

Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland) – undertracks and other subsurface deformation structures revealed

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Tracks and trackways of theropod dinosaurs (*Grallator* footprints) are abundant in the Late Triassic lake sediments of East Greenland. For this study we selected a rather diffuse theropod track preserved on the upper surface of a red heterolithic mudrock, and a better preserved track seen on the upper surface of a greyish mudrock. In order to examine undertracks and other subsurface deformation structures, both slabs were sectioned vertically at closely-spaced intervals, perpendicular to the length of the axis of the impression of digit III. Each section was subsequently polished and internal structures revealed. The digit impressions of both tracks were associated with well-defined undertracks which were cut by deep and narrow claw imprints at the distal end of the digit impressions. Marginal ridges at the tracking surfaces were typically associated with subsurface marginal folds. The marginal ridges were asymmetrically developed suggesting an outward movement of the proximal part of the foot, probably during the kick-off; this is in contrast to what is observed in tracks from Lower Jurassic theropods. The study shows that cross-sections through dinosaur tracks display large structural variation and it is suggested that some disturbed layers in continental deposits could be the result of trampling by vertebrates. □ *Lake sediments, Late Triassic, Theropod tracks, undertracks, walking dynamics.*

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Vertebrate tracks should not be regarded as deformation structures in the sediment surface only. The weight of an animal not only affects the surface it walks upon, the tracking surface *sensu* Fornós *et al.* (2002), but subjacent horizons are also subject to deformation caused by the pressure from the foot transferred radially outwards during the stride (Allen 1997). This leads to the formation of undertracks and other sub-sediment deformation structures.

Only within the last years has the formation of undertracks and sub-sediment deformation structures been systematically described and incorporated into the description and interpretation of the footprints. Gatesy *et al.* (1999) sectioned transversely or sagittally Late Triassic theropod tracks made in deep mud to allow examination and reconstruction of the sub-sediment foot movements of the trackmaker, and Fornós *et al.* (2002) described in detail the sub-sediment deformation structures associated with Pleistocene goat tracks in aeolianites from Mallorca.

Experimental work with artificial sediments (Jackson 2002; Milan & Bromley 2002, 2003; Milàn & Bromley in press), has greatly added to the under-

standing of the formation of undertracks and other related deformation structures. Avanzini (1998) examined the walking dynamics of theropod dinosaurs by sectioning *Grallator* footprints and studied the horizontal deformation of the layers resulting from sideways foot movements during the stride.

The aim of this paper is to supplement the study of Gatesy *et al.* (1999) by the method of Avanzini (1998) and examine vertebrate tracks in vertical section, by sectioning two slabs of ancient lake deposits, each containing a theropod track. The slabs are from the Late Triassic Fleming Fjord Formation in central East Greenland (Fig. 1). Vertical sectioning is an additional method to reveal the complex formation of undertracks, deep cuts from claw imprints and other subsurface deformation structures, resulting from the dynamic interaction between the trackmaker and the substrate.

Stratigraphy

The uppermost part of the Late Triassic Flemming

Fjord Formation, the Ørsted Dal Member, is well-exposed in mountain slopes along Carlsberg Fjord in central East Greenland (Fig. 1) (Clemmensen *et al.* 1998). In this region the Ørsted Dal Member has a thickness of approximately 135 m and is composed of a lower unit of cyclically-bedded, structureless red, clay-rich mudrocks and thin greyish red or green siltrich, heterolithic mudrocks with wave-ripples (the Carlsberg Fjord Beds) and an upper unit of cyclically bedded variegated or grey mudrocks and yellowish grey marlstones (the Tait Bjerg Beds). Both units are lacustrine and formed in a large lake system that was situated at approximately 35° N in the central part of Laurasia (Clemmensen *et al.* 1998). The climate of the area was initially dry and steppe-like but gradually changed to a more humid and temperate climate.

Palaeomagnetic and cyclostratigraphic studies by Kent & Clemmensen (1996) and Clemmensen *et al.* (1998) suggest that the Ørsted Dal Member is of Late Norian to Early Rhaetian age and covers a time span of c. 2.m.y.

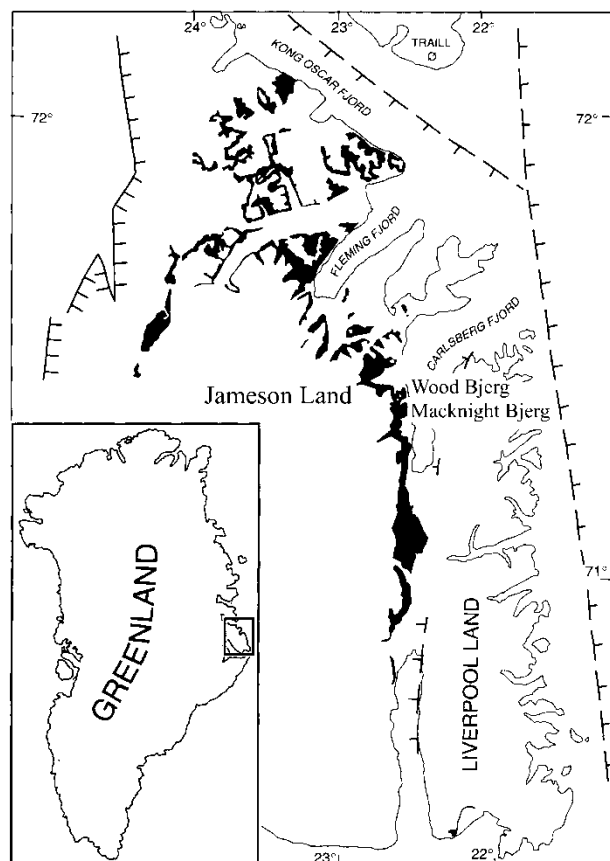


Fig. 1. Jameson Land, East Greenland. Outcrops of Late Triassic lake sediments (Fleming Fjord Formation) are indicated in black. The tracks were collected at the two localities with thick successions of mudrocks in the Ørsted Dal Member, Wood Bjerg and Macknight Bjerg. Modified after Clemmensen *et al.* (1998).

