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

30 3 million km^2 - is a significant gap in our knowledge of the Quaternary. Such data are critical lines of

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.

33 Here, we describe an important contribution to the record and report stratigraphically-constrained

34 fossils of mammals, birds and reptiles from recent excavations at Ti's al Ghadah in the southwestern

35 Nefud Desert. Combined U-series and ESR analyses of *Oryx* sp. teeth indicate that the assemblage is

36 Middle Pleistocene in age and dates to ca. 500 ka. The identified fauna is a biogeographical admixture

37 that consists of likely endemics and taxa of African and Eurasian affinity and includes extinct and extant

38 (or related Pleistocene forms of) mammals (*Palaeoloxodon* cf. *recki*, *Panthera* cf. *gombaszogenis*,

39 *Equus hemionus*, cf. *Crocuta crocuta*, *Vulpes* sp., *Canis anthus, Oryx* sp.), the first Pleistocene records

40 of birds from the Arabian Peninsula (*Struthio* sp., *Neophron percnopterus*, *Milvus* cf. *migrans*,

41 *Tachybaptus* sp. *Anas* sp., *Pterocles orientalis*, *Motacilla* cf. *alba*) and reptiles (Varanidae/*Uromastyx*

42 sp.). We infer that the assemblage reflects mortality in populations of herbivorous animals and their

43 predators and scavengers that were attracted to freshwater and plant resources in the inter-dune basin.

44 At present, there is no evidence to suggest hominin agency in the accumulation of the bone assemblages.

45 The inferred ecological characteristics of the taxa recovered indicate the presence, at least periodically,

46 of substantial water-bodies and open grassland habitats.

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56 **1. Introduction**

57 The Arabian Peninsula (defined here as the landmass from the southern borders of Iraq and Jordan, to

58 the southern coastline of Yemen; **Fig. 1A**) is a key theatre to consider hominin dispersals between

59 Africa and Eurasia (e.g. Rose and Petraglia, 2009; Dennell and Petraglia, 2012; Groucutt and Petraglia,

60 2012). While the geographical significance of this landmass of over 3 million km^2 as a link between

61 these continents is self-evident, the potential routes and timing of dispersals and exchange by animals

62 and hominins in the Pleistocene (2.6 Ma to 0.011 Ma) are much-debated (e.g. O'Regan et al., 2005;

63 Beyin, 2006; Fernandes et al., 2006; Fernandes, 2009; O'Regan et al., 2011; Groucutt et al., 2015a).

64 As studies continue to unveil a complex climatic and environmental history (e.g. Fleitmann et

65 al., 2003; Fleitmann and Matter, 2009; Parker, 2009; Fleitmann et al., 2011; Rosenberg et al., 2011;

66 Rosenberg et al., 2013; Breeze et al., 2015; Jennings et al., 2015; Matter et al., 2015; Parton et al.,

67 2015a; Parton et al., 2015b) and the Palaeolithic archaeological record develops (e.g. Armitage et al.,

68 2011; Delagnes et al., 2012; Groucutt and Petraglia, 2012; Petraglia et al., 2012) it is now clear that

69 Pleistocene hominins penetrated the interior of the Peninsula (Groucutt et al., 2015b; Groucutt et al.

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

72 chronologically-constrained records of vertebrates. Here, we describe an important step towards

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

76 and Oriental (e.g. Portik and Papenfuss, 2012) and the historical vertebrate fauna is an admixture of

77 endemic species with taxa of African and Eurasian affinity (e.g. Delany, 1989; Harrison and Bates,

78 1991; Cox et al., 2012; Portik and Papenfuss, 2012). The opening of the Red Sea and climatic shifts in

79 the late Miocene were major drivers of diversification and dispersal of the biota of the region and a

80 combination of harsh arid environments, periodic humid events and geological evolution has shaped

81 the fauna of the Peninsula (e.g. Metallinou et al., 2012). Genetic studies of a small number of species

82 (*Papio hamadryas*, *Ichneumia albicauda* and *Varanus yemenensis*) have shed light on the

83 biogeographical history of aspects of the regional Pleistocene fauna (Fernandes, 2009 and Kopp et al.,

84   2014; Fernandes, 2011; Portik and Papenfuss, 2012, respectively) but, in contrast to works on Miocene

85   vertebrates (e.g. Whybrow and Hill, 1999; Beech and Hellyer, 2005), the paucity of Pleistocene records

86   from the Arabian Peninsula remains a major limiting factor in modelling the dynamics of Quaternary

87   animal populations (e.g. Fernandes, 2009; O'Regan et al., 2011; Stimpson et al., 2015). Furthermore,

88   while records of vertebrate taxa cannot be considered as direct or unequivocal proxies for the dispersal

89   of hominins (e.g. Bar-Yosef and Belmaker, 2011) and species responses to climatic and environmental

90   changes are individualistic (e.g. Stewart, 2009), such data are critical lines of contextual evidence in

91   considering Pleistocene environments and hominin palaeoecology in the interior (e.g. Belmaker, 2009).

92   The Arabian Peninsula today comprises of a heterogeneous suite of habitats, including tropical,

93   sub-tropical and montane biomes in the south and western coastal regions. The interior, however, is

94   dominated by basalt flows, salt flats and (overwhelmingly) sand and gravel deserts (Mallon, 2011; Cox

95   et al., 2012). These hyper-arid habitats are embodied by three major sand seas that collectively occupy

96   over 700,000 km^2: the Rub' al Khali (also known as the Empty Quarter) and Wahiba Sands in the south

97   and southeast, respectively, and the Nefud Desert in the north (**Fig. 1A**). During the Pleistocene,

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

100 et al., 2015; Matter et al., 2015; Parton et al., 2015b; **Fig. 1A, B**). As the volume and periodicity of

101 available moisture increased plant biomass will have responded accordingly (e.g. Southgate et al., 1996)

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).

108   Excavations of the Late Pleistocene site Shi'bat Dihya (SD-1) in Yemen, dated to 55 ka, by

109 Delagnes et al. (2012) recovered poorly preserved assemblages of bone. Remains of the post-cranial

110 skeleton were impossible to identify. Tooth fragments could be assigned to four mammalian families:

111   Bovidae, Suidae, Hystricidae and Equidae. A tentative identification of Asiatic wild ass (cf. *Equus*

112   *hemionus*) was proposed from an intact third molar.

113   Pleistocene fossils have also been recovered from the two largest sand seas: the Rub' al Khali

114   and the Nefud Desert (**Fig. 1A**). Collections made by McClure (1984) during pioneering studies of

115   lacustrine deposits in the Rub' al Khali resulted in confident identifications of *Oryx* ("presumably

116   *leucoryx*"), *Bos* (cf. *primigenius*), *Equus* (cf. *hemionus*), *Gazella* sp. ("apparently *G. arabica*"), *Bubalus*

117   sp. and *Hippopotamus* ("presumably *amphibius*"). Remains of the Caprinae included a possible record

118   of the endemic *Hemitragus* (*Arabitragus*) *jayakari*. McClure points out, however, that collection was

119   not systematic and information for exact geographical provenance and chronological affinities of the

120   fossil assemblages was lacking. Essentially, the "fossil vertebrate suite should therefore be taken as

121   representing the general lacustrine periods of both late Pleistocene and Holocene" (McClure, 1984, 179)

122   with the proviso that it was likely that the hippopotamus and large water buffalo "belong to the earlier

123   (Late Pleistocene) period" (McClure, 1984, 181).

124   In the north of the Peninsula, Pleistocene fossils are known to be associated with lacustrine

125   deposits in the Nefud Desert (Thomas et al., 1998; Rosenberg et al., 2013). The first Pleistocene taxa

126   were reported by Thomas et al. (1998) from collections at three sites in the southwestern Nefud Desert

127   (Locality #1: Khall Amayshan; Locality #2: Ti's al Ghadah, the focus of this study, and an unnamed

128   site: Locality #3; **see Fig. 1B**). Despite relatively small sample sizes, a total of 14 taxa (including fish,

129   reptiles and mammals) were identified (**Table 1**).

130   Thomas et al. (1998) report fossils of *Equus* sp., a large bovid (identified as *Pelorovis* cf.

131   *oldawayensis*) and a reportedly gracile hippopotamid (*Hexaprotodon* sp.?) from the site at Khall

132   Amayshan (KAM-1 – Thomas locality 1; **Fig. 1B**). Thomas et al. (1998) also report fossils from an

133   unnamed site ("Locality 3"; **Fig. 1B**) that is likely to be site "16.1" of Rosenberg et al. (2013) and dated

134   between 419 ± 39 ka and 286 ± 30 ka, which included large bovids (referred to *Pelorovis* cf.

