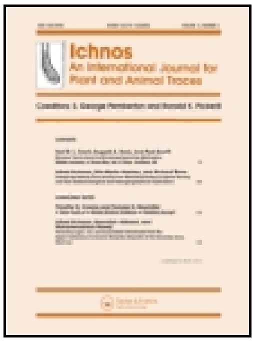

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A Dinosaur Ichnocoenosis from the Waterberg Plateau (Etjo Formation, Lower Jurassic), Namibia

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ABSTRACT
About a hundred dinosaur tracks, mostly preserved as isolated footprints, have been recorded at a single site within the borders of the Waterberg National Park, Otjozondjupa Region, north-central Namibia. They are found in an interdune setting within the Lower Jurassic Etjo Formation and represent medium-sized theropods with slender digits and high projection of digit three. From an ichnotaxonomic point of view, the Namibian tracks are intermediate in morphology between *Grallator* (which is known to occur at other localities within the same Etjo Formation) and *Anchisauripus*, being otherwise in a size range that is usually considered typical for the latter ichnotaxon or even for *Eubrontes*. The Waterberg tracks do not match the allometric growth model proposed by Olsen et al. (1998) for the Early Jurassic theropod track assemblage of the North American Connecticut Valley, and they highlight the difficulties of consistently discriminating between theropod ichnotaxa in the *Grallator-Anchisauripus-Eubrontes* plexus. The Waterberg ichnosite adds important data to our understanding of the ichnological diversity of the Etjo Formation, raising to three the dinosaur localities in Namibia with revised and updated ichnofaunas. The dinosaur ichnofauna from Namibia, of which the Waterberg tracksite is a basic component, shows high ichnotaxonomic similarity with coeval assemblages from the northern hemisphere. This points to an overall homogeneity of the global ichnofaunistic composition, even at lower latitudes.

KEYWORDS
Dinosaur footprints Waterberg Plateau; Namibia; Etjo Formation; Early Jurassic; tridactyl dinosaur tracks

Introduction

The presence of dinosaur footprints in the Waterberg Plateau has been known for decades (Cosburn, 1980, 1990; Pickford, 1994, 1995), albeit a detailed description and interpretation of these ichnites has never been attempted so far. The importance of this site is both scientific and historical, as it is one of the few windows on the Early Jurassic vertebrate life of this region and a significant addition to the ichnological record from the Etjo Formation, which has a long research history dating back to the first decades of the 20th century (Huene, 1925; Gürich, 1926) and is recognized by the Namibian government as part of the natural and cultural heritage of the country. The whole Namibian dinosaur track record is in the process of being reevaluated in a series of works that focus on the occurrences in the Waterberg range, such as the Omuramba Omambonde tracksite (D'Orazi Porchetti et al., 2015) and the historical occurrence at the Otjihaenamaparero 92 Farm (Wagensommer et al., 2016). All these tracksites occur in the Etjo Formation, a Lower Jurassic unit representing arid to hyper-arid paleoenvironments. In all cases, dinosaur tracks are found in interdune settings and represent small to medium bipedal dinosaurs. So far, no quadrupedal trackways have been found. The Etjo ichnofauna reveals a strong overall resemblance to coeval ichnoassemblages from North America, pointing to a relatively homogeneous distribution of trackmakers in the Early Jurassic. A comparison with the geographically closer and coeval ichnofauna of Lesotho (Ellenberger, 1972, 1974; Olsen and Galton, 1984; Smith et al., 2009) is not attempted herein, as the ichnotaxonomy of this assemblage needs to be revised. A major problem is that the monumental pioneering work of Ellenberger focused mainly on somehow defining idealized track types without assessing their morphological ranges. This makes any comparison with other occurrences problematic.

Being inside the borders of the Waterberg National Park, and being one of the few dinosaur records from Namibia, the Waterberg Plateau tracksite should be considered part of a potential paleontological heritage system, and as such, it deserves to be protected and promoted.

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Geological framework

The Großer Waterberg is a large plateau in the Otjozondjupa Region, north-central Namibia, which reaches a maximum height of 1885 meters in the area of the Waterberg National Park (Fig. 1). Its reddish, vertical cliffs originate from erosive processes of the Etjo and underlying Omingonde formations. The Etjo Formation forms the high and steep walls at the top of the plateau, reaching a maximum thickness of about 140 meters in outcrop (Wanke, 2000), while the more erodible mudstones of the Omingonde Formation (Lower to Middle Triassic) form the gentle slopes of the Waterberg and are mostly covered by debris. The two formations are separated by a sharp erosive contact thought to represent a hiatus of about 35 myr (Smith and Swart, 2002). The Plateau stretches along a northeast-southwest line, bordered to the north by the Omaruru-Waterberg fault. The Etjo Formation is dominated by siliciclastic rocks, deposited in semi-arid to hyper-arid environments. It has been divided into three informal members (Lower, Middle, and Upper Units) by Holzförster et al. (1999), who distinguish three main depositional phases with increasing aridity. The Lower Unit is represented by 25 meters of well-sorted, massive sandstone interbedded with thin pebbly gravel layers. The Middle Unit is dominated by massive and homogeneous sandstone beds and reaches a thickness of about ten meters in the Waterberg area. The Upper Unit is dominant in terms of thickness, being about 100 meters thick on the northern part of the Waterberg. Cross-bedded sandstone is the dominant feature of this member of the Etjo Formation, testifying to the presence of a large erg (Holzförster et al., 1999; Wanke, 2000) (Fig. 2A).

