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Darting towards Storm Shelter: A minute dinosaur trackway from southern Africa

Theropod dinosaurs are considered the main terrestrial carnivores in the Jurassic and Cretaceous. Their rise to dominance has been linked to, among others, body size changes in their early history, especially across the Triassic–Jurassic boundary. However, to qualitatively assess such temporal trends, robust skeletal and trace fossil data sets are needed globally. The richly fossiliferous southern African continental rock record in the main Karoo Basin offers an unparalleled perspective for such investigations. Herein, by documenting a newly discovered Early Jurassic trackway of very small, functionally tridactyl tracks near Storm Shelter (Eastern Cape) in South Africa, the track record can be expanded. Based on ichnological measurements at the ichnosite and digital 3D models, the footprint dimensions (length, width, splay), locomotor parameters (step length, stride, speed), and body size estimates of the trackmaker are presented. In comparison to other similar tracks, these footprints are not only the smallest *Grallator*-like tracks in the Clarens Formation, but also the most elongated dinosaur footprints in southern Africa to date. The tracks also show that the small-bodied bipedal trackmaker dashed across the wet sediment surface at an estimated running speed of ~12.5 km/h. During the dash, either as a predator or as a prey, the trackmaker's small feet sunk hallux-deep into the sediment. The tracking surface is overgrown by fossilised microbial mats, which likely enhanced the footprint preservation. Based on track morphometrics and the regional dinosaur skeletal record, the trackmakers are attributed to *Megapnosaurus rhodesiensis* (formerly *Syntarsus rhodesiensis*), a small-to-medium-sized, early theropod common in southern Africa.

Significance:

- A newly discovered Early Jurassic theropod trackway in South Africa contains not only the smallest tracks in the Clarens Formation, but also the most elongated dinosaur footprints in southern Africa to date.
- The tracks show that the small bipedal trackmaker dashed across the wet sediment surface at an estimated running speed of ~12.5 km per hour.
- During the run, the trackmaker's feet sunk so deeply into the sediment that even the forwards-directed halluces were impressed.

Introduction

Mounting evidence for body size changes in theropods^{1–3}, a class of carnivorous dinosaurs, during the dawn of the dinosaurs is increasingly placing the southern African fossil record into the focus of global palaeontological studies. Late Triassic to Early Jurassic dinosaur footprints, for which southern Gondwana, especially southern Africa, is an excellent archive, are particularly useful proxies for such biogeological investigations. In particular, the Lower Jurassic of southern Africa (i.e. the upper Stormberg Group; Figure 1) is key in this regard as: (1) it was deposited in a semi-arid continental ecosystem of rivers, lakes and deserts; (2) it is richly fossiliferous, and (3) it provides clues on how life recovered after the global biodiversity crisis event that occurred ~200 million years ago.^{4,5}

This study reports on the smallest dinosaur footprints, forming a single trackway, in the Clarens Formation (uppermost Stormberg Group; Figure 1) of South Africa and shows that these tracks are also, to date, the most elongated dinosaur footprints from the Early Jurassic of southern Africa. These tiny, slender tracks in the lower Clarens Formation are part of the Lower Jurassic footprint assemblage, which in southern Africa is contained in the upper Elliot Formation (Hettangian–Sinemurian) and in the conformably overlying Clarens Formation (Sinemurian–Pliensbachian).⁴ These two rock units also contain the two largest (footprint lengths: 55–57 cm)^{6–9} and the smallest (footprint length: ~6.5 cm)¹⁰ tridactyl tracks on record thus far, all reported from Lesotho. Because the current tracks are part of the ichnofauna of the lower Clarens Formation, which is likely Sinemurian⁴, they enrich the Early Jurassic track record locally and globally, and thus can contribute to the evaluation of the temporal patterns in the footprint record, which, in turn, can add to the ongoing debate on dinosaur body size changes across the Triassic–Jurassic boundary^{1–3,11}.

Geological background

The dinosaur footprints investigated in this study were discovered north of Maclear in the Eastern Cape of South Africa (Figure 1) by a local resident, Mrs Adele Moore, and her field party in 2014 along a footpath leading to the Storm Shelter archaeological site.¹³ Found at the same altitude as the rock art site, the very fine-grained sandstone slab, containing the single trackway of five well-impressed dinosaur footprints, is part of the lowermost Clarens Formation (Figure 1). Here, at Storm Shelter, and throughout the main Karoo Basin (South Africa and Lesotho), the basal Clarens Formation, which is likely Sinemurian^{4,14} in age, is characterised by tabular, fine- to medium-grained sandstone beds and subordinate mudstones. Suites of sedimentary structures (e.g. horizontal lamination, cross-bedding, ripple cross-lamination, desiccation cracks; [Supplementary figure 1](#)) in these rocks point to deposition in decelerating powerful traction currents and stagnant water.^{15,16} Overall, these rocks indicate

that the ancient wet aeolian ecosystem was prone to intermittent flash flooding and drying episodes.^{15,16} While being less fossiliferous than the conformably underlying Hettangian to Sinemurian upper Elliot Formation, the palaeontological record of the Clarens Formation is diverse, both in vertebrate skeletal remains and trace fossils^{4,6,14,17,18}, particularly in footprints, and most notably in dinosaur tracks, as recently summarised by Mukaddam et al.¹⁹

Methods

The footprints investigated in this study were subjected to morphometric measurements as shown in Figure 2. Moreover, for comparative purposes, four additional footprints collected from Lesotho, two *Grallator*-like (LES 283 and 288) and two *Anomoepus*-like (LES 111 and 112) tracks from the Clarens and upper Elliot Formations, respectively, were also briefly analysed for this study. These four Lesotho tracks were

collected by Dr Paul Ellenberger pre-1970, and are now housed in the Ellenberger Collection at the University of Montpellier (France).

