

Interpreting ecology and behaviour from the vertebrate fossil track record

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Abstract

Fossil tracks represent a direct window onto the lives of extinct organisms, being formed and preserved *in situ*. Because track morphology is determined by limb motion, foot anatomy and substrate consistency, studies of fossil tracks can provide insight into producer, behaviour and palaeoenvironment. However, each determining factor is subject to variation, either continuous or discrete, and this variation may be co-dependent, making it difficult to correctly interpret a track. In addition to variance from the track-forming variables, tracks and tracksites are subject to further obfuscation because of time averaging, even before the effects of weathering, erosion and exposure are accounted for. This paper presents a discussion of the factors that may confound interpretation of fossil tracks, trackways and tracksites, and reviews experimental studies that have attempted to elucidate and eliminate these sources of confusion.

Introduction

The fossilized tracks and trackways of extinct vertebrates can offer a wealth of information about locomotion (Castanera *et al.*, 2013), behaviour (Bibi *et al.*, 2012), anatomy (Milner *et al.*, 2009), ecology (Lockley, Hunt & Meyer, 1994a; Lockley *et al.*, 2009) and evolution (Lockley *et al.*, 1992) that complements the body fossil record (Thulborn, 1990), either by preserving complimentary information or by providing a secondary, independent source of data (Carrano & Wilson, 2001). Making inferences about such aspects of extinct organisms is made possible because track morphology (at the time of formation) is entirely determined by three factors: limb dynamics, substrate properties and foot shape (Padian & Olsen, 1984; Minter, Braddy & Davis, 2007), which means that the type of animal, the way the animal moves and the environment it moves through will all affect the shape of the track left behind.

Locomotion – Because tracks are a direct record of limb motion, they often receive particular attention for their utility in understanding the locomotion of extinct animals, particularly when the fossil taxa in question have no modern analogue (Farlow *et al.*, 2000; Day *et al.*, 2002; Wilson, Marsicano & Smith, 2009). For the majority of studies, general trackway parameters tend to be used to make inferences about locomotion; stride length and foot length, enabling the calculation of speed (Alexander, 1976; Thulborn, 1990) are the most common, frequently accompanied by other

metrics such as pace angulation and track rotation (Leonardi, 1987). Relative placements (or even presence/absence) of the manus and pes can be informative as to the gait of the track maker – quadrupedal or bipedal, wide or narrow gauge, whether the tail was held high, all of which may be difficult to ascertain from bones alone (Wilson & Carrano, 1999; Wilson & Fisher, 2003; Henderson, 2006; Romano, Whyte & Jackson, 2007; Castanera *et al.*, 2013).

However, features of morphology within individual tracks can also be highly informative. Particularly, deep tracks will, by their very nature, record more of the foot motion than shallow tracks. Such deep tracks can be used to describe the path of the foot through the substrate (Gatesy *et al.*, 1999; Avanzini, Piñuela & García-Ramos, 2012). Although shallower tracks may record less motion, skin impressions and scale drag marks can still elucidate the angles at which the foot contacted and subsequently moved off the substrate (Gatesy, 2001).

The motion of distal elements of the limb (i.e. the manus or pes) is directly linked to the motion of more proximal limb elements, and ultimately of the animal itself. As such, changes in contact area, centre of pressure, and ground reaction force orientation and magnitude occur throughout the step cycle (Panagiotopoulou *et al.*, 2012; Bates *et al.*, 2013). As the pressure exerted by the foot increases (e.g. during toe-off when contact area is at a minimum), or when the applied force changes angle, the load may overcome the substrate shear strength and cause localized deformation (Falkingham *et al.*,

2011a), resulting in deeper areas within a track (Thulborn, 1990; Manning, 2004). The variation in topography of individual tracks within a trackway may therefore be indicative of differences in limb dynamics between foot falls, although it may also simply be a function of a spatially heterogeneous substrate. The double peak pressure curve observed in extant bipeds (Usherwood *et al.*, 2012) has been posited as the mechanism necessary for the generation of tracks in which the anterior and/or posterior are impressed to a greater depth than the centre of the track (Manning, 2004). Accelerations and decelerations result in differences between relative forces exerted by the foot at either foot strike or kick-off (Thulborn, 1990; Manning, 2004), with deceleration increasing force at the rear of the foot during initial contact and acceleration increasing that force anteriorly at kick-off. These forces may in turn directly affect the relative depths of the front and rear of a track, observable as variations in pitch or depth profile that may correlate with other speed-related features such as stride length (Mossman, Brünig & Powell, 2003; Bates *et al.*, 2013; Pataky *et al.*, 2013).

