DINOSAUR BEHAVIOUR IN AN EARLY JURASSIC PALAEOECOSYSTEM – UPPERMOST ELLIOT FORMATION, HA NOHANA, LESOTHO

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Abstract: The Ha Nohana palaeosurface in southern Lesotho preserves tridactyl and tetradactyl tracks and trackways attributable to Early Jurassic bipedal, theropod-like dinosaurs. Complementary sedimentological and ichnological observations along the palaeosurface and in the strata below and above it allow detailed interpretations of climatically driven changes in this southern Gondwana palaeoecosystem. Sedimentological evidence suggests trackmaking under a semi-arid climate with heavy storms and episodic flash flooding that induced ephemeral, unconfined sheetwashes. The palaeosurface is overlain by rhythmically bedded, organic-matter rich mudstones that formed in a deep, stratified lake indicative of a longer and wetter period in the history of the site. The unique morphological details of the Ha Nohana tracks help refine the properties of the substrate during track making, the ichnotaxonomic affinities of the footprints and the interpretation of the foot movement relative to the substrate. Two footprint morphotypes, ~ 300 m apart, are defined on the palaeosurface. Tracks of morphotype I are tridactyl, shallow, contain digital pad impressions and were impressed on a firm, sand rippled substrate that underwent desiccation. Conversely, tracks of morphotype II are tetradactyl, deep, and have an elongated posterior region. These tracks are preserved on the surface of a massive sandstone and are associated with soft sediment collapse structures related to the animal's foot sinking into the water-saturated, malleable sediment layer. Morphotype II tracks show that as the animal waded across the substrate, the liquefied sediment lost its cohesive strength and could only partially support the weight of the animal. In so doing, the animal's foot sunk deep enough into the sediment such that the impression of the metatarsal and digit I (hallux) are now visible. Thus, the palaeosurface was walked on by small-to-medium sized theropods that traversed over ripple marks in firmer moist sand, as well as a larger theropod that tottered through water-logged sand.

Key words: Vertebrate ichnology, tridactyl, tetradactyl, climate change, southern Gondwana, Karoo, upper Elliot Formation.

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INTRODUCTION

The continental red beds of the Upper Triassic to Lower Jurassic Elliot Formation (Fig. 1) were deposited during dynamically changing climatic conditions in southern Gondwana and preserve a rich history of life before and after the end-Triassic mass extinction event (e.g., Ellenberger *et al*., 1969; Ellenberger, 1970; Bordy *et al*., 2004; McPhee *et al*., 2017). This diverse palaeontological heritage, comprising of both body and trace fossils, provides valuable insight into biodiversity, environmental conditions and behaviour of animals during this dynamic period (Bordy and Eriksson, 2015).

The most notable trace fossils preserved in the Elliot Formation are the vertebrate ichnofossils, elements of which were first discovered during the mid-1880's by French missionaries in Lesotho (Ambrose, 1991; 2016). Since then, diverse vertebrate ichnofauna assemblages, especially of dinosaurs, have been recovered in the exceptionally well-exposed strata of the Elliot Formation of western Lesotho and South Africa (e.g., Ellenberger, 1970; Olsen and Galton, 1984; Smith *et al.,* 2009; Sciscio *et al.,* 2016; Abrahams *et al.,* 2017; Bordy *et al*., 2017).

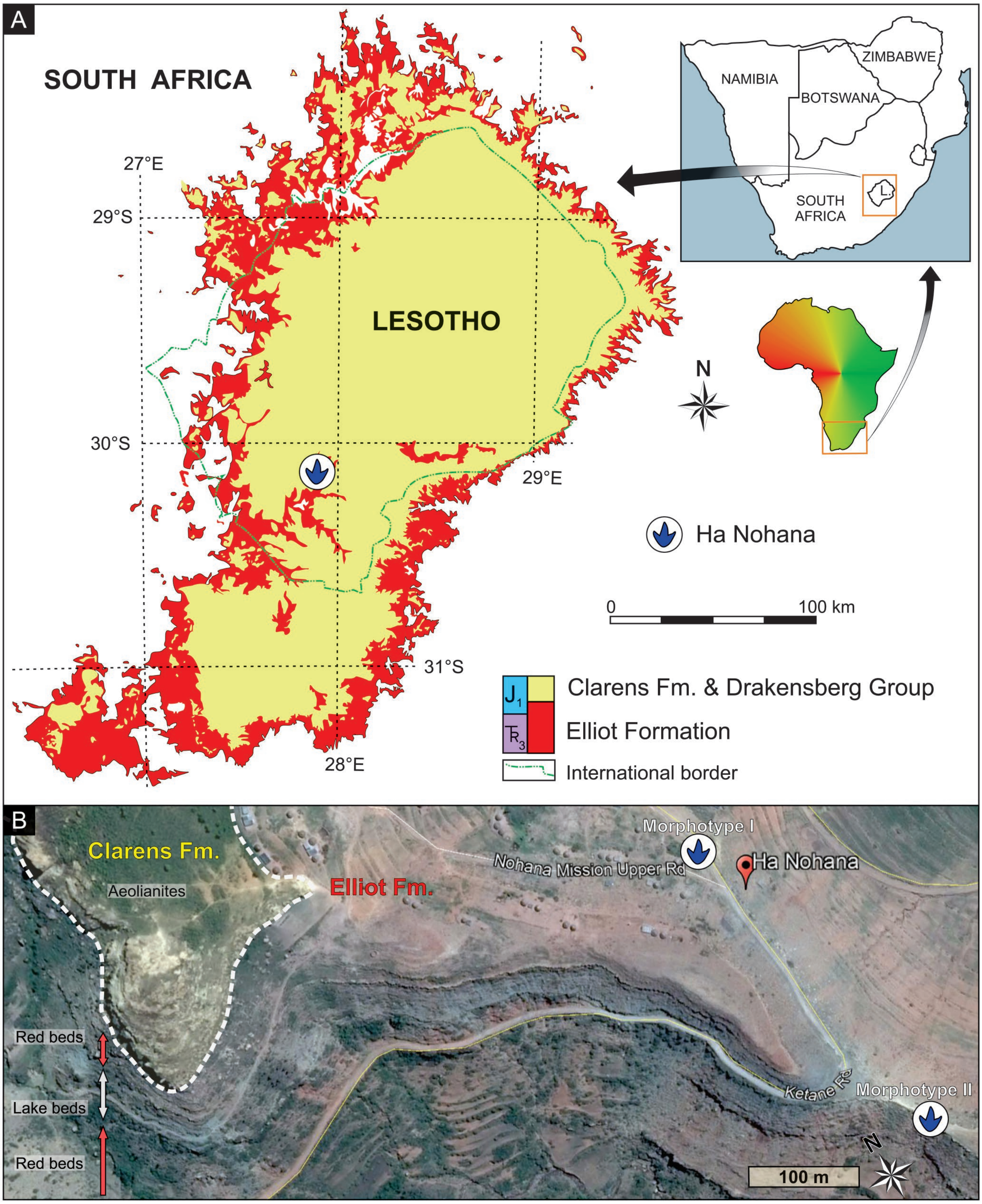

Fig. 1. Locality maps of the Ha Nohana ichnosite. **A.** A simplified geological map of the Upper Triassic to Lower Jurassic Elliot and Clarens formations, and Drakensberg Group in South Africa and Lesotho. **B.** Close-up of the Ha Nohana ichnosite showing the lateral extent of the track-bearing sandstone as well as the under- and overlying deposits in the uppermost Elliot Formation (studied stratigraphic interval: ~ 50 m). Maps derived from combining data from Google Earth images, Council for Geoscience (2008) and own mapping.

Vertebrate ichnofauna are important in refining the continental biostratigraphy in southern Africa and establishing correlations with global successions from the Late Triassic and Early Jurassic. The first vertebrate-based ichnozonation scheme of the Stormberg Group, which in addition to the Elliot Formation, encompasses the underlying Molteno and overlying Clarens Formations, was attempted by Ellenberger (1970; 1972), and later revised by Olsen and Galton (1984). While the biostratigraphic utility of these vertebrate tracks had been attempted before, their application in palaeoenvironment and palaeoecosystem reconstructions is lagging (Lockley, 1986; Whyte and Romano, 2001; Falkingham *et al.,* 2010), especially in southern Africa. This is despite the wealth of information in ichnite-bearing rocks that pertain to the conditions of the track-bearing sediments at the time of track formation. Because the final depth and morphology of a footprint are principally controlled by the rheological properties of the substrate, the pedal anatomy of the track maker, and the locomotor dynamics of the animal (e.g., Avanzini, 1998; Gatesy *et al.*, 1999; Milàn and Bromley, 2006; Jackson *et al.,* 2009; Huerta *et al.,* 2012), tracks can reveal subtle, but important clues on the moisture level of the substrate on which animals walk. In this way, substrates, with a higher degree of water saturation, are more conducive to forming penetrative and deep tacks, while hard, less pliable, drier substrates are more prone to producing shallow tracks (e.g., Gatesy *et al.*, 1999; Razzolini *et al.,* 2014; Sciscio *et al.,* 2016; Falk *et al.,* 2017).