Footprints have been found on a flat surface (Fig. 2B), exposed over a few hundred square meters, moderately to highly weathered, depending on the sectors. Dinoturbation occurred on a package of thin parallel sandstone layers, interpreted here as an interdune deposit. Above the printed surface, columnar remains of cross-bedded sandstone are preserved, which are similar to those observed at the Omuramba Omambonde tracksite (Wiechmann, 1983; Grote, 1984; D'Orazi Porchetti et al., 2015) (Fig. 2C,D). They represent the remnants of a dune deposit that eventually covered the track-bearing interdune surface. Here at the Waterberg tracksite, as well as at the Omuramba Omambonde locality, the footprint-bearing layer belongs to the uppermost member of

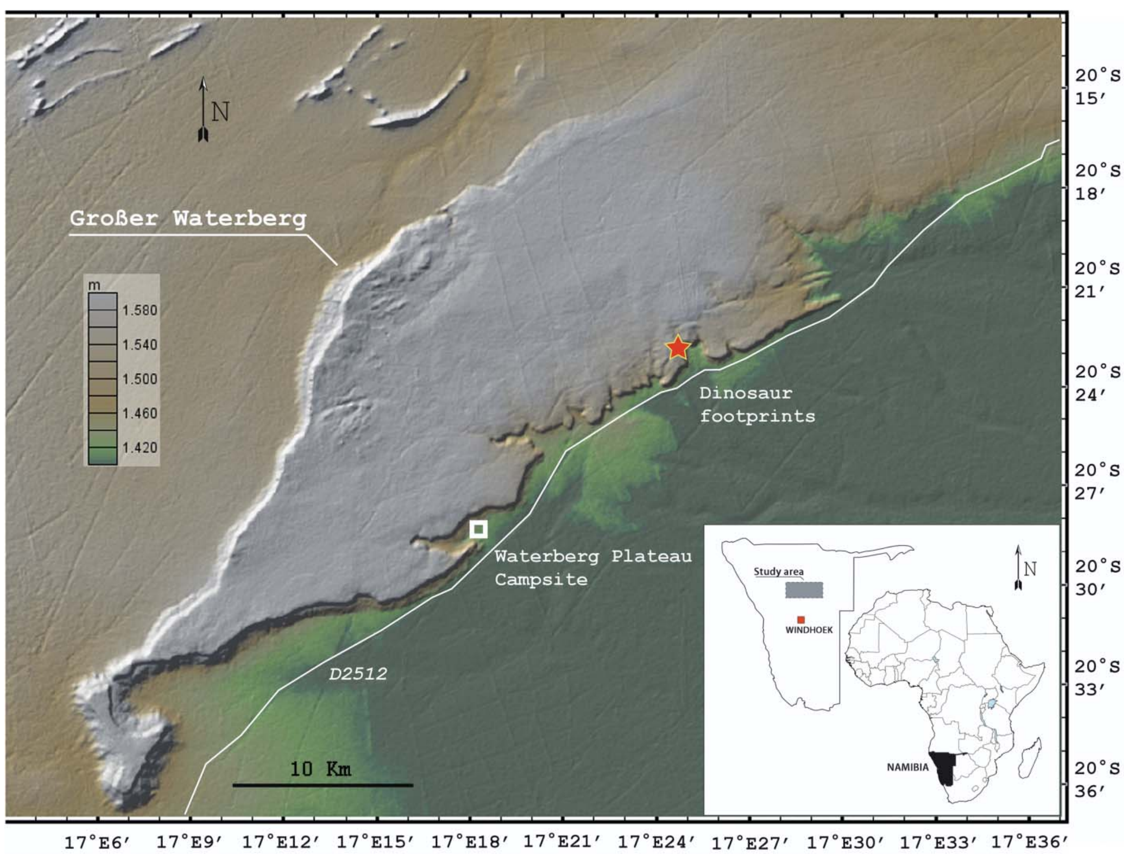

Figure 1. Geographic location of the dinosaur tracksite at the Waterberg Plateau (red star). Base map generated in GeoMapApp (http://www.geomapapp.org).

