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Reevaluation of the Lark Quarry dinosaur Tracksite (late Albian-Cenomanian Winton Formation, central-western Queensland, Australia): no longer a stampede?

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ARTICLE

REEVALUATION OF THE LARK QUARRY DINOSAUR TRACKSITE (LATE ALBIAN–CENOMANIAN WINTON FORMATION, CENTRAL-WESTERN QUEENSLAND, AUSTRALIA): NO LONGER A STAMPEDE?

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ABSTRACT—The Lark Quarry dinosaur tracksite has previously been recognized as recording the stampede of a mixed herd of dozens of small theropod and ornithopod dinosaurs. A reexamination of trackway material reveals that the small theropod-type tracks, previously assigned to the ichnotaxon *Skartopus*, can co-occur within individual trackways of the ornithopod-type tracks assigned to *Wintonopus*. Moreover, in singular deep tracks where the overall surface outline resembles *Skartopus*, the base of the track can also resemble *Wintonopus*. Whereas the *Wintonopus* holotype may reflect the pedal anatomy of a short-toed or subunguligrade ornithopod trackmaker, the elongate 'toe' impressions typically associated with *Skartopus* (including the holotype) primarily provide information on digit movement through the sediment and, in many instances, may represent swim traces. The morphological differences between the two ichnotaxa are therefore not taxonomically significant and we formally propose that *Skartopus australis* should be considered a junior synonym of *Wintonopus latomorum*. Longitudinal depth profiles through tracks indicate that many are swim traces. The sedimentology and lithology of Lark Quarry further indicates the site represents a time-averaged assemblage formed in a fluvial-dominated floodplain under variable subaqueous conditions, with the parallel orientation of the numerous trackways formed by trackmakers under the influence of downstream current flow. This indicates that the fluvial environment may have been a preferred route for hydrophilic bipedal dinosaurs. We thus do not consider the Lark Quarry dinosaur tracksite to represent a 'stampede.' Instead, the tracksite may represent part of a riverine setting, where the water was shallow, in which small dinosaurs swam and/or waded.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Lark Quarry, 95 km south-west of Winton, central-western Queensland, is arguably one of the most complex dinosaur tracksites in the world, containing a very high concentration of tracks, a wide spectrum of ichnotaxon morphotypes, and what are thought to be most of the world's known running dinosaur trackways. In a combined study by The University of Queensland and the Queensland Museum, spanning the mid-1970s to late 1980s, Thulborn and Wade (1979, 1984, 1989) provided major contributions to the science of dinosaur (paleo)ichnology through their analysis of the site. This work included, but was not limited to, the documentation of over 3000 individual tracks, the interpretation of a track horizon that preserved four sequential generations of tracks, the description of extramorphological track features formed from variable pedal kinematics and substrate interactions, the estimation of trackmaker height and speed through the development of updated calculations (modified from Alexander, 1976), and the formulation of a scenario in which all the small bipedal tracks were formed by running trackmakers, thereby providing evidence for the world's only known dinosaur stampede.

The research findings of Thulborn and Wade (1979, 1984, 1989) were pivotal in getting Lark Quarry conserved and included on the Australian National Heritage listing. The site is now fully protected within a purpose-built, temperature-controlled building (completed in 2002), permitting public access and ongoing research activities. In 2004, the site was renamed Dinosaur Stampede National Monument (Australian National Heritage List, Place ID 105664).

Although the original study by Thulborn and Wade (1984) utilized dozens of trackways to calculate trackmaker hip height and speed, only two trackway diagrams were presented, one referable to a large theropod, assigned to cf. *Tyrannosauropus* (now considered the ornithopod ichnotaxon *Amblydactylus* cf. *A. gethingi*; Romilio and Salisbury, 2011a), and the other assigned to a medium-sized *Wintonopus* trackmaker. Significantly, neither trackway formed part of the 'stampede.' A partial trackway of *Skartopus* was subsequently included in a later study (Wade, 1989). Due to the wide variation in the morphology of individual tracks shown to occur in both *Wintonopus* and *Skartopus* ichnotaxa by Thulborn and Wade (1984), some researchers have commented on the resemblance of some of these tracks to swim traces (e.g., Moreno et al., 2004). This becomes an important issue if one is to consider that the range of Lark Quarry 'stampede' tracks were supposedly formed by running animals in a terrestrial setting.

For many years, the standard procedure in dinosaur ichnology was to identify tracks as two-dimensional (2D) outlines, a practice that was employed at Lark Quarry by Thulborn and Wade (1979, 1984, 1989). However, as many studies have shown in recent years, tracks are complex three-dimensional (3D) structures (Arakawa et al., 2002; Gatesy et al., 2005; Bates et al., 2008a, 2008b; Jackson et al., 2009) that can appear very different when viewed in only 2D (Padian, 2003). Sectioning through tracks can reveal the 3D surface deformations within and around tracks, providing a useful means of investigating dinosaur pedal

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kinematics (e.g., Avanzini, 1998; Gatesy et al., 1999; Manning, 2004, 2008; Milàn et al., 2004, 2006; Bates et al., 2008a). Although the Lark Quarry surface track outlines described by Thulborn and Wade (1979, 1984, 1989) are accurate, the absence of 3D information has hindered a more detailed understanding of track morphology, trackmaker identification, and trackmaker pedal kinematics. Although Thulborn and Wade (1984, 1989) illustrated longitudinal depth profiles for idealized *Wintonopus* and *Skartopus* (e.g., Thulborn and Wade, 1984:figs. 7 and 12, respectively), it is unclear how these profiles were obtained because methods for the acquisition of the requisite data are not presented. As such, the accuracy of the subsequent portrayals of pedal kinematics for each of the respective trackmakers is uncertain (e.g., Thulborn and Wade, 1984:figs. 7 and 12).

There are many challenges associated with the identification of in situ Lark Quarry trackways and thus confirmation of many of the findings of Thulborn and Wade (1984). The high density of tracks makes distinguishing individual trackways extremely difficult, particularly in the absence of trackway diagrams. This problem is exacerbated by the fact that the track surface has deteriorated considerably in parts since it was first excavated and subsequently described by Thulborn and Wade (1979, 1984, 1989). As summarized by Agnew and Oxnam (1983), Agnew et al. (1989), and Cook (2004), the deterioration of the Lark Quarry track surface has been due to a variety of factors, including the susceptibility of the track surface to rapid weathering, the presence of direct pedestrian traffic, vandalism and theft of track material, degradation due to faunal defecation and carcass putrefaction, the accidental burning of 'protective' plastic and its subsequent melting into the tracks, and surface damage due to the collapse of a rammed earth wall. Restoration of the deteriorated areas has modified the surface (including the largest tracks; see Agnew and Oxnam, 1983). As a consequence, individual track dimensions and trackway parameters such as pace, stride, and pace angulation as listed in Thulborn and Wade (1979, 1984, 1989) have become very difficult to confirm. Although Thulborn and Wade (1984) identified 56 *Wintonopus* and 34 *Skartopus* trackways, they provide only minimal photographic or schematic documentation of their location at the tracksite: only one *Wintonopus* trackway (described as from a trotting animal; Thulborn and Wade, 1984:fig. 3b) and a partial *Skartopus* trackway (described as from a running animal; Wade, 1989:fig. 8.5) are available.

Fortunately, the type specimens of both *Wintonopus latomorum* (QM F10319) and *Skartopus australis* (QM F10330) have avoided deterioration due to their housing at the Queensland Museum. These specimens are presumably in a condition that is comparable to those of other tracks left in situ after their excavation in 1976 (Wade, 1979a), and are therefore ideal for the reinvestigation of the depth profiles of individual tracks. Because many of the tracks photographed by Thulborn and Wade (1984) were of replica specimens (QM F10322), the replicas are necessarily included in the current comparative study. However, as noted by Wade (1979b:290), details such as depth can be misrepresented when based solely on the investigation of cast or replica material, because the uniform texture and coloring may mask any previous "failure to clean out some [Lark Quarry] tracks before casting."

As new tracks are documented from Australia and in other places around the world that resemble *Wintonopus* (Long, 1998; Gierlinski and Pienkowski, 1999; Li et al., 2006) and *Skartopus* (Gierlinski and Nowacki, 2008; Gierlinski et al., 2009; Cook et al., 2010), it becomes increasingly important to properly understand the nature and diagnosis of these ichnotaxa. In this investigation, we analyzed the tridactyl tracks at Lark Quarry assigned to *Wintonopus latomorum* and *Skartopus australis* in light of recent advances in trackway documentation and analysis, with the primary goal of gaining a better understanding the 3D track morphology of these ichnotaxa. This research forms part of a wider reevaluation of the locomotor abilities of the Lark Quarry trackmakers, and the evaluation of the lithology, sedimentology, and stratigraphy of the region and Winton Formation in general.

Institutional Abbreviations—CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **QM**, Queensland Museum, Brisbane, Australia; **YPM**, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

REGIONAL AND LOCAL GEOLOGY

The 'mid'-Cretaceous (late Albian–Cenomanian) Winton Formation is restricted to the Eromanga Basin, which geographically forms a major component of the Great Australian Artesian Basin of northeastern Australia (Dunstan, 1916; Whitehouse, 1955; Vine, 1966; Gallagher and Lambeck, 1989; Angevine et al., 1990; Draper, 2002; Dettmann et al., 2009; Fig. 1). The drag and cooling of the Australian plate over the subducting Pacific plate resulted in the subsidence of the Australian margin in the Triassic, which continued into the Middle–Late Jurassic (Gallagher and Lambeck, 1989; Draper, 2002). Upon termination of subduction (Jurassic to very Early Cretaceous), the rebound of the Australian plate induced erosion of the eastern Australian continent, supplying depositional sediment during the Jurassic to 'mid'-Cretaceous (Gallagher and Lambeck, 1989; Draper, 2002). Sedimentation in the Jurassic (Aalenian–Tithonian) is dominated by fluvial deposition, including three cycles of upward-fining clastics (Hutton, Birkhead, Adori, Westbourne, Namur, and Hooray formations). In the Early Cretaceous (Berriasian), a broad shallow epicontinental seaway covered much of the Eromanga Basin (Wallumbilla, Toolebuc, Allaru, Mudstone, and Mackunda Formations) at least four times, with the final regression of this seaway occurring in the late Albian. Continued fluvial deposition during the late Albian–Cenomanian identifies the Winton Formation (Fig. 2).

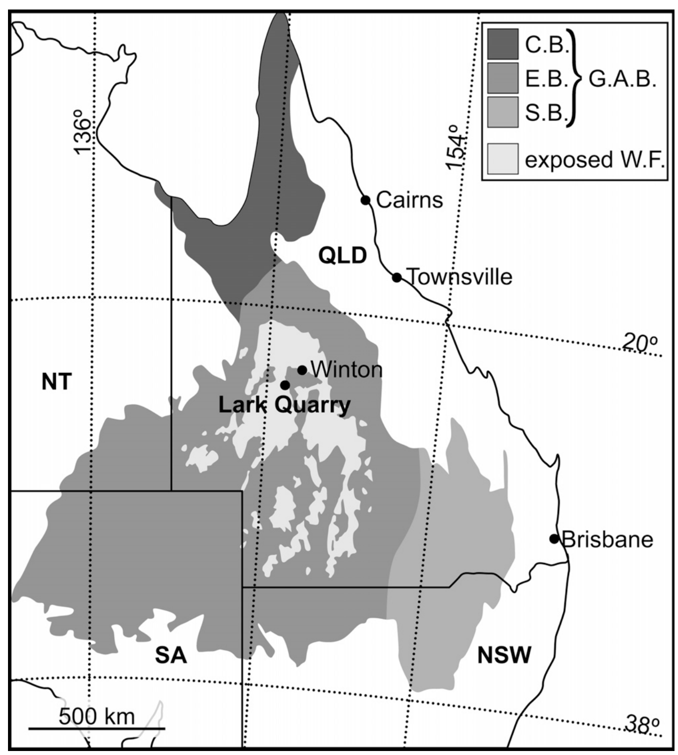

FIGURE 1. A map of northeastern Australia. **Abbreviations**: **C.B.**, Carpenteria Basin; **E.B.**, Eromanga Basin; **S.B.**, Surat Basin; **G.A.B.**, Great Artesian Basin; **W.F.**, exposed Winton Formation; **QLD**, Queensland; **NSW**, New South Wales; **SA**, South Australia; **NT**, Northern Territory.

