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DOI:

[10.1038/s41559-018-0698-9](https://doi.org/10.1038/s41559-018-0698-9)

*Document Version*

Peer reviewed version

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*Citation for published version (APA):*

Roberts, P., Stewart, M., Alagaili, A. N., Breeze, P., Candy, I., Drake, N., Groucutt, H. S., Scerri, E. M. L., Lee-Thorp, J., Louys, J., Zalmout, I. S., Al-Mufarreah, Y. S. A., Zech, J., Alsharekh, A. M., al Omari, A., Boivin, N., & Petraglia, M. (2018). Fossil herbivore stable isotopes reveal middle Pleistocene hominin palaeoenvironment in 'Green Arabia'. *Nature Ecology and Evolution*, 2(12), 1871-1878. <https://doi.org/10.1038/s41559-018-0698-9>

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1 **Fossil herbivore stable isotopes reveal Middle Pleistocene hominin palaeoenvironment**  
2 **in ‘Green Arabia’**

3  
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26  
27  
28 **Abstract:**

29  
30 Despite its largely hyper-arid and inhospitable climate today, the Arabian Peninsula is  
31 emerging as an important area for investigating Pleistocene hominin dispersals. Recently, a  
32 member of our own species was found in northern Arabia dating to *c.* 90 ka, while stone tools  
33 and fossil finds have hinted at an earlier, Middle Pleistocene, hominin presence. However,  
34 there remain few direct insights into Pleistocene environments, and associated hominin  
35 adaptations, that accompanied the movement of populations into this region. Here, we apply  
36 stable carbon and oxygen isotope analysis to fossil mammal tooth enamel (n=21) from the  
37 Middle Pleistocene locality of Ti’s al Ghadah in Saudi Arabia associated with newly-  
38 discovered lithics and probable cutmarks. The results demonstrate productive grasslands in  
39 the interior of the Arabian Peninsula *c.* 300-500 ka, as well as aridity levels similar to those  
40 found in open savanna settings in eastern Africa today. The association between this  
41 palaeoenvironmental information and the earliest traces for hominin activity in this part of the  
42 world lead us to argue that Middle Pleistocene hominin dispersal into the interior of the  
43 Arabian Peninsula required no major novel adaptation.

44 **Introduction**

45

46 Studies of Pleistocene hominin dispersals beyond Africa are important for understanding the  
47 course of global human evolution and prehistory. In particular, analysis of the environmental  
48 context under which members of the genus *Homo* moved into Europe and Asia in the Early  
49 and Middle Pleistocene (2.6 Ma to 126 ka) relative to that of *Homo sapiens* populations  
50 expanding around the globe in the Late Pleistocene (126-12 ka) can provide insight into the  
51 potential ecologically unique nature of our species<sup>1-3</sup>. It has recently been highlighted that our  
52 species occupied and utilized a diversity of extreme environments, including deserts, tropical  
53 rainforests, palaeartic, and high-altitude settings, around the world during the Late  
54 Pleistocene<sup>3</sup>. By contrast, the dispersals of other earlier and contemporaneous *Homo* species  
55 into Europe and Asia appear to be best associated with generalized utilization of different  
56 forest and grassland mosaics proximate to riverine and lacustrine settings<sup>2,4</sup>. Yet, a paucity of  
57 associated palaeoenvironmental information has made it difficult to systematically test this  
58 distinction and many hold that non-*H. sapiens* members of the genus *Homo* demonstrate  
59 significant cultural<sup>5-6</sup> and ecologically adaptive<sup>7-9</sup> flexibility.

60 In spite of its crucial geographic position at the interface of Africa and Eurasia, the Arabian  
61 Peninsula has remained remarkably absent from adaptive models of Pleistocene hominin  
62 expansions until relatively recently, owing to a lack of well-constrained archaeological and  
63 palaeoecological data. Climate modeling<sup>10</sup>, speleothem records<sup>11</sup>, palaeontological findings<sup>12-  
64 15</sup>, and geomorphological studies of palaeolake records<sup>16-17</sup> have been used to argue that at  
65 intervals in the past, notably during interglacials, the harsh, hyper-arid deserts that cover  
66 much of Arabia today were replaced by 'moister' and 'greener' conditions more hospitable to  
67 foraging occupation<sup>18-19</sup>. Furthermore, the find of a *H. sapiens* phalanx, in association with  
68 Middle Palaeolithic stone tools, at the site of Al Wusta dated to *c.* 90 ka provides definitive  
69 evidence for the early presence of our species in the interior of the Arabian Peninsula<sup>20</sup>.  
70 There have also been suggestions that stone tools in the Arabian interior are associated with  
71 an earlier period of Middle Pleistocene hominin dispersal<sup>21-24</sup>. However, despite the  
72 significance of climate and environmental change for hominin dispersal into the region, there  
73 has been no direct means of determining what 'wetter' represents in the context of regional  
74 ecology nor definitive identification of Middle Pleistocene hominin presence.

