










## FRONTIERS IN PALAEOLOGY

# A STANDARD PROTOCOL FOR DOCUMENTING MODERN AND FOSSIL ICHNOLOGICAL DATA

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**Abstract:** The collection and dissemination of vertebrate ichnological data is struggling to keep up with techniques that are becoming commonplace in the wider

palaeontological field. A standard protocol is required to ensure that data is recorded, presented and archived in a manner that will be useful both to contemporary

researchers, and to future generations. Primarily, our aim is to make the 3D capture of ichnological data standard practice, and to provide guidance on how such 3D data can be communicated effectively (both via the literature and other means) and archived openly and in perpetuity. We recommend capture of 3D data, and the presentation of said data in the form of photographs, false-colour images, and interpretive drawings. Raw data (3D models of traces) should

always be provided in a form usable by other researchers (i.e. in an open format). If adopted by the field as a whole, the result will be a more robust and uniform literature, supplemented by unparalleled availability of datasets for future workers.

**Key words:** track, trace, digitization, ichnology, photogrammetry, standard protocol, 3D data.

THE study of trace fossils is of major significance to the wider field of palaeontology. Tracks, traces and footprints can offer us insights that are unlikely, or even impossible, to preserve in the osteological fossil record. Information about trackmaker anatomy, behaviour, motions and ecology is tied up in the three-dimensional morphology that we ultimately call a track (Padian & Olsen 1984a; Minter *et al.* 2007; Falkingham 2014). Fully extracting that information requires knowledge of both track size and shape, and of the processes and mechanisms involved in the foot–sediment interaction. Great progress has been made in understanding the mechanics of track formation and taphonomy (Padian & Olsen 1984b; Allen 1989; Thulborn & Wade 1989; Lockley *et al.* 1994; Avanzini 1998; Gatesy *et al.* 1999; Manning 2004; Milàn 2006; Milàn & Bromley 2006, 2008; Milàn *et al.* 2006; Graversen *et al.* 2007; Marty *et al.* 2009; Avanzini *et al.* 2012; Bates *et al.* 2013; Castanera *et al.* 2013; Ellis & Gatesy 2013; Falkingham & Gatesy 2014) but communication of track form has long been hampered by traditional means of recording and disseminating information.

For the vast majority of time since Edward Hitchcock formalized ichnology as a science (Hitchcock 1836), communication has been almost exclusively limited to printed papers and books. This 2D medium restricted the recording of tracks to sketches and lithographs, and later with the rise of the camera, photographs. Most ichnological literature, perhaps until only a few years ago, continued to rely solely on photos and drawings. Workers have thus spent the majority of their time reporting linear measurements in the horizontal plane (e.g. length, width and interdigital angle (IDA, or digit divarication); Leonardi 1987) occasionally supplementing such metrics with a single measure of depth.

But all tracks consist of a three-dimensional topographic surface. Whether preserved as a ‘negative’ depression or as a ‘positive’ relief feature, this 3D characteristic is fundamental to the existence of a track. In more complex scenarios, where laminations in the sediment are preserved, this 3D morphology is volumetric, extending above and below the foot–sediment interface as overprints and undertracks, respectively (Avanzini 1998; Manning 2004; Milàn & Bromley 2006; Marty *et al.* 2016).

The importance of that third dimension in the scientific study of tracks cannot be understated. In the simplest

scenario, we might consider a track to be a perfect mould of the foot that made it. In such a scenario, the topography within the track is a direct record of the soft-tissue anatomy of the trackmaker and can provide information regarding the size and distribution of under-foot pads, claws, or other features of the autopodium. However, this mould-based perspective is not always applicable, and such a mindset may ultimately be detrimental to our understanding of ichnological data (Gatesy & Falkingham 2017).

Generally, the foot–sediment interaction is more complex than a simple vertical ‘stamp’, involving forces varying in magnitude and direction throughout the stance phase. This dynamic force will differentially deform the substrate, leaving deeper or shallower areas within a track (Thulborn 1990). Any horizontal (anterior/posterior or lateral/medial) motions of the foot may act upon the sediment in such a way as to produce uneven raised rims around the track itself, or extensive zones of disturbed sediment around and below the actual track, which, when encountered in different states of erosion, can make it very hard to identify the boundaries of the true track (Graversen *et al.* 2007; Milàn & Loope 2007).

Even if we were to have no interest in trackmaker kinematics, and were instead focused on trackmaker identity, diversity or distribution, even basic measurements such as length and width are fundamentally altered depending on how they are measured and defined on that 3D surface (Falkingham 2016). Such measurements, of course, have a direct impact on interpretation, classification and ichnotaxonomy, particularly when used in geometric morphometrics or other numerical analyses. Some modern techniques attempt to avoid making specific measurements and apply a ‘whole track’ approach (Belvedere *et al.* 2018), though even here extents of the track must be defined to avoid incorporating too much undisturbed tracking surface into the analysis.

Unfortunately, given this importance, adequately conveying 3D form in a two-dimensional medium is (or at least, has been) a non-trivial task. However, in recent years we have seen a considerable rise in the availability, affordability, and ease of use of digitization techniques including laser scanning and photogrammetry. This has

been coupled with advances in web-based technology facilitating the acquisition, processing, archiving and sharing of large volumes of complex digital data. As these technologies mature, it is important that we as a field set down guidelines to ensure standardization of techniques and data.

In this paper, we propose a standard protocol for the collection and dissemination of 3D track data with the hope of achieving two specific aims. First, that such data is accurately recorded; we shall briefly discuss means of doing so later. Second, that the data is put into a communicable form that allows others to: (1) reproduce the work (a fundamental tenet of science); and (2) build upon it (thus advancing scientific knowledge). While our focus is primarily on tracks and trackways, the principles we shall discuss will be equally applicable to most other forms of trace fossil.

