Paläontol Z
DOI 10.1007/s12542-015-0264-6

RESEARCH PAPER

A vertebrate trackway from the Twyfelfontein Formation (Lower Cretaceous), Damaraland, Namibia

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Received: 24 December 2014 / Accepted: 15 April 2015

Abstract A trackway of 22 footprints is the first definite evidence of vertebrate life from the Main Aeolian Unit of the Twyfelfontein Formation (Lower Cretaceous), Kunene region, Northwestern Namibia. Footprints were left on the lee slope of an ancient dune in a hyper-arid, erg-dominated paleo environment. The new material is reminiscent of the Mesozoic ichnotaxon *Brasilichnium*, which is exclusively found on the slip face of sand dunes, from both South and North America. The Twyfelfontein Formation is considered a lateral equivalent of the Brazilian Botucatu Formation in which *Brasilichnium* is a common trace fossil, but correlation was formerly based exclusively on sedimentologic and lithostratigraphic homologies. Aside from being the first vertebrate evidence from the Cretaceous of Namibia, and possibly the first African *Brasilichnium*, this new find enforces the correlation between the Botucatu and the Twyfelfontein formations.

Keywords Lower Cretaceous · Twyfelfontein Formation · Sand dunes · Vertebrate trackway · *Brasilichnium*

Kurzfassung Eine aus 22 aufeinanderfolgenden Trittsiegeln bestehende Fährte ist der erste Nachweis eines Wirbeltiers aus der Main Aeolian Unit der Twyfelfontein–Formation (Unterkreide), Region Kunene, nördwestliches Namibia. Die Fährte entstand auf der Leeseite einer Düne in einem hyperariden, Erg–artigen Lebensraum. Sie erinnert an das mesozoische Ichnotaxon *Brasilichnium*, das bisher ausschließlich von fossilen Sanddünen in Süd–und Nordamerika beschrieben wurde. Die Twyfelfontein–Formation wird als afrikanisches Gegenstück zur brasilianischen Botucatu–Formation angesehen, obgleich die Korrelierung bislang nur auf sedimentologischen und lithostratigraphischen Homologien basierte. Dieser neue Fund ist nicht nur der erste Nachweis eines Wirbeltiers aus der Kreide Namibias und möglicherweise der erste Beleg von *Brasilichnium* auf dem afrikanischen Kontinent, sondern er untermauert auch die Korrelierung zwischen der Botucatu–und der Twyfelfontein–Formation.

Schlüsselwörter Unterkreide · Twyfelfontein–Formation · Sanddünen · Wirbeltierfährte · *Brasilichnium*

Introduction

Fossil deserts might be extremely poor in fossils, and especially in body fossils. It is, however, not uncommon to find in such extreme paleoenvironments vertebrate and invertebrate ichno fossils, which might turn out to be useful tools for correlation and dating. The Twyfelfontein Formation of Namibia is no exception, and until this discovery, neither vertebrate body fossils nor their footprints were known from this unit. Only invertebrate burrows (*Skolithos*) were described from the supersurface at the base of the Main Aeolian Unit in the so called Huab Outliers area (Mountney et al. 1999b, 2000).

During a field survey in summer 2014, the authors discovered a sequence of footprints organized in a clear

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Published online: 01 May 2015

trackway on a fallen block of the Twyfelfontein Formation, not far from the renowned rock petroglyphs site in the homonymous area (Fig. 1). This paper deals with the description and interpretation of this material, which is the first of its kind from the Twyfelfontein Formation.

Geological setting

The Huab Basin (Horsthemke et al. 1990) is a marginal rift basin, recording Karoo and Post–Karoo deposits. In the Huab area, Karoo sediments are represented by the Permian–Triassic Gai–As and Doros formations (Stanistreet and Stollhofen 1999) whereas post–Karoo deposits include the Cretaceous Etendeka Group (Twyfelfontein Formation, Awahab and Tafelberg formations; Milner et al. 1994; Stollhofen 1999; Fig. 2).

The Twyfelfontein Formation in the Huab Basin covers about 5000 square kilometres (Mountney and Howell 2000, 1998, 1999a, b) and reaches a maximum thickness of 200 metres (Mountney and Howell 2000) in the basin depocenter, whereas it is about 30 m thick in the area where fieldwork has been carried out. The Twyfelfontein Formation rests unconformably on the Gai–As Formation and interfingers with the Etendeka volcanics in its uppermost section. Mountney et al. (1998, 1999b) distinguished four lithostratigraphic units in the Twyfelfontein Formation, from the base to the top: the Krone Fluvial Member, the Mixed Aeolian–Fluvial Unit, the Main Aeolian Unit and the Upper Aeolian Unit. From a paleoenvironmental point of view, these units record a shift from semi-arid to hyper-arid conditions.

