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Stuttgart, August 2016 **Article**

Dinosaur diversity in an Early Jurassic African desert: the significance of the Etjo Sandstone ichnofauna at the Otjihaenamaparero locality (Namibia)

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With 19 figures

Abstract: About 350 dinosaur footprints, including the longest dinosaur trackway currently on record in Africa, are preserved in the Lower Jurassic Etjo Formation at the Otjihaenamaparero 92 Farm in north-central Namibia. This historically significant locality was among the first dinosaur tracksites ever to be reported from the African continent and is today a National Monument and tourist destination. Nevertheless, its ichnofauna was never described in any detail. Herein we discuss its significance for southern African palaeontology. Although originally described in the 1920ies as new ichnotaxa and later compared to other ichnotaxa described from Lesotho, most tracks of the Namibian Etjo Formation are referable to the classic North American ichnogenera *Eubrontes*, *Anchisauripus* and *Grallator*. A single median-sized theropod trackway is cautiously assigned to *Kayentapus*, but shows characters that differ from North American and European *Kayentapus*, linking it to other "*Kayentapus*-like" tracks from Lesotho and Madagascar. A small-sized functionally tridactyl morphotype with posteriorly directed hallux, common at Otjihaenamaparero, appears to represent a genuinely African form that may also occur in Lesotho. This ichnofauna strengthens the assignment of an Early Jurassic age to the Etjo Formation and opens a window on the diversity of dinosaur communities in arid environments of Early Jurassic southern Gondwana.

Key words: Theropod tracks, Ichnotaxonomy, Early Jurassic, Dinosaurs, Namibia, Africa.

1. Introduction

The occurrence of dinosaur tracks in the vicinity of the Otjihaenamaparero 92 Farm in north-central Namibia (Fig. 1) has long been known in literature and is frequently reported on tourist maps and websites promoting the natural heritage of the country. Being a National Monument since 1951, the locality is visited by about two to three thousand visitors every year, but despite its easy accessibility it was never studied in any detail after its original description in the first decades of the 20th century. Nevertheless, the tracks have frequently been cited and reported under different names, and knowledge about this intricate history is important for a better understanding of this locality and its relevance to Southern African ichnology.

The first report of this locality (v. Huene 1925), although very concise, is historically significant as it is one of the oldest reports on dinosaur footprints from sub-Saharan Africa, predated only by a few reports from Lesotho (Dornan 1907; Haughton 1924). One year later, a second more detailed study on this occurrence was published by Gürich (1926). Like v. Huene, Gürich never visited the site, but he could rely on a detailed description made by a Mr Elmenhorst, who also managed to send some plaster casts of a selection

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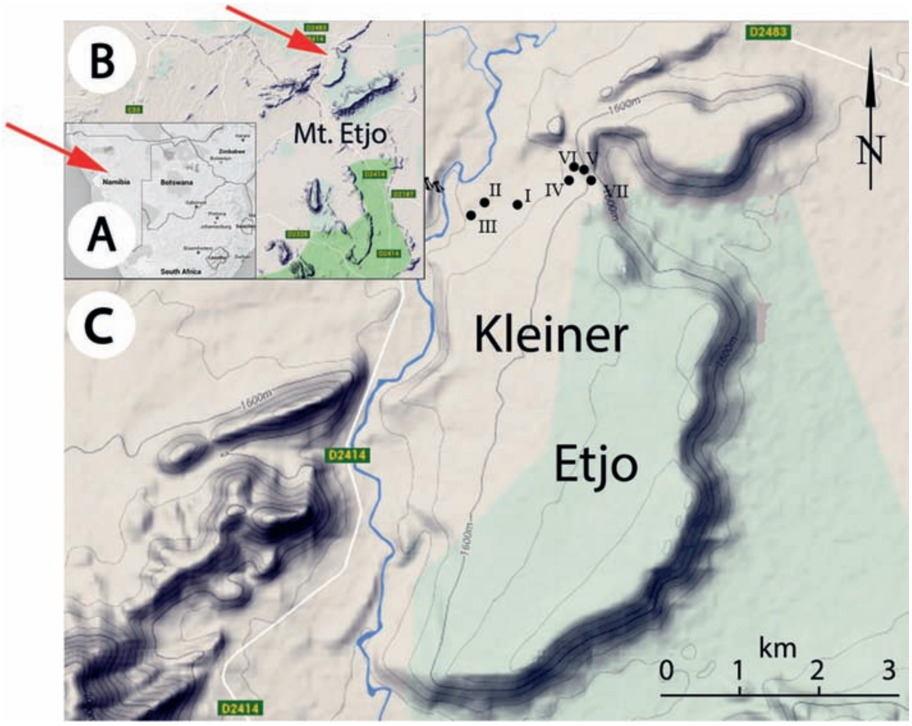

Fig. 1. Geographic location of the Otjihaenamaparero tracksites. Inserts in the upper left corner show the position of the Mount Etjo complex within Namibia (**A**) and of the Otjihaenamaparero 92 Farm (**B**). Positions of the seven tracksites at Otjihaenamaparero are labelled with Roman numerals I-VII (**C**). Base maps from Creative Commons.

of footprints to Germany. Based on this material, which the author reports as being "stored at the Mineralogisch-Geologisches Staatsinstitut, Hamburg", Gürich erected two new ichnogenera and five ichnospecies, the validity of which will be discussed herein. A few years later, Heinz (1932) published a brief note on the ichnofauna of Otjihaenamaparero after personally visiting the place. He was unable to identify all the ichnotaxa erected by Gürich (1926) and concluded that only two different kinds of tracks occurred at the locality, namely *Saurichnium damarense* and *S. tetractis.*

After these first three reports, now dating from almost a century ago, the dinosaur tracks at Otjihaenamaparero were never revised, although they were occasionally cited in works dealing with the paleontology (Pickford 1995) and geology (Löffler & Porada 1998; Holzförster et al. 1999) of Karoo sediments in Namibia or attempting to summarize the fossil record of the country (Pickford 1994; Schneider & Marais 2004) or the worldwide dinosaur record (Weishampel 1990; Weishampel et al. 2004).

A joint field campaign by the authors in 2013-2014 provided the first systematic data collection on the dinosaur tracks at Otjihaenamaparero. Seven different outcrops exposing dinosaur tracks (tracksites) have been detected at this locality, including the two historical tracksites mentioned by Gürich (1926) and Heinz (1932) and five new sites that are herein reported for the first time.

In addition to the sites at Otjihaenamaparero, two more tracksites were investigated at different localities within the same lithological unit (the Etjo Formation), namely at the Waterberg Plateau (about 130 km northeast of Otjihaenamaparero) and at Omuramba Omambonde (about 185 km northeast of Otjihaenamaparero). Although never published in paleontological literature, these sites have previously been reported in non-technical journals (Wiechmann 1983; Pickford 1994) as well as unpublished reports (Cosburn 1980, 1990; Grote 1984). Our revision of these two localities is being published separately (D'Orazi Porchetti et al. 2015; Wagensommer et al. in press).

Being an important and rich source of information from a geographic area with an otherwise poorly known dinosaur record, the ichnofauna of the Etjo Sandstone, and particularly that of the Otjihaenama-

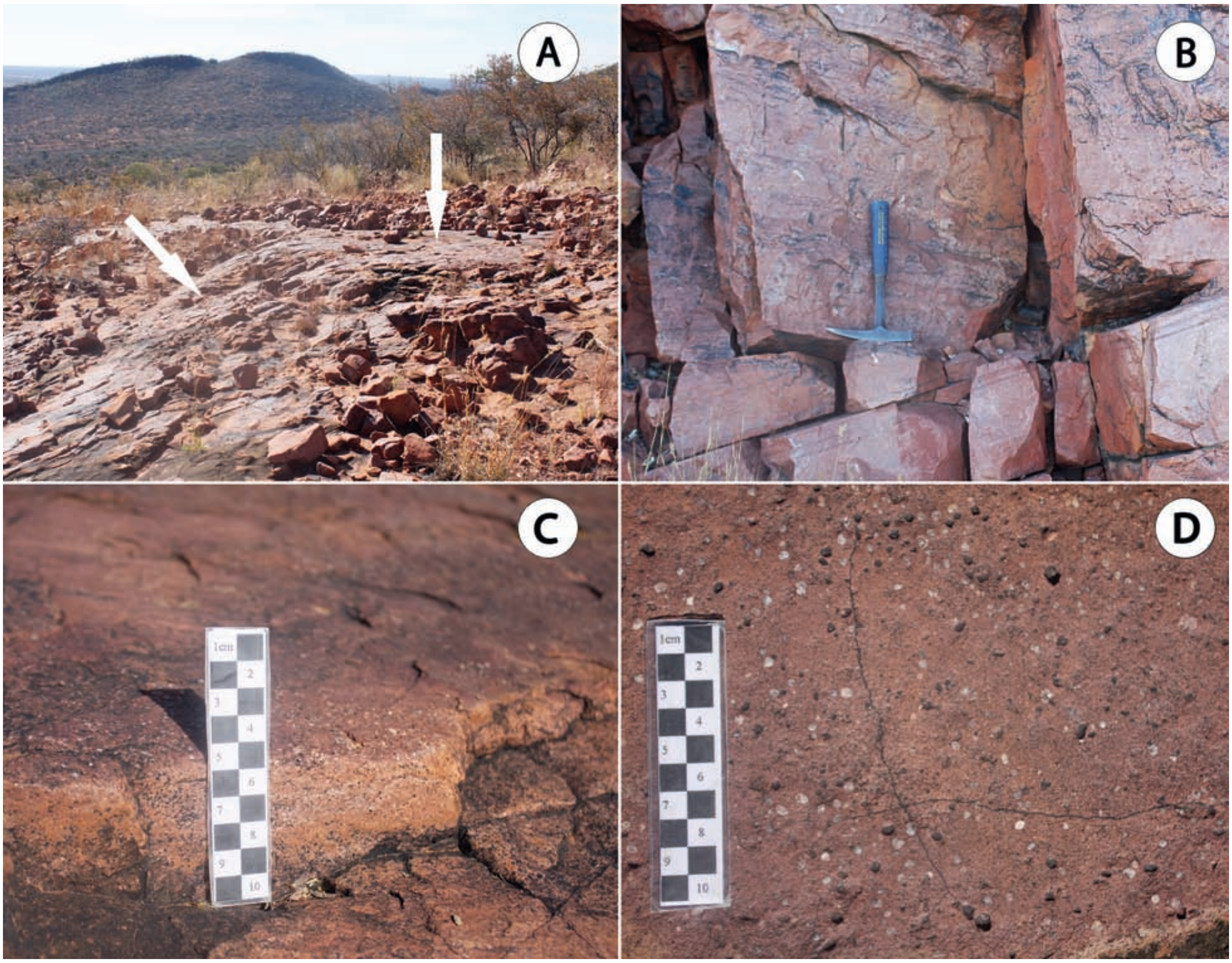

Fig. 2. The Etjo Formation as seen in outcrop along the northern slope of the Klein Etjo. **A** – Interdune surface (vertical arrow) intersecting an underlying dune slope surface (inclined arrow). Both arrows are perpendicular to the surfaces they refer to. Dinosaur tracks are found on the once horizontal (now tectonically tilted) surfaces; no record from the dune facies has been reported so far from anywhere in the Etjo Formation. **B** – Cross-bedding of the eolian facies, some 10–20 m above the trampled surfaces near tracksite ONP VII. Hammer for scale (33 cm long). **C**, **D** – Details of the track bearing surface at site ONP IV. Note the white fine gravel particles that characterize the trampled surface. Scale bar equals 10 cm.

parero locality, was urgently in need of a revision. In this paper we will discuss its potential in assessing the diversity of Early Jurassic ichnofaunas in southern Africa and compare them to coeval ichnofaunas from other parts of the world.

2. Geological setting

The Etjo Formation is the only lithostratigrapic unit recording Jurassic continental sediments in Namibia. Major outcrops are in the north-central region, the Waterberg Mountain being the most impressive and extensive in terms of thickness and area. Minor outcrops are found at the Großer Etjo and at the Kleiner Etjo mountains (Fig. 2). The sequence reaches its maximum thickness (about 140 metres) at the contact with the Waterberg-Omaruru Fault (Wanke 2000), and rapidly thins out moving southward, with thinnest outcrops encountered at the Omatako Mountains. The Etjo Formation is almost devoid of body fossils, and its age was originally estimated on the basis of lithologic similarities with other African formations and by its position on top of the fossil-rich Omingonde Formation (Lower to Middle Triassic). The occurrence of a skeleton cast assigned to *Massospondylus* (Holzförster 1999; Holz-

Förster et al. 1999) in the Middle Unit of the Etjo, and the identification of a trackway referred to *Otozoum moodii* at the Omuramba Omambonde locality, northeast of the Waterberg Plateau (D'Orazi Porchetti et al. 2015), have consistently constrained the age of this Formation to the Early Jurassic.

The Etjo Formation records a sequence of increasingly drier deposits, shifting from a semi-desertic environment with ephemeral water supplies, to hyper–arid conditions, with dominance of erg facies in the uppermost section. Holzförster et al. (1999) divide this sequence into three informal units (Lower, Middle and Upper Unit) that record this climatic shift, and interpret the Otjihaenamaparero footprint-bearing horizons as belonging to the Upper Unit. In contrast, Smith & Swart (2002), consider the stratigraphic position of the dinosaur tracks as resting much lower in the stratigraphy of the Etjo Formation, close to the contact with the Triassic Omingonde Formation.