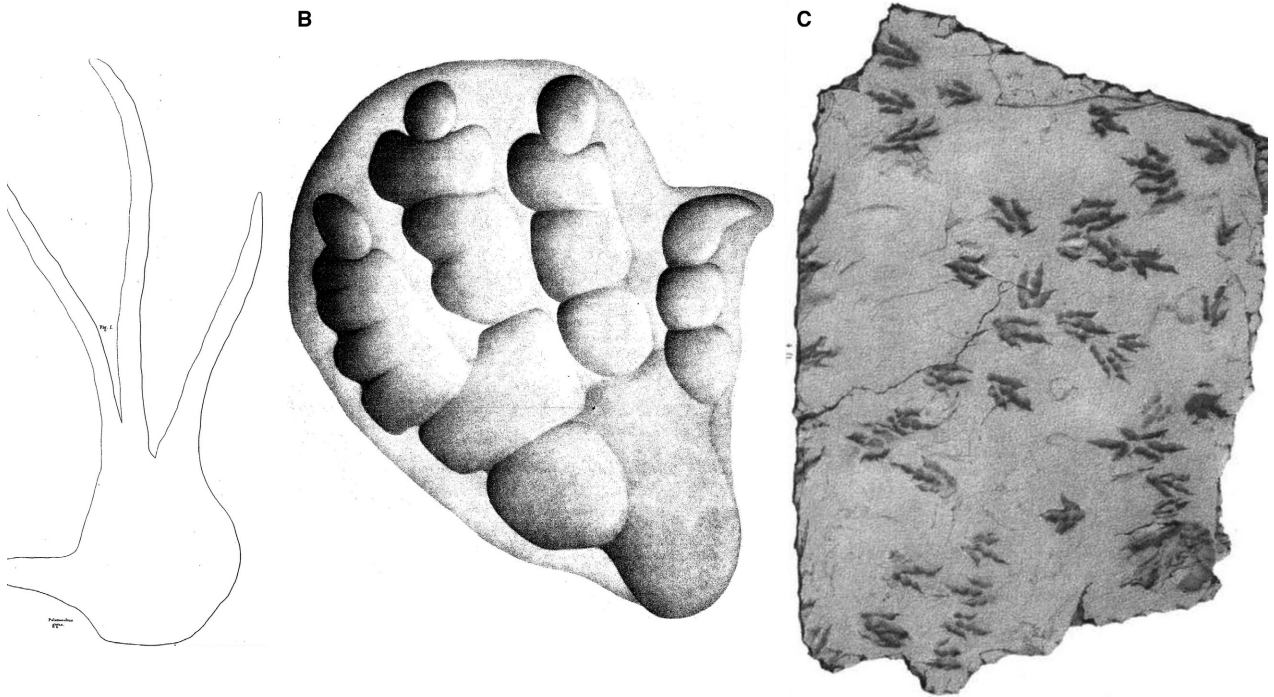
## CURRENT PRACTICE

Before discussing the methods that we recommend for capturing, recording, storing and disseminating 3D data, it is worth reviewing current and historical practice in the field.

As previously noted, since the early 1800s the standard in documenting tracks was to produce a drawing or photograph, usually in top-down view (that is, normal to the

tracking surface). The unstated priority in doing so was to record the outline, such that metrics like length, width and interdigital angle can be measured, as well as pace angulation and stride length in the case of multiple tracks constituting a trackway. Hitchcock himself reported tracks in a variety of ways, including photographs, shaded sketches and simple outlines, even within a single publication (e.g. Hitchcock 1858). Looking at Figure 1, readers will quickly come to the obvious conclusion that a simple outline alone lacks a significant amount of information.

The largest problem with such outlines is not just the lack of data, but the reproducibility of what data are recorded. There are many examples of tracks for which it can be hard to determine where the track ends and the surrounding undeformed tracking surface begins. While any given worker may be able to reproduce outlines consistently, between-worker variation is an unknown which makes comparison of data between studies difficult and prone to error (though this between-worker error may be relatively low; M. Belvedere unpub. data). This is particularly true for ichnotaxonomy, where new ichnotaxa are erected but often presented in the literature only as outlines. Ultimately, an outline should be considered an interpretation, *not* data. When working with osteological material, this issue is partially negated because all new taxa are (or should be) deposited with museums and other such



**FIG. 1.** Three dinosaur tracks as presented by Edward Hitchcock in 1858. A, outline drawing of *Polemarchus gigas* (Hitchcock 1858, pl. 18 fig. 1). B, shaded sketch of *Otozoum moodii* (Hitchcock 1858, pl. 22). C, 'ambrotype sketch' of a slab with *Brontozoum exsertum* (Hitchcock 1858, pl. 40 fig. 3).

institutions, and another worker can visit the specimen directly (funds and time permitting). With tracks, this is not always the case; new ichnotaxa can be erected on specimens that remain in the field and are ultimately subject to weathering, erosion or poaching. While plaster, fibreglass, silicone or latex casts might be made in such scenarios, they may be more prone to breakage, distortion, degradation or even disposal over time.

Acknowledging this subjectivity in track outlines is nothing new, and workers have always been attempting to mitigate or remove it where possible. Placing transparent plastic over a track and tracing outlines directly onto it offers some level of reproducibility, though even here there is an element of subjectivity between workers. Photographs also provide a level of objectivity, and many workers have adopted a process of publishing a photograph beside their drawing, essentially presenting data and interpretation beside each other. Best practice in such cases involves the photograph being taken in low-angle light, usually from the upper left (the direction of which is noted on the photograph or in the figure caption), which casts strong shadows and portrays topography more clearly, though this is not always possible, particularly with specimens in the field. Still, the fundamental fact remains that even in this case, 3D morphology is not being adequately recorded or communicated.

The goal of data collection is to record the morphology in full; objectively, repeatably, and to as high a degree of accuracy and precision as is feasible. Until relatively recently, capturing 3D morphology in such a way was prohibitively expensive or difficult, requiring laser scanners (Bates *et al.* 2008a, b, 2009; Petti *et al.* 2008; Falkingham *et al.* 2009; Adams *et al.* 2010; Belvedere & Mietto 2010; Bennett *et al.* 2013; Castanera *et al.* 2013; Marsicano *et al.* 2014; Razzolini *et al.* 2014; Klein *et al.* 2016) or expensive proprietary software (Breithaupt *et al.* 2004; Matthews *et al.* 2016). However, recent advances in both consumer hardware (Falkingham 2013) and software (Falkingham 2012; Mallison & Wings 2014; Matthews *et al.* 2016; Belvedere *et al.* 2018) have made such methods available to all.

Our aim here is to propose a standardized method of data collection within our field, such that full 3D data is captured, communicated and archived in an objective, repeatable and precise manner. To this end, we have together developed guidelines to help researchers ensure they capture the maximum amount of data, and that it can be communicated and archived effectively.

## A STANDARD PROTOCOL

Here we present a new standard protocol for data collection, data presentation, and data dissemination of tracks and traces.

### Data collection

Our stated aim is to record the 3D morphology of a trace. Ultimately it does not matter what method is used to capture the data, providing it does so reliably, to a necessary degree of accuracy, and captures the 3D form to the fullest extent possible. Until recently the prohibitive cost or complexity of 3D digitization techniques would make any request for researchers to incorporate such data collection as standard unreasonable. However, such techniques (particularly photogrammetry) are now so cheap and easy to use that we consider it realistic to suggest that all reports of traces include 3D data collection, especially when new ichnotaxa are being erected. A growing number of ichnologists are now collecting such data regularly, and we wish to codify the practice here.

The capture of 3D morphology essentially comes down to photogrammetry and laser scanning. We will assume that if one has access to a laser scanner, one is familiar with its use and software. Photogrammetry is the more accessible method, available to anyone with access to a camera (even if only a camera phone) and computer. The method has come a long way in terms of ease of use and required hardware over the last ten years (Breithaupt *et al.* 2004; Matthews *et al.* 2006; Bates *et al.* 2009; Petti *et al.* 2008). There are several publications already available explaining best practice in producing 3D models from photographs, and the available software packages that can be used (Falkingham 2012; Mallison & Wings 2014; Matthews *et al.* 2016). We will not detail such methods here, but instead refer readers to the above publications, and to the wider literature (both academic and web) to seek out the most up-to-date programs and techniques as they need them.

