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Early evidence for complex social structure in Proboscidea from a late Miocene trackway site in the United Arab Emirates

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Many living vertebrates exhibit complex social structures, evidence for the antiquity of which is limited to rare and exceptional fossil finds. Living elephants possess a characteristic social structure that is sex-segregated and multi-tiered, centred around a matriarchal family and solitary or loosely associated groups of adult males. Although the fossil record of Proboscidea is extensive, the origin and evolution of social structure in this clade is virtually unknown. Here, we present imagery and analyses of an extensive late Miocene fossil trackway site from the United Arab Emirates. The site of Mleisa 1 preserves exceptionally long trackways of a herd of at least 13 individuals of varying size transected by that of a single large individual, indicating the presence of both herding and solitary social modes. Trackway stride lengths and resulting body mass estimates indicate that the solitary individual was also the largest and therefore most likely a male. Sexual determination for the herd is equivocal, but the body size profile and number of individuals are commensurate with those of a modern elephant family unit. The Mleisa 1 trackways provide direct evidence for the antiquity of characteristic and complex social structure in Proboscidea.

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1. INTRODUCTION

Among living mammals, elephants are remarkable for their hierarchical and complex social behaviour. Living *Loxodonta* and *Elephas* species are matrilineal, forming stable matriarchal social units, termed families, consisting of related females and their offspring [1–3]. Male elephants are raised in the family unit until adolescence, after which point they separate to lead lives that are primarily solitary, re-uniting with female-led groups only intermittently, e.g. for mating [3–5]. Despite a rich fossil record [6], the origin and evolution of social structure in Proboscidea is virtually unknown. Herd structure and social behaviour have been previously inferred for both the extinct mastodon (*Mammuth*) and mammoth (*Mammuthus*) from Pleistocene mass-death assemblages and trackways [7–9], but little else is known about proboscidean behaviour prior to this time. Numerous trackway sites are known—as old as the early Miocene of Europe [10] and the middle Miocene of North America [11]—but none adequately records herd structure or social complexity. We here describe an exceptional trackway site from the United Arab Emirates that documents the movements of both a proboscidean herd and a solitary individual, demonstrating the presence of social complexity in Proboscidea of late Miocene age.

2. MATERIAL AND METHODS

Detailed methods and contextual information is provided in the electronic supplementary material. The site of Mleisa 1 is part of the Baynunah Formation, which has been biochronologically dated to between 8 and 6 Ma [12–14]. The site was imaged by kite aerial photography to produce an orthographically corrected photomosaic from which stride length measurements were taken. Body mass estimates were calculated using a regression of body mass against stride length in 189 measurements of African and Asian elephants (provided by J. Hutchinson). The full resolution orthophotomosaic is permanently archived and viewable at <http://gigapan.org/gigapans/78542>.

3. RESULTS

No less than 14 different trackways at Mleisa 1 are attributable to Proboscidea on the basis of the round shape and large size of the prints, coupled with very large trackway stride lengths (figure 1). All the Mleisa 1 trackways occur within a single carbonate level of microbial mat origin, indicating their relative contemporaneity. A solitary trackway (track 1 and 2 in figure 1b) extends over a distance of 260 m, making this one of the longest continuous fossil trackways in the world. The remaining proboscidean trackways are exposed over a distance of 190 m and are tightly grouped (20–30 m span), in sub-parallel alignment, and with little incidence of intersection or overlap, indicating simultaneous movement as a herd across the ancient landscape. Living elephants are known to create trails and regularly traverse these for rapid resource access [15], but the lack of overlapping and intersecting trackways indicates this was not the case at Mleisa 1. A count of non-overlapping trackways indicates a minimum number of 13 proboscidean individuals in the herd. The herd trackways show continuous small variations in directionality along their length, with more common occurrence of doubled prints that probably indicate

