Middle Pleistocene vertebrate fossils from the Nefud Desert, Saudi Arabia, and their 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 the site at Ti’s al Ghadah in the southwestern Nefud Desert. U series and combined US-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. Crocuta 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/Uromastyx 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.

Keywords: vertebrates, Pleistocene, desert, Saudi Arabia, lacustrine, palaeoecology, biogeography
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. Dennell and Petraglia, 2012; Groucutt and Petraglia, 2012; Rose and Petraglia, 2010). While the geographical significance of this landmass of over 3 million km$^2$ 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 to 0.011 Ma) are much-debated (e.g. Beyin, 2006; Fernandes, 2009; Fernandes et al., 2006; Groucutt et al., 2015a; O’Regan et al., 2005, O’Regan et al., 2011).

As studies continue to unveil a complex climatic and environmental history (e.g. Breeze et al., 2015; Fleitmann and Matter, 2009; Fleitmann et al., 2003; Fleitmann et al., 2011; Jennings et al., 2015; Matter et al., 2015; Parker, 2009; Parton et al., 2015a; Parton et al., 2015b; Rosenberg et al., 2011; Rosenberg et al., 2013) and the Palaeolithic archaeological record develops (e.g. Armitage et al., 2011; Delagnes et al., 2012; Delagnes et al., 2013; 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; Groucutt et al. 2015c; Scerri et al., 2015; Shipton et al., 2014) 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. Cox et al., 2012; Delany, 1989; Harrison and Bates, 1991; 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 and Kopp et al.,
2014; Fernandes, 2011; 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).

**Fig. 1.** A: The Arabian Peninsula and B: location of Ti’s al Ghadah (TAG-1) and Thomas et al. (1998) fossil sites in the southwestern Nefud.

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 (Cox et al., 2012; Mallon, 2011). These hyper-arid habitats are embodied by three major sands seas that collectively occupy over 700,000 km$^2$: 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 (Breeze et al., 2015; Matter et al., 2015; Parker, 2009; Parton et al., 2015b; Rosenberg et al., 2013; Fig. IA, 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 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, recovered poorly preserved assemblages of bone (Delagnes et al., 2012). 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 of in the interior: the Rub’ al Khali and the Nefud Desert (Fig. IA). 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 amphibious”). 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 in the Nefud Desert (Rosenberg et al., 2013; Thomas et al., 1998). Thomas and colleagues (1998) reported the first Pleistocene fossil collections from a survey of three sites in the southwestern
Nefud Desert (including the site at Ti’s al Ghadah, the focus of this study; Figs. 1B, 2). Despite relatively small sample sizes, a total of 14 taxa (including fish, reptiles and mammals) were identified (Table 1).

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, Thomas et al. (1998), taxa, Stimpson et al. (2015), dates, Rosenberg et al. (2013). X = present; / = no record.

<table>
<thead>
<tr>
<th>REGION</th>
<th>Southwest</th>
<th>Rub’ al Khali</th>
<th>Nefud Desert</th>
</tr>
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<tbody>
<tr>
<td>SITES</td>
<td>Shi’bat Dihya (SD-1)</td>
<td>lacustrine deposits</td>
<td>Khall Amayshan (Thomas loc-1)</td>
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<tr>
<td>DATES (ka)</td>
<td>55</td>
<td>/</td>
<td>99±7/117±8</td>
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<td>Inferred MIS</td>
<td>3</td>
<td>1-3?</td>
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<td>TAXA</td>
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<td>ACTINOPTERYGII</td>
<td>Osteoglossiformes</td>
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<td>SAUROPSIDA</td>
<td>Geochelone cf. sulcata</td>
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<td>REPTILIA</td>
<td>Squamata</td>
<td>/</td>
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<td>AVES</td>
<td>Tachybaptus sp.</td>
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<td>MAMMALIA</td>
<td>Equus sp.</td>
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<td></td>
<td>cf. E. hemionus</td>
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<td>cf. Palaeoloxodon (recki)</td>
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<td></td>
<td>cf. Hexaprotodon sp.</td>
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<td>Hippopotamus sp.</td>
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<td>X</td>
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<td></td>
<td>Suidae: gen et sp. indet.</td>
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<td></td>
<td>Panthera cf. gombazogensis</td>
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<td>Vulpes (cf. vulpes)</td>
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<td>Crocuta crocuta</td>
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<td></td>
<td>Bovidae: gen et sp. indet.</td>
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<td></td>
<td>Pelorovis (cf. oldawayensis)</td>
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<td></td>
<td>Bos cf. primigenius</td>
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<td>Bubalus sp.</td>
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<td>Oryx sp.</td>
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<td>Gazella sp.</td>
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<td>cf. Arbitragus javakari</td>
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<td></td>
<td>Camelidae gen et sp. indet.</td>
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The site at Khall Amayshan (KAM-1 – Thomas locality 1; Fig. 1B) yielded fossils of Equus sp., a large bovid (identified as Pelorovis cf. oldawayensis) and a reportedly gracile hippopotamid...
(Hexaprotodon sp.? that, upon review, is more likely to be Hippopotamus sp. (White et al., forthcoming). Fossils from an unnamed site (“Locality 3” in Thomas et al., 1998; Fig. IB) that is likely site 16.1 of Rosenberg et al. (2013), which yielded OSL dates between 419 ± 39 ka and 286 ± 30 ka, included large bovids (referred to Pelorovis cf. oldawayensis), a well preserved left mandible of Crocuta 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. 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 fish (a specimen we were unfortunately unable to relocate and review), Equus sp., Vulpes sp. and a specimen conferred to the extinct Eurasian jaguar, Panthera (onca) gombaszogensis (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 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.

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 these 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,
and palaeoenvironmental implications of the identified taxa.

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 highlighted in red). C: Excavation of trenches 1 and 2 (numbered in red) 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.

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 (Fig. 1B). 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. 2A, 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. 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-H; 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).
Fig. 3. Plan view of the ridge at the fossil site of Ti’s al Ghadah, showing location of trenches.

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 SCTH. 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 et al.
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 Graeme 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 (Tring- NHM-T) and palaeontological comparative specimens at the NHM-SK.

3.3 Chronology

A sample for OSL dating was 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 deposit and the fossiliferous stratum that underlies it, we sampled the lake deposit for OSL dating (Unit 7) and five fossil cheek teeth (Oryx sp.) that were recovered from Unit 5 were submitted for U-series and combined US-ESR dating (Table S1 supplementary data). Additionally, a series of sediment samples were collected from different depths within Unit 5 to evaluate the variability of the sediment radioactivity.