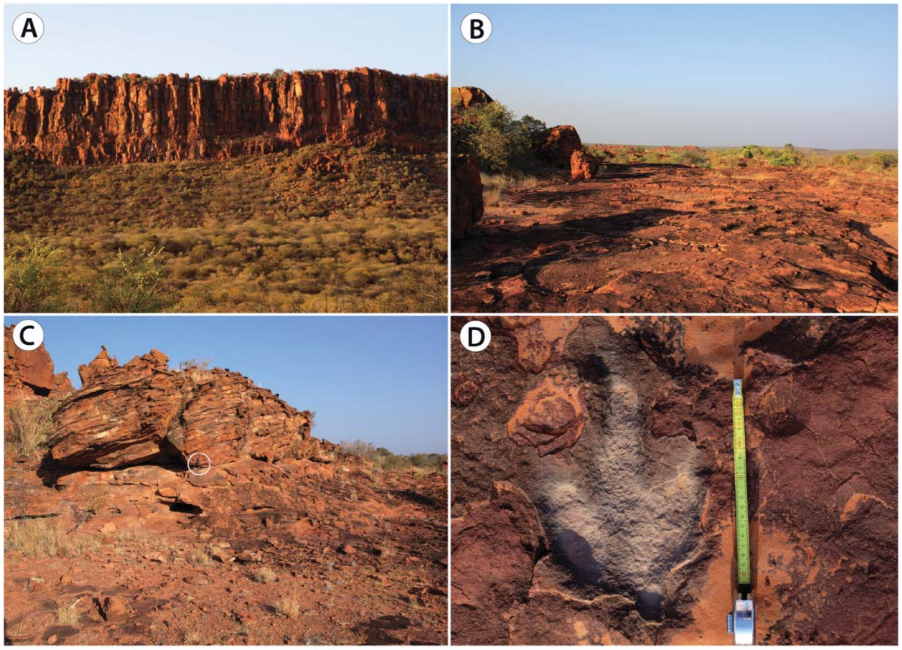

Figure 2. A. The steep cliffs of the Etjo Formation as visible from the Waterberg Plateau Campsite. A large talus hides the contact with the Omingonde Formation, densely covered by vegetation. B. North to South view of the track-bearing surface. The surface is better preserved on the left side of the photograph, where large blocks of cross-bedded sandstone are visible. C. Detail of the first-order contact between the trampled surface, interdune, and cross-bedded strata of a dune. Hammer in the centre of the photograph (white circle) for scale. D. One tridactyl footprint is highlighted here in order to show the quality of preservation. Delamination is visible around the footprint itself. Difference in color depends on the presence of sand inside the digit traces, removed before shooting. The scale is set on 20 cm.

the Etjo Formation (Fig. 3A), and these two sites can be correlated stratigraphically. The historical Otjihaenamaparero 92 locality, which is discussed in detail elsewhere (Wagensommer et al., 2016), is more difficult to relate in stratigraphic terms to the Waterberg and Omuramba Omambonde tracksites, but might represent an older level.

The presence of *Otozoum moodi* at the Omuramba Omambonde locality (D'Orazi Porchetti et al., 2015) represents an important age constraint for the Etjo Formation, as this ichnotaxon is exclusively known from the Early Jurassic. This find strongly supports a Lower Jurassic age for the Etjo Formation, as does a mould of a possible *Massospondylus* skeleton from the Middle Unit of the Etjo Formation (Holzförster, 1999; Holzförster et al., 1999),

Materials and methods

Over a hundred footprints have been identified at the Waterberg Plateau tracksite. Direction of travel has been estimated from 88 tracks, and some 24 footprints have been measured in the field (Appendix). Many more footprints might have been lost to erosion, and some might have been overlooked during fieldworks because of compelling time constraints and suboptimal light conditions. However, the surface appears to be medium-to-highly trampled, according to the dinoturbation index proposed by Lockely (1991). Selected tracks have been reproduced on transparent peels, photographed, and, in two cases, molded with silicon rubber. Close range photogrammetry on selected specimens resulted in 3D models of the tracks, obtained following the method in Falkingham (2012) (Fig. 4). Linear track parameters measured in the field include footprint length (FL), footprint width (FW), and projection of digit three beyond the tips of digits two and four ("toe extension"; te). FL has been measured as distance between the tip of digit three (excluding claw mark where this could be differentiated from the most distal interphalangeal pad) and the proximal margin of digit four (alternatively, where the rear margin of the digits appeared to be fused to a "heel," the hindmost end of the track was chosen). FW has been measured as distance between the tips of digits two and four (excluding claw marks where visible), and te has been measured as distance between the tip of digit three (as defined for FL) and the line connecting the tips of the lateral digits. The only angular value measured is total divarication of the outer digits. In order to compare the Waterberg tracks with other Early Jurassic tridactyl ichnotaxa, especially with the classical ichnotaxa from North America, the linear measurements FL, FW, and te were plotted on a