Behaviour – Locomotion is implicit in the formation of a track (at least, a non-termination trace). However, tracks may offer glimpses of rare locomotory behaviours that an organism may undertake even if the skeleton does not display evolutionary adaptations indicating such behaviour. There are, for instance, several examples of potential swimming (or punting) traces made by dinosaurs (Coombs, 1980; Ishigaki, 1989; Wilson & Fisher, 2003; Milner, Lockley & Kirkland, 2006; Ezquerro *et al.*, 2007; Xing *et al.*, 2013) indicating behaviour that would otherwise remain unknown, although in many cases such interpretations remain untested.

Behaviours other than locomotion may also be expressed, including actions such as feeding (Ensom, 2002; Falk, Hasiotis & Martin, 2010; Kim *et al.*, 2012) or resting (Hitchcock, 1858; Milner *et al.*, 2009), which may be inferred from a single trace, or behaviours observable at the larger scale of tracksites such as gregarious behaviour (Lockley, Meyer & Santos, 1994b; Bibi *et al.*, 2012) or predator–prey interactions.

Palaeoecology – As noted above, tracksites can potentially record both inter- and intraspecific interactions. The *in situ* nature of tracks, in contrast to the transportability of body fossils, makes tracksites a more confident indicator of diversity in a given environment (Dentzien-dias, Schultz & Bertoni-Machado, 2008; Smith, Marsicano & Wilson, 2009; Kurihara & Lockley, 2012) as each track represents an animal that lived, at least temporarily, in that location, the sedimentology of which can directly inform us of the palaeoenvironment (Phillips *et al.*, 2007). The necessity of water in making a substrate soft enough to form and preserve tracks means that many tracksites can be focal points for communities of animals, being formed around watering holes or along shores for example.

There is, therefore, a wealth of information to be read from the morphology of a track. However, reading that information requires understanding how a track is formed. The best way to attain that understanding is through experimental neoichnology, and many authors have pursued this to great effect, using live animals, cadaveric feet or models, or basic

shapes to produce tracks in real, artificial and virtual simulated substrates (Davis, Minter & Braddy, 2007; Marty, Strasser & Meyer, 2009).

The contributions of limb dynamics, anatomy and substrate to track morphology

The idea that foot anatomy affects the shape of the track is, of course, obvious. The substrate is directly deformed by the contact between the foot and the ground. A large round elephant foot will produce a very different track to one produced by a slender toed bird, irrespective of any other considerations. The converse is also true, that animals sharing a common pedal morphology will, if substrate and motion are consistent, produce tracks that are fundamentally alike. It is for this latter reason that neoichnological studies can be so enlightening – the conservative pedal morphology of theropods and their avian descendants has enabled workers to draw insightful conclusions about theropod dinosaur tracks from work with extant birds (Gatesy *et al.*, 1999; Milàn, 2006; Milàn & Bromley, 2006; Ellis & Gatesy, 2013).

Track morphology is also intuitively linked to substrate – one only has to walk along a beach, moving closer to or further from the water to see a distinct change in the shape of the footprints left behind. A substrate can be described either morphologically (as grain size, angularity, composition) or mechanically (with terms such as stiffness, strength, compressibility, and cohesion). Although it is the latter that describes how a substrate will respond to load, palaeontologists are predominantly limited to observing the former. Unfortunately, most of the mechanical properties of a substrate are highly dependent upon water content, which can be almost impossible to determine from a lithified sediment. Instead, experimental data must be used to produce tracks in a range of substrates and compare these to fossil specimens. This is easier for some organisms, where body weight and kinematics can be relatively well constrained, such as with hominid tracks (e.g. Hatala *et al.*, 2013; Morse *et al.*, 2013), but can become somewhat circular in nature if the track maker and associated mass are unknown; are the experimental track and fossil track at the same depth because the substrate is the same, or because the experimental track was produced with a greater or lesser force than the fossil track?

The dynamics of the distal limb, which include both the motion of the foot and the associated forces applied to the substrate, represent the third contributor to track morphology. The orientation and force with which the foot interacts with the substrate will ultimately determine the directions in which the substrate deforms, and consequently the track morphology. A foot which encounters the substrate while moving forward at a low angle may produce a shallow rear to the track from the metatarsus (Gatesy *et al.*, 1999) while a vertically emplaced foot will produce a track with steep, vertical walls (providing the sediment can sufficiently hold such a form) (Milàn, Christiansen & Mateus, 2005). The dynamic nature of the foot-sediment interface and of the animal's mass passing

