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True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field

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Abstract

To be able to distinguish between true tracks, undertracks and tracks altered by erosion is of great importance in tetrapod track ichnotaxonomy. This paper reports three experimental approaches to the study of undertracks using the footprints of an emu (*Dromaius novaehollandiae*). Experiment 1 describes successive horizontal sections down through a plaster cast of an emu footprint emplaced in soft mud, revealing a steady downward decrease in the area of the track, particularly the length. This is the result of the movements of the trackmaking limb during impact, forward swing of the body and final kick-off. Experiments 2 and 3 describe vertical sections cut through footprints emplaced in packages of layered, coloured cement, admixed with water to produce different consistencies, firm and semi-fluid. After hardening, the cement block was serial-sectioned vertically, and removal of a lightly cemented layer gave access to two undertrack bedding-plane views. Successive undertracks downward show an increase in horizontal dimensions and decrease in vertical topography of the structure, representing gradual degradation of the track anatomy with depth. In experiment 3, the true track at the tracking surface was deformed by collapse and flow of the substrate after withdrawal of the foot. In this case the undertracks that were formed in layers subjacent to the foot reproduced the morphology of the foot more faithfully than did the true track.

Keywords: Footprint morphology; Undertracks; Erosion; Cement substrate; Sediment properties

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1. Introduction

Fossil vertebrate footprints do not only represent the mere impression made by the trackmaker's foot; they also reflect the local sedimentological conditions, at the moment when the tracks were emplaced as well as information about the trackmaker's behaviour and mode of progression. The intimate relationship between the properties of the substrate and the morphology of the tracks emplaced within it, has only been discussed seriously within the latest years (Allen, 1997; Gatesy et al., 1999; Nadon, 2001; Diedrich, 2002; Fornós et al., 2002; Mazin et al., 2003) and experimental work using artificial sub-

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strates, has greatly added to the understanding of the factors involved in the formation of tracks and undertracks (Allen, 1997; Jackson, 2002; Milàn, 2003; Milàn and Bromley, 2002, 2003, in press; Romano and Whyte, 2003; Manning, 2004). Tracks exposed to different degrees of erosion or tracks exposed in vertical sections can display widely diverging morphologies, in addition to the formation of undertracks. It is most important to be able to recognize vertebrate tracks in vertical sections because most potential track-bearing strata are exposed in steep sections where the cross sections of the tracks traditionally have been described as load casts or slump structures (Loope, 1986). In the latest years, however, more workers have identified and described tracks exposed in cross section (Difley and Ekdale, 2002; Fornós et al., 2002; Currie et al., 2003).

The surface on which the trackmaker walks is termed the tracking surface (Fornós et al., 2002). The foot (manus or pes) of the trackmaker forms a track in the tracking surface. The bottom of the track contains the direct impression of the trackmaker's foot, and is termed the true track. If the sediment is soft enough to allow the foot to sink to a certain depth during foot-fall, vertical, or near-vertical walls are formed from the true track up to the tracking surface; these are termed track walls (Brown, 1999). If the track walls have a slope, produced by the dynamic movement of the foot during the foot-fall, the track at the tracking surface can appear larger than the true track, and is termed the overall track (Brown, 1999). Surrounding the track on the tracking surface, a raised rim can be present, consisting of sediment displaced by the pressure of the foot (Fornós et al., 2002).

The weight and momentum of the trackmaker not only deforms the surface layer, but is also transferred outward and down into the layers subjacent to the trackmaker's foot (Allen, 1997), causing the formation of a stacked succession of the same footprint at several subjacent horizons.

Thulborn (1990) developed two scenarios for undertrack formation that he termed underprints and transmitted prints or ghost prints. Underprints in the sense of Thulborn are produced when the foot penetrates down through the layers in laminated sediments, and these are filled in with sediment of another consistency. In this model the sediment is supposed to be split at successively deeper levels to reveal less complete sections of the footprint. The other model, employing the two terms transmitted prints and ghost prints, occurs when the weight of the foot does not penetrate the layered sediments but deforms them under the foot, thereby making it possible to split the sediment package at successively deeper levels and reveal correspondingly shallower and less detailed versions of the whole footprint.