3.3.1 Optically Stimulated Luminescence

One sample for luminescence dating was collected from the palaeolake sediments capping the excavated sequence (Unit 7; Fig. 4). A metal tube was hammered into a cleaned section, capped, and transported to the Research Laboratory for Archaeology and the History of Art (University of Oxford) for preparation and measurement. Coarse-grained potassium feldspars (180-255 μm) were extracted.
from the consolidated sample via hydrochloric acid treatment, wet sieving, and density separation with sodium polytungstate ($\rho < 2.58 \text{ g cm}^{-3}$). Luminescence measurements were conducted with the *lexsyg smart*, a smaller and simpler version of the *lexsyg research* TL/OSL reader (Richter et al., 2013).

Infrared stimulation was provided by LEDs emitting $850 \pm 20 \text{ nm (} \sim \text{ mW cm}^{-2}\text{)}$ and emissions were detected with a standard bi-alkaline cathode PMT (Hamamatsu) with peak sensitivity at 420 nm. The *lexsyg smart* incorporates a 90Sr/90Y beta ‘flat source’ with a dose rate ~0.15 Gy s\textsuperscript{-1}.

Equivalent doses were measured for ten multigrain feldspar aliquots (1 mm diameter) via the single aliquot regeneration (SAR) post-IR, IR stimulation at 290ºC (pIRIR290) protocol (Thiel et al., 2011). This protocol includes recycling and thermal transfer (‘zero dose’) tests. Net signals were calculated by integrating the first two seconds of emission and subtracting an average background found from the last 50 s. Aliquots were accepted if their recycling ratios were within 10% of unity or overlapped unity at two sigma uncertainty, and if the zero dose step yielded a signal less than 5% of the normalized natural signal or was indistinguishable from 0 at two sigma. Saturated aliquots that passed these two criteria were also rejected from the population used to calculate the luminescence age.

Equivalent doses were calculated with Luminescence Analyst v. 4.11, and the central age model was used to calculate overdispersion values and the population De for age determination (Galbraith et al., 1999). The reported ages have not been corrected for fading (Thiel et al., 2010; Thomsen et al., 2011).

External alpha, beta, and gamma dose rates were calculated from elemental concentrations obtained from homogenized sample sediment via ICP-MS analysis (Activation Laboratories, Ltd., Canada). For internal dose rate calculations, grains are assumed to contain 12.5 ± 0.5% potassium (Huntley and Baril, 1997) and 400 ± 100 ppm rubidium-87 (Huntley and Hancock, 2001). Dose rate conversion factors were obtained from Adamiec and Aitken (1998) for potassium, thorium, and uranium. Grain attenuation for these elements was calculated for alpha and beta dose rates according to Brennan et al. (1991) and Brennan (2003), respectively. The internal absorbed dose rate from rubidium was taken directly from Readhead (2002). This results in an internal feldspar dose rate of 0.91 ± 0.15 Gy ka\textsuperscript{-1}. The external dose rate was corrected according to Zimmerman (1971) for sediment water content assuming a burial average of 5 ± 3 % (water/wet sediment). Cosmic dose rates were
calculated using the modern day burial depths, corrected for geomagnetic latitude and altitude (Prescott

3.3.2 U-series analysis of teeth

Laser ablation U-series analyses were carried out at the Research School of Earth Sciences of the
Australian National University (Australia), using a custom-built laser sampling system interfaced
between an ArF Excimer laser and a MC-ICP-MS Finnigan Neptune (for details, see Eggins et al., 2003;
Eggins et al., 2005), following principles and procedures described in Grün et al. (2014). Enamel and
dentine of teeth were analysed along separate lines. No individual age calculation was carried when the
U-concentrations were below about 0.5 ppm and/or detrital $^{232}\text{Th}$ was observed (elemental U/Th ratios
below 300). The analytical data of the enamel and dentine sections were integrated to provide the data
input for the ESR age calculations.

3.3.3 Combined US-ESR dating of fossil teeth

Fossil teeth were prepared following a standard ESR dating procedure for enamel powder (e.g. Duval
et al., 2011): the enamel layer was mechanically separated from the other dental tissues and both inner
and outer surfaces were removed with a dentist drill to eliminate the volume that received an external
alpha dose. The samples were then ground and sieved to recover the size fraction of $<$200 µm. Dose
evaluation utilised the multiple aliquot additive dose method. The powder was split into several aliquots
and irradiated up to 4019 Gy with a Gammacell1000 Cs-137 gamma source. ESR measurements were
carried out with a Bruker Elexsys 500 spectrometer at the Research School of Earth Sciences (RSES)
of the Australian National University, using the following acquisition parameters: 3–5 scans, 2 mW
microwave power, 1024 points resolution, 12 mT sweep width, 50 kHz modulation frequency, 0.1 mT
modulation amplitude, 20 ms conversion time and 5 ms time constant. The ESR intensities were
extracted from T1-B2 peak-to-peak amplitudes of the ESR signal (Grün, 2000), and then normalised on
the number of scans and mass. All aliquots of a given sample were measured within a short time interval
($<$1 h). This procedure was repeated twice over two successive days without removing the enamel from
the ESR tubes between measurements in order to evaluate measurement precision and thus $D_E$
reproducibility: the latter was found to be excellent, with a variability of <2% between the two repeated measurements.

For dose evaluations, fitting procedures were carried out with the Microcal OriginPro 9.1 software using a Levenberg-Marquardt algorithm by chi-square minimisation. Data were weighted by the inverse of the squared ESR intensity \(1/I^2\) (Grün and Brumby, 1994). Final equivalent dose (\(D_E\)) values were obtained by fitting a single saturating exponential (SSE) through the pooled ESR intensities obtained from the two repeated measurements. Given the magnitude of the \(D_E\) values (>2000 Gy), a maximum irradiation dose (\(D_{\text{max}}\)) of 4019 Gy was used, so that \(D_{\text{max}}/D_E\) ratio remains around 1 as recommended by Duval and Grün (2016) to ensure reliable fitting. The final dose response curves (DRCs) are shown in Fig. S1 (supplementary data).

For the dose rate calculations, the following parameters were used: an alpha efficiency of 0.13±0.02 (Grün and Katzenberger-Apel, 1994), Monte Carlo beta attenuation factors from Marsh (1999), dose-rate conversion factors from Guérin et al. (2011), an estimated water content of 5±3 wt.% in dentine and 10±5 wt.% in sediment. U and Th and K concentrations in raw sediment were determined by ICP-OES and ICP-MS analysis on samples collected within Unit 5 (Table S2 supplementary data).

