

Light grey layer 1 undergoes deformation similar to, although less dramatic than, the true track surface (Fig 2B). Light-dark interfaces above and below layer 1 represent undertracks, which could be exposed by splitting at these interfacial boundaries. More specifically, we distinguish such surfaces as ‘transmitted undertracks’ (see Terminology). Unlike more superficial particles, the light grey particles never come in contact with the toe model. Rather, the cylinder affects layer 1 only indirectly (Gatesy, 2003) by transmitting forces through the intervening dark grey material. Displacement decreases with distance from the cylinder, as forces dissipate over an ever-larger volume (Allen, 1997; Manning, 2004; Falkingham et al., 2011b). In this case, particles starting more than about one cylinder diameter deep undergo only subtle movement (Fig. 2C). Light grey layer 2 exhibits just a very slight depression (Fig. 2B–C). Thus, in accordance with ichnological dogma, the true track records the greatest relief, while undertracks suffer a progressive reduction in topography and detail with depth.

Leptodactylous Track Formation and Penetrative Tracks—A simulation of the cylinder descending more deeply portrays leptodactylous track formation (Fig. 3A–D). Virtual substrate flows around and over the cylinder, collapsing to create a shallow surficial furrow atop a deep vertical seam. Unlike the circular cross-section of the cylinder, the furrow is V-shaped with a sharp median cleft. Moreover, the furrow’s cleft is created not by the nadir of the cylinder, which continues down almost five times deeper, but by the slumping track walls. The form of this surficial mark varies with consistency; non-cohesive and semi-fluid substrates collapse more readily (Allen, 1997; Loope, 2006; Milàn, 2006; Jackson et al., 2010; Falkingham and Gatesy, 2014; Gatesy and Falkingham, 2017).

As the cylinder approaches each light grey layer in turn, indirect transmission induces deformation (Fig. 3B, layer 2; Fig. 3C, layer 3; Fig. 3D, layer 6), just as in the pachydactylous mechanism (Fig. 2B). Layers 1-5 undergo further distension, being drawn down into teardrop profiles by the cylinder as their upper arms buckle inward (Fig. 3C, layer 2; Fig. 3D, layer 5). The upper arms of layers 1-4 subsequently pinch off completely (Fig. 3D), giving rise to a characteristic pattern of nested V's when viewed in cross-section (Gatesy et al., 1999; Olsen, 2002; Gatesy, 2003; Loope, 2006; Milàn and Bromley, 2008; Falkingham and Gatesy, 2014).

Trajectories of a dozen particles from within layer 2 (Fig. 3E–I) exemplify the displacements underlying such deformation structures (Fig. 3J). Traced particles move downward and outward as the cylinder descends (Fig. 3B, F). Soon after, however, the overlying trench collapses (Fig. 3C), sealing off the toe model from the air above. The eight most lateral particles follow loop-like trajectories as they pass the cylinder on either side and converge (Fig. 3F–G). A wedge-shaped group of previously overlying particles prevents these eight from reaching the midline, resulting in a V-configuration (Fig. 3G–I). The four particles starting closest to the midline are drawn progressively deeper. Three follow cusped trajectories as they bifurcate left or right, pass the cylinder's widest point (Fig. 3G–H), and then collapse in and down to extend the seam (Fig. 3H–I). When the simulation ends, the cylinder has yet to pass the particle pushed below the level of layer 6 (Fig. 3D, I, J). Similar particle motions have been documented in a real substrate (Fig. 3K) using biplanar X-rays (Ellis and Gatesy, 2013).

Leptodactylous data exhibit a more complex sequence of undertrack development than the pachydactylous simulation. The cylinder continuously produces transmitted undertracks as it nears each light/dark interface, but for the upper five layers such simple deformations are transient. Midline particles become trapped and drawn downward (Fig. 3G–I) to contribute to the seam. Being composed of discrete particles, layers (nor the surfaces between them) are not infinitely stretchable rubber sheets (Gatesy, 2003). Particles contributed from adjacent layers fill the enlarging gaps, which eventually expand to the point that the original layer can no longer be considered continuous (Gatesy, 2003; Gatesy and Ellis, 2016). Midline seam particles become so dispersed and intermingled that individual layers and layer interfaces are obliterated.

Given their distinctive formation mechanism and morphology, we refer to surfaces bearing these V-shaped furrows as ‘penetrative tracks’ (see Terminology). Rather than merely distorting layer boundaries, penetrative tracks are formed when layer boundaries are perforated. Although we propose different terms, transmitted undertracks and penetrative tracks form a continuum. At the end of the simulation (Fig. 3D), tracks bordering layers 6 and 7 are transmitted, those bordering layers 1-4 are penetrative, and those bordering layer 5 are in intermediate states. Transmitted undertracks form below the descending toe model like the bow wave of a ship. If the cylinder continues to sink, penetrative tracks are left above the descending toe model in a manner akin to that ship’s trailing wake.

Actual fossils share deformation patterns closely corresponding to our leptodactylous simulation. A cross section from YPM VP.057950 affords great detail (Fig. 4A). Distinctly colored laminae clearly reveal nested V’s and a midline seam left by toe entry. Sections through two leptodactylous furrows (Fig. 4B) in a drill core from the Portland Formation, Hartford, Connecticut (Olsen, 2002:fig. 33C) show a similar pattern.

Terminology

Here we discuss our choice of terms (‘transmitted undertracks’ and ‘penetrative tracks’) relative to existing alternatives. The word ‘undertrack’ has a complex history. Goldring and Seilacher (1971:424) introduced the term in their study of limulid ichnites for “duplicate imprints on lower surfaces.” The relatively sharp legs of horseshoe crabs pierce down into deeper sedimentary layers (Seilacher, 2007) and leave distinct tracks across a range of depths. Similarly, the cylinder in our leptodactylous track simulation (Fig. 3D) perforates superficial layers to directly interact with lower material. Unfortunately, ‘undertrack’ has contracted a second meaning as well. In vertebrate ichnology, the term generally implies the indirect transmission of deformation beneath the foot-sediment interface, as in our pachydactylous track simulation (Fig. 2B). To confuse matters further, undertracks have been used more or less synonymously with terms such as under-traces (Langston, 1986; Allen, 1989), transmitted prints/tracks (Smith, 1993; Farlow and Langston, 2006), ghost prints/tracks (Farlow and Langston, 2006), and transmitted reliefs (Thulborn, 2012), all of which are contrary to the original meaning (Goldring and Seilacher, 1971).

Given such ambiguity, we follow Seilacher (2007), who distinguished ‘compressive undertracks’ from ‘penetrative undertracks,’ but with slight variations. We prefer the modifier ‘transmitted’ over ‘compressive’ because of its use for displacement by sediment-sediment force transfer (Deane, 1861; Smith, 1993; Thulborn, 2012), and its lack of unnecessary connotations of compaction. We therefore suggest the term ‘transmitted undertracks’ to specify the well-established, indirect mechanism for vertebrate undertrack formation (Leonardi, 1987; Thulborn, 1990; Lockley, 1991; Allen, 1997). Our choice of ‘penetrative track’ (Getty et al., 2017:29-36) is adopted from Rainforth (2005). A penetrative track found below another penetrative track can be confidently identified as an undertrack, but perhaps not if found in isolation. Surficial penetrative tracks typically lack detailed pad, claw, and skin impressions, making them indistinguishable from interfacial penetrative undertracks (Figure 3D). In the absence of strong, consistent morphological criteria, we fall back on the more generic term.

Penetrative Track Presentation Modes

Based on our survey of the entire HIC, we recognize three basic ways in which penetrative tracks are exposed on the surfaces of fossil slabs. These ‘presentation modes’ affect the way penetrative tracks appear both in the field and in collections.

Fully Excavated Penetrative Tracks—If a penetrative track is cleared of infilling matrix, the V-shaped furrows are well exposed (Fig. 5A). Examples that have some digit entries prepared in this way include two tracks that record foot perforation through their slabs. ACM-ICH 32/23 consists of two slabs that sit below ACM-ICH 32/24. The middle slab of the three was broken longitudinally and suffered some damage (Fig. 5B), but this fracture appears to have allowed the furrow of digit III on its upper surface to have been almost entirely cleared during the repair. ACM-ICH 32/28 consists of two slabs. On the upper surface of the bottom slab (Fig. 5C), the furrows created by digits I and IV are fully prepared of overlying matrix.

When fully excavated, furrow walls converge to extremely thin slits (Fig. 5B–C, white transect lines) “as if the mud had been impressed by the blade of a knife” (Hitchcock 1848:140). Although such exposure follows an interfacial contour most faithfully (Fig. 5A), equating topography with toe shape leads to a flawed reconstruction of pedal anatomy. Hitchcock (1848, 1858) went so far as to invoke “keel-shaped” toes in several leptodacylous taxa. But as simulations (Fig. 3) and physical experiments (Gatesy et al., 1999; Manning, 2004; Milàn, 2006; Ellis and Gatesy, 2013; Falkingham and Gatesy, 2014) show, soft substrates collapse, either during the foot’s descent or soon after. Furrows faithfully record neither toe diameter nor integumentary details.