Based on the $^{40}Ar/^{39}Ar$ method, Renne et al. (1996) dated the Etendeka lava flows to ~132 Ma, which is the minimum age for the Twyfelfontein Formation. No definitive constraint is known so far for the base of this unit, but an Early Cretaceous age is generally accepted as most probable (Stollhofen 1999; Wanke 2000). The Twyfelfontein Formation is considered as a lateral equivalent of the Brazilian Botucatu Formation (Stollhofen 1999), which might have supplied sand to its African extension (Dingle 1992), at least for the Main Aeolian Unit (Mountney et al. 1999b).

Materials and methods

Footprints were found on a dislodged boulder (coo. 20°35′01″S–14°23′45″E, elevation ~600 m AMSL) on the NE face of a hill that borders the road to the Twyfelfontein World Heritage site. The block originates from the overlying units and rests mid-height on the side of the hill as part of a large talus (Fig. 3a). The boulder is roughly rectangular, 5.5 m long by 2.5 m wide. The thickness is around 1.1 m, where measurable (Fig. 3b). The trackway crosses the entire block along its downslope margin (Fig. 3c), but its orientation is not determinable, given that the original position of the boulder is unknown. The block

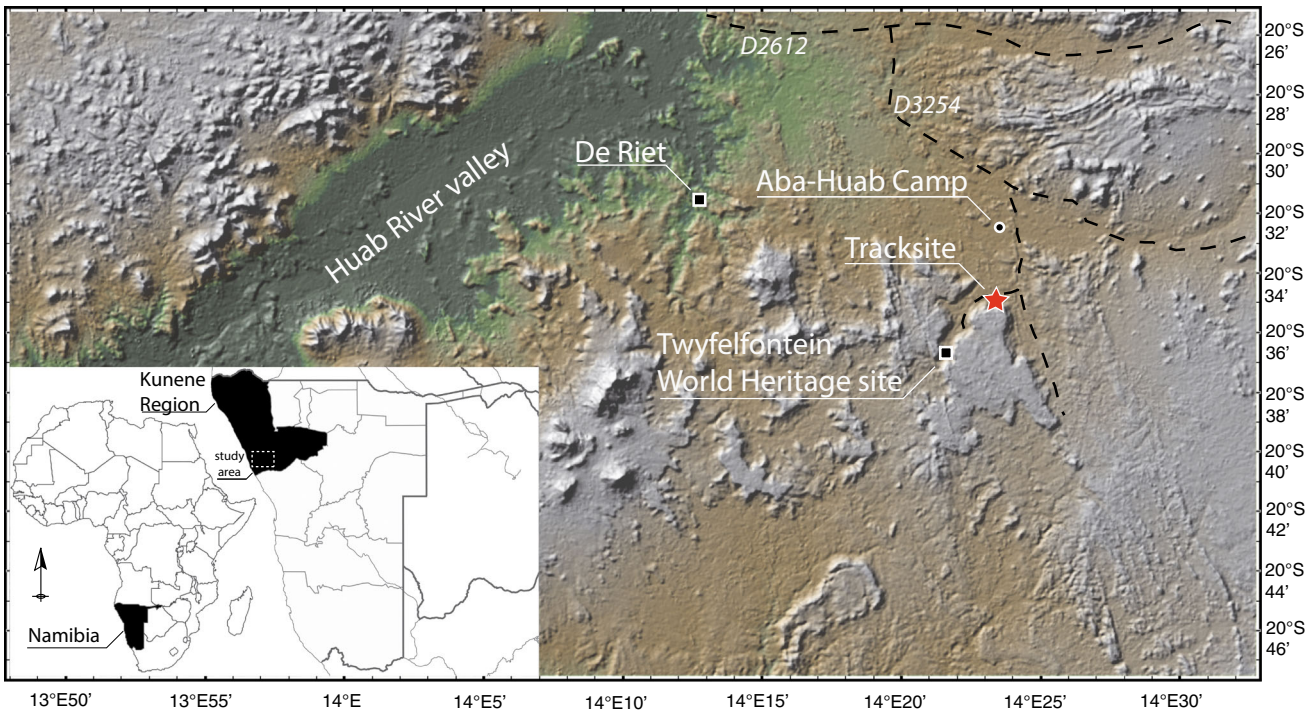

Fig. 1 Location map of the new tracksite (*star*). Base map generated by GeoMapApp (http://www.geomapapp.org)