135   *oldawayensis*), a well preserved left mandible of *Crocuta crocuta*, and post-crania and a molar from an

136   elephant. Examination of the incomplete, hypsodont molar plate resulted in a cautious referral to the

137   extinct African elephant taxon *Palaeoloxodon recki*. An aberrant horn-core (originally reported to be

138   from Ti's al Ghadah) that possibly represented an undescribed taxon was also recovered from this site.

139   The site at Ti's al Ghadah (**Fig. 2**) yielded the largest and most diverse sample reported by

140   Thomas et al. (1998). The collection included a relative abundance of fossils from *Oryx* sp. together

141   with small numbers of specimens attributable to tortoise (*Geochelone* cf. *sulcata*), a large

142   Osteoglossiforme (an order of primitive, ray-finned freshwater fish) specimen we were unfortunately

143   unable to relocate and review), *Equus* sp., *Vulpes* sp. and a specimen conferred to the extinct Eurasian

144   jaguar, *Panthera (onca) gombaszogensis* (see also Stimpson et al., 2015). Unidentified, potentially

145   novel bovid and camelid taxa were also reported. Re-inspection of the bovid remains from the collection

146   at Ti's al Ghadah by one of us (CMS) suggested that the crania may be attributable to a Pleistocene

147   *Oryx* sp. (see also section **4.2.3.4**). A poorly preserved maxilla fragment appears to be camelid, but with

148   no discernible difference to extant *Camelus*.

149   While these collections provide some insight into the Pleistocene vertebrates of the interior,

150   they were the product of surface collections and their stratigraphic and chronological affinities are not

151   clear (Stimpson et al., 2015). In the original report by Thomas et al. (1998), for example, the collections

152   were considered as a whole and an Early Pleistocene age and an Ethiopian affinity were inferred on the

153   basis of taxonomic composition and "stage of evolution" (Thomas et al., 1998, 150). Subsequent dating

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

156   Middle and Late Pleistocene age (**Table 1**). As such, further work to resolve the identity and

157   chronological affinities of the Nefud fauna is warranted.

158   Here we describe an important step towards resolving the character and chronological context

159   of the Pleistocene vertebrates of the Nefud Desert. Following collaborative investigations of the fossil

160   site of Ti's al Ghadah by the Saudi Commission for Tourism and National Heritage (SCTH), Saudi

161   Geological Survey (SGS) and the Palaeodeserts project (University of Oxford), we describe

162   stratigraphically-constrained records of mammals, birds and reptiles. We report the results of our

163   chronometric and stratigraphic investigations and consider the biostratigraphic and palaeoecological

164   implications of the identified taxa.

165

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,

168   approximately 95 km southeast of the city of Tayma (**Fig. 1B**). The basin is bordered to the west by a

169   large (ca. 60 m high) compound barchan dune ridge, while smaller branching linear dunes extend to the

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

172   marls (**Fig. 2B**) that rises approximately 6 m above the floor of the basin, and is approximately 1 km in

173   length. It dips gently to the south of the basin and interdigitates with low branching dunes in the east.

174   Lacustrine and diatomaceous marls are exposed vertically along the western edge of the ridge (**Fig. 2C**)

175   and dip gently to the east where they are overlain by modern dune sands. Ephemeral gullies run

176   perpendicular to the long axis of the ridge towards the west of the basin and at the foot of the large

177   barchan dune. These have eroded fossils from the main lake ridge, re-depositing them unconformably

178   downslope in sinuous ridges comprised of heavily indurated, coarse, red-brown sand. Pale cream-grey

179   sands are exposed along the southeastern corner of the basin, and represent an older palaeodune

180   configuration that lies beneath the present day rubified sand sea. Exposed within the centre of the basin,

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.

183   0.4 m) beds of diatomaceous marls outcrop from the smaller branching linear dunes and represent a

184   phase of lake formation that postdates the formation of the main lake ridge. The lacustrine silts and

185   diatomaceous marls of the ridge have formed an armoured cap to the thick beds of interdigitated sands

186   that lie beneath, including the principal fossiliferous deposit: Unit 5.

187

188   **3. Materials and Methods**

189   **3.1 Excavation**

190   Excavations on the ridge focused on Unit 5 (**Fig. 2A-H**; **Fig. 4**): methodology is described in Stimpson

191   et al. (2015). The general lithofacies described in Stimpson et al. (2015; n.b. Unit 5 = "Layer 5") were

192   found throughout the excavations with major variation between trenches limited to the relative thickness

193   of the lacustrine deposit and the greenish grey sands overlying Unit 5. All overlying deposits were

194   removed following stratigraphic boundaries and all fragments in Unit 5 were collected. The locations

195   of diagnostic specimens (> 5 mm in maximum dimension with anatomical landmarks) were recorded

196   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.

202

203   **3.2 Fossil analyses**

204   The identification of the fossils was conducted in the UK with the permission of the SCTH. Fossils

205   were identified by morphological and morphometric comparisons with comparative museum

206   specimens, published descriptions and morphometric data. Measurements of bones generally follow the

207   schemes described in Von den Driesch (1976), and for elephant molars Maglio (1973) but are defined

208   in the text. Measurements were taken with dial callipers to the nearest 0.01 mm. Morphometric analyses

209   were carried out in PAST (Hammer et al., 2001) following conventions described in Hammer and

210   Harper (2006). A preliminary macroscopic taphonomic investigation was conducted and surface

211   condition and modifications to bones were noted. Weathering stages were characterised following

212   Behrensmeyer (1978) and interpreted following Andrews and Whybrow (2005).

213   For mammals and reptiles, modern reference materials were consulted at the Oxford University

214   Museum of Natural History (OUMNH), the Graeme Clark Zooarchaeology Laboratory, University of

215   Cambridge (GCZL) and the Harrison Zoological Institute (HZM). Palaeontological specimens and

216   modern comparatives were also consulted at the Department of Earth Sciences at the Natural History

217   Museum (South Kensington – NHM-SK). For birds, recent comparative materials were consulted at the

218   Bird Group, Natural History Museum (NHM-Tring) and palaeontological comparative specimens at the

219   NHM-SK.

220

221   **3.3 Chronology**

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222   A sample for OSL dating was probably recovered from a stratum that directly underlies, or is equivalent

223   to the main bone-bearing layer (Units 4 or 5, respectively; **Fig. 4**) by Rosenberg et al. (2013). This

224   sample yielded OSL and TT-OSL (thermally-transferred optically stimulated luminescence) ages of

225   328 ± 26 ka and 318 ± 25 ka, respectively. The overlying lake formation was interpreted as an MIS 9

226   deposit (Rosenberg et al., 2013).

227   To refine our understanding of the chronology of the lacustrine deposit and the fossiliferous

228   stratum that underlies it, we collected an OSL sample (**methods S1 supplementary data**) from the

229   palaeolake sediments capping the excavated sequence (Unit 7; see **Fig. 4**). Five fossil cheek teeth (*Oryx*

230   sp.) that were recovered from Unit 5 were also submitted for U-series and combined US-ESR dating

231   and a series of sediment samples were collected from different depths within Unit 5 to evaluate the

232   variability of the sediment radioactivity (**methods S2 supplementary data**).

233

234   **4. Results**

235   **4.1 Stratigraphy, bone distribution and taphonomy**

236   The deepest sedimentary sequence uncovered at the site comprised a total of 9 stratigraphic units (**Fig.**

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.

241   Granulitic inclusions of well-rounded quartz occur throughout the unit, which displays a diffuse contact

242   with both the overlying and underlying units. This is overlain by a thin layer (Unit 3) of very poorly

243   sorted greenish sands with no bedding structures and numerous, well-rounded quartz pebble inclusions.

244   The unit is heavily cemented and calcritized at the base, with iron staining and iron-stained root voids

245   throughout. Unit 4 comprises pale cream-grey, very poorly sorted, coarse, horizontally bedded sands.

246   Bedding is variable, being generally weak throughout, but strongly bedded and cemented in places.

247   Vertical and horizontal iron-stained root impressions occur throughout, along with numerous well-

248   rounded quartz granules and small (< 10 mm) pebbles. There is a notable increase in iron staining at the

249   base of the unit, along with generally coarser clasts, while a diffuse contact is present with both over

250   and underlying units.