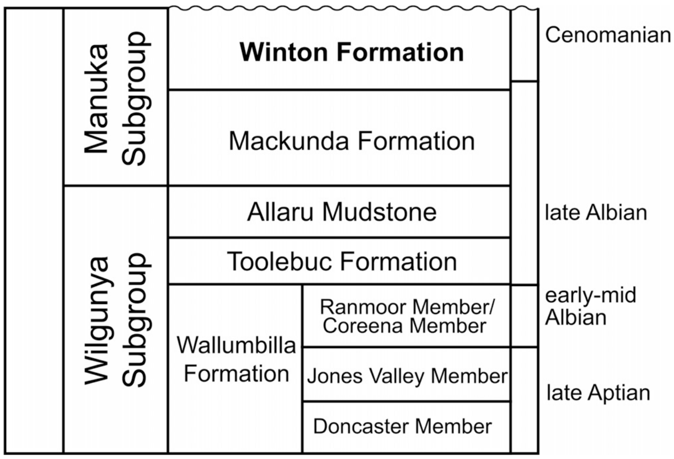

FIGURE 2. Stratigraphy of the Eromanga Basin, central-western Queensland. Adapted from Draper (2002). Lark Quarry's stratigraphic position in the Winton Formation is yet to be determined.

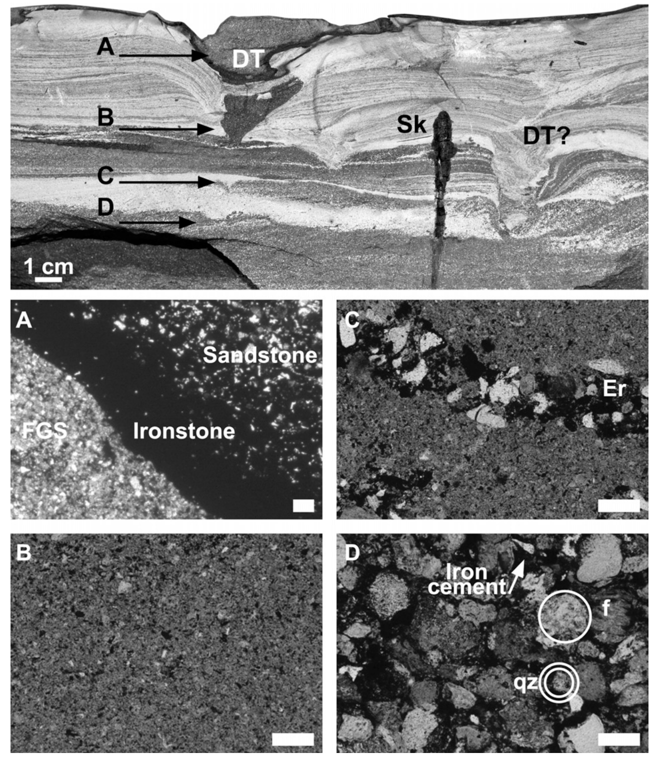

FIGURE 3. Lithologic section through the track-bearing horizon at Lark Quarry Conservation Park. **A**, sandstone with ironstone at its base, positioned above the upper laminae of the track horizon, characterized by fine-grained sandstone; **B**, fine siltstone with sand grain inclusions, and horizontal to cross-bedded laminae; **C**, erosive contact (Er) between the fine siltstone and the underlying sandstone; **D**, underlying cross-bedded feldspathic sandstone. **Abbreviations**: **DT**, dinoturbation; **f**, potassium feldspar; **FGS**, fine-grained sandstone; **qz**, quartz; **Sk**, *Skolithos* invertebrate trace fossil. Distal track to the right. Scale bars equal 1 mm.

The Winton Formation (late Albian–Cenomanian), originally described by Dunstan (1916) as the 'Winton Series,' consists of sandstones, shales, and minor coal seams that stratigraphically overlie the predominantly marine sediments of the Makunda Formation. The two formations together comprise the Manuka Subgroup, which is the uppermost unit of the Rolling Downs Group (Dunstan, 1916; Whitehouse, 1954, 1955; Exon, 1966; Casey, 1970; Draper, 2002; Fig. 2). The Winton Formation itself consists of complex repetitive sequences of fine- to medium-grained feldspatholithic or lithofeldspathic arenite, siltstones, mudstones, and claystones with minor inclusions of thinly bedded mudclast conglomerates, and rare limestone (montomorillonite is abundant, and trace amounts of illite and kaolinite have been identified; Senior and Mabbutt, 1979; Coote, 1987; Draper, 2002).

Sedimentology and Depositional Environment

Previous lithological descriptions of the track-bearing strata at Lark Quarry Conservation Park by Thulborn and Wade (1979, 1984, 1989) lack localized stratigraphic or regional lithological details. These authors described the track horizon as soft and fine-grained arkosic sandstones of reddish-buff color, interbedded with thin indurated pink claystone, with dinosaur footprint impressions occurring within an 8–10-cm seam of finally laminated claystone that was "evidently of lacustrine origin" (Thulborn and Wade, 1979:275), but provided no supporting lithostratigraphic or architectural evidence for this interpretation. Thulborn and Wade (1984) define the track horizon as a pink claystone containing iron-staining, and noted that above and below the track horizon are thick beds of finely cross-bedded arkosic sandstone. These claystone/sandstone couplets are numerous throughout the local outcropping Winton Formation, and suggested that the "creek bed" drained into a lake or watering hole (Thulborn and Wade, 1989:52).

A reexamination of the Lark Quarry lithology reveals that the track horizon consists of a layer of siltstone/fine-grained sandstone overlying a relatively homogeneous sandstone layer (Fig. 3). This contrasts to the separate claystone and sandstone layers previously interpreted by Thulborn and Wade (1979, 1984, 1989). The rock specimen Thulborn and Wade (1984:pl. 2) cited as containing 'claystone' could not be located for this study; instead, we examined other topotype material under the same collection number (i.e., QM F10321). The track horizon (Fig. 3) consists of feldspatholithic fine-grained sandstone to siltstone (50–60% potassium feldspar, 40–30% quartz [poly/monocrystaline], and 10–20% volcano/sedimentary-lithics), with grains overall submoderate to moderately round, much less mature quartz grains, and diagentic iron as the dominant cement. Throughout the track horizon numerous sedimentary structures were identified, including planar and cross-bedding along with the inclusion of rip-up clasts from the underlying sandstone, along with several instances of 'dinoturbation' (Fig. 3), where the siltstone lamina have been deformed due to loading and unloading pressures by trackmakers during possibly saturation of the horizon. The lamina at the base of the track horizon is fine siltstone, but larger individual grains of potassium feldspar or quartz also occur. The lamina at the upper portion of the track horizon exhibits nonparallel to parallel planar bedding to convolute bedding, coarsening upwards from siltstone to fine sandstone. This horizon is dominated by medium-grained, feldspatholithic siltstone to fine sandstone, containing distinctive cross-bedded lamina, characterized by an erosive contact with the above sandstone. This sandstone layer is of similar lithology to the sandstone layer below the track horizon, and contains rip-up clasts from the underlying track horizon. This suggests a period when the track horizon ceased deposition, hardened (perhaps subaerially), prior to the high-energy regime when sand was deposited. The excavated surface of Lark Quarry is not the uppermost surface of the track horizon but rather an ironstone layer formed from the lowermost portion of sandstone overlying the track horizon (Fig. 4). This ironstone effectively 'drapes' a protective layer over the tracks, marginally reducing their dimensions, and may have formed when iron-rich water met a differential grain boundary between the more porous overlying sandstone and the less porous

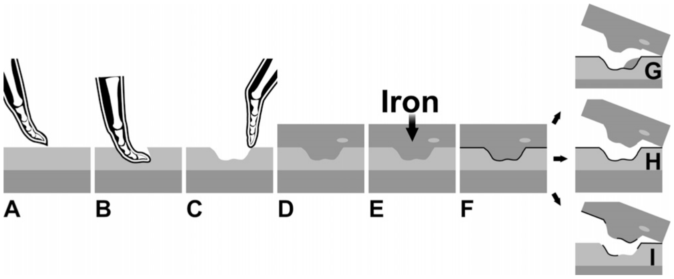

FIGURE 4. Sequence of Lark Quarry track preservation. **A**, deposition of fluvial silt and fine sand (light gray) on top of sand (dark gray); **B**, dinosaur trackmaker steps into the silt and fine-sand layer; **C**, dinosaur exits substrate leaving a track; **D**, deposition of fluvial sand (gray) and occurrence of rip-up clast (light gray oval); **E**, diagenetic iron permeates through the overlying rock and sandstone layers; **F**, a thin veneer of ironstone forms at the base of the sandstone layer overlying the track horizon; **G**, excavation removes most of the sandstone above the ironstone layer leaving some track infill; **H**, excavation removes the sandstone above the ironstone layer; **I**, excavation removes the sandstone and some of the ironstone layer exposing parts of the underlying track horizon. **Abbreviation**: **Iron**, water-soluble iron.

underlying track horizon siltstone. During excavation, much of the sandstone above the ironstone layer was removed to expose the tracks (Fig. 4H). In some tracks, the sandstone was not completely removed and infill remains (Fig. 4G), whereas in other instances portions of ironstone have been removed exposing the upper portions of the track horizon (Fig. 4I).

The upper surface of the track horizon we interpret as representing the original paleosurface that the dinosaur trackmakers contacted, and agree with previous findings that there is "no indication that any of them [i.e., the tracks] are 'underprints' [undertracks sensu Marty, 2008] transmitted through the overlying sediments" (Thulborn and Wade, 1989:51). Had they been undertracks resulting from the animals having contacted the overlying layers (i.e., the overlying sandstone), then there would likely have been disruption of rip-up clasts that occur as part of track infill, a disturbance between the sandstone and track horizon, and potentially a lack of overhanging structures within tracks. We have not observed any of the latter features so conclude that none of the tracks is an undertrack.

We find no evidence of a lake environment as proposed by Thulborn and Wade (1979, 1984). Instead, the sediments and associated sedimentary structures at Lark Quarry indicate minor cycles of increased and decreased flow velocities at overall higher rates of flow than the supposedly lacustrine environment. This includes the bedding pattern, grain maturity, and grain distribution being distinctive of fluvial rather than lacustrine environments. We interpret the sedimentary patterns and structures as most likely generated by a secondary or tertiary fluvial channel with waxing and waning flow velocities, with the lower sandstone unit suggestive of higher flow rates and the overlying siltstone suggestive of a decline in flow. The numerous larger grain inclusions within the siltstone are indicative of changes in flow velocities. The uppermost section of the track-bearing strata coarsens upwards, indicating an overall increase in flow rate. The occurrence of only one invertebrate ichnogenus, *Skolithos*, characterized by simple vertical burrows and escape trace fossils (~3 mm in diameter; see Fig. 3), is attributable to high-energy flow regimes typical of fluvial channels (Buatois and Mangano, 2011). Parallel to 'stampede' direction are vegetation drag marks (sensu Thulborn and Wade, 1984) that may have required considerable aquatic flow rate to maintain their sublinear formation.

MATERIALS AND METHODS

This study examined the Lark Quarry ichnites located in situ and specimens housed at the Queensland Museum (holotypes, QM F10319 and QM F10330; paratype, QM F10320; topotypes, QM F10321; and replicas, QM F10322). Trackways were identified as a collection of ichnites with similarities in trackway measurements, including track size, pace, and stride measurements, and track rotation relative to the trackway axis. Because catalogue numbers have not previously been assigned to any Lark Quarry trackways, those identified in this study were labeled with the locality prefix 'LQ' (Lark Quarry), a trackway number (using Arabic numerals), and individual tracks within these labeled as left ('L') or right ('R') and numbered separately from '1' onwards. For example, LQ-2(L3) denotes the 3rd left track from trackway 2. This trackway numbering system does not relate to the numbered trackways tabulated by Thulborn and Wade (1984). We labeled the most recognizable trackway, *Amblydactylus* cf. *A. gethingi* (sensu Romilio and Salisbury, 2011a), as trackway '1' (i.e., LQ-1(L1–L6) for the entire set of 11 tracks of this trackway), and all subsequent trackways onwards from this number.

Single and stereoscopically paired photographs were taken of the tracks using digital cameras (either a Nikon D70 with an 18–55 mm Nikor lens, or a Nikon D80 with a 28–105 mm Nikor lens), with shutter speeds set manually to achieve the appropriate exposure, and illuminated either by natural light or by a remotely activated flash (Nikon SB-600 Speedlight). Track outlines were drawn based on first-hand examination and tracings of in situ tracks, photographs, and reconstructed 3D images of the respective tracks. In the illustrations of individual tracks, continuous lines represent internal track, dotted lines represent external track, dashed lines represent slide/drag marks, and gray continuous lines represent proximal semicircular shapes. For clarity, however, in the illustration of tracks within trackways, continuous lines represent the track and its extramorphological features and dotted lines represent repaired areas (sensu Agnew and Oxnam, 1983). Stereoscopic photographs were converted to 3D digital images using AgiSoft StereoScan (1.0.1 beta 64 bit), and then saved as PDF and movie files to allow visualization of the track depth (see Supplementary Data). To quantify the track depth profile, a 15-cm contour gauge was pressed along the length of each footprint's digits (digits II, III, and IV), removed, and the profile photographed. For tracks with lengths greater than 15 cm, depth profiles were determined from the 3D digital images created in AgiSoft StereoScan. Digital images were placed into Adobe InDesign CS4 and the profiles traced, and compared with the pedal stance range that could be reconstructed for the pes skeleton of *Dryosaurus altus* (based on CM 21786, YPM 1876, YPM 1884).