Lockley (1991) further discussed the phenomenon of undertrack formation, restricting his discussion to Thulborn's (1990) transmitted prints or ghost prints model. In Lockley's (1991) view the undertrack is formed when the weight of an animal deforms the layers below the surface that the animal trod upon, which allows the possibility to expose the same track at different horizons. This model takes an important phenomenon into account. If the tracks from an assemblage consisting of both large and small animals are exposed at the tracking surface, the ichnofauna will consist of both large and small tracks, but if the ichnofauna is exposed along one of the subjacent horizons, only the tracks from the large animals will be present as the heavier animals leave deeper undertracks than the smaller ones (Lockley, 1991). This makes it important to be able to discriminate between true tracks and undertracks when describing fossil track assemblages. The terminology of Lockley (1991) with true tracks and undertracks is the simplest and is today standard terminology in most works on fossil footprints.

However, erosion of a track can further alter its appearance significantly enough to cause misidentification or give rise to the erection of additional ichnotaxa. In that case Thulborn's (1990) model of underprints can be useful to add to the tracking terminology as it describes the case where a track is eroded to different levels.

An emu (*Dromaius novaehollandiae*) was chosen as a trackmaker as the feet, and thus the tracks of emus, bear strong similarities to tridactyl Mesozoic dinosaur footprints and thereby allow almost direct comparison between the experimental and fossil tracks (Milàn, 2003). The digits have all the anatomical details found in theropod footprints, including the small tubercles in the skin, and the configuration of the digital pads around the phalangeal joints. The emu foot is tridactyl, consisting of digits II, III and IV. Digit I is the hallux, which in modern birds is posteriorly directed and used for grasping branches, and which occurs uncommonly as posterolateral traces in dinosaur footprints (Irby, 1995). The hallux is absent in all the ratites, except for the kiwi (Davies, 2002).

The aim of this study is to demonstrate two contingencies. (1) The differences in the morphology of tracks in artificial layered sediments of two different consistencies, by the method developed by Milàn and Bromley (2003); and further to describe and compare the morphology of the undertracks with that of the true track. (2) To make horizontal sections through a plaster cast of an emu track emplaced in deep firm mud to demonstrate the changes in the morphological appearance in a track as it undergoes erosion to different levels, underprints sensu Thulborn (1990), and discuss implications of these sections for the interpretation of fossil footprints.

2. Methods

2.1. Experiment 1

Horizontal sections were cut through a plaster cast of an emu track that was emplaced in deep, firm mud, to simulate the conditions whereby fossil tracks are exposed to different degrees of erosion and to record the changes in footprint morphology occurring with depth. The track was made by an emu walking on mud of a consistency that allowed the foot to sink to a depth of 4.5 cm. The mud was mixed by adding water to the dark organic-rich soil of the emu paddock. To support the plaster cast and make it strong enough to be cut in thin horizontal sections, the whole cast was subsequently embedded in plaster of a different colour.

The blade of the rocksaw is 3 mm wide, so that the distance between each successive section is 3 mm, while slice thickness was maintained at approximately 1 cm to avoid breakage of the slices. The images on one of the two sides of each slice was flipped mirror-wise in order to make adjacent sections comparable.

2.2. Experiments 2 and 3

A package of six layers of coloured cement was produced, each layer of approximately 1 cm thickness, to create a tracking substrate able to record the formation of both true tracks and undertracks, and which was stable enough to be sectioned vertically. The coloured layers consisted of three colours repeated two times, red, blue and natural cement grey. The colours applied to the cement were blue powder colour and red water-based paint.

The foot of an emu was impressed in the package of cement with the approximate weight of an adult emu, 40 kg. A real emu foot was used in the experiments, since it has several advantages over a model. Because the emu foot was fresh, containing freely moving sinews and flexible joints, its behaviour during the experiment closely mimicked a living foot. When weight is applied to the middle digit III in the T-phase, the outer and inner digits II and IV diverge, and when the metatarsus is lifted and moved forward in the K-phase (see below), the digits converge and fold backwards as in the living emu, thus making the footprints very authentic.

The terminology of Thulborn and Wade (1989) is adapted to describe the foot movements during walk. The walking cycle is divided into three distinct phases. The first phase is the touch-down phase (T), where the foot is extended forward, and planted on the ground while the digits diverge. Then follows the weight-bearing phase (W), where the metatarsus is moved forward and the centre of gravity of the animal passes over the foot, which becomes impressed into the substrate. This is succeeded by the kick-off phase (K), where the proximal parts of the foot are raised and the weight is transferred to the distal parts of the digits as the body moves forward. The foot subsequently is lifted in preparation for a new T-phase.