251   Unit 5 is the main fossil layer at the site and comprises weakly cross-bedded, very poorly sorted,

252   coarse, reddish sands with occasional iron-stained root voids, fine (ca. 5 -10 mm max length) rounded

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

255   fractured laminae intruding vertically from the overlying lake beds. The unit is indicative of the small-

256   scale, localised mobilisation of waterlain sands, displaying evidence of both bioturbation and sediment

257   reworking in the form of small (< 20 cm) infills. Unit 5 is representative of wetted and partially

258   vegetated sands. The characteristics of the underlying unit (Unit 4) indicate initial sediment deposition

259   under low energy (localised) sheetflood conditions, following increased rainfall in the basin. A lack of

260   channel incisions or large clasts throughout the sequence precludes major sediment mobilisation, and

261   is more indicative of continual localised slopewash events. This phase of surface water and sediment

262   mobilisation culminated in the development of vegetation and stabilisation of the landscape represented

263   by Unit 5.

264   Fossil specimens were mineralised and ranged from a pale, yellowish-brown to (more

265   frequently) a dark reddish-brown: iron-staining was prevalent the latter resulting from the leaching and

266   downward percolation of iron derived from Fe-rich sands within the overlying sedimentary units.

267   Consolidated sand particles were frequently adhered to the bone surface, though were relatively easy to

268   remove with brush or wooden pick. Post-depositional movement and reworking appears to be have been

269   minimal. While minor abrasion was occasionally observed, there was no evidence to suggest rolling or

270   significant water transport. As a general rule, there was a contrast in the degree of weathering between

271   the area of bone in contact with the substrate (less abraded) than the upper surface exposed in excavation

272   (more abraded). Some trampling was evident in the form of the presence of fine striae on the surfaces

273   of bones and "sharp breaks" to specimens (e.g. see **Fig. 12F, H** and **J**). In addition to direct physical

274   evidence of the presence of predators and scavengers on site, carnivore pits and tooth marks indicate

275   the activity of small and large-bodied carnivores. Tooth marks were identified in the small sample of

276   recovered bird bones (**section 4.2.2**) and were detected on the bones of *Equus* sp. (**section 4.2.3.2**) and

277 *Oryx* sp. (**section 4.2.3.4**). No lithics were recovered during our excavations and the association

278 between the artefacts reported previously in the basin (Scerri et al., 2015) and the fossiliferous strata

279 remains unclear.

280   Within the limits of our investigations, there was lateral variation in taxonomic diversity and in

281 the preservation of the recovered specimens between the northern and southern limits of the excavations

282 (**Fig. 3**). Fossils attributable to the Bovidae were numerically dominant throughout although trenches

283 in the south of the site (trenches 1 and 2) yielded a greater range of taxa compared with the northern

284 excavations (trenches 5 and 6; **Fig. 5A**). Weathering profiles generated from examination of bovid long

285 bones from trenches 1,2 and 5 and 6 (**Fig. 5B** and **5C**, respectively) indicate that specimens from the

286 south of the site were generally well-preserved: maximally to Behrensmeyer's (1978) weathering stage

287 3, rarely to stage 4 (**Fig. 5B**). Conversely, specimens from the northerly trenches were paler in colour,

288 more friable and weathering profiles suggest that these specimens were subject to sub-aerial weathering

289 for longer than in the southern trenches (**Fig. 5C**). In summary, fossil assemblages from the

290 investigations of the southern end of the ridge were more diverse and better preserved than the

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

299 mark an influx of sand into the basin. These are generally laterally variable and well cemented in places

300 (Unit 7). Unit 8 comprises a series of interdigitated sands and marls, possibly reflecting variations in

301 lake water levels in the basin. Marls are highly cemented and gypsiferous, while sand content is coarse

302 and non-laminar. The sequence is capped by beds of sandy, gypsiferous marls (Unit 9). These are

303 heavily indurated and unevenly bedded in desiccation 'curls': blocks of marl that have undergone

304 polygonal cracking as a result of drying, and have deformed to make bowl-shaped structures. These are

305   interdigitated due to the extent of deformation, and are predominantly infilled with sand and infrequent

306   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**

311   Thomas et al. (1998) report the remains of tortoise (*Geochelone* cf. *sulcata*) from Ti's al Ghadah. While

312   a small fragment of carapace was recovered from the surface of the ridge deposit (Unit 9), however, no

313   further remains of the Testudinidae have been identified in the excavated materials from Unit 5. In

314   contrast, the Squamata (an order containing c. 95% of all living reptiles) are represented by a small

315   number of relatively large trunk (mid-dorsal) vertebrae and a single cervical vertebra (**Fig 6A, B**; **Table**

316   **2**). Osteological nomenclature and description follow Hoffstetter and Gasc (1969) and Holmes et al.

317   (2010).

318

319   **4.2.1.1 Squamata**

320   Varanidae and/or Agamidae - *Uromastyx* sp.

321   The centra are procoelous. The cotyles are widest dorsally with a relatively flat dorsal edge and narrow

322   ventrally to a curved ventral margin. The condyles are orientated postero-dorsally, with a flatter ventral

323   margin than the cotyles. The cotyles are orientated antero-ventrally and, unlike the majority of

324   procoelous lizards, the ventral rim is retracted and exposes the entirety of ventral concave surface of

325   the cotyle (**Fig. 6A-1**). There is no sagittal crest present on the ventral surface. These characters suggest

326   the varanids (Varanidae) or the agamid *Uromastyx*. The cervical vertebra (TAG14/706), however, lacks

327   a marked hypapophyseal peduncle (**Fig. 6B-2**), which suggests *Uromastyx* sp. rather than the Varanidae

328   (Holmes et al., 2010).

329

330   **4.2.2 Aves**

331   Ten specimens are attributable to six orders, six families, seven genera and seven species (**Table 3**).

332   Taxonomic conventions follow Porter and Aspinall (2010) and osteological nomenclature follows

333   Baumel and Witmer (1993).

334

335   **4.2.2.1 Struthioniformes**

336   Struthionidae (ostrichs)

337   *Struthio* sp.

338   A thirteenth cervical vertebra (TAG14/318) is attributable to an ostrich, *Struthio* sp. (**Fig. 6C**). The

339   specimen is stained light-brown in colour with minimal weathering or abrasion. All articular surfaces

340   are well-defined, although the specimen has been crushed and is slightly compressed in the

341   dorsal/ventral direction. The facies articularis caudalis of the corpus vertebra has broken off, as have

342   the processes costalis.

343   TAG14/318 was compared with the type specimen (NHM - 23105) of the extinct Asiatic

344   ostrich, *Struthio asiaticus*, Milne Edwards 1871. This taxon, of uncertain stratigraphic provenance from

345   the Siwaliks, is generally regarded as a large-form of ostrich and a range Pliocene- and Pleistocene-age

346   osteological remains from Eurasia have been referred to it (Mourer-Chauviré and Geraards, 2008).

347   Comparison with the type specimen suggests that the specimen from Ti's al Ghadah was

348   derived from a bird with similarly-sized cervical vertebrae. The series of articulated cervical vertebrae

349   in the type, however, are fused in matrix to an atlas, distal tarsometatarsus and phalanx and this state of

350   preservation precludes detailed morphological and metric comparison. In terms of overall dimensions

351   (**Table S3 supplementary data**) though, there is no evidence to suggest an affinity with "giant"

352   Pleistocene ostrich taxa reported from the Caucasus (Burchak-Abramovich and Vekua, 1990; Vekua,

353   2013).

354   Morphological and morphometric comparisons (**Table S3 supplementary data**) were also

355   conducted with specimens from extant taxa (*S. camelus camelus*, *S. c. australis*, *S. c. massaicus* and *S.*

356   *molybdophanes*) and recently extinct sub-species (*S. c. syriacus*). TAG14/318 differs from comparative

357   specimens from extant *S. c. australis* and extinct *S. c. syriacus*. Viewed from the dorsal aspect, the

358   opening to the foramen vertebra forms a much more acute angle between the zygapophyses cranialis in

359 TAG14/318 (**Fig. 6C-3**) than in the comparative specimens for these taxa. The articular surfaces of

360 zygapophyses cranialis are also much more developed and robust in TAG14/318 (**Fig 6C-4**). At the

361 caudal end, the lacuna interzygapophyses is very square in TAG14/318 (**Fig. 6C-5**), as indeed are the

362 caudal articular facets (**Fig. 6C-6**): these characters are rounded in the comparative specimens.

363 However, comparison with material from *S. molybdophanes* (NHM-Tring: 1888.5.5.1) indicates that

364 these characters are similar. From the dorsal aspect, the lacuna interzygapophyses caudalis is square

365 and the lacuna interzygapophyses is v-shaped, rather than u-shaped in *S. molybdophanes* (**Table S3**

366 **supplementary data**).

367   The Pleistocene fossil record of *Struthio* is sparse and the taxonomic and geographic affinities

368 of Pleistocene ostriches are poorly known. As such, it is not feasible to identify this specimen beyond

369 genus. However, it is notable that of all the compared specimens the closest match on morphological

370 and morphometric grounds is *S. molybdophanes*, an ostrich recently promoted to full species status

371 (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.