This paper reports the ichnological and sedimentological findings of an ichnosite with multiple dinosaur trackways from the Lower Jurassic uppermost Elliot Formation at Ha Nohana in the Quthing District of southern Lesotho (30°3'12.01"S; 27°51'29.91"E). The tridactyl dinosaur footprints at Ha Nohana were discovered by Father Francis Makhetha in 2005 and have briefly been mentioned in Ambrose (2016), but to date, have not been described in the published ichnological literature. Our recent investigation of the originally reported trackways resulted in the documentation of the original tridactyl tracks and an additional, previously unknown tetradactyl trackway, as well as the sedimentological context of the track-bearing surface and strata below and above it over a vertical stratigraphic distance of ~ 50 m (Fig. 1B). The Ha Nohana tracks are preserved on the upper bedding plane of a sandstone layer within a ~ 1 m-thick sandstone package that is at the base of an interbedded succession of black, organic matter rich mudstone and laterally persistent, 10–50-cm-thick sandstone layers. The tracks are preserved on the same laterally continuous sandstone palaeosurface, with a local road separating the palaeosurface into two exposures that are approximately 300 m apart (Fig. 1B).

Ichnology, sedimentary facies analysis and stratigraphy were combined to provide the palaeoecological context of the Ha Nohana dinosaur ichnites in the Lower Jurassic upper Elliot Formation. More specifically, this study aims to: 1) document the sedimentological and ichnological contexts of Ha Nohana dinosaur tracks and trackways; 2) reconstruct locomotor dynamics and behaviour of the trackmaker dinosaurs; and 3) integrate the sedimentological and ichnological findings to establish the palaeoenvironmental conditions that occurred prior, during and after the tracks formed in the Early Jurassic.

GEOLOGICAL SETTING

The Ha Nohana palaeosurface is located within the upper Elliot Formation, stratigraphically 40-50 m below the base of the Clarens Formation (Fig. 1). The rocks of the Elliot Formation are underlain by the Molteno Formation and conformably overlain by the Clarens Formation, and together these comprise the continental Stormberg Group of the Karoo Supergroup in southern Africa (Fig. 1).

The Elliot Formation is informally divided into the upper and lower Elliot formations, abbreviated as lEF and uEF, based on distinct sedimentary facies changes (Bordy *et al*., 2004). This informal subdivision is also, coincidentally, the current biostratigraphic boundary between the '*Euskelosaurus*' and *Massospondylus* zones (Kitching and Raath, 1984; McPhee *et al*., 2017). Depositional history of the Elliot Formation, based on the sedimentological evidence, suggests a predominantly fluvio-lacustrine system for the unit, with a change in fluvial style from meandering rivers and floodplains in the lEF to ephemeral rivers and lakes in the uEF (Bordy *et al.,* 2004). This environmental change has been linked to foreland basin tectonics as well as a gradual aridification during the Early Jurassic of southern Gondwana (Bordy *et al.,* 2004; Sciscio and Bordy, 2016). This aridification culminated during the deposition of the overlying Sinemurian to Pliensbachian Clarens Formation.

The focus of this study, the uEF, is composed of fine- to medium-grained sandstones and mudstones (Bordy *et al.,* 2004). Sedimentary structures in the sandstones range from horizontal and ripple cross-lamination, planar cross-bedding, low-angle cross-bedding to massive beds (Bordy *et al.,* 2004). The sandstone units are separated by mostly massive as well as horizontally laminated mudstone layers that vary in thickness from 0.1 to maximum of 10 m (Bordy *et al.,* 2004). The uEF contains an abundance of vertebrate fossils, ranging from theropods and sauropodomorphs to fossils of fish, amphibians, cynodonts, basal crocodylomorphs, basal turtles and mammals (Kitching and Raath, 1984; Bordy and Eriksson, 2015; McPhee *et al*., 2017). An abundance of invertebrate and vertebrate trace fossils as well as some plant remains are also found within the uEF (Bordy *et al.,* 2004; Knoll, 2005).

METHODS AND MATERIALS

The exceptional three-dimensional outcrop exposure at the Ha Nohana ichnosite permitted detailed field-based investigations of the ichnology and sedimentology (Figs 2–7). All field observations were photographically documented. Vertical and lateral changes in the rocks were described using methods of sedimentary facies analysis on centimetre to decimetre scale. Miall (1996) provides full details of the analytical procedures applied to the sedimentary rocks observed in field in a road cut and adjacent natural exposures.

The high-quality exposure of the uEF rocks at Ha Nohana is provided by the curving nature of the road and its locally steep gradient (Figs 1, 3). Trackway surfaces were

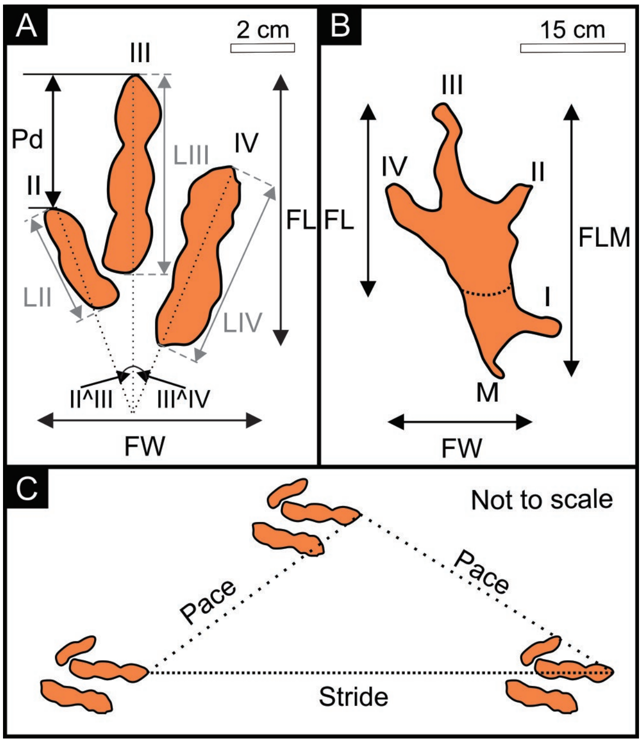

Fig. 2. Measurements obtained for the ichnological analyses and their abbreviations used in this work. **A**. Measurements of morphotype I tracks (example used: track 23). **A**. Measurements of morphotype II tracks (example used: track C2). **C.** Pace and stride lengths. Abbreviations: roman numerals I–IV for digits; M – metatarsal impression; FL – foot length, FW – foot width; FLM – foot length with metatarsus; Pd – protrusion of digit III; interdigit angles between digits II^III and III^IV.

thoroughly cleaned to accommodate accurate on-site measurements, comprehensive ichnological descriptions and photographic recording of the footprints for photogrammetric analyses. The latter includes 3D photogrammetric models of one trackway (Trackway C) and of its best individual tracks. The models were made using the Agisoft Photoscan software (standard version 1.1.4) applying methods described by Mallison and Wings (2014). Over 200 photographs were taken using a Canon PowerShot EOS D1200 (Focal length 28 mm, 5184 x 3456 resolution) and input into the software to generate digital point clouds. Cloud Compare (software v.2.6.1) and Paraview (v. 5.5.1) were used to produce depth-colour image analyses.

The measured dimensions of the dinosaur tracks were described as follows: footprint length (FL), footprint length with metatarsal (FLM), footprint width (FW), interdigit angles between digits (II^III, III^IV, II^IV), digit length (LII–IV), pace length (PL) and stride length (SL) (Fig. 2; Tabs 1–3, Appendix Tab. 1). The track length was measured from the end of digit III to the metatarso-phalangeal pad of digit III, and where applicable to the end of the metatarsal. Interdigit angles were measured using ImageJ (Fig. 2). The calculations of Thulborn (1990) were used to estimate body dimensions of track makers, namely hip height (H) and body length (L). The morphometric and allometric hip height (H) ratios and body length (L) were calculated using different foot lengths (FL) for theropod trackmakers as defined by Thulborn (1990). Dinosaur gaits were calculated according to Thulborn and Wade (1984), using the ratio of footprint stride length (λ) to hip height (H). Walking gaits are characterised as $\lambda/H \leq 2.0$, "trotting" gaits are $2.0 < \lambda/H < 2.9$ and running gaits have $\lambda/H \geq 2.9$. Speed estimates of trackmakers' were calculated as per Alexander (1976).

RESULTS

Sedimentology

The tracks at Ha Nohana are preserved on the upper bedding plane of a ~ 1 m-thick cream, very fine- to fine-grained, tabular sandstone unit that is underlain by a red bed succession and overlain by grey to black mudstones, which in turn are overlain by an additional 20–35 m of red beds and finally the Clarens Formation (Figs 1B, 3).

Underlying the track-bearing sandstone unit, the red beds are dominated by mudstones that are massive, deep red to maroon coloured, except for immediately below the sandstone unit where colour mottling and light grey colours are common (Fig. 3B, C). The red mudstones are interbedded with < 30 cm-thick very fine grained massive sandstones and siltstones, and contain pedogenic alteration features (e.g., calcareous nodules, fossil plant roots, desiccation cracks) that are otherwise common in the uEF (Fig. 3B, C).

The track-bearing sandstone unit extends over the entire length of the outcrop area (~ 900 m), and therefore its true width is unknown (Figs 1B, 3A). It comprises horizontally laminated and massive beds, ripple cross-lamination, asymmetrical ripple marks as well as mud-films with desiccation cracks (Fig. 3A–D). Furthermore, the track-bearing sandstone unit also contains invertebrate trace fossils (Fig. 3B) in association with the several levels of mud films with desiccation cracks (Fig. 3B, D, E).

Overlying the track-bearing sandstone unit, the mudstones are light to dark grey and black in colour and free of any pedogenic overprinting (Fig. 3F, G). Interbedding of massive and horizontally laminated mudstone (Fig. 3G) is common, however desiccation cracks (Fig. 3H) and fossil conchostracan shells (Fig. 3I) are only found in the lowermost strata. The total thickness of these grey to black mudstones is 10–12 m, and they are overlain by a 20–35-m-thick red bed succession (Fig. 1B). These younger red beds have sedimentary facies similar to the red beds that underlie the track-bearing sandstone unit, and are in turn conformably overlain by the aeolian Clarens Formation (Fig. 1B).