3. Results

3.1. Experiment 1

3.1.1. Horizontal sections

The track selected for sectioning is the impression of a right foot and has digit III most deeply impressed to a depth of 4.5 cm, followed by the metatarsal pad. The impression of Digit II, in this case, is slightly deeper than that of digit IV. The cast of the track is well defined, and shows evidence of the dynamic movement of the foot during the stride, indicated by sloping of the track walls in the metatarsal area, that results from the forward movement of the foot in the T-phase. A long drag trace from the claw of digit III projects distally away from the tip of the digit, originating from the forward movement of the foot while this was lifted towards a new T-phase (Fig. 1A).

The following measurements were taken for each horizontal section cut through the cast of the track. Track length is measured from the proximal end of the metatarsal pad impression to the termination of the impression of digit III. Track width is measured between the terminations of the impressions of digits II and IV. Width of digits is measured in the middle of each digit. All measurements are listed in Table 1.

3.1.1.1. Section 1. The first section is cut approximately 3 mm below the tracking surface. The shape of the track is partly obscured owing to unevenness in

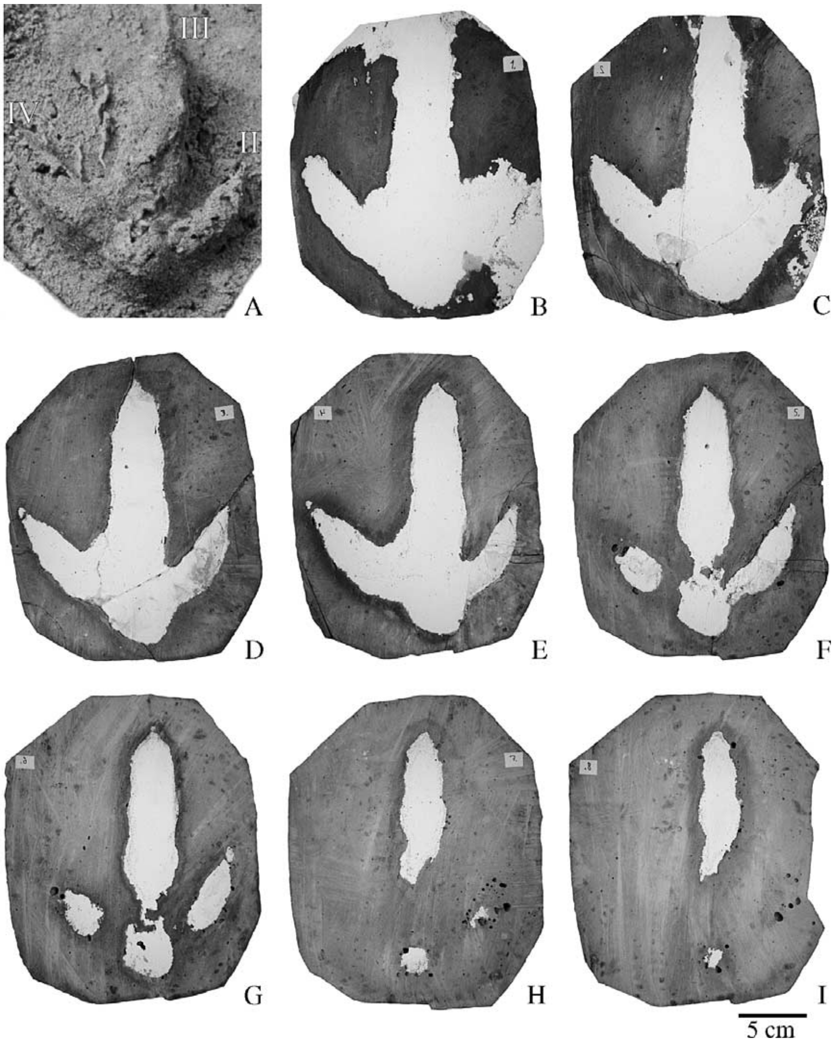

Fig. 1. Horizontal sections through a plaster cast of a true track from the left foot of an emu. (A) The plaster cast of the track as obtained in the field. Notice the presence of the drag trace from the forward movement of the claw of digit III. (B, C) Horizontal sections through the track near the surface. (D, E) Sections cut at 14 and 17 mm depth. The outline of the track at this depth is unbroken. (F, G) The individual digit impressions detach from each other at depths of 25 and 28 mm. (H, I). At depths of 38–41 mm only the most deeply impressed parts of the foot have left impressions. All figures to scale. Digit numbers are indicated by roman numbers. Scale bar 5 cm.