At both Omuramba Omambonde and the Waterberg, the track-bearing layers are associated with abundant eolian cross-strata sets, which Holzförster et al. (1999) recognized as the typical facies of the Upper Unit of the Etjo Formation. Thus, the dinosaur tracks at these two localities occur in the youngest levels of the Etjo. At the Otjihaenamaparero 92 Farm, tracksites all occur on the uppermost levels exposed, but their stratigraphic position within the Etjo Formation is less easy to assess. As stated above, different authors have divergent interpretations, considering the tracks at this locality as pertaining either to the Upper (Holzförster et al. 1999) or to the Lower (Smith & Swart 2002) Unit of the Etjo. A main issue in interpreting the correct position of the footprint-bearing layers is that the thickness of the Etjo Formation is low at Otjihaenamaparero (about ten metres), and dinosaur tracks are only a few metres above the contact between the Etjo and the Omingonde formations. In our view, the close vicinity to the Waterberg-Omaruru Fault might have favoured disruption and erosion of the upper portions of the sequence and subsequent exposure of older levels. As a matter of fact, the Etjo Formation is indeed much thicker at the top of the Großer Etjo, only 3.5 kilometres away from the tracksites, and is less tectonically disturbed than at the Kleiner Etjo. However, the possibility of extreme facies etheropy may not be completely discarded.

At Otjihaenamaparero, the Etjo Formation reveals an alternation of the typical hyper-arid depositional environment, dominated by large cross-strata sets and interdune deposits, with humid episodes possibly related to flooding events. Aeolianites are represented by well-sorted, small, rounded grains of windblown sand, brown-red to reddish in colour, rarely associated with isolated pebbles of white quartz. Patches of coarser sand are found locally, sometimes infilling dinosaur tracks. The occurrence of mudcracks on some surfaces, along with a few levels where sandstone grains are associated with a larger amount of matrix, deposited in plano-parallel layers, are clear evidence of the ephemeral presence of water in the area. Sedimentological features are presented in more detail in chapter 4, where the single tracksites are described.

3. Materials and methods

About 350 dinosaur footprints are preserved at the seven tracksites so far recognized at Otjihaenamaparero. Most of them are organized in trackways. To facilitate future reference we assigned an acronym to each track. The acronyms summarize information about tracksite and trackway to which the individual footprint belongs. A general acronym, ONP (Otjihaenamaparero), precedes all footprints and is followed by a Roman numeral that identifies the outcrop (i.e., the tracksite) inside the broader area. Each tracksite is separated from the others by physical obstacles, might they be vegetated areas, soil cover, or erosion channels. Tracksites might also be at different stratigraphic positions, though some might represent different exposures of a single laterally extensive surface. An Arab number identifies the trackway within a given tracksite and a second Arab number, separated from the first by a dot, specifies the footprint within the trackway. For example, the fourth footprint in the third trackway at the second tracksite is ONP II_3.4. Footprints and trackways have been measured in the field, reproduced on plastic peels, photographed, and selected footprints have been moulded with silicon rubber. The moulds have been reproduced as 3D images following the method described by Falkingham (2012).

In order to divide the overall sample into distinct morphological groups, we plotted linear and angular values of each well–preserved footprint on different kinds of diagrams. Where "clusters" or "clouds" formed, we considered each of them as representing a morphotype. This method has the advantage of minimizing subjective selection of "representative" tracks, which in some instances might lead to an overestimation of diversity. On the other hand, to avoid losing qualitative characters that might be difficult to represent by numerical plots, we coupled this quantitative analysis with a more qualitative one (i.e., comparison of the best preserved tracks and trackways with the diagnosis of coeval ichnotaxa), as suggested by LOCKLEY (2000).

We adopted two main quantitative approaches. A first carthesian diagram plots footprint length (FL) against footprint width (FW), thus employing the two most widely used and easiest–to–get linear measures. The second one plots (FL–te)/FW against te/FW, where "te" is the projection of digit III beyond the tips of digits II and IV ("toe extension"). This diagram was introduced by WEEMS (1992) to discriminate between Early Jurassic ichnotaxa from North America and has since been used by some other workers (GIERLIŃSKI 1996; PIUBELLI et al. 2005; WAGENSOMMER et al. 2012) for comparisons of Jurassic ichnofaunas from other parts of the world with the classical North American ichnotaxa. For this reason, the "Weems diagram" allows a straightforward comparison of the Namibian record with other coeval ichnofaunas. Being based on proportions, the Weems diagram does not account for the absolute size of the tracks, which in turn shows up in the FL/FW diagram. For direct comparison with North American ichnotaxa we used a simplified version of the Weems diagram, which needs a few words of explanation. WEEMS (1992) originally defined the fields of all Early Jurassic tridactyl tracks attributed to theropods that had previously been described from North America and concluded that only nine morphological groups could be consistently differentiated. He then grouped these nine ichnospecies into three ichnogenera, namely *Grallator*, *Eubrontes* and *Kayentapus*. For better readability of the diagram, we did not draw the fields of all nine ichnotaxa identified by WEEMS, but fused them into larger fields encompassing the morphological range of the ichnogenera. In doing so, however, we applied the definitions of OLSEN et al. (1998) for *Eubrontes*, *Anchisauripus* and *Grallator*. Thus, our fields for *Eubrontes* and *Kayentapus* are the same as defined by WEEMS (1992), while our field for *Grallator* includes all the "small" (FL < 15 cm) grallatorid tracks (roughly the fields for *Grallator cursorius* and *G. tenuis* in WEEMS), while our field for *Anchisauripus* encompasses the larger (15 < FL < 25) forms assigned by WEEMS to the ichnospecies *Grallator sillimani*, *G. parallelus* and *G. tuberosus*.

4. Tracksites

The seven tracksites we identified at Otjihaenamaparero are spread over an area of about 0.5 x 1.5 km along the northern edge of the Klein Etjo Mountain, about 190 km NNW of Windhoek. The geographic coordinates of these tracksites are listed in Fig. 3. Tectonics related to the Waterberg-Omaruru Fault hampers an easy interpretation of the stratigraphic relationships among different track-bearing levels within the area. Strata show an overall northern dip, but the surface is fractured in several blocks, tilted to various degrees with respect to each other. Direct stratigraphic relationships can only be observed among tracksites ONP V, ONP VI and ONP VII. In any case, the trampled levels all belong to a relatively thin succession, possibly less than ten metres thick. Each single ichnosite is described hereafter.

Tracksite acronym	Coordinates
ONP_I	21°02'31.4" S / 16°24'18.7" E
ONP_II	21°02'30.3" S / 16°24'03.4" E
ONP_III	21°02'36.4" S / 16°23'57.8" E
ONP_IV	21°02'20.6" S / 16°24'41.3" E
ONP_V	21°02'16.6" S / 16°24'46.4" E
ONP_VI	21°02'16.2" S / 16°24'43.8" E
ONP_VII	21°02'21.7" S / 16°24'50.9" E

Fig. 3. Location of the seven tracksites identified at Otjihaenamaparero. The coordinates were taken by a GPS device at a point of interest within the tracksite, usually about halfway along the longest and/or best preserved trackway of each site.

4.1. Site ONP I

This is the largest dinosaur tracksite at this locality and one of the two mentioned by v. HUENE (1925), GÜRICH (1926) and HEINZ (1932). It is also the type locality of four among the five ichnotaxa erected by GÜRICH (1926). A bedding plane gently dipping towards the northwest is exposed for about 100 x 60 metres. At the position given by the coordinates in Fig. 3, two trackways of medium-sized tridactyl footprints intersect at almost right angles, trackway ONP I_1 heading NW and trackway ONP I_2 heading SW (Fig. 4). This is the "main site" mentioned by v. HUENE (1925) and discussed in some detail by GÜRICH (1926). Despite the fact that early researchers at Otjihaenamaparero paid much attention to the two intersecting trackways ONP I_1 and ONP I_2, their actual length was never really appreciated. GÜRICH (1926) states that they consist of "about 15 footprints each", HEINZ (1932) records 34

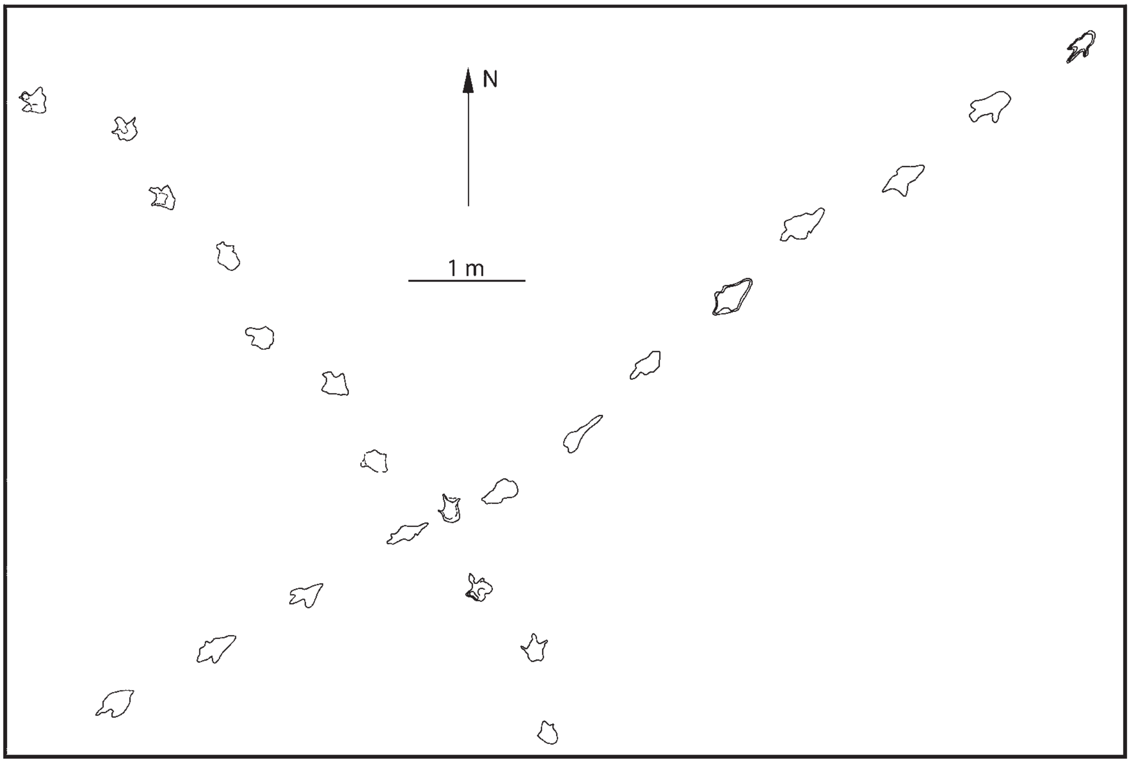

Fig. 4. Partial site map of ONP I, with the two intersecting trackways ONP I_1 and ONP I_2.

footprints in one of the trackways and 35 footprints in the other, while Schneider & Marais (2004) report about 30 footprints in each trackway. Actually, trackway ONP I_1 has 41 preserved footprints and trackway ONP I_2 no less than 73. Both trackways have some minor gaps due to erosion. The distance between first and last preserved/exposed footprint is 28 m in trackway ONP I_1 and 93.5 m in trackway ONP I_2. Trackway ONP I_2 thus qualifies as the longest dinosaur trackway on record on the African continent, and indeed as one of the longest in the world, as trackways approaching or exceeding 100 metres are known from only about a dozen localities in Bolivia (Lockley et al. 2002; Marty, pers. comm.), Turkmenistan (Lockley et al. 1996; Meyer & Lockley 1997; Fanti et al. 2013), England (Day et al. 2002; 2004), France (Mazin & Hantzpergue 2010), Switzerland (Meyer 1990; Marty et al. 2010), Portugal (Santos et al. 1992; Lockley & Meyer 2000), Germany (Fischer 1998), and the United States (Lockley et al. 1986; Lockley & Hunt 1995). An updated review of this topic can be found in Xing et al. (2015).

Besides these two intersecting trackways there is another short trackway segment (three consecutive footprints) a few metres to the west, at the coordinates 21°02'31.4" S / 16°24'17.4" E. This trackway ONP I_3 is different from the first two in that the tracks are considerably smaller, but also much shallower, so that they can easily be overlooked.

Gürich (1926) reports that in addition to the two long trackways (our trackways ONP I_1 and ONP I_2), "the surface is intensively covered by countless isolated tracks of all sizes" (our translation). We cannot agree with this statement, evidently based on Mr Elmenhorst's description, as Gürich himself puts the sentence in brackets. We spent more than a week at this site and intensively searched for tracks under different light conditions during the day. The surface is certainly very irregular, with countless bulges and shallow depressions, and it is heavily weathered mostly in its uphill (southern) section. Some of these non-biogenic features bear a vague resemblance with dinosaur tracks, but we could not find any unequivocal footprint beyond those pertaining to the three trackways mentioned above. This observation is of some relevance as three of the five ichnotaxa erected by Gürich (1926) are based on plaster casts of such “isolated tracks” and among these, two are so shallow and featureless that they probably are no tracks at all.

4.2. Site ONP II

A bedding plane with dinosaur tracks crops out on an area of 30 x 200 m, about 400 m to the west of ONP I. This is the second historical tracksite at Otjihaenamaparero and contains the holotype trackway of *Saurichnium tetractis* Gürich, 1926. As in ONP I, the surface is freshest in its northern part, while to the south it becomes more and more heavily affected by erosion. More than a hundred dinosaur tracks organized in 11 trackways are preserved on this surface. Stratigraphically, this tracksite is not easily related to ONP I. No direct relationship between the two surfaces has been observed in the field. We tentatively consider it as lying above ONP I, on the base of the general dip of the area. All tracks on this surface are small (FL = 6-8 cm). Some are rather shallow, but many are deeply impressed (up to a depth of about 3 cm), with clear outlines and steep track walls. Some trackways consistently show hallux impressions in almost every footprint, while others do not.