The mean radioelement concentration values were used for the age calculations. Combined US-ESR ages were calculated with DATA, a DOS-based programme (Grün, 2009) using the US model defined by Grün et al (1988). Further details about this dating method applied to fossil teeth may be found in Duval (2015).

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.
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 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 area of bone in contact with the substrate (less abraded), as exposed during excavation, than the upper surface that was presumably exposed prior to burial (more abraded). Some trampling was evident in the form of the presence of fine stria on the surfaces of bones and “sharp breaks” to specimens (e.g. see Fig. 15F, 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. (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 5C, 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). Following Andrews and Whybrow (2005), the weathering profiles collectively suggest that carcasses were exposed maximally (in arid conditions) for approximately 15 years before burial. However, 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.

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.

4.2 Vertebrate Palaeontology

4.2.1 Reptila

While a small fragment of carapace was recovered from the surface of the ridge deposit (Unit 9), no remains of the Testudinidae have been identified in the excavated materials from Unit 5 (cf. Thomas et al., 1998). However, the Squamata are represented by a small number of relatively large trunk (mid-
dorsal) vertebrae and a single cervical vertebrae (Fig 6A, B; Table 2). Osteological nomenclature and description follows Hoffstetter and Gasc (1969) and Holmes et al. (2010).

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.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Description</th>
<th>GL (mm)</th>
<th>AW (mm)</th>
<th>PW (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAG14/307</td>
<td>mid-dorsal vertebra</td>
<td>13.74</td>
<td>13.6</td>
<td>13.19</td>
</tr>
<tr>
<td>TAG13/049</td>
<td>mid-dorsal vertebra</td>
<td>16.69</td>
<td>17.42</td>
<td>/</td>
</tr>
<tr>
<td>TAG13/Hc-T1</td>
<td>mid-dorsal vertebra</td>
<td>16.26</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>TAG14/706</td>
<td>cervical vertebra</td>
<td>12.24</td>
<td>9.34</td>
<td>6.95</td>
</tr>
</tbody>
</table>


4.2.1.1 Squamata
Varanidae and/or Agamidae - *Uromastyx* 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 *Uromastyx*. The cervical vertebra (TAG14/706), however, lacks a marked hypapophyseal peduncle (Fig. 6B-2), which suggests *Uromastyx* 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) and are the first Pleistocene records of birds to be reported from the Arabian Peninsula. Taxonomic conventions follow Porter and Aspinall (2010) and osteological nomenclature follows Baumel and Witmer (1993).

#### Table 3

Bird fossils recovered from Unit 5 at Ti’s al Ghadah. GL = greatest length; Bp = proximal breadth; Sc = minimum width of shaft; Bd = distal breadth; Dp = proximal depth and Dd = distal depth. All measurements are in millimetres.

<table>
<thead>
<tr>
<th>SPECIMEN</th>
<th>ELEMENT</th>
<th>side</th>
<th>TAXA</th>
<th>GL</th>
<th>Bp</th>
<th>Sc</th>
<th>Bd</th>
<th>Dp</th>
<th>Dd</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAG13/038</td>
<td>tarsometatarsus</td>
<td>L</td>
<td><em>Tachybaptus</em> sp.</td>
<td>32.72</td>
<td>6.50</td>
<td>2.68</td>
<td>5.89</td>
<td>7.14</td>
<td>4.76</td>
</tr>
<tr>
<td>TAG14/185</td>
<td>humerus</td>
<td>L</td>
<td><em>Anas</em> sp.</td>
<td>/</td>
<td>/</td>
<td>6.74</td>
<td>13.50</td>
<td>/</td>
<td>8.04</td>
</tr>
<tr>
<td>TAG14/225</td>
<td>femur</td>
<td>R</td>
<td><em>Milvus cf. migrans</em></td>
<td>/</td>
<td>/</td>
<td>6.44</td>
<td>13.30</td>
<td>/</td>
<td>10.07</td>
</tr>
<tr>
<td>TAG14/246</td>
<td>humerus</td>
<td>R</td>
<td><em>Motacilla cf. alba</em></td>
<td>/</td>
<td>6.34</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>TAG14/251</td>
<td>ulna</td>
<td>L</td>
<td>cf. <em>Motacilla</em></td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>TAG14/259-269</td>
<td>humerus</td>
<td>R</td>
<td><em>Neophron percnopterus</em></td>
<td>/</td>
<td>/</td>
<td>9.64</td>
<td>24.36</td>
<td>/</td>
<td>13.26</td>
</tr>
<tr>
<td>TAG14/270</td>
<td>humerus</td>
<td>L</td>
<td><em>Pterocles orientalis</em></td>
<td>16.34</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>10.98</td>
<td>/</td>
</tr>
<tr>
<td>TAG14/286</td>
<td>ulna</td>
<td>R</td>
<td><em>Neophron percnopterus</em></td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>TAG14/287</td>
<td>cranium</td>
<td>/</td>
<td><em>Neophron percnopterus</em></td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
<td>/</td>
</tr>
<tr>
<td>TAG14/318</td>
<td>c. vertebra XIII</td>
<td>/</td>
<td><em>Struthio</em> sp.</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>

* see Table 4
4.2.2.1 Struthioniformes

Struthionidae

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.

Comparison with the type specimen for the Pleistocene taxon *Struthio asiaticus* (NHM - 23105) suggests that the Nefud specimen was derived from a similarly-sized bird. The type, however, includes a series of articulated cervical vertebrae that are fused in matrix to an atlas, distal tarsometatarsus and phalanx and this state of preservation precludes detailed morphological and metric comparison. However, in terms of overall dimensions, there is no evidence to suggest an affinity with “giant” Pleistocene ostrich taxa reported from the Caucuses (Burchak-Abramovich and Vekua, 1990; Vekua, 2013).

Morphological and morphometric comparisons were also conducted with specimens from extant species (*S. camelus camelus, S. c. australis, S. c. massaicus* and *S. molybdophanes*) and recently extinct species (*S. c. syriacus*); these data are summarised in Table 4. TAG14/318 differs from comparative specimens from the extant and recently-extinct species, *S. c. australis* and *S. c. syriacus*, respectively. 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-3) 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* (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 4).
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.

Table 4

Characters and measurements for specimen TAG14/318 and comparative *Struthio* spp. examined at NHM-Tring.

Measurements: GL = greatest length; B cran = cranial breadth; B caud = caudal breadth; H cran = cranial height.

