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Large dinosaurian tracks from the Upper Cretaceous (Cenomanian–Turonian) portion of the Winton Formation, Lark Quarry, central-western Queensland, Australia: 3D photogrammetric analysis renders the 'stampede trigger' scenario unlikely

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ABSTRACT

The largest dinosaurian tracks at Lark Quarry, central-western Queensland, Australia, were re-examined using revised analytical protocols that incorporate three-dimensional (3D) structure. Comparisons were made with archival photographs, replica specimens (c. 1977) and the *in situ* tracks (2013) to account for changes to the track surface. Damage caused both during and after the excavation of the tracks was evident, and in cases where the archival photographs and 1970's replicas strongly differ from the *in situ* tracks, it is apparent that restoration has modified the original track morphology.

Even after accounting for recent damage and alteration, several of the track morphologies obtained from new 3D evaluation models differ considerably from the track outlines that were published in the original description of the site. Compared with the new set of representations, some of the original outlines seem to represent simpler, stylized versions of the tracks. A number of the original outlines are >20% larger than the *in situ* tracks, while others appear to incorporate cracks as part of the margin of digit impressions. Overall, the best-preserved tracks show blunt digit impressions, reaffirming the idea that the trackmaker was a large ornithopod and supporting a reassignment to cf. *Iguanodontipus*. The new analysis also reveals the nature of the displacement rims associated with the tracks, and the overprinting of these rims by other ichnites—initially by tool marks (presumably caused by floating vegetation) and then by other dinosaurian tracks (assignable to *Wintonopus latomorum*). In the context of these observations, we see no evidence for an interaction between the cf. *Iguanodontipus* trackmaker and the smaller-bodied *W. latomorum* trackmakers, as neither can be inferred to have been present at the tracksite at, or even close to the same time. Similarly, there is no evidence to support the idea that the approach of the cf. *Iguanodontipus* trackmaker in some way triggered the movement of the *W. latomorum* trackmakers. Rather than a snap-shot of dinosaurian 'stampede', this study supports the idea that Lark Quarry most likely represents a complex time-averaged assemblage of multiple dinosaurian ichnites, preserved over an extended period of time (hours to days) and bracketed by discrete phases of trackmaker activity and fluctuations in water depth.

1. Introduction

Dinosaurian tracks and trackway data preserved in a single bedding horizon have the potential to reveal information on the abundance and diversity of contemporaneous dinosaurian trackmakers in a given area (Fastovsky and Smith, 2004; Matsukawa and Lockley, 2007). This information may in turn provide insights into the composition of dinosaurian communities and palaeoecology (Adams and Breithaupt, 2003; Matsukawa and Lockley, 2007). In instances where several ichnotaxa are represented on the same track surface, some researchers (e.g. Bird, 1954, 1985; Farlow et al., 2012) have also speculated on possible palaeobiological interactions between trackmakers with similarly oriented trackways. However, the presence of multiple tracks on a track surface typically indicates the formation of ichnites within a single recording period, and not necessarily the presence of multiple trackmakers at the same moment (Fastovsky and Smith, 2004).

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The Lark Quarry dinosaurian tracksite (within the Cenomanian–Turonian portion of the Winton Formation), located 95 km south-west of Winton, central-western Queensland (Fig. 1), has multiple tracks assigned to different ichnotaxa. The tracks occur on a single track surface (Fig. 2), arousing speculations of possible interactions between the dinosaurian trackmakers (e.g. Thulborn and Wade, 1984; Paul, 1988; Lockley and Matsukawa, 1999; Roach and Brinkman, 2007; Thulborn, 2013). Numerous tracks have been interpreted as preserving evidence for the presence of two types of small dinosaurian trackmakers—small-bodied ornithopods and theropods—and a much larger bipedal dinosaurian trackmaker, initially considered to be a theropod (Thulborn and Wade, 1984). Most of the trackways produced by the small-bodied dinosaurs have the same orientation, and it was originally speculated that their trackmakers formed a co-operative, mixed herd of more than 150 individuals caught up in a terrestrial stampede (Thulborn and Wade, 1984). Several alternative interpretations have also been proposed: the small-bodied theropodan trackmakers were an avian or near-avian species posing no threat to the co-herding ornithopodan trackmakers (Roach and Brinkman, 2007); the small-bodied theropodan trackmakers were a threat and co-operatively hunted the herding ornithopodan trackmakers (Paul, 1988); some of the small-bodied trackmakers were swimming (Moreno et al., 2004; Romilio et al., 2013); the small-bodied trackmakers were either two types of theropods, two types of ornithopods, or “a single taxon of either group” (Matsukawa and Lockley, 2007: 30). Romilio et al. (2013) re-evaluated the small dinosaurian tracks and concluded that the two previously recognized ichnotaxa (i.e. *Wintonopus latomorum* and *Skartopus australis*) represented ichnomorphs (*sensu* Fastovsky and Smith, 2004) and not separate ichnotaxa, with all of these tracks being assignable to the ornithopodan ichnotaxon *W. latomorum*.

The complex track patterns present at Lark Quarry had also led to speculation that the small-bodied dinosaurian trackmakers may have interacted or responded in some way to the presence of a much larger one (Thulborn and Wade, 1984). In the context of this interpretation, the largest Lark Quarry trackmaker was considered to have ‘approached’ the smaller trackmakers (Thulborn and Wade, 1984: 413, 443, 445, 455)—even though the trackway data indicates the large-bodied trackmaker “was heading in the opposite direction” (Thulborn, 2013: 3)—and in some way “triggered” a stampede (Thulborn and Wade, 1984: 413, 443). This scenario requires the largest Lark Quarry tracks to have been formed at “*about* the same time” as the small-bodied dinosaur traces (Thulborn and Wade, 1984: 446). Thulborn and Wade (1984) described the largest tracks and those formed by small-bodied dinosaurian trackmakers

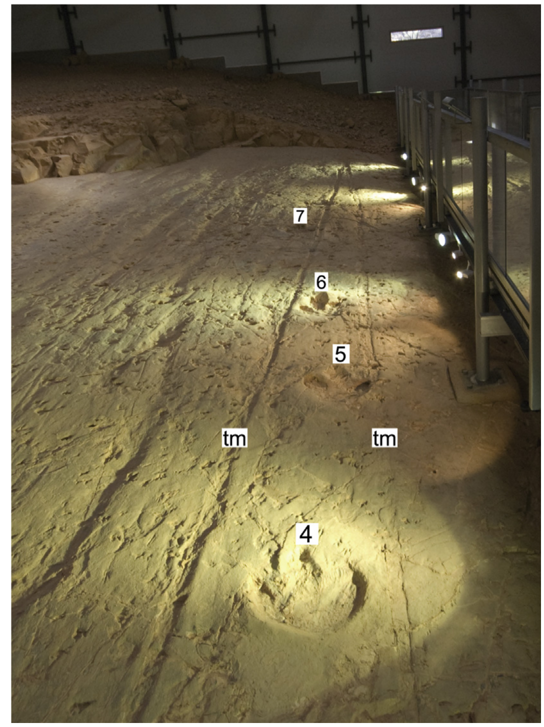

Fig. 2. Lark Quarry tracksite, April 2013. Several of the largest tracks (tracks 4–7; R2–L4) are discernable, as are tool marks (tm) possibly caused by partially buoyed vegetation. Thousands of very small dinosaur tracks appear as numerous ‘pits’ over the exposed surface. Photograph © S. W. Salisbury.

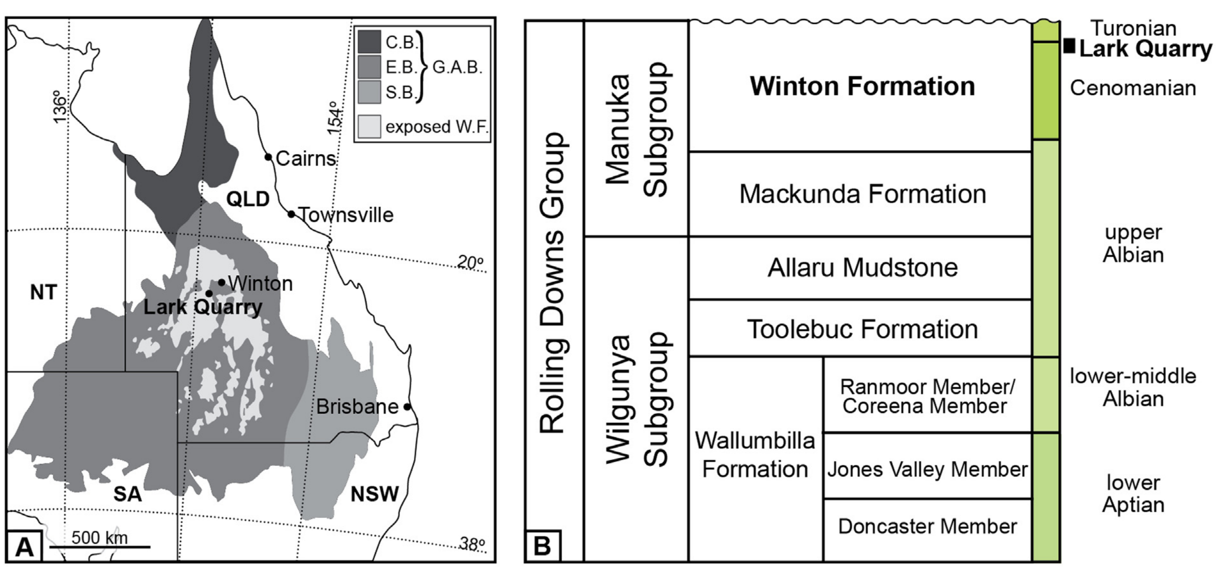

Fig. 1. A, A map of north-eastern Australia, with the position of the Lark Quarry dinosaur tracksite (23.0161° S, 142.4114° E); B, Stratigraphy of the Eromanga Basin, central-western Queensland. Abbreviations: C.B., Carpenteria Basin; E.B., Eromanga Basin; S.B., Surat Basin; G.A.B., Great Artesian Basin; W.F., exposed Winton Formation; QLD, Queensland; NSW, New South Wales; SA, South Australia; NT, Northern Territory. Adapted from Romilio et al. (2013), Tucker et al. (2013: 1) and Berrell et al. (in press).

as having been formed only when a period of subaqueous conditions had lapsed, leaving the surface subaerially exposed. During the inferred initial period of subaqueous exposure, partially buoyed vegetation floated over the site, leaving a series of parallel drag marks (tool marks). In this scenario, the tool marks are made prior to the large dinosaurian tracks.

Romilio et al. (2013) examined the Lark Quarry dinosaurian ichnites and concluded that the apparent *en masse* interactions of the small-bodied dinosaurian trackmakers—which would be necessary for a stampede—as proposed by Thulborn and Wade (1984), was highly unlikely. Instead, Romilio et al. (2013) proposed that different sized swim traces could be linked to likely fluctuations in water depth at the site during the time the tracks were recorded, such that the formation of tracks assignable to *W. latomorum* (including tracks previously assigned to '*S. australis*') could not have been synchronous. The occurrence of small-bodied dinosaurian swim traces at the site also discounted the original interpretation that *all* the small-bodied dinosaurian trackmakers traversed the site during subaerial conditions.

Other authors have also questioned Thulborn and Wade's (1984) identification of the large dinosaurian tracks at Lark Quarry, along with proposed behavioural interactions of this trackmaker with the smaller ones (e.g. Norman in Thulborn and Wade, 1984: 421; Paul, 1988). Thulborn and Wade (1984: 420) originally compared the large Lark Quarry tracks to *Tyrannosauropus* and placed them in cf. *Tyrannosauropus*. *Tyrannosauropus* has subsequently been considered a *nomen dubium* by Lockley and Hunt (1994), and the majority of tracks previously assigned to it are now regarded as being ornithopodan in origin (Lockley and Hunt, 1994; Manning et al., 2008). Assuming that the original comparisons to *Tyrannosauropus* still hold, it follows that the largest Lark Quarry tracks may also have been left by an ornithopod. Indeed, in our own initial review of these tracks, we noted that the original published outline of the "best-preserved and most complete footprint" (track 3; Thulborn and Wade, 1984: 434) closely resembled the holotype of the ornithopodan ichnotaxon *Amblydactylus gethingi* Sternberg, 1932 (Romilio and Salisbury, 2011). We also examined the shape of the original published two-dimensional (2D) track outlines from Thulborn and Wade (1984) using the multi-bivariate analysis of Moratalla et al. (1988), which provides proportional criteria to distinguish tridactyl tracks presumed to pertain to ornithopodan trackmakers from those presumed to pertain to theropodan trackmakers. Based on the results of this analysis, we concluded that the large trackmaker was likely to have been an ornithopod, and considered hostile interactions between this trackmaker and the small-bodied dinosaurian trackmakers to have been unlikely (Romilio and Salisbury, 2011).

To facilitate our initial analysis of the large Lark Quarry tracks we adapted the original outlines of Thulborn and Wade (1984) to include missing or dotted (contentious) sections (see Romilio and Salisbury, 2011: Fig. 2). The missing/dotted portions of the track outlines were added following an examination of replica specimens, the *in situ* tracks and a compilation of alternative versions of the same outlines that have appeared in the literature (see Long, 1990: 66 unnumbered figure; Thulborn, 1990: Fig. 11.10a; Molnar, 1991: Fig. 37r; Long, 1998: 127 unnumbered figure; Scanlon, 2006: Fig. 5e; Thulborn, 2013: Fig. 1; Appendix Fig. 1). Thulborn (2013) criticized our inclusion of a proximal track outline for some of the tracks, considering it a misrepresentation of the original published 2D outlines (*sensu* Thulborn and Wade, 1984), and, on the basis of this criticism proposed that "claims" by Romilio and Salisbury (2011) that the large Lark Quarry trackmaker was an ornithopod were "groundless…based partly on misconceptions and partly on fabricated data" (Thulborn, 2013: 1). Thulborn (2013) instead maintained that the original identification of these tracks and the overall interpretation of the site proposed by Thulborn and Wade (1984) were correct.

While documenting tracks as 2D drawn outlines has been one of the traditional methods employed in dinosaur ichnology, there is no escaping the fact that the vast majority of tracks are 3D structures. Any representations of tracks in 2D means that information relating to depth is subsequently lost or 'compressed', with the depicted outlines being reliant on the interpretation of the investigator, making them highly subjective (Bates et al., 2008b). Thulborn and Wade (1984) documented the largest Lark Quarry tracks using traditional methods of photography and drawn outlines. All the tracks were depicted in dorsal view as 2D outlines (Thulborn and Wade, 1984: Figs. 3, 4, Pl. 17), but only tracks 3 (as a replica track) and 6–8 (as *in situ* tracks) have accompanying photographs that are in the same view (Thulborn and Wade, 1984: Pls. 4, 5B, 6), while photographs of tracks 9–11 are not included. Because of this, subsequent assessments of these tracks have relied largely on the 2D outlines, including the analysis that we published in 2011 (see Romilio and Salisbury, 2011). However, whether these outlines actually reflect the morphology displayed by the *in situ* tracks is questionable, since most of "…the 11 large footprints at Lark Quarry are so imperfect it proved impossible [for Thulborn and Wade, 1984] to detect their complete outlines" (Thulborn, 2013: 17).

The aim of this study was to document the 3D morphology of the tracks of the largest Lark Quarry trackmaker, along with associated surface structures (e.g. displacement rims), using objective methods that retain 3D track information, and in so doing, determine how well these ichnites have been approximated in the original published 2D track outlines of Thulborn and Wade (1984). Additionally, our 3D track surface investigation allows for the reexamination of the sequence of ichnite formation through the determination of a hierarchy of trace overprinting. Should it be established that the largest dinosaurian Lark Quarry tracks were not formed synchronously (or near-synchronously) with tracks formed by the small-bodied dinosaurs, then the associated trackmaker behaviour as proposed by Thulborn and Wade (1984) will require critical reevaluation.

1.1. Institutional abbreviations

LQ, Lark Quarry, Lark Quarry Conservation Park, Queensland, Australia; **QM**, Queensland Museum, Brisbane, Australia.

2. Methods

Data on the largest Lark Quarry tracks were obtained through the analysis of the tracksite (examined during April 2013), replicas (made c. 1977, L. Beirne pers. comm. 2013), and archival photographs (taken c. 1977). Numbering of the *in situ* tracks follows that given in Romilio et al. (2013), with the trackway given the number LQ-1 and the eleven tracks numbered consecutively from left pes 1 (L1) to left pes 6 (L6) (but see Fig. 14D for alternatively numbering where the first track is considered to have been made by the right pes). There are two 'sets' of replicas, all given the same museum accession number (QM F10322): those of individual tracks (tracks 1–6; LQ-1(L2–L6)) and a wall-mounted exhibition replica of part of the track surface (tracks 3–11; LQ-1(L1–R3)) that is currently on display at the Queensland Museum, Brisbane. The individual track replicas are stored in association with preparation mounts, suggesting to us that they are likely to be a more accurate representation of the original track topography than the large exhibition replica. Both the replicas and the *in situ* tracks were used to evaluate the displacement rim morphology.