We note here that where possible, digitization should be carried out prior to any physical replication (e.g. moulding or casting; see Maceo & Riskind 1991) as the physical replication process may alter the fossil either physically or chemically. Indeed, for these reasons (as well as reasons of archiving and sharing that we discuss below) digital replicas are favourable to physical ones.

Several key works have detailed the measurements that should (or can) be taken from a track (Haubold 1971; Leonardi 1987; Thulborn 1990; Lockley 1991; Farlow *et al.* 2012) and researchers can adhere to these guidelines by taking measurements either directly from the track (or cast/peel) or from the digital model. Best practice dictates that researchers should detail either in figures or text how and where measurements were taken. Armed with a digital model of the specimen, a researcher can be confident that their measurements are verifiable, and that should another worker use different definitions (see Falkingham 2016) they can make their own measurements directly. Alternatively, 3D data can be incorporated into analyses

that rely on automatic analysis and measurement of tracks, such as in the mediotype analysis recently proposed by Belvedere *et al.* (2018)

#### *Summary.*

1. Collect 3D data of any traces that will be core to the conclusions of the study.
2. These data should be of a high resolution, such that other researchers can replicate and build upon the original findings.
3. Data is method agnostic; i.e. it does not matter if data is captured through photogrammetry, laser scanning, or other means, providing the resolution/accuracy is high enough that conclusions are replicable and other workers can find value in the data. File format issues will be discussed in Data archiving below.
4. As much data should be collected as possible, but at the very least:
  - a. Digital models of potential new ichnotaxa or other figured specimens
  - b. Representative tracks from within a long trackway or larger tracksite (we recognize that large-scale data collection is not always feasible, though should be attempted if possible).

#### *Data presentation*

Having collected three-dimensional data, said data must be communicated effectively. In line with the growing number of authors now collecting 3D data, many recent papers describing traces have presented 3D height maps of specimens recorded in 3D (e.g. Castanera *et al.* 2013; Bennett *et al.* 2014; Fiorillo *et al.* 2014; McCrea *et al.* 2014; Razzolini *et al.* 2014, 2017; Xing *et al.* 2014, 2016a, b; Cifton *et al.* 2015; Díaz-Martínez *et al.* 2016; Klein *et al.* 2016; Salisbury *et al.* 2016; Marty *et al.* 2017) and we propose that such practice becomes standard for the field, whether digital models are produced via photogrammetry, laser scanning or other means.

We recommend that best practice is to present a ‘true colour’ image (e.g. a photograph, orthophoto or textured render) side-by-side with a ‘false colour’ image (e.g. a height/depth map, contour map or simply a solid colour lit to accentuate topography) of the 3D model in the same orientation, scale and position (Fig. 2A). These may be further enhanced by a third panel presenting the author’s interpretation in the form of a line drawing. In this way, the original, processed and interpreted data are presented together for easy comparison by readers (e.g. Marty *et al.* 2017; Razzolini *et al.* 2017; Xing *et al.* 2016b). The same process can be used for individual tracks, trackways or entire tracksites. In cases where the morphology of the track includes significant overhanging

or occluding features, it is advisable to present also an oblique view of the track, enabling readers to see the pertinent features. Workers may wish to provide such a view in any case, to convey 3D topography. We provide an example following this protocol in Fig. 2A. More advanced visualizations such as cross-section profiles may be employed as necessary (Fig. 2B–N). It would be difficult to standardize techniques for making line drawings as the reason for including such will vary from study to study. Authors may wish to include outlines in order to remove background noise they consider ‘extramorphological’, and as such clean line drawings that highlight the edges of the trace are recommended.

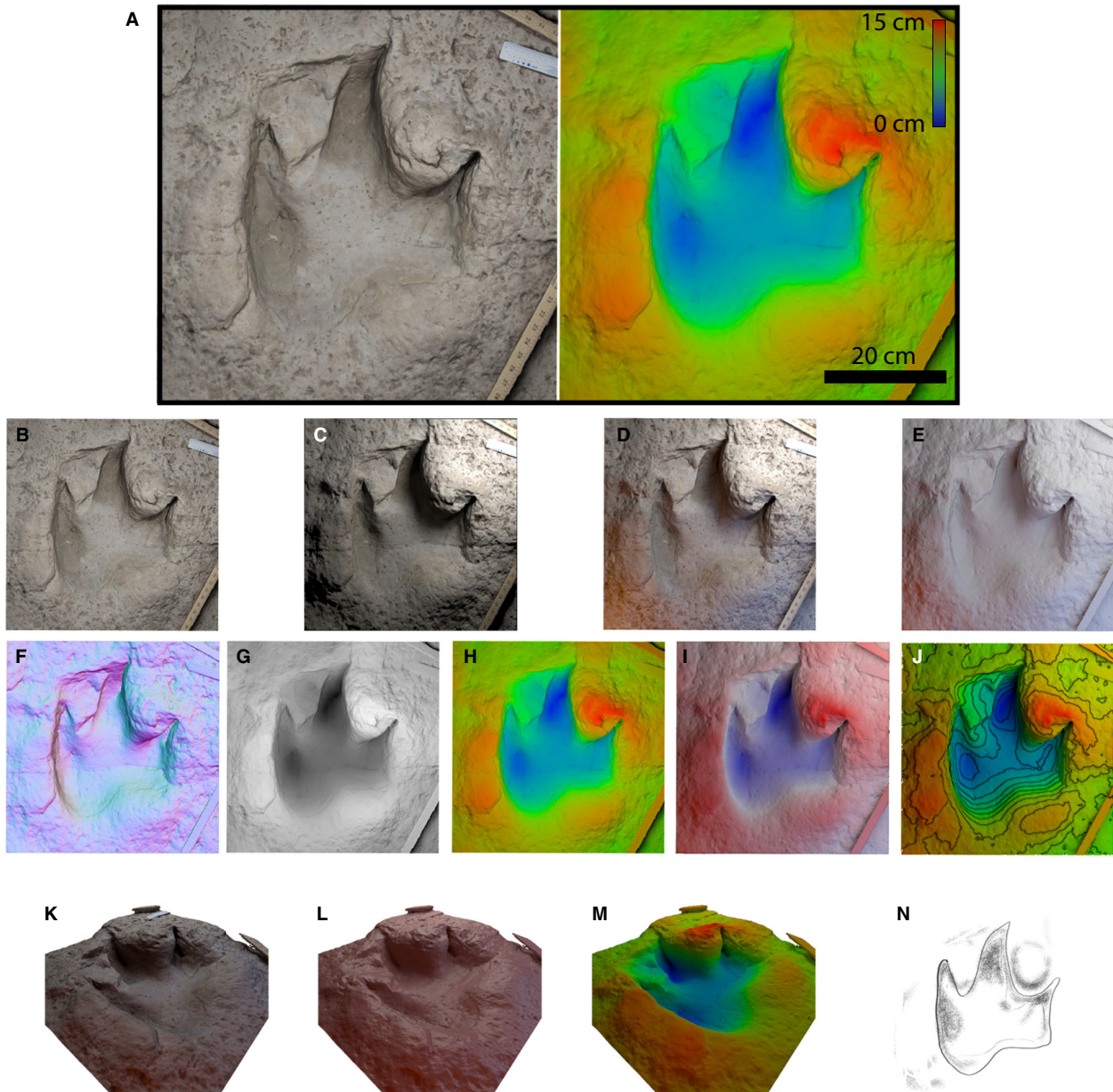
In our example (Fig. 2), we have presented a range of possible height-map colour scales, including greyscale. We leave specific colour choice at the discretion of individual authors, who may wish to use different colours for various reasons (e.g. the common red–green–blue colour scale is difficult to read by sufferers of colour-blindness; some journals charge for colour figures).