A hypothetical subdigitigrade (sensu Leonardi, 1987) *Dryosaurus* track was reconstructed based on the reconstructed pes skeleton of *Dryosaurus altus* (based on CM 21786, YPM 1876, YPM 1884) and the ichnotaxon *Dinehichnus socialis* (Gierlinski and Sabath, 2008). The hypothetical track was scaled to the width of studied Lark Quarry tracks, along with a reconstructed subunguligrade (sensu Moreno et al., 2007) hind limb skeleton of *Dryosaurus altus* (based on CM 21786, YPM 1876, YPM 1884) in order to estimate trackmaker hip height. Although we acknowledge that hip height calculating formulae exist (Alexander, 1976; Thulborn, 1990), these rely on digitigrade (rather than subdigitigrade) track measurements. In the reconstruction of the hypothetical *Dryosaurus* track, we note that the digit impressions are longer than that of the (presumably) walking trace of the *Wintonopus* holotype. Although differences occur in the digit lengths between the hypothetical *Dryosaurus* track and *Wintonopus*, we regard *Dryosaurus* as an appropriate model for a generalized small-bodied, basal iguanodontian ornithopod.

Trackmaker gait was estimated by comparing the calculate relative stride (stride/hip height; λ/h) with the specific values determined by Alexander (1976) and Thulborn and Wade (1984) for the different dinosaur gaits, including walking (λ/h < 2), 'trotting' (2 < λ/h < 2.9), and running (λ/h > 2.9). Although we are aware that trotting should be referable to quadrupedal and not bipedal gaits, we acknowledge that this represents a slow run that has a 'suspended phase' where both feet are off the ground.

DESCRIPTION OF TRACKS AND TRACKWAYS

Given the difficulties of identifying trackways, not all trackways present at Lark Quarry were mapped. Ten trackways were located (Figs. 5–7), containing between 3 and 18 tracks (average 6.5), with most orientated to the northeast with relatively long stride lengths (Table 1). Trackways that deviated from this trend were LQ-4 and LQ-11, with the former having a short stride lengths (average 19 cm) and the first track oriented to the east and the last oriented to the northeast, and the latter oriented to the south. A walking gait is estimated for trackway LQ-4 (λ/h = 0.7), a slow running gait for trackways LQ-6 and 8–11, and a running gait for LQ-2, 3, 5, and 7 (Table 1; Appendix 1). *Characichnos*-type swim traces were observed in trackways LQ-2, 4, 5, 7, and 8 (Fig. 5).

The track morphologies are highly variable, even within singular trackways (Figs. 6–7), varying from deep to very shallow (e.g., LQ-2(L1) and LQ-2(R5), respectively), long- and short-toed traces (e.g., LQ-2(L10) and LQ-2(R6), respectively), and traces with '*Skartopus*' outlines at the surface but *Wintonopus* features at the track base (e.g., LQ-2(L1); Fig. 11). We could not find any distinction between the ichnotaxa *Wintonopus latomorum* and '*Skartopus australis*.' Consequently, we attribute all tracks and trackways to the ichnospecies *W. latomorum*. For example, both *Wintonopus* and '*Skartopus*' tracks are found within singular individual trackway LQ-7 (Fig. 6): track L1 has *Wintonopus*-like characteristics with short digit impressions, track R3 has '*Skartopus*'-like characteristics, with elongated digit impressions with sharp claw impressions, whereas track R1 has both *Wintonopus*-like and '*Skartopus*'-like characteristics, with short toe impressions and a divergent digit II diagnostic of *Wintonopus* and the sharp claw impressions that characterize '*Skartopus*.' This was not the case with all trackways. For instance, in LQ-10 (Fig. 6) all the tracks appears consistent with *Wintonopus* morphotypes, and trackway LQ-5 (Fig. 5) appears to have '*Skartopus*' track morphotypes (but we note that these latter tracks are also characteristic of *Characichnos*-type swim traces; see below). Some individual tracks have surface outlines resembling '*Skartopus*' and the base track outline resembling *Wintonopus* (e.g., the '*Skartopus*' holotype and LQ-2(L1); Figs. 10 and 11, respectively).

The previously published Lark Quarry trackways attributed to *Wintonopus* and '*Skartopus*' (Thulborn and Wade, 1984:fig. 3, and Wade, 1989:fig. 8.5, respectively) were located, but notable differences occur in our interpretation of these ichnites. The *Wintonopus* trackway Thulborn and Wade (1984) interpreted as consisting of seven tracks in a trackway oriented to the northeast. We interpret this trackway as having five tracks (trackway LQ-10), with the 'sixth' as first track (L1) of trackway LQ-11, oriented to the south (Figs. 5 and 7), and the 'seventh' track missing, but we note that the region that it possibly occurs has extensive surface damage. Although track LQ-11(L1) is in a position consistent with it being be part of trackway LQ-10, its track orientation, size, and proximal displacement rim suggest that L1 is not a track of the LQ-10 trackway (Fig. 7). The '*Skartopus*' trackway illustrated by Wade (1989:fig. 8.5) is a partial trackway of six tracks purportedly of a larger trackway of 24 tracks. This corresponds to trackway LQ-2(L1–L10) of only 18 tracks (excluding the possible trace at position LQ-2(L8) that is covered in concrete; Fig. 6). The difference in our number of tracks within this trackway relates to our exclusion of traces we considered possibly made by different trackmakers.

The depth profiles of individual tracks display variations of four general (and even overlapping) categories (Fig. 8): (1) shallow longitudinal scratches with a flat track base (e.g., Fig. 12); (2) tracks with a steep proximal and distal track margin (e.g., Figs. 14B, ii and 15); (3) tracks with a steep proximal track margin and an inclined distal track margin (e.g., Fig. 14B, iv); and (4) tracks with steep proximal and distal track margins, and a flat track base (e.g., Fig. 9). When viewed from above, category 1 tracks are shallow traces that mainly appear as subparallel scratch marks (Fig. 12) or as tridactyl scratches where digit II and IV impressions appear as convex (relative to the axis of the central digit impression) scratches. Category 2 typically have a surface outline of three aligned circles, but can also have digit and claw impressions at the track's proximal and distal margins (Fig. 15). The distal incline of the category 3 track profiles forms an elongated digit impression. Some of these tracks have a rounded shaped immediately caudal to the track that spans the track width (Figs. 14 and 16). Others have a short horizontal portion at the base of the track that may correspond to the digit impression (e.g., the holotype '*Skartopus*'; Fig. 10), with at least one having the cranial edge of the profile overhanging the deepest part of the print, as revealed by the only 'naturally' sectioned track (on the broken edge of the *Wintonopus* holotype block; Fig. 3). The relatively large track base of tracks within category 4 may relate to the plantar surface of the trackmaker being impressed into the substrate, although some tracks have the proximal margin of the trace elongated, presumably by trackmaker dragging its toes (Fig. 11).

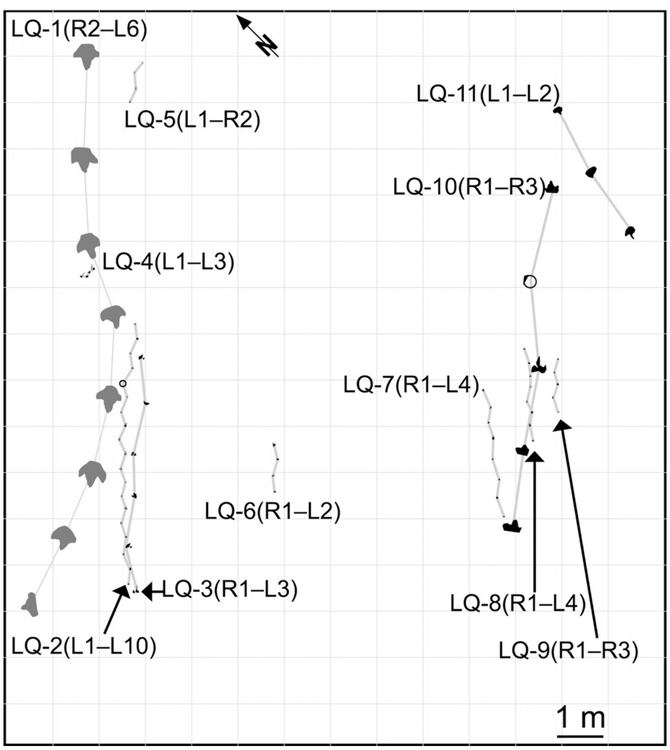

FIGURE 5. Interpretative map of the Lark Quarry tracksite, showing *Amblydactylus* cf. *A. gethingi* (adapted from Romilio and Salisbury, 2011b), as trackway LQ-1, and 10 *Wintonopus latomorum* Thulborn and Wade, 1984, trackways, LQ-2 to LQ-11. *Wintonopus* tracks obscured by concrete are indicated by open circles. **Abbreviations**: **LQ-1–11**, Lark Quarry trackway numbers; **L**, left track; **R**, right track. Scale bar equals 1 m.

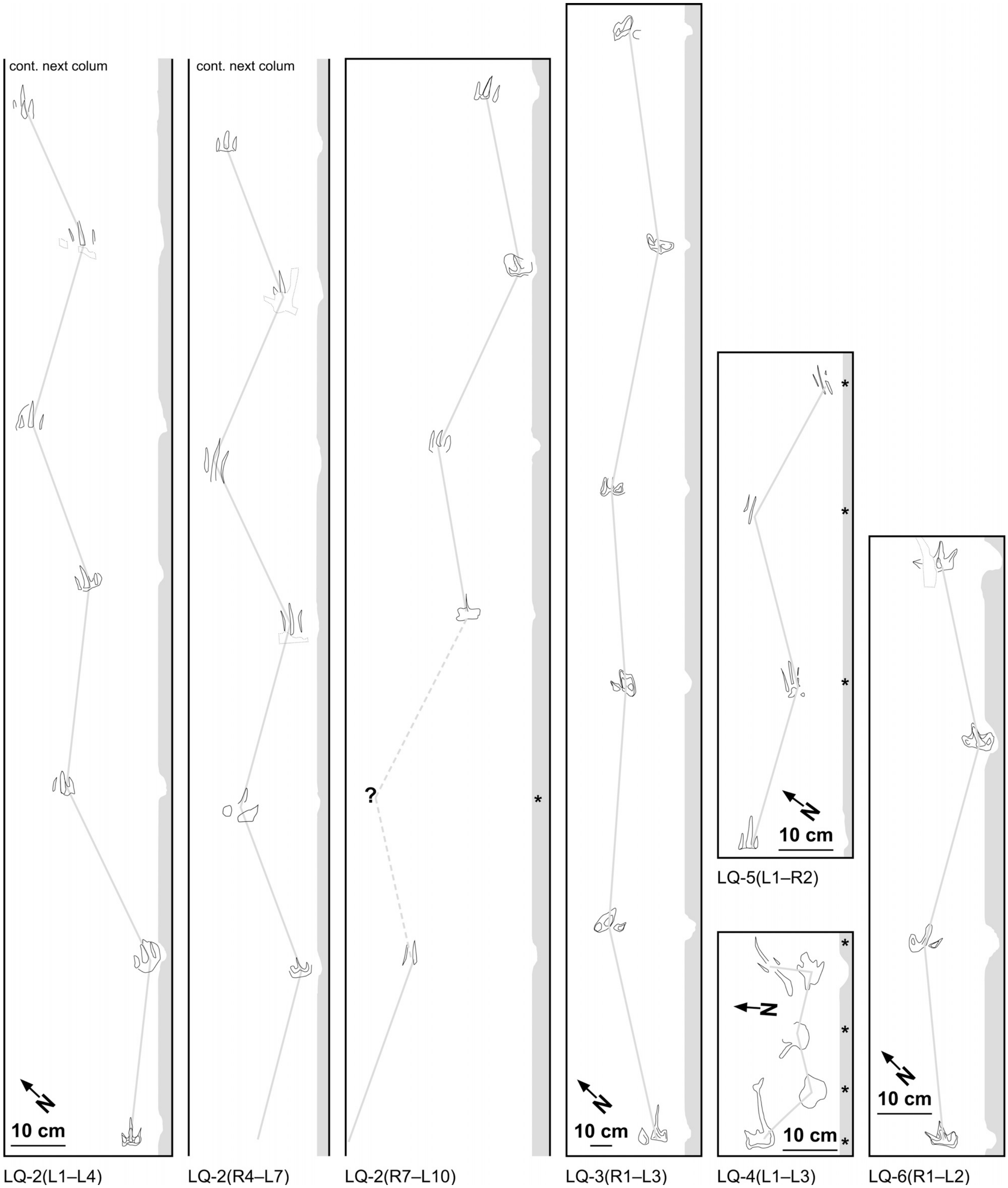

FIGURE 6. *Wintonopus latomorum* Thulborn and Wade, 1984. Trackways LQ-2 to LQ-6 discussed in this study. Gray columns to the right of their respective trackways indicate the track depth profile measured along the principle axis of the digit III impression. Estimated hip height for LQ-2 is 19 cm; LQ-3, 62.5 cm; LQ-4, 25 cm; LQ-5, 18 cm; and LQ-6, 25 cm. A continuous line represents track outlines, and a dotted line represents the repaired track surface in contact with the track. **Abbreviations**: **LQ-2–6**, Lark Quarry trackway numbers; **L**, left track; **R**, right track. *, depth profile not recorded. Distal track to the top. Scale bars equal 10 cm.

