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Early Evidence for Complex Social Structure in Proboscidea from a Late Miocene Trackway Site in the United Arab Emirates

Authorship

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• Site Description and Discovery

The site of Mleisa 1, located at 23.948N, 53.061E, is today a flat plain with extensive aerial exposure of multiple carbonate levels. A single level of these preserves fossil vertebrate trackways that in total comprise over 1500 footprints over an area of 50 hectares (ESM Figs. 1–2). Fossil trackway sites in the Al Gharbia region have been long known to local Emiratis, and were taken to be the prints of dinosaurs or giant men of ancient myth. In April 2001, Mubarak bin Rashid Al Mansouri led staff of the Abu Dhabi Islands Archaeological Survey to footprint sites in the Niqa and Mleisa areas [1]. A second visit in February 2003 included present author M.B. and allowed for further assessment of the Mleisa 1 trackway site [2]. The site was subsequently visited in successive years by teams led by F.B., A.H., and M.B., but it was not until January 2011, with the production of the kite aerial orthophotomosaic by N.C., that the extent and distribution of the trackways could be properly visualised and analysed. The full resolution orthophotomosaic is permanently archived and viewable at <http://gigapan.org/gigapans/78542> .

• Straigraphic and Sedimentological Context

The Baynunah Formation is a sequence of predominantly fluvial sands and silts exposed over a wide area of the Al Gharbia region of the United Arab Emirates. Coarse sands and conglomerates mostly from the lower half of the Baynunah Formation have produced diverse vertebrate, invertebrate, and plant fossils [3]. The upper parts of the Baynunah Formation comprises sands and clays alternating with thin to thick ($\geq 2\text{m}$) white carbonate and carbonate-rich beds. About 20km inland, from the area of Mleisa to Umm al-Ushtan, these carbonate layers are widely exposed aerially, forming an extensive and fairly flat landscape that is highly reflective on satellite imagery. These exposures preserve footprints of

proboscideans and at least one type of medium-sized ungulate animal from at least four different sites. Among these is the site of Mleisa 1.

The Mleisa 1 fossil trackways are preserved in a single carbonate level (ESM Fig. 3). As is the case for the other levels (ie levels -1, +1 and +2 in ESM Fig. 2) this is made of a finely laminated carbonate that is silty to sandy, preserving gastropod moulds and small, non-marine ostracod shells. These laminated carbonates further display characteristic and distinctive desiccation polygons and cracks, as well as a bioturbated upper surface, all pointing to a microbial mat origin. Thus, the depositional environment is that of a wide, ephemeral, flat-bottomed, and very shallow water body that covered at least the area of the whole Mleisa 1 site and supported microbial mat growth.

Modern microbial mats are found in a wide range of watered environments, from marine to freshwater and saline. Comparisons to studies of footprints in modern microbial mats [4] suggest the Mleisa 1 trackway level microbial mat had begun superficial desiccation while water remained in the carbonate mud just below. In several places, the characteristic desiccated polygons can be seen to have been displaced by the track-making activity. Once dry and consolidated, modern microbial mats become too elastic or rigid to further register footprints, even for a heavy track-maker, and they are furthermore strongly resistant to re-humidification [4] at this point. Thus, the entire Mleisa 1 trackway level must have been imprinted in a relatively short time, being that between initial desiccation and full drying and consolidation of the microbial mat. Lithification would have followed quickly thereafter, fossilising the footprints and rendering the sediments impermeable to any further imprinting, as they remain today.

• **Chronological Context of Mleisa 1**

The Baynunah Formation has been assigned an age of between 8 and 6 Ma on the basis of several taxa linked to radiometrically dated sites in Africa and southern Asia. These include *Nyzanzachoerus syrticus*, *Propotamochoerus hysudricus* [5], *Stegotetralodon syrticus* [6], and *Diamantornis laini* [7]. The footprint sites are laterally correlated to the alternating carbonate beds of the upper parts of the Baynunah Formation, and accordingly are assigned to the same age range.