*Linear or logarithmic scales?* It may not always be ideal to apply the height map as a linear scale. In cases where tracks have large, broad features at depth, but detail at the top (e.g. shallow displacement rims around a deep track), or vice versa (subtle changes in depth at the base of a track), it may be more appropriate to apply a logarithmic (or exponential) scale to highlight the features of interest to readers. Doing so requires explicitly stating that this is the case in the figure caption, and ensuring that a labelled colour scale is present as part of the figure.

*Video and embedded 3D.* Some publishing venues are moving towards using ‘rich media’ in online versions of papers; videos, 3D PDF and embedded 3D objects to name a few. While this practice should of course be encouraged, we caution that such methods should be used as a supplement to presenting 3D data in the manuscript as figures, and not a replacement. We also argue that such means of presentation are not a substitute for providing the actual data as Supporting Information, as we discuss below.

#### *Summary.*

1. Tracks and traces should be presented as photo (or ‘true colour’ image) and heightmap (or other ‘false colour’ image), side-by-side, in the same orientation.
2. These may be supplemented with interpretive line drawings.
3. Oblique views should be used to reveal otherwise occluded features, or to better convey 3D morphology.
4. In addition to scale bars and labels, a colour scale should ideally be included in the figure, or at least described in the figure caption.



**FIG. 2.** A range of ways to present 3D data. We consider a combination of true-colour and ‘false colour’ image (A) to be a minimum for communicating 3D morphology in published work. True-colour images may come from photos taken in the field, or renders of textured models in flat light (B), a single directed light (C, light from upper right), or multiple lights of different hue (D). Morphology may also be communicated through images of untextured models (E). False-colour images are used to convey 3D morphology, and might include normal maps (F), or height maps in a range of colours, e.g. black–white (G), blue–green–red (H) or blue–white–red (I). Height contours may also be added (J). Additionally, authors may wish to include oblique views, e.g.: K, textured mesh; L, false-colour mesh; M, height mapped mesh. Finally, interpretive images including outline or shaded drawings (N) may be included as well. Scale bar in A represents 20 cm. Height maps range over 15 cm. Contours in J are at 1 cm increments. Scale bars are not present on smaller images B–N for clarity, but should normally be included. Photos and model of this track (a theropod track from Glen Rose, Texas) are available in Falkingham (2018).

5. We do not recommend any specific colour scale.
6. Videos, 3D PDFs, and embedded objects should be considered supplementary to the above, but not as a replacement for providing usable 3D data.

#### *Data archiving*

Possibly the most crucial part of our protocol is in archiving the collected data in a way that enables other

researchers to work with it. It is a core part of the scientific method that experiments should be repeatable and testable. It is imperative, therefore, that 3D data collected in the study of tracks and traces adheres to the guiding principles currently being more broadly applied in palaeontology (Davies *et al.* 2017). Here, we outline archival principles that we hope will become standard practice in ichnology.

Any publication using 3D data should ideally make that data available at the time of publication. Indeed, this is now widely a fundamental criterion for publication in many peer-reviewed scientific journals anyway (Davies *et al.* 2017) and can similarly be a requirement for many funding agencies or government bodies. If data upon which descriptions or measurements are based are not made available, conclusions cannot be verified by other researchers. One may argue that repeatability exists on some level in so much as another worker may visit the field site or museum where the original fossil exists. But this line of thinking is flawed in two ways. First is that, in the case of tracks and traces left in the field, the fossils are subject to change through weathering and erosion, etc., and therefore no longer exist in the form in which they were described. It may also be the case that fossil traces are found on private land, or are potentially vulnerable to being stolen, vandalized or destroyed; in these and other cases, publishing specific locality information may not be feasible. The second is that in an age where we can transfer gigabytes (even terabytes) of data with relative ease, and view 3D data at our desks, we should do so in favour of requiring other researchers to travel the globe. Of course, visiting specimens first hand is always preferable, but in many cases time or financial constraints make this difficult or impossible.

It is important that when the digital data is made available, it is archived in such a way as to ensure that it will continue to be available, and discoverable, for the foreseeable future. The most obvious way of doing so is to include the data as Supporting Information. In this case, the data will be available and discoverable for as long as the paper itself is. However, we recognize that many journals have limits (or costs) related to the possible size of supplemental data, which may make hosting gigabytes of data with the publisher difficult. Books pose a different problem; including disks increases publishing costs and limits data availability, not to mention that disks are frequently lost and that the time of compatibility for CDs, DVDs and other physical media is probably limited. We therefore suggest that when archiving is not possible with the publisher, that an open repository such as Figshare (<https://figshare.com>), Zenodo (<https://zenodo.org/>) or similar is used, and that the data should be linked directly from the published work (journal article, book or online

resource). Both of the repositories mentioned above are backed by major institutions and journals, and ensure the data is available for the lifetime of the repository (currently 10 and 20 years respectively). These services provide free hosting for large files, and can allocate a DOI which, if data is uploaded prior to publication, can be linked to in the paper, book or other work (note that these services can allow workers to upload data and reserve a DOI, but not make the data publicly available until the associated work is published). Several authors have already used such a system, archiving data with these repositories and providing a link in the paper (e.g. Lallensack *et al.* 2016; Marty *et al.* 2017; Lomax *et al.* 2017). Using these services, rather than institutional or personal servers, ensures long-term access and discoverability, which in turn will help to drive citations of associated works.

Having made the case that data should be archived, let us address exactly *what* that data should be, both in terms of content, and format.

#### *Content and raw data*

The most important data to archive is that upon which any descriptions or conclusions are based. Generally, this will consist of cleaned and aligned 3D models that enable other researchers to replicate the original findings.

However, we acknowledge that processed data may introduce inaccuracies or discrepancies. For instance, when meshing point cloud data, the process will generally involve a level of interpolation and retopologizing. Also, the scaling process inherent in most photogrammetry workflows may be a source of error if not carried out correctly.

