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VARIATIONS IN THE MORPHOLOGY OF EMU (*DROMAIUS NOVAEHOLLANDIAE*) TRACKS REFLECTING DIFFERENCES IN WALKING PATTERN AND SUBSTRATE CONSISTENCY: ICHNOTAXONOMIC IMPLICATIONS

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Abstract: Fossil footprints appear in a variety of preservational states, each revealing a different morphology that can give rise to misidentification and misinterpretations. Comparative ichnological work was conducted using living emus (*Dromaius novaehollandiae*). It was clearly demonstrated that the morphological variation that occurred in footprints of the same animal, walking in the same manner, was caused by variation in substrate consistency. Dry sand substrates are unlikely to preserve any anatomical details of the foot, whereas damp sand or mud of firm consistency preserves a high level of anatomical detail. The finest anatomical details, such as skin impressions, are only preserved in firm mud or clay. In semi-fluid to fluid mud the track walls collapse, destroying the shape of the footprint. Increased speed of progression affects the shape of the footprint dramatically as the distal ends of the digits become more deeply impressed in the substrate during acceleration. Plantigrade stance adopted by the emu while feeding produces highly elongated footprints. Applying these observations to the study of fossil footprints demonstrates that great care should be paid to the original sedimentary conditions at the time of track making, as well as to the stance and gait of the trackmaker.

Key words: Emu tracks, field experiments, sediment properties, footprint morphology.

THAT variation in substrate consistency exercises a strong control on the morphology of fossil tracks and traces has long been well documented among marine invertebrate trace fossils (Bromley 1996). Only recently has the same awareness about the relationship between the morphology of a vertebrate track and the consistency of the substrate in which it is emplaced been the topic of systematic study. Bromley (1996, fig. 7.1) used his own footprint emplaced on photographic paper, dry sand, damp sand and in deep mud on an intertidal mud flat to demonstrate how different tracks from the same action can appear in different substrates.

Laporte and Behrensmeyer (1980) described the connection between grain size and water content of the sediment and the potential for tracks to be preserved, on the basis of field observations of tracks in Recent and Plio/Pleistocene sediments in Kenya. According to their observations, tracks are unlikely to be preserved in dry sediments, since dry sand is too loose to preserve tracks, and dry clay is simply too hard to allow the formation of a track. If the sediment is saturated with water, sand will be too loose to preserve tracks and clay will be too fluid. The optimal parameters for track preservation, according to Laporte and Behrensmeyer (1980), are when the sediment is moist, and has a grain size between sand and clay.

Allen (1997) made several observations on subfossil human and cattle tracks in the Severn Estuary, south-west England. A human footprint imprinted in deep, fluid to semi-fluid mud would collapse and the sediment would gradually flow back and fill the track, obscuring it from the bottom up. Such a track would, if fossilized, reveal little about the nature of the trackmaker, and may be recognized only as a mass of disrupted sediments below a slight depression in the sediment surface (Allen 1997). Tracks emplaced in soft mud have a much less pronounced tendency to flow and collapse, but are generally poor in detail because of the tendency for the mud to adhere to the trackmaker's foot and create adhesion spikes as the foot is withdrawn, leaving the footprint blurred. In some cases the movement of the foot leaves striations on the track walls. Tracks preserved in such sediments are likely to show only gross anatomical features (Allen 1997). Firm mud, according to Allen's (1997) observations, is likely to produce very well-defined but shallow tracks and, if fossilized, should preserve even fine details, such as skin impressions. These observations were backed up by an intensive study of cross-sections through artificially produced tracks in layered plasticine, to reveal and describe the various subsediment deformation structures that occur beneath and around a vertebrate footprint. A similar study, designed to describe the influence that substrate consistency exercises on the morphology of tracks and undertracks was carried out by Milàn and Bromley (in press) using vertical sections through emu tracks emplaced in layered cement packages of different consistencies.

Diedrich (2002) demonstrated several different preservational variants of Triassic rhynchosaurid tracks caused by differences in water content of the sediments. Tracks made in dry subaerial sediments consist of little more than faint claw imprints. With increasing water content of the sediment, shallow tracks are found having skin texture preserved. In more water-rich and thus softer sediments, the tracks become deeper and more blurred in shape, and finally, subaquatic tracks produced by a swimming trackmaker are found as elongated, parallel scratch traces.

Using live animals has several advantages over previous experiments using models of feet. While the track experiments using artificial model feet (Allen 1997; Manning 2004) are easier to conduct and, importantly, much easier to document as one is in total control of all parameters, one important factor is missing: the dynamic interaction between the animal and the substrate emphasized by Baird (1957). By using live animals, all the factors resulting from differences in gait, individual behaviour and mode of progression are reflected in the footprints.

The extant emu, *Dromaius novaehollandiae*, and other large cursorial birds are the best living analogues to Mesozoic theropods. The emu and the rhea, *Rhea americana*, having a pedal skeleton and footprint morphology resembling that of non-avian theropods, are especially obvious candidates for comparative ichnological work.

The first comparison of footprints from ratitous birds and theropods was by Sollas (1879), who compared casts of emu and cassowary tracks with what he then believed to be tracks of giant extinct birds in the Triassic conglomerates of South Wales. Padian and Olsen (1989) demonstrated that the stance and gait of theropods and small bipedal ornithopods were similar to those of the extant rhea, by comparing trackways from rheas with those of theropods. Farlow (1989) made similar observations of tracks and trackways of an ostrich, and pointed out that an ostrich might not be the best of the large flightless birds to use for comparison with theropods, because of its didactyl foot. To help interpret strange collapsed theropod tracks from the Upper Triassic deposits of Jameson Land, East Greenland, Gatesy *et al.* (1999) used a turkey, *Meleagris gallopavo*, and a helmeted guineafowl, *Numida meleagris*, running and walking in mud of different consistencies, producing tracks at several states of collapse. Recent studies by Farlow *et al.* (2000) and Smith and Farlow (2003) of the interspecific variations in footprints and foot morphology of the ratites and other cursorial birds further demonstrate the value of incorporating studies of extant animals in palaeoichnological studies.

The aim of this paper is to describe the range of morphological variation in tridactyl footprints, owing to differences in substrate consistency and mode of progression, by using an emu as a trackmaker. The extant tracks are described and comparisons made with fossil tracks and trackways that show similar sediment-induced differences in morphology.

METHODS

The emus used for the experiment belong to breeder Karin Holst, Mønge, Denmark. In order to record tracks, two types of sediment were used as substrate: (1) local organic-rich, dark soil from within the emu enclosure mixed with different quantities of water, in order to record tracks in mud having consistencies from firm to liquid; and (2) glaciofluviatile sand from a nearby sandpit. Each sediment type was analysed following Tucker (2001), with the mean grain-size, median grain size and degree of sorting calculated by the methods advised by Folk and Ward (1957). The local organic-rich soil is poorly sorted (degree of sorting, 1·57), and has a median grain size of 2·2 and a mean grain size of 2·18 mm. The glaciofluvatile sand is poorly sorted (degree of sorting, 1·42), and has a median grain size of 2·4 and mean grain size 2·38 mm. The sand grains are angular with a high sphericity in the terminology of Tucker (2001).

Eight different substrates were prepared in which the emus were encouraged to walk: dry loose sand, damp sand, wet sand, thin layer of soft mud, deep firm mud, deep semi-firm mud, deep semi-fluid mud and deep fluid mud. In order to obtain an emu track with as many anatomical details preserved as possible, a fresh, severed emu foot was impressed in a sheet of soft potter's clay. This track serves as a reference for discussing the amount of preserved anatomical details in the tracks from the field experiments.

To record longer trackways, sand patches were laid out on the paths preferred by the emus within the fenced paddock. Selected tracks and trackways were recorded photographically and relevant measurements were taken in the field. Where the consistency of the sediment allowed, plaster casts were made. The plaster casts depicted herein are curated by the Geological Museum, University of Copenhagen, numbers MGUH 27474–27479.

