



Middle Pleistocene vertebrate fossils from the Nefud Desert, Saudi Arabia: Implications for biogeography and palaeoecology

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ABSTRACT

The current paucity of Pleistocene vertebrate records from the Arabian Peninsula – a landmass of over 3 million km² – is a significant gap in our knowledge of the Quaternary. Such data are critical lines of contextual evidence for considering animal and hominin dispersals between Africa and Eurasia generally, and hominin palaeoecology in the Pleistocene landscapes of the Arabian interior specifically. Here, we describe an important contribution to the record and report stratigraphically-constrained fossils of mammals, birds and reptiles from recent excavations at Ti's al Ghadah in the southwestern Nefud Desert. Combined U-series and ESR analyses of *Oryx* sp. teeth indicate that the assemblage is Middle Pleistocene in age and dates to ca. 500 ka. The identified fauna is a biogeographical admixture that consists of likely endemics and taxa of African and Eurasian affinity and includes extinct and extant (or related Pleistocene forms of) mammals (*Palaeoloxodon* cf. *recki*, *Panthera* cf. *gombaszogenis*, *Equus hemionus*, cf. *Crocota crocuta*, *Vulpes* sp., *Canis anthus*, *Oryx* sp.), the first Pleistocene records of birds from the Arabian Peninsula (*Struthio* sp., *Neophron percnopterus*, *Milvus* cf. *migrans*, *Tachybaptus* sp., *Anas* sp., *Pterocles orientalis*, *Motacilla* cf. *alba*) and reptiles (*Varanidae/Uromastix* sp.). We infer that the assemblage reflects mortality in populations of herbivorous animals and their predators and scavengers that were attracted to freshwater and plant resources in the inter-dune basin. At present, there is no evidence to suggest hominin agency in the accumulation of the bone assemblages. The inferred ecological characteristics of the taxa recovered indicate the presence, at least periodically, of substantial water-bodies and open grassland habitats.

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1. Introduction

The Arabian Peninsula (defined here as the landmass from the southern borders of Iraq and Jordan, to the southern coastline of Yemen; Fig. 1A) is a key theatre to consider hominin dispersals between Africa and Eurasia (e.g. Rose and Petraglia, 2009; Dennell and Petraglia, 2012; Groucutt and Petraglia, 2012). While the

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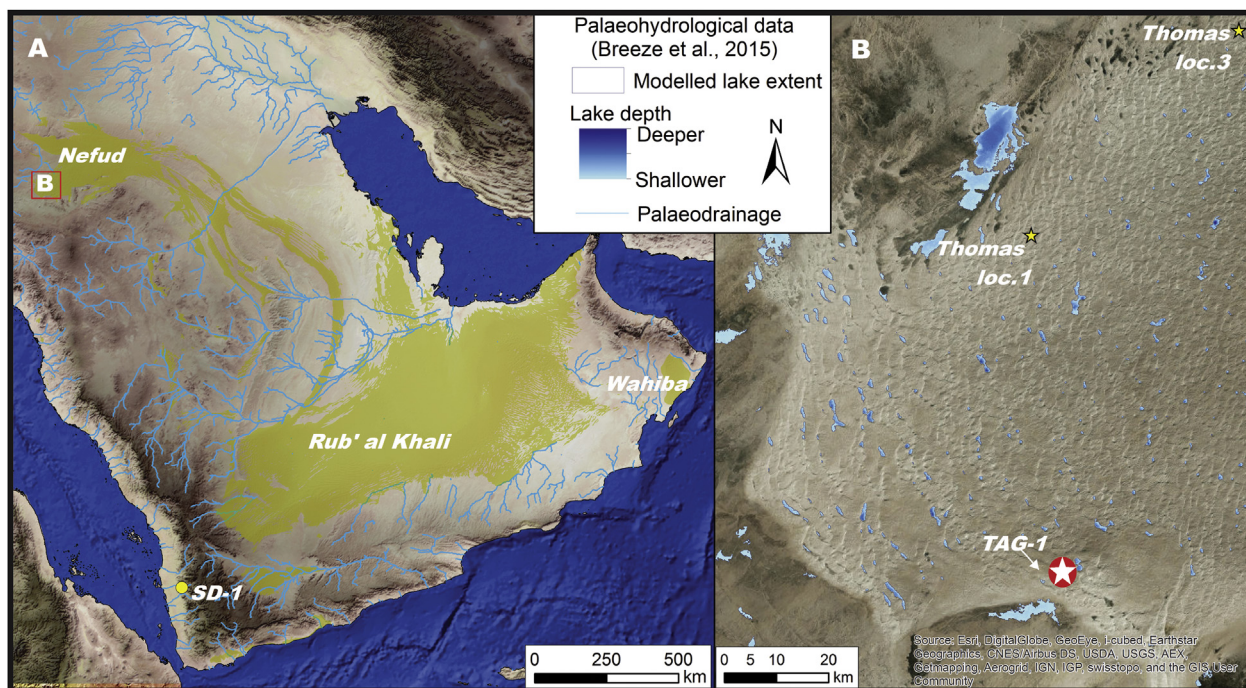


Fig. 1. A: The Arabian Peninsula, showing locations of three major sand seas and the site of Shi'bat Dihya (SD-1) and B: Southwestern Nefud Desert showing location of Ti's al Ghadah (TAG-1) and other Thomas et al. (1998) fossil sites.

geographical significance of this landmass of over 3 million km² as a link between these continents is self-evident, the potential routes and timing of dispersals and exchange by animals and hominins in the Pleistocene (2.6 Ma–0.011 Ma) are much-debated (e.g. O'Regan et al., 2005; Beyin, 2006; Fernandes et al., 2006; Fernandes, 2009; O'Regan et al., 2011; Groucutt et al., 2015a).

As studies continue to unveil a complex climatic and environmental history (e.g. Fleitmann et al., 2003; Fleitmann and Matter, 2009; Parker, 2009; Fleitmann et al., 2011; Rosenberg et al., 2011, 2013; Breeze et al., 2015; Jennings et al., 2015; Matter et al., 2015; Parton et al., 2015a, 2015b) and the Palaeolithic archaeological record develops (e.g. Armitage et al., 2011; Delagnes et al., 2012; Groucutt and Petraglia, 2012; Petraglia et al., 2012) it is now clear that Pleistocene hominins penetrated the interior of the Peninsula (Groucutt et al., 2015b, 2015c; Shipton et al., 2014; Scerri et al., 2015) in regions that are today harsh, hyper-arid habitats. A key line of evidence to contextualise these movements is, however, lacking: stratigraphically- and chronologically-constrained records of vertebrates. Here, we describe an important step towards addressing this issue.

North Africa and the Middle East are biogeographically complex regions. The Arabian Peninsula is situated at the junction of three biogeographic realms, the Afrotropical, Western Palearctic and Oriental (e.g. Portik and Papenfuss, 2012) and the historical vertebrate fauna is an admixture of endemic species with taxa of African and Eurasian affinity (e.g. Delany, 1989; Harrison and Bates, 1991; Cox et al., 2012; Portik and Papenfuss, 2012). The opening of the Red Sea and climatic shifts in the late Miocene were major drivers of diversification and dispersal of the biota of the region and a combination of harsh arid environments, periodic humid events and geological evolution has shaped the fauna of the Peninsula (e.g. Metallinou et al., 2012). Genetic studies of a small number of species (*Papio hamadryas*, *Ichneumia albicauda* and *Varanus yemenensis*) have shed light on the biogeographical history of aspects of the regional Pleistocene fauna (Fernandes, 2009, 2011 and Kopp

et al., 2014; Portik and Papenfuss, 2012, respectively) but, in contrast to works on Miocene vertebrates (e.g. Whybrow and Hill, 1999; Beech and Hellyer, 2005), the paucity of Pleistocene records from the Arabian Peninsula remains a major limiting factor in modelling the dynamics of Quaternary animal populations (e.g. Fernandes, 2009; O'Regan et al., 2011; Stimpson et al., 2015). Furthermore, while records of vertebrate taxa cannot be considered as direct or unequivocal proxies for the dispersal of hominins (e.g. Bar-Yosef and Belmaker, 2011) and species responses to climatic and environmental changes are individualistic (e.g. Stewart, 2009), such data are critical lines of contextual evidence in considering Pleistocene environments and hominin palaeoecology in the interior (e.g. Belmaker, 2009).

The Arabian Peninsula today comprises of a heterogeneous suite of habitats, including tropical, sub-tropical and montane biomes in the south and western coastal regions. The interior, however, is dominated by basalt flows, salt flats and (overwhelmingly) sand and gravel deserts (Mallon, 2011; Cox et al., 2012). These hyper-arid habitats are embodied by three major sand seas that collectively occupy over 700,000 km²: the Rub' al Khali (also known as the Empty Quarter) and Wahiba Sands in the south and southeast, respectively, and the Nefud Desert in the north (Fig. 1A). During the Pleistocene, oscillations between hyper-arid and humid conditions saw periodic increases in precipitation, humidity and the activation of river and lake systems in the interior (Parker, 2009; Rosenberg et al., 2013; Breeze et al., 2015; Matter et al., 2015; Parton et al., 2015b, Fig. 1A, B). As the volume and periodicity of available moisture increased plant biomass will have responded accordingly (e.g. Southgate et al., 1996) and an availability of fresh water resources would have led to a "greening" of the interior that in turn would have provided windows of opportunity for dispersal for animals and hominins (e.g. Parton et al., 2015a). However, the character and composition of the animal populations of these landscapes is poorly known. The existing collections of Pleistocene fossils have provided taxonomic insights (Table 1) but are beset by

Table 1

Pleistocene vertebrate taxa from the Arabian Peninsula reported prior to this study. Sources: Shi'bat Dihya – taxa and dates, [Delagnes et al. \(2012\)](#); Rub' al Khali – taxa, [McClure \(1984\)](#); Nefud Desert – taxa^a, [Thomas et al. \(1998\)](#), taxa^b, [Stimpson et al. \(2015\)](#), dates, [Rosenberg et al. \(2013\)](#). X = present; /= no record.

Region	Southwest	Rub' al Khali	Nefud desert		
Sites	Shi'bat Dihya (SD-1)	Lacustrine deposits	Khall Amayshan (Thomas loc-1)	Ti's al Ghadah (TAG-1)	"Locality #3" (Thomas loc-3)
Dates (ka)	55	/	99 ± 7/117 ± 8	318 ± 25/328 ± 26	419 ± 39 to 286 ± 30
Inferred MIS	3	1–3?	5c/5e	9 ^a	9–11
Taxa				^a	^b
Actinopterygii					
Osteoglossiformes	/	/	/	X	/
Sauropsida					
<i>Geochelone</i> cf. <i>sulcata</i>	/	/	/	X	/
Reptilia					
Squamata	/	/	/	/	X
Aves					
<i>Tachybaptus</i> sp.	/	/	/	/	X
Mammalia					
<i>Equus</i> sp.	/	/	X	X	/
cf. <i>E. hemionus</i>	X	X	/	/	/
cf. <i>Palaeoloxodon</i> (<i>recki</i>)	/	/	/	/	X
cf. <i>Hexaprotodon</i> sp.	/	/	X	/	/
<i>Hippopotamus</i> sp.	/	X	/	/	/
Suidae: gen. et sp. indet.	X	/	/	/	/
<i>Panthera</i> cf. <i>gombaszogensis</i>	/	/	/	X	X
<i>Vulpes</i> (cf. <i>vulpes</i>)	/	/	/	X	X
<i>Crocota</i> <i>crocota</i>	/	/	/	/	X
Bovidae: gen. et sp. indet.	X	/	/	X	/
<i>Pelorovis</i> (cf. <i>oldowayensis</i>)	/	/	X	/	X
<i>Bos</i> cf. <i>primigenius</i>	/	X	/	/	/
<i>Bubalus</i> sp.	/	X	/	/	/
<i>Oryx</i> sp.	/	X	/	X	X
<i>Gazella</i> sp.	/	X	/	/	/
cf. <i>Arabitragus jayakari</i>	/	X	/	/	/
Camelidae gen. et sp. indet.	/	/	/	X	/
Hystricidae gen. et sp. indet.	X	/	/	/	/

problems of preservation, provenance and chronological control ([O'Regan et al., 2011](#); [Stimpson et al., 2015](#)).

Excavations of the Late Pleistocene site Shi'bat Dihya (SD-1) in Yemen, dated to 55 ka, by [Delagnes et al. \(2012\)](#) recovered poorly preserved assemblages of bone. Remains of the post-cranial skeleton were impossible to identify. Tooth fragments could be assigned to four mammalian families: Bovidae, Suidae, Hystricidae and Equidae. A tentative identification of Asiatic wild ass (cf. *Equus hemionus*) was proposed from an intact third molar.

Pleistocene fossils have also been recovered from the two largest sand seas: the Rub' al Khali and the Nefud Desert ([Fig. 1A](#)). Collections made by [McClure \(1984\)](#) during pioneering studies of lacustrine deposits in the Rub' al Khali resulted in confident identifications of *Oryx* ("presumably *leucoryx*"), *Bos* (cf. *primigenius*), *Equus* (cf. *hemionus*), *Gazella* sp. ("apparently *G. arabica*"), *Bubalus* sp. and *Hippopotamus* ("presumably *amphibius*"). Remains of the Caprinae included a possible record of the endemic *Hemitragus* (*Arabitragus*) *jayakari*. McClure points out, however, that collection was not systematic and information for exact geographical provenance and chronological affinities of the fossil assemblages was lacking. Essentially, the "fossil vertebrate suite should therefore be taken as representing the general lacustrine periods of both late Pleistocene and Holocene" ([McClure, 1984, 179](#)) with the proviso that it was likely that the hippopotamus and large water buffalo "belong to the earlier (Late Pleistocene) period" ([McClure, 1984, 181](#)).

In the north of the Peninsula, Pleistocene fossils are known to be associated with lacustrine deposits ([Thomas et al., 1998](#); [Rosenberg et al., 2013](#)). The first Pleistocene taxa were reported by [Thomas et al. \(1998\)](#) from collections at three sites in the southwestern

Nefud Desert (Locality #1: Khall Amayshan; Locality #2: Ti's al Ghadah, the focus of this study, and an unnamed site: Locality #3; see [Fig. 1B](#)). Despite relatively small sample sizes, a total of 14 taxa (including fish, reptiles and mammals) were identified ([Table 1](#)).

[Thomas et al. \(1998\)](#) report fossils of *Equus* sp., a large bovid (identified as *Pelorovis* cf. *oldowayensis*) and a reportedly gracile hippopotamid (*Hexaprotodon* sp.?) from the site at Khall Amayshan (Thomas locality 1; [Fig. 1B](#)). [Thomas et al. \(1998\)](#) also report fossils from an unnamed site ("Locality 3"; [Fig. 1B](#)) that is likely to be site "16.1" of [Rosenberg et al. \(2013\)](#) and dated between 419 ± 39 ka and 286 ± 30 ka, which included large bovids (referred to *Pelorovis* cf. *oldowayensis*), a well preserved left mandible of *Crocota crocuta*, and post-crania and a molar from an elephant. Examination of the incomplete, hypsodont molar plate resulted in a cautious referral to the extinct African elephant taxon *Palaeoloxodon recki*. An aberrant horn-core (originally reported to be from Ti's al Ghadah) that possibly represented an undescribed taxon was also recovered from this site.