Incompletely Excavated Penetrative Tracks—The vast majority of penetrative tracks in the Beneski Museum collection are incompletely excavated. Separation of slabs, whether by natural weathering or during collection/preparation, causes overlying material to remain in the furrows of penetrative tracks. “For often it is difficult to cleave a specimen so perfectly, that the portions of the rock which fills the depression, shall all be got out …” (Hitchcock 1836:310-311). Cracks initiated between horizontal laminae are free to propagate relatively unimpeded until they encounter a downturned furrow. Rather than continuing to follow the ever-steepening laminar boundaries, fractures typically jump from one wall to the other, more parallel with the overall bedding plane. When viewed from above, the layers of broken overlying material resemble a valley floor (Fig. 6A). When laminae break at a consistent depth, the furrow walls and floor can combine into a U-shaped profile (Fig. 6B, 6D, white transect lines). The midline groove characteristic of penetration is typically obscured. Insidiously, the fill’s exposed edges can blend with the downturned walls to give the appearance of a continuous surface—a false bottom. Such a deceptive presentation mode can cause a penetrative track to resemble a transmitted undertrack. If such tracks are encountered without the aid of cross-sections or additional surfaces, the potential for misinterpretation is very high.

The amount of material remaining in a furrow after splitting is critical to the perception of a toe impression’s depth and width. Specimens in substrates with less distinct laminae tend to fail higher across the furrow, revealing a broader floor that converges on a thick-toed appearance. For example, ACM-ICH 18/2 (Fig. 6B) and its counterpart ACM-ICH 18/1 comprise the “Great Folio” (Hitchcock 1858)—the classic specimens brought to Hitchcock’s attention by Deane in 1835 (Hitchcock 1836). The pair of slabs bears clear evidence of “impressions having been made through them both” (Hitchcock 1865:53), yet the tracks as exposed appear broad and shallow. Extremely obdurate specimens can fail by shearing almost flush with the main track surface.

Tracks on three slabs (ACM-ICH 27/6, 27/7, and 27/8) figured in Hitchcock's original description (1836) exemplify this low profile presentation.

Penetrative tracks on lower surfaces appear as truncated crests and ridges—the convex counterparts of variably excavated furrows (Fig. 6C). A track on the lower surface of ACM-ICH 31/23 demonstrates a range of fracture depths (Fig. 6D). Material filling the metatarsal furrow fractured quite low, leaving a pronounced ridge. By contrast, two of the digital furrows broke very high, shearing almost flush with the bedding surface and appearing much wider than the third. Broken laminations parallel to the furrow axis are evident in some areas (Fig. 6B, D), as predicted by the flow-collapse-fracture sequence (Fig.6A).

Penetrative Tracks Above Transmitted Undertracks—Our leptodactylous simulation predicts that transmitted undertracks could be left behind in the deepest part of the volume (Fig. 3, borders of layers 6 and 7). Several specimens clearly exhibit the lower portion of this sequence, in which penetrative tracks lie above transmitted undertracks (Fig. 7A). For example, ACM-ICH 37/24 is composed of two slabs with penetrative tracks on the uppermost (Fig. 7B, D) and two internal surfaces. However, the lower surface of the bottom slab retains a pachydactylous track with impressions of digital pads and claws (Fig. 7C, E). Although rare for the entire foot (other complete examples include ACM-ICH 41/21 and 32/30), this phenomenon is not uncommon for individual digit impressions. As pointed out by Milàn and Bromley (2008), the juxtaposition of thick-toed tracks below collapsed furrows sets the traditional dogma on its head—morphological detail increasing with depth.

Recognizing Penetrative Tracks

Leptodactylous tracks have been, and continue to be, confusing (Getty et al., 2017:29-36). Workers not aware of the penetrative formation mechanism may assume that transmission-based deformation is responsible for all tracks. Even those familiar with deep sinking feet and collapse may miss clues to the penetrative nature of their specimens. To avoid misinterpretations, a first step is a healthy skepticism. Just as not all tracks are ‘true’ tracks, not all undertracks are transmitted.

A primary reason we focused this study on the HIC is the vast number and unrivaled accessibility of its penetrative tracks. Most of Hitchcock’s ichnotaxa are represented by multiple tracks on multiple specimens, often from multiple localities. Even more significantly, dozens of track volumes have been split into two or more stacked slabs, allowing penetrative track morphologies to be assessed on several surfaces in context. These multi-slab specimens, in turn, serve as critical references for isolated slabs sampled from unknown depths.

Penetrative tracks are easiest to identify when clearly revealed in cross-section. Laminated rocks deformed into a set of nested V’s with a median seam can confirm the formational flow of sediment around and over each toe (Fig. 4). Unfortunately, a straightforward determination is more commonly hampered by poor clarity and unresolved laminar boundaries. Natural breaks often transect digital furrows obliquely, and many exposed faces lack well-defined layering.

Context is also important, as the distribution of penetrative tracks should vary within the disturbed track volume. A slab collected from the middle depths should show associated leptodactylous tracks on both its upper and lower surfaces. Passage of the foot through a slab’s thickness leaves tracks exposed as partially filled furrows on top, complemented by tracks bearing truncated crests and ridges beneath (Fig. 6). However, complete perforation lapses high and low in the volume. A slab bracketing the originally exposed tracking surface (Fornós et al., 2002) only shows a penetrative track on its lower surface. Likewise, a slab encompassing deformation left by the foot's deepest descent only bears penetrative tracks on its upper surface. Therefore, absence of perforation does not exclude a penetrative origin.

If information from cross-sections or other surfaces is not available, as for a large slab *in situ*, the appearance of the track surface itself becomes more critical. The key features of penetrative tracks we focus on here are the slit-like furrows formed during toe entry. Detailed impressions of soft tissue pads, claws, and skin texture will normally (but not always) be obliterated by sediment flow. Furrow margins can be angular near the top of the volume, but elsewhere exhibit smoothly rounded contours (Figs. 3–6). Given that incomplete excavation (Fig. 6) is by far the most common presentation mode for Connecticut Valley penetrative tracks, close scrutiny of furrow morphology can offer essential clues. When cracks break across, rather than between, laminae, the slope and curvature often change sharply at the wall-floor transition (Fig. 6). Furrow floors, being made up of laminae broken in section, frequently exhibit a coarser texture than the walls and sometimes show a longitudinal 'grain' (Fig. 6B). Exposure of multiple laminae means that the floor's coloring can also differ from that of the surrounding rock (Fig. 6A). Such discontinuities offer evidence that a wedge of overlying material is occluding full exposure of a deeper digital furrow.

Implications for Connecticut Valley Track Diversity

In his 1858 monograph, Hitchcock described 89 species within 43 genera of Early Jurassic tetrapods based on their fossil tracks. Modern workers name tracks, not the animals that made them, but quantifying diversity continues as a common practice. Rainforth (2005) undertook a thorough examination of Connecticut Valley footprints and traced the convoluted history of Hitchcock's ichnotaxonomy. She considered 79 of his ichnospecies and 38 of his ichnogenera to be of tetrapod origin. Of these 79, we recognize 43 (54.4%) as definitively leptodactylous ichnospecies (Table 1), compared with 32 as pachydactylous and four as ambiguous. Relative percentages of the 38 ichnogenera are comparable: 21 leptodacylous (55.3%), 15 pachydactylous, and two mixed.

Upon inspection of the four holotypes, 34 lectotypes, one paralectotype, and four neotypes of Rainforth's (2005) leptodactylous ichnospecies that we considered most similar to Hitchcock's from 1858, we find that all 43 (100%) of these type specimens are penetrative tracks (Appendix 1). Somewhat less than half (20, 46.5%) record perforation of the foot through both upper and lower surfaces of at least one slab. Thus, these representative specimens support the direct relationship between a penetrative flow pattern and an overall leptodactylous morphology.

Of the 266 specimens listed by Hitchcock (1858) that we could evaluate, we judge 238 (89.5%) to be penetrative. Among the penetrative specimens, 112 (47.1%) are perforated, displaying associated penetrative tracks on both surfaces of a slab. Based on our sample, 30 of Hitchcock's 43 lists of specimens are exclusively penetrative, ranging from singletons for seven ichnospecies to a maximum of 33 for *Triaenopus leptodactylus* (Table 1). We rate 17 specimens (6.4%) as ambiguous. Some of these appear to be exposed at depths intermediate between transmitted and fully penetrative endpoints (Fig. 3). Others have suffered damage from preparation or breakage, show penetration of only distal toe tips, or are too small to easily assign a formation mechanism. Only eleven specimens (4.1%) from five ichnospecies are considered to be transmitted undertracks. A more detailed breakdown listing specimen numbers is given in Appendix 1.