All measurements were taken from the dorsal surface and are in millimetres.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Taxon</th>
<th>Characters</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>GL (dor)</th>
<th>B cran</th>
<th>B caud</th>
<th>H cran</th>
<th>notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAG14/318</td>
<td><em>Struthio</em> sp.</td>
<td>v-shaped</td>
<td>square</td>
<td>flat</td>
<td>71.96</td>
<td>38.64</td>
<td>38.73</td>
<td>(27.96)</td>
<td>crushed d/v</td>
<td></td>
</tr>
<tr>
<td>1857.2.24.10</td>
<td><em>S. australis</em></td>
<td>u-shaped</td>
<td>round</td>
<td>rounded</td>
<td>73.61</td>
<td>40.7</td>
<td>42.16</td>
<td>32.12</td>
<td>female</td>
<td></td>
</tr>
<tr>
<td>1888.3.5.1</td>
<td><em>S. molybdophanes</em></td>
<td>v-shaped</td>
<td>square</td>
<td>flat</td>
<td>70.4</td>
<td>40.05</td>
<td>43.02</td>
<td>28.42</td>
<td>Somalialia</td>
<td></td>
</tr>
<tr>
<td>1846.10.17.7</td>
<td><em>S. camelus</em></td>
<td>u-shaped</td>
<td>round</td>
<td>rounded</td>
<td>77.24</td>
<td>42.43</td>
<td>44.05</td>
<td>35.52</td>
<td>male - Gambia</td>
<td></td>
</tr>
<tr>
<td>1915.3.30.1</td>
<td><em>S. massaicus</em></td>
<td>inter.</td>
<td>round</td>
<td>flat</td>
<td>71.7</td>
<td>35.42</td>
<td>37.12</td>
<td>29.98</td>
<td>male</td>
<td></td>
</tr>
<tr>
<td>S.1972.1.2</td>
<td><em>S. camelus</em></td>
<td>inter.</td>
<td>round</td>
<td>rounded</td>
<td>75.48</td>
<td>42.02</td>
<td>44.96</td>
<td>29.96</td>
<td>female - captive</td>
<td></td>
</tr>
<tr>
<td>S.1954.5.1</td>
<td><em>S. camelus</em></td>
<td>u-shaped</td>
<td>round</td>
<td>rounded</td>
<td>70.84</td>
<td>36.91</td>
<td>40.79</td>
<td>31.16</td>
<td>female - captive</td>
<td></td>
</tr>
<tr>
<td>1923.6.10.1</td>
<td><em>S. syriacus</em></td>
<td>u-shaped</td>
<td>square</td>
<td>rounded</td>
<td>61.42</td>
<td>31.96</td>
<td>38.32</td>
<td>24.36</td>
<td>extinct</td>
<td></td>
</tr>
<tr>
<td>1924.4.81</td>
<td><em>S. syriacus</em></td>
<td>u-shaped</td>
<td>square</td>
<td>rounded</td>
<td>62.06</td>
<td>36.24</td>
<td>40.08</td>
<td>27.64</td>
<td>extinct</td>
<td></td>
</tr>
</tbody>
</table>

1 – shape of foramen vertebra; 2 – shape of lacuna interzygapophyses 3 – shape of caudal articular facets.

4.2.2.2 Podicipediformes

Podicipedidae

*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, *T. 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 height to the condylus interarticularis (cf. Fjeldså, 2004, 214).
TAG13/038 is notably shorter overall (Fig. 7A), 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 S3 supplementary data) and extant Oriental subspecies are “generally smaller” than their counterparts from higher latitudes (Fjeldså, 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 comparatives. 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.

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**Fig. 7.** Bivariate plots to show A: measurements of tarsometatarsus TAG13/038, Tachybaptus sp., with comparative specimens of *T. ruficollis* (open square) and *T. pelzelnii* (closed square) at NHM-Tring. GL = greatest length; Bp = proximal breadth. B: measurements of the proximal humerus TAG14/270, Pterocles orientalis with comparative specimens of *Pterocles* spp. and Syrrhaptes sp. Bp = proximal breadth; Dp = proximal depth.
4.2.2.3 Accipitriformes

Accipitridae

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 was recovered in two pieces (Fig 6E iii and iv). There is extensive evidence of gnawing/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 × 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.

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).
4.2.4 Pteroclidiformes

Pteroclididae

*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. 7B; Table S4 supplementary data) and all observable characteristics match those of *P. orientalis*.

4.2.5 Anseriformes

Anatidae

*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*)

4.2.6 Passeriformes

Motacillidae

*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 *M. alba*.

4.2.3 Mammalia

4.2.3.1 Carnivora
Felidae

Panthera

A total of four specimens known from Ti’s al Ghadah are attributable to the genus Panthera (Table 5).

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 (onca) 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 P. onca gombaszogensis (Table S5, Fig. S2 supplementary data). The genus is also represented by a phalanx (TAG14/339) and broken mandibular canine (TAG13/145) (Fig. 8A, B).

Table 5

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 = breath across jugal processes; Ltald = length of talonid. All measurements are in millimetres.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Element</th>
<th>Taxon</th>
<th>Measurements</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>JMI 27</td>
<td>left metacarpal III</td>
<td>Panthera cf. gombaszogensis</td>
<td>GL = 91.94; Bp = 22.16; Dp = 20.70; MDAP = 11.74; MWML = 12.05; Bd = 20.75; Dd = 18.21</td>
<td>Thomas et al. (1998); metrics: this study</td>
</tr>
<tr>
<td>TAG13/097</td>
<td>right metacarpal IV</td>
<td>Panthera cf. gombaszogensis</td>
<td>GL = 88.72; Bp = 17.16; Dp = 19.14; MDAP = 11.74; MWML = 11.40; Bd = 17.30; Dd = 18.04</td>
<td>Stimpson et al. (2015)</td>
</tr>
<tr>
<td>TAG13/145</td>
<td>mandibular canine</td>
<td>Panthera sp.</td>
<td>M-D = &gt; 17.00; B-L = 13.22</td>
<td>this study</td>
</tr>
<tr>
<td>TAG14/339</td>
<td>phalanx I</td>
<td>Panthera sp.</td>
<td>GL = 48.70; Bp = 19.20; Dp = 14.91</td>
<td>this study</td>
</tr>
<tr>
<td>TAG14/245</td>
<td>occipital</td>
<td>Canis sp.</td>
<td>HFM = 16.1; WFM = 18.30; WOC = 30.77; BJP = 42.58</td>
<td>this study</td>
</tr>
<tr>
<td>TAG14/184</td>
<td>M1 (carnassial)</td>
<td>Canis anthus</td>
<td>M-D = 21.20; B-L = 8.04; Ltald = 6.22</td>
<td>this study</td>
</tr>
</tbody>
</table>

Hyaenidae
cf. Crocuta crocuta
A total of seven coprolites were during the excavations: six specimens from trench 1 and a one specimen from trench 6. The general morphology of intact specimens - a near circular cross-section, with convex and concave ends - closely resembles hyena, most likely *Crocuta crocuta* (Larkin pers comm.; Parfitt pers. comm). Measurements (following Larkin et al., 2000) of one complete specimen, TAG14/256 (Fig. 8C: 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).

