

A FOOTPRINT AS A HISTORY OF MOVEMENT

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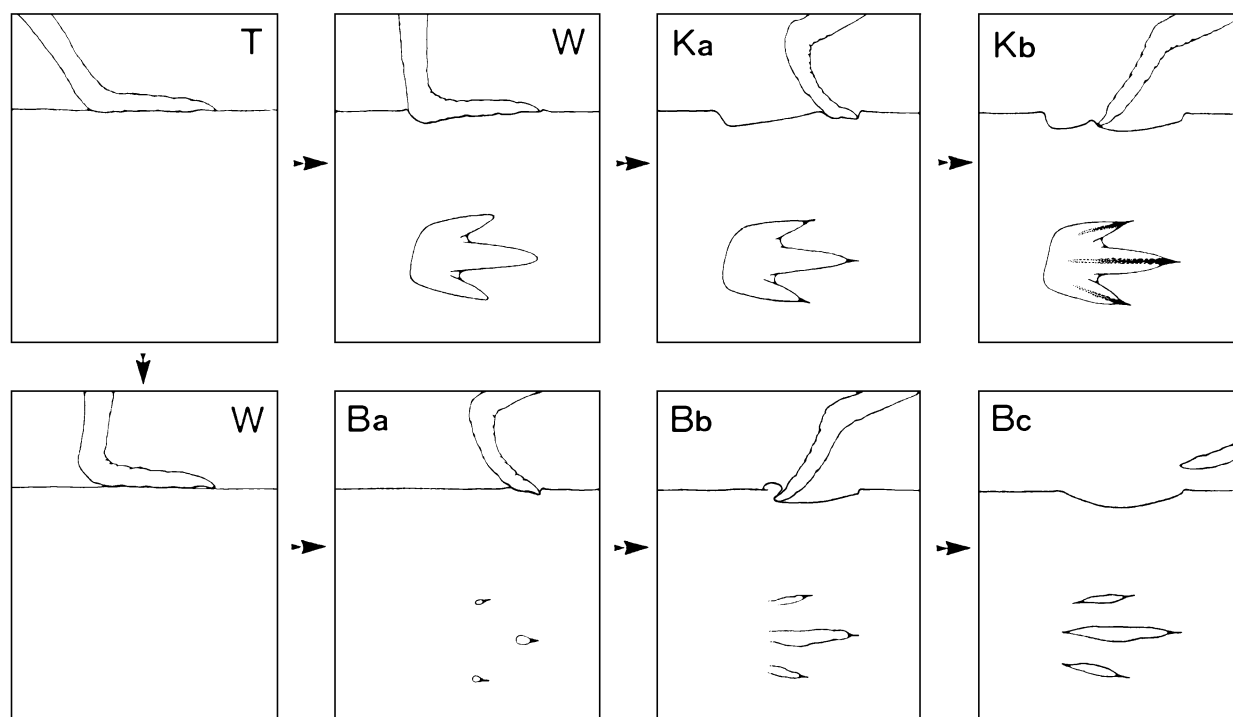


Figure 1. Morphological features of coelurosaur footprints (*Skartopus australis*) at Lark Quarry site, related to events during the trackmaker's step-cycle (see also Fig. 6). Each diagram shows position of foot in profile (above) and corresponding plan view of the right footprint (below). **T**, touch-down phase; the foot makes little or no impression on the substrate. **W** (upper row), weight-bearing phase; the foot sinks into the substrate. **Ka**, kick-off phase; as foot is lifted from substrate the tips of the toes produce sharp imprints of the claws. **Kb**, kick-off phase (frequently following **Ka**); tips of the toes slip backwards, incising grooves in floor of footprint. **W** (lower row), weight-bearing phase; the relatively large and broad-spreading foot fails to sink into the substrate. **Ba**, kick-off phase; only the tips of toes break through the surface of the substrate. **Bb**, **Bc** (frequently following **Ba**), kick-off phase; tips of the toes break through the surface of the substrate and slip backwards to form sub-parallel furrows.