4.3. Site ONP III

Located about 200 m southwest of site ONP II (600 m from site ONP I), this tracksite was discovered by Reinhold Strobel, owner of the Otjihaenamaparero farm since 1999. It contains a single trackway of 10 small (FL = 7 cm) tetradactyl footprints. The footprint bearing surface lies topographically about 2 m below ONP II. In this case too, however, there is no possibility to directly determine their stratigraphic relationships. Similarity in lithology and footprint morphotype links this site to ONP II and the two sites might well represent outcrops of the same surface. Their different topographic height would in this case have to be explained by tectonic displacement.

4.4. Site ONP IV

Located about 700 m northeast of site ONP I, this tracksite too was discovered by Reinhold Strobel. On an area of a few hundreds of square metres, it contains about 20 small tridactyl footprints organized in two trackways. Its stratigraphic position relatively to the other sites is not assessable because of lack of continuity with other footprint-bearing outcrops.

4.5. Site ONP V

Located about 1 km northeast of site ONP I (200 m away from site ONP IV), this outcrop lies inside a narrow erosional channel. It contains about 40 small footprints, organized in 7 trackways.

4.6. Site ONP VI

This tracksite is located only about 70 m west of site ONP V, downslope along the same erosional channel, and about 1 m lower in the stratigraphic column. It contains two trackways of small tridactyl footprints, altogether about 20 footprints.

4.7. Site ONP VII

Located about 200 m southeast of site ONP V (1 km from ONP I), this site contains a single trackway of large (FL = 34 cm) tridactyl footprints. The footprints are not so deeply impressed as in site ONP I but show very clear outlines and digital pads. The surface is heavily affected by erosion, so that many tracks are missing. Only 18 footprints are preserved on a total length of the exposed trackway segment of 48 m. Given a pace length of about 1 m, this implies that more than half of the footprints are lost to erosion. This is the uppermost level in the sequence ONP V-VII. However, no direct correlation between these sites and sites ONP I-IV can be established.

At tracksites ONP V-VII, isolated quartz pebbles occur (Fig. 5A) in association with unsorted coarse sand to fine gravel particles. Patches of coarse sand randomly occur on the surfaces and sometimes infill the dinosaur footprints at ONP VII (Fig. 5B). This is possibly an example of the “*pebble to coarse sand-covered surfaces*” described by Holzförster et al. (1999) and interpreted as deflation lag surfaces. We also observed ripple marks and desiccation cracks at various levels within the track-bearing sequence at Otjihaenamaparero (Fig. 5C, D). Close association of small-scale ripples and mud cracks is visible at site ONP V. Here the mud cracks are preserved as counterprints (convex epireliefs), probably because they formed on a thin layer of finer sediments that once covered the sandstone surface and successively eroded, leaving only the infill of the cracks visible on the underlying surface. This interpretation is enforced by the presence of a cm-sized

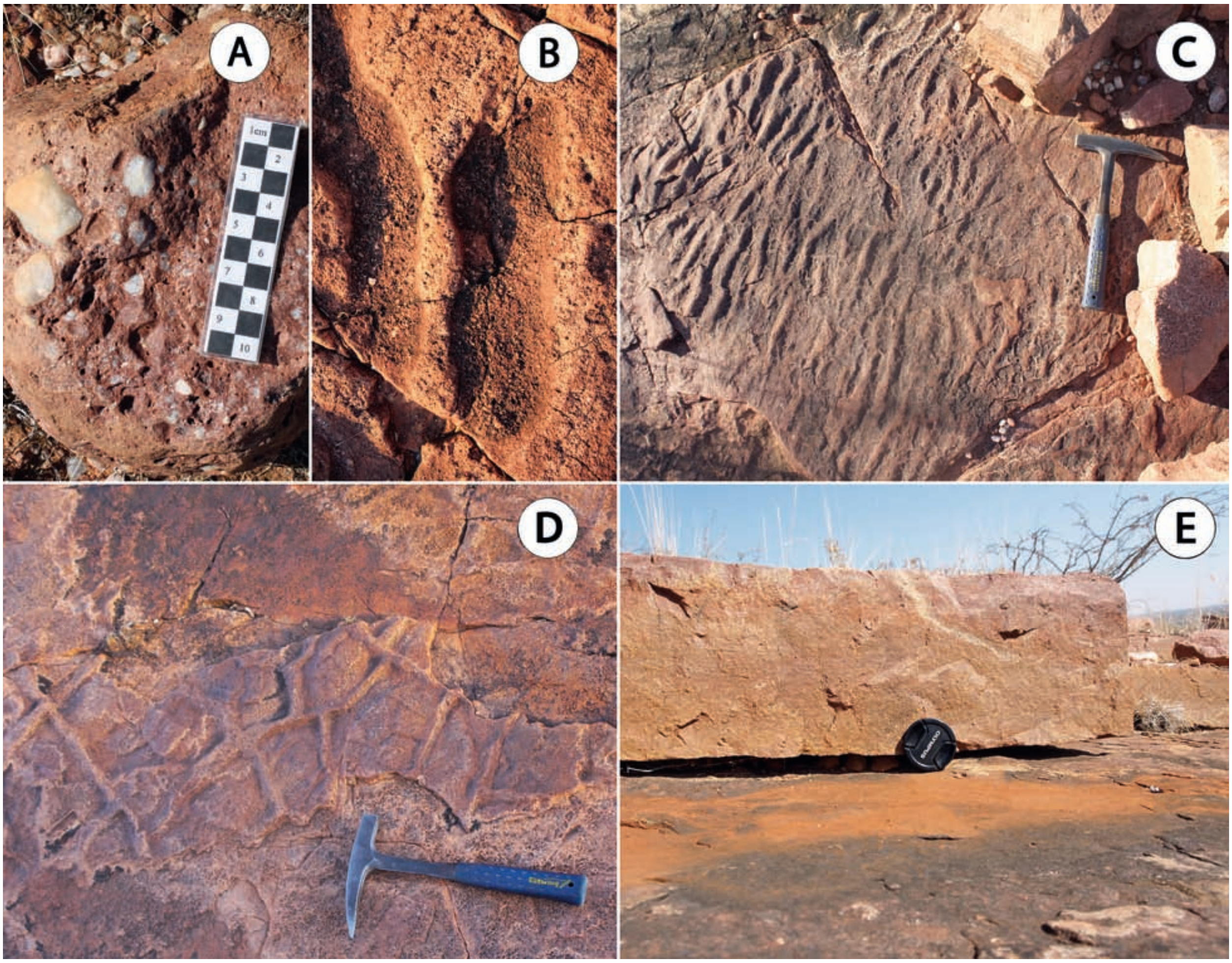

Fig. 5. Details of the dinosaur track bearing surface at tracksites ONP V-VII. **A** – Cm-sized quartz pebbles occur in one or multiple levels associated with the track-bearing surface, though not in the trampled level itself. Scale bar equals 10 cm. **B** – Patches of coarse sand infilling a dinosaur track (digit II and part of digit III shown in the picture) at tracksite ONP VII. The track itself is impressed in fine-grained sandstone. **C** – Small scale ripple marks at tracksite ONP V. The rippled surface lies about 2-3 cm above the track bearing surface. Hammer is 33 cm long. **D** – Desiccation cracks at tracksite ONP V. Note that the cracks are preserved as counterprints. Hammer for scale (33 cm). **E** – A cm-sized gap separates the track bearing surface at site ONP VI (lower half of the picture) from the overlying sandstone bed, testifying to the presence of a more erodible thin layer which may be the level originally trampled by the dinosaurs. Camera lens cap for scale is 58 mm.

gap between the track-bearing surface and the overlying sandstone bed (Fig. 5E), possibly left by a thin more erodible layer. The dinosaur tracks were possibly emplaced on this finer sediment, in which case the footprints now exposed on the surface would be slight undertracks.

5. Track morphology and ichnotaxonomy

Ever since v. Huene (1925) published his first report of this ichnofauna, all workers recognized the fact that the dinosaur tracks at Otjihaenamaparero can be assigned to two different size classes, which we can provisionally refer to as "small" and "large" forms. The small forms, represented by 24 trackways in our sample, range in footprint length between 5.5 and 11 cm, whereas the large forms, represented by three trackways, have a range of FL between 25 and 35 cm. Thus there is a considerable size gap between the largest "small" forms and the smallest "large" forms, which allows a clear separation of the two groups. This can be visualized by plotting the values for FL and FW of every individual footprint on a FL/FW diagram (Fig. 6). This exercise

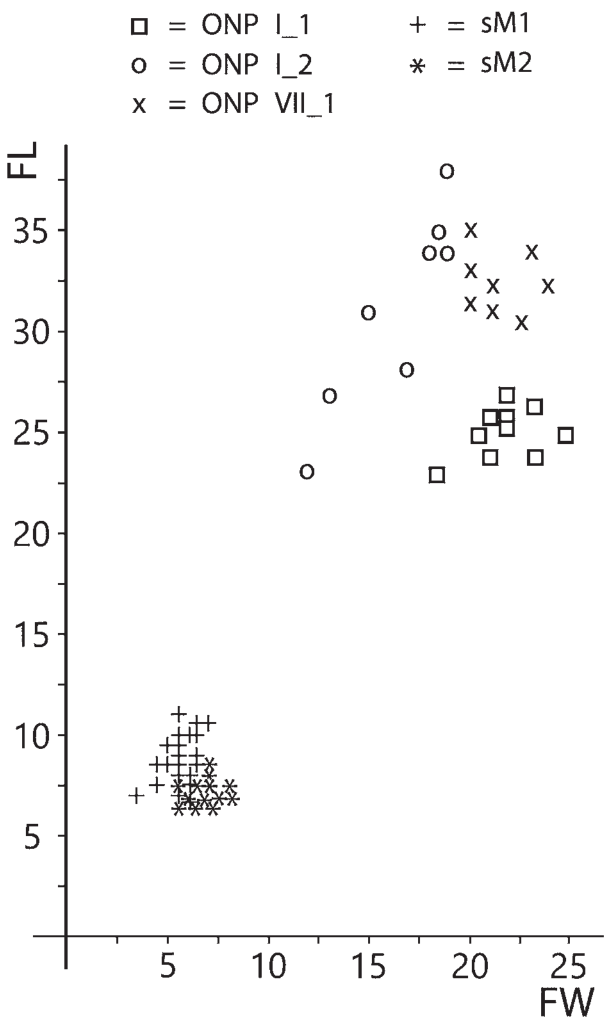

Fig. 6. A diagram plotting footprint length (FL) versus footprint width (FW) shows that dinosaur tracks at Otjihaenamaparero belong to two neatly separated size classes. Each of the three "large" trackways is represented by a different symbol, while the "small" tracks are grouped into the two morphotypes sM1 and sM2 for better readability. Scale is in centimetres.

also reveals that the "small forms" form a relatively narrow cluster, while the "large forms" display more variability. For this reason, we will discuss the three "large" trackways separately, while such a discussion "trackway by trackway" appears to be redundant for the "small" forms, which we will treat as a single sample.

5.1. Trackway ONP I_1

This is the holotype trackway of Gürich's (1926) *Saurichnium damarense* (as well as Ellenberger's 1972, *Anatrisauropus hereroensis*; see discussion below). The preserved trackway segment is about 30 metres long and comprises 41 recognizable tracks; a few more are lost to erosion. The average stride length is about 140 cm. The footprints are almost as wide as long (FL= 25 cm and FW = 21 cm on average) and are deeply impressed (up to 5.5 cm), with steep side walls and without appreciable sediment displacement rims. No metatarsal nor hallux impressions have been observed. The digits appear to be quite stout (width of digit III about one third of its length). In the best preserved tracks, the last pad of the outer digits is markedly bent outwards, allowing for a moderately high projection of digit III. This outward bending, which brings the tips of digits II and IV to point almost at opposite directions, was considered a diagnostic feature by Ellenberger (1972). The total divarication angle of the footprints averages just over 40°, with an asymmetrical position of digit III: interdigital angle II-III about 10°-15°, interdigital angle III-IV about 25°-30°. A 3D photogrammetric model of two of the best preserved tracks is shown in Fig. 7; photographs are provided in Fig. 18.

Three common ichnotaxa of tridactyl dinosaurs from the Early Jurassic of North America are within the size range of trackway ONP I_1, namely *Eubrontes*, *Anchisauripus* and *Kayentapus*. On the Weems diagram, the footprints of trackway ONP I_1 form a relatively narrow cluster that is well outside the range of *Anchisauripus* and *Eubrontes*, but partly covers the range of *Kayentapus* (Fig. 8). On a qualitative basis, the slender digits, narrow divarication angle and high toe extension of *Anchisauripus* allow an easy differentiation from trackway ONP I_1. The comparison with *Eubrontes* and *Kayentapus* proves more problematic. ONP I_1 displays two characters that are "*Kayentapus*–like": first, it is relatively short (FL/FW about 1.2) and second, its toe extension is higher than in *Eubrontes*. These two characters are responsible for its position on the Weems diagram. But it also displays characters that are "invisible" to the Weems diagram and are more "*Eubrontes*-like", such as stout digits, digit divarication angle around 40°, and short step. The latter feature was suggested as possibly significant for differentiation between *Eubrontes* and *Kayentapus* by Lockley et al. (2011).