Vertebrate ichnology

Sixty-one tracks, preserved as hyporeliefs, were identified at the Ha Nohana ichnosite and were grouped into two morphotypes (morphotype I and II) based on their respective morphologies and dimensions. Morphotype I is tridactyl and occurs exclusively on the palaeosurface that is exposed parallel to the road in the northern part of the study area. Morphotype II is a single tetradactyl trackway and occurs in the south-eastern part of the study area, ~ 300 m away,

Table 1

Average track measurements, and their standard deviations, of morphotype I and II at Ha Nohana. Where specific measurements could not be taken either due to the track features being absent or the track morphology being obscured, the measurement is regarded as not applicable (N/A).

	FLM	FL	FW	FL/ FW	Pd	Pd/W	Interdigit angle			Digit length (cm)		
	(cm)				(cm)		II^III	III^IV	II^IV	LII	LIII	LIV
Average Morphotype I	N/A	10.1	8.8	1.2	3.7	0.4	39	34	69	5.7	7.3	6.5
STD DEV	N/A	0.53	0.83	0.11	0.64	0.08	6.2	5.37	9.56	0.68	0.8	0.8
Average Morphotype II	37	27.9	19.1	1.5	8.7	0.5	N/A	N/A	N/A	N/A	N/A	N/A
STD DEV	3.7	4.11	1.53	0.19	1.16	0.06	N/A	N/A	N/A	N/A	N/A	N/A

Table 2

Measurements of the individual tracks comprising trackways A, B (morphotype I) and C (morphotype II) at Ha Nohana. For a complete set of measurements on all 61 tracks of Ha Nohana, see Appendix Table 1.

Fooprint #	FLM	FL	FW	FL/FW	Pd	Pd/W	Interdigit angle			Digit length (cm)		
	(cm)				(cm)		II^III	III^IV	II^IV	LII	LIII	LIV
A1	N/A	9.0	8.0	1.1	4.0	0.5	46	31	78	4.3	6.8	5
A2	N/A	9.5	8.0	1.2	2.7	0.3	40	36	73	5	7.8	6.2
A3	N/A	10.0	9.0	1.1	2.5	0.3	40	32	73	6.6	7.3	7.5
A4	N/A	10.5	8.5	1.1	4.0	0.5	34	37	70	3.9	4.8	4.4
Average	***N/A***	***9.8***	***8.4***	***1.1***	***3.3***	***0.4***	***40***	***34***	***74***	***5.0***	***6.7***	***5.8***
B1	N/A	10.5	9.0	1.2	5.0	0.6	46	32	77	7.3	8.5	8.2
B2	N/A	9.5	8.5	1.1	4.8	0.6	42	38	75	4.5	7.6	6
B3	N/A	10.0	10.0	1	3.4	0.3	44	39	78	5.2	6.7	5.5
B4	N/A	11.5	9.0	1.3	3.5	0.4	45	34	72	5	6.4	5.4
Average	***N/A***	***10.4***	***9.1***	***1.2***	***4.2***	***0.5***	***44***	***36***	***76***	***5.5***	***7.3***	***6.3***
C1	N/A	30.0	20.0	1.5	9.1	0.5	N/A	N/A	N/A	N/A	N/A	N/A
C2	40	31.0	20.0	1.6	8.5	0.4	N/A	N/A	N/A	N/A	N/A	N/A
C3	37	20.0	19.0	1.1	6.7	0.4	N/A	N/A	N/A	N/A	N/A	N/A
C4	39	31.0	19.0	1.6	10.4	0.5	N/A	N/A	N/A	N/A	N/A	N/A
C5	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
C6	39	29.0	19.0	1.5	7.8	0.4	N/A	N/A	N/A	N/A	N/A	N/A
C7	38	30.0	21.0	1.4	9.8	0.5	N/A	N/A	N/A	N/A	N/A	N/A
C8	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
C9	29	24.0	16.0	1.5	8.3	0.5	N/A	N/A	N/A	N/A	N/A	N/A
Average	***37***	***27.9***	***19.1***	***1.5***	***8.7***	***0.5***	***N/A***	***N/A***	***N/A***	***N/A***	***N/A***	***N/A***

but on the same sandstone palaeosurface (Fig. 1B). Track preservation is highly variable laterally along the palaeosurface, but the main morphological features are discernible with digital pad impressions occasionally being preserved (e.g., Fig. 4).

Morphotype I

A total of fifty-two tracks are tridactyl and have been classified as morphotype I. They occur mostly as shallow impressions on a small-scale ripple marked surface that was covered by a < 1 cm-thin layer of mud that subsequently desiccated (see inset in Fig. 3D). The tracks are likely true tracks (cf., Lockley, 1991; Citton *et al.*, 2016; Marty *et al.*, 2016), because of their morphological detail (i.e., some preserve digital pad impressions, are associated with weak expulsion rims, are superimposed onto ripple marks, which they locally slightly disrupt; Fig. 4). These asymmetrical, tridactyl pes tracks are small with an average FL of 10.1 cm, an average FW of 8.8 cm (Tab. 1; Fig. 4), and an average FL/FW ratio of 1.2 (Tabs 1, 2, Appendix Tab.1). Digit III extends further than the other digits (average

Table 3

Calculations of hip height, gait and speed as well as body length of the trackmakers at Ha Nohana. Estimated lengths are shown by an asterisk (*).

Footprint #	FL	Stride	Morphometric			Allometric			Body length
			Hip height	Gait	Speed	Hip height	Gait	Speed	
	(cm)	(m)			(m/s)	(m)		(m/s)	(m)
A1 - A3	9.5	0.68	0.43	1.6	1.12	0.40	1.7	1.22	1.71
A2 - A4	9.5	0.5	0.43	1.2	0.67	0.40	1.3	0.73	1.71
Average			***0.43***	***1.4***	***0.90***	***0.40***	***1.5***	***0.97***	***1.71***
B1 - B3	10.3	0.55	0.46	1.2	0.72	0.43	1.3	0.77	1.85
B2 - B4	10.5	0.65	0.47	1.4	0.93	0.45	1.4	0.99	1.89
Average			***0.47***	***1.3***	***0.82***	***0.44***	***1.4***	***0.88***	***1.87***
C1 - C3	25.0	1.54	1.23	1.3	1.28	1.32	1.2	1.17	4.90
C2 - C4	31.0	1.59	1.52	1.1	1.05	1.59	1.0	0.99	6.08
C3 - C5	20.0	1.62	0.98	1.7	1.82	1.10	1.5	1.59	3.92
C4 - C6	30.0	1.56	1.47	1.1	1.06	1.55	1.0	0.99	5.88
C5 - C7	30.0	1.56	1.47	1.1	1.05	1.55	1.0	0.99	5.88
C6 - C8	29.0	1.60*	1.31	1.2	1.26	1.42	1.1	1.14	5.46
C7 - C9	27.0	1.67	1.21	1.4	1.47	1.22	1.3	1.34	5.10
Average			***1.31***	***1.2***	***1.28***	***1.39***	***1.2***	***1.17***	***5.32***

Pd ~ 3.7 cm), with digits II and IV sub-equal in length and curving outwards from the track midline (divergent). Digit III appears straight in all tracks. The average interdigital angles between digits II and III, III and IV, and II and IV are 39˚, 34˚ and 69˚, respectively (Tabs 1, 2, Appendix Tab. 1). The metatarsophalangeal pad is almost always preserved (Fig. 4), whereas digital pad impressions and claw marks are rarely preserved (e.g., Fig. 4D).

Two morphotype I trackways, both consisting of four consecutive steps, have been identified (trackway A and B; Fig. 5; Tabs 2, 3). The trackways are oriented to the north, as are most of the elongation axes of the other isolated tracks. Pes impressions making up the trackway are forward facing with no apparent rotation relative to the trackway midline and the trackway width is very narrow (Fig. 5). Trackway A has an average pace of 0.28 m and variable strides ranging from 0.5 m to 0.68 m (Tab. 3). The average gait is 1.4 and 1.5 (walking gaits), with an average speed of 0.90 and 0.97 ms^{-1}, for morphometric and allometric hip heights, respectively (Tab. 3). A body length of 1.71 m was determined for the trackmaker of trackway A and both the morphometric and allometric equations suggest that trackmaker A had a hip height < 0.5 m (Tab. 3). Trackway B has an average pace of 0.27 m and variable strides that a range between 0.55 m and 0.65 m (Tab. 3). The average gait is 1.3 and 1.4 (walking gaits), with an average speed of 0.82 ms^{-1} and 0.88 ms^{-1}, for morphometric and allometric hip heights respectively (Tab. 3). An average body length of 1.87 m was calculated for trackmaker B, with a morphometric and allometric hip height < 0.5 m (Tab. 3). Although the gaits in trackway A and B are variable, the gait never surpasses 2, suggesting that the trackmakers had a walking gait throughout the trackway.

Morphotype II

Nine morphotype II tracks are preserved as tetradactyl impressions because, in addition to preserving the impression of digits II, III and IV, the tracks also include the impression of digit I (hallux; Fig. 6). Moreover, seven of these tracks display the impression of the metatarsal ('M' in Fig. 6). These tracks are considered true tracks as they were formed by the direct interaction of the trackmaker's foot with the subsurface sediment layers and occur mostly as deep impressions with associated sediment collapse structures in a massive sandstone (cf., Lockley, 1991; Gatesy, 2003; Citton *et al*., 2016; Marty *et al*., 2016; Figs 6, 7). Morphotype II tracks form trackway C (Fig. 7), which comprises nine consecutive steps orientated towards SE, essentially parallel to the trackway midline and with a narrow the gauge.

