Track formation mechanisms elucidated by computer simulation and bi-planar X-ray

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Abstract:

We demonstrate, through the use of computer simulation and bi-planar X-ray data, that track volumes formed by narrow-toed feet, such as those of theropods and birds, may be penetrative, rather than transmissive in nature. Penetrative tracks and undertracks do not look like the feet that made them, which has made them less attractive to study. Despite the lack of anatomical correlates, penetrative tracks can be exquisitely preserved and provide a wealth of information about their track makers and vertebrate track formation more broadly.

Key words: simulation; dinosaur; DEM; digitization; biomechanics

Tracks are three-dimensional structures whose initial morphology is defined entirely by the anatomy of the foot, consistency of the substrate, and dynamics of the lower limb (and ultimately the whole animal). This Anatomy-Substrate-Dynamics concept has been invoked by several authors in different forms, including ternary diagrams (Padian and Olsen 1984), Venn diagrams (Minter, Braddy, & Davis 2007) and multi-dimensional axes (Falkingham 2014). Understanding the formational process then, can potentially shed light on soft-tissue anatomy, environmental conditions when the track was made, and locomotor kinematics of the track maker.

Whilst anatomy will remain relatively constant throughout a trackway (indeed, throughout many trackways left by that animal), substrate and dynamics will vary far more dramatically. Changes in substrate can be highly localized (e.g. walking on a beach from dry sand to the water's edge), and as substrates become softer, the foot will sink deeper. Relative to a firm substrate standard, deeper sinking entails altered movement and the potential for greater step-step kinematic variation. Tracks made in deep, soft, substrates will necessarily record a more complete and complex foot-substrate interaction (Gatesy et al. 1999; Milàn, Christiansen & Mateus 2005; Cobos et al. 2016) than tracks left on shallow firm substrates. The deeper the foot sinks, the more motion is recorded in the reorganisation of sediment grains.

When the sediment behaviour includes an element of flow, grains and particles are free to move around pedal structures under load. The weight of the animal will not be supported and the foot will descend, perforating superficial layers before reaching its maximum depth. We refer to tracks created by this mechanism as 'penetrative' tracks, because the foot does not simply deform, but actually perforates the surface (and subsurface; 'penetrative undertracks') layers (Gatesy & Falkingham , in Review). The result is a sequence of interfacial surfaces below the original tracking surface that record the motion of the foot.

The concept of a 'track volume' is not new. Indeed, it was the 'father of ichnology' Edward Hitchcock that first illustrated the concept of 'undertracks' (Hitchcock 1858, 1841). Hitchcock's figures have generally been interpreted as describing the transmission of displacement beneath the foot-sediment interface, producing 'transmitted undertracks'. As we have discussed elsewhere (Gatesy & Falkingham, in review), it is not clear if this was in fact Hitchcock's original understanding.

Undertracks were an under-acknowledged phenomenon in vertebrate ichnology for well over 100 years, until work in the 1980's and onwards emphasised the importance of sub-surface deformations (Allen 1989, 1997; Jackson, Whyte & Romano 2010; Jackson, Whyte & Romano 2009; Manning 2004; Milàn & Bromley 2006, 2008; Milàn, Clemmensen & Bonde 2004; Falkingham et al. 2011). Much of this work concerned transmission of displacement beneath the foot-sediment interface, producing progressively less defined copies of the "True track" with depth.

However, our experimental work with a chicken-like bird, the guineafowl, employing bi-planar X-rays and computer simulation (Falkingham & Gatesy 2014; Gatesy & Falkingham 2017), has shown that very little deformation is actually transmitted below the sinking foot, at least for relatively narrow-toed feet such as birds and other theropods. Instead, the narrow toes penetrate sediment layers, leaving behind a series of nested V's beneath the tracking surface, all of which are "direct tracks" that have been formed through explicit contact with the trackmaker's foot (Gatesy 2003).

To illustrate sediment flow and penetrative track and undertrack formation, Figure 1 shows a computer simulation carried out using the discrete element method to simulate particle motions around a vertically indenting cylinder. The simulation shows how sediment collapses behind the descending cylinder and creates v-shaped penetrative tracks. This phenomenon is not limited to arbitrary indenters, but occurs with real foot morphologies and motions too, with individual toes behaving just like the cylinder in our simulation (Ellis & Gatesy 2013; Milàn & Bromley 2008).