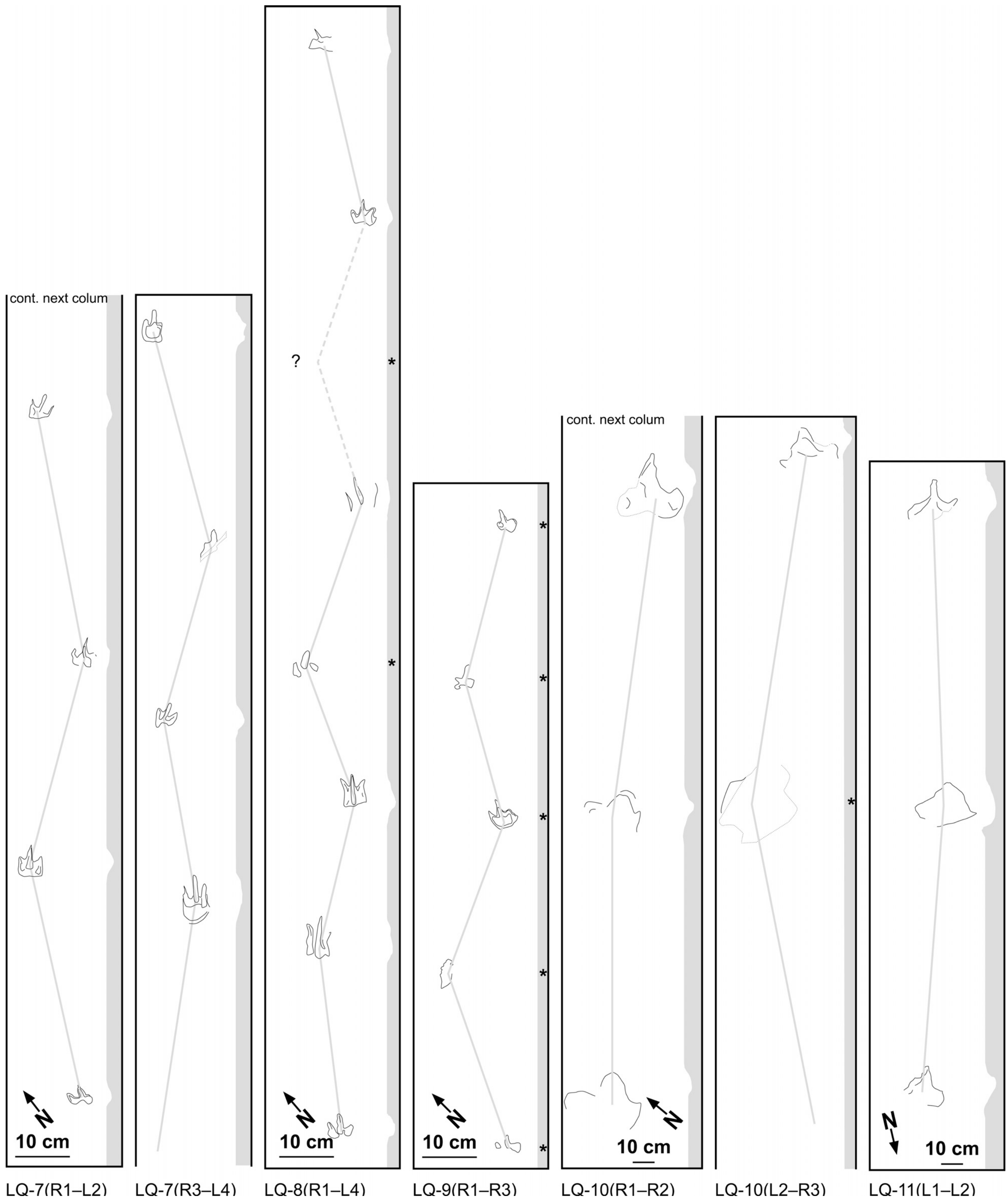

FIGURE 7. *Wintonopus latomorum* Thulborn and Wade, 1984. Trackways LQ-7 to LQ-11 discussed in this study. Gray columns to the right of their respective trackways indicate the track depth profile measured along the principle axis of the digit III impression. Estimated hip height for LQ-7 is 19 cm; LQ-8, 20 cm; LQ-9, 20 cm; LQ-10, 160 cm; and LQ-11, 110 cm. A continuous line represents track outlines, and a dotted line represents the repaired track surface in contact with the track. **Abbreviations**: **LQ-7–11**, Lark Quarry trackway numbers; **L**, left track; **R**, right track. *, depth profile not recorded. Distal track to the top. Scale bars equal 10 cm.

TABLE 1. Average trackway measurements of 10 Lark Quarry (LQ) trackways.

Trackway	Track length (cm)	Track width (cm)	Pace (cm)	Stride (cm)	Pace angle (°)	Height (cm)	Relative stride (stride/hip height)
LQ-2	4.8	4.1	32	62	141	19	3.3 (run)
LQ-3	11	11	98	193	165	62.5	3.1 (run)
LQ-4	9.2	4.9	11	19	119	25	0.7 (walk)
LQ-5	6.3	3.5	27	58	140	18	3.2 (run)
LQ-6	5.4	6.5	35	70	154	25	2.8 (slowrun)
LQ-7	5.3	4.1	40	78	159	19	4.1 (run)
LQ-8	5.6	4.9	30	55	162.5	20	2.7 (slowrun)
LQ-9	4	3.5	30	56	146	20	2.8 (slowrun)
LQ-10	26.3	32.4	168.5	336	167	160	2.1 (slowrun)
LQ-11	22.2	25.8	155	308	173	110	2.8 (slowrun)

DISCUSSION

Lark Quarry Ichnotaxa

Thulborn and Wade (1979, 1984, 1989) show, perhaps unintentionally, that the track morphologies associated with *Wintonopus* and '*Skartopus*' ichnotaxa overlap (Fig. 17). Our study supports this view, with the overlap not only occurring within singular trackways (e.g., LQ-7; Fig 7), but also within individual tracks, either by a combination of diagnostic features (e.g., LQ-7(R1)) or the occurrence of different 'ichnotaxa' at different depths with a track (e.g., holotype '*Skartopus*,' and LQ-2(L1); Figs. 10 and 11). We are in agreement with Lockley and Foster (2006) that it is problematic to assign two ichnogenera to tracks within a single trackway (as well as to varying depths within a single track) and consider, as has been proposed by Farlow and Chapman (1997:540), that fossilized tracks "should be given names only when they display a distinctive shape that is unlikely to be an artifact of their formation, a shape that to some extent reflects the skeletal structure of the trackmaker. Furthermore, the foot structure inferred from the footprint should be different from the foot structure inferred from previously named ichnotaxa." Our findings indicate that '*Skartopus*' is a track variant of *Wintonopus*, and as such we regard '*Skartopus australis*' as a junior synonym of *Wintonopus latomorum*. Additionally, the findings of this study provide a useful understanding of the range of extramorphological variation within the *Wintonopus* ichnotaxon.

The separation of the small Lark Quarry tracks into two ichnotaxa permitted Thulborn and Wade (1979, 1984, 1989) to interpret the close track association as evidence for mixed herding behavior between small ornithischian and theropod dinosaurs. Some authors have speculated that this mixed herd could only occur if the theropods posed no threat to the ornithischians, with the '*Skartopus*' trackmaker possibly being an "avian or near-avian theropod species" (e.g., Roach and Brinkman, 2007:130). Others consider this 'mixed-herd' as unlikely, and that the identity of the trackmakers may represent two different groups of either ornithopods or theropods (e.g., Paul, 1988; Lockley and Matsukawa, 1999), or possibly a single taxon of either group (Paul, 1988; Lockley, 1991; Lockley and Matsukawa, 1999; Romilio and Salisbury, 2011b, 2011c). Our study supports this latter view; namely, that the *Wintonopus* and '*Skartopus*' tracks are formed from extramorphological track variations rather than pedal differences between unrelated types of trackmakers.

FIGURE 8. Four general categories of track depth profiles when measured longitudinally along digit III. Distal track to the right (see text for details). Images not to scale.

Pedal Kinematics and Posture

Dinosaur limb posture and foot movements can been ascertained from the deformed substrate within and surrounding the tracks (Avanzini, 1998; Brown, 1999; Gatesy et al., 1999; Manning, 2004, 2008; Bates et al., 2008a, 2008b). Thulborn and Wade (1984, 1989) recognized this pes-substrate interaction as having a great effect on the Lark Quarry track morphologies, and considered them to have been made by digitigrade *Wintonopus* and '*Skartopus*' trackmakers. This interpretation contrasts with their earlier account of the small-bodied Lark Quarry trackmaker's having "the metatarso-phalangeal joints lifted clear of the ground at foot-strike" (Thulborn and Wade, 1979:277)—an interpretation that has been accepted by others (e.g., Gierlinski and Pienkowski, 1999; Li et al., 2006, Gierlinski et al., 2009). Our interpretation of the longitudinal depth track profiles supports Thulborn and Wade's (1979) earlier account, with some tracks having been made by animals with a subunguligrade posture (Fig. 21). Some of the tracks, however, could only have been formed by animals with an unguligrade posture, with only the unguals having contacted the substrate (e.g., those with a depth profile of categories 1 and 2 and at least some of category 3). Because a digitigrade posture is typical for bipedal dinosaurs (sensu Lockley and Gillette, 1989), the occurrence of alternate postures may suggest that the Lark Quarry trackmakers were externally supported at the time they contacted the substrate. This may have been particularly relevant for unguligrade

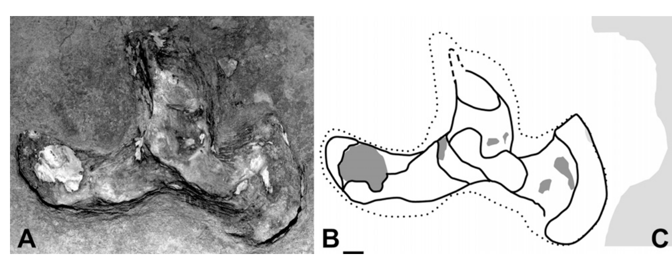

FIGURE 9. *Wintonopus latomorum* Thulborn and Wade, 1984, QM F10319, holotype, category 4 track. **A**, photograph; **B**, interpretive drawing; **C**, track depth profile along the principal axis of the digit III impression. Estimated trackmaker hip height of 69 cm (see text for details). Continuous line represents internal track; dotted line represents external track outline; dashed line represent drag marks. Dark gray regions represent exposed portions of the underlying track horizon. Distal track to the top. Scale bar equals 1 cm.

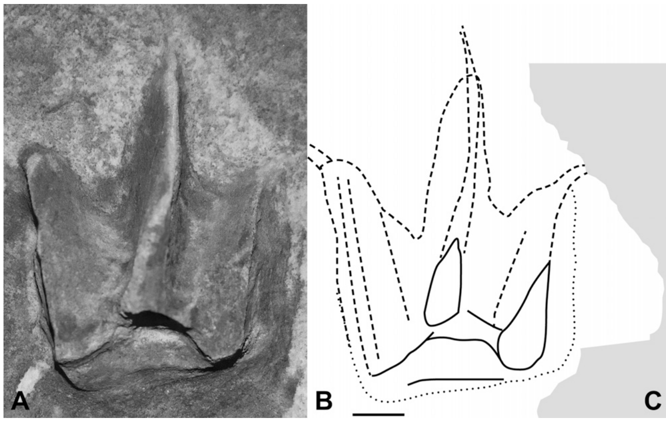

FIGURE 10. *Wintonopus latomorum* Thulborn and Wade, 1984, QM F10330, category 3b track. **A**, photograph; **B**, interpretive drawing; **C**, track depth profile along the principal axis of the digit III impression. This track was previously designated the holotype '*Skartopus australis*' by Thulborn and Wade (1984). Estimated trackmaker hip height of 23 cm (see text for details). Continuous line represents internal track; dotted line represents external track outline; dashed line represents drag marks. Distal track to the top. Scale bar equals 1 cm.

tracks, which, in agreement with Paul (1988), we suspect would have been a highly unstable posture for a bipedal dinosaur. A subunguligrade posture has been proposed for the theropod trackmaker of the ichnotaxon *Carmelopodus*, which may have habitually moved with the metatarsophalangeal pad of digit IV elevated off the ground (Lockley et al., 1998). Some large styracosternan ornithopods have also been reconstructed with a pes skeleton that enabled a subunguligrade posture (Moreno et al., 2007). Lark Quarry tracks with a depth profile of category 4 and at least some of category 3 may have formed from the distal portions of the digits contacting the substrate when the pes was in a subunguligrade posture, but whether this capacity was due to the trackmakers having supported themselves or being buoyed is not clear.