Table 1
Measurements of successive horizontal sections 1–8 through the emu footprint

Section (Figure no.)	Depth below surface (mm)	Footprint Length (mm)	Footprint Width (mm)	Width digit II middle (mm)	Width digit III middle (mm)	Width digit IV middle (mm)
1 (Fig. 1B)	3	230+	181	–	45	34
2 (Fig. 1C)	6	230+	181	34	44	34
3 (Fig. 1D)	14	211	174	26	44	32
4 (Fig. 1E)	17	204	174	26	43	30
5 (Fig. 1F)	25	199	149	24	42	29
6 (Fig. 1G)	28	196	140	24	42	23
7 (Fig. 1H)	38	189	69	9	39	–
8 (Fig. 1I)	41	185	33	–	33	–

The footprint length in sections 1 and 2 are in excess of the length of the slab owing to the elongated drag trace from the claw of digit III. The missing measurement in section 1 is due to unevenness in the sediment surface which obliterated the shape of digit II. Missing measurements in sections 7 and 8 are due to the different penetration depths of the digits into the substrate, compare with Fig. 1A–I.

the original sediment surfaces making it difficult to obtain measurements. The drag trace from the claw of digit III causes the track to extend beyond the edge of the slab (Fig. 1B).

3.1.1.2. Section 2. The drag trace from the claw of digit III still prevents measurements of the track length to be obtained, however the contour of the track is better defined than in Section 1 (Fig. 1C).

3.1.1.3. Sections 3 and 4. These sections are below the level of disturbance from unevenness in the sediment surface and the outline of the track is complete (Fig. 1D, E). The track width does not change in the two sections, but the track becomes 7 mm shorter and the width of digit III's impression becomes 1 mm thinner from Sections 3 to 4.

3.1.1.4. Sections 5 and 6. The track becomes divided as the sections pass through the deep interpad spaces dividing the impressions of the digital pads from the metatarsal pad impression (Fig. 1F, G). In Section 5, the impression of digit IV is disconnected from the metatarsal pad impression, while the impressions of digits III and II still are connected to the metatarsal pad impression by a thinner area. Section 6 shows complete separation of the impressions of digits II and IV from the metatarsal pad impression, and the impression of digit III is still connected by a narrow area.

3.1.1.5. Sections 7 and 8. The impression of digit III becomes separated from the metatarsal pad impression in Sections 7 and 8 and the impression of digit IV disappears in Section 7, as it was impressed less deeply into the substrate than digits II and III (Fig. 1H, I). Digit II, however, is only represented by a small impression in section 7, and disappears completely in Section 8, which represents the very bottom of the track, where only impressions of the distal part of digit III and the metatarsal pad are represented, being the parts of the foot carrying the most weight during the W-phase.

3.2. Experiments 2 and 3

Two tracks in packages of layered cement, produced during the initial phases of the experiments, turned out to be indeed very interesting as failures in the mixtures resulted in unexpected applications. The two tracks are hereafter referred to as tracks 1 and 2.

3.2.1. Track 1, vertical sections

The water:cement ratio for the mixture of the sediment in which track 1 was emplaced was 143 ml/kg. The true track on the surface appears well defined with distinct impressions of the individual digital pads and claws (Fig. 2). The track walls have converged somewhat after removal of the foot owing to the softness of the sediment. The block containing the track was cut in five sections, lettered A–E, perpendicular to the length axis of the digit III impression (Fig. 3).

3.2.1.1. Section A. The claw has cut right through the upper layers and pressed the displaced material

Fig. 2. Experiment 2: track emplaced in layered cement of firm consistency, using a fresh severed emu foot. Digit numbers are indicated with Roman numbers. The true track as it appears on the tracking surface is well defined, showing clear impressions of individual digital pads and claw imprints. Lettered lines correspond to the locations of vertical sections through the track in Fig. 3. Digit numbers are indicated by roman numbers. Scale bar 5 cm.

down into the lower layers, creating a V-shaped undertrack in the lower layers. The width of the undertrack is almost double that of the true track on the surface (Fig. 3A).

3.2.1.2. Section B. Track walls are vertical in this section through the middle of the impression made by digit III. The layers bend nicely around the digit and are unbroken but thinner. The undertracks in the lower layers created by the pressure from the digit, become progressively wider and their relief shallower downwards (Fig. 3B).

3.2.1.3. Section C. This section shows undertrack formation below the impression of all three digits. The sediment between the digits was pressed up by the vertical pressure exercised on the sediment by the foot. As in section B the undertrack becomes wider and its relief shallower with depth (Fig. 3C).

3.2.1.4. Section D. This section passes through the shallow impression from the interpad space separating the digits from the metatarsal pad. Individual digit impressions in the undertrack are only recognizable in the upper layers. The undertrack in the lower layers consists of a single low-relief depression spanning the width of all three digits (Fig. 3D).