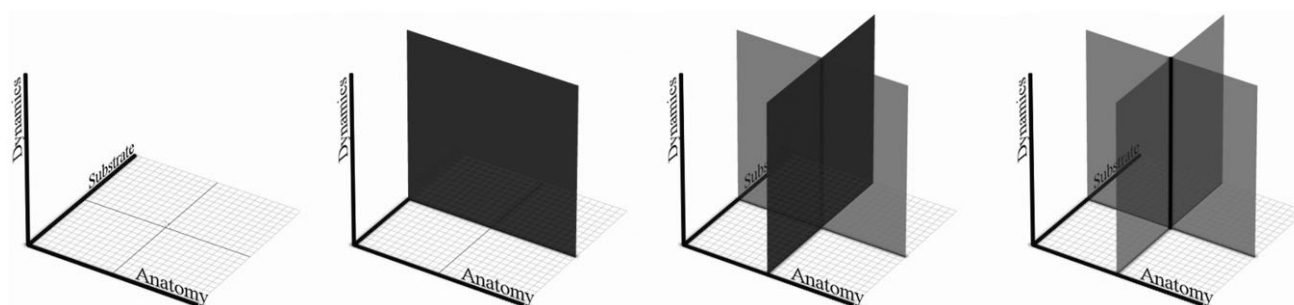


Figure 1 A conceptual morphospace of track morphology. From left to right: The 3D morphospace is defined by the three axes Substrate, Anatomy and Dynamics. For a given substrate, the morphospace is limited to a plane, where track morphology varies only because of anatomy or dynamics. If anatomy is also fixed (i.e. a single animal on a single substrate), variations in track morphology are limited to those resulting from changes in foot dynamics, that is the intersection between the 'substrate' and 'anatomy' planes, constraining potential track morphology to a one-dimensional morphospace. If limb dynamics were also known, the morphospace would be reduced to a single point, and only one track morphology could be possible.

over the foot means that throughout the stance phase of the step cycle (i.e. while the foot is in contact with the substrate) the load applied to the substrate will vary in position, direction and magnitude, dynamically affecting the formation of the track.

Each of the above factors can vary independently or in conjunction with each other (e.g. when an organism must adapt limb kinematics to deal with changes in substrate consistency), and these variations can be both continuous (e.g. substrate moisture content) and discrete (number of digits on the foot). While Baird (1957) noted that a track was the by-product of dynamic contact between an organism and its environment, Padian & Olsen (1984) were the first to conceptualize the contributions to track morphology from anatomy, kinematics and substrate by placing the three factors into a ternary diagram. Their goal was to illustrate that the morphology of a particular track (in this case, *Pteraichnus*) was heavily influenced by substrate, to the extent that foot anatomy was obscured, making track maker identification difficult. Minter *et al.* (2007) presented a variation of these three factors in a Venn diagram, using substrate, behaviour and producer as the formational factors not only for tracks, but for all trace fossils. Here, I suggest that, at least for tracks, the terms dynamics, anatomy and substrate are the most apt descriptors of the contributing factors to track morphology. 'Dynamics' encompasses both kinematics (motion) and kinetics (forces), and is the means by which any given behaviour is expressed as a trace. 'Anatomy' is preferable over 'producer', as producer may vary while pedal anatomy remains conserved, and thus 'producer' *sensu stricto* is not the variable affecting the track shape. Substrate is perhaps the most nebulous term of the three, referring to a complex range of morphological and mechanical properties, and to say that 'the substrate varies' is to paint a broad brush over a highly complex factor. Nevertheless, substrate is discrete from anatomy and dynamics, and it serves to consider it as an independent variable, or at least suite of variables, when discussing track morphology.

Together, these three variables control all possible track morphologies (at least prior to preservation), and therefore

define a morphospace (Fig. 1). If any one of these variables is known (or constrained), the morphospace becomes a two-dimensional plane. Fixing a second or third variable will reduce the morphospace further, first to a one-dimensional line, and finally to a single point.

Difficulties in interpreting tracks and experimental work shedding light on these difficulties

The three-dimensional (3D) nature of tracks – volumes and topology

Because dynamics, substrate and anatomy ultimately determine the 3D morphology of the track, ichnologists can attempt to reverse engineer track formation in order to tease out data about how the limb moved, the shape of the foot (and subsequently the identity of the producer) and the environmental conditions when the track was formed. However, the interplay of the three factors results not only in 3D topography at the surface, but also 3D deformation subsurface either through transmission of force (Allen, 1989, 1997; Manning, 2004; Milàn, Clemmensen & Bonde, 2004; Milàn & Bromley, 2006, 2008; Falkingham *et al.*, 2011a; Thulborn, 2012) and/or penetration of the sediment by the foot leading to the formation of deep tracks (Gatesy, 2003).