Abstract

The foot of a moving animal interacts with the substrate in three phases: touch-down, weight-bearing and kick-off. We examine the morphological effects of these phases in footprints of Cretaceous dinosaurs (theropods and ornithopods) at the Lark Quarry Environmental Park, western Queensland, Australia.

Introduction

A footprint gives only an imperfect idea of a trackmaker's foot structure. The footprint maybe incomplete, because parts of the foot were not impressed into the substrate, or it may be obscured by adventitious or extramorphological features (following terminology of Peabody 1948). Some of these deficiencies and

extramorphological features result from local variations in the physical properties of the substrate; others originate from the dynamic interaction between foot and substrate. That complex interaction may be envisaged as a sequence of three phases: (i) touch-down (abbreviation T-phase), (ii) weight-bearing (W-phase), and (iii) kick-off (K-phase). Touch-down is normally on the functional ball of the foot, with the tips of the toes turned slightly upwards. In the W-phase the trackmaker's center of gravity passes over the planted foot, which usually sinks to some degree into the substrate. The K-phase entails a backwards sweep of the toes. All three phases may be seen in living tetrapods, particularly in those such as kangaroos that move the hind feet synchronously. Similar

phases are evident in barefoot humans and probably occurred in dinosaurs too. In some instances a trackmaker's foot makes little impression on the substrate until the K-phase. Then, as the rear part of the foot is being lifted from the ground, the toes break through the surface to produce a foreshortened footprint. Such distinctive one-phase footprints, formed during a brief episode of breakthrough, are identified in our illustrations by the code-letter B.

We illustrate the morphological effects of these phases in a variety of footprints made by Cretaceous dinosaurs, both theropods and ornithopods. These footprints were found at a site known as Lark Quarry, in western Queensland, Australia (see Thulborn and Wade 1979, 1984; and Agnew et al. 1989)

Substrate and Paleoenvironment

The sediments at Lark Quarry are interbedded sandstones and claystones. These accumulated in the floor of a broad creekbed that drained into a lake or waterhole to the southwest. Each sandstone/claystone couplet presumably originated from a single major influx of sediment charged water. Dinosaur footprints occur at several horizons in the succession. At the single horizon discussed here nearly 4,000 footprints were excavated in the form of natural molds (concave epireliefs). All these footprints were impressed in a single bedding plane which defines the top of a laminated claystone bed with a total thickness ranging between 6 cm and 12 cm. The claystone is overlain and underlain by finely cross-bedded arkosic sandstones.

Footprints

The Lark Quarry footprint horizon bears several generations of dinosaur tracks (Fig. 2), which are examined in chronological order. All the footprints are original impressions; there is no indication that any of them are "underprints" transmitted through the overlying sediments.

First Generation

This category comprises a few scattered and poorly preserved footprints attributed to moderately large ornithopods. The tridactyl foot-