Canidae

*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 a medium-sized canid. The skull fragment consists of the occipital region and a fragment of the supra-occipital (Fig. 8D). 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*: measurements indicate that it derived from a relatively large individual (Table 5).

**Fig. 8.** Carnivora fossils from 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. *Crocuta 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.

*Canis anthus* (syn. *Canis aureus* [lupaster]; *Canis lupus lupaster*)

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. 8E). 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 burial as there is minimal modification to this surface of the tooth (Fig. 8E i). Conversely, the lingual side is abraded across the entire surface (Fig. 8E ii).

TAG14/184 is too large to have derived from any known *Vulpes* sp. and is from a medium-sized canid (Table 5). The carnassial is trenchant, with a sub-equal bicuspid talonid (Fig. 8E ii-1) and a relatively well-developed metaconid (Fig. 8E 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 and regional *C. lupus lupus* (cf. Flower and Shreve, 2014; Sansalone et al., 2015), recent records of *C. lupus pallipes* (cf. Dayan, 1994) and Pleistocene and recent records of *C. lupus arabs* from the Levant (Fig. 9). Conversely, measurements from TAG14/184 suggest that it derived from an animal that is larger than recent European jackals, recent and Pleistocene African jackals (*C. aureus s.s*) and match equivalent measurements of a large form of jackal, variously classified as *Canis aureus lupaster* or *Canis lupus lupaster* (Fig. 9).

Osteological studies have long recognised the likelihood of a large extant form of jackal in North Africa (Huxley, 1880) and “large” jackal fossils (classified as *Canis aureus*) are known from Middle to Late Pleistocene in Northwest Africa (Geraads, 2011). Recent work with mitochondrial and nuclear genome data, however, has indicated that these North African “jackals” are a cryptic species more closely related to grey wolves (*C. lupus*) and occupy a much wider geographical area and range.
of habitats in Africa than was previously thought (Rueness et al., 2011; Gaubert et al., 2012; Koepfli et al., 2015). The trenchant morphology and morphometric characteristics of TAG14/184 are a close match for these “large forms” and we follow Koepfli et al. (2015) and refer this specimen to *Canis anthus*, the African golden wolf.

Fig. 9. 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 (M1) from recent and fossil *Canis* sp. with fossil specimen TAG14/184. Data compiled from Kurten, 1965; Dayan et al., 1992; Dayan, 1994; Rook and Azzaroli Puccetti, 1996; Baryshnikov, 2012; Stoyanov, 2012; Measurements of recent *C. lupus arabs* were also taken from comparative specimens at the HZM.

*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.

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

**Equidae**

In addition to small numbers of rib fragments and a thoracic vertebrae, three well preserved specimens attributable to the Equidae were recovered (Table 6): a fragment of a right mandible (TAG14/329; Fig. 10A, B), a complete left astragalus (TAG14/342; Fig. 10C) and a near-complete left femur (TAG13/146; Fig. 10D).

#### Table 6

Measurements of fossils of the Equidae from 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.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Element</th>
<th>MD</th>
<th>BL</th>
<th>Lo</th>
<th>lo</th>
<th>LDB</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAG14/329</td>
<td>right mandible</td>
<td>M3 (c.33.85)</td>
<td>15.98</td>
<td>(c. 32)</td>
<td>13.2</td>
<td>14.81</td>
</tr>
<tr>
<td></td>
<td></td>
<td>M2</td>
<td>25.6</td>
<td>18.88</td>
<td>25.08</td>
<td>14.18</td>
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<table>
<thead>
<tr>
<th>Specimen</th>
<th>Element</th>
<th>GL</th>
<th>mL</th>
<th>Bp</th>
<th>Sc</th>
<th>Bd</th>
<th>Dd</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAG13/146</td>
<td>left femur</td>
<td>c. 350</td>
<td>306</td>
<td>c. 114.66</td>
<td>43.77</td>
<td>96.68</td>
<td>c. 100</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Element</th>
<th>1</th>
<th>2</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAG14/342</td>
<td>left astragalus</td>
<td>65.16</td>
<td>66.5</td>
<td>67.91</td>
<td>56.16</td>
<td>37.9</td>
<td>57.65</td>
</tr>
</tbody>
</table>

The Pleistocene equids of the Middle East are generally thought to comprise of *E. caballus*, *E. hydruntinus* and *E. 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 unequivocal (e.g. Azzaroli and Stanyon, 1991; Giegl and Grange, 2012) and the nomenclature employed in schemes varies between authorities. For TAG14/329, we follow criteria described in Davis.
Stimpson et al. Ti’s al Ghadah vertebrates - 12/01/2016


**Fig. 10.** Fossils of Equidae from 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.

*Equus hemionus*

TAG14/329 is a fragment of a robust right mandible (Fig. 10A). The first molar is broken off at the root below the alveolus, but the worn second and third molars are in situ. The M₂ is intact. The M₃ is largely complete but is there is a break to the distal occlusal surface (Fig. 10B). Cabaloid horses can be discounted as the double knots on M₂ and M₃ are rounded (Fig. 10B-1) with v-shaped (rather than u-shaped) lingual valleys (linguaflexids; Fig. 10B-2) and rounded (rather than flat) buccal margins of the protoconid and hypoconid (Fig. 10B-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. 10B-4). This would discounts zebras and zebra-like taxa, the extinct *E. hydruntinus* and Pleistocene stenonine horses and indicate the hemione, *E. hemionus*. Morphometric comparisons using the intact M₂ of TAG14/329 suggest the dimensions of the occlusal surface are larger than equivalent
data from 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, *E. kiang* (Fig. 11).

**Fig. 11.** Bivariate plot to show length of occlusal surface (Lo) and width of occlusal surface (lo) of second lower molars (*M₂*) for five subspecies of *Equus hemionus*, *E. kiang* and *E. africanus* with fossil specimen TAG14/329. Comparative data compiled from [http://www.vera-eisenmann.com/](http://www.vera-eisenmann.com/). Convex hulls fitted in PAST (Hammer et al., 2001).