Our aim here is not to advocate for the legitimacy of Hitchcock's ichnospecies or to question his assignment of certain specimens. Nor do we believe that naming taxa, while valuable, should overshadow or interfere with discerning the larger meaning of tracks. Rather, Hitchcock's 1858 ichnotaxonomy serves as a touchstone from which to assess the impact of penetrative tracks on his conception of ancient life in the Connecticut Valley. Every one of the 43 leptodactylous animal species is established on penetrative tracks. Therefore, if the thick-toed trackmakers responsible for thin-toed tracks are already represented by pachydactylous ichnotaxa, the biological diversity of his tetrapod species would be immediately halved. Hitchcock's hypothesis of thin-toed animals from familiar groups (birds, lizards, batrachians, chelonians) and unfamiliar composites (ornithoid lizards, ornithoid batrachians) is not supported by such 'phantom taxa' (Haubold, 1996; Haubold et al., 2005).

Hitchcock's Views on Track Formation

In his very first publication on fossil tracks, Hitchcock observed that specimens broken in cross section often revealed "successive layers of rock bent downward" (1836:310). Later he openly acknowledged the phenomena of deep sinking and collapse: "where the materials were very soft, it would seem as if the toes sank considerably into the mud, and… the edges of the impression thus made approached each other." (1848:144). From these and other statements, one might conclude that Hitchcock was fully aware of the mechanism of penetrative track formation shown in our leptodactylous simulation (Fig. 3). Yet his conviction about thin-toed trackmakers remained steadfast.

Reality of Thin-Toed Trackmakers—Hitchcock's acceptance of the Leptodactyli is foundational in his approach to Connecticut Valley diversity. In earlier treatments (Hitchcock

1836, 1841), differences between thick-toed and thin-toed tracks underlay his classification scheme, being the first character listed (Hitchcock 1848). A decade later he shifted away from using toe width as the basis for his monographic classification, but still asserted that, “this distinction is a natural and important one” (Hitchcock 1858:30). Hitchcock explicitly defended the existence of thin-toed animals based on three lines of reasoning (1848, 1858). He argued that if thick-toed feet created leptodactylous tracks, such tracks should: 1) be wider on deeper layers, 2) retain some indication of digital pads, and 3) not be found on the same layer as pachydactylous tracks.

First, we concur that the vast majority of leptodactylous specimens appear thin-toed, with no obvious widening on deeper exposed surfaces. Yet as Hitchcock was aware (1858), a pachydactylous track has occasionally been found beneath leptodactylous tracks as part of the same track volume (Fig. 7). Despite being predicted by our simulation (Fig. 3), such examples are likely uncommon because so few survived the disruption of foot withdrawal. Moreover, sampling probabilities do not favor their discovery. The relatively narrow zone of potential pachydactylous surfaces at the bottom (Fig. 3, layer 6) has a very low likelihood of being uncovered and, if found in isolation, might easily be misinterpreted as a shallow transmitted undertrack. Only when such volumes are fortuitously split to reveal both pachydactylous and leptodactylous tracks simultaneously is their true context revealed (Fig. 7).

Second, Hitchcock is correct that most leptodactylous tracks show no evidence of digital pad and claw marks. Yet penetrative tracks on ACM-ICH 31/42 and 31/30 exhibit pad and claw silhouettes (Fig. 8). We also found toe impressions showing evidence of digital pads in six other leptodactylous specimens (ACM-ICH 27/20, 31/36, 32/56, 34/33, 37/22, and 41/46). Exceptions aside, most relevant to our discussion is the issue of substrate flow. Hitchcock claimed that, “no sliding back of the mud, after a thick-toed animal trod upon it, would obliterate the distinct phalangeal protuberances" (1848:141). But based on our experience with both physical and simulated substrates (Gatesy et a., 1999; Ellis and Gatesy, 2013; Falkingham and Gatesy, 2014; Gatesy and Falkingham, 2017) as well as on the results of published indenter experiments (Manning, 2004; Jackson et al., 2009, 2010; White et al., 2017), we do not find the loss of pad detail at all surprising.

Third, Hitchcock argued that if pachydactylous animals made thin- and thick-toed tracks, both should not be found on the same slab. He listed five large specimens as evidence for their genuine distinction (1858). We confirmed the presence of mixed types on three of these (ACM-ICH 9/10, 10/6, and 25/1), as well as on other large slabs (ACM-ICH 2/1, 12/1, 19/9, 30/2, 51/17, and 63/9). His fourth (ACM-ICH 6/1) shows both types of tracks, but on distinct layers; we could not locate leptodactylous tracks on the fifth (ACM-ICH 22/1). Yet co-occurrence of tracks need not reflect the coexistence of animals with these specific pedal characteristics (Deane, 1847, 1861; Rainforth, 2005; Pérez-Lorente, 2015). Changes over time, particularly in the degree of water saturation, are known to affect track morphology on a single surface (e.g. Marty et al., 2009; Scott et al., 2010, 2012; Gatesy and Falkingham, 2017). Leptodactylous tracks might have been made on initially soft ground, which then progressively dried enough to yield pachydactylous tracks. Conversely, a substrate suitably firm for thick-toed tracks could have been rehydrated and become soft enough to be penetrated.

Hitchcock's Model—Hitchcock came tantalizingly close to understanding thin-toed tracks, but we are unable to find an explicit recognition of transmitted and penetrative deformation patterns in any of his publications. Rather, his discussions of this topic are unclear and sometimes contradictory. We suggest this ambiguity stems from his struggle to formulate a single formation mechanism to account for both track types. In his 1858 monograph, Hitchcock illustrated (pl. VI, fig. 1) a hypothetical transverse section (Fig. 9A) through a track showing, “how the layers are bent by the three front toes” (1858:33). Each layer is contiguous, with no sharp furrows or obvious collapse. Hitchcock never provided specific names for interfacial tracks, but a modern ichnologist may interpret his representation as a true track surface nestled amidst transmitted undertracks below and contoured layers of later-deposited sediment (overtracks) above. However, compared to our pachydactylous simulation (Fig. 2B), deformation extends across a very large vertical range. Some of this extra range can be attributed to overtrack layers, which we did not simulate, but we believe the vertical span was intentional and has significance.

Hitchcock’s 1858 section (Fig. 9A) is a redrawing of an earlier figure (Fig. 9B) from his Final Report on the Geology of Massachusetts (1841:fig. 104). In the older version, a greater number of thinner layers form sharper, narrower furrows in the middle depths. He stated, “the depression is communicated to several layers… Sometimes indeed, they make almost a right angle with the general surface” (1841:468). The nested configuration of such acutely deformed layers bears some resemblance to our leptodactylous simulation (Fig. 3D). However, Hitchcock’s figures lack the tell-tale median seams indicative of penetration and collapse, revealing his reliance on transmission alone. The broken edges of HIC slabs often reveal the general cross-sectional shape of digital entry furrows. One of the best penetrative examples are the four slabs of ACH-ICH 41/4, which are broken to expose two sets of deflected laminae (Fig. 9C). Slab boundaries and internal cracks imply the presence of nested V’s, but complete laminar details and seams (Fig. 4A–B) are not discernible. Thus, the precise organization of each furrow’s tapered convergence could easily have remained obscured. Given that thin-toed tracks featured so prominently in Hitchcock's 1841 Report, observations from such penetrative specimens may have strongly affected his perspective on all tracks.

We propose that Hitchcock's original 1841 illustration correctly characterized neither pachydactylous nor leptodactylous track formation. The result was a chimera—a non-existent hybrid never seen in any one fossil—that drew inspiration from the deformations he observed in both thin- and thick-toed tracks. Exactly how Hitchcock arrived at this single hypothesis remains speculation. Perhaps he quickly deduced the existence of two foot types from two track types, which were then reconciled by one mechanism. Alternatively, his perception of a common deformation pattern may have steered him toward two foot types as the most likely explanation for two track types. Regardless, Hitchcock became entrenched in this perspective from his first track publication to the end of his career. A century and a half later, we can now more accurately perceive substrate flow and its significance for producing pachydactylous and leptodactylous formational variants from a single foot type.

Long-Distance Transmission

Hitchcock's hypothetical sections (Fig. 9A–B) portray deformations duplicated across bedding planes spanning a wide range of depths. Given this conceptualization as an inter-nested set of Russian dolls, it is no surprise that Hitchcock was often uncertain about the exact "layer on which the impression was originally made" (Hitchcock, 1841:468). However, it is apparent that he believed toes could transmit toe-shaped depressions far below their point of deepest descent. Hitchcock is not alone in this opinion. To illustrate our point, we refer to one of the best-known fossils in the HIC. ACM-ICH 27/4, acquired by Hitchcock in 1853 from the estate of Dexter Marsh, consists of five split slabs (Fig. 10) that were attached by metal hinges and dramatically exhibited as what Hitchcock called the “Fossil Volume” (Hitchcock, 1858, 1865). The four upper and four lower inter-slab surfaces bear what appear to be pairs of shallow tracks. Hitchcock remarked that, “though so thick, the impressions are nearly alike on all the layers” (Hitchcock, 1858:33). If transmitted, undertracks maintaining such clearly-defined track morphology across such depths poses a puzzle.