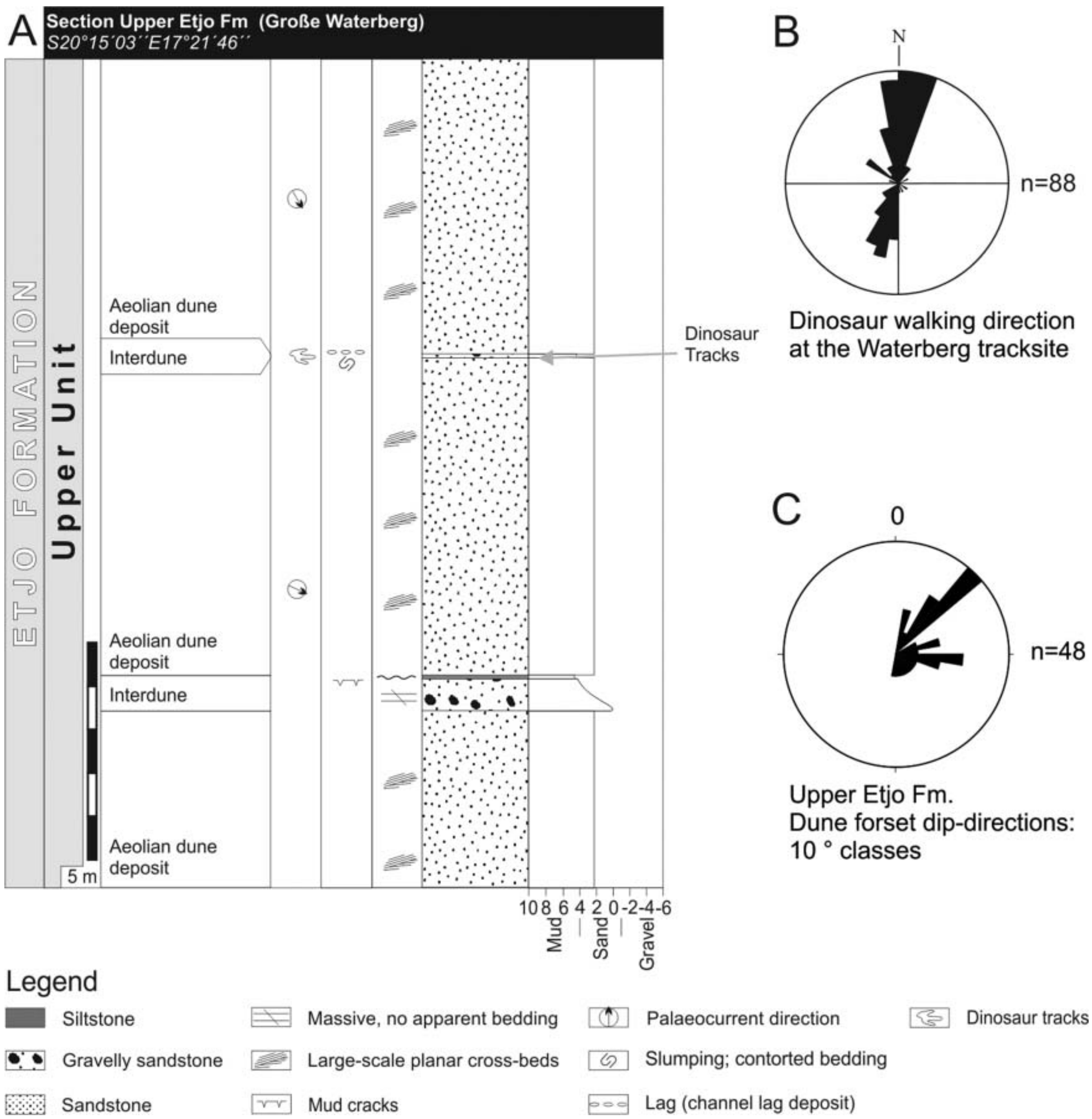

Figure 3. A. Stratigraphic section of the Upper Unit at the Waterberg Plateau, see coordinates for the exact location of the section. B. Rose diagram showing the walking direction of 88 tracks from the Waterberg tracksite. Note the symmetrical distribution of the two main directions, hinting at the presence of a physical obstacle that forced the animals to follow a given path. C. Dune foreset dip orientation diagram, as from 48 samples. As the dune crests would be oriented at 90° to the direction of dip, the secondary peak, dipping roughly towards the east, correlates well with the walking direction of dinosaurs at the Waterberg tracksite.

diagram comparing the proportions of "anterior" and "posterior triangle" (*sensu* Lockley 2009), as proposed by Weems (1992). This diagram will be referred to as the "Weems diagram" herein.

Discussion and remarks

Footprints at the Waterberg tracksite mostly occur as isolated tracks or short trackway segments (up to five consecutive tracks). Orientation of digit three has been measured for 88 tracks and is assumed to match closely the direction of travel of the trackmaker, as the few trackway segments preserving three or more tracks show no appreciable rotation with respect to the trackway midline. The resulting rose diagram (Fig. 3B) highlights two main directions, which are exactly opposite to each other, one heading NNE and the other SSW. This correlates well with one trend of fossil dunes in the Etjo Formation as measured in the Waterberg area (Wanke, 2000) (Fig. 3C). We infer that the animals moving over the flat interdune surface were probably forced to follow a preferential path by some kind of physical obstacle, most likely a nearby dune.

The ichnocoenosis preserved at the Waterberg tracksite appears to be morphologically homogenous. All the

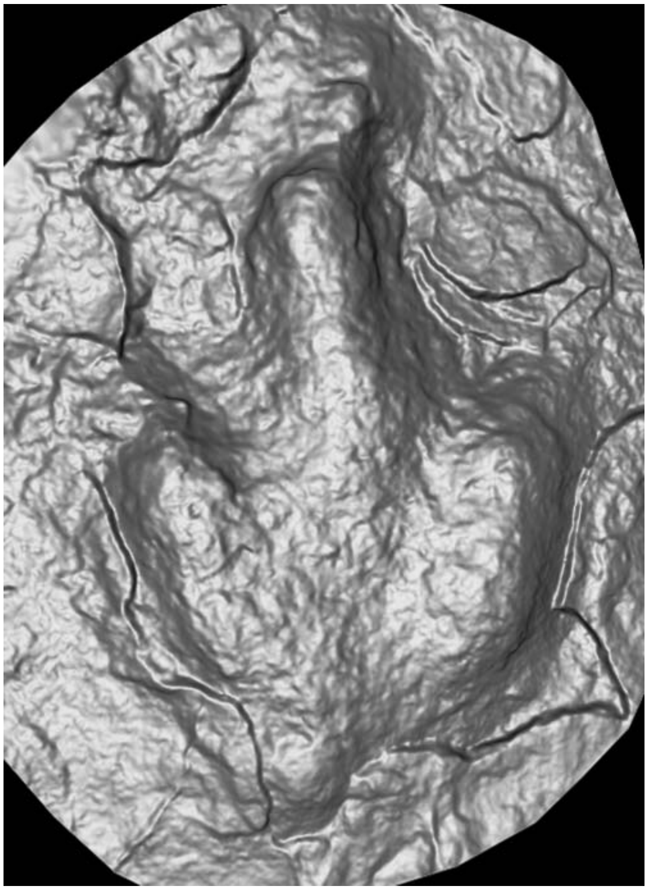

Figure 4. Three dimensional digital model based on close range photogrammetry on a silicon rubber mould. Footprint unnumbered. The total length of the footprint is 25 cm. The original footprint is reproduced in Fig. 2D.