*Equus* sp.

In terms of the small sample of post-crania, the specimens are rather robust. The dimensions of a nearly complete left femur TAG13/146 (Table 6; Fig. 10D), notable for the presence of carnivore pits on the caudal surface, near to the proximal end (Fig. 10D-5), indicate that this specimen is large and robust in comparison to extant hemiones (Fig. 12A). The dimensions of a complete left astragalus (TAG14/342; Fig. 10C), which was found in close association with mandible TAG14/329, are also large and robust in comparison to extant hemiones (Fig. 12B). We cannot assume, however, that the two specimens derived from the same individual and a PCA analyses of six variables (Table 6) suggests that is also of a size and proportion of larger equid taxa than the extant hemiones, equivalent perhaps to *Equus oldowayensis* (Fig. 12B). 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.

**Fig. 12.** A: Bivariate plot to show medial length (mm) and distal breath measurements of fossil femur TAG13/146 with comparative data from five sub-species of *E. hemionus*, *E. kiang* and *E. gevyi*. Comparative data compiled from [http://www.vera-eisenmann.com/](http://www.vera-eisenmann.com/). Convex hulls fitted in PAST (Hammer et al., 2001). B: Principal components analysis scatter for six metric variables of fossil astragalus TAG14/342 and comparative data from extant and extinct *Equus* spp. Data compiled from [http://www.vera-eisenmann.com/](http://www.vera-eisenmann.com/), Alberdi and Palombo (2013) and comparative specimens at NHM-SK.

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 indicates, or secondly that the equid remains at Ti’s al Ghadah 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; Fig. 5A*). Here, we focus on the taxonomic diagnosis of two diagnostic specimens, an upper molar TAG14/301 (*Fig. 13A, B*) and a mandible of a young animal, TAG14/281 (*Fig. 13C, D*).

**Elephantidae**

*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. 13A*). 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 molar in early to mid-wear.
Fig. 13. Elephantidae fossils from 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.

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
is problematic for TAG14/301. The width of the crown reduces very slightly from front to back (Table
7), 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 7 shows measurements
for the Ti’s al Ghadah teeth, in comparison with published data for $P. antiquus$ and $P. recki recki$, the
latest chrono-subspecies, with a chronological range in East Africa of ca. 1.2 – 0.5 Ma.

Table 7

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 ± standard deviation for samples where \( n > 5 \).

<table>
<thead>
<tr>
<th>Width</th>
<th>Length</th>
<th>Plate number</th>
<th>Lamellar Frequency</th>
<th>Enamel Thickness</th>
<th>Hypsodonty Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>M(^2)TAG 14/301</td>
<td>90.5</td>
<td>&gt;171</td>
<td>( \geq 15 )</td>
<td>6.40</td>
<td>2.7</td>
</tr>
<tr>
<td>M(^2) <em>P. recki recki</em></td>
<td>65-80</td>
<td>250</td>
<td>10</td>
<td>5.0-6.8</td>
<td>2.0-2.5</td>
</tr>
<tr>
<td>M(^3) <em>P. recki recki</em></td>
<td>89.2 ± 7.6</td>
<td>315-360</td>
<td>13-19</td>
<td>5.82 ± 0.74</td>
<td>2.73 ± 0.29</td>
</tr>
<tr>
<td>M(^3) <em>P. antiquus</em></td>
<td>74.1 ± 7.99</td>
<td>200 ± 33</td>
<td>11.7 ± 1.0</td>
<td>6.57 ± 0.99</td>
<td>2.33 ± 0.38</td>
</tr>
<tr>
<td>M(^4) <em>P. antiquus</em></td>
<td>83.4 ± 6.89</td>
<td>284 ± 40</td>
<td>17.3 ± 1.5</td>
<td>6.18 ± 0.82</td>
<td>2.68 ± 0.51</td>
</tr>
<tr>
<td>dP(_4) TAG 14/281</td>
<td>[( \geq 44 )]</td>
<td>128</td>
<td>10</td>
<td>9.13</td>
<td>1.3</td>
</tr>
<tr>
<td>dP(_4) <em>P. recki recki</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>dP(_4) <em>P. antiquus</em></td>
<td>47.3 ±6.5</td>
<td>98-145</td>
<td>9-11</td>
<td>8.92 ± 1.43</td>
<td>1.50 ± 0.31</td>
</tr>
</tbody>
</table>

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.

The juvenile mandible TAG 14/281 preserves dP\(_4\) complete: its lamellar formula is x10x (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 M\(^3\) and dP\(_4\) 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 M\(^3\) and 136° for the dP\(_4\). The dP\(_4\) 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 Middle 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 7). 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

**Hippotraginae**

*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. 14).

![Skeletal element representation of *Oryx* sp. expressed as % Number of Identified Specimens (NISP), with estimates of Minimum Number of Individuals (MNI) and location of carnivore pits, compiled from trenches 1 and 2 and trenches 5 and 6 at Ti’s al Ghadah.](image)

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. 15K) 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. 15F, H and J) suggests that trampling by large animals may also have been a destructive factor.


Cheek teeth are robust and hypsodont (Fig. 15A-D) although on all fully-erupted adult teeth in wear abrasion appears to have been considerable (Fig. 15B), 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, *O. leucoryx* and *O. dammah*, rather than *O. gazella* or *O. 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. 15B).

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. 15B).

A small sample of horn-cores (e.g. Fig 15E) are characteristic of 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; medial 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 S6 supplementary data). A morphometric examination of the maximum dimensions of proximal epiphyses of fossil metapodia was employed as an index to consider relative body size with available data from extant taxa. While sample sizes of comparative data from *O. leucoryx* are small, measurements of metacarpals (Fig. 16A) and metatarsals (Fig. 16B) indicate that the specimens from Ti’s al Ghadah were larger animals than the endemic species and approach the size of equivalent measurements 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 suggest 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

TAG1-OSL4 aliquots 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, though, age underestimation due to signal saturation is not a concern for this sample. Equivalent dose overdispersion (23.8 ± 7.1 %) is among the lowest values measured with the same protocol for similar samples in the Nefud (Clark-Balzan et al., in prep; White et al., in prep). This level of overdispersion both supports the assumption of signal stability, as fading values vary significantly between feldspar grains from the Rub’ al Khali (Trauerstein et al., 2012) and would be unlikely to average each other so precisely, and suggests that partial bleaching is a negligible issue. The palaeolake sediments capping the ridge (Unit 7) have a luminescence age of 291 ± 34 ka (Table 8).