Surface morphology can – and should – readily be captured and analysed. Historically vertebrate ichnology has been limited to recording only two dimensions, initially by outline and/or shaded drawings, later accompanied by photographs. An initial movement towards adopting 3D documentation techniques such as moiré photography (Ishigaki & Fujisaki, 1989), anaglyph stereo imaging (Gatesy, Shubin & Jenkins, 2005), photogrammetry (Breithaupt & Matthews, 2001; Breithaupt *et al.*, 2001; Breithaupt, Matthews & Noble, 2004; Matthews, Noble & Breithaupt, 2006) and laser scanning (Bates *et al.*, 2008a,b) has grown towards becoming a standard for ichnological documentation (Bates *et al.*, 2009;

Remondino *et al.*, 2010; Farlow *et al.*, 2012; Belvedere *et al.*, 2013; Bennett *et al.*, 2013), aided by advances in consumer digitization, particularly with photogrammetry (Falkingham, 2012, 2013).

It is not always possible to see beneath the exposed surface of a fossil track, requiring either natural breaks or deliberate cross-sectioning, both of which are destructive and thus not possible for protected tracksites. It may also be that a track is emplaced in what becomes a homogeneous rock layer, where subsurface deformation cannot be observed even if the subsurface sediment is exposed, because the necessary delineations created by laminations are absent. Nevertheless, an appreciation of subsurface geometry is required in order to attempt to identify exposed surfaces as 'true tracks' or 'undertracks' (Milàn & Bromley, 2006). This is important because apparent track morphology changes within the volume, and so interpretations based on misidentified surfaces can be flawed. Many experimental studies have focused on this difficulty in considering tracks as 3D volumes, and have presented numerous methods for 'seeing' beneath the foot-sediment interface including using plaster or cement between friable layers (Manning, 2004; Milàn & Bromley, 2008), coloured plasticine (Allen, 1989, 1997), biplaner X-rays (Ellis & Gatesy, 2013) and computer simulation (Falkingham *et al.*, 2009; Falkingham, Margetts & Manning, 2010b; Falkingham *et al.*, 2011a,b). Even observing or defining the foot-sediment interface can be difficult if the sediment has sealed upon removal of the trackmaker's foot; the interface or direct track *sensu* Gatesy (2003), will then exist within the volume and is unlikely to be exposed at any natural break.

Time averaging

A fossil track is a recording of a brief moment in an animal's life. In this regard, a track represents a very narrow window of time preserved in the rock. A tracksite (multiple tracks and trackways on a single surface), however, cannot be constrained so confidently, and while time averaging of a tracksite is considered to operate over a much briefer time scale than for body fossils (Cohen *et al.*, 1991), it may still be significant. It may be tempting to view a tracksite as being produced by contemporaneous animals, particularly if tracks appear parallel or associated in some other way, but a sediment may be exposed and susceptible to track formation continuously or sporadically over minutes, days, months or even years. This can make interpretations of gregarious behaviour and population dynamics (Ostrom, 1972; Lockley *et al.*, 2002, 2009; Myers & Fiorillo, 2009) from fossil tracks difficult to substantiate. While time averaging is difficult to investigate experimentally, at least for specific sites, hypotheses of contemporaneity can be tested by examining the morphology of individual tracks – do the tracks show similar deformation structures that would indicate comparable substrate conditions at the time the tracks were made? For example, do displacement rims around tracks indicate a similar level of consistency and incompressibility within the substrate, or does the sediment show shearing or cracking in the same way between tracks? To phrase this differently, if all tracks at a site were placed con-

ceptually into the 3D morphospace of dynamics-substrate-anatomy (Fig. 1), would the substrate contribution to morphology remain constant?

Covariance of dynamics-substrate-anatomy

As mentioned briefly above, there are occasions when two or more of the formational variables (dynamics, substrate, anatomy) become intrinsically linked. An animal is unlikely to be able to use the same gait to move over firm sand as for deep, soupy mud and this can be seen in neoichnological experiments (Falkingham, pers. obs. 2013). As such, tracks made in two mechanically very different substrates will differ in morphology because both sediments behave differently, and from a change in the dynamics of the foot. Taken to an extreme, a submerged substrate may result in the preservation of tracks recording swimming (or at least 'punting'), rather than terrestrial locomotion (Milner *et al.*, 2006).

Alternatively, substrate and limb dynamics may determine which parts of the foot are able to make an impression, shifting the morphospace of track morphology with respect to the anatomy axis. The variable distribution of under-foot pressure may mean that some parts of the pedes may fail to deform the substrate; for instance, a tridactyl foot may produce enough pressure under two digits to indent the substrate but fail to leave a mark for the third, resulting in apparently didactyl tracks (Falkingham *et al.*, 2010a; fig. 5). In the same way, as a substrate becomes softer and the foot sinks deeper, more of the anatomy becomes involved in forming the track (e.g. Gatesy *et al.*, 1999). For instance, two tridactyl feet, identical save for the orientation of the hallux, may produce identical shallow tracks (providing dynamics and substrate remain consistent) which occupy the same point in morphospace, but produce tracks differing in morphology in deep substrates.