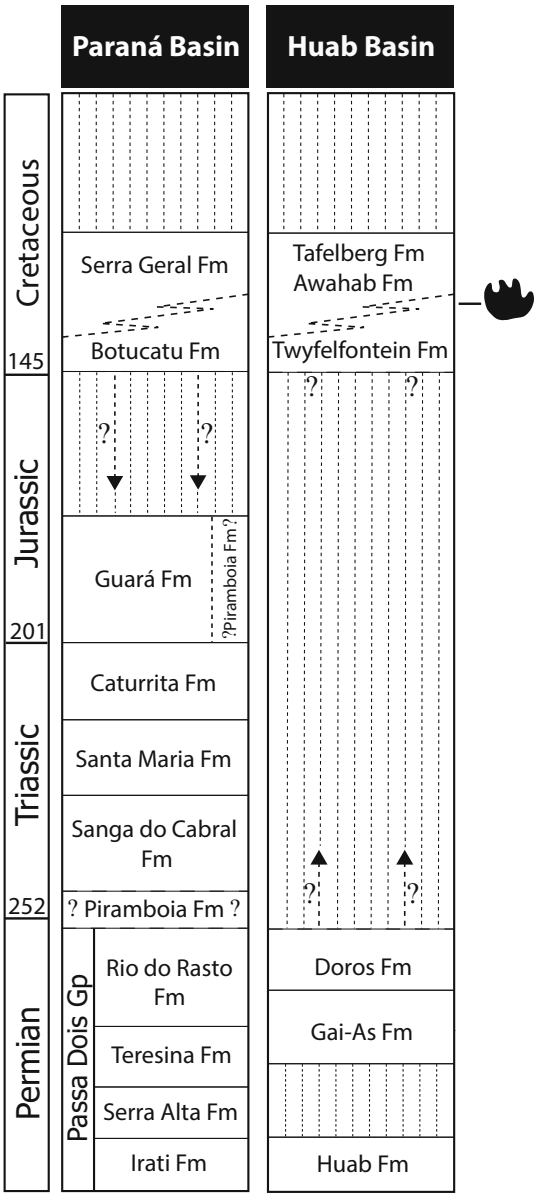

Fig. 2 Lithostratigraphy of the Huab (Namibia) and Paraná (Brazil) Basins, showing a correlation between Brazilian and African units (modified after Jerram et al. 1999 and references therein; Warren et al. 2001; David et al. 2011). The age of the Piramboia Formation is doubtful, and it is considered either Permian (Scherer 2000) or Mesozoic (Soares 1975; Soares et al. 2009), thus it is represented twice in the left column, with question marks

is made of well-sorted, rounded, homogeneous, medium-sized sand grains, pale orange in colour (Fig. 3d). This sandstone shows the 'millet seed' texture described by Mountney et al. (1998) and Mountney and Howell (2000, Fig. 3a). No gradation is observable. The block preserves sets of parallel layers, whose thickness decreases moving toward the trampled surface. This 'millet seed' texture represents a signature for the block origin, which is considered as fallen from the Main Eolian Unit. Other indirect evidence regarding the provenance of the block includes the absence of the Mixed Aeolian–Fluvial and of the Upper Aeolian Unit in this specific area, and a clear sedimentologic difference from the Krone Fluvial Member.

The specimen has been left in situ, and recorded by photographs and measurements. A cast was made with plaster that is now stored at the Geological Survey of Windhoek (Namibia) under the repository number F1528. A close-range photogrammetric record of a portion of the trackway (footprints 10–20) was performed following the procedure described by Falkingham (2012). All measurements and terminology follow Thulborn (1990) and Leonardi (1987).