Figure 5. Detail of preservational styles; some tracks appear to be raised above the surrounding surface due to higher degree of erosion around the track. Scale bar is 10.

tracks are within a relatively narrow size range (20 < FL < 27.5), without gaps in size distribution that could have hinted at the presence of distinct trackmaker populations. Some tracks are well defined, with slender digits, clear pads and claw marks, whereas others display broader digit marks without recognizable interphalangeal pads. This is interpreted here as a preservational difference, best explained as a gradient of shallow versus deeper undertracks. As a matter of fact, the tracking surface is subject to erosional exfoliation; i.e., the bed on which the tracks are preserved is laminated and the individual laminae tend to detach in places, exposing successively deeper surfaces. Typically, a lamina weathers more easily around the track than inside the track itself, so that often the tracks preserve remnants of younger laminae and in some instances appear to be raised with respect to the surrounding surface (Fig. 5). The deeper the exposed lamina is positioned with respect to the surface on which the animals walked, the more a track becomes blurred and displays broad digits without recognizable pads. Relative proportions of the tracks also change with the depth of the exposed lamina; deeper undertracks display a higher FW relative to their FL. As this shallow-vs-deep undertrack gradient best explains the slight morphological difference between the tracks, we infer that all footprints at the Waterberg site represent a single ichnotaxon, thus representing a monotypic ichnoassemblage.

All footprints at the Waterberg tracksite are tridactyl (Figs. 6 and 7). No hallux marks or metatarsal impressions were observed. Footprint length is about 24 cm on average, for an average width of 16 cm. In qualitative terms the footprints have a slender morphology, with low angle of digit divarication. Digit three has a remarkable extrusion respect to the laterals, and the proximal end of digit four is distinctively withdrawn with respect to the base of digit three. All digits are narrow (width of the digits about 1/4 of their length) and end in sharply pointed claw marks. On the basis of these features, we assign the footprints to a medium-sized theropod trackmaker.

For ichnotaxonomical purposes, we focused on those few tracks that show well-defined outlines and clear digital pads that allow an unequivocal assessment of the basic linear measurements FL, FW, and te. This sample

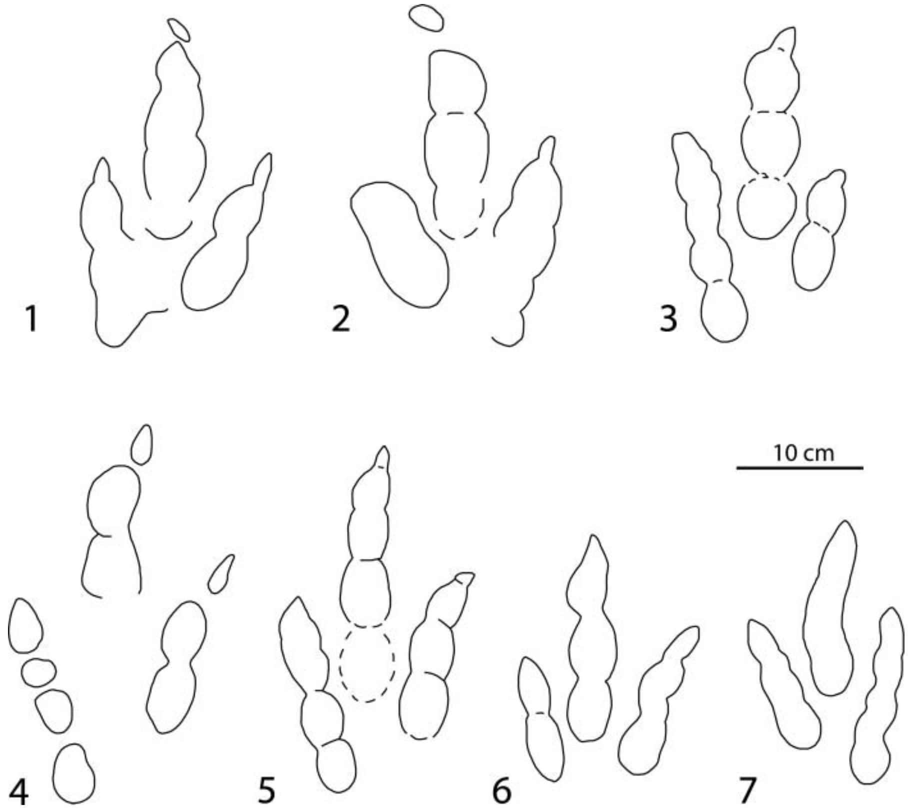

Figure 6. Outline drawings of selected dinosaur tracks from the Waterberg tracksite. Footprint no. 2 is the same shown in Fig. 2 (photograph) and Fig. 4 (3D model). Scale bar is 10 cm.

(which we will refer to as "elite tracks" from here on) encompasses about 10% of all tracks preserved on the surface.