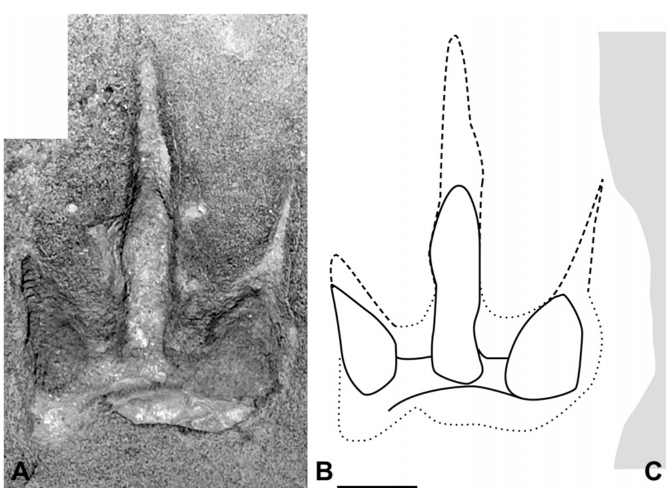

FIGURE 11. *Wintonopus latomorum* Thulborn and Wade, 1984, LQ-2(L1), category 4 track. **A**, photograph; **B**, interpretive drawing; **C**, track depth profile along the principal axis of the digit III impression. Estimated trackmaker hip height of 19 cm (see text for details). Continuous line represents internal track; dotted line represents external track outline; dashed line represents slide/drag marks. Distal track to the top. Scale bar equals 1 cm.

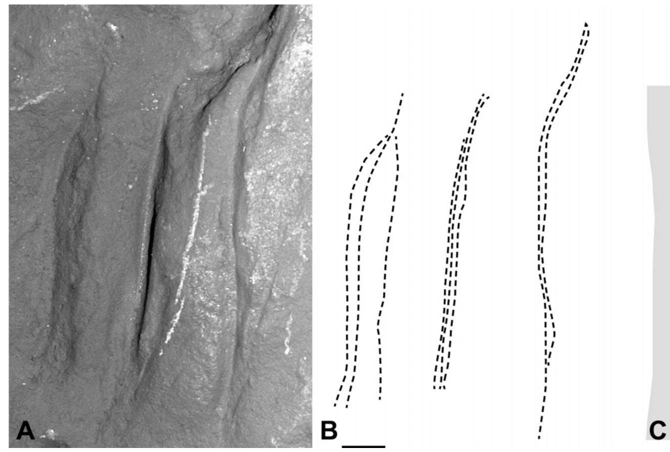

FIGURE 12. *Wintonopus latomorum* Thulborn and Wade, 1984, QM F10322 (replica), category 1 swim trace. **A**, photograph; **B**, interpretive drawing; **C**, track depth profile along the principal axis of the digit III impression. Thulborn and Wade (1984:pl. 14a) consider this *Wintonopus*. Estimated trackmaker hip height of 21 cm (see text for details). Dashed lines represent scratch marks. Distal track to the top. Scale bar equals 1 cm.

Category 1 Tracks—The elongated, didactyl or tridactyl, longitudinal scratches that characterize category 1 tracks strongly resemble previously recognized dinosaur swim traces (e.g., McAllister, 1989; Whyte and Romano, 2001; Gierlinski et al., 2004; Lockley and Foster, 2006; Milner et al., 2006; Ezquerra et al., 2007). Whyte and Romano (2001) assigned similar traces from the Middle Jurassic, Saltwick Formation, United Kingdom, to the ichnogenus *Characichnos*, interpreting them as the swim traces of theropod dinosaurs. However, such tracks may not be restricted to theropod trackmakers, having been observed to occur within trackways of the ornithopod ichnotaxon *Dinehichnus* (Lockley and Foster, 2006). We suspect that many of the Lark Quarry tracks formed as a result of the backwards sweeping of the tips

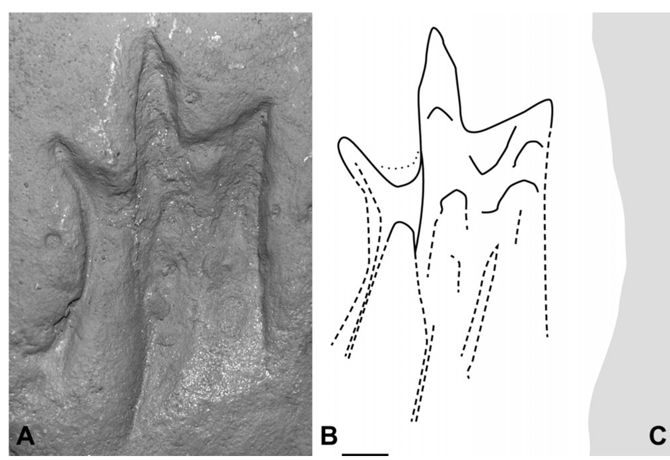

FIGURE 13. *Wintonopus latomorum* Thulborn and Wade, 1984, QM F10322, category 1 swim trace. **A**, photograph; **B**, interpretive drawing; **C**, track depth profile along the principal axis of the digit III impression. This track was previously described "with deeply incised scratches" by Thulborn and Wade (1984:pl. 12c, caption). Estimated trackmaker hip height of 22 cm (see text for details). Continuous line represents internal track; dotted line represents external track outline; dashed line represents scratch marks. Distal track to the top. Scale bar equals 1 cm.

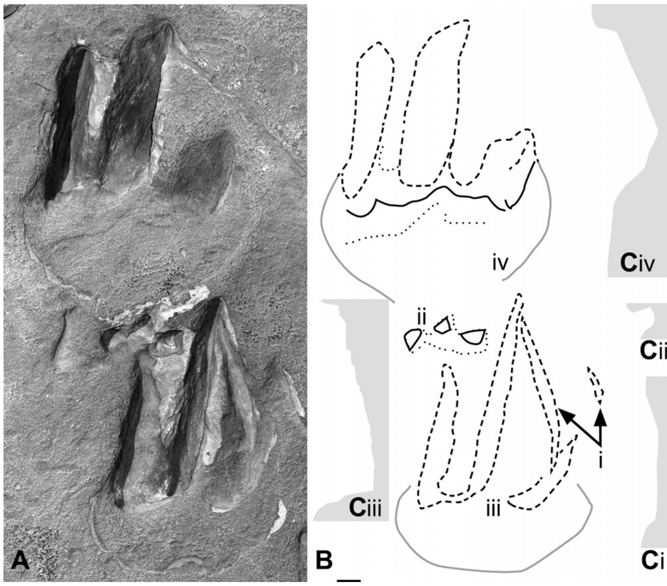

FIGURE 14. *Wintonopus latomorum* Thulborn and Wade, 1984, QM F10321, four swim traces. **A**, photograph; **B**, interpretive drawing; **C**, track depth profile along the principal axis of the digit III impression. **i**, A didactyl category 1 swim trace with an estimated trackmaker hip height of 24 cm. **ii**, A tridactyl swim trace of category 2 with an estimated trackmaker hip height of 18 cm. **iii**, A tridactyl swim trace of category 3 with an estimated trackmaker hip height of 30 cm. **iv**, A tridactyl swim trace of category 3 with an estimated trackmaker hip height of 42 cm representing the largest individual of this category from this study (see text for details). Continuous line represents internal track; dotted line represents external track outline; dashed line represents scratch marks; continuous gray line represents proximal round shape. Distal track to the top. Scale bar equals 1 cm.

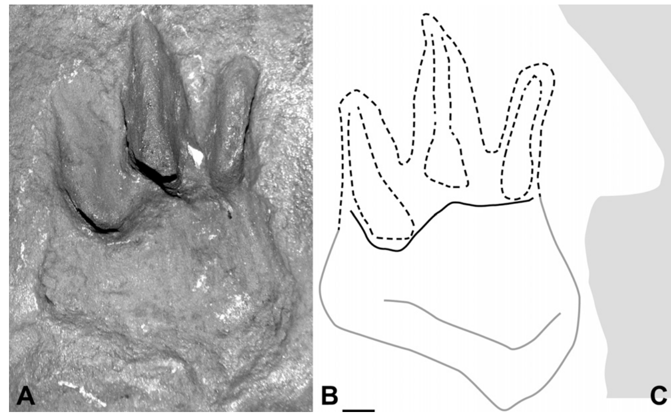

FIGURE 16. *Wintonopus latomorum* Thulborn and Wade, 1984, QM F10322, category 3 swim trace. **A**, photograph; **B**, interpretive drawing; **C**, track depth profile along the principal axis of the digit III impression. This track was previously described as preserving a 'metapodium' impression by Thulborn and Wade (1984). Estimated trackmaker hip height of 28 cm (see text for details). Dotted line represents external track outline; dashed line represents scratch marks; continuous gray line represents proximal round shape. Distal track to the top. Scale bar equals 1 cm.

of the digits contacting the substrate while the trackmaker was buoyed by water (Fig. 18B). Some category 1 tracks differ from the typical three longitudinal scratches, and instead have digit impressions instead of distal scratch marks (e.g., Thulborn and Wade, 1984:pl. 12c; Fig. 13). Thulborn and Wade (1984, 1989) proposed that these types of tracks were assignable to '*Skartopus*.' As such, they interpreted the '*Skartopus*' trackmaker to have had relatively large digitigrade pedes that were functionally analogous to "snow-shoes" (Thulborn and Wade, 1984:418), with "broad-spreading feet, and some of [these trackmakers] might have traversed the site without leaving any recognizable trackways" (Thulborn, 1990:329). Upon exiting, Thulborn and Wade (1984) interpret the tips of the unguals to have impressed into the substrate, scratched the substrate, and lengthened the track proximally as the trackmaker kicked-back (Fig. 18A). Thulborn and Wade (1984) do not provide an explanation for the occurrence of these scratch marks within *Wintonopus* tracks (Thulborn and Wade, 1984:pl. 14a), whose trackmaker presumably did not have pedes that were analogous to snowshoes. The snowshoe analogy is probably based (in part) on the assumption that the '*Skartopus*' trackmakers had elongated digits to aid weight distribution across the foot. However, we do not consider long 'digit impressions' associated with tracks such as the '*Skartopus*' holotype to represent anamomical imprints of the toes sensu stricto; instead, we consider these traces to represent drag or scratch marks associated with a much shorter, subunguligrade pes (i.e., category 3 tracks; Fig. 20). Also, Thulborn and Wade's (1984) model seems problematic for terrestrial locomotion on account of the caudally moving pes failing to grip the substrate sufficiently in order to reaccelerate the body into the next step. It is conceivable that such a kinematic movement is likely to have caused the animal to

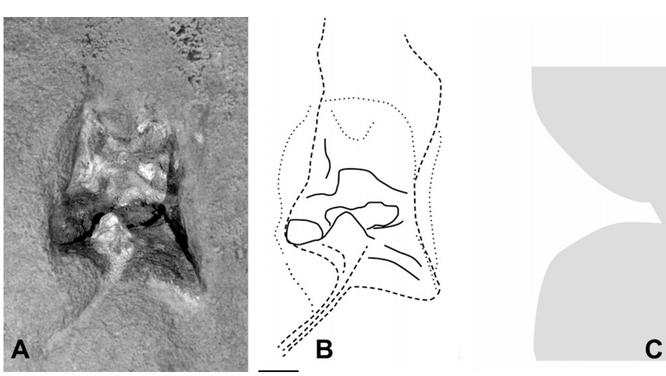

FIGURE 15. *Wintonopus latomorum* Thulborn and Wade, 1984, QM F10321, category 2 swim trace. **A**, photograph; **B**, interpretive drawing; **C**, track depth profile along the principal axis of the digit III impression. Estimated trackmaker hip height of 14 cm representing the smallest individual from this study (see text for details). Continuous line represents internal track; dotted line represents external track outline; dashed line represents scratch/drag marks. Distal track to the top. Scale bar equals 1 cm.