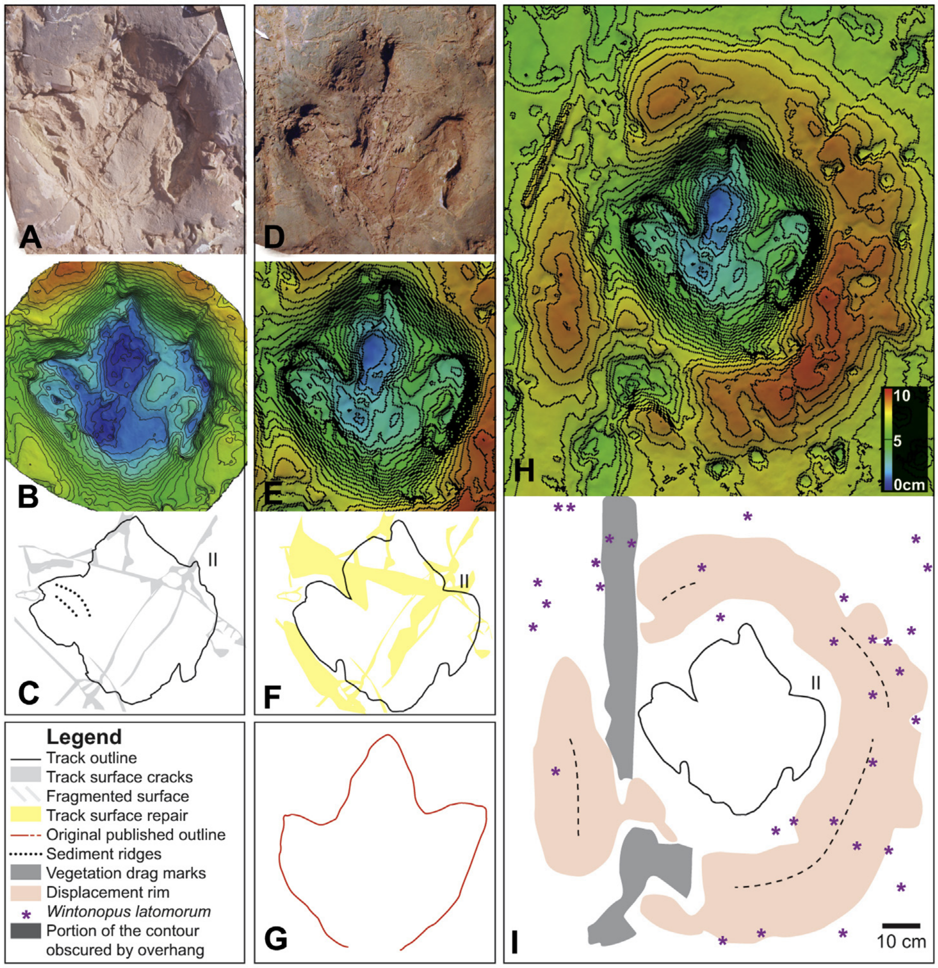

Fig. 3. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 1 (L1), a left pes impression. A, Photograph of the *in situ* track taken c. 1977 (photograph © Queensland Museum); B, colour-coded 3D relief of the track based on a fibreglass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track and surface features based on A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on photographs of the *in situ* specimen taken in 2013; F, single contour line of the track and surface features based on D and E; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to track 3, which was given a length of 64 cm by Thulborn and Wade (1984: 434); H, 3D relief of the *in situ* track (based on photographs taken during 2013); I, single contour line of the track and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *Wintonopus latomorum* (*). The depth range of the surface is approximately 10 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Multiple photographs (30–80 photographs per track) of each track were taken from varying angles, using a digital camera (either a Nikon D70 with an 18–55 mm Nikkor lens, or a Nikon D80 with a fixed 24 mm Nikkor lens), with shutter speeds set to achieve the appropriate exposure, and illuminated by artificial light (either a Nikon Speedlight SB-600 or Arlec 1000 W R7S Halogen Worklight mounted on a tripod). Virtual 3D reliefs were created by importing the multiple photographs into Agisoft PhotoScan Standard Edition (version 0.8.3 beta 64 bit), with PLY files imported into Paraview (version 3.98.0 64 bit) for the production of digital 3D reliefs with 30 contour intervals. We chose to false colour the 3D reliefs with a gradient of blue-to-red (as in Adams et al., 2010; Castanera et al., 2013), with cool colours representing the lowermost parts of the track and warm colours the higher parts. Two-dimensional outlines of tracks were then constructed by using one of the contour lines from the track 3D relief, thereby removing any ambiguity as to how they were created. No attempt was made to adjust these outlines to account for track surface heterogeneity, which includes, but is not limited to, erosional features, fragmentation and restoration. Image J (Java 1.6.0_15 (32 bit; http://imagej.nih.gov/ij)) was used to calculate track dimensions, using the 3D reliefs of both replica and *in situ* tracks, whereas trackway dimensions were measured by hand at the tracksite. Because the track surface has been modified since the initial excavation (for a summary, see Romilio et al., 2013: 103), hand measurements taken from replica specimens were considered the most reliable method to verify the measurements derived from Image J. Track and trackway orientation was recorded relative to magnetic north (inclination at Lark Quarry—4°NW).

3. Results

3.1. How well do the replicas approximate the original tracks and the surrounding 'track surface'?

Overall, the archival track photographs compared favourably with the respective 3D reliefs of the replicas (e.g. Fig. 5A,B). Strong similarities are observed in the track morphology (e.g. the presence/absence of individual digit impressions, and the lack of digital pad impressions) and the position of non-track features (e.g. surface cracks) providing assurances that these "high-fidelity replicas"

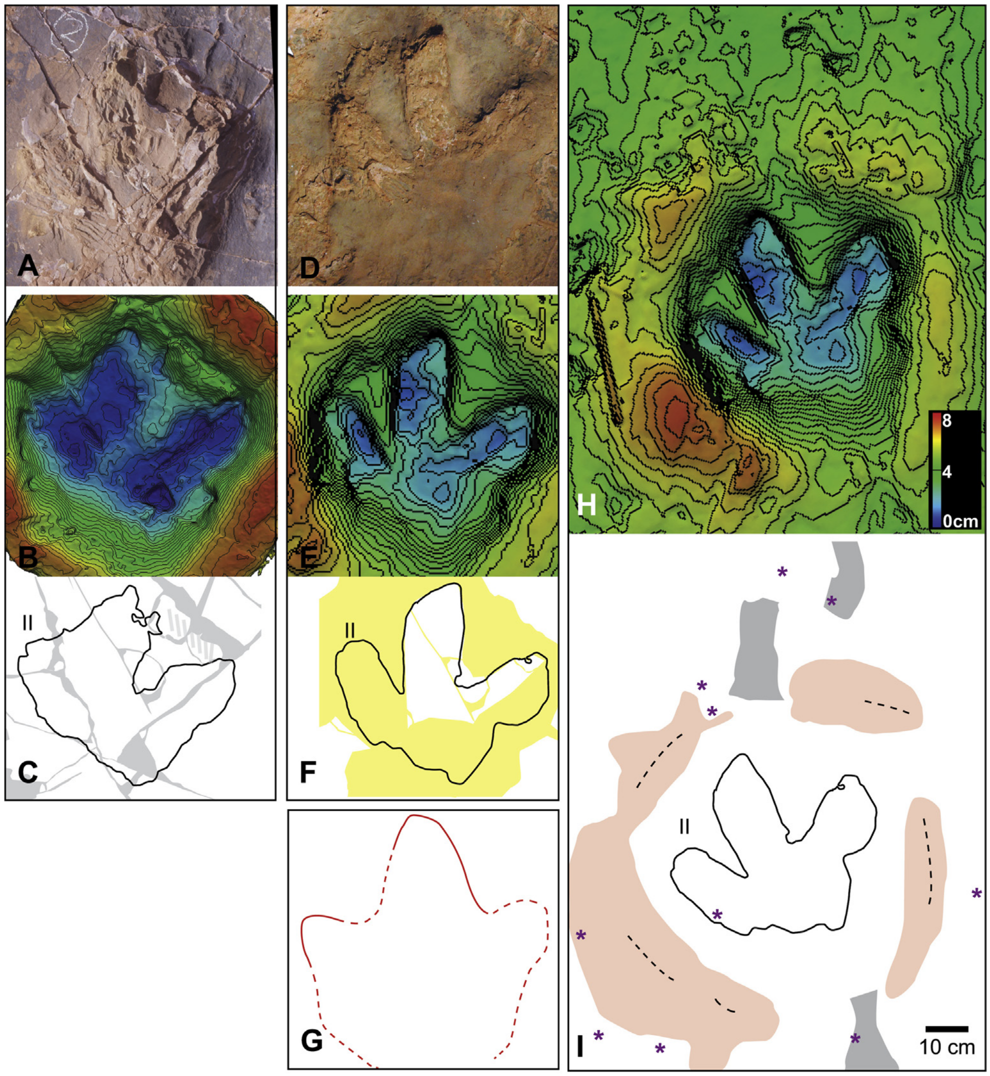

Fig. 4. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 2 (R1), a right pes impression. A, Photograph of the *in situ* track taken c. 1977 (photograph © Queensland Museum); B, colour-coded 3D relief of the track based on a fibreglass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track and surface features based on A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on photographs of the *in situ* specimen taken in 2013; F, single contour line of the track and surface features based on D and E; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to track 3, which was given a length of 64 cm by Thulborn and Wade (1984: 434); H, 3D relief of the *in situ* track (based on photographs taken during 2013); I, single contour line of the track, and schematic interpretation the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*). The depth range of the surface is approximately 8 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Thulborn and Wade, 1984: 416) are an accurate topographical representation of the *in situ* tracks as they appeared soon after excavation (c. 1977).

Nonetheless, some differences are evident between the archival photographs of the *in situ* tracks and their 3D reliefs of the respective replicas. The archival photographs appear to have been taken under conditions of bright natural light, with the tracks lacking sufficient shadowing that subsequently has resulted in the apparent loss of some surface topography. Specifically, most tracks appear shallower in the archival photographs than they actually are, and some track margins appear indistinct (particularly in the proximal track margin) than that revealed by the replicas (tracks 1, 2, 5–11; LQ-1(L1, R1, L3–L6); Figs. 3A,B, 4A,B, 7–11A,B).

Other differences also occur between the archival photographs and the replicas. The 3D relief of track 1 (LQ-1(L1); Fig. 3B) more clearly reveals morphological features (i.e. the digit III impression is broad and round in morphology; and a hypex is present between digit impressions II and III) than is apparent from the photograph (Fig. 3A). Similarly, although paired sediment ridges in the digit IV impression are evident in the archival photograph (Fig. 3A), it is only in the 3D relief that the groove (~2 cm wide) between these ridges is revealed to be quite deep (i.e. dark blue in Fig. 3B). For track 2 (LQ-1(R1)), the archival photograph shows a poorly defined tridactyl track (Fig. 4A), while the 3D relief of this track provides greater resolution of the digit IV impression (Fig. 4B). For track 3 (LQ-1(L2)), the lateral margin of the digit III impression in the archival photograph appears highly fragmented (Fig. 5A). This same region appears consolidated on the small replica (Fig. 5B), and is absent (or less raised) on the exhibition replica (Fig. 5K). For track 4 (LQ-1(R2)), the archival photograph shows a lot of unconsolidated material at the proximal track margin (Fig. 6A), and while present in the replicas, not all of this material is arranged the same way

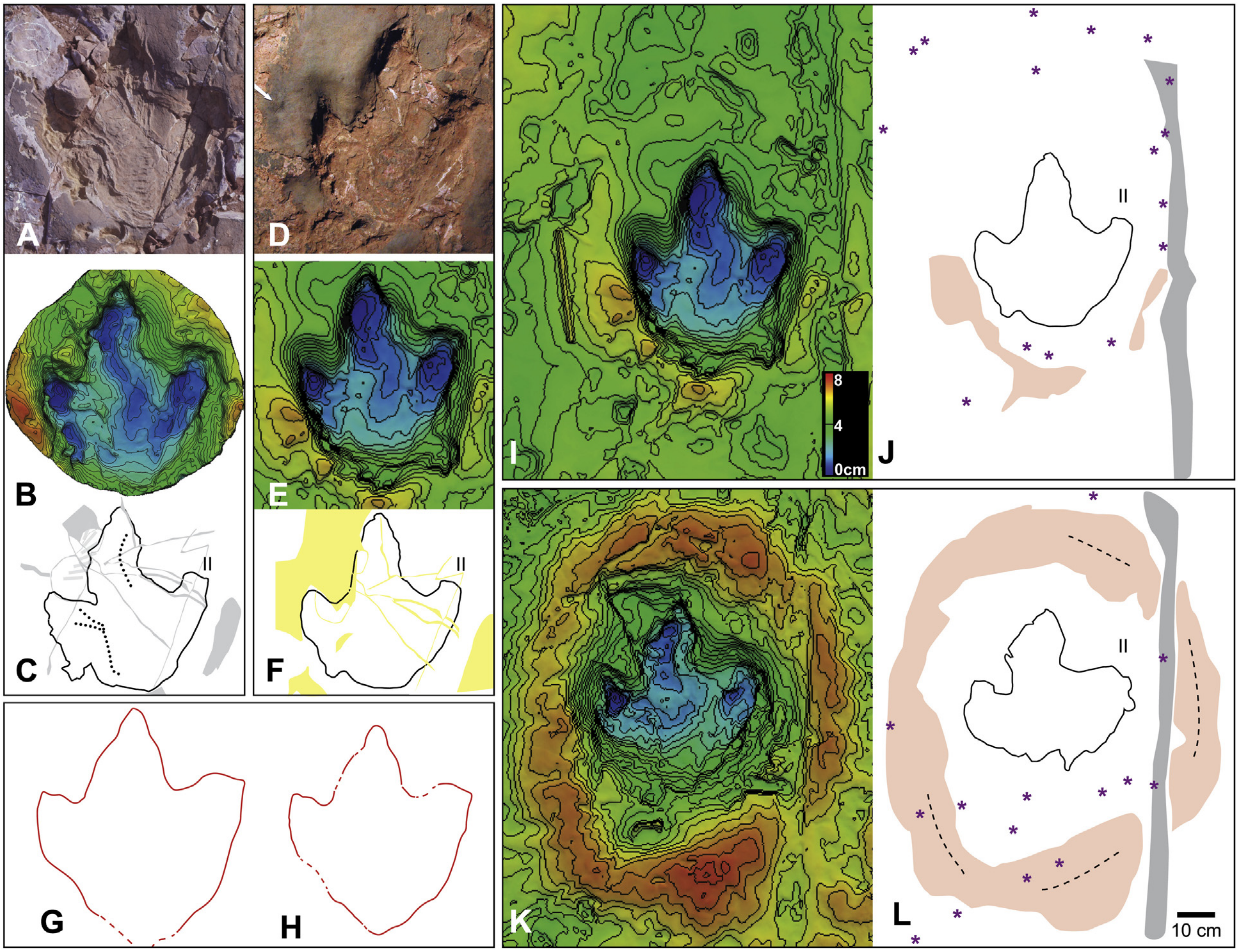

Fig. 5. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 3 (L2), a left pes impression. A, Photograph of the *in situ* track taken c. 1977 (A; photograph © Queensland Museum); B, colour-coded 3D relief of the track based on a fibreglass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track based on A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on photographs of the *in situ* specimen taken in 2013; F, single contour line of the track based on D and E; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to the given length of 64 cm by Thulborn and Wade (1984: 434); H, schematic interpretation of the track adapted from Thulborn and Wade (1984: Fig. 4); I, 3D relief of the *in situ* track (based on photographs taken during 2013); J, single contour line of the track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); K, 3D relief of the exhibition fibreglass replica (based on photographs taken during 2013); L, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*). Track depth range approximately 8 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Fig. 6B,K). Additionally, the exhibition replica of track 4 (LQ-1(R2)) shows a digit impression II that is separate from the remainder of the track (Fig. 6K), whereas the same digit impression is continuous with the other regions of the track in the archival photograph and small replica (Fig. 6A,B). Track 5 (LQ-1(L3)) appears well preserved in the archival photograph (Fig. 7A), and the same general shape is mirrored in the 3D relief of the small replica (Fig. 7B). However, the 3D relief of the track 5 (LQ-1(L3)) exhibition replica (Fig. 7K) only vaguely resembles the track portrayed in the archival photograph and small replica.

For track 6 (LQ-1(R3)), the digit III impression appears, at first glance, rather narrow in the archival photograph (Fig. 8A), but this is due to shadowing that reduces the apparent digit impression width by approximately one third, as is evident in the 3D relief (Fig. 8B). Sediment overhang occurs at the distal (for digit impressions II and III) and medial (for digit impression IV) portions of the rounded digit impressions (see Fig. 8C).