The tetradactyl morphotype II tracks have an average FL of 27.9 cm without the metatarsal, and 37.0 cm with the metatarsal impression, and an average FW of 19.1 cm (Tabs 1, 2). The average FL/FW ratio is 1.5 (Tabs 1, 2). Morphotype II are posteriorly elongated by the presence of a metatarsal impression, except for tracks C8 and C9 (Fig. 7B). The hallux (digit I) impression is notable in most tracks as a posteromedially oriented short projection (Figs 6, 7). In addition to the characteristic tetradactyl morphology, these tracks also preserve sloping track walls and extramorphological sediment collapse features (e.g., sediment slumping around digit impressions and exit peaks at the front of tracks as sediment was dragged out during foot withdrawal; Figs 6, 7B). The best-preserved footprints display narrow digits with sharp claws that curve inwards towards the track midline (Figs 6, 7). Preservational changes are also noted

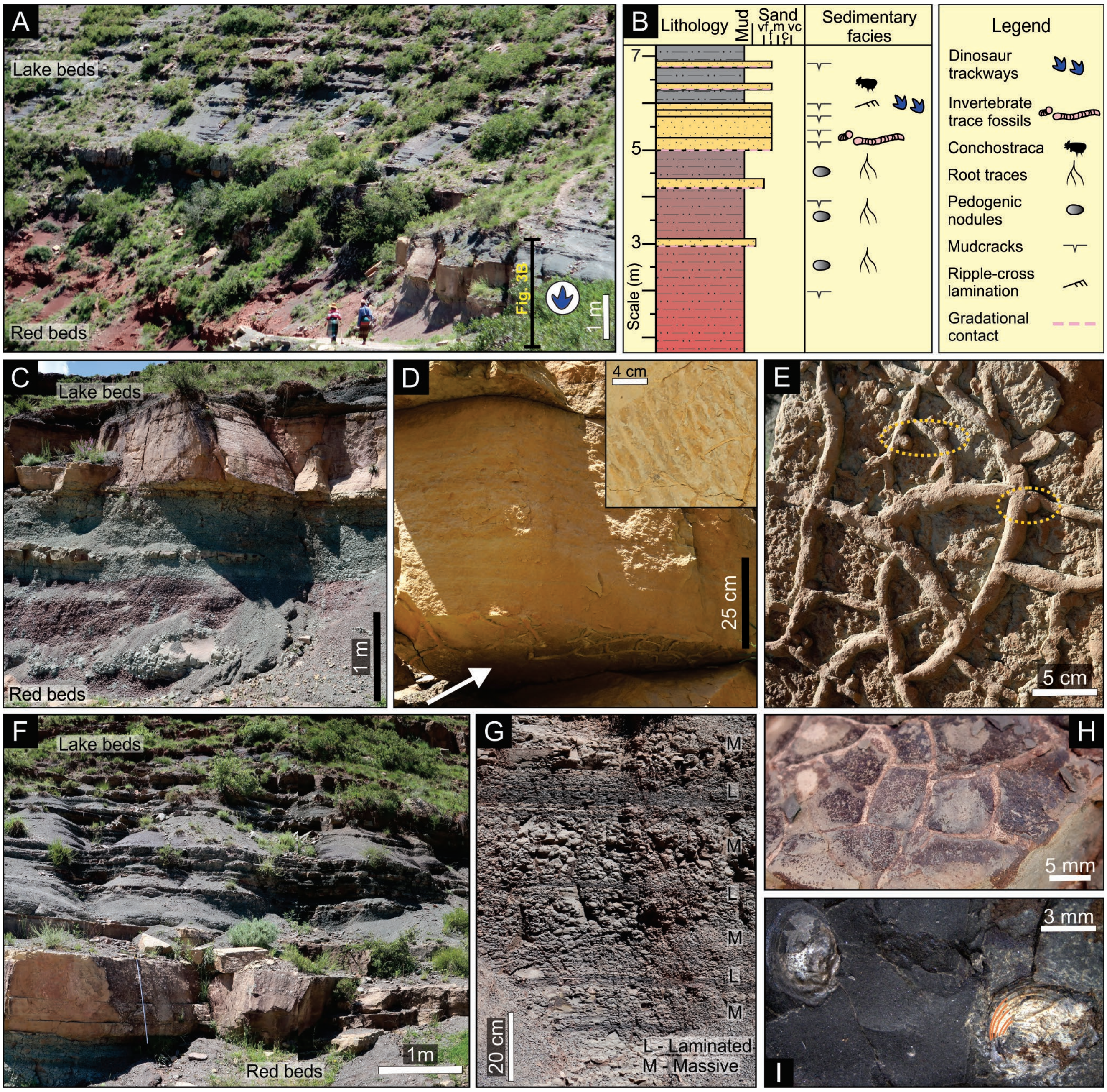

Fig. 3. Sedimentary facies of the upper Elliot Formation at Ha Nohana. **A.** An overview picture of the main sandstone unit with the underlying red beds and overlying grey to black lake beds. **B.** A sedimentological log of the sandstone unit and adjacent strata. **C.** Section of the main sandstone unit and the underlying red beds with several pedogenic features, including colour mottling, nodules, fossil plant roots. **D.** Close-up of the main sandstone unit showing horizontal lamination in fine- to very fine-grained sandstone (a typical upper flow regime sedimentary structure), and multiple desiccation crack surfaces (lower one arrowed). Note the asymmetrical ripple marks in the inset. **E.** Invertebrate burrows (some circled) are both perpendicular to and parallel to sandstone bedding planes; here within a network of desiccation crack casts. **F.** Section of the main sandstone unit and the overlying grey to black lake beds. **G.** Close-up of the first lake beds comprising interbedded massive and laminated, light to dark grey to black mudstone. **H.** Casts of desiccation cracks. **I.** Fossil conchostracan shells with growth rings in dark grey to black mudstone (H and I are limited to the lowermost lake beds).

along the length of trackway C with proximal tracks (tracks C2, C3 and C4) showing the most deformation and deeper impressions, while the most distal track (C9) is the most shallowly impressed.

The average pace in trackway C is 0.97 m and the strides are variable with a range between 1.5 and 1.7 m (Tab. 3). The average gait is 1.20 for both morphometric and allometric hip heights, with an average speed of 1.28 ms^{-1} and 1.17 ms^{-1}, respectively (Tab. 3). Although the gait is variable along the trackway (ranging from 1.0 to 1.5 using allometric hip heights), the animal maintains a walking gait across the trackway (Tab. 3). An average body length of 5.32 m was determined for the trackmaker of trackway C, with an average morphometric and allometric hip height > 1 m (Tab. 3).

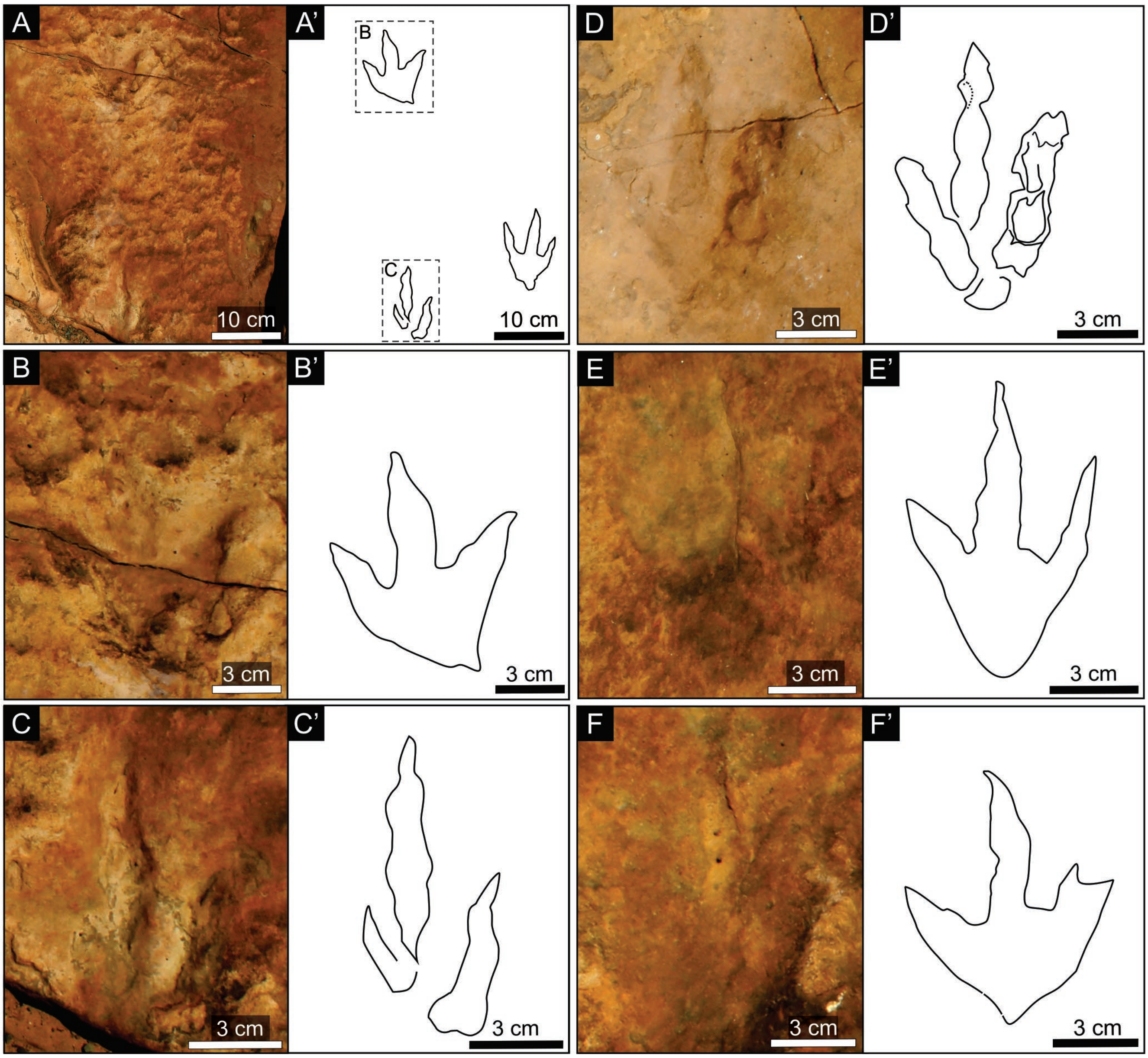

Fig. 4. Field photographs and interpretative outlines of the small, tridactyl tracks of morphotype I at Ha Nohana. **A.** Overview of a trackway section where the tracks are preserved sub-perpendicular to the crests of the asymmetrical ripple marks. **B, C.** Close-ups of two consecutive steps (their positions within A' are marked with rectangles). **D.** Track of morphotype I with digital pad impressions and claw marks. **E, F.** Examples of slightly impressed tracks of morphotype I showing limited morphological detail.