Lockley (1991) followed Hitchcock (Fig. 10A) in describing a mechanism “analogous to writing on a sheet of paper... leaving colorless impressions on several sheets in a pad” (1991:28). Likewise, Manning (2004, 2008) interpreted Hitchcock’s “stony volumes” as stacked sets of transmitted undertracks created by a pressure bulb rather than deep sinking. Neither explained how toes not directly contacting deeper layers yielded distant tracks with sharp contours. Seilacher’s (2007) interpretation of ACM-ICH 27/4 (Fig. 10B) goes into greater detail: “impressions can be followed through successive bedding planes over a thickness that may exceed the diameter of a single footprint… the dinosaur foot did not pierce through all this thickness… but stamped identical copies from the top by bed-to-bed deformation” (2007:8). He then invoked a hypothetical “pressure prism” mechanism to prevent the dissipation of displacement with depth.

We find no support for the transmission of detailed undertracks long distances beneath the deepest penetration of the foot. Despite Seilacher’s conjecture about putative anisotropy, plastic sediments do not behave like an array of metal rods in a pin art toy. On a firm substrate, the same resistance to particle motion that keeps the foot from sinking also prevents deep transmission. Nearby layers are deformed to create undertracks, but the magnitudes of displacement drop off steeply. Softer substrates do not significantly improve transmission of deformation farther below the foot; particles that are easier to move merely allow the foot itself to sink deeper. There may be sedimentary scenarios that combine shallow sinking with deep, high fidelity transmission, but we see no evidence for these in the Connecticut Valley material.

Confusion surrounding ACM-ICH 27/4 arises from the fundamental misconception that its tracks are transmitted. The feet actually perforated down into the bottom slab (Marsh, 1848; Getty et al., 2017:29-36). Toe impressions, although relatively wide, are still leptodactylous. Their deceptively transmitted appearance stems from how layers have separated (Fig. 10D–G). Just as in our examples of incompletely excavated penetrative tracks (Fig. 6), split slabs fracture across downturned laminae (Fig. 10C, E), leaving a valley floor composed of overlying material within each digital furrow (Fig. 10D). These false bottoms blend with the furrow walls to masquerade as a continuous surface (Fig. 10F, G). In “stony volumes” with multiple slabs, this breakage pattern is repeated, thus creating the illusion of a nested set of similarly-shaped transmitted tracks. Deane (1861) accurately described this penetrative phenomenon, but seems to have been ignored by subsequent workers.

The feet responsible for ACM-ICH 27/4 followed relatively vertical trajectories into the substrate. In many other leptodactylous specimens the foot’s entry was more canted. Hitchcock’s illustrations accompanying this topic (1841, fig. 105 and 1858, pl. VI, fig. 2) show track silhouettes at the top and bottom of a volume of laminated substrate (Fig. 11A). Relatively thick specimens that may have inspired these figures include ACM-ICH 32/24 and 32/41. Tracks on the upper (Fig. 11B) and lower (Fig. 11C) surfaces of ACM-ICH 32/24 are noticeably offset. Our updated version of Hitchcock’s figure shows linked homologous landmarks inside our cropped photogrammetric model (Fig. 11D). Once such tracks are recognized as penetrative rather than transmitted, their morphology becomes manifest. The foot perforated entirely through a slab, leaving behind tracks of consistent clarity in its wake.

Penetrative Dinosaur Tracks in Space and Time

Penetrative tracks are not oddities restricted to just one locality. Although many specimens in the HIC are from Wethersfield, Connecticut, Lull's assertion that leptodactylous tracks were "found practically nowhere else" (Lull, 1915:91) is not supported. In fact, only 11 of the 43 type specimens designated by Rainforth (2005) are from Wethersfield. All the remainder are from Massachusetts: Turners Falls and Gill (26), Chicopee (4), Montague (1), and Northampton (1). Thus, Hitchcock found penetrative tracks widespread along the length of the Connecticut Valley.

Tracks attributed to dinosaurs that we deem penetrative have been described from throughout the Mesozoic and from all continents except Antarctica, including: the Triassic of northeastern USA (Bock, 1952) and Greenland (Gatesy et al., 1999); the Jurassic of northeastern (Olsen, 2002) and southwestern (Loope, 2006; Milner et al., 2006; Clark and Brett-Surman, 2008) USA, England (Romano and Whyte, 2003), Spain (Avanzini et al., 2012), Germany (Lallensack et al., 2015), Morocco (Boutakiout et al., 2006; Ishigaki and Lockley, 2010; Belvedere et al., 2011), and Madagascar (Wagensommer et al., 2012); Jurassic/Cretaceous of Spain (Pérez-Lorente, 2015); and the Cretaceous of Texas (Kuban, 1989; Farlow et al., 2012), Canada (McCrea et al., 2014), England (Shillito and Davies, 2019), Spain (Romero-Molina et al., 2003; Razzolini et al., 2014), Italy (Citton et al., 2015), Chile (Rubilar-Rogers et al., 2008), Mongolia (Ishigaki, 2010), China (Xing et al., 2013, 2018), Korea (Kim and Huh, 2010), and Australia (Martin et al., 2014). We are much less familiar with the track record from other tetrapods, but clear examples from the Pennsylvanian (Haubold et al., 2005), Permian (Haubold et al., 1995; Marchetti, 2018), and Triassic (Peabody, 1956) attest to the commonality of penetrative tracks.

The treatment of penetrative tracks varies widely among publications. Perhaps the best described area is La Rioja, Spain (Pérez-Lorente, 2015 and references therein), from which collapsed, ‘filiform’ toe and metatarsal marks have been documented from many sites. Yet more commonly, reports neither use the terms leptodactylous/penetrative nor recognize thin-toed tracks as deeply impressed. We are confident in our assessment of a penetrative formation mechanism in the majority of these examples, but for others we cannot be sure without seeing the original material. Nonetheless, it is likely that the true frequency of penetrative tracks is extremely under-reported.

Implications for Track Analysis

At the heart of this study are two fundamental issues for assessing track morphology: how was sediment displaced during a footstep, and how have these displacements been exposed as fossil surfaces? Our elucidation of penetrative tracks leads to several general observations. First, thin-toed tracks are not poorly preserved thick-toed tracks that have suffered damage or deformation. Leptodactylous tracks arose through their inception by a fundamentally different mechanism. Variation in substrate consistency induced disparities in sinking depth, altered sub-surface foot kinematics, and modified sediment flow. Thus, even a single individual could have produced multiple leptodactylous forms (Gatesy and Falkingham, 2017:fig. 2). Hitchcock’s 43 ichnospecies are not an accurate record of animal diversity, but rather a graphical embodiment of the one-to-many nature of the track formation process.

Second, our “footprints are not feet” dictum (Gatesy and Falkingham, 2017:7) is nowhere more applicable. One issue deserving caution is footprint depth, which is easily calculated from 3D models (Falkingham et al., 2018). The maximum depth of a leptodactylous furrow is misleading, as resealing of the collapsed surface severs any relationship between a track's local minimum and overall foot movement. Likewise, Hitchcock's assiduously reported digital lengths and angles need not reflect the geometry of the toes that made them (Deane, 1861; Falkingham and Gatesy, 2014; Gatesy and Falkingham, 2017). Sediment flow around and over the sinking foot is affected by interdigital interactions far more complex than our single cylinder simulations imply.

Third, we emphasize that ichnologists should avoid falling into the same trap as Hitchcock. Many specimens from the Connecticut Valley appear superficially bird-like (Figs. 1C, 5C, 6B). Mesozoic tridactyl tracks with thin toe impressions and large divarication angles may be avian (Belvedere et al., 2011; Falk et al., 2011; Martin et al., 2014; Xing et al., 2015; Buckley et al., 2016), but furrow lengths and inter-furrow angles are warped by sediment flow. To support the hypothesis of a thin-toed trackmaker based on thin-toed tracks, evidence against their penetrative formation is essential. Likewise, if penetrative tracks are recognized, the temptation to treat them as transmitted must be resisted. Researchers confronted with tetrapod tracks exposed on different layers have sought out those with minimal 'extramorphologic' influence (Peabody, 1948; Haubold et al., 1995, 2005). But in most cases, none of these penetrative tracks accurately represent pedal anatomy.

Fourth, differentiating among transmitted and penetrative formation mechanisms by explicit terminology could, if widely accepted, minimize misunderstandings. For example, Marchetti (2018) recently drew attention to large amphibian tracks exposed on multiple layers. He deemed these "the first unequivocal fossil evidence" of undertracks that are "better-preserved and diagnostic than the footprints on the actual trampled surface, which can be deformed and collapsed" (Marchetti, 2018:11). Identifying portions of these specimens as penetrative tracks, rather than as transmitted undertracks, immediately removes the motivating expectation of a reduction in quality with depth. Moreover, the allegedly novel relationship among tracks is quite common in the Connecticut Valley (Hitchcock, 1848, 1858; Marsh, 1848). Indeed, dozens of HIC specimens display associated penetrative tracks more distinctly on their lower than upper surfaces.