The ichnological morphometric measurements and the standard proxies derived from them, which estimate the trackmaker's hip height, gait, body length and speed, are summarised in Table 1 and detailed in Supplementary tables 1–5 (with references). The relevant *modus operandi* is explained elsewhere^{5,8,9,10,19} and in references therein. The track measurements were taken physically in the field using a calliper. After photographing each track with a Nikon D5100 digital camera (focal length 50 mm), individual photogrammetric 3D models and false-colour depth maps were generated with Agisoft Metashape Professional (version 1.6.4) and CloudCompare (v.2.11.0) software packages, respectively. Following the standard protocol of Falkingham et al.²⁰, the photogrammetric 3D models and relevant raw data are publicly available online via this open access data repository link: <https://doi.org/10.6084/m9.figshare.13007240>

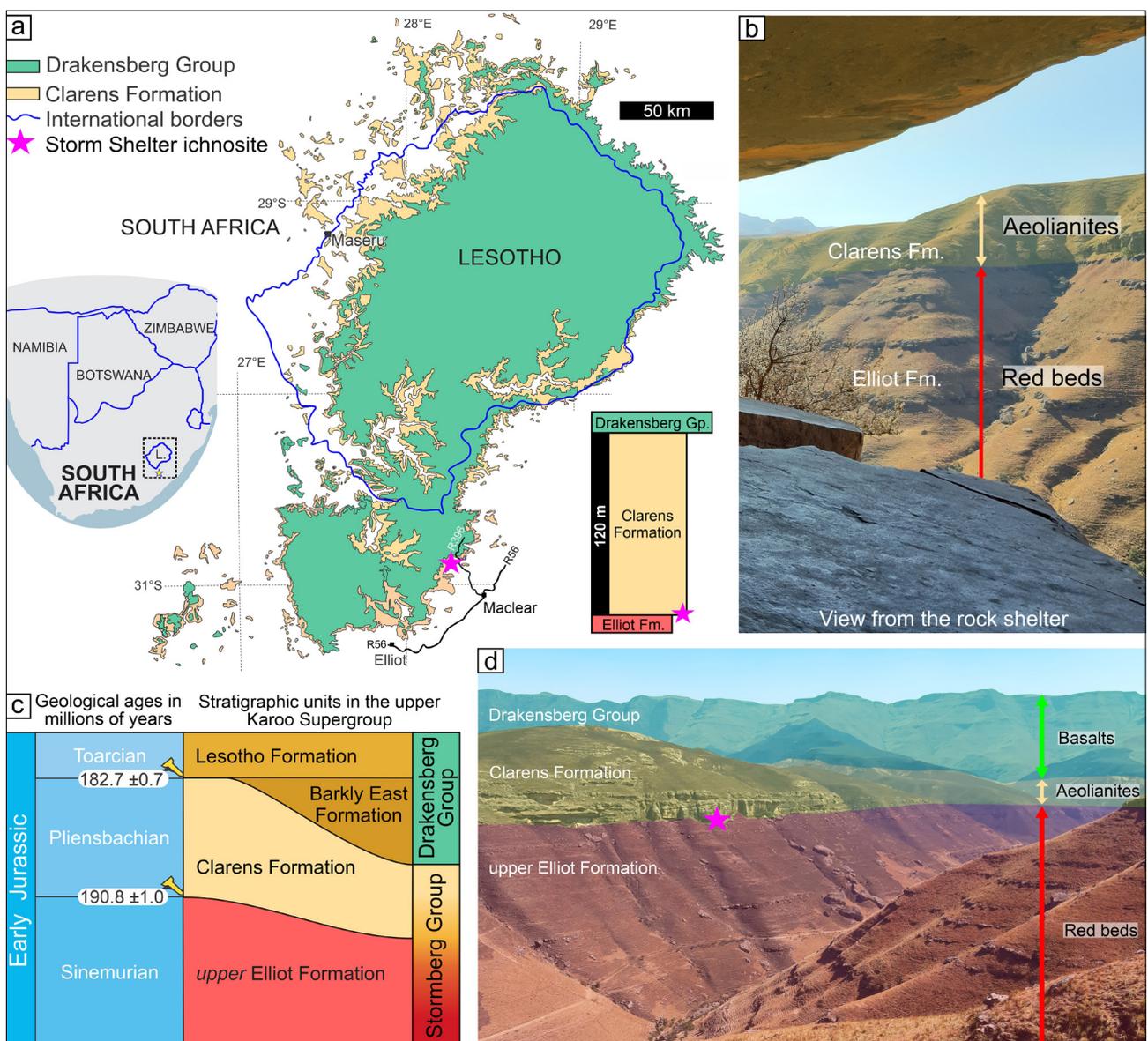
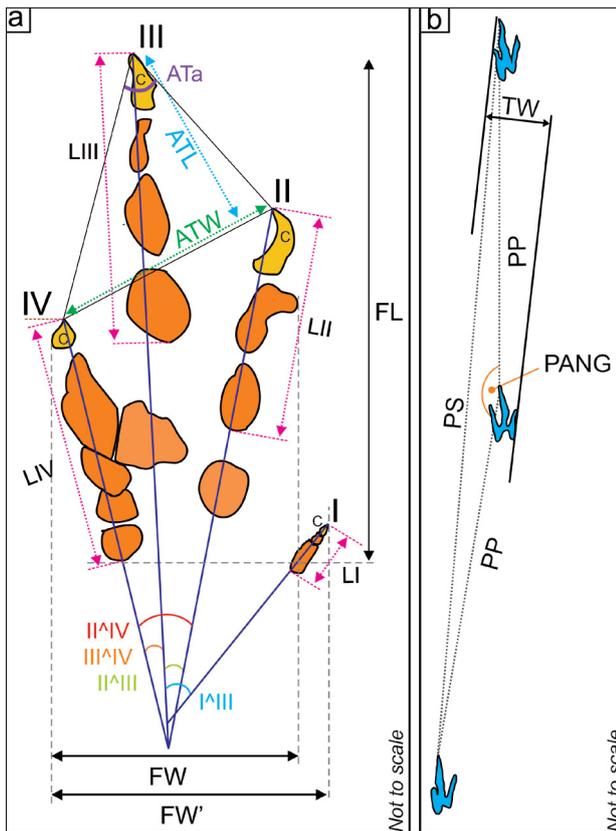


Figure 1: Geological context of the Storm Shelter ichnosite. (a) Simplified geological map of the upper part of the Karoo Supergroup in the Republic of South Africa and Lesotho, showing the position of the study locality northwest of Maclear (Eastern Cape). Inset log shows the local thickness of the Clarens Formation and the relative position of the ichnosite within it. (b–d) Stratigraphic details of the ichnosite within the upper Karoo Supergroup. Map derived by combining data from Johnson and Wolmarans¹² and own mapping.



