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

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1	Middle Pleistocene vertebrate fossils from the Nefud Desert, Saudi Arabia:
2	implications for biogeography and palaeoecology
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#### 28 Abstract

29 The current paucity of Pleistocene vertebrate records from the Arabian Peninsula - a landmass of over 3 million km<sup>2</sup> - is a significant gap in our knowledge of the Quaternary. Such data are critical lines of 30 31 contextual evidence for considering animal and hominin dispersals between Africa and Eurasia 32 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 33 fossils of mammals, birds and reptiles from recent excavations at Ti's al Ghadah in the southwestern 34 Nefud Desert. Combined U-series and ESR analyses of *Oryx* sp. teeth indicate that the assemblage is 35 Middle Pleistocene in age and dates to ca. 500 ka. The identified fauna is a biogeographical admixture 36 that consists of likely endemics and taxa of African and Eurasian affinity and includes extinct and extant 37 (or related Pleistocene forms of) mammals (Palaeoloxodon cf. recki, Panthera cf. gombaszogenis, 38 Equus hemionus, cf. Crocuta crocuta, Vulpes sp., Canis anthus, Oryx sp.), the first Pleistocene records 39 of birds from the Arabian Peninsula (Struthio sp., Neophron percnopterus, Milvus cf. migrans, 40 Tachybaptus sp. Anas sp., Pterocles orientalis, Motacilla cf. alba) and reptiles (Varanidae/Uromastyx 41 sp.). We infer that the assemblage reflects mortality in populations of herbivorous animals and their 42 predators and scavengers that were attracted to freshwater and plant resources in the inter-dune basin. 43 At present, there is no evidence to suggest hominin agency in the accumulation of the bone assemblages. 44 45 The inferred ecological characteristics of the taxa recovered indicate the presence, at least periodically, of substantial water-bodies and open grassland habitats. 46

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48 Keywords: vertebrates, Pleistocene, desert, Saudi Arabia, lacustrine, palaeoecology, biogeography

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#### 56 1. Introduction

The Arabian Peninsula (defined here as the landmass from the southern borders of Iraq and Jordan, to the southern coastline of Yemen; **Fig. 1A**) is a key theatre to consider hominin dispersals between Africa and Eurasia (e.g. Rose and Petraglia, 2009; Dennell and Petraglia, 2012; Groucutt and Petraglia, 2012). While the geographical significance of this landmass of over 3 million km<sup>2</sup> 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. O'Regan et al., 2005; Beyin, 2006; Fernandes et al., 2006; Fernandes, 2009; O'Regan et al., 2011; Groucutt et al., 2015a).

As studies continue to unveil a complex climatic and environmental history (e.g. Fleitmann et 64 al., 2003; Fleitmann and Matter, 2009; Parker, 2009; Fleitmann et al., 2011; Rosenberg et al., 2011; 65 Rosenberg et al., 2013; Breeze et al., 2015; Jennings et al., 2015; Matter et al., 2015; Parton et al., 66 67 2015a; Parton et al., 2015b) and the Palaeolithic archaeological record develops (e.g. Armitage et al., 2011; Delagnes et al., 2012; Groucutt and Petraglia, 2012; Petraglia et al., 2012) it is now clear that 68 Pleistocene hominins penetrated the interior of the Peninsula (Groucutt et al., 2015b; Groucutt et al. 69 70 2015c; Shipton et al., 2014; Scerri et al., 2015) in regions that are today harsh, hyper-arid habitats. A 71 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 72 73 addressing this issue.

74 North Africa and the Middle East are biogeographically complex regions. The Arabian 75 Peninsula is situated at the junction of three biogeographic realms, the Afrotropical, Western Paleartic and Oriental (e.g. Portik and Papenfuss, 2012) and the historical vertebrate fauna is an admixture of 76 77 endemic species with taxa of African and Eurasian affinity (e.g. Delany, 1989; Harrison and Bates, 1991; Cox et al., 2012; Portik and Papenfuss, 2012). The opening of the Red Sea and climatic shifts in 78 the late Miocene were major drivers of diversification and dispersal of the biota of the region and a 79 combination of harsh arid environments, periodic humid events and geological evolution has shaped 80 the fauna of the Peninsula (e.g. Metallinou et al., 2012). Genetic studies of a small number of species 81 (Papio hamadryas, Ichneumia albicauda and Varanus yemenensis) have shed light on the 82 83 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 84 vertebrates (e.g. Whybrow and Hill, 1999; Beech and Hellyer, 2005), the paucity of Pleistocene records 85 from the Arabian Peninsula remains a major limiting factor in modelling the dynamics of Quaternary 86 animal populations (e.g. Fernandes, 2009; O'Regan et al., 2011; Stimpson et al., 2015). Furthermore, 87 88 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 89 changes are individualistic (e.g. Stewart, 2009), such data are critical lines of contextual evidence in 90 91 considering Pleistocene environments and hominin palaeoecology in the interior (e.g. Belmaker, 2009).

The Arabian Peninsula today comprises of a heterogeneous suite of habitats, including tropical, 92 sub-tropical and montane biomes in the south and western coastal regions. The interior, however, is 93 dominated by basalt flows, salt flats and (overwhelmingly) sand and gravel deserts (Mallon, 2011; Cox 94 95 et al., 2012). These hyper-arid habitats are embodied by three major sand seas that collectively occupy over 700,000 km<sup>2</sup>: the Rub' al Khali (also known as the Empty Quarter) and Wahiba Sands in the south 96 and southeast, respectively, and the Nefud Desert in the north (Fig. 1A). During the Pleistocene, 97 98 oscillations between hyper-arid and humid conditions saw periodic increases in precipitation, humidity 99 and the activation of river and lake systems in the interior (Parker, 2009; Rosenberg et al., 2013; Breeze et al., 2015; Matter et al., 2015; Parton et al., 2015b; Fig. 1A, B). As the volume and periodicity of 100 available moisture increased plant biomass will have responded accordingly (e.g. Southgate et al., 1996) 101 102 and an availability of fresh water resources would have led to a "greening" of the interior that in turn 103 would have provided windows of opportunity for dispersal for animals and hominins (e.g. Parton et al., 104 2015a). However, the character and composition of the animal populations of these landscapes is poorly 105 known. The existing collections of Pleistocene fossils have provided taxonomic insights (Table 1) but 106 are beset by problems of preservation, provenance and chronological control (O'Regan et al., 2011; 107 Stimpson et al., 2015).