However, due to the unique preservation of morphotype II tracks, the estimation of the trackmaker's body dimensions should be considered very tentatively.

DISCUSSION

Palaeoenvironmental context

The studied rock interval intersects two sets of continental red bed units that are separated by grey to black mudstones (Figs 1B, 3A). The red beds contain sedimentary features (e.g., carbonate nodules, fossil roots, desiccation cracks) that are typical to the pedogenically altered floodplain facies within the uEF in southern Africa (see Bordy *et al.,* 2004), and thus their interpretation is not repeated here.

Overlying the lower red bed unit, within the track-bearing sandstone unit, massive and horizontally laminated sandstone beds represent periods of upper flow regime conditions, while asymmetrical ripple marks and ripple cross-lamination are indicative of migrating sand ripples during decelerating flows under low energy conditions (Fig. 3B–D). The interbedded mud films with desiccation cracks (Fig. 3D, E) are evidence for cessation of the ephemeral currents and temporal drying out of initially wet sediment layers under subaerial conditions. The track-bearing sandstone unit is identified as a flash flood deposit based on its sheet-like geometry and associated sedimentary structures (Fig. 3A, B). The desiccation crack surfaces between the sandstone layers (Fig. 3B, D, E) represent consecutive, short-lived flooding and drying events within a longer flooding period. Asymmetrical ripple marks covered by a thin, desiccated mudfilm and preserved on top of the last, footprint-bearing sandstone bed are evidence for the last shallow water, unidirectional currents and subsequent subaerial conditions. Along the palaeosurface, there were distinct differences in substrate consistency, and ranged from firmer, moist substrates with ripple marks and a desiccating mud layer to water logged, massive sediments (see next section). In summary, the deposition of the track-bearing interval occurred under a semi-arid climate prone to storm induced flash flooding. The multiple short-lived, high energy sheet flooding events were punctuated by episodic periods of drying out, during which ephemeral and typically unchannelized water courses were drained and transformed into temporary ponds (Bordy *et al*., 2004). These ephemeral pools of water served as local watering holes, which were visited by animals either in search for food or drinking water (Fig. 8).

Overlying the track-bearing sandstone unit, pedogenic alteration-free, massive to laminated grey to black mudstones indicate inundation and subaqueous conditions during a longer and wetter period in the history of the study area. Within this succession, the laminated mudstones were deposited in stable, low-energy settings as fine-grained particles settled out of suspension, while the massive layers were possibly deposited during higher energy, mudflow events. These grey to black mudstones indicate deposition under anoxic conditions in a deep stratified lake (cf. Tänavsuu-Milkeviciene and Sarg, 2012), which was at least 900 m wide. However, desiccation cracks within the lowermost lake beds (Fig. 3H) indicate the drying out during its early history of the lake and possibly initial shallower water conditions. The presence of fossil conchostracan shells in the basal beds lends further support of an initially shallow lacustrine setting (Fig. 3I). Conchostracans are bivalved, filter-feeding shrimps that are often found in shallow, freshwater lakes, and can be common in semi-arid lakes due to their short life span (approximately 5–23 days in modern species) and strong tolerance to dry environments (Kozur and Mock, 1993; Kozur and Weems, 2010). After the initial period, when the lake was shallower and prone to drying, the conditions in the interior of the lake became unsuitable for animal life, possibly because the lake became deeper and more anoxic. The rhythmically interbedded massive and laminated, grey to black mudstone facies, which lacks evidence of pedogenic alteration (Fig. 3B, D), is interpreted as a deposit of a deeper lake that likely experienced recurring and increasing storm activity. Such interstratifications are considered common in arid to semi-arid lacustrine depositional environments, prone to flash flooding during storms (Nichols, 2009, p. 159). Repeated cycles of desiccation and flash flooding have also been associated with ephemeral pond settings where sediment is washed in during storm events (Gates, 2005). The lacustrine conditions at Ha Nohana were also temporary, and were followed by a final phase of red bed deposition before the onset of the desert conditions that were typical during the Clarens Formation (Fig. 1).

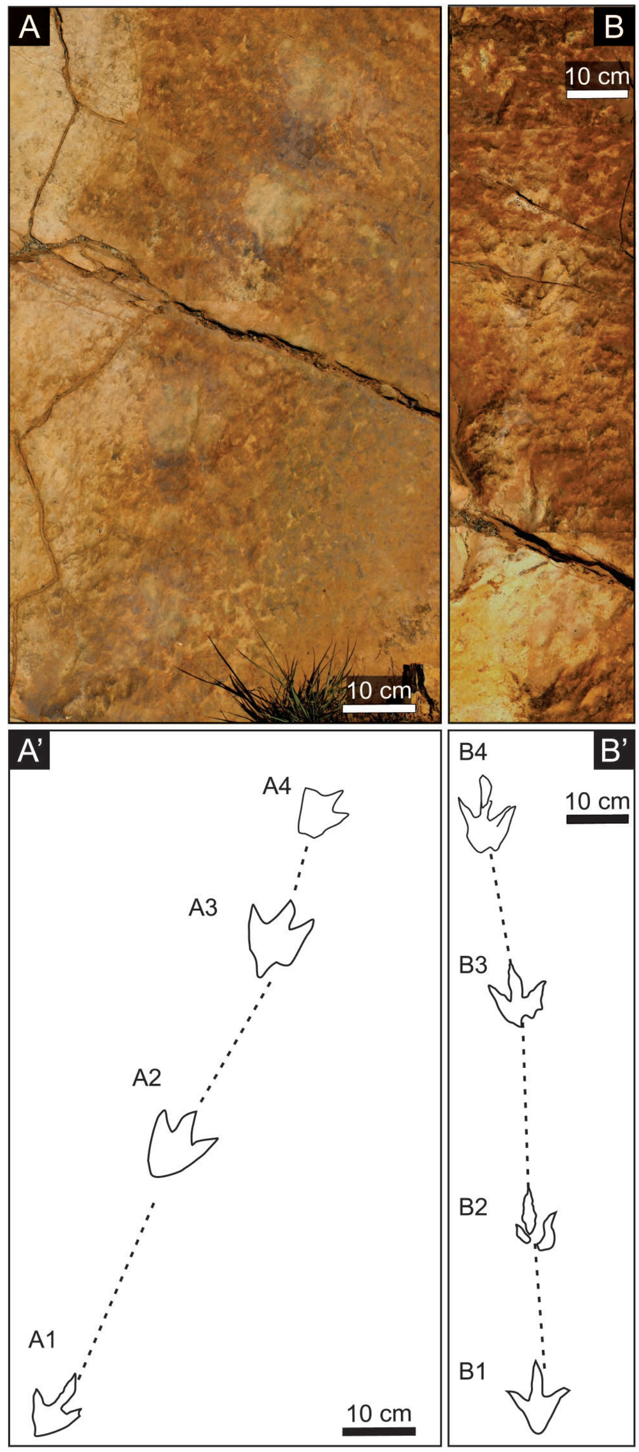

Fig. 5. Overview of bipedal trackways A and B of morphotype I tridactyl tracks at Ha Nohana. **A.** Field photographs and interpretative outlines of trackway A. **B.** Field photographs and interpretative outlines of trackway B. Each trackway comprises 4 consecutive steps of a northwards walking theropod. Tracks in both trackways show limited morphological detail, likely because of the relative firmness of the substrate at time of track formation.