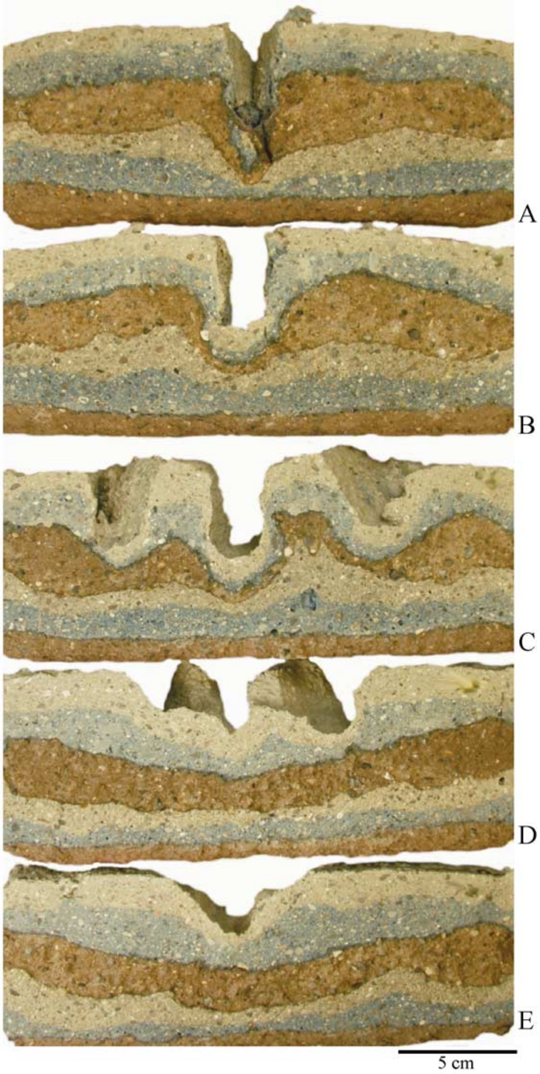

Fig. 3. Five successive vertical sections through the package of layered cement, demonstrating the formation of undertracks below the digits. Notice how the undertracks become successively broader and shallower downward. The distinct layer in the middle of the package was removed to reveal two surfaces with undertracks (Figs. 4 and 5). All sections are seen in rear view. Scale bar 5 cm.

Fig. 4. Hyporelief undertrack of the track shown in Fig. 2, formed approximately 2 cm below the tracking surface. Digit numbers are indicated by roman numbers. Scale bar 5 cm.

3.2.1.5. Section E. The rounded metatarsal pad has left a V-shaped depression at the surface. Low-relief undertracks are formed in the upper layers (Fig. 3E). The lower layers are deformed in the same way as section D.

Fig. 5. Epirelief undertrack of the track shown in Fig. 2, formed approximately 3 cm below the tracking surface. Digit numbers are indicated by roman numbers. Scale bar 5 cm.

3.2.2. Track 1, horizontal sections

The water-based paint used to colour the red cement layer in the middle of the package had an unforeseen effect on the cement. The red layer never really hardened and easily crumbled when touched by hand. This enabled the red layer to be decomposed in water and removed, revealing a complete subsurface horizon with the undertrack exposed. Both the cast of the undertrack in the former red horizon, and the undertrack in the lower layer are revealed in this way (Figs. 4, 5).

The cast of the undertrack represents a surface approximately 2 cm below the tracking surface (Fig. 4). The impressions from the digits are clearly recogniz-

