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LARGE TRIDACTYL DINOSAUR TRACKS FROM THE EARLY JURASSIC OF SOUTHERN GONDWANA – UPPERMOST ELLIOT FORMATION, UPPER MOYENI, LESOTHO

Miengah ABRAHAMS[1], **Lara SCISCIO**[1,2], **Mhairi REID**[1,3], **T'Nielle HAUPT**[1] **& Emese M. BORDY**[1*]

[1] Department of Geological Sciences, University of Cape Town, Rondebosch 7701, South Africa;
e-mails: miengah.abrahams@uct.ac.za; reid.mhairi@gmail.com;
l.sciscio@gmail.com; tnielleh@gmail.com; emese.bordy@uct.ac.za
[2] Current address: Department of Geology, University of Johannesburg,
Kingsway and Auckland Park, 2006 Johannesburg, South Africa
[3] Current address: Department of Geology, University of Oxford, Oxford, England
**Corresponding author*

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Abstract: A new ichnosite in southwest Lesotho (Upper Moyeni, Quthing District) is located within the uppermost part of the highly fossiliferous Elliot Formation, ~35 m below the conformably overlying Clarens Formation and ~65 m above the world-renowned Lower Moyeni ichnosite. While the Lower Moyeni site preserves diverse Early Jurassic ichnofossils, the ichnites at Upper Moyeni comprise one vertebrate burrow and ~50 tridactyl tracks with footprint lengths between 15 and 51 cm. Many of the tracks preserve digital pad impressions, claw marks and displacement rims, all related to substrate conditions. The morphometric parameters of the Upper Moyeni tracks are consistent with *Grallator*, *Eubrontes* and *Kayentapus*. Several larger tracks with footprint lengths > 40 cm are *Kayentapus*-like and *Eubrontes*-like, and are comparable to previously described very large theropods tracks with lengths > 50 cm from the uppermost Elliot and Clarens formations. On the basis of sedimentological and ichnological evidence, the Upper Moyeni ichnofossils were formed in a palaeolandscape with small rivers and shallow lakes by burrowing tetrapods and a variety of bipedal dinosaurs (theropods), some of which were up to 7–8 m in body length. The Upper Moyeni tracks, together with the other very large tracks from coeval locations in southern Africa, collectively highlight the tendency towards increasing diversity in size of tridactyl tracks and by extension theropod trackmaker body size body size, which runs in tandem with the increasing diversity of non-sauropod, sauropodomorph body fossils in the Sinemurian–Pliensbachian of southern Gondwana.

Key words: Vertebrate ichnology, tridactyl, large theropods, southern Gondwana, Karoo, upper Elliot Formation.

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INTRODUCTION

Dinosaurs, as part of the clade of *Dinosauromorpha*, emerged relatively soon after the Permo–Triassic mass extinction event (e.g., Sereno and Arcucci, 1993, 1994; Langer *et al.,* 2010, 2017; Brusatte *et al*., 2011; Benson *et al*., 2014). However, the exact timing of the origin of dinosaurs is contested and is hindered by scarce body fossil material and obscure, unreliable ichnofossils (e.g., Demathieu, 1990; Rogers *et al*., 1993; Sereno, 1999; Carrano and Wilson, 2001; Thulborn, 2006; Marsicano *et al*., 2007; Brusatte *et al*., 2011). During the Triassic, dinosaurs were geographically widespread but had a low degree of diversity and a limited abundance, though they experienced a significant increase in disparity and diversity during the Carnian–Norian, possibly in response to climatic, floral and ecosystem changes (e.g., Brusatte *et al*., 2008; Bernardi *et al.,* 2018). The Early Jurassic marked a pivotal period for dinosaurs, evidenced by a significant increase in both abundance and diversity (e.g., Irmis *et al*., 2007; Brusatte *et al*., 2008; Olsen *et al*., 2010; Baron, 2019). This occupation of a larger morphospace has been linked by some authors to the end-Triassic Mass Extinction events (ETE) and the resultant removal of crurotarsans, the primary dinosaur competitor, indicating that the success of dinosaurs is attributed to "opportunity" rather than "superiority" (Benton, 1983; Olsen *et al*., 2002).

The upper Norian–Sinemurian Elliot Formation in the upper Stormberg Group (main Karoo Basin) is a continental red bed succession that encompasses the Triassic–Jurassic boundary (TJB), although the precise placement of this boundary within the formation is still unresolved (Olsen and Galton, 1984; Lucas and Hancox, 2001; Sciscio *et al*., 2017a; Bordy *et al*., 2020). This fluvio-lacustrine formation (e.g., Bordy *et al*., 2004a, b, c) is highly fossiliferous, both in body and trace fossils, with the latter skewed towards theropods (e.g., Ellenberger *et al*., 1964; Ellenberger, 1970, 1972, 1974; Kitching and Raath, 1984; Munyikwa and Raath, 1999; Ambrose, 2003; Yates, 2003; Knoll, 2004, 2005; Butler, 2005; Yates, 2005; Sciscio *et al*., 2016; Abrahams *et al.,* 2017, in press; Bordy *et al*., 2017; McPhee *et al*., 2017; Sciscio *et al*., 2017b, c; Chapelle and Choiniere, 2018; Rampersadh *et al*., 2018). As is the case with its global Upper Triassic–Lower Jurassic counterparts, theropod osteological material is scarce in the upper Stormberg Group and is limited to isolated teeth and fragmentary or partial cranial material (e.g., Kitching and Raath, 1984; Smith and Kitching, 1997; Ray and Chinsamy, 2002; Yates, 2005). Consequently, the wealthy ichnological record especially in the Lower Jurassic upper Elliot Formation offers a crucial opportunity to examine theropods during a period of post-extinction recovery. It has been suggested, primarily based on the track record of the Newark Supergroup (USA), that in response to the ETE and across the TJB, theropod body size increased significantly and abruptly (Olsen *et al*., 2002). This proposal, at least on a global scale, is contested, with numerous authors highlighting that osteological and ichnological evidence indicates that large theropods were present already in the Late Triassic, though less prevalent than in the Early Jurassic populations (e.g., Lucas *et al*., 2006; Lucas and Tanner, 2007; Irmis, 2011; Griffin and Nesbitt, 2019). Instead, these authors posit that theropod body size increased steadily from the Late Triassic to Early Jurassic. In southern Africa, tentative increases in theropod body size have been noted within the Elliot Formation (Ellenberger, 1972) and the largest known Early Jurassic theropod body size, deduced from a single trackway, has recently been presented (Sciscio *et al*., 2017b).

Herein, we describe the newly discovered Upper Moyeni ichnosite from the upper Elliot Formation (southwest Lesotho; Fig. 1), stratigraphically ~65 m above the renowned Lower Moyeni ichnosite first reported on by Ellenberger *et al.* in 1963. Forty-nine tridactyl tracks, preserved as trackways and in isolation, are documented across the ~130 m palaeosurface, which serves as a busy informal suburban road. This study documents the sedimentological context of the ichnites and their morphology and assigns most of the tracks to known ichnotaxa. The detailed ichnological assessment presented in this paper contributes to the understanding of theropod diversity and body size distributions in the Early Jurassic of southern Gondwana. These findings can be collated with global theropod trends during the ETE recovery period.

GEOLOGICAL SETTING

The area around the Upper Moyeni ichnosite (Fig. 1) is dominated by Lower Jurassic rocks: the sedimentary succession of the upper Stormberg Group and the conformably overlying lower Drakensberg Group, which comprises mostly igneous rocks that formed ~183±1 Ma ago (Duncan *et al*., 1997; Moulin *et al*., 2017). Within the main Karoo Basin, the Stormberg Group, an over 1500-m-thick succession that records the final stages of the basin evolution, comprises three fossiliferous continental units. From oldest to youngest, these are the fluvial sandstones, plant-fossil-rich carbonaceous mudstones and coal seams of the Carnian Molteno Formation; the fluvio-lacustrine red beds of the Norian to Sinemurian Elliot Formation, and the predominantly aeolian Sinemurian to Pliensbachian Clarens Formation (e.g., Bordy *et al*., 2004 a, b, 2020; Catuneanu *et al*., 2005; Johnson *et al*., 2006). The latter unit has gradational, conformable lower and upper contacts, and generally consists of cream-yellow fine-, medium- to coarse-grained sandstones (mostly arenites) with subordinate mudstones, especially in its lower part (Eriksson, 1981, 1986; Bordy and Catuneanu, 2001; Bordy and Head, 2018).

The Upper Moyeni palaeosurface is located in the uppermost part of the Elliot Formation, stratigraphically ~35 m below the base of the conformably overlying Clarens Formation (Fig. 1). The middle unit of the Stromberg Group, the Norian to Sinemurian Elliot Formation was deposited from ~215 to ~190 Ma, from the Late Triassic to the Early Jurassic (Sciscio *et al*., 2017a; Bordy *et al*., 2020). It consists of red, pink, purple and maroon mudstones, siltstones and medium- to very fine-grained sandstones, with a thickness of up to 480 m in the south and less than 30 m in the north of its outcrop area in the main Karoo Basin (Fig. 1; Bordy *et al*., 2004b; Bordy and Eriksson, 2015). There are several sedimentary characteristics (e.g., rock types, palaeocurrents, associations of sedimentary structures) of the Elliot Formation that are significantly different in the upper and lower parts of the formation, thus the unit is informally subdivided into the lower Elliot (lEF) and the upper Elliot (uEF) formations (Bordy *et al*., 2004a, b). Caused by climatic and tectonic changes during deposition, this switch in facies characteristics at the lEF-uEF boundary marks a major depositional style change from a mainly meandering river and floodplain sedimentation in the lEF to essentially ephemeral stream and lake deposition in the uEF (Bordy *et al*., 2004a, b; Catuneanu *et al*., 2005). Moreover, synsedimentary normal faults and purported seismites in the uppermost uEF are taken as evidence for the initial stages in the inversion of the regional tectonic regime from compressional to extensional already in the Sinemurian (Bordy *et al*., 2004a, b). In addition, the Elliot Formation is highly fossiliferous with major groups of vertebrate fossils, comprising dinosaurs, turtles, fish, amphibians and early mammals, as well as crustaceans ("conchostracans"), and fossilized wood (e.g., Kitching and Raath, 1984; Knoll, 2004, 2005; Bordy and Eriksson, 2015; Abrahams *et al*., 2017; Bordy *et al*., 2017, 2020; McPhee *et al*., 2017; Sciscio *et al*., 2017a, b, c).

In addition to a plethora of skeletal remains, a diverse array of trace fossils, especially tetrapod footprints but also vertebrate burrows (e.g., Bordy *et al*., 2016), are also common in the Elliot Formation (e.g., Ellenberger, 1970, 1972, 1974; Sciscio *et al*., 2016, 2017b, c; Abrahams *et al*., 2017; Bordy *et al*., 2017; Rampersadh *et al*., 2018). Notably, the most diverse, extensive and well-known ichnological