376 A well-preserved, complete left tarsometatarus (**Fig. 6D**) first reported in Stimpson et al. (2015) is

377 derived from a small grebe of the genus *Tachybaptus*, which contains one species, *T. ruficollis*. The

378 specimen is an excellent match for the genus. At the distal end of the element, the end of the lateral

379 edge of the trochlea metatarsi II curves to the diaphysis and the lateral side of the trochlea metatarsi IV

380 is flat. At the proximal end, the hypotarsus is equal in height to the condylus interarticularis (cf. Fjeldså,

381 2004, 214).

382   TAG13/038 is notably shorter overall (**Fig. S2A supplementary data**), but is not less robust

383 than the comparative material at NHM-Tring. To date, morphological and metric comparisons have

384 been limited to comparative material of European provenance (**Table S4 supplementary data**) and

385 extant Oriental subspecies are "generally smaller" than their counterparts from higher latitudes (Fjeldså,

386 2004, 153). There are differences, however, between the relative positions of the medial trochlea (**Fig**

387 **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*

394 The mineralised remains of a cranium (TAG14/287- **Fig. 6E i** and **ii**), a complete right humerus

395 (recovered in two pieces, TAG14/259 and 269**; Fig. 6E iii** and **iv**) and a complete, but very friable right

396 ulna (TAG14/286) were found in close proximity in trench one and are clearly attributable to Egyptian

397 vulture, *Neophron percnopterus* (cf. NHM 1847.10.21.25). These specimens are a relatively early

398 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 semi-

400 circular puncture (maximum dimensions = 11.60 mm × 8.78 mm) is evident to the right side of the

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 × 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

409 edge and is likely to have been re-exposed and weathered. The ulna has also been chewed, apparently

410 by a small to medium-sized carnivore.

411

412 *Milvus* sp. (cf. *migrans*)

413 A fragment of a distal end of a right femur (TAG14/225) indicates the presence of a kite. While it is

414 notoriously difficult to separate skeletal elements of the genus *Milvus* sp. (e.g. Morales Muniz, 1993),

415 the relatively small size of the specimen and comparison with the specimens at Tring is suggestive of

416 black 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*

438 Two small, mineralised and well preserved specimens - a fragment of a right proximal humerus

439 (TAG14/246) and a left ulna (TAG14/251) - are derived from passerines. Comparisons under a lower

440 power microscope with the comparative collections at NHM-Tring indicate that they are both

441 attributable to the genus *Motacilla* (wagtails), most likely *M. alba*.

442

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**).

448 Two of these, a left third metacarpal (JMI 27) and a right fourth metacarpal (TAG13/097), have been

449 referred to the extinct Eurasian jaguar, *Panthera gombaszogensis* (see Thomas et al., 1998 and Stimpson

450 et al., 2015, respectively). Morphological and morphometric analyses of TAG13/097 are described in

451 Stimpson et al. (2015). While comparative sample sizes are small, measurements for JMI 27 appear

452 equivalent with published measurements for Pleistocene jaguars, *P. onca augusta* and *P.*

453 *gombaszogensis* (**Table S6**; **Fig. S3 supplementary data**). The genus is also represented by a phalanx

454 (TAG14/339) and broken mandibular canine (TAG13/145) (**Fig. 7A**, **B**).

455

456 Hyaenidae

457 cf. *Crocuta crocuta*

458 A total of seven coprolites were during the excavations: six specimens from trench 1 and a one specimen

459 from trench 6. The general morphology of intact specimens - a near circular cross-section, with convex

460 and concave ends - closely resembles hyaena, most likely *Crocuta crocuta* (Larkin pers comm.; Parfitt

461 pers. comm). Measurements (following Larkin et al., (2000)) of a complete specimen, TAG14/256 (**Fig.**

462 **7C**: axial length 40.58 mm; diameter A 29.85 mm, diameter B 28.43 mm) fall within reported ranges

463 of coprolites from this taxon (cf. Larkin et al., 2000; Lewis et al., 2010).

464

465 Canidae

466 *Canis* sp.

467 A fragment of the base of the skull (TAG14/245), a lower right carnassial (TAG14/184) and a fragment

468 of a lumbar vertebra (TAG14/208) are attributable to medium-sized canids. The skull fragment consists

469 of the occipital region and a fragment of the supra-occipital (**Fig. 7D**). The foramen magnum, occipital

470 condyles and condylar foramen are intact and portions of the par-occipital process and basi-occipital

471   are present. This specimen is a good morphological match with comparative material for the golden

472   jackal, *Canis aureus*: measurements indicate that it derived from a relatively large individual (**Table 4**).

473

474   *Canis anthus*

475   TAG14/184 is a trenchant, lower right carnassial (M_1). With the exception of the break to the mesial

476   root, the specimen is complete and is relatively unworn (**Fig. 7E**). The specimen, however, appears

477   iron-stained and there is marked "sidedness" in weathering: it appears that the tooth ultimately lay on

478   its buccal side prior to burial as there is minimal modification to this surface of the tooth (**Fig. 7E i**).

479   Conversely, the lingual side is abraded across the entire surface (**Fig. 7E ii**).

480   TAG14/184 is too large to have derived from any known *Vulpes* sp. and is from a medium-

481   sized canid. The carnassial is trenchant, with a sub-equal bicuspid talonid (**Fig. 7E ii-1**) and a relatively

482   well-developed metaconid (**Fig. 7E ii-2**). The hypoconid is not centrally-located and is angular rather

483   than conical. These characters indicate *Canis* sp. and discount the hypercarnivorous *Cuon* and *Lycaon*

484   (cf. Baryshnikov and Tsoukala, 2010; Baryshnikov, 2012; Brugal and Boudadi-Maligne, 2011; Petrucci

485   et al., 2012).

486   The morphometric characteristics of TAG14/184 indicate that it derived from a smaller animal

487   than Pleistocene and recent records of European and regional *C. lupus lupus* (cf. Flower and Shreve,

488   2014; Sansalone et al., 2015), recent records of *C. lupus pallipes* (cf. Dayan, 1994) and Pleistocene and

489   recent records of *C. lupus arabs* from the Levant (**Fig. 8**). Conversely, measurements from TAG14/184

490   suggest that it derived from an animal larger than recent European golden jackals, recent and Pleistocene

491   African golden jackals (*C. aureus* s.s) and match equivalent measurements of a large form, variously

492   classified as "*Canis aureus lupaster*" or "*Canis lupus lupaster*" ("*Canis lupus lupaster*" in **Fig. 8**).

493   Osteological studies have long recognised the likelihood of a large extant form of jackal in

494   North Africa (e.g. Huxley, 1880) and "large" golden jackal fossils are known from Middle to Late

495   Pleistocene in Northwest Africa (Geraads, 2011). Recent work with mitochrondrial and nuclear genome

496   data has indicated that some populations of North African golden jackals are a cryptic species distinct

497   from Eurasian golden jackals, which occupies a much wider geographical area in Africa than was

498   previously thought (Rueness et al., 2011; Gaubert et al., 2012; Koepfli et al., 2015). Koepfli et al.

18

499   (2015) recommend that *Canis lupus lupaster* (and *Canis aureus* sensu lato) be classified as *Canis*

500   *anthus*, the African golden wolf. Given the trenchant morphology and that the morphometric

501   characteristics of TAG14/184 are a close match for fossil (Levant) and recent (North Africa) data for

502   these "large forms", we follow the taxonomic proposal of Koepfli et al. (2015) and refer TAG14/184 to

503   *Canis anthus*.

504

505   *Vulpes* sp.

506   Thomas et al. (1998) reported the presence of the bones of foxes with no discernible morphological

507   differences from extant *Vulpes vulpes*. Small cranial fragments were recovered in 2013 (Stimpson et

508   al., 2015), but no further specimens have yet been identified in Unit 5.

509

510   cf. Mustelidae

511   A single left mandibular canine (antero-posterior length = 3.56 mm; buccal-lingual width = 2.34 mm)

512   with a marked cingulum on the medial side of the tooth is most likely attributable to the Mustelidae.

513   Measurements suggest that it derived from an animal similar in size to a large *Mustela* sp. or *Vormela*

514   sp. but further comparative material is required.

515

516   **4.2.3.2 Perissodactyla**

517   Equidae

518   In addition to small numbers of rib fragments and a thoracic vertebrae, three well preserved specimens

519   attributable to the Equidae were recovered (**Table 5**): a fragment of a right mandible (TAG14/329; **Fig.**

520   **9A**, **B**), a complete left astragalus (TAG14/342; **Fig. 9C**) and a near-complete left femur (TAG13/146;

521   **Fig. 9D**).