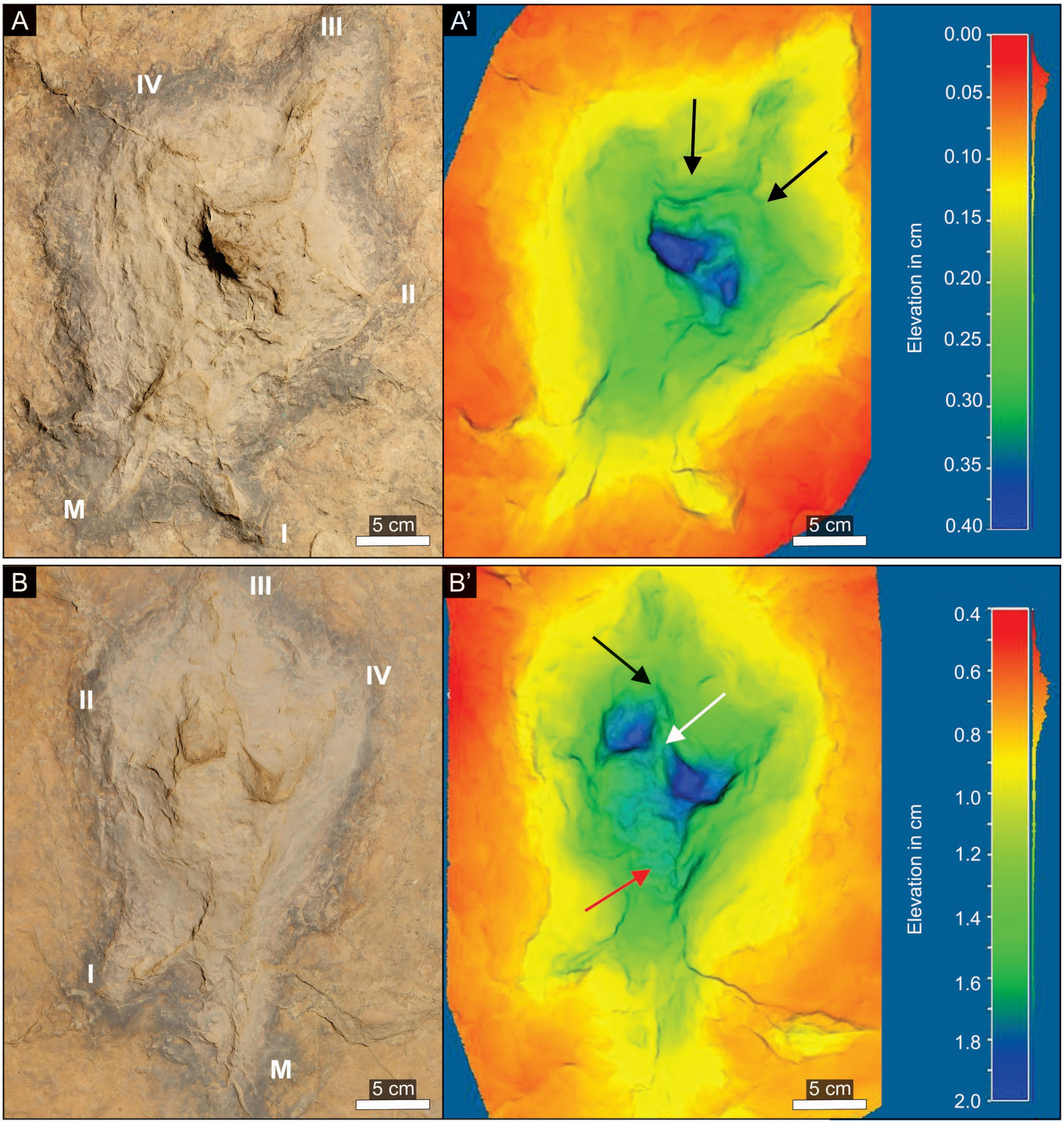

Fig. 6. Photographs (left A, B) of two representative, deeply, penetrative tetradactyl tracks of morphotype II at Ha Nohana and their false depth-colour maps (right A', B'), where dark blue is for the deeply impressed areas of the foot. Note the highly deformed morphology due to the water-saturated substrate "trapping" the foot and allowing for the preservation of both digit I and the metatarsal ('M'). Also note the extramorphological collapse features shown by the arrows in the depth-colour map and the appearance of a more posteromedially orientated hallux in B'. Black arrows indicate sediment collapse along digit walls; white arrow indicates slumping of sediment into the deepest part of the footprint; red arrow indicates sloping of the track wall at the proximal end of the track.

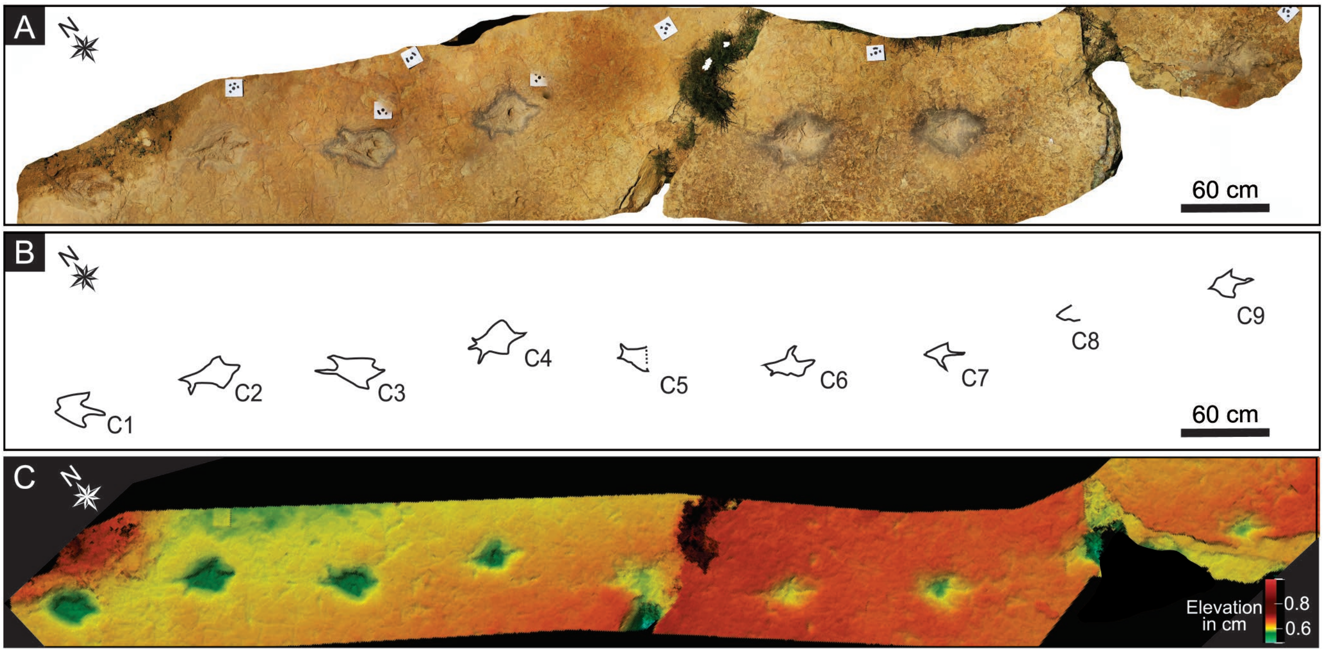

Fig. 7. Overview of trackway C comprising nine morphotype II tetradactyl tracks at Ha Nohana. **A.** Orthophoto. **B.** Interpretive outline drawing overlying the orthophoto. **C.** Colour-depth model. Note that the degree of deformation and penetration of the tracks decreases along the length of the trackway with the distal tracks (C8, C9) being more shallowly impressed and showing the least amount of soft sediment deformation (collapse) structures.