Tracks 7–11 (LQ-1(L4–L6)) also reveal differences between archival photographs and their respective replica 3D reliefs. In track 7 (LQ-1(L4)), the archival photograph appears to show a narrow digit III impression, a widely divergent digit II impression, and an isolated impression medially, possibly pertaining to digit IV (Fig. 9A). However, the replica and its 3D relief show the seemingly narrow digit III impression to be a deeper portion of a much broader digit impression (Fig. 9B), consistent with the broad digit impressions of the other tracks. The 3D relief also shows that the distal portion of the seemingly 'narrow' digit III impression kinks laterally then distally in a manner that is inconsistent with the digit impressions of the other tracks. Additionally, the possible digit IV impression could easily represent a track assignable to *W. latomorum*. Two smaller circular depressions cranial to this impression are evident in the 3D relief (Fig. 9B,H), although only one of these is distinct in the archival photograph (Fig. 9A). With track 8 (LQ-1(R4)), the intense lighting conditions evident in the archival photograph (Fig. 10A) makes discerning much of the track margin difficult. Ascertaining track morphology from the 3D relief (Fig. 10B) is not nearly as difficult, but some aspects of the track are initially surprising, specifically that of the seemingly distally

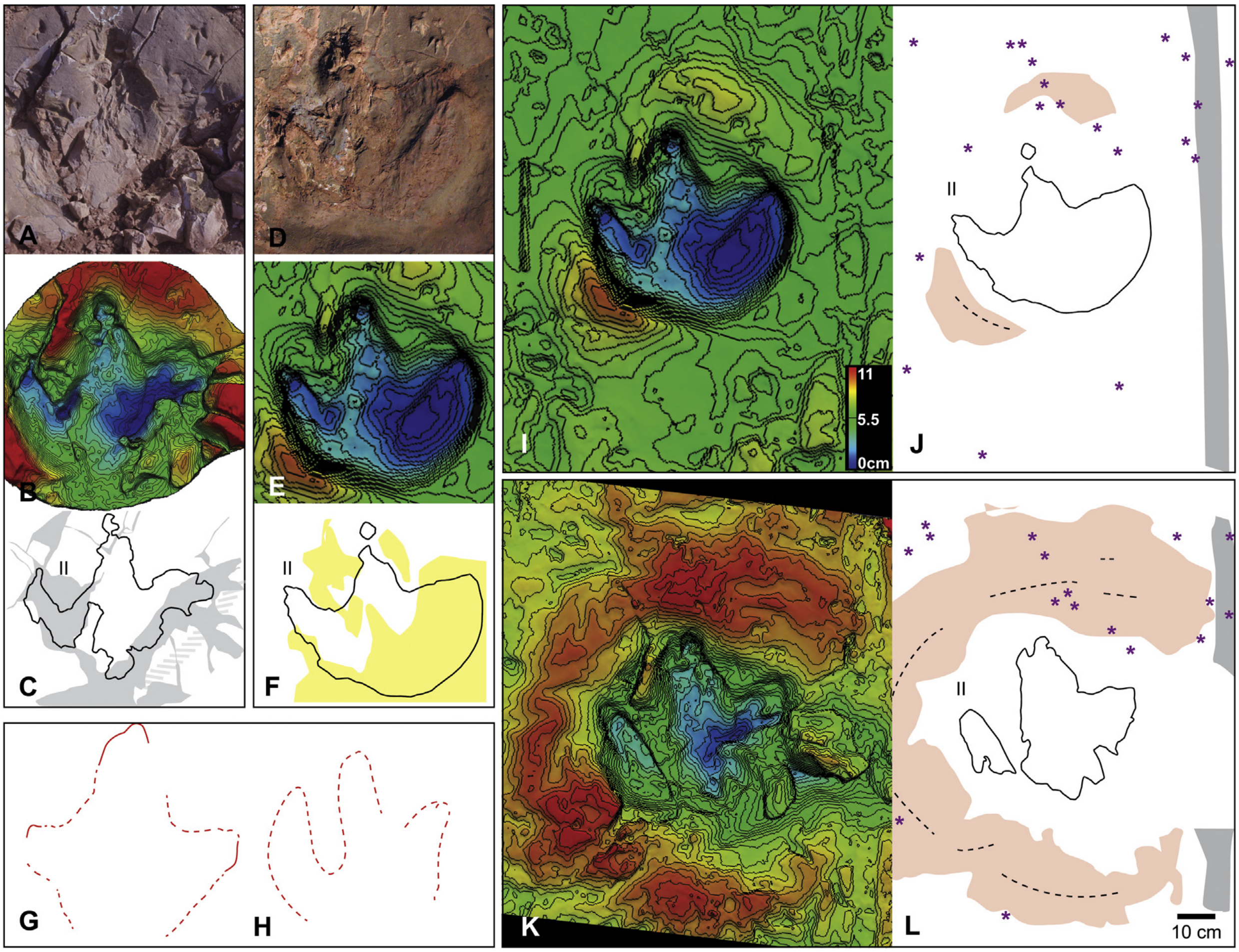

Fig. 6. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 4 (R2), a right pes impression. A, Photograph of the *in situ* track taken c. 1977 (A; photograph © Queensland Museum); B, colour-coded 3D relief of the track based on a fibreglass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track based on A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on photographs of the *in situ* specimen taken in 2013; F, single contour line of the track based D and E; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to track 3, which was given a length of 64 cm by Thulborn and Wade (1984: 434); H, schematic interpretation of the track adapted from Thulborn and Wade (1979: Fig. 2a); I, 3D relief of the *in situ* track (based on photographs taken during 2013); J, single contour line of the track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); K, 3D relief of the exhibition fibreglass replica (based on photographs taken during 2013); L, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*). Track depth range approximately 11.5 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bilobed digit III impression. This anomaly is likely the result of sediment movement at the time of track formation, rather than a consequence of an unusual pedal anatomy. Within this digit impression paired sediment ridges connect to the bilobed portion of the track. Between these paired sediments ridges is a deep, narrow groove. With track 9 (LQ-1(L5)), the archival photograph shows converging cracks and fragmentation of the track surface, but provides little information with regard to track morphology (Fig. 11A). The 3D relief of track 9 (LQ-1(L5)) shows the cracks and fragmented areas and a roughly sub-rectangular shaped track that lacks digit impressions (Fig. 11B).

The archival photograph of track 10 (LQ-1(R5)) shows a narrow groove between paired sediment ridges that seem to represent edges of the impression of digit III (Fig. 12A). This feature is very similar with that observed within the digit IV impression of track 1 (LQ-1(L1); Fig. 3B) and the groove within the digit III impression of track 7 and 8 (LQ-1(L4, R4); Figs. 9A, 10A). The 3D reliefs of track 10 (LQ-1(R5)) show that this narrow groove sits within a much broader digit III impression (Fig. 12B). Multiple sediment ridges (and grooves) are also present in the digit IV impression (Fig. 12A,B). The archival photograph for track 11 (LQ-1(L6); Fig. 13A) has considerable shadowing of a triangular region that gives the illusion of a strongly shaped and deep digit impression. However, the 3D relief shows that much of this region is considerably shallower than the actual track impression and actually represents a triangular cluster of cracks, cranial to and separate from track 11 (LQ-1(L6)), which lacks clear digit impressions (Fig. 13B).

In the majority of instances discussed above, most of the replicas and the subsequent 3D reliefs may be regarded as reasonably accurate representations of the 'original' track surface. In the case of tracks 3–5 (LQ-1(L2–L3)), where small- and exhibition-replicas are known, the small replica tracks appear to reflect the track morphology apparent in the archival photographs more accurately than that of the exhibition replicas. These differences in the replicas of the same track can likely be accounted for through differences in casting processes, assuming that the same latex peels were used.

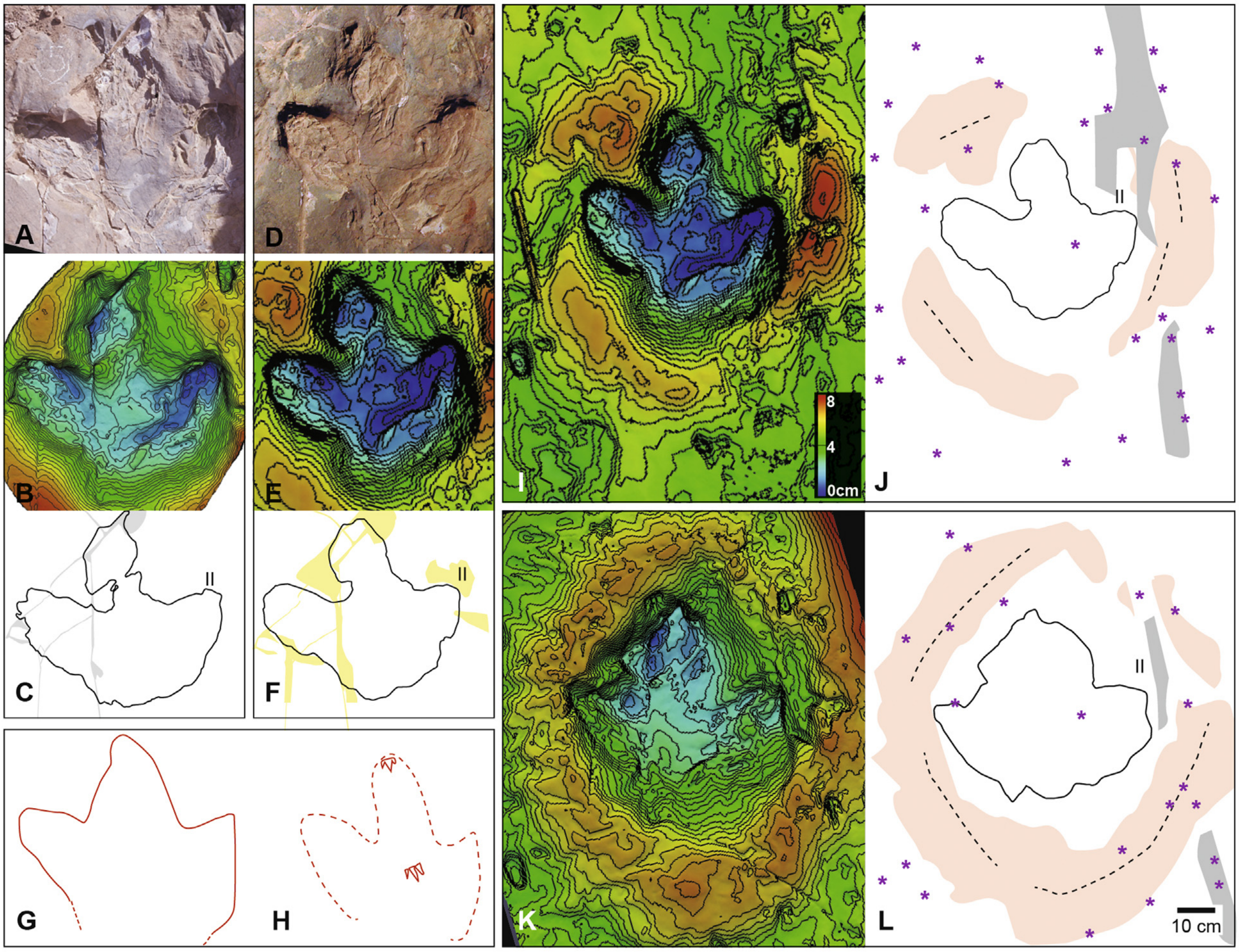

Fig. 7. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 5 (L3), a left pes impression. A, Photograph of the *in situ* track taken c. 1977 (A; photograph © Queensland Museum); B, colour-coded 3D relief of the track based on a fibreglass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track based on A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on photographs of the *in situ* specimen taken in 2013; F, single contour line of the track based on D and E; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to track 3, which was given a length of 64 cm by Thulborn and Wade (1984: 434); H, schematic interpretation of the track adapted from Thulborn and Wade (1979: Fig. 2b); I, 3D relief of the *in situ* track (based on photographs taken during 2013); J, single contour line of the track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); K, 3D relief of the exhibition fibreglass replica (based on photographs taken during 2013); L, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*). Track depth range approximately 8 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The favourable comparisons between the replica specimens and the archival photographs can be used to verify a number of unusual surface features. In track 3 (LQ-1(L2)), for instance, the distal-most portion of the digit III impression is pointed, but an examination of both the archival photograph (Fig. 5A) and the 3D relief (Fig. 5B) reveals that the medial edge of this 'digit impression' is actually a surface crack (Fig. 5A), with the entire area 'shelved' on a topographically higher surface to that of the digit impression immediately proximal to it (Fig. 5B). As such, we consider the area delineated by these cracks to be unrelated to the track. In addition, the narrow elongate impression between paired sediment ridges within the digit IV impressions of tracks 1 and 10 (LQ-1(L1, R5); Figs. 3B, 12B), and the digit III impressions of tracks 7, 8 and 10 (LQ-1(L3, R4, R5); Figs. 9B, 10B, 12B), most likely represent areas where sediment has partially adhered to the underside of the trackmaker's pes upon exiting the track. As a result we consider the broader impressions that surround these grooves to provide a more accurate representation of the track outline, and specifically the respective digits.

3.2. How well do the *in situ* tracks approximate the original track surface?

The 3D reliefs of the *in situ* tracks created from photographs taken in April 2013 (e.g. Fig. 8E) also compare well with those of the replicas (e.g. Fig. 8B) in terms of overall general track morphology. However, much of the originally exposed cracks have been infilled, and the fragmented track sections have been consolidated (e.g. track 3; LQ-1(L2); Fig. 5D,E), removed (e.g. track 9; LQ-1(L5); Fig. 11D,E), or remodelled (e.g. track 4; Fig. 6D,E). The surfaces of the *in situ* tracks are topographically smoother, due to the application of silicone and cement (Agnew and Oxnam, 1983; Agnew et al., 1989) when compared with the 'original' tracks (e.g. as represented by the 3D reliefs of the replicas).

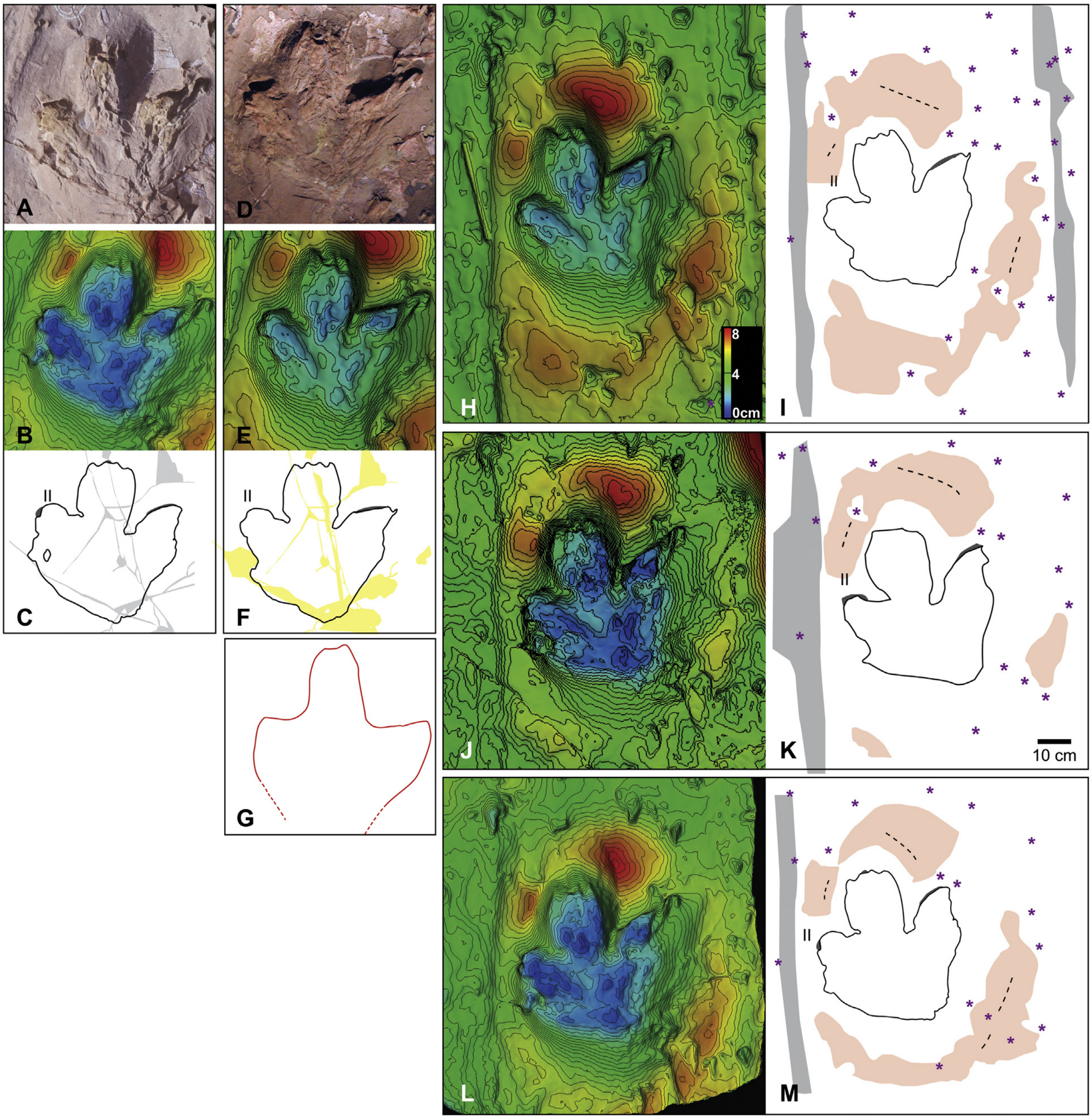

Fig. 8. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 6 (R3), a right pes impression. A, Photograph of the *in situ* track taken c. 1977 (A; photograph © Queensland Museum); B, colour-coded 3D relief of the track based on a fibreglass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track based on A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on photographs of the *in situ* specimen taken in 2013; F, single contour line of the track based on D and E; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to track 3, which was given a length of 64 cm by Thulborn and Wade (1984: 434); H, 3D relief of the *in situ* track (based on photographs taken during 2013); I, single contour line of the track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); J, 3D relief of the exhibition fibreglass replica (based on photographs taken during 2013); K, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); L, 3D relief of the small replica (based on photographs taken during 2013); M, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*). Track depth range approximately 8.2 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

A likely result of the restoration processes that have been applied to these tracks is that some track margins have been altered. In the *in situ* track 1 (LQ-1(L1)), for instance, the margin between the digit III and IV impressions is more clearly defined (Fig. 3D,E), whereas for the *in situ* tracks 2 and 4 (LQ-1(R1, R2); Figs. 4D,E and 6D,E) the margins have been changed considerably. For tracks 2 and 4 (LQ-1(R1, R2)), the restoration processes have resulted in the *in situ* tracks appearing more ‘track-like’ than was apparent with the ‘original’ track surface (Figs. 4A–C and 6A–C).