Roman numerals I–IV denote digits; L, length of digit; C, claw trace; FL, foot length; FW, foot width; FW', foot width including digit I; ATW, anterior triangle width; ATL, anterior triangle length; Ata, anterior triangle angle; interdigital angles between digits I[^]III, II[^]III, III[^]IV and II[^]IV; TW, trackway width; PP, pace; PS, stride; PANG, pace angulation

Figure 2: Key morphological features of the tracks and their measurements obtained for the ichnological analyses: (a) track measurements and (b) trackway measurements.

Results

The Storm Shelter ichnosite preserves a single trackway of five, very small, narrow, elongated and strongly mesaxonic footprints (Figure 3, Table 1, Supplementary table 1) with the following main parameters (average values): length 7.5 cm, width 3.6 cm, length/width ratio >2.1. The ratios of the anterior triangle²¹ length to width and the anterior triangle length to track width are 1 and 0.9, respectively. Manus tracks were not observed.

These elongate, digitigrade tracks preserve evidence for claw marks at the tips of the three well-impressed digits and one lightly impressed digit, indicative of a hindfoot that was functionally tridactyl and featured a well-developed hallux (digit I). The slender digit impressions only sporadically show discrete, oval digital pads, most likely due to extensive sediment collapse within the tracks, which would also suggest that these are likely penetrative tracks^{22,23} (i.e. the foot penetrated the substrate much more deeply than is apparent from the track outlines on the tracking surface). The penetrative nature of the tracks is further supported by the very narrow distal portion of digit III. Relative to digits II and IV, digit III is better impressed and extends beyond digits II and IV, which are subequal. Both the apex of the anterior triangle and the divarication between digits II and IV form acute angles of 54° and 29°, respectively. On average, digit I is ~1 cm long and its long axis encloses an acute angle of 54° with the long axis of digit III. The variability of the position of the digit I impression relative to the other digits (Figure 3, Table 1) indicates that the hallux did not have any functional use for locomotion or stability.

The single trackway that these five pes tracks form is narrow (~6.1 cm), and relative to the footprint length of 7.5 cm, preserves long strides of nearly 1 m (Figure 4, Table 1, Supplementary table 2). The long axis of

digit III is essentially parallel to the trackway axis. The average pace is 47.6 cm with an angulation of 172°, and the track width to trackway width ratio is 59%, which define a narrow-gauge trackway. Along the trackway, the morphological quality of the tracks is uniform, although well-developed wrinkle structures, a type of microbially induced sedimentary structure, are present both inside and outside the tracks on the tracking surface (Figure 4 and Supplementary figure 1), and interfere with the outlines of some of the tracks (e.g. see the posterior of track #1 in Figure 3). The microbially induced sedimentary structures and the digit I impression demonstrate that the tracks are not underprints, but rather primary, penetrative footprints impressed directly and deeply on the tracking surface.

Because of the incomplete/missing digital pad impressions, some ill-defined imprint walls, and superimposition of microbial structures, all five Storm Shelter tracks rank low, around 1.5 on the recently proposed^{24,25}, four-point (0-1-2-3) track-grading scale. Because of the suboptimal morphological quality of the digital pad impressions, only a very tentative phalangeal formula of 1(?)2-3(?)4-0 (not counting the claw traces) is inferred from the collective assessment of the five tracks.

Using standard ichnological formulae^{26,27} (detailed in Supplementary tables 3 and 4), the trackmaker's hip height, body length, body mass, gait and speed were estimated as summarised in Table 1. Based on these parameters, which are essentially derived from the average foot length and stride values, the trackmaker's hip height was ~32 cm, its body length was ~120 cm and it weighed ~3–4 kg (Table 1, Supplementary table 3). The body size of this digitigrade, obligate bipedal trackmaker thus is comparable to small-sized, long-legged, ground-dwelling extant birds, which fall into a size class between a very tall domestic rooster and a bustard or a wild turkey (hip height 0.39 m and body mass of ~5–7 kg; cf.²⁸). The track data are insufficient to determine whether the small trackmaker was a juvenile or a small-sized but fully grown adult.

The trackmaker's allometric and morphometric gait values are 3.2 and 2.9, respectively, indicating a constant 'running' gait^{26,27} across the sediment surface (Table 1, Supplementary tables 3 and 4). The allometric and morphometric speed estimations show that the trackmaker ran at an average speed of 3.45 m/s (i.e. ~12.42 km/h). The relatively rapid locomotion of the trackmaker is also suggested by the narrow trackway, as during fast movement, running bipedal animals place their feet closer to the midline (cf.²⁹). The stride/footprint length ratio for the Storm Shelter trackway is 12.9 and thus is only slightly greater than the median value³⁰ for trackways in this size category (i.e. foot length of 5–10 cm) from the early Mesozoic and attributed to theropods. This suggests that the trackmaker was moving in a typical manner for a small theropod.

Discussion

The morphological characteristics describing the Storm Shelter footprint proportions (Table 1) closely resemble those of *Grallator*-like tracks; however, due to the moderate to low quality of these tracks, their ichnotaxonomic treatment is not warranted here. *Grallator* is an ichnogenus that refers to globally occurring tracks of bipedal theropod dinosaurs of early Mesozoic age. *Grallator* tracks are small (<15 cm long), elongate with a footprint length/width ratio of ≥2, narrow digit divarication angles (10–30°) of the slender, pointy toes and a great anterior projection of digit III (i.e. mesaxonic tracks; e.g.^{21,26,31,32}). Moreover, *Grallator* tracks are digitigrade, often preserve claw traces and occasionally also the impression of digit I²⁸, and thus the ichnogenus refers to functionally tridactyl tracks.

In the early Mesozoic ichnological record of the main Karoo Basin of southern Africa, tracks referable to *Grallator* are not rare.^{6-10,33-37} Being only ~1 cm longer than the smallest *Grallator* tracks in southern Africa (described¹⁰ from the lower part of the upper Elliot Formation in Lesotho), the Storm Shelter tracks, with their average footprint length of 7.5 cm, are among the smallest *Grallator*-like tracks in the Lower Jurassic of this region, and certainly the smallest of all dinosaur tracks in the Clarens Formation to date.



Table 1: Summary of the morphometric measurements and derived parameters of the Storm Shelter tracks. See Supplementary tables 1–4 for full morphometric measurements and calculations. Length measurements are in centimetres.