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

Pleistocene fossils have also been recovered from the two largest sand seas: the Rub' al Khali 113 and the Nefud Desert (Fig. 1A). Collections made by McClure (1984) during pioneering studies of 114 115 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 116 sp. and *Hippopotamus* ("presumably *amphibius*"). Remains of the Caprinae included a possible record 117 of the endemic Hemitragus (Arabitragus) jayakari. McClure points out, however, that collection was 118 not systematic and information for exact geographical provenance and chronological affinities of the 119 fossil assemblages was lacking. Essentially, the "fossil vertebrate suite should therefore be taken as 120 121 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 122 123 (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 (Thomas et al., 1998; Rosenberg et al., 2013). The first Pleistocene taxa were reported by Thomas et al. (1998) from collections at three sites in the southwestern Nefud Desert (Locality #1: Khall Amayshan; Locality #2: Ti's al Ghadah, the focus of this study, and an unnamed site: Locality #3; **see Fig. 1B**). Despite relatively small sample sizes, a total of 14 taxa (including fish, reptiles and mammals) were identified (**Table 1**).

130 Thomas et al. (1998) report fossils of Equus sp., a large bovid (identified as Pelorovis cf. oldawayensis) and a reportedly gracile hippopotamid (Hexaprotodon sp.?) from the site at Khall 131 Amayshan (KAM-1 – Thomas locality 1; Fig. 1B). Thomas et al. (1998) also report fossils from an 132 unnamed site ("Locality 3"; Fig. 1B) that is likely to be site "16.1" of Rosenberg et al. (2013) and dated 133 between  $419 \pm 39$  ka and  $286 \pm 30$  ka, which included large bovids (referred to *Pelorovis* cf. 134 oldawayensis), a well preserved left mandible of Crocuta crocuta, and post-crania and a molar from an 135 elephant. Examination of the incomplete, hypsodont molar plate resulted in a cautious referral to the 136 extinct African elephant taxon Palaeoloxodon recki. An aberrant horn-core (originally reported to be 137 138 from Ti's al Ghadah) that possibly represented an undescribed taxon was also recovered from this site.

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139 The site at Ti's al Ghadah (Fig. 2) yielded the largest and most diverse sample reported by Thomas et al. (1998). The collection included a relative abundance of fossils from Oryx sp. together 140 with small numbers of specimens attributable to tortoise (Geochelone cf. sulcata), a large 141 Osteoglossiforme (an order of primitive, ray-finned freshwater fish) specimen we were unfortunately 142 unable to relocate and review), Equus sp., Vulpes sp. and a specimen conferred to the extinct Eurasian 143 jaguar, Panthera (onca) gombaszogensis (see also Stimpson et al., 2015). Unidentified, potentially 144 novel bovid and camelid taxa were also reported. Re-inspection of the bovid remains from the collection 145 at Ti's al Ghadah by one of us (CMS) suggested that the crania may be attributable to a Pleistocene 146 Orvx sp. (see also section 4.2.3.4). A poorly preserved maxilla fragment appears to be camelid, but with 147 no discernible difference to extant Camelus. 148

While these collections provide some insight into the Pleistocene vertebrates of the interior, 149 150 they were the product of surface collections and their stratigraphic and chronological affinities are not clear (Stimpson et al., 2015). In the original report by Thomas et al. (1998), for example, the collections 151 were considered as a whole and an Early Pleistocene age and an Ethiopian affinity were inferred on the 152 basis of taxonomic composition and "stage of evolution" (Thomas et al., 1998, 150). Subsequent dating 153 154 work by Rosenberg et al. (2013) using luminescence techniques at these fossil localities indicated that 155 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 156 chronological affinities of the Nefud fauna is warranted. 157

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

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#### 166 2. Site location and geological setting

167 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 168 large (ca. 60 m high) compound barchan dune ridge, while smaller branching linear dunes extend to the 169 170 northern and southern ends of the basin. Relict lacustrine deposits form a distinct ridge that runs broadly 171 northwest to southeast (Fig. 2, Fig. 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 172 length. It dips gently to the south of the basin and interdigitates with low branching dunes in the east. 173 Lacustrine and diatomaceous marls are exposed vertically along the western edge of the ridge (Fig. 2C) 174 and dip gently to the east where they are overlain by modern dune sands. Ephemeral gullies run 175 perpendicular to the long axis of the ridge towards the west of the basin and at the foot of the large 176 barchan dune. These have eroded fossils from the main lake ridge, re-depositing them unconformably 177 178 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 179 configuration that lies beneath the present day rubified sand sea. Exposed within the centre of the basin, 180 181 are heavily indurated, iron-stained marl beds ca. 0.6 m thick, reflecting the formation of an older lake 182 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 183 184 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 185 186 that lie beneath, including the principal fossiliferous deposit: Unit 5.

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#### 188 **3. Materials and Methods**

#### 189 **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).

197 Searches for possible, earlier fossil-bearing strata in the ridge and in the wider basin area were 198 made by the creation of step trenches in the north and south of the ridge (Fig. 3) and a series of test pits 199 in the basin. While the deep section exposed by the step trenches provided further sedimentological 200 information regarding the geomorphological evolution of the basin, no further fossiliferous layers were 201 detected.

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# 203 3.2 Fossil analyses

The identification of the fossils was conducted in the UK with the permission of the SCTH. Fossils 204 were identified by morphological and morphometric comparisons with comparative museum 205 206 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 207 in the text. Measurements were taken with dial callipers to the nearest 0.01 mm. Morphometric analyses 208 were carried out in PAST (Hammer et al., 2001) following conventions described in Hammer and 209 210 Harper (2006). A preliminary macroscopic taphonomic investigation was conducted and surface condition and modifications to bones were noted. Weathering stages were characterised following 211 212 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 (NHM-Tring) and palaeontological comparative specimens at the NHM-SK.

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221 **3.3** Chronology

A sample for OSL dating was probably recovered from a stratum that directly underlies, or is equivalent to the main bone-bearing layer (Units 4 or 5, respectively; **Fig. 4**) by Rosenberg et al. (2013). This sample yielded OSL and TT-OSL (thermally-transferred optically stimulated luminescence) ages of  $328 \pm 26$  ka and  $318 \pm 25$  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 collected an OSL sample (**methods S1 supplementary data**) from the palaeolake sediments capping the excavated sequence (Unit 7; see **Fig. 4**). Five fossil cheek teeth (*Oryx* sp.) that were recovered from Unit 5 were also submitted for U-series and combined US-ESR dating and a series of sediment samples were collected from different depths within Unit 5 to evaluate the variability of the sediment radioactivity (**methods S2 supplementary data**).

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#### **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. 236 237 4), and is underlain by coarse, well-cemented, cross-bedded, pale cream-grey sands (Unit 1). These 238 contain occasional calcareous nodules and iron-stained root impressions throughout the upper ca. 0.6 239 m of the unit. Unit 2 comprises weakly horizontally bedded, pale cream-white, coarse, poorly sorted 240 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 241 with both the overlying and underlying units. This is overlain by a thin layer (Unit 3) of very poorly 242 sorted greenish sands with no bedding structures and numerous, well-rounded quartz pebble inclusions. 243 The unit is heavily cemented and calcritized at the base, with iron staining and iron-stained root voids 244 throughout. Unit 4 comprises pale cream-grey, very poorly sorted, coarse, horizontally bedded sands. 245 Bedding is variable, being generally weak throughout, but strongly bedded and cemented in places. 246 Vertical and horizontal iron-stained root impressions occur throughout, along with numerous well-247 rounded quartz granules and small (< 10 mm) pebbles. There is a notable increase in iron staining at the 248

base of the unit, along with generally coarser clasts, while a diffuse contact is present with both overand underlying units.