The site at Ti's al Ghadah ([Fig. 2](#)) yielded the largest and most diverse sample reported by [Thomas et al. \(1998\)](#). The collection included a relative abundance of fossils from *Oryx* sp. together with small numbers of specimens attributable to tortoise (*Geochelone* cf. *sulcata*), a large Osteoglossiforme (an order of primitive, ray-finned freshwater fish) specimen we were unfortunately unable to relocate and review, *Equus* sp., *Vulpes* sp. and a specimen conferred to the extinct Eurasian jaguar, *Panthera gombaszogensis* ([Thomas et al., 1998](#); see also [Stimpson et al., 2015](#)). Unidentified, potentially novel bovid and camelid taxa were also reported. Re-inspection of the bovid remains from the collection at Ti's al Ghadah by one of us (CMS) suggested that the crania may be attributable to a

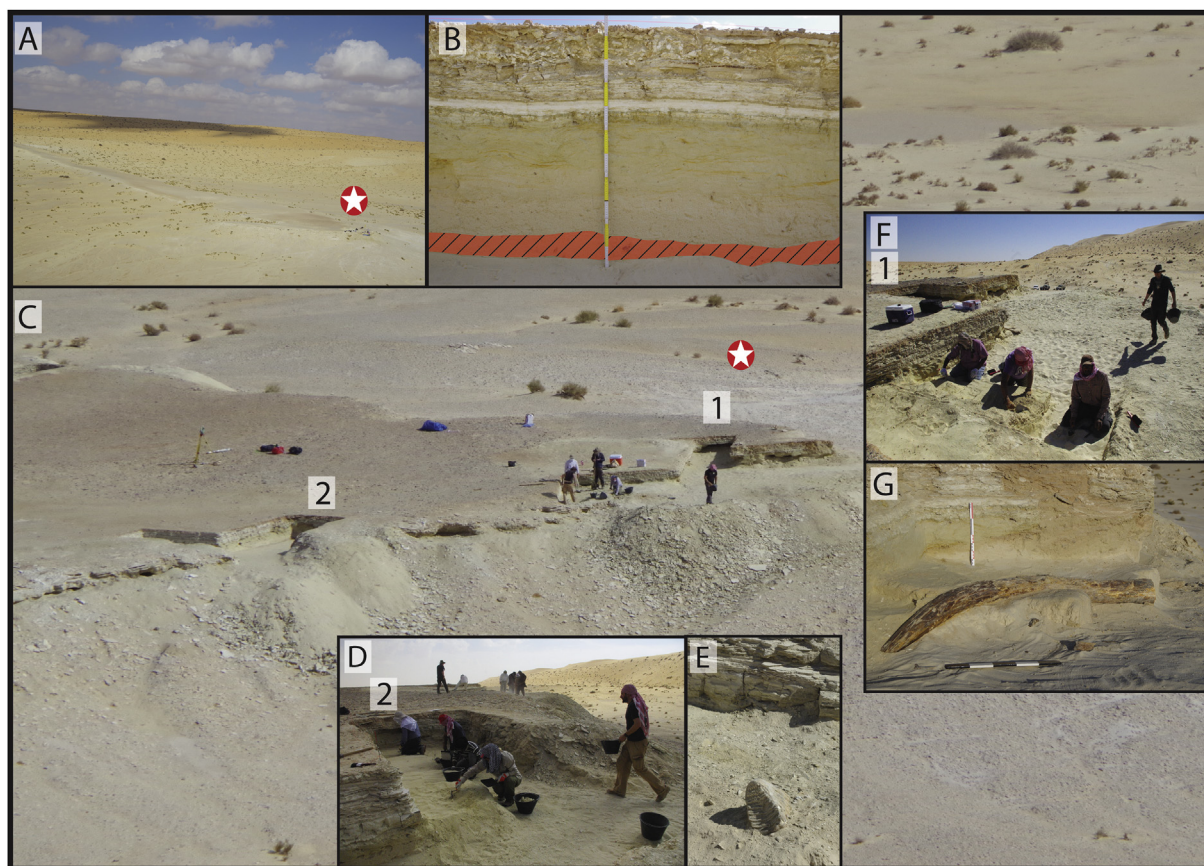


Fig. 2. The fossil site of Ti's al Ghadah. A: the ridge viewed from the southwest from the adjacent barcan dune. B: Section through the ridge deposit after excavation (scale = 10 cm increments: the position of the fossil layer within Unit 5 is hatched and highlighted in red). C: Excavation of trenches 1 and 2 (numbered) at the southern end of the ridge, viewed from the southwest. D: Excavation of trench 2, viewed from the west. E: TAG14/301 – *Palaeoloxodon* molar, in situ in trench 2. F: Excavation of trench 1, viewed from the north. G: TAG13/052 – elephant tusk, in situ in trench 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Pleistocene *Oryx* sp. (see also Section 4.2.3.4). A poorly preserved maxilla fragment appears to be camelid, but with no discernible difference to extant *Camelus* (Thomas et al., 1998).

While these collections provide some insight into the Pleistocene vertebrates of the interior, they were the product of surface collections and their stratigraphic and chronological affinities are not clear (Stimpson et al., 2015). In the original report by Thomas et al. (1998), for example, the collections were considered as a whole and an Early Pleistocene age and an Ethiopian affinity were inferred on the basis of taxonomic composition and “stage of evolution” (Thomas et al., 1998, 150). Subsequent dating work by Rosenberg et al. (2013) using luminescence techniques at these fossil localities indicated that this fauna was younger and derived from different temporal episodes and incorporated fossils of likely Middle and Late Pleistocene age (Table 1). As such, further work to resolve the identity and chronological affinities of the Nefud fauna is warranted.

Here we describe an important step towards resolving the character and chronological context of the Pleistocene vertebrates of the Nefud Desert. Following collaborative investigations of the fossil site of Ti's al Ghadah by the Saudi Commission for Tourism and National Heritage (SCTH), Saudi Geological Survey (SGS) and the Palaeodeserts project (University of Oxford), we describe stratigraphically-constrained records of mammals, birds and reptiles. We report the results of our chronometric and stratigraphic investigations and consider the biostratigraphic and palaeoecological implications of the identified taxa.

2. Site location and geological setting

The site at Ti's al Ghadah is situated within an interdunal basin in the southwest of the Nefud Desert, approximately 95 km southeast of the city of Tayma. The basin is bordered to the west by a large (ca. 60 m high) compound barchan dune ridge, while smaller branching linear dunes extend to the northern and southern ends of the basin. Relict lacustrine deposits form a distinct ridge that runs broadly northwest to southeast (Figs. 2 and 3). This ridge is comprised of a sequence of stratified sands and marls (Fig. 2B) that rises approximately 6 m above the floor of the basin, and is approximately 1 km in length. It dips gently to the south of the basin and interdigitates with low branching dunes in the east. Lacustrine and diatomaceous marls are exposed vertically along the western edge of the ridge (Fig. 2C) and dip gently to the east where they are overlain by modern dune sands. Ephemeral gullies run perpendicular to the long axis of the ridge towards the west of the basin and at the foot of the large barchan dune. These have eroded fossils from the main lake ridge, re-depositing them unconformably downslope in sinuous ridges comprised of heavily indurated, coarse, red-brown sand. Pale cream-grey sands are exposed along the southeastern corner of the basin, and represent an older palaeodune configuration that lies beneath the present day rubified sand sea. Exposed within the centre of the basin, are heavily indurated, iron-stained marl beds ca. 0.6 m thick, reflecting the formation of an older lake that predates the main lake ridge deposit. Conversely, at the northwestern edge of the basin, thin (ca.

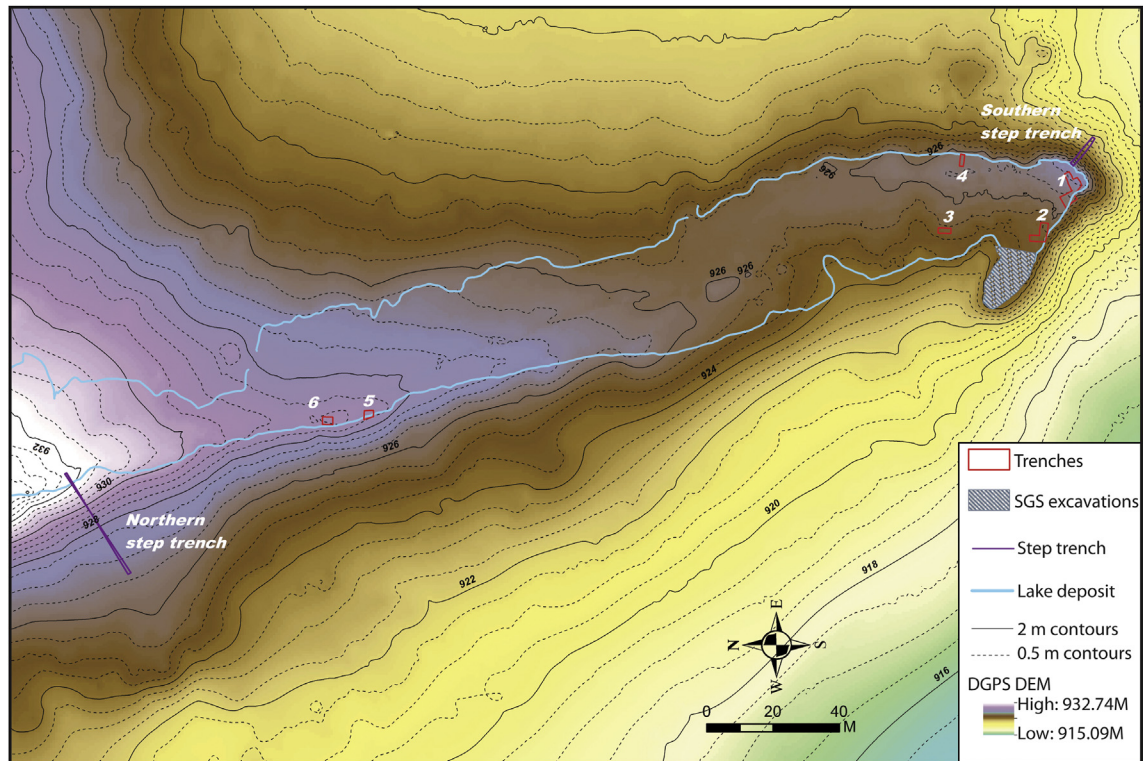


Fig. 3. Plan view of the ridge at the fossil site of Ti's al Ghadah, showing location of trenches.

0.4 m) beds of diatomaceous marls outcrop from the smaller branching linear dunes and represent a phase of lake formation that postdates the formation of the main lake ridge. The lacustrine silts and diatomaceous marls of the ridge have formed an armoured cap to the thick beds of interdigitated sands that lie beneath, including the principal fossiliferous deposit: Unit 5.

3. Materials and methods

3.1. Excavation

Excavations on the ridge focused on Unit 5 (Fig. 2A–G; Fig. 4); methodology is described in Stimpson et al. (2015). The general lithofacies described in Stimpson et al. (2015; n.b. Unit 5 = “Layer 5”) were found throughout the excavations with major variation between trenches limited to the relative thickness of the lacustrine deposit and the greenish grey sands overlying Unit 5. All overlying deposits were removed following stratigraphic boundaries and all fragments in Unit 5 were collected. The locations of diagnostic specimens (>5 mm in maximum dimension with anatomical landmarks) were recorded in three dimensions by Leica Flexline Total Station (Fig. 5A).

Searches for possible, earlier fossil-bearing strata in the ridge and in the wider basin area were made by the creation of step trenches in the north and south of the ridge (Fig. 3) and a series of test pits in the basin. While the deep section exposed by the step trenches provided further sedimentological information regarding the geomorphological evolution of the basin, no further fossiliferous layers were detected.

3.2. Fossil analyses

The identification of the fossils was conducted in the UK with the permission of the SETH. Fossils were identified by

morphological and morphometric comparisons with comparative museum specimens, published descriptions and morphometric data. Measurements of bones generally follow the schemes described in Von Den Driesch (1976), and for elephant molars Maglio (1973) but are defined in the text. Measurements were taken with dial callipers to the nearest 0.01 mm. Morphometric analyses were carried out in PAST (Hammer et al., 2001) following conventions described in Hammer and Harper (2006). A preliminary macroscopic taphonomic investigation was conducted and surface condition and modifications to bones were noted. Weathering stages were characterised following Behrensmeyer (1978) and interpreted following Andrews and Whybrow (2005).

For mammals and reptiles, modern reference materials were consulted at the Oxford University Museum of Natural History (OUMNH), the Grahame Clark Zooarchaeology Laboratory, University of Cambridge (GCZL) and the Harrison Zoological Institute (HZM). Palaeontological specimens and modern comparatives were also consulted at the Department of Earth Sciences at the Natural History Museum (South Kensington – NHM-SK). For birds, recent comparative materials were consulted at the Bird Group, Natural History Museum (NHM-Tring) and palaeontological comparative specimens at the NHM-SK.

3.3. Chronology

Prior to this study, the only available chronological control was one luminescence sample that was probably recovered from a stratum that directly underlies, or is equivalent to the main bone-bearing layer (Units 4 or 5, respectively; Fig. 4) by Rosenberg et al. (2013). This sample yielded OSL and TT-OSL (thermally-transferred optically stimulated luminescence) ages of 328 ± 26 ka and 318 ± 25 ka, respectively. The overlying lake formation was interpreted as an MIS 9 deposit (Rosenberg et al., 2013).