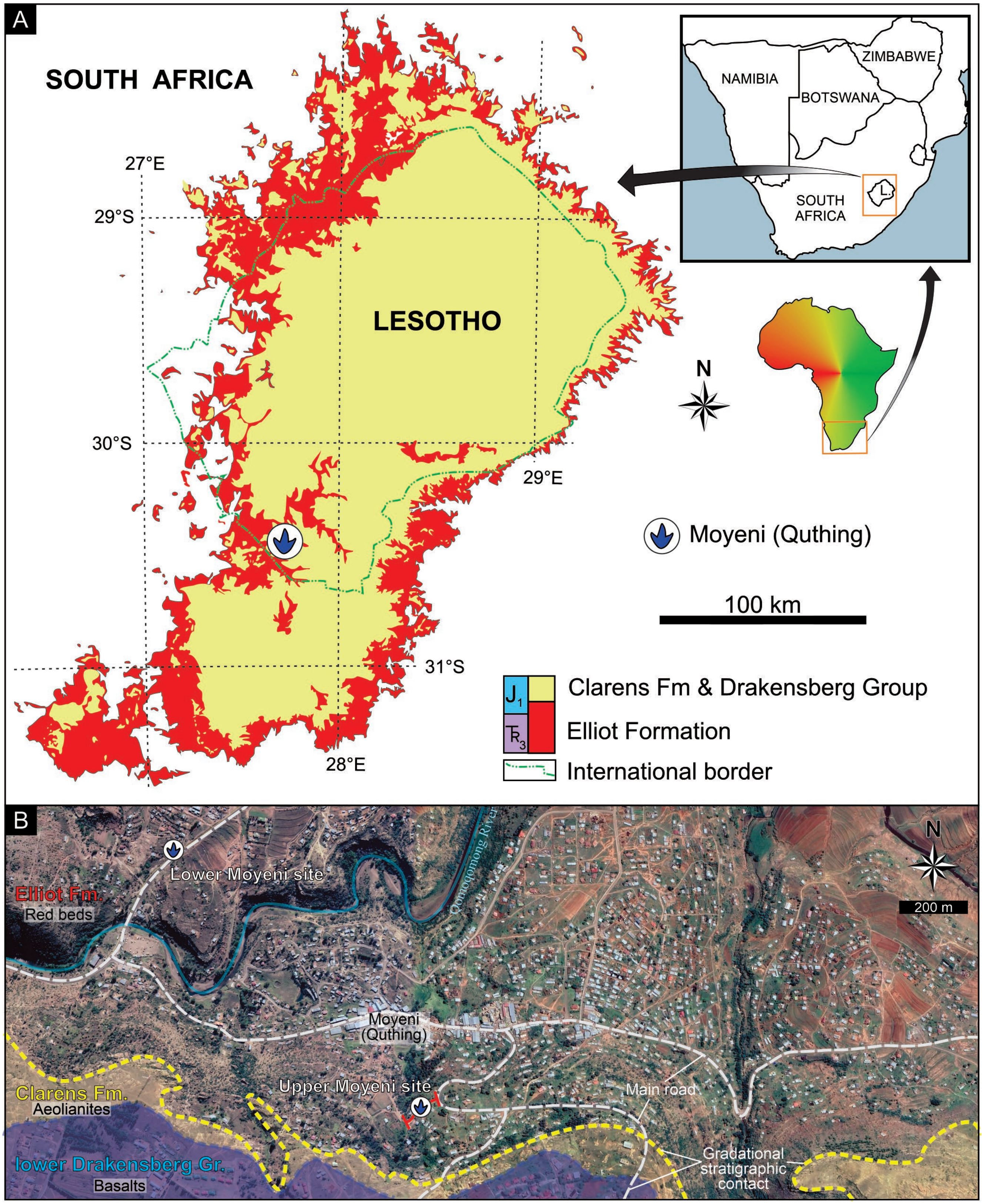

Fig. 1. Locality maps of the Upper Moyeni ichnosite. **A.** A simplified geological map of the Upper Triassic to Lower Jurassic Elliot and Clarens formations, and Drakensberg Group in South Africa and Lesotho. **B.** A simplified geological map of the area near Moyeni town (also called Quthing), showing the Upper Moyeni and Lower Moyeni ichnosites. The latter is the largest dinosaur ichnosite in southern Africa (see e.g., Ellenberger, 1970, 1972; Smith *et al*., 2009). Maps derived from combining data from Google Earth images, Council for Geoscience (2008) and own mapping.

site in the Stormberg Group is in Lower Moyeni (Fig. 1), stratigraphically ~65 m below the Upper Moyeni ichnosite. Situated in the lower uEF, this exceptional ichnosite was discovered and extensively studied by Paul and François Ellenberger and co-workers (see Ellenberger *et al*., 1963; Ellenberger 1970, 1974), and re-investigated in detail using modern techniques by Smith *et al*. (2009), Wilson *et al*. (2009) and Marsicano *et al*. (2014). Originally, the palaeosurface exposed a diverse ichnofauna (e.g., ichnites of theropods, ornithischians, amphibians, crocodylomorphs) of more than 450 tracks, but about 200 tracks were obliterated in spite of conservation efforts in the late 1980s (e.g., building of a protective shelter and visitors centre).

METHODS AND MATERIALS

At the Upper Moyeni tracksite, standard field techniques in both ichnology and sedimentology were used to record, photograph and document the host rock and the ichnite-bearing trackway surface. Macroscopic observations of the host sedimentary rocks were made along a road cutting that transects the rock units immediately above and below the tracksite. In addition, regional sedimentological fieldwork was conducted in the area of the tracksite to provide its broader stratigraphic context and relationships to near-by track-bearing surfaces (Haupt, 2018). Standard-practice sedimentological procedures, detailed in Miall (1996), were used to document the sedimentology of the site, which included the rock types, geometry of sedimentary facies, primary and secondary sedimentary structures, and vertical and lateral grain-size variations. In documenting the trace fossils preserved on the Upper Moyeni palaeosurface, the authors used line drawings, photographs, and photogrammetry. Moreover, silicon rubber casts of several tracks were made using the methods outlined in Sciscio *et al*. (2016) and these are now hosted in the Ichnology Collection of the Evolutionary Studies Institute (ESI) at the University of Witwatersrand, South Africa (accession numbers: BP/6/752-3). All photographs were taken using photogrammetric techniques, outlined in Mallison and Wings (2014), on a Canon PowerShot EOS D1200 (Focal length 28 mm, 5184 x 3456 resolution). These were used to build photogrammetric 3-D models using Agisoft Photoscan Professional (standard version 1.1.4) software. Scaling of the models was done in Agisoft using target-based calibrated scale bars. Markers are placed on targets on the physical scale bars in each image, two markers are then chosen to create a digital scale bar of known length. The horizontal plane of the models was determined using the freeware Cloud Compare (software v. 2.6.1) and the orthographic depth-colour maps and contour lines were generated using the freeware Paraview (v. 5.5.1). Models were additionally manipulated in Meshlab (v. 2016.12) in order to add lighting and shadow effects. Several individual tracks and trackways were photographed to produce 3-D models and can be found in the supplementary files (DOI: 10.6084/m9.figshare.12318848). Standard measurements for tridactyl tracks were recorded from the ichnofossils on site or using ImageJ. These measurements include: track length (TL), track width (TW), track span (TS), digit III projection relative to digit II and IV (Dp), digit length (LII–IV), divarication angles (II^III, III^IV, II^IV) and where tracks were part of a trackway, the pace length (PL) and stride length (λ) were also recorded. All measurements taken are illustrated on Figure 2. The anterior triangle morphology of the tracks is expressed in the Dp/TS ratio, to quantify the medial digit III emphasis of the tracks (*sensu* Lockley, 2009). Hip heights (*h*), and gaits (λ/*h*), of trackway-makers were calculated using the allometric and morphometric equations, outlined by Thulborn (1990). Trackway gauge (TW relative to trackway width) was determined using the methods, outlined by Romano *et al*. (2007). A morphological preservation grade (Pm) was assigned to each track to quantify the amount of detail the track preserves and its usefulness for ichnotaxonomic assignment (Belvedere and Farlow, 2016; Marchetti *et al.,* 2019).

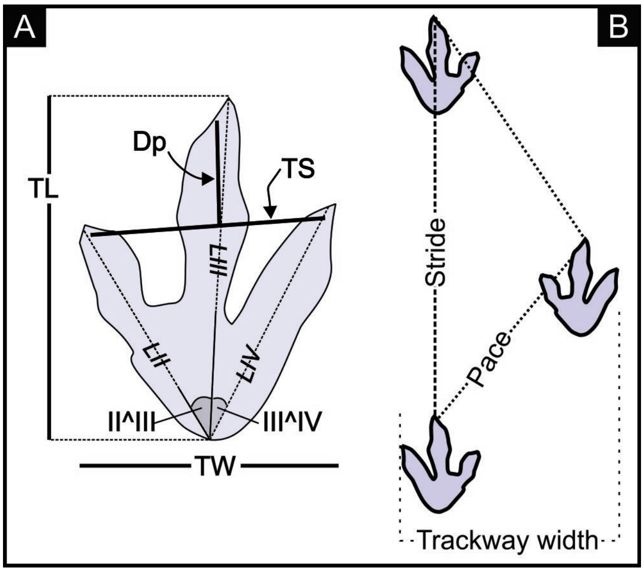

Fig. 2. Measurements taken from the tridactyl ichnites at Upper Moyeni. Abbreviations: TL – track length, TW – track width, TS – track span, Dp – digit III projection, LII/III/IV – respective digit lengths, II^III/III^IV – respective inter-digit angles.

RESULTS

Geological context of the Upper Moyeni ichnosite

The Upper Moyeni ichnosite is stratigraphically ~35 m below the Elliot-Clarens contact, and ~65 m above the lower Moyeni ichnosite in the uppermost uEF. The track-bearing surface is ~130 m long and 2–2.25 m wide. It represents the upper bedding plane of the youngest layer in an upward-fining, tabular sandstone unit (Fig. 3A–C) that is laterally mappable for ~300 m. This fine- to medium-grained sandstone unit is 1.5–3.5 m thick and comprises upward-thinning, tabular beds. Moreover, the beds also fine upwards from a < 3-cm-thick intraformational mudstone-clast breccia with an uneven, erosional base (Gmm in Fig. 3A, C) to the overlying, mostly fine-grained sandstones. The breccia stringer is succeeded first by cross-bedded, medium-grained, and then by horizontally laminated and massive, fine-grained sandstones (Fig. 3A–C). The vertebrate tracks are preserved among asymmetrical ripple marks at the top of the sandstone unit (Fig. 3A, B). Although obscured by thick vegetation, the overlying strata are likely to be red mudstones, as attested by a few patchy outcrops. The adjacent main road cutting (Fig. 3A–D) exposes a ~15 m-thick vertical section of the strata that underlie the track-bearing, upward-fining sandstone package. This succession (Fig. 3A) comprises two 1-1.5 m-thick, tabular sandstone units, which are interbedded with purple-red, massive, silty mudstones that show several pedogenic alteration features (e.g., colour mottling, white blotches, *in-situ* carbonate nodules). Some ~13 m below the track-bearing Upper Moyeni palaeosurface, an isolated, semi-horizontal vertebrate burrow cast with a bilobate cross-sectional shape was also located in a purple-red, massive silty mudstone bed (Fig. 3D). This semi-horizontal burrow cast has a maximum diameter of 23 cm, and a maximum height and exposed length of 10 and 45 cm, respectively. The sides of the burrow cast preserve oblique scratch marks that are arranged in subparallel to criss-crossing subsets (see inset in Fig. 3D). The scratch marks dissipate towards the smooth upper surface of the

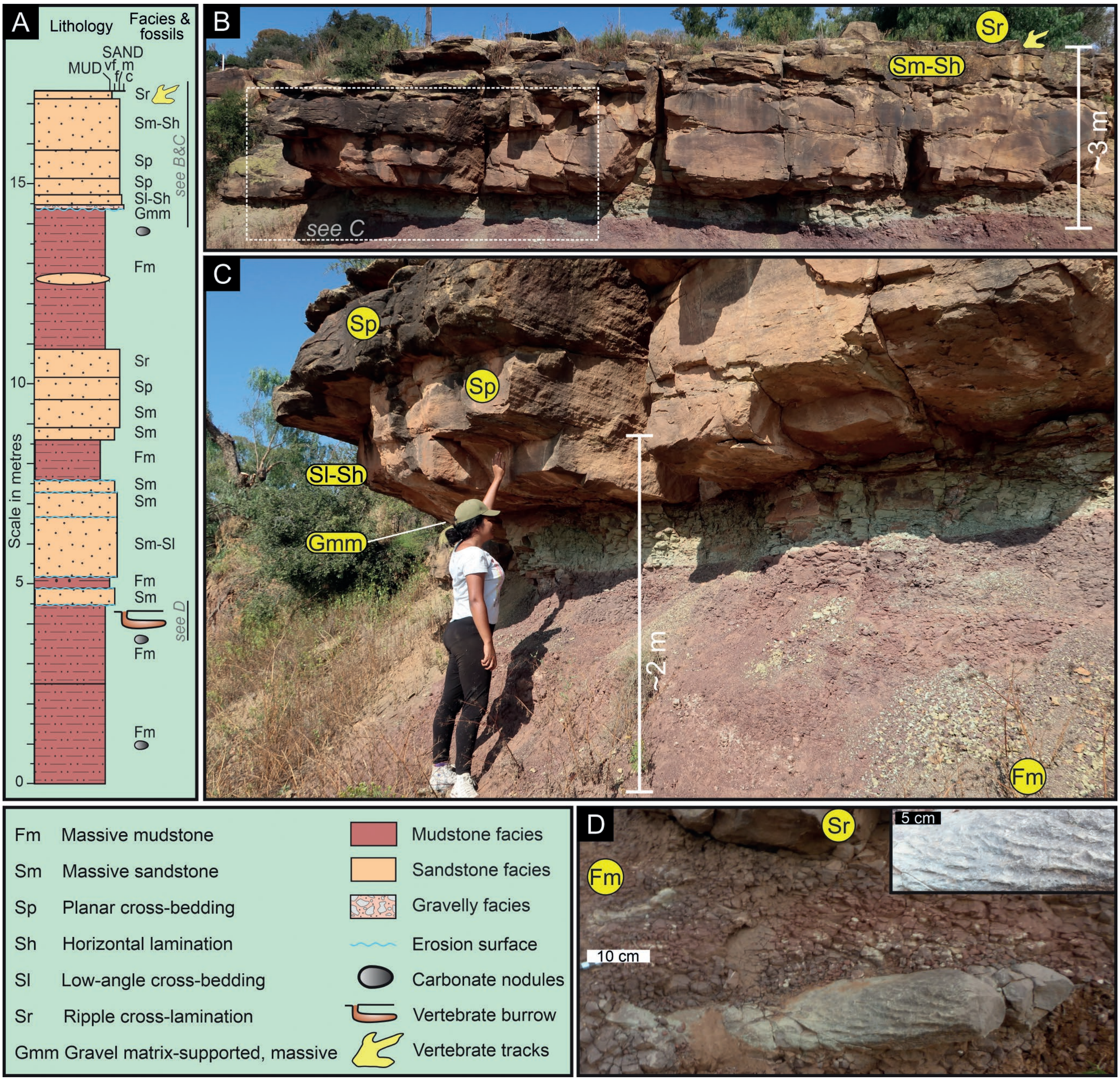

Fig. 3. Sedimentary facies of the upper Elliot Formation at Upper Moyeni. **A.** Sedimentological log, showing key sedimentary features and trace fossils. Capital letters B, C and D denote corresponding images on the right. For key, including facies codes, see legend box below the log. **B.** Overlying sandy siltstones with *in-situ* carbonate nodules, the mostly fine-grained sandstone beds thin and fine upward and terminate in the track-bearing, ripple-marked surface. **C.** Close-up view of the area marked with the white rectangle in B. **D.** Side view of the vertebrate burrow cast with slightly converging scratch marks along its side (see inset image for a close-up view). Note the pedogenic alteration in the host mudstone, which includes carbonate nodules and white mottling.

burrow cast, on which mm-scale bioturbation structures can be observed. The fill of the burrow is massive, fine-grained sandstone.