At first it proved to be difficult to persuade the emus to walk on the prepared sediments. Emus act very suspiciously to changes in their environment, and were very reluctant to enter the patches of sediment prepared for them. By placing the sediments on their preferred paths along the paddock, and encouraging them by holding a bucket of seed at the other end of the prepared sediment, the birds were tempted to co-operate. After a period of getting used to walking in the sediments, the opposite problem arose: the emus started to walk back and forth through the sediments. Hence it became necessary to prevent them from trampling the tracks already made.

The terminology used to describe the emu tracks is based on Lockley (1991) and Allen (1997) to ease comparison with fossil footprints. Where no sufficient palaeoichnological terms exist, the neoichnological terminology of Brown (1999) is adopted. To describe the emu foot, and the anatomical features recognizable in the footprints, the terminology of Lucas and Stettenheim (1972) is employed. The terminology used to describe the foot movements during the walking phases is based on Thulborn and Wade (1989) and Avanzini (1998).

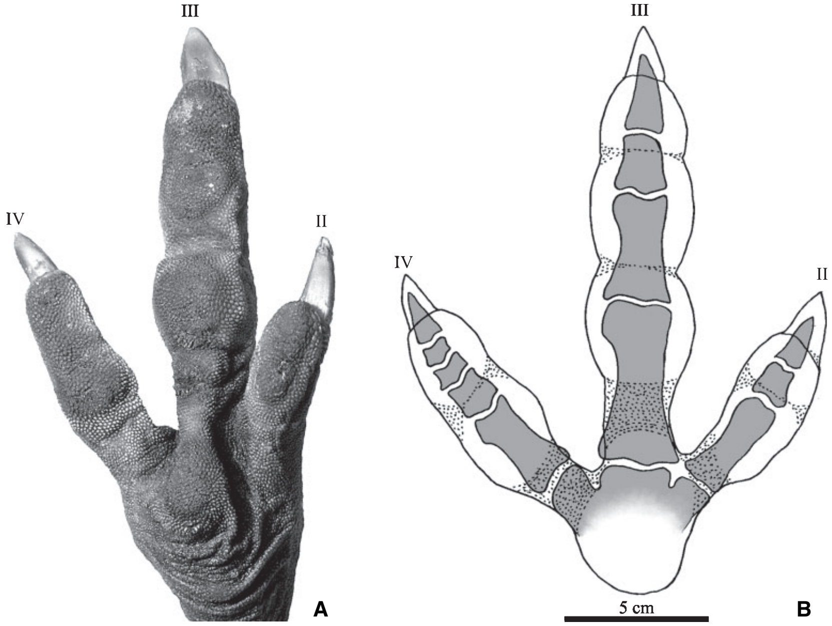
RESULTS

The emu foot

The emu foot is tridactyl, 18–20 cm long, consisting of digits II, III and IV; digit I, the hallux, is absent in the emu. Digit III is the longest with the shorter digits II and IV of subequal length, making the foot close to symmetrical about the length axis of digit III. Each digit terminates in a long blunt claw (Text-fig. 1A). The integument on the sole of the emu foot consists of fleshy digital pads covering the joints between the phalanges. The ventral surfaces of the digital pads are covered with small, closely situated, horny tubercles of millimetre size. Each digital pad is separated from the next by a small gap, situated approximately at the middle of the phalanx. The joint between the basal phalanges and the tarsometatarsus is covered by a single round pad, the metatarsal pad, which in the case of the emu is clearly separated from the other digital pads by a broad, deep interpad space. Digit II, consisting of three phalanges, has two digital pads covering the joints. Owing to the shortness of the digit, however, the interpad space is weakly developed. Digit III, which has four phalanges, bears three prominent digital pads that are clearly separated by interpad spaces. Digit IV, which consists of one long basal phalanx and four short phalanges, has only developed what seems to be one long digital pad, weakly divided in two by a shallow part in the middle. Whereas digital pads in digits II and III clearly reflect the number of phalanges in the digits, the pads on digit IV do not reflect the number of phalanges in the digit (Text-fig. 1B).

Foot movements during walk

Like all birds, the emu walks in a digitigrade fashion, with the elongated tarsometatarsus lifted clear of the ground. According to the terminology of Thulborn and Wade



TEXT-FIG. 1. The emu foot and pedal skeleton. A, right foot of an emu in dorsal view. Each digit bears a number of fleshy digital pads and terminates in a blunt claw. The skin is covered with small horny tubercles each 1–2 mm in size. B, pedal skeleton of the same foot, redrawn from a radiograph, and superimposed on its footprint. The fleshy digital pads are situated around the phalangeal joints in digits II and III. The four short distal phalanges of digit IV are covered by a single digital pad, giving the digit only two weakly divided digital pads. The joint between the metatarsus and the phalanges is partly covered by a single rounded pad separated from the digital pads by a deep, broad interpad space. Photograph, O. B. Berthelsen.

(1989) and Avanzini (1998), there are three distinct phases of foot contact during walking: the touch-down phase (T) is the phase where the foot is extended forward and planted on the ground. This initial phase of ground contact is followed by the weight-bearing phase (W), where the animal's centre of gravity passes over the animal's foot, which becomes impressed into the substrate. The last phase is the kick-off phase (K). In this phase 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 and the foot is subsequently lifted and swung towards a new T-phase. When the foot is lifted, the digits converge and bend backwards to a nearly vertical position while the foot is moved forward (Text-fig. 2).

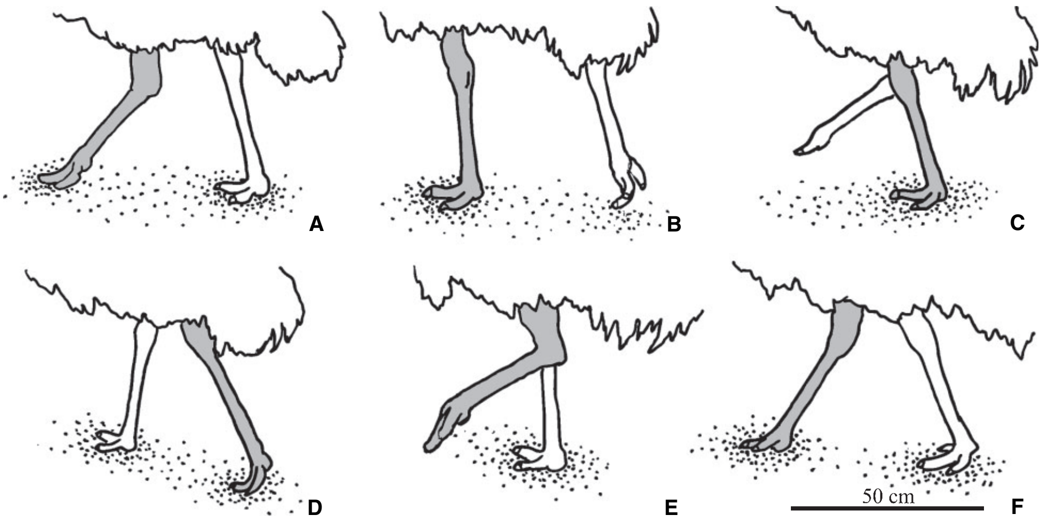
Footprint morphology in different substrates

Since a footprint can be described as the by-product of dynamic contact between an organism and its environment (Baird 1957), both the movement of the animal that produced the track and the physical nature of the environment in which the animal trod have a considerable effect on the morphology of the track produced.