Fauna

The vertebrate assemblages of the Fleming Fjord Formation are very rich and diverse (Jenkins *et al.* 1994) including several dinosaurs. Based on skeletal material, the dominating element in the dinosaur fauna were prosauropods (*Plateosaurus engelhardti*) of which several well-preserved specimens have been found, while only a single incomplete, so far indeterminate, theropod skeleton has been found (Jenkins *et al.* 1994). The non-dinosaurian vertebrate fauna comprises a rich fish fauna (hybodont sharks, actinopterygians, coelacanths and lungfish). Labyrinthodont amphibians are common, with the plagiosaurid *Gerrothorax* being the most frequently encountered vertebrate in these deposits, and several larger stereospondyls such as cyclotosaurs, capitosaurids and metoposaurs. The reptilian fauna consists of turtles (cf. *Proganochelys*), phytosaurs, aetosaurs (*Aetosaurus ferratus* and *Paratypothorax*) and pterosaurs (*Eudimorphodon cromptonellus* Jenkins *et al.* 2001). Furthermore the fauna contains a diverse mammalian assemblage including teeth of *Kuehneotherium*, cf. *Brachyzostrodon* and triconodonts, as well as a skull with postcranial elements of *Haramiyavia clemmenseni* (Jenkins *et al.* 1997), the only skeleton known worldwide. This faunal assemblage is one of the richest Late Triassic, Norian, occurrences of continental vertebrates in the world.

The vertebrate ichnofauna is dominated by tridactyl tracks of small theropod dinosaurs. The tracks are common at many levels in the Ørsted Dal Member, and are particularly abundant on the upper surfaces of the wave-rippled heteroliths or the grey mudrocks. One locality was so rich in tracks that it was referred to as 'The Raceway' by Jenkins *et al.* (1994). In contrast to the numerous theropod trackways, only three trackways can be attributed to prosauropod dinosaurs (Jenkins *et al.* 1994; Clemmensen *et al.* 1998; Gatesy *et al.* 1999; Gatesy 2001). This contradicts the skeletal records from the area, in which the prosauropods by far outnumber the theropods. There are many smaller footprints and trackways distributed in the Fleming Fjord Formation, some of which seem to be amphibian and others possibly of crocodilian origin (Jenkins *et al.* 1994) and a single hitherto undescribed *Chirotherium* trackway (Bonde pers. obs.). The formation further comprises an extensive invertebrate ichnofauna (Bromley & Asgaard 1979).

Methods

For this study we selected a rather diffuse theropod

track preserved on the upper surface of a red heterolithic mudrock (track 1), and a better-defined theropod track preserved in a grey mudrock (track 2). The two slabs were sliced vertically, perpendicular to the long axis of the impression of digit III using a stationary rock saw. The surface of each slice of rock was subsequently polished to allow examination of the internal structures of the slab. The track formed in reddish heterolith showed very little contrast in the colours, and in order to enhance the sedimentary structures, the slice was submerged for 20 minutes in a 10 % acetic acid solution, which enhanced the structures significantly.

Each section was afterwards scanned directly on a flatbed scanner at 600 dpi. To protect the glass surface of the scanner a sheet of transparent plastic was placed between the rock slice and the glass. Alcohol was used as a contact medium between the rock and the plastic sheet. Digital colour and contrast enhancing was subsequently performed using Corel Photo-paint 11. Four sections (A–D) from each of the two tracks were examined. For each track, section A is cut through the claw imprint of digit III, section B is from the middle of the impression of digit III, section C is cut through the middle of the impressions of digits II and IV and through the basal part of the impression of digit III. Section D is cut through the proximal part of the footprint, the metatarsal area.

Grallator footprints

Grallator Hitchcock, 1858 (Fig. 2) is one of the oldest scientifically named tetrapod ichnogenera, first described by Hitchcock (1858) as the footprints of large flightless birds under the name *Ornithichnites*. The ichnogenus spans from the Late Triassic throughout the Jurassic, and was presumably made by several different small to medium sized theropods. *Grallator* tracks are mostly tridactyl, consisting of impressions digits II, III and IV. In rare specimens, traces of digit I, the posteromedially-orientated hallux (Irby 1995) are preserved. Since digit I is situated at an elevated position on the metatarsus (Christiansen 1997), impressions of the digit mostly occur in tracks deep tracks such as those described by Gatesy *et al.* (1999).

The individual digit impressions in *Grallator* footprints have well-defined digital pads and impressions of long, slender claws, reflecting the phalangeal skeleton inside. Digit II, which consists of three phalanges, has two prominent pads covering the joints. The three phalangeal pads cover the four phalanges in digit III. The claw of digit III is offset towards the midline of the trackway. Digit IV consists of four or five small phalangeal pads.

The proximal end of *Grallator* tracks is asymme-

trical as the proximal pad impressions of digit IV extend further back than those of digits III and II. The claw impressions of digit III is always directed inward towards the midline of the trackway (Lockley 1991; Farlow *et al.* 2000).

The asymmetry of the proximal end of the foot and the orientation of the claw of digit III are important indicators of right or left feet if only single footprints are examined, as these characters can be recognized even in weathered and eroded tracks. The producers of Late Triassic *Grallator* tracks are supposed to be small to medium-sized *Coelophys*-like theropods (Lockley 1991).