Vertebrate tracks

The Upper Moyeni ichnosite preserves in excess of 50 tridactyl tracks, of which 18 comprise 5 trackways that are dispersed across the palaeosurface. Both the isolated tracks and the trackways show no observable preferred orientation. The morphological preservation grade of the tracks varies, with no discernible trend across the track-bearing surface (Fig. 4A; Appendix Fig. 1; Appendix Tab. 1). Some tracks are preserved with digital pad impressions or claw marks (or both), while others are incomplete or have their morphologies distorted by substrate-controlled modifications, such as displacement rims and sediment collapse features (Fig. 4A; Appendix Fig. 1). About 20% of the documented tracks are preserved with their infilling still in place, thus distorting the track morphology (Appendix Fig. 1).

The Upper Moyeni tracks generally share a similar asymmetrical, elongate morphology with medial digit III protruding beyond digits II and IV. All digits are tapering and have V-shaped tips and a total digit divarication of less than 90°(Fig. 4; Appendix Fig. 1; Appendix Tab. 1). Given the overall similar morphology of the tracks, the focus herein is on the five trackways (A, B, C, D, E) and select, key isolated tracks (26, 27, 28, 36, 40, 48) preserved at Upper Moyeni. The five trackways considered all have narrow trackway widths and gauges (> 50%) and were produced by bipedal, digitigrade trackmakers (Fig. 4; Tab. 1; Appendix Fig. 1). The isolated tracks were selected because their morphology is either similar to or distinctly different from tracks in trackways A–E and additionally, they preserve more morphological detail than other isolated tracks on the palaeosurface.

Trackway A (track #5, 6, 7) comprises three tracks, which decrease in morphological preservation grade along the trackway (Pm between 2 and 2.5; Fig. 4B; Appendix Fig. 1; Appendix Tab. 1). Track 7, which has the lowest morphological preservation grade, deviates from the consistent track dimensions of tracks 5 and 6 with a lower TL/TW (1.17 vs 1.5 and 1.48, respectively; Appendix Tab. 1) and a higher total digit divarication (63° vs 40° and 42°, respectively, where II^III and III^IV are subequal, with a maximum difference of 5°, for all three tracks; Appendix Tab. 1). Tracks 5 and 6 preserve digital pad impressions and claw marks on nearly all digits, while track 7 preserves a single claw mark on digit IV (Fig. 4B; Appendix Fig. 1). Tracks 5 and 6 are preserved as distinct digit impressions, whereas track 7 has a merged, tulip-shaped "heel". The elongate tracks have an intermediate mesaxony (*sensu* Lockley, 2009), which is consistent between the tracks (Dp/TS ranges from 0.47 to 0.5; Appendix Tab. 1). Average morphometric and allometric hip heights, estimated for the trackmaker, are 154 and 161 cm, respectively (Tab. 1). With a single stride length of 227 cm, a walking gait (λ/h) of 1.48 and 1.41, respectively, is determined for the trackmaker.

Trackway B (track #43, 9, 11) comprises some of the smallest tracks of all the Upper Moyeni trackways (mean TL of 27.5 cm; Tab. 1). The morphological preservation grade varies significantly in the trackway, with incomplete track 43 preserving only two digits and no meaningful morphological detail (Fig. 4A, C; Appendix Fig. 1; Appendix Tab. 1). Track 9 has gracile digits and preserves the most morphological detail (Pm = 2.5; Appendix Tab. 1): digital pad impressions and claw marks are clearly preserved on digits III and IV, and faint pad impressions are preserved on digit II (Fig. 4A; Appendix Fig.1). Track 11 (Fig. 4C) is more deeply impressed and preserves claw mark impressions on digits II and IV. The tracks have tulip-shaped heels and robust, tapering digits, which terminate in V-shaped tips, or occasionally U-shaped tips (digit III of tracks 11 and 43; Appendix Fig. 1). Tracks 9 and 11 are elongate (mean TL/TW of 1.4) and have a variable Dp/TS (0.45 and 0.53, respectively; Appendix Tab. 1). The total digit divarication is variable amongst trackway B (ranging from 38° to 65°), with subequal II^III and III^IV for tracks 9 and 43 (18° and 20°, and 31° and 34°, respectively; Appendix Tab. 1). Average morphometric and allometric hip heights estimated for the trackmaker are 135 and 144 cm, respectively (Tab. 1). With a single stride length of 204 cm, a walking gait (λ/h) of 1.51 and 1.42, respectively, is determined for the trackmaker.

Trackway C (track #12, 20, 21, 22, 23, 24, 25, 44) comprises eight of the largest tracks (average TL of 41.4 cm) and is the longest trackway preserved at the Upper Moyeni ichnosite (Fig. 4A, C; Tab. 1; Appendix Fig.1). There is

Table 1

Average track measurements of trackways identified at Upper Moyeni. Blank fields indicate that the specific parameter could not be measured, owing to obscured track morphology or absence of the necessary feature.

Trackway	TL (cm)	TW (cm)	TS (cm)	TL/TW	Dp (cm)	Dp/TS	Dp/TL %	LII (cm)	LIII (cm)	LIV (cm)	Interdigit angles (°)			Allometric		Morphometric		Gauge % (TW/trackway width)
											II^IV	II^III	III^IV	h (cm)	λ/h	h (cm)	λ/h	
A	31.3	22.7	23	1.38	11.3	0.49	36	15.9	22.6	19.8	48	25.7	22.7	154	1.48	161	1.41	
B	27.5	19.5	19	1.41	9.25	0.49	34	13.9	15.1	20.0	52	24.5	27.0	135	1.51	144	1.42	75
C	41.4	34.3	35.8	1.25	16.68	0.47	40	24.1	28.7	26.9	60			200	2.17	201	2.15	80
D	23.3	16.5		1.42				11.2		12.9				111	1.48	119	1.39	72
E	30.5	24.0		1.27										142	1.20	157	1.08	69

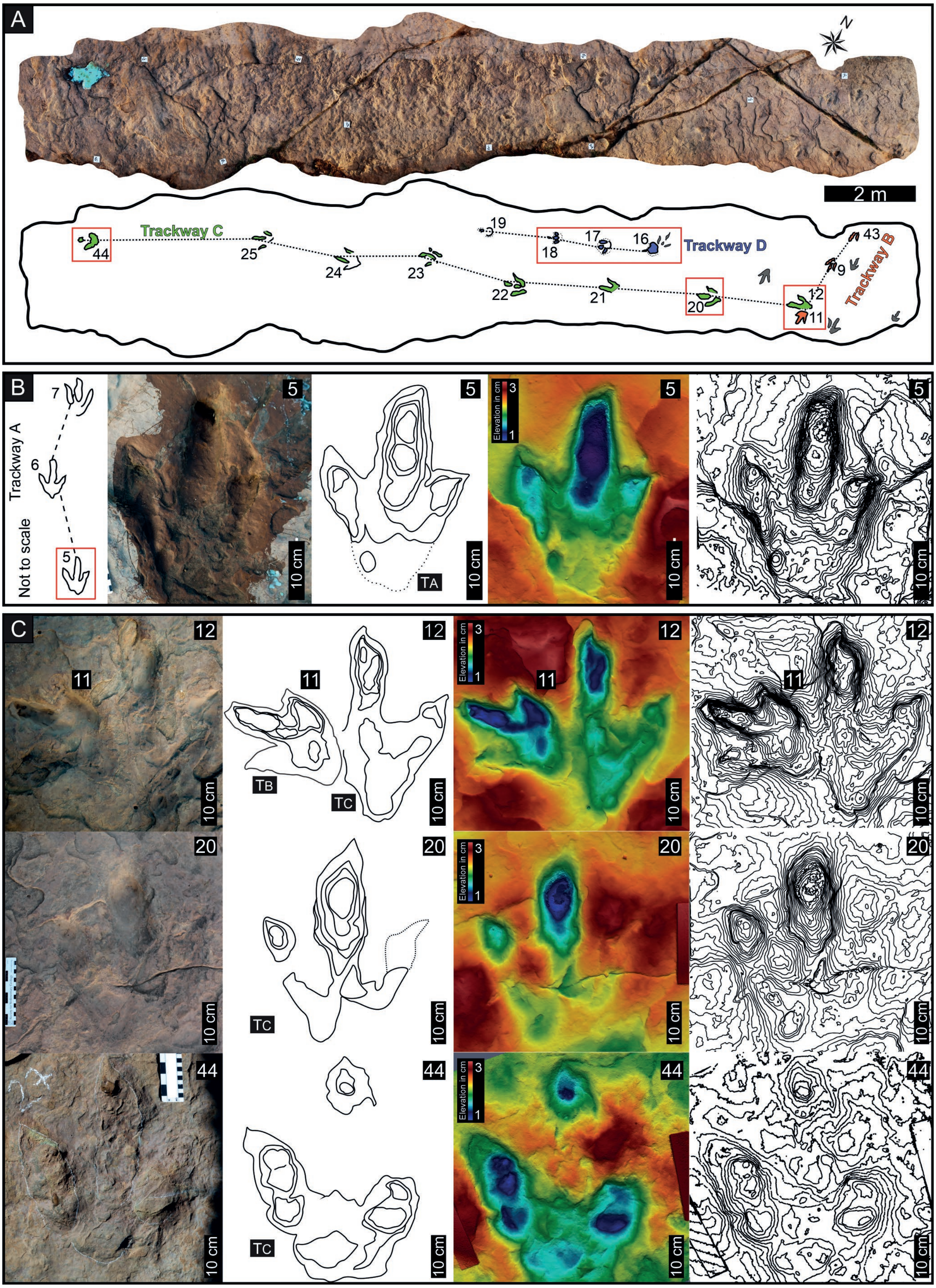

Fig. 4. Tridactyl ichnites from Upper Moyeni illustrated here by field photographs, interpretative outlines, false-coloured depth models and relative-depth maps (with a contour line spacing of 1 mm). **A.** Overview of the ichnite-rich segment of the palaeosurface. **B.** Trackway A schematic and a close-up of high morphological grade track 5, preserving claw marks and digital pad impressions. **C.** Close-ups of selected tracks from Trackways B and C, preserving digital pad impressions and claw marks. **D.** Partial overview of Trackway D with associated sediment collapse and expulsion rim features. **E**. Overview of Trackway E composed of natural cast infilled tracks. See Appendix Fig. 1 for individual track illustrations.

a distinct curvature along the trackway (involving tracks 22, 23, 24 and 25), which corresponds to smaller stride lengths within the trackway (Fig. 4A). The morphological preservation grade is variable, with no discernible pattern along the trackway and half of the trackway C tracks are incomplete (e.g., tracks 12, 21, 23, 25, 44; Fig. 4A, C; Appendix Fig. 1). When preserved, the digit impressions are gracile and commonly taper to V-shaped tips. Tracks 20, 21 and 25 preserve sporadic digital pad impressions and tracks 12, 21, 24 and 41 preserve claw mark impressions. Where a "heel" morphology is preserved, it is lily-shaped (e.g., tracks 12, 20, 24, 25; Fig. 4A, C; Appendix Fig. 1). The tracks are elongate (average TL/TW of 1.25), have an intermediate mesaxony (mean Dp/TS of 0.47) and a wide mean total digit divarication of 60° (Tab. 1). The average morphometric and allometric hip heights, estimated for the trackmaker C (from 8 tracks), are 200 and 201 cm, respectively, with an averaged body length estimate of 7.5 m (Tabs 1, 2). With an average stride of 433 cm, a fast walking gait of 2.17 and 2.15, respectively, is determined for the trackmaker.