75 We undertook renewed archaeological and taphonomic analysis of fossil fauna found at the  
76 Middle Pleistocene (*c.* 500-300 ka) fossil locality of Ti's al Ghadah in the Nefud Desert of  
77 Saudi Arabia (Fig. 1; Supplementary Text 1 and 2; Supplementary Figures 1 and 2) and  
78 report, for the first time at the site, lithic artefacts in direct stratigraphic association with the  
79 fossil fauna. Ti's al Ghadah is one of the most important palaeontological sites in the region,  
80 representing the only dated faunal assemblage recovered from Middle Pleistocene Arabia<sup>12-14</sup>.  
81 Previous analyses have identified a suite of terrestrial and aquatic animals, including extinct  
82 elephants (*Palaeoloxodon* sp.), horses (*Equus hemionus*), and water birds (*Tachybaptus* sp.  
83 and *Anas* sp.)<sup>12-14</sup> (Supplementary Table 2), that have been used to argue the western Nefud  
84 Desert was significant less arid at times during the Middle Pleistocene than it is today.  
85 'Middle Palaeolithic' artefacts of unknown age have also been recovered from the surface of  
86 the basin<sup>24</sup>. Yet, the lack of taphonomic analysis and scarcity of anthropogenic remains has  
87 made evaluating the relationship between hominins and fossil fauna difficult.

88 There has also been no way of analyzing, in detail, the vegetation and relative aridity  
89 associated with the Middle Pleistocene fossil assemblage, and potential hominin presence, at  
90 Ti's al Ghadah. Here, we performed stable carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope analysis

91 of 21 fossil fauna recovered from the site.  $\delta^{13}\text{C}$  analysis of faunal tooth enamel is used to  
92 assess different types of biomass in animal diets<sup>25-27</sup>. Most terrestrial plants, including trees,  
93 herbs, shrubs, and shade-loving grasses follow the  $\text{C}_3$  photosynthetic pathway<sup>28</sup>.  $\text{C}_4$   
94 photosynthesis is followed by most arid-adapted grasses and some sedges<sup>29</sup>.  $\text{C}_3$  and  $\text{C}_4$  plants  
95 have distinct and non-overlapping  $\delta^{13}\text{C}$  values<sup>30</sup> that are passed into faunal consumers  
96 allowing reliance on tree and shrub versus grassland biomass to be determined in global  
97 ecosystems, including those of Arabia<sup>12</sup>. In faunal diets, prior to the impact of significant  
98 fossil fuel emission, average herbivore  $\delta^{13}\text{C}$  values for  $\text{C}_3$  and  $\text{C}_4$  reliance are *c.* -12‰ and ~  
99 0‰, respectively<sup>25-27</sup> (Fig. 3).

100  $\delta^{18}\text{O}$  data from fossil herbivore tooth enamel reflect precipitation source, humidity,  
101 temperature, and also plant water. These multiple influences can often make faunal enamel  
102  $\delta^{18}\text{O}$  difficult to interpret as a past environmental signal. This is particularly the case in areas  
103 like the Arabian Peninsula where the source water, and therefore  $\delta^{18}\text{O}$ , for precipitation may  
104 have changed over time<sup>10</sup>. Evaporation exerts a positive effect on  $\delta^{18}\text{O}$ , particularly in arid  
105 desert regions such as the centre of the Arabian Peninsula, so that continental water bodies  
106 and soils in areas with a water deficit are  $^{18}\text{O}$ -enriched. This effect is even stronger in plants  
107 due to the process of evapo-transpiration<sup>32-33</sup>. The difference between the  $\delta^{18}\text{O}$  from tooth  
108 enamel of obligate drinkers such as equids (that must drink from open water sources) and  
109 non-obligate drinkers such as *Oryx* spp. (that can meet their water requirements through the  
110 consumption of plants) will be strongly influenced by palaeoaridity<sup>34-35</sup> at a given locale, and  
111 will not be effected by changes in the precipitation or source water baseline (Supplementary  
112 Text 2). Finally, due to the fact that tooth enamel forms incrementally, sequential  $\delta^{13}\text{C}$  and  
113  $\delta^{18}\text{O}$  analysis of animal tooth enamel can be used to look at temporal changes in vegetation  
114 and water source during the period of tooth enamel formation<sup>36</sup>. The preservation of all  
115 samples was also checked using FTIR as per<sup>31</sup> (Supplementary Text 3).