Track #	#1	#2	#3	#4	#5	Average
Footprint length (FL)	7.47	7.85	7.05	7.47	7.76	7.5
Footprint width (FW)	3.06	3.71	3.38	4.37	3.33	3.6
Footprint width' (FW')	3.21	4.39	3.81	3.35	3.33	3.6
FL/FW ratio	2.4	2.1	2.1	1.7	2.3	2.1
AT angle (degrees)	52	64	57	45	49	54
ATL	3.04	2.79	2.84	3.92	3.44	3.2
ATW	3.09	3.69	3.24	3.23	3.13	3.3
ATL/ATW ratio	1.0	0.8	0.9	1.2	1.1	1.0
ATL/FW ratio	1.0	0.8	0.8	0.9	1.0	0.9
II ^ IV (degrees)	26	34	25	32	30	29
II ^ III (degrees)	16	14	14	12	20	15
III ^ IV (degrees)	11	20	11	21	10	15
I ^ III (degrees)	66	62	45	42	53	54
No. of toes	4	4	4	4	4	4
LI	1.07	1.08	0.87	1.42	1.12	1.1
LII	3.11	4.26	3.16	2.80	3.04	3.3
LIII	4.08	4.51	4.07	5.46	4.22	4.5
LIV	3.77	4.29	3.48	4.05	3.74	3.9
Pace	–	–	–	–	–	47.17
Stride	–	–	–	–	–	96.75
Pace angulation (degrees)	–	–	–	–	–	174.0
Trackway width (TW)	–	–	–	–	–	6.1
Trackway ratio (FW/TWx100)	–	–	–	–	–	59
Allometric	Hip height	–	–	–	–	30.2
	Gait	–	–	–	–	3.2
	Speed (m/s)	–	–	–	–	3.6
Morphometric	Hip height	–	–	–	–	33.5
	Gait	–	–	–	–	2.9
	Speed (m/s)	–	–	–	–	3.3
Body length	–	–	–	–	–	120.6
Body mass (kg)	Allometric	–	–	–	–	2.91
	Morphometric	–	–	–	–	3.98

AT, anterior triangle; ATL, anterior triangle length; ATW, anterior triangle width; ATL/FW, anterior triangle length to footprint width ratio; II ^ IV, total divarication between digits II and IV; (II ^ III, divarication between digits II and III; III ^ IV, divarication between digits III and IV; I ^ III, divarication between digits I and III; no. of toes, number of visible digit marks on the footprint; LI–LIV: length of digits I, II, III and IV, respectively, inclusive of the claw trace

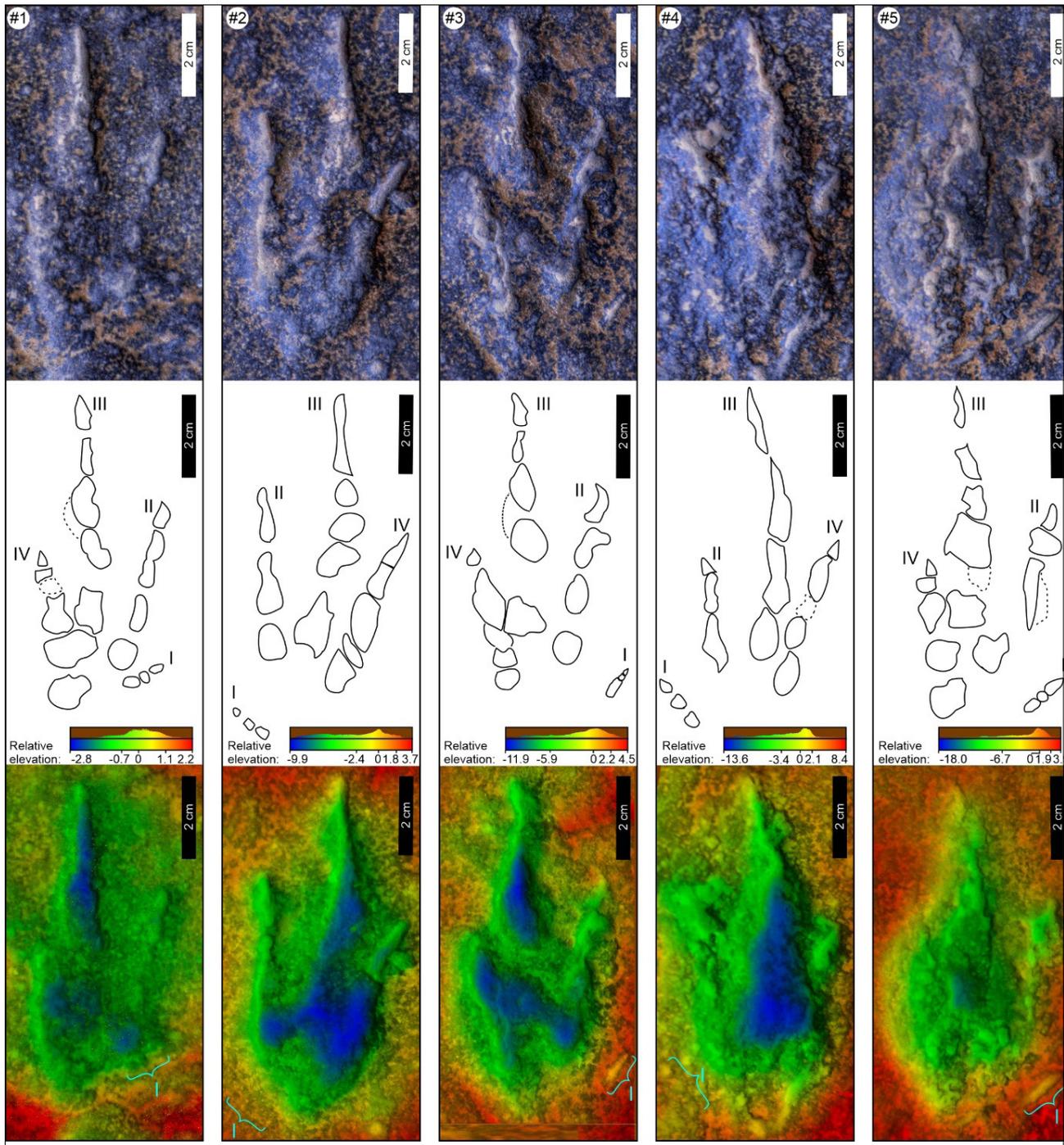


Figure 3: Five *Gallator* tracks from the lower Clarens Formation at the Storm Shelter ichnosite. Each track (#1–#5) is illustrated with three different images: *top* – orthophoto derived from photogrammetric model; *middle* – interpretive outline drawing; *bottom* – false-colour depth map (dark red is the highest point; blue is the lowest). See Supplementary table 1 for track morphometric measurements and <https://doi.org/10.6084/m9.figshare.13007240> for the photogrammetric models. Roman numerals I–IV denote digits; for clarity, the length of digit I is marked with curly brackets on the false-colour depth maps.