Description

The Twyfelfontein trackway consists of a sequence of 22 footprints arranged in a sigmoid path (Fig. 4a). Along its length (139 cm), the trail shows slight variations in width, pace angulation, and stride. The mean width of footprints is 18 mm, for an average length of 24 mm; widths of the footprints seem to be more stable, less variable then those related to the length. No definite *manus* prints were identified on the trackway. The pace has a mean value of 73 mm (varying between 66 and 86 mm). Pace angulation is on average 122.6° (min 112°, max 132°), with higher values in the second half of the trackway. The trackway width has a mean value of 35.5 mm (28–42 mm) and tends to be constant in the first half of the trackway, decreasing toward the end of it. The path is slightly sigmoidal, with two sensible variations in the direction of movement. No tail marks were observed on the trackway. All measurements are reported on Table 1.

The quality of preservation of single footprints is generally poor, either as a consequence of erosion or because the sediment was too coarse to record finer details. However, at least one footprint (number 13) shows relatively well-preserved digit marks, helping to define the shape of the trackmaker's foot (Fig. 4b). This footprint is tetradactyl, and apparently digitigrade. Digit marks have more or less the same length and are arranged to form an arc. Digits are short and distally sharpened. Digit I lies posterior to the other digits. Digit II is advanced with respect to digit I, whereas digit III is the most extended anteriorly. Digit IV is as extended as digit II.

Discussion and remarks

The trackway is apparently bipedal. However, the absence of *manus* traces might be interpreted as a preservational artefact, and a quadrupedal trackmaker cannot be excluded.

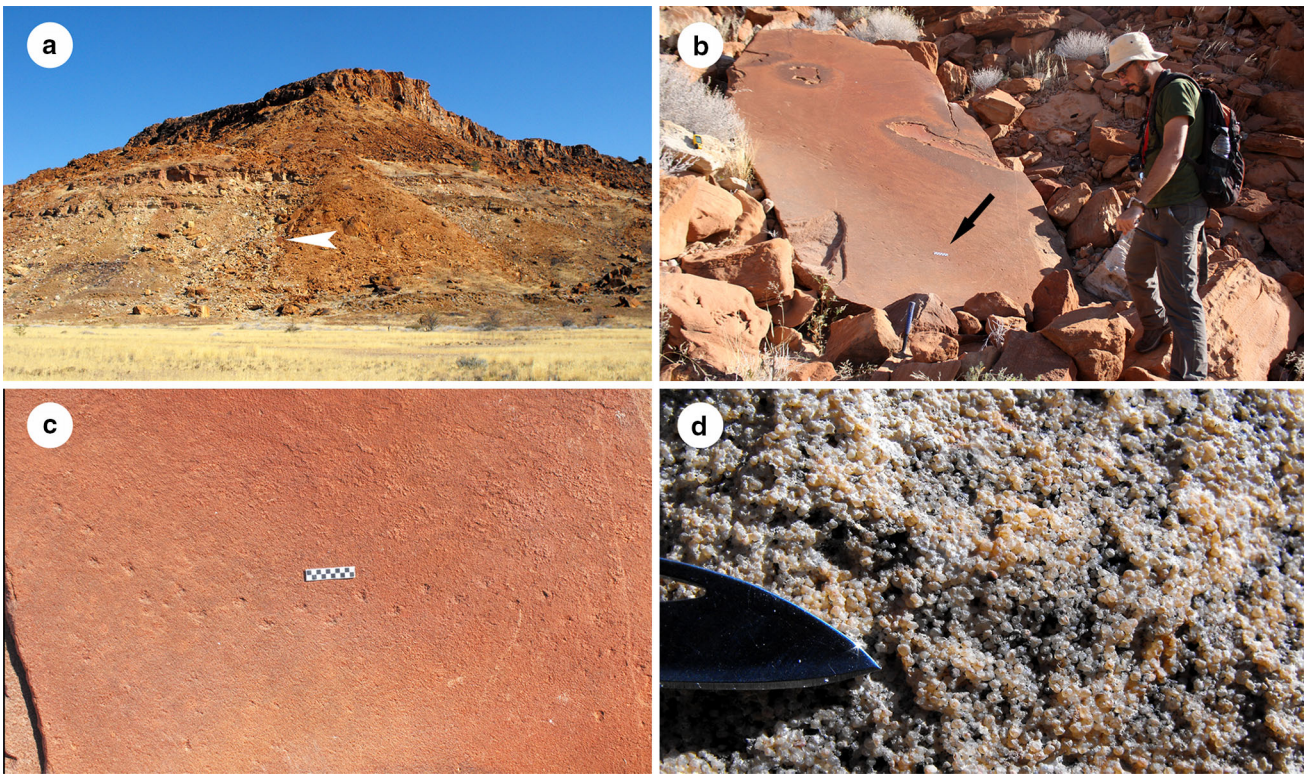

Fig. 3 **a** Position of the footprint–bearing block along the scree on the northern side of the hill (*white arrow*). **b** The footprint–bearing boulder, with the trackway running on its downslope portion, below the *black arrow* (*scale bar* 10 cm). **c** Close–up of the vertebrate trackway (*scale bar* 10 cm). **d** "Millet seed" sandstone, typical of the Main Eolian Unit, (blade maximum height is 1 cm)