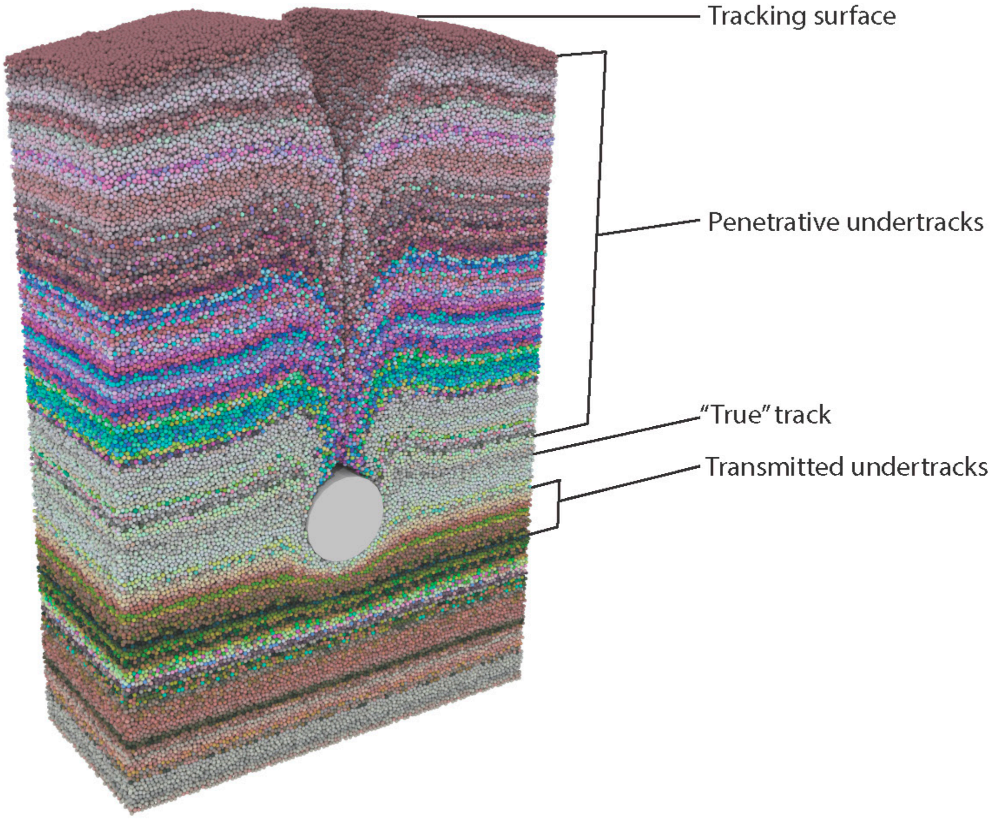

Fig. 1 - Discrete Element simulation demonstrating penetrative track and penetrative undertrack formation. Note that the depth beneath the indenter that transmitted undertracks occur is very shallow compared to the distance over which penetrative undertracks occur. From Gatesy and Falkingham (in review).

We have previously demonstrated the 3D capture of subsurface foot motions in guineafowl traversing soft substrates (Falkingham & Gatesy 2014), through the use of XROMM; X-ray Reconstruction of moving morphology (Gatesy et al. 2010; Brainerd et al. 2010). Incorporating the foot motions captured with XROMM into our DEM simulations results in surface tracks almost identical to the real tracks, but allows us to expose subsurface deformations as layers or slices.

Vertical slices through our simulations exhibit nested 'V' shapes where the toe has passed through laminations. These are identical to our abstract indenter simulations, but also to cut sections through dinosaur tracks (Figure 2), demonstrating that this mechanism occurs in both computational and real-world cases.

Our footprint simulations also provide a means of identifying what these tracks will look like if exposed at some surface beneath the original layer the animal walked on. The fossil track collections held at the Beneski Museum of Natural History, Amherst College – many of which were collected and curated by Edward Hitchcock, contain a wide range of penetrative dinosaur tracks. Hitchcock collected many tracks that appeared to have been made by animals with extremely thin toes. Hitchcock named these tracks 'leptodactylous' to reflect this interpretation. However, exposing our simulated penetrative tracks on sub-surface layers presents thin impressions much narrower than the toes that made them. Flow and collapse of soft sediment behind the sinking digits creates slit-like impressions. The degree to which these slits are prepared or naturally broken can determine how thick they appear.