522   The Pleistocene equids of the Middle East are generally thought to comprise of *E. caballus*, *E.*

523   *hydruntinus* and *E. hemionus* (Eisenmann et al., 2002). The separation of different equids on the basis

524   of dental morphology, however, is not a straightforward issue. Morphological criteria can be equivocal

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

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

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

528

529   *Equus hemionus*

530   TAG14/329 is a fragment of a robust right mandible (**Fig. 9A**). The first molar is broken off at the root

531   below the alveolus, but the worn second and third molars are in situ. The M_2 is intact. The M_3 is largely

532   complete but there is a break to the distal occlusal surface (**Fig. 9B**). Caballoid horses can be discounted

533   as the double knots on M_2 and M_3 are rounded (**Fig. 9B-1**) with v-shaped (rather than u-shaped) lingual

534   valleys (linguaflexids; **Fig. 9B-2**) and rounded (rather than flat) buccal margins of the protoconid and

535   hypoconid (**Fig. 9B-3**), although this last characteristic is regarded as an unreliable means to

536   discriminate between taxa (Davis, 1980). While tooth wear is marked, the vestibular grooves

537   (ectoflexids) on each molar appear shallow and they do not penetrate the isthmus of the double-knot

538   (**Fig. 9B-4**). This would discount zebras and zebra-like taxa, the extinct *E. hydruntinus* and Pleistocene

539   stenonine horses and indicate the hemione, *E. hemionus*. Morphometric comparisons using the intact

540   M_2 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

542   Mongolian subspecies *E. h. hemionus* and the Tibetan species, *E. kiang* (**Fig. S4 supplementary data**).

543

544   *Equus* sp.

545   The few specimens of recovered post-crania are rather robust. The dimensions of a near-complete left

546   femur TAG13/146 (**Table 5**; **Fig. 9D**), notable for the presence of carnivore pits on the caudal surface,

547   near to the proximal end (**Fig. 9D-5**), indicate that this specimen is large and robust in comparison to

548   extant hemiones (**Fig. S5A supplementary data**). A complete left astragalus (TAG14/342; **Fig. 9C**),

549   which was found in close association with mandible TAG14/329, is also large and robust (**Fig. S5B**

550   **supplementary data**). A PCA analyses of six variables suggests that the astragalus is of a size and

551   proportions of larger equid taxa, equivalent perhaps to *Equus oldowayensis,* rather than extant hemiones

552   (**Fig. S5B supplementary data**). This would be consistent with the findings reported in Thomas et al.

553 (1998) who also describe relatively large and robust bones from the site, possibly from a robust stenonid

554 horse or species of zebra.

555 Given that Eisenmann et al. (2008) report that the various subspecies of *E. hemionus*, as they

556 are known from the fossil record, appear to have been conservative in terms of overall dimensions and

557 proportions there are two possible scenarios for the interpretation of the equid remains in hand. Firstly,

558 that there are the remains of more species of equid preserved at the site than the available dental material

559 currently indicates, or secondly that the equid remains at Ti's al Ghadah collectively represent a large

560 and robust Pleistocene form of *E. hemionus*.

561

562 **4.2.3.3 Proboscidea**

563 The presence of bones from a large elephant was identified in 2013, with a 2.25 m long tusk

564 (TAG13/052) and right magnum (carpal III - TAG13/104) recovered. Stimpson et al. (2015) tentatively

565 proposed that these remains were attributable to the extinct genus *Palaeoloxodon* (sometimes classified

566 as *Elephas*). In 2014, collaborative investigations of the elephant remains of Ti's al Ghadah began

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

581 posterior end lamellae have been lost post-mortem. Specimen TAG14/281 is a portion of a juvenile

582 mandible including a complete molar in early to mid-wear.

583   The molars show features which strongly suggest referral to the genus *Palaeoloxodon*. In

584 particular, the occlusal wear figures show lamellae with distinctly but roughly folded enamel, and

585 irregular expansions at roughly the mid-line of the molar, extending in both the anterior and posterior

586 directions from the anterior and posterior enamel bands, respectively. These features are distinctive of

587 *Palaeoloxodon* and distinguish these molars from other candidate genera, *Loxodonta* (African

588 elephants), *Mammuthus* (mammoths) and *Elephas* s.s. (lineage of Asian elephant). Another common

589 feature of *Palaeoloxodon*, rings of enamel medial and lateral to each lamella in early wear, are not

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

593 preserved crown is worn to the root at the front, and the isolated 'anterior root' has been lost through

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^2 (the penultimate of the series) or M^3 (the last of the series). In a more complete

601 specimen, this can easily be determined from the shape of the posterior end of the crown, which tapers

602 in M^3 but is blunt and wide in M^2. Unfortunately, breakage makes the determination of this characteristic

603 problematic for TAG14/301. The width of the crown reduces very slightly from front to back (**Table**

604 **6**), which might suggest M^3, but this is insufficient for certainty. A second factor is crown height, which

605 tends to be maximal near the front of the molar in M^3 and near the back in M^2. However, because only

606 the posterior two preserved lamellae of this specimen are unworn and allow measurement of crown

607 height, this cannot be determined. The crown is relatively high (133 mm, for a molar width of 90.5 mm,

608 giving a preserved hypsodonty index of 100 x 133/90.5 = 147), which would be consistent with either

22

609   a lamella close to the original posterior end of an M^2, or a lamella half to two-thirds down the crown of

610   an M^3. The remaining exterior surface of the molar near the posterior break provides some evidence:

611   especially near the top of the crown on the lateral side it curves medially to a degree that suggests it is

612   close to the natural posterior end of the tooth, rather than that the tooth extended much beyond the

613   break. In this case, the molar would be an M^2, but this cannot be considered certain. If it is an M^2, then

614   the curvature of the surface suggests that approximately two lamellae (plus the posterior talon) should

615   be added to the preserved number. That would give an approximate total of at least 15 (two or more at

616   the front, two at the back, and 11 preserved). If, however, the molar is an M^3, then an unknown number

617   is missing at the back and the total is known only to be greater than 15. **Table 6** shows measurements

618   for the Ti's al Ghadah teeth, in comparison with published data for *P. antiquus* and *P. recki recki*, the

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

621   we are correct that at least two lamellae are missing from each of its anterior and posterior ends, so that

622   its original value was at least 15, this places it in M^3 range. M^2 of *P. recki recki* is represented by only

623   one specimen, with 10 plates, but the range probably extended to 12 as this value is found even in earlier

624   samples referred to *P. recki ileretensis* and *P. recki atavus* (Beden, 1979). However, 15 plates have not

625   been recorded in any M^2 of *P. recki* and even in the more advanced *P. antiquus* of Europe: 11-14 is

626   typical for M^2 (and 16-19 in M^3). The rather thick enamel of TAG14/301 also supports identification as

627   M^3, although this is less secure. Following Laws (1966) scheme, TAG14/301, if it is an M^3 as here

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_4 complete: its lamellar formula is x10x (10

630   lamellae plus anterior and posterior talons). Its crown is part-buried in the jaw, but from a micro-CT

631   scan its crown height is ca. 57 mm and width 44 mm, giving a hypsodonty index of ca. 130. Mesowear

632   angles were measured on the M^3 and dP_4 following Saarinen et al. (2015). The angles are measured

633   between the ridges of enamel bounding each lamella, and the floor of dentine inside. Averaged over

634   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

635   to mid-wear and at wear stage V in Laws (1966) scheme, which corresponds to an age at death of

636   approximately 3 years.

637   Having established the generic attribution and the likely position of the teeth in the tooth-row,

638   the question of species attribution can be considered. *Palaeoloxodon* from Africa are generally

639   identified as *P. recki*; those from mainland Europe as *P. antiquus*. Remains from the Levant have

640   generally been equated with *P. antiquus* but Saegusa and Gilbert (2008) identified *P. recki* among the

641   earliest (ca. 800 ka) records. The identity of remains from the Arabian Peninsula therefore cannot be

642   assumed, and the situation is further complicated by the evolving molar morphology of *P. recki* through

643   its 3 million year history, with increasing plate number and crown height (Beden, 1979; Todd, 2001;

644   Lister, 2013). However, given the independent evidence for a Middle Pleistocene age of the Ti's al

645   Ghadah assemblage (**section 4.3**), we restrict our comparisons to the latest subspecies, *P. recki recki*,

646   with a known duration of ca. 1.5 – 0.4 Ma or possibly a little younger (Sanders et al., 2010). We

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.