The trackway width and pace angulation are in fact not consistent with a bipedal gait. The trackmaker was probably a quadruped, even if only marks of the *pes* are preserved. This might be due to erosion of existing *manus* prints, which may have penetrated the sand to a lower depth relative to the *pes* (see Loope 2006) or, alternatively, it might be a genuine absence, in the sense that the *manus* exerted load forces below the threshold for deforming the sediment. The absence of *manus* prints in several, if not most, of the trackways referred to *Brasilichnium* has been also interpreted as the result of overstepping (*pes* walking over *manus* traces) (Leonardi 1981). However, extensive revision of a large number of specimens (convex hyporeliefs and concave epireliefs) did not reveal any feature (i.e., partial preservation of a *manus* trace) helpful to support this statement. Results of this revision will be discussed elsewhere.

The features observed on the Twyfelfontein material suggest a direct comparison with a specific ichnotaxon typical of desert environments, *Brasilichnium elusivum* Leonardi 1981 (Fig. 4c, d).

We consider the Twyfelfontein material as cf. *Brasilichnium*, for the following reasons: both have tetradactyl *pes* prints (Fernandes and Carvalho 2008; Lockley 2011), and digit marks that are arranged in a very similar pattern; although quadrupedal, *Brasilichnium* is commonly made by *pes*–only sequences (Leonardi and Oliveira 1990; Fernandes and Carvalho 2008; Lockley 2011). Finally, both are found on the lee side of dunes in hyper-arid environments, usually ergs, even if this is not an inherent feature of the footprint itself.

Nonetheless, the Namibian material shows some characteristics different from the common Brazilian morphotype of *Brasilichnium*. *Brasilichnium elusivum* shows different gaits (i.e., walk, gallop, ricochet) and variability in trackway parameters (stride, pace angulation, *pes* rotation, etc.) inside each specific gait. Although pace values reported for *Brasilichnium* are usually small, some trackways show higher values, much closer to those observed on the Twyfelfontein trackway.

Brazilian *Brasilichnium* usually shows a neat expulsion rim, which is here identified as a pressure pad, according to the nomenclature proposed by Fornós et al. (Fornós et al. 2002). Even if pressure pads are not necessarily associated with *Brasilichnium*, and this structure does not represent any anatomical feature of the trackmaker's foot, it is nevertheless a "typical" extramorphologic mark for this ichnogenus. The position and shape of the pressure pads vary depending on the orientation of the *Brasilichnium* (e.g., uphill, downhill). The inclination of the substrate on

