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SHORT COMMUNICATION

Theagarten Lingham-Soliar · Tim Broderick ·
Ali Ait Kaci Ahmed

Closely associated theropod trackways from the Jurassic of Zimbabwe

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Abstract Eighty-eight tracks of large theropod dinosaurs were found in the mid-Jurassic of Zimbabwe. Among the tracks, at least five adjacent trackways are recorded. The adjacent tracks were probably made by animals traveling as a group, given that they are in relatively close succession; that there are three overlapping tracks (among just 23) suggesting reasonably close associations of the animals; that all the tracks are apparently of the same ichnotaxon; that the preservational types of the tracks are similar; and that the tracks are all of animals traveling in one general direction closely associated in time (there are no returning tracks of the same animals or of those of other species; presence of such tracks would be highly probable if the tracks were made over a period of time of even several hours). Nearby, recently discovered giant sauropod tracks, the first in sub-Saharan Africa, indicate a realistic potential of predator/prey interactions between the two groups of dinosaurs.

Introduction

Four new Mid-Late Jurassic dinosaur track sites were recently discovered in the Ntumbe area, Zimbabwe. They occupy an area no more than 400 m long by 150 m wide in micaceous sandstone beds closely related in time. The location is about 400–500 m northwest of the first trackway found (site 1; e.g. Broderick 1985) and falls on the Kachowe 1/50,000 scale toposheet (1629 B2), 30°00′E and 16°10′S. Ninety-four footprints were found in total, 88 of large theropod dinosaurs and 6 of large sauropods.

The present report concentrates on one of the four new sites (site 5) occupying an area 0.6 km^2. It contains 45 tracks of a large theropod dinosaur taxon (Figs. 1, 2) and includes at least 5 closely associated trackways. Track sites 2 and 4 contain 43 similar theropod tracks. Site 3 contains 6 sauropod tracks.

The sauropod footprints (Ait-Kaci Ahmed and Mukandi 2001), the first found in sub-Saharan Africa, are mentioned briefly in terms of the paleobiology of the region.

Geology

The Ntumbe trackway locality lies within strata of the post-Karoo Dande Sandstone Formation (Fig. 2d), the beds of which are correlative to those of the Kadzi area (Raath and McIntosh 1987). A recent study (Ait-Kaci Ahmed and Mukandi 2001) indicates that the Ntumbe strata has a Middle to Upper Jurassic affinity as opposed to Early Jurassic (Lingham-Soliar and Broderick 2000). More detailed geology is presented by Ait-Kaci Ahmed and Mukandi (2001 and references therein).

The sedimentary sub-environment of the Ntumbe dinosaur tracks

Oesterlen and Millsteed (1994) note the development of bituminous mudstones that indicate a shallow-water lake (or quiet overbank) sub-environment where crusts of gypsum and possibly halite reflect periodic aridity. Ripple marks and desiccation features on alternate beds, and sometimes on the same bed, show that periodic precipitation occurred in this semi-arid to arid environment (Collinson 1986). The dinosaur footprints were preserved in an overbank adjacent to the river channel in which

T. Lingham-Soliar (✉)
Department of Zoology,
University of Durban-Westville,
Private Bag X54001, 4000 Durban, Kwazulu-Natal, South Africa
e-mail: lsoliar@pixie.udw.ac.za
Fax: +27-31-2044790