To refine our understanding of the chronology of the lacustrine

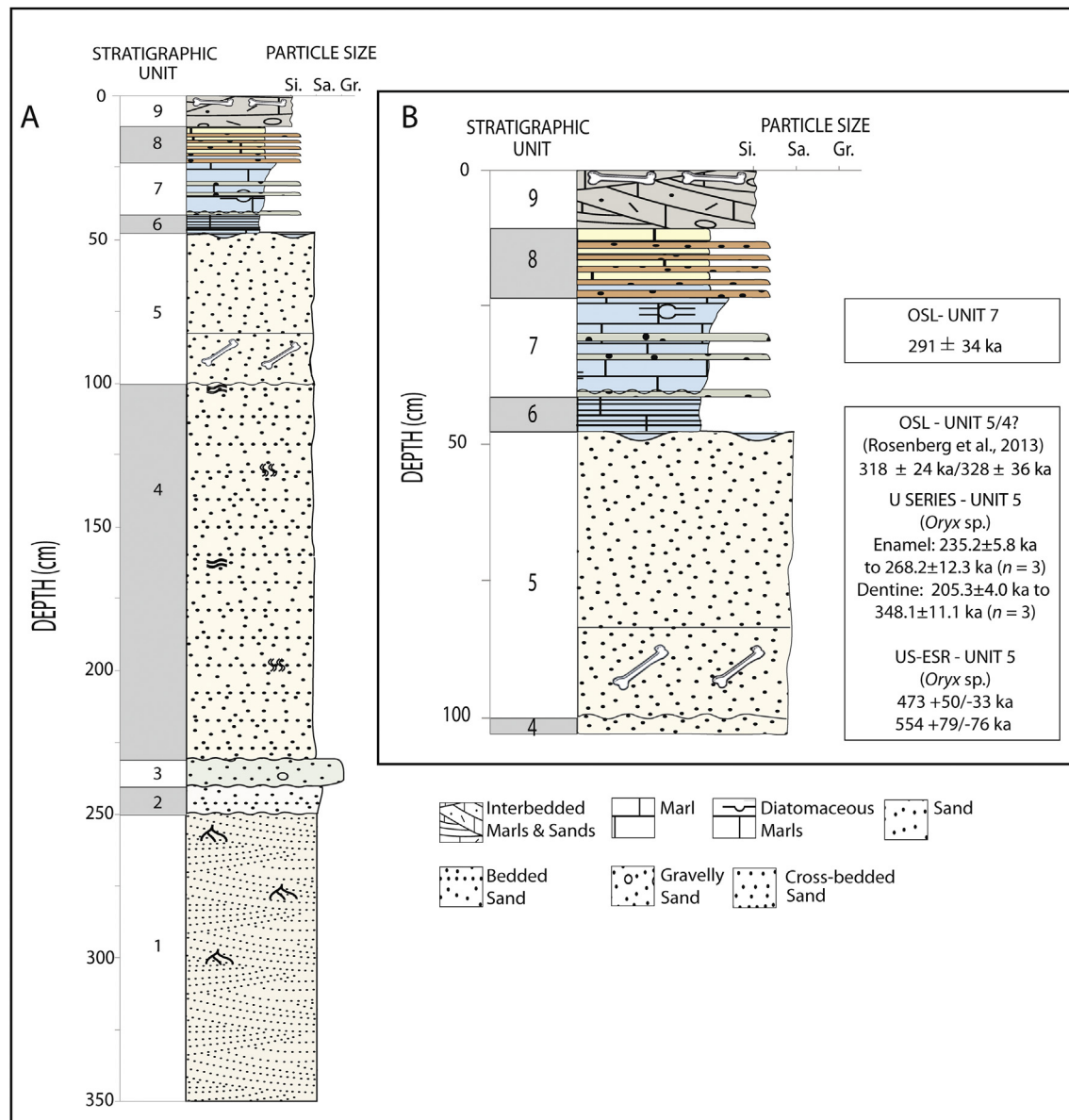


Fig. 4. A: Stratigraphic log of the ridge deposits at Ti's al Ghadah with, B: upper metre of section annotated with OSL and US/ESR dates.

deposit and the fossiliferous stratum that underlies it, we collected an OSL sample (Methods S1 supplementary data) from the palaeolake sediments capping the excavated sequence (Unit 7; see Fig. 4). Five fossil cheek teeth (*Oryx* sp.) that were recovered from Unit 5 were also submitted for U-series and combined US-ESR dating and a series of sediment samples were collected from different depths within Unit 5 to evaluate the variability of the sediment radioactivity (Methods S2 supplementary data).

4. Results

4.1. Stratigraphy, bone distribution and taphonomy

The deepest sedimentary sequence uncovered at the site comprised a total of 9 stratigraphic units (Fig. 4), and is underlain by coarse, well-cemented, cross-bedded, pale cream-grey sands (Unit 1). These contain occasional calcareous nodules and iron-stained root impressions throughout the upper ca. 0.6 m of the

unit. Unit 2 comprises weakly horizontally bedded, pale cream-white, coarse, poorly sorted sands, which feature iron staining and occasional root voids infilled with coarse, dark brown sand. Granulitic inclusions of well-rounded quartz occur throughout the unit, which displays a diffuse contact with both the overlying and underlying units. This is overlain by a thin layer (Unit 3) of very poorly sorted greenish sands with no bedding structures and numerous, well-rounded quartz pebble inclusions. The unit is heavily cemented and calcritized at the base, with iron staining and iron-stained root voids throughout. Unit 4 comprises pale cream-grey, very poorly sorted, coarse, horizontally bedded sands. Bedding is variable, being generally weak throughout, but strongly bedded and cemented in places. Vertical and horizontal iron-stained root impressions occur throughout, along with numerous well-rounded quartz granules and small (<10 mm) pebbles. There is a notable increase in iron staining at the base of the unit, along with generally coarser clasts, while a diffuse contact is present with both over and underlying units.

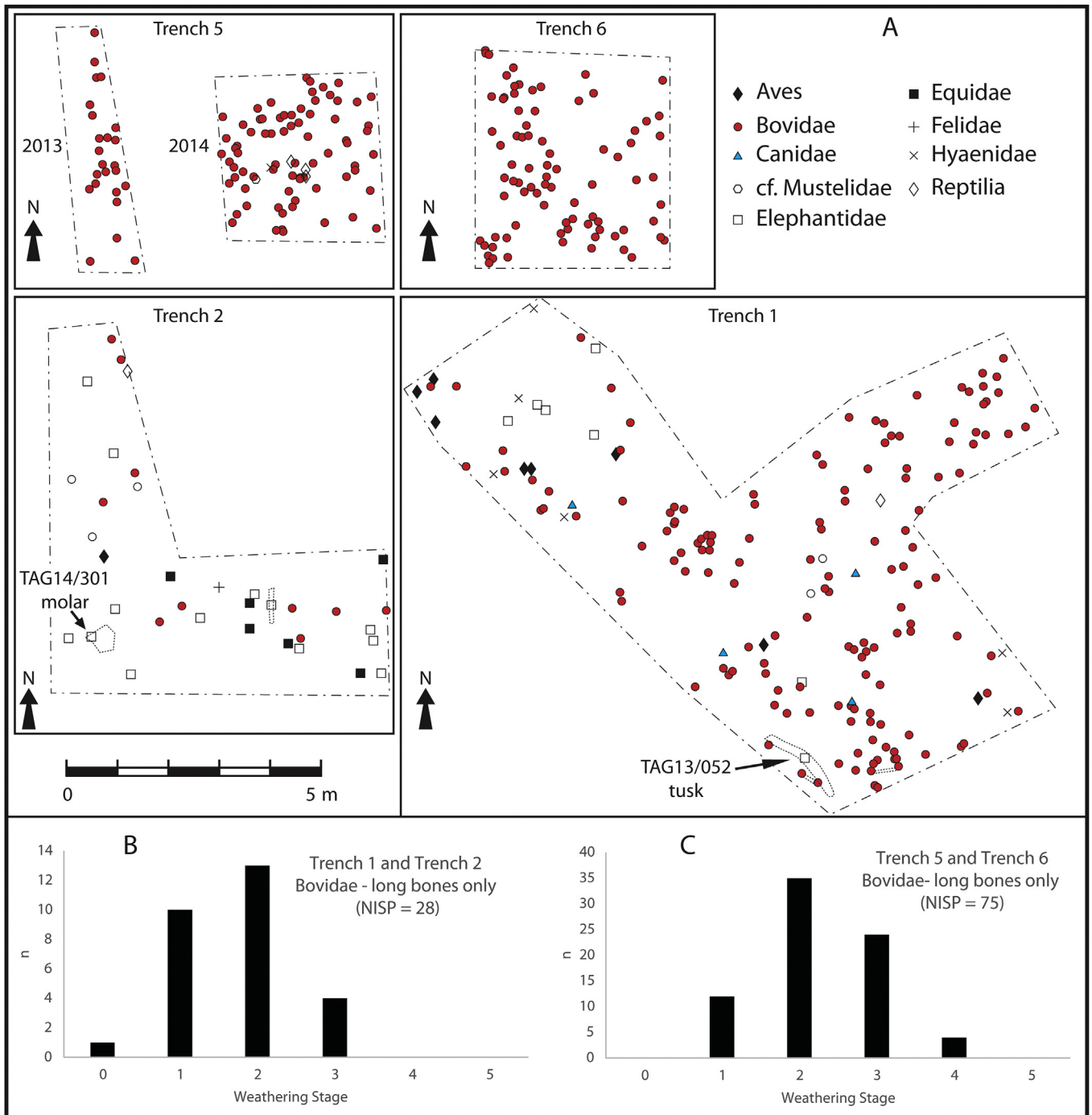


Fig. 5. A: Plots of fossil locations in western trenches 1, 2, 5 and 6, with cumulative weathering profiles (long bones – Bovidae) for B: trenches 1 and 2 and, C: trenches 5 and 6 at Ti's al Ghadah.

Unit 5 is the main fossil layer at the site and comprises weakly cross-bedded, very poorly sorted, coarse, reddish sands with occasional iron-stained root voids, fine (ca. 5–10 mm max length) rounded quartz pebbles, and calcareous drapes throughout. The unit becomes notably redder up-profile, while the contact with the overlying unit is characterised as sharp and laterally variable, with marl chunks and fractured laminae intruding vertically from the overlying lake beds. The unit is indicative of the small-scale, localised mobilisation of waterlain sands, displaying evidence of both bioturbation and sediment reworking in the form of small

(<20 cm) infills. Unit 5 is representative of wetted and partially vegetated sands. The characteristics of the underlying unit (Unit 4) indicate initial sediment deposition under low energy (localised) sheetflood conditions, following increased rainfall in the basin. A lack of channel incisions or large clasts throughout the sequence precludes major sediment mobilisation, and is more indicative of continual localised slopewash events. This phase of surface water and sediment mobilisation culminated in the development of vegetation and stabilisation of the landscape represented by Unit 5.

Fossil specimens were mineralised and ranged from a pale,

yellowish-brown to (more frequently) a dark reddish-brown: iron-staining was prevalent the latter resulting from the leaching and downward percolation of iron derived from Fe-rich sands within the overlying sedimentary units. Consolidated sand particles were frequently adhered to the bone surface, though were relatively easy to remove with a brush or wooden pick. Post-depositional movement and reworking appears to have been minimal. While minor abrasion was occasionally observed, there was no evidence to suggest rolling or significant water transport. As a general rule, there was a contrast in the degree of weathering between the areas of bone in contact with the substrate (less abraded) than the upper surface exposed in excavation (more abraded). Some trampling was evident in the form of the presence of fine striae on the surfaces of bones and “sharp breaks” to specimens (e.g. Fig. 12F, H and J). In addition to direct physical evidence of the presence of predators and scavengers on site, carnivore pits and tooth marks indicate the activity of small and large-bodied carnivores. Tooth marks were identified in the small sample of recovered bird bones (Section 4.2.2) and were detected on the bones of *Equus* sp. (Section 4.2.3.2) and *Oryx* sp. (Section 4.2.3.4). No lithics were recovered during our excavations and the association between the artefacts reported previously in the basin (Scerri et al., 2015) and the fossiliferous strata remains unclear.

Within the limits of our investigations, there was lateral variation in taxonomic diversity and in the preservation of the recovered specimens between the northern and southern limits of the excavations (Fig. 3). Fossils attributable to the Bovidae were numerically dominant throughout although trenches in the south of the site (trenches 1 and 2) yielded a greater range of taxa compared with the northern excavations (trenches 5 and 6; Fig. 5A). Weathering profiles generated from examination of bovid long bones from trenches 1, 2 and 5 and 6 (Fig. 5B and C, respectively) indicate that specimens from the south of the site were generally well-preserved: maximally to Behrensmeyer's (1978) weathering stage 3, rarely to stage 4 (Fig. 5B). Conversely, specimens from the northerly trenches were paler in colour, more friable and weathering profiles suggest that these specimens were subject to sub-aerial weathering for longer than in the southern trenches (Fig. 5C). In summary, fossil assemblages from the investigations of the southern end of the ridge were more diverse and better preserved than the assemblages from the northern limits of our investigations. The weathering profiles collectively suggest that carcasses were exposed maximally (in arid conditions) for approximately 15 years before burial. If conditions were more humid at the time of deposition then the duration of exposure would likely have been less (Behrensmeyer, 1978; Andrews and Whybrow, 2005).

The overlying unit (Unit 6) marks the onset of lake formation in the sequence, and comprises a series of interstratified, finely laminated diatomaceous marls. Iron staining occurs throughout, and is prevalent between laminae, however, Fe content is not associated with sand content. Lenses of greenish mark an influx of sand into the basin. These are generally laterally variable and well cemented in places (Unit 7). Unit 8 comprises a series of interdigitated sands and marls, possibly reflecting variations in lake water levels in the basin. Marls are highly cemented and gypsiferous, while sand content is coarse and non-laminar. The sequence is capped by beds of sandy, gypsiferous marls (Unit 9). These are heavily indurated and unevenly bedded in desiccation ‘curls’: blocks of marl that have undergone polygonal cracking as a result of drying, and have deformed to make bowl-shaped structures. These are interdigitated due to the extent of deformation, and are predominantly infilled with sand and infrequent fossil fragments (that have not yet been studied in detail). The unit marks the final phase of drying at the site and desiccation of the lake that forms the main

ridge in the basin.

4.2. Vertebrate palaeontology

4.2.1. Reptilia

Thomas et al. (1998) report the remains of tortoise (*Geochelone* cf. *sulcata*) from Ti's al Ghadah. While a small fragment of carapace was recovered from the surface of the ridge deposit (Unit 9), however, no further remains of the Testudinidae have been identified in the excavated materials from Unit 5. In contrast, the Squamata (an order containing c. 95% of all living reptiles) are represented by a small number of relatively large trunk (mid-dorsal) vertebrae and a single cervical vertebra (Fig. 6A, B; Table 2). Osteological nomenclature and description follow Hoffstetter and Gasc (1969) and Holmes et al. (2010).

4.2.1.1. Squamata

4.2.1.1.1. *Varanidae* and/or *Agamidae* – *Uromastix* sp.. The centra are procoelous. The cotyles are widest dorsally with a relatively flat dorsal edge and narrow ventrally to a curved ventral margin. The condyles are orientated postero-dorsally, with a flatter ventral margin than the cotyles. The cotyles are orientated antero-ventrally and, unlike the majority of procoelous lizards, the ventral rim is retracted and exposes the entirety of ventral concave surface of the cotyle (Fig. 6A-1). There is no sagittal crest present on the ventral surface. These characters suggest the varanids (*Varanidae*) or the agamid *Uromastix*. The cervical vertebra (TAG14/706), however, lacks a marked hypapophyseal peduncle (Fig. 6B-2), which suggests *Uromastix* sp. rather than the *Varanidae* (Holmes et al., 2010).

4.2.2. Aves

Ten specimens are attributable to six orders, six families, seven genera and seven species (Table 3). Taxonomic conventions follow Porter and Aspinall (2010) and osteological nomenclature follows Baumel and Witmer (1993).

4.2.2.1. *Struthioniformes*

4.2.2.1.1. *Struthionidae* (*ostriches*)

4.2.2.1.1.1. *Struthio* sp.

A thirteenth cervical vertebra (TAG14/318) is attributable to an ostrich, *Struthio* sp. (Fig. 6C). The specimen is stained light-brown in colour with minimal weathering or abrasion. All articular surfaces are well-defined, although the specimen has been crushed and is slightly compressed in the dorsal/ventral direction. The facies articularis caudalis of the corpus vertebra has broken off, as have the processes costalis.