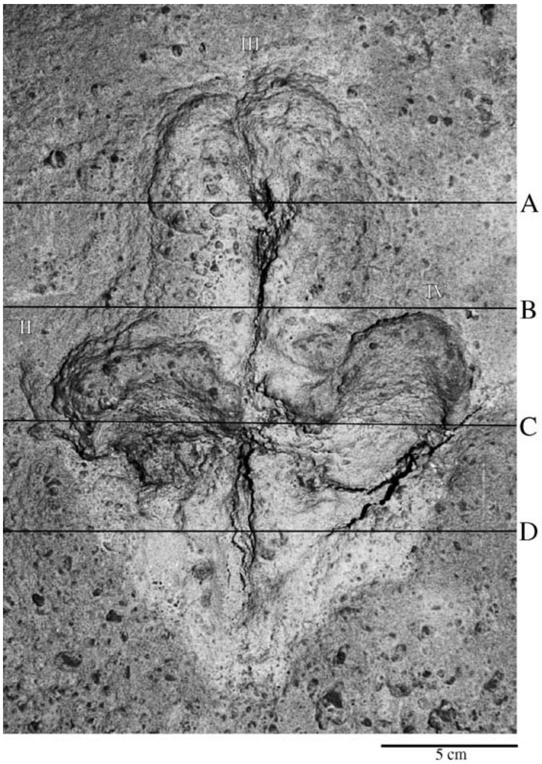

Fig. 6. Experiment 3: track emplaced in a package of layered cement of semi-liquid consistency. After withdrawal of the foot the cement collapsed; notice the prominent rounded “exit hole” from the impression of digit III. Lettered lines correspond to the location of vertical sections in Fig. 7. Digit numbers are indicated by roman numbers. Scale bar 5 cm.

able in hyporelief in the cast as they are the deepest impressed in the cement; compare with sections A–E (Fig. 3). Individual features of the digits, such as digital pads and claw imprints, are not recognizable in the undertrack. The metatarsal area is only represented in slight relief but is still recognizable. At the surface at approximately 4 cm depth, the undertrack is much less well defined, but an imprint of digit III is still represented by a prominent depression, although significantly wider than in the true track (Fig. 5). Digits II and IV are harder to recognize, but shallow depressions in the cement hint at their existence. The overall track shape is hard to recognize at this depth.

3.2.3. Track 2, vertical sections

The water:cement ratio for this sediment was 171 ml/kg. The true track has a collapsed appearance at the surface because of the softness of the cement (Fig. 6). The soft cement that collapsed over the digits during the W-phase, was lifted forward during the K-phase and deployed in front of the digits, forming mounds in front of digits II and IV and a rounded mound containing a centrally placed "exit hole" in front of, and around the impression of digit III.

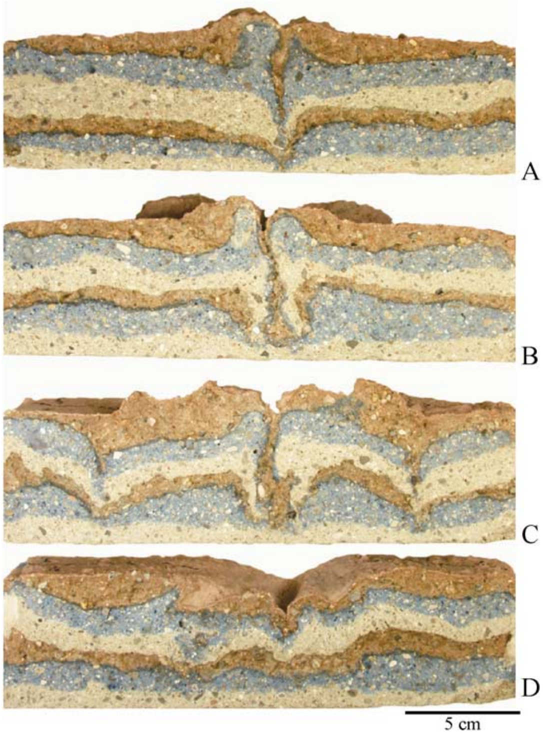

Fig. 7. Four transverse sections cut, after hardening, through the package of layered semi-fluid cement, demonstrating the formation of undertracks and structures resulting from collapse of the fluid sediment, see text for details. All sections seen in frontal view. Scale bar 5 cm.

Fig. 8. Hyporelief undertrack of the track shown in Fig. 6. The undertrack is formed approximately 3 cm below the tracking surface. The impressions from the claws of digits II and III are still recognizable. Digit numbers are indicated by roman numbers. Scale bar 5 cm.

Four sections, lettered A–D, cut perpendicular to the length axis of the impression of digit III, reveal the deformation of the layers and formation of undertracks in soft sediment (Fig. 7).

3.2.3.1. Section A.

This section shows the part of the track where the sharp edges of the claw of digit III has cut through the layers. The upper three layers have been cut by the claw, but owing to the semi-liquid consistency of the sediment, subsequent flow closed the claw impression after lifting of the foot. Shallow V-shaped undertracks from the claw impression are formed within the bottom layers. During lifting of the foot an amount of the soft cement has been dragged upwards causing the formation of a raised rim in the upper layers on both sides of the digit (Fig. 7A).

3.2.3.2. Section B.

The upward and downward movement of the digit has produced a zone of vertical mixing of the layers. An amount of the upper layers appears as a raised rim on both sides of the digit impression and in the undertracks. A drop-like inclusion of the red surface layer is enclosed in the bottom of the digit imprint. A wide undertrack is formed in the bottom blue layer (Fig. 7B).