T. Broderick
Makari, 19 Jenkinson Road, Chisipite, Harare, Zimbabwe

A. Ait Kaci Ahmed
Geological Survey of Zimbabwe,
The Causeway, Harare, Zimbabwe

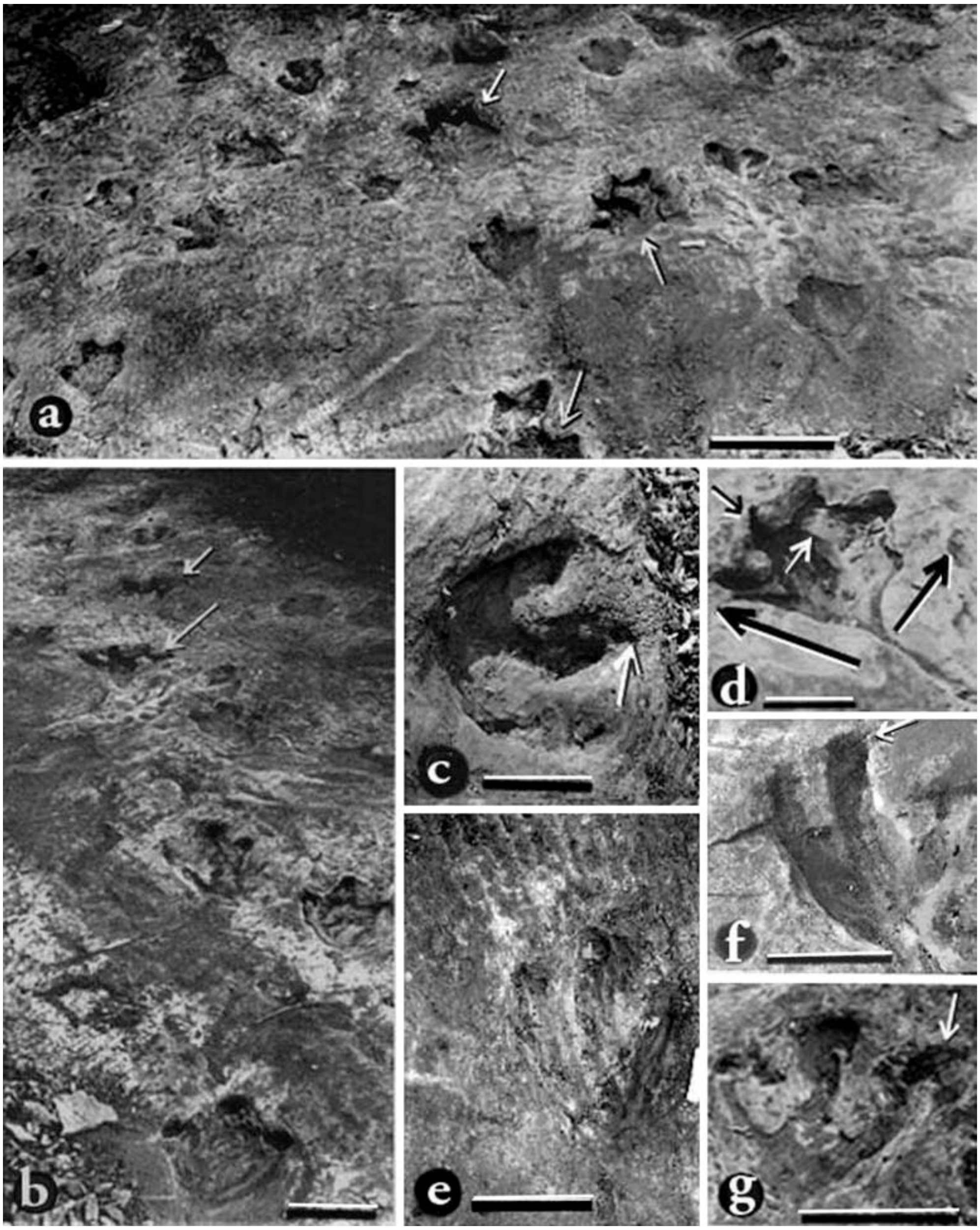

Fig. 1a–g Jurassic theropod trackways in Zimbabwe. **a** A number of trackways cross the dry river bed (*white arrows* show three double tracks. **b** The longest series of nine footprints (track I) extends parallel to the river bed before turning into the right bank. **c** Detail of one of the tracks (R; *arrow* shows claw). **d** Detail of the best double track showing different depths of the two tracks (*white arrow*); sediment collapse of both digit IIIs (*top, left and right*); long metatarsal impression (narrow because of angle of photo, see Fig. 2); *small black arrow* shows curved claw; *large black arrows* indicate direction of tracks. **e** Track (L) to the east–northeast of site (see Fig. 2) on ripple bed, photographed directly overhead. **f** One of the well-preserved tracks west–northwest in a narrow strip (see text and Fig. 2b); *white arrow* shows distinctive slender claw; digit pads are evident including skin creases. **g** Detail of a track (L) photographed from about 1 m behind, hence somewhat compressed lengthwise (*arrow* shows large claw on digit II that apparently curved under the digit). *L* left track; *R* right track. Scale in **a** 50 cm, in all others 25 cm