As of 2013, the condition of the *in situ* tracks 5–11 (LQ-1(L3–L6)), indicates that they have received relatively minor modifications since excavation and may be regarded as reasonably good representations of the ‘original’ track surface. However, the current state of the *in situ* tracks 1–4 (LQ-1(L1–R2)), suggests

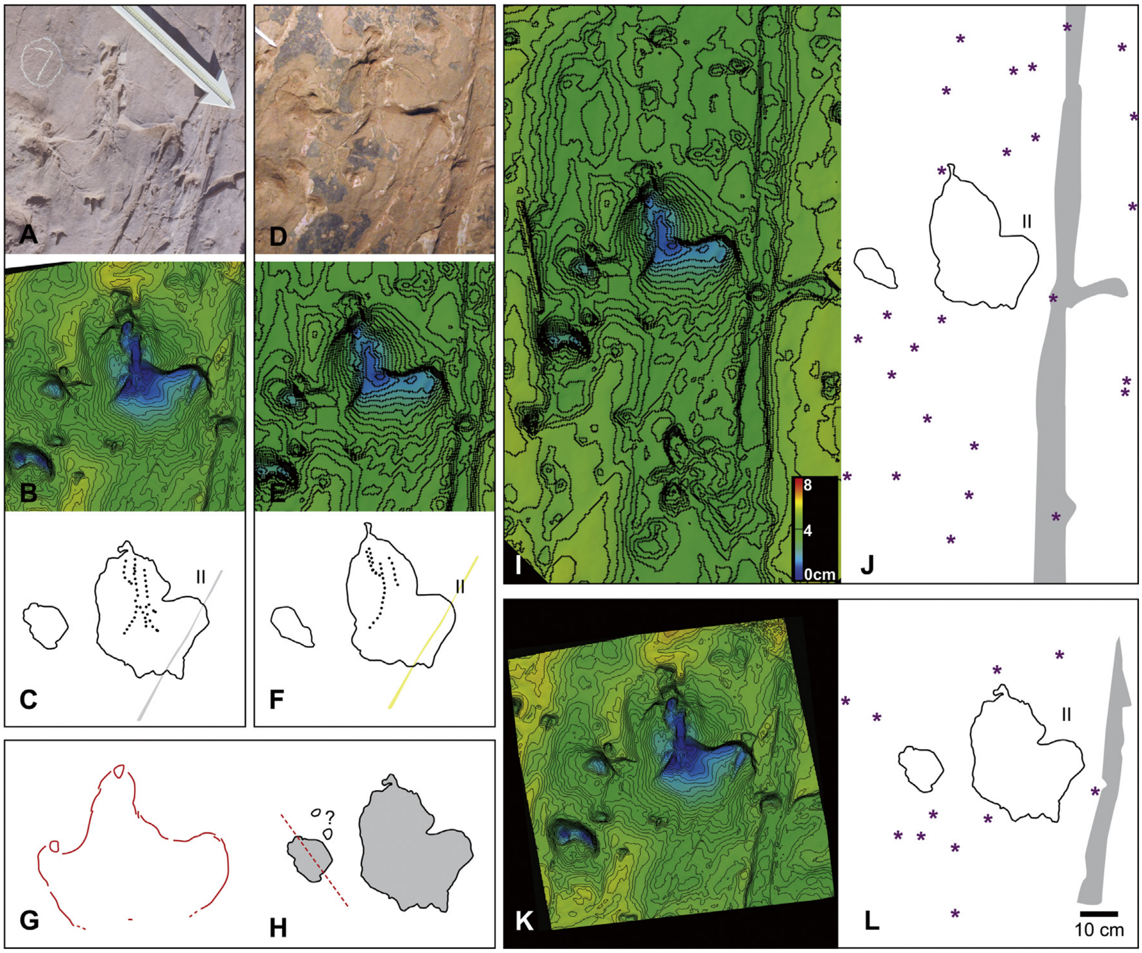

Fig. 9. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 7 (L4), a left pes impression. A, Photograph of the *in situ* track taken c. 1977 (A; photograph © Queensland Museum); B, colour-coded 3D relief of the track based on a fibreglass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track based A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on photographs of the *in situ* specimen taken in 2013; F, single contour line of the track based D and E; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: Fig. 4); H, single contour of the track based on the replica (QM F10322) and a photograph of the *in situ* specimen taken c. 1977, showing relative positions of circular depressions ('?') and longitudinal axis of the digit IV impression (dotted line); I, 3D relief of the *in situ* track (based on photographs taken during 2013); J, single contour line of the track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); K, 3D relief of the exhibition fibreglass replica (based on photographs taken during 2013); L, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*). Track depth range approximately 5 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are <30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

extensive track surface modifications since excavation, such that the 3D reliefs generated from photographs taken in 2013 cannot be regarded as accurate reflections of the original tracks.

3.3. Track and trackway measurements

When analysed in detail, the 3D reliefs of the replicas and *in situ* tracks show a high degree of morphological variability between individual tracks within the trackway (Figs. 3A,B,C–13A,B,C). Of the replica tracks, the dimensions range from 21.5 to 52.4 cm in proximodistal length and 39.5–53.4 cm in mediolateral width (Table 1). The dimensions of the *in situ* tracks are similar to the measurements obtained for the respective replica tracks, and range from 18.0 to 51.5 cm in proximodistal length and 38.8–53.0 cm in mediolateral width (Table 1).

The trackway data (Fig. 14B–D) show the track orientation is generally to the southwest, with the exception of tracks 10 and 11 (LQ-1(R5, L6)) that are aligned approximately west (266°N) and northwest (295°N), respectively.

The pace and stride lengths of the *in situ* trackway are 1.42–2.10 m and 2.90–3.84 m, respectively (Table 1). The hip height (h) for the trackmaker can be estimated using Alexander's (1976) formula (i.e. $h = 4 \times$ track length), although caution should be exercised when using this formula as some extinct (see Paul, 2002: appendix fig. 8) and extant dinosaurian taxa may deviate from this hip height estimation. For example, some extant avian taxa have proportionately large feet relative to limb lengths (e.g. jacanids; Jenni, 1996) whilst others have proportionately small feet relative to limb length ratios (e.g. burhinids; Hume, 1996). The Lark Quarry tracks are highly variable in length, yet occur in two size groupings: tracks 1–6 (excluding damaged track 4), which have an average track length of 47.7 cm; and tracks 7–11 (LQ-1(L4–L6)), which have an average track length of 33.4 cm. The latter track group includes "foreshortened footprint[s]" (Thulborn and Wade, 1989: 53) and are excluded from hip height calculations, which requires the measurement of the entire pedal impression length. Our calculations estimate trackmaker hip height as being approximately 1.91 m.

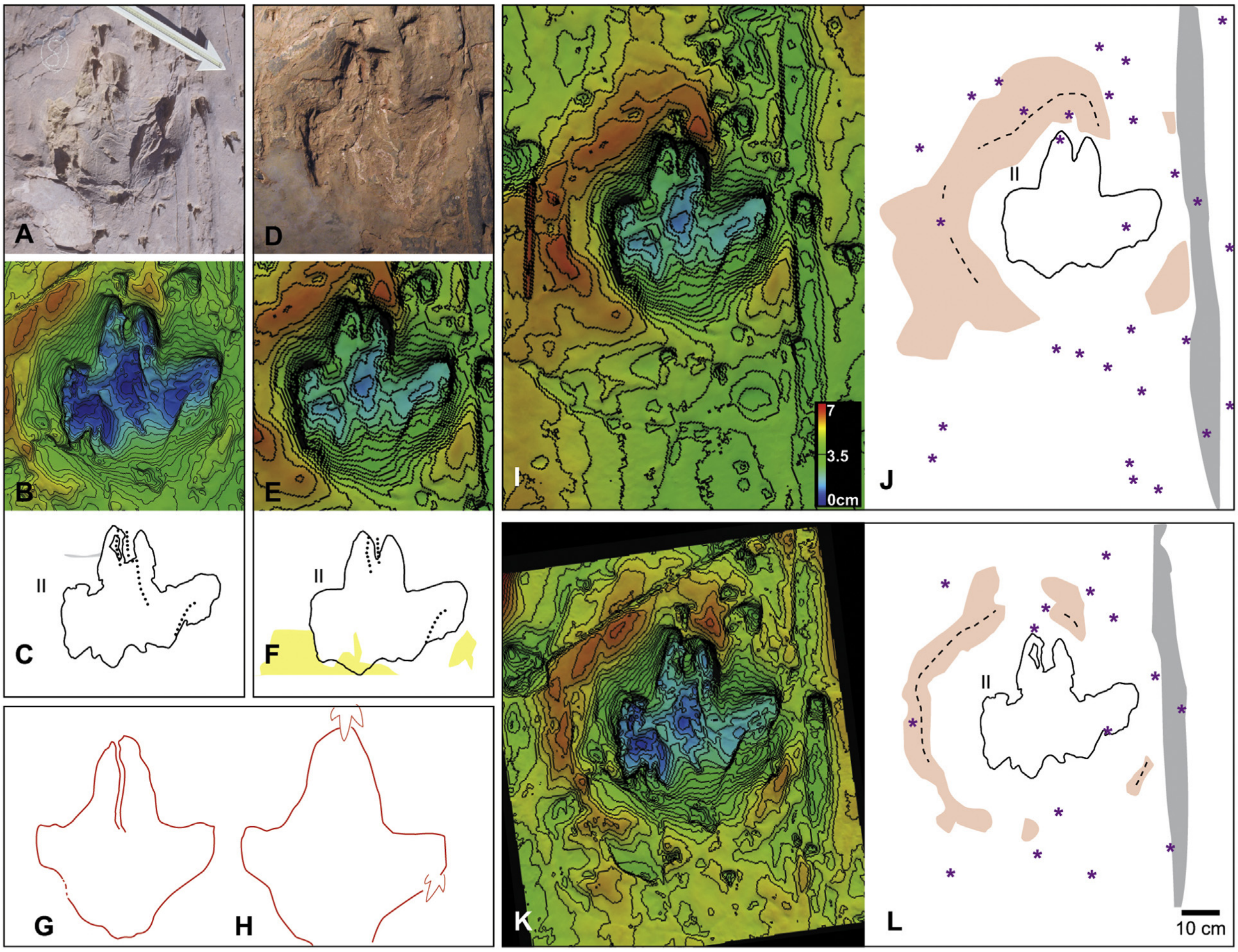

Fig. 10. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 8 (R4), a right pes impression. A, Photograph of the *in situ* track taken c. 1977 (A; photograph © Queensland Museum); B, colour-coded 3D relief of the track based on a fibreglass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track based on A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on D and E; F, single contour line of the track based on colour-coded 3D relief created from photographs of the *in situ* specimen taken in 2013; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: Fig. 4); H, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to track 3, which was given a length of 64 cm by Thulborn and Wade (1984: 434); I, 3D relief of the *in situ* track (based on photographs taken during 2013); J, single contour line of the track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); K, 3D relief of the exhibition fibreglass replica (based on photographs taken during 2013); L, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); Track depth range approximately 7 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The stride lengths and hip height can be used to estimate the trackmaker's gait at the time of track formation using relative stride length (relative stride length = stride/hip height): less than 2.0 indicates walking; 2.0–2.9 indicates trotting in quadrupedal animals (equivalent to slow run in bipeds); and greater than 2.9 indicates running (Alexander, 1976). The relative stride length for the large Lark Quarry tracks is approximately 1.53–2.01, suggesting the trackmaker was employing a walking gait to the very lower limits of a slow run.

Many of the tracks are positioned either very close to, on, or cross the stride midline (Fig. 14C,D). When combined with the individual track variability, this makes the precise determination of left or right pes impressions extremely difficult. If the odd numbered tracks represent left pes impressions (Fig. 14C) then tracks 2, 4, 5, and 8 (LQ-1(R1, R2, L3, R4)) cross the stride midline, with tracks 3 and 10 (LQ-1(L2, R5)) being on the midline, resulting in a trackway average pace angulation of approximately 179.6°. Alternatively, if the odd numbered tracks represent right pes impressions (Fig. 14D) then crossovers occur at tracks 6, 7 and 9 (LQ-1(R3, L4, L5)), with an overall average trackway pace angulation of approximately 180.4°. We are in agreement with Thulborn and Wade (1984) that the odd numbered tracks most likely represent the left pes impressions. Our interpretation is based on the pace angulation between tracks 9 and 11 (i.e. 180°) and the relative orientation of track 11 (LQ-1(L6)), since such an arrangement would make it much easier for a biped to turn left from track 9 (LQ-1(L5)) if the odd numbered tracks had been formed by the left pes. The alternative movement would have required a long, straight stride with the right leg that ended with the pes being rotated laterally nearly 45° as it was placed down; a move that we imagine would be worthy of entry into Monty Python's ‘Ministry of Silly Walks’ (see Thulborn, 2013: 15).

3.4. Displacement rims

In addition to the general features of the tracks, displacement rims (see Bates et al., 2008a) are associated with both the *in situ* and replica specimens (Figs. 3–13). Displacement rims—also referred to

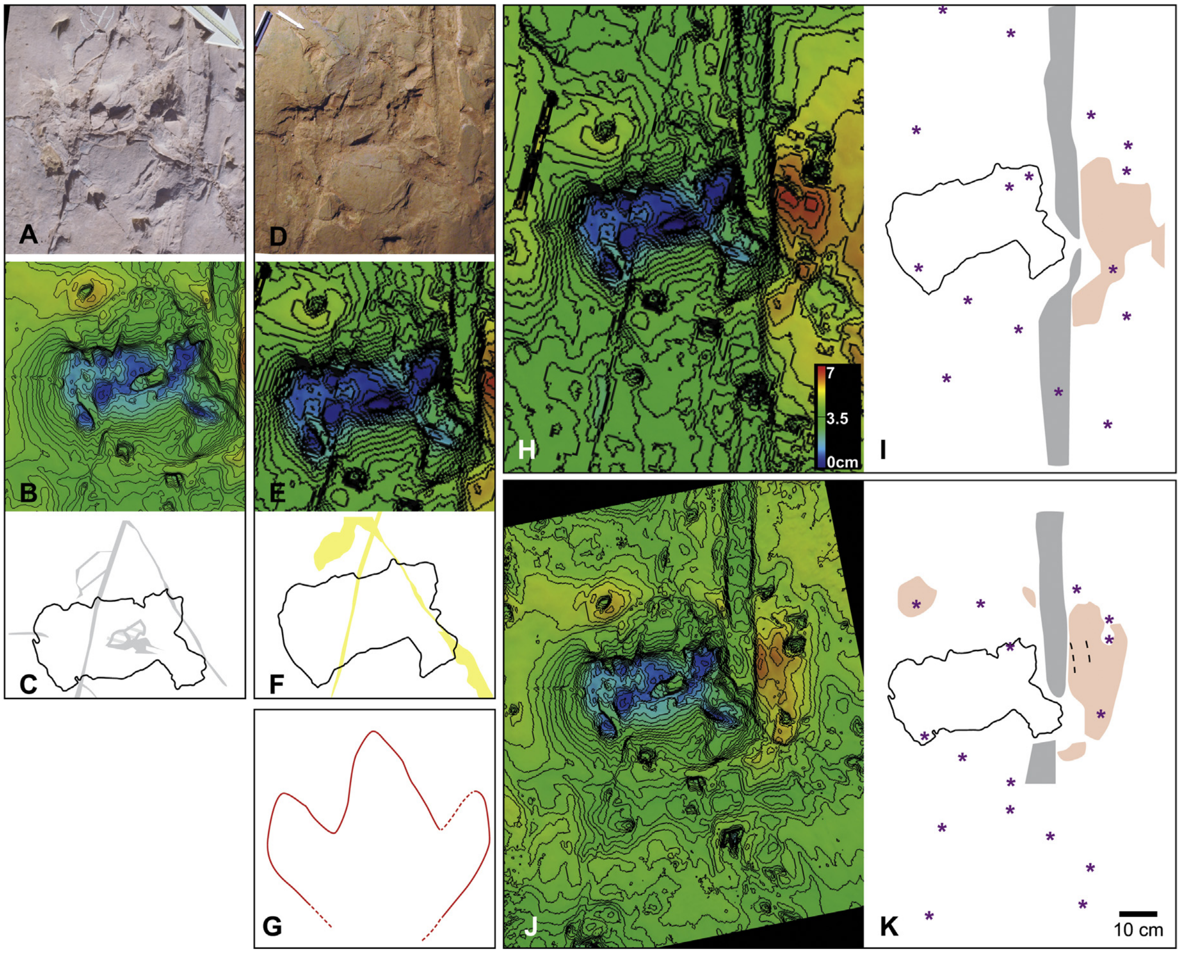

Fig. 11. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 9 (L5), a left pes impression. A, Photograph of the *in situ* track taken c. 1977 (A; photograph © Queensland Museum); B, colour-coded 3D relief of track based on fibre-glass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track based on A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on D and E; F, single contour line of the track based on colour-coded 3D relief created from photographs of the *in situ* specimen taken in 2013; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to track 3, which was given a length of 64 cm by Thulborn and Wade (1984: 434); H, 3D relief of the *in situ* track (based on photographs taken during 2013); I, single contour line of the track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); J, 3D relief of the exhibition fibreglass replica (based on photographs taken during 2013); K, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); Track depth range approximately 9 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

as ‘marginal ridges’ (see Allen, 1997)—are typically regarded as having been formed from sediment that was displaced during track formation rather than from sediment that was in direct contact with the trackmaker's pes (Gatesy, 2003). Some of the Lark Quarry tracks (e.g. tracks, 1, 2, 5 and 6; LQ-1(L1, R1, L3, R3); Figs. 3H, 4H, 7I, 8H) are completely encircled by prominently raised rims, while on others, these rims are much less pronounced (e.g. tracks 8–10; LQ-1(R4–R5) Figs. 10J, 11J, 12J) or absent (i.e. track 7; LQ-1(L4); Fig. 9I–L). The displacement rim for track 11 (LQ-1(L6); Figs. 13J,K) is prominent yet located caudal to the proximal track margin.