649   Insufficient comparative work has been done between the molars of *P. recki recki* and *P.*

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

654   potentially separable on plate number and hypsodonty index of complete third molars, where their

655   ranges overlap but the variation in both variables extends to lower values in *P. r. recki* and to higher

656   values in *P. antiquus*. The recovery of further dental remains of elephant from Ti's al Ghadah may

657   therefore allow a clearer taxonomic designation in the future. For the present, we follow precedent in

658   referring them to *Palaeoloxodon* cf. *recki* in view of their more likely geographical origin from African

659   populations than European.

660

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

666   were relatively high compared to other taxa, estimates of minimum numbers of individuals (MNI)

667   compiled for trenches 1 and 2 and 5 and 6, indicated a MNI of 5 (five left mandibles) and 6 (six right

668   metatarsals), respectively and suggest that a relatively low number of individuals were represented.

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.

671   The entire skeleton was represented, although the assemblages were characterised by a relative low

672   abundance of specimens from the proximal axial skeleton (humerus and femur; **Fig. 11**).

673   A number of factors can mediate attrition in different portions of the skeleton and the analysis

674   of skeletal element representation is not a straightforward issue (e.g. Marean et al., 2004). Given the

675   direct evidence of carnivores recovered on site and the presence of carnivore pits on recovered

676   specimens (**Fig. 12K**) however, it is plausible to suggest that the relative low abundance of these

677   appendicular elements may have resulted from removal and/or destruction by scavengers; the presence

678   of "sharp" breaks to specimens (**Fig. 12F**, **H** and **J**) suggests that trampling by large animals may also

679   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

683   simple and we concur with the observations of Thomas et al. (1998) that the dental morphology of the

684   specimens from Ti's al Ghadah is more similar to extant desert-dwelling species, *O. leucoryx* and *O.*

685   *dammah*, rather than *O. gazella* or *O. beisa*. Accessory columns on the lingual face of upper molars are

686   present in *O. gazella* and *O. beisa* but are poorly developed (if present at all) in *O. dammah* and *O.*

687   *leucoryx* and these characters are not present or prominent in the specimens from Ti's al Ghadah (**Fig.**

688   **12B**).

689   Further examination of maxilla fragments indicates that the infra orbital foramen is located

690   posteriorly to P^2, as in the genus, although the posterior palatine foramen appears to be located more

691   distally in the fossil specimens, than in comparative material. The curved edge of the posterior palatine

692   encroaches mesially in line with the M^3 in *O. beisa*, *O. dammah*, and *O. gazella*, but it does not extend

693   beyond the posterior column of the M^3 in comparative material for *O. leucoryx* or the specimens from

694   Ti's al Ghadah (**Fig. 12B**).

695   A small sample of horn cores (e.g. **Fig 12E**) are characteristic of the genus and rounded in

696   cross-section, although are rather robust in comparison with available reference material (basal

697   measurements: anterior-posterior mean = 43.00 mm; medio-lateral mean = 41.15 mm, *n* = 4). Thomas

698   et al. (1998) report that Nefud specimens differ from extant *Oryx* spp. by degree of horn core divergence

699   of ca. 35° (Thomas et al. 1998, 149). From the small number of newly recovered specimens (*n* = 4) we

700   estimate a divergence of closer to 20°, but the degree of divergence appears greater than available

701   comparative material for *O. dammah* and *O. leucoryx* and closer to *O. gazella*.

702   Elements from the post cranial skeleton appear to be relatively large and robust (**Table S8**

703   **supplementary data**). Measurements of proximal ephiphyses of the fossil metapodia were used as a

704   proxy for body size and compared with available data from extant taxa. While sample sizes of

705   comparative data from *O. leucoryx* are small, measurements of metacarpals (**Fig. 13A**) and metatarsals

706   (**Fig. 13B**) indicate that the specimens from Ti's al Ghadah were larger animals than the endemic

707   Arabian species and approach the size of *O. beisa*.

708   In summary, the fossil specimens recall *O. leucoryx* in tooth and palatine morphology, but

709   appear to differ in horn core characteristics. The available data show that the Middle Pleistocene oryx

710   at Ti's al Ghadah were larger and more robust animals than the extant Arabian endemic and closer in

711   size to extant *O. beisa*. We withhold a species attribution, but suspect that the oryx of Ti's al Ghadah

712   represents a larger-bodied Pleistocene form of the extant endemic.

713

714   **4.3 Chronology**

715   **4.3.1 Optically Stimulated Luminescence**

716   Aliquots from sample TAG1-OSL4 from Unit 7 (**Fig. 4**) are 'well-behaved' according to standard SAR

717   protocol rejection criteria, and signal saturation in one aliquot suggests that the pIRIR290 protocol is

718   yielding a stable luminescence emission without the need for fading correction. Given that all other

719   aliquots were unsaturated, age underestimation due to signal saturation is not a concern for this sample.

720   Equivalent dose overdispersion (23.8 ± 7.1 %) supports the assumption of signal stability, as fading

721 values vary significantly between feldspar grains from the Rub' al Khali (Trauerstein et al., 2012) and

722 would be unlikely to average each other so precisely, and suggests that partial bleaching is a negligible

723 issue. The palaeolake sediments capping the ridge (Unit 7) have a luminescence age of 291 ± 34 ka

724 (**Table 7**).

725

726 **4.3.2 U-series dating**

727 U-series results are shown in **Tables 8** and **9** for samples 3536 and 3538 and in supplementary

728 information (**Tables S9 – S11**) for the other teeth. The tooth samples have unusually high uranium

729 concentrations, on average between 2.0 ppm (3536) and 61.1 ppm (3540) in the enamel and from 139

730 ppm (3536) to 188 (3540) in the dentine.

731 Two tissues show evidence of apparent uranium leaching (3536 dentine and 3538 dentine), for

732 which U-series age cannot be calculated. The enamel sections show consistent mean apparent U-series

733 ages ranging from 235.2 ± 5.8 ka to 268.2 ± 12.3 ka, whereas dentine results are somewhat more

734 scattered from 205.3 ± 4.0 ka to 348.1 ± 11.1 ka. U-series results on skeletal materials have generally

735 to be regarded as minimum age estimates (Grün et al., 2014). The finite dentine ages indicate that the

736 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

741 issue for accurate age estimation (see Duval et al., 2012). The results of the age calculations are shown

742 in **Table 10**. The samples display characteristics that are usually found in Early Pleistocene teeth:

743 extremely high D_E values (>3500 Gy), apparent U-leaching in dentine, and high U-concentration values

744 in dentine and enamel. Age calculations were performed by assuming early U uptake for the dentine

745 that showed U-leaching (i.e. p = -1). Combined US-ESR age calculations yielded 473 +50/-33 ka and

746 554 +79/-76 ka for samples 3536 and 3538, respectively, resulting in a mean value of 512 ± 59 ka (1-σ

747 error). The teeth could be somewhat older if sediment cover was thicker in the past. In the age

748 calculations, a depth of 1.0 + 0.5 m was used for the calculation of the cosmic ray contribution.

749   However, even when assuming an average depth of 30 ± 5 m, the resulting ages increase only by 1.3 %

750   for sample 3536 and 2.2% for sample 3538. This is due to the fact that 95% of the total dose rate is

751   generated within the tooth from the high U-concentrations in the dental tissues. Similarly, water content

752   variability has virtually no impact on the final age results: by considering either 15 or 20%, instead of

753   10%, the ages slightly increase by <0.5%.

754

755   **5. Discussion**

756   The vertebrate record of Ti's al Ghadah is an important step toward our understanding of the Pleistocene

757   biogeography in the Arabian Peninsula. While we are mindful that these records derived from a single

758   site, we consider the wider chronological context of the identified taxa with regional biostratigraphic

759   records and then describe the palaeoecological and palaeoenvironmental inferences that may be drawn

760   from the inferred ecological characteristics of the fauna.

761

762   **5.1 Chronological context**

763   Our initial interpretation of the formation of the Unit 5 assemblages was that they derived from animals

764   moving into the basin with the onset of wetter conditions and that the overlying lake deposit in the ridge,

765   as observed in section (Unit 7; see Fig. 4), represented a later expansion of a contemporaneous lake

766   formation (Stimpson et al., 2015). The earlier work by Rosenberg et al. (2013) suggested a date

767   equivalent to MIS 9 for Unit 5. However, an uncertain stratigraphic position of the sample reported by

768   Rosenberg et al. (2013) may explain the contrast with the findings of our US-ESR analyses from Unit

769   5 and our OSL date from Unit 7, which suggest that Unit 7 was formed later, likely in MIS 7.