sediment accumulated during flooding. Presence of choncostracans (Lingham-Soliar and Broderick 2000) suggests ephemeral water bodies (Tasch 1984). The footprints are preserved in a rapidly drying silty sand (indicated by desiccation cracks and ripples) and infilled by a softer, more erodible muddy sediment. Theropod tracks are also found extensively elsewhere in the Ntumbe environment, on different bedding planes, indicating the presence of predaceous dinosaurs over a period of several thousand years.

Morphological description

Forty-five large theropod dinosaur tracks are preserved in site 5, 37 of which occur in an area 15 m long by 3 m wide (Figs. 1a, 2a). The remaining 8 tracks occur west–northwest in a long adjacent narrow strip (one is shown in Figs. 1f, 2b). All tracks are oriented in the same general direction (N to NW). Over half of these footprints form five trackways (Figs. 1a, 2a). The longest trackway (I) consists of nine footprints (Table 1), which extend roughly parallel to the tributary bed before they turn and converge with the other trackways crossing the bed. Because of the shortness of the other trackways, trackway I is the only one in which pace, stride, and pace angulation were measured. All the tracks disappear under

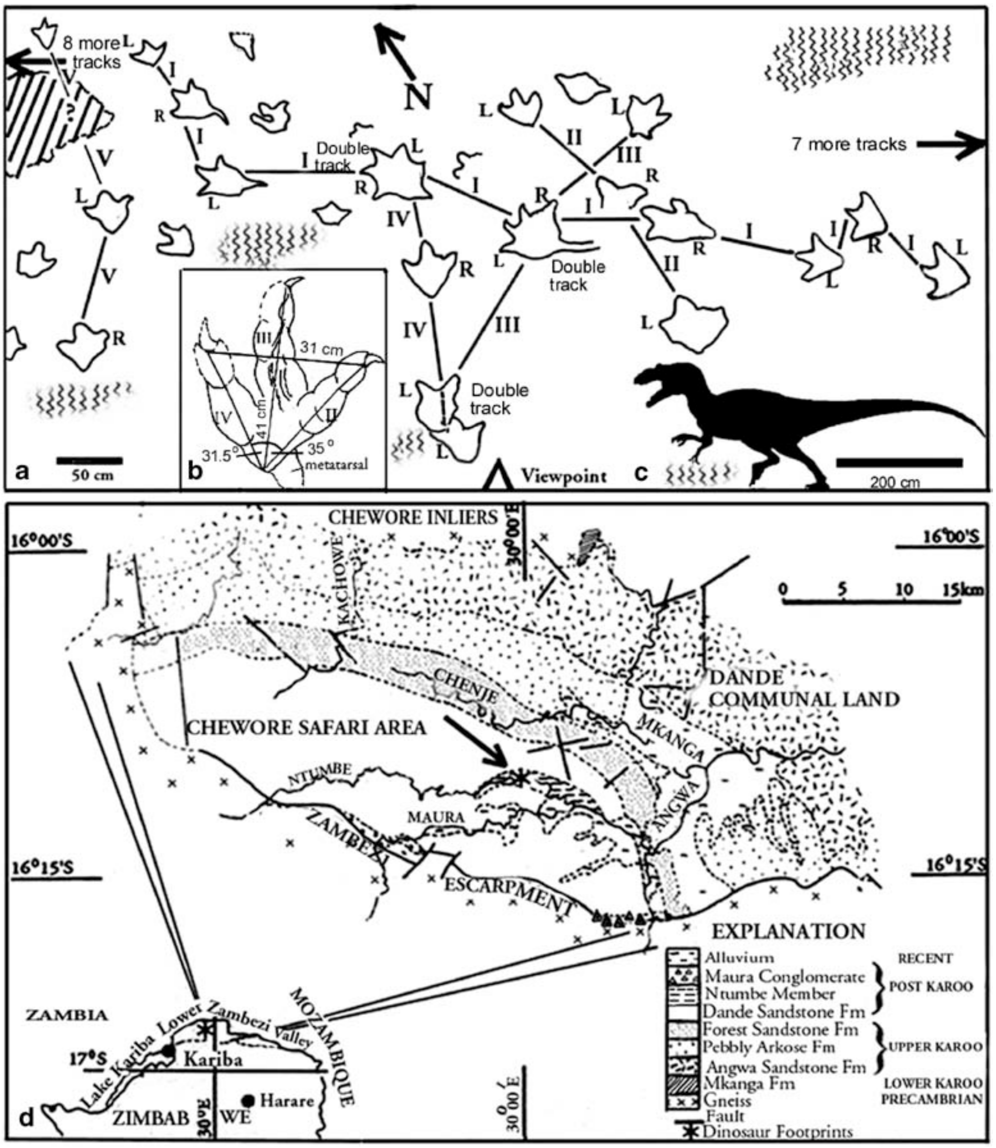

Fig. 2a–d The main area of site 5 containing 30 tracks (based on tracing of a detailed photo). **a** Five trackways are identified (I–V). The *hatched area* to the left represents a lower bed. *Zig-zag patterns* are a schematic representation of some areas in which ripples are preserved within the track site. Three of the double tracks are indicated. **b** Tracing of Fig. 1f, with foot structure and dimensions. **c** Silhouette of a large theropod trackmaker with suggested posture (ca. 3 m tall). **d** Map and stratigraphic log of the Chewore area of Zimbabwe

overlying strata exposed in the banks on either side of the narrow tributary bed. Several features of the tracks show with reasonable certainty that they belong to theropods: (1) they are tridactyl and significantly longer than wide (ratio of foot length:foot width is 4:3); (2) distinctive curved claws are present on a number of tracks; (3) they have tapering digits (Figs. 1f, 2b) and (4) curvature of digits II