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

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

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28 **Abstract**

29 The current paucity of Pleistocene vertebrate records from the Arabian Peninsula - a landmass of over
30 3 million km² - 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. *Crocota 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.

47

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

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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 km² 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 Palearctic
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 km²: 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**

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 calcitized 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 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 (ostriches)

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 tarsometatarsus (**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 platyrhynchos*).

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 mitochondrial 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.

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 M₂ is intact. The M₃ 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 M₂ and M₃ 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 M₂ 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 $100 \times 133/90.5 = 147$), which would be consistent with either

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

661 **4.2.3.4 Bovidae (Hippotragini)**

662 *Oryx* sp.

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

665 post-crania were attributable to the genus *Oryx*. While NISP (number of identified specimens) counts
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 P², 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 M³ in *O. beisa*, *O. dammah*, and *O. gazella*, but it does not extend

693 beyond the posterior column of the M³ 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 epiphyses 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 ($1-\sigma$
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 M³) 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 hyaena (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 dP₄ (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.

933

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968

969

970

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1443

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); Beau = 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
 1473 *P. antiquus*. Comparative data for *P. r. recki* compiled from Beden (1979), Ferretti et al., (2003), Saegusa and

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 \pm 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 $2\text{-}\sigma$.

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 $2\text{-}\sigma$.

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-
 1491 1) and B: Southwestern Nefud Desert showing location of Ti's al Ghadah (TAG-1) and other Thomas et al.
 1492 (1998) fossil sites.

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
 1496 within Unit 5 is hatched and highlighted in red). C: Excavation of trenches 1 and 2 (numbered) at the southern
 1497 end of the ridge, viewed from the southwest. D: Excavation of trench 2, viewed from the west. E: TAG14/301 -
 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
 1507 bones - Bovidae) for B: trenches 1 and 2 and, C: trenches 5 and 6 at Ti's al Ghadah.

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,
 1512 *Tachybaptus* sp. E i: TAG14/287 occipital region and base of skull of *Neophron percnopterus*, lateral aspect. E
 1513 ii: TAG14/287, maxilla of *Neophron percnopterus*, lateral aspect. E iii: TAG14/269 right humerus proximal end
 1514 of *Neophron percnopterus*, caudal aspect. E iv: TAG14/259 right humerus distal end of *Neophron percnopterus*,
 1515 caudal aspect. F: TAG14/270 proximal end of left humerus of *Pterocles orientalis*, caudal aspect. Scale bars = 10
 1516 mm. Numbered features are referred to in the text.

1517

1518 **Fig. 7.** Carnivora fossils from Unit 5 at Ti's al Ghadah A: TAG14/339 phalanx, volar and plantar aspects, *Panthera*
 1519 sp. B: TAG13/145 broken mandibular canine, *Panthera* sp. C: TAG14/256 coprolite, cf. *Crocota crocuta*. D:
 1520 TAG14/245, occipital region, caudal aspect, *Canis* sp. E: TAG14/184, right M₁ (carnassial), *Canis anthus*, buccal
 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 (M₁) from recent and fossil
 1525 *Canis* spp. with fossil specimen TAG14/184. Data compiled from Kurtén, 1965; Dayan et al., 1992; Dayan,
 1526 1994; Rook et al., 1996; Aouraghe, 2000; Baryshnikov, 2012; Stoyanov, 2012. Measurements of recent *C. lupus*
 1527 *arabs* were taken from comparative specimens at the HZM. REVISE figures.

1528

1529 **Fig. 9.** Fossils of Equidae from Unit 5 at Ti's al Ghadah. TAG14/329 right mandible, *Equus hemionus*, in A:
 1530 lateral and B: occlusal views. C: TAG14/342 left astragalus, *Equus* sp., dorsal aspect. D: TAG13/146 left femur,
 1531 *Equus* sp., cranial and caudal views. Scale bars = 50 mm. Numbered features are referred to in the text.

1532

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
 1535 bars = 100 mm.

1536

1537 **Fig. 11.** Skeletal element representation of *Oryx* sp. expressed as % Number of Identified Specimens (NISP; see
1538 **Table S7 supplementary data**), with estimates of Minimum Number of Individuals (MNI) and location of
1539 carnivore pits, compiled from excavations of Unit 5 in trenches 1 and 2 and trenches 5 and 6 at Ti's al Ghadah.

1540

1541 **Fig. 12.** Examples of fossil crania and post-crania of *Oryx* sp. from Ti's al Ghadah. TAG13/109 right maxilla
1542 and tooth row in A: lateral and B: occlusal views. TAG13/147, right mandible and tooth row in C: lateral and D:
1543 occlusal views. E: TAG14/216, right horn core and cranial fragment, anterior aspect. F: TAG13/099, left
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)
1550 and proximal depth (Dp) of metacarpals. B: proximal breadth (Bp) and proximal depth (Dp) of metatarsals.
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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