Unit 5 is the main fossil layer at the site and comprises weakly cross-bedded, very poorly sorted, 251 coarse, reddish sands with occasional iron-stained root voids, fine (ca. 5 -10 mm max length) rounded 252 253 quartz pebbles, and calcareous drapes throughout. The unit becomes notably redder up-profile, while 254 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-255 scale, localised mobilisation of waterlain sands, displaying evidence of both bioturbation and sediment 256 reworking in the form of small (< 20 cm) infills. Unit 5 is representative of wetted and partially 257 vegetated sands. The characteristics of the underlying unit (Unit 4) indicate initial sediment deposition 258 under low energy (localised) sheetflood conditions, following increased rainfall in the basin. A lack of 259 260 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 261 mobilisation culminated in the development of vegetation and stabilisation of the landscape represented 262 263 by Unit 5.

264 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 265 266 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 267 remove with brush or wooden pick. Post-depositional movement and reworking appears to be have been 268 minimal. While minor abrasion was occasionally observed, there was no evidence to suggest rolling or 269 270 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) than the upper surface exposed in excavation 271 (more abraded). Some trampling was evident in the form of the presence of fine striae on the surfaces 272 of bones and "sharp breaks" to specimens (e.g. see Fig. 12F, H and J). In addition to direct physical 273 evidence of the presence of predators and scavengers on site, carnivore pits and tooth marks indicate 274 the activity of small and large-bodied carnivores. Tooth marks were identified in the small sample of 275 276 recovered bird bones (section 4.2.2) and were detected on the bones of Equus sp. (section 4.2.3.2) and Oryx sp. (section 4.2.3.4). No lithics were recovered during our excavations and the association
between the artefacts reported previously in the basin (Scerri et al., 2015) and the fossiliferous strata
remains unclear.

Within the limits of our investigations, there was lateral variation in taxonomic diversity and in 280 281 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 282 in the south of the site (trenches 1 and 2) yielded a greater range of taxa compared with the northern 283 excavations (trenches 5 and 6; Fig. 5A). Weathering profiles generated from examination of bovid long 284 bones from trenches 1,2 and 5 and 6 (Fig. 5B and 5C, respectively) indicate that specimens from the 285 south of the site were generally well-preserved: maximally to Behrensmeyer's (1978) weathering stage 286 3, rarely to stage 4 (Fig. 5B). Conversely, specimens from the northerly trenches were paler in colour, 287 288 more friable and weathering profiles suggest that these specimens were subject to sub-aerial weathering for longer than in the southern trenches (Fig. 5C). In summary, fossil assemblages from the 289 investigations of the southern end of the ridge were more diverse and better preserved than the 290 291 assemblages from the northern limits of our investigations. Following Andrews and Whybrow (2005), 292 the weathering profiles collectively suggest that carcasses were exposed maximally (in arid conditions) 293 for approximately 15 years before burial. However, if conditions were more humid at the time of 294 deposition then the duration of exposure would likely have been less (Behrensmeyer 1978; Andrews 295 and Whybrow, 2005).

296 The overlying unit (Unit 6) marks the onset of lake formation in the sequence, and comprises a 297 series of interstratified, finely laminated diatomaceous marls. Iron staining occurs throughout, and is 298 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 299 300 (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 301 and non-laminar. The sequence is capped by beds of sandy, gypsiferous marls (Unit 9). These are 302 heavily indurated and unevenly bedded in desiccation 'curls': blocks of marl that have undergone 303 304 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
- 307 the site and desiccation of the lake that forms the main ridge in the basin.
- 308

# 309 4.2 Vertebrate Palaeontology

# 310 4.2.1 Reptilia

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

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# 319 4.2.1.1 Squamata

320 Varanidae and/or Agamidae - Uromastyx sp.

The centra are procoelous. The cotyles are widest dorsally with a relatively flat dorsal edge and narrow 321 322 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 323 procoelous lizards, the ventral rim is retracted and exposes the entirety of ventral concave surface of 324 the cotyle (Fig. 6A-1). There is no sagittal crest present on the ventral surface. These characters suggest 325 the varanids (Varanidae) or the agamid *Uromastyx*. The cervical vertebra (TAG14/706), however, lacks 326 a marked hypapophyseal peduncle (Fig. 6B-2), which suggests *Uromastyx* sp. rather than the Varanidae 327 (Holmes et al., 2010). 328

329

330 4.2.2 Aves

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

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#### 335 4.2.2.1 Struthioniformes

336 Struthionidae (ostrichs)

337 *Struthio* sp.

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

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

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

Morphological and morphometric comparisons (**Table S3 supplementary data**) were also conducted with specimens from extant taxa (*S. camelus camelus, S. c. australis, S. c. massaicus* and *S. molybdophanes*) and recently extinct sub-species (*S. c. syriacus*). TAG14/318 differs from comparative specimens from extant *S. c. australis* and extinct *S. c. syriacus*. Viewed from the dorsal aspect, the opening to the foramen vertebra forms a much more acute angle between the zygapophyses cranialis in

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359 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 360 caudal end, the lacuna interzygapophyses is very square in TAG14/318 (Fig. 6C-5), as indeed are the 361 caudal articular facets (Fig. 6C-6): these characters are rounded in the comparative specimens. 362 363 However, comparison with material from S. molybdophanes (NHM-Tring: 1888.5.5.1) indicates that these characters are similar. From the dorsal aspect, the lacuna interzygapophyses caudalis is square 364 and the lacuna interzygapophyses is v-shaped, rather than u-shaped in S. molvbdophanes (Table S3 365 supplementary data). 366

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.

372

#### 373 4.2.2.2 Podicipediformes

374 Podicipedidae (grebes)

375 *Tachybaptus* sp.

A well-preserved, complete left tarsometatarus (**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 in height to the condylus interarticularis (cf. Fjeldså, 2004, 214).

TAG13/038 is notably shorter overall (**Fig. S2A supplementary data**), but is not less robust than the comparative material at NHM-Tring. To date, morphological and metric comparisons have been limited to comparative material of European provenance (**Table S4 supplementary data**) and extant Oriental subspecies are "generally smaller" than their counterparts from higher latitudes (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 comparative material.

388 We withhold a specific attribution until it can be determined if this variation falls within specific limits

- 389 for *T. ruficollis* or represents a novel Pleistocene form.
- 390

#### 391 **4.2.2.3** Accipitriformes (diurnal birds of prey)

392 Accipitridae

393 *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).