and III; (5) there is a narrow gauge of the trackways, that is, right–left bipedal progression along a narrow midline. Further supportive evidence exists: (6) a tracing (Fig. 2b) of one of the best-preserved tracks (Fig. 1f) graphically depicts theropod track characteristics, and (7) the Ntumbe trackway (site 1), which is similar to the present trackways, was interpreted as being made by a theropod in two separate studies (Broderick 1985; Munyikwa 1996).

Tracks are on average 5 cm deep in the anterior toe region, about a third deeper than in the posterior part of the foot (excluding the metatarsal impression), and most show a strong medial curvature and angulation of digits II and III, suggesting a species trait. Figure 2c shows the suggested walking posture and average size of the dinosaur (adjacent scale).

Long slip marks associated with metatarsal impressions (Figs. 1d, 2a) and short and blunt digit impressions in some tracks (see, for example, Fig. 1d), presumably a consequence of sediment collapse or backflow (Kuban 1989; Brenchley and Harper 1998), suggest that the tracks were made in soft sediment. The blunt digit impressions are not primary conditions since elongated toe and/or claw impressions (e.g. Fig. 1e, f) are seen elsewhere in the same sequence of tracks. This emphasizes the important role played by local variations in the physical properties of the substrate and by the dynamic interaction between foot and substrate (Thulborn and Wade 1979).

Four sets of double imprints, that is, pairs of overlapping tracks, were recorded in the site. Three of the double imprints occur in trackways I, III, and IV (Figs. 1a, 2a). A

Table 1 Trackway I, nine consecutive footprints. The average depth anteriorly is 5 cm and posteriorly about a third less. Stride and pace measurements were taken from tip of digit III to tip of digit III of succeeding tracks

Trackway I	Measurement
Pace (cm)	
1 to 2	125
2 to 3	60
3 to 4	119
4 to 5	92
5 to 6	117
6 to 7	118
7 to 8	115
8 to 9	103
Stride (cm)	
1 to 3	180
2 to 4	160
3 to 5	189
4 to 6	197
5 to 7	230
6 to 8	212
7 to 9	210
Pace angle (degrees)	
1 to 3	122
2 to 4	138
3 to 5	147
4 to 6	148
5 to 7	155
6 to 8	128
7 to 9	178
Track width (cm)	
1 to 3	36
2 to 4	64
3 to 5	48
4 to 6	68
5 to 7	88
6 to 8	48
7 to 9	60