TAG14/318 was compared with the type specimen (NHM – 23105) of the extinct Asiatic ostrich, *Struthio asiaticus*, Milne Edwards 1871. This taxon, of uncertain stratigraphic provenance from the Siwaliks, is generally regarded as a large-form of ostrich and a range Pliocene- and Pleistocene-age osteological remains from Eurasia have been referred to it (Mourer-Chauviré and Geraads, 2008).

Comparison with the type specimen suggests that TAG14/318 was derived from a bird with similarly-sized cervical vertebrae. The series of articulated cervical vertebrae in the type, however, are fused in matrix to an atlas, distal tarsometatarsus and phalanx and this state of preservation precludes detailed morphological and metric comparison. In terms of overall dimensions (Table S3 supplementary data) though, there is no evidence to suggest an affinity with “giant” Pleistocene ostrich taxa reported from the Caucasus (Burchak-Abramovich and Vekua, 1990; Vekua, 2013).

Morphological and morphometric comparisons (Table S3 supplementary data) were also conducted with specimens from extant



Fig. 6. Reptile and bird fossils from Unit 5 at Ti's al Ghadah. A: TAG13/049 mid-dorsal (trunk) vertebra, ventral aspect, cf. *Varanidae/Uromastix* sp. B: TAG14/706 cervical vertebra, lateral aspect, cf. *Uromastix*. C: TAG14/318 13th cervical vertebra, dorsal aspect, *Struthio* sp. D: TAG13/038 left tarsometatarsus, dorsal aspect, *Tachybaptus* sp. E i: TAG14/287 occipital region and base of skull of *Neophron percnopterus*, lateral aspect. E ii: TAG14/287, maxilla of *Neophron percnopterus*, lateral aspect. E iii: TAG14/269 right humerus proximal end of *Neophron percnopterus*, caudal aspect. E iv: TAG14/259 right humerus distal end of *Neophron percnopterus*, caudal aspect. F: TAG14/270 proximal end of left humerus of *Pterocles orientalis*, caudal aspect. Scale bars = 10 mm. Numbered features are referred to in the text.

Table 2

Measurements of greatest length (GL), anterior width (AW) and posterior width (PW) of reptile vertebrae recovered from Unit 5 at Ti's al Ghadah. All measurements are in millimetres and are taken from the dorsal surface.

Specimen	Description	GL (mm)	AW (mm)	PW (mm)
TAG14/307	Mid-dorsal vertebra	13.74	13.60	13.19
TAG13/049	Mid-dorsal vertebra	16.69	17.42	/
TAG13/Hc-T1	Mid-dorsal vertebra	16.26	/	/
TAG14/706	Cervical vertebra	12.24	9.34	6.95

Table 3

Bird fossils recovered from Unit 5 at Ti's al Ghadah. Measurements: GL = greatest length; Bp = proximal breadth; Sc = minimum width of shaft; Bd = distal breadth; Dp = proximal depth and Dd = distal depth; Bcra = cranial breadth (dorsal surface); Bcau = caudal breadth (dorsal surface). All measurements are in millimetres.

Specimen	Element	Side	Taxa	GL	Bp	Sc	Bd	Dp	Dd
TAG13/038	Tarsometatarsus	L	<i>Tachybaptus</i> sp.	32.72	6.50	2.68	5.89	7.14	4.76
TAG14/185	Humerus	L	<i>Anas</i> sp.	/	/	6.74	13.50	/	8.04
TAG14/225	Femur	R	<i>Milvus</i> cf. <i>migrans</i>	/	/	6.44	13.30	/	10.07
TAG14/246	Humerus	R	<i>Motacilla</i> cf. <i>alba</i>	/	6.34	/	/	/	/
TAG14/251	Ulna	L	cf. <i>Motacilla</i>	/	/	/	/	/	/
TAG14/259–269	Humerus	R	<i>Neophron percnopterus</i>	/	/	9.64	24.36	/	13.26
TAG14/270	Humerus	L	<i>Pterocles orientalis</i>	/	16.34	/	/	10.98	/
TAG14/286	Ulna	R	<i>Neophron percnopterus</i>	/	/	/	/	/	/
TAG14/287	Cranium	/	<i>Neophron percnopterus</i>	/	/	/	/	/	/
/	/	/	/	GL	Bcra	Bcau	/	/	/
TAG14/318 ^a	c. vertebra XIII	/	<i>Struthio</i> sp.	71.96	38.64	38.73	/	/	/

^a See also Table S3.

taxa (*Struthio camelus camelus*, *S. c. australis*, *Struthio c. massaicus* and *S. molybdophanes*) and recently extinct sub-species (*S. c. syriacus*). TAG14/318 differs from comparative specimens from extant *S. c. australis* and extinct *S. c. syriacus*. Viewed from the dorsal aspect, the opening to the foramen vertebra forms a much more acute angle between the zygapophyses cranialis in TAG14/318 (Fig. 6C–38) than in the comparative specimens for these taxa. The articular surfaces of zygapophyses cranialis are also much more developed and robust in TAG14/318 (Fig. 6C–4). At the caudal end, the lacuna interzygapophyses is very square in TAG14/318 (Fig. 6C–5), as indeed are the caudal articular facets (Fig. 6C–6): these characters are rounded in the comparative specimens. However, comparison with material from *S. molybdophanes* (NHM-Tring:

1888.5.5.1) indicates that these characters are similar. From the dorsal aspect, the lacuna interzygapophyses caudalis is square and the lacuna interzygapophyses is v-shaped, rather than u-shaped in *S. molybdophanes* (Table S3 supplementary data).

The Pleistocene fossil record of *Struthio* is sparse and the taxonomic and geographic affinities of Pleistocene ostriches are poorly known. As such, it is not feasible to identify this specimen beyond genus. However, it is notable that of all the compared specimens

the closest match on morphological and morphometric grounds is *S. molybdophanes*, an ostrich recently promoted to full species status (Sangster et al., 2015; see also Miller et al., 2011) and currently restricted to the horn of Africa.

4.2.2.2. Podicipediformes

4.2.2.2.1. Podicipedidae (grebes)

4.2.2.2.1.1. *Tachybaptus* sp.

A well-preserved, complete left tarsometatarsus (Fig. 6D) first reported in Stimpson et al. (2015) is derived from a small grebe of the genus *Tachybaptus*, which contains one species, *Tachybaptus ruficollis*. The specimen is an excellent match for the genus. At the distal end of the element, the end of the lateral edge of the trochlea

metatarsi II curves to the diaphysis and the lateral side of the trochlea metatarsi IV is flat. At the proximal end, the hypotarsus is equal in height to the condylus interarticularis (cf. Fjelds , 2004, 214).

TAG13/038 is notably shorter overall (Fig. S2A supplementary data), but is not less robust than the comparative material at NHM-Tring. To date, morphological and metric comparisons have been limited to comparative material of European provenance (Table S4 supplementary data) and extant Oriental subspecies are “generally smaller” than their counterparts from higher latitudes (Fjelds , 2004, 153). There are differences, however, between the relative positions of the medial trochlea (Fig. 6D–7) and foramen vasculare distale (Fig. 6D–8) in the TAG specimen and the comparative material. We withhold a specific attribution until it can be determined if this variation falls within specific limits for *T. ruficollis* or represents a novel Pleistocene form.

4.2.2.3. Accipitriformes (diurnal birds of prey)

4.2.2.3.1. Accipitridae

4.2.2.3.1.1. Neophron percnopterus

The mineralised remains of a cranium (TAG14/287– Fig. 6E i and ii), a complete right humerus (recovered in two pieces, TAG14/259 and 269; Fig. 6E iii and iv) and a complete, but very friable right ulna (TAG14/286) were found in close proximity in trench one and are clearly attributable to Egyptian vulture, *Neophron percnopterus* (cf. NHM 1847.10.21.25). These specimens are a relatively early record of this species, which is present in the Ti’s al Ghadah area today (CMS, personal observation).

The remains of the cranium consist of the occipital region and cranial vault (Fig. 6E i). A semi-circular puncture (maximum dimensions = 11.60 mm × 8.78 mm) is evident to the right side of the vault, which we interpret as a tooth mark (Fig. 6E i–9). There may also be a second puncture just above the foramen magnum although this may be a break associated with weakening of the bone around the edge of the foramen. The maxilla is also present and is complete from os nasale to rostrum maxillare (Fig. 6E ii). The humerus is complete though it was recovered in two pieces (Fig. 6E iii and iv). There is extensive evidence of gnawing and chewing on the caudal and cranial surfaces. The crista deltopectoralis appears gnawed along much of the dorsal edge (Fig. 6E iii–10) and there are multiple small (maximum dimensions: 2.5 mm × 2.5 mm) pits in the cranial surface of the distal end of the element (Fig. 6E iv–11). The ulna is complete, but friable. It was recovered much closer to the section edge and is likely to have been re-exposed and weathered. The ulna has also been chewed, apparently by a small to medium-sized carnivore.

4.2.2.3.1.2. Milvus sp. (cf. migrans)

A fragment of a distal end of a right femur (TAG14/225) indicates the presence of a kite. While it is notoriously difficult to separate skeletal elements of the genus *Milvus* sp. (e.g. Morales Muniz, 1993), the relatively small size of the specimen and comparison with the specimens at Tring is suggestive of black kite (*Milvus migrans*).

4.2.2.4. Pteroclidiformes

4.2.2.4.1. Pteroclididae (sandgrouse)

4.2.2.4.1.1. Pterocles orientalis

TAG14/270 is a fragment of a left proximal humerus from a large sandgrouse species (Fig. 6F). While it is a reasonable morphological match for *Syrhaptes* sp., TAG14/270 is markedly larger and more robust: the caput humeri (Fig. 6F–12) is more developed and more prominent as in *Pterocles* sp. It can be difficult to separate the skeletal elements of different *Pterocles* species (e.g. Dobney et al., 1999) but TAG14/270 is clearly from a large bird (Fig. S2B, Table S5 supplementary data) and all observable characteristics

match those of *Pterocles orientalis*, the black-bellied sandgrouse.

4.2.2.5. Anseriformes

4.2.2.5.1. Anatidae (ducks and geese)

4.2.2.5.1.1. Anas sp.

Two fragments of the distal end of a left humerus (TAG14/285) is from a dabbling duck of the genus *Anas*. It is not possible to identify this specimen to species, but it derived from a bird equivalent in size to a mallard (*Anas platyrhynchos*).

4.2.2.6. Passeriformes

4.2.2.6.1. Motacillidae (wagtails)

4.2.2.6.1.1. Motacilla cf. alba

Two small, mineralised and well preserved specimens – a fragment of a right proximal humerus (TAG14/246) and a left ulna (TAG14/251) – are derived from passerines. Comparisons under a lower power microscope with the comparative collections at NHM-Tring indicate that they are both attributable to the genus *Motacilla* (wagtails), most likely *Motacilla alba*.

4.2.3. Mammalia

4.2.3.1. Carnivora

4.2.3.1.1. Felidae

4.2.3.1.1.1. Panthera sp.

A total of four specimens known from Ti’s al Ghadah are attributable to the genus *Panthera* (Table 4). Two of these, a left third metacarpal (JMI 27) and a right fourth metacarpal (TAG13/097), have been referred to the extinct Eurasian jaguar, *Panthera gombaszogensis* (see Thomas et al., 1998 and Stimpson et al., 2015, respectively). Morphological and morphometric analyses of TAG13/097 are described in Stimpson et al. (2015). While comparative sample sizes are small, measurements for JMI 27 appear equivalent with published measurements for Pleistocene jaguars, *P. onca augusta* and *Panthera gombaszogensis* (Table S6; Fig. S3 supplementary data). The genus is also represented by a phalanx (TAG14/339) and broken mandibular canine (TAG13/145) (Fig. 7A, B).

4.2.3.1.2. Hyaenidae

4.2.3.1.2.1. cf. Crocuta crocuta

A total of seven coprolites were during the excavations: six specimens from trench 1 and a one specimen from trench 5. The general morphology of intact specimens – a near circular cross-section, with convex and concave ends – closely resembles hyaena, most likely *Crocuta crocuta* (Larkin pers comm., Parfitt pers. comm). Measurements of a complete specimen, TAG14/256 (Fig. 7C: axial length 40.58 mm; diameter A 29.85 mm, diameter B 28.43 mm) fall within reported ranges of coprolites from this taxon (cf. Larkin et al., 2000; Lewis et al., 2010).

4.2.3.1.3. Canidae

4.2.3.1.3.1. Canis sp.

A fragment of the base of the skull (TAG14/245), a lower right carnassial (TAG14/184) and a fragment of a lumbar vertebra (TAG14/208) are attributable to medium-sized canids. The skull fragment consists of the occipital region and a fragment of the supra-occipital (Fig. 7D). The foramen magnum, occipital condyles and condylar foramen are intact and portions of the par-occipital process and basi-occipital are present. This specimen is a good morphological match with comparative material for the golden jackal, *Canis aureus* (but see below): measurements indicate that it derived from a relatively large individual (Table 4).

4.2.3.1.3.2. Canis anthus

TAG14/184 is a trenchant, lower right carnassial (M₁). With the exception of the break to the mesial root, the specimen is complete and is relatively unworn (Fig. 7E). The specimen, however, appears iron-stained and there is marked “sidedness” in weathering: it appears that the tooth ultimately lay on its buccal side prior to

Table 4

Carnivora measurements from Unit 5 at Ti's al Ghadah. Measurements: GL = greatest length; Bp = proximal breadth; Dp = proximal depth; MDAP = minimum antero-posterior diameter of diaphysis; MWML = minimum medio-lateral width of diaphysis; Bd = distal breadth; Dd = distal breadth; M-D = mesio-distal length; B-L = buccal-lingual width; HFM = height of foramen magnum; WFM = width of foramen magnum; WOC = width across occipital condyles; BJP = breadth across jugal processes; Ltald = length of talonid. All measurements are in millimetres.

Specimen	Element	Taxon	Measurements	Source
JMI 27	Left metacarpal III	<i>Panthera cf. gombaszogensis</i>	GL = 91.94; Bp = 22.16; Dp = 20.70; MDAP = 11.74; MWML = 12.05; Bd = 20.75; Dd = 18.21	Thomas et al. (1998); metrics: this study
TAG13/097	Right metacarpal IV	<i>Panthera cf. gombaszogensis</i>	GL = 88.72; Bp = 17.16; Dp = 19.14; MDAP = 11.74; MWML = 11.40; Bd = 17.30; Dd = 18.04	Stimpson et al. (2015)
TAG13/145	Mandibular canine	<i>Panthera sp.</i>	M-D = >17.00; B-L = 13.22	This study
TAG14/339	Phalanx I	<i>Panthera sp.</i>	GL = 48.70; Bp = 19.20; Dp = 14.91	This study
TAG14/245	Occipital	<i>Canis sp.</i>	HFM = 16.1; WFM = 18.30; WOC = 30.77; BJP = 42.58	This study
TAG14/184	M ₁ (carnassial)	<i>Canis anthus</i>	M-D = 21.20; B-L = 8.04; Ltald = 6.22	This study



Fig. 7. Carnivora fossils from Unit 5 at Ti's al Ghadah A: TAG14/339 phalanx, volar and plantar aspects, *Panthera sp.* B: TAG13/145 broken mandibular canine, *Panthera sp.* C: TAG14/256 coprolite, cf. *Crocota crocuta*. D: TAG14/245, occipital region, caudal aspect, *Canis sp.* E: TAG14/184, right M₁ (carnassial), *Canis anthus*, buccal (i) and lingual (ii) aspects. Scale bars = 10 mm. Numbered features are referred to in the text.

burial as there is minimal modification to this surface of the tooth (Fig. 7E i). Conversely, the lingual side is abraded across the entire surface (Fig. 7E ii).