Table 8

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.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Meas. (#)</th>
<th>Number Rejected</th>
<th>Accepted</th>
<th>CAM D$_{\text{e}}$ (Gy)</th>
<th>Overdispersion (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>TAG1-OSL4</td>
<td>10</td>
<td>0 RR</td>
<td>0 Zero</td>
<td>8 Sat.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>628.6 ± 57.8</td>
<td>23.8 ± 7.1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Sample</th>
<th>Sample Composition</th>
<th>Burial Depth (m)</th>
<th>Internal Dose Rate (Gy ka$^{-1}$)</th>
<th>Total Wet Dose Rate (Gy ka$^{-1}$)</th>
<th>Age (ka)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>TAG1-OSL4</td>
<td>0.41 K (ppm)</td>
<td>3.4 Th (ppm)</td>
<td>0.25 U (ppm)</td>
<td>0.91 ± 0.15</td>
</tr>
</tbody>
</table>

*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).

4.3.2 U-series dating

U-series results are shown in Tables 9 and 10 for samples 3536 and 3538 and in supplementary information (Tables S7 – S9) 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.
Table 9

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.

<table>
<thead>
<tr>
<th>Sample 3536</th>
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</tr>
</thead>
<tbody>
<tr>
<td>Spot</td>
<td>U (ppm)</td>
<td>Th (ppb)</td>
<td>U/Th</td>
<td>$^{230}$Th/$^{238}$U</td>
<td>$^{230}$Th/$^{238}$U</td>
<td>Age (ka)</td>
</tr>
<tr>
<td>1</td>
<td>1.41</td>
<td>0.2</td>
<td>-6337</td>
<td>0.8490</td>
<td>0.0293</td>
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</tr>
<tr>
<td>2</td>
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<td>0.3</td>
<td>5380</td>
<td>1.1222</td>
<td>0.0322</td>
<td>1.0588</td>
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<tr>
<td>3</td>
<td>1.64</td>
<td>0.7</td>
<td>-2443</td>
<td>1.0063</td>
<td>0.0390</td>
<td>1.0548</td>
</tr>
<tr>
<td>4</td>
<td>2.60</td>
<td>0.3</td>
<td>9061</td>
<td>0.9908</td>
<td>0.0270</td>
<td>1.0888</td>
</tr>
<tr>
<td>5</td>
<td>2.83</td>
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<td>1.0468</td>
<td>0.0290</td>
<td>1.0955</td>
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<td>6</td>
<td>132.0</td>
<td>1.2</td>
<td>110175</td>
<td>1.8516</td>
<td>0.0114</td>
<td>1.6562</td>
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<tr>
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<td>0.0090</td>
<td>1.6984</td>
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<td>8</td>
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<tr>
<td>9</td>
<td>3</td>
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<td>112505</td>
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<td>0.0233</td>
<td>1.6855</td>
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<tr>
<td>10</td>
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<td>67061</td>
<td>1.9047</td>
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<td>1.6095</td>
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<tr>
<td>11</td>
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<td>18.4</td>
<td>11125</td>
<td>1.6274</td>
<td>0.0100</td>
<td>1.4786</td>
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</table>

Mean values

<p>| | | | | | | |</p>
<table>
<thead>
<tr>
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<th></th>
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</thead>
<tbody>
<tr>
<td>1-5</td>
<td>2.01</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Enamel</td>
<td>±0.29</td>
<td>1.0096</td>
<td>0.0242</td>
<td>1.0955</td>
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<tr>
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<td>1.9837</td>
<td>0.0075</td>
<td>1.6741</td>
<td>0.0027</td>
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</tr>
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</table>

Table 10

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.

<table>
<thead>
<tr>
<th>Sample 3538</th>
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</thead>
<tbody>
<tr>
<td>Spot</td>
<td>U (ppm)</td>
<td>Th (ppb)</td>
<td>U/Th</td>
<td>$^{230}$Th/$^{238}$U</td>
<td>$^{230}$Th/$^{238}$U</td>
<td>Age (ka)</td>
</tr>
<tr>
<td>1</td>
<td>0.9</td>
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<td>166300</td>
<td>0.5428</td>
<td>0.0290</td>
<td>1.2435</td>
</tr>
<tr>
<td>2</td>
<td>4.8</td>
<td>0.1</td>
<td>37935</td>
<td>1.0823</td>
<td>0.0141</td>
<td>1.3052</td>
</tr>
<tr>
<td>3</td>
<td>3.2</td>
<td>0.2</td>
<td>18040</td>
<td>1.0047</td>
<td>0.0221</td>
<td>1.1484</td>
</tr>
<tr>
<td>4</td>
<td>2.8</td>
<td>-0.1</td>
<td>-45258</td>
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<td>0.0328</td>
<td>1.1622</td>
</tr>
<tr>
<td>5</td>
<td>4.4</td>
<td>1.2</td>
<td>3705</td>
<td>1.3042</td>
<td>0.0263</td>
<td>1.3248</td>
</tr>
<tr>
<td>6</td>
<td>11.6</td>
<td>0.3</td>
<td>36259</td>
<td>1.1768</td>
<td>0.0185</td>
<td>1.1827</td>
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<tr>
<td>7</td>
<td>137.0</td>
<td>3.4</td>
<td>40150</td>
<td>1.8820</td>
<td>0.0141</td>
<td>1.5268</td>
</tr>
<tr>
<td>8</td>
<td>140.5</td>
<td>5.1</td>
<td>45896</td>
<td>1.9089</td>
<td>0.0117</td>
<td>1.5597</td>
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<tr>
<td>9</td>
<td>145.5</td>
<td>5.6</td>
<td>26034</td>
<td>1.9141</td>
<td>0.0133</td>
<td>1.5738</td>
</tr>
<tr>
<td>10</td>
<td>164.5</td>
<td>6.9</td>
<td>23999</td>
<td>1.7657</td>
<td>0.0116</td>
<td>1.5362</td>
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<tr>
<td>11</td>
<td>213.0</td>
<td>11.5</td>
<td>18540</td>
<td>1.4530</td>
<td>0.0078</td>
<td>1.4416</td>
</tr>
</tbody>
</table>

Mean values

<p>| | | | | | | |</p>
<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td>1-6</td>
<td>4.62</td>
<td>1.321</td>
<td>0.0115</td>
<td>1.2223</td>
<td>0.0064</td>
<td>234.7</td>
</tr>
<tr>
<td>Enamel</td>
<td>±1.50</td>
<td>1.7545</td>
<td>0.0070</td>
<td>1.5204</td>
<td>0.0020</td>
<td>n/a</td>
</tr>
<tr>
<td>7-11</td>
<td>160.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dentine</td>
<td>±14.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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 US-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 11. 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+50-33 ka and 554+79-76 ka for samples 3536 and 3538, respectively, resulting in a mean value of 512+59 ka (1-$\sigma$ error).