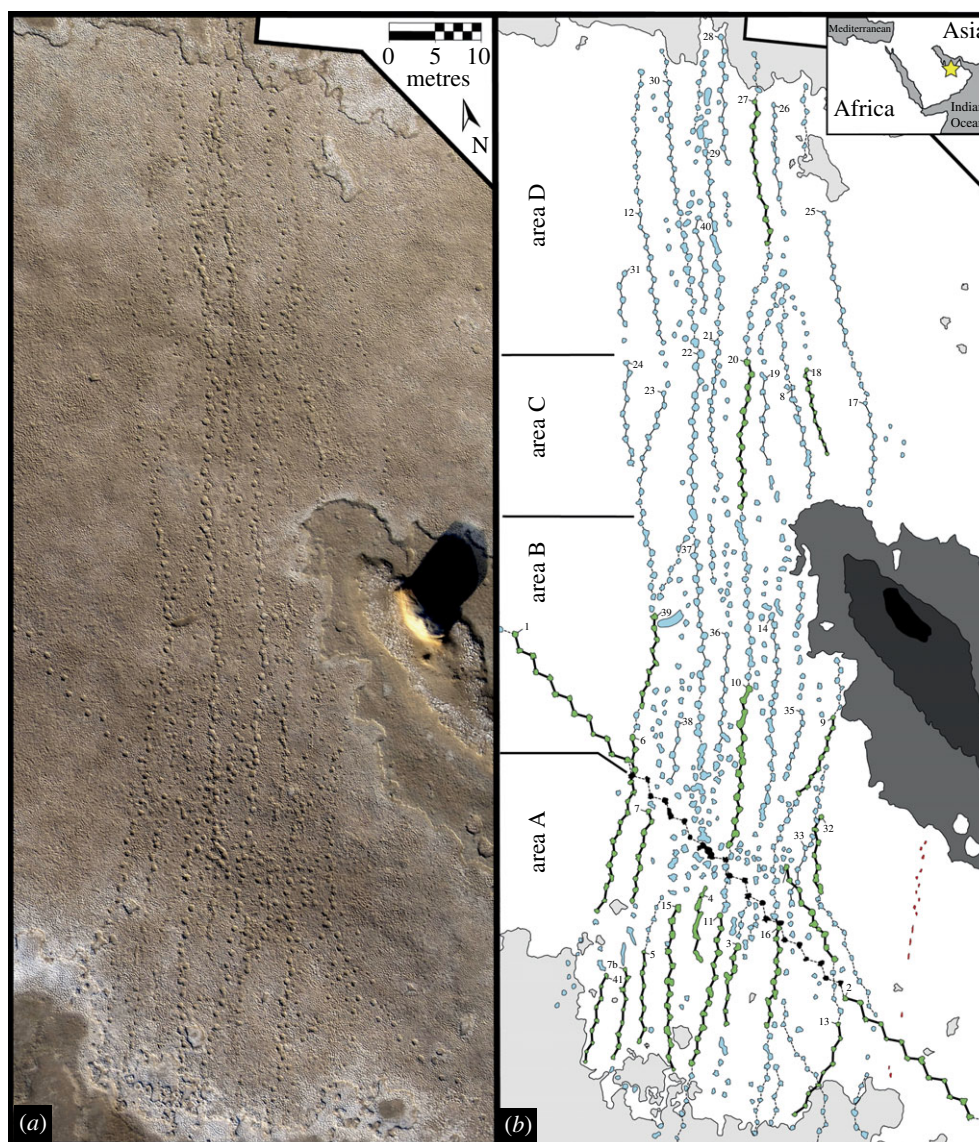


Figure 1. Close-up of the central portion of Mleisa 1. (a) The kite aerial orthophotomosaic. (b) Corresponding colour map of the trackways, with the prints forming each trackway connected by lines. Track sections that were measured and reported in figure 2a are connected by solid lines and numbered, with tracks sections in green indicating those used to calculate the minimum herd profile (figure 2b). Remaining proboscidean prints are shown in blue (herd) or black (solitary individual in the herd area). A single non-proboscidean trackway is shown in red. The full site aerial photograph and map are presented as electronic supplementary material.

minor changes in the makers' speed [16], as might be expected for a group that was moving and interacting simultaneously. In contrast, the solitary trackway is very straight along most of its length, with a more consistent and wider stride pattern which suggests its maker may have been walking at a slower and more steady speed. In this case, our estimate of the solitary individual's size relative to those of the herd may be underestimated.