The Mleisa 1 carbonates are a stratigraphic and lithological match with those from coastal sites, comprising multiple carbonate layers alternating with sands and silts, and consistently producing a similar invertebrate microfauna. At the sites of Jebel Barakah and Umm al-Khabir, fossil remains typical of the Baynunah Formation have been found interbedded between successive carbonate beds, including eggshell of *Diamantornis laini*, hippopotamid and proboscidean tooth fragments, crocodile bones and crocodile-like coprolites, and shells of *Mutela* and *Leguminaia*. At Umm al-Khabir, 20km to the west of Mleisa 1, the fossil remains derive from sands and conglomerates just above a sandy carbonate-rich layer preserving proboscidean trackways in relief. Furthermore, the absence of any regionally extensive erosional contact within the Baynunah Formation, the absence of regional and local faulting in the Baynunah Formation, a practically negligible regional dip, and the continuation of similar lithologies and fossils into its upper half supports the relative contemporaneity of the entire formation. All stratigraphic, lithological, and fossil evidence therefore confidently places the Mleisa 1 trackway deposits within the late Miocene Baynunah Formation.

- **Identification of the Trackways and Number of Individuals**

Trackways are recognised based on the regular spacing of consistently-sized prints in a predictable and unchanging left-right pattern for stretches of several meters or more.

Walking elephants are known to place the hind foot into the same spot made by the forelimb of the same side, which effectively results in the creation of only two footprints for every movement of all four limbs [8]. This is the predominant pattern seen at Mleisa 1, and allowed us to assume walking speeds of 1.0 to 1.6 m/sec in performing the estimated body mass calculations. Occasional elongate or doubled prints reflecting slightly advanced or delayed hind foot contact appear to indicate changes in the animal's velocity [8], and these are much more common in the herd trackways than in that of the solitary individual. When doubled prints were encountered, these were measured to the print providing the stride length most consistent with that of contiguous sections of the trackway.

None of the prints preserves clear details of foot morphology, presumably because of the elastic, fibrous, and muddy nature of the original substrate, in addition to possible microbial mat regrowth after the prints were made [4]. In the absence of features such as foot outlines or ungual impressions, the actual direction of movement of the track-makers was not evident. Furthermore, detailed examination of the prints could not conclusively reveal the temporal sequence of events, i.e. whether the solitary individual crossed the Mleisa 1 paleo-landscape before or after the group had already done so, though apparent perturbations in the directionality and stride lengths of the herd in the vicinity of the solitary trackway suggest the latter may have already been in place when the herd traversed the area.

To provide a count of individuals and to guide measurement and analysis, the herd trackway was divided among four sampling areas A–D. On the aerial photomosaic, transects more-or-less perpendicular to the main herd axis allowed the determination of the minimum number of individuals represented in each area. Trackways were taken to represent different

individuals if they could be counted along the transect or if their location clearly indicated they represented an individual that had not yet been counted. Certain trackways could be recognised as representing unique individuals but were not adequately preserved to permit measurement. The minimum number of individuals counted / measured in each area are: A: 13/10, B: 11/11, C: 9/9, D: 10/9.

In calculating the minimum measurable number of individuals for the total herd (manuscript Fig. 2B), we selected the minimum number of measurable individuals from area A (n=10), plus that of trackway section 32 as it is clearly traceable lateral to area A, plus that of trackway section 18 as it represents a very small individual clearly distinguishable in size from all those in area A.

• **Imaging the Mleisa 1 Site**

Along the main concentration of tracks, a series of photographic targets was placed and measured to provide ground controls. Suspended in a downward looking gyro-stabilised mount, a Canon S90 camera was lifted by a Rokkaku kite. Using this equipment, parallel transects of overlapping (>30%) low-altitude vertical aerial photographs of the trackway site were captured. Photographs from this sortie were processed with the structure from motion photogrammetry application PhotoScan Professional to produce an image for measurement purposes. Lens distortion was estimated and corrected based on focal length and sensor size. On each individual image, reference points were established; between each image, reference points were matched. From these matches and the viewing parameters, the bundle adjustment was solved, and this provided an estimation of camera orientations and overall scene structure. Using PhotoScan's height field routine, the surface geometry of the site was computed. The scale of this reconstructed surface was established from the measured ground

controls visible in the photographs, and an orthographically corrected photomosaic was produced.

• **Trackway Measurement**

Trackway stride lengths were measured digitally in Adobe Photoshop from the orthographically corrected photomosaic. The length of Trackway T1 as measured with tape in the field was used for scale. Stride and total track lengths taken in the field for measured trackway sections 1–16 were used to assess the accuracy of the digitally-derived measurements from the photomosaic. Total measured track section lengths averaged 2.23% (SD = 1.54%) difference between field and digital measurements; stride length data averaged 3.72% (SD = 2.45%) difference between field and digital measurements (i.e. well under an average 5% error).