### Table 11

<table>
<thead>
<tr>
<th>Sample</th>
<th>Beta dose rate dentine (µGy/a)</th>
<th>Beta dose rate sediment (µGy/a)</th>
<th>Total dose rate + cosmic (µGy/a)</th>
<th>Enamel thick. (µm)</th>
<th>Removed surface layer (µm) on each side</th>
<th>$D_E$ (Gy)</th>
<th>$p$-parameter</th>
<th>US-ESR age (ka)</th>
</tr>
</thead>
<tbody>
<tr>
<td>3536</td>
<td>213 ±405</td>
<td>1805 ±1317</td>
<td>32 ±35</td>
<td>9485 ±1378</td>
<td>800 ±20</td>
<td>4457 ±399</td>
<td>-0.83</td>
<td>470 ±50-32</td>
</tr>
<tr>
<td>3538</td>
<td>1425 ±707</td>
<td>24 ±15</td>
<td>336 ±35</td>
<td>6910 ±1100</td>
<td>20 ±2</td>
<td>3831 ±535</td>
<td>-0.58</td>
<td>554 ±79-76</td>
</tr>
</tbody>
</table>

## 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.

The OSL date from the “capping” lacustrine deposits of the ridge, however, suggests that this formation was later, likely 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 an older age and that the assemblages derived from 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 lake formation, 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.

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 their utility is limited, except to say the identified species are relatively early records and are known from regional records today (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 hyena (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 inferred presence of these predators at Ti’s al Ghadah is further indication of a Middle Pleistocene context for this species. The spotted hyena is known from Levantine sites until at least the Middle Pleistocene (e.g. Bar-Yosef and Belmaker, 2011) and it appears that it was also a component of the fauna of the Arabian Peninsula during this time.

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. This species clearly has a larger extant geographic range in Africa than previously thought and the record from Ti’s al Ghadah suggests 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 of P. recki, 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 lack 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, 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 *Equus hemionus* is consistent with regional fossils records. *Equus hemionus* appears as part of fauna of SW Asia and the Levant in the Middle Pleistocene. Specimens are reported from Nadaouiyeh Ain 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 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; White et al., forthcoming).

### 5.3 Vertebrate palaeoecology and palaeoenvironments and 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, herbivorous mammals 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 whether 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 these resources more substantial and long-standing at Ti’s al Ghadah or in the wider Nefud Desert?

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 at 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; White et al., forthcoming). Rosenberg et al. (2013) suggest the possibility 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 of a fossil of a relatively large Osteoglossiforme fish (although his 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, wolf and hyaena and the attention of carnivores is evidenced by tooth marks. Although it was not possible to identify to 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 Uromastyx spp. are primarily herbivorous. It is plausible that the Egyptian vulture also scavenged at the site, but it is notable that one of these birds were 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 hyena (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 dunefields (Kok and Nel, 1996) and these antelopes and the mountain zebra (Equus zebra hartmannae) are important prey animals for local populations of spotted hyena (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 litres 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 indicates that the specimens approach the size of the 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. 16). 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.

6. Conclusion

The Middle Pleistocene fauna of Ti’s al Ghadah reported here, dated to ca. 500 ka, comprises of 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. The identified vertebrate taxa indicate that areas of the southwest Nefud Desert in MIS 11 held (at least periodically) substantial freshwater and plant resources and were a focal point in the landscape for birds and populations of herbivores (including very large mammals) and their predators and scavengers.

Acknowledgements

For permission to conduct this study, we thank HRH Prince Sultan bin Salman, President of the Saudi Commission for Tourism and National Heritage (SCTH) and Professor Ali I. Al-Ghabban, Vice President. We thank Jamal Omar and Sultan Al-Fagir of the SCTH for their support and assistance with the field investigations. Particular thanks to Abdullah Alsharekh of King Saud University for discussions and long term support. We thank Heidi Eager, Muhammed Zahir, Oshan Wedage, Marco Bernal, Patrick Cuthbertson, Patrick Roberts, Margaret Ashley-Veall and Helena White (Palaeodeserts) and Saleh A. Soubhi, Mohammed A. Haptari, Adel H. Matari, Abdu M. Al-Masary, Ahmad A.
Bahameem and Ammar Jamal Jamalaldeen (Saudi Geological Survey) for their contributions in the field. Sandra Chapman and Pip Brewer provided access to comparative specimens at the Natural History Museum (Palaeontology), as did Jo Cooper and Judith White at the Bird Group in Tring. CMS thanks Jo Cooper for helpful discussion. Malgosia Nowak-Kemp and Eliza Howlett assisted with access to specimens in the Oxford University Museum of Natural History (OUMNH) and CMS is grateful to Darren Mann and Bethany Columbo for permission and assistance while working in the osteological collections. Jess Rippengal helped with access to the reference collections in Cambridge, as did Malcolm Pearch at the Harrison Institute (Sevenoaks). We thank Nigel Larkin for his conservation work on TAG14/301 and his advice on the identification of hyaena coprolites; discussions with Simon Parfitt were also particularly helpful in this regard. Juha Saarinen kindly measured the mesowear angles of the elephant molars, and provided discussion. This study also benefited from discussions with Chris Jarvis (OUMNH), Matt Freidman and Roger Benson (University of Oxford). We thank Heidi Eager and Laura Bishop for valuable and constructive comments on an early draft of the manuscript. CMS thanks Ian Cartwright for the photographs of specimens shown in Figs. 10A and B and 15A and B. The ESR dating study has received funding from a Marie Curie International Outgoing Fellowship of the European Union's Seventh Framework Programme (FP7/2007-2013) awarded to MD under REA Grant Agreement nº PIOF-GA-2013-626474. MDP acknowledges financial support from the European Research Council (grant no. 295719, to MDP) and from the SCTH. Author contributions: CMS wrote the paper, with contributions from all authors; fossil analysis was undertaken by CMS (except elephant fossils) and AL (elephant fossils); Stratigraphic analysis was undertaken by AP; OSL dating was undertaken by LCB; U-series and ESR dating was undertaken by MD and RG; Mapping, and site survey was undertaken by PB; RJ collated fossil survey data; study was conceived by MDP and supervised in the field by AA-O and RJ (2013) and AA-O, KSMAM, CMS, ISZ, YAM and AMM (2014).

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