Some of the displacement rims associated with the replica tracks do not compare favourably with the respective rims of the *in situ* tracks. In the exhibition replicas of tracks 3–5 (LQ-1(L2–L3); Figs. 5K,L, 6K,L, 7K,L) the displacement rims are more extensive than those on the respective *in situ* tracks (Figs. 5I,J, 6I,J, 7I,J). It is not possible for us to judge what the exact cause of these differences is. If the reduced size of the *in situ* displacement rims for tracks 3–5 (LQ-1(L2–L3)) were the result of erosion, then the overprinted smaller dinosaurian tracks (see below) would also be expected to be absent or significantly eroded relative to what is observed in the replica specimens (see Romilio et al., 2013: 103), but this is not the case. The differences are more likely to be the result of the casting and replication process, with the flexible latex peels possibly having been set to a slightly incorrect shape at the onset of the production of the polyester resin and fibreglass replicas. This may account for the exhibition replica track 5 (Fig. 7K,L) having a considerably different in morphology to that of the small replica (Fig. 7B,C) and the *in situ* track (Fig. 7D,C). However, given the lack of detailed historical descriptions of how the *in situ* track surface has altered over time, combined with the obvious complications associated with the production of such a large replica specimen, we are unable to determine exactly what has happened and thus account for the differences that are now apparent.

Published photographs of the original *in situ* track surface in oblique-view (Thulborn and Wade, 1984: Pl. 5B) show displacement rims surrounding tracks 1 and 2 (LQ-1(L1, R1)), with at least a partial rim close to the proximolateral margin of track 3 (LQ-1(L2)) and the proximomedial margin of track 4 (LQ-1(R2)). These are consistent with what we observed in the 3D reliefs of the *in situ*

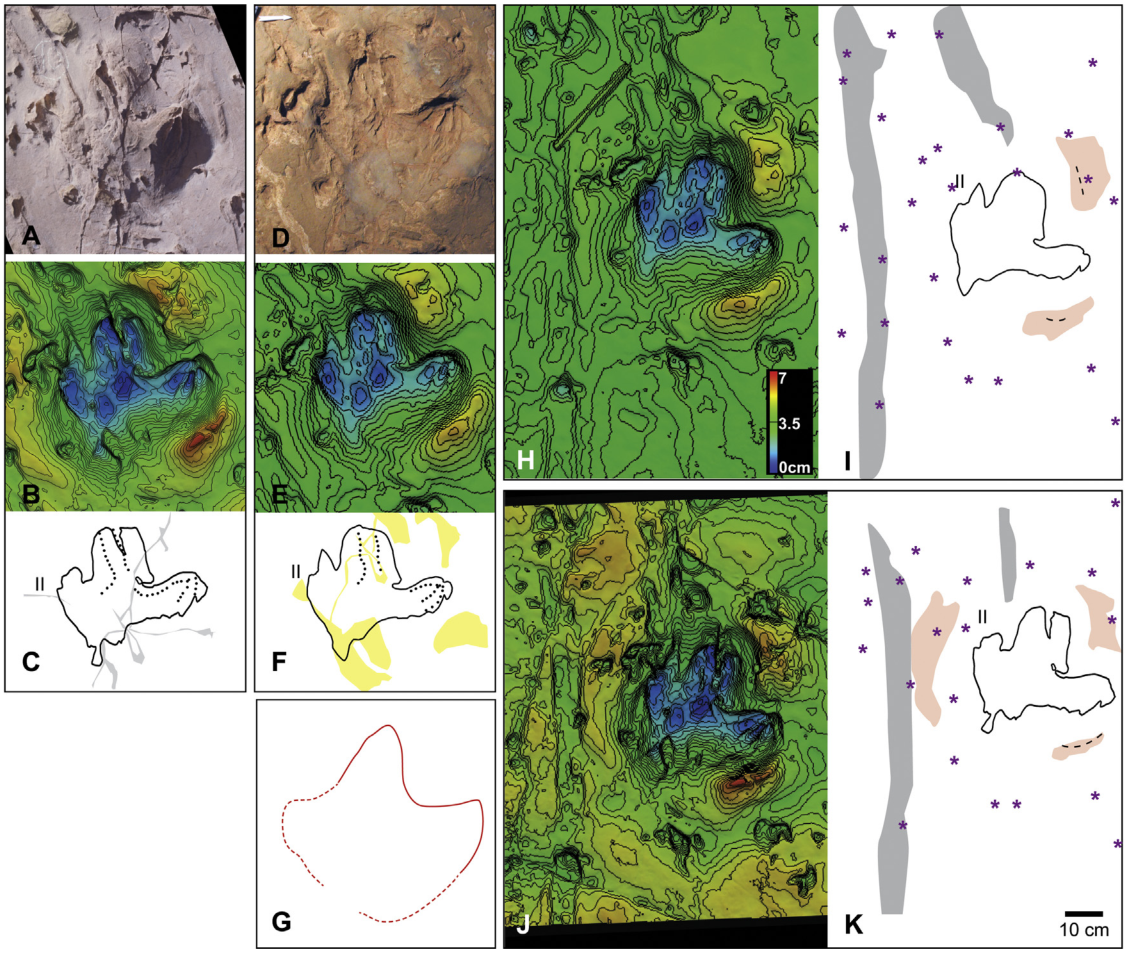

Fig. 12. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 10 (R5), a right pes impression. A, Photograph of the *in situ* track taken c. 1977 (A; photograph © Queensland Museum); B, colour-coded 3D relief of track based on fibre-glass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track based A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on photographs of the *in situ* specimen taken in 2013; F, single contour line of the track based on D and E; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to track 3, which was given a length of 64 cm by Thulborn and Wade (1984: 434); H, 3D relief of the *in situ* track (based on photographs taken during 2013); I, single contour line of the track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); J, 3D relief of the exhibition fibreglass replica (based on photographs taken during 2013); K, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); Track depth range approximately 7 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

tracks 1, 2 and 4 (LQ-1(L1, R1, R2), Figs. 3H, 4H, and 6I, respectively), but the displacement rim measured for track 3 (Fig. 5I) seems smaller than that shown in the original publication. The value of the displacement rims associated with tracks 3–5 (LQ-1(L2–L3)) is difficult to judge due to the unexplainable differences that are apparent between the 3D reliefs obtained from the *in situ* and exhibition replica specimens. Thus the displacement rims present in these tracks will not be considered further.

The small replicas of tracks 1–5 (LQ-1(L1–L3)) are not big enough to include their associated displacement rim. The small track 6 (LQ-1(R3)) replica does have the associated displacement rim (Fig. 8L,M). Although prominent, this displacement rim differs from that on the exhibition replica (Fig. 8J,K) and the *in situ* specimen (Fig. 8H,I), the latter being more pronounced despite any anticipated effects of erosion. While differences occur between these specimens, all have a rim bordering the digit III impression and near to both the proximomedial and the proximolateral track margin. The lack of a more complete displacement rim in the replicas, particularly that of the exhibition replica (Fig. 8J,K), may be due to discrepancies associated with how each cast was produced.

Many of the displacement rims associated with the large tracks are overprinted by tool marks (Figs. 3H, 4H, 8H, 10I, 11H), with all the displacement rims, as well as the tool marks, being overprinted with small dinosaurian tracks assignable to *W. latomorum* (e.g. track 5, LQ-1(L3), Fig. 7I–L). The hierarchy of overprinting indicates that the large dinosaurian tracks were formed before the tool marks, and that these were formed prior to the recording of the smaller dinosaurian tracks assignable to *W. latomorum*. The lack of overprinting in other sections of Lark Quarry makes the determination of tracemaker succession much more difficult, if not impossible.

4. Discussion

4.1. *Comparisons of the replica and* in situ *tracks with the original published data*

The documentation of tracks through the description and visualization of the 3D topography is important for the retention of morphological information (Petti et al., 2008), and was achieved at Lark Quarry soon after excavation through the creation of large

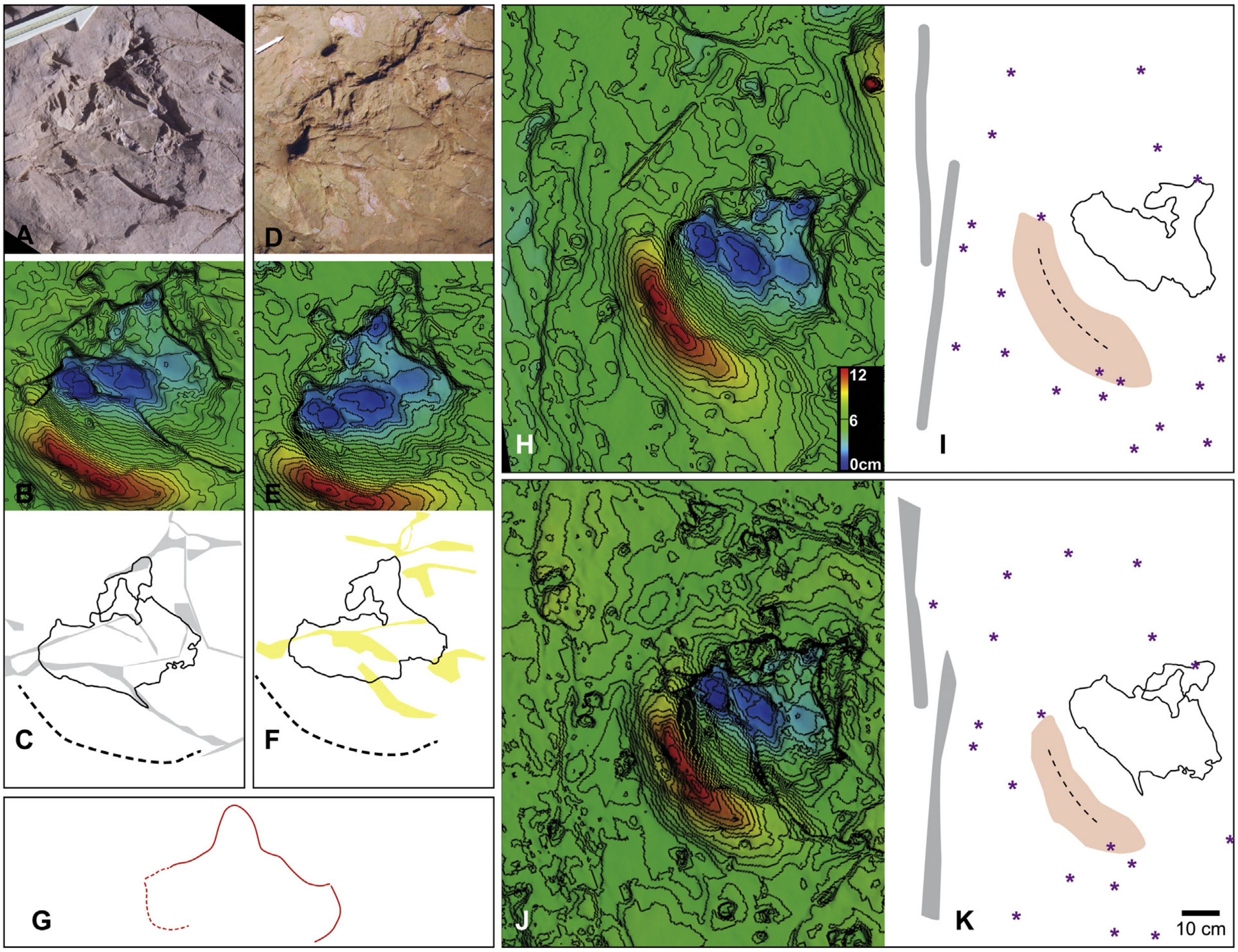

Fig. 13. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Image comparison of track 11 (L6), a left pes impression. A, Photograph of the *in situ* track taken c. 1977 (A; photograph © Queensland Museum); B, colour-coded 3D relief of track based on fibre-glass replica (QM F10322; made c. 1977 using a latex cast, also made c. 1977); C, single contour line of the track based on A and B; D, photograph of the *in situ* track taken in 2013; E, colour-coded 3D relief based on D and E; F, single contour line of the track based on colour-coded 3D relief created from photographs of the *in situ* specimen taken in 2013; G, schematic interpretation of the track adapted from Thulborn and Wade (1984: pl 17), and scaled to track 3, which was given a length of 64 cm by Thulborn and Wade (1984: 434); H, relief of the *in situ* track (based on photographs taken during 2013); I, single contour line of the track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); J, 3D relief of the exhibition fibreglass replica (based on photographs taken during 2013); K, single contour line of the exhibition fibreglass replica track, and schematic interpretation of the associated displacement rim, neighbouring tool marks and smaller tracks assignable to *W. latomorum* (*); Track depth range approximately 12.5 cm; cooler colours represent deeper portions of the surface and warmer colours higher portions. Within this depth range there are 30 evenly spaced contour intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

latex peels and the subsequent production from these of "high-fidelity replicas" (Thulborn and Wade, 1984: 416). However, access to the accessioned replica specimens (QM F10322), particularly the large exhibition specimen, is limited. Instead, the most widely communicated morphology for the largest Lark Quarry tracks has been the 2D drawn outlines that appeared in Thulborn and Wade (1984). Since 2D outlines may rely on the subjective interpretation of the investigator (Bates et al., 2008b), the accuracy of the original published outlines (and other ichnological data that is derived from them) can now be critically assesses in light of the results of this study.

An important limitation of examining non-*in situ* 3D track surface topography (e.g. replicas, photogrammetry, laser scans) is that these techniques do not distinguish between the heterogeneity of surfaces. As a tracksite, Lark Quarry is extremely complex, and caution must be exercised when it is interpreted, since the track surface *sensu stricto* is for the most part not exposed at the site. The true track surface became enveloped in a millimetre thin veneer of dark coloured ironstone when iron-laden water penetrated the fine-grained sandstone that overlies the siltstone/fine-grained sandstone in which the tracks were formed (Romilio et al., 2013: Fig. 4). The ease with which the ironstone and overlying sandstone can be separated from each other, along with the difference in colour, was the main factor that facilitated the 1970's excavation of the current 'track surface' (Thulborn and Wade, 1984: 416). However, there are many instances where, during excavation, the ironstone layer has been penetrated, exposing and in the process damaging portions of the underlying fine-grained sandstone/siltstone track surface (e.g. Figs. 4A, 6A). Further processes have also modified the surface of the tracksite since the initial excavation, both to its detriment and its restoration (for a summary, see Romilio et al., 2013: 103). The resulting heterogeneity of the surface is not apparent when it is rendered digitally into a 3D model through photogrammetry or laser scanning (e.g. Falkingham, 2011), or physically into a cast (e.g. QM F10322), thus necessitating our use of archival and recent photographs of the *in situ* material to help ascertain modifications to surface features (e.g. fragmentation, cracks, restoration artifacts, etc).

Some of the ichnological data obtained from the current study compares favourably with the findings of Thulborn and Wade

Table 1
cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Track and trackway measurements. *Average hip height measurement of tracks 1–6. Values in parentheses indicate dimensions with the inclusion of contentious track features (in text for details).

Track	Specimen	Length	Width	L/W	Te	Te/L	Direction °N	Pace angulation	pace	Stride	h (m)	Stride/1.91*
1	Replica small	49.5	51.5	0.96	15.3	0.31					1.98	
1	*In situ*	50	48.5	1.03	16.5	0.33	208				2	
2	Replica small	50.5	53.4	0.95	16.1	0.32					2.02	
2	*In situ*	47.5	52	0.91	14.7	0.31	194		2.1		1.9	
3	Replica small	47.3 (52.4)	43.4	1.09 (1.21)	19.3	0.37					1.89 (2.10)	
3	Replica large	46 (51.5)	42	1.23 (1.10)	24	0.47					1.84 (2.06)	
3	*In situ*	47.1 (51.5)	41.5	1.14 (1.24)	20.2	0.39	208	187.5	1.74	3.84	1.88 (2.06)	2.01 (1.97)
4	Replica small	44.5	46.4	0.96	13.8	0.31					1.78	
4	Replica large	43	44.1	0.98	14.2	0.33					1.72	
4	*In situ*	47	53	0.89	16.5	0.35	200	180	1.69	3.4	1.88	1.78
5	Replica small	48.3	47.5	1.02	13.6	0.28					1.93	
5	Replica large	44	50	0.88	18	0.41					1.76	
5	*In situ*	48.8	52.1	0.94	16.4	0.34	218	189.5	2.08	3.76	1.95	1.97
6	Replica small	46	41	1.12	14.7	0.32					1.84	
6	Replica large	47.8	43	1.11	15.1	0.32					1.91	
6	*In situ*	48.2	44	1.10	15.3	0.32	218	192.00	1.69	3.8	1.93	1.99
7	Replica large	30.5	41.4	0.74	13.2	0.43					1.22	
7	*In situ*	32.1	42.7	0.75	13.5	0.42	217	170.00	1.51	3.22	1.28	1.69
8	Replica large	41	42	0.98	15.7	0.38					1.64	
8	*In situ*	43.5	41.8	1.04	14.8	0.34	217	161.00	1.67	3.1	1.74	1.62
9	Replica large	30	42	0.71							1.2	
9	*In situ*	18.3	39.9	0.46			232	190	1.57	3.24	0.73	170
10	Replica large	34	39.5	0.86	11.7	0.34					1.36	
10	*In situ*	32.2	38.8	0.83	12	0.37	266	166	1.42	2.93	1.29	1.53
11	Replica large	36	41.7	0.86							1.44	
11	*In situ*	36.8	41.8	0.88			295	180	1.47	2.9	1.47	
Average				0.93 (0.95)								

(1984). These include: the high variability between tracks; the tracks of the first half of the trackway being proximodistally longer than those tracks of the latter half; the odd numbered tracks likely corresponding to left pes impressions; and many of the tracks being overprinted by traces formed by small-bodied dinosaurian trackmakers.