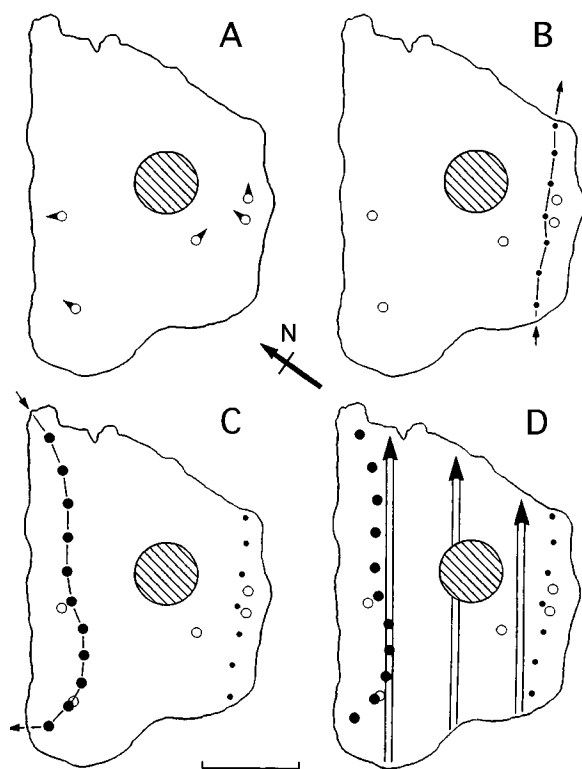


Figure 2. Sequence in which dinosaur tracks were formed at the Lark Quarry site, Queensland. Each of the four charts shows outline of area excavated at the site; cross-hatched circle indicates approximate location of an outlier of undisturbed overburden; scale bar indicates approximately 5 m. A, randomly-oriented footprints produced by ornithopods crossing the area while it was still under water (not all examples illustrated). B, moderately large ornithopod traverses southern part of the area from west southwest to east-northeast while it is draining free of water. C, carnosaur walks across northern part of the area from northeast to southwest. D, whole area is traversed by more than 160 small ornithopods and coelurosaur running from southwest to northeast.

prints have rather short, thick and bluntly-rounded digits and are randomly oriented (Fig. 2A). They were formed, and then eroded and filled with water-laid sediment, well before the substrate was exposed to the air and other dinosaurs traversed the area.

These scattered prints were probably made by ornithopods that were swimming and only occasionally touching down on the bottom—much like the hadrosaur footprints described by Currie (1983) in the Cretaceous of Canada. The prints trapped some residual quartz sand, without appreciable feldspar, that had been winnowed across the subaqueously hardening mud, along with a few streaks of muddy sediment that was probably stirred up by dinosaurs venturing across the area before it drained free of water. The footprints represent fairly large animals; smaller dinosaurs might also have crossed the submerged area at about the same time, but these would not have left any traces if their legs were too short to have touched down.

Second Generation

At least one moderately large ornithopod traversed the area as it was draining free of water. This animal, estimated to have been about 1.6 m high at the hip, trotted across the southern part of the site from west-southwest to east-northeast (Fig. 2B). Some of its footprints were deeply impressed in saturated mud, which bulged up between the toes and behind the foot. This upwelling is most pronounced *behind* the footprint, indicating some backwards displacement of sediment at the end of the W-phase and during the K-phase. It is worth emphasizing that this displacement occurred in an almost horizontal substrate: evidently an upwelling of sediment behind a footprint does not necessarily indicate that the trackmaker was ascending a slope. Other footprints in the same trackway are not so deeply impressed nor so well preserved; they seem to have been formed in slightly lower-lying areas that were subject to scouring as the substrate finally drained free of water and became exposed to the air.

Third Generation

This category comprises the trackway of a single carnosaur (large theropod) that walked across the northern part of the site from north-

east to southwest (fig. 2C). The trackway comprises 11 tridactyl footprints, each with tapering or V-shaped digits and, in some cases, with clear indications of large and sharply-pointed claws.

The footprints resemble those in the ichnogenus *Tyrannosauropus* and were probably made by a carnosaur about 2.6 m high at the hip (Thulborn and Wade 1984).