399 The remains of the cranium consist of the occipital region and cranial vault (Fig.6E i). A semicircular puncture (maximum dimensions =  $11.60 \text{ mm} \times 8.78 \text{ mm}$ ) is evident to the right side of the 400 401 vault, which we interpret as a tooth mark (Fig. 6E i-9). There may also be a second puncture just above 402 the foramen magnum although this may be a break associated with weakening of the bone around the 403 edge of the foramen. The maxilla is also present and is complete from os nasale to rostrum maxillare 404 (Fig. 6E ii). The humerus is complete though it was recovered in two pieces (Fig 6E iii and iv). There 405 is extensive evidence of gnawing and chewing on the caudal and cranial surfaces. The crista 406 deltopectoralis appears gnawed along much of the dorsal edge (Fig. 6E iii-10) and there are multiple 407 small (maximum dimensions: 2.5 mm  $\times$  2.5 mm) pits in the cranial surface of the distal end of the 408 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 409 by a small to medium-sized carnivore. 410

411

412 *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 ofblack kite (*Milvus migrans*).
- 417

# 418 4.2.2.4 Pteroclidiformes

- 419 Pteroclididae (sandgrouse)
- 420 *Pterocles orientalis*
- 421 TAG14/270 is a fragment of a left proximal humerus from a large sandgrouse species (**Fig. 6F**). While
- 422 it is a reasonable morphological match for *Syrrhaptes* sp., TAG14/270 is markedly larger and more
- 423 robust: the caput humeri (Fig. 6F-12) is more developed and more prominent as in *Pterocles* sp. It can
- 424 be difficult to separate the skeletal elements of different *Pterocles* species (e.g. Dobney et al., 1999) but
- 425 TAG14/270 is clearly from a large bird (Fig. S2B, Table S5 supplementary data) and all observable
- 426 characteristics match those of *P. orientalis*, the black-bellied sandgrouse.
- 427

#### 428 4.2.2.5 Anseriformes

- 429 Anatidae (ducks and geese)
- 430 *Anas* sp.
- 431 Two fragments of the distal end of a left humerus (TAG14/285) is from a dabbling duck of the genus

432 *Anas.* It is not possible to identify this specimen to species, but it derived from a bird equivalent in size

- 433 to a mallard (*Anas platyrhynchous*).
- 434

# 435 4.2.2.6 Passeriformes

- 436 Motacillidae (wagtails)
- 437 *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*.

#### 443 **4.2.3 Mammalia**

#### 444 **4.2.3.1** Carnivora

- 445 Felidae
- 446 *Panthera* sp.

447 A total of four specimens known from Ti's al Ghadah are attributable to the genus Panthera (Table 4). Two of these, a left third metacarpal (JMI 27) and a right fourth metacarpal (TAG13/097), have been 448 referred to the extinct Eurasian jaguar, Panthera gombaszogensis (see Thomas et al., 1998 and Stimpson 449 et al., 2015, respectively). Morphological and morphometric analyses of TAG13/097 are described in 450 Stimpson et al. (2015). While comparative sample sizes are small, measurements for JMI 27 appear 451 equivalent with published measurements for Pleistocene jaguars, P. onca augusta and P. 452 gombaszogensis (Table S6; Fig. S3 supplementary data). The genus is also represented by a phalanx 453 454 (TAG14/339) and broken mandibular canine (TAG13/145) (Fig. 7A, B).

455

456 Hyaenidae

457 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 hyaena, most likely *Crocuta crocuta* (Larkin pers comm.; Parfitt
pers. comm). Measurements (following Larkin et al., (2000)) of a complete specimen, TAG14/256 (Fig.
7C: axial length 40.58 mm; diameter A 29.85 mm, diameter B 28.43 mm) fall within reported ranges
of coprolites from this taxon (cf. Larkin et al., 2000; Lewis et al., 2010).

464

465 Canidae

466 *Canis* sp.

A fragment of the base of the skull (TAG14/245), a lower right carnassial (TAG14/184) and a fragment
of a lumbar vertebra (TAG14/208) are attributable to medium-sized canids. The skull fragment consists
of the occipital region and a fragment of the supra-occipital (Fig. 7D). The foramen magnum, occipital
condyles and condylar foramen are intact and portions of the par-occipital process and basi-occipital

are present. This specimen is a good morphological match with comparative material for the golden
jackal, *Canis aureus*: measurements indicate that it derived from a relatively large individual (Table 4).

473

474 *Canis anthus* 

TAG14/184 is a trenchant, lower right carnassial (M<sub>1</sub>). With the exception of the break to the mesial
root, the specimen is complete and is relatively unworn (Fig. 7E). The specimen, however, appears
iron-stained and there is marked "sidedness" in weathering: it appears that the tooth ultimately lay on
its buccal side prior to burial as there is minimal modification to this surface of the tooth (Fig. 7E i).
Conversely, the lingual side is abraded across the entire surface (Fig. 7E ii).

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

The morphometric characteristics of TAG14/184 indicate that it derived from a smaller animal than Pleistocene and recent records of European 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. 8**). Conversely, measurements from TAG14/184 suggest that it derived from an animal larger than recent European golden jackals, recent and Pleistocene African golden jackals (*C. aureus* s.s) and match equivalent measurements of a large form, variously classified as "*Canis aureus lupaster*" or "*Canis lupus lupaster*" ("*Canis lupus lupaster*" in **Fig. 8**).

Osteological studies have long recognised the likelihood of a large extant form of jackal in North Africa (e.g. Huxley, 1880) and "large" golden jackal fossils are known from Middle to Late Pleistocene in Northwest Africa (Geraads, 2011). Recent work with mitochrondrial and nuclear genome data has indicated that some populations of North African golden jackals are a cryptic species distinct from Eurasian golden jackals, which occupies a much wider geographical area in Africa than was previously thought (Rueness et al., 2011; Gaubert et al., 2012; Koepfli et al., 2015). Koepfli et al.

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(2015) recommend that *Canis lupus lupaster* (and *Canis aureus* sensu lato) be classified as *Canis anthus*, the African golden wolf. Given the trenchant morphology and that the morphometric characteristics of TAG14/184 are a close match for fossil (Levant) and recent (North Africa) data for these "large forms", we follow the taxonomic proposal of Koepfli et al. (2015) and refer TAG14/184 to *Canis anthus*.

504

505 *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.

509

510 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.

515

# 516 4.2.3.2 Perissodactyla

517 Equidae

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

521 Fig. 9D).

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 equivocal (e.g. Azzaroli and Stanyon, 1991; Geigl and Grange, 2012) and the nomenclature employed in schemes

varies between authorities. For TAG14/329, we follow criteria described in Davis (1980), Eisenmann

et al. (2008), van Asperen et al. (2012), Geigl and Grange (2012) and Alberdi and Palombo (2013).