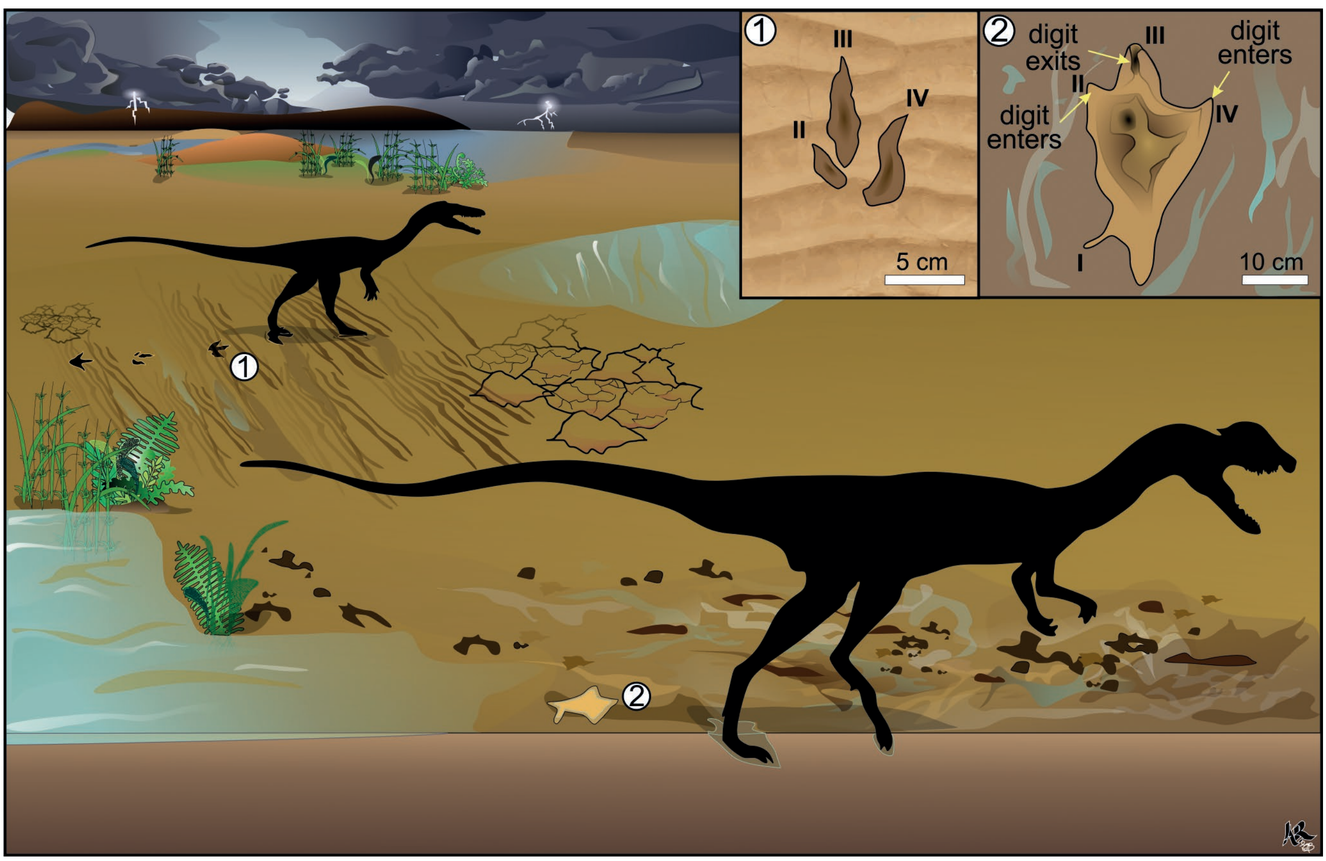

Fig. 8. Palaeoenvironmental reconstruction of the Ha Nohana palaeosurface. This Early Jurassic snapshot captures the depositional dynamics in the fluvio-lacustrine upper Elliot Formation after the passing of a heavy storm and the generation of theropod-like tracks around ephemeral ponds by small (? juvenile) and moderate size bipedal theropod dinosaurs. Numbers refer to tridactyl, theropod-like tracks (see inset): 1 - morphotype I preserved on a firm ripple marked surface; 2 - morphotype II preserved on soft, water-saturated sediment. See text and Tables for details regarding ichnotaxonomic measurements. *Dracovenator* and *Coelophysis* outlines are adapted from Ornitholestes (2018) and Martz (2012), respectively. Artwork by Akhil Rampersadh and Emese M. Bordy.

Dinosaur footprints

Morphotype I tridactyl tracks are small (average FL: 10.1 cm, FW: 8.8 cm) with a low FL/FW ratio of 1.2 (Tab. 1) and slightly asymmetrical interdigital angles (II^III: 39°; III^IV: 34°; Tab. 1). The average total interdigital divarication angle (II^IV) is large at 69° (Tab. 1). These tracks preferentially preserve claw marks, have V-shaped digital tips and occasionally display digital pad impressions. In general, most morphological features presented by morphotype I are aligned with the ichnotaxon *Grallator*, which forms part of the *Grallator-Anchisauripus-Eubrontes* plexus, in which inchotaxa are largely distinguishable by their size with *Grallator* being < 15 cm, *Anchisauripus* being between 15–25 cm and *Eubrontes* being > 25 cm in length, respectively. *Grallator* tracks are characterized by a footprint length-to-width ratio of ~ 2, narrow digits with digit IV slightly longer than digit II, a strong mesaxonic index (1.22 Pd/FW ratio for the *Grallator* type species; see Lockley, 2009) and narrow total interdigital angles II^IV of between 10 and 30° (Olsen *et al*., 1998). Furthermore, like morphotype I, *Grallator*-like tracks have a digit III that extends further than digits II and IV (Appendix Tab. 1). The main differences between morphotype I tracks and *Grallator*-like are the wider total divarication angle, the smaller FL/FW ratio and weaker mesaxony in the Ha Nohana tracks (i.e., total divarication average 69°, average FL/FW ratio 1.2 and mesaxony 0.4; Tab. 1).

In several ways, these dimensions also match those of the pes of *Anomoepus,* which are similar to *Grallator*-like tracks in size and largely in morphology but differ in the greater total divarication angle and weaker mesaxony (Pd/FW ranging from 0.2 to 0.47; e.g., Olsen and Rainforth, 2003; Lockley, 2009). Importantly the position of the metatarsal-phalangeal pad in *Anomoepus* walking traces is often nearly in line with the axis of digit III, while the metatarsal-phalangeal pads in seated traces bear a similar resemblance to grallatorid tracks, where the metatarsal-phalangeal pad of digit IV is positioned to the side of the axis of digit III (Olsen and Rainforth, 2003). This position of the metatarsal-phalangeal pad seen in grallatorid footprints is also consistent with early theropod tracks (Getty, 2005). Furthermore, it should be noted that while both ichnogenera have a digit III that extends farther than other digits, *Anomoepus* exhibits a shorter digit III than *Grallator* (e.g., Olsen and Rainforth, 2003; Knoll, 2005; Dalman and Weems, 2013). The higher divarication angles for morphotype I tracks in comparison to *Grallator*-like tracks, although similar to *Anomoepus*, can be accounted for by the animals' foot interaction with substrate (Olsen and Rainforth, 2003), and this can largely vary and deform with changes in substrate. Based on the gross morphological similarities, morphotype I tracks are more allied with *Grallator,* and can be considered *Grallator*-like because of the features mentioned above (e.g., foot lengths < 15 cm, an asymmetric morphology with digit III extending further than digits II and IV, metatarsal-phalangeal pads of digit IV that lie lateral to the axis of digit III, some digits terminating in sharp claw marks). Both *Anomoepus*-like and *Grallator*-like tracks are common in the Lower Jurassic of southern Africa (e.g., Ellenberger, 1970; Olsen and Galton, 1984; Knoll, 2005; Wilson *et al*., 2009). *Anomoepus*-like tracks are considered to be made by ornithischian dinosaurs (Olsen and Rainforth, 2003; Dalman and Weems, 2013), whereas *Grallator* is considered to be made by theropod dinosaurs (e.g., Thulborn, 1990; Olsen *et al*., 1998).

In southern Africa, the Early Jurassic osteological record, to-date, contains evidence for only two theropod taxa, namely that of the larger *Dracovenator regenti* (Yates, 2005) and a smaller *Coelophysis rhodesiensis* (Bristowe and Raath, 2004). Morphometric and allometric hip heights for the Ha Nohana trackways (Tab. 3) were calculated and revealed consistent results supporting Henderson's (2003) conclusion that different hip height calculations will return consistent results for smaller theropods. Hip height estimations are not as reliable for trackmaker identification as footprint characters, which mirror the anatomy of the foot (e.g., Sacchi *et al*., 2014; Romano and Citton, 2016; Romano *et al.*, 2016), although the < 1 m hip height estimated for morphotype I (Tab. 3) being comparable to body size estimates for the theropod genus *Coelophysis* makes this common southern African theropod a possible trackmaker of morphotype I tracks. The speed calculations indicate that these trackmakers were walking slowly over the ripple marked surface of a sand layer. The trackways being positioned sub-perpendicular to the crestlines of the asymmetrical ripple marks possibly indicate that the trackmakers walked towards a nearby pool of floodwater to drink (Fig. 8; cf., Paik and Kim, 2006; Sciscio *et al*., 2016).

Tetradactyl morphotype II was made by a bipedal animal with comparatively larger pes (average 27.9 cm) than the maker of morphotype I. Our measurements also show an average FL/FW ratio of 1.5 and the average Pd/FW ratio of 0.5 (Tabs 1, 2). Due to the overall preservation of the deep footprints with claw marks, metatarsal and posteromedially oriented hallux impressions, morphotype II is cautiously attributed to a theropod-like trackmaker, but more detailed taxonomic analysis and trackmaker identification of morphotype II are not possible. Based on the average footprint size of 28.5 cm, estimated body length of 5.32 m and the very limited variety of theropod bone fossils in southern Africa, morphotype II tracks are very tentatively attributed to *Dracovenator regenti* (Yates, 2005).

Morphotype II tracks, with their tetradactyl shape and associated soft sediment deformation features (Figs 6, 8), uniquely preserve the 3D foot motion of the trackmaker (e.g., Gatesy *et al.,* 1999), despite their otherwise poorly defined morphological features. The tracks illustrate a trackmaker walking through a viscous and malleable sediment, which caused its foot to sink deeply into the substrate such that even the metatarsal and the hallux where impressed. Because these anatomical features are otherwise nearly never in contact with firm ground in theropod dinosaurs (Gatesy *et al.,* 1999), morphotype II tracks are unique for the Lower Jurassic ichnological record in southern Africa. Trackway C of morphotype II demonstrates the pattern of foot motion described by Gatesy *et al*. (1999), whereby the animal steps into a wet substrate with an initially splayed foot and while the foot is emplaced, the sediment in the footwalls collapsed over the digits and is displaced during the kick-off phase of the foot (Milàn and Bromley, 2006). The resultant sloping track walls are generated by the dynamic motion of the foot during track formation (Milàn and Bromley, 2006).

The angle of preservation of the hallux impression is related to the angle of foot penetration in more malleable substrates, where a foot with an anteromedially directed hallux is also capable of preserving a posteromedially directed furrow (Gatesy *et al*., 1999). In morphotype II, the angle of the hallux impression is at 109˚ relative to digit III and the metatarsal impression is posteriorly orientated. Metatarsal impressions have also been linked to theropods resting, squatting, foraging for food or crouching while watching prey (Romero-Molina *et al.,* 2003). However, in trackway C, we associate the metatarsal and hallux impressions with a walking trackmaker trudging through a water-saturated medium (e.g., Kuban, 1989; Citton *et al.*, 2015; 2017). The trackmaker's pace and stride do not change significantly along the trackway, although the track morphology changes from deeper, highly deformed proximal tracks to shallower, less deformed distal tracks (Fig. 7; Tab. 3). Assuming that the distal tracks in trackway C formed in a relatively firmer substrate, acceleration along the trackway would be expected (Thulborn, 1990) as the animal should have found the firmer substrate easier to increase its stride over. This, however, does not occur in trackway C and seems to be line with the suggestion by Wilson *et al*. (2009) who state that, unlike ornithischians, theropod dinosaurs did not significantly adapt their locomotive mode with changing substrate conditions. However, due to the lack of resting or stopping traces (and lacking preceding or succeeding tridactyl tracks) along the trackway, it is not impossible that the trackmaker did adapt its walking style by lowering its center of balance to maintain stability as it squelched across this softer section of the substrate (cf. Belvedere *et al.*, 2010). Moreover, the intratrackway variably in the depth of the foot impressions (Fig. 7) may also be due a gentle palaeoslope along the shoreline of a temporary pond (Fig. 8).