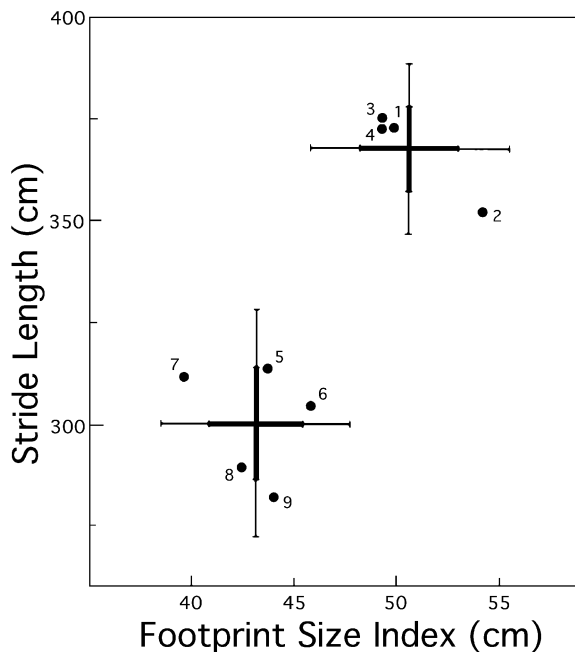


Figure 3. Variation in stride length and footprint size in the single carnosaur trackway (cf. *Tyrannosauropus*) at Lark Quarry. Footprint size index is the square root of footprint length x footprint width; it is plotted as the mean for the two footprints defining each stride. Data for each of the carnosaur's nine strides indicated by number. Note that the data fall into two distinct groups (strides 1 to 4 versus strides 5 to 9). Crosses indicate mean values plus and minus two standard deviations.

The first part of the carnosaur's trackway is noticeably different from the second (Fig. 3). Initially (strides 1-4) the footprints are relatively large and the animal took long strides; thereafter (strides 5-9) the footprints are smaller and stride length is reduced. This weaving trackway ends with an abrupt turn to the right, which presumably reflects a change in the trackmaker's behavior. We suspect that the carnosaur might have been approaching or stalking a group of dinosaurs gathered around the waterhole to the southwest (Thulborn and Wade 1984).

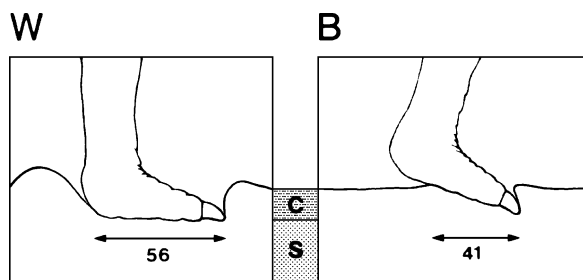


Figure 4. Two footprint morphologies in the carnosaur trackway at Lark Quarry. **W**, full-length footprint formed during weight-bearing phase of the step-cycle. Note that the foot penetrated the muddy surface sediment (c), which bulged up around the footprint, and came to rest on the firmer sandy sediment beneath (s). **B**, foreshortened footprint made by the foot breaking through the surface sediment during kick-off phase of the step-cycle. Approximate lengths of the two types of footprints indicated in cm.

The first part of the trackway comprises deep foot prints, each surrounded by a prominent raised rim of sediment. Evidently the trackmaker's foot plunged right through the muddy surface layer and rested on the firmer sandy sediments beneath (Fig. 4W). In this W-phase the muddy sediment bulged between the toes and around the perimeter of the foot. Once again it is noteworthy that this upwelling of sediment also occurred *behind* the foot on a more or less horizontal substrate. In the second part of the trackway the foot sometimes made little impression on the substrate until the K-phase. Then, as the rear part of the foot lifted