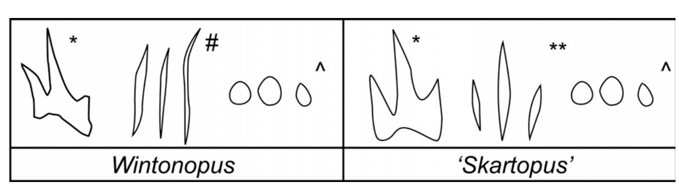

FIGURE 17. Interpretive diagram of previously published *Wintonopus latomorum* and '*Skartopus australis*' where ichnotaxa share morphological traits. *, adapted from Thulborn and Wade (1979:fig. 2am labeled as 'ornithopod' and 'coelurosaur' tracks); **#**, adapted from Thulborn and Wade (1984:pl. 14a); **, adapted from Thulborn and Wade (1984:fig. 12); ^, adapted from Thulborn and Wade (1989:fig. 6.6). Distal track to the top. Images not to scale.

stumble rather than achieve the steady pace lengths that are observed in trackways containing category 1 tracks (e.g., LQ-5). We are therefore of the opinion that category 1 tracks were formed when the trackmakers were partially buoyed, their feet contacting the substrate in a caudally directed power stroke that was more analogous to paddling rather than running or walking (Fig. 18B). This supposition is supported by the similarity of these tracks to other dinosaur swim traces (e.g., McAllister, 1989; Whyte and Romano, 2001; Gierlinski et al., 2004; Milner et al., 2006; Ezquerra et al., 2007).

Category 2 Tracks—These tracks typically appear as three circle-shaped impressions in dorsal view, with steep distal and proximal margins in the track depth profile width (Figs. 8, 14 ii and 15). In the explanation for the formation of these tracks, Thulborn and Wade (1989) proposed that the trackmaker's digitigrade, 'snow-shoe'-like pes failed to impress into the substrate until the end of the contact phase, at which point the unguals penetrate vertically into the sediment (Fig. 19A). We consider an alternative explanation with the tracks formed by a buoyed, unguligrade trackmaker, moving the pes caudocranially (Fig. 19B), with a near vertical entering and exiting of the sediment almost vertically with very little longitudinal movement within the substrate. Some tracks show proximal entry and distal exit drag marks of the digits and/or unguals (Fig. 19C). The latter pose no problem for a swim trace, but become problematic in the context of the digitigrade model proposed by Thulborn and Wade (1989).

Category 3 Tracks—These tracks typically have long distal digit impressions, occasionally with a rounded shape immediately caudal to the proximal track margin (e.g., Figs. 14, iii/iv and 16). These have a longitudinal depth profile characterized by a steep proximal margin and a sloping distal margin that we categorize as category 3a tracks. Some others also have long digits impressions with a very similar depth profile but also have a short horizontal base close to the proximal track margin (e.g., Fig. 10) that we refer as category 3b tracks.

Category 3a tracks may have formed by deeply penetrating scratches formed from by a buoyed trackmaker (Fig. 20D) similar to the paddling we propose for category 1 tracks, where the digit elongated the track craniocaudally. However, the vertical proximal track margin indicates that the caudad-directed pes movement was halted, perhaps due to resistance of compacting the sediment behind the digits. The rounded shape immediately caudal to some tracks (Figs. 14iii, iv and 16) may have formed as a result of this sediment compaction, although it has previously been described as an "imprint of [the] metapodium" (Thulborn and Wade, 1984:pl. 13b caption). The (apparent) 'heel' and digit impressions strongly contrast in depth profiling (e.g., Fig. 16) and their previously association with some *Charachichos* swim traces (Whyte and Romano, 2001) leads us to consider that these do not represent metatarsal impressions but rather are swim traces, with the rounded shapes formed by sediment compaction associated with a caudally moving unguligrade/subunguligrade pes.

Alternatively, category 3b tracks may have been formed from digits elongating the track caudocranially (similar to category 2 tracks). We consider that the trackmaker's pes entered the substrate steeply and deeply in a subunguligrade or unguligrade stance, and then exited the substrate by dragging the digits cranially and dorsally for such tracks as the holotype of '*Skartopus*' (Fig. 20C). Whether tracks of this type were formed subaerially or subaqueously is unclear, because both modes of formation seem plausible for subunguligrade trackmakers.

Thulborn and Wade (1984:428) propose a different kinematic model for the "sharp-toed tridactyl footprints such as the [*Skartopus australis*] holotype," and suggested that the '*Skartopus*' trackmaker failed to register a foot impression until in mid-stance, and then exited the track with digits scratching along the length of the digit impressions (Fig. 20A). When this pedal kinematic model is applied to our measured holotype '*Skartopus*' track profile (Fig. 20B), the movement appears cumbersome and unnatural: the trackmaker's metatarsophalangeal joint is required to hyperextend to approximately 90° in order for digit III to fit into the track (possibly disarticulating the joint unless the trackmaker had extreme joint mobility similar to that of *Rahonavis*; Senter, 2009); the trackmaker is required to exit the track without placing body weight on the distal portion of the digits (or a different longitudinal depth profile would have been formed distally); and after the trackmaker has exited the track, it has to reenter the distal portion of the track to scratch along the midline of the digit impressions (perhaps particularly remarkable for a trackmaker maintaining forward momentum). We consider Thulborn and Wade's (1984) holotype '*Skartopus*' foot movement model problematic, and instead favor our caudocranial pes movement model in the formation of these tracks.

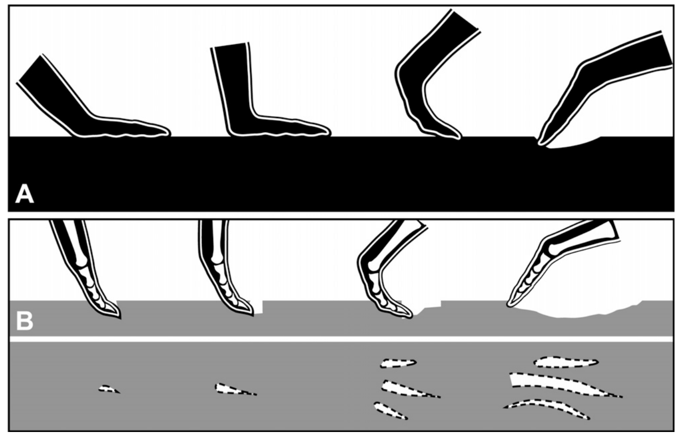

FIGURE 18. Models of pedal kinematics in the formation of category 1 tracks. **A**, original kinematic model proposed for the formation of these tracks (adapted from Thulborn and Wade, 1984:fig. 12); **B**, this study's kinematic model for the formation of these tracks using track LQ-2(L6) as a guide. The schematic of the pes (through metatarsal III and digit III) is based on the reconstructed pes skeleton of *Dryosaurus altus* (CM 21786, YPM 1876, YPM 1884). Continuous line represents internal track; dotted line represents external track outline; dashed line represents scratch marks. Distal track to the right.

The 'naturally' sectioned *Wintonopus* print (Fig. 3) that we consider is a modified category 3 track and interestingly bears a longitudinal profile resembling the theropod track contours shown by Gatesy et al. (1999) and Avanzini et al. (2012) (i.e., with the cranial edge of the profile overhanging the deepest part of the print). These researchers indicated that track formation occurred with a caudocranial movement of the pes movement and accounted for the 'overhanging' portion of the track profile formed when the toes were partially lifted caudally prior to being dragged cranially through the substrate upon exit. We consider it likely that this movement was responsible for the formation of the 'naturally' sectioned *Wintonopus* track. The tracks studied by Gatesy et al. (1999) and Avanzini et al. (2012) indicated that the trackmakers converged the digits upon exiting the tracks. Category 3b tracks show no digit convergence when viewed dorsally (Fig. 10), possibly indicating different pedal kinematics between theropods and ornithopods.

Category 4 Tracks—The steep proximal and distal track margins indicate that the trackmaker's pes entered and exited the track at a steep angle, and the relatively long flat track base suggests that much of the track length represents the anatomical impression of the pes (e.g., *Wintonopus* holotype; Figs. 9 and 21). Tracks such as LQ-2(L1) may be considered variants of this category because they have a large, flat track base, but are

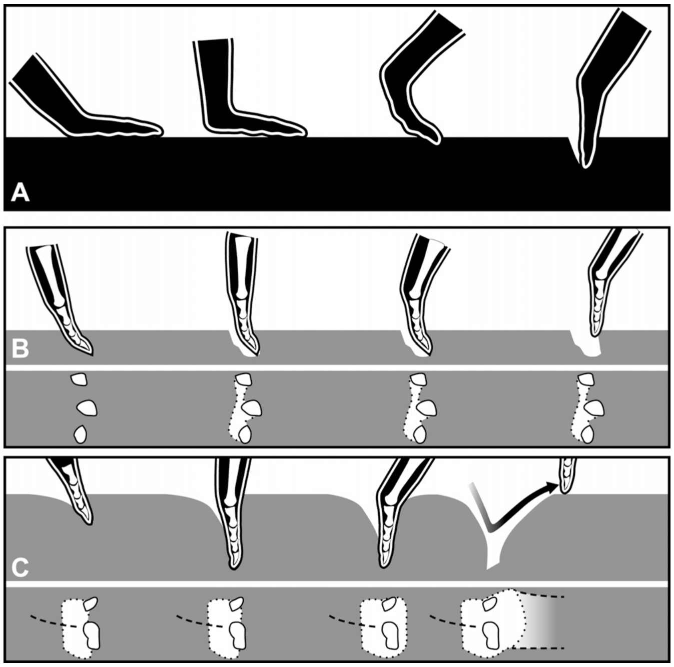

FIGURE 19. Models of pedal kinematics in the formation of category 2 tracks. **A**, original kinematic model proposed for the formation of these tracks (adapted from Thulborn and Wade, 1989:fig. 6.6); **B**, this study's kinematic model for the formation of the track using the track from Figure 14ii as a guide; **C**, this study's kinematic model for the formation of the track using the track from Figure 15 as a guide. The schematic of the pes (through metatarsal III and digit III) is based on the reconstructed pes skeleton of *Dryosaurus altus* (CM 21786, YPM 1876, YPM 1884). Continuous line represents internal track; dotted line represents external track outline; dashed line represents scratch marks; continuous gray line represents proximal round shape. Distal track to the right.

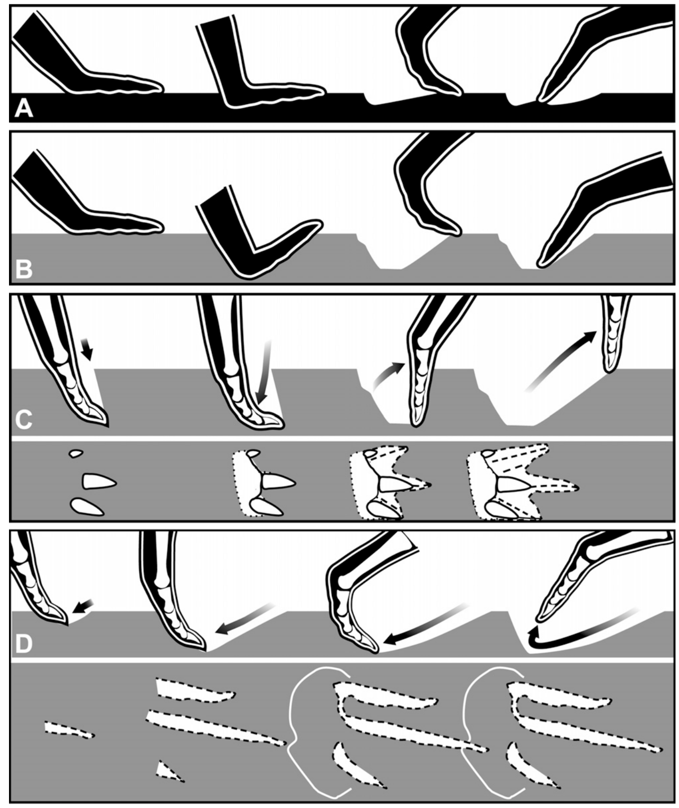

FIGURE 20. Models of pedal kinematics in the formation of category 3 tracks. **A**, original proposed kinematics of '*Skartopus australis*' holotype trackmaker (adapted from Thulborn and Wade, 1984:fig. 12); **B**, original proposed kinematics of '*Skartopus australis*' holotype trackmaker applied to the track's measured depth profile; **C**, this study's kinematic model for the formation of the track using the '*S. australis*' holotype as a guide; **D**, this study's kinematic model for the formation of the track using the track from Figure 14iii as a guide. The schematic of the pes (through metatarsal III and digit III) is based on the reconstructed pes skeleton of *Dryosaurus altus* (CM 21786, YPM 1876, YPM 1884). Continuous line represents internal track; dotted line represents external track outline; dashed line represents scratch marks; continuous gray line represents proximal round shape. Distal track to the right.

distally elongated due to the additional presence of drag marks (Fig. 10).