On a qualitative basis (Table 1), the elite tracks from the Waterberg correlate well with the revised diagnosis of *Anchisauripus* as defined by Olsen et al. (1998). If plotted on the Weems diagram, however, the tracks define a field which is intermediate between the ranges of *Eubrontes, Anchisauripus* and *Grallator* (Fig. 8). About half of the tracks are within the range of *Grallator*, though very close to *Anchisauripus*. This result highlights the difficulties of consistently discriminating between tracks within these three classical Early Jurassic ichnotaxa, which led different authors either to synonymizse them all under a single label (Olsen, 1980; Rainforth 2005), or recognize *Eubrontes* and *Grallator* as distinct ichnogenera and synonymize *Anchisauripus* with the latter (Weems, 1992; Lockley, 2009).

On a regional scale, the dinosaur tracks preserved at the Waterberg site can be compared with the rich and diverse assemblage at the Otjihaenamaparero 92 Farm. The ongoing revision of this locality (Wagensommer et al., 2016) shows that moderately large tracks (FL in the range 25–30 cm) occur together with numerous small tracks (FL mostly in the range 7–10 cm). The former include a trackway that is virtually identical to Northern American *Eubrontes giganteus*, a second well-preserved trackway with foot proportions more typical of *Kayentapus*, and a third long trackway (identified by the acronym ONP I_2) that plots as *Anchisauripus* on the Weems diagram, although the track outlines are slightly biased due to preservational factors. The small tracks are partly referable to *Grallator* isp., though a recurrent morphotype with neat hallux impressions and wide divarication of the digits may represent a different ichnotaxon.

Viewed in this context, the Waterberg assemblage probably represents the same ichnotaxon as trackway ONP I_2 at Otjihaenamaparero. The shared characters include similar size, general digit slenderness, and similar relative proportions. ONP I_2 plots a bit higher in the Weems diagram and compares better to North American *Anchisauripus*, but we do not think that this difference is significant for ichnotaxonomy in view of the preservational conditions of trackway ONP I_2, which will be discussed elsewhere (Wagensommer et al., 2016). On the other hand, the Waterberg assemblage is clearly distinct from other "large" forms at Otjihaenamaparero (assigned to *Eubrontes* and *Kayentapus*), not only by its different relative proportions, but also by its appreciably more slender digits. Some of the "small" tracks at Otjihaenamaparero (referred to *Grallator* isp.) are morphologically similar to the Waterberg tracks, but are