Terminology

The animal responsible for fossil footprints is termed the 'trackmaker', and the sediment surface it walks upon is termed the 'tracking surface' *sensu* Fornós *et al.* (2002) (Fig. 3). The track emplaced on the actual tracking surface is termed the 'true track' (Lockley 1991). The sedimentary filling of the track forms a 'natural cast' of the track (Lockley 1991). If the trackmaker's foot sinks to a considerable depth in the sediment, then the vertical parts of the track is termed 'track walls' (Brown 1999). If the track walls are sloping as a result of the dynamic movement of the trackmaker's foot during the stride, then the actual

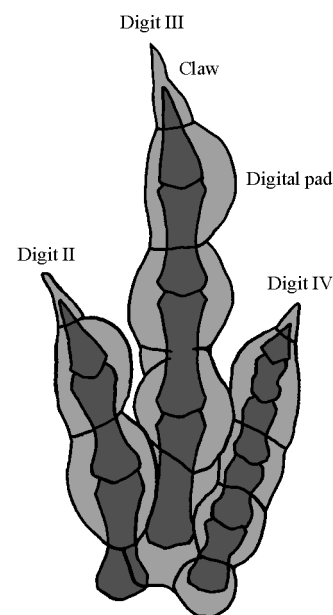


Fig. 2. Idealized *Grallator* track from a right foot with pedal skeleton superimposed. The digital pads correspond with number of phalanges in digit II and III, but not in digit IV where the individual phalanges are too short. Notice the inward orientation of the claw of digit III and the pronounced asymmetry in the proximal part of the track. Modified after Olsen *et al.* (1998).

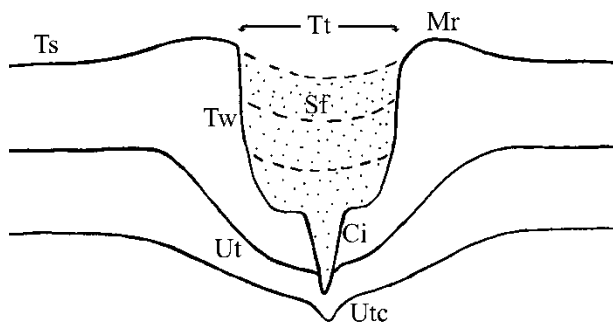


Fig. 3. Schematic section through the distal end of a theropod digit impression, with features mentioned in text. Tracking surface (Ts), marginal ridge (Mr), sedimentary fill (Sf), track wall (Tw), claw imprint (Ci), true track (Tt), undertrack (Ut) and undertrack formed by the claw impression (Utc).

impression of the track will appear longer at the surface than at the bottom of the track. In this case the track in the bottom is the true track and the hole in the sediment surface is termed the 'overall track' (Brown 1999). On the surface around the track, a marginal rim of displaced material is formed, and depending on the substrate consistency, marginal thrusts in the rim and radial fractures in the sediment around the track can form (Allen 1997). The weight of the trackmaker's foot is transferred radially outward into the sediment around and below the trackmaker's foot (Allen 1997). If the track is made in layered sediments an impression of the track will be formed at horizons subjacent to the tracking surface; these tracks are termed 'undertracks' (Lockley 1991) or 'transmitted Tracks' (Thulborn 1990), for this study the term undertracks *censu* Lockley (1991) will be used. Undertracks differ from true tracks in being less detailed downward as demonstrated by experimental work by Milàn & Bromley (2003, in press). If the trackmaker possesses sharp claws on the digits, these will, depending on the properties of the substrate leave deep claw imprints, usually to a deeper level than the digit impressions. In some cases the deep imprints of the claws can cut through the layers with undertracks from the digit impressions and form their own undertracks in the subjacent layers.

Material

Track 1

This track was collected in 1991 from the track-bearing beds in the Carlsberg Fjord Formation at Wood Bjerg. At the surface the track appears shallow (14 mm at the deepest) (Fig. 4A). The appearance of the track is typical of what could be expected from an

undertrack according to experimental work by Milàn & Bromley (2003, in press), in that the track appears broad and rounded and apparently lacks preservation of finer anatomical features, but the digit impressions and gross overall shape of the track.

The track is approximately 24 cm long and 14 cm wide, and shows a divarication angle of 56 degrees between the impression of digits II and IV. The shallow and undefined nature of the track makes it difficult to obtain accurate measurements. When the footlength of 24 cm is used in the formula developed by Alexander (1976), that hip-height equals approximately 4 times the foot length, we arrive at an estimated hip-height of the trackmaker of 1 m. From this an estimated total length of the animal, supposing that it fits the *Coelophysus* bodyplan, would be around 4 m (Per Christiansen, personal communication 2002).

No division of phalangeal pads is visible and the shape of the digit impressions appears rounded with short, blunt digits. The outline, however, reflects the slight turn of the claw of digit III and the asymmetry in the proximal end of the track, identifies the track as a right pes.

A raised rim of displaced material is present at the proximal part of digit II's impression, suggesting the trackmaker made a slight outward movement of the proximal part of the foot during progression. Lateral movements in the proximal parts of theropod feet during walking, have previously been described by Avanzini (1998), and in that case the movement occurred inward contrary to track 1 in which the movement was outward.

The slab containing the track is a reddish heterolith 40–45 mm thick. Grain size varies from clay to fine-grained sand. The silt-sized particles are clastic grains (predominantly quartz and a few clay peloids) while the sand-sized particles are rounded clay peloids, and these grains form well-defined laminae separated by more clay-rich laminae. The clay-rich laminae are red-coloured and contain about 55% of carbonate. The clay-rich matrix displays a clotted texture indicating a pedogenic overprint.