The original interpretation by Thulborn and Wade (1984:425) was that the *Wintonopus* trackmakers were "thoroughly digitigrade," and contrasts with other descriptions of *Wintonopus*-like tracks as subdigitigrade traces (e.g., Gierlinski and Pienkowski, 1999). We consider the lack of a metatarsophalangeal pad impression to be a clear indication that these traces were at the very least made by a trackmaker with a subdigitigrade stance (sensu Leonardi, 1987). The proportionately short digit impressions further indicate that this track is likely to have been made by a trackmaker whose typical, weight-supporting pedal stance was subunguligrade (sensu Moreno et al., 2007). If correct, these tracks could have been made during terrestrial locomotion, or during wading in water that was relatively shallow (i.e., not deep enough to have buoyed the trackmaker's body). If, however, the trackmaker had a typically digitigrade pedal stance during terrestrial locomotion, then this track is an atypical representation, and may instead have been formed when the animal's body was partially buoyed by water. Some *Wintonopus* have very long drag marks (Thulborn and Wade, 1984:pls. 8a, 10d), which may suggest a partially buoyed trackmaker because to have dragged the pes to such a degree during terrestrial running seems hard to envisage, but not so if the trackmaker was buoyed in water and only just capable of touching the bottom.

We consider the similarity of the Lark Quarry tracks with recognized dinosaur swim traces elsewhere, and the presence of unguligrade prints, as evidence that many trackmakers passed the area when buoyed by water. This interpretation of the tracksite preserving swim traces contrasts with the original explanation that it represents traces of numerous terrestrially running dinosaurs, and as such we do not support the idea of the occurrence of a dinosaur 'stampede.'

Possible Trackmaker Affinities

Distinguishing the tracks of non-avian theropod and bipedal ornithischian dinosaurs can be problematic, because the feet of both groups are functionally tridactyl with mesaxonic symmetry (Moratalla et al., 1988; Thulborn, 1994; Fastovsky and Smith, 2004; Mateus and Milàn, 2008; Lockley, 2009; Romilio and Salisbury, 2011a). However, a suite of general criteria can be used to help distinguish 'typical' tracks of theropod and bipedal ornithischian dinosaurs (Lockley, 1991; Wright, 2004). Theropod tracks tend to been relatively long, narrow impressions, with digits II and IV extending to roughly the same point distally, but with digit IV extending farther proximally than digit II, thereby making the footprints appear asymmetrical. Claw impressions may be sharp or blunt, with claw phalanx impressions (where present) directed medially for digits II and III and laterally for digit IV (Wright, 2004). Theropod tracks also tend to be slightly out-turned relative to the trackway axis; however, this is not always the case, even within individual trackways (Day et al., 2002). Ornithopod tracks, on the other hand, typically tend to be wider than they are long. Tracks that are thought to have been made by more plesiomorphic ornithopods are typically asymmetrical (e.g., *Anomoepus*; Olsen and Rainforth, 2003), whereas those thought that have been made by more derived taxa are symmetrical (e.g., *Iguanodontipus*; Lockley and Wright, 2001), with tracks turned inward relative to the trackway axis for ornithopods. *Wintonopus* tend to be an asymmetrical track, wider than longer, with blunt to pointed claw impressions, have an asymmetrical proximal track margin, and are turned inwards relative to the trackway axis. *Wintonopus* in this case combines features 'typical' of both theropod and ornithopod tracks, with a slight favoring towards ornithopod traits.

Multivariate analysis provides a quantitative means of discriminating between tridactyl ornithischian pes tracks and theropod pes tracks (Moratalla et al., 1988; Lockley, 1998; Mateus and Milàn, 2008). The analysis has been used previously at the Lark Quarry tracksite (Romilio and Salisbury, 2011a) to support the view that the large trackmaker was an ornithopod. However, this type of multivariate analysis is dependent on the trackmaker leaving digitigrade foot impressions (J. Moratalla, pers. comm., 2011) and may not be relevant for use with subdigitigrade-unguligrade tracks, such as *Wintonopus*.

Tracks made by small-bodied ornithopods with a subdigitigrade pedal stance have been described previously (e.g., Gierlinski and Pienkowski, 1999; Li et al., 2006). Similarly, tracks from Poland (cf. *Carmelopodus*; Gierlinski and Pienkowski, 1999) and Italy (Conti et al., 2005:fig. 18) have been assigned to what are assumed to be theropods with a subdigitigrade pedal stance. However, the assignment of both sets of tracks to either ornithopod or theropod trackmakers is not without its problems. Although it is likely that the cf. *Carmelopodus* trackmaker elevated the proximal portions of all its pedal digits off the ground preventing their impression, we disagree with their apparent similarity to the ichnogenus *Carmelopodus* (sensu Lockley et al., 1998) that has only the proximal part of digit IV elevated off the ground, with digits II and III fully digitigrade. In this respect, we regard the tracks assigned to cf. *Carmelopodus* as bearing a much stronger resemblance to cf. *Wintonopus* from the same track horizon (Gierlinski and Pienkowski, 1999:pl. IV, fig. 2). On the other hand, we agree with Conti et al. (2005) that the 'heel'-less Mattinata tracks from Italy (Conti et al., 2005:fig. 18), with their elongate digit impressions, do appear to have been made by a theropod. Quadrupedal cf. *Wintonopus* footprints have been reported (Thulborn, 1999), which provides support that the trackmaker may have been an ornithopod, but because this publication lacks images or descriptions, it is unclear if these were made by resting or moving animals.

The trackmaker pedal movement revealed by tracks has enabled some researchers to conclude that, like birds, non-avian theropods converged the digits upon exiting the track (Gatesy et al., 1999; Avanzini et al., 2012). *Wintonopus* category 3b tracks we interpret as formed from the caudocranial pedal kinematics similar to those made by theropod tracks (e.g., Gatesy et al., 1999; Avanzini et al., 2012) but contrast in the lack of digital adduction, as indicated by track exit drag marks (Fig. 10). This suggests that this trackmaker had pedal kinematics that differed from those of theropods, and in light of these observations, we conclude that *Wintonopus latomorum* probably represents the traces of an ornithopod trackmaker.

SYSTEMATIC PALAEONTOLOGY

WINTONOPUS Thulborn and Wade, 1984

'Coelurosaur' tracks, Thulborn and Wade, 1979:fig. 2.
Skartopus australis, Thulborn and Wade, 1984:427, fig. 12, pls. 1c, 1d, 7b, 10b, 12, 13a, 13b, 14b, 15a, 16a, 16c (original description).
Skartopus Thulborn and Wade, 1984; Haubold, 1984:195.
Small theropod tracks, Paul, 1988:36.
Skartopus australis Thulborn and Wade, 1984; Kuban, 1989:fig. 7:17h.
Skartopus australis Thulborn and Wade, 1984; Thulborn and Wade, 1989:figs. 6.6, 6.8.
Skartopus australis Thulborn and Wade, 1984; Wade, 1989:fig. 8.5.
Skartopus australis Thulborn and Wade, 1984; Long, 1990:66.
Skartopus australis Thulborn and Wade, 1984; Thulborn, 1990:figs. 5.7f, 5.16b, 6.10a, 6.10c, pls. 6, 8, 9, 10.
Small theropod tracks, Lockley, 1991:79.
Skartopus australis Thulborn and Wade, 1984; Molnar, 1991:fig. 37r, s.
Skartopus australis Thulborn and Wade, 1984; Dettman et al., 1992:230.
Skartopus australis Thulborn and Wade, 1984; Long, 1998:128.
Skartopus Thulborn and Wade, 1984; Lockley and Matsukawa, 1999:29.
Skartopus Thulborn and Wade, 1984; Lockley et al., 2003:175.
Skartopus Thulborn and Wade, 1984; Milàn, 2003:27.
Skartopus Thulborn and Wade, 1984; Rich and Vickers-Rich, 2003:72.
Skartopus australis Thulborn and Wade, 1984; Conti et al., 2005:545.
Skartopus australis Thulborn and Wade, 1984; Scanlon, 2006:fig. 5e.
Skartopus Thulborn and Wade, 1984; Gierlinski and Nowacki, 2008:fig. 1c.
Skartopus australis Thulborn and Wade, 1984; Marty, 2008:179.
Skartopus Thulborn and Wade, 1984; Belvedere, 2009:72.
Skartopus australis Thulborn and Wade, 1984; Gierlinski et al., 2009:fig. 4b.
Skartopus australis Thulborn and Wade, 1984; Hocknull et al., 2009:table 1.
Skartopus Thulborn and Wade, 1984; Kim and Huh, 2010:table 1.
Skartopus australis Thulborn and Wade, 1984; Romilio and Salisbury, 2011a:135.
Skartopus australis Thulborn and Wade, 1984; Romilio and Salisbury, 2011b:72.
Skartopus australis Thulborn and Wade, 1984; Romilio and Salisbury, 2011c:32.

Revised Ichnogeneric Diagnosis—Small- to medium-sized (<0.3 m long), tridactyl, mesaxonic pes impressions that are wider than long. Digit impressions are cranially directed and are short in length, with digit III being the longest, and digit IV being equivalent to or longer than digit II. The proximal track margin is more concave proximomedially than proximolaterally, with the proximal margin of the digit IV impression more proximally positioned relative to the impression of digit II. Both digit II and IV impressions extend farther proximally than the digit III impression. A metatarsophalangeal pad impression is absent, and claw impressions, when present, are pointed to rounded.

Valid Ichnospecies—*Wintonopus latomorum* Thulborn and Wade, 1984; holotype, QM F10319 (Thulborn and Wade, 1984:pl. 7, fig. A).

Distribution—Early to 'middle' Cretaceous: late Albian–Cenomanian Winton Formation, Queensland, Australia (Thulborn and Wade, 1984); Berriasian–Barremian Broome Sandstone, Western Australia (Long, 1998).

Comparisons—Footprints identified as cf. *Wintonopus* are known from several sites of varying ages around the world: the Early Jurassic (late Hettangian), Przysucha Formation of the Holy Cross Mountains, Poland (Gierlinski and Pienkowski, 1999); the 'Middle' Jurassic Balgowan Colliery, Darling Downs, Australia (Thulborn, 1999; Turner et al., 2009); and the Early

Cretaceous Hekou Group, Gansu Province, China (Li et al., 2006). Cf. *Carmelopodus* sp. from the Przysucha Formation of the Holy Cross Mountains, Poland (Gierlinski and Pienkowski, 1999), should be referred to as cf. *Wintonopus*. A single *Skartopus* from the Early Jurassic, Razorback Beds (equivalent with the Evergreen Formation of the Precipice Sandstone) of Mount Morgan, central Queensland, Australia (Cook et al., 2010), should be referred to as an indeterminate theropod print. The *Skartopus* sp. specimen (QM F52282) from the Winton Formation, central-western Queensland, Australia, should also be referred to as indeterminate theropod track.

WINTONOPUS LATOMORUM Thulborn and Wade, 1984

Holotype—QM F10319, a right pes track (natural mould).

Referred Specimens—QM F10320, left track on the same slab as the holotype but made by a smaller individual (also a natural mould); QM F10322, fiberglass replicas of various tracks and trackways; QM F10330 ('*Skartopus*' holotype, left pes track, natural mould). QM F10321, multiple specimens (~53 slabs >0.3 m length, 100+ rock slabs <0.3 m length, all natural moulds).

Ichnospecies Diagnosis—As for ichnogeneric diagnosis.

Horizon and Type Locality—Winton Formation, late Albian–Cenomanian, 'mid'-Cretaceous; Lark Quarry, Lark Quarry Conservation Park, Queensland, Australia.

Synonyms—'*Skartopus australis*' Thulborn and Wade, 1984 (diagnosis by Thulborn and Wade, 1984). The '*S. australis*' holotype was originally described as having narrow, elongate digit impressions; however, these were based on the 2D surface track outline. The 3D analysis of the track reveals that the digit impressions are elongate as a result of the digits passing through the substrate. New discoveries of '*Skartopus*' sp. (Cook et al., 2010; QM F52282) resemble the '*Skartopus*' holotype (QM F10330) in track outline but differ by being relatively shallow prints. This suggests that the elongate, narrow digit impressions are likely formed from anatomical impressions of the trackmaker's digits rather than by toes scratching and/or dragging through the substrate. In our opinion, these traces are indeterminate tridactyl dinosaur tracks.