Finally, we hope that penetrative tracks can become fully integrated into a more complete perspective on footprint variation. Despite increased awareness over the last two decades, tracks not fitting a pachydactylous search image are likely overlooked in the field, deemed poorly preserved when found, and judged below the standard for publication. Conversely, we believe that penetrative tracks are routinely mistaken for transmitted undertracks when exposed via the incomplete excavation presentation mode (Figs. 6, 8, 10). Mapping, measuring, describing, naming, and attributing specimens based on such erroneous assumptions is flawed.

CONCLUSION

Dinosaurs walking through soft substrates sank to significant depths, often leaving behind collapsed furrows that have been mistaken for the tracks of thin-toed animals. Hitchcock's assessment of the Early Jurassic fauna of the Connecticut Valley was significantly inflated by such disparate leptodacylous specimens, which account for more than half of his nominal tetrapod diversity. Penetrative tracks can be difficult to distinguish from transmitted undertracks, particularly if entry furrows remain partially filled with overlying laminae. Perforated slabs and fossil volumes showing clearly defined tracks across significant depths are products of penetration, not long-distance transmission. Simulations and cut sections provide a clear visualization of sediment displacement unavailable to Hitchcock, perhaps explaining his invocation of a single, hybrid deformation pattern for all tracks. Although transmitted and penetrative undertracks represent two ends of a continuum, distinguishing between these two track formation mechanisms advances our understanding of the track making process. Recognition of penetrative tracks offers an alternative search image for workers in the field and collections, fosters the extraction of biological information inherent in such trace fossils, and should help reduce nomenclatural confusion.

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DATA ARCHIVING STATEMENT

3D models of tracks, plus input files for simulation data, will be uploaded to Figshare (or Dryad, if the journal prefers) upon acceptance.

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FIGURE CAPTIONS

FIGURE 1. Nineteenth century images of Early Jurassic tracks from the Connecticut Valley (Hitchcock, 1858). **A**, part and counterpart of a pachydactylous track (pl. LII, fig. 7). **B**, part and counterpart of a leptodactylous track (pl. LII, fig. 1). **C**, a sampling of thin-toed morphological diversity (pl. XIV, XX, XVII, and XV). Additional labels designate ichnotaxa figured later in this paper: *Triaenopus leptodactylous* (Figs. 6D, 8A), *Platypterna varica* (Fig. 10), *Platypterna deaniana* (Figs. 5B, 11), *Ornithopus gallinaceus* (Figs., 4A–B, 7), *Tridentipes elegans* (Fig. 6B), *Plectropterna minitans* (Fig. 5C). [planned for column width]

FIGURE 2. Cross-sectional view of pachydactylous track formation. **A**–**B**, two time steps from a computer simulation of a cylindrical toe model descending into a layered substrate. Light grey layers 1 and 2 reveal subsurface deformation. A ‘true’ track is created at the air-sediment boundary, with transmitted undertracks at layer interfaces beneath. Detailed transmission is limited to nearby layers. **C**, four time steps tracing the trajectories of black particles (shown 1.5X size for visibility). Particles directly beneath the cylinder are driven downward and apart to contribute to the floor and walls of the true track. More peripheral superficial particles move laterally and are uplifted into the marginal ridges on each side. Scale bar equals 1 cm. [planned for 2/3 page width]

FIGURE 3. Cross-sectional view of leptodactylous track formation. **A**–**D**, four time steps from a computer simulation of a cylindrical toe model descending into a layered substrate. Light grey layers 1-7 reveal subsurface deformation. **E**–**I**, five time steps tracing the trajectories of 12 black

particles from layer 2 (shown 3X size for visibility). Dotted line is the original air-sediment boundary. Particles move down and around the descending cylinder before collapsing inward, with midline particles being driven deepest. Trajectory cusps (arrows) mark passage of particles past the cylinder's widest point (asterisks). **J**, particles rendered with a random greyscale layering pattern show the continuous nature of the deformation. **K**, trajectories of actual beads displaced by a physical toe model (data from from Ellis and Gatesy, 2013; fig. 7.1 vertically offset to the same starting depth). Scale bars equal 2 cm. [planned for 2/3 page width]

FIGURE 4. Leptodactylous furrows in cross-section. A, cut section of YPM VP.057950 showing deflected laminae converging at a midline seam. **B**, leptodactylous penetrative tracks exposed within a drill core from the Portland Formation, Hartford, Connecticut (modified from Olsen, 2002: fig. 33C). Scale bars equal 5 cm. [planned for column width]

FIGURE 5. Well excavated penetrative tracks exhibit deep, sharp furrows with a V-shaped profile. **A**, oblique view of a simulated track section fully cleared of overlying layers. **B**–**C**, rendered models of ACM-ICH 32/23 and 32/28 shown with photo-textures (left), height maps (middle), and white transect lines in oblique close-up (right). Not all furrows are equally excavated. Height maps are inconsistently scaled so as to capture each specimen's full depth. Scale bars equal 3 cm in **B** and 5 cm in **C**. [planned for page width]

FIGURE 6. Incomplete excavation of penetrative undertracks reveals furrows with a U-shaped profile. **A**, two views of a simulated track section with material from overlying layers creating a 'false bottom'. **B**, rendered models of ACM-ICH 18/2 shown with photo-textures (left), height

maps (middle), and white transect lines in oblique close-up (right). Note the longitudinal ridges present in DIII. **C**, inverted section of simulated track showing the truncated profile characteristic of penetrative tracks on lower surfaces. **D**, rendered models of the lower surface of ACM-ICH 31/23 reveal tall crests left by the metatarsus and one toe, but the ridges of the other two toes are broken almost flush (close-up). Height maps are inconsistently scaled so as to capture each specimen's full depth. Scale bars equal 5 cm in **B** and 3 cm in **D**. [planned for page width]

FIGURE 7. Penetrative tracks above transmitted undertracks. **A**, deep section of a simulated track exposing a partially excavated furrow above and a transmitted undertrack beneath. **B**–**C**, rendered models of the uppermost and lowermost surfaces of ACM-ICH 37/24 shown with height maps. **D**–**E**. the transition in DIII from leptodactylous to pachydactylous is shown by the white transect lines in oblique close-up. Height maps are inconsistently scaled so as to capture each specimen's full depth. Scale bar equals 5 cm. [planned for column width]

FIGURE 8. Evidence of digital pads and claws in leptodactylous tracks. **A**, impression of digit III on ACM-ICH 31/42. **B**, impression of digit II on ACM-ICH 31/30. Entry furrows sometimes retain constrictions marking claw/pad (asterisks) and pad/pad (arrows) transitions. Scale bars equal 2 cm. [planned for column width]

FIGURE 9. Hitchcock's hypothetical cross-sections of layer deformation. **A**, figure 1 from Plate VI of his 1858 monograph. **B**, figure 104 from his 1841 Final Report. **C**, traced broken edge of of ACM-ICH 41/4 showing penetration of two toes through four slabs (1-4, * missing). Laminar

details, particularly seams, are difficult to discern. Scale bar equals 2 cm. [planned for column width]

FIGURE 10. The penetrative origin of ACM-ICH 27/4. **A**, Lockley‘s schematic based on a ‘pen and pad of paper’ mechanism (1991: fig. 3.3). **B**, Seilacher‘s hypothetical ‘pressure prisms” transmitting high-fidelity track below foot depth (2007: pl. 2). **C**, section of a simulated track split into three slabs. **D**, rendered model of ACM-ICH 27/4 shown with phototextures in digital cross-sections. **E**, our hypothesized pattern of nested DIII furrows. **F**, close-up photograph of an incompletely excavated furrow showing longitudinal ridges of broken laminae. **G**, oblique views of the posterior track on the upper surface of the third slab. Transmitted undertracks (dashed lines, left) cannot propagate toe contours over long distances. Repeated fracture of penetrative furrows (solid lines, right) accounts for this and other fossil volumes. Scale bars equal 2 cm. [planned for page width]

FIGURE 11. Oblique penetration through thick slabs. **A**, Hitchcock’s text-fig. 105 (1841) has been interpreted as representing transmitted undertracks. Penetrative tracks on the upper (**B**) and lower (**C**) surfaces of ACM-ICH 32/24 are offset, indicating diagonal entry. **D**, cropping the photogrammetric model of this slab reveals the 3-D relationship of these perforated surfaces. Scale bar equals 3 cm in **B**–**C** and 4 cm in **D**. [planned for 2/3 page width]