Trackway D (track #16, 17, 18, 19) comprises tracks of consistently low morphological preservation grade along the trackway, with track 19 preserving almost no morphological information (Fig. 4A, D; Appendix Fig. 1). The tracks are deep and are associated with sediment collapse features at the digit tips and displacement rim features at the "heel" region (i.e., the posterior margin of the track). This indicates that the track morphology, at the time of track registration, was strongly controlled by saturated substrate conditions. Despite this, the morphology of the tracks is still partly discernible. The tracks are elongate (average TL/TW of 1.42; Tab. 1), and tracks 16, 17 and 18 preserve three distinct digit impressions, with a pronounced medial digit III projection (Fig. 4A, D; Appendix Fig. 1). The apparent digit lengths of digit II and IV, where measurable, are subequal (mean LII:LIV of 1:1.2; Appendix Tab. 1). Unlike the other tracks at the Upper Moyeni ichnosite, trackway D tracks predominantly have robust, rounded outer digits with U-shaped tips. Where the distal ends of digit III are preserved, e.g., tracks 16, 18 and 19, deep claw mark features are observed (Fig. 4A, D; Appendix Fig. 1). Average morphometric and allometric hip heights calculated for the trackmaker are 111 and 119 cm, respectively (Tab. 1). A walking gait (λ/h) of 1.48 and 1.39, respectively, is determined for the trackmaker.

Trackway E (track #36, 45, 49) consists of three tracks preserved with their infilling (Fig. 4E). The little morphological detail preserved decreases along the trackway, with track 49 being so morphologically indistinct that it could not be measured (Fig. 4E). Despite the infilling, impressions of three digits can be observed for tracks 36 and 45. Track 36 has a protruding feature near its "heel" region, which may resemble a digit I, though it is unclear (Fig. 4E; Appendix Fig. 1). Displacement rims are observed around the "heel" region of track 45. The tracks have an average TL and TW of 30.5 and 24 cm, respectively (mean TL/TW of 1.27; Tab. 1). Average morphometric and allometric hip heights estimated for the trackmaker are 142 and 157 cm, respectively (Tab. 1). With a single stride length of 170 cm, a walking gait (λ/h) of 1.2 and 1.1, respectively, is determined for the trackmaker.

Isolated tracks with TL > 40 cm, are not exclusive to trackway C at the Upper Moyeni ichnosite e.g., tracks 1, 2, 8, 26, 27, 28, 34, 38, 39 (Appendix Fig. 1; Appendix Tab. 1). The true TL of tracks 27 and 28 are likely higher than the measured TL because the tracks are incomplete. These large tracks preserve little morphological detail, with few preserving claw marks or digital pad impressions (e.g., tracks 8, 28, 34, 38, 39; Appendix Fig. 1). Of these, track 26 is truly outstanding, having a TL of 51 cm, which makes it the largest measured track at Upper Moyeni (Appendix Fig. 1). Tracks 26 and 27 are noteworthy as their morphologies are akin to Trackway C. The tracks preserve distinct, lily-shaped "heels" and possess relatively narrow digits, which taper to V-shaped tips. They lack additional morphological detail, except for a single claw mark impression preserved on digit II of track 26. Tracks 26 and 27 have a TL/TW of 1.31 and total digit divarication of 61° and 64°, respectively (vs Trackway C average TL/TW of 1.25 and II^IV of 60°; Appendix Fig. 1; Appendix Tab. 1). Track 38 is one of the only large tracks that preserves claw marks (on all three digits) and faint digital pad impressions (on digit II and III), which are obscured by infilling preserved in digit III (Appendix Fig. 1). It has a TL/TW of 1.33, a Dp/TS of 0.47 and a II^IV of 54°, with II^III 6° > III^IV, similar to trackways A and B (Tab. 1; Appendix Tab. 1). It also preserves a rounded, tulip-shaped "heel" and has subequal digit II and IV lengths (25 and 30 cm, respectively; Appendix Fig. 1; Appendix Tab. 1). Like track 36 from trackway E, isolated track 33 is preserved with its infilling and has a protruding feature near its "heel" region, resembling digit I (Appendix Fig. 1). The discernible digit tips taper to V-shapes but little else can be discerned about the morphology of this track. Distinct from the trackways described herein, tracks 40 and 48 are small with TLs of 15 and 17 cm, respectively (Appendix Fig. 1; Appendix Tab. 1). The morphology of track 40 is unclear as it preserves no additional morphological details. Track 48 is elongate (TL/TW of 1.3), has a tulip-shaped "heel" region, and higher-intermediate mesaxony (Dp/TS of 0.66) with digit III accounting for 51% of the total TL (Appendix Tab. 1). Digits II and IV have subequal lengths (10.6 and 9.4 cm, respectively), terminate in rounded, blunt tips and are widely splayed (II^IV of 74°; Appendix Fig. 1). No claw mark or digital pad impressions are associated with track 48.

DISCUSSION

Palaeoenvironmental context

The rock interval studied at the Upper Moyeni ichnosite contains continental red beds with sedimentary characteristics that are typical in the fluvio-lacustrine uEF, not only around the town of Moyeni, but also within southern Africa, and have been described previously by Visser and Botha (1980), Eriksson (1985), Smith *et al.* (1993), and Bordy *et al.* (2004b). For example, the track-bearing sandstone unit that comprises upward-fining and thinning, tabular beds as well as upper and lower flow regime sedimentary structures in its lower and upper part, respectively (see facies Sl, Sh vs Sr with tracks in Fig. 3), can be interpreted as flood deposits.

These likely formed in vast, laterally extensive sheets of shallow, unidirectional water courses. In these sheet washes, the initially high-energy, erosive currents decelerated with time and deposited asymmetrical sand ripples that migrated in downcurrent direction in gentle currents that would form owing to the waning of the flash floods. The dinosaurs walked on this rippled sand surface, while the sediment was still moist.

The more localised sandstone units (lower part of Fig. 3A) either formed in single flash-flood events or several short-lived flooding events that were separated by periods of non-deposition and drying (Hogg, 1982; Bordy *et al*., 2004b). The thickness of the sandstone units (up to 3.5 m; Fig. 3A, B) may also give insight into the size of the channels, which on a regional scale ranged from small channels in streams of a water depth of ~1 m to deeper channels with depths of at least 2 to 3 m (Bordy *et al*., 2004b).

The massive silty mudstones with pedogenic alteration features indicate low-energy depositional settings and are interpreted as floodplain deposits that supported soil development, similar to other track-bearing palaeosurfaces in the uEF (e.g., Sciscio *et al*., 2016, 2017b; Abrahams *et al*., 2017; Rampersadh *et al*., 2018). The presence of the pedogenic alteration features, especially *in-situ* carbonate nodules in the silty mudstones (Fig. 3A), serves as evidence for the climatic conditions during the deposition of the mudstones. These early post-depositional features are characteristic of palaeosols in semi-arid environments, where pedogenic alteration and precipitation of carbonates in soil profiles are linked to seasonal fluctuations from wet to dry conditions (e.g., Blodgett, 1988; Wright and Tucker, 1991; Bordy *et al*, 2004b). *In-situ* carbonate nodules associated with ancient soil profiles are especially common in depositional environments, in which clastic sediment input came to a halt or was low enough at least periodically for the carbonate-bearing palaeosol horizons to develop (e.g., Blodgett, 1988; DeCelles, 2012).

The vertebrate burrow cast found ~13 m below the track-bearing surface is interpreted to be a tetrapod burrow similar in size and morphology to the only other vertebrate burrow cast that was reported to-date from the uEF (Bordy *et al*., 2016). Because of its kidney-shaped cross-sectional outline, the Upper Moyeni vertebrate burrow cast can be attributed to *Reniformichnus* ichnogenera (Krummeck and Bordy, 2018). On the basis of the presence of the scratch marks on the side of the burrow cast (Fig. 3D), the burrowing animal was a tetrapod with claws and excavated sideways in a downward motion (Bordy *et al*., 2011, 2019). These kidney-shaped uEF burrow casts were likely generated by synapsids, a prominent group of reptiles with a rich record of skeletal remains (e.g., Kitching and Raath, 1984; Bordy *et al*., 2016, 2020) and footprints (e.g., Ellenberger, 1970; Haubold, 1987) in the Sinemurian of southern Gondwana.

The burrow-hosting, pedogenically altered mudstone unit (Fig. 3A, D) indicates that the animal likely burrowed into a soil-supporting substrate. The scratch marks also indicate that the sediment was competent enough, possibly owing to some slight pedogeneis, to prevent caving-in of the open burrow, but was also moist enough to preserve the scratch marks (Bordy *et al*., 2011, 2019). The isolated, semi-horizontal burrow cast with its fairly uniform diameter indicates that the burrow could have been a temporary hiding or resting place and not necessarily a permanent habitat (e.g., Groenewald *et al*., 2001; Bordy *et al*., 2011, 2019). The bioturbation structures on the topside of the burrow cast indicate that the burrow-filling sediment was nutrient-rich for other smaller, burrowing invertebrate organisms that were likely part of the soil fauna.

In summary, the laterally continuous sheet-like sandstone units that are interbedded with massive, pedogenically altered silty mudstones (Fig. 3) are interpreted as products of short-lived, high-energy fluvial depositional events on an extensive, low-gradient, vegetated land surface. These flash floods distributed sandy sediments in shallow, wide water courses over the low gradient, low energy land surface. During the uEF depositional period, the climate was hot, semi-arid and prone to short-lived, high-energy flash floods that were followed by periods of drying out (e.g., Visser and Botha, 1980; Bordy and Catuneanu, 2002; Bordy *et al*., 2004a, b, c; Rampersadh *et al*., 2018). The environment was able to support not only dinosaurs but other burrowing tetrapods as well, which were likely synapsids.

Ichnotaxonomic assignment

Although the Upper Moyeni tracks considered in this study preserve a similar morphology, being elongate, mesaxonic tridactyl tracks that commonly preserve claw marks and digital pad impressions, there are distinct differences amongst the tracks.

Trackways A and B comprise large track lengths (average TL of 31.3 and 27.5 cm, respectively; Tab. 1) and have comparable morphologies. The tracks are elongate (average TL/TW of 1.38 and 1.41, respectively), moderately mesaxonic (average Dp/Ts of 0.49) and have a pronounced Dp which accounts for 34–36% of the TL (Tab. 1). The digits are robust, taper to V-shaped tips, often preserving claw mark impressions. Moreover, four digital pads associated with digit IV can be identified within both trackways (tracks 5 and 9, respectively; Fig. 4A, B; Appendix Fig. 1). The posterior (“heel” region) of the tracks are primarily rounded and U-shaped e.g., tracks 5, 7, 11, 43 (Fig. 4A–C; Appendix Fig. 1). These morphological characteristics are comparable with the globally abundant ichnotaxon *Eubrontes*, which is defined as having a TL > 25 cm, a strong medial digit projection and robust digits (Olsen *et al.,* 1998). Furthermore, the anterior projection of digits II and IV along the axis of digit III for trackways A and B are near equal, which is consistent with *Eubrontes*. The relative dimensions of trackways A and B are comparable to *Eubrontes* and *K. minor* (Fig. 5), but their larger track lengths (TL > 25 cm) and overall morphologies, i.e., robust digits and narrower total digit divarication, are more consistent with *Eubrontes*. *Eubrontes*-like tracks have been identified at numerous Early Jurassic Stormberg Group ichnosites (e.g., Ellenberger, 1974; Olsen and Galton, 1984; Ambrose, 2003; Raath and Yates, 2005; Sciscio *et al*., 2016, 2017b). Isolated track 38, which notably shared morphological characters with trackways A and B, plots within the *Eubrontes* ichnotaxon field, near the average ratio dimensions of trackways A and B (Fig. 5).

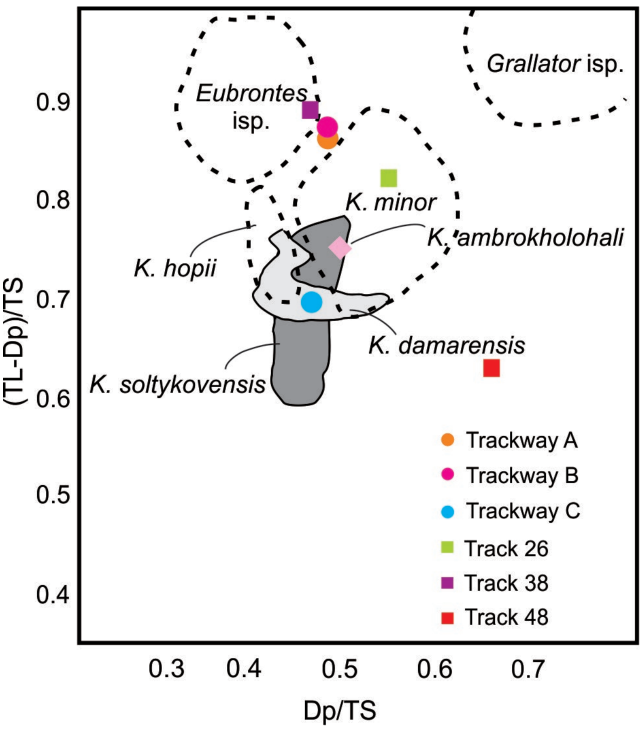

Fig. 5. Bivariate plot comparing the anterior and posterior triangle ratios of known theropod ichnotaxa and the Upper Moyeni trackways and select isolated ichnites. Upper Moyeni trackways are represented by their mean track measurements, while isolated tracks are represented by their absolute track measurements. Modified after Sciscio *et al*. (2017b).