Since none of the footprints preserves clear detailed foot morphology all measurements were taken from and to the centre of each footprint as this was determined to be the most reliably retrievable point. Trackway strides were measured from the centre-point of a footprint to the centre-point of the next footprint of the same body side.

• **Body Mass Estimation**

Body mass estimates using the mean $\pm 95\%$ stride lengths of each trackway were calculated using a regression of body mass against stride length in 189 measurements of African and Asian elephants walking at speeds of 1.0 to 1.6 m/sec (dataset kindly provided by J. Hutchinson). This dataset is comprised of both African and Asian elephants, including juveniles to adults, and both males and females. Among adult individuals, the dataset is

biased towards females with only one adult male represented. The resulting regression formula is as follows:

$$\ln(m) = 5.100075 + 3.0513 * \ln(s)$$

$$\text{whereby: } m = 164.03s^{3.0513}$$

and where m is body mass in kilograms and s is trackway stride length in meters ($R^2=0.77$). Calculations were performed in the application JMP 8 (SAS Institute Inc.).

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ESM TABLE 1

Stride lengths (in cm) of the trackways measured. Areas and trackway numbers follow manuscript Fig. 1 (and ESM Fig. 2). Measurements are taken starting at the first labelled print in that image.

		Stride number														
Trac Area	Trac kway #	1-3	2-4	3-5	4-6	5-7	6-8	7-9	8-10	9-11	10-1 2	11-1 3	12-1 4	13-1 5	14-1 6	15-1 7
-	1	311	303	309	326	312	299	315	307	303	310	320				
-	2	324	330	313	304	318	292	324	348	322	305	310				
A	3	271	275	282	314	298										
A	4	247	235	231	270	248										
A	5	234	249	268	249	239	232	243								
A	6	260	231	233	240	217	239	245	244	227	239	268	265	247	271	284
A	7	237	262	278	263	241	235	237								
A	7b	212	217	219	275	280	256	262								
A	11	273	273	277	279	278	284	273	279	283	286	280				
A	13	283	297	287	281	276	274	281								
A	15	305	340	349	333	305	272	265	275	312	296	270				
A	16	248	240	249	239	234	247	226	242	267						
A	41	258	237	242	258	247	245	235								
B	9	237	239	228	242	232	231	233								
B	10	268	284	275	262	265	278	264	255	267	274	267				
B	14	229	241	261	269	266	275	235	186	188						
B	32	282	290	278	275	279										
B	33	258	259	257	242											
B	34	285	284	287	282	278	284	299								
B	35	247	250	249	270											
B	36	253	255	232	230	249	243	243	254	264						
B	37	268	260	253	259	262	258	249	269	311	295	278				
B	38	340	306	300												
B	39	249	242	261	244	242	253	256								
C	8	249	244	238	249	254	233	250	242	246						
C	17	237	234	255	256	236	244	254								
C	18	150	142	145	186	189	177	187	195	178						
C	19	315	300	307	325	303										
C	20	270	279	266	272	265	268	274	270	270	260	262				

C	21	204	221	225	222	228	200	207	215	213	224	213				
C	22	297	308	302	302	300	274	259	287	316	311	319				
C	23	252	228	261	258	252	245	244								
C	24	241	287	316	318	293	281	287								
D	12	248	238	240	238	249	244	241	244	241	231	224				
D	25	235	236	252	247	252	250	249	252	242	240	252				
D	26	252	244	237	251	254	277	295								
D	27	276	278	262	260	268	264	261	250	258	273	270				
D	28	304	296	287	311	328	300	317								
D	29	207	225	220	248	246	220	234								
D	30	236	227	243	241	241	252	240	240	243	249	244				
D	31	295	300	268												
D	40	285	302	304	290	291	295									

ESM FIGURE CAPTIONS

ESM Fig.1 The Mleisa 1 site kite aerial orthophotomosaic. The full resolution orthophotomosaic is permanently archived and viewable at <http://gigapan.org/gigapans/78542>

ESM Fig.2 The Mleisa 1 colour-coded site map.

ESM Fig.3 Local stratigraphy and sediments at Mleisa 1. **A.** Local stratigraphy as observed in the site surface and central yardang, and a view of the solitary trackway. **B.** View to the west showing the trackway level and trackways from within the herd. **C.** Close-up of one of the better-preserved prints in the herd.