Because of this, it is essential that where possible raw data (e.g. captured laser scans or photographs used in photogrammetry) and any metadata (e.g. auto-generated 3D reconstruction reports) are included with data. Especially for photogrammetry, this has the added benefit of making raw data available in the future when software and workflows are inevitably improved, potentially making more accurate or higher resolution models available down the line.

*Format.* With regards to the format, important factors are that the data are open, and not reliant on proprietary software (which may become deprecated, or simply remain unaffordable to many). For processed 3D data, the most common open formats are \*.PLY and \*.OBJ. Both formats are open and can generally be accessed using any 3D software. Colour information can be stored either directly, associated with each vertex (as in PLY or XYZ), or as a separate texture file. Given that digital storage capacity is

continuously increasing (Kryder's law), we recommend against downsampling data unless absolutely necessary. Whilst large files of several gigabytes may be unwieldy now, in only a few years we will see them as inconsequential; consider how large a file of several tens of megabytes seemed in the mid 1990s. Formats that do not allow easy manipulation or extraction of the data, such as 3D PDFs should not be used as a means of making data available.

Photographs are best stored in the original format in which they were taken; usually JPG. RAW or TIFF files may also be stored, as unlike JPGs they are lossless formats. However, because of this, RAW and TIFF files are considerably larger, and consequently many people do not take or use photographs in these formats. When archiving, we recommend storing the original JPG (or other) files within a zipped folder. The original files will contain EXIF data regarding the camera make, lens and settings that may be useful in future analyses, particularly in photogrammetric techniques where such EXIF data can make the difference between a great reconstruction and a failed one.

When raw data is collected in a proprietary format, for instance when using LiDAR or other laser scanning techniques, it may be prudent to convert that data into a more open format. For instance, exporting raw laser scan data as ASCII text files containing XYZ vertices, luminance and colour values makes the data available to all workers, and future proofs against the proprietary format becoming obsolete. This recommendation comes from personal experience, as some of us (PLF, KTB, M. Belvedere) have laser scan data which was collected a decade ago, but no longer possess the software required to open it.

#### Summary.

1. 3D data should be made freely available at the time of publication.
2. The data should be archived with a digital object identifier (DOI), and permanently associated with the publication as supplemental data, hosted either by the publisher, or by an external, public, repository.
3. Data should be in a non-proprietary format to facilitate accessibility to those without specialist (expensive) software licenses.
4. Raw data should be included if possible:
  - a. In the case of photogrammetry, all photos used to reconstruct the model should be included
  - b. Photogrammetric models should be cleaned and aligned, and the process documented
  - c. For laser scans, cleaned and aligned point clouds are preferable (noise can be much harder to differentiate post-hoc/if not familiar with it); again, the cleaning and aligning process should be stated
  - d. Downsampling should be avoided if possible (a large file now will seem tiny in 10 years)
- e. Other methods (e.g. CT) should follow the policies outlined in Davies *et al.* (2017).

## DISCUSSION AND CONCLUDING REMARKS

Going forward, we hope that the field as a whole will be receptive to the primary aspects of our proposal: that tracks should be digitally recorded; that the 3D data should be used in communication and analyses; and that said data be made available with the associated work at the time of publication. While 3D data collection and availability are important to all aspects of ichnology, we note that it is essential when new ichnotaxa are being erected (Belvedere *et al.* 2018). Undoubtedly there shall be nuanced or outlier cases in which some aspect of the above is not feasible and, when such cases occur, we implore authors to explicitly state why 3D data was not collected, presented or made available. The result will, hopefully, be that our science becomes simultaneously more robust and more accessible over time.

We consider a bare minimum of our protocol to be the collection of 3D data of individual tracks of interest, especially in the case of type specimens. Larger scale 3D data, such as that pertaining to whole track-sites, is currently more difficult to obtain, process and archive, and it is understandable that including such data is not always feasible. Still, we hope that colleagues will make every effort to include such data when they can, particularly when conclusions and interpretations are drawn from larger scale features such as trackway parameters.

What we have not covered is how all of this data we encourage generating and archiving will be discoverable. A number of us have in the past considered an online repository specifically for digitized tracks (M. Belvedere *et al.* unpub. data) but so far this has failed to gain traction for a number of logistical reasons. If we look at what is happening in the wider field, we can see several repositories for morphological data (e.g. MorphoSource, MorphoBank, Aves3D). Whilst these resources are of immense use to science, there is an element of fragmentation in where and how 3D data are stored, which can make meta-analyses difficult. There is also confusion arising over the different policies regarding access to data on these repositories (which is one of the reasons we strongly recommend making data fully available at time of publication). It may be best in future to rely on data repositories such as those listed above (e.g. Figshare, Zenodo), and instead focus on creating front-facing searchable databases that link directly to these repositories. This would ideally create multiple means of finding the data while maintaining universal access and longevity of the data itself.



**TABLE 1.** List of ichnological papers for which 3D data were made available after publication.

References	Description of data	Data DOI
Abrahams <i>et al.</i> (2017)	Photos and PLY of tracks	<a href="https://doi.org/10.6084/m9.figshare.5683732">https://doi.org/10.6084/m9.figshare.5683732</a>
Belvedere & Mietto (2010)	PLY derived from laserscans of the cast of the tracks	<a href="https://doi.org/10.6084/m9.figshare.5531170">https://doi.org/10.6084/m9.figshare.5531170</a>
Falkingham <i>et al.</i> (2010)	Photos and model of bird track	<a href="https://doi.org/10.6084/m9.figshare.5590396">https://doi.org/10.6084/m9.figshare.5590396</a>
Falkingham <i>et al.</i> (2014)	Photos and model of Bird's 'Chase Sequence' 1946	<a href="https://doi.org/10.6084/m9.figshare.1297750">https://doi.org/10.6084/m9.figshare.1297750</a>
Klein <i>et al.</i> (2015)	PLY file, texture file, and 3D PDF of tracks	<a href="https://doi.org/10.6084/m9.figshare.c.2133546">https://doi.org/10.6084/m9.figshare.c.2133546</a>
Milàn & Bromley (2008)	Photos and models of emu track and undertrack in cement	<a href="https://doi.org/10.6084/m9.figshare.5554147">https://doi.org/10.6084/m9.figshare.5554147</a>
Milàn & Hedegaard (2010)	Tracks from 12 species of crocodile, models and photos	<a href="https://doi.org/10.5281/zenodo.31711">https://doi.org/10.5281/zenodo.31711</a>
Manning <i>et al.</i> (2008)	Possible tyrannosaurid track photogrammetric model and photos	<a href="https://doi.org/10.6084/m9.figshare.1117833">https://doi.org/10.6084/m9.figshare.1117833</a>
Xing <i>et al.</i> (2016a)	Photos and model of sauropod tracks	<a href="https://doi.org/10.6084/m9.figshare.3203359">https://doi.org/10.6084/m9.figshare.3203359</a>
Xing, <i>et al.</i> (2016b)	Photos and model of ornithischian track	<a href="https://doi.org/10.6084/m9.figshare.4231679">https://doi.org/10.6084/m9.figshare.4231679</a>