Many of the archival photographs were taken in such a way as to render the margins of some tracks indistinct (e.g. tracks 1, 2, 4–7, 9–11; Figs. 3A, 4A, 6A–9A, 11A–13A). These same margins are considered either missing or contentious in the outlines provided by Thulborn and Wade (1984; see Figs. 3G, 4G, 6G–9G, 11G–13G; also see Thulborn, 2013). However, our study indicates apparent absences of some portions of the track margins are a consequence of the intense natural lighting conditions under which the tracks were originally photographed, inadvertently reducing the topographical appearance of the track surface. The 3D reliefs of various tracks (from multiple sources) show that these contentious margins are indeed present and distinct, albeit highly variable (Figs. 3B–13B).

Other ichnological data obtained during the current investigation that was not consistent with the information presented by Thulborn and Wade (1984) includes: additional details relating to track morphology (including dactyly); track dimensions; estimated trackmaker hip height; and the proposed sequence of track formation at the site.

Some relatively minor differences relating to track morphological may be explained by the subjective interpretation of different investigators on what constituents the track margin. For example, Thulborn and Wade (1984) depict track 3 (LQ-1(L2); Fig. 5G,H) as having wider bases to the digit impressions than is proposed here (Fig. 5B). Another is the inclusion of surface features that have been subjectively interpreted as constituting part of the track, such as for track 5 (LQ-1(L3)), where Thulborn and Wade (1984) consider the distolateral portion of digit III impression to be slightly kinked (Fig. 7G), a feature that we identify as being an overprinted small track assignable to *W. latomorum*. Also, some track features have been exaggerated. Thulborn and Wade's (1984) published outline of track 8 shows a pair of sediment ridges that extend the full length of the digit III impression (Fig. 10G), but the results of this study show that these ridges are restricted to the distal portion of the digit impression and a separate single sediment ridge extends distally (Fig. 10B,E).

The morphology of all the other tracks obtained in the current study is significantly different to the respective 2D track outlines published by Thulborn and Wade (1984). Most consistent is our finding that all the tracks have entire track margins (Figs. 3B–13B), which contrasts with the Thulborn and Wade's (1984) depiction of the portions of some track margins as either missing or contentious (Figs. 3G–9G, 11G–13G). Since the archival photographs also give the illusion of missing track portions (Figs. 3A–13A) we suspect that some of outlines published in Thulborn and Wade (1984) were based on these photographs. This supposition is supported by the original published outline of track 6 (LQ-1(R3)) having a relatively narrow digit III impression (Fig. 8G), with the archival photograph 'narrowing' this digit impression as a consequence of shadowing (Fig. 8A).

Additionally, Thulborn and Wade (1984: 419) state that "Each footprint is tridactyl, with clear imprints of digits 2, 3 and 4". The current study does not support this observation. Only six of the eleven tracks in the trackway are clearly tridactyl (Fig. 15). Tracks 9 and 11 (LQ-1(L5, L6)) lack digit impressions entirely (Figs. 11, 13). Thulborn and Wade (1984: pl 17) depicted track 9 (LQ-1(L5)) as having three prominent digit impressions (Fig. 11G), but the apparent lateral and medial margins of track 9's digit III impression are not track features at all, rather two cracks that converge cranial to the actual track (Fig. 11A,B,D). Because of this, it seems likely that the outline of this track that was published by Thulborn and Wade (1984) was based solely on the archival photograph (despite the fact that this photograph clearly shows these two cracks continuing cranially and caudally through the track; Fig. 11A). Cracks have also been interpreted by Thulborn and Wade (1984) as incorrectly representing 'digit impressions' for track 11. In this case, the cluster

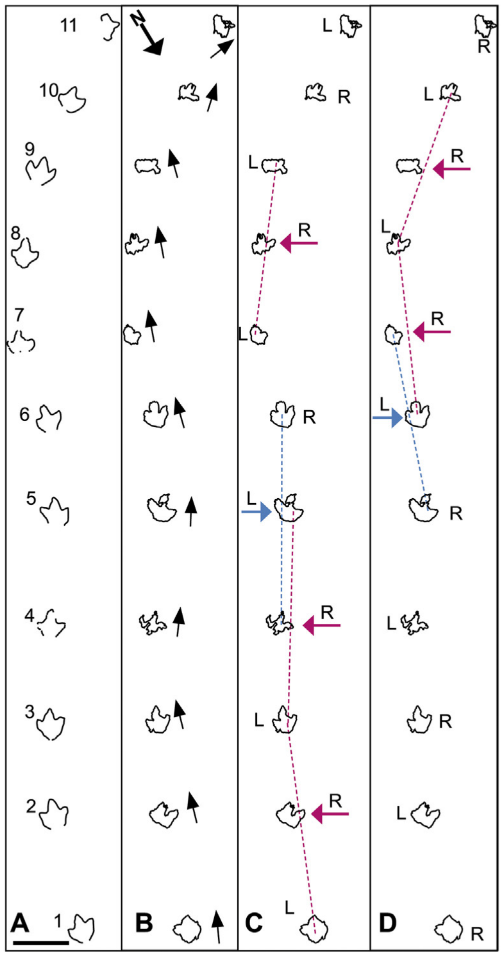

Fig. 14. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. A, Original trackway schematic, adapted from Thulborn and Wade (1984: pl 17); B, current trackway interpretation with track orientations; C, tracks crossing over the stride midline (dotted line) assuming odd numbered tracks are left pes impressions; D, tracks crossing over stride midline (dotted line) assuming odd numbered tracks are right pes impressions. Scale equals 1 m.

of cracks is cranial to the track, which lacks digit impressions (Fig. 13A,G).

Overall, we regard the 2D drawn outlines presented by Thulborn and Wade (1984) to be inadequate and inaccurate representations of the 3D morphology of the largest Lark Quarry tracks.

Thulborn and Wade (1984) provide only patchy accounts of track dimensions. On page 420 they provide values for 'average track length and width' (51.4 cm, $n = 7$; 46.1 cm, $n = 10$), but the only track for which an individual dimension is given is track 3 (LQ-1(L2)), which, on page 434 is stated as having a 'footprint length' of 64 cm. On the same page an unspecified track is given an "estimated" minimum 'footprint length' of 41 cm. Based on the relative sizes of the track outlines presented by Thulborn and Wade (1984: Pl 17), the latter track is likely either track 7 or track 11 (LQ-1(L4, L6)).

While Thulborn and Wade (1984) obtained track lengths ranging from 41 to 64 cm, our own proximodistal length measurements ranged from 21.5 to 52.4 cm for the replicas and 18.0 to 51.5 cm for the *in situ* tracks. Our values for the replicas and *in situ* tracks closely correspond with each other, yet differ significantly from the original published values provided by Thulborn and Wade (1984). To explain these differences in track dimensions, we question the methods that were used by Thulborn and Wade (1984). Thulborn and Wade (1984: 419) state that the "Measurements of the carnosaur trackway were taken directly from the bedding plane at Lark Quarry and were checked on fibreglass replicas (QM F10322) at the Queensland Museum". While cross-checking the measurements of the *in situ* specimens with the replica material may be regarded as standard procedure and was also employed in the current study (Table 1), the results obtained in the our study casts doubt as to how effectively this procedure was carried out by Thulborn and Wade (1984). For example, Thulborn and Wade (1984: 434) state that the length of track 3 (LQ-1(L2)) is 64 cm. A photograph of the small replica of this track is later shown with a 15 cm ruler for scale (Thulborn and Wade, 1984: Pl. 5A). Our direct measurement of the entire replica (i.e. inclusive of the surface surrounding the track) gives a maximum length of 60.1 cm (i.e. less than the maximum track length given by Thulborn and Wade, 1984). The maximum length of the actual track on the small replica is 52.4 cm. Unless we have missed something, the actual maximum length of track 3 (LQ-1(L2)) is around 82% less than the measurement provided by Thulborn and Wade (1984). However, in stating this, we recognize that the actual track length could be smaller still. The distal-most portion of the digit III impression sits on a topographically higher 'shelf' to the digit impression immediately proximal to it (Fig. 5B), and given that the medial edge of this digit impression traces a surface crack (Fig. 5A), we suspect this elevated region does not represent the anatomical impression of the distal portion of the pes. Excluding the latter feature, we estimate the length of track 3 (LQ-1(L2)) to be closer to 47.3 cm, which is only 74% of the original documented length (Thulborn and Wade, 1984). Perhaps not surprisingly, using the 15 cm ruler as a scale, the size of

Track	Number of clear digit impressions	Large track overprinted by small tracks	Displacement rim overprinted	
			small tracks	vegetation drag marks
1	2		✓	✓
2	2	✓	✓	✓
3	3		✓	✓
4	3		✓	✓
5	3	✓	✓	✓
6	3		✓	✓
7	2 or 3		NA	NA
8	3		✓	✓
9	0	✓	✓	✓
10	3	✓	✓	
11	0		✓	

Fig. 15. cf. *Iguanodontipus*, Upper Cretaceous (upper Cenomanian–lower Turonian), Winton Formation, Lark Quarry, central-western Queensland, Australia. Dactyly and overprinting: a tick denotes evidence of overprinting; NA denotes not applicable.

the small track 3 (LQ-1(L2)) replica that is illustrated in Thulborn and Wade (1984: Pl. 5A) is consistent with our findings.

Track 3 was also regarded by Thulborn and Wade (1984: 434) as "the best-preserved and most complete footprint". However, the archival photograph and replicas (Fig. 5A–C) show that this track suffered considerable damage during excavation: the track surface along the margins of the impressions of digits III and IV is fragmented and the mediodistal edge of the digit III impression is disrupted by a crack. Track 3 (LQ-1(L2)) has undergone significant reconstruction resulting in a much smoother surface with consolidated track margins (Fig. 5D–F). Since a number of other tracks show far less excavation damage and less track surface remodelling (e.g. tracks 5 and 6; LQ-1(L3, R3); Figs. 7A–F, 8A–F), we disagree with Thulborn and Wade (1984) and do not regard track 3 (LQ-1(L2)) as the best track within the trackway sequence.

Thulborn and Wade (1984) used a value of 64 cm for track 3 (LQ-1(L2)) to estimate the hip height of the trackmaker at 2.56 m, based on a formula by Alexander (1976) of 'hip height equals four times track length'. Given that the value of 64 cm is erroneous, it follows that the original calculated trackmaker hip height based on this value is also erred. Our own calculations, using the same formula, but based on revised measurements of tracks where the entire pedal impression is preserved, given a trackmaker hip height of approximately 1.91 m, representing 75% of that value obtained by Thulborn and Wade (1984).

We are in agreement with Thulborn and Wade (1984) that the approximately 10 cm wide, SE–NW aligned tool marks (Fig. 2) were likely formed when portions of floating vegetation—either branches or roots—were dragged along the sediment surface in line with the predominant current flow (Thulborn and Wade, 1984: 419; Romilio and Salisbury, 2011: 105). Thulborn and Wade (1984: 419) interpreted these tool marks to have been formed prior to the tracks of the largest trackmaker but did not demonstrate how this assessment was made. Thulborn and Wade (1984: 446) continued their interpretation of the succession of tracemakers, proposing that the largest dinosaurian tracks were formed under subaerial conditions "at *about* the same time" as the small-bodied dinosaurian tracks. By restricting the formation of these different dinosaurian tracks within a period where "very little time would have elapsed" (Thulborn and Wade, 1984: 446), these authors thus had grounds upon which to speculate that these trackmakers were present at the site at or near the same time, and thus may have interacted. Within the context of this scenario, they put forward the idea that the large-bodied trackmaker may have "triggered" the stampede of the small-bodied dinosaurian trackmakers (Thulborn and Wade, 1984: 413, 443).

Several of the displacement rims associated with the large Lark Quarry tracks are in close proximity to the vegetation tool marks. Where they coincide, the tool marks overprint the displacement rims (e.g. Fig. 3I), indicating that the tool marks could have only formed *after* the large dinosaurian tracks were made, and not before-hand as proposed by Thulborn and Wade (1984). Significantly, the occurrence of floating vegetation between the formation of the large and small tracks extends the time between the events of dinosaurian track formation and reduces the likelihood that the large trackmaker was present at the site at the same time as the small dinosaurian trackmakers.

In summary, the results of this investigation contrast strongly with the ichnological data provided by Thulborn and Wade (1984) for the largest Lark Quarry tracks. The majority of the Thulborn and Wade's (1984) track outlines appear to have been based on photographs taken under relatively intense natural light that 'hid' the proximal margins of some track; the original track length dimensions are much larger than the actual proximodistal track lengths, which have subsequently lead to an exaggeration of the trackmaker's estimated hip height estimate. Our investigation indicates that the original 2D published outlines do not accurately reflect the morphology of these tracks, and any reliance on these outlines as a comparative resource is therefore inherently flawed. Additionally, the current study has revealed that displacement rims, associated with the large tracks, are overprinted by tool marks and tracks assignable to *W. latomorum*, indicating that the largest Lark Quarry dinosaurian trackmaker was present at the site before the current assisted movement of partially buoyed vegetation that formed the tool marks, and not after as proposed by Thulborn and Wade (1984).

4.2. Determining the likely identity of the large Lark Quarry trackmaker

The actual morphologies of the large Lark Quarry tracks are highly variable, and the ability to systematically categorize them and determine the likely identity of the trackmaker is not straightforward. Establishing "an unequivocal relationship between a fossil track and its possible producer is highly speculative" (Apesteguía and Gallina, 2011: 271), and as such most dinosaur palaeoichnologists usually do not assign a specific ichnite to a specific zoological (body fossil) taxon. Absolute certainty can only be achieved when a direct association can be made between a body fossil and its tracks (Voigt et al., 2007). In the absence of such rare finds, the most common approach has been to identify trackmakers "on the basis of general similarity between the track and the foot skeleton" (Carrano and Wilson, 2001: 565), or their morphological similarity with other ichnotaxa that have previously been attributed to particular zoological taxa (e.g. Meyer and Thüring, 2003).

The morphology of the largest Lark Quarry tracks was originally considered "closer in appearance to *Tyrannosauropus* than to any other form of carnosaur footprint so far described" (Thulborn and Wade, 1984:420). As discussed previously, since the majority of tracks assigned to this ichnogenus—which was considered a *nomen dubium* by Lockley and Hunt (1994)—have subsequently been regarded as ornithopodan in origin (Lockley and Hunt, 1994; Manning et al., 2008), it follows that the largest Lark Quarry tracks may also have been made by an ornithopod. Romilio and Salisbury (2011) took this view further, showing that the published outline of track 3 (LQ-1(L2)), being the "best-preserved and most complete footprint" (Thulborn and Wade, 1984: 434) resembled the ornithopodan ichnotaxon *Amblydactylus gethingi*. However, the results of this study show that placing confidence in the original published track outlines is fundamentally unsound, as is the subsequent use of such outlines for the purpose of ichnotaxonomic reassignment. Nevertheless, the occurrence of these ichnites within a single trackway precludes the possibility of them having been made by both theropodan and ornithopodan trackmakers.

Thulborn and Wade (1984) used several lines of evidence to interpret the largest Lark Quarry tracks as having been made by a large-bodied theropodan trackmaker. These included: the tracks being longer than wide; the presence of claw impressions; and the digit III impression being 'V'-shaped (Thulborn and Wade, 1984: 421).

Tridactyl dinosaurian tracks that are longer than wide are typically regarded as pertaining to theropodan trackmakers (although not universally so; see Castanera et al., 2013). Conversely, tridactyl tracks wider than long are considered representative of those formed by ornithopodan trackmakers (Lockley, 2009). Thulborn and Wade (1984: 419–420) considered the best-preserved tracks to be longer than wide, although these authors did not explicitly state which tracks. From our study, of the best preserved tracks, the dimensions of track 5 (LQ-1(L3), as calculated from the exhibition replica and *in situ* track) indicate that it is wider than long, while track 6 (LQ-1(R3)) has dimensions that are longer than wide (Table 1). Overall, the tracks in the latter portion of the Lark Quarry trackway tend to be wider than long, while some of the tracks at the start of the trackway are longer than wide. This may indicate that the large trackmaker shifted between pedal postures as it traversed the tracksite.