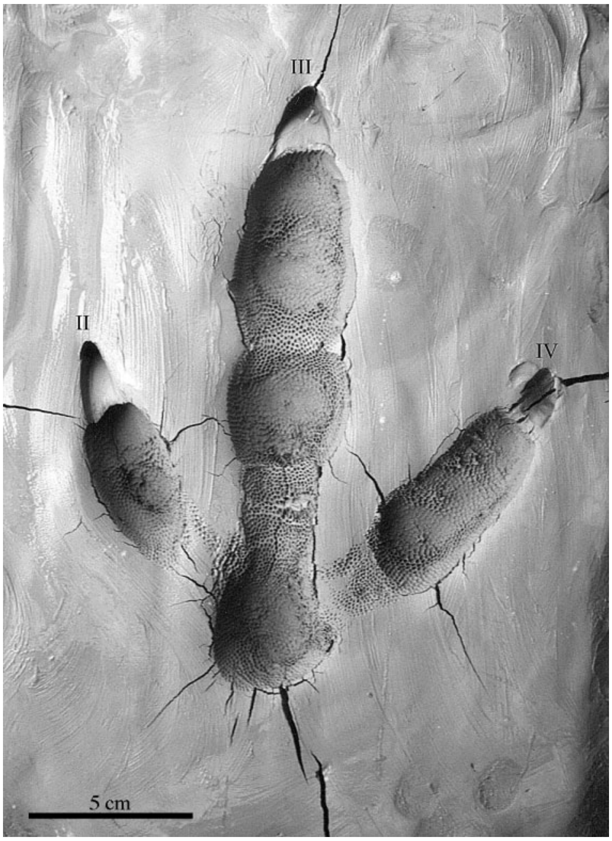
In the present experiment, the first track produced was emplaced in potter's clay. Owing to the very fine-grained composition and good moulding properties of the clay, the track is very detailed. The impressions of the individual digital pads, and the shallow gaps dividing them, are well defined and clearly visible, as well as the impressions of the blunt claws. The tuberculate skin covering the sole of the digital pads left clear impressions in the sides and bottom of the digit impressions. As the clay was allowed to dry slowly for 2 days, large fractures formed, radiating outward from the claw impressions and the impression of the metatarsal pads. In all cases the formation of the fractures was initiated by small fractures in the sediment created during the formation of the track, which then acted as agents for the formation of desiccation cracks in the clay (Text-fig. 3).

Dry loose sand has no cohesive properties and the footprints emplaced within it collapsed immediately after the foot was lifted. No fine anatomical details of the track are preserved, except for the overall shape of the metatarsal pad and the digits. The collapsing of the sand caused the digits to appear significantly broader and more rounded that they are. In many cases even the outline of the track was not recognizable and the track appeared only as a shallow depression in the sand (Text-fig. 4).

Adding water to sand significantly enhances its cohesive properties, and thus its ability to preserve tracks. The tracks emplaced in damp sand are well defined, with the impressions of all digits clearly formed. The impressions of the claws, the individual digital pads and the shallow gaps separating them are recognizable. Faint impressions of the tuberculate skin are visible, but the grain size of the sand prevents fine details from being preserved (Text-fig. 5). As the sand dried during the day, the shape of the track slowly degraded and the morphology came to resemble that of the track emplaced in dry sand.



TEXT-FIG. 2. The walking phases of the emu, illustrated by the movements of the left leg indicated in grey; sketched from photographs. A, the foot is put forward and down in the touch-down phase (T-phase). B–C, the centre of gravity passes directly over the left foot in the weight-bearing phase (W-phase), while the right foot is swung forward to the T-phase. D, the left foot is in the kick-off phase (K-phase); the tips of the digits are the last to lose contact with the ground. E–F, the left foot is swung forwards to the next T-phase.



TEXT-FIG. 3. Emu track emplaced in potter's clay. Anatomical details such as skin texture, number and arrangement of digital pads and claw imprints are preserved in exquisite detail. Small radiating fractures were formed around the digits during impression of the foot. The radiating fractures acted subsequently as sites for the formation of larger desiccation cracks in the clay.

Water-saturated sand allowed the emu foot to sink to a depth of approximately 10 cm during the stride. At the moment of formation, the track was well defined with clear impressions of each digit. Subsequently the softness of the sediment caused water to flow from the sediment into the track, filling it from the bottom up. During that process the track walls flowed together and the shape of the track slowly degraded as the track became filled with sand. During the impression of the foot, fractures radiating outwards from the track were created in the metatarsal area and between the digits (Text-fig. 6).

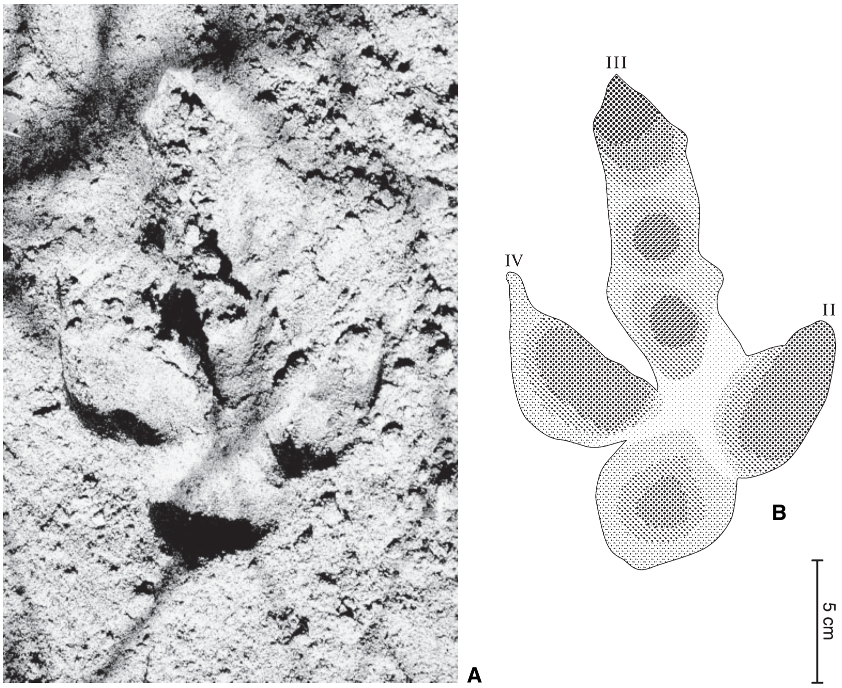
A thin layer of soft mud applied over a firm base proved to be an excellent medium in which to record tracks. The features of the track are very well preserved, with the impressions of the individual digital pads and claws clearly recognizable. Impressions of the fine anatomical details of the skin, such as skin tubercles and small wrinkles, are preserved in detail. A certain amount of mud was pressed up between the proximal parts of digits III and IV during the weight-bearing phase. After removal of the foot, the upward-pressed mud collapsed down into the impression of digit IV, partly covering it (Text-fig. 7). The quality of anatomical detail preserved in this track rivals that of the experimental track in potter's clay (Text-fig. 3).

Deep mud of a firm consistency produced deep, well-defined tracks. In this case the consistency of the mud was firm enough to prevent collapsing of the track walls subsequent to removal of the foot. The track was approximately 8 cm deep, and the impression of the foot is perfectly preserved in the bottom of the track, with the impressions of claws, digital pads and even skin structure recognizable. The depth of the mud caused the parasaggital movement that the foot performs during the stride to be reflected in the track, thereby making the overall track at the surface 8 cm longer than the true track preserved at the bottom (Text-fig. 8).

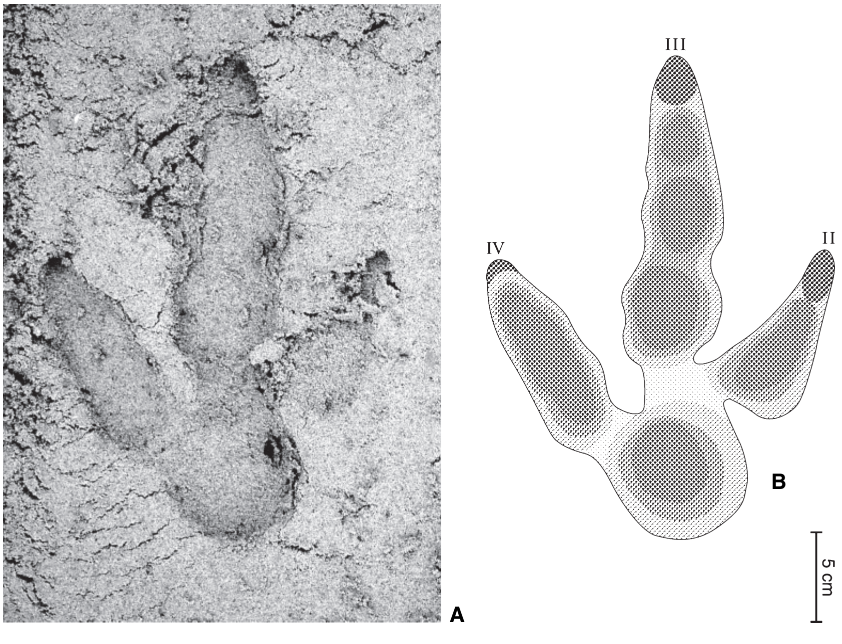
In deep, semi-firm mud, the softness of the sediment caused the track walls to collapse slowly over the digit imprints. The collapse is most prominent between the digit impressions where two lobes of mud have converged and closed the proximal part of the impression of digit III, leaving the overall track shape to be that of a triangular depression formed by the metatarsal pad and the outer sides of digits II and IV, with the impression of digit III represented as an oval hole (Text-fig. 9). Faint striations created by the tubercles during the impression of the foot are preserved in the metatarsal area of the track.