528

529 *Equus hemionus* 

TAG14/329 is a fragment of a robust right mandible (Fig. 9A). The first molar is broken off at the root 530 below the alveolus, but the worn second and third molars are in situ. The  $M_2$  is intact. The  $M_3$  is largely 531 532 complete but there is a break to the distal occlusal surface (Fig. 9B). Caballoid horses can be discounted as the double knots on M<sub>2</sub> and M<sub>3</sub> are rounded (Fig. 9B-1) with v-shaped (rather than u-shaped) lingual 533 valleys (linguaflexids; Fig. 9B-2) and rounded (rather than flat) buccal margins of the protoconid and 534 hypoconid (Fig. 9B-3), although this last characteristic is regarded as an unreliable means to 535 536 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 537 (Fig. 9B-4). This would discount zebras and zebra-like taxa, the extinct *E. hydruntinus* and Pleistocene 538 stenonine horses and indicate the hemione, E. hemionus. Morphometric comparisons using the intact 539 540 M<sub>2</sub> of TAG14/329 show that the dimensions of the occlusal surface are larger than in extant and recently 541 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. S4 supplementary data). 542

543

544 *Equus* sp.

The few specimens of recovered post-crania are rather robust. The dimensions of a near-complete left 545 femur TAG13/146 (Table 5; Fig. 9D), notable for the presence of carnivore pits on the caudal surface, 546 near to the proximal end (Fig. 9D-5), indicate that this specimen is large and robust in comparison to 547 548 extant hemiones (Fig. S5A supplementary data). A complete left astragalus (TAG14/342; Fig. 9C), which was found in close association with mandible TAG14/329, is also large and robust (Fig. S5B 549 supplementary data). A PCA analyses of six variables suggests that the astragalus is of a size and 550 proportions of larger equid taxa, equivalent perhaps to Equus oldowayensis, rather than extant hemiones 551 552 (Fig. S5B supplementary data). This would be consistent with the findings reported in Thomas et al.

(1998) who also describe relatively large and robust bones from the site, possibly from a robust stenonidhorse or species of zebra.

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

561

#### 562 **4.2.3.3 Proboscidea**

The presence of bones from a large elephant was identified in 2013, with a 2.25 m long tusk 563 564 (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 565 as *Elephas*). In 2014, collaborative investigations of the elephant remains of Ti's al Ghadah began 566 567 between the SCTH, SGS and Palaeodeserts project, with the establishment of large-scale investigations 568 by the SGS at the south of the ridge (Fig. 3). Here, we focus on the taxonomic diagnosis of two 569 diagnostic specimens, an upper molar TAG14/301 (Fig. 10A, B) and a mandible of a young animal, 570 TAG14/281 (Fig. 10C, D).

571

# 572 Elephantidae

# 573 Palaeoloxodon cf. recki

574 The lineage of the straight-tusked elephant is generally included within *Elephas* Linnaeus, 1758 by
575 workers on African material (e.g. Sanders et al., 2010) but *Palaeoloxodon* Matsumoto, 1924 or *Elephas*

576 (*Palaeoloxodon*) by those studying Eurasian remains (e.g. Palombo and Ferretti 2005; Lister, 2016).

577 Pending resolution of the relationships among elephant genera we here retain the genus *Palaeoloxodon* 

578 for clarity (cf. Shoshani and Tassy 1996).

579 Specimen TAG14/301 is a portion of an adult left upper molar in mid-wear (**Fig. 10A**). The 580 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.

The molars show features which strongly suggest referral to the genus Palaeoloxodon. In 583 particular, the occlusal wear figures show lamellae with distinctly but roughly folded enamel, and 584 585 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 586 Palaeoloxodon and distinguish these molars from other candidate genera, Loxodonta (African 587 elephants), Mammuthus (mammoths) and Elephas s.s. (lineage of Asian elephant). Another common 588 feature of *Palaeoloxodon*, rings of enamel medial and lateral to each lamella in early wear, are not 589 590 visible these specimens; this character is not, however, invariably present in the genus.

591 Upper molar TAG14/301 preserves 11 enamel lamellae, but this is incomplete and the original 592 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 593 594 wear, so it is not possible to reconstruct the number of lamellae lost (Lister and Sher, 2015; Sher and 595 Garutt, 1987). The base of a somewhat isolated root is visible at the antero-lateral corner of the crown, 596 but it is not of the correct shape or position to be the true 'anterior root' and must therefore be one of 597 the 'paired roots' behind it. It is therefore likely that at least 2-3 lamellae have been lost through wear, 598 but the precise number is unknown.

599 Loss at the posterior end is also difficult to quantify. The large size of the molar makes it very 600 likely to be either M<sup>2</sup> (the penultimate of the series) or M<sup>3</sup> (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 601 602 in M<sup>3</sup> but is blunt and wide in M<sup>2</sup>. Unfortunately, breakage makes the determination of this characteristic problematic for TAG14/301. The width of the crown reduces very slightly from front to back (Table 603 6), which might suggest M<sup>3</sup>, but this is insufficient for certainty. A second factor is crown height, which 604 tends to be maximal near the front of the molar in  $M^3$  and near the back in  $M^2$ . However, because only 605 the posterior two preserved lamellae of this specimen are unworn and allow measurement of crown 606 height, this cannot be determined. The crown is relatively high (133 mm, for a molar width of 90.5 mm, 607 608 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<sup>2</sup>, or a lamella half to two-thirds down the crown of 609 610 an M<sup>3</sup>. 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 611 close to the natural posterior end of the tooth, rather than that the tooth extended much beyond the 612 break. In this case, the molar would be an  $M^2$ , but this cannot be considered certain. If it is an  $M^2$ , then 613 the curvature of the surface suggests that approximately two lamellae (plus the posterior talon) should 614 be added to the preserved number. That would give an approximate total of at least 15 (two or more at 615 the front, two at the back, and 11 preserved). If, however, the molar is an  $M^3$ , then an unknown number 616 is missing at the back and the total is known only to be greater than 15. Table 6 shows measurements 617 for the Ti's al Ghadah teeth, in comparison with published data for *P. antiquus* and *P. recki recki*, the 618 619 latest chrono-subspecies, with a chronological range in East Africa of ca. 1.2 - 0.5 Ma.

620 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 621 its original value was at least 15, this places it in M<sup>3</sup> range. M<sup>2</sup> of *P. recki recki* is represented by only 622 one specimen, with 10 plates, but the range probably extended to 12 as this value is found even in earlier 623 624 samples referred to P. recki ileretensis and P. recki atavus (Beden, 1979). However, 15 plates have not been recorded in any M<sup>2</sup> of *P. recki* and even in the more advanced *P. antiquus* of Europe: 11-14 is 625 typical for M<sup>2</sup> (and 16-19 in M<sup>3</sup>). The rather thick enamel of TAG14/301 also supports identification as 626  $M^3$ , although this is less secure. Following Laws (1966) scheme, TAG14/301, if it is an  $M^3$  as here 627 628 suggested, is probably around wear stage XXII-XXIII, suggesting an age of roughly 40 years.