## 116 **Results**

117  
118 The fossil faunal remains and newly-discovered stone tools analysed in this study were  
119 recovered from a sandy horizon ('Unit 5') directly beneath a palaeolake deposit in the Ti's al  
120 Ghadah basin<sup>14</sup> (Fig. 2). The lithic artefacts, coupled with new taphonomic evidence  
121 suggestive of anthropogenic accumulation of bones on-site, confirm a hominin presence in  
122 association with the faunal remains analysed here (Fig. 2; see also Supplementary Text 4).  
123 These findings represent the oldest radiometrically dated hominin presence in the Arabian  
124 Peninsula, as well as the first anthropogenically modified faunal assemblage from the  
125 Pleistocene. In total, six unretouched flakes and one retouched flake were recovered from  
126 Unit 5. A further six chunks were recovered with the artefacts and likely represent highly  
127 fragmented debitage. The lithics and debitage fragments are made on a brown coloured  
128 lacustrine chert, and this material is known from lakebeds across the Nefud<sup>18-20</sup>. At the MIS 5  
129 site of Al Wusta, 3km from Ti's al Ghadah, similar lacustrine chert was the main raw  
130 material used by hominins<sup>20</sup>. Despite difficulties in knapping such material, the artefacts are  
131 finely made and similar to one another in terms of technology (Fig. 2A). The lithics consist of  
132 small flakes struck from prepared cores and a side-retouched flake ('side scraper').  
133

134 In addition, associated faunal material includes two medium-sized ungulate rib fragments that  
135 bear tentatively assigned cut marks (TAG13/133 and TAG13/900; Fig. 2D and E). These  
136 markings are V-shaped in cross-section and run parallel to each other and either  
137 perpendicular or obliquely to the long axis of the bone. Shoulder effect and shoulder flaking

138 is apparent, the latter in the form of Hertzian cones. No internal microstriations were  
139 observed, although fine-scale features, such as microstriations, are quickly removed during  
140 chemical alteration<sup>37</sup>. The direction and location of the markings is consistent with cut marks  
141 produced during filleting of meat from around the rib<sup>38</sup>. Notches with a broad arcuate  
142 planform and conchoidal medullary flake scar, reminiscent of notches produced during  
143 hammerstone percussion, were also identified and suggest hominins may have broken open  
144 long bones to exploit marrow (Suppelementary Text 4; Figs 2B and Suppelementary Figure  
145 12). Together with the evidence of the newly-identified associated lithics, this makes Ti's al  
146 Ghadah the first, at least partially anthropogenic faunal assemblage from the Arabian  
147 Peninsula in the Pleistocene.

148 The  $\delta^{13}\text{C}$  data from all of the sampled fossil mammals (elephants, *Oryx* sp., hartebeest,  
149 equids, and unidentified bovids) associated with this hominin presence show an unequivocal  
150 dominance of  $\text{C}_4$  vegetation in the diets of herbivores ( $\delta^{13}\text{C}$  range = -0.8 to 3.3‰), (Fig. 3)  
151 (Supplementary Table 5), and suggests that rainfall occurred during the warm season. The  
152  $\delta^{13}\text{C}$  evidence also fits with climate simulations suggesting that the periodic amelioration of  
153 Arabian environments reflects the incursion of the African monsoon system<sup>10</sup>. The  
154 uniformity of  $\text{C}_4$  consumption by all animals suggests the presence of extensive, productive  
155  $\text{C}_4$  grasslands in the vicinity of the palaeolake. The  $\delta^{18}\text{O}$  range of fauna from Ti's al Ghadah  
156 is high ( $\delta^{18}\text{O}$  range = -5.6 to 6.2‰) – though not higher than Pliocene, Pleistocene, and  
157 contemporary African ecosystems<sup>34-35,39-40</sup>. Differences in  $\delta^{18}\text{O}$  between obligate drinking  
158 equids, hartebeest, and elephants and non-obligate drinking *Oryx* sp. allow more detailed  
159 estimations of relative environmental aridity to be made (Suppelementary Text 2).