Tracks assigned to ornithischian trackmakers reveal that some were capable of shifting between a digitigrade and plantigrade pedal postures (Gierlinski and Sabath, 2008; Wilson et al., 2009). Similarly, the Lark Quarry ichnotaxon *Wintonopus* is now thought to represent a subunguligrade ornithopodan trackmaker, with the tracks assigned to it being characterized by having only the distal portions of the digits being impressed and lacking a metatarsodigital pad impression (Romilio et al., 2013). Osteological studies also indicate that the majority of derived hadrosauroid ornithopods likely had a skeletally subunguligrade pedal posture (Moreno et al., 2007). Depending on their pedal pad morphology, such dinosaurs could therefore produce tracks that are proportionately short proximodistally. Given that other morphological characteristics of the large Lark Quarry tracks indicate that the trackmaker was an ornithopod, the foreshortening of some of the tracks is unusual but not unexpected. The only theropodan ichnotaxon for which the tracks suggest a subunguligrade trackmaker is *Carmelopodus* (Gierlinski and Pienkowski, 1999), which lacks any indication of a proximal pad on the digit IV impression (Lockley et al., 1998). However, tracks assigned to *Carmelopodus* are distinctly theropodan in other aspects of their morphology, with narrow digit impressions that have pronounced phalangeal pad impressions; features that are not apparent on the largest Lark Quarry tracks.

Thulborn and Wade (1984) regarded the 'V'-shaped digit III impressions of tracks 1, 3, 5, 9, and 10 (LQ-1(L1, L2, L3L, L5, R5)) to be indicative of tracks formed by a theropod. Our examination of these tracks does not support Thulborn and Wade's (1984) observation. Track 1 (LQ-1(L1)) displays a digit III impression that is clearly broad and non-theropodan-like (Fig. 3B). With regard to track 3 (LQ-1(L2); Fig. 5B), although the 3D relief compares somewhat favourably with what may be expected for a theropodan track with a proportionately elongate and pointed digit III impression, this is a damaged track (Fig. 5A). The pointed tip to the digit III impression is most likely not an anatomical feature and the value of using this feature in evaluating trackmaker identity is ambiguous at best, and when excluded, the actual distal digit III impression is rounded and not 'V'-shaped (see Fig. 5B). For tracks 5 and 10 (LQ-1(L3, R5)), digit III impressions are rounded distally, not pointed, and track 9 (LQ-1(L5)) lacks digit impressions altogether, with the 'V'-shape of the original outline derived from misinterpretation of converging cracks cranial to track as the medial and lateral margins of the digit III impression (Fig. 11).

All the tracks lack digital pad impressions, and most have digit impressions with distinctly broad, rounded outlines (e.g. tracks 1, 2, 5, 6, 8, 10; LQ-1(L1, R1, L3, R3, R4, R5); Figs. 3, 4, 7, 8, 10, 12), which contrasts with typical theropodan tracks that have the impressions of digital pads within the impressions of relatively narrow digits (see Lockley, 2009). Theropodan tracks may form ichnites that have broad, blunt digit impressions, although these are generally considered to be undertracks (Piñuela, 2012). The presence of overhangs and sediment ridges indicates that the large tracks at Lark Quarry are not undertracks. Tracks that have proportionately wide digit impressions are typically attributed to ornithopodan trackmakers (Lockley, 2009). However, tracks with more pointed and/or narrow digit impressions have been assigned to ornithopodan ichnotaxa such as *Iguanondontipus* (Meyer and Thüring, 2003: Fig. 5; Diedrich, 2004: Fig. 8), *Caririchnium* (Matsukawa et al., 1999: Fig. 3; Mangano et al., 2012: Fig. 1d) and *Hadrosauropodus* (Currie et al., 1991: Fig. 5). It is possible that similarly pointed digit impressions could be associated with some of the Lark Quarry tracks (e.g. tracks 3, 7; LQ-1(L1, L4)), but most can be explained as either being the result of track surface damage (i.e. track 3; LQ-1(L2); Fig. 5), or sediment movement (i.e. tracks 7 and 10; LQ-1(L4, R5); Figs. 9, 12).

Thulborn and Wade (1984) regarded the presence of claw impressions as the most convincing evidence that the large Lark Quarry trackmaker was a theropod. Although several tracks were implied as containing claw impressions, Thulborn and Wade (1984: 420) only state track 7 (LQ-1(L4)) as having them, and more recently Thulborn (2013:18) has stated the presence of claw impressions on track 6 (LQ-1(R3)).

Track 7 (LQ-1(L4)) was originally considered to have claw impressions associated with digit impressions III and IV (Thulborn and Wade, 1984: 420, Pl. 6). We interpret the 'claw impressions' at the distal portion of the digit III impression (Fig. 9B) to be a rounded structure that is continuous with the groove between the aforementioned paired sediment ridges. This groove forms a deeper portion of the track. As such, rather than representing part of the anatomy of the trackmaker's pes, we regard it a portion of sediment between others that had adhered to the underside of the trackmaker's pes as it was lifted from the track. Similar grooves also occur within the digit III impression of tracks 8 and 10 (LQ-1(R4, R5); Figs. 10B, 12B) and digit IV impression for tracks 1 and 10 (LQ-1(L1, R5); Figs. 3B, 12B), and, similar to track 7 (LQ-1(L4)), in some cases they are deeper than other portions of the broader digit impression. With respect to track 7 (LQ-1(L4)), we regard the 'claw impression' not to be an anatomical feature, but an extramorphological structure associated with sediment movement, as exemplified by a similar structure formed sub-distally on the digit IV impression of track 10 (LQ-1(R5)) where multiple sediment ridges converge (Fig. 12B).

The 'claw impression' considered by Thulborn and Wade (1984: 420, P1. 6) to be associated with the digit IV impression of track 7 (LQ-1(L4)) occurs separate to and at the medial margin of the digit IV impression (Fig. 9A–C, H). This contrasts with typical claw impressions that are expected to be continuous with the distal portion of the digit impression (e.g. Lockley, 2009: Fig. 2). Thulborn and Wade (1984: Pl. 6 caption) note the occurrence of pick-marks near this track, presumably formed during the excavation process (Fig. 9H), and it is possible that this circular structure may in fact be a similar excavation artifact. In light of these observations, we consider this particular feature to be an unreliable characteristic on which to base the identity of the largest Lark Quarry trackmaker.

Thulborn (2013: 18) found "the existence of [the impressions of] claws is apparent even in the [archival] photograph of footprint 6… especially if this is viewed at arm's length". This is not the case, regardless of what distance the photograph is viewed at. The archival photograph of track 6 (LQ-1(R3); Fig. 8A) has sediment overhang that obscures rather than reveals the distal-most portions of the digit impressions. Our observations of this portion of the track indicate a well-rounded distal digit II impression that continues approximately 2 cm beneath a sediment overhang. There is a very small (approximately 0.5 cm) concavity at the distal end of the digit III impression. A similar concavity is apparent along most of the medial edge of the digit IV impression, but only part of the medial portion of this digit impression is obscured by overhang (Fig. 8B). Thulborn and Wade (1984: 420) describe the 'claw impressions' on all the tracks as being conical. This is clearly not the case with the 'claw impression' associated with track 6 (LQ-1(R3)). The slight concavity that is apparent distal to the digit III impression is probably the result of sediment movement. The same holds true for the medial sediment overhang associated with the digit IV impression, which is not in the expected anatomical position of a claw impression.

Some authors have considered the relative width of a trackway as potentially providing insights into the identification of tridactyl trackmakers, with theropods considered more likely to display a narrow gauge trackway, and ornithopods a more wide gauge trackway (e.g. Lockley et al., 1998; Day et al., 2004; Kim et al., 2009; Mateus and Milàn, 2010). However, this is not diagnostic within either trackmaker grouping, as both can have a range of gauge widths (e.g. Day et al., 2002, 2004; Kim et al., 2009; Mateus and Milàn, 2010). Similar to theropodan trackmakers, ornithopodan trackmakers appear to have been capable of very narrow pedal gauges (e.g. dos Santos et al., 2013: Fig. 4), even when in a quadrupedal stance (e.g. Diedrich, 2004: Fig 8a; dos Santos et al., 2013: Fig. 4). Also, the occurrence of short pace length has been considered characteristics of ornithopods (Lockley, 1991). However, this trait is more likely to be an indication of gait used at the time of track formation (see Alexander, 1976) rather than an indicator of likely trackmaker identity.

Overall, we consider the combination of (1) broad digit impressions and the lack digital pad impressions on the better-preserved tracks, (2) the majority of tracks being on average wider than long, and (3) the absence of any definitive claw impressions to strongly support the idea that the trackmaker responsible for the large Lark Quarry tracks was probably an ornithopod.

In light of these new observations, we find it necessary to update the ichnotaxonomic status of the largest Lark Quarry tracks. The track outlines originally published by Thulborn and Wade (1984) were obtained via different and subjective methods, and do not accurately reflect the morphology of the tracks. As a consequence, the use of these outlines for comparisons and ichnotaxonomic assignment is flawed. Based on these outlines, these tracks have been previously assigned to cf. *Tyrannosauropus* (Thulborn and Wade, 1984) and *Amblydactylus* cf. *A. gethingi* (Romilio and Salisbury, 2011), but based on the results of this new study both assignments are problematic.

Based on our evaluation of the morphology of these tracks using digital 3D reliefs, we cannot confidently assign the large Lark Quarry tracks to either a new or an existing ichnotaxon. However, the tracks do share similarities with the ichnogenus *Iguanodontipus*: the trackway in which they occur has a narrow gauge (Sarjeant et al., 1998), and the digit impressions, where well preserved, have a rounded outline (Sarjeant et al., 1998: Fig. 16), with those of digits II and IV being directed abaxially (Sarjeant et al., 1998) to distally (Sarjeant et al., 1998; dos Santos et al., 2013). Sarjeant et al. (1998: 195) diagnosed *Iguanodontipus* on the basis of a "semi-digitigrade" pedal impression (see Leonardi, 1987), which is a term equivalent to subunguligrade as used here and elsewhere (see Moreno et al., 2007), where only the distal portions of the digits are impressed, a feature displayed by tracks 7–11 (LQ-1(L4–L6)) of the large Lark Quarry tracks. However, *Iguanodontipus* tracks typically have an impression of the metatarsodigital pad (e.g. Sarjeant et al., 1998: Fig. 15; Meyer and Thüring, 2003: Fig. 5; Diedrich, 2004: Fig. 5) that may range from having a proximal margin that is narrow to broad, features apparent only in Lark Quarry tracks 1–6 (LQ-1(L1–R3)). The broad digit impressions of the large Lark Quarry tracks are also similar to those associated with *Caririchnium* (e.g. Leonardi, 1984; Xing et al., 2007; Lim et al., 2012). However, this ichnotaxon is characterized by separations between the impressions of each digit, as well as that of the metatarsodigital pad. No such separation is observed in the large Lark Quarry tracks, with the notable exception of the digit IV impression of track 7 (LQ-1(L4)), but this bears no resemblance to the digit impressions documented for *Caririchnium*. On the basis of these observations we propose that the large Lark Quarry tracks should be referred to cf. *Iguanodontipus*, pending the discovery and subsequent analysis of other tracks within the Winton Formation that can be linked to this track type and which may better elucidate its morphology and ichnotaxonomic affinity.

4.3. Systematic palaeoichnology

cf. *Iguanodontipus*

v. 1979 'carnosaur footprints' Thulborn and Wade, pp. 275–279; figs 1–2.
v. 1984 cf. *Tyrannosauropus* Thulborn and Wade, pp. 419–421, 455; figs 4, 22; pls 3, 5, 6, 17; table 8 (original description);
v. 2011 *Amblydactylus* cf. *A. gethingi* Romilio and Salisbury, pp. 135–142; figs 1–3, 5–8.

Referred material—QM F10322, a set of seven fibreglass replicas; eleven *in situ* tracks (LQ-1(L1–L6)) (Romilio et al., 2013, fig. 5).
Horizon, age and locality—Winton Formation, Cenomanian–Turonian (Upper Cretaceous); Lark Quarry, Lark Quarry Conservation Park, Queensland, Australia.

4.4. Sequence of track events

Based on the hierarchical overprinting of traces, we propose (in part) a new sequence of events associated with the formation of the Lark Quarry trace fossils. Given that the displacement rims associated with the largest Lark Quarry tracks are overprinted by tool marks made by partially buoyed vegetation, it seems only reasonable to assume that the largest Lark Quarry dinosaur trackmaker was present at the site prior to the formation of the tool marks. This indicates that water was present at the site after the progression of the largest trackmaker. Smaller dinosaurian tracks overprint the largest dinosaurian tracks (e.g. tracks 2, 5, 6 and 10, LQ-1(R2, L3, R3, R5); Figs. 4H, 7I, 8H and 12H, respectively), the associated displacement rims (all except track 7, LQ-1(L1–R3, R4–L6); Figs. 3H, 4H, 5I, 7I, 8H, 10I, 11H, 12J and 13H), and the tool marks (e.g. associated with tracks 1, 2, 6, 8 and 9, LQ-1(L1, R1, R3, R4, L5); Figs. 3H, 4H, 8H, 10I and 11H, respectively), and indicate that these small dinosaurian tracks were formed after the passage of the floating vegetation.

We also recognize the largest dinosaurian tracks are highly variable in morphology, with sediment ridges present within the digit impressions, well-developed associated displacement rims, and lack desiccation cracks. These are all indicators that the track surface at the time of recording the traces consisted of soft sediment of high water content (see Marty, 2008: Table 4.2), but that it was probably not completely saturated or submerged. This suggests that the largest Lark Quarry trackmaker very likely traversed the site during subaerial exposure. For the tool marks to have been made, the water level at the site must have risen. Sometime after the tool marks were formed, the site was traversed by numerous smaller dinosaurian trackmakers. The required time delay between the formation of both sets of ichnites means the largest Lark Quarry dinosaurian trackmaker could not been present at or near the same time as the smaller dinosaurian trackmakers. Indeed Thulborn and Wade (1984: Pl. 5A caption) note the presence of "ripples of sandy sediment in the floor of the [foot]print 3", and while they did not elaborate further, these may also suggest the presence of subaqueous conditions after the largest Lark Quarry tracks were made (see within 'heel' region of track 3, Fig. 5A).

In the context of these observations, we regard the Lark Quarry tracksite to have recorded trace information over an extended period of time, spanning events that can be bracketed by the passage of the large trackmaker and at least some of the smaller dinosaurian trackmakers (Fig. 16). The revised sequence of events that we propose is therefore as follows:

- The largest dinosaurian trackmaker (a large-bodied, bipedal ornithopod; tracks assigned to cf. *Iguanodontipus*) traversed the site, most likely when it was subaerially exposed (Fig. 16A);
- Water was present at least for a period of time after the large tracks assigned to cf. *Iguanodontipus* were formed, with a current strong enough to carry partially floating vegetation across the site to form tool marks (Fig. 13B), some of which disrupted the displacement rims associated with the large tracks;
- At least some of the smaller dinosaurian trackmakers (small-bodied, bipedal ornithopods; tracks assignable to *W. latomorum*) moved non-synchronously across the site during fluctuating subaqueous conditions (Fig.16C), with some traces overprinting the tool marks and the tracks assigned to cf. *Iguanodontipus*.

An important consideration is that this succession of trace-makers is relative only to cf. *Iguanodontipus*, or more precisely to the displacement rims associated with the Lark Quarry cf. *Iguanodontipus*. For traces farther away from the tracks assigned to cf. *Iguanodontipus*, overprinting cannot be tested, such that it is more difficult or impossible to ascertain the sequence in which these traces were formed.

Since all the tracks at Lark Quarry have a similar style of preservation, it seems probable that all of them were likely recorded and preserved before significant track deterioration and loss of detail occurred through erosion—either by water movement or aerial exposure, for instance—perhaps over a period of hours or days rather than several weeks.

The proposed sequence of events presented herein is consistent with the site being a time-averaged assemblage (Romilio et al., 2013). Our examination of the site provides no evidence for the formation of the largest Lark Quarry tracks at, or near the same time as the formation of the smaller dinosaurian tracks. Instead, our findings suggest that a considerable period of time may have lapsed between both events. As such, our findings do not support previous accounts in which the largest Lark Quarry trackmaker "triggered" the movement of the smaller dinosaurs (Thulborn and Wade, 1984: 413, 443), or engaged in some form of "pursuit" (Wade, 1979: 16, 18 unnumbered figure captions) or "approached" them (Thulborn and Wade, 1984: 445). In a recent description of Lark Quarry, Thulborn (2013: 1) maintained there was no "substantial flaw in the existing [i.e. Thulborn and Wade's (1984)] interpretation of the [sequence of] Lark Quarry dinosaur tracks", and continued speculation that the "presence of a theropod [the cf. *Iguanodontipus* trackmaker] might help explain [the movement of the smaller dinosaurian trackmakers]". The results of our study suggests otherwise.

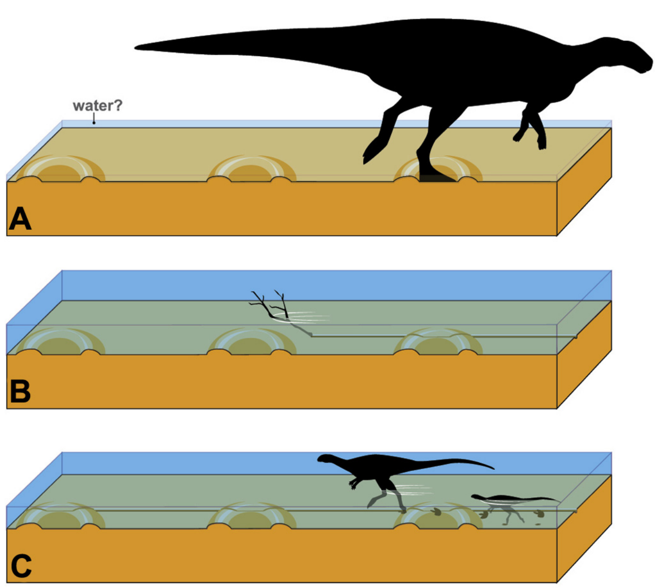

Fig. 16. The possible succession of Lark Quarry tracemakers. A, Progression of the cf. *Iguanodontipus* trackmaker during likely subaerial track surface conditions; B, the formation of tool marks by partially buoyed vegetation; and C, the progression of at least some *W. latomorum* trackmaker, some of which were swimming.