In the Clarens Formation, only four tracks that are morphologically similar to *Gallator* were mentioned by Ellenberger⁶ from Lesotho: three tracks of similar size (~10 cm long) from zone B5 (his figures 127–129) and one from zone B6 (no illustration). In spite of efforts to relocate these tracks in the field, only the latter track (*G. molapo* – Leribe-Molapo) as well as *G. (Paragallator) matsiengensis* (Matsieng, his figure 128) are available for direct study as specimens LES 288 (holotype) and LES 283 (the only replica of the now lost holotype), respectively, in the Ellenberger Collection at the University of Montpellier (France). Because these ichnotaxa are partially preserved, severely obscured by extramorphological features

and lacking information regarding the foot anatomy of the trackmaker, they can be considered *nomina nuda*, but being the only tracks identified as ‘*Gallator*’ from the Clarens Formation, the digital 3D models of these tracks are documented here (Figure 5, Supplementary table 5) for sake of completeness. Morphometric measurements show that these ‘*Gallator*’ tracks are >33% longer (average length: 11.3 cm) than the Storm Shelter tracks. The only other footprints in the Clarens Formation that have been likened to *Gallator* are large, ~40-cm-long tridactyl tracks reported³³ from the eastern Free State (Uniondale) in South Africa. However, these large, broad tracks, due to their key track morphological

parameters (e.g. length-to-width ratio of 1.2; total divarication of 71°), are not considered here to be attributable to *Grallator* (see ^{8,21,32,35} and references therein for a more detailed discussion on the ichnotaxonomic considerations of these tracks).

Very small tridactyl tracks from Lesotho have been reported^{5,6,10} from the upper Elliot Formation (Hettangian–Sinemurian, zone B1 of Ellenberger). However, with the exception of the minute *Grallator* tracks¹⁰ in the lower part of the upper Elliot Formation at Lephotu in the Roma valley, compared to which the Storm Shelter tracks are similar in length but more elongated, all other very small tridactyl tracks (footprint length <9

cm) from the Elliot Formation seem to be consistent with ichnological parameters of either *Trisauropodiscus*-like or *Anomoepus*-like tracks (Figure 6, Supplementary table 1; also see^{5,10}). Compared to these older, likely pre-Sinemurian⁴, tridactyl tracks (Figure 6), the Storm Shelter tracks are typically more elongated with narrow digit divarication angles ($10\text{--}30^\circ$) and a greater anterior projection of digit III (i.e. more mesaxonic; see Supplementary table 1). All in all, these comparisons show that, thus far, the Storm Shelter tracks are among the most elongated (i.e. high length/width ratio) *Grallator*-like tracks reported from the Lower Jurassic of southern Africa, and the smallest in the Clarens Formation.