Using a wetter mixture, a deeper layer of semi-fluid mud was created. The semi-fluid consistency caused the track walls to collapse over the digits while these were impressed in the sediment, in turn causing the material covering the digits to be lifted up by the foot, transported and dropped onto the tracking surface in front of the track. Striations in the track walls created by the forward movement of the foot are preserved in the proximal part of the track. The consistency and water content of the mud caused water to flow into the track and the track walls subsequently to collapse slowly, largely destroying the shape of the track (Text-fig. 10).

The wettest mixture used produced a deep fluid mud so soft that the sediment flowed instantly together over the digits during the impression in the sediment. The softness of the sediment prevented the mud from adhering to the dorsal side of the foot, and thus little sediment was ejected in front of the track during the lifting of the foot. After the lifting of the foot, the track immediately flowed together leaving only an angular, water-filled depression in the mud. Owing to the depth of the mud, the foot was not lifted totally clear of the sediment while it was swung towards the next step. This caused the tip of digit III to create a long, narrow drag trace in the tracking surface in front of the track (Text-fig. 11).



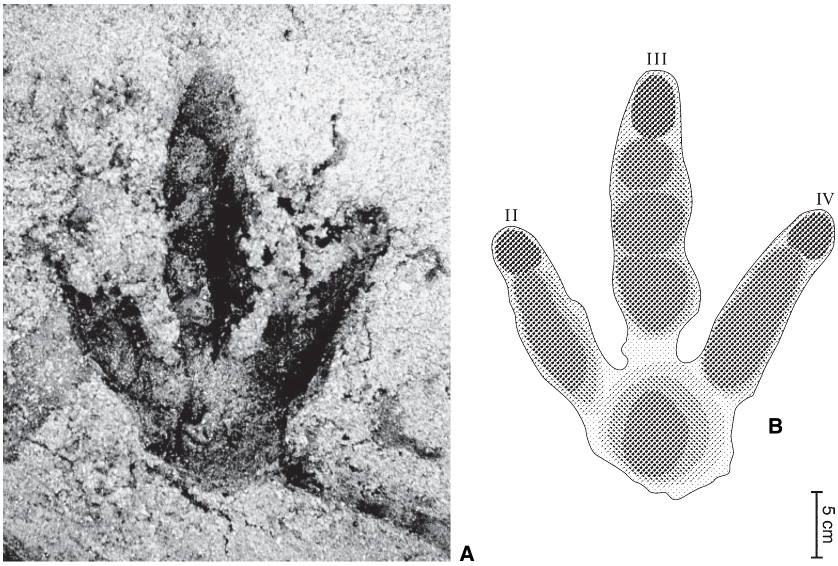
TEXT-FIG. 4. Track emplaced in dry sand. A, the dry sand has no cohesive properties and no anatomical details, except for the gross overall shape of the foot, are preserved. B, interpretative drawing showing the overall shape and dimensions of the track, with all disturbing surface features and shadows removed.



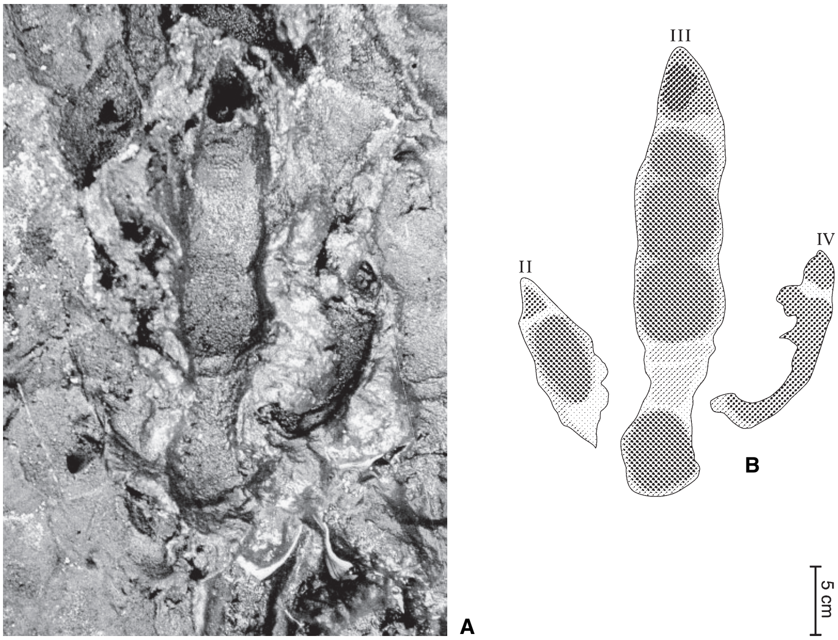
TEXT-FIG. 5. Track emplaced in damp sand. A, the track is well defined, with impressions of individual digital pads and claw impressions preserved. The coarseness of the sand prevented fine anatomical details like skin texture from being preserved. B, interpretative drawing showing only the shape and dimensions of the track.

'Didactyl' emu footprints

While the emus were walking on relatively firm substrates such as damp sand, it was noticed that digit II became less impressed in the sediment than digits III and IV, which were always impressed to about equal depth. All tracks examined in trackways from emus walking on damp sand showed digit II to be less impressed than digits III and IV (Text-fig. 12A). The interpad space between the proximal digital pad of digit II and the metatarsal pad often left no impression in the sand (Text-fig. 12B), indicating that the proximal part of digit II is held higher than in digits III and IV. In most tracks the impression of digit II is faint but



TEXT-FIG. 6. Track emplaced in wet sand. A, the foot has sunk deeply into the substrate and formed steep track walls. The imprints of the digital pads and claws are present in the bottom of the track. Radiating fractures are formed in the sand around the track. B, interpretative drawing showing only the track as it appeared subsequent to the lifting of the foot.

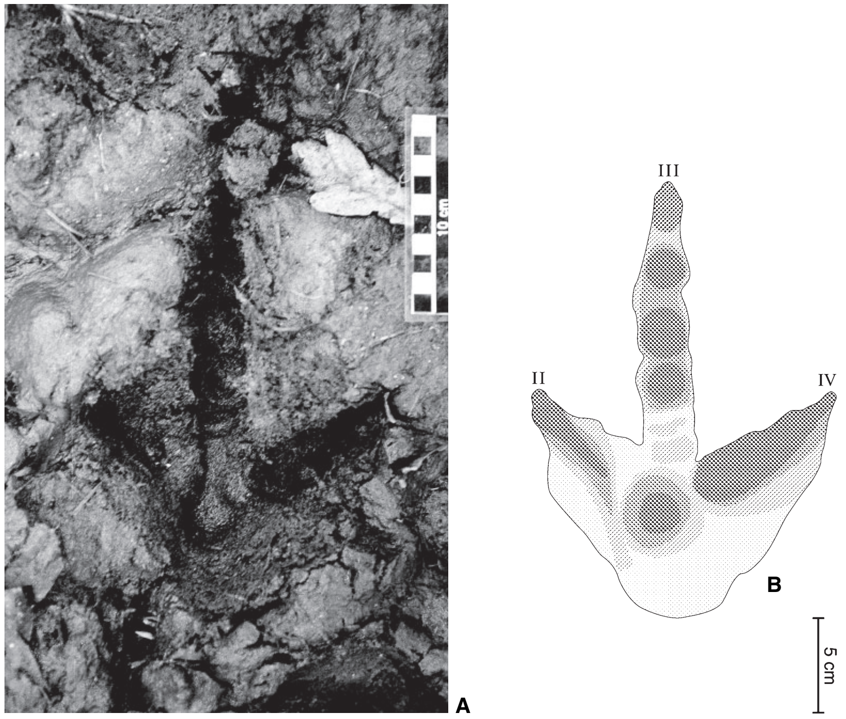


TEXT-FIG. 7. Track emplaced in a thin layer of soft mud. A, impressions of the claws, digital pads and the tuberculate skin texture are well preserved in the soft mud. A mound of mud which was pressed up between digits III and IV during the W-phase now partly fills the impression of digit IV. B, interpretative drawing of the track. Disturbing surface features from previous trampling have been removed.