The slab is divided into three units; a basal laminated (10 mm) unit, a middle unit with small-scale cross-lamination (20–25 mm), and an upper unit (10 mm) displaying a vague and indistinct lamination (Fig. 5A). The unidirectionally dipping cross-lamination suggests that sediment transport can be of current or combined current and wave-induced origin. All units display a fining-upward trend suggesting deposition during gradually decreasing energy. At the very top of the slab is the tracking surface, which consists of red mudstone. In the deeper part of the track there is a filling of light-coloured mudstone with intrafor-

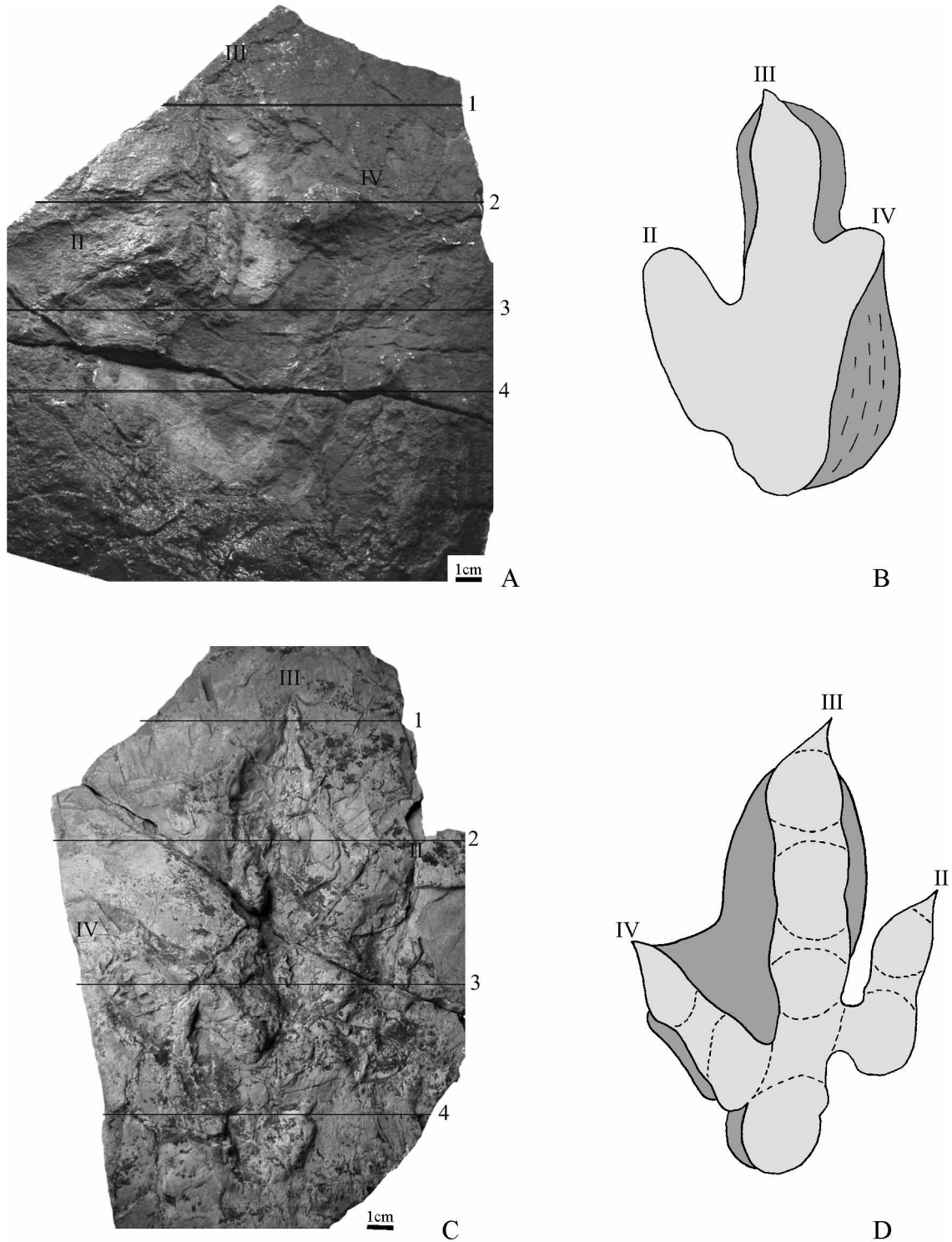


Fig. 4. The two *Grallator* tracks as they appeared on the surface. The termination of each digit impression is indicated by roman letters, according to digit number. Numbered lines indicates the sections used in this study. □ A. Track 1 is badly preserved and displays little more than the gross outline of the track. Of finer anatomical details, only the claw impression of digit III is vaguely recognizable. □ B. Interpretative drawing of track 1, with the marginal rims of displaced material indicated by shaded colour. □ C. Track 2 exhibits a higher state of preservation. Individual digital pads are distinguishable on digit III's impression and prominent claw marks are present at the end of all three digit impressions. □ D. Interpretative drawing of track 2, showing the individual phalangeal pads. Marginal rims of displaced material is indicated by shaded colour.

mational mud clasts that clearly originated from the semi-lithified tracking surface. The surface of the slab, including the track is cut by several orders of polygonal desiccation structures. The underside of the slab is covered with numerous small *Diplichnites* trackways preserved in positive relief and the arthropod resting trace *Rusophycus*, indicating a fluvial and possibly lacustrine environment before the track-bearing layer was deposited (Bromley & Asgaard 1979). Clemmensen *et al.* (1998) suggested that most of the track-bearing beds formed during flooding of marginal mud flats by lake water. Most of the dinosaur tracks and trackways apparently formed during subsequent periods of exposure and desiccation of the flood-generated deposits.

Track 2

This track was collected in 1995 at MacKnight Bjerg in the transition zone between the Carlsberg Fjord Beds and the Tait Bjerg Beds. The track is tridactyl with long slender digit impressions each terminating in narrow claw imprints. The claw imprint of digit III is offset to the right of the long axis of the digit impression, and the impressions of the digital pads in the proximal end of the track have a pronounced asymmetry towards the right side which identifies the track as a left pes

(Fig. 4C). The length is 21.3 cm and the width is 14.9 cm, suggesting a trackmaker with a hip height of around 85 cm and a total estimated body-length of 3.5 m, a little smaller than the trackmaker responsible for track 1. The divarication angle between digits II and IV is 50 degrees, which is within the normal range for small to medium sized theropods (Farlow *et al.* 2000). The track was emplaced in a layer of relatively thin and firm mud, which has caused the imprints of the digits to be only slightly connected as the shallow interpad spaces separating the digits did not reach the tracking surface and failed to leave imprints. Impressions of the individual digital pads are recognizable in digits II and III, while the imprint of digit IV still contains some of the covering sediments, hindering identification of individual digital pads. Impressions of long slender claws are present at the ends of the impressions of digits II and III while the proximal part of digit IV's impression is partly filled with clay. A prominent rim of material displaced by the digits is present between the impressions of digit IV and III, caused by the upward and forward movement when the foot is lifted. Low rims of displaced material are present along the outline of the track.