Conclusions

The wealth of information recorded in a track, trackway or tracksite is immense and ranges from the specific locomotor dynamics and behaviours of individual animals to the complex interactions between multiple individuals and species. Unfortunately, disentangling the contributions to track morphology from dynamics, anatomy and substrate is not trivial. It is not as though one factor contributes to track morphology and is then subsequently altered by another factor, enabling us to work backwards in a step-wise fashion. Rather, it is that the three factors combine simultaneously to produce a single morphology. Adding to this complexity, the final morphology is inherently volumetric, but is almost always expressed only as a single surface (which may or may not represent the surface upon which the track was made), limiting what data can be used to reverse engineer the formation of the track.

Experimental ichnology is the means with which we explore the contributing factors and essentially 'fill in' track morphospace with the resultant morphologies of known dynamics, anatomy and substrate. In order to do this, it is imperative that experimental neoichnological work details the

sediment properties (ideally both mechanical and morphological), the shape (and stiffness) of the foot, and the movement and forces with which the foot was indented. Ideally, 3D digital models of experimental tracks should be made and distributed, enabling ichnologists to compare the experimental tracks with exposed surfaces seen in fossil tracks, and provide more confidence with which to interpret the producers, behaviours and palaeoenvironments of extinct organisms from their tracks.

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References

- Alexander, R.M. (1976). Estimates of speeds of dinosaurs. *Nature* **261**, 129–130.
- Allen, J.R.L. (1989). Fossil vertebrate tracks and indenter mechanics. *J. Geol. Soc. London* **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. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **352**, 481–518.
- Avanzini, M., Piñuela, L. & García-Ramos, J.C. (2012). Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. *Lethaia* **45**, 238–252.
- Baird, D. (1957). Triassic reptile footprint faunules from Milford, New Jersey. *Bull. Mus. Comp. Zool.* **117**, 449–520.
- Bates, K.T., Falkingham, P.L., Hodgetts, D., Farlow, J.O., Breithaupt, B.H., O'Brien, M., Matthews, N.A., Sellers, W.I. & Manning, P.L. (2009). Digital imaging and public engagement in palaeontology. *Geol. Today* **25**, 134–139.
- Bates, K.T., Manning, P.L., Vila, B. & Hodgetts, D. (2008a). Three dimensional modelling and analysis of dinosaur trackways. *Palaeontology* **51**, 999–1010.
- Bates, K.T., Rarity, F., Manning, P.L., Hodgetts, D., Vila, B., Oms, O., Galobart, À. & Gawthorpe, R. (2008b). High-resolution LiDAR and photogrammetric survey of the Fumanya dinosaur tracksites (Catalonia): implications for the conservation and interpretation of geological heritage sites. *J. Geol. Soc. London* **165**, 115–127.
- Bates, K.T., Savage, R., Pataky, T.C., Morse, S.A., Webster, E., Falkingham, P.L., Ren, L., Qian, Z., Bennett, M.R., McClymont, J. & Crompton, R.H. (2013). Does footprint depth correlate with foot motion and pressure? *J. R. Soc. Interface* **10**, 20130009.