Trackway C differs from trackways A and B in that the tracks are very large (average TL of 41.4 cm), have widely splayed digits (average II^IV of 60° vs 48° and 52°; Tab. 1) and have a relatively reduced elongation (average TL/TW of 1.25; Fig. 4A, C; Appendix Fig. 1). The digits are gracile, occasionally taper to claw mark impressions and digital pad impressions are rarely preserved. The “heel” region, when preserved, is lily- or V-shaped. These morphological characteristics are comparable to *Kayentapus*, an ichnotaxon first appearing from the Early Jurassic. *Kayentapus* is defined as being tridactyl, with a TL ranging between 11.5 and 40 cm and having a wide total digit divarication where II^III < III^IV (Welles, 1971; Piubelli *et al*., 2005; Lockley *et al.,* 2011). The gracile digits and high digit splay distinguish it from the contemporaneous *Eubrontes*. The relative dimensions of trackway C are comparable to *K. soltykovensis* and *K. damarensis* (Fig. 5). *Kayentapus*-like tracks are known from the uEF and Clarens Formation in southern Africa (e.g., Ellenberger 1970, 1974; Olsen and Galton, 1984; Sciscio *et al*., 2017b; Abrahams *et al*., in press). Isolated track 26, which has a comparable morphology to trackway C, may also be assigned to *Kayentapus* (Fig. 5).

Trackway D comprises elongate tracks (average TL/TW of 1.4) with round, robust digit II and IV impressions (Fig. 4A, D; Appendix Fig. 1). Unlike the lateral digits, medial digit III is often preserved as a discontinuous impression, separate from the main track, and is narrow, tapering to a V-shaped tip or deep claw mark impression. The tracks are associated with extramorphological features, such as expulsion rims and sediment-collapse structures, indicating that the substrate had a strong control on the ultimate track morphology (Fig. 4A, D; Appendix Fig. 1). The digit impression depth increases towards the anterior of the impression and the digit morphology is obscured by overlying sediment as the digits penetrate beneath the sediment surface (Fig. 4D). A confident ichnotaxonomic assignment, therefore, may not be performed for trackway D. The robust, rounded nature of the digit impressions and lack of a consistently clear, asymmetrical posterior is comparable to the Early Jurassic ichnogenus *Anomoepus,* which is attributed to an ornithischian trackmaker. *Anomoepus* is defined as having a small (TL < 20 cm), functionally tridactyl pes that may be preserved with pentadactyl manus impressions. The ichnite is distinguished by the placement of the metatarsophalangeal pad of digit IV, which is directly in line with the digit III impression. This, however, is not observed for trackway D. Furthermore, *Anomoepus* classically has a TL/TW of ~1 or less (Olsen and Rainforth, 2003), though TL > TW have been recorded (Dalman and Weems, 2013). *Anomoepus*-like tracks are known from the uEF (e.g., Ellenberger, 1974; Smith *et al*., 2009). The distinct claw marks associated with digit III, the TL/TW of 1.4 and asymmetrical posterior seen for tracks 16 and 18 are more comparable to a theropod trackmaker than an ornithischian trackmaker. Furthermore, the measured digit lengths for digits II and IV are subequal (11.2 vs 12.9 cm, respectively), which is a characteristic of tracks on the *Grallator-Anchisauripus-Eubrontes* plexus (Olsen *et al*., 1998). The overall morphology of trackway C resembles deep tracks from the Late Triassic of Greenland that are interpreted as theropod tracks, modified by substrate conditions (Gatesy *et al*., 1999; their fig. 6).

Trackway E and isolated track 33 are completely obscured by infilling and have a low morphological preservation grade of 0–1 (Fig. 4E; Appendix Tab. 1). Consequently, their ichnotaxonomy remains unresolved.

Isolated tracks 40 and 48, are distinct from other Upper Moyeni tracks because of their small size (TL = 15 and 17 cm, respectively; Appendix Tab. 1). Of the two tracks, track 48 has the more distinct morphology and, therefore, the more complete measurement dataset. Track 48 is elongate (TL/TW of 1.31), has an intermediate-high mesaxony (Dp/TS of 0.66), and its medial digit projection accounts for 51% of the TL (Appendix Tab. 1). In track 48, the small TL, tulip-shaped “heel” region and strong emphasis of digit III is consistent with the ichnotaxon *Grallator*, which is a functionally tridactyl ichnite, defined as having a TL < 15 cm, a high digit III projection and TL/TW of ~2 (Olsen *et al.,* 1998). Track 48 has a significantly smaller track elongation and larger total digit divarication than classical *Grallator* but is consistent with other southern African *Grallator*-like tracks (e.g., Sciscio *et al*., 2016; Abrahams *et al*., 2017; Rampersadh *et al.,* 2018).

Comparisons with the southern African large tridactyl tracks

The first, very large tridactyl track to be documented in the ichnite record of southern Africa was reported by

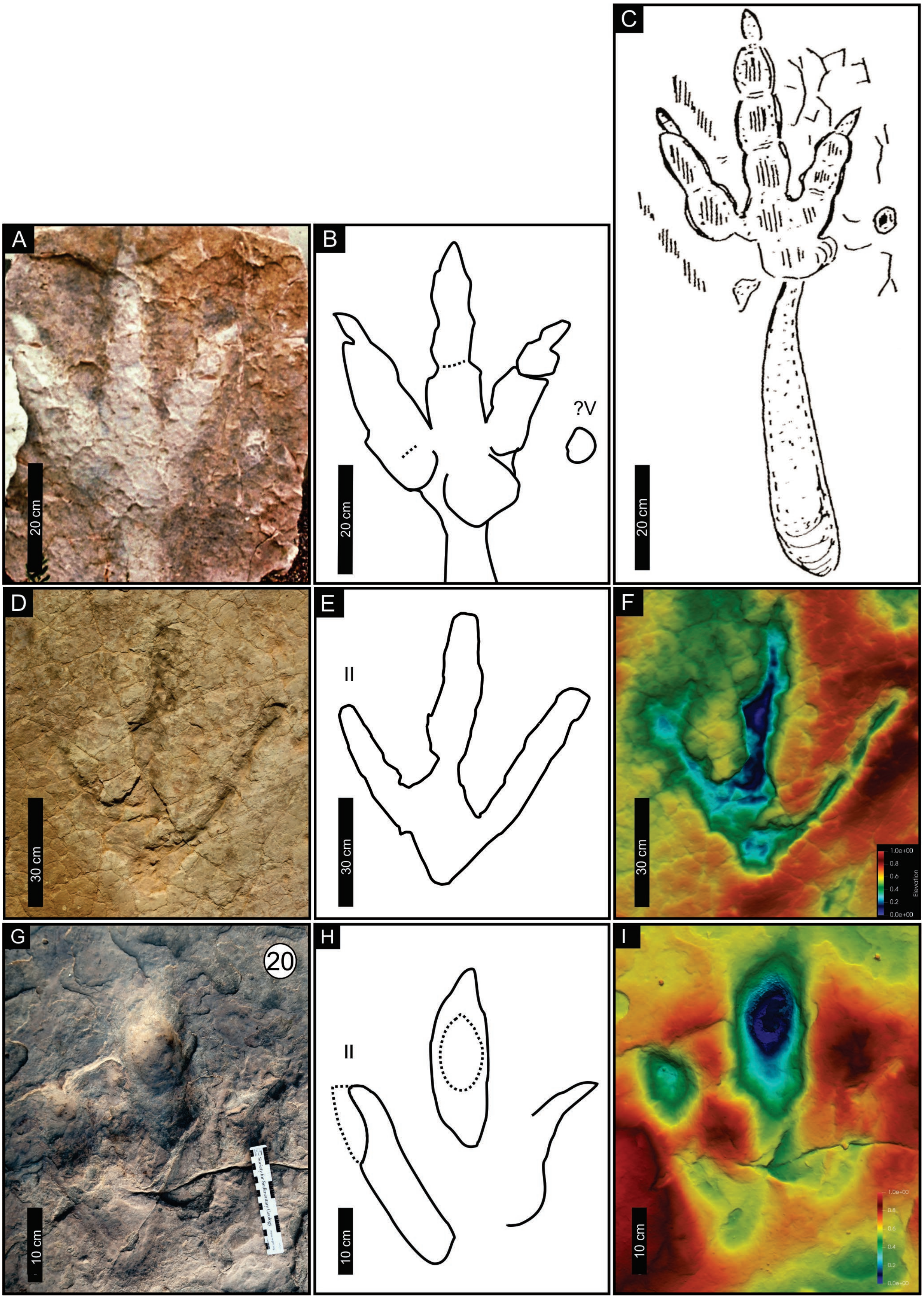

Fig. 6. The three largest tridactyl tracks from the Lower Jurassic of southern Africa to date. **A.** *Megatrisauropus malutiensis* plaster cast from the upper Clarens Formation at Mokae (SW Lesotho; this is an unpublished photograph from the Ellenberger Collection at the University of Montpellier, France). **B.** Line drawing from a photograph of the cast. **C.** Line drawing taken from Ellenberger (1970). **D–F.** Photograph, line drawing and false colour-depth model *Kayentapus ambrokholohali* from the uppermost upper Elliot Formation at Roma-Matobo (central-western Lesotho; Sciscio *et al.*, 2017b). **G–I.** Photograph, line drawing and false colour-depth model of track 20 from the uppermost uEF at the Upper Moyeni ichonsite (SW Lesotho; this study). Roma-Matobo and Mokae are ~100 km to the north and ~32 km to the north-east of Upper Moyeni, respectively (see Fig. 1A).

Ellenberger (1970; pl. VII, fig. 126) as *Megatrisauropus malutiensis* (Fig. 6A–C). This trackway is located in the upper Clarens Formation (Zone B/5) near the village of Mokae (Quthing District, Lesotho), some ~32 km to the NE from Upper Moyeni (see Fig. 1A). Recent attempts to relocate the ichnosite at Mokae were unsuccessful, and the casts (LES281.1,2) in the Ellenberger Collection (University of Montpellier, France) could not be located either, despite a carefully conducted inspection of all specimens in that collection. However, unpublished photographs (Fig. 6A) by Paul Ellenberger (University of Montpellier) and a brief description and accompanying illustration (Fig. 6B, C) in Ellenberger (1970) permit comparison with the largest tridactyl tracks studied by the present authors at Roma (Sciscio *et al*., 2017b) and Upper Moyeni (this study).

Megatrisauropus malutiensis comprises one figured pes track (pl. VII, fig. 126, p. 364 in Ellenberger 1970), although a stride measurement of 250 cm indicates that it may form part of a trackway. The TL is 55 cm with TL/TW of 1.3 and Dp of 23 cm providing a Dp/TW of 0.6 (intermediate mexasony). The total divarication is 59° with the divarication between digits II^III and digits III^IV nearly equal at 30° and 28°, respectively. Claw marks are sharply defined and present on all digits, with digit II being the longest (Fig. 6A). Digital pads are preserved and the distinct metatarsophalangeal pad traces below digit II and IV are defined. The track also preserves a 30-cm-long posterior, elongate mark that is the impression of the metatarsal (Fig. 6C). Ellenberger (1970, 1972) recorded and illustrated (Fig. 6A, C) a small circular structure parallel to digit IV and with a diameter of 4.5 cm, which may be the impression of digit V. The average calculated morphometric and allometric hip heights are 220 and 210 cm, respectively, giving a predicted averaged body length of 7.8 m (Tab. 2). In comparison to other large tridactyl tracks of the upper Stromberg Group, *M. malutiensis* is distinguished by the clear impression of the metatarsophalangeal pads, metatarsal and the possible impression of digit ?V, although the latter is brought into question herein. In all other respects, the gracile digits, size, ratios and divarication of the digits are closely comparable with uEF *Kayentapus ambrokholohali* and *M. malutiensis* may be considered *Kayentapus*-like, despite its larger size.

Kayentapus ambrokholohali (Fig. 6D–F) was discovered in the uppermost uEF (Roma, Lesotho) and consists of two consecutive pes tracks on a palaeosurface with other tridactyl ichnites. These *K. ambrokholohali* tracks are gracile, very large (TL: 57 cm, TL/TW: 1.14), have a V-shaped “heel” region (posterior margin), a total divarication of 63° and Dp/TW ratio of 0.4 (Sciscio *et al*., 2017b). The step is not deeply impressed, does not display digital pads or claw marks and is, unfortunately, heavily weathered by the passage of carts over the palaeosurface. On the same palaeosurface, other large tridactyl tracks, assigned to the ichnogenus *Eubrontes*, were also reported but these were more robust, with fleshed digit impressions, U-shaped “heel” regions and a TL of up to 40 cm (TW = 30 cm, TL/TW = 1.2; Sciscio *et al*., 2017b). *K. ambrokholohali* tracks represent the largest Early Jurassic *Kayentapus* and are of the largest and earliest, tridactyl tracks attributed to theropods, globally.