Comparison with ichnotaxa from southern Africa does not prove easier. In his monumental work on the ichnofauna of Lesotho, Ellenberger (1972: 37) included "*en complement d'information*" (for completeness of information) the description of a cast which reportedly was taken at Otjihaenamaparero in 1967 and

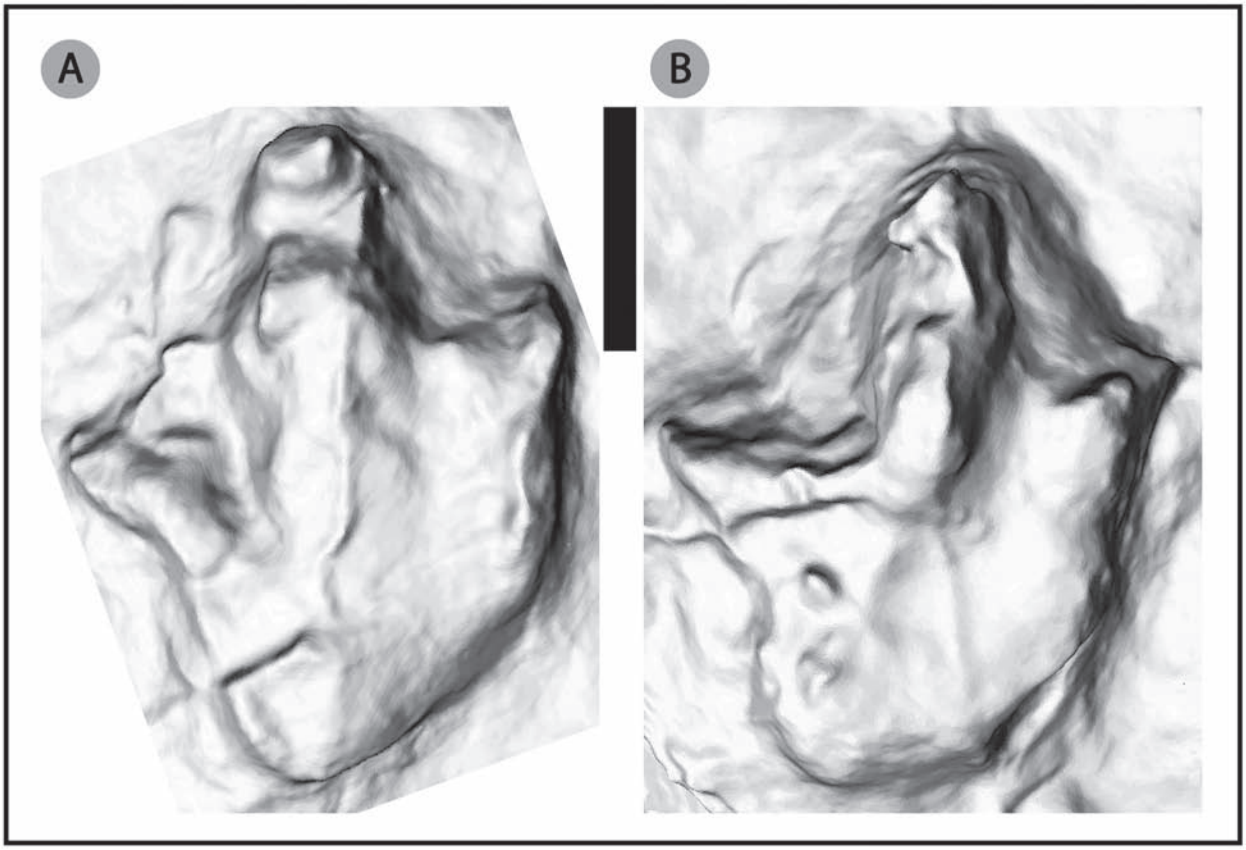

Fig. 7. 3D photogrammetric models of track ONP I_1.9 (**A**) and ONP I_1.13 (**B**). Black bar equals 10 cm.

was shown to him by the curator of the museum in Windhoek. Ellenberger evidently was not aware of the German literature on this locality, as he does not cite any of those works and explicitly writes that the tracks "were never studied systematically" (our translation). Based on this cast, which is no longer present in the collections of the Geological Survey Museum in Windhoek and thus has to be regarded as lost, Ellenberger (1972) erected the new ichnospecies *Anatrisauropus hereroensis.* Although the cast is lost, both Ellenberger's description and his drawing leave no doubt that he describes a track of trackway ONP I_1, almost certainly track ONP I_1.13 (see Fig. 9 for a comparison). He does not refer any material from Lesotho to *A. hereroensis,* but he includes a second species in the same ichnogenus: *A. ginsburgi* (Ellenberger 1972) from the "Lower Stormberg" of Maphutseng (Lesotho). As a matter of fact, his description and figure of the type of this ichnospecies reveals a striking similarity with trackway ONP I_1. In Ellenberger's (1972) own words, *A. ginsburgi* and *A. hereroensis* are of roughly

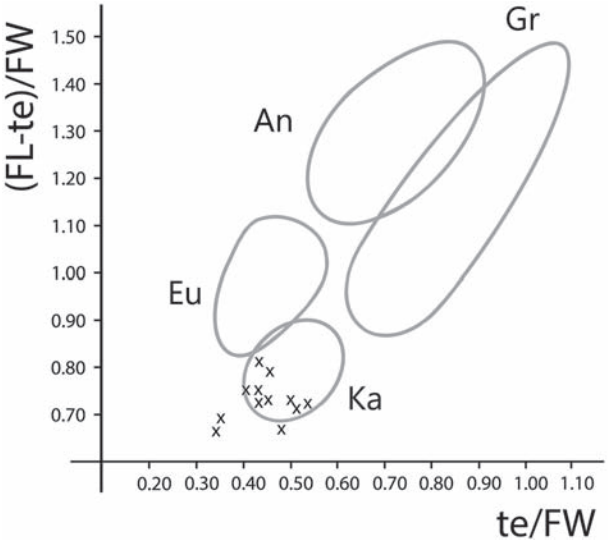

Fig. 8. Weems diagram displaying the relative proportions of footprints belonging to trackway ONP I_1 (X), compared to the ranges of common ichnogenera from the Early Jurassic of North America (grey circles). An = *Anchisauripus*; Eu = *Eubrontes*; Gr = *Grallator*; Ka = *Kayentapus.*

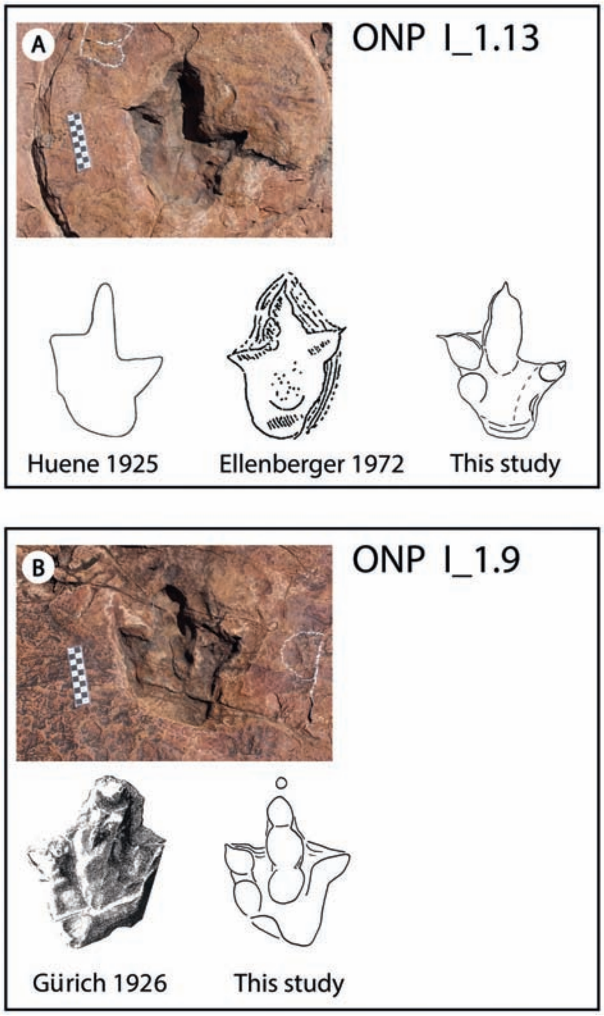

Fig. 9. Two footprints in trackway ONP I_1 (herein referred to as *Kayentapus damarensis* comb. nov.) have been figured in previous publications. **A** – Photograph of footprint ONP I_1.13 compared to the outline drawings published by v. Huene (1925) and Ellenberger (1972) and our interpretation. Note that Ellenberger's drawing is based on a cast and thus left side and right side are inverted. **B**: Photograph of ONP I_1.9 compared to the figure published by Gürich (1926) and our interpretation. Gürich's drawing is based on a cast and thus left side and right side are inverted.

the same size and differ only in the degree of outward bending of the distal pads of digits II and IV (which form an angle of 160° in the former and 180° in the latter ichnospecies) and in the development of a broader heel ("talon") in *A. hereroensis*. As noted, Ellenberger based his diagnosis on the cast of only a single track, while we had the opportunity to study the entire trackway. Both characters used to differentiate the two ichnospecies of *Anatrisauropus* are very variable. The divergence of the tip of digits II and IV apparently approaches 180° only in tracks ONP I_1.13 and ONP I_1.39, while it is as little as 110° in ONP I_1.9. The distinction between *A. ginsburgi* and *A. hereroensis* is therefore a clear case of oversplitting based on characters that lack any consistency. Interestingly, Ellenberger (1972) compares his *Anatrisauropus* to *Apatichnus* from the Newark Basin. Weems (1992) reassigned the ichnospecies *Apatichnus minor* to *Kayentapus*, a label that almost certainly was unknown to Ellenberger, as it was introduced by Welles (1971) only one year before the work of Ellenberger (1972) was published. Thus, Ellenberger acknowledged some similarity between *Anatrisauropus* and forms today referred to as *Kayentapus*, although he considered the African form different because of its bigger size, broader sole impression and high degree of outward bending of the tips of outer digits. All three characters are dubious. As for size, Ellenberger probably refers to the type ichnospecies of *Apatichnus*, *A. circumagens* (FL = 7.5 cm), which is considered an ornithischian footprint (Lull 1953; Weems 1992). Instead, *A. minor* (*Kayentapus minor* in Weems 1992), now regarded as a theropod track, has reported footprint lengths of about 22–25 cm, which is exactly the size range of *Anatrisauropus*. The broadness of the sole might be a function of substrate consistency, while the degree of outward bending of the outer digits is highly variable within trackway ONP I_1. A feature that Ellenberger (1972) regards as diagnostic for *Anatrisauropus* is that digits II and III are allegedly nearly parallel and fused to "*une seule sole pédieuse*" (a single foot sole), leaving only the tip of digit II free, while digit IV would be separated from the other two and more highly diverging. We disagree with this interpretation. While we measured the same narrow interdigital angle II-III (about 10°-15°) as Ellenberger did, we do not think that the two digits were fused. The apparent lack of separation between digits II and III observed in some of the deepest tracks may be more parsimoniously explained by extramorphological processes, e.g. mud adhering at the trackmaker's foot could have filled the narrow gap between digits II and III, or the sediment was not firm enough to retain the narrow ridge between two nearly parallel digits sinking some 5 cm deep into the sediment. Some of the best–preserved tracks, like ONP I_1.9 (the one figured by Gürich 1926 as holotype of *Saurichnium damarense*), actually show a clear separation of digits II and III. We also disagree with Ellenberger's measurement of the interdigital angle III-IV, which he gives as 48°, leading

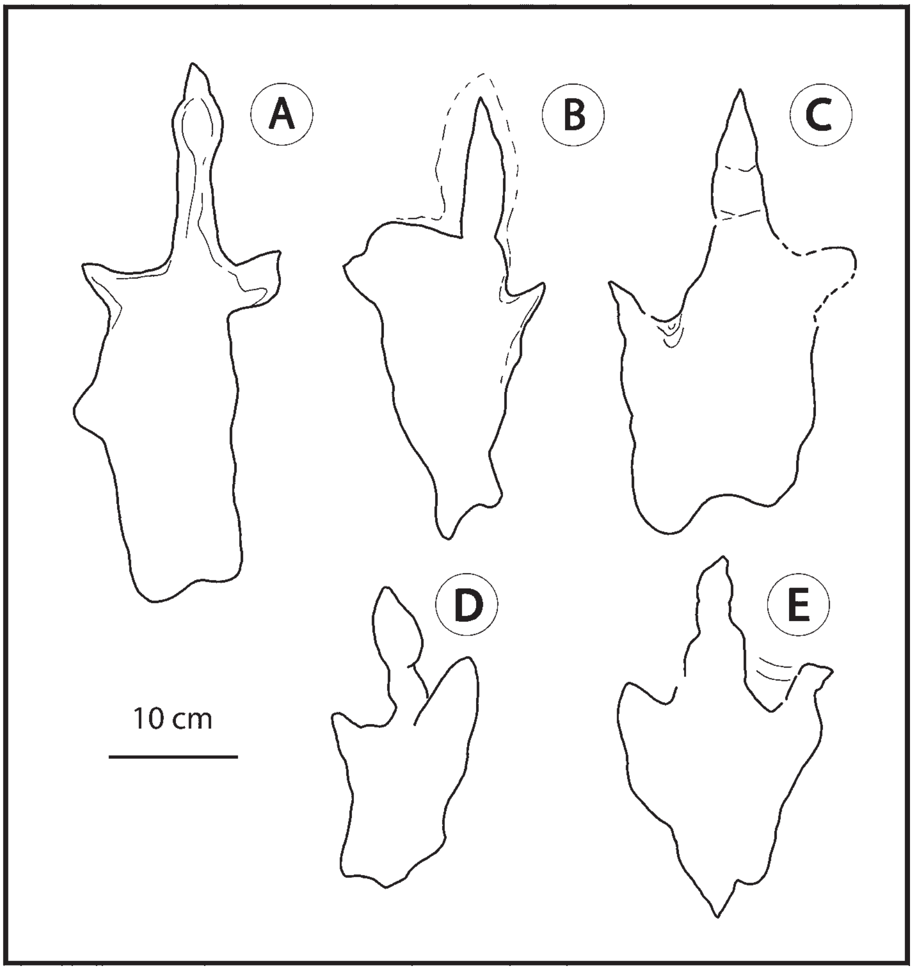

Fig. 10. Outline drawings of a selection of footprints belonging to trackway ONP I_2 (herein referred to as cf. *Anchisauripus* isp.). A: ONP I_2.6; B: ONP I_2.14; C: ONP I_2.34; D: ONP I_2.49; E: ONP I_2.58.