- Belvedere, M., Jalil, N.-E., Breda, A., Gattolin, G., Bourget, H., Khaldoune, F. & Dyke, G.J. (2013). Vertebrate footprints from the Kem Kem beds (Morocco): a novel ichnological approach to faunal reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **383–384**, 52–58.
- Bennett, M.R., Falkingham, P.L., Morse, S.A., Bates, K. & Crompton, R.H. (2013). Preserving the impossible: conservation of soft-sediment hominin footprint sites and strategies for three-dimensional digital data capture. *PLoS ONE* **8**, e60755.
- Bibi, F., Kraatz, B., Craig, N., Beech, M., Schuster, M. & Hill, A. (2012). Early evidence for complex social structure in Proboscidea from a late Miocene trackway site in the United Arab Emirates. *Biol. Lett.* **8**, 670–673.
- Breithaupt, B.H., Matthews, N. & Noble, T. (2004). An integrated approach to three-dimensional data collection at dinosaur tracksites in the Rocky Mountain West. *Ichnos* **11**, 11–26.
- Breithaupt, B.H. & Matthews, N.A. (2001). *Preserving paleontological resources using photogrammetry and geographic information systems*. in Harmon, D., ed., Crossing Boundaries in Park Management: Proceedings of the 11th Conference on Research and Resource Management in Parks and Public Lands, The George Wright Society, Inc.
- Breithaupt, B.H., Southwell, E.H., Adams, T. & Matthews, N.A. (2001). *Innovative documentation methodologies in the study of the most extensive dinosaur tracksite in Wyoming*. 6th Fossil Research Conference Proceedings Volume, pp. 113–122.
- Carrano, M.T. & Wilson, J.A. (2001). Taxon distributions and the tetrapod track record. *Paleobiology* **27**, 564–582.
- Castanera, D., Vila, B., Razzolini, N.L., Falkingham, P.L., Canudo, J.I., Manning, P.L. & Galobart, À. (2013). Manus track preservation bias as a key factor for assessing trackmaker identity and quadrupedalism in basal ornithopods. *PLoS ONE* **8**, e54177.
- Cohen, A., Lockley, M., Halfpenny, J. & Michel, A.E. (1991). Modern vertebrate track taphonomy at Lake Manyara, Tanzania. *Palaio* **6**, 371–389.
- Coombs, W.P. (1980). Swimming ability of carnivorous dinosaurs. *Science* **207**, 1198–1200.
- Davis, R.B., Minter, N.J. & Braddy, S.J. (2007). The neoichnology of terrestrial arthropods. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **255**, 284–307.
- Day, J.J., Upchurch, P., Norman, D.B., Gale, A.S. & Powell, H.P. (2002). Sauropod trackways, evolution, and behavior. *Science* **296**, 1659.
- Dentzien-dias, P., Schultz, C. & Bertoni-Machado, C. (2008). Taphonomy and paleoecology inferences of vertebrate ichnofossils from Guarà Formation (Upper Jurassic), southern Brazil. *J. South Am. Earth Sci.* **25**, 196–202.
- Ellis, R.G. & Gatesy, S.M. (2013). A biplanar X-ray method for three-dimensional analysis of track formation. *Palaeontol. Electron.* **16**, 1T:16p; palaeo-electronica.org/content/2013/371-x-ray-track-analysis
- Ensom, P.C. (2002). Vertebrate trace fossils in the Purbeck Limestone Group of southern England. *Life Environ. Purbeck Times* **68**, 203–220.
- Ezquerro, R., Doublet, S., Costeur, L., Galton, P.M. & Pérez-Lorente, F. (2007). Were non-avian theropod