Table 2 Measurements of best preserved tracks in each trackway. Length was taken from tip of digit III to heel, width across the base of claw of digit II to digit IV (see Fig. 2b)

Footprint track	Trackway				
	1	2	3	4	5
Length (cm)	47	43	42	40	41
Width (cm)	36	34	30	32	32

fourth double track imprint (not shown) occurs about 3 m to the southeast of those shown. Two of the double tracks in trackways I and III and trackways I and IV (Figs. 1a, 2a) show the successive track distinctly cut within the preceding track and deeper (see Fig. 1d, white arrow).

For the large theropods we use the measurement of 4. 5×foot length to calculate hip height (Alexander 1976; Thulborn 1990). The greatest hip height was 211.5 cm. The footprints averaged about 40 cm long (Table 2), giving an average hip height of about 180 cm. An estimated average speed of 4–5 km h^{-1} was derived from trackway I (Table 1).

Discussion

Locomotion and inferences on group behavior

Day et al. (2002) described a trackway showing theropod gait switching from wide to narrow gauges with increased speed. Locomotory features are also noted in our trackway 1 (Table 1), where a sudden widening of tracks 2–3 indicates a pause, and of tracks 7–8 a sudden veering of the dinosaur to the right (Fig. 2a).

Multiple trackways of a large theropod dinosaur taxon in a relatively small area suggest gregarious behavior (cf. Ostrom 1972, 1986), a relatively infrequent observation and consequently important for its potential in furthering our understanding of theropod behavior. However, establishing the contemporaneity of the trackways, that they were made almost simultaneously or within minutes of one another, is difficult and subject to varying interpretations (e.g. Lark Quarry tracks; Thulborn and Wade 1979). A reasonable hypothesis invariably depends on support from a number of coinciding factors. We propose the following points in support of our view that the prints were closely connected in time:

1. All the footprints belong to large theropods of apparently a single species.
2. In a rapid-drying environment the substrate should, in our view, show footprints of different preservational types, for example, if they were laid down with longer time intervals separating them. This is apparently not the case since most of the tracks have remarkably similar shapes and depths. It is pertinent too that the tracks forming double imprints are equally sharply defined (Figs. 1d, 2a). This is unlikely were there a significant time interval between the first and second imprints since desiccation, for example, would likely result in differences in track quality as a consequence of destruction of the earlier-formed track by the later. On the contrary, the track of trackmaker I cuts precisely into that of the preceding trackmaker III, cutting deeper but with little interference to the latter (see Fig. 1d).
3. Tracks are aligned in one general direction, that is, there are no returning or random tracks or those of other species. The most parsimonious explanation is that individuals of the same taxon made the tracks within a relatively short space of time.
4. Three sets of double imprints in a relatively small number of tracks suggest animals traveling in relatively close association.

Crossing over of the trackways, as opposed to the side by side alignment of sauropod (herbivore) trackways, is considered reasonable and inevitable in predatory pack-hunting animals (personal observation of wolves in northern Europe and numerous carnivores in Africa), in which hierarchies (e.g. in wolves denoted by alpha, beta, and omega males/females) prompt 'safe' distances being maintained between pack members.

Paleobiology

The first sub-Saharan sauropod tracks are also the first of a large herbivorous dinosaur that can be associated with the Ntumbe theropod dinosaurs in both time and space. The present dinosaur associations in Zimbabwe are interesting in the context of the African dinosaur fauna. *Brachiosaurus* was first discovered in Africa in Tendaguru, Tanzania (e.g. see Fastovsky and Weishampel 1996) although there was no record of association with large theropods, in contrast to the theropod/sauropod associations of the Morrison Formation in the United States (Prince and Lockley 1989). Thus the Ntumbe region in Zimbabwe, as with the Morrison Formation, speaks to a theropod fauna with associated giant sauropods.

If large theropods did cooperate in feeding on the gigantic sauropods (see Gurche and Miller 1989; Farlow 1993; Farlow and Brett-Surman 1997; Thomas and Farlow 1997), then based on such studies, group interaction (predatory unions) among the Ntumbe theropods would seem consistent.

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