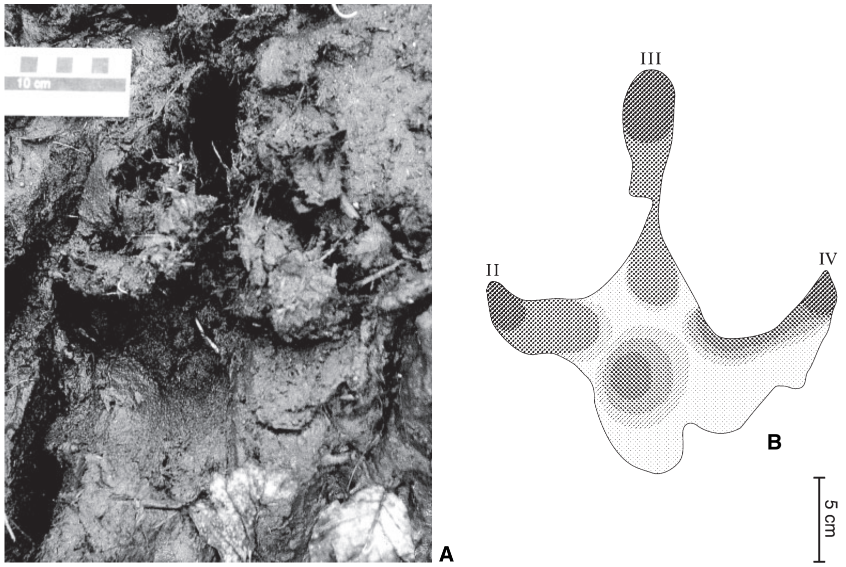
recognizable. In one track, however, the only hint of digit II is a shallow pinch trace produced by the tip of the claw, which at first glance makes the track appear perfectly didactyl (Text-fig. 12C).

Plantigrade emu tracks

The normal stance of the emu is digitigrade, with the elongated tarsometatarsus held at a steep angle to the ground. During feeding on seeds strewn on the ground, the emu adopted a plantigrade stance and walked around with the metatarsus making full contact with the ground. The plantigrade tracks comprised the impressions of the three digits, the metatarsal pad impression and the long impression of the metatarsus. The metatarsus impressions were deepest proximally, at the anatomical heel, shallowing distally towards the metatarsal pad. Impressions of the pointed scales covering the ventral side of the metatarsus were present in the tracks (Text-fig. 13).



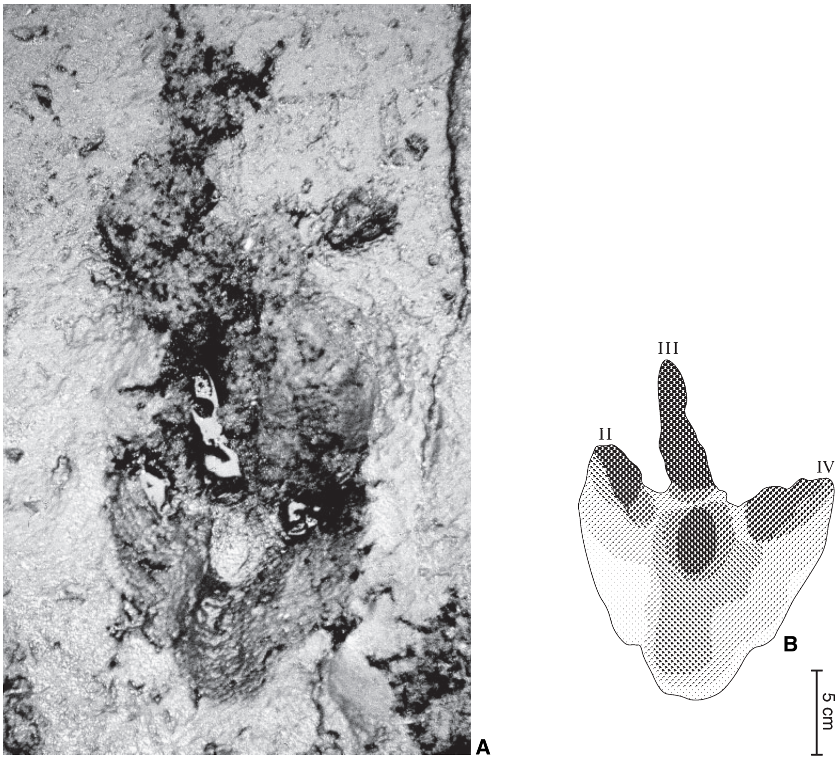
TEXT-FIG. 8. Track emplaced in deep firm mud. A, The foot has sunk to a considerable depth in the substrate, creating steep track walls. Impressions of digital pads and skin texture are preserved in the bottom of the track. The tubercles covering the sole and sides of the digital pads have created striations in the track walls. Owing to the dynamic movement of the foot during the stride, the track walls slope, causing an elongation of the track at the surface. B, interpretative drawing of the track. Note the prominent elongation of the proximal part of the track, caused by the sloping track walls.



TEXT-FIG. 9. Track emplaced in deep semi-firm mud. A, two lobes of mud formed between the digits have converged and closed off the proximal end of the impression of digit III. At the surface the track appears as a triangular impression of the metatarsal pad and digits II and IV, plus an oval hole from the tip of digit III. The track wall at the proximal end of the track slopes where the foot sank deeply into the substrate. B, interpretative drawing showing the track as it appears on the tracking surface.

Striations from skin tubercles

In tracks produced in deep mud of a firm consistency, the skin tubercles covering the sides and sole of the digital pads left clear striations in the track walls as they were dragged through the sediment during walking. A plaster cast of a well-preserved emu footprint (Text-fig. 14A) shows variation in the direction of the striations in different parts of the footprint. The striations in the impressions of the proximal part of digit III and the metatarsal pad are orientated forward and down and are formed during the impression of the foot, the T-phase. However, the striations in the impressions of the two proximal digital pads of digit III are directed forward and upward, having originated from the subsequent lifting of the foot, the K-phase. This double origin allows the striations formed during the footfall to be



TEXT-FIG. 10. Track emplaced in deep, semi-fluid mud. A, the foot has sunk deeply into the substrate forming deep, sloping track walls. During impression of the foot the mud collapsed over the digits and was ejected and carried in front of the track as the foot was subsequently lifted and swung forward. After the foot was lifted, the track was gradually degraded because of inflow of water from the sediment. B, interpretative drawing showing only the direct track as it appears on the surface. The track is highly elongated with prominent sloping track walls at the proximal end.

partly overprinted by the striations formed during the lifting of the foot (Text-fig. 14B).