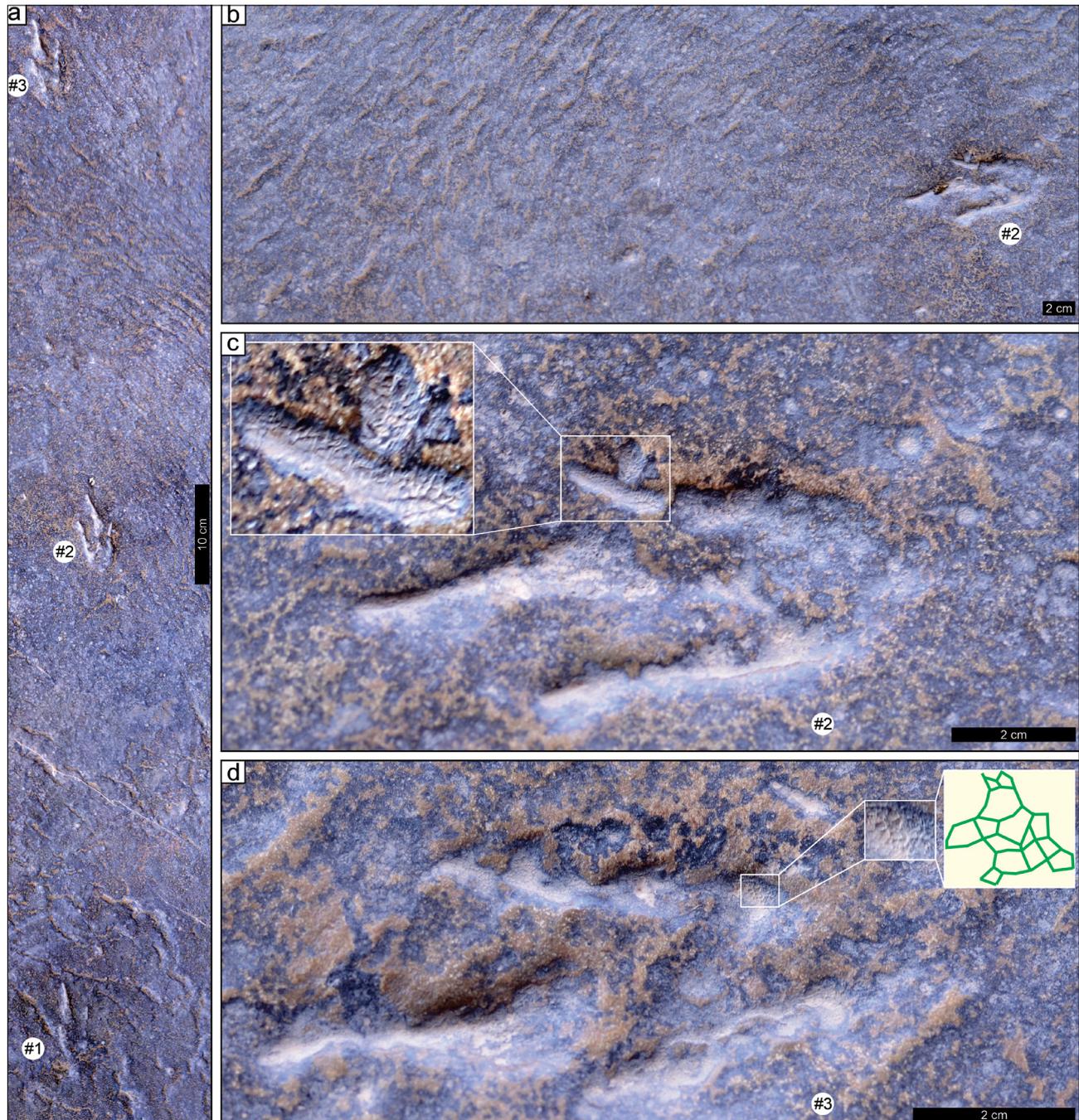


Figure 4: Details of the *Grallator* trackway in the lower Clarens Formation at the Storm Shelter ichnosite. (a) Orthophoto of the first three tracks within the trackway (image derived from photogrammetric model) showing random, parallel as well as curving ridges on the surface, which are interpreted as wrinkle structures – a type of microbially induced sedimentary structure. (b) Details of the tracking surface around track #2. (c and d) Close-up images of track #2 and #3 showing the millimetre-scale polygonal pattern inside small depressions both within and next to the tracks. The small-scale, polygonal pattern is interpreted as dried-out, microbially bound surfaces that draped the entire tracking surface soon after the tracks were formed. See Supplementary table 2 for trackway morphometric measurements, <https://doi.org/10.6084/m9.figshare.13007240> for the trackway photogrammetric model and Supplementary figure 1 for further details on the sedimentological context of the ichnosite.

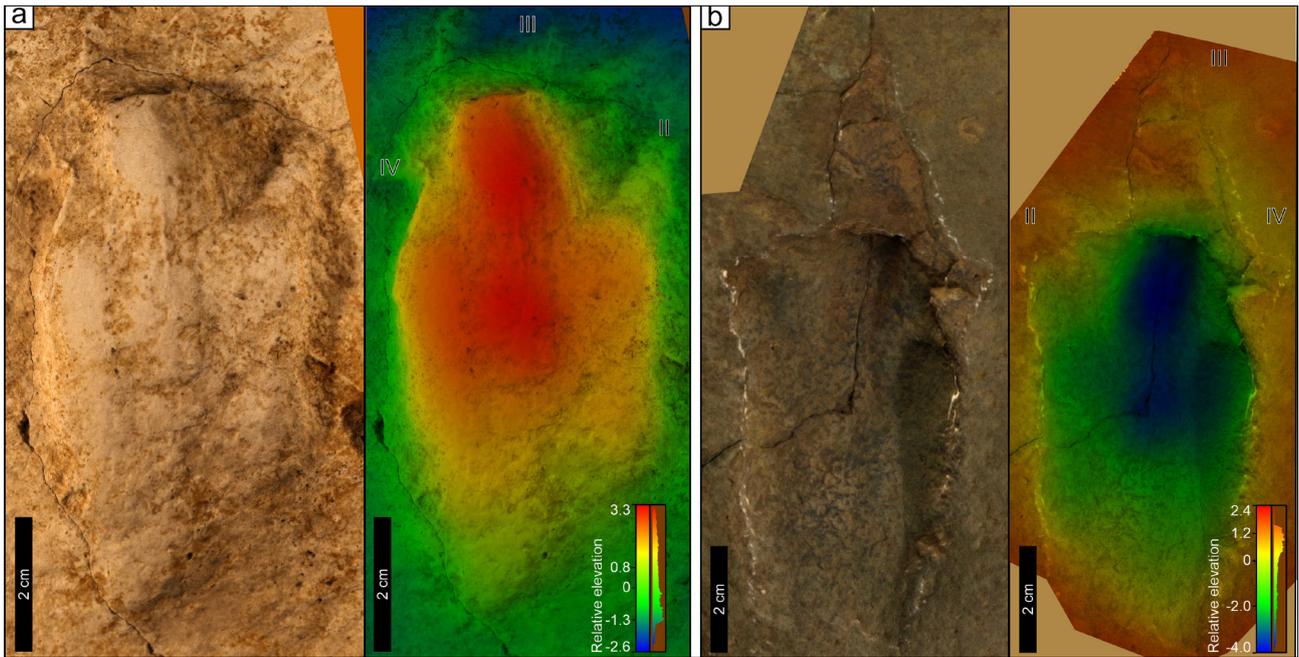


Figure 5: *Grallator* tracks from the Clarens Formation in Lesotho. Left image: orthophoto derived from photogrammetric modelling; right image: false-colour depth model generated using CloudCompare version 2.11.3 (dark red is the highest point, dark blue the lowest). (a) *Grallator* (*Paragrallator*) *matsiengensis* (^{6,7} figure 128, LES 283) from Matsieng (Zone B/5). This broken, plaster-of-Paris cast is the only replica of the lost holotype. (b) *Grallator molapo* (^{6,7} LES 288, holotype) from Leribe-Molapo (Zone B/6). Both specimens are housed in the Ellenberger Collection at the University of Montpellier (France). See Supplementary table 5 for their morphometric measurements and <https://doi.org/10.6084/m9.figshare.13007240> for their photogrammetric models. Roman numerals I–IV denote digits.

Although *Grallator* tracks rarely preserve²⁸ impressions of digit I, remarkably, all *Grallator*-like tracks at Storm Shelter are associated with hallux (digit I) traces (Figure 3). Moreover, unlike in typical *Grallator* tracks^{26,31,39}, the impression of the hallux is not directed medially or to the rear, but forward. Figure 3 shows how these ~1-cm-long impressions point in the forward direction, at ~54° (average) away from the long axis of digit III. The hallux impressions are not only important for identifying the trackmaker (see below) but also for determining that the trackmaker's feet sunk hallux-deep into the wet, soft sediment while the animal ran across the surface. A pliable, squidgy tracking surface also explains why digits II, III and IV in these tracks lack well-defined digital pad impressions, imprint walls, etc. (Figure 3), and thus limit the tracks' ichnotaxonomic assessment and conclusive attribution to any specific trackmaker. The wrinkle structures (Figure 4, Supplementary figure 1), which are linked to fossilised microbial mats and are abundant on this tracking surface, were possibly present already at the time of trackmaking and thus enhanced the footprint generation and overall preservation. Microbially induced sedimentary structures are known to be associated with dinosaur tracks in the southern African^{10,34,35} and global^{40–42} ichnofossil record. Likely, these sediment-binding biofilms developed as localised algal blooms flourished in shallow, stagnant pools of water that were generated in ephemeral downpours and that evaporated over time (Figure 7). Although the host Clarens Formation at Storm Shelter does preserve desiccation cracks (Supplementary figure 1), there are none preserved on the tracking surface itself, which possibly remained wet, or at least moist, until it was buried by the next layer of flash flood generated sediment (Figure 7).