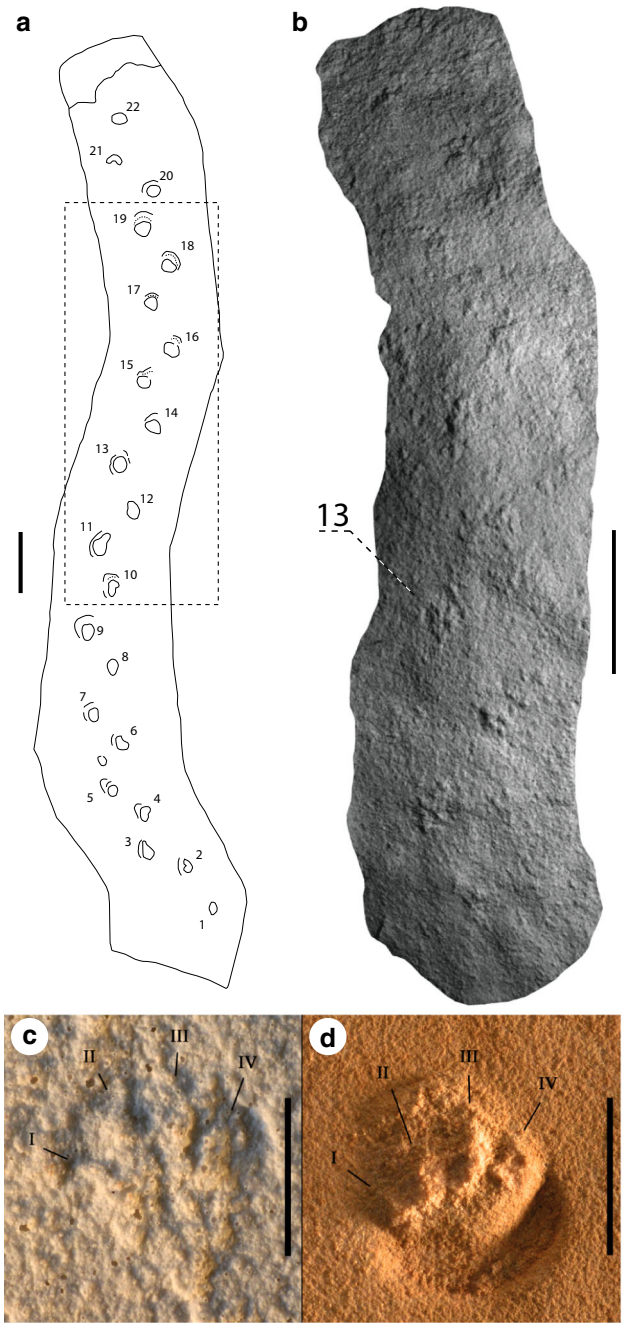

Fig. 4 **a** Map of the entire trackway (*scale bar* 10 cm). **b** 3D photograph of a portion of the trackway (from footprint *10 to 19*, see *dotted box on A*). **c** Close up of footprint 13 (*scale bar* 2 cm) and **d** of *Brasilichnium elusivum* from slab URCM.41, Museu de Paleontologia e Estratigrafia, "Prof. Dr. Paulo Milton Barbosa Landim", Rio Claro Campus, Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP), São Paolo State, Brazil. (Courtesy of Prof. Reinaldo J. Bertini)

which the animal moved is an extremely influential factor, as the steepness might influence the angle of impact of the trackmaker's foot onto the sediment, and, consequently, the final shape of the footprint. It is suggested here that minor morphological differences between the Twyfelfontein trackway and the classic *Brasilichnium* from Brazil may be a consequence of different inclination of the original surface. For the African material the angle might have been quite low.

The Twyfelfontein material is, therefore, provisionally labelled as cf. *Brasilichnium*, until more abundant and better preserved material helps to refine or change this attribution.

Brasilichnium has apparently an extensive stratigraphic distribution, having been reported from Upper Triassic (Apachean, Redonda Formation, Lucas et al. 2010) to Lower Cretaceous units. *Brasilichnium* was first described from the Botucatu Formation (Paraná Basin, Brazil) by Leonardi (1977, 1981), and successively reported from several localities in and outside Brazil (Leonardi 1980, 1981, 1984; Leonardi and Sarjeant 1986; Leonardi and Oliveira 1990; Leonardi and Carvalho 2002). The age of *Brasilichnium* in South America is problematic, as it is found in rocks originally considered as Lower to Middle Jurassic by Leonardi and Oliveira (1990). A Late Jurassic age has been inferred for the Botucatu Formation by Bonaparte (1996) on the basis of the ichnologic content. A similar age was suggested by Soares et al. (2009), with only the highest portion of the Botucatu Formation being Cretaceous in age.

Scherer (2000, 2002) proposed an Early Cretaceous age for the Botucatu Formation based on the assumption that the Botucatu desert was still active at the time of the Serra Geral lava extrusion. Recent paleomagnetic dating of the Botucatu Formation in Rio Grande do Sul outcrops (Southern Brazil) confirmed a Lower Cretaceous age for this unit (Tamrat and Ernesto 2006). In any case, the debate on the age of the Botucatu Formation, especially in the São Paulo region, is not concluded, and more definite dating seems to be necessary.

Abundant material from North America has been ascribed to *Brasilichnium*. The occurrences, at least those unequivocally referring to this ichnotaxon, are from the Navajo Sandstone and the Aztec Sandstone, late Early Jurassic in age (Lockley 2011; Rowland and Mercadante 2014). Other material, originally allocated under different ichnotaxonomic labels (e.g., *Bipedopus* and *Semibipedopus*) is now considered a preservational variation, and, therefore, a synonym of *Brasilichnium* (Lockley 2011).