Knowing that toes have penetrated through the exposed surface can provide information regarding the path of the foot. Many of the tracks in the Hitchcock collection appear on both upper and lower surfaces of specimens, and sometimes over multiple slabs. Tracking foot features over multiple surfaces can provide a means of documenting the path the foot took, and providing information about foot anatomy and motion, as well as substrate behaviour, that would not be available from a single surface.

Ironically, these highly informative tracks are often ignored or treated superficially in the literature, cast aside in preference of 'footprints' that appear more like a mould of an animal's foot. This second class status extends to terminology; the terms 'well preserved' or 'elite' have been used by some authors to exclusively refer to those tracks with clear anatomical features. We have previously made the case that such deep and 'messy' tracks should be considered no less well-preserved than a perfect impression of a foot in firm clay, if we are to maintain any consistency between osteological and ichnological vocabulary (Gatesy & Falkingham 2017). This has met with some resistance (e.g. Marchetti et al. 2019), but we maintain that calling the guineafowl tracks in Figure 3, recorded immediately after they were made, anything but 'well preserved' is misleading and incorrect. Further, to focus on anatomical correlates is to take vertebrate ichnology back to a time when ichnotaxa were analogous to species taxa, and raises points for discussion about what ichnotaxonomy is for; is it purely to communicate morphology, or is it to attempt to quantify biological diversity?