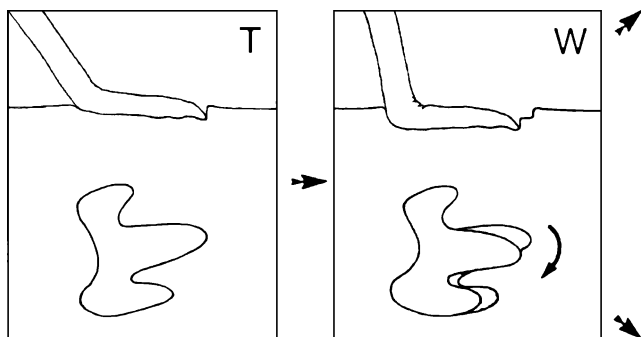


Figure 5. Morphological features of ornithopod footprints (*Wintonopus latomorum*) at Lark Quarry site, related to events during the trackmaker's step-cycle. Each diagram shows position of foot in profile (above) and corresponding plan view of the right footprint (below). **T**, touch-down phase; initial footprint (shaded) is shallow and inwardly rotated. **W**, Weight-bearing phase; the foot sinks deeper, and may rotate laterally and/or slip backwards (unshaded footprint). **Ka**, end of kick-off phase; tips of one or more toes drag through the front rim of the footprint, forming forwardly-directed scrape-marks. **Kb**, kick-off phase; the tips of toes slip backwards, incising grooves in the floor of the footprint. **Kc**, kick-off phase (continued from **Kb**); toes continue to slip backwards, producing retro-scratches behind footprint.

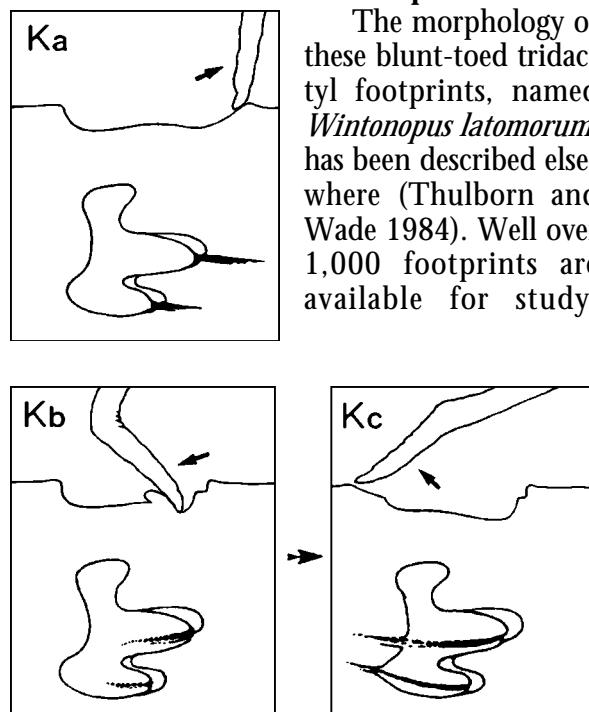
clear of the ground, the distal parts of the toes broke through the surface to produce a foreshortened footprint (Fig. 4B).

Fourth Generation

Finally a large number (160+) of small bipedal dinosaurs ran across the area from southwest to northeast. This unusual event has been interpreted as a dinosaur stampede, which was presumably triggered by the approach of the carnosaur (Thulborn and Wade 1979, 1984). By this time the muddy substrate had been exposed long enough to have achieved a firm plastic consistency. The substrate was not waterlogged, for none of the thousands of footprints slumped or collapsed; nor was it very tenacious, for it rarely adhered to a trackmaker's foot. The numerous small dinosaurs were of two types—ornithopods and coelurosaurs (small theropods)—each indicated by its own distinctive footprint morphology.

Ornithopod Footprints

The morphology of these blunt-toed tridactyl footprints, named *Wintonopus latomorum*, has been described elsewhere (Thulborn and Wade 1984). Well over 1,000 footprints are available for study;



these show tremendous morphological variation, much of it related to events during the trackmaker's step-cycle (Figs. 5-8). At the start of this cycle (T-phase) the forwardly extended foot was planted on the substrate with slight

positive (inwards) rotation (Fig. 5T). Initially there would have been a very shallow footprint, or none at all. At mid-step (W-phase) the trackmaker's center of gravity passed forwards above the planted foot, which then sank deeper into the substrate. The degree to which the foot sank depended on many and variable factors, including the size and weight of the trackmaker, the attitude of its foot, and the local consistency of the substrate. Sometimes the foot sank up to, or beyond, the distal end of the metapodium, leaving a print that comprised three digital impressions joined together along a continuous posterior margin (Fig. 6C,D).