Grallator is commonly attributed to early theropod dinosaurs that were obligatory bipeds with long, thin toes, including well-developed halluces (e.g.^{21,26,31,32}). Based on the morphometric parameters of the Storm Shelter tracks (Figure 3, Table 1, Supplementary table 1) and the regional Early Jurassic bone fossil record, a likely trackmaker candidate is *Megapnosaurus rhodesiensis* (formerly *Syntarsus rhodesiensis* and *Coelophysis rhodesiensis*^{39,40}). This early theropod is a coelophysoid dinosaur (Figure 7) that is common in the same stratigraphic interval (i.e. Lower Jurassic) of southern Africa, especially in Zimbabwe

(e.g.^{43–45}). A similar coelophysoid dinosaur, *Coelophysis bauri*, is often assumed to have made the early Mesozoic *Grallator* tracks in North America (e.g.^{26,31,32,46–48}). Both of these early theropods were small-to-medium-sized, lightly built, agile, carnivorous bipeds and are often found in richly fossiliferous strata where entire animal populations are jumbled together as partially intact or complete skeletons that also include articulated foot bones.⁴³ Foot reconstructions show that these early theropods had four pedal digits and a pes phalangeal formula (inclusive of unguals) of 2:3:4:5:0.⁴³ Reconstructions also show that digit I (the hallux; Figure 7b) did not touch the ground during the steeply digitigrade locomotion of the animal (Figure 7a; e.g.^{43,48,49}). Moreover, the well-formed hallux and associated foot bones of *Megapnosaurus rhodesiensis* preserve anatomical features that indicate that the hallux was forwards directed^{26,43}, alongside digit II (Figure 7b). Raath^{43(p.93)} remarked that the hallux 'retained a specialised function in life. Its use as a grooming accessory seems quite feasible'. The congruence in the morphological features of this foot skeleton and the tracks (including the non-reversed hallux configuration) is used here to suggest that the Storm Shelter footprints likely belong to *Megapnosaurus rhodesiensis*. It is noteworthy that in other early Mesozoic *Grallator* tracks^{26,31,39,48}, the orientation of the hallux impression is reversed (posterior directed) in contrast to the original anatomical configuration. This backward-directed hallux mark resulted from the way the forward-directed hallux interacted with the sediment during the track-generating process as demonstrated by Gatesy et al.⁴⁸ In the Storm Shelter tracks, however, the hallux impression closely corresponds to the typical anatomical (forward) orientation of the digit I in coelophysoid dinosaurs^{43,48}, and this makes the Storm Shelter tracks unique among *Grallator*-like tracks. It is probable that this anterior-directed hallux impression resulted from the fortuitous combination of the microbially influenced substrate consistency that allowed the penetrative tracks to form, the trackmaker's tiny body proportions and the fast speed of motion.

Theropods were the main terrestrial carnivores in the post-Triassic part of the Mesozoic. Their smaller bodied varieties, like the trackmaker of the Storm Shelter tracks, most probably took on the dual role of predator and prey, and thus had good reason to leave behind tracks indicative of

a running gait. The ability to run and occasionally sprint at speeds up to 12.5 km/h, even in the smallest individuals, must have been a great advantage for these agile, highly successful predators⁴³ that had to adapt to an increasingly harsh, desert ecosystem, prone to flash flooding and dry spells in the Early Jurassic of southern Africa⁴ (Figure 7).

The minute, elongated Storm Shelter tracks together with the region's smallest¹⁰ and two largest⁶⁻⁹ tridactyl tracks are taken as evidence, not only of the abundance but also the size diversity of the Early Jurassic

theropod dinosaurs in southern Africa. Given the regional abundance and diversity of the footprint record, the dinosaur tracks of southern Africa, in all shapes and sizes, remain an important proxy for meaningfully assessing concepts on macroevolutionary changes in dinosaur body size during the early Mesozoic.^{1-3,50} The true potential of this rich ichnological record is only achievable if the collected, but largely undescribed materials in various museum collections, as well as new discoveries like this one at the Storm Shelter, are quantified and integrated with the global early Mesozoic ichnological and osteological fossil records.