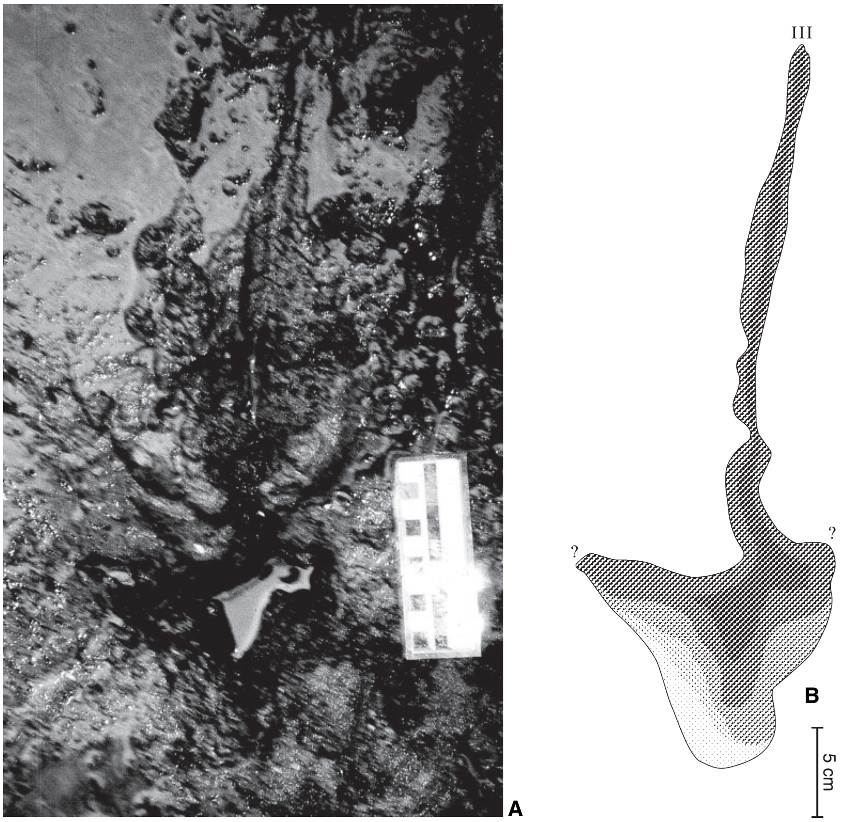
In another track, impressed in deep semi-firm mud, the sediment collapsed over the digit impressions at the surface but left the digit impressions open at the bottom of the track (Text-fig. 14C). On the plaster cast the striations in the impression of digit IV change direction with depth, thus reflecting the subsediment movements of the foot. The striations reflect first the downward movement of the foot during the footfall and then a change of direction as the digit is dragged backwards and up during the kick-off (Text-fig. 14D).

An acceleration footprint

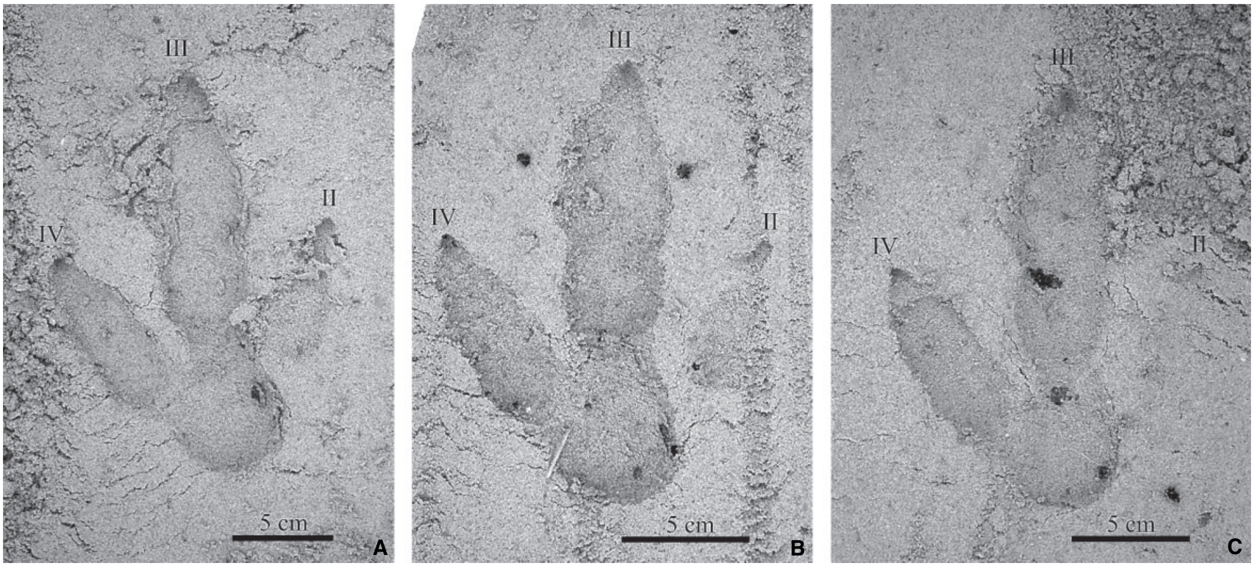
Acceleration from normal walking speed to running changes the shape of the footprints significantly. During normal walking the different parts of the foot are impressed to almost equal depth in the sediment, showing an even distribution of the weight (Text-fig. 15A), but during acceleration the weight of the animal is transferred to the tips of the toes, causing the digit impressions to be significantly deeper distally (Text-fig. 15B). A plaster cast of the acceleration track shows that the tip of digit III is most deeply impressed in the sediment, and that the digit impression shallows proximally. The claw of the digit has left a clear cut down through the sediment. Digit IV is also most deeply impressed in the distal parts and shallows proximally. Only the claw and the distal digital pad of digit II are present in the track. The metatarsal pad is only represented by a very shallow impression, and is hardly recognizable in the cast. The track walls of the digits slope to each side; this shows that the divarication angle between digits II and IV increased from the tracking surface to the bottom of the footprint during acceleration (Text-fig. 15B). The angle between digits III and IV increases by 27 degrees from surface to the bottom, while the angle between digits II and III decreases by 11 degrees, leaving a total increase in divarication angle of 15 degrees from the tracking surface to the bottom of the footprint.

DISCUSSION

The pedal morphology of the emu, and especially the similarity between the morphology of its footprints and those of small- to medium-sized theropods, makes it an ideal animal to use for comparative ichnological work. When studying the curiously collapsed theropod footprints from Jameson Land, East Greenland, Gatesy *et al.* (1999) used a turkey and a helmeted guineafowl walking in mud of different consistencies to re-create the different stages of collapse they observed in the footprints. While turkeys and guineafowl are fairly large



TEXT-FIG. 11. Track emplaced in deep fluid mud. A, the soft mud collapsed immediately after the foot was lifted, leaving only a low-relief, angular, water-filled depression in the surface. The claw of digit III left a long drag trace in the tracking surface in front of the track, as the depth of the mud prevented the emu from lifting the foot totally clear of the sediment. B, interpretative drawing showing only the direct track features recognizable on the tracking surface. Note the long drag trace from digit III.