The slab containing the track is a greyish mudrock with a thickness of about 40 mm. A thin section study indicates that the mudrock contains a little (10–20%)

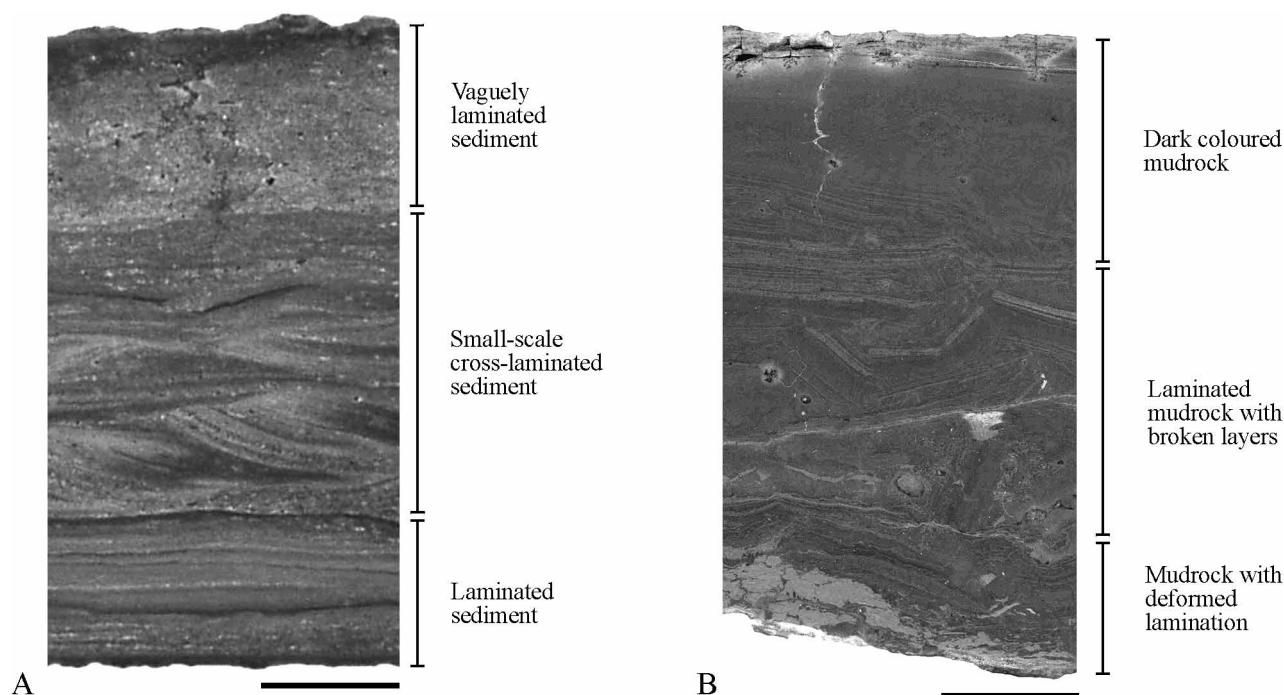


Fig. 5. Sections showing structures in the track-bearing slabs. □ A. Reddish heterolith composed of three distinct units. The basal unit is finely laminated, then follows a unit with small-scale cross lamination and the top unit is vaguely laminated. Total thickness of slab is 40–45 mm. □ B. Grey mudrock divided into three units. The basal unit has deformed lamination, the middle unit is well laminated, but contain also layers that have been broken up. The top unit is structure less to vaguely laminated. Total thickness of the slab is 40 mm. Scale bar 1 cm.

clastic material. The clastic material is composed of silt-sized grains (predominantly quartz) set in a fine-grained matrix. There is around 30% carbonate in the matrix. The slab is composed of three units (Fig. 5B).

At the base is a unit (about 10 mm thick) with chaotic or deformed lamination. Then follows laminated sediment (about 20 mm thick), with two or three layers that have been broken up either during subaerial