5. Conclusion

A main limitation associated with the traditional approach to track analysis of subjectively utilizing hand drawn track outlines is the lack of reproducibility, which becomes particularly relevant for the interpretation, understanding and monitoring of significant ichnological data. Without accurate, objectively reproducible representations of track morphology, we are limited in the usefulness that such outlines can provide for potential applications in future research. More objective methods, such as digital photogrammetry, are now available to ichnologists, and are inexpensive and easy to use, enabling the documentation of 3D information of tracks and related structures.

The rounded digit impressions and the lack of both claw and digital pad impressions, indicate that the largest Lark Quarry tracks were likely ornithopodan in origin, and that they can be reassigned to cf. *Iguanodontipus*. Track features indicate that the cf. *Iguanodontipus* trackmaker may have traversed the site during subaerial exposure in conditions where the soft sediment had a high water content. Displacement rims overprinted by subaqueously formed tool marks extends the time period between the formation of the large dinosaur tracks and at least some of the much smaller dinosaurian tracks assignable to *W. latomorum*. The current study finds no evidence to suggest that both types of dinosaurian track types formed (near) simultaneously, and any proposals for inferred interactions between the single large ornithopodan trackmaker and other Lark Quarry trackmakers seem hard to rationalize or substantiate.

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References

Adams, T.L., Breithaupt, B.H., 2003. Middle Jurassic dinosaurs of northern Wyoming: evidence from the Yellow Brick Road dinosaur tracksite, Bighorn Basin, Wyoming. Wyoming Geo-Notes 78, 39–48.

Adams, T.L., Strganac, C., Polcyn, M.J., Jacobs, L.L., 2010. High resolution three-dimensional laser-scanning of the type specimen of *Eubrontes* (?) *glenrosensis* Shuler, 1935, from the Comanchean (Lower Cretaceous) of Texas: implications for digital archiving and preservation. Palaeontologica Electronica 13.

Agnew, N.H., Griffin, H., Wade, M.J., Tebble, T., Oxnam, W., 1989. Strategies and techniques for the preservation of fossil tracksites: an Australian example. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 397–407.

Agnew, N.H., Oxnam, W.B., 1983. Conservation of the Lark Quarry dinosaur trackway. Curator 26, 219–233.

Alexander, R.M., 1976. Estimates of speeds of dinosaurs. Nature 261, 129–130.

Allen, J.R.L., 1997. Subfossil mammalian tracks (Flandrian) in the Severn Estuary, S.W. Britain: mechanics of formation, preservation and distribution. Philosophical Transactions of the Royal Society of London, B 352, 481–518.

Apesteguía, S., Gallina, P.A., 2011. Tunasniyoj, a dinosaur tracksite from the Jurassic-Cretaceous boundary of Bolivia. Anais da Academia Brasileirna de Ciencias 83, 267–277.

Bates, K.T., Manning, P.L., Vila, B., Hodgetts, D., 2008a. Three-dimensional modelling and analysis of dinosaur trackways. Palaeontology 51, 999–1010.

Bates, K.T., Rarity, F., Manning, P.L., Hodgetts, D., Vila, B., Oms, O., Galobart Lorente, À., Gawthorpe, R.T., 2008b. High-resolution LiDAR and photogrammetric survey of the Fumanya dinosaur tracksites (Catalonia): implications for the conservation and interpretation of geological heritage sites. Journal of the Geological Society, London 165, 115–117.

Berrell, R.W, Alvarado-Ortega, J., Yabumoto, Y., Salisbury, S.W. In press. First record of the ichthyodectiform fish *Cladocyclus* from eastern Gondwana: an articulated skeleton from the Early Cretaceous of Queensland, Australia. Acta Palaeontologica Polonica. (http://dx.doi.org/10.4202/app.2012.0019).

Bird, R.T., 1954. We captured a 'live' brontosaur. National Geographic 105, 707–722.

Bird, R.T., 1985. Bones for Barnum Brown: Adventures of a Dinosaur Hunter. Texas Christian University Press, Fort Worth, TX.

Carrano, M.T., Wilson, J.A., 2001. Taxon distributions and the tetrapod track record. Paleobiology 27, 564–582.

Castanera, D., Pascual, C., Razzolini, N.L., Vila, B., Barco, J.L., Canale, J.I., 2013. Discriminating between medium-sized tridactyl trackmakers: tracking ornithopod tracks in the base of the Cretaceous (Berriasian, Spain). PLoS One 8. http://dx.doi.org/10.1371/journal.pone.0081830.

Currie, P.J., Nadon, G.C., Lockley, M.G., 1991. Dinosaur footprints with skin impressions from the Cretaceous of Alberta and Colorado. Canadian Journal of Earth Sciences 28, 102–115.

Day, J.J., Norman, D.B., Gale, A.S., Upchurch, P., Powell, H.P., 2004. A Middle Jurassic dinosaur trackway site from Oxfordshire, UK. Palaeontology 47, 319–348.

Day, J.J., Norman, D.B., Upchurch, P., Powell, H.P., 2002. Dinosaur locomotion from a new trackway. Nature 415, 494–495.

Diedrich, C.G., 2004. New important iguanodontid and theropod trackways of the tracksite Obernkirchen in the Berriasian of NW Germany and megatracksite concept of central Europe. Ichnos 11, 215–228.

dos Santos, V.F., Callapez, P.M., Rodrigues, N.P.C., 2013. Dinosaur footprints from the Lower Cretaceous of the Algarve Basin (Portugal): New data on the ornithopod palaeoecology and palaeobiogeography of the Iberian Peninsuln. Cretaceous Research 40, 158–169.

Falkingham, P.L., 2011. Applying objective methods to subjective track outlines. In: Richter, A., Hübner, T., van der Lubbe, T. (Eds.), Dinosaur Track Symposia 2011 Obernkirchen, abstracts volume, p. 6.

Farlow, J.O., Brien, M.O., Kuban, G.J., Dattilo, B.F., Bates, K.T., Falkingham, P.L., Piñuela, L., Rose, A., Freels, A., Kumagai, C., Libben, C., Whitcraft, J., 2012. Dinosaur tracksites of the Paluxy River valley (Glen Rose Formation, Lower Cretaceous), Dinosaur Valley State Park, Somervell County, Texas, Actas de Las V Jornadas Internacionales Sobre Paleontología de Dinosaurios y su Entorno, Salas de Los Infantes, Burgos, Espana, 16-18 de Septiembre de 2010. Colectivo Arquecologico-Paleonotologico de Salas, C. A. S., Burgos, Spain, pp. 41–69.

Fastovsky, D.E., Smith, J.B., 2004. Dinosaur paleoecology. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria, 2nd edition. University of California Press, Berkeley, pp. 614–626.

Gatesy, S.M., 2003. Direct and indirect track features: what sediment did a dinosaur touch? Ichnos 10, 91–98.

Gierlinski, G.D., Pienkowski, G., 1999. Dinosaur track assemblages from the Hettangian of Poland. Geological Quarterly 43, 329–346.

Gierlinski, G.D., Sabath, K., 2008. Stegosaurian footprints from the Morrison Formation of Utah and their implications for interpreting other ornithischian tracks. Oryctos 8, 29–46.

Hume, R.A., 1996. Family Burhinidae (Thick-knees). In: del Hoyo, J., Elliott, A., Jordi, S. (Eds.), Handbook of the Birds of the World. Lynx Edicions, Barcelona, Spain, pp. 348–363.

Jenni, D.A., 1996. Family Jacanidae (Jancanas). In: del Hoyo, J., Elliott, A., Jordi, S. (Eds.), Handbook of the Birds of the World. Lynx Edicions, Barcelona, Spain, pp. 276–291.

Kim, J.Y., Lockley, M.G., Kim, H.M., Lim, J.-D., Kim, K.-S., 2009. New dinosaur tracks from Korea, *Ornithopodichnus masanensis* ichnogen. et ichnosp. nov. (Jindong Formation, Lower Cretaceous): implications for polarities in ornithopod foot morphology. Cretaceous Research 30, 1387–1397.

Leonardi, G., 1984. Le impronte fossile di dinosauri. In: Bonaparte, J.F., Colbert, E.H., Currie, P.J., de Ricqlès, A.J., Kielan-Jaworowska, Z., Leonardi, G., Morello, N., Taquet, P. (Eds.), Sulle Orme dei Dinosauri. Erizzo Editrice, Venice, pp. 165–186.

Leonardi, G., 1987. Glossary and manual of tetrapod footprint palaeoichnology. Departmento Nacional da Producao Mineral, Brasilia, Brazil, 117.

Lim, J.-D., Lockley, M.G., Kong, D.Y., 2012. The trackway of a quadrupedal ornithopod from the Jindong Formation (Cretaceous) of Korea. Ichnos 19, 101–104.

Lockley, M.G., 1991. Tracking dinosaurs: a new look at an ancient world. Cambridge University Press, Cambridge.

Lockley, M.G., 2009. New perspectives on morphological variation in tridactyl foot prints: clues to widespread convergence in developmental dynamics. Geological Quarterly 53, 415–432.

Lockley, M.G., Garcia-Ramos, J.C., Piñuela, L., Avanzini, M., 2008. A review of vertebrate track assemblages from the Late Jurassic of Asturias, Spain with comparative notes on coeval ichnofaunas from the western USA: implications for faunal diversity in siliciclastic facies assemblages. Oryctos 8, 53–70.

Lockley, M.G., Hunt, A.P., 1994. A track of the giant theropod dinosaur *Tyrannosaurus* from close to the Cretaceous/ Tertiary boundary, northern New Mexico. Ichnos 3, 213–218, 227.

Lockley, M.G., Hunt, A.P., Paquette, M., Bilbey, S.A., Hamblin, A.H., 1998. Dinosaur tracks from the Carmel Formation, northeastern Utah: implications for Middle Jurassic paleoecology. Ichnos 5, 255–267.

Lockley, M.G., Matsukawa, M., 1999. Some observations on trackway evidence for gregarious behavior among small bipedal dinosaurs. Palaeogeography, Palaeoclimatology, Palaeoecology 150, 25–31.

Long, J.A., 1990. Dinosaurs of Australia and other animals of the Mesozoic Era. Reed Books Pty Ltd, Balgowlah.

Long, J.A., 1998. Dinosaurs of Australia and New Zealand and other animals of the Mesozoic Era. UNSW Press, Sydney.

Mangano, M.G., Buatois, L.A., MacNaughton, R.B., 2012. Ichnostratigraphy. Elsevier, Amsterdam.

Manning, P.L., Ott, C.J., Falkingham, P.L., 2008. A probable tyrannosaurid track from the Hell Creek Formation (Upper Cretaceous), Montana, United States. Palaios 23, 645–647.

Marty, D., 2008. Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez—Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology. GeoFocus 21, 1–278.

Mateus, O., Milàn, J., 2010. A diverse Upper Jurassic dinosaur ichnofauna from central-west Portugal. Lethaia 43, 245–257.

Matsukawa, M., Lockley, M.G., 2007. Speculations on Cretaceous ornithopod trackway distributions in east Asia: comparisons with extant ungulate migration patterns, Proceedings of the 2007 Haenam Uhangri International Dinosaur Symposium. Chunnam National University Press, Gwangju, pp. 177–232.

Matsukawa, M., Lockley, M.G., Hunt, A.P., 1999. Three age groups of ornithopods inferred from footprints in the Mid-Cretaceous Dakota Group, eastern Colorado, North America. Palaeogeography, Palaeoclimatology, Palaeoecology 147, 39–51.

Meyer, C.A., Thüring, B., 2003. The first iguanodontid dinosaur tracks from the Swiss alps (Schrattenkalk Formation, Aptian). Ichnos 10, 221–228.

Molnar, R.E., 1991. Fossil reptiles in Australia. In: Vickers-Rich, P., Monaghan, J.M., Baird, R.F., Rich, T.H., Thompson, E.M., Williams, C. (Eds.), Vertebrate Palaeontology of Australasia. Pioneer Design Studio, and Monash University Publications Committee, Melbourne, pp. 605–702.

Moratalla, J.J., Sanz, J.L., Jimenez, S., 1988. Multivariate analysis of Lower Cretaceous dinosaur footprints: discrimination between ornithopods and theropods. Geobios 21, 395–408.

Moreno, K., Blanco, N., Tomlinson, A., 2004. Nuevas huellas de dinosaurios del Jurásico Superior en el norte de Chile. Ameghiniana 41, 535–544.

Moreno, K., Carrano, M.T., Snyder, R., 2007. Morphological changes in pedal phalanges through ornithopod dinosaur evolution: a biomechanical approach. Journal of Morphology 268, 50–63.

Paul, G.S., 1988. Predatory dinosaurs of the world: a complete illustrated guide. Simon and Schuster, New York.

Paul, G.S., 2002. Dinosaurs of the Air: The Evolution and Loss of Flight in Dinosaurs and Birds. Johns Hopkins University Press., Baltimore.

Petti, F.M., Avanzini, M., Belvedere, M., de Gasperi, M., Ferrertti, P., Girardi, S., Remondino, F., Tomasoni, R., 2008. Digital 3D modelling of dinosaur footprints by photogrammetry and laser scanning techniques: integrated approach at the Coste dell'Anglone tracksite (Lower Jurassic, Southern Alps, Northern Italy). Studi Trentini di Scienze Naturali. Acta Geologica 83, 303–315.

Piñuela, L., 2012. Dinosaur true tracks and undertracks. Recognition criteria and nomenclature problems. The Asturian case (Spain). In: Xing, L., Lockley, M. (Eds.), 2012 Abstract book of Qijinag International dinosaur track symposium, Chongqing Municipality, China. Boulder Publishing, Boulder, pp. 91–95.

Roach, B.T., Brinkman, D.L., 2007. A reevaluation of cooperative pack hunting and gregariousness in *Deinonychus antirrhopus* and other nonavian theropod dinosaurs. Bulletin of the Peabody Museum of Natural History 48, 103–138.

Romilio, A., Salisbury, S.W., 2011. A reassessment of large theropod dinosaur tracks from the mid-Cretaceous (late Albian—Cenomanian) Winton Formation of Lark Quarry, central-western Queensland, Australia: A case for mistaken identity. Cretaceous Research 32, 135–142.

Romilio, A., Tucker, R.T., Salisbury, S.W., 2013. Re-evaluation of the Lark Quarry dinosaur tracksite (late Albian—Cenomanian Winton Formation, central-western Queensland, Australia): no longer a stampede? Journal of Vertebrate Paleontolology 33, 102–120.

Sarjeant, W.A.S., Delair, J.B., Lockley, M.G., 1998. The footprints of *Iguanodon*: a history and taxonomic study. Ichnos 6, 183–202.

Scanlon, J.D., 2006. Dinosaurs and other Mesozoic reptiles of Australasia. In: Merrick, J.R., Archer, M., Hickey, G.M., Lee, M.S.Y. (Eds.), Evolution and

biogeography of Australian vertebrates. Australian Scientific Publishing, Sydney, pp. 265–290.
Sternberg, C.M., 1932. Dinosaur tracks from Peace River, British Columbia. Canada National Museum Bulletin 68, 59–85.
Thulborn, R.A., 2013. Lark Quarry revisted: a critique of methods used to identify a large dinosaurian track-maker in the Winton Formation (Albian–Cenomanian), western Queensland, Australia. Alcheringa: An Australasian Journal of Palaeontology 37, 312–330.
Thulborn, R.A., Wade, M.J., 1979. Dinosaur stampede in the Cretaceous of Queensland. Lethaia 12, 275–279.
Thulborn, R.A., Wade, M.J., 1984. Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. Memoirs of the Queensland Museum 21, 413–517.
Thulborn, R.A., Wade, M.J., 1989. A footprint as a history of movement. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 51–56.
Thulborn, T., 1990. Dinosaur tracks. Chapman and Hall, London.
Tucker, R.T., Roberts, E.M., Hu, Y., Kemp, A.I.S., Salisbury, S.W., 2013. Detrital zircon age constraints for the Winton Formation, Queensland: contextualizing Australia's Late Cretaceous dinosaur faunas. Gondwana Res 24, 767–779.
Voigt, S., Berman, D.S., Henrici, A.C., 2007. First well-established track-trackmaker association of paleozoic tetrapods based on *Ichniotherium* trackways and diadectid skeletons from the Lower Permian of Germany. Journal of Vertebrate Paleontology 27, 553–570.
Wade, M.J., 1979. A minute—a hundred million years ago. Hemisphere 23, 16–21.
Wilson, J.A., Marsicano, C.A., Smith, R.M.H., 2009. Dynamic locomotor capabilities revealed by early dinosaur trackmakers from southern Africa. Public Library of Science PLoS ONE, 8.
Xing, L., Wang, F., Pan, S., Chen, W., 2007. The discovery of dinosaur footprints from the middle Cretaceous Jiaguan Formation of Qijiang County, Chongqing City. Acta Geologica Sinica 81, 1591–1602.

Appendix A. Supplementary data

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