to a total divarication angle of 63°. Our measures for interdigital angle III-IV are about half that reported by Ellenberger (1972), and the total divarication angle quite consistently is in the range 35°-45° in all clearly outlined tracks. If the "fusion" of digits II and III is regarded as an extramorphological feature, *Anatrisauropus* may well be a synonym of other medium–sized, moderately divaricated, "short" (with respect to the FL/FW ratio) ichnotaxa erected in the same work (Ellenberger 1972), like *Neotrisauropus* and *Kleitotrisauropus*. These two ichnogenera, in turn, have been considered as possible African examples of *Kayentapus* in some recent revisions (Piubelli et al. 2005; Lockley et al. 2011). We note that among all "*Kayentapus*-like" footprints reported from around the world, *Kleitotrisauropus* is the one with the stoutest digits and the lowest total divarication (about 40° based on the outline drawings of Ellenberger 1972), two characters that link it to trackway ONP I_1. Stouter digits and lower divarication angle in comparison with the holotype of *Kayentapus hopii* also characterize a sample of Middle Jurassic tracks from Madagascar assigned to *Kayentapus* isp. (Wagensommer et al. 2012), though these tracks are larger (FL = 35 cm on average) and have a slightly higher divarication angle (47° on average) than trackway ONP I_1. Thus, trackway ONP I_1 from Namibia, *Kleitotrisauropus* from Lesotho and *Kayentapus* isp. from Madagascar all share the following characters: they are similar to *Kayentapus* in relative proportions of FL and FW, in having a moderately high projection of digit III ("toe extension") and in possessing an interdigital angle III-IV appreciably higher than interdigital angle II-III, but they resemble *Eubrontes* in having stout digits. The total divarication angle of all three track types is at the upper end of the range of *Eubrontes* or slightly higher. Although any conclusion about these southern Gondwanan “robust” *Kayentapus*-like ichnomorphs is premature until more material emerges, we carefully hypothesize that they represent a recurrent track type that occurs in the Jurassic of southern Africa and Madagascar, two landmasses that were completely adjacent until the Toarcian (Geiger et al. 2004) and preserved a connection through Antarctica until at least the Late Jurassic (Smith et al. 1994; Sereno et al. 2004).

As the distinction between *Eubrontes* and *Kayentapus* stands upon relatively subtle differences (Lockley et al. 2011), it may be unadvisable to distinguish ONP I_1 as a third ichnogenus. Given that it shares more characters with *Kayentapus*, we assign it to this ichnogenus, but we think that its stout digits and relatively low divarication angle allow distinction from other ichnospecies currently recognized under this label (i.e., *K. hopii* Welles 1971; *K. minor*, Weems 1992; and *K. soltykovensis*, Gierliński 1991, 1996). We therefore retain the specific name assigned to this trackway by Gürich (1926) and assign trackway ONP I_1 to *Kayentapus damarensis* comb. nov. The nomenclatural implications of this assignment are discussed at 6.2.

5.2. Trackway ONP I_2

Gürich (1926) refers this trackway to *Saurichnium damarense*. In his description, he notes that this trackway has a slightly longer step than the holotype trackway (85-90 cm instead of 70-75 cm) and that the tracks are less well preserved. We identified 73 tracks in this trackway; the exposed segment is 93.5 metres long. The average stride length is about 185 cm. The footprints appear to be markedly longer than wide (FL = 30 cm and FW = 17 cm on average), but both FL and FW are subject to relevant variations (Fig. 10), which is mainly due to unclear outlines of the tracks, likely a consequence of substrate conditions at the time of track formation. Some tracks apparently penetrated into the sediment to a considerable depth and collapsed after withdrawal of the foot; they show the typical features described by Gatesy et al. (1999) for deep tracks, i.e. increased apparent footprint length, presence of a metatarsal impression and reduction of digit impressions to narrow slits. A few tracks collapsed to the degree that they are only visible as narrow, elongated, shallow depressions that would hardly be interpreted as tracks if they were found in isolation and were not part of a trackway (Fig. 18.8). The sediment retained the details of trackway ONP I_1 much better than those of ONP I_2, which is most likely due to a change in substrate conditions, e.g. wet vs. dry sediment. Given that the two trackways intersect and that the differences in the degree of preservation are much higher between the two trackways than they are within tracks of the same trackway, this difference in substrate conditions is likely not a spatial, but a temporal difference. In other words, the two trackmakers passed at different moments and the time that elapsed between the two passages was sufficiently long to allow the substrate to change, most likely to dry out after a phase of wetting.

Although very few tracks in trackway ONP I_2 are so well preserved to allow univocal recognizing of the pads or even of the lengths of individual digits, a number of tracks allow to locate with confidence at least the tips of the three functional digits and thus to identify the “anterior triangle” *sensu* Weems (1992) and Lockley (2009). This reveals a moderately high projection of digit III (te about 1/3 FL). Although the “posterior triangle” is more difficult to assess because of the difficulty of identifying the limit between digits and metatarsal impressions, a few tracks allow the identification of the posterior margin of digit IV and thus a measure of FL without metatarsus. In these tracks, the measured value of FL is about 27-28 cm, whereas FW is 16-17 cm. We regard this figure as the best estimate we can get of the trackmaker’s foot proportions. Although many tracks within ONP I_2 show metatarsal impressions of varying length, we could not confidently identify any hallux impressions, which might be due to either a genuine absence of digit I, or to unfavourable preservation. Divarication angles are difficult to assess because the position of the axis of individual digits is unclear, but they are in the range of about 30°.

Although Gürich (1926) referred this trackway to *Saurichnium damarense* and thus considered it as similar to trackway ONP I_1, we observe that there are a few differences that can be identified notwithstanding the bad preservation of the trackway. First, while FL (without metatarsus) is comparable in the two trackways, FW is consistently lower in ONP I_2. Second, the maximal divarication angle appears to be lower and third, the digits of ONP I_2 are much more slender than those of ONP I_1, even in those tracks that allow identification of the pads and therefore cannot be regarded as much distorted by the interaction with the sediment. For these reasons, we disagree with the conclusion of Gürich (1926) and consider the two forms different.

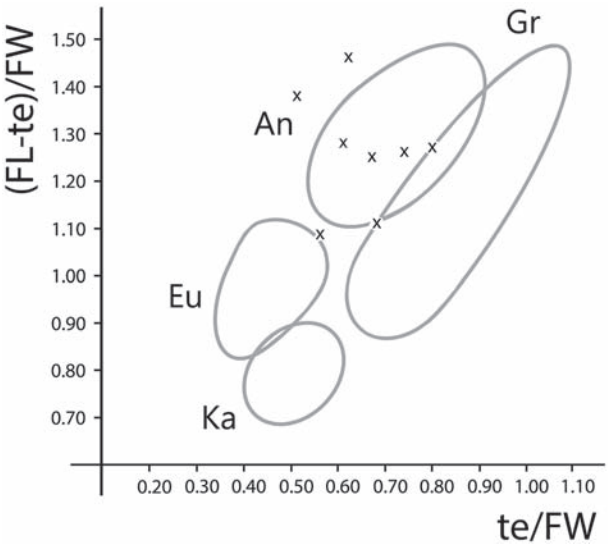

Fig. 11. Weems diagram displaying the relative proportions of footprints belonging to trackway ONP I_2 (X), compared to the ranges of common ichnogenera from the Early Jurassic of North America (grey circles). An = *Anchisauripus*; Eu = *Eubrontes*; Gr = *Grallator*; Ka = *Kayentapus.*

On the WEEMS diagram, trackway ONP I_2 broadly overlaps the range of *Anchisauripus* (Fig. 11). Among the material described by ELLENBERGER (1972) from Lesotho, the highest similarity with trackway ONP I_2 is given in the ichnogenus *Prototrisauropus*, of which the author distinguishes four ichnospecies. Although we had no opportunity to see the material on which these ichnotaxa are based, we observe that based on both the description and the outline drawings, *Prototrisauropus* comprises small to medium sized theropod tracks with slender digits, narrow interdigital angles and long projection of digit III. A comparison between the diagnoses of *Prototrisauropus* (ELLENBERGER 1972) and *Anchisauripus* (LULL 1915, 1953; OLSEN et al. 1998) shows that the two ichnogenera are very similar, and should probably be treated as synonyms. The status of *Anchisauripus* is not clear even in its type area in North America. Some authors (OLSEN 1980; RAINFORTH 2005a) argued that *Grallator*, *Anchisauripus* and *Eubrontes* form a continuous allometric growth series and should thus be synonymised. Others (WEEMS 1992; LOCKLEY & HUNT 1995) keep the separation between *Grallator* and *Eubrontes* but find it difficult to identify *Anchisauripus* as a separate form. While we are conscious of these difficulties, the purpose of this study is to compare the Etjo Formation ichnofauna with coeval ichnofaunas in other parts of the world, rather than adding to the discussion about the possibilities of discriminating different kinds of Early Jurassic tridactyl tracks. We observe that trackway ONP I_2 compares well with North American *Anchisauripus*, although it is slightly larger than the 25-cm-limit assigned by OLSEN et al. (1998) as maximum FL for this ichnogenus. The poor preservation of the tracks however yields some uncertainty about their exact proportions. For these reasons we assign trackway ONP I_2 to cf. *Anchisauripus* isp. Similar material from the Waterberg National Park has recently been revised by these authors (WAGENSOMMER et al. in press).

5.3. Trackway ONP VII_1

This is the only "large" dinosaur trackway preserved at Otjihaenamaparero other than the two intersecting trackways ONP I_1 and ONP I_2 discussed above. It was never before reported in paleontological literature. The trackway is heavily affected by erosion of the exposed surface, so that several tracks are missing. In fact, the preserved trackway segment is about 48 metres long, with several interruptions. Over this distance, only 18 footprints are preserved. Since the average stride is about 2 metres (pace about 1 m), some 30 footprints must be missing along the sequence. As in trackways ONP I_1 and ONP I_2, all missing footprints correspond to missing portions of the surface, and it must be assumed that prior to erosion the sequence was continuous. Despite the many tracks lost to erosion, those that are still in place are often very finely preserved and show much more detail than the two trackways at site ONP I. The outlines of the digits and individual pads are clearly recognizable (Fig. 12). The tracks are shallow if compared with those at site ONP I; the indentation depth is around 2 cm. This implies that the substrate was much firmer at the time of track formation than it was in site ONP I. Footprints are rather elongate; FL is 32 cm on average and FW 21 cm on average. Total divarication averages 35°-40°, interdigital angle II-III being around 12°-15° and interdigital angle II-IV around 20°-25°. The measured parameters show little variation from one footprint to another.

Toe extension is lower than in trackways ONP I_1 and ONP I_2. The cluster that the tracks of ONP VII_1 form on the Weems diagram mostly overlaps the range of *Eubrontes* (Fig. 13). Size and stoutness of digits agree well with this ichnogenus, and the total divarication angle, while slightly higher than in "typical" North American *Eubrontes*, is still within

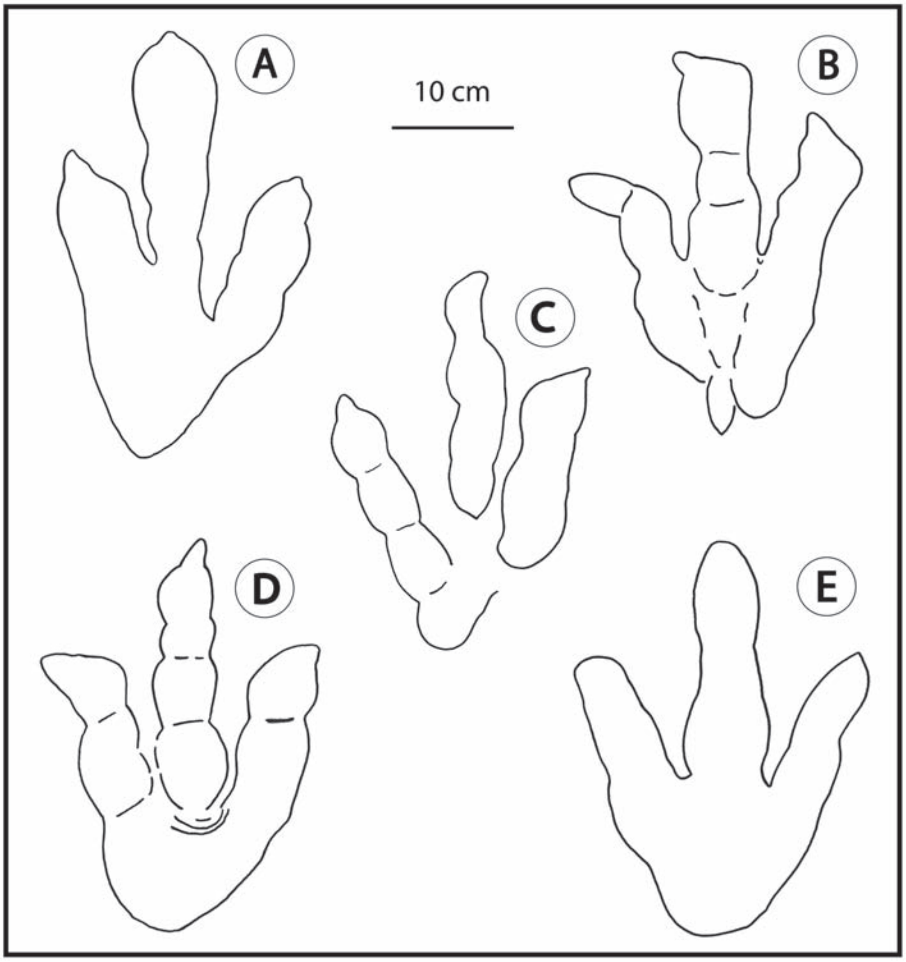

Fig. 12. Outline drawings of a selection of footprints belonging to trackway ONP VII_1 (herein referred to as *Eubrontes giganteus*). **A**: ONP VII_1.3; B: ONP VII_1.7; C: ONP VII_1.8; D: ONP VII_1.17; E: ONP VII_1.18.

the range given by OLSEN et al. (1998). A comparison of the outline drawings of type *Eubrontes giganteus* with the tracks of ONP VII_1 gives an almost perfect match. We therefore assign trackway ONP VII_1 to this ichnotaxon.