629 The juvenile mandible TAG 14/281 preserves dP<sub>4</sub> 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 630 scan its crown height is ca. 57 mm and width 44 mm, giving a hypsodonty index of ca. 130. Mesowear 631 angles were measured on the M<sup>3</sup> and dP<sub>4</sub> following Saarinen et al. (2015). The angles are measured 632 between the ridges of enamel bounding each lamella, and the floor of dentine inside. Averaged over 633 several lamellae the angles are 120° for the M<sup>3</sup> and 136° for the dP<sub>4</sub>. The dP<sub>4</sub> in TAG14/281 is in early 634 to mid-wear and at wear stage V in Laws (1966) scheme, which corresponds to an age at death of 635 636 approximately 3 years.

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637 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 638 identified as P. recki; those from mainland Europe as P. antiquus. Remains from the Levant have 639 generally been equated with P. antiquus but Saegusa and Gilbert (2008) identified P. recki among the 640 641 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 642 its 3 million year history, with increasing plate number and crown height (Beden, 1979; Todd, 2001; 643 Lister, 2013). However, given the independent evidence for a Middle Pleistocene age of the Ti's al 644 Ghadah assemblage (section 4.3), we restrict our comparisons to the latest subspecies, *P. recki recki*, 645 with a known duration of ca. 1.5 - 0.4 Ma or possibly a little younger (Sanders et al., 2010). We 646 647 provisionally exclude its Middle to Late Pleistocene descendent P. iolensis of North Africa, as its molar 648 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. 649 650 antiquus. However, in terms of occlusal morphology, the two molars available from Ti's al Ghadah 651 can be closely matched with available specimens of both taxa (see, for example, illustrations of *P. recki* 652 recki in Beden (1979), and of *P. antiquus* in Guenther (1977)). Similarly, the measurements that could 653 be taken on these specimens are within the known ranges of both species (Table 6). The taxa are potentially separable on plate number and hypsodonty index of complete third molars, where their 654 ranges overlap but the variation in both variables extends to lower values in P. r. recki and to higher 655 values in *P. antiquus*. The recovery of further dental remains of elephant from Ti's al Ghadah may 656 therefore allow a clearer taxonomic designation in the future. For the present, we follow precedent in 657 referring them to Palaeoloxodon cf. recki in view of their more likely geographical origin from African 658 populations than European. 659

660

661 4.2.3.4 Bovidae (Hippotragini)

662 *Oryx* sp.

663 The vertebrate remains from Unit 5 were numerically dominated by elements from the Bovidae (Fig.
664 5A), although it is not a diverse assemblage: all examined cranial and dental remains, and identifiable

665 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) 666 compiled for trenches 1 and 2 and 5 and 6, indicated a MNI of 5 (five left mandibles) and 6 (six right 667 metatarsals), respectively and suggest that a relatively low number of individuals were represented. 668 669 Specimens were rarely encountered in strict anatomical position (occasional cervical vertebrae) but it 670 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 671 abundance of specimens from the proximal axial skeleton (humerus and femur; Fig. 11). 672

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

680 Cheek teeth are robust and hypsodont (Fig. 12A-D) although on all fully-erupted adult teeth in 681 wear abrasion appears to have been considerable (Fig. 12B), which we interpret to reflect the presence 682 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 683 684 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 685 686 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. 687 12B). 688

Further examination of maxilla fragments indicates that the infra orbital foramen is located posteriorly to  $P^2$ , 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 M<sup>3</sup> in *O. beisa*, *O. dammah*, and *O. gazella*, but it does not extend beyond the posterior column of the M<sup>3</sup> in comparative material for *O. leucoryx* or the specimens from
Ti's al Ghadah (Fig. 12B).

A small sample of horn cores (e.g. **Fig 12E**) are characteristic of the genus and rounded in cross-section, although are rather robust in comparison with available reference material (basal measurements: anterior-posterior mean = 43.00 mm; medio-lateral mean = 41.15 mm, n = 4). Thomas et al. (1998) report that Nefud specimens differ from extant *Oryx* spp. by degree of horn core divergence of ca. 35° (Thomas et al. 1998, 149). From the small number of newly recovered specimens (n = 4) we estimate a divergence of closer to 20°, but the degree of divergence appears greater than available comparative material for *O. dammah* and *O. leucoryx* and closer to *O. gazella*.

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

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

713

# 714 **4.3** Chronology

# 715 4.3.1 Optically Stimulated Luminescence

Aliquots from sample TAG1-OSL4 from Unit 7 (**Fig. 4**) are 'well-behaved' according to standard SAR protocol rejection criteria, and signal saturation in one aliquot suggests that the pIRIR290 protocol is yielding a stable luminescence emission without the need for fading correction. Given that all other aliquots were unsaturated, age underestimation due to signal saturation is not a concern for this sample. Equivalent dose overdispersion ( $23.8 \pm 7.1$  %) 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  $291 \pm 34$  ka (Table 7).

725

# 726 4.3.2 U-series dating

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

Two tissues show evidence of apparent uranium leaching (3536 dentine and 3538 dentine), for which U-series age cannot be calculated. The enamel sections show consistent mean apparent U-series ages ranging from  $235.2 \pm 5.8$  ka to  $268.2 \pm 12.3$  ka, whereas dentine results are somewhat more scattered from  $205.3 \pm 4.0$  ka to  $348.1 \pm 11.1$  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.

737

# 738 4.3.3 Combined U-series and ESR dating

739 Only two fossil teeth were dated by means of the combined US-ESR approach (samples 3536 and 3538) 740 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 741 in **Table 10**. The samples display characteristics that are usually found in Early Pleistocene teeth: 742 extremely high D<sub>E</sub> values (>3500 Gy), apparent U-leaching in dentine, and high U-concentration values 743 in dentine and enamel. Age calculations were performed by assuming early U uptake for the dentine 744 that showed U-leaching (i.e. p = -1). Combined US-ESR age calculations yielded 473 +50/-33 ka and 745 554 + 79/-76 ka for samples 3536 and 3538, respectively, resulting in a mean value of  $512 \pm 59$  ka  $(1-\sigma)$ 746 error). The teeth could be somewhat older if sediment cover was thicker in the past. In the age 747 748 calculations, a depth of 1.0 + 0.5 m was used for the calculation of the cosmic ray contribution.

However, even when assuming an average depth of  $30 \pm 5$  m, the resulting ages increase only by 1.3 % for sample 3536 and 2.2% for sample 3538. This is due to the fact that 95% of the total dose rate is generated within the tooth from the high U-concentrations in the dental tissues. Similarly, water content variability has virtually no impact on the final age results: by considering either 15 or 20%, instead of 10%, the ages slightly increase by <0.5%.