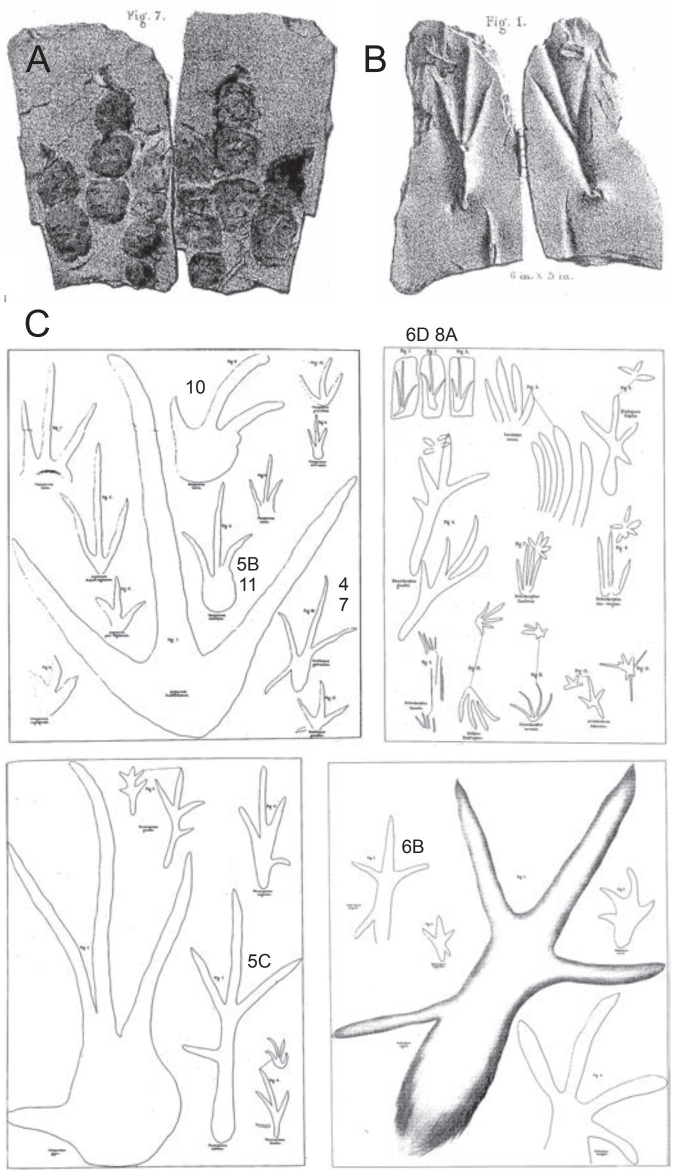
Fig. 7.
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Fig. 1.
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C
10
5B
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6D 8A
5C
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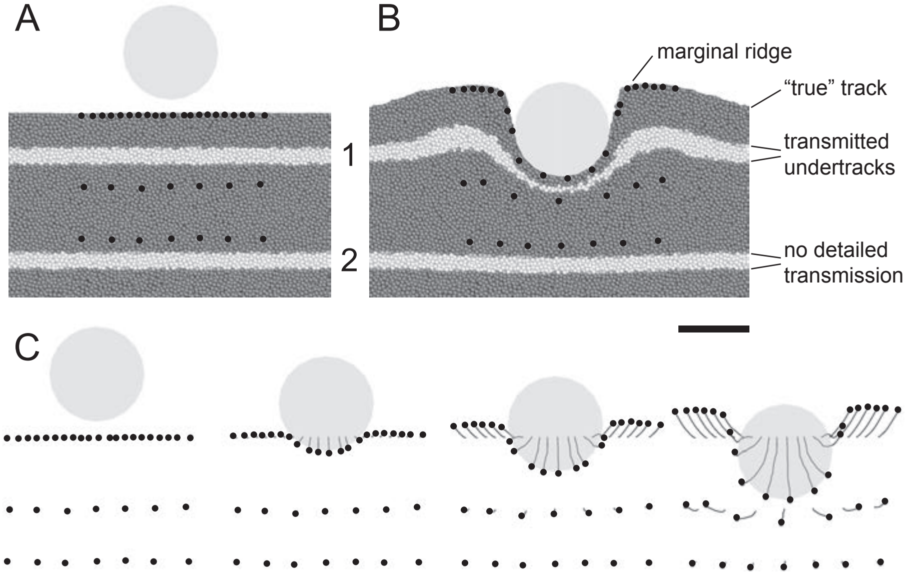