5.4. "Small" forms

"Small" (FL = 5.5-11 cm) dinosaur footprints have been identified at six among the seven tracksites investigated

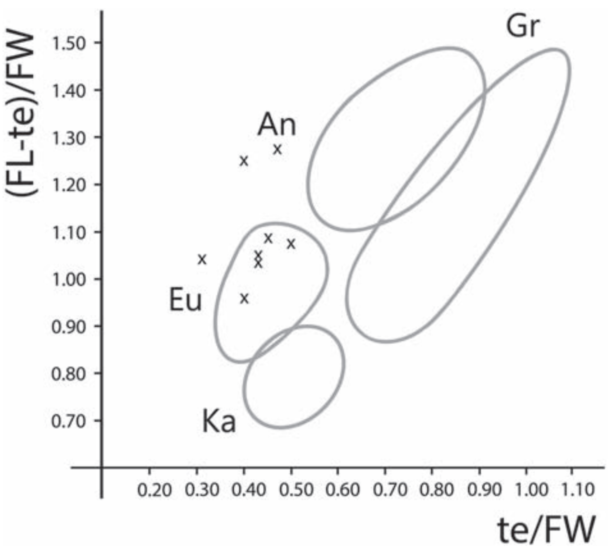

Fig. 13. Weems diagram displaying the relative proportions of footprints belonging to trackway ONP VII_1 (X), compared to the ranges of common ichnogenera from the Early Jurassic of North America (grey circles). An = *Anchisauripus*; Eu = *Eubrontes*; Gr = *Grallator*; Ka = *Kayentapus*.

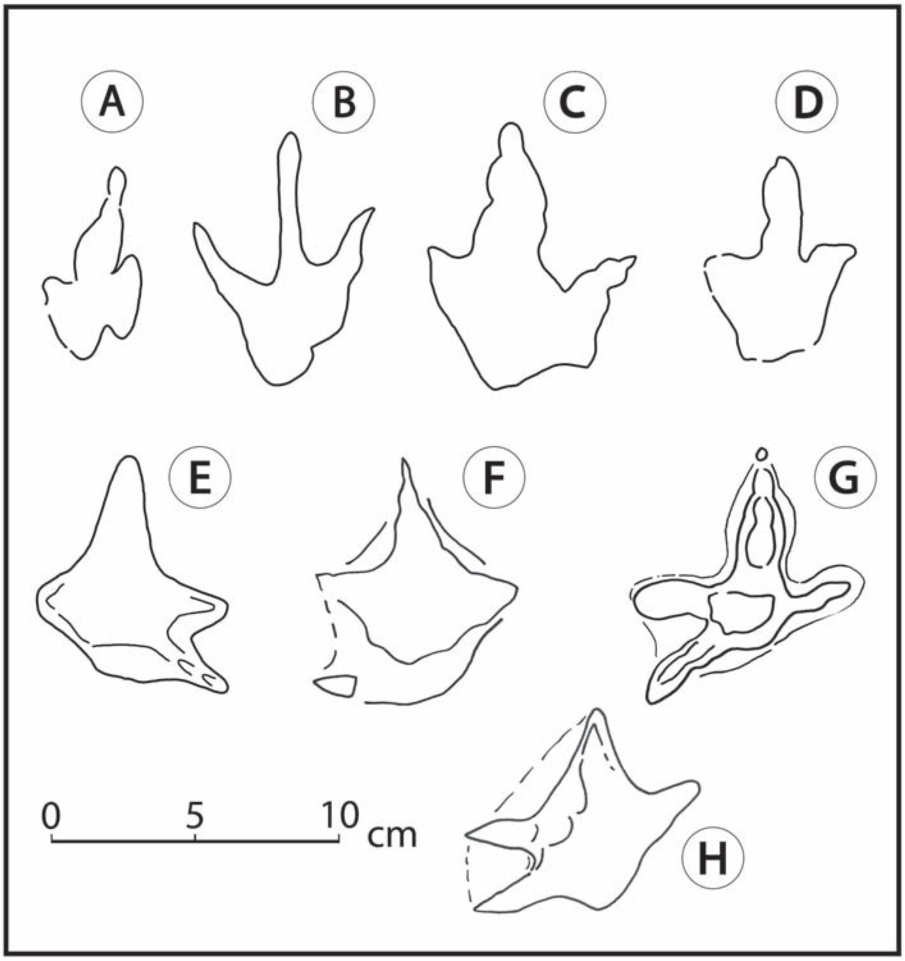

Fig. 14. Outline drawings of a selection of "small" footprints from Otjihaenamaparero. **A-D** – morphotype I (A: ONP I_3.1; B: ONP IV_1.9; C: ONP V_5.11; D: ONP VI_1.1); **E-H** – morphotype II (E: ONP II_1.28; F: ONP II_3.8; G: ONP II_9.1; H: ONP III_1.6).

at Otjihaenamaparero; the only site yielding only "large" tracks is ONP VII (single *Eubrontes* trackway). A total of 24 "small" trackways have been recorded during the 2013-2014 field campaign; these sum up to a total of 220 individual footprints. This sample includes short trackway segments of just two or three consecutive footprints, and longer segments of up to 31 consecutive footprints (ONP II_1). The tracks display a wide array of preservational conditions, from shallow faint undertracks (e.g. ONP IV_1 and ONP IV_2) to deep (up to 3 cm), irregular indentations with steep side walls (e.g. ONP II_1). About 20% of the sample is suitable for identification of the parameters needed to plot a track on the Weems diagram (i.e., FL, FW, and te). A few footprints preserve details such as claw marks and digital pads. The overall sample can be divided into two morphotypes.

We define morphotype I as follows: small (FL about 7 to 11 cm), tridactyl tracks with divarication angles mostly between 30° and 45°; no hallux impression has been observed in our sample. The trackway is narrow (pace angulation mostly in the range 160°-175°) with a long stride, commonly in the range of about 10-12 FL (Fig. 14A-D).

We define morphotype II as follows: small (FL about 5 to 10 cm), functionally tridactyl tracks with divarication angles mostly between 75° and 100°; hallux impressions have been observed in most (but not all) trackways assigned to this morphotype and are often consistently present in sets of consecutive footprints. When present, the hallux mark always points backwards, typically almost exactly the opposite direction

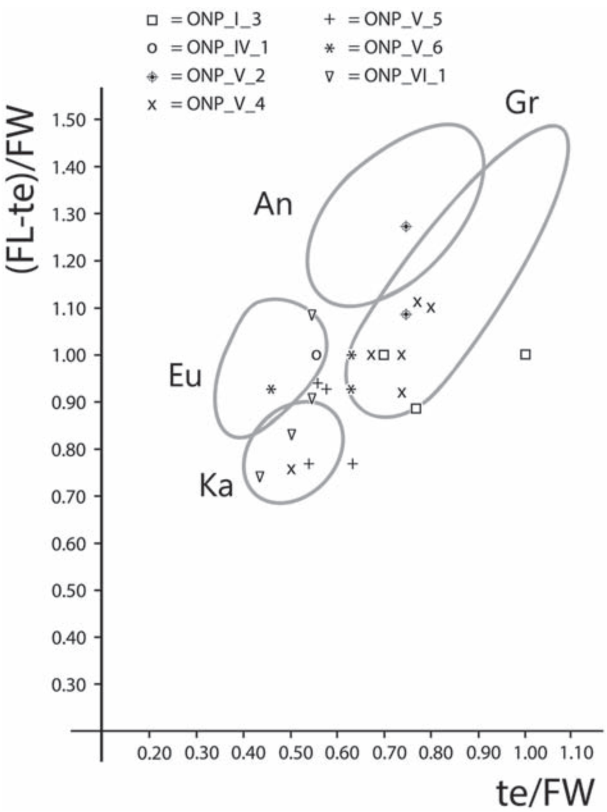

Fig. 15. Weems diagram displaying the relative proportions of footprints belonging to "small" morphotype I, compared to the ranges of common ichnogenera from the Early Jurassic of North America (grey circles). An = *Anchisauripus*; Eu = *Eubrontes*; Gr = *Grallator*; Ka = *Kayentapus*.

than digit IV. The trackway is narrow (pace angulation mostly in the range 160°-175°) with a long stride, though usually shorter than in morphotype I (commonly in the range of about 8-9 FL) (Fig. 14E-H).

Whether the two morphotypes represent distinct ichnotaxa or preservational variants of a same ichnotaxon is not easily resolved. When plotted on the Weems diagram, most tracks assigned to morphotype I fall either inside the range of *Grallator* isp. or slightly outside (Fig. 15), although some (mainly belonging to trackways ONP V_5 and ONP VI_1) fall quite far apart of it. This high degree of spread is most likely a function of suboptimal preservation and is expected to be seen in small tracks, because the material allows measures to be rounded off only to about the nearest half centimetre. While this is true for both the large and the small morphotypes in our sample, an error in the range of 5 mm will not seriously affect the position on the diagram of a track some 250 mm long, while it is more likely to affect a track in the range of 100 mm or less. Even so, the diagram shows that values oscillate around a centre that lies within the "lower" (= relatively higher values of FW) portion of the *Grallator* field. On a qualitative basis, morphotype I tracks match the revised diagnosis of *Grallator* as given by Olsen et al. (1998), except for a higher divarication of the outer digits (30°-45° instead of 10°-30°) and lower FL/FW ratio (1.5-2.0 instead of > 2 as in type *Grallator*), which is a consequence of higher FW values. It has to be stated, however, that the values given by Olsen et al. (1998) refer to the type ichnospecies *Grallator parallelus* (syn. *G. cursorius*), which occupies the "upper" half of the *Grallator* field in the Weems diagram. Other North American ichnospecies referred to the same ichnogenus, like *G. tenuis* and *G. cuneatus* as diagnosed by Lull (1904, 1915, 1953), perfectly match the Namibian "small" morphotype I tracks under every respect (see Fig. 16 for a comparison). They also occupy the same "lower" part of the *Grallator* field on the Weems diagram. To discuss the validity of ichnospecies within *Grallator* is beyond the aims of this paper. For our purposes it is enough to note that morphotype I tracks are perfectly within the variability range of North American *Grallator*. For this reason, we refer them to this ichnogenus.

Morphotype II tracks are the form referred to as *Saurichnium tetractis* by Gürich (1926) and Heinz

	FL (cm)	FW (cm)	Divarication	Stride (cm)
Grallator cursorius (Olsen et al. 1998)	< 8	n.a.	28°	n.a.
Grallator cursorius (Lull, 1915)	7.9	3.1	26°	120
Grallator tenuis (Lull, 1915)	7.3	3.7	40°-45°	40
Grallator cuneatus (Lull, 1915)	12.5	8	46°	90-100
ONP morphotype I tracks	7-11	3.5-6.5	30°-45°	70-100

Fig. 16. Key measurements for different North American ichnospecies assigned to *Grallator*, compared to the variability range of morphotype I tracks from Otjihaenamaparero.

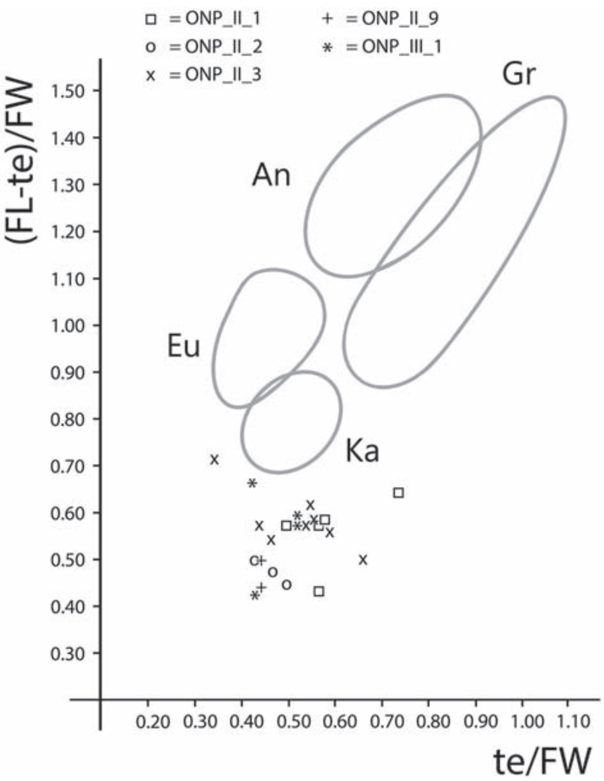

Fig. 17. Weems diagram displaying the relative proportions of footprints belonging to "small" morphotype II, compared to the ranges of common ichnogenera from the Early Jurassic of North America (grey circles). An = *Anchisauripus*; Eu = *Eubrontes*; Gr = *Grallator*; Ka = *Kayentapus*.