160 The  $\delta^{18}\text{O}$  difference (non-obligate drinker median = 0.0‰, obligate drinker median = 1.7‰,  
161 difference = 1.7‰) between these taxa is 6.0‰ lower than that found between modern  
162 equids/camels (median = 0.7‰) and Arabian oryx (8.4‰) in central Arabia today (difference  
163 = 7.7 ‰), demonstrating that conditions were considerably wetter in the region's past. This  
164 difference is compared to  $\delta^{18}\text{O}$  datasets of obligate drinking and non-obligate drinking  
165 mammals in present day East Africa (where sample size for each group exceeds  $n=5$ )<sup>35</sup> (Fig.  
166 4) (Supplementary Text 2; Supplementary Table 9). While caution is warranted given that  
167 taxon-specific habits could vary through time, when the difference between obligate and non-  
168 obligate drinker  $\delta^{18}\text{O}$  from Ti's al Ghadah is compared to that of modern day Tsavo (1.7‰)  
169 and Laikipia (1.3‰), Middle Pleistocene ecological conditions in the interior of Arabia  
170 appear to approximate that of a relatively humid African savanna today (Fig. 4)  
171 (Supplementary Text 2). Such a reconstruction is supported by the results of a mixed  
172 ANOVA performed to compare the difference between obligate drinkers and non-obligate  
173 drinkers at each site (Supplementary Tables 10 and 11). While Tsavo and Laikipia show no  
174 significant difference between these 'drinker' groups, there is a significant difference found  
175 between these groups at Ti's al Ghadah.

176 There is no correlation between the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values in the Ti's al Ghadah fossil dataset  
177 (Multiple R-squared=0.04,  $p<0.01$ , adjusted R-squared=-0.01,  $p<0.01$ ), indicating that access  
178 to vegetation was independent of factors affecting faunal  $\delta^{18}\text{O}$ . This is also borne out in  
179 sequential  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  analyses of selected fossil teeth that enables the identification of  
180 potential environmental seasonality or mobility. The sequential  $\delta^{13}\text{C}$  data, from all taxa,  
181 document a homogeneous source of lush  $\text{C}_4$  vegetation, likely in the form of grasses, at Ti's  
182 al Ghadah (Figs. 5-6, Supplementary Tables 5 and 7). This could either be linked to the  
183 persistence of  $\text{C}_4$  vegetation in the western Nefud Desert or animal movements tracking  
184 seasonal availability of  $\text{C}_4$  resources. Sequential  $\delta^{18}\text{O}$  provided more insights in this regard  
185 and *Oryx* sp.  $\delta^{18}\text{O}$  documents clear, sigmoidal fluctuations usually associated with seasonal

186 variations in regional environmental conditions rather than use of different water sources<sup>36,40</sup>  
187 – in this case seasonal variation in the evaporative stresses placed on plants consumed (Fig.  
188 5). Similar, although dampened, sigmoidal curves can also be seen in the equid individuals  
189 sampled, suggesting seasonal changes in the level of evaporation affecting the drinking water  
190 imbibed by these individuals (Fig. 6). These results are consistent with environmental  
191 seasonality in ranges covered by the two taxa sampled. Furthermore, the difference in the  
192 degree of acuteness of these seasonal changes between the *Oryx* sp. and equids further  
193 highlights the validity of using the relative magnitude  $\delta^{18}\text{O}$  distinctions between non-obligate  
194 and obligate drinking taxa as a palaeoaridity indicator.

195 The two *Palaeoloxodon recki* specimens demonstrate very little variation in either  $\delta^{13}\text{C}$  or  
196  $\delta^{18}\text{O}$  through the formation of the tooth, suggesting reliable access to stable water bodies and  
197  $\text{C}_4$  grasses (Fig. 6). Given documentation of seasonal patterns in  $\delta^{18}\text{O}$  in *Oryx* sp. and equids  
198 with more limited ranges, the fact that *Palaeoloxodon recki* documents limited changes  
199 suggests that these animals were migrating over much larger distances, perhaps following  
200 lake and river systems with relatively similar  $\delta^{18}\text{O}$  values. Furthermore, geomorphological  
201 insights have also suggested that the Ti's al Ghadah palaeolake would have been relatively  
202 shallow (Supplementary Text 1), further suggesting that *Palaeoloxodon recki* had to range to  
203 obtain enough water throughout the year. The potential undertaking of significant, long-  
204 distance migrations in search of water and vegetation would fit with the behaviours  
205 documented among African elephants today<sup>41</sup>. Furthermore, such results are also compatible  
206 with suggestions based on palaeolake and palaeoriver modeling, using Geographical  
207 Information Systems, that indicate that Ti's al Ghadah was not an isolated oasis, but rather  
208 part of a broader, often interconnected, chain of palaeolakes during wet intervals<sup>19</sup>.