- dinosaurs able to swim? Supportive evidence from an Early Cretaceous trackway, Cameros Basin (La Rioja, Spain). *Geology* **35**, 507–510.
- Falk, A.R., Hasiotis, S.T. & Martin, L.D. (2010). Feeding traces associated with bird tracks from the lower cretaceous Haman formation, Republic of Korea. *Palaio* **25**, 730–741.
- Falkingham, P.L. (2012). Acquisition of high resolution three-dimensional models using free, open-source, photogrammetric software. *Palaeontol. Electron.* **15**, 1T:15p.
- Falkingham, P.L. (2013). Low cost 3D scanning using off-the-shelf video gaming peripherals. *J. Paleontol. Tech.* **11**, 1–9.
- Falkingham, P.L., Agenbroad, L.D., Thompson, K. & Manning, P.L. (2010a). Bird tracks at the hot springs mammoth site, South Dakota, USA. *Ichnos* **17**, 34–39.
- Falkingham, P.L., Bates, K.T., Margetts, L. & Manning, P.L. (2011a). The ‘Goldilocks’ effect: preservation bias in vertebrate track assemblages. *J. R. Soc. Interface* **8**, 1142–1154.
- Falkingham, P.L., Bates, K.T., Margetts, L. & Manning, P.L. (2011b). Simulating sauropod manus-only trackway formation using finite-element analysis. *Biol. Lett.* **7**, 142–145.
- Falkingham, P.L., Margetts, L. & Manning, P.L. (2010b). Fossil vertebrate tracks as paleopenetrometers: confounding effects of foot morphology. *Palaio* **25**, 356–360.
- Falkingham, P.L., Margetts, L., Smith, I. & Manning, P.L. (2009). Reinterpretation of palmate and semi-palmate (webbed) fossil tracks; insights from finite element modelling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **271**, 69–76.
- Farlow, J.O., Gatesy, S.M., Holtz, T.R., Hutchinson, J.R. & Robinson, J.M. (2000). Theropod locomotion. *Am. Zool.* **40**, 640–663.
- Farlow, J.O., O’Brien, M., Kuban, G.J., Dattilo, B.F., Bates, K.T., Falkingham, P.L., Piñuela, L., Rose, A., Freels, A., Kumagai, C., Libben, C., Smith, J. & Whitcraft, J. (2012). *Dinosaur tracksites of the Paluxy River Valley (Glen Rose Formation, Lower Cretaceous), Dinosaur Valley State Park, Somervell County, Texas*. Proceedings of the V International Symposium about Dinosaur Palaeontology and their Environment, pp. 41–69.
- Gatesy, S.M. (2001). Skin impressions of Triassic theropods as records of foot movement. *Bull. Mus. Comp. Zool.* **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., Middleton, K.M., Jenkins, F.A. & Shubin, N.H. (1999). Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature* **399**, 141–144.
- Gatesy, S.M., Shubin, N.H. & Jenkins, F.A. (2005). Anaglyph stereo imaging of dinosaur track morphology and microtopography. *Palaeontol. Electron.* **8**, 1–12.
- Hatala, K.G., Dingwall, H.L., Wunderlich, R.E. & Richmond, B.G. (2013). The relationship between plantar pressure and footprint shape. *J. Hum. Evol.* **65**, 21–28.
- Henderson, D.M. (2006). Burly Gaits: centers of mass, stability, and the trackways of sauropod dinosaurs. *J. Vertebrate Paleontol.* **26**, 907–921.
- Hitchcock, E. (1858). *Ichnology of New England. A Report on the Sandstone of the Connecticut Valley, Especially its Fossil Footmarks*, p. 220.
- Ishigaki, S. (1989). Footprints of swimming sauropods from Morocco. In *Dinosaur tracks and traces*: 83–86. Gillette, D.D. & Lockley, M.G. (Eds). Cambridge: Cambridge University Press.
- Ishigaki, S. & Fujisaki, T. (1989). Three dimensional representation of eubrontes by the method of Moiré topography. In *Dinosaur tracks and traces*: 421–425. Gillette, D.D. & Lockley, M. (Eds). Cambridge: Cambridge University Press.
- Kim, J.Y., Lockley, M.G., Seo, S.J., Kim, K.S., Kim, S.H. & Baek, K.S. (2012). A paradise of mesozoic birds: the world’s richest and most diverse cretaceous bird track assemblage from the early cretaceous haman formation of the Gajin Tracksite, Jinju, Korea. *Ichnos* **19**, 28–42.
- Kukihara, R. & Lockley, M.G. (2012). Fossil footprints from the Dakota Group (Cretaceous) John Martin Reservoir, Bent County, Colorado: new insights into the paleoecology of the Dinosaur Freeway. *Cret. Res.* **33**, 165–182.
- Leonardi, G. (1987). *Glossary and Manual of Tetrapod Footprint Palaeoichnology*.
- Lockley, M., Chin, K., Houck, K., Matsukawa, M. & Kukihara, R. (2009). New interpretations of Ignotornis, the first-reported Mesozoic avian footprints: implications for the paleoecology and behavior of an enigmatic Cretaceous bird. *Cret. Res.* **30**, 1041–1061.
- Lockley, M.G., Hunt, A.P. & Meyer, C.A. (1994a). Vertebrate tracks and the ichnofacies concept: implications for paleoecology and palichnostratigraphy. In *The paleobiology of trace fossils*: 241–268. Donovan, S. (Ed.). New York: Wiley and Sons, Inc.
- Lockley, M.G., Meyer, C.A. & Santos, V.F. (1994b). Trackway evidence for a herd of juvenile sauropods from the Late Jurassic of Portugal. *Gaia* **10**, 27–35.
- Lockley, M.G., Schulp, A.S., Meyer, C.A., Leonardi, G. & Kerumba Mamani, D. (2002). Titanosaurid trackways from the Upper Cretaceous of Bolivia: evidence for large manus, wide-gauge locomotion and gregarious behaviour. *Cret. Res.* **23**, 383–400.
- Lockley, M.G., Yang, S.Y., Matsukawa, M., Fleming, F. & Lim, S.K. (1992). The track record of mesozoic birds: evidence and implications: philosophical transactions. *Biol. Sci.* **336**, 113–134.
- Manning, P.L. (2004). A new approach to the analysis and interpretation of tracks: examples from the dinosauria. *Geol. Soc. Lond., Spec. Publ.* **228**, 93–123.
- Marty, D., Strasser, A. & 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. *Int. J. Plant Anim. Traces* **16**, 127–142.
- Matthews, N.A., Noble, T.A. & Breithaupt, B.H. (2006). The application of photogrammetry, remote sensing and