In this study, tracks from trackway C (Fig. 6G–I; Appendix Fig. 1; Appendix Tab. 1), represent a large (TL > 40 cm;) and relatively gracile morphotype at the Upper Moyeni ichnosite. These tracks average 41.4 cm in length, TL/TW of 1.3, Dp of 16.7 cm (Dp/TW: 0.5) and total divarication of 60° (Appendix Tab. 1). Other large tracks, e.g., Tracks 26 and 27, are of similar morphology and have comparable TL/TW and total digit divarication. These are assigned to *Kayentapus* and *Kayentapus*-like tracks and are comparable with both *K. ambrokholohali* (uEF) and *M. malutiensis* (upper Clarens Formation). However, the latter taxa show more gracile digits than the Upper Moyeni isolated tracks and trackway C. It is possible that this is a function of preservation given that the Upper Moyeni palaeosurface shows more pliability and variability in water saturation relative to Roma-Matobo and Mokae sites. This substrate plasticity allows for morphological and formational variation (Gatesy *et al*., 1999; Gatesy and Falkingham, 2017), and an exemplar of these substrate-controlled variants is illustrated in the trackway D (e.g., tracks 16–19; e.g., Appendix Fig. 1).

Table 2

Comparison of the hip heights and body lengths of the large *Kayentapus*-like tracks from the upper Elliot and Clarens formations. N – number of tracks.

Track	Reference	N	TL (cm)	Allometric hip height, *h* (m)	Morphometric hip height, *h* (m)	Body length (m)		
						Allometric	Morphometric	Averaged
Megatrisauropus malutiensis	Ellenberger, 1970	1	55	2.6	2.7	8.7	8.9	8.8
Eubrontes (Matobo B)	Sciscio *et al*., 2017b	2	40	2.0	2.0	7.5	7.4	7.4
Kayentapus ambrokholohali	Sciscio *et al*., 2017b	2	57	2.7	2.8	8.8	9.1	9.0
#38; *Eubrontes*-like	this study	1	44	2.1	2.2	7.8	7.8	7.8
#12, 20, 21, 22, 23, 24, 25, 44 (Trackway C); *Kayentapus*-like	this study	8	41	2.0	2.01	7.5	7.5	7.5

Thus, the increased robustness of the larger Upper Moyeni tracks and trackways is a function of substrate conditions preserving a more complete 3-D morphology of the pes than at sites that contain *K. ambrokholohali* (uEF at Roma-Matobo) and *M. malutiensis* (upper Clarens Formation at Mokae).

M. malutiensis is an exceptional track given both its significant length (TL = 55 cm) and its high preservation grade (2.0–3.0). The description, photograph of the cast and its illustration show desiccation cracks, digital pads, sharp claw marks and trackmaker behaviour as well as substrate-related structures. The latter relates to the 30 cm long "heel" region of metatarsal and digit V impressions. Ellenberger (1970, 1972) suggested the 4.5 cm diameter circular impression parallel to digit IV is the mark of the claw tip of digit V and inferred the track to be made by a non-sauropod sauropodomorph. Cooper (1981) suggested that *M. malutiensis* was made by *Massospondylus*, a common non-sauropod sauropodomorph in the uEF and lower Clarens Formation. However, Lockley *et al*. (2003) consider the track a theropod trace, with the elongate posterior trace that of the metatarsal, but did not discuss or illustrate the impression of "digit V". In many bipedal theropods and non-sauropod sauropodomorphs, digit I acts as a dewclaw and digit V is vestigial and neither are typically expected to be impressed. There are exceptions and the hallux (digit I) may be impressed as a function of both biological variation and substrate (e.g., Lockley *et al*., 2003; Farlow *et al*., 2013; Xing *et al*., 2014). The impression of either, in addition to the record of the metatarsal, is likely a function of behaviour (i.e., locomotion or resting) on a pliable substrate.

M. malutiensis was preserved on a relatively firm mud-covered surface given the well-preserved, fine desiccation cracks that crosscut the cast. Furthermore, the track is shallowly impressed, allowing distinct digital pad and claw impressions, elongate posterior margin (30 long) and potentially the presence of a forward and medially-directed ?claw mark (digit V) or related impression. Importantly, the elongate "heel" mark (i.e., posterior margin of the track) described by Ellenberger (1970) is most probably the metatarsal impression, as considered by Lockley *et al*. (2003, see their fig. 8, p. 173). Given the preservation quality, a firm substrate is likely to register the stationary anatomy of the trackmaker and this impression could be produced when the animal is crouching in a resting position (Gatesy and Falkingham, 2017). During a resting, crouched stance, the digit I may be medially directed relative to digit II, producing a mark as opposed to the posterolateral position, typically recorded by moving animals in pliable substrates (Gatesy *et al*., 1999). However, it is unlikely that a similar mark could be made parallel to digit IV by a vestigial digit V as suggested by Ellenberger (1970). Given neither the original palaeosurface nor the cast can be located to-date, we cannot further speculate on the origin of this mark.

In comparison, *K. ambrokholohali* (uEF at Roma-Matobo) is preserved as a shallow impression on a sandy substrate (Fig. 6D). No morphological features are preserved and a heavy reliance on the ratios, digit proportions and divarication are needed to describe this trackway (Sciscio *et al*., 2017b). Therefore, no extramorphological features are noted, nor digital pads or distinct claw marks, as in *M. malutiensis*. Despite these preservational differences, the morphometrics of these tracks are comparable and indicate that these large morphotypes reflect animals with similar pedal structures and body proportions. The Upper Moyeni ichnosite reflects another series of large tracks from the uEF that can be assigned to *Kayentapus*. The Upper Moyeni tracks are on the same morphological spectrum as the above two very large tracks, even though they are slightly smaller in size, having TLs between 40–51 cm. Spatiotemporally, the track record in the upper Stromberg Group reflects not only the expansion of body size in the Early Jurassic, but also a more complex ecological disparity than currently hypothesised on the basis of the conservative nature of theropod pedal structures and limited fossil remains (Farlow *et al*., 2013). Moreover, the very large Pliensbachian track from the Clarens Formation at Mokae indicates a complex history and long persistence of larger-bodied animals under increasing aridity than is currently expressed in the body-fossil record from southern Africa.

In summary, the uppermost uEF and upper Clarens Formation preserve some of the earliest and largest tridactyl tracks, known regionally and globally. The convergence of several large tridactyl tracks in the upper Sinemurian to Pliensbachian of southern Africa expresses a diversity of large-bodied (theropod) dinosaurs that are not currently reflected in the regional body fossil record. To date, this fossil bone record is assigned only two theropod genera: *Megapnosaurus* (a coelophysoid; Bristowe and Raath, 2004) and *Dracovenator* (a dilophosaurid; Yates, 2005) and neither represent the body proportions indicated by the large tracks, analysed and compared herein from the uppermost uEF and Clarens Formation. However, dilophosaurids were capable of reaching upwards of 7 m in body length, which would cater to the lower end of the track spectrum (~40 cm TL) of the present account. The diversity of medium- to large-sized sized tridactyl tracks with TL between 30–50 cm and exceptionally large tracks with TL > 50 cm in southern Africa collectively indicate the expansion of body size of theropods that far outstrips their body fossil record regionally and globally. Moreover, these tracks can be placed in the robust stratigraphic context and the improved temporal framework of the upper Stormberg Group (Bordy *et al*., 2020), adding greater value to their occurrences and biostratigraphic associations. The importance of this is reinforced by the global disparity between the body and trace-fossil records and the rarity of medium- to large-sized tridactyl tracks, with those exceeding 50 cm in length being exceptional (Lucas *et al*., 2006; Irmis, 2011; Griffin and Nesbitt, 2019).

CONCLUSION

The forty-nine tracks, described from the Upper Moyeni palaeosurface, were registered by tridactyl bipeds under variable substrate conditions. The morphological preservation grade of the tracks is non-uniform along the palaeosurface, with low grades relating to the initial track registration, preservation style or erosion, which is aggravated by the palaeosurface currently serving as a busy informal suburban road. The sedimentological evidence indicates that during the deposition of the uEF, Upper Moyeni was prone to flash floods and drying in a generally low-energy, depositional system with small streams and vegetated, low-gradient floodplains. The climate was semi-arid, with seasonal and likely high-intensity rain, and the palaeoenvironment was able to support large vertebrates, such as carnivorous theropods, herbivorous ornithischian dinosaurs, burrowing tetrapods (possibly synapsids). Although the Upper Moyeni tracks appear superficially similar, i.e., mesaxonic, tridactyl tracks, there are morphological distinctions between the tracks. These distinctions primarily relate to the digit width of the tracks, medial digit projection and total digit divarication, though the latter is treated with caution, as it is naturally variable (Moratalla *et al.*, 1988; Lockley, 2009). Therefore, the Upper Moyeni tracks are assigned to at least three ichnotaxa, commonly preserved in the Early Jurassic: *Grallator, Eubrontes* and *Kayentapus*. Recent in-depth, statistical analyses suggest that these ichnites can be attributed to three distinct trackmakers (Farlow, 2018), which are near-universally accepted to be theropods (Olsen, 1980; Lockley, 1991; Olsen *et al*., 1998; Li *et al*., 2006; Sciscio *et al.,* 2016, 2017b; Farlow, 2018 but cf. Weems, 2019). Consequently, the ichnoassemblage identified at Upper Moyeni expands the theropod diversity known from the Early Jurassic of southern Africa, where the osteological record is limited to fragmentary theropod bone material. Moreover, the Upper Moyeni ichnoassemblage also increases the abundance of *Kayentapus* recorded in the upper Stormberg Group, being the fourth site, where this taxon occurs (see Discussion). Tracks of large and very large tridactyl animals, attributable to theropod dinosaurs, provide a good source of independent information as to the fauna, occupying niche space during the Early Jurassic in southern Africa. The tendency towards increasing diversity in size of tridactyl tracks, and by extension their body size, runs in tandem with the increasing diversity of non-sauropod, sauropodomorph body fossils at this time and particularly within the uEF (Bordy *et al*., 2020; Viglietti *et al*., 2020). Moreover, the expansion in size-class diversity of theropod-attributed tracks during the Early Jurassic can be discussed in the light of rebound and recovery after the ETE. Finally, more detailed biostratigraphic work on the upper Stromberg may place these very large (> 50 cm) tracks with theropod affinity in the ecological context of the contemporaneous, very large (12-tonne) sauropodomorphs, such as *Ledumahadi mafube* (McPhee *et al*., 2018) in this southern part of Gondwana in the Sinemurian and Pliensbachian.

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Supplementary Data Archiving

Supplementary data (i.e., photogrammetric models) for the Upper Moyeni project are available on Figshare: https://doi.org/10.6084/m9.figshare.12318848.