770   Conversely, U-series analyses of oryx teeth from Unit 5 suggest a minimum age for the Unit 5

771   fossils of ca. 350 ka and combined US-ESR dating indicates on older age and that the assemblages

772   derived from ca. 500 ka, likely MIS 11. A strict interpretation of the available dating information would

773   be that the Unit 5 assemblages derived from animals associated with an earlier phase of wetting, not

774   represented in section in the ridge, and that there was significant erosion and/or depositional hiatuses

775   after the formation of the Unit 5 stratum and the overlying lacustrine deposits in the ridge. We suspect

776   that the iron-rich, relict lake deposit in the centre of the basin (**section 4.1**) represents the

777   contemporaneous lake and the key water resource for faunal populations from which the Unit 5

778   assemblages 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

782   Peninsula. In terms of biostratigraphy, the utility of the bird fossils identified to species is limited, except

783   to say the identified species are early records and are known from the region today. The Egyptian vulture

784   is resident in the Arabian Peninsula (and occurs around Ti's al Ghadah) and is widely distributed from

785   southern Europe, North Africa and east to the Indian sub-continent. Black kites are relatively common

786   passage visitors to the Peninsula; a closely related species, *Milvus aegypticus*, is restricted to the

787   southwest. White wagtails (*Motacilla alba*) are also relatively common winter or passage visitors.

788   Although no aquatic taxa were confidently identified to species is worthy of note that little grebes

789   (*Tachybaptus ruficollis*) are resident and readily colonise well-vegetated bodies of water. The black-

790   bellied sandgrouse (*Pterocles orientalis*) is found in Iberia, North Africa and Asia: it is regarded as rare

791   winter visitor to the Arabian Peninsula (Hollom et al., 1998; Porter and Aspinall, 2010).

792   The extinct *Panthera gombaszogensis* is regarded as Eurasian taxon and is known from the

793   Early to Middle Pleistocene (e.g. Marciszak, 2014). Records for this enigmatic fossil felid are sparse in

794   SW Asia. The specimens from Ti's al Ghadah are the most southerly known records of this taxon,

795   although with the present dating information for the site these records fit well within the chronological

796   range of this taxon. The Eurasian jaguar is known from the Kudaro faunal unit (MIS 9-11) in the

797   Caucasus and is described from Layer 5c from Kudaro 1, which yielded two thermoluminescence dates

798   of 360 ± 90 ka and 350 ± 70 ka (Baryshnikov, 2002).

799   We infer the presence of the spotted hyaena (currently restricted to Sub-Saharan Africa) at Ti's

800   al Ghadah from coprolites. A well-preserved mandible is an unequivocal fossil record from elsewhere

801   in the southwestern Nefud Desert, from Locality # 3 (Thomas et al., 1998). It is likely that this locality

802   is site 16.1 of Rosenberg et al. (2013), which yielded OSL dates between 419 ± 39 ka and 286 ± 30 ka

803   (**Table 1**). While there is no strict evidence of any chronological affinity between Locality # 3 and Ti's

804   al Ghadah, the coprolites are further indication that the spotted hyaena was present in the Arabian

805   Peninsula in the Middle Pleistocene.

806   The biogeographic implications of the record of the African golden wolf, *Canis anthus*, are

807   more difficult to consider as the taxonomic affinity of this cryptic canid was clarified only recently. The

808   record from Ti's al Ghadah, however, indicates that it ranged into the Arabian Peninsula in the Middle

809   Pleistocene.

810   The extinct elephant, *Palaeoloxodon recki*, is known from the Middle Pliocene until the Middle

811   Pleistocene in Africa, where it is conventionally divided into five chronological stages. The elephants

812   of Ti's al Ghadah are morphologically consistent with the latest stage, *P. recki recki*, with known

813   occurrence in East Africa between ca. 1.5-0.4 Ma, although it is not possible to rule out an earlier stage

814   for the small sample of two molars: the potentially diagnostic specimen (the M^3) is incomplete. After

815   0.5 Ma, the African species *P. iolensis*, is believed to be the lineal descendent of *P. recki* and persists

816   until the Late Pleistocene, possibly as late as 75 ka (Sanders et al., 2010). *P. iolensis* lacks the median

817   enamel expansions of *P. recki* that are also seen in the molars from Ti's al Ghadah. However, that a

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

824   (Goren-Inbar et al., 1994), has been regarded as one of the earliest representatives of this species, and

825   the species has also been identified at Revadim Quarry ("ca. 500-300 ka or possibly more": Rabinovich

826   et al., 2012). However, Saegusa and Gilbert (2008), on the basis of cranial characters, suggested that

827   the GBY cranium might actually be *P. recki*, while the morphology of the Revadim elephants has not

828   been described in sufficient detail to discriminate between the two species. The taxonomic boundary

829   between *P. recki* and *P. antiquus*, in this geographical region and time-interval, is therefore currently

830   blurred, but it cannot be ruled out that the elephants of Ti's al Ghadah might have derived from Europe

831   and eventually be considered to belong to *P. antiquus*.

832   Further samples from Ti's al Ghadah are required to clarify the range of the equid taxa that are

833   represented at the site, although our identification of a mandible of *E. hemionus* is consistent with

834   regional fossil records. *Equus hemionus* appears as part of fauna of SW Asia and the Levant in the

835   Middle Pleistocene. Specimens are reported from Nadaouiyeh Aïn Askar (El Kown) in Syria (Savioz

836   and Morel, 2005) and from Levantine sites (Bar-Yosef and Belmaker, 2011) and dated to 300-500 ka,

837   and 100-300 ka, respectively.

838   We suspect that the *Oryx* sp. of Ti's al Ghadah is likely to be a large but closely-related

839   Pleistocene form of the extant endemic *Oryx leucoryx*. Ancestral populations of early Hippotragini were

840   probably established in the Miocene and these antelopes will likely have been a long-standing presence

841   in the Arabian Peninsula. Fossils of this genus have proved to be common in Pleistocene assemblages

842   of different ages in the southwestern Nefud Desert (Thomas et al., 1998).

843   Our interpretation of the taxonomic composition of the vertebrates of Ti's al Ghadah is that,

844   like the historical fauna of the Arabian Peninsula, it is a distinct biogeographical admixture. While the

845   evidence from Ti's al Ghadah is further support for assertions that distinct regional zoogeographies

846   were established by the Middle Pleistocene (e.g. O'Regan et al., 2005), it does not necessarily indicate

847   that they were isolated.

848

849   **5.3 Vertebrate palaeoecology and palaeoenvironments and at Ti's al Ghadah.**

850   The identified taxa indicate that the Ti's al Ghadah basin was, at least at times, a focal point in the

851   landscape for birds, herbivorous mammals and predators and scavengers. However, given that there

852   have been suggestions that Pleistocene lacustrine deposits in the Nefud Desert may represent ephemeral

853   marsh-like habitats, rather than the formation of substantial bodies of water (Enzel et al., 2015), this

854   raises the question of if the Unit 5 assemblages represent animals that were attracted to an ephemeral

855   water source and a relatively brief flush of plants in the dune fields, or were freshwater and plant

856   resources more substantial and long-standing?

857   At present, it is not possible to determine the degree of time-averaging of the Unit 5

858   assemblages, although the fossil stratum appears to be a rather discrete unit with little evidence of

859   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

862   Pleistocene onward (Rosenberg et al., 2013). Rosenberg et al. (2013) suggest that large-scale lake and

863   wetland habitats developed across the western Nefud during MIS 11. The inferred presence of a lake at

864   Ti's al Ghadah would be supported by previous reports (Thomas et al., 1998) of a fossil of a relatively

865   large Osteoglossiforme fish (although this was an unstratified specimen) and consistent with the aquatic

866   affinities of two of the identified avian taxa (grebe, duck). Indeed, the presence of the bird taxa identified

867   at the site may parsimoniously be explained as attracted to habitat (grebe, duck, wagtail), to drink

868   (sandgrouse, ostrich) or in a scavenging role (Egyptian vulture, kite).

869   Oryx, equids and elephant will likewise have been attracted to fresh water and plant resources

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

872   attention of carnivores is evidenced by tooth marks. Although it was not possible to identify the

873   reptilian fossils to genus it is worth noting that, in this context, the majority of extant *Varanus* spp. are

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

878   behaviour of large felids (e.g. Valeix et al., 2010) and the presence of a large-bodied pantherine (ca.