3.2.3.3. Section C. The claws of digits II and IV have cut the upper layers, forming narrow imprints in the sediments. The structures formed by the impression of digit III are similar to those observed in Section 2. A clear undertrack showing imprints of all three digits has been formed in the lower red and blue layers (Fig. 7D).

3.2.3.4. Section D. A rounded depression in the surface represents the rounded metatarsal pad impression. The shallow interpad spaces separating the digits have formed a shallow-relief undertrack that shows vague impressions of the three digits (Fig. 7D).

3.2.4. Track 2, horizontal sections

As it was in the case of track 1, the red water-based paint that was used to colour the cement, prevented the cement from hardening properly and made it possible to break it down in water afterwards (Figs. 2–5). The two hereby exposed surfaces at approximately 3 and 4 cm depth, display clear undertracks comprising three well defined digit impressions (Figs. 8 and 9). The undertrack preserved in hyporelief on the surface at approximately 3 cm depth is indeed very well preserved and anatomical details like claw impressions are recognizable in the impressions of digits II and III (Fig. 8). The undertrack in epirelief at the surface approximately 4 cm below the tracking surface is not as detailed but still clearly recognizable as a tridactyl footprint (Fig. 9). In the impression of digit III, the division of the digital pads and a faint claw impression are recognizable.

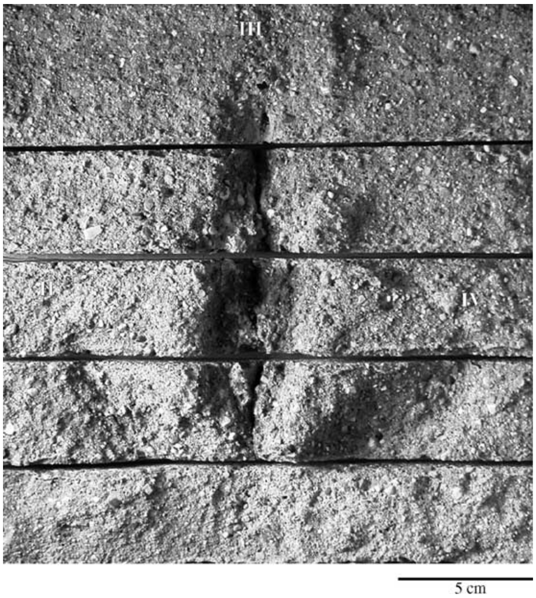

Fig. 9. Epirelief undertrack of the track shown in Fig. 6, formed approximately 4 cm below the tracking surface, notice the distinct impressions of the digits. Digit numbers are indicated by roman numbers. Scale bar 5 cm.

4. Discussion

Although cement is not a naturally occurring sediment, its physical properties closely resemble those of natural damp sediments, and the experimentally obtained tracks and undertracks are comparable to those found in natural sediments. The thickness of the cement package prevented the foot from penetrating the cement to deeper levels than were observed, which means that the experiments must be compared with a sedimentary situation consisting of a layer of 6 cm thick soft mud overlying a firm base. This situation is not uncommon in track-bearing sedimentary systems, which commonly consist of floodplain or similar deposits in connection with fluvial systems (Nadon, 1993, 2001), and can thus be considered as models of realistic tracking environments. In fact, the bottom layer, supported on the incompressible base, has resisted deformation and its upper surface has acted to some extent like a tectonic detachment surface. Here, the overlying layers are well deformed, and the undeformed contact with the bottom layer must have acted as a basement thrust surface on a very small scale.

The horizontal sections through the emu track (experiment 1) show that the area of the tracks is significantly larger in the surface sections than in the sections near the bottom of the true track (Fig. 1B–D). This increase in area is especially due to a decrease in length of the track from more than 230 mm at the tracking surface to 185 mm at the bottom of the track (Table 1), showing that the walls of the track are not vertical but sloping. This sloping of the trackwalls occurs because the formation of the track not only is the result of a unidirectional downward and upward movement of the foot, but is a complex three dimensional movement with both horizontal and vertical components (Brown, 1999). In the present case the firmness of the mud prevented the track walls from collapsing after withdrawal of the foot. The larger track outline in the upper track sections is a combination of two factors. The first is that the pressure transmitted to the sediment by the foot is directed radially away from the digits, giving the deformation a horizontal as well as a vertical component (Allen, 1997). The second factor is the forward movement of the foot during walk, which in deep sediments causes the track walls in the distal and proximal parts of the track to slope. The area around the metatarsal pad and the proximal end of the digits tends especially to increase in the surface layers of the track. This is because of the narrow gap between the proximal end of the digits which, when the foot is moved forward and up, will deform the surrounding sediments and cause the track to appear larger in that area.