- geographic information systems (GIS) to fossil resource management. *Bull. N. M. Mus. Nat. Hist. Sci.* **34**, 119–131.
- 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. & Bromley, R.G. (2006). True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **231**, 253–264.
- Milàn, J. & 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., Clemmensen, L.B. & 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. & 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.
- Milner, A.R.C., Lockley, M.G. & Kirkland, J.I. (2006). A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah: Jurassic Terrestrial Transition. *Bull. N. M. Mus. Nat. Hist. Sci.* **37**, 44–47.
- Milner, A.R.C., Harris, J.D., Lockley, M.G., Kirkland, J.I. & Matthews, N.A. (2009). Bird-like anatomy, posture, and behavior revealed by an early jurassic theropod dinosaur resting trace. *PLoS ONE* **4**, e4591.
- Minter, N.J., Braddy, S.J. & Davis, R.B. (2007). Between a rock and a hard place: arthropod trackways and ichnotaxonomy. *Lethaia* **40**, 365–375.
- Morse, S.A., Bennett, M.R., Liutkus-Pierce, C., Thackeray, F., McClymont, J., Savage, R. & Crompton, R.H. (2013). Holocene footprints in Namibia: the influence of substrate on footprint variability. *Am. J. Phys. Anthropol.* **151**, 265–279.
- Mossman, D.J., Brüning, R. & Powell, H.P. (2003). Anatomy of a Jurassic theropod trackway from Ardley, Oxfordshire, U.K. *Ichnos* **10**, 195–207.
- Myers, T.S. & Fiorillo, A.R. (2009). Evidence for gregarious behavior and age segregation in sauropod dinosaurs. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **274**, 96–104.
- Ostrom, J.H. (1972). Were some dinosaurs gregarious? *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **11**, 287–301.
- Padian, K. & Olsen, P.E. (1984). The fossil trackway pteraichnus: not pterosaurian, but crocodilian. *J. Paleontol.* **58**, 178–184.
- Panagiotopoulou, O., Pataky, T.C., Hill, Z. & Hutchinson, J.R. (2012). Statistical parametric mapping of the regional distribution and ontogenetic scaling of foot pressures during walking in Asian elephants (*Elephas maximus*). *J. Exp. Biol.* **215**, 1584–1593.
- Pataky, T.C., Savage, R., Bates, K.T., Sellers, W.I. & Crompton, R.H. (2013). Short-term step-to-step correlation in plantar pressure distributions during treadmill walking, and implications for footprint trail analysis. *Gait Posture* **38**, 1054–1057.
- Phillips, J.P.L., Ludvigson, G.A., Matthew Joeckel, R., Gonzalez, L.A., Brenner, R.L. & Witzke, B.J. (2007). Sequence stratigraphic controls on synsedimentary cementation and preservation of dinosaur tracks: example from the lower Cretaceous, (Upper Albian) Dakota Formation, Southeastern Nebraska, U.S.A. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **246**, 367–389.
- Remondino, F., Rizzi, A., Girardi, S., Petti, F.M. & Avanzini, M. (2010). 3D Ichnology – Recovering digital 3D models of dinosaur footprints. *Photogramm. Rec.* **25**, 266–282.
- Romano, M., Whyte, M.A. & Jackson, S.J. (2007). Trackway ratio: a new look at trackway gauge in the analysis of quadrupedal dinosaur trackways and its implications for ichnotaxonomy. *Ichnos* **14**, 257–270.
- Smith, R.M.H., Marsicano, C.A. & Wilson, J.A. (2009). Sedimentology and paleoecology of a diverse Early Jurassic tetrapod tracksite in Lesotho, southern Africa. *Palaios* **24**, 672–684.
- Thulborn, R.A. (1990). *Dinosaur tracks*: London: Chapman & Hall.
- Thulborn, T. (2012). Impact of sauropod dinosaurs on lagoonal substrates in the Broome Sandstone (Lower Cretaceous), Western Australia. *PLoS ONE* **7**, e36208.
- Usherwood, J.R., Channon, A.J., Myatt, J.P., Rankin, J.W. & Hubel, T.Y. (2012). The human foot and heel-sole-toe walking strategy: a mechanism enabling an inverted pendular gait with low isometric muscle force? *J. R. Soc. Interface* **9**, 2396–2402.
- Wilson, J.A. & Carrano, M.T. (1999). Titanosaurs and the origin of ‘wide-gauge’ trackways: a biomechanical and systematic perspective on sauropod locomotion. *Palaeobiology* **25**, 252–267.
- Wilson, J.A. & Fisher, D. (2003). Are manus-only sauropod trackways evidence of swimming, sinking, or wading? *J. Vertebrate Paleontol.*, SVP Abstracts Book **23**, 111A.
- Wilson, J.A., Marsicano, C.A. & Smith, R.M.H. (2009). Dynamic locomotor capabilities revealed by early dinosaur trackmakers from Southern Africa. *PLoS ONE* **4**, e7331.
- Xing, L., Lockley, M.G., Zhang, J., Milner, A.R.C., Klein, H., Li, D., Persons, W.S. & Ebi, J. (2013). A new Early Cretaceous dinosaur track assemblage and the first definite non-avian theropod swim trackway from China. *Chin. Phys. Lett. Sci. Bull.* **58**, 2370–2378.