At other times the foot did not sink so deeply, so that the three digital impressions are partly or completely separated and there is no continuous rear margin to the footprint (Fig. 6A,B). Other variations in footprint shape depended on the attitude of the foot during the T-phase and are examined elsewhere (see Thulborn and Wade 1984, Fig. 5); so too are size related variations, such as the fact that the tips of the digits appear to have been distinctly sharper in small footprints. Variation in footprint shape with depth of tracks is a widespread phenomenon. In some sedimentary successions it may result in underprints which differ considerably from the true footprints.

During the W-phase the foot sometimes slipped backwards as it sank deeper, so that the front margins of the digital impressions are distinctly stepped or terraced (Fig. 5W). In addition the foot sometimes rotated outwards, so that digit III pointed directly ahead; similar traces of rotation or sideways slippage of the foot were described by Soergel (1925) in *Chirotherium* footprints. Since the foot was planted into the substrate (T-phase) with inwards rotation, but was withdrawn (K-phase) in a different direction (forwards or antero-laterally), the tip of digit III may appear to be forked or Y-shaped (e.g., Fig. 5W).

During the K-phase the tips of the toes were the last parts of the foot to be withdrawn from the substrate. Sometimes the toes slipped backwards as they were being withdrawn, thus incising slots in the floor of the footprint (Fig. 5Kb). Occasionally the tips of the toes slipped

back so far that they breached the rear wall of the footprint to leave retro-scratches (Fig. 5Kc). In some instances the tips of the toes did not slip backwards during the K-phase; instead they sometimes dragged through the front rim of the newly-formed footprint, to leave forwardly-directed scrape marks (Fig. 5Ka). Digit III was the longest in the trackmaker's foot and, for that reason, formed a scrape mark most frequently; digit II was the shortest in the foot and rarely produced a scrape mark.

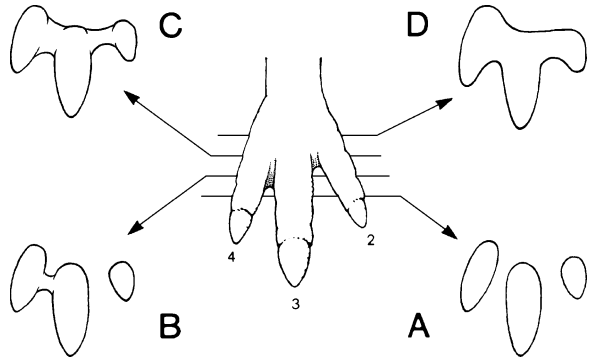
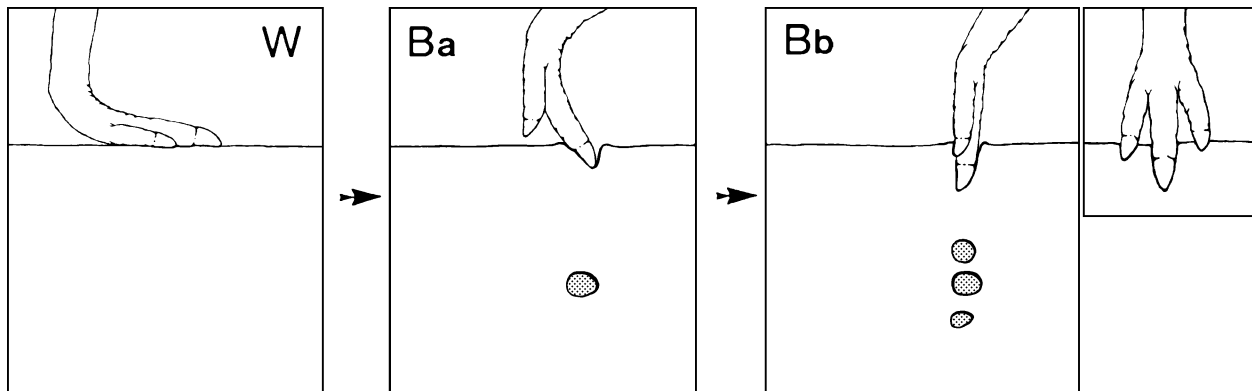