TAG14/184 is too large to have derived from any known *Vulpes sp.* and is from a medium-sized canid. The carnassial is trenchant, with a sub-equal bicuspid talonid (Fig. 7E ii-1) and a relatively well-developed metaconid (Fig. 7E ii-2). The hypoconid is not centrally-located and is angular rather than conical. These characters indicate *Canis sp.* and discount the hypercarnivorous *Cuon* and *Lycaon* (cf. Baryshnikov and Tsoukala, 2010; Baryshnikov, 2012; Brugal and Boudadi-Maligne, 2011; Petrucci et al., 2012).

The morphometric characteristics of TAG14/184 indicate that it

derived from a smaller animal than Pleistocene and recent records of European *Canis lupus lupus* (cf. Flower and Shreve, 2014; Sansalone et al., 2015) and recent records of *C. lupus pallipes* (cf. Dayan, 1994) and *C. lupus arabs* from the Levant (Fig. 8). Conversely, measurements from TAG14/184 suggest that it derived from an animal larger than recent European golden jackals, recent and Pleistocene African golden jackals (*Canis aureus s.s.*) and match equivalent measurements of a large form, variously classified as “*Canis aureus lupaster*” or “*Canis lupus lupaster*” (see data for “*Canis lupus lupaster*” in Fig. 8).

Osteological studies have long recognised the likelihood of a large extant form of “jackal” in North Africa (e.g. Huxley, 1880) and

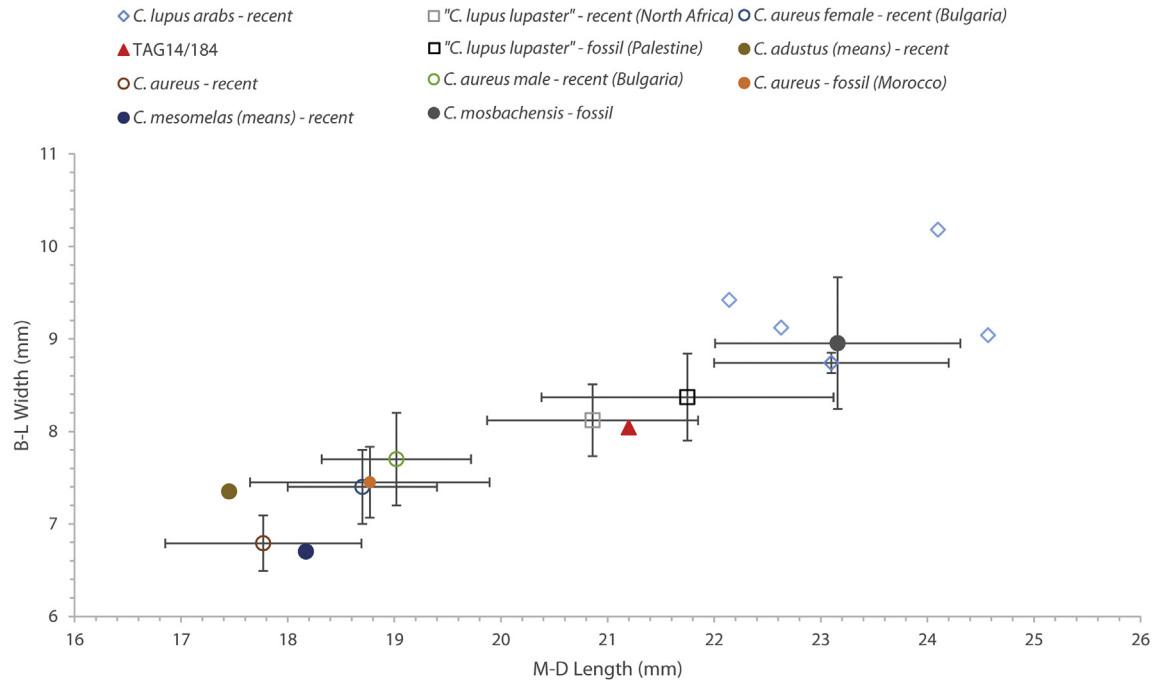


Fig. 8. Bivariate plot to show mean values, ranges (1 sigma) and single observations of length (M-D = mesio-distal) and width (B-L = buccal-lingual) measurements for lower carnassial teeth (M_1) from recent and fossil *Canis* spp. with fossil specimen TAG14/184. Data compiled from Kurtén, 1965; Dayan et al., 1992; Dayan, 1994; Rook et al., 1996; Aouraghe, 2000; Baryshnikov, 2012; Stoyanov, 2012. Measurements of recent *C. lupus arabs* were also taken from comparative specimens at the HZM.

“large” golden jackal fossils are known from Middle to Late Pleistocene in Northwest Africa (Geraads, 2011). Recent work with mitochondrial and nuclear genome data has indicated that some populations of North African “golden jackals” are a cryptic species, distinct from Eurasian golden jackals, which occupies a much wider geographical area in Africa than was previously thought (Rueness et al., 2011; Gaubert et al., 2012; Koepfli et al., 2015). Koepfli et al. (2015) recommend that *Canis lupus lupaster* (and some animals recognised as *Canis aureus*, sensu lato) be classified as *Canis anthus*, the African golden wolf. Given the trenchant morphology and morphometric characteristics of TAG14/184, we follow this proposal and refer TAG14/184 to *Canis anthus*.

4.2.3.1.3.3. *Vulpes* sp.

Thomas et al. (1998) reported the presence of the bones of foxes with no discernible morphological differences from extant *Vulpes vulpes*. Small cranial fragments were recovered in 2013 (Stimpson et al., 2015), but no further specimens have yet been identified in Unit 5.

4.2.3.1.4. cf. *Mustelidae*. A single left mandibular canine (antero-posterior length = 3.56 mm; buccal-lingual width = 2.34 mm) with a marked cingulum on the medial side of the tooth is most likely attributable to the *Mustelidae*. Measurements suggest that it derived from an animal similar in size to a large *Mustela* sp. or *Vormela* sp. but further comparative material is required.

4.2.3.2. *Perissodactyla*

4.2.3.2.1. *Equidae*. In addition to small numbers of rib fragments and a thoracic vertebrae, three well preserved specimens attributable to the *Equidae* were recovered (Table 5): a fragment of a right mandible (TAG14/329; Fig. 9A, B), a complete left astragalus (TAG14/342; Fig. 9C) and a near-complete left femur (TAG13/146; Fig. 9D).

The Pleistocene equids of the Middle East are generally thought to comprise of *Equus caballus*, *Equus hydruntinus* and *Equus*

hemionus (Eisenmann et al., 2002). The separation of different equids on the basis of dental morphology, however, is not a straightforward issue. Morphological criteria can be equivocal (e.g. Azzaroli and Stanyon, 1991; Geigl and Grange, 2012) and the nomenclature employed in schemes varies between authorities. For TAG14/329, we follow criteria described in Davis (1980), Eisenmann et al. (2008), van Asperen et al. (2012), Geigl and Grange (2012) and Alberdi and Palombo (2013).

4.2.3.2.1.1. *Equus hemionus*

TAG14/329 is a fragment of a robust right mandible (Fig. 9A). The first molar is broken off at the root below the alveolus, but the worn second and third molars are in situ. The M_2 is intact. The M_3 is largely complete but there is a break to the distal occlusal surface (Fig. 9B). Cabaloid horses can be discounted as the double knots on M_2 and M_3 are rounded (Fig. 9B-1) with v-shaped (rather than u-shaped) lingual valleys (linguaflexids; Fig. 9B-2) and rounded (rather than flat) buccal margins of the protoconid and hypoconid (Fig. 9B-3), although this last characteristic is regarded as an unreliable means to discriminate between taxa (Davis, 1980). While tooth wear is marked, the vestibular grooves (ectoflexids) on each molar appear shallow and they do not penetrate the isthmus of the double-knot (Fig. 9B-4). This would discount zebras and zebra-like taxa, the extinct *E. hydruntinus* and Pleistocene stenonine horses and indicate the hemione, *E. hemionus*. Morphometric comparisons using the intact M_2 of TAG14/329 show that the dimensions of the occlusal surface are larger than in extant and recently extinct regional sub-species (*E. h. onager* and *E. h. hemippus*, respectively) and equivalent to extant Mongolian subspecies *E. h. hemionus* and the Tibetan species, *Equus kiang* (Fig. S4 supplementary data).

4.2.3.2.1.2. *Equus* sp.

The few specimens of recovered post-crania are rather robust. The dimensions of a near-complete left femur TAG13/146 (Table 5; Fig. 9D), notable for the presence of carnivore pits on the caudal surface, near to the proximal end (Fig. 9D-5), indicate that this specimen is large and robust in comparison to extant hemiones

Table 5

Measurements of fossils of the Equidae from Unit 5 at Ti's al Ghadah. Abbreviations: TAG14/329 – MD = mesial-distal length; BL = buccal-lingual width; Lo = length of occlusal surface; lo = width of occlusal surface; LDB = length of double knot. TAG13/146 – GL = greatest length; mL = medial length; Bp = proximal breadth; Sc = minimum width of diaphysis; Bd = distal breadth; Dd = distal depth. TAG14/342 – astragalus measurements follow the locations and conventions described in Alberdi and Palombo (2013). All measurements are in millimetres.

Specimen	Element		MD	BL	Lo	lo	LDB
TAG14/329	Right mandible	M ₃ M ₂	(c.33.85) 25.6	15.98 18.88	(c. 32) 25.08	13.2 14.18	14.81 15.31
Specimen	Element	GL	mL	Bp	Sc	Bd	Dd
TAG13/146	Left femur	c. 350	306	c. 114.66	43.77	96.68	c. 100
Specimen	Element	1	2	4	5	6	7
TAG14/342	Left astragalus	65.16	66.5	67.91	56.16	37.9	57.65

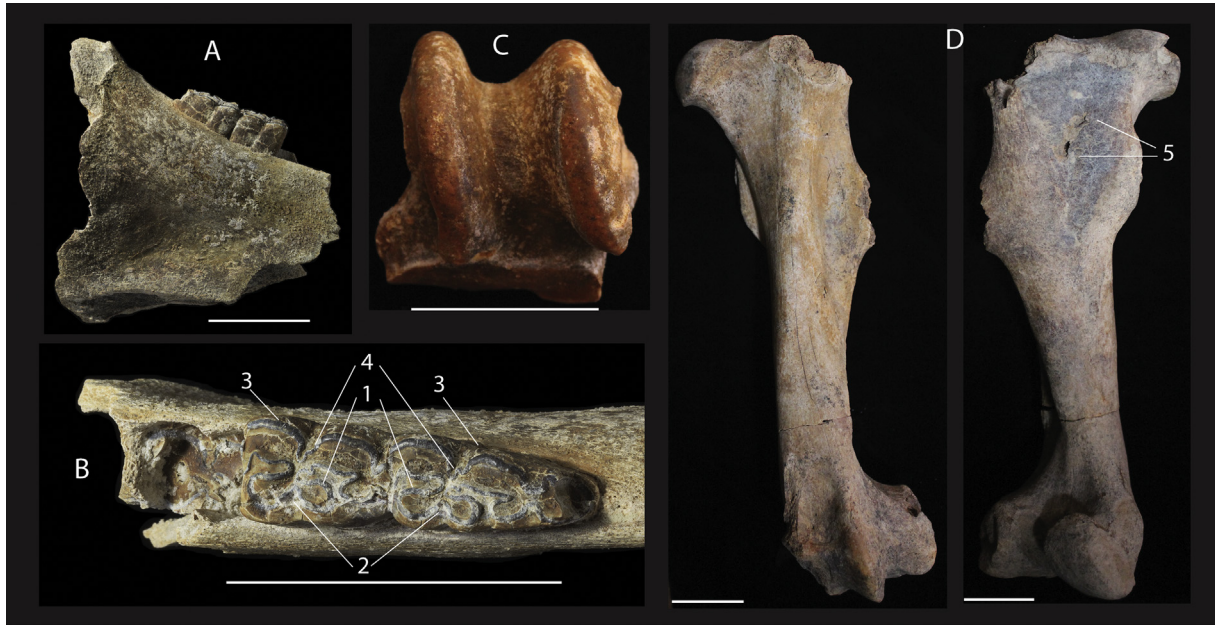


Fig. 9. Fossils of Equidae from Unit 5 at Ti's al Ghadah. TAG14/329 right mandible, *Equus hemionus*, in A: lateral and B: occlusal views. C: TAG14/342 left astragalus, *Equus* sp., dorsal aspect. D: TAG13/146 left femur, *Equus* sp., cranial and caudal views. Scale bars = 50 mm. Numbered features are referred to in the text.

(Fig. S5A supplementary data). A complete left astragalus (TAG14/342; Fig. 9C), which was found in close association with mandible TAG14/329, is also large and robust (Fig. S5B supplementary data). A PCA analyses of six variables suggests that the astragalus is of a size and proportions of larger equid taxa, equivalent perhaps to *Equus oldowayensis*, rather than extant hemionos (Fig. S5B supplementary data). This would be consistent with the findings reported in Thomas et al. (1998) who also describe relatively large and robust bones from the site, possibly from a robust stenonid horse or species of zebra.

Given that Eisenmann et al. (2008) report that the various subspecies of *E. hemionus*, as they are known from the fossil record, appear to have been conservative in terms of overall dimensions and proportions there are two possible scenarios for the interpretation of the equid remains in hand. Firstly, that there are the remains of more species of equid preserved at the site than the available dental material currently indicates, or secondly that the equid remains at Ti's al Ghadah collectively represent a large and robust Pleistocene form of *E. hemionus*.

4.2.3.3. Proboscidea. The presence of bones from a large elephant was identified in 2013, with a 2.25 m long tusk (TAG13/052) and right magnum (carpal III – TAG13/104) recovered. Stimpson et al.

(2015) tentatively proposed that these remains were attributable to the extinct genus *Palaeoloxodon* (sometimes classified as *Elephas*). In 2014, collaborative investigations of the elephant remains of Ti's al Ghadah began between the SCTH, SGS and Palaeodeserts project, with the establishment of large-scale investigations by the SGS at the south of the ridge (Fig. 3). Here, we focus on the taxonomic diagnosis of two diagnostic specimens, an upper molar TAG14/301 (Fig. 10A, B) and a mandible of a young animal, TAG14/281 (Fig. 10C, D).