We close with the message that 'it's never too late'. Because photogrammetry requires only digital photographs as input in order to generate a 3D model, it is possible to generate models using photographs that were taken long before the method was feasible. In an extreme sense, there is no real age limit on photos that can retrospectively generate useful 3D data (Falkingham *et al.* 2014; Lallensack *et al.* 2015). While collections of old digitized photos might prove usable, more practical scenarios may involve more recent collections of digital photos taken for documentation purposes, but perhaps without photogrammetry in mind at the time. Those photographs may now be used to generate new 3D data via post-hoc photogrammetry, preserving and making accessible specimens first described some years ago. In doing so, authors will rejuvenate past publications, benefiting from additional citations while the wider community benefits from increased access to data. By way of example, we present in Table 1 a list of publications for which 3D data has since been made available, and the DOI/links to said data. In this way we hope to formally

associate the data and publications, and aid in future discoverability. We caution, however, that going forward this should not be interpreted as a precedent for refusing to make data available at the time of publication. Individuals, palaeoichnology and the wider palaeontological community as a whole, can only benefit from an attitude that encourages data generation and sharing in this way, and we look forward to continuing to work in such a collegial field.

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## REFERENCES

- ABRAHAMAS, M., BORDY, E. M., SCISCIO, L. and KNOLL, F. 2017. Scampering, trotting, walking tridactyl bipedal dinosaurs in southern Africa: ichnological account of a Lower Jurassic palaeosurface (upper Elliot Formation, Roma Valley) in Lesotho. *Historical Biology*, **29**, 1–18.
- ADAMS, T., STRGANAC, C., POLCYN, M. J. and JACOBS, L. L. 2010. High resolution three-dimensional laser-scanning of the type specimen of *Eubrontes* (?) *glenrosensis* Shuler, 1935, from the Comanchean (Lower Cretaceous) of Texas: implications for digital archiving and preservation. *Palaeontologia Electronica*, **13.3.1T**, 11 pp.
- ALLEN, J. R. L. 1989. Fossil vertebrate tracks and indenter mechanics. *Journal of the Geological Society*, **146**, 600–602.
- AVANZINI, M. 1998. Anatomy of a footprint: bioturbation as a key to understanding dinosaur walk dynamics. *Ichnos*, **6**, 129–139.
- PIÑUELA, L. and GARCÍA-RAMOS, J. C. 2012. Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. *Lethaia*, **45**, 238–252.
- BATES, K. T., BREITHAUP, B. H., FALKINGHAM, P. L., MATTHEWS, N. A., HODGETTS, D. and MANNING, P. L. 2009. Integrated LiDAR & photogrammetric documentation of the Red Gulch dinosaur tracksite (Wyoming, USA). 101–103. In FOSS, S. E., CAVIN, J. L., BROWN, T., KIRKLAND, J. I. and SANTUCCI, V. L. (eds). *Proceedings of the Eighth Conference on Fossil Resources*, May 19–21, St George, Utah. <https://www.nps.gov/subjects/fossils/research-volumes.htm>
- MANNING, P. L., VILA, B. and HODGETTS, D. 2008a. Three dimensional modelling and analysis of dinosaur trackways. *Palaeontology*, **51**, 999–1010.
- RARITY, F., MANNING, P. L., HODGETTS, D., VILA, B., OMS, O., GALOBART, À. and 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. *Journal of the Geological Society*, **165**, 115–127.