Figure 6. Morphology of ornithopod footprints (*Wintonopus latomorum*) at Lark Quarry site, related to various depths to which the foot sank during the weight-bearing phase. Right foot is shown in anterior outline (center) with diagrams of corresponding right footprints at various depths. A, shallow footprint; only the undersurfaces of three separate digits are impressed. B, deeper footprint, with hypex (re-entrant) between digits III and IV impressed. C, still deeper footprint, with hypex between digits II and III also impressed. D, deep footprint, with extensive and continuous rear margin.

In a few cases the foot made no impression during the T-phase and W-phase, but broke through the surface during the K-phase, when a considerable fraction of the animal's body mass was supported only by the distal parts of the toes. The tip of the long middle toe (III) sank into the substrate, anchoring itself in place (Fig. 7Ba), then, as the K-phase continued, the flanking toes (III and IV) swung forwards to touch down alongside the anchored digit III (Fig. 7Bb). The result was an extremely distinctive one-phase footprint consisting of three puncture-like markings arranged side-by-side. Such footprints are noticeably narrower than those "normal" footprints where the trackmaker's toes splayed out sideways during the W-phase (cf. figs. 5, 6, 8).

Figure 7. Unusual form of footprint formed by limited penetration of toes into substrate during the kick-off phase. **W**, weight-bearing phase; foot makes no impression on substrate. **Ba**, at kick-off phase the tip of digit III penetrates the substrate and is anchored in place. **Bb**, as the kick off phase continues, digits II and IV swing forwards to touch down alongside the anchored digit III. Note that the digits are not splayed out (anterior view of foot, top right), so that the resulting footprint is distinctly narrower than a footprint formed during the W-phase (e.g., Figs. 6, 7, 8). Footprints of this type were produced by both ornithopods and coelurosaurs.



The axial digit (III) was probably the thickest in the trackmaker's foot and normally produced a correspondingly broad impression in the footprint (Fig. 8A,E-G). Sometimes the impact of this principal weight-bearing digit generated a thixotropic reaction in the underly-

ing sediment; then, when the trackmaker's foot was withdrawn from the substrate, the fluid sediment flowed (or was sucked) inwards to leave a secondarily narrowed imprint of digit III (Fig. 8B-D).

Coelurosaur Footprints

These tridactyl and almost symmetrical footprints, named *Skartopus australis*, have also been described elsewhere (Thulborn and Wade 1984). They are readily distinguished from the ornithopod footprints on account of their narrow, tapering and sharply pointed digits. Many hundreds of footprints are available for study, but they show rather less morphological variation than the ornithopod footprints at the same site. Once again, the variations that do exist are best explained by reference to events during the trackmaker's step-cycle (Figs. 7, 1).

At the start of this cycle (T-phase) the forwardly-extended foot was planted on the substrate, producing a very shallow footprint or no perceptible footprint at all (Fig. 1T). At mid-step (W-phase) the trackmaker's center of gravity passed forwards above the planted foot, which in some cases sank deeper into the substrate (Fig. 1W, upper row). During the K-phase the tips of the toes pressed down and slightly backwards to leave imprints of the sharply pointed claws (fig. 1Ka). Sometimes the tips of the toes slipped backwards during the K-phase, incising grooves in the floor of the footprint (Fig. 1Kb). Occasionally the tips of the toes continued to slip backwards, forming