(1932). They form a relatively narrow cluster on the Weems diagram (Fig. 17), which does not match the field of any of the North American ichnotaxa considered by Weems (1992). The size of morphotype II tracks is in the range of *Grallator*, but the high divarication angle, low FL/FW ratio and common presence of a hallux do not agree with the diagnosis of this ichnogenus and imply either assignment to a different ichnotaxon or a sedimentological explanation for the origin of such striking morphological differences. Small size, high divarication and presence of hallux marks are characters shared with the North American ornithischian track *Anomoepus*, which is also found in Lesotho, where it has been named *Moyenisauripus* (Ellenberger 1972, 1974). Weems (1992) did not include *Anomoepus* in his diagram, but the track parameters he gives for type material of this ichnogenus would place it in a field with (FL–te)/FW values as high as in *Eubrontes*, but lower te/FW values. This position is quite far from that of the Namibian morphotype II tracks from Otjihaenamaparero, which have different relative proportions. Furthermore, hallux marks in *Anomoepus* point anteromedially, forming an angle of 90° or less with the axis of digit IV, and are usually associated with metatarsal impressions and manus prints in the typical 'sitting' posture, whereas *Saurichnium tetractis* displays posteromedially oriented hallux marks in normal bipedal walking, quite consistently forming an angle of about 180° with digit IV. Last but not least, the narrow trackway and long stride of *S. tetractis* suggest a theropod trackmaker instead of the ornithischian *Anomoepus*, which usually has a wider trackway and shorter step (Olsen & Rainforth 2003; Lockley et al. 2009). A reversed hallux "rotated so as to be in line with the fourth digit" (Lull 1915) is found in some forms of the Connecticut Valley ichnofauna, such as *Steropoides* and *Sillimanius*, but the status of these ichnogenera is dubious, as they were not reported again after their original description in the 19th century (Hitchcock 1845) and were never formally revised since the work of Lull (1915, 1953). Rainforth (2005a, b) considers these forms as preservational variants of "normal" grallatorid tracks, but no model as to how they could have arisen has been proposed. *Saurichnium tetractis* resembles *Trisauropodiscus* and *Masitisisauropezus* from Lesotho, but a closer comparison is hampered by the lack of a conspicuous documentation about these and other purportedly "proavian" forms from the Lesotho ichnofauna. According to the illustrations provided by Ellenberger (1972, 1974) none of these forms displays comparably well-developed hallux marks as the Namibian tracks, perhaps except *Trisauropodiscus superaviforma*, although Ellenberger's (1972) diagnosis is not clear on this point. *Trisauropodiscus* has also been reported from western North America (Lockley et al. 1992) and possibly Europe (Lockley & Meyer 2000), but these northern hemisphere examples all lack hallux impressions and have been considered as possi-

Fig. 18. Dinosaur tracks from the Otjihaenamaparero locality. **1-6** – A selection of footprints belonging to trackway ONP I_1, referred to *Kayentapus damarensis* comb. nov. **7-12** – A selection of footprints belonging to trackway ONP I_2, referred to cf. *Anchisauripus* isp.

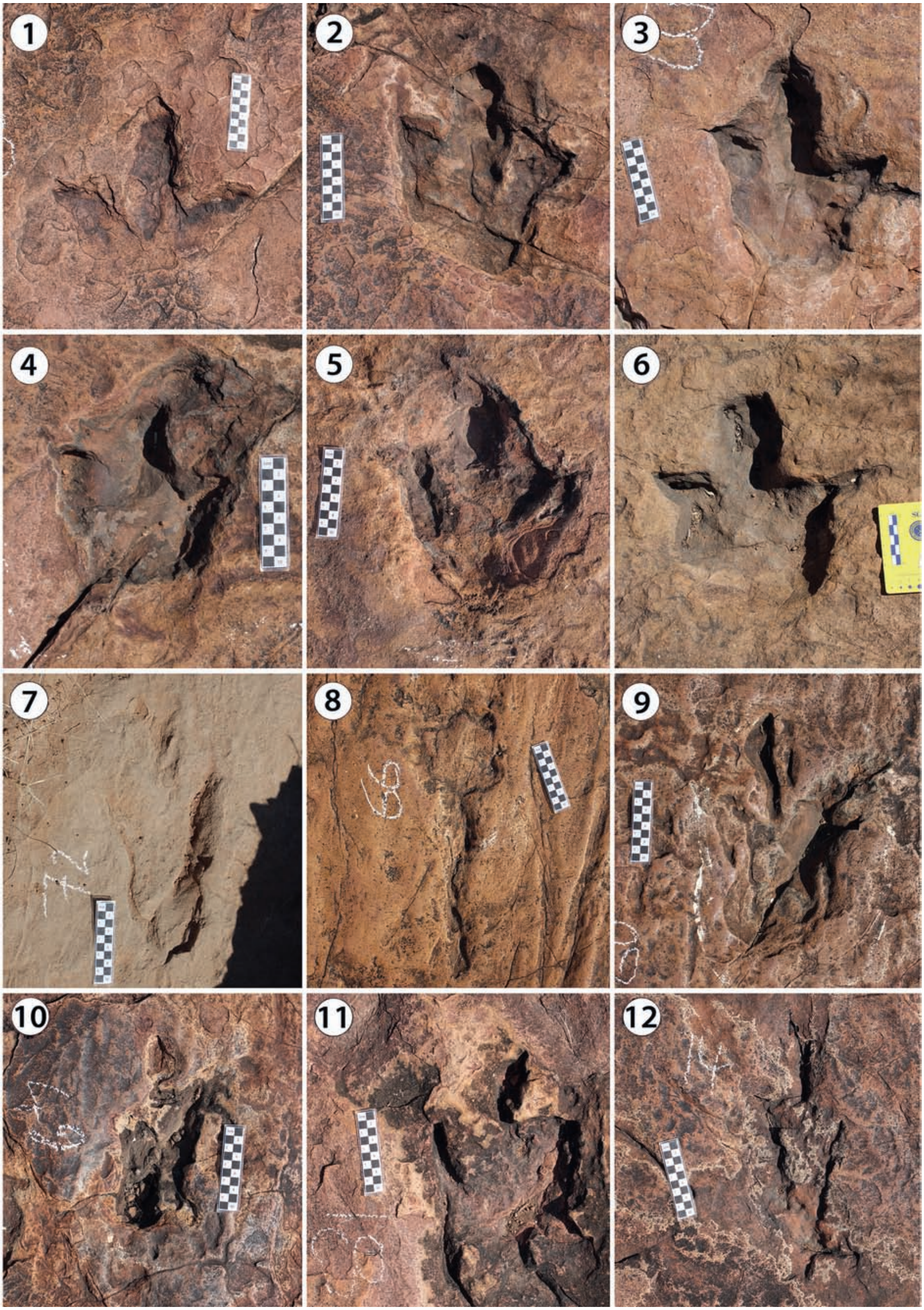

Fig. 18.

ble *Anomoepus* specimens by later workers (Lockley & Rainforth 2002; Lockley & Gierliński 2006; Belvedere et al. 2011). There seems to be no close match between *Saurichnium tetractis* and any Early Jurassic tracks currently known from outside Africa, while comparable forms have been reported from Lesotho (Ellenberger 1972, 1974) under a variety of names and are in need of a revision. Pending this revision, we provisionally retain, as an informal label, the name assigned by Gürich (1926) to the tetradactyl footprints of Otjihaenamaparero, although we are conscious that *"Saurichnium" tetractis* cannot be a valid name, if only because the type ichnospecies of *Saurichnium* is *S. damarense*, which is certainly different enough from both "small" morphotypes to warrant distinction at the ichnogenus level.

6. Discussion

The ichnofauna preserved within the Etjo Formation opens an interesting window on the Early Jurassic dinosaur communities in an otherwise poorly known area. Several issues can be addressed in evaluating this source of information.

6.1. Dinosaur diversity as mirrored by the ichnofauna

It is generally acknowledged that ichnotaxa are not the equivalent of osteological taxa, and that a same track type could have been produced by different species or genera of trackmakers. The number of ichnotaxa identified at a given locality should thus be treated as an indicator of the minimum faunal diversity at this site. However, there is also an increasing awareness that the opposite might be true in some cases, i.e. different track morphologies that have been assigned formal names (ichnotaxa) may have been produced by the same trackmaker. For instance, end members in a growth series of a single animal population may be mistaken to represent different trackmakers rather than juveniles and adults of the same population, as suggested by Olsen (1980) for North American Early Jurassic theropod ichnotaxa. A second mechanism that might lead to an overestimate of trackmaker diversity is the production of differently shaped tracks when the same foot morphology impacts different kinds of sediment (Gatesy et al. 1999; Milàn & Bromley 2005; Milàn 2006; Milàn & Bromley 2008). At Otjihaenamaparero we identified five morphotypes of tracks that can be assigned to different formally named ichnotaxa. How do they relate to the actual dinosaur diversity in this ancient environment? The total recorded number of 350 tracks in 27 trackways represents a sample which is large enough to make it statistically unlikely that the gap in size distribution between "large" and "small" forms could have arisen from random sampling in a population including a complete growth series from juveniles to adults. It is more parsimonious to assume that the dinosaur fauna at this locality really included both small and larger theropods, the former being more abundant, and that the two size classes represent different dinosaur taxa rather than juveniles and adults of a same species. Within the "large" forms, trackways ONP I_1 and ONP VII_1 (assigned to *Kayentapus damarensis* and *Eubrontes giganteus*, respectively) are sufficiently well preserved to be differentiated with confidence. Trackway ONP I_2 (cf. *Anchisauripus*) appears to be different from both, but as most of its tracks are distorted by deeply sinking into the sediment its actual morphology remains uncertain. A case could also be made that "*Saurichnium*" *tetractis* and *Grallator* may have been produced by the same trackmaker, the former representing the track of a deeply sunken foot in which the hallux contacted the ground and the total divarication is exaggerated by the interaction between the digits and the sediment, as has been suggested for similar forms in North America (Rainforth 2005b). A comparison between "*S.*" *tetractis* and deep theropod tracks of small size from the Triassic of Greenland showing a posteromedially directed hallux trace (Gatesy et al. 1999), however, highlights some significant differences, such as the presence of metatarsal impressions,

Fig. 19. Dinosaur tracks from the Otjihaenamaparero locality. **1-3** – A selection of footprints belonging to trackway ONP VII_1, referred to *Eubrontes giganteus*. **4-6** – Footprints assigned to "small" morphotype I. **7-9** – Footprints assigned to "small" morphotype II. **10** – Partial view of trackway ONP I_1. Hammer (inside white circle) is 33 cm long. **11** – A row of white quartz pebbles, each put inside a footprint of trackway ONP IV_1, helps visualize the narrow trackway pattern of "small" morphotype I. Hammer for scale (33 cm). **12** – Two parallel trackways assigned to "small" morphotype I at site ONP V.

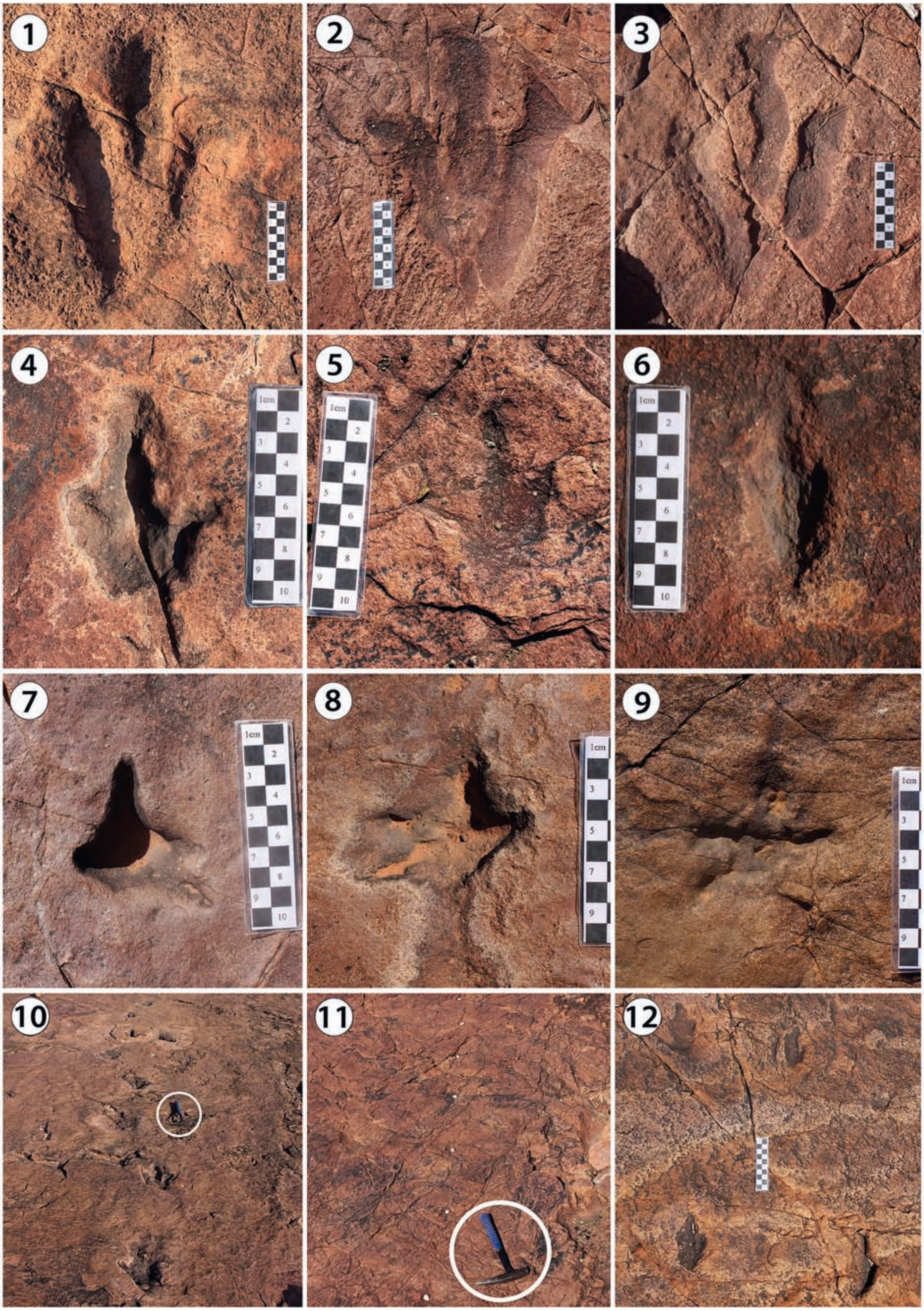

Fig. 19.

an increasing anterior elongation and the presence of a rounded "exit hole" of the foot at the tip of digit III in the Greenland material, as opposed to short and wide tracks without metatarsal impression and without any appreciable "exit hole" in "*S.*" *tetractis*. It cannot be ruled out that the two morphotypes of "small" tracks at Otjihaenamaparero may have been produced by a same foot morphology impacting sediments of different consistency, but at present there is no known mechanism that could explain the differences between the two by sedimentologic or kinetic processes alone. We therefore provisionally treat them as separate ichnotaxa, pending further research on the possibilities of distortion of track parameters by the foot/sediment interaction. Thus the track record at Otjihaenamaparero allows to infer some 3-5 different foot morphologies as a minimum diversity index for different dinosaurian trackmakers represented at this locality.