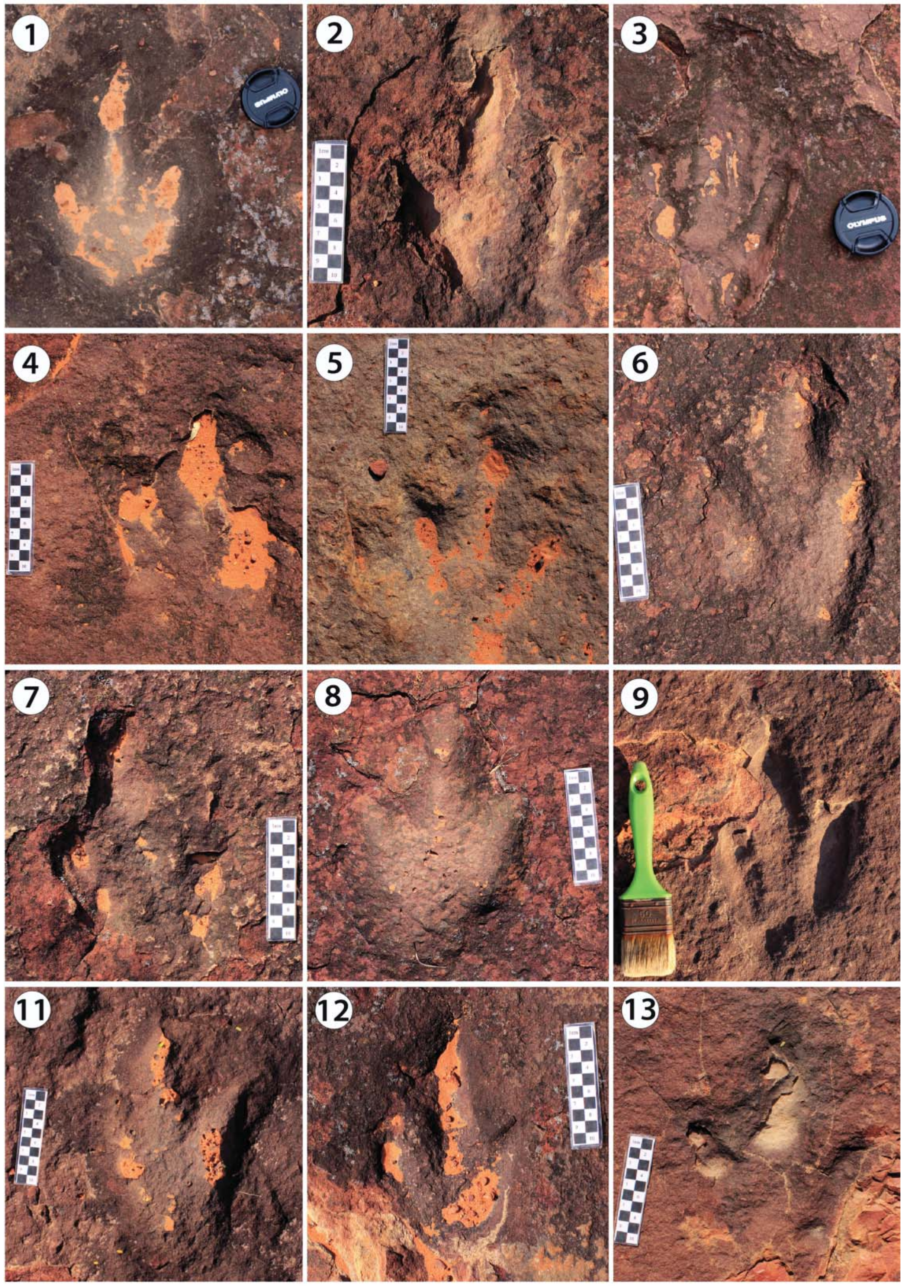

Figure 7. A selection of footprints from the Waterberg tracksite. Brush length is about 21 cm. Camera's cap diameter is 4.8 cm. Scale bar is 10 cm.

Table 1. A comparison of track parameters in the types of the three ichnogenera in the GAE plexus, as defined by Olsen et al. (1998), and the equivalent parameters in the Waterberg tracks and in trackway ONP I_2 at Otjihaenamaparero shows that these Namibian ichnites compare best with North American *Anchisauripus*.

	FL (mm)	FW (mm)	(FL-te)/te	FL / FW - ratio	Total divarication
Grallator (after Olsen et al. 1998)	< 150	n.a.	1.0 – 1.5	> 2	10°–30°
Anchisauripus (after Olsen et al. 1998)	150–250	n.a.	1.3 – 1.8	about 2	20°–35°
Eubrontes (after Olsen et al. 1998)	> 250	n.a.	2.2 – 2.5	1.4–1.5	25°–40°
Waterberg site "elite tracks"	200–280	120–200	1.3 – 1.9	1.4–1.8	25°–45°
Trackway ONP I_2 (Otjihaenamaparero)	280–300	160–170	1.6 – 2.0	1.6–2.1	30°–40°

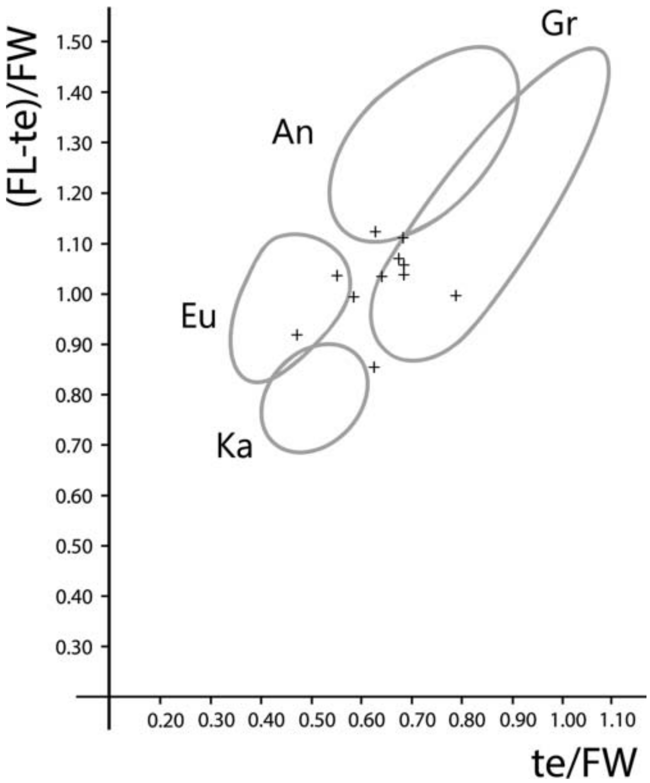

Figure 8. A comparison of the relative proportions of the best preserved footprints (elite tracks) at the Waterberg site (represented by +) with the morphological ranges of Early Jurassic theropod ichnotaxa from North America (elliptical fields). The fields for North American ichnogenera are simplified after Weems (1992). Ka: *Kayentapus*; Eu: *Eubrontes*; An: *Anchisauripus*; Gr: *Grallator*.

considerably smaller. Although it is often argued that size alone should not be used as a criterion to distinguish different ichnotaxa, we observe that even the smallest tracks at the Waterberg site are twice the size of the biggest *Grallator* tracks at Otjihaenamaparero and that no tracks in the intermediate size range (FL between 10 and 20 cm) are currently known from the Etjo Formation. Until more tracksites are discovered and studied in the Early Jurassic of Namibia, possibly closing this gap, we prefer to consider them as different forms.