- SAVAGE, R., PATAKY, T. C., MORSE, S. A., WEBSTER, E., FALKINGHAM, P. L., REN, L., QIAN, Z., BENNETT, M. R., McCLYMONT, J. and CROMPTON, R. H. 2013. Does footprint depth correlate with foot motion and pressure? *Journal of the Royal Society: Interface*, **10**, 20130009.
- BELVEDERE, M. and MIETTO, P. 2010. First evidence of stegosaurian *Deltapodus* footprints in North Africa (Iouaridène Formation, Upper Jurassic, Morocco). *Palaeontology*, **53**, 233–240.
- BENNETT, M. R., MARTY, D., BUDKA, M., REYNOLDS, S. C. and BAKIROV, R. 2018. Stat-tracks and mediotypes: powerful tools for modern ichnology based on 3D models. *PeerJ*, **6**, e4247.
- BENNETT, M. R., FALKINGHAM, P. L., MORSE, S. A., BATES, K. and 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.
- MORSE, S. A. and FALKINGHAM, P. L. 2014. Tracks made by swimming Hippopotami: an example from Koobi Fora (Turkana Basin, Kenya). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **409**, 9–23.
- BREITHAUPT, B. H., MATTHEWS, N. and NOBLE, T. 2004. An integrated approach to three-dimensional data collection at dinosaur tracksites in the Rocky Mountain West. *Ichnos*, **11**, 11–26.
- CASTANERA, D., VILA, B., RAZZOLINI, N. L., FALKINGHAM, P. L., CANUDO, J. I., MANNING, P. L. and GALOBART, À. 2013. Manus track preservation bias as a key factor for assessing trackmaker identity and quadrupedalism in Basal Ornithopods. *PLoS One*, **8**, e54177.
- CITTON, P., NICOSIA, U., NICOLOSI, I., CARLUCCIO, R. and ROMANO, M. 2015. Elongated theropod tracks from the Cretaceous Apenninic Carbonate Platform of southern Latium (central Italy). *Palaeontologia Electronica*, **18**.3.49A, 12 pp.
- DAVIES, T. G., RAHMAN, I. A., LAUTENSCHLAGER, S., CUNNINGHAM, J. A., ASHER, R. J., BARRETT, P. M., BATES, K. T., BENGTON, S., BENSON, R. B. J., BOYER, D. M., BRAGA, J., BRIGHT, J. A., CLAESSENS, L. P. A. M., COX, P. G., DONG, X.-P., EVANS, A. R., FALKINGHAM, P. L., FRIEDMAN, M., GARWOOD, R. J., GOSWAMI, A., HUTCHINSON, J. R., JEFFERY, N. S., JOHANSON, Z., LEBRUN, R., MARTÍNEZ-PÉREZ, C., MARUGÁN-LOBÓN, J., O'HIGGINS, P. M., METSCHER, B., ORLIAC, M., ROWE, T. B., RÜCKLIN, M., SÁNCHEZ-VILLAGRA, M. R., SHUBIN, N. H., SMITH, S. Y., STARCK, J. M., STRINGER, C., SUMMERS, A. P., SUTTON, M. D., WALSH, S. A., WEISBECKER, V., WITMER, L. M., WROE, S., YIN, Z., RAYFIELD, E. J. and DONOGHUE, P. C. J. 2017. Open data and digital morphology. *Proceedings of the Royal Society B*, **284**, 20170194.
- DÍAZ-MARTÍNEZ, I., SUAREZ-HERNANDO, O., MARTÍNEZ-GARCÍA, B. M., LARRASOÑA, J. C. and MURELAGA, X. 2016. First bird footprints from the lower Miocene Lerín Formation, Ebro Basin, Spain. *Palaeontologia Electronica*, **19**.1.7A, 15 pp.
- ELLIS, R. G. and GATESY, S. M. 2013. A biplanar X-ray method for three-dimensional analysis of track formation. *Palaeontologia Electronica*, **16**.1.1T, 16 pp.
- FALKINGHAM, P. L. 2012. Acquisition of high resolution three-dimensional models using free, open-source, photogrammetric software. *Palaeontologia Electronica*, **15**.1.1T, 15 pp.
- 2013. Low cost 3D scanning using off-the-shelf video gaming peripherals. *Journal of Paleontological Techniques*, **11**, 1–9.
- 2014. Interpreting ecology and behaviour from the vertebrate fossil track record. *Journal of Zoology*, **292**, 222–228.
- 2016. Applying objective methods to subjective track outlines. 72–81. In FALKINGHAM, P. L., MARTY, D. and RICHTER, A. (eds). *Dinosaur tracks: the next steps*. Indiana University Press.
- 2018. Tridactyl dinosaur track - Glen Rose, TX, USA. *Figshare*. <https://doi.org/10.6084/m9.figshare.5674696>
- and GATESY, S. M. 2014. The birth of a dinosaur footprint: subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. *Proceedings of the National Academy of Sciences*, **111**, 18279–18284.
- MARGETTS, L., SMITH, I. and MANNING, P. L. 2009. Reinterpretation of palmate and semi-palmate (webbed) fossil tracks; insights from finite element modelling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **271**, 69–76.
- AGENBROAD, L. D., THOMPSON, K. and MANNING, P. L. 2010. Bird tracks at the Hot Springs Mammoth Site, South Dakota, USA. *Ichnos*, **17**, 34–39.
- BATES, K. T. and FARLOW, J. O. 2014. Historical photogrammetry: Bird's Paluxy River dinosaur chase sequence digitally reconstructed as it was prior to excavation 70 years ago. *PLoS One*, **9**, e93247.
- FARLOW, J. O., CHAPMAN, R. E., BREITHAUPT, B. H. and MATTHEWS, N. 2012. The scientific study of dinosaur footprints. 713–759. In BRETT-SURMAN, M. K., HOLTZ, T. R. and FARLOW, J. O. (eds). *The complete dinosaur*. 2nd edn. Indiana University Press.
- FIORILLO, A. R., CONTESSI, M., KOBAYASHI, Y., McCARTHY, P. J., LOCKLEY, M. and LUCAS, S. 2014. Theropod tracks from the lower Cantwell Formation (Upper Cretaceous) of Denali National Park, Alaska, USA with comments on theropod diversity in an ancient, high-latitude terrestrial ecosystem. 429–439. In LOCKLEY, M. and LUCAS, S. G. (eds). *Tracking dinosaurs and other tetrapods in North America*. New Mexico Museum of Natural History & Science, Albuquerque.
- GATESY, S. M. and FALKINGHAM, P. L. 2017. Neither bones nor feet: track morphological variation and 'preservation quality'. *Journal of Vertebrate Paleontology*, **37**, e1314298.
- MIDDLETON, K. M., JENKINS, F. A. and SHUBIN, N. H. 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature*, **399**, 141–144.
- GRAVERSEN, O., MILÀN, J. and LOOPE, D. B. 2007. Dinosaur tectonics: a structural analysis of theropod

- undertracks with a reconstruction of theropod walking dynamics. *Journal of Geology*, **115**, 641–654.
- HAUBOLD, H. 1971. Ichnia amphibiorum et reptiliorum fossilium. *Handbuch der Paläoherpetologie. Part 18*. G. Fischer, Stuttgart.
- HITCHCOCK, E. 1836. Ornithichnology. Description of the foot marks of birds (Ornithichnites) on new Red Sandstone in Massachusetts. *American Journal of Science*, **29**, 307–340.
- 1858. Ichnology of New England: A report on the Sandstone of the Connecticut Valley, especially its fossil footmarks. W. White, Boston, 220 pp.
- KLEIN, H., MILÀN, J., CLEMMENSEN, L. B., FROBØSE, N., MATEUS, O., KLEIN, N., ADOLFSEN, J. S., ESTRUP, E. J. and WINGS, O. 2015. Archosaur footprints (cf. *Brachychirotherium*) with unusual morphology from the Upper Triassic Fleming Fjord Formation (Norian–Rhaetian) of East Greenland. Geological Society, London, Special Publications, 434, 71–85.
- WIZEVICH, M. C., THÜRING, B., MARTY, D., THÜRING, S., FALKINGHAM, P. and MEYER, C. A. 2016. Triassic chirotheriid footprints from the Swiss Alps: ichnotaxonomy and depositional environment (Cantons Wallis & Glarus). *Swiss Journal of Palaeontology*, **135**(2), 295–314.
- LALLENSACK, J. N., SANDER, P. M., KNÖTSCHKE, N. and WINGS, O. 2015. Dinosaur tracks from the Langenberg Quarry (Late Jurassic, Germany) reconstructed with historical photogrammetry: evidence for large theropods soon after insular dwarfism. *Palaeontologia Electronica*, **18**.2.31A, 34 pp.
- HETEREN, A. H. VAN and WINGS, O. 2016. Geometric morphometric analysis of intratrackway variability: a case study on theropod and ornithopod dinosaur trackways from Münchhagen (Lower Cretaceous, Germany). *PeerJ*, **4**, e2059.
- LEONARDI, G. 1987. *Glossary and manual of tetrapod footprint palaeoichnology*. Publicação do Departamento Nacional da Produção Mineral Brasil, Brazil.
- LOCKLEY, M. G. 1991. *Tracking dinosaurs*. Cambridge University Press, 252 pp.
- MEYER, C. A. and SANTOS, V. F. 1994. Trackway evidence for a herd of juvenile sauropods from the Late Jurassic of Portugal. *Gaia*, **10**, 27–35.
- LOMAX, D. R., FALKINGHAM, P. L., SCHWEIGERT, G. and JIMÉNEZ, A. P. 2017. An 8.5 m long ammonite drag mark from the Upper Jurassic Solnhofen Lithographic Limestones, Germany. *PLoS One*, **12**, e0175426.
- MACEO, P. J. and RISKIND, D. H. 1991. Field and laboratory moldmaking and casting of dinosaur tracks. 419. In GILLETTE, D. D. and LOCKLEY, M. G. (eds). *Dinosaur tracks and traces*. Cambridge University Press.
- MALLISON, H. and WINGS, O. 2014. Photogrammetry in paleontology – a practical guide. *Journal of Paleontological Techniques*, **12**, 1–31.
- MANNING, P. L. 2004. A new approach to the analysis and interpretation of tracks: examples from the Dinosauria. *Geological Society, London, Special Publications*, **228**, 93–123.
- OTT, C. and FALKINGHAM, P. L. 2008. A probable tyrannosaurid track from the Hell Creek Formation (Upper Cretaceous), Montana, United States. *Palaios*, **23**, 645–647.
- MARSICANO, C. A., WILSON, J. A. and SMITH, R. M. 2014. A temnospondyl trackway from the early Mesozoic of western Gondwana and its implications for basal tetrapod locomotion. *PLoS One*, **9**, e103255.
- MARTY, D., STRASSER, A. and MEYER, C. A. 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: implications for the study of fossil footprints. *Ichnos*, **16**, 127–142.
- FALKINGHAM, P. L. and RICHTER, A. 2016. Dinosaur track terminology: a glossary of terms. 399–402. In FALKINGHAM, P. L., MARTY, D. and RICHTER, A. (eds). *Dinosaur tracks: the next steps*. Indiana University Press.
- BELVEDERE, M., RAZZOLINI, N. L., LOCKLEY, M. G., PARATTE, G., CATTIN, M., LOVIS, C. and MEYER, C. A. 2017. The tracks of giant theropods (*Jurabrontes curtedulensis* ichnogen & ichnosp. nov.) from the Late Jurassic of NW Switzerland: palaeoecological & palaeogeographical implications. *Historical Biology*, **2017**, 1–29.
- MATTHEWS, N. A., NOBLE, T. A. and BREITHAUP, B. H. 2006. The application of photogrammetry, remote sensing and geographic information systems (GIS) to fossil resource management. *Bulletin New Mexico Museum of Natural History & Science*, **34**, 119–131.
- NOBLE, T. and BREITHAUP, B. H. 2016. Close-range photogrammetry for 3-D ichnology: the basics of photogrammetric ichnology. 28–55. In FALKINGHAM, P. L., MARTY, D. and RICHTER, A. (eds). *Dinosaur tracks: the next steps*. Indiana University Press.
- MCCREA, R. T., BUCKLEY, L. G., FARLOW, J. O., LOCKLEY, M. G., CURRIE, P. J., MATTHEWS, N. A. and PEMBERTON, S. G. 2014. A ‘terror of tyrannosaurs’: the first trackways of tyrannosaurids and evidence of gregariousness and pathology in Tyrannosauridae. *PLoS One*, **9**, e103613.
- 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.
- and BROMLEY, R. G. 2006. True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **231**, 253–264.
- — 2008. The impact of sediment consistency on track and undertrack morphology: experiments with emu tracks in layered cement. *Ichnos*, **15**, 19–27.
- and HEDEGAARD, R. 2010. Interspecific variation in tracks and trackways from extant crocodiles. *New Mexico Museum of Natural History & Science Bulletin*, **51**, 15–30.
- and LOOPE, D. B. 2007. Preservation and erosion of theropod tracks in eolian deposits: examples from the Middle Jurassic Entrada Sandstone, Utah, U.S.A. *Journal of Geology*, **115**, 375–386.
- AVANZINI, M., CLEMMENSEN, L. B., GARCÍA-RAMOS, J. C. and PINUELA, L. 2006. Theropod foot