A
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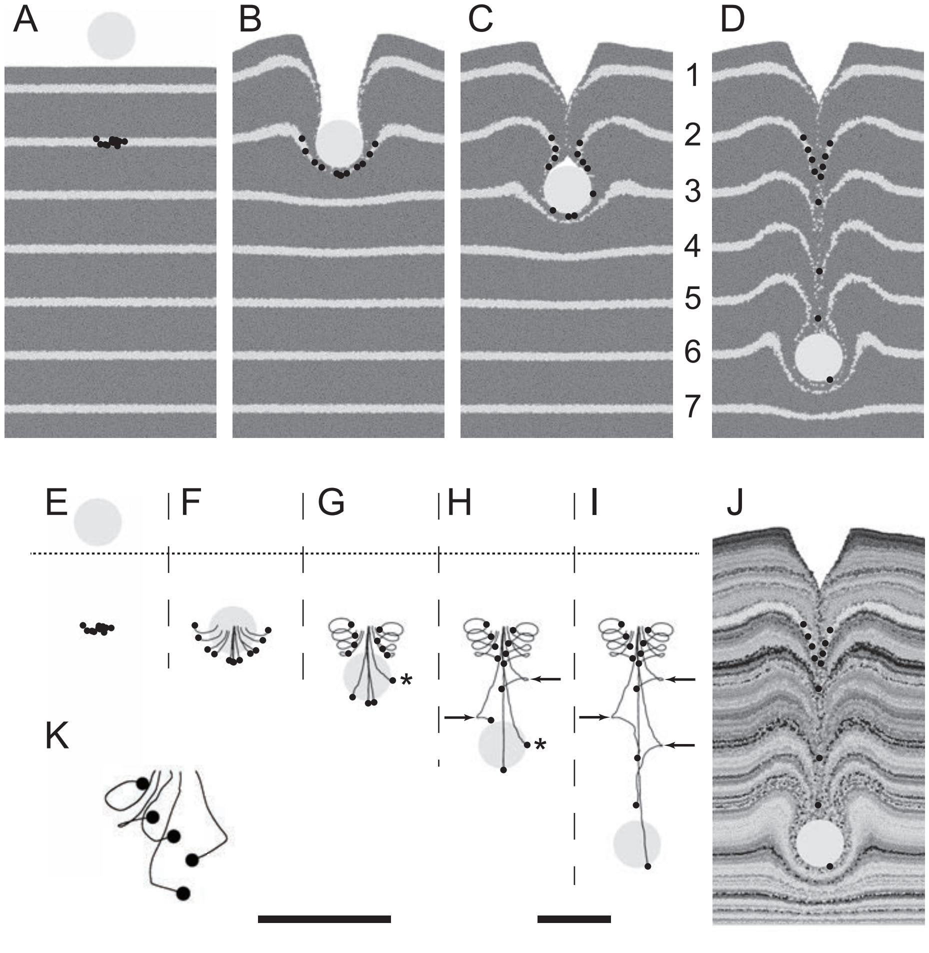
marginal ridge
"true" track
1
transmitted
undertracks
2
no detailed
transmission
C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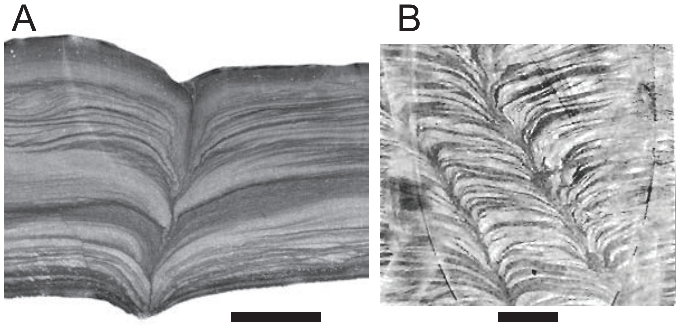
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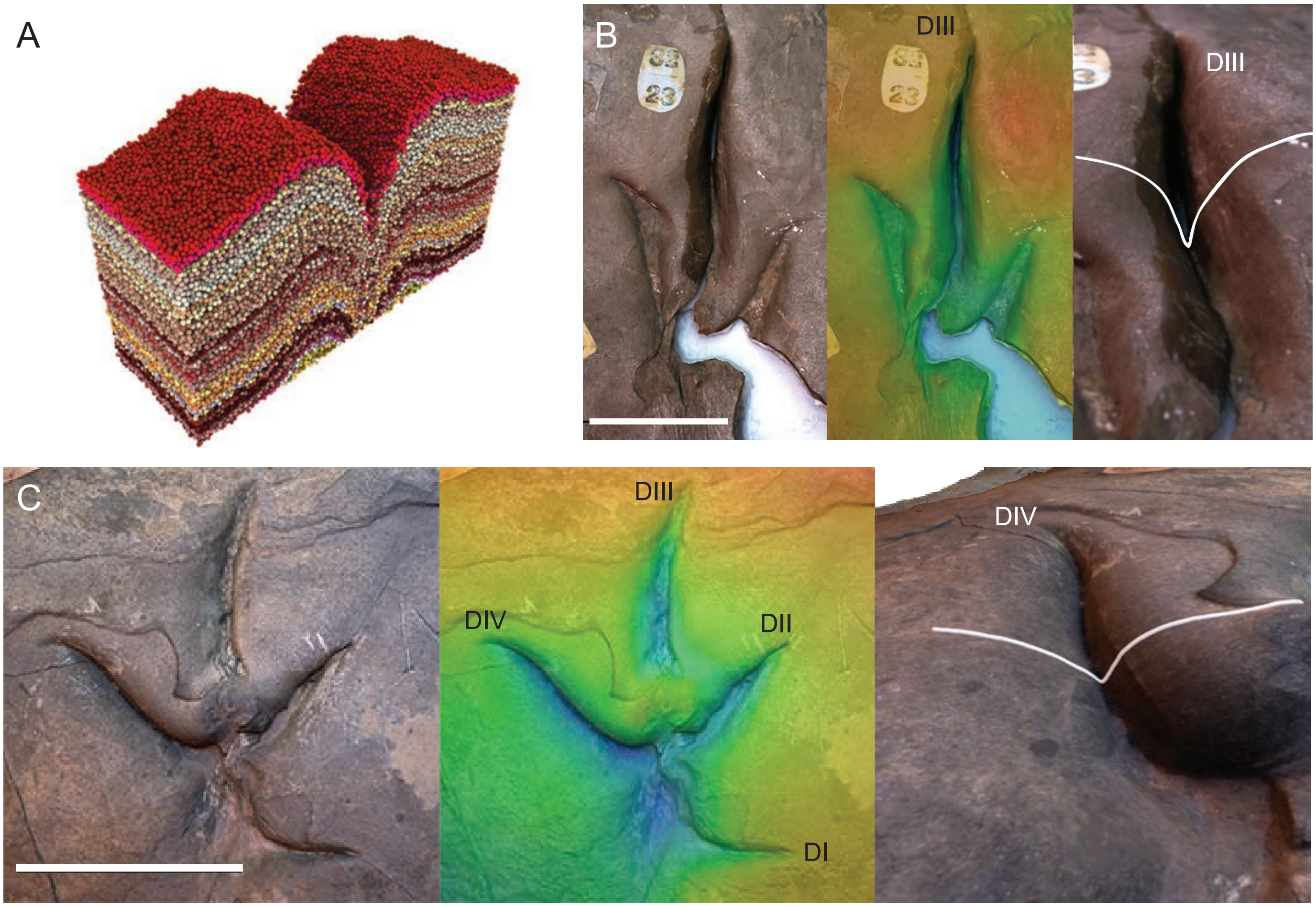
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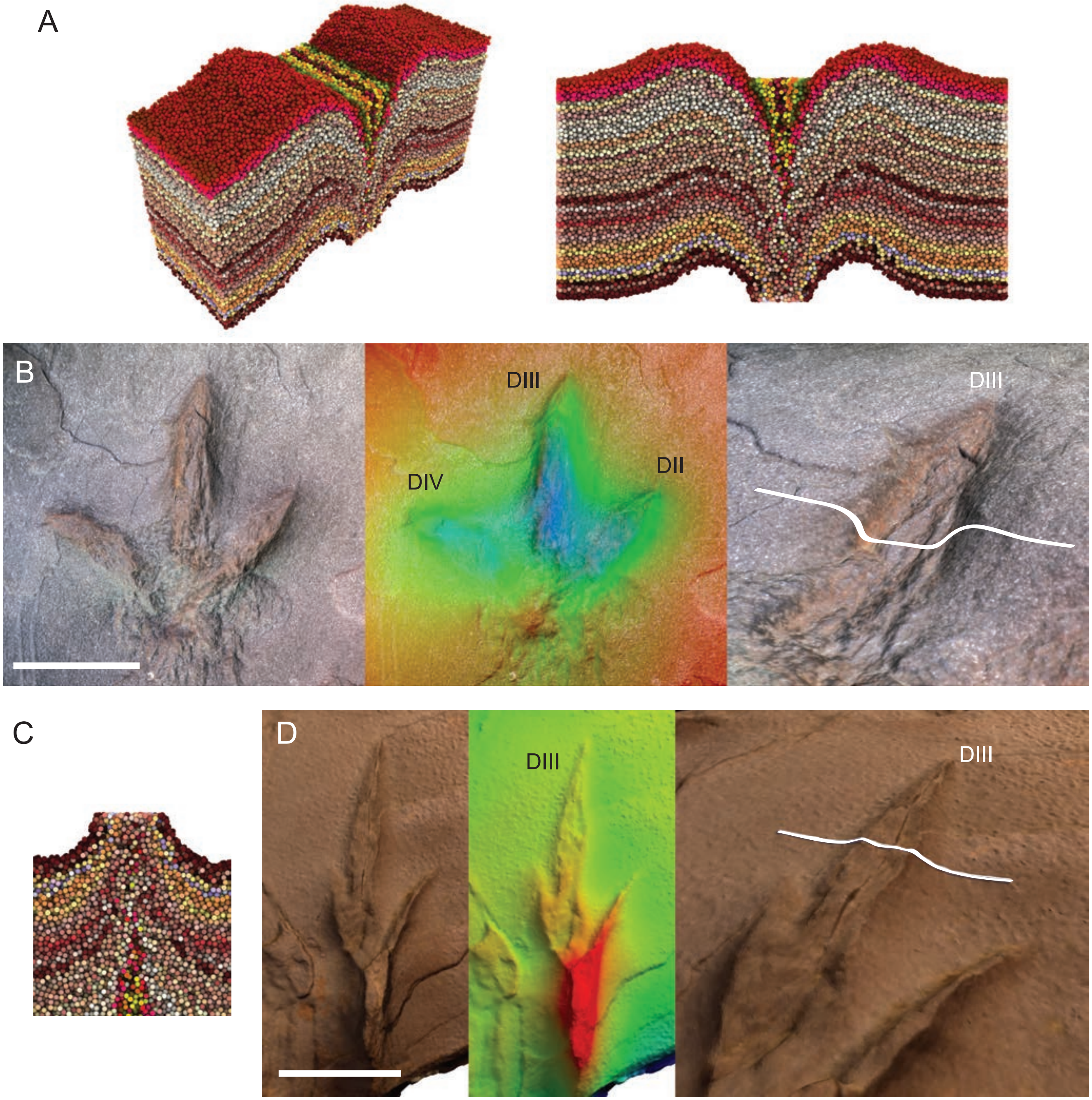