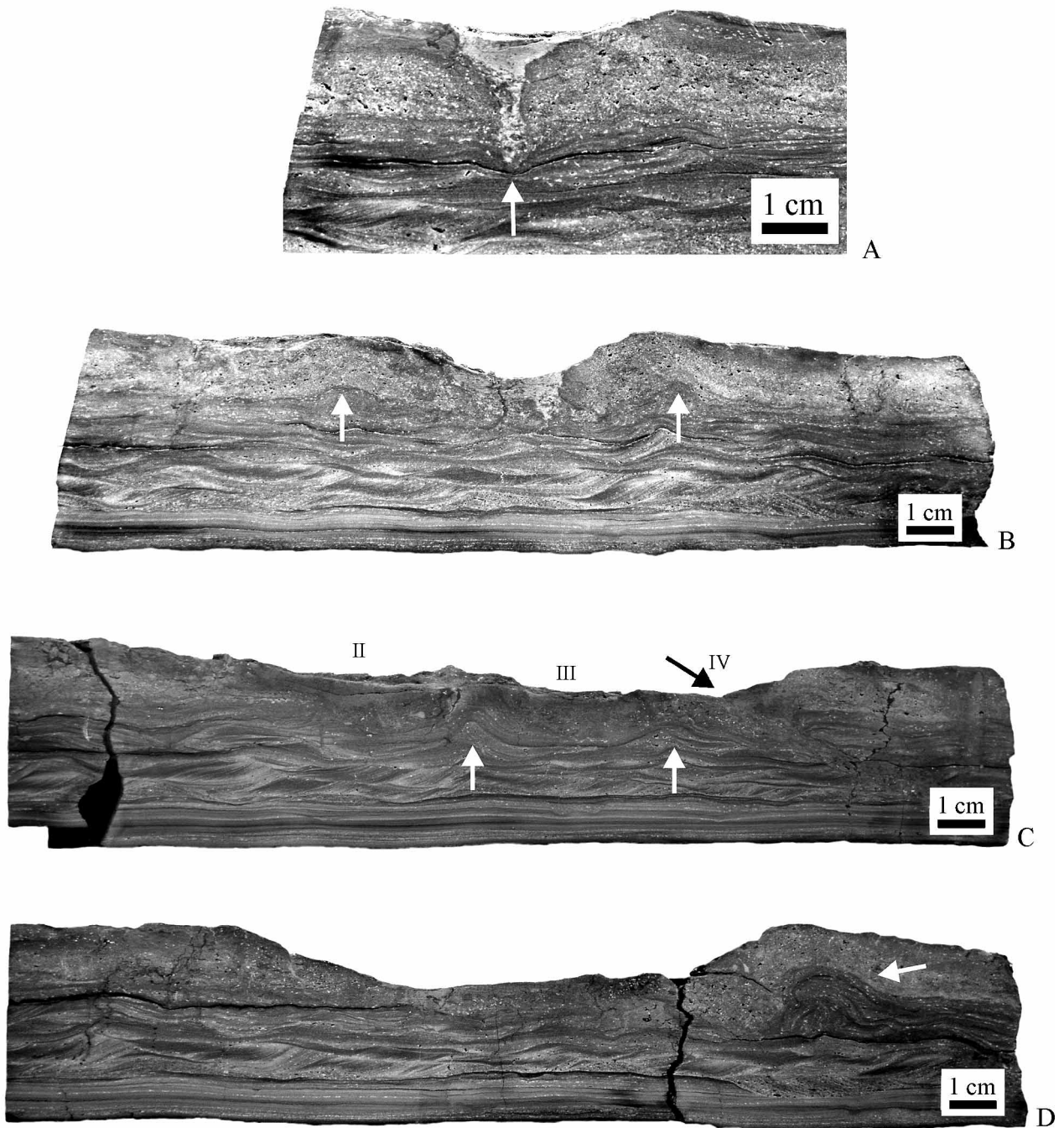


Fig. 6. Vertical sections through track 1. The sections are cut perpendicular to the length axis of digit III, see text for details. Section A is cut through the tip of digit III's impression. Arrow indicates the undertrack formed by the claw impression. Section B is cut through the middle of digit III's impression. Arrows mark the width of the undertrack formed at the horizon approximately 1 cm below the tracking surface. Section C is cut through the impressions of digits II, III and IV. The division of the digits are best recognizable in the undertracks, white arrows indicate the up-bulged material between the digits. The black arrow marks a deep outward directed fault. Section D is cut through the proximal end of the track, notice prominent disturbance from a sideways movement of the foot in the right side of the track (indicated by arrow). All sections in rear view.

exposure or by an earlier phase of trampling, and finally a unit (about 15 mm) of structureless to vaguely laminated sediment. At the top is the tracking surface of dark-coloured mudrock. The bottom of the track is filled with light-coloured muddy sediment containing numerous intraformational clasts. These clasts originate from the semi-lithified tracking surface and were deposited in the track simultaneously with or immediately after track formation.

Track 1, section A

This section passes through the tip of the claw impression of digit III where the slender, sharp claw has cut down through the vaguely laminated unit and left a narrow groove, traceable in the cross-stratified layer (Fig. 6A). The soft parts, surrounding the base of the claw, have formed a bowl-shaped depression in the tracking surface, from which the claw cut protrudes downward, suggesting that the foot was at first placed flat on the ground, and the deep cut from the claw was made during the subsequent kick-off where the weight was transferred to the tip of the digit. Both the bowl-shaped depression and the cut from the claw are filled with sediment of a slightly lighter colour than that of the mudstone. The broad, upper part of the digit impression has formed an undertrack in the layers directly below it. On the tracking surface a shallow up-bulged area of displaced material is present on the right side of the digit impression, suggesting a sideways movement of the foot.

Track 1, section B

This section was cut through the middle of the impression from digit III, and is expressed as a bowl-shaped depression in the tracking surface (Fig. 6B). The vertical pressure exercised on the sediment by the digit has caused the formation of a rim of displaced sediment on either side of the digit, most pronounced on the right side of the digit. The undertrack is evident in the layer 1 cm below the tracking surface. It appears shallower and wider than the true track. The rim of material displaced by the sideways pressure of the digit can also be recognized in the undertrack, although less pronounced.

Track 1, section C

The bottom of the track shows the initial division between digits II and III. The separation between digits III and IV are not evident at the bottom of the true track (Fig. 6C). Digit II is partly filled with sediment and so appears very shallow and hardly recognizable at the tracking surface. The undertrack in this section

reveals more information about the configuration of the digits than the true track, as the separation between digits II, III and IV is represented by a prominent upward bulging of the layers between the digit impressions. This interdigital upward bulging of the sediment must also have been present at the true track, but has been secondarily lost. A prominent fault cut the layers, projecting downward and outward from the bottom of the right side of the surface track (see arrow on Fig. 6C).

Track 1, section D

This section is through the proximal part of the track, close to the metatarsal joint. The track is formed in the upper vaguely stratified unit of the slab (Fig. 6D). A prominent raised marginal rim of displaced surface material is present at the right side of the footprint, originating from a sideways and outwards movement of the foot during the stride. While the track itself has only left a very shallow undertrack, the marginal rim is also prominent in the undertrack.

Track 2, section A

This section is through the claw imprint of digit III (Fig. 7A). The claw has left a clear, narrow cut down through the upper part of the slab and the upper layer has only been dragged a little down by the pressure from the claw. The cut from the claw protrudes 15 mm down from the tracking surface and is filled with sediment of a lighter colour. A shallow v-shaped undertrack is formed in the layers below the claw mark.