On the other hand, the zoological attribution of *Brasilichnium* is stable, as it is usually considered the *repichnia* of a "mammaloid", possibly a tritylodontid therapsid (Leonardi 1980, 1981, 1984; Leonardi and Sarjeant 1986; Leonardi and Oliveira 1990; Leonardi and Carvalho 2002; Fernandes and Carvalho 2008; Lockley 2011; Rowland and Mercadante 2014).

Table 1 Measurements of the new trackway from the Twyfelfontein Formation, Huab Basin, Namibia

Footprint no.	F. length	F. width	Pace	Value	Stride	Value
1	24	15	2–3	70	2–4	122
2	24	15	3–4	76	4–6	124
3	22	16	4–5	70	6–8	127
4	23	15	5–6	81	8–10	127
5	20	14	6–7	66	10–12	127
6	24	20	7–8	86	12–14	135
7	23	16	8–9	68	14–16	127
8	27	17	9–10	84	16–18	129
9	32	18	10–11	69	18–20	123
10	27	17	11–12	79	20–22	127
11	38	24	12–13	72	3–5	131
12	28	20	13–14	80	5–7	129
13	24	20	14–15	71	7–9	135
14	21	21	15–16	68	9–11	140
15	n/a	n/a	16–17	74	11–13	133
16	24	n/a	17–18	67	13–15	137
17	20	20	18–19	71	15–17	123
18	20	21	19–20	64	17—19	120
19	26	21	20–21	77	19–21	118
20	18	20	21–22	68		
21	19	25				
22	n/a	22				
Standard deviation	4708	3133		6278		5915

All measurements are in millimetres

Although Mesozoic footprints referred to synapsids are known from the African continent, most of them have uncertain ichnotaxonic status, having been named, but not always described, by Paul Ellenberger in a series of different publications on the ichnofauna of Lesotho (1972, 1975). A re–evaluation of some of these ichnotaxa (Lockley et al. 2004) did not refer any of the Ellenberger ichnites to *Brasilichnium*. Moreover, the age of the Elliot and Clarens Formation, which yielded most of the African material, is older than the purported age of the Twyfelfontein Formation. Lower Cretaceous mammaliamorph tracks have been recently reported from a diamond mine in Angola, and referred to as *Ameghinichnus* (Marzola et al. 2014).

To our knowledge, ichnites ascribed to *Brasilichnium* are not known to be from Africa. The Twyfelfontein material is, therefore, the first potential occurrence of *Brasilichnium* from this continent.

Conclusions

This is the first record of vertebrate life obtained from the Twyfelfontein Formation. The scarcity of fossil footprints in this paleoenvironment might be well explained by invoking taphonomic bias, but, at the same time, it is well understood that erg biotas are usually depauperate in terms of species richness and show shortened food webs (Ward 2009). The possible presence of *Brasilichnium* in this environment would be in line with previous discoveries in very similar environments, and seems to point to a consistent association between this ichnotaxon and erg deposits.

Before the discovery of the material from the Twyfelfontein Formation, *Brasilichnium* was apparently restricted to the American continents. This material is possibly a further constraint to the link between the Brazilian Botucatu Formation and the African Twyfelfontein Formation. There would be reasonable paleogeographic conditions to favour such an occurrence, as the Twyfelfontein Formation is interpreted as the African extension of the huge Brazilian Botucatu erg (Bigarella 1970; Zalan et al. 1991), which probably supplied most of the sand for the Twyfelfontein sand sea (Dingle 1992).

Acknowledgments Dr. Nigel P. Mountney (University of Leeds) is greatly acknowledged for sharing with us information on the Twyfelfontein Formation. We would like to express our gratitude to Helke G. Mocke (Geological Survey of Namibia) for her constant help and assistance. Donovan Wagner is acknowledged for supplying logistic support during fieldworks. We are indebted to Prof. Reinaldo

J. Bertini (UNESP Rio Claro) for allowing us to access the collection of Botucatu slabs under his care. Spencer G. Lucas (New Mexico Museum of Natural History, Albuquerque) and David J. Loope (University of Nebraska, Lincoln) are kindly acknowledged for improving the final quality of the manuscript with their comments and suggestions. D'Orazi Porchetti's research is supported by a Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) post–doctoral grant (Process Number 2013/01930–1).

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