- movement recorded from Late Triassic, Early Jurassic and Late Jurassic fossil footprints. *New Mexico Museum of Natural History & Science Bulletin*, **37**, 352–364.
- MINTER, N. J., BRADDY, S. J. and DAVIS, R. B. 2007. Between a rock and a hard place: arthropod trackways and ichnotaxonomy. *Lethaia*, **40**, 365–375.
- PADIAN, K. and OLSEN, P. E. 1984*b*. Footprints of the Komodo monitor and the trackways of fossil reptiles. *Copeia*, **1984**, 662–671.
- 1984*a*. The fossil trackway *Pteraichnus*: not pterosaurian, but crocodylian. *Journal of Paleontology*, **58**, 178–184.
- PETTI, F. M., AVANZINI, M., BELVEDERE, M., DE GASPERI, M., FERRETTI, P., GIRARDI, S., REMONDINO, F. and TOMASONI, R. 2008. Digital 3D modelling of dinosaur footprints by photogrammetry and laser scanning techniques: evaluation of the integrated approach at the Coste dell'Anglone tracksite (Lower Jurassic, Southern Alps, Northern Italy). *Studi Tridentini Scienze Naturali, Acta Geologica*, **83**, 303–315.
- RAZZOLINI, N. L., VILA, B., CASTANERA, D., FALKINGHAM, P. L., BARCO, J. L., CANUDO, J. I., MANNING, P. L. and GALOBART, À. 2014. Intra-trackway morphological variations due to substrate consistency: the El Frontal Dinosaur Tracksite (Lower Cretaceous, Spain). *PLoS One*, **9**, e93708.
- BELVEDERE, M., MARTY, D., PARATTE, G., LOVIS, C., CATTIN, M. and MEYER, C. A. 2017. *Megalosauripus transjuranicus* ichnosp. nov. A new Late Jurassic theropod ichnotaxon from NW Switzerland and implications for tridactyl dinosaur ichnology and ichnotaxonomy. *PLoS One*, **12**, e0180289.
- SALISBURY, S. W., ROMILIO, A., HERNE, M. C., TUCKER, R. T. and NAIR, J. P. 2016. The dinosaurian Ichnofauna of the Lower Cretaceous (Valanginian–Barremian) Broome Sandstone of the Walmadany Area (James Price Point), Dampier Peninsula, Western Australia. *Journal of Vertebrate Paleontology*, **36**, 1–152.
- THULBORN, R. A. 1990. *Dinosaur tracks*. Chapman & Hall, 410 pp.
- and WADE, M. 1989. A footprint as a history of movement. 51–56. In GILLETTE, D. D. and LOCKLEY, M. G. (eds). *Dinosaur tracks and traces*. Cambridge University Press.
- XING, L.-D., PENG, G.-Z., YE, Y., LOCKLEY, M. G., McCREA, R. T., CURRIE, P. J., ZHANG, J.-P. and BURNS, M. E. 2014. Large theropod trackway from the Lower Jurassic Zhenzhuchong Formation of Weiyuan County, Sichuan Province, China: review, new observations and special preservation. *Palaeworld*, **23**, 285–293.
- XING, L., LI, D., FALKINGHAM, P. L., LOCKLEY, M. G., BENTON, M. J., KLEIN, H., ZHANG, J., RAN, H., PERSONS, S. and DAI, H. 2016*a*. Digit-only sauropod pes trackways from China – evidence of swimming or a preservational phenomenon? *Scientific Reports*, **6**, 21138.
- LOCKLEY, M. G., KLEIN, H., FALKINGHAM, P. L., KIM, J. Y. U. L., McCREA, R. T., ZHANG, J., PERSONS, W. S. IV, WANG, T. A. O. and WANG, Z. 2016*b*. First Early Jurassic small ornithischian tracks from Yunnan Province, Southwestern China. *Palaio*, **31**, 516–524.