4.2.3.3.1. Elephantidae

4.2.3.3.1.1. *Palaeoloxodon cf. recki*

The lineage of the straight-tusked elephant is generally included within *Elephas* Linnaeus, 1758 by workers on African material (e.g. Sanders et al., 2010) but *Palaeoloxodon* Matsumoto, 1924 or *Elephas* (*Palaeoloxodon*) by those studying Eurasian remains (e.g. Palombo and Ferretti, 2005; Lister, 2016). Pending resolution of the relationships among elephant genera we here retain the genus *Palaeoloxodon* for clarity (cf. Shoshani and Tassy, 1996).

Specimen TAG14/301 is a portion of an adult left upper molar in mid-wear (Fig. 10A). The anterior end of the crown shows signs of both natural (lifetime) wear and post-mortem breakage; at the posterior end lamellae have been lost post-mortem. Specimen TAG14/281 is a portion of a juvenile mandible including a complete



Fig. 10. Elephantidae fossils from Unit 5 at Ti's al Ghadah. TAG14/301, upper left molar, *Palaeoloxodon*, in A: occlusal view and B: lateral view. TAG14/281, right mandible in C: occlusal view, and D: lateral view. Scale bars = 100 mm.

molar in early to mid-wear (Fig. 10C, D).

The molars show features which strongly suggest referral to the genus *Palaeoloxodon*. In particular, the occlusal wear figures show lamellae with distinctly but roughly folded enamel, and irregular expansions at roughly the mid-line of the molar, extending in both the anterior and posterior directions from the anterior and posterior enamel bands, respectively. These features are distinctive of *Palaeoloxodon* and distinguish these molars from other candidate genera, *Loxodonta* (African elephants), *Mammuthus* (mammoths) and *Elephas* s.s. (lineage of Asian elephant). Another common feature of *Palaeoloxodon*, rings of enamel medial and lateral to each lamella in early wear, are not visible these specimens; this character is not, however, invariably present in the genus.

Upper molar TAG14/301 preserves 11 enamel lamellae, but this is incomplete and the original number (and the original length of the tooth) are difficult to reconstruct. At the anterior end, the preserved crown is worn to the root at the front, and the isolated 'anterior root' has been lost through wear, so it is not possible to reconstruct the number of lamellae lost (Lister and Sher, 2015; Sher and Garutt, 1987). The base of a somewhat isolated root is visible at the antero-lateral corner of the crown, but it is not of the correct shape or position to be the true 'anterior root' and must therefore be one of the 'paired roots' behind it. It is therefore likely that at least 2–3 lamellae have been lost through wear, but the precise number is unknown.

Loss at the posterior end is also difficult to quantify. The large size of the molar makes it very likely to be either M^2 (the penultimate of the series) or M^3 (the last of the series). In a more complete specimen, this can easily be determined from the shape of the posterior end of the crown, which tapers in M^3 but is blunt and wide in M^2 . Unfortunately, breakage makes the determination of this characteristic problematic for TAG14/301. The width of the crown reduces very slightly from front to back (Table 6), which might suggest M^3 , but this is insufficient for certainty. A second factor is crown height, which tends to be maximal near the front of the molar in M^3 and near the back in M^2 . However, because only the

posterior two preserved lamellae of this specimen are unworn and allow measurement of crown height, this cannot be determined. The crown is relatively high (133 mm, for a molar width of 90.5 mm, giving a preserved hypsodonty index of $100 \times 133/90.5 = 147$), which would be consistent with either a lamella close to the original posterior end of an M^2 , or a lamella half to two-thirds down the crown of an M^3 . The remaining exterior surface of the molar near the posterior break provides some evidence: especially near the top of the crown on the lateral side it curves medially to a degree that suggests it is close to the natural posterior end of the tooth, rather than that the tooth extended much beyond the break. In this case, the molar would be an M^2 , but this cannot be considered certain. If it is an M^2 , then the curvature of the surface suggests that approximately two lamellae (plus the posterior talon) should be added to the preserved number. That would give an approximate total of at least 15 (two or more at the front, two at the back, and 11 preserved). If, however, the molar is an M^3 , then an unknown number is missing at the back and the total is known only to be greater than 15. Table 6 shows measurements for the Ti's al Ghadah teeth, in comparison with published data for *Palaeoloxodon antiquus* and *Palaeoloxodon recki recki*, the latest chrono-subspecies, with a chronological range in East Africa of ca. 1.2–0.5 Ma.

The measurement data tend to identify the upper molar TAG14/301 as an M^3 rather than M^2 . If we are correct that at least two lamellae are missing from each of its anterior and posterior ends, so that its original value was at least 15, this places it in M^3 range. M^2 of *P. recki recki* is represented by only one specimen, with 10 plates, but the range probably extended to 12 as this value is found even in earlier samples referred to *P. recki ileretensis* and *P. recki atavus* (Beden, 1979). However, 15 plates have not been recorded in any M^2 of *P. recki* and even in the more advanced *P. antiquus* of Europe: 11–14 is typical for M^2 (and 16–19 in M^3). The rather thick enamel of TAG14/301 also supports identification as M^3 , although this is less secure. Following Laws (1966) scheme, TAG14/301, if it is an M^3 as here suggested, is probably around wear stage XXII–XXIII, suggesting an age of roughly 40 years.

Table 6

Measurements of Ti's al Ghadah elephant molars compared to East African *P. recki recki* and European *P. antiquus*. Comparative data for *P. r. recki* compiled from [Beden \(1979\)](#), [Ferretti et al. \(2003\)](#), [Saegusa and Gilbert \(2008\)](#), and for *P. antiquus* from unpublished data of AML and P. Davies. Measurements are in millimetres and are shown as ranges for samples where $n \leq 5$, and mean $\pm$ standard deviation for samples where $n > 5$.

	Width	Length	Plate number	Lamellar Frequency	Enamel thickness	Hypsodonty Index
M^{2/3} TAG 14/301	90.5	>171	≥ 15	6.40	2.7	≥ 147
M ² <i>P. recki recki</i>	65–80	250	10	5.0–6.8	2.0–2.5	198
M ³ <i>P. recki recki</i>	89.2 $\pm$ 7.6	315–360	13–19	5.82 $\pm$ 0.74	2.73 $\pm$ 0.29	180 $\pm$ 16
M ² <i>P. antiquus</i>	74.1 $\pm$ 7.99	200 $\pm$ 33	11.7 $\pm$ 1.0	6.57 $\pm$ 0.99	2.33 $\pm$ 0.38	221 $\pm$ 34
M ³ <i>P. antiquus</i>	83.4 $\pm$ 6.89	284 $\pm$ 40	17.3 $\pm$ 1.5	6.18 $\pm$ 0.82	2.68 $\pm$ 0.51	213 $\pm$ 16
dP₄ TAG 14/281	[≥ 44]	128	10	9.13	1.3	ca. 130
dP ₄ <i>P. recki recki</i>	—	—	—	—	—	—
	(dP ⁴ = 55)	(dP ⁴ = 89)	(dP ⁴ = 8)	(dP ⁴ = 7.7–8.9)	(dP ⁴ = 1.3–1.7)	(dP ⁴ = 130)
dP ₄ <i>P. antiquus</i>	47.3 $\pm$ 6.5	98–145	9–11	8.92 $\pm$ 1.43	1.50 $\pm$ 0.31	164 $\pm$ 3.4

Ti's al Ghadah specimens are shown in bold.

The juvenile mandible TAG 14/281 ([Fig. 10C, D](#)) preserves dP₄ complete: its lamellar formula is $\times 10x$ (10 lamellae plus anterior and posterior talons). Its crown is part-buried in the jaw, but from a micro-CT scan its crown height is ca. 57 mm and width 44 mm, giving a hypsodonty index of ca. 130. Mesowear angles were measured on the M³ and dP₄ following [Saarinen et al. \(2015\)](#). The angles are measured between the ridges of enamel bounding each lamella, and the floor of dentine inside. Averaged over several lamellae the angles are 120° for the M³ and 136° for the dP₄. The dP₄ in TAG14/281 is in early to mid-wear and at wear stage V in [Laws \(1966\)](#) scheme, which corresponds to an age at death of approximately 3 years.

Having established the generic attribution and the likely position of the teeth in the tooth-row, the question of species attribution can be considered. *Palaeoloxodon* from Africa are generally identified as *P. recki*; those from mainland Europe as *P. antiquus*. Remains from the Levant have generally been equated with *P. antiquus* but [Saegusa and Gilbert \(2008\)](#) identified *P. recki* among the earliest (ca. 800 ka) records. The identity of remains from the Arabian Peninsula therefore cannot be assumed, and the situation is further complicated by the evolving molar morphology of *P. recki* through its 3 million year history, with increasing plate number and crown height ([Beden, 1979](#); [Todd, 2001](#); [Lister, 2013](#)). However, given the independent evidence for a Middle Pleistocene age of the Ti's al Ghadah assemblage (Section 4.3), we restrict our comparisons to the latest subspecies, *P. recki recki*, with a known duration of ca. 1.5–0.4 Ma or possibly a little younger ([Sanders et al., 2010](#)). We provisionally exclude its Little to Late Pleistocene descendent *P. iolensis* of North Africa, as its molar morphology shows derived characteristics not shared with *P. recki* or the Ti's al Ghadah molars.

Insufficient comparative work has been done between the molars of *P. recki recki* and *P. antiquus*. However, in terms of occlusal morphology, the two molars available from Ti's al Ghadah can be closely matched with available specimens of both taxa (see, for example, illustrations of *P. recki recki* in [Beden \(1979\)](#), and of *P. antiquus* in [Guenther \(1977\)](#)). Similarly, the measurements that could be taken on these specimens are within the known ranges of both species ([Table 6](#)). The taxa are potentially separable on plate number and hypsodonty index of complete third molars, where their ranges overlap but the variation in both variables extends to lower values in *P. r. recki* and to higher values in *P. antiquus*. The recovery of further dental remains of elephant from Ti's al Ghadah may therefore allow a clearer taxonomic designation in the future. For the present, we follow precedent in referring them to *Palaeoloxodon* cf. *recki* in view of their more likely geographical origin from African populations than European.

4.2.3.4. Bovidae (*Hippotragini*)

4.2.3.4.1. *Oryx* sp.. The vertebrate remains from Unit 5 were

numerically dominated by elements from the Bovidae ([Fig. 5A](#)), although it is not a diverse assemblage; all examined cranial and dental remains, and identifiable post-crania were attributable to the genus *Oryx*. While NISP (number of identified specimens) counts were relatively high compared to other taxa, estimates of minimum numbers of individuals (MNI) compiled for trenches 1 and 2 and 5 and 6, indicated a MNI of 5 (five left mandibles) and 6 (six right metatarsals), respectively and suggest that a relatively low number of individuals were represented. Specimens were rarely encountered in strict anatomical position (occasional cervical vertebrae) but it was clear that multiple skeletal elements from single individuals were recovered in close proximity. The entire skeleton was represented, although the assemblages were characterised by a relative low abundance of specimens from the proximal axial skeleton (humerus and femur; [Fig. 11](#); [Table S7](#) supplementary data).

A number of factors can mediate attrition in different portions of the skeleton and the analysis of skeletal element representation is not a straightforward issue (e.g. [Marean et al., 2004](#)). Given the direct evidence of carnivores recovered on site and the presence of carnivore pits on recovered specimens ([Fig. 12K](#)) however, it is plausible to suggest that the relative low abundance of these appendicular elements may have resulted from removal and/or destruction by scavengers; the presence of “sharp” breaks to specimens ([Fig. 12F, H and J](#)) suggests that trampling by large animals may also have been a destructive factor.

Cheek teeth are robust and hypsodont ([Fig. 12A–D](#)) although on all fully-erupted adult teeth in wear abrasion appears to have been considerable ([Fig. 12B](#)), which we interpret to reflect the presence of abrasives (i.e. sand) in the diet. In all examined maxillary tooth rows, the occlusal morphology is simple and we concur with the observations of [Thomas et al. \(1998\)](#) that the dental morphology of the specimens from Ti's al Ghadah is more similar to extant desert-dwelling species, *Oryx leucoryx* and *Oryx dammah*, rather than *Oryx gazella* or *Oryx beisa*. Accessory columns on the lingual face of upper molars are present in *O. gazella* and *O. beisa* but are poorly developed (if present at all) in *O. dammah* and *O. leucoryx* and these characters are not present or prominent in the specimens from Ti's al Ghadah ([Fig. 12B](#)).

Further examination of maxilla fragments indicates that the infra orbital foramen is located posteriorly to P², as in the genus, although the posterior palatine foramen appears to be located more distally in the fossil specimens, than in comparative material. The curved edge of the posterior palatine encroaches mesially in line with the M³ in *O. beisa*, *O. dammah*, and *O. gazella*, but it does not extend beyond the posterior column of the M³ in comparative material for *O. leucoryx* or the specimens from Ti's al Ghadah ([Fig. 12B](#)).

A small sample of horn cores (e.g. [Fig. 12E](#)) are characteristic of

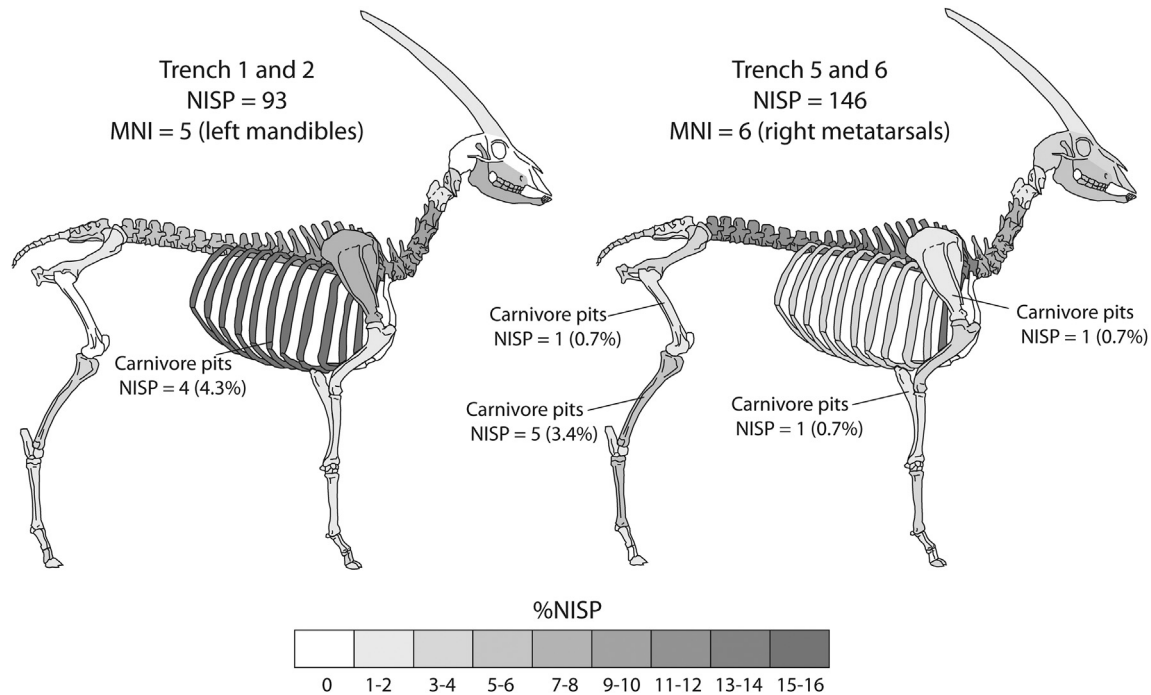


Fig. 11. Skeletal element representation of *Oryx* sp. expressed as % Number of Identified Specimens (NISP; see Table S7 supplementary data), with estimates of Minimum Number of Individuals (MNI) and location of carnivore pits, compiled from excavations of Unit 5 in trenches 1 and 2 and trenches 5 and 6 at Ti's al Ghadah.

the genus and rounded in cross-section, although are rather robust in comparison with available reference material (basal measurements: anterior-posterior mean = 43.00 mm; medio-lateral mean = 41.15 mm, $n = 4$). Thomas et al. (1998) report that Nefud specimens differ from extant *Oryx* spp. by degree of horn core divergence of ca. 35° (Thomas et al., 1998, 149). From the small number of newly recovered specimens ($n = 4$) we estimate a divergence of closer to 20°, but the degree of divergence appears greater than available comparative material for *O. dammah* and *O. leucoryx* and closer to *O. gazella*.