The vertical sections through the experimentally produced tracks clearly demonstrate the different appearances of tracks when viewed in vertical sections, both according to location of the section and properties of the sediments, which are both very important factors. The pattern of undertrack formation and deformation of the layers in track 1 (Fig. 3), is comparable to that observed in vertical sections through Early Jurassic theropod tracks from Italy (Avanzini, 1998) and Late Triassic Theropod tracks from Greenland (Milàn et al., 2004).

The experimentally obtained undertracks presented here supplement and expand initial experimental work of Milàn and Bromley (in press), thus the present study demonstrates undertrack formation in both firm and semi-fluid sediments, as well as demonstrating the importance of considering the level of erosion the track has been exposed to (Fig. 1). Furthermore, it supports parts of the study by Nadon (2001) in demonstrating that undertracks never are more detailed than the true track. However, the following claims by Nadon (2001) are not supported: (1) that undertracks are rare and the majority of tracks interpreted as undertracks are the result of erosion; (2) that the apparent lack of anatomical details in the track are caused by mud adhering to the trackmaker's foot, and which blurs the shape of the track.

Contrary to this, the experiments with layered cement clearly demonstrate that undertracks form, and are recognizable at several horizons subjacent to the true track, even in sediments having very different properties. An interesting feature about the track in the semi-fluid cement is that the true track at the surface has collapsed through flow of the cement subsequent to lifting of the foot (Fig. 6). In this case, the shape of the true track is erased and bears little similarity to the shape of the trackmaker's foot. A similar effect was seen in the fossil tracks described by Gatesy et al. (1999) from the Upper Triassic of Jameson Land, East Greenland. The shallow undertracks formed 3 and 4 cm below the tracking surface (Figs. 8 and 9) in this case reflects the anatomy of the trackmaker's foot much better than the true track on the surface.

The apparent lack of anatomical details in undertracks and the generally broader, more rounded and less defined nature of the undertracks compared with the true tracks, has some interesting ichnotaxonomical implications. At least one dinosaur ichnogenus, *Therangospodus oncalensis* Lockley et al. (1998), has been diagnosed as having broad, undefined digit impressions and lacking distinct division of digital pads and other anatomical features (Lockley et al., 1998). Upper Triassic theropod tracks from Jameson Land, demonstrate a wide variety of morphologies owing to different sediment properties (Gatesy et al., 1999), where tracks range from well defined to elongated collapsed structures comparable to that of track 2 (Fig. 6). Rhynchosaurid tracks from the Middle Triassic of Germany display a comparable range of preservational states originating from different sediment properties (Diedrich, 2002).

These examples demonstrate that close attention should be paid to the sedimentary context of tracks because erosion, sediment properties and the formation of undertracks can give rise to a wide range of diverging track morphologies in tracks deriving from the same trackmaker.

5. Conclusions

1. A plaster cast of a track, produced by a walking emu in mud, was sectioned horizontally. Succes-

sive sections downward showed a steady downward reduction of the dimensions of the track, indicating that the track walls are inclined. This inclination and downward track-size reduction were caused by the combined movements of impact, forward swing and kick-off by the walking limb.

2. Tracks were impressed into two packages of colour-layered cement, using the fresh, severed right pes of an emu. The two packages had different water contents, rendering the one substrate fairly firm and the other nearly liquefied. After hardening of the cement, the packages were serially sectioned in the vertical lateral plane. In each case, subsequent removal of a poorly hardened median layer displays the bedding-plane morphology of two undertrack levels, in epirelief and hyporelief, respectively.
3. The firmer cement substrate shows the progressive enfeeblement of successive undertracks. Successive undertracks also show gradual increase in horizontal dimensions and were therefore wider and longer than the true track, while vertical sculpture is gradually reduced. Thus, the undertracks showed a steady degradation of the morphology of the true track.
4. The nearly liquefied cement substrate shows the same downward trends of the undertracks. However, collapse of the wet cement at the tracking surface as the foot was removed resulted in severe distortion of the true track. Thus, in contrast to the firmer substrate, the upper levels of undertracks in this case show a closer resemblance to the anatomy of the emu foot than did the true track.
5. Comparison of the emu tracks with published tracks of dinosaurs in firmer and liquefied mud substrates shows close correspondence in morphology of both true tracks and successive undertracks.

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