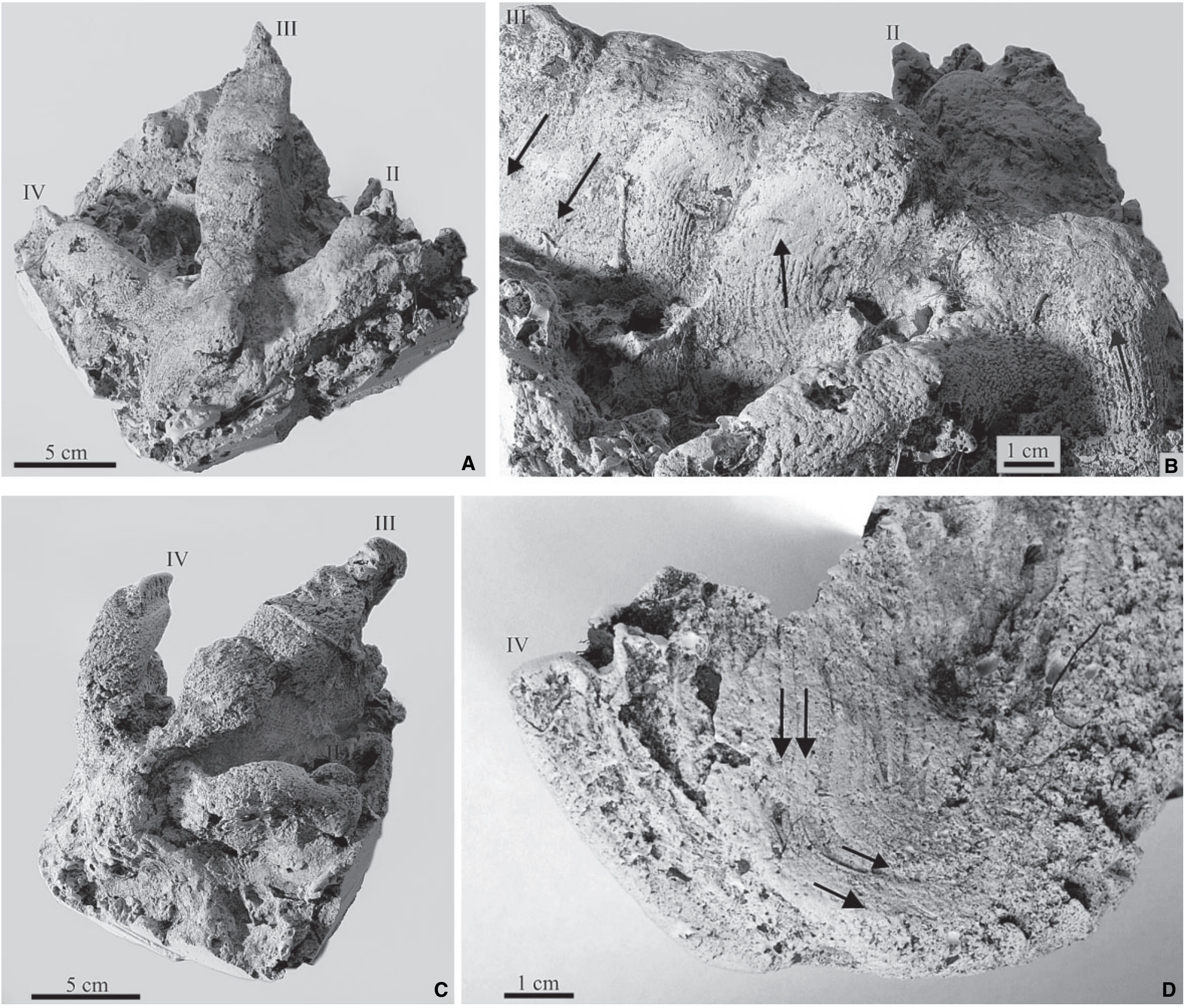
TEXT-FIG. 12. Various degrees of impression of digit II in emu tracks made in damp sand during normal walking. A, digit II impressed to approximately the same depth as digits III and IV. B, digit II only slightly impressed, leaving a faint trace of the digit and the claw. C, the fleshy parts of digit II are not impressed in the sediment, and only a small pinch trace from the tip of the claw represents the digit; a plaster cast of the didactyl track exists as MGUH 27474. All examples shown as left feet.

birds, their footprints are only 5–10 cm long and they have narrow toes lacking prominent digital pads. The larger size of the emu foot, 18–20 cm, with its broader and fleshier digital pads, favours a direct comparison with track features of especially theropod and small ornithopod tracks.

TEXT-FIG. 13. Plaster cast of emu track with full metatarsus impression (MGUH 27475). During feeding on seeds strewn on the ground the emu adopted a plantigrade stance with the full length of the metatarsus in contact with the ground. The length of the metatarsus impression is indicated by a dashed line. The pointed scales covering the ventral surface of the metatarsus have left clear impressions in the cast. Birdseed from the feeding session still adheres to parts of the plaster cast.

The artificially obtained track emplaced in potter's clay (Text-fig. 3) represents the optimal sediment for track preservation, and the fine-grained texture of the clay preserves even minute details of the skin. Clay has a high potential for fossilization because it hardens as it dries. All vertebrate tracks showing good skin impressions are found in clay or very fine-grained sediments (Laporte and Behrensmeyer 1980; Woodhams and Hines 1989; Currie *et al.* 1991; Allen 1997; Gatesy *et al.* 1999; Gatesy 2001; McCrea *et al.* 2001; Diedrich 2002). The emu track in dry sand (Text-fig. 4) shows little detail, but the gross overall shape of the track has some preservation potential. Damp sand (Text-fig. 5) preserved anatomical details of the foot such as digital pads and even faint skin impressions. It is possible to preserve tracks in damp sand because aeolian sediments have been shown to be rich sources of fossil footprints (McKeever 1991; Fornós *et al.* 2002; Loope and Rowe 2003); furthermore, the consistency of damp sand proved rigid enough to allow plaster casts to be made of the footprints. Wet sand (Text-fig. 6) produced deep, well-defined tracks, but the wetness of the substrate caused the tracks to flow together slowly, obliterating the shape of the track. In this case, the radial cracks formed around the track are solely the result of the horizontal pressure applied to the sediment as the foot was impressed. A thin layer of soft mud (Text-fig. 7) produced very detailed footprints showing a high degree of anatomical detail, such as digital pads and skin impressions. Tracks impressed in mud have a high preservational potential if allowed to dry a little before burial.

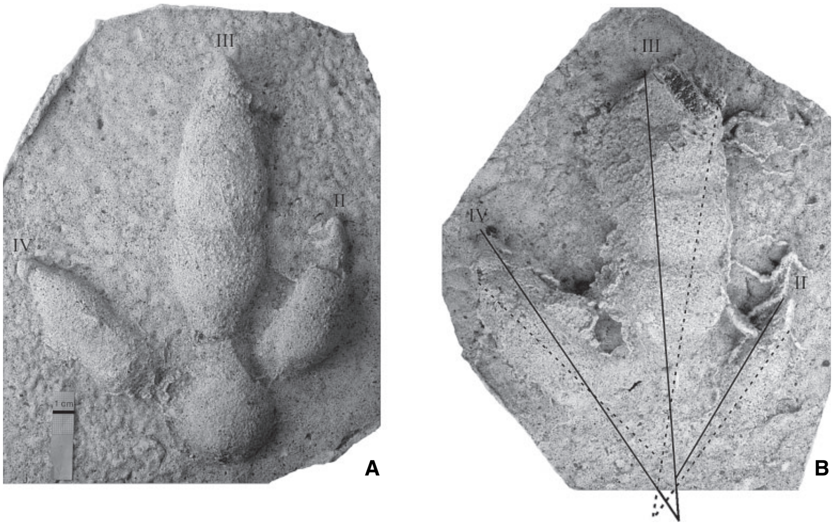
The amount of detail preserved in deep, firm mud is similar to that of a thin mud layer, and the fossilization potential is high (Text-fig. 8). In addition to the skin impressions from the sole of the digital pads preserved in a thin layer of mud, the tubercles on the sides of digital pads produced striations in the track walls, representing the dynamic movement of the foot as it was dragged through the sediment (Text-fig. 14). This adds valuable information about the gait and walking dynamics of the trackmaker, a phenomen hitherto studied by cutting sections through well-preserved footprints (Avanzini 1998; Gatesy *et al.* 1999; Milàn *et al.* 2004). When the deep mud has a slightly softer consistency the track walls collapse over the digit impressions after uplifting of the foot, leaving a track consisting of a triangular 'heel' area and an oval hole where digit III left the sediment (Text-fig. 9). This elongated and partly collapsed footprint morphology is known in Triassic theropod tracks from East Greenland (Gatesy *et al.* 1999). In even softer mud, the softness of the mud caused the track walls to collapse over the digits, smothering the foot in sediment, which caused a certain amount of mud to be thrown up in front of the track during the K-phase (Text-figs 10, 11). Tracks imprinted in this kind of sediment are not likely to reveal many details if fossilized because the sediment slowly flows together after the foot has been lifted, leaving only an area of disturbed mud on the surface. However, even



TEXT-FIG. 14. Plaster casts of emu footprints from deep, firm mud; striations caused by the skin tubercles preserved. The orientation and directions of the striations are indicated by arrows. Roman numbers indicate terminations of each digit. A, plaster cast of emu footprint emplaced in firm mud (MGUH 27476). B, detail of A, showing the striations formed in the track walls of the metatarsal pad and digit III. The striations on the metatarsal pad and the proximal digital pad of digit III were created during the T-phase when the foot was brought down through the sediment. The striations in the distal end of digit III were formed during the K-phase when the foot was lifted up and forward through the sediment. C, plaster cast of track emplaced in deep, semi-firm mud; the track walls are partly collapsed at the surface, but the digit impressions are open at the bottom (MGUH 27477). D, multidirectional striations on the side of the digit IV reflecting the sub-sediment movement of the digit as it was first pressed down in the T- and W-phase, and afterwards dragged backwards and up in the K-phase. Photographs, O. B. Berthelsen.

if the footprint at the surface is collapsed and hardly recognizable as a footprint at all, experimental work by Milàn and Bromley (in press) has demonstrated that the footprint in such cases can be preserved both clearly and recognizably as an undertrack in the sediment layers just beneath the true track.