754

#### 755 **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.

761

# 762 **5.1 Chronological context**

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

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

779

# 780 5.2 Biogeographical and biostratigraphical implications of the Ti's al Ghadah fauna

781 The fossils of Ti's al Ghadah include the first Pleistocene-age bird bones to be reported from the Arabian Peninsula. In terms of biostratigraphy, the utility of the bird fossils identified to species is limited, except 782 to say the identified species are early records and are known from the region today. The Egyptian vulture 783 is resident in the Arabian Peninsula (and occurs around Ti's al Ghadah) and is widely distributed from 784 southern Europe, North Africa and east to the Indian sub-continent. Black kites are relatively common 785 passage visitors to the Peninsula; a closely related species, Milvus aegypticus, is restricted to the 786 southwest. White wagtails (Motacilla alba) are also relatively common winter or passage visitors. 787 788 Although no aquatic taxa were confidently identified to species is worthy of note that little grebes (Tachybaptus ruficollis) are resident and readily colonise well-vegetated bodies of water. The black-789 bellied sandgrouse (Pterocles orientalis) is found in Iberia, North Africa and Asia: it is regarded as rare 790 791 winter visitor to the Arabian Peninsula (Hollom et al., 1998; Porter and Aspinall, 2010).

The extinct *Panthera gombaszogensis* is regarded as Eurasian taxon and is known from the Early to Middle Pleistocene (e.g. Marciszak, 2014). Records for this enigmatic fossil felid are sparse in SW Asia. The specimens from Ti's al Ghadah are the most southerly known records of this taxon, although with the present dating information for the site these records fit well within the chronological range of this taxon. The Eurasian jaguar is known from the Kudaro faunal unit (MIS 9-11) in the Caucasus and is described from Layer 5c from Kudaro 1, which yielded two thermoluminescence dates of  $360 \pm 90$  ka and  $350 \pm 70$  ka (Baryshnikov, 2002).

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

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

The extinct elephant, Palaeoloxodon recki, is known from the Middle Pliocene until the Middle 810 Pleistocene in Africa, where it is conventionally divided into five chronological stages. The elephants 811 of Ti's al Ghadah are morphologically consistent with the latest stage, P. recki recki, with known 812 occurrence in East Africa between ca. 1.5-0.4 Ma, although it is not possible to rule out an earlier stage 813 for the small sample of two molars: the potentially diagnostic specimen (the  $M^3$ ) is incomplete. After 814 815 0.5 Ma, the African species *P. iolensis*, is believed to be the lineal descendent of *P. recki* and persists until the Late Pleistocene, possibly as late as 75 ka (Sanders et al., 2010). P. iolensis lacks the median 816 enamel expansions of P. recki that are also seen in the molars from Ti's al Ghadah. However, that a 817 818 population of the *recki-iolensis* lineage existed in the Arabian peninsula in the Middle Pleistocene is 819 perfectly plausible.

820 A descendant of Palaeoloxodon recki, P. antiquus, is known from Europe from Middle to Late 821 Pleistocene (ca. 780 to 50 ka), where it underwent relatively little evolutionary change before going 822 extinct during the last glaciation (Lister, 2004, 2016). Palaeoloxodon antiquus has also been identified 823 in the Levant. A Palaeoloxodon cranium from Gesher Benot Ya'aqov (GBY), Israel, dated to 780 ka (Goren-Inbar et al., 1994), has been regarded as one of the earliest representatives of this species, and 824 the species has also been identified at Revadim Quarry ("ca. 500-300 ka or possibly more": Rabinovich 825 et al., 2012). However, Saegusa and Gilbert (2008), on the basis of cranial characters, suggested that 826 the GBY cranium might actually be P. recki, while the morphology of the Revadim elephants has not 827 been described in sufficient detail to discriminate between the two species. The taxonomic boundary 828 between P. recki and P. antiquus, in this geographical region and time-interval, is therefore currently 829 blurred, but it cannot be ruled out that the elephants of Ti's al Ghadah might have derived from Europe 830 831 and eventually be considered to belong to P. antiquus.

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

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

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

848

# 849 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 if the Unit 5 assemblages represent animals that were attracted to an ephemeral water source and a relatively brief flush of plants in the dune fields, or were freshwater and plant resources more substantial and long-standing?

At present, it is not possible to determine the degree of time-averaging of the Unit 5 assemblages, although the fossil stratum appears to be a rather discrete unit with little evidence of significant reworking or redeposition. There is clear evidence, however, of a least three discrete 860 episodes of the formation of standing water within the Ti' al Ghadah basin and there is regional evidence 861 of the periodic formation of water bodies throughout southwestern Nefud Desert dating from the Middle Pleistocene onward (Rosenberg et al., 2013). Rosenberg et al. (2013) suggest that large-scale lake and 862 wetland habitats developed across the western Nefud during MIS 11. The inferred presence of a lake at 863 864 Ti's al Ghadah would be supported by previous reports (Thomas et al., 1998) of a fossil of a relatively large Osteoglossiforme fish (although this was an unstratified specimen) and consistent with the aquatic 865 affinities of two of the identified avian taxa (grebe, duck). Indeed, the presence of the bird taxa identified 866 at the site may parsimoniously be explained as attracted to habitat (grebe, duck, wagtail), to drink 867 (sandgrouse, ostrich) or in a scavenging role (Egyptian vulture, kite). 868

Oryx, equids and elephant will likewise have been attracted to fresh water and plant resources 869 870 and we infer that the remains recovered in Unit 5 reflect die-off in populations of these animals. Animal 871 carcasses will have attracted mammalian scavengers such as fox, golden wolf and hyaena and the attention of carnivores is evidenced by tooth marks. Although it was not possible to identify the 872 reptilian fossils to genus it is worth noting that, in this context, the majority of extant Varanus spp. are 873 874 carnivorous and will scavenge animal carcasses, whereas *Uromastyx* spp. are primarily herbivorous. It 875 is plausible that the Egyptian vulture also scavenged at the site and it is notable that one of these birds 876 were in turn subject to the attentions of a carnivore.

877 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. 878 879 100 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 880 881 resources. We also infer the presence of hyeana (cf. Crocuta crocuta) from coprolites. While these animals are famed as scavengers and for the demolition of bone, they are dynamic and capable 882 predators. Modern analogues should be applied with caution but it is notable that the taxonomic and 883 ecological composition of the fossil fauna from Ti's al Ghadah bears some resemblance to Namibian 884 desert ecosystems that experience flushes of plant growth in response to increased precipitation. For 885 example, increased wetting prompts a seasonal influx of large number of gemsbok (Oryx gazella) to 886 887 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 hyaena
(Tilson and Henschel, 1986).