Track 2, section B

Section B is cut through the middle part of the impression of digit III (Fig. 7B). The digit has not penetrated the surface layer, which has been depressed below the digit. The material laterally displaced by the pressure of the digit, has caused an upward bulging of the sediment on both sides of the digit impression. The upward bulging is more prominent at the outer (left) side of the digit impression, suggesting an outwards movement of the digit, during the stride. The bottom of the digit imprint is covered with later filled sediment having a lighter colour. The upward bulging of the sediment is visible in the undertrack at 20 mm depth. The structure here is shallower and wider than at the tracking surface.

Track 2, section C

This section is through the imprints of digits II, III and

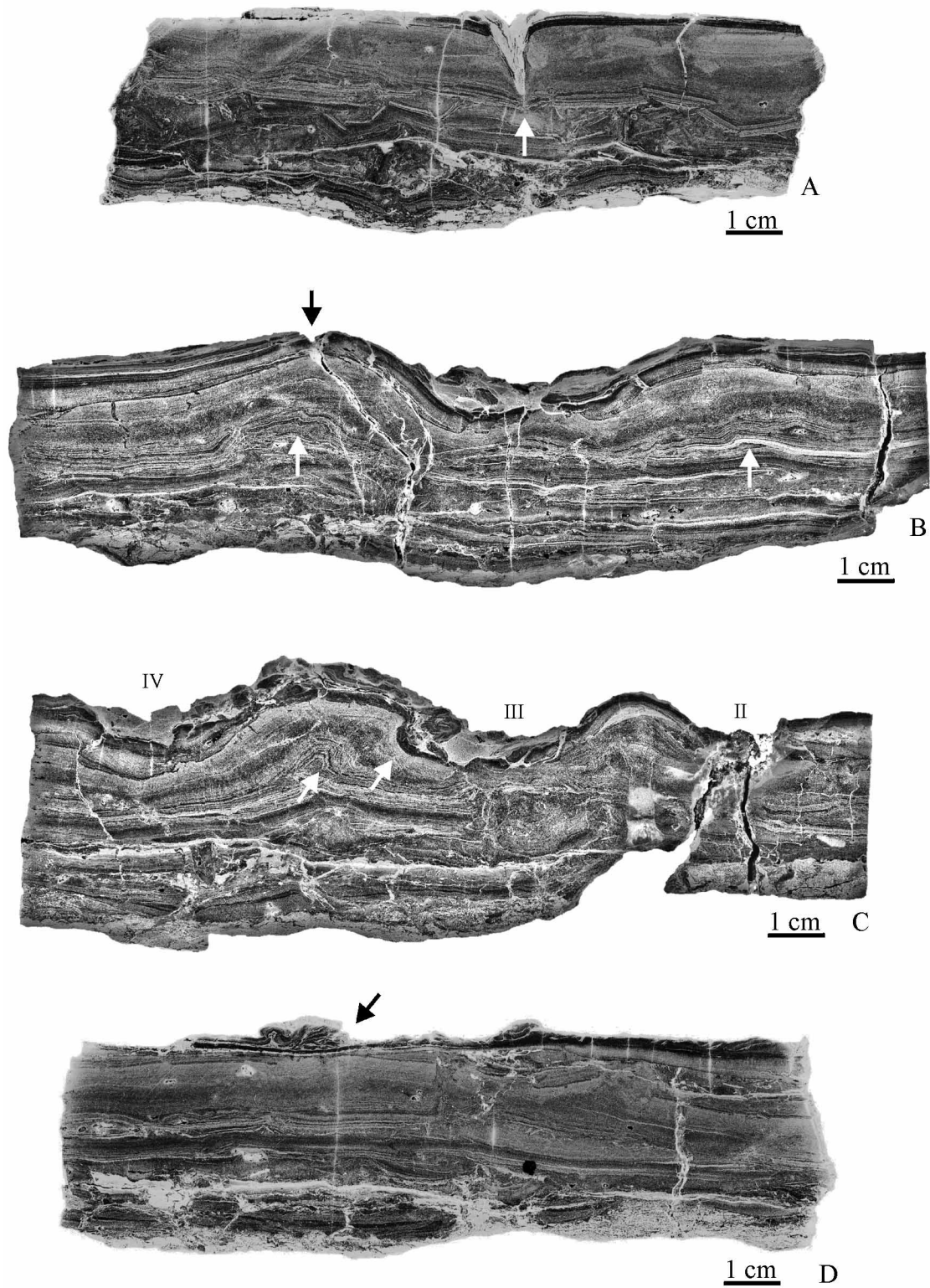


Fig. 7. Vertical sections through track 2, see text for details. Section A is cut through the claw impression from digit III. Arrow marks the faint undertrack formed below the claw impression. Section B is from the middle of digit III's impression. The marginal ridge of up bulged material is most prominent on the left (outward) side of the track, indicated by black arrow. Notice the prominent undertrack at the horizon 2.3 cm below the tracking surface. White arrows indicate the width of undertrack. Section C represents a cut through the impressions of digits II, III and IV. Notice the folding of the prominent up-bulged material between the impressions of digit IV and III, marked by arrows, which indicates a sideways movement of the foot. Section D is cut through the impression of the proximal end of the track. The foot has only caused slight sideways disturbance in the thin surface layer (arrow). All sections in rear view.

IV (Fig. 7C). The track is deepest at digit III, which is 9 mm deep measured from the original tracking surface. The bottoms of the digit imprints are disturbed and filled with sediment of a lighter colour. The upward sediment bulge between the digit impressions, most pronounced between digits IV and III, and is asymmetric, a feature that is also clearly evident in the undertracks, although the individual digit impressions become less wide and shallow downward. The deformation structures around and below the track all indicate an outward movement of the foot during the stride.