209  
210

## Discussion

211 The recovery of unambiguous hominin-produced lithic material, in association with evidence  
212 from the fossil record suggestive of hominin butchery activities, reported here and dated to *c.*  
213 500-300 ka, represents the oldest dated hominin occupation in Arabia. While the small  
214 sample size makes detailed descriptions of the assemblage's lithic technology and cultural  
215 attributions currently difficult, they demonstrate a Middle Pleistocene hominin presence in  
216 Arabia. It is considerably older than the previously oldest site of Jebel Qattar-1 at *c.* 210 ka<sup>23</sup>  
217 and, alongside recent research<sup>42</sup>, highlights the benefits of systematic, detailed taphonomic  
218 study of fossil material when exploring hominin arrival in different parts of the world. In  
219 addition to recent finds of *H. sapiens* in the Arabian interior *c.* 90 ka<sup>20</sup>, the Ti's al Ghadah  
220 evidence highlights that focus on Pleistocene *Homo* expansions should not solely be limited  
221 to Eurasia, Africa, and the Levant. The identification of Afro-tropical, Saharao-Arabian, and  
222 Palearctic fauna<sup>12-15</sup> in association with hominin presence also highlights the possibility of  
223 Middle, and perhaps also Early, Pleistocene hominin migrations into the Arabian Peninsula  
224 from Africa and Eurasia. Future systematic survey and excavation will help to further  
225 constrain the chronology and nature of hominin dispersal into this part of the world.

226 The stable isotope data from fauna directly associated with these traces of hominin activity at  
227 Ti's al Ghadah provide detailed insights into palaeoaridity and palaeovegetation in this part  
228 of Arabia during periods of hominin migration. A substantial corpus of environmental data  
229 exists for the Late Pleistocene (from MIS7 onwards) documenting recurrent humid  
230 episodes<sup>17,19,43-44</sup> (Supplementary Text 5), although generally deficient knowledge of  
231 evapotranspiration and insufficient on-the-ground testing of the results of climate change  
232 models has led to limited understanding as to what 'wetter' represents in the context of  
233 regional vegetation and biomass. Meanwhile, modern Arabian landscapes, to which we might

234 look for analogues, have been heavily modified by Holocene anthropogenic activity. The  
235 situation is even worse for the Middle Pleistocene (pre-MIS6 on the MIS stage of the date  
236 mean). As Supplementary Table 13 shows (Supplementary Text 5), the majority of these  
237 three proxies from from three locales (the Hoti and Al Mukalla caves in Oman and Yemen,  
238 and the alluvial fan complexes of the Hajar mountains. Only a few exist for northern Arabia,  
239 demonstrating the importance of the Ti's al Ghadah assemblage for studying environmental  
240 conditions associated with hominin incursions

241 The data presented here highlight the presence of abundant C<sub>4</sub> grasslands and aridity levels  
242 somewhat similar to those found in East Africa today. The comparison of obligate and non-  
243 obligate drinker stable oxygen isotopes has been little-developed beyond Africa, yet we hope  
244 to have shown here that this methodology could and should be applied to other parts of Asia,  
245 such as the Thar Desert, central Asia, and eastern Asia in order to develop more detailed  
246 understandings of hominin adaptations to semi-arid and arid environments in these parts of  
247 the world. The data reported here also fits with palaeoecological reconstructions based on the  
248 fossil taxa identified at Ti's al Ghadah<sup>12-15</sup> (Supplementary Table 2). The presence of various  
249 grassland taxa (*Palaeoloxodon* and an alcelaphine), fish and birds with strong affinities  
250 toward water (e.g. *Anas* and *Tachybaptus*) imply the presence of expansive grasses and large  
251 perennial water sources<sup>12-15</sup> (Supplementary Figure 3; Supplementary Table 2). The presence  
252 of a large felid (*Panthera gombaszoegensis*) and hyena indicate that the western Nefud  
253 Desert was also host to a substantial prey-biomass<sup>13-14</sup>. Alongside evidence from sequential  
254 isotopic analysis of the wide-ranging *Palaeoloxodon recki* reported here, attainment of lake  
255 sequences should also help to clarify wider, regional environmental trends during the earliest  
256 arrival of hominins into Arabia. Overall, however, Early and Middle Pleistocene hominin  
257 populations would seemingly have been able to extend not only into the Levant, but also deep  
258 into the Arabian Peninsula, potentially making use of access to a combination of African and  
259 Eurasian medium and large sized mammals, as well as similar grassland habitats<sup>4,15,45</sup>.