Elements from the post cranial skeleton appear to be relatively large and robust (Table S8 supplementary data). Measurements of proximal epiphyses of the fossil metapodia were used as a proxy for body size and compared with available data from extant taxa. While sample sizes of comparative data from *O. leucoryx* are small, measurements of metacarpals (Fig. 13A) and metatarsals (Fig. 13B) indicate that the specimens from Ti's al Ghadah were larger animals than the endemic Arabian species and approach the size of *O. beisa*.

In summary, the fossil specimens recall *O. leucoryx* in tooth and palatine morphology, but appear to differ in horn core characteristics. The available data show that the Middle Pleistocene oryx at Ti's al Ghadah were larger and more robust animals than the extant Arabian endemic and closer in size to extant *O. beisa*. We withhold a species attribution, but suspect that the oryx of Ti's al Ghadah represents a larger-bodied Pleistocene form of the extant endemic.

4.3. Chronology

4.3.1. Optically stimulated luminescence

Aliquots from sample TAG1-OSL4 from Unit 7 (Fig. 4) are 'well-behaved' according to standard SAR protocol rejection criteria, and signal saturation in one aliquot suggests that the pIRIR290 protocol is yielding a stable luminescence emission without the need for fading correction. Given that all other aliquots were unsaturated, age underestimation due to signal saturation is not a concern for

this sample. Equivalent dose overdispersion ($23.8 \pm 7.1\%$) is low, and suggests that partial bleaching in this unit is a negligible issue. The palaeolake sediments capping the ridge (Unit 7) have a luminescence age of 291 ± 34 ka (Table 7).

4.3.2. U-series dating

U-series results are shown in Tables 8 and 9 for samples 3536 and 3538 and in supplementary information (Table S9–S11 supplementary data) for the other teeth. The tooth samples have unusually high uranium concentrations, on average between 2.0 ppm (3536) and 61.1 ppm (3540) in the enamel and from 139 ppm (3536) to 188 (3540) in the dentine.

Two tissues show evidence of apparent uranium leaching (3536 dentine and 3538 dentine), for which U-series age cannot be calculated. The enamel sections show consistent mean apparent U-series ages ranging from 235.2 ± 5.8 ka to 268.2 ± 12.3 ka, whereas dentine results are somewhat more scattered from 205.3 ± 4.0 ka to 348.1 ± 11.1 ka. U-series results on skeletal materials have generally to be regarded as minimum age estimates (Grün et al., 2014). The finite dentine ages indicate that the minimum age of the faunal remains within Unit 5 is around 350 ka.

4.3.3. Combined U-series and ESR dating

Only two fossil teeth were dated by means of the combined US-ESR approach (samples 3536 and 3538) as all the other samples show U-concentration values in enamel >5 ppm, which is known to be a major issue for accurate age estimation (see Duval et al., 2012). The results of the age calculations are shown in Table 10. The samples display characteristics that are usually found in Early Pleistocene teeth: extremely high D_E values (>3500 Gy), apparent U-leaching in dentine, and high U-concentration values in dentine and enamel. Age calculations were performed by assuming early U uptake for the dentine that showed U-leaching (i.e. $p = -1$). Combined US-ESR age calculations yielded $473 \pm 50/-33$ ka and $554 \pm 79/-76$ ka for samples 3536 and 3538, respectively, resulting



Fig. 12. Examples of fossil crania and post-crania of *Oryx* sp. from Ti's al Ghadah. TAG13/109 right maxilla and tooth row in A: lateral and B: occlusal views. TAG13/147, right mandible and tooth row in C: lateral and D: occlusal views. E: TAG14/216, right horn core and cranial fragment, anterior aspect. F: TAG13/099, left humerus cranial view. G: TAG14/901, complete left metatarsal, dorsal view. H: TAG14/195, fragment of distal left tibia, ventral view. I: TAG14/1518 left astragalus, dorsal aspect. J: TAG13/003 distal metacarpal fragment, dorsal view. K: TAG14/205, rib fragment with carnivore pits. Scale bars = 50 mm.

in a mean value of 512 ± 59 ka (1- σ error). The teeth could be somewhat older if sediment cover was thicker in the past. In the age calculations, a depth of 1.0 ± 0.5 m was used for the calculation of the cosmic ray contribution. However, even when assuming an average depth of 30 ± 5 m, the resulting ages increase only by 1.3% for sample 3536 and 2.2% for sample 3538. This is due to the fact that 95% of the total dose rate is generated within the tooth from the high U-concentrations in the dental tissues. Similarly, water content variability has virtually no impact on the final age results: by considering either 15 or 20%, instead of 10%, the ages slightly increase by <0.5%.

5. Discussion

The vertebrate record of Ti's al Ghadah is an important step toward our understanding of the Pleistocene biogeography in the Arabian Peninsula. While we are mindful that these records derived from a single site, we consider the wider chronological context of the identified taxa with regional biostratigraphic records and then describe the palaeoecological and palaeoenvironmental inferences that may be drawn from the inferred ecological characteristics of the fauna.

5.1. Chronological context

Our initial interpretation of the formation of the Unit 5 assemblages was that they derived from animals moving into the basin with the onset of wetter conditions and that the overlying lake deposit in the ridge, as observed in section (Unit 7; see Fig. 4), represented a later expansion of a contemporaneous lake formation (Stimpson et al., 2015). The earlier work by Rosenberg et al. (2013) suggested a date equivalent to MIS 9 for Unit 5. However, an uncertain stratigraphic position of the sample reported by Rosenberg et al. (2013) may explain the contrast with the findings of our US-ESR analyses from Unit 5 and our OSL date from Unit 7, which suggest that Unit 7 was formed later, likely in MIS 7.

Conversely, U-series analyses of oryx teeth from Unit 5 suggest a minimum age for the Unit 5 fossils of ca. 350 ka and combined US-ESR dating indicates on older age of ca. 500 ka, likely MIS 11. A strict interpretation of the available dating information would be that the Unit 5 assemblages derived from animals associated with an earlier phase of wetting, not represented in section in the ridge, and that there was significant erosion and/or depositional hiatuses after the formation of the Unit 5 stratum and the overlying lacustrine deposits in the ridge. We suspect that the iron-rich, relict lake deposit in the centre of the basin (Section 4.1) represents the contemporaneous lake and the key water resource for faunal populations from which the Unit 5 assemblages derived.

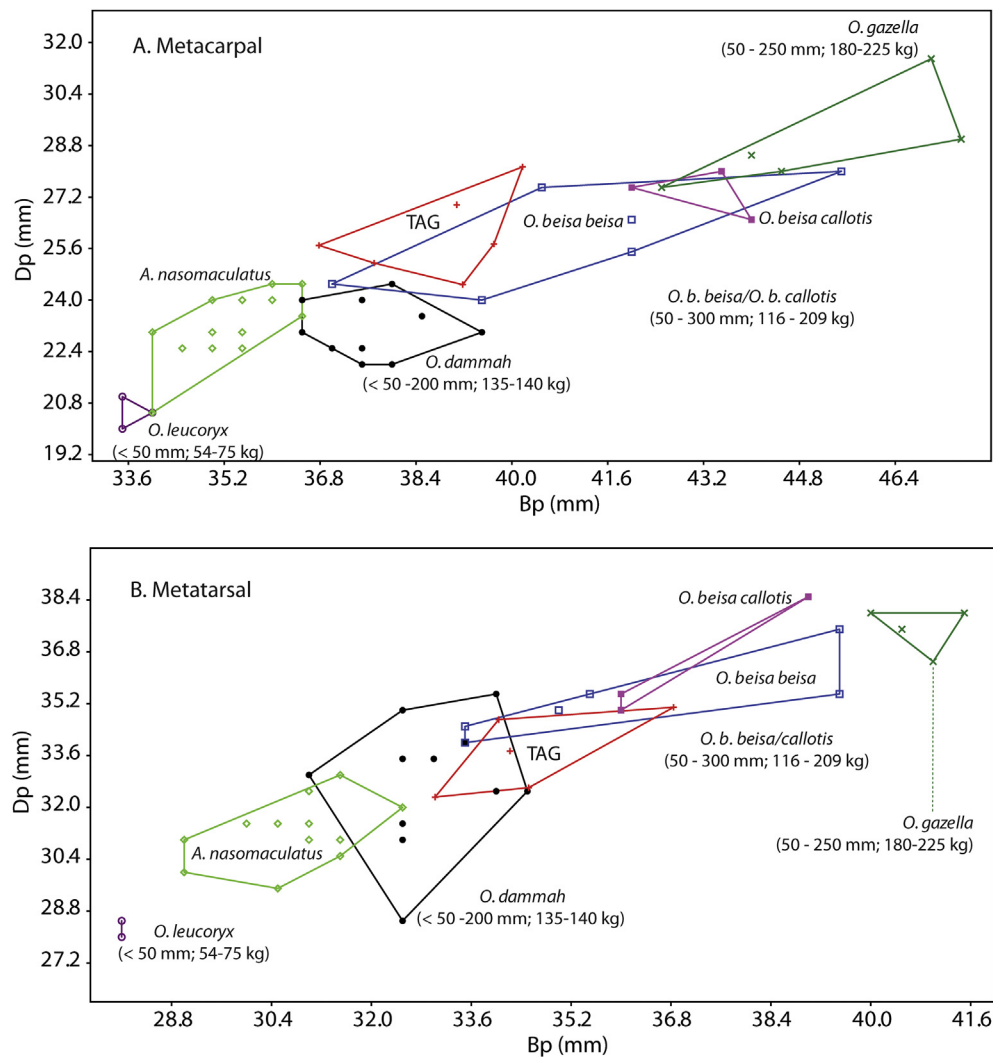


Fig. 13. Measurements of proximal metapodia from fossil *Oryx* sp. from Unit 5 at Ti's al Ghadah, with comparative morphometric data from four extant *Oryx* spp. and *Addax nasomaculatus*. A: proximal breadth (Bp) and proximal depth (Dp) of metacarpals. B: proximal breadth (Bp) and proximal depth (Dp) of metatarsals. Morphometric data compiled from Peters et al. (1997). Ranges of annual rainfall within *Oryx* spp. extant distributions and body weight ranges (from Stanley Price, 1989, 29) are also annotated. Convex hulls fitted in PAST (Hammer et al., 2001).

Table 7
Luminescence dating results for sample TAG1-OSL4. A: pIRIR290 equivalent dose measurements: number of aliquots excluded according to each rejection criterion, and central age model values calculated for the accepted population. B: Values for dose rate calculations and the final sample age.

	Sample	Meas. (#)	Number rejected			Accepted (#)	CAM D _e (Gy)	Overdispersion (%)
			RR	Zero	Sat.			
A	TAG1-OSL4	10	0	1	1	8	628.6 ± 57.8	23.8 ± 7.1

	Sample	Sample Composition			Burial Depth (m)	Internal Dose Rate (Gy ka ⁻¹)	Total Wet Dose Rate (Gy ka ⁻¹)	Age (ka)
		K (%)	Th (ppm)	U (ppm)				
B	TAG1-OSL4	0.41	3.4	1.8	0.25	0.91 ± 0.15	2.16 ± 0.16	291 ± 34

'RR': The ratio of the repeated dose step to the first given dose ('recycling ratio').
'Zero': The ratio of the normalized OSL response of the zero dose step to the natural signal ('zero ratio').
'IR': The ratio of the post-IR repeated dose step to the first given dose ('IR depletion ratio').
'Sat': Aliquots were considered to be saturated if the natural response plus error was greater than the fitted exponential (i.e. Analyst returns an infinite error).

5.2. Biogeographical and biostratigraphical implications of the Ti's al Ghadah fauna

The fossils of Ti's al Ghadah include the first Pleistocene-age bird bones to be reported from the Arabian Peninsula. In terms of biostratigraphy, the utility of the bird fossils identified to species is limited, except to say the identified species are early records and

are known from the region today. The Egyptian vulture is resident in the Arabian Peninsula (and occurs around Ti's al Ghadah) and is widely distributed from southern Europe, North Africa and east to the Indian sub-continent. Black kites are relatively common passage visitors to the Peninsula; a closely related species, *Milvus aegypticus*, is restricted to the southwest. White wagtails (*Motacilla alba*) are also relatively common winter or passage visitors.

Table 8

U-series results on sample 3536. Negative U/Th are due to the background being higher than the measurement. n/a: age calculations not possible, leaching is indicated. All errors are 2- σ .

Sample 3536									
Spot	U (ppm)	Th (ppb)	U/Th	$^{230}\text{Th}/^{238}\text{U}$	$^{230}\text{Th}/^{238}\text{U}$ error	$^{234}\text{U}/^{238}\text{U}$	$^{234}\text{U}/^{238}\text{U}$ error	Age (ka)	Age error (ka)
1	1.41	−0.2	−6337	0.8490	0.0293	1.1960	0.0176	128.4	9.0
2	1.55	0.3	5380	1.1222	0.0322	1.0588	0.0154	n/a	
3	1.64	−0.7	−2443	1.0063	0.0390	1.0548	0.0151	304.6	68.0
4	2.60	0.3	9061	0.9908	0.0270	1.0888	0.0126	241.2	25.9
5	2.83	0.4	7240	1.0468	0.0290	1.0955	0.0175	291.2	46.5
6	132.0	1.2	110,175	1.8516	0.0114	1.6562	0.0030	405.1	17.6
7	133.4	1.6	84,429	2.0311	0.0090	1.6984	0.0040	n/a	
8	145.3	1.3	107,694	2.1153	0.0084	1.7224	0.0059	n/a	
9	131.23	1.2	112,505	2.0140	0.0233	1.6885	0.0071	n/a	
10	152.0	2.3	67,061	1.9047	0.0155	1.6095	0.0035	n/a	
11	204.7	18.4	11,125	1.6274	0.0100	1.4786	0.0054	430.4	26.6
Mean values									
1–5 Enamel	2.01 ± 0.29			1.0096	0.0242	1.0955	0.0112	251.0	25
6–10 Dentine	138.8 ± 4.2			1.9837	0.0075	1.6741	0.0027	n/a	

Table 9

U-series results on sample 3538. Negative U/Th are due to the background being higher than the measurement. n/a: age calculations not possible, leaching is indicated. All errors are 2- σ .