SWIMMING LARK QUARRY DINOSAURS

Thulborn and Wade (1984, 1989) considered the long stride lengths and parallel orientation of *Wintonopus* and '*Skartopus*' trackways at Lark Quarry as evidence that the tracksite recorded a terrestrial stampede. However, long stride lengths can also occur when trackways are oriented with downstream flow direction (Whyte and Romano, 2001; Lockley and Foster, 2006). Our reinterpretation of many of the Lark Quarry tracks as swim traces suggests that rather than a 'stampede,' the site instead preserves evidence of trackmakers using current flow to assist their movements. The large numbers of singularly oriented tracks may indicate that the site was a favored dinosaur route (contra Thulborn and Wade, 1984). The tracksite's vegetation drag marks (sensu Thulborn and Wade, 1984:419) are sublinear traces, suggesting that the northeast current flow may have been quite strong (at times). The 'gaps' or incomplete nature of many of the trackways, previously thought to be related to the fact that the trackmakers were "so light that their broad-spreading and rather springy feet simply failed to break through the surface of the sediment" (Thulborn and Wade, 1984:443), are far more likely to be a consequence of buoyed trackmakers only occasionally contacting the substrate with their feet as they drifted or swam downstream. According to Wade (1989:77), the fact that the '*Skartopus*' trackmaker "had no need to place its feet below the center of gravity" explained the "considerable individual variation in lateral foot[-print] position," which we suggest may also be explained by these trackmakers having been buoyed.

It appears that not all *Wintonopus* trackways were made by running animals or by animals moving in the same direction. Trackway LQ-3 appears to have been made by a dinosaur that was moving slowly (equivalent to a terrestrial walking gait), with short stride lengths and an overall trackway orientation that was initially perpendicular to the inferred current direction but then turned downstream. It is unclear why this trackmaker was moving slowly, because the tracks indicate that the animal was buoyed. Other *Wintonopus* trackways (LQ-6, LQ-8, LQ-9, LQ-10, LQ11) indicate the equivalent to a terrestrial slow run, which implies that not all the *Wintonopus* trackmakers were "flat-out running" (Wade, 1989:77). Trackway LQ-11 is oriented to the south rather than to the northeast, which we suggest was the downstream course. This particular trackmaker was considerably larger than most of the other trackmakers at the site, and as such appears to have been able to have walked or waded in water that was too shallow to have buoyed its body.

Our approach of scaling a hypothetical *Dryosaurus*-like track gives us hip-height estimates of 14–160 cm for the *Wintonopus* trackmakers, which is comparable to the values obtained by Thulborn and Wade (1984) of 13.3–158.4 cm. The highest value relates to the same trackmaker (LQ-10), with only a different of 1.6 cm in our calculation and that of Thulborn and Wade (1984). Because many of the tracks and trackways indicate swimming traces, our height estimates provide a useful guide for estimating paleowater depth.

Considering that a digitigrade posture is typical for bipedal dinosaur (Lockley and Gillette, 1989), one possibility is that the subdigitigrade tracks (requiring a subunguligrade posture; sensu Moreno et al., 2007) were formed by trackmakers that were buoyed by water. Because "hip height gives an estimate of the water depth" (Whyte and Romano, 2001:229), the largest Lark Quarry trackmaker that impressed subdigitigrade tracks (LQ-10) indicates a water depth of 160 cm at the time of its passage, whereas the smallest trackmaker size (based on the track shown in Fig. 15) indicates a depth of only 14 cm. If correct, this scenario indicates that the site experienced wide fluctuations in water levels (i.e., at least 146 cm) over the time that the tracks were formed, with the different-sized animals progressed through the area at different time intervals as water depth permitted.

An alternate possibility is that the trackmakers were capable of supporting their weight on subunguligrade feet. Even in the presence of a subaqueous substrate, relatively tall trackmakers would not need to be buoyed by water to form subdigitigrade tracks. Although it is unclear to us if all the subdigitigrade tracks were made when the trackmaker fully supported its body weight on its feet, the unguligrade tracks and swim traces certainly would have required their makers to be buoyed. We estimate that these trackmakers range in hip heights from 14 to 42 cm (Figs. 15 and 14Civ, respectively). Swim traces can be found in close proximity to each other (e.g., Figs. 14 and 22) from animals with a range of

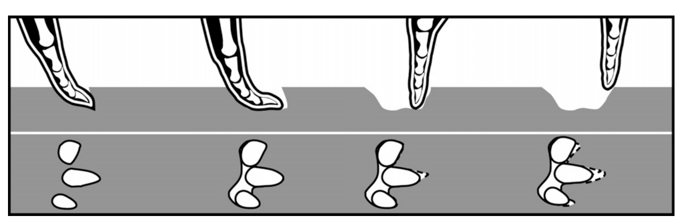

FIGURE 21. Models of pedal kinematics in the formation of category 4 tracks. This study's kinematic model for the formation of the track using the *Wintonopus latomorum* holotype as a guide. The schematic of the pes (through metatarsal III and digit III) is based on the reconstructed pes skeleton of *Dryosaurus altus* (CM 21786, YPM 1876, YPM 1884). Continuous line represents internal track; dotted line represents external track outline. Distal track to the right.

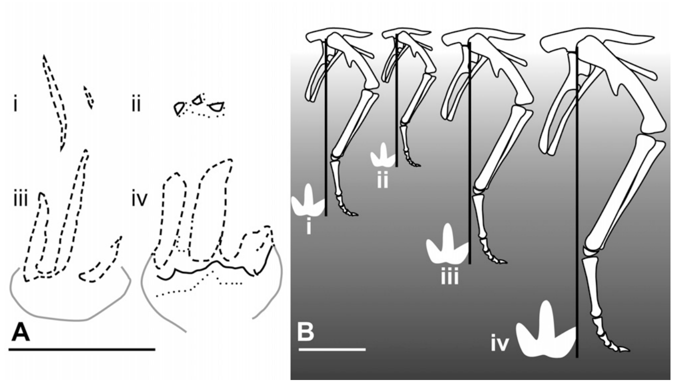

FIGURE 22. Determining hip height and water depth. **A**, four swim traces as shown in Figure 13; **B**, estimating trackmaker hip heights based on scaling the width of a hypothetical *Dryosaurus* track and associated hind limb skeleton to the width of the studied tracks (see text for details). Each of these swim tracks could only have formed when the water level was at a specific depth, because the smaller-sized buoyed trackmakers are unable to contact the substrate at the water level when the largest tracks formed. The implication is that these tracks could only have formed at different time intervals as water levels at the tracksite fluctuated from at least 18–42 cm. Continuous line represents internal track; dotted line represents external track outline; dashed line represents scratch marks; continuous gray line represents proximal round shape. Distal track to the top. Scale bar equals 10 cm.

hip heights (e.g., 18, 24, 30, and 42 cm). We consider it unlikely that the smaller trackmaker (18 cm hip height) would have been able to touch the substrate when the water depth enabled the larger trackmaker (e.g., 42 cm hip height) to be buoyed. It is likely that these trackmakers passed at the area at different times when water level differed.

The inference of both scenarios is that the large number of *Wintonopus* tracks could not have been formed at the same time. The variability in the size of the swim traces, and, by inference, that of their makers means that not all the animals could have been swimming and touching the substrate at the same water depth. In the context of this interpretation, Lark Quarry most likely represents an accumulation of tracks over a period of time (perhaps days), during which water level fluctuated, with the majority of the smaller animals swimming or wading, and the larger animals walking or wading, and many animals using the current to assist their movements.

In presenting this interpretation of Lark Quarry, we are aware of the fact that we may be considered iconoclasts by some members of the paleoichnological community and public alike, many of whom have become enamored with the idea that the site preserves a dinosaurian stampede. However, it should be realized that both the original scenario and the one we propose are interpretations that should be assessed on their merit based on the evidence available. If we are correct in our interpretations, Lark Quarry can now be regarded as a site that preserves one of the highest concentrations of dinosaur swim traces in the world, providing valuable information in the understanding of the kinematics of swimming dinosaurs. The ongoing scientific evaluation of Lark Quarry has a historical significance in that it additionally demonstrates how changes in the analysis and documentation of paleoichnological data can lead to markedly different site interpretations.

CONCLUSIONS

Our investigation of the Lark Quarry tracksite shows that a wide range of track morphologies can be assigned to the *Wintonopus latomorum* ichnospecies, including '*Skartopus australis*,' which we regard as a junior synonym of the former. This finding eliminates any evidence of mixed herding between ornithopod and theropod dinosaurs at the site. The presence of swim traces, long stride lengths, and preferred trackway orientation indicates that the majority of Lark Quarry trackmakers moved downstream and were current assisted. The paleo-water depth would have had to vary in order to allow different-sized buoyed trackmakers to contact the substrate, indicating that animals passed through the area at different time intervals. In the absence of evidence for the single mass of running terrestrial trackmakers, we consider that Lark Quarry is not representative of a 'dinosaurian stampede.'

The sedimentologic and ichnological observations are consistent with interpretations of the area being a fluvial-dominated floodplain under variable subaqueous conditions. Given the extent of this geological setting, the apparent hydrophilic nature of the Lark Quarry ornithopod trackmakers, and the recent renewed interest in researching the paleobiology of the region, we anticipate similar tracks and trackways to the ones described herein from Lark Quarry will be found elsewhere in the Winton Formation.

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APPENDIX 1. Track dimensions within 10 Lark Quarry (LQ) trackways. **L**, left; **R**, right. Numbers refer to sequences of individual tracks within trackways. Bold numbers indicate averages.

Trackway	Track length (cm)	Track width (cm)	Pace (cm)	Stride (cm)	Pace angle (°)	Average height (cm)	Relative stride (stride/hip height)
LQ-2							
L1	5	3.5					
R1	4	4.5	33		149		
L2	4.5	4	34	64	146		
R2	4.5	4	39	69	149		
L3	5	4.5	31	67	143		
R3	4.5	4.5	35	63	139		
L4	6.5	3.5	26	68	140		
R4	3	3.5	31	55	140		
L5	6.5	6	32	59	140		
R5	6	4	31	60	136		
L6	8.5	4	31	60	128		
R6	4.5	2	31	59	139		
L7	4	4	31	58	140		
R7	2.5	5	35	62			
L8							
R8	5	4.5		62			
L9	4	4	30		144		
R9	4	3.5	34	62	144		
L10	5	4	34	65			
	4.8	**4.1**	**32**	**62**	**141**	**19.0**	**3.3**
LQ-3							
R1	13	11					
L1	12	11	97				
R2	10.5	11	100		165		
L2		11	86	199	171		
R3	10	10	108	187	165		
L3	10	12	100	194	160		
	11	**11**	**98**	**193**	**165**	**62.5**	**3.1**
LQ-4							
L1	13	5.5					
R1	6	5.5	13		116		
L2	7.5	5	11	20	154		
R2	7	5	12	22	87		
L3	12.5	3.5	8	14			
	9.2	**4.9**	**11**	**19**	**119**	**25.0**	**0.7**
LQ-5							
L1	6.5	4					
R1	7	4.5	31		148		
L2	5.5	2.5	22	60.5	131		
R2	6	3	28	55			
	6.25	**3.5**	**27**	**58**	**140**	**18.0**	**3.2**
LQ-6							
R1	4.5	6					
L1	6	6	34		154		
R2	5.5	6	37	70	154		
L2	5.5	8	34	69			
	5.4	**6.5**	**35**	**70**	**154**	**25.0**	**2.8**
LQ-7							
R1	3.6	4.5					
L1	6	4.5	43		158		
R2	5.5	4.5	40	82	156		
L2	5	4	44	82	165		
R3	6	4.5	48	90	165		
L3	5	4	33	79	157		
R4	5	3	35	64	151		
L4	6	3.5	40	71			
	5.3	**4.1**	**40**	**78**	**159**	**19.0**	**4.1**
LQ-8							
R1	4.5	4.5					
L1	8	4.5	33		161		
R2	6	4.5	29	61	159		
L2	5	5.5	25	52	141		
R3	6.5	6	30	51	164		
L3					186		
R4	5	4.5			164		
L4	4	4.5	33				
	5.6	**4.9**	**30**	**55**	**162.5**	**20.0**	**2.7**
LQ-9							
R1	3	4.5					
L1	5	2.5	33		143		

(Continued on next page)

APPENDIX 1. Track dimensions within 10 Lark Quarry (LQ) trackways. **L**, left; **R**, right. Numbers refer to sequences of individual tracks within trackways. *(Continued)*

Trackway	Track length (cm)	Track width (cm)	Pace (cm)	Stride (cm)	Pace angle (°)	Average height (cm)	Relative stride (stride/hip height)
R2	3.5	3.5	30	60	146		
L2	4.5	3.5	26	54	149		
R3	4	3.5	30	55			
	4	**3.5**	**30**	**56**	**146**	**20.0**	**2.8**
LQ10							
R1	29	45.5					
L1	21	30	155		175		
R2	34	34	169	325	167		
L2			173	339	160		
R3	21	20	177	345			
	26.25	**32.375**	**168.5**	**336**	**167**	**160.0**	**2.1**
LQ-11							
L1	20.5	21.5					
R1	23	32	143		173		
L2	23	24	167	308			
	22.2	**25.8**	**155**	**308**	**173**	**110.0**	**2.8**