Trackway stride lengths (figure 2a and electronic supplementary material, table S1) are relatively consistent within any given trackway. The solitary trackway records a large individual with a mean stride length of over 3 m. From within the herd, the size of the solitary trackway stride lengths is rivalled by those of at least a single individual. Among measured areas A–D, a consistent herd profile is recovered with the presence of 8–11 medium to large-sized individuals (figure 2a). Area C uniquely records the presence of a single small-sized individual (trackway 18 in figure 1b), the

prints of which are faint, perhaps on account of its lighter weight. Wide variation in stride lengths among measured trackways confirms the assertion that the trackways were made by many different individuals. The resulting body mass estimates lie within the total body mass range recorded for males and females of the living elephants *Elephas maximus* and *Loxodonta africana* [2,5,17,18] (figure 2b). However, body mass estimates for the largest individuals in the Mleisa herd are greater than the range recorded for adult females of *L. africana* and *E. maximus*.

4. DISCUSSION

The majority of mammalian species (including elephants) exhibit male-based natal dispersal [19,20], and in living elephants males tend to leave the group at sexual maturity, or around 14 years in age [4]. In living elephants, males are also consistently the larger

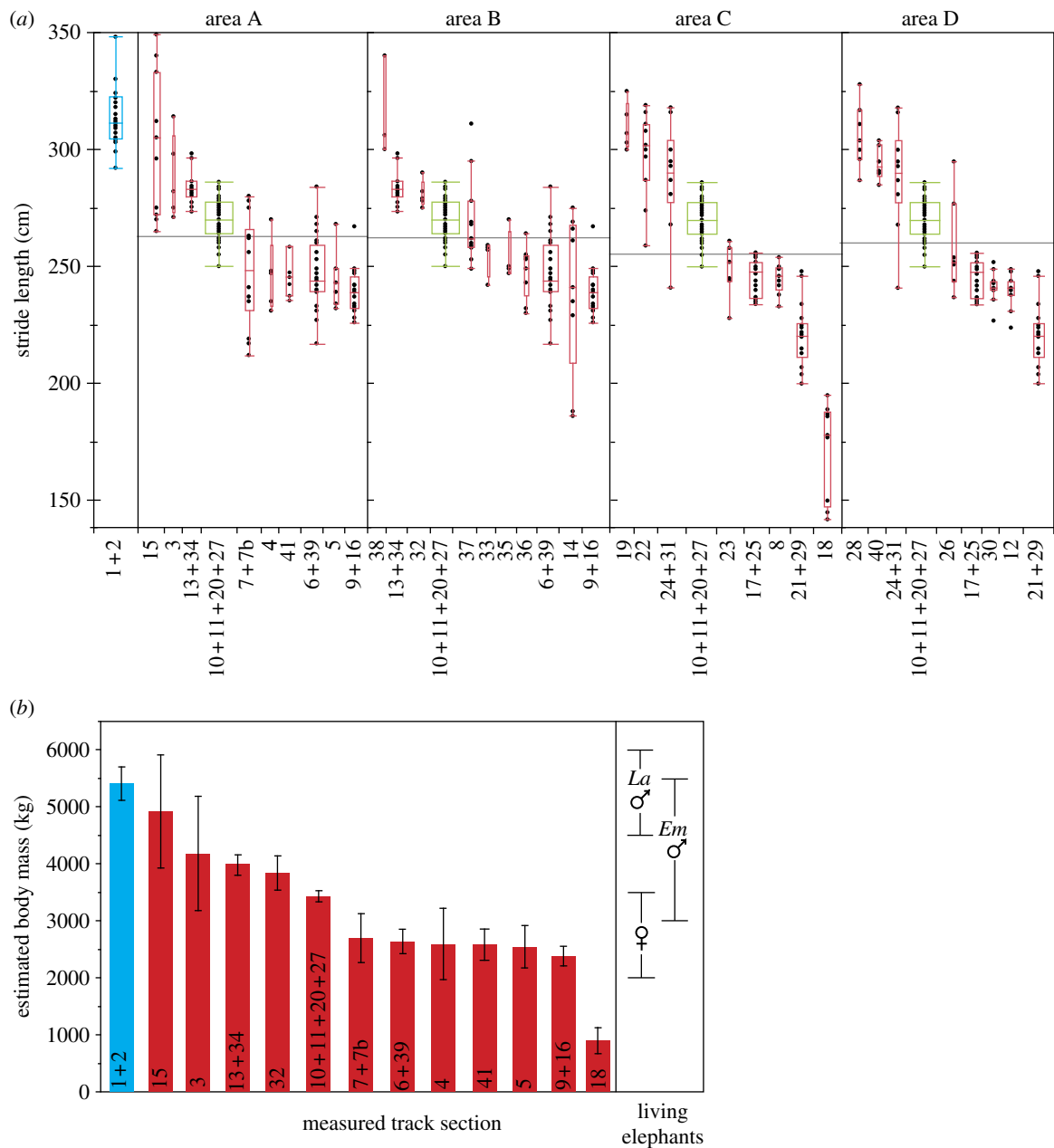


Figure 2. (a) Stride lengths for the solitary and herd trackways. Trackways and areas are numbered according to figure 1b. Box plots show median, first and third quartiles, and bars reaching the outermost data points within a 1.5 interquartile range. The horizontal grey lines mark the value of each area's average stride length. Only a single trackway could be traced throughout all measured areas of the herd (in green). In all areas A–D, 8–11 individuals of intermediate to large size are recovered. Area C additionally records the presence of a small individual (trackway 18). (b) Estimated body mass profile for the minimum number of measurable Mleisa 1 proboscideans. These comprise the solitary individual (blue), and all individuals from area A plus trackways 32 from area B and 18 from area C (red). Shown also are reported body mass ranges for adult males of *Loxodonta africana* (*La*) and *Elephas maximus* (*Em*) and adult females of both species [2,5,17,18].