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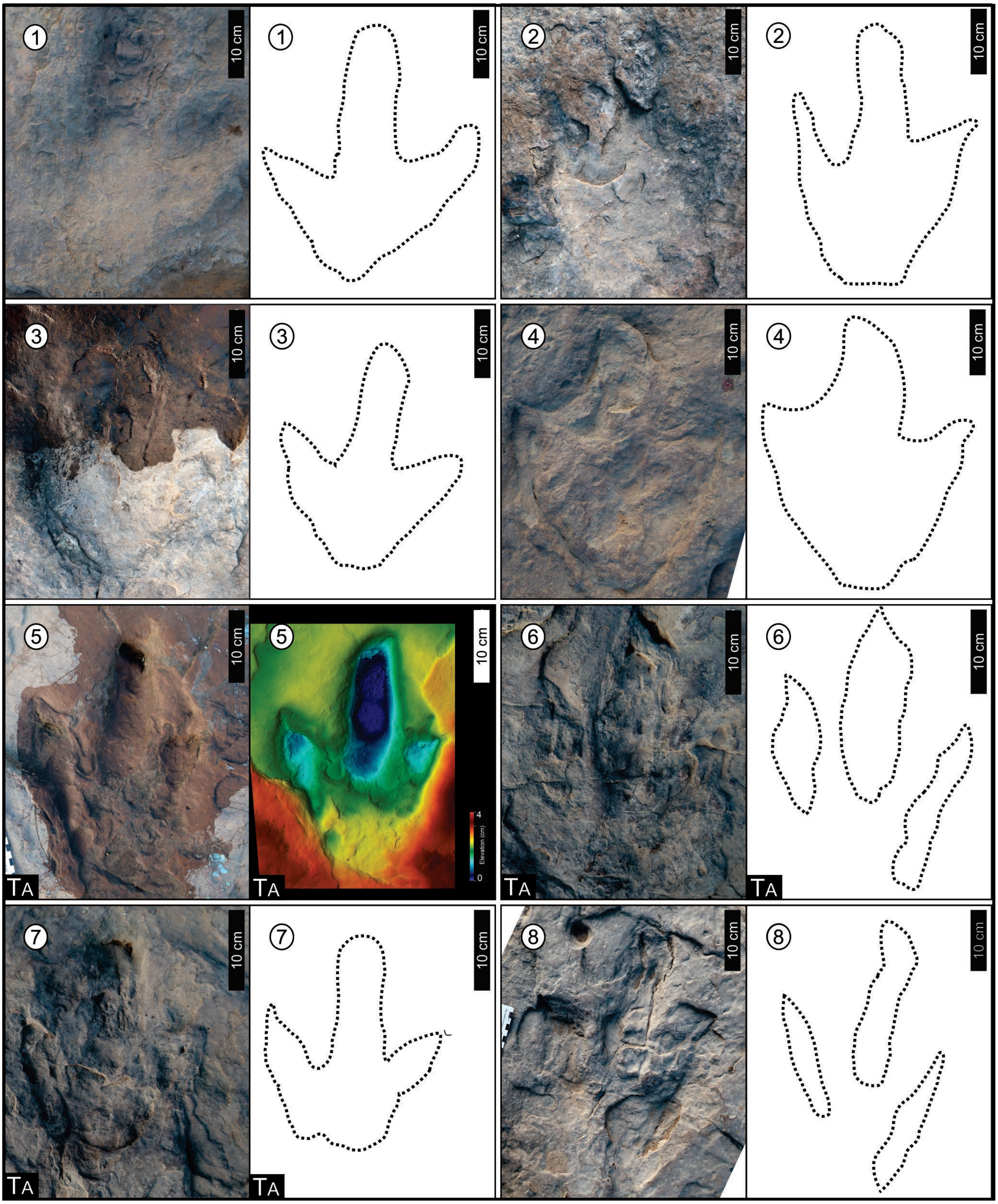
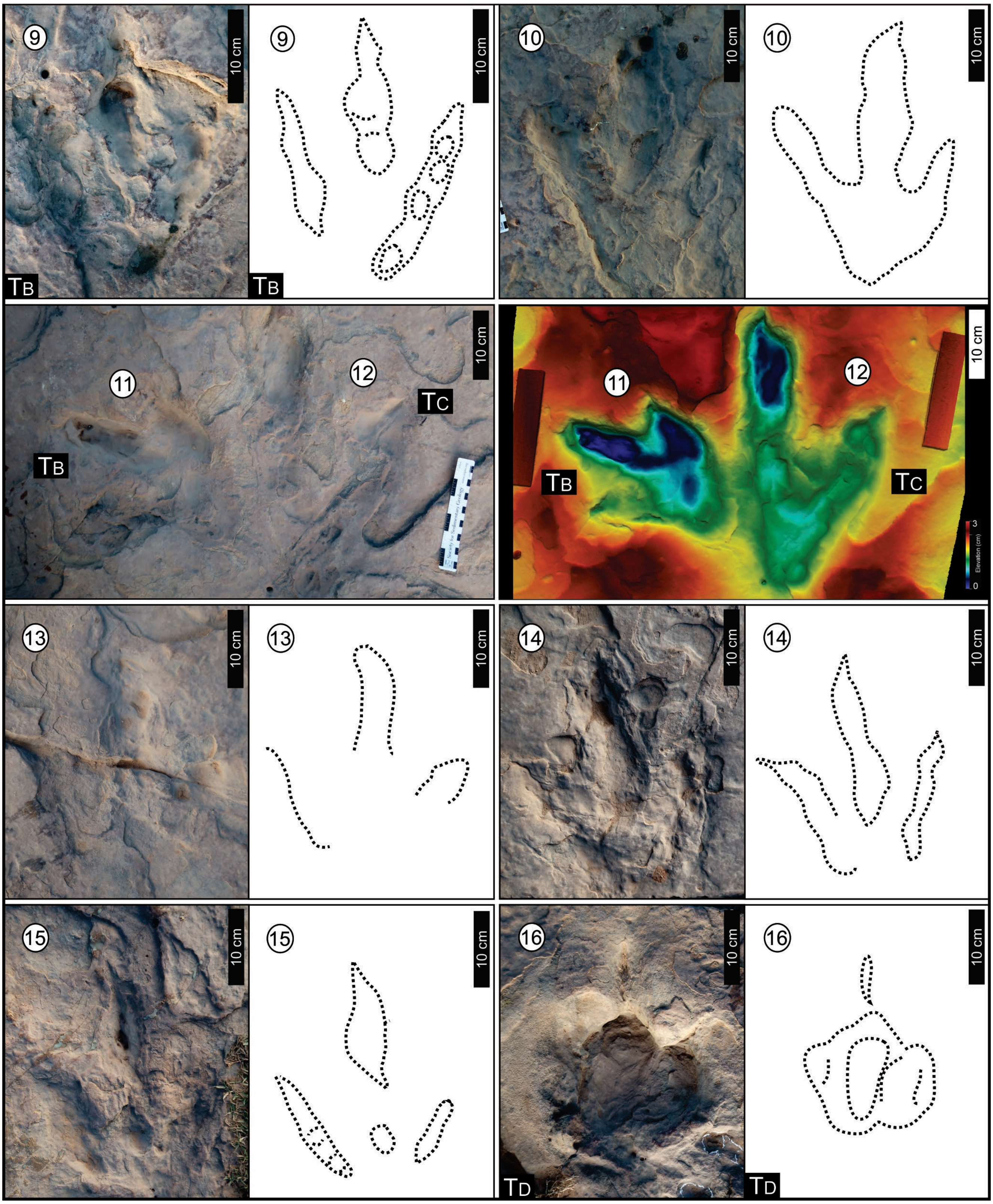
Appendix Fig. 1.

Photographs and interpretative outlines and some false-coloured depth model maps of tridactyl ichnites documented at the Upper Moyeni ichnosite. See Fig. 4 for individual trackway illustrations. Abbreviations: TA – Trackway A, TB – Trackway B, TC – Trackway C, TD – Trackway D, TE – Trackway E.




⑨
10 cm
TB
⑨
10 cm
TB
⑩
10 cm
⑩
10 cm
⑪
⑫
TC
TB
10 cm
⑪
⑫
TB
TC
10 cm
3
Elevation (cm)
0
⑬
10 cm
⑬
10 cm
⑭
10 cm
⑭
10 cm
⑮
10 cm
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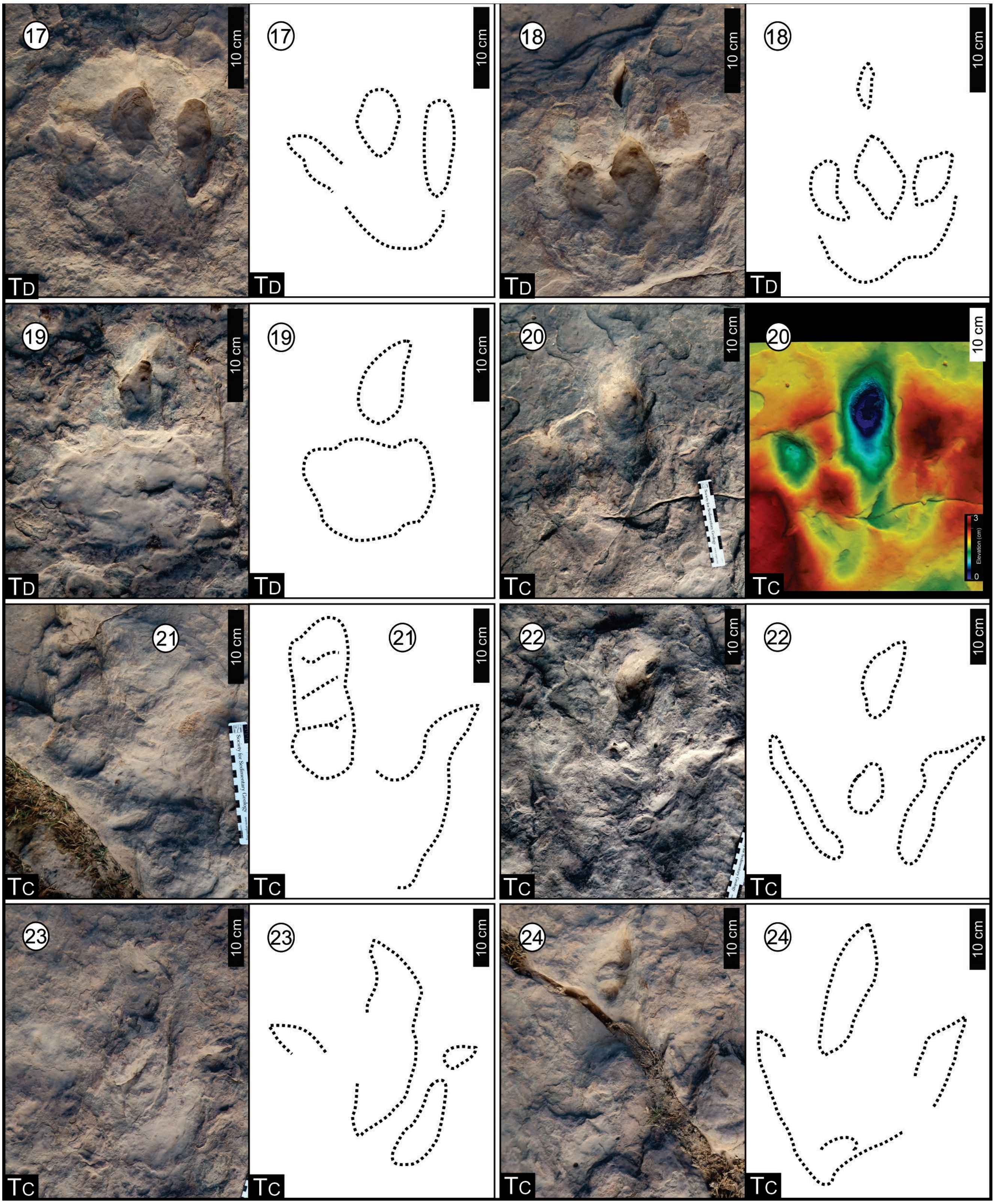
10 cm
⑯
10 cm
TD
⑯
10 cm
TD


17
10 cm
TD
17
10 cm
TD
18
10 cm
TD
18
10 cm
TD
19
10 cm
TD
19
10 cm
TD
20
10 cm
TC
20
10 cm
3
Elevation (cm)
0
TC
21
10 cm
Society for Sedimentary Geology
TC
21
10 cm
TC
22
10 cm
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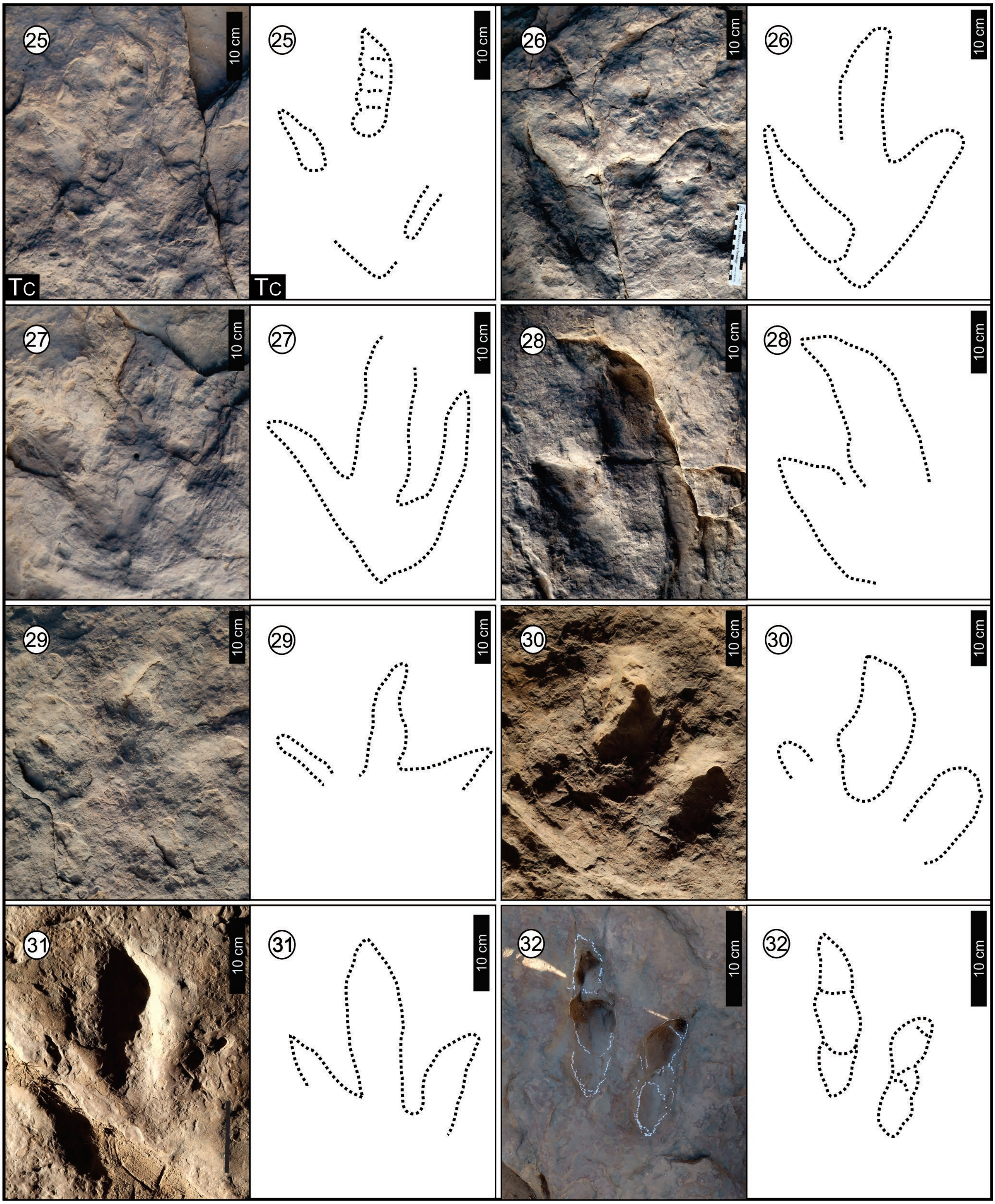
24
10 cm
TC
24
10 cm
TC