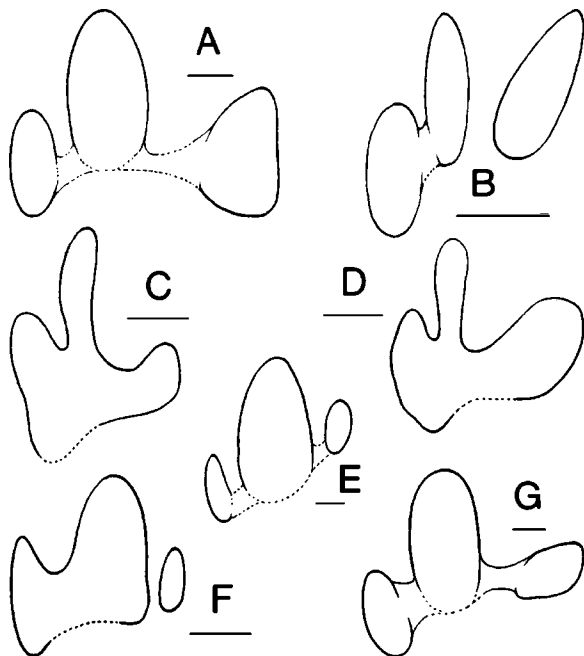


Figure 8. Ornithopod footprints (*Wintonopus latomorurum*) showing variation in size and shape of the middle digit (3). All outlines are traced from photographs of footprints at Lark Quarry, with morphological features such as scrape-marks and retro-scratches omitted for sake of clarity. All examples are illustrated as left footprints (C,D and E reversed from right footprints), and each scale bar indicates 2 cm. Digit III was the stoutest in the trackmaker's foot and appears as such in many other footprints (A, E-G). In other footprints (B-D) the imprint of digit III was secondarily narrowed by inwards suction of fluid sediment during withdrawal of the foot.

retro-scratches that breach the rear wall of the footprint (cf. Fig. 1Kb). Retro-scratches are commoner than in the ornithopod footprints, possibly because the coelurosaurs had less flexible toes. There is no obvious indication that the coelurosaur foot rotated in its footprint during the W-phase (as it did in the ornithopods, cf. Fig. 5W) nor of forwardly directed scrape marks from the tips of the digits (cf. Fig. 5Ka).

In many cases the foot did not sink into the substrate during the T-phase or the W-phase (Fig. 1W, lower row). This seems to have happened very frequently, judging from the large number of “gaps” or “missing” footprints in the coelurosaur trackways at Lark Quarry. We suspect that the coelurosaurs had relatively large and broad-spreading feet that acted as analogues of snowshoes. Nevertheless the sharp tips of their claws did commonly break through the surface of the substrate during the K-phase, when the animal’s body mass would have been supported by a small (and diminishing) area of the foot’s undersurface (Fig. 1Ba). Then, quite frequently, the sunken tips of the toes lost their purchase in the muddy substrate and slithered backwards to leave a footprint consisting of superficial furrows or retro-scratches (Fig. 1Bb, Bc). Sometimes only one or two of the three

digits broke through and furrowed the surface in this fashion. The coelurosaurs commonly produced distinctive one-phase footprints consisting of three puncture-like markings arranged side-by-side (Fig. 7).

Finally, a few of the coelurosaur footprints include a trace of the metapodium (Thulborn and Wade 1984, plates 12, 13B, 14B). This is a large subrectangular impression behind the three digit impressions; it is no wider than the maximum spread of the digits and is roughly as long as the imprint of digit III. Such footprints are rare and seem to occur randomly within otherwise normal *Skartopus* trackways; however, one section of trackway shows a sequence of four such footprints. Presumably these footprints originated when the normally digitigrade trackmakers used a “flat-footed” gait. Kuban (1986) described somewhat similar footprints from the Cretaceous of the Paluxy River, Texas, but these appear to differ in one respect from those at Lark Quarry: the metapodium imprint is *deeper* than the digit imprints in the Paluxy River examples whereas it is *shallower* than the digit impressions in the Lark Quarry footprints. The significance of this distinction remains unknown.

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