Although morphotypes I and II are found on the same palaeosurface, their preservational differences can, to some extent, be related to the different sizes (and masses) of the trackmaker animals (estimated from their foot lengths). However, it is more likely that the differences are accentuated by the substrate heterogeneity, which is further supported by the local sedimentary facies variations along the palaeosurface (i.e., the same sandstone layer at trackway B is massive, structureless, but some 300 m to the ~ N, it displays ripple marks and desiccation cracks - Fig. 1B). The substrate heterogeneity might also be due to the position of the sites relative to the pools that were likely left behind major flash floods (Fig. 8). Moreover, the different track preservations might also be linked to the relative timing of the impressions – i.e., morphotype II could have been impressed earlier on the substrate when it was more water-saturated.

CONCLUSION

Ichnites on the Ha Nohana palaeosurface are preserved as two morphotypes that can be attributed with variable certainty to theropod-like trackmakers. Moreover, morphotype II displays anatomical details of the trackmaker's foot that are not common with respect to most tridactyl morphologies but are well-documented in the ichnological record of theropods (e.g., Kuban, 1989; Olsen *et al*., 1998; Gatesy *et al*., 1999; Gatesy, 2003; Lockley *et al*., 2003; Nicosia *et al*., 2007; Milàn *et al*., 2008; Lockley *et al*., 2013; Citton *et al*., 2015; Romano and Citton, 2016; Citton *et al*., 2017). Here, the metatarsal and digit I are present in the track impression suggesting that as the animal's foot sunk a significant amount into the substrate and probably had to walk while waddling through the water-logged sand. However, sediment cohesion was high enough that on extracting the foot the tetradactyl impression was not completely lost.

From a sedimentological viewpoint, the Ha Nohana site preserves an ancient ecosystem that was dominated by extensive, low-gradient, vegetated floodplains and multiple periods of flash flooding and drying out in a semi-arid climate. Within this system, vertebrate tracks were generated on a single palaeosurface by walking bipedal dinosaurs after flooding events deposited laterally persistent sheet sandstones of variable water-saturation levels and that are dominated by both upper flow regime sedimentary structures and desiccation cracks. The two different modes of footprint preservation within a single sandstone bed demonstrate the spatially heterogenous moisture content of the sand layers. Large, deep tracks were produced as the animal's foot sank into the malleable, more water-saturated sediment, while the smaller, shallower tracks were preserved on a drier and firmer substrate that contains small-scale ripple marks and desiccation cracks.

Based on morphological parameters, the tracks and trackways were generated by theropod-like trackmakers. Considering the currently known theropod body fossil record of the Lower Jurassic upper Elliot Formation, the trackmakers are very tentatively identified as *Dracovenator regenti* and *Coelophysis rhodesiensis*. Following the multiple sheet flooding events and trampling of the surface by dinosaurs, the area was occupied by a progressively deepening, temporal lake in which water stagnation lead to stratification and anoxia on the lake floor. Initially, the lake was shallow, prone to desiccation, and suitable for occupation by conchostracans. Subsequent to the lake drying up, subaerial semi-arid conditions returned and 20–35 m of pedogenically altered red beds were deposited at Ha Nohana, before the onset of desert conditions that characterized the sedimentary dynamics of the conformably overlying Clarens Formation.

Overall, this study advances the reconstruction of the Early Jurassic (Hettangian to Sinemurian) environments in southern Africa by providing some fine-scale details of these semi-arid ecosystems. This southern Gondwana palaeoenvironment was characterized not only by a diverse biota of plants, invertebrates and vertebrates, including two different taxa of theropods, but also by dynamically changing environmental conditions driven by extreme fluctuations in precipitation, which caused flash floods, and locally, the establishment of deep, stratified lakes on one end, and repeated drying out on the other.

Acknowledgments

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Supplementary data archiving

Supplementary data for the Ha Nohana project are available on Figshare:https://figshare.com/s/ac86a240eeb5ab09fc1c
The data include Appendix Tab. 1, text Tabs 1–3 in MS Excel version, field photographs and photogrammetric models and figures in in high resolution version (TIFF).

Appendix Table 1

Ichnological measurements of 44 of the 52 morphotype I tracks at Ha Nohana.
Note that 17 tracks could not be measured due to their poor preservation.
Abbreviations: II, III, IV – digits; ^ – interdigit angles; FL – foot length;
FW – foot width; FLM – foot length with metatarsus; Pd – protrusion of digit III.

Footprint#	FL	FW	FL/FW	Pd	Pd/FW	Interdigit angle				Digit length	
						II^III	III^IV	II^IV	LII	LIII	LIV
	(cm)			(cm)						(cm)	
5	10.0	10.0	1.0	4.6	0.5	42	40	81	6.8	9.1	7.9
6	9.0	9.0	1.0	2.9	0.3	39	38	81	5.2	7.3	6.5
7	11.0	10.0	1.1	3.2	0.3	49	44	84	5.9	8.4	7.5
8	10.0	9.0	1.1	2.9	0.3	39	36	76	7	7.9	7.7
9	10.5	8.5	1.2	3.9	0.5	41	29	65	6.3	8.2	6.4
10	10.0	9.5	1.1	3.2	0.3	36	47	80	5.9	7.4	6.8
11	9.5	9.5	1.0	2.9	0.3	40	35	66	6.6	7.7	6.7
12	9.5	9.0	1.1	3.6	0.4	N/A	N/A	N/A	N/A	N/A	N/A
13	10.0	9.0	1.1	3.4	0.4	54	39	77	5.2	7.3	7.5
14	10.0	10.0	1.0	3.7	0.4	43	39	83	6.4	7.9	6.7
15	9.5	9.5	1.0	3.0	0.3	39	37	71	6	6.9	5.3
16	9.0	8.5	1.1	3.8	0.4	N/A	N/A	N/A	N/A	N/A	N/A
19	11.0	9.0	1.2	2.9	0.3	44	39	78	6.4	8.1	7.4
22	11.5	11.0	1.0	4.9	0.4	39	29	69	5.9	7.5	6.1
23	10.5	9.0	1.5	2.9	0.3	48	40	71	5.4	7.7	7.8
24	10.0	9.5	1.2	2.9	0.3	48	37	80	4.6	5.6	5.4
25	10.0	8.5	1.0	4.5	0.5	N/A	N/A	N/A	N/A	N/A	N/A
26	10.0	8.0	1.2	3.4	0.4	N/A	N/A	N/A	N/A	N/A	N/A
27	9.5	7.5	1.2	3.6	0.5	33	34	65	5.4	6.6	7.6
28	10.0	8.5	1.2	3.3	0.4	46	34	84	5.7	6.6	6.8
29	10.0	7.5	1.3	3.4	0.5	34	29	60	5.9	7.8	6.2
30	11.0	10.0	1.2	4.7	0.5	N/A	N/A	N/A	N/A	N/A	N/A
31	10.0	9.1	1.2	4.4	0.5	N/A	N/A	N/A	N/A	N/A	N/A
33	10.0	9.0	1.5	3.6	0.4	36	37	70	4.9	6.9	5.3

Footprint#	FL	FW	FL/FW	Pd	Pd/FW	Interdigit angle				Digit length	
						II^III	III^IV	II^IV	LII	LIII	LIV
	(cm)			(cm)						(cm)	
35	10.0	8.5	1.1	4.5	0.5	52	36	84	4.9	5.7	5.3
36	10.0	9.0	1.3	3.7	0.4	38	36	66	5.6	7	6.3
39	10.0	8.0	1.2	4.4	0.6	35	26	59	5.4	6.7	6.3
40	10.0	8.0	1.3	4.2	0.5	N/A	N/A	N/A	N/A	N/A	N/A
41	10.0	8.5	1.2	4.6	0.5	N/A	N/A	N/A	N/A	N/A	N/A
42	10.0	8.0	1.3	3.5	0.4	N/A	N/A	N/A	N/A	N/A	N/A
43	10.0	8.5	1.3	3.4	0.4	N/A	N/A	N/A	N/A	N/A	N/A
44	10.5	8.0	1.1	3.0	0.4	N/A	N/A	N/A	N/A	N/A	N/A
45	10.5	10.0	1.2	3.2	0.3	32	25	53	6.5	8.2	7
46	10.5	7.0	1.1	4.2	0.6	N/A	N/A	N/A	N/A	N/A	N/A
47	10.3	8.5	1.1	4.5	0.5	29	30	55	5.7	7.9	6.3
48	10.5	8.5	1.1	3.6	0.4	30	27	58	6.4	7.6	7
49	10.0	8.0	1.3	4.3	0.5	29	28	53	4.9	7.6	5.2
50	10.5	9.0	1.2	4.3	0.5	N/A	N/A	N/A	N/A	N/A	N/A
51	10.5	9.0	1.3	4.2	0.5	41	29	64	4.7	7.7	6.7
52	10.0	8.5	1.3	3.8	0.4	35	26	59	5.6	7.2	6.7
53	10.0	10.0	1.2	4.1	0.4	41	37	83	5.6	6.3	6.5
54	10.0	8.5	1.1	3.4	0.4	40	28	61	4.5	6.2	5.2
55	9.5	6.5	1.2	3.7	0.6	36	26	62	5.11	6.7	6.2
56	10.5	9.0	1.2	4.4	0.5	28	26	56	4.9	6.5	6.2
Average	10.1	8.8	1.2	3.7	0.4	39	34	69	5.7	7.3	6.5

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