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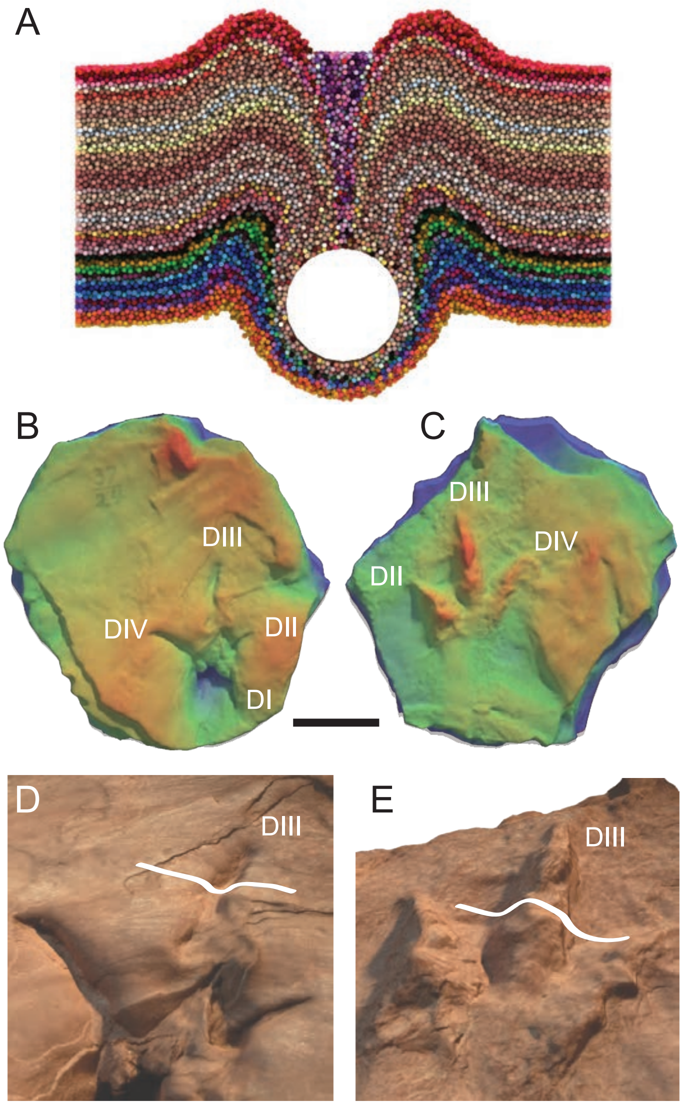
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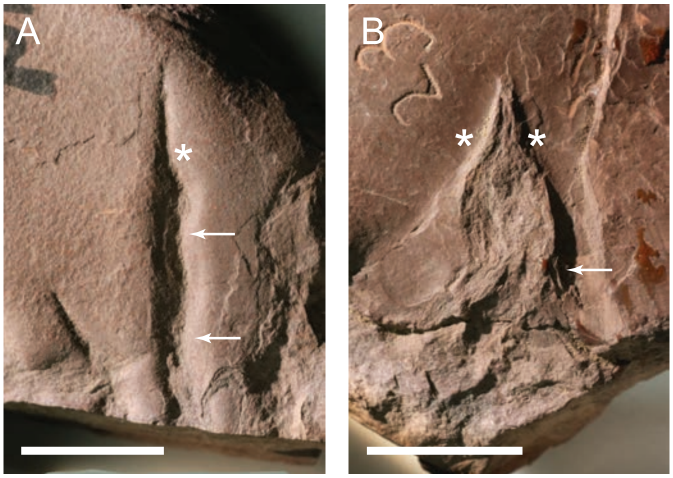
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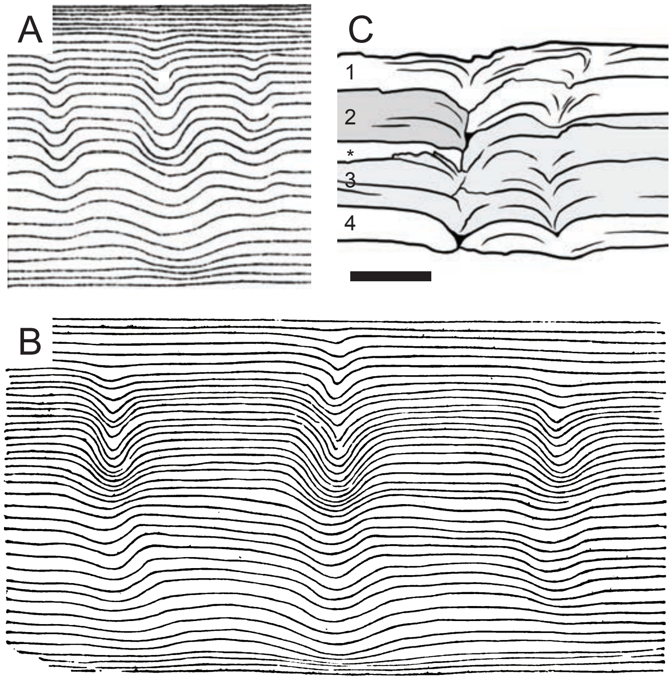
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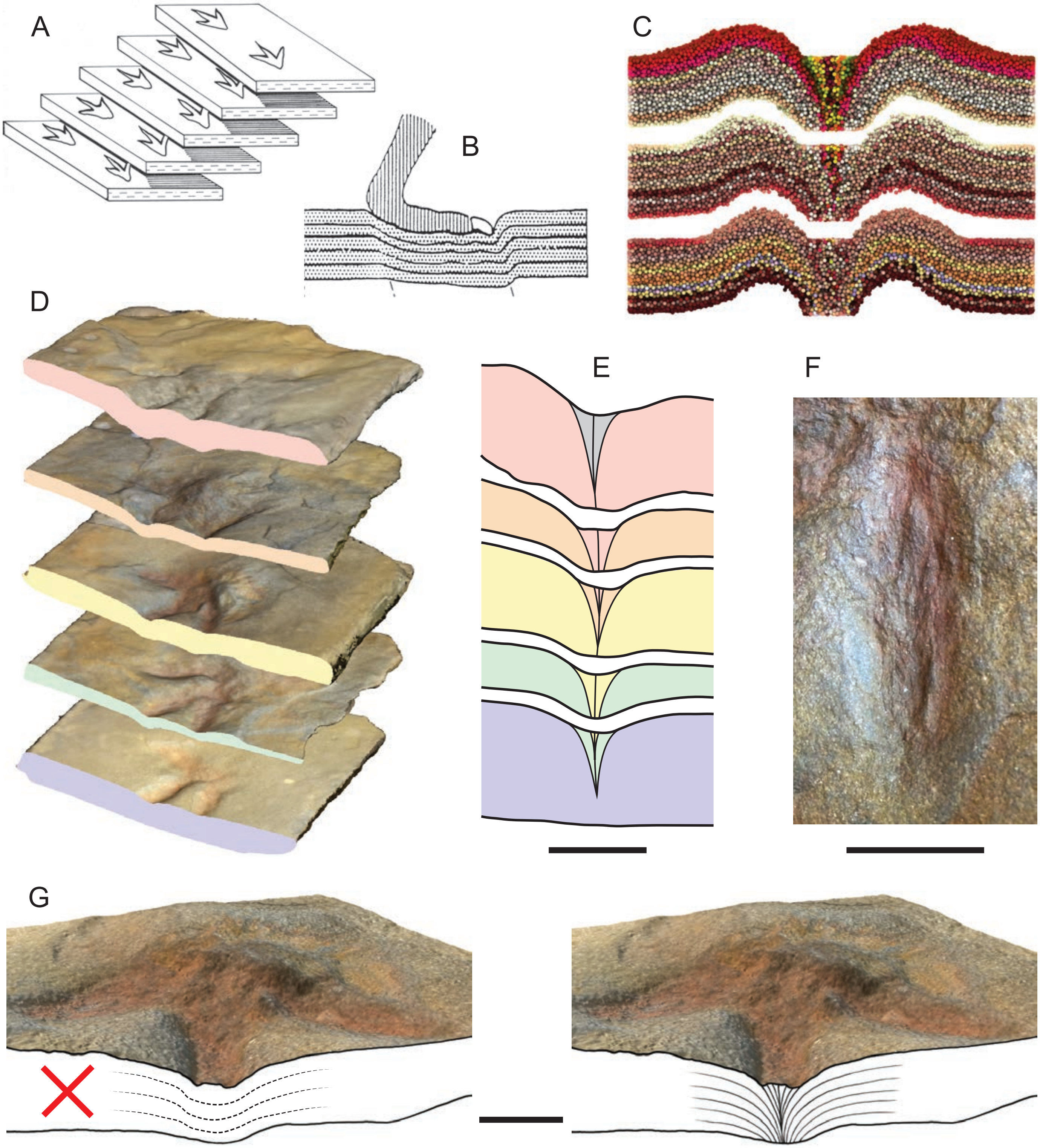
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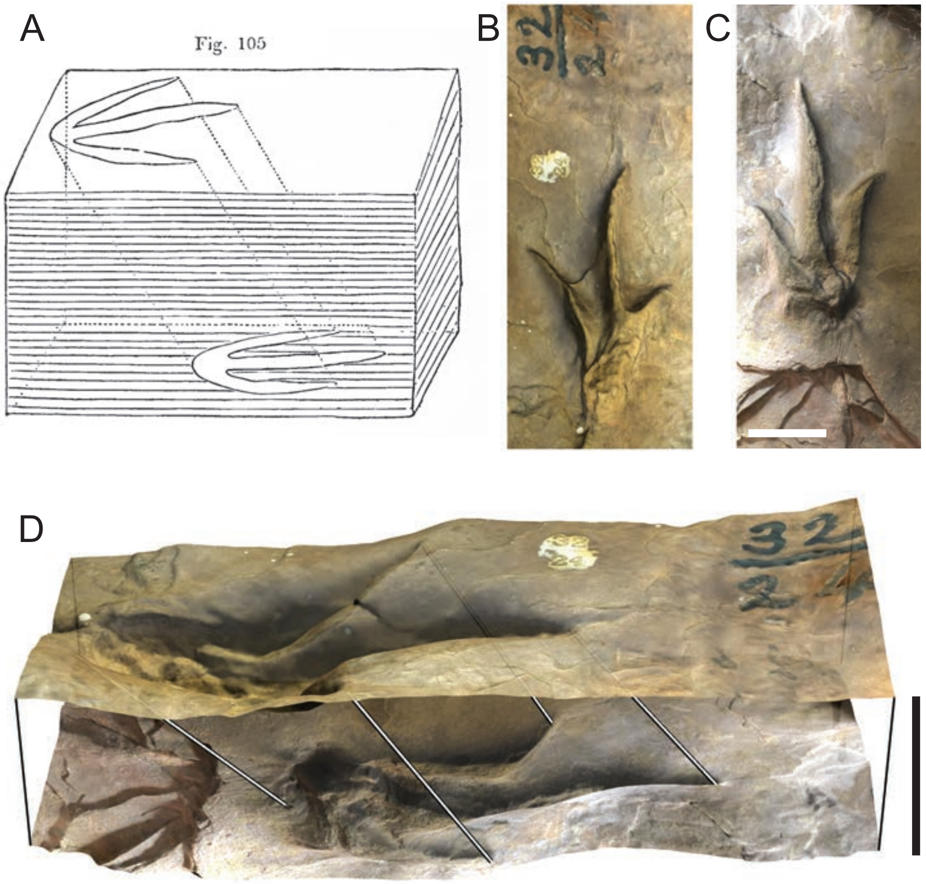
A
Fig. 105
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