879   100 kg: see Stimpson et al., 2015) suggests that the biomass of potential vertebrate prey would likely

880   have been substantial in the area (e.g. Carbone and Gittleman, 2002) as would, by inference, plant

881   resources. We also infer the presence of hyeana (cf. *Crocuta crocuta*) from coprolites. While these

882   animals are famed as scavengers and for the demolition of bone, they are dynamic and capable

883   predators. Modern analogues should be applied with caution but it is notable that the taxonomic and

884   ecological composition of the fossil fauna from Ti's al Ghadah bears some resemblance to Namibian

885   desert ecosystems that experience flushes of plant growth in response to increased precipitation. For

886   example, increased wetting prompts a seasonal influx of large number of gemsbok (*Oryx gazella*) to

887   the Kuiseb river from surrounding dunefields (Kok and Nel, 1996) and these antelopes and the mountain

888   zebra (*Equus zebra hartmannae*) are important prey animals for local populations of spotted hyaena

889   (Tilson and Henschel, 1986).

890   For the *Palaeoloxodon* remains, there is clearly more than one individual preserved at the site:

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*

893   and *P. antiquus* are estimated to have had a body mass of ca. 10-12 tonnes (Larramendi, 2015) and

894   would have been a social animal living in family groups like living elephants. Elephants require a

895   substantial intake of water (up to 360 litres a day in an adult), implying local availability of water.

896   Elephants in semi-desert areas of Africa (Mali and Namibia) undertake substantial migrations in search

897   of food and water, and focus on moist riverside vegetation (e.g. Viljoen, 1989a, b) but Ramey et al.

898   (2013) have demonstrated a reliance on clean, un-fouled water resources.

899   While the fossil elephants of the Nefud were not necessarily there year round, but perhaps only

900   when food and water supplies allowed, a substantial biomass of vegetation is required to support an

901   elephant herd, even though elephants can survive on relatively low-quality herbage. Microwear and

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_4 (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

911   relatively large-bodied form and available data indicate that the specimens approach the size of extant

912   *O. beisa*. While *Oryx* spp. display marked physiological adaptations to tolerate drought conditions (e.g.

913   Ostrowski et al., 2006), available data for four species indicate that there is a broad but positive

914   correlation between annual rainfall and body weight (**Fig. 16**). It is plausible to suggest that the relative

915 size of the oryx of Ti's al Ghadah reflected more amenable habitats and that climatic and environmental

916 amelioration was of a sufficient duration to support populations of this larger-bodied form.

917   In summary, our interpretation of the vertebrate fauna of Ti's al Ghadah is that parts of the

918 southwestern Nefud Desert were characterised by the longstanding (but possibly periodic) presence of

919 substantial water bodies and grassland ecosystems in the Middle Pleistocene. As a case study, the

920 evidence from Ti's al Ghadah is further indication that, at times, the Pleistocene habitats in the Nefud

921 Desert contrasted markedly with the hyper-arid environments of today and contained freshwater and

922 game resources with the potential to support by occupation by hominins.

923

924 **6. Conclusion**

925 The Middle Pleistocene fauna of Ti's al Ghadah reported here, dated to ca. 500 ka, comprises reptiles,

926 birds and mammals. The bird fossils are the first Pleistocene-age records to be reported from the Arabian

927 Peninsula. The mammalian fauna consists of an admixture of African, Eurasian and likely endemic

928 taxa, which we interpret to reflect the geographic situation of the Arabian Peninsula as a crossroads

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.

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1444 **List of Tables**

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[a], Thomas

1447 et al. (1998), taxa[b], 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

1450 recovered from Unit 5 at Ti's al Ghadah. All measurements are in millimetres and are taken from the dorsal

1451 surface.

1452

1453 **Table 3** Bird fossils recovered from Unit 5 at Ti's al Ghadah. Measurements: GL = greatest length; Bp =

1454 proximal breadth; Sc = minimum width of shaft; Bd = distal breadth; Dp = proximal depth and Dd = distal

1455 depth; Bcra = cranial breath (dorsal surface); Bcau = caudal breadth (dorsal surface). All measurements are in

1456 millimetres.

1457

1458 **Table 4** Carnivora measurements from Unit 5 at Ti's al Ghadah. Measurements: GL = greatest length; Bp =

1459 proximal breadth; Dp = proximal depth; MDAP = minimum antero-posterior diameter of diaphysis; MWML =

1460 minimum medio-lateral width of diaphysis; Bd = distal breadth; Dd = distal breadth; M-D = mesio-distal length;

1461 B-L = buccal-lingual width; HFM = height of foramen magnum; WFM = width of foramen magnum; WOC =

1462 width across occipital condyles; BJP = breath across jugal processes; Ltald = length of talonid. All measurements

1463 are in millimetres.

1464

1465 **Table 5** Measurements of fossils of the Equidae from Unit 5 at Ti's al Ghadah. Abbreviations: TAG14/329 - MD

1466 = mesial-distal length; BL = buccal-lingual width; Lo = length of occlusal surface; lo = width of occlusal surface;

1467 LDB = length of double knot. TAG13/146 – GL = greatest length; mL = medial length; Bp = proximal breadth;

1468 Sc = minimum width of diaphysis; Bd = distal breadth; Dd = distal depth. TAG14/342 - astragalus measurements

1469 follow the locations and conventions described in Alberdi and Palombo (2013). All measurements are in

1470 millimetres.

1471

1472 **Table 6** Measurements of Ti's al Ghadah elephant molars compared to East African *P. recki recki* and European

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1474   Gilbert (2008), and for *P. antiquus* from unpublished data of AML and P. Davies. Measurements are in millimetres

1475   and are shown as ranges for samples where $n \leq 5$, and mean ± standard deviation for samples where $n > 5$.

1476

1477   **Table 7** Luminescence dating results for sample TAG1-OSL4. A: pIRIR290 equivalent dose measurements:

1478   number of aliquots excluded according to each rejection criterion, and central age model values calculated for the

1479   accepted population. B: Values for dose rate calculations and the final sample age.

1480

1481   **Table 8** U-series results on sample 3536. Negative U/Th are due to the background being higher than the

1482   measurement. n/a: age calculations not possible, leaching is indicated. All errors are 2-σ.

1483

1484   **Table 9** U-series results on sample 3538. Negative U/Th are due to the background being higher than the

1485   measurement. n/a: age calculations not possible, leaching is indicated. All errors are 2-σ.

1486

1487   **Table 10** ESR parameters and combined ESR-U-series age calculations for samples 3536 and 3538.

1488

1489   **List of Figures**

1490   **Fig. 1.** A: The Arabian Peninsula, showing locations of three major sand seas and the site of Shi'bat Dihya (SD-
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1493

1494   **Fig. 2.** The fossil site of Ti's al Ghadah. A: the ridge viewed from the southwest from the adjacent barcan dune.
1495   B: Section through the ridge deposit after excavation (scale = 10 cm increments: the position of the fossil layer
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1498   *Palaeoloxodon* molar, in situ in trench 2. F: Excavation of trench 1, viewed from the north. G: TAG13/052 –
1499   elephant tusk, in situ in trench 1.

1500

1501   **Fig. 3.** Plan view of the ridge at the fossil site of Ti's al Ghadah, showing location of trenches.

1502

1503   **Fig. 4.** A: Stratigraphic log of the ridge deposits at Ti's al Ghadah with, B: upper metre of section annotated with
1504   OSL and US/ESR dates.

1505

1506   **Fig. 5.** A: Plots of fossil locations in western trenches 1, 2, 5 and 6, with cumulative weathering profiles (long

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1508

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,

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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

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1517

1518   **Fig. 7.** Carnivora fossils from Unit 5 at Ti's al Ghadah A: TAG14/339 phalanx, volar and plantar aspects, *Panthera*

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1521   (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-

1524   distal) and width (B-L = buccal-lingual) measurements for lower carnassial teeth (M_1) from recent and fossil

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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

1533   **Fig. 10.** Elephantidae fossils from Unit 5 at Ti's al Ghadah. TAG14/301, upper left molar, *Palaeoloxodon*, in A:

1534   occlusal view and B: lateral view. TAG14/281, right mandible in C: occlusal view, and D: lateral view. Scale

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1536

1537   **Fig. 11.** Skeletal element representation of *Oryx* sp. expressed as % Number of Identified Specimens (NISP; see

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1540

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

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1544   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,

1546   dorsal view. K: TAG14/205, rib fragment with carnivore pits. Scale bars = 50 mm.

1547

1548   **Fig. 13.** Measurements of proximal metapodia from fossil *Oryx* sp. from Unit 5 at Ti's al Ghadah, with

1549   comparative morphometric data from four extant *Oryx* spp. and *Addax nasomaculatus*. A: proximal breadth (Bp)

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1551   Morphometric data compiled from Peters et al. (1997). Ranges of annual rainfall within *Oryx* spp. extant

1552   distributions and body weight ranges (from Stanley Price, 1989, 29) are also annotated. Convex hulls fitted in

1553   PAST (Hammer et al., 2001).

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