There is a general consensus that *Grallator*, *Anchisauripus*, *Eubrontes* and *Kayentapus* are the tracks of theropods. Claims that *Eubrontes* might be the track of a prosauropod (Weems 2003) have widely been dismissed (Smith & Farlow 2003; Lucas et al. 2006a). As for *"Saurichnium" tetractis*, we assign this tracktype to a theropod trackmaker too, on the basis of the following characters: narrow, sharply pointed digit marks and narrow trackway with long stride. Thus the assemblage at Otjihaenamaparero, though moderately diverse, appears to be exclusively characterized by theropods.

6.2. Biogeographic affinity of the Etjo Formation ichnofauna

The ichnofauna preserved at Otjihaenamaparero is markedly similar to coeval faunas from North America. The twofold size-classing observed at Otjihaenamaparero, with "small" and "large" tracks separated by a considerable dimensional gap, is also given at several Lower Jurassic localities in North America (Lockley & Hunt 1995; Hamblin et al. 2006; Williams et al. 2006). Three out of five ichnotaxa recognized at Otjihaenamaparero (namely *Eubrontes*, *Anchisauripus* and *Grallator*) have been originally named in North America, where they are the most common dinosaur tracks in Lower Jurassic sediments. While the remaining two forms appear to be genuinely African, one of them (*Kayentapus damarensis*) is similar enough to North American forms to warrant inclusion in the same ichnogenus. In addition to the rich record at Otjihaenamaparero, D'Orazi Porchetti et al. (2015) recently reported *Otozoum moodii* trackways from the Etjo Formation at the Omuramba Omambonde tracksite, some 185 km NE of Otjihaenamaparero, adding another classical North American ichnotaxon to the Namibian Early Jurassic ichnofauna. The same ichnotaxon has recently been reported also from Northern Africa (Masrour & Pérez-Lorente 2014). There is an increasing awareness that the ichnotaxa originally described from North America also characterize the Early Jurassic record from Europe (Gierliński 1995; Lange-Badré & Lafon 2000; Montenat & Bessonnat 2003; Gierliński et al. 2004; Piubelli et al. 2005), Asia (Lockley et al. 2003; Lockley & Matsukawa 2009; Pieńkowski et al. 2015) and Australia (Cook et al. 2010), which points at a rather uniform, "pangaean" distribution of track morphologies in this period. Earlier claims for a highly distinct southern African ichnofauna sharing less than 2% of its ichnotaxa with North America (Ellenberger 1972) can be rejected. While these claims have long been doubted (Olsen & Galton 1984; Haubold 1986; Wilson et al. 2009), this assumption was based mainly on literature data. Our field-based study confirms these doubts and underlines the broad similarity of southern African and northern American ichnofaunas in the Early Jurassic.

6.3. Age constraints for the Etjo Formation

The age of the Etjo Formation has been a quite controversial issue, the unit being referred to the Late Triassic (Cosburn 1980, 1990; Dingle et al. 1983), the Early Jurassic (Holzförster 1999; Holzförster et al. 1999), crossing the Triassic/Jurassic boundary (Löffler & Porada 1998) or even extending to the Early Cretaceous (Pickford 1994, 1995). The occurrence of *Otozoum* in the higher levels of the Etjo Formation (Upper Unit *sensu* Holzförster et al. 1999) at Omuramba Omambonde sets a clear constraint for an Early Jurassic age at least of this portion of the sequence (D'Orazi Porchetti et al. 2015). Holzförster et al. (1999) refer the dinosaur tracks at Otjihaenamaparero to the same Upper Unit of the Etjo Formation, but given the contrasting view of Smith & Swart (2002) and the position of the tracksites only a few metres above the Omingonde/Etjo contact, they may actually be older than the *Otozoum*-bearing levels at Omuramba Omambonde.

Though quite diverse, the theropod ichnofauna of Otjihaenamaparero lacks specific biostratigraphic markers. While *Grallator* is abundant in Upper Triassic as well as Lower Jurassic strata (e.g., Lockley & Hunt 1995; Lockley & Eisenberg 2006; Lockley & Gierliński 2009), *Eubrontes* appears to be more common in the Early Jurassic and it has in fact been argued that the lowest occurrence of this ichnogenus can be used as a marker for the Triassic/Jurassic boundary (SILVESTRI & SZAJNA 1993; OLSEN et al. 2002), a view though that has been contradicted by other workers (THULBORN 2003; LUCAS et al. 2006a), who convincingly demonstrated that *Eubrontes* does occur in the Late Triassic. *Anchisauripus* has a range spanning both the Late Triassic and the Early Jurassic (SILVESTRI & SZAJNA 1993). *Kayentapus* has mostly been reported from Jurassic strata, but WEEMS (1992, 2006) reports *K. minor* from the Upper Triassic of Virginia.

Although none of the ichnotaxa recorded at Otjihaenamaparero is exclusively Jurassic, their association and the lack of typical Triassic track types is more reminiscent of Early Jurassic than Late Triassic assemblages if compared with the North American record (e.g., LUCAS et al. 2006b). Therefore, an Early Jurassic age seems to be likely for this locality as well. By now, there is no reason to assume that the Etjo Formation might extend downwards into the Triassic.

6.4. Taxonomical status of the ichnotaxa erected by GÜRICH (1926)

In his original report on the dinosaur tracks at Otjihaenamaparero, GÜRICH (1926) used the plaster casts that were sent to him to describe different track types, which he formally named, erecting five new ichnospecies accommodated within two new ichnogenera. These casts are no longer present in the collections of the University of Hamburg and have probably been lost during World War II (KOTTHOFF, pers. comm.), so all that is left over are the descriptions and figures published by GÜRICH (1926). GÜRICH's work was unknown to ELLENBERGER (1972), who named a new ichnospecies *Anatrisauropus hereroensis* based on the same trackway used by GÜRICH (1926) as a holotype for *Saurichnium damarense*. This again was not noticed by later authors (STANISTREET & STOLLHOFEN 1999; HOLZFÖRSTER et al. 1999; SCHNEIDER & MARAIS 2004) who compared the tracks to other forms described by ELLENBERGER (1972, 1974) from Lesotho, such as *Qemetrisauropus* and *Prototrisauropus*, further complicating the ichnotaxonomic status of the Namibian material. Such a comparison is obviously pointless in the view of ELLENBERGER's own awareness of the Namibian tracks, but the case invites us to stress the importance of a specialist approach to the footprint record, especially when dealing with ichnotaxa that might be used as biomarkers and, moreover, reminds us of the compelling necessity of revising the footprint record from Lesotho with a strong stratigraphical control, in order to set this key record from Gondwana in a clear stratigraphical framework.

Whatever the status of the ichnotaxa described from Lesotho concerns, the names introduced by GÜRICH (1926) have priority on all names introduced by ELLENBERGER (1972, 1974). Despite being widely ignored, GÜRICH's naming of the tracks was technically valid, as he designated holotypes for each of his new ichnospecies, deposited plaster casts of them in a public institution for future reference, figured them and published a clear diagnosis of each new ichnotaxon, including comparisons with North American forms, based on the literature available at his time. In the following we discuss the significance that has to be assigned to these ichnotaxa.

Saurichnium damarense was erected by GÜRICH based on the plaster cast of a single track and a number of sketches of the most prominent trackway at the "main tracksite". His accurate description and figures leave no doubt that he was referring to trackway ONP I_1, which we identify as the holotype. The figured track (GÜRICH 1926, fig. 1) is ONP I_1.9, identifiable by its outline and the rock fracture pattern around the footprint. GÜRICH compared this form to both *Anchisauripus* and *Gigandipus* from North America and decided it was different enough to warrant the erection of a new ichnogenus and species. Our assignment of this trackway to *Kayentapus* (see details at 5.1.) arises a nomenclatural problem, as *Saurichnium damarense* was formally erected about half a century before WELLES (1971) introduced the name *Kayentapus*. This implies that the latter label should be considered a junior synonym of *Saurichnium*. Besides being a quite unfortunate name, meaning nothing more than "reptile trace", *Saurichnium* was never used in paleontological literature after HEINZ (1932) revisited the dinosaur tracks at Otjihaenamaparero, and it was never applied to any dinosaur track other than the type material. As opposed to this, *Kayentapus* is a widely employed and well known label that has been used in quite a number of studies published in recent years (see LOCKLEY et al. 2011, and references therein). For these reasons, we suggest that in case future research confirms that *Saurichnium* and *Kayentapus* are synonyms, the latter name be retained for this ichnogenus, as *Saurichnium* can be considered a *nomen oblitum*. The correct label for trackway ONP I_1 in this case would be *Kayentapus damarensis* comb. nov.

Saurichnium tetractis is the name GÜRICH applied to our "small" morphotype II tracks. The type locality is certainly ONP II, and the holotype trackway probably ONP II_1, although it is not clear which tracks of this sequence are actually represented in Gürich's figure. He compares this form to *Anomoepus* but considers it different because of its wider digit divarication and because he mistakenly assumes the reversed hallux to be a metatarsal impression and thus writes that a hallux mark is missing. His inclusion of this form within the same ichnogenus as trackway ONP I_1 would be unconceivable today, as the two forms greatly differ in size, shape and relative proportions. The type ichnospecies of *Saurichnium* is *S. damarense*, and for this reason *"Saurichnium" tetractis* should be moved into a different ichnogenus. But given the uncertainties about the influence of sediment consistency on this morphotype and its relationship to similar tracks in Lesotho, we retain the name *"Saurichnium" tetractis* in this study.

Gürich included two more ichnospecies in *Saurichnium*: *S. parallelum* and *S. anserinum*. Both are small (FL about 10 cm) and the type locality of both is ONP I, "slightly more uphill and to the SW of the *Saurichnium damarense* trackway, but on the same surface" (our translation). *S. parallelum* is based on isolated tracks, while *S. anserinum* is said to be based on a short trackway, although Gürich figures one track only. We were not able to relocate these tracks. Judging from Gürich's figures, *S. parallelum* appears to be a rather featureless shallow depression, and since the sandstone surface at ONP I is very irregular due to both primary (sedimentation) and secondary (erosion) features, we doubt it is a track at all. As opposed to this, the plaster cast of *S. anserinum* (Gürich 1926, fig. 4) looks convincing and we cannot rule out that it was based on a real trackway that may since have been eroded or that we may have overlooked. Its proportions would perfectly fit our "small" morphotype I tracks, of which a short trackway is present at ONP I (but in a different position from the one given by Gürich). Since we referred this morphotype to *Grallator* isp., the correct name for this form would be *Grallator anserinum*, but given that the holotype is lost and Gürich's description does not allow a clear differentiation of this track type from other ichnospecies within *Grallator*, we consider this label as a *nomen dubium*.

Roundish, shallow, featureless depressions about 30 cm in length were described by Gürich as a new form, which he named *Tetrapodium elmenhorsti*, assuming a quadrupedal trackmaker. The type locality is ONP I; from his description it is not clear whether the "tracks" were arranged in a trackway or isolated. After careful inspection of the tracksite, we are convinced that no such form exists at ONP I; *Tetrapodium elmenhorsti* is most likely based on a non–biogenic feature of the sandstone surface and thus is not a valid name.

7. Conclusions

The ichnofauna preserved at the seven tracksites on the land of the Otjihaenamaparero 92 Farm represents about 80% of the entire dinosaurian record of Namibia. This locality, registered as a National Monument by the Namibian government, has a long and complex research history as one of the earliest discoveries of dinosaur tracks on the African continent. Nevertheless, prior to this revision, the ichnofauna preserved at Otjihaenamaparero had been described in a rather superficial manner, leading to the naming and renaming of the tracks without a proper ichnotaxonomical discussion. Our study leads to the recognition of five ichnotaxa, namely *Eubrontes giganteus*, *Kayentapus damarensis* comb. nov., cf. *Anchisauripus*, *Grallator* isp. and a small widely divaricated track with hallux impression for which we provisionally retain the name *"Saurichnium" tetractis*, pending a further comparison with similar ichnomorphs from Lesotho. All five are considered to have been made by theropods. The ichnofauna is markedly similar to coeval ichnofaunas from North America and Europe. Although the ichnofauna lacks unequivocal biostratigraphic markers, its overall character strengthens the assignment of the Etjo Formation to the Lower Jurassic.

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