25
10 cm
Tc
25
10 cm
Tc
26
10 cm
26
10 cm
27
10 cm
27
10 cm
28
10 cm
28
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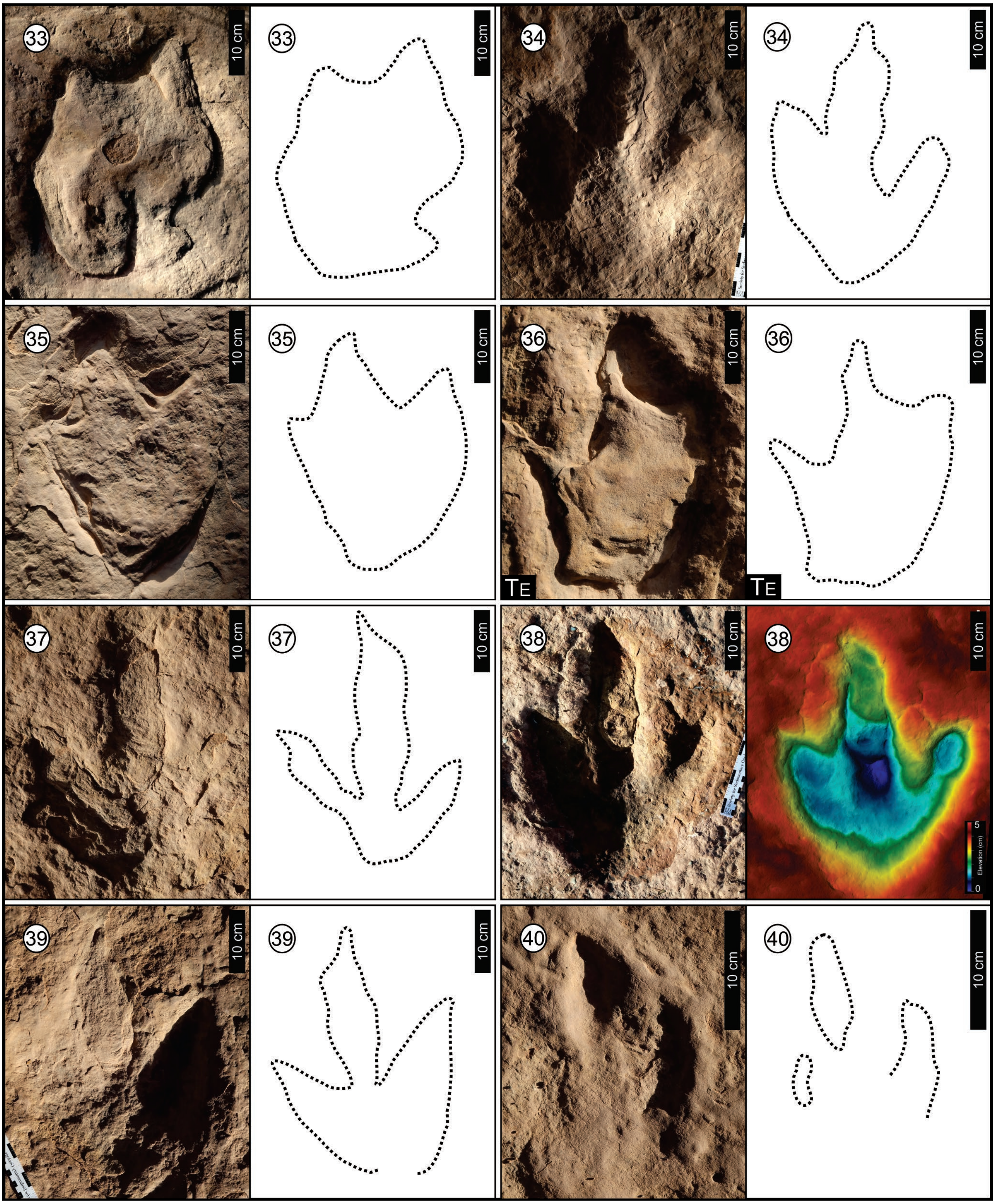
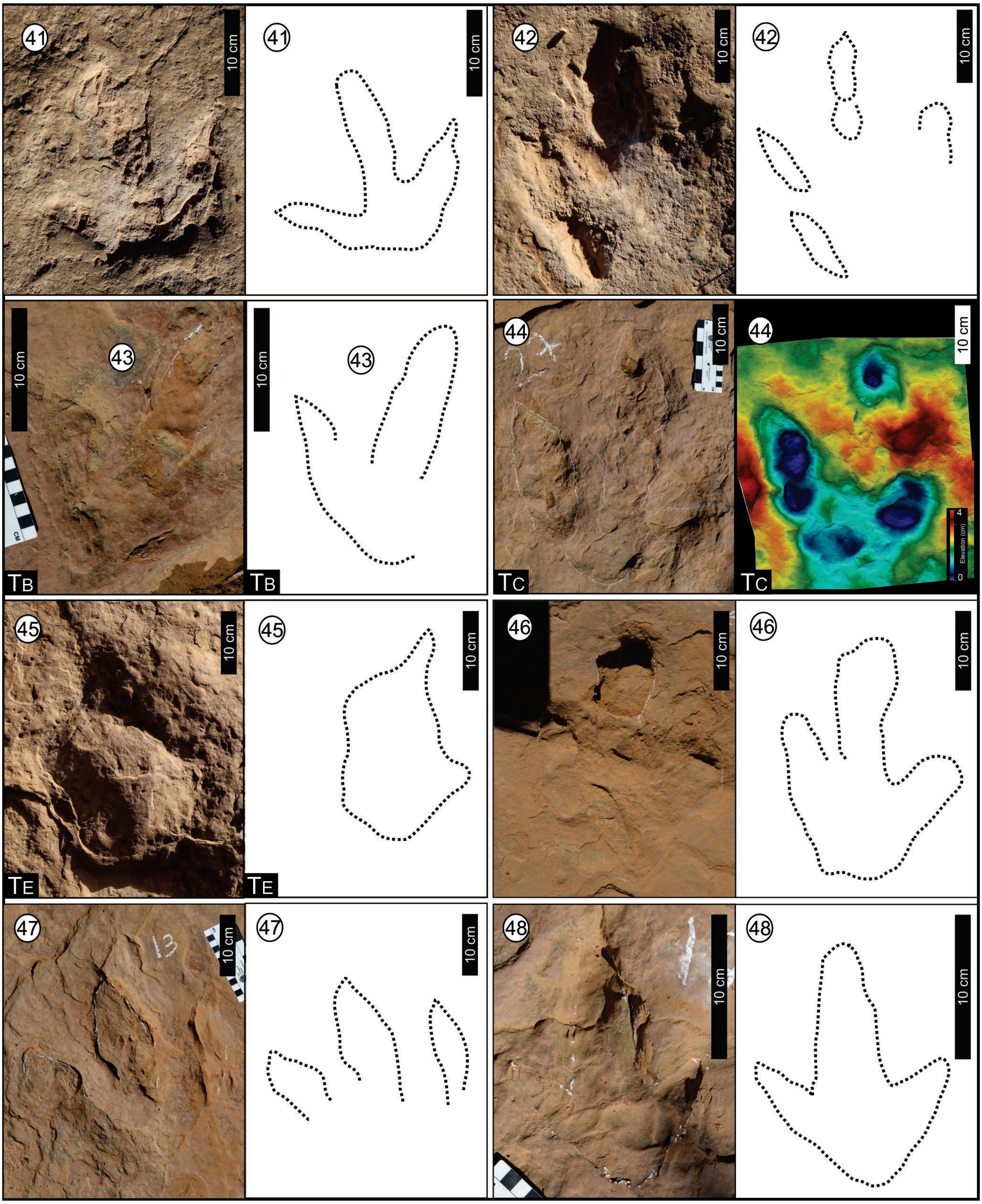
31
10 cm
32
10 cm
32
10 cm


33
10 cm
33
10 cm
34
10 cm
34
10 cm
35
10 cm
35
10 cm
36
10 cm
TE
36
10 cm
TE
37
10 cm
37
10 cm
38
10 cm
38
10 cm
5
Elevation (cm)
0
39
10 cm
39
10 cm
40
10 cm
40
10 cm


41
10 cm
41
10 cm
42
10 cm
42
10 cm
43
10 cm
TB
43
10 cm
TB
44
10 cm
TC
44
10 cm
4
Elevation (cm)
0
TC
45
10 cm
TE
45
10 cm
TE
46
10 cm
46
10 cm
47
13
10 cm
47
10 cm
48
10 cm
48
10 cm

Appendix Table 1

Track measurements and morphological preservation grades of documented ichnites preserved at Upper Moyeni. Blank fields indicate that the specific parameter could not be measured due to obscured track morphology or absence of the necessary feature. Abbreviations: TL – track length, TW – track width, TS – track span, Dp – digit III projection, II, III, IV – digits, L – digit length, ^ – interdigit angles, Pm – morphological preservation grade. See Appendix Fig. 1 for individual track illustrations.

Track	**TL (cm)**	**TW (cm)**	**TS (cm)**	**TL/ TW**	**Dp (cm)**	**Dp/TS**	**Dp/TL %**	**LII (cm)**	**LIII (cm)**	**LIV (cm)**	**II^IV (°)**	**II^III (°)**	**III^IV (°)**	**Pm**
1	40	33	33	1.21	17.4	0.53	44	21.8		24.9	70	34	36	1
2	42	30	29	1.40	12.3	0.42	29				53			1
3	33	27	26	1.22	13.8	0.53	42				70			1
4	41	31	31	1.32	14.8	0.48	36				62			1
5	33	22	23	1.50	11.5	0.50	35		22		40	22	18	2.5
6	34	23	23	1.48	11.6	0.50	34	15.8	23.1	21.3	42	21	21	2
7	27	23	23	1.17	10.8	0.47	40	15.9		18.2	63	34	29	2
8	44	27	28	1.63	16.7	0.60	38	20.2	24.6	22.7	45	25	20	2a
9	28	20	20	1.40	8.9	0.45	32	15.3	14.8	20	38	18	20	2.5
10	36	24	24	1.50	14.3	0.60	40	22.9			52			2
11	27	19	18	1.42	9.6	0.53	36	12.4	15.4		65	31	34	2
12	41													2c
13	27	25	24		13									1p
14	29	24	24	1.21	11.9	0.50	41	16.3	22.5	19.5	51	27	24	2
15	30	23	23	1.30	18.1	0.79	60				57			1p?
16	24	17		1.41				11.2		12.8				0a
17	23	18		1.28										0a
18	25	17		1.47				11.8		15				0a
19	21	14		1.50				10.6		10.8				0a
20	45	36	36	1.25	16.1	0.45	36	23.2	25.6	29.7	51	25	26	1
21	35													1p
22	41	37	38	1.11	17	0.45	41	26	30	24	66	28	38	2
23	38	36	36	1.06	15.6	0.43	41		32		55			1p
24	44	34	35	1.29	17.7	0.51	40				62			1c
25	46	30		1.53							65			2c
26	51	39	37	1.31	20.3	0.55	40				61			2
27	42+	32	31	1.31	12.8+	0.41	30				64			2
28	43													1p
29			40								100			0
30	36		34		18.1	0.53	50							1p
31	26	26	26		13.4	0.52					63			2p
32									17					3p
33	38	25		1.52										0a
34	45	31	27	1.45	16.9	0.63	38				56			2
35	35	22	22	1.59	10.3	0.47	29				55			1a
36	32	25		1.28										1a
37	39	30	29	1.30	20.6	0.71	53		29		76			2p?
38	44	33	32	1.33	15.1	0.47	34	25	28	30	54	30	24	2
39	40	29	26	1.38					26.1		62			1
40	15		11											1p

Track	**TL (cm)**	**TW (cm)**	**TS (cm)**	**TL/ TW**	**Dp (cm)**	**Dp/TS**	**Dp/TL %**	**LII (cm)**	**LIII (cm)**	**LIV (cm)**	**II^IV (°)**	**II^III (°)**	**III^IV (°)**	**Pm**
41	22	23	23	0.96	10.8	0.47	49				93			1
42	33	27	25	1.22	11.5	0.46	35				58			2p
43	22+													1p
44	41	33	34	1.24	17.0	0.5	41	23.0	27.0					2
45	29	23		1.26										0
46	30.5	22.8	21.4	1.34	12.2	0.57					57			2
47		31.5												1p
48	17	13	13.1	1.31	8.7	0.66	51	10.6		9.4	74			2
49														0