Track 2, section D

A section through the impression of the proximal pad of digit IV represents the metatarsal area of the track (Fig. 7D). The imprint is here very shallow and has only disturbed the upper 2 mm layer of the surface. The pressure from this part of the foot has been too light to initiate the formation of undertracks. A shallow rim of laterally displaced material is present on both sides of the impression, most pronounced on the outside of the track.

Discussion

At the surface, the two tracks exhibit very different states of preservation. Owing to the shallow appearance and the vaguely defined rounded shape of the digit impression, track 1 was initially identified as an undertrack. However, the presence of sediment filling of a slightly different colour in some of the slices and especially the deep cut from the claw of digit III proves that the track is an eroded true track. The presence of undertracks in the layers subjacent to the track cannot solely be used to argue that the track is an undertrack, since undertracks form at several horizons subjacent to the tracking surface (Milàn & Bromley in press), so even if the track at the apparent surface is an undertrack, then it would still be possible to find undertracks at the subjacent horizons.

The rounded and undefined appearance of the track at the surface is the result of subaerial erosion of the track, and the fact that parts of the track still retain the sedimentary filling. Whether the erosion of the track occurred before burial, or has happened after the track bearing layers were re-exposed at the surface recently, is not known. The presence of desiccation cracks in the surface around the track witnesses a certain time of subaerial exposure of the tracking surface prior to burial.

Track 2 exhibits at the surface a much better defined appearance than track 1, as the digits are well-defined

and anatomical details, like digital pads, are recognizable in two of the digits. The state of preservation of this track is comparable to the one described by Gatesy *et al.* (1999, fig. 1b).

At the surface, the differences in preservation of the two tracks make direct comparisons difficult, but when viewed in cross-section, a number of similarities become apparent. The narrow cut from the claw of digit III shows that the trackmaker in both cases possessed sharp laterally compressed claws. The apparent shortness of the digits in track 1 is shown to be an artefact of erosion, as the undertracks reveals that the division of the digits occurs well before this can be recognized in the track at the surface. In both tracks the undertracks are well-defined, although wider and shallower than the true tracks. Undertracks are recognizable at horizons down to 2 cm depth.

The sectioning of the two tracks further reveals that parts of the tracks still retain some of the sedimentary filling, which blurs the shape and anatomical details, and in the case of track 1, combined with erosion gives the true track the appearance of an undertrack.

The asymmetry of the two footprints with the marginal rim of displaced material on the outer side of the track, in fact displays many similarities with asymmetrical deformation of tracks described in Lower Jurassic *Grallator* tracks from Italy (Avanzini 1998). However, in that case the asymmetry occurred in the opposite side of the track. Avanzini (1998) used this deformation to infer information about the walking dynamics of theropod dinosaurs and incorporated a slight inwards turn of the foot in his reconstruction of theropod foot movements during a stride. The material studied by Avanzini (1998) consisted of vertical sections of six tracks where the sideways deformation structure in the proximal end of the track occurred in two of the tracks (Marco Avanzini, personal communication 2003). The sideways deformation structures in the two tracks herein described is similar to, but occurs on the opposite side of the tracks described by Avanzini (1998). This shows a clear difference in the foot movements of the dinosaurs responsible for the tracks in Greenland and those in Italy. Although the tracks belong to the same ichnogenus (*Grallator*), the temporal gap between the Upper Triassic, (Late Norian to Early Rhetian) beds from Greenland to the Lower Jurassic beds from Italy, suggest different genera of trackmakers in the two cases.

This study demonstrates that evidence obtained from ichnology is very important in the study of dinosaur walking dynamics; in this case it suggests a change in walking dynamics across the Triassic-Jurassic border. However, further sectioning of tracks from different localities and geological stages should

be conducted to examine the full range of walking dynamics of dinosaurs, before any firm conclusions can be drawn.

Sideways deformation structures in tracks can also occur when an animal changes its direction of progression (Brown 1999) or if the tracking surface is sloping. Such things need to be taken into consideration when deformation structures around tracks are interpreted.

The marginal ridge formed on the right side of the proximal part of track 1 (Fig. 6D) shows in section a deep disturbed zone undercutting the rim of displaced material. A possible origin of the structure is that it is a fault formed during the formation of the raised pad of displaced material caused by a sideways and downwards movement of the foot during the stride. That microfaulting occurs in sediments in connection with track formation has been established experimentally by Allen (1997) and Jackson (2002). However, the uniform bending of the layers down into the structure (Fig. 6C) does not correspond with what would be expected of a fault. Instead the architecture suggests that the structure is caused by sediment flow and is in fact similar to the structures termed 'Cave' and 'Cave-in' by Brown (1999). Cave is the situation where a slight turn of the trackmaker's foot during the stride causes the foot to slightly undermine the track wall, leaving parts of the trackwall as an overhang, whereas cave-in is the situation where the overhang afterwards collapses over the cave.

Conclusion

Although in its infancy, the method of studying vertebrate tracks in vertical section has proved to be indeed very useful, as information crucial to the correct interpretation of both the trackmaker and the substrate consistency at the time of trackmaking is concealed below the tracking surface.

The initial identification of track 1 as an undertrack, based on the shallow, rounded and poorly-defined appearance of the track was shown to be incorrect, as the vertical sections through the track demonstrated that the undertrack-like appearance was an artefact of subaerial erosion, and that 'real' undertracks were present in the layers subjacent to the track.

In both tracks the narrowness of the claw incisions observed in the sections show that the theropods responsible for the tracks had laterally compressed, sharp claws. The pronounced outward rotation of the foot observed in both tracks, show that Upper Triassic theropods had a walking pattern, which included an outward movement of the proximal part of the foot,

probably during the kick-off. This is in contrast to the pattern described from Lower Jurassic theropods.

A track exposed in cross-section can express different morphologies, of which some are hardly recognizable as tracks. This is important to bear in mind when studying exposures of continental deposits, as horizons with apparent disturbance of the layers may be the result of trampling by vertebrates.

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