sex. The solitary proboscidean trackway at Mleisa 1 represents an individual that was very large in size (figure 2), leading us to infer that it was made by a male that was at least of sexually mature age.

Sex determination for the larger members of the herd is less clear given the absence of any major size difference between them and the solitary individual, as might be expected for modern female and male elephants (figure 2b). Accepting that the Mleisa 1 proboscideans consisted of a solitary male and a female-led herd would require either that the Mleisa proboscideans exhibited significantly less sexual dimorphism than do elephants today, or that the solitary male was not yet fully grown.

These ideas could be further tested using the abundant Neogene record of proboscidean body fossils.

In terms of herd profile, the range of body sizes calculated for the Mleisa 1 herd is commensurate with that of a modern elephant family unit, allowing for greater average body size than observed in living elephant females. Furthermore, herd size at Mleisa 1, being a minimum of 13 individuals, is consistent with data from Amboseli [1] and Hwange [7] which places average family unit size between five and 16 individuals.

The earliest fossils attributable to *Loxodonta* and *Elephas* are recorded from late Miocene and early Pliocene Africa, respectively [6]. Neither genus is

represented in the Baynunah Formation, which instead has yielded many remains of *Stegotetabelodon syrticus* and a small number of specimens of *Deinotherium* sp. and ‘*Mastodon*’ *grandincisivus* [21]. We therefore cannot be certain which proboscidean made the Mleisa 1 tracks, nor even that the solitary and herd trackways were made by the same species. But as well as being the most abundant, *Stegotetabelodon* is the most likely of the three to have been found in open habitats [6]. Regardless of the identity of the track maker, the Mleisa 1 trackways present direct evidence that proboscidean social structure in the late Miocene comprised both herding and solitary behavioural modes, and that these modes were most likely to have been sexually determined. These behavioural aspects are characteristic of living elephants, and since the most recent common ancestor of *Loxodonta* and *Elephas* is estimated to date back to the late Miocene [22], one would expect modern elephant social behaviour to date back to this time as well. However, there has been no direct evidence to bear on this issue, until now.

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