The fact that tracks produced by the same trackmaker can appear significantly different morphologically as the substrate properties change can cause confusion when fossil tracks are described and can lead to the erection of unnecessary numbers of ichnotaxa. The Triassic theropod tracks found in East Greenland are supposed to originate from the same type of dinosaur (Gatesy *et al.* 1999), so the great morphological variation within the tracks is in this case solely a result of changes in substrate consistency. Diedrich (2002) described preservational variants of vertebrate tracks ranging from forms only preserved as shallow claw marks, over well-preserved imprints with skin impressions to semi-aquatic swimming traces, all presumably from the same animal, although very different



TEXT-FIG. 15. Plaster casts of tracks, at the same scale, from an emu walking on damp sand. A, track produced during normal walking is equally impressed and well defined (MGUH 27478). B, track where the emu is accelerating to a run (MGUH 27479). The distal parts of the digit impressions are significantly deeper, while the impression of the rounded metatarsal pad is shallow and hard to recognize. The digits have diverged during the impression in the sediment causing the track walls of the digit impressions to slope. The divarication angle between digits II and IV is increased from 62 degrees at the track surface to 77 degrees at the bottom of the track, an all-round increase in divariation angle of 15 degrees. Solid lines represent length axes of the digits at the track surface and dotted lines at the bottom of the track.

in appearance. A revision of Permian vertebrate ichnogenera from Scotland and Germany showed that many ichnogenera are simply substrate or behavioural variants of tracks from the same trackmaker (McKeever and Haubold 1996). Local changes in substrate consistency have been reported in a sauropod trackway in the Upper Cretaceous of Bolivia, where the individual footprints within the same trackway gradually change morphology from well defined to small, collapsed, rounded holes, indicating a progressive increase in water content of the sediment (Lockley *et al.* 2002). The present study in substrate consistency and footprint morphology supplements the above studies in documenting the different footprint morphologies, in this case evidently from the same trackmaker with the same type of gait.

The formation of radiating fractures in the sediment around footprints has hitherto received little attention. Allen (1997) described a case where a recent cattle footprint emplaced in stiff mud acts as a localizing agent for desiccation cracks forming during initial drying of the sediment. Similar radiating fractures in the sediment are occasionally described in connection with fossil footprints. On a track-bearing slab containing both ornithopod and bird tracks from the Middle Cretaceous Dakota Formation in Colorado, radiating fractures in the sediment were present around some of the large ornithopod tracks (Lockley *et al.* 1989), and radiating fractures around depressions in sediments in the Upper Cretaceous St. Mary Formation of Montana were interpreted as caused by footprints (Nadon 1993). The experimental track in potter's clay (Text-fig. 3) demonstrates clearly how the initial radiating fractures in the sediment caused by the horizontal pressure of emplacement of the foot in the sediment act as an agent for the subsequent development of a set of larger desiccation cracks.

Striations and skin impressions are rarely preserved in fossil footprints since these features can only be preserved in sediments of the right consistency. Furthermore, skin impressions can be preserved only in the true track or the natural cast thereof, and because of the delicacy of the structures they are easily erased even by mild erosion. Skin impressions preserved in dinosaur tracks were depicted for the first time, but not described, by Hitchcock (1848, pl. 13) in a tetradactyl footprint of presumably prosauropod origin and in a theropod track, *Brontozoum* (*Eubrontes*) *giganteus* (Hitchcock 1858, pl. 10). In both cases the skin impressions occurred on the digital and metatarsal pads and were those of closely packed skin tubercles. Well-preserved ornithopod tracks, *Caririchnium leonardii*, in the Cretaceous South Platte Formation of Colorado (Currie *et al.* 1991) and the Lower Cretaceous, Wealden strata of East Sussex, England (Woodhams and Hines 1989) show preservation of skin impressions. In both cases the impression is that of closely packed skin tubercles averaging 3–5 mm in size on the digits and up to 10 mm in the metatarsal region. Probable ankylosaur footprints from the Upper Cretaceous Dunvegan Formation in Alberta show both manus and pes imprints with impressions of skin tubercles, and in one case the tubercles of the manus have left clear striations in the track walls (McCrea *et al.* 2001, fig. 20.24a–b). Preserved skin impressions and striations found in Late Triassic theropod footprints in Jameson Land, East Greenland, show that the feet of these theropods were covered with small skin tubercles; they were used by Gatesy (2001) to re-create the foot movement during the stride. The tubercular skin texture preserved in the footprints that he described is very similar in both pattern and size to that covering the sole of the emu foot.

That the emu, when walking on firm substrates, carries the least weight on digit II and then occasionally produces didactyl tracks is important to bear in mind when interpreting purported didactyl dinosaur footprints. Thulborn (1990) discussed substrate-related didactyli in emu footprints, and suggested that didactyl variants of both ornithopod and theropod footprints could be related to the consistency of the substrate rather than to didactyl dinosaurs. Some theropods, however, show clear adaptations in digit II that made them unsuitable for walking. The dromaeosaurs and the troodonts carry an elongated sickle claw on a hyper-extensible digit II, used for killing prey. The length and shape of the claw implies that the digit had to be lifted clear of the ground during walking, potentially producing didactyl tracks. So far, however, no convincing tracks, except perhaps for *Deinonychosauripus*, have been attributed to the sickle-clawed theropods (Lockley 2002).

It is interesting that the emu, in spite of its highly elongated metatarsus, is capable of plantigrade, though ineffective, walking, since plantigrade theropod trackways from Paluxy River, Texas, show that theropods occasionally were capable of plantigrade walking at normal speeds (Kuban 1989). The Early Jurassic ichnogenus *Anomoepus*, which is referred to small ornithopod dinosaurs, includes a variant where the trackmaker is resting with the metatarsus fully impressed in the sediment, as well as impressions of the ischium and belly and five-fingered manus imprints (Hitchcock 1858, pls 8–9). Interestingly the metatarsus impressions in these resting traces is impressed in the sediment in a way similar to that of the emu resting track, with the proximal part of the metatarsus most deeply impressed, shallowing distally. In this case the metatarsal joint is not represented by any pad impressions. Unfortunately the body of the emu failed to leave impressions in the sediment, hindering further comparisons with dinosaur resting traces.

During my study, the divarication angles were measured on 30 footprints representing different sediment consistencies and progression speeds. When measured in only 30 tracks, the divarication angle of emu tracks was found to be very inconsistent, ranging from 61 to 102 degrees, with a mean of 76·8 degrees. Even within tracks from the same trackway and same progression speed the angle can vary from footprint to footprint. However, measurements from several hundred tracks of emus and other large flightless birds show that the divarication angles show something like a normal distribution about mean values (J. O. Farlow, pers. comm. 2003). Interspecific and intraspecific variation in footprints of emus and related flightless birds has been discussed in detail by Farlow *et al.* (1997, 2000). Interestingly, my study shows that the divarication angle can also change as a function of depth within the same track (Text-fig. 15B). This is important to bear in mind as experimental work with successive sections down through an emu footprint shows great morphological variation in digit shape and dimensions with depth (Milàn and Bromley in press). Furthermore, if the divarication angle can vary with depth in the footprint, great care should be taken when describing and interpreting footprints that have been exposed to erosion.

CONCLUSION

By conducting practical field experiments with living animals, valuable insight into the processes of track making and track preservation can be obtained, insight that is hard to obtain from laboratory controlled experiments. This is owing to the fact that the formation of a track is the result of the dynamic interaction between the trackmaker and the substrate. The close similarities between the tracks of emus and especially tracks of theropods and small ornithopods make emus ideal for comparative studies in track formation and taphonomy, as experimental results will be directly comparable with fossil tracks. The consistency of the substrate exercises a strong control on the track morphology and the amount of anatomical details preserved within it. This means that close attention should be paid to the sedimentary context of the tracks when they are described, because footprints from the same trackmaker can appear significantly different morphologically according to the properties of the sediment in which they were impressed. Differences in gait further affect the morphology of the footprints, although not as dramatically as differences in substrate consistency.

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