Sample 3538									
Spot	U (ppm)	Th (ppb)	U/Th	$^{230}\text{Th}/^{238}\text{U}$	$^{230}\text{Th}/^{238}\text{U}$ error	$^{234}\text{U}/^{238}\text{U}$	$^{234}\text{U}/^{238}\text{U}$ error	Age (ka)	Age error (ka)
1	0.9	0.0	166,300	0.5428	0.0290	1.2435	0.0270	61.3	4.7
2	4.8	0.1	37,935	1.0823	0.0141	1.3052	0.0104	170.7	6.0
3	3.2	0.2	18,040	1.0047	0.0221	1.1484	0.0137	206.0	15.0
4	2.8	−0.1	−45258	1.1074	0.0328	1.1622	0.0107	269.6	33.6
5	4.4	1.2	3705	1.3042	0.0263	1.3248	0.0131	272.9	23.9
6	11.6	0.3	36,259	1.1768	0.0185	1.1827	0.0079	321.0	29.9
7	137.0	3.4	40,150	1.8820	0.0141	1.5268	0.0059	n/a	
8	140.5	3.1	45,896	1.9089	0.0117	1.5597	0.0022	n/a	
9	145.5	5.6	26,034	1.9141	0.0133	1.5738	0.0048	n/a	
10	164.5	6.9	23,999	1.7657	0.0116	1.5362	0.0029	714.2	185.2
11	213.0	11.5	18,540	1.4530	0.0078	1.4416	0.0049	279.8	7.0
Mean values									
1–6 Enamel	4.62 ± 1.50			1.1321	0.0115	1.2223	0.0064	234.7	8.9
7–11 Dentine	160.1 ± 14.1			1.7545	0.0070	1.5204	0.0020	n/a	

Table 10

ESR parameters and combined ESR-U-series age calculations for samples 3536 and 3538.

	Int. Dose rate ($\mu\text{Gy/a}$)	Beta dose rate dentine ($\mu\text{Gy/a}$)	Beta dose rate sediment ($\mu\text{Gy/a}$)	Gamma dose rate + cosmic ($\mu\text{Gy/a}$)	Total dose rate ($\mu\text{Gy/a}$)	Enamel thick. (μm)	Removed surface layer (μm) on each side	D_E (Gy)	p-parameter		US-ESR age (ka)
									En.	De.	
3536	213 ± 405	8905 ± 1317	32 ± 15	336 ± 35	9485 ± 1378	800 ± 80	20 ± 2	4457 ± 399	−0.83	−1	473 +50/−33
3538	1425 ± 707	5125 ± 863	24 ± 12	336 ± 35	6910 ± 1116	1100 ± 110	20 ± 2	3831 ± 535	−0.58	−1	554 +79/−76

Although no aquatic taxa were confidently identified to species it is worthy of note that little grebes (*Tachybaptus ruficollis*) are resident and readily colonise well-vegetated bodies of water. The black-bellied sandgrouse (*Pterocles orientalis*) is found in Iberia, North Africa and Asia: it is regarded as rare winter visitor to the Arabian Peninsula (Hollom et al., 1998; Porter and Aspinall, 2010).

The extinct *Panthera gombaszogensis* is regarded as Eurasian taxon and is known from the Early to Middle Pleistocene (e.g. Marciszak, 2014). Records for this enigmatic fossil felid are sparse in SW Asia. The specimens from Ti's al Ghadah are the most southerly known records of this taxon, although with the present dating information for the site these records fit well within the

chronological range of this taxon. The Eurasian jaguar is known from the Kudaro faunal unit (MIS 9–11) in the Caucasus and is described from Layer 5c from Kudaro 1, which yielded two thermoluminescence dates of 360 ± 90 ka and 350 ± 70 ka (Baryshnikov, 2002).

We infer the presence of the spotted hyaena (currently restricted to Sub-Saharan Africa) at Ti's al Ghadah from coprolites. A well-preserved mandible is an unequivocal fossil record from elsewhere in the southwestern Nefud Desert, from Locality # 3 (Thomas et al., 1998). It is likely that this locality is site 16.1 of Rosenberg et al. (2013), which yielded OSL dates between 419 ± 39 ka and 286 ± 30 ka (Table 1). While there is no strict

evidence of any chronological affinity between Locality # 3 and Ti's al Ghadah, the coprolites are further indication that the spotted hyaena was present in the Arabian Peninsula in the Middle Pleistocene.

The biogeographic implications of the record of the African golden wolf, *Canis anthus*, are more difficult to consider as the taxonomic affinity of this cryptic canid was clarified only recently. The record from Ti's al Ghadah, however, indicates that it ranged into the Arabian Peninsula in the Middle Pleistocene.

The extinct elephant, *Palaeoloxodon recki*, is known from the Middle Pliocene until the Middle Pleistocene in Africa, where it is conventionally divided into five chronological stages. The elephants of Ti's al Ghadah are morphologically consistent with the latest stage, *P. recki recki*, with known occurrence in East Africa between ca. 1.5–0.4 Ma, although it is not possible to rule out an earlier stage for the small sample of two molars: the potentially diagnostic specimen (the M³) is incomplete. After 0.5 Ma, the African species *P. iolensis*, is believed to be the lineal descendent of *P. recki* and persists until the Late Pleistocene, possibly as late as 75 ka (Sanders et al., 2010). *P. iolensis* lacks the median enamel expansions of *P. recki* that are also seen in the molars from Ti's al Ghadah. However, that a population of the *recki-iolensis* lineage existed in the Arabian peninsula in the Middle Pleistocene is perfectly plausible.

A descendant of *Palaeoloxodon recki*, *P. antiquus*, is known from Europe from Middle to Late Pleistocene (ca. 780 to 50 ka), where it underwent relatively little evolutionary change before going extinct during the last glaciation (Lister, 2004, 2016). *Palaeoloxodon antiquus* has also been identified in the Levant. A *Palaeoloxodon* cranium from Gesher Benot Ya'aqov (GBY), Israel, dated to 780 ka (Goren-Inbar et al., 1994), has been regarded as one of the earliest representatives of this species, and the species has also been identified at Revadim Quarry ("ca. 500–300 ka or possibly more": Rabinovich et al., 2012). However, Saegusa and Gilbert (2008), on the basis of cranial characters, suggested that the GBY cranium might actually be *P. recki*, while the morphology of the Revadim elephants has not been described in sufficient detail to discriminate between the two species. The taxonomic boundary between *P. recki* and *P. antiquus*, in this geographical region and time-interval, is therefore currently blurred, but it cannot be ruled out that the elephants of Ti's al Ghadah might have derived from Europe and eventually be considered to belong to *P. antiquus*.

Further samples from Ti's al Ghadah are required to clarify the range of the equid taxa that are represented at the site, although our identification of a mandible of *E. hemionus* is consistent with regional fossil records. *Equus hemionus* appears as part of fauna of SW Asia and the Levant in the Middle Pleistocene. Specimens are reported from Nadaouiye Aïn Askar (El Kown) in Syria (Savioz and Morel, 2005) and from Levantine sites (Bar-Yosef and Belmaker, 2011) and dated to 300–500 ka, and 100–300 ka, respectively.

We suspect that the *Oryx* sp. of Ti's al Ghadah is likely to be a large but closely-related Pleistocene form of the extant endemic *Oryx leucoryx*. Ancestral populations of early Hippotragini were probably established in the Miocene and these antelopes will likely have been a long-standing presence in the Arabian Peninsula. Fossils of this genus have proved to be common in Pleistocene assemblages of different ages in the southwestern Nefud Desert (Thomas et al., 1998).

Our interpretation of the taxonomic composition of the vertebrates of Ti's al Ghadah is that, like the historical fauna of the Arabian Peninsula, it is a distinct biogeographical admixture. While the evidence from Ti's al Ghadah is further support for assertions that distinct regional zoogeographies were established by the Middle Pleistocene (e.g. O'Regan et al., 2005), it does not necessarily indicate that they were isolated.

5.3. Vertebrate palaeoecology and palaeoenvironments at Ti's al Ghadah

The identified taxa indicate that the Ti's al Ghadah basin was, at least at times, a focal point in the landscape for birds, herbivores and predators and scavengers. However, given that there have been suggestions that Pleistocene lacustrine deposits in the Nefud Desert may represent ephemeral marsh-like habitats, rather than the formation of substantial bodies of water (Enzel et al., 2015), this raises the question of if the Unit 5 assemblages represent animals that were attracted to an ephemeral water source and a relatively brief flush of plants in the dune fields, or were freshwater and plant resources more substantial and long-standing?

At present, it is not possible to determine the degree of time-averaging of the Unit 5 assemblages, although the fossil stratum appears to be a rather discrete unit with little evidence of significant reworking or redeposition. There is clear evidence, however, of a least three discrete episodes of the formation of standing water within the Ti' al Ghadah basin and there is regional evidence of the periodic formation of water bodies throughout southwestern Nefud Desert dating from the Middle Pleistocene onward (Rosenberg et al., 2013). Rosenberg et al. (2013) suggest that large-scale lake and wetland habitats developed across the western Nefud during MIS 11. The inferred presence of a lake at Ti's al Ghadah would be supported by previous reports (Thomas et al., 1998) of a fossil of a relatively large Osteoglossiforme fish (although this was an unstratified specimen) and consistent with the aquatic affinities of two of the identified avian taxa (grebe, duck). Indeed, the presence of the bird taxa identified at the site may parsimoniously be explained as attracted to habitat (grebe, duck, wagtail), to drink (sandgrouse, ostrich) or in a scavenging role (Egyptian vulture, kite).

Oryx, equids and elephant will likewise have been attracted to fresh water and plant resources and we infer that the remains recovered in Unit 5 reflect die-off in populations of these animals. Animal carcasses will have attracted mammalian scavengers such as fox, golden wolf and hyaena and the attention of carnivores is evidenced by tooth marks. Although it was not possible to identify the reptilian fossils to genus it is worth noting that, in this context, the majority of extant *Varanus* spp. are carnivorous and will scavenge animal carcasses, whereas *Uromastix* spp. are primarily herbivorous. It is plausible that the Egyptian vulture also scavenged at the site and it is notable that one of these birds was in turn subject to the attentions of a carnivore.

The establishment of water holes has been shown to have a significant effect on the hunting behaviour of large felids (e.g. Valeix et al., 2010) and the presence of a large-bodied pantherine (ca. 100 kg: see Stimpson et al., 2015) suggests that the biomass of potential vertebrate prey would likely have been substantial in the area (e.g. Carbone and Gittleman, 2002) as would, by inference, plant resources. We also infer the presence of hyaena (cf. *Crocuta crocuta*) from coprolites. While these animals are famed as scavengers and for the demolition of bone, they are dynamic and capable predators. Modern analogues should be applied with caution but it is notable that the taxonomic and ecological composition of the fossil fauna from Ti's al Ghadah bears some resemblance to Namibian desert ecosystems that experience flushes of plant growth in response to increased precipitation. For example, increased wetting prompts a seasonal influx of large number of gemsbok (*Oryx gazella*) to the Kuiseb river from surrounding dune fields (Kok and Nel, 1996) and these antelopes and the mountain zebra (*Equus zebra hartmannae*) are important prey animals for local populations of spotted hyaena (Tilson and Henschel, 1986).

For the *Palaeoloxodon* remains, there is clearly more than one

individual preserved at the site: further excavation is likely to reveal the remains of further elephants and may allow assessment of the age profile of the assemblage, with possible relevance to mode of accumulation. *Palaeoloxodon recki* and *P. antiquus* are estimated to have had a body mass of ca. 10–12 tonnes (Larramendi, 2015) and would have been a social animal living in family groups like living elephants. Elephants require a substantial intake of water (up to 360 L a day in an adult), implying local availability of water. Elephants in semi-desert areas of Africa (Mali and Namibia) undertake substantial migrations in search of food and water, and focus on moist riverside vegetation (e.g. Viljoen, 1989a, b) but Ramey et al. (2013) have demonstrated a reliance on clean, un-fouled water resources.

While the fossil elephants of the Nefud were not necessarily there year round, but perhaps only when food and water supplies allowed, a substantial biomass of vegetation is required to support an elephant herd, even though elephants can survive on relatively low-quality herbage. Microwear and isotopic studies of *Palaeoloxodon* indicate a mixed-feeder taking both graze and browse (Grube et al., 2010; Rivals et al., 2012). The mesowear method of Saarinen et al. (2015) has been applied to the upper molar (TAG14/301) and lower dP₄ (TAG14/281) from Ti's al Ghadah: the former gave an average mesowear angle of 120°, indicating a grass-dominated mixed-feeder (50–70% grass); the latter an angle of 136°, indicating a strongly graze-dominated diet (>90% grass).

The presence of a robust hemione and the feeding habits of extant oryx species are also suggestive of the presence of open, grassland habitats. Extant oryx species are mixed feeders although the majority of the diet consists of coarse grasses occasionally supplemented by ephemeral forbs (Stanley Price, 1989). The Pleistocene oryx of Ti's al Ghadah, however, appears to have been a relatively large-bodied form and available data indicate that the specimens approach the size of extant *O. beisa*. While *Oryx* spp. display marked physiological adaptations to tolerate drought conditions (e.g. Ostrowski et al., 2006), available data for four species indicate that there is a broad but positive correlation between annual rainfall and body weight (Fig. 13). It is plausible to suggest that the relative size of the oryx of Ti's al Ghadah reflected more amenable habitats and that climatic and environmental amelioration was of a sufficient duration to support populations of this larger-bodied form.

In summary, our interpretation of the vertebrate fauna of Ti's al Ghadah is that parts of the southwestern Nefud Desert were characterised by the longstanding (but possibly periodic) presence of substantial water bodies and grassland ecosystems in the Middle Pleistocene. As a case study, the evidence from Ti's al Ghadah is further indication that, at times, the Pleistocene habitats in the Nefud Desert contrasted markedly with the hyper-arid environments of today and contained freshwater and game resources with the potential to support occupation by hominins.

6. Conclusion

The Middle Pleistocene fauna of Ti's al Ghadah reported here, dated to ca. 500 ka, comprises reptiles, birds and mammals. The bird fossils are the first Pleistocene-age records to be reported from the Arabian Peninsula. The mammalian fauna consists of an admixture of African, Eurasian and likely endemic taxa, which we interpret to reflect the geographic situation of the Arabian Peninsula as a crossroads between continents. Chronometric data and the identified vertebrate taxa indicate that areas of the southwest Nefud Desert held (at least periodically) substantial freshwater and plant resources in MIS 11 and were a focal point in the landscape for birds and populations of herbivores (including very large mammals) and their predators and scavengers.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2016.05.016>.

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