According to the classification of grallatorid tracks proposed by Olsen et al. (1998), the Waterberg assemblage would have to be labelled as *Anchisauripus* isp., despite the slight differences in relative proportions that distinguish this African record from North American tracks referred to this ichnogenus. From an ichnotaxonomic point of view, however, the status of *Anchisauripus* is not clear, and probably few authors would still consider it a valid ichnogenus. While the ichnotaxonomic problems concerning the *Grallator-Anchisauripus-Eubrontes* (GAE) plexus will ultimately have to be solved by an in-depth restudy of the types and additional material from the type area (i.e., North America), we observe that as far as the record from the Etjo Formation is concerned, *Grallator* and *Eubrontes* are distinct by a number of characteristics including size, relative proportions (mainly controlled by differences in the anterior projection of digit three), and slenderness/broadness of the digits. Instead, tracks of intermediate size from the Etjo Formation (comparable to North American *Anchisauripus*) are separated from *Grallator* by a considerable size gap and can be differentiated from *Eubrontes* by their higher projection of digit III and by a more slender morphology. The Waterberg footprints are morphologically closer to the *Grallator* tracks from Otjihaenamaparero (the only record of this ichnogenus in Namibia so far) than they are to *Eubrontes*, as the Namibian *Grallator* has lower values of te and higher values of FW as the type ichnospecies *G. cursorius*, though within the range of other North American forms assigned to the same ichnogenus. Thus, the track record from the Etjo Formation does not fit the model proposed by Olsen (1980), according to whom the GAE plexus represents an allometric growth series, where toe extension and FL/FW ratio steadily decrease with increasing size of the track. This strengthens the view that *Eubrontes* and *Grallator* deserve the status of separate ichnogenera, while forms referred to *Anchisauripus* might possibly be accommodated within *Grallator*, although distinguished at the ichnospecies level, as proposed by Weems (1992) for the North American track record. Since a widely shared consensus on the validity and limits of ichnotaxa within the GAE plexus has still to be achieved, and given that the Namibian *Anchisauripus*-like tracks do not closely match the type ichnospecies *A. sillimani*, we refer to this African record as cf. *Anchisauripus* isp. or, more informally, as "large grallatorid" tracks, as opposed to the "small grallatorids" from Otjihaenamaparero that can safely be labelled as *Grallator* isp. It has to be stated that our concept of grallatorid tracks differs from that of Rainforth (2005) in that we limit it to forms with slender digits and high projection of the middle digit, and thus we do not include *Eubrontes*.

Conclusions

The ichnocoenosis preserved at the Waterberg tracksite represents an important addition to the track record of the Etjo Formation. The assemblage, which we regard as monospecific, is made up of "large" grallatorid tracks, distinct from "small" grallatorids recorded elsewhere within the same Formation by a considerable difference in size, and from other "large" forms by slender digits and high projection of digit three. A further record from the Etjo Formation that may represent the same morphotype occurs at the at the Otjihaenamaparero tracksite. As far as the dinosaur track record of Namibia is concerned, tracks referred to cf. *Anchisauripus* are closer in morphology to local *Grallator* than they are to *Eubrontes*, although they are much closer in size to the latter. Since many horizontal outcrops of the Etjo Formation remain as yet unexplored because they are hardly accessible, it may be expected that more tracksites will be discovered in the future. The Etjo Formation represents a promising opportunity in terms of potential new discoveries. A rapid inspection of the outcrops at the Etjo Mountain top (pers. obs. AW and SDP) revealed widespread bioturbation of fossil sand dunes, mostly by invertebrates, and additional fieldwork may add important data to the overall ichnofaunistic composition of the area.

Any new record of tridactyl footprints from the Etjo Formation will help refine current ichnotaxonomical models and may possibly clarify the relationship of "small" and "large" grallatorid tracks, provisionally referred to as *Grallator* isp. and cf. *Anchisauripus* isp.

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Appendix: Measures taken from 24 among the best preserved tracks at the Waterberg site; 11 are considered as "elite tracks" because they show clear outlines, including recognizable digital pads. All measurements are in cm, except for the altitude of the tracksite above the sea level (ASL), which is in meters.

	Locality: WATERBERG Acronym: WTB_I Date: July 2013				GPS coordinates: 20°22′41.0″S/17°24′35.3″E		
Track no	FL	FW	te	α	elite	te/FW	Elevation ASL: 1,590 m (FL-te)/FW
N 1	23	14.5	8	35	Y	0.55	1.03
N 2	23.5	15	8.5	35	Y	0.57	1.00
N 3	23.5	14	8	40	N	0.57	1.11
N 4	21.5	18	7.5	25	N	0.42	0.78
N 5	26	19.5	12	70	N	0.62	0.72
N 6	23.5	13	9	45	Y	0.69	1.12
N 7	26	15.5	10	35	Y	0.64	1.03
N 8	21	12	7.5	35	Y	0.625	1.125
N 9	27.5	20.5	10	50	N	0.49	0.85
N 10	22	16	7.5	25	Y	0.47	0.91
N 11	25.5	17	7.5	40	N	0.44	1.06
N 12	n/a	n/a	n/a	n/a	N	n/a	n/a
N 13	20	15.5	7.5	30	N	0.48	0.81
N 14	26	18.5	9	55	N	0.49	0.92
N 15	26	15	10	30	Y	0.67	1.07
N 16	25.5	17.5	9	50	N	0.51	0.94
N 17	19.5	15	9	40	N	0.60	0.70
N 18	22	16	n/a	n/a	N	n/a	n/a
N 19	n/a	n/a	n/a	n/a	N	n/a	n/a
N 20	n/a	15	n/a	n/a	N	n/a	n/a
N 21	24	16.5	10	45	Y	0.61	0.85
N 22	25	14	11	35	Y	0.79	1.00
N 23	27	15.5	10.5	30	Y	0.68	1.06
N 24	24	14	9.5	30	Y	0.68	1.04
	Average FL (all tracks)		23.90	—	Average FL (elite tracks)		23.82
	Average FW (all tracks)		15.80	—	Average FW (elite tracks)		15.41
	Average te (all tracks)		9.05	—	Average te (elite tracks)		9.19
	Average α (all tracks)		39	—	Average α (elite tracks)		37