For the *Palaeoloxodon* remains, there is clearly more than one individual preserved at the site: 890 891 further excavation is likely to reveal the remains of further elephants and may allow assessment of the 892 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 893 would have been a social animal living in family groups like living elephants. Elephants require a 894 substantial intake of water (up to 360 litres a day in an adult), implying local availability of water. 895 Elephants in semi-desert areas of Africa (Mali and Namibia) undertake substantial migrations in search 896 of food and water, and focus on moist riverside vegetation (e.g. Viljoen, 1989a, b) but Ramey et al. 897 (2013) have demonstrated a reliance on clean, un-fouled water resources. 898

899 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 900 elephant herd, even though elephants can survive on relatively low-quality herbage. Microwear and 901 902 isotopic studies of *Palaeoloxodon* indicate a mixed-feeder taking both graze and browse (Grube et al., 903 2010; Rivals et al. 2012). The mesowear method of Saarinen et al. (2015) has been applied to the upper 904 molar (TAG14/301) and lower dP<sub>4</sub> (TAG14/281) from Ti's al Ghadah: the former gave an average 905 mesowear angle of 120°, indicating a grass-dominated mixed-feeder (50-70 % grass); the latter an angle 906 of 136°, indicating a strongly graze-dominated diet (> 90 % grass).

907 The presence of a robust hemione and the feeding habits of extant oryx species are also 908 suggestive of the presence of open, grassland habitats. Extant oryx species are mixed feeders although 909 the majority of the diet consists of coarse grasses occasionally supplemented by ephemeral forbs 910 (Stanley Price, 1989). The Pleistocene oryx of Ti's al Ghadah, however, appears to have been a relatively large-bodied form and available data indicate that the specimens approach the size of extant 911 O. beisa. While Oryx spp. display marked physiological adaptations to tolerate drought conditions (e.g. 912 Ostrowski et al., 2006), available data for four species indicate that there is a broad but positive 913 correlation between annual rainfall and body weight (Fig. 16). It is plausible to suggest that the relative 914

size of the oryx of Ti's al Ghadah reflected more amenable habitats and that climatic and environmental
amelioration was of a sufficient duration to support populations of this larger-bodied form.

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

923

#### 924 6. Conclusion

The Middle Pleistocene fauna of Ti's al Ghadah reported here, dated to ca. 500 ka, comprises reptiles, 925 926 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 927 taxa, which we interpret to reflect the geographic situation of the Arabian Peninsula as a crossroads 928 929 between continents. Chronometric data and the identified vertebrate taxa indicate that areas of the 930 southwest Nefud Desert held (at least periodically) substantial freshwater and plant resources in MIS 931 11 and were a focal point in the landscape for birds and populations of herbivores (including very large 932 mammals) and their predators and scavengers.

933

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1445	Table 1 Pleistocene vertebrate taxa from the Arabian Peninsula reported prior to this study. Sources: Shi'bat
1446	Dihya - taxa and dates, Delagnes et al. (2012); Rub' al Khali - taxa, McClure (1984); Nefud Desert - taxa <sup>a</sup> , Thomas
1447	et al. (1998), taxa <sup>b</sup> , Stimpson et al. (2015), dates, Rosenberg et al. (2013). X = present; / = no record.
1448	
1449	Table 2 Measurements of greatest length (GL), anterior width (AW) and posterior width (PW) of reptile vertebrae
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bones - Bovidae) for B: trenches 1 and 2 and, C: trenches 5 and 6 at Ti's al Ghadah.



1509 Fig. 6. Reptile and bird fossils from Unit 5 at Ti's al Ghadah. A: TAG13/049 mid-dorsal (trunk) vertebra, ventral 1510 aspect, cf. Varanidae/Uromastyx sp. B: TAG14/706 cervical vertebra, lateral aspect, cf. Uromastyx. C: 1511 TAG14/318 13th cervical vertebra, dorsal aspect, Struthio sp. D: TAG13/038 left tarsometatarsus, dorsal aspect, 1512 Tachybaptus sp. E i: TAG14/287 occipital region and base of skull of Neophron percnopterus, lateral aspect. E 1513 ii: TAG14/287, maxilla of Neophron percnopterus, lateral aspect. E iii: TAG14/269 right humerus proximal end 1514 of Neophron percnopterus, caudal aspect. E iv: TAG14/259 right humerus distal end of Neophron percnopterus, 1515 caudal aspect. F: TAG14/270 proximal end of left humerus of *Pterocles orientalis*, caudal aspect. Scale bars = 10 1516 mm. Numbered features are referred to in the text. 1517 1518 Fig. 7. Carnivora fossils from Unit 5 at Ti's al Ghadah A: TAG14/339 phalanx, volar and plantar aspects, Panthera 1519 sp. B: TAG13/145 broken mandibular canine, Panthera sp. C: TAG14/256 coprolite, cf. Crocuta crocuta. D: 1520 TAG14/245, occipital region, caudal aspect, Canis sp. E: TAG14/184, right M<sub>1</sub> (carnassial), Canis anthus, buccal

(i) and lingual (ii) aspects. Scale bars = 10 mm. Numbered features are referred to in the text.

1522

1523 Fig. 8. Bivariate plot to show mean values, ranges (1 sigma) and single observations of length (M-D = mesio-

distal) and width (B-L = buccal-lingual) measurements for lower carnassial teeth  $(M_1)$  from recent and fossil

1525 Canis spp. with fossil specimen TAG14/184. Data compiled from Kurtén, 1965; Dayan et al., 1992; Dayan,

1526 1994; Rook et al., 1996; Aouraghe, 2000; Baryshnikov, 2012; Stoyanov, 2012. Measurements of recent C. lupus

1527 *arabs* were taken from comparative specimens at the HZM. REVISE figures.

1528

1529 Fig. 9. Fossils of Equidae from Unit 5 at Ti's al Ghadah. TAG14/329 right mandible, *Equus hemionus*, in A:

1530 lateral and B: occlusal views. C: TAG14/342 left astragalus, *Equus* sp., dorsal aspect. D: TAG13/146 left femur,

1531 *Equus* sp., cranial and caudal views. Scale bars = 50 mm. Numbered features are referred to in the text.

1532

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

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

1540

1541 Fig. 12. Examples of fossil crania and post-crania of *Oryx* sp. from Ti's al Ghadah. TAG13/109 right maxilla

and tooth row in A: lateral and B: occlusal views. TAG13/147, right mandible and tooth row in C: lateral and D:

1543 occlusal views. E: TAG14/216, right horn core and cranial fragment, anterior aspect. F: TAG13/099, left

humerus cranial view. G: TAG14/901, complete left metatarsal, dorsal view. H: TAG14/195, fragment of distal

1545 left tibia, ventral view. I: TAG14/1518 left astragalus, dorsal aspect. J: TAG13/003 distal metacarpal fragment,

dorsal view. K: TAG14/205, rib fragment with carnivore pits. Scale bars = 50 mm.

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

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