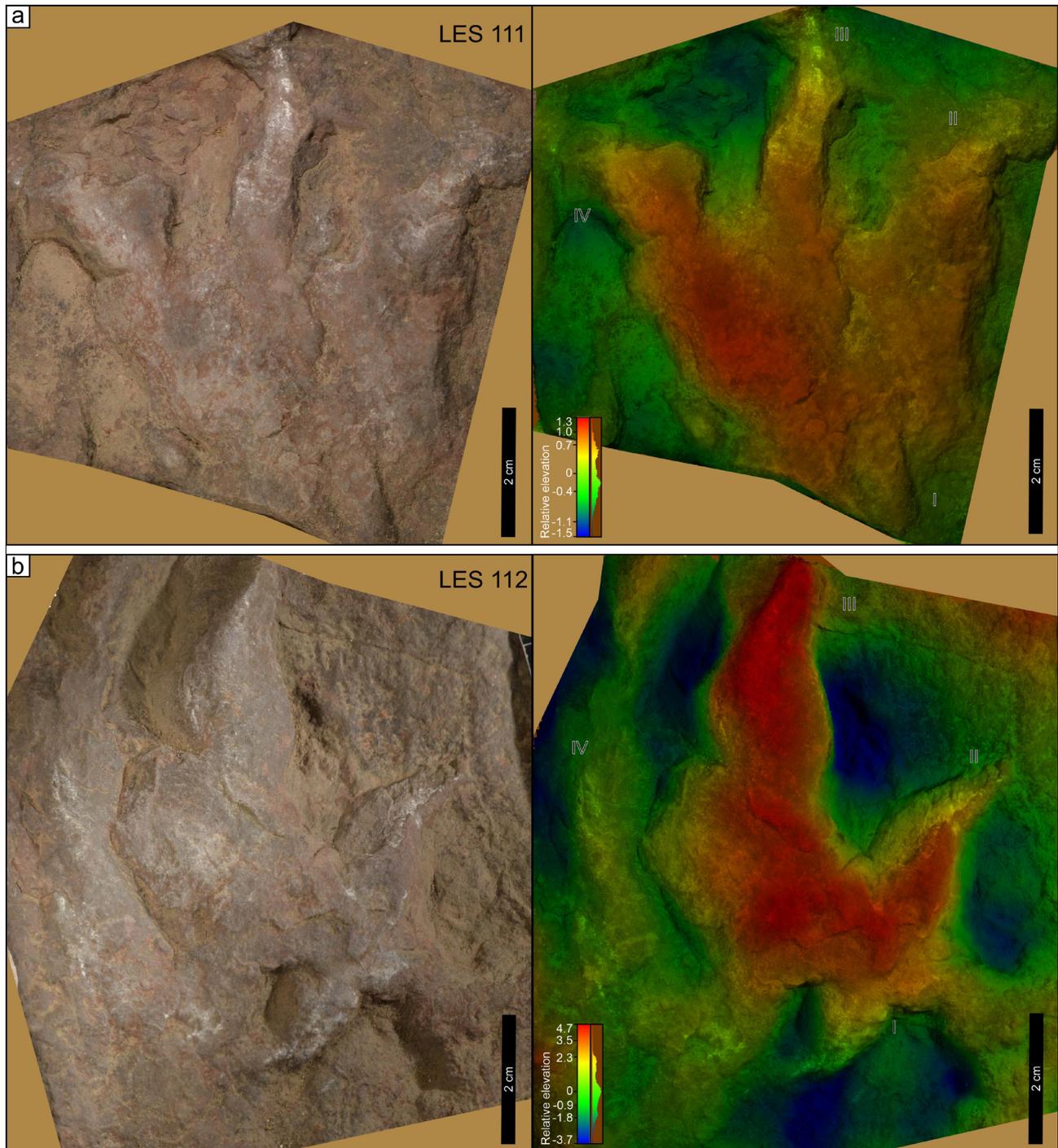
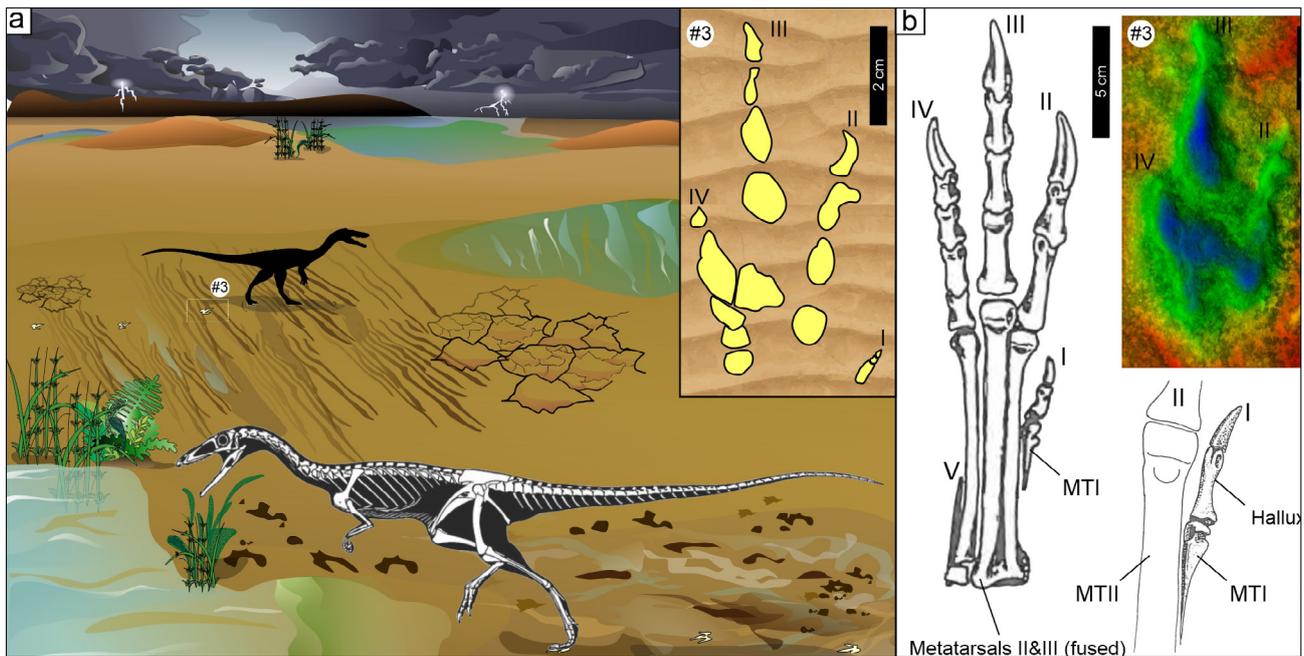


Figure 6: Two examples of small, ~7.7-cm-long tridactyl tracks from the Lower Jurassic of southern Africa. Left image: orthophoto derived from photogrammetric modelling; right image: false-colour depth model generated using CloudCompare version 2.11.3 (dark red is the highest point, dark blue the lowest). (a and b) *Masitisisauropus palmipes* (LES 111 and LES 112, respectively³⁸) from the lower part of the upper Elliot Formation at Mokanametsong in southwest Lesotho (Quthing district). Compared to these tracks, *Grallator* tracks are narrower with more slender toe impressions. Both specimens are housed in the Ellenberger Collection at the University of Montpellier (France). See Supplementary table 5 for their morphometric measurements and <https://doi.org/10.6084/m9.figshare.13007240> for their photogrammetric models. Roman numerals I-IV denote digits.



MT, metatarsal; Roman numerals I–V denote digits and corresponding MTs

Figure 7: Interpretation of the *Grallator* trackway in the lower Clarens Formation at the Storm Shelter ichnosite. (a) Palaeoenvironmental reconstruction (modified from original artwork by Akhil Rampersadh and Emese M. Bordy). Dinosaur outlines are adapted from Paul⁴⁷ (foreground) and Rampersadh et al.³⁶ (background). Inset shows the interpretative outline of track #3. (b) Skeletal reconstructions of the left foot and hallux of *Megapnosaurus rhodesiensis* are adopted from Raath⁴³ (his figure 20). Inset shows the relative position of the hallux trace in this left footprint of the *Grallator* trackmaker (false-colour depth map of track #3).

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Competing interests

I declare that there are no competing interests.

Data availability

The ichnological photogrammetric data that support the findings of this study are openly available in Figshare at <https://doi.org/10.6084/m9.figshare.13007240>, and include photographs used in the photogrammetric models, and the cleaned and aligned 3D models of the tracks figured in this paper (Figures 3, 5, 6).

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