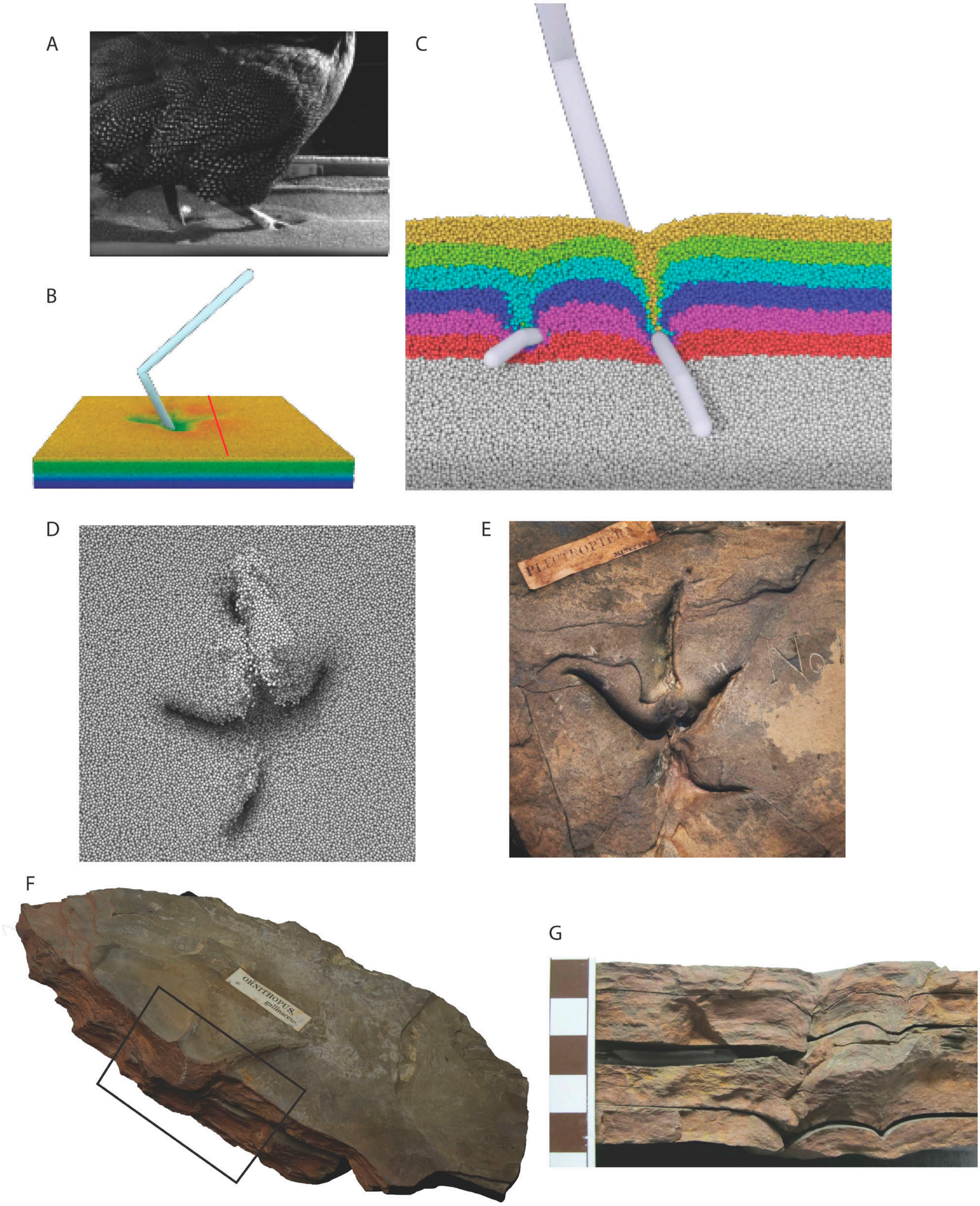

Figure 2 - Simulations and fossil tracks showing penetrative formation. Video (A) and XROMM-DEM simulation (B) of guineafowl track formtion, presented as a cross section in C. D) sub-surface layer exposed as though the track volume was broken along a lamination, displaying narrow, V-like digits very similar to the fossil specimen (E) ACM-ICH 32/28 from the Beneski Museum of Natural History. F & G show a track preserved in cross-section (specimen ACM-ICH 41/4).

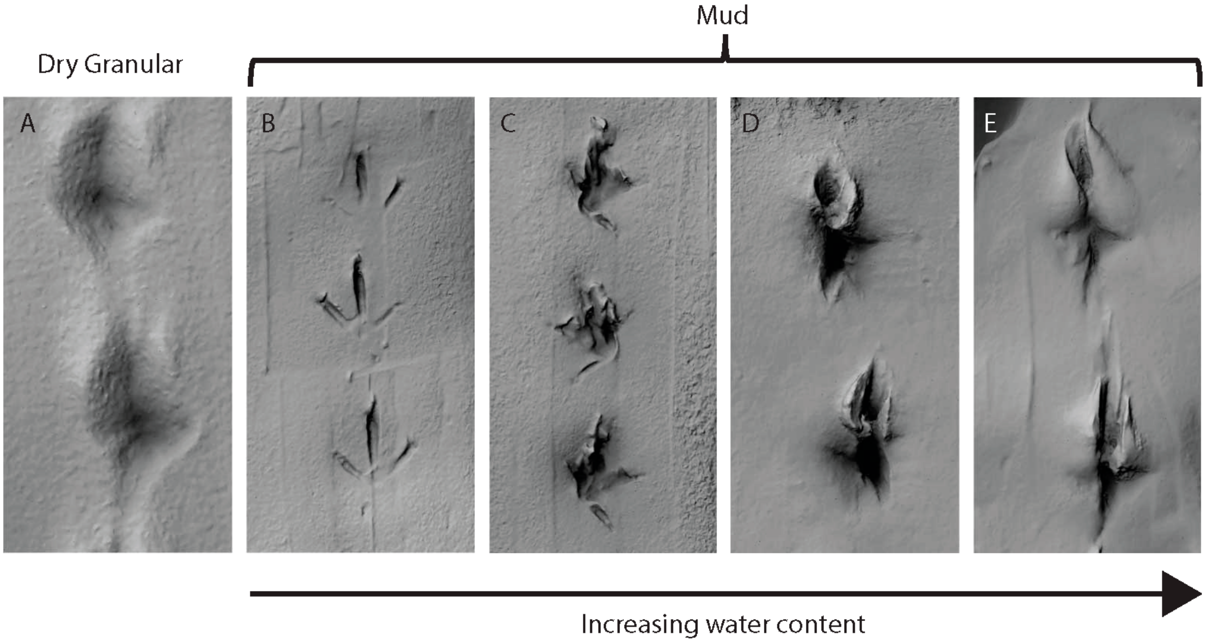

Figure 3 - Photogrammetric models of Guineafowl tracks recorded immediately after formation. A Dry granular medium (poppy seeds, behaving similar to dry sand). B-E Tracks left in a clay mixture at various levels of hydration. Note that only when walking over a firm mud (B) does the Guineafowl leave tracks that record anatomical correlates. Fossil tracks similar to those in A, C-E are often referred to incorrectly as 'poorly preserved' due to a lack of anatomical fidelity. Modified from Gatesy and Falkingham (2017).

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