260 The identification of Late Pleistocene *H. sapiens* and Middle Pleistocene hominins in the  
261 interior of the Arabian Peninsula opens up the possibility of exploring the adaptive capacities  
262 of different hominin taxa in what is, today, an extreme environment. The proto-global  
263 distribution of non-*H. sapiens* Middle Pleistocene *Homo*, as well as growing evidence for its  
264 cultural capacity<sup>5-6</sup>, have been argued to represent a potential adaptive threshold,  
265 demonstrating the exploitation of new environments (e.g.<sup>7,46</sup>). In line with previous  
266 suggestions<sup>4-15</sup>, we demonstrate that Middle Pleistocene hominin expansions into this region  
267 would not necessarily have required new innovations or adaptations to harsh desertic aridity  
268 and imply a range expansion similar to other large and medium sized mammal populations  
269 moving between Africa, the Levant, and Eurasia<sup>15</sup>. By contrast, although our own species  
270 was also reliant on periods of increased precipitation to access the Arabian Peninsula<sup>20</sup>, it  
271 appears to have had a wide geographic spread<sup>20-21,47</sup>, penetrating further into the dunefields  
272 and living under conditions that were perhaps harsher than their Middle Pleistocene  
273 predecessors<sup>16,48</sup>. Recent research in the Kalahari and Namib Deserts of southern Africa has  
274 also highlighted that our species was potentially uniquely able to occupy arid regions during  
275 periods of limited surface water in the Late Pleistocene<sup>49-50</sup>. Future work, and the application  
276 of palaeoenvironmental methodologies akin to that developed here, should enable further  
277 testing as to whether our species is ecologically unique within the genus *Homo*.

## 279 **Methods**

### 281 *Lithic and faunal analysis*

282 Lithic artefacts were recovered from Unit 5 of trench 6. The lithic material and debitage was  
283 measured, recorded, and drawn following previously published protocols<sup>51</sup>.

284 Fossil identification and analysis was conducted at the Australian National University (ANU)  
285 and the University of New South Wales (UNSW), Australia, and facilitated by comparative  
286 osteological material. Each specimen was examined by eye and hand-lens (10-20x) and at  
287 different angles to identify fine-scale surface modifications that only become apparent at  
288 certain angles of light exposure. Bone surface modifications, such as tooth and percussion  
289 marks, were analyzed and recorded following standard methodologies for taphonomic  
290 analysis of fossil faunal assemblages (e.g. <sup>52-53</sup>). Cut marks are defined as V-shaped grooves  
291 and are often accompanied with features such as shoulder effect, flaking and microstriations<sup>54</sup>,  
292 and were considered when analyzing modifications in this study. Markings suspected of  
293 being cut marks were further inspected by Scanning Electron Microscopy (SEM)  
294 (Supplementary Text 4). Notches were defined as circular to semi-circular breaks in the edge  
295 of midshaft fragments and are typically produced by both hominins and large carnivores  
296 when exploiting within bone nutrients (i.e. marrow)<sup>52</sup>. Dynamic loading forces associated  
297 with hammerstone percussion tend to produce notches that are wider and shallower than  
298 those generated by carnivores, allowing notches to be quantitatively differentiated. Notch  
299 morphology was determined following the protocol described in Capaldo and  
300 Blumenschine<sup>52</sup> and notches were compared to those generated by carnivores, un-modified  
301 hammerstones, and modified hammerstones under experimental settings<sup>52,55</sup> (Supplementary  
302 Figure 13) (Supplementary Text 4).

### 303 *Stable isotope analysis*

304 Tooth enamel samples were selected from the available fauna from deposits at Ti's al Ghadah  
305 dated to *c.* 300-500 ka (Supplementary Texts 1 and 2, Supplementary Table 3). Fossil equids,  
306 extinct elephants, and hartebeest were targeted for stable oxygen isotope measurement as  
307 abundant obligate drinkers, while *Oryx* sp. comprise the non-obligate drinker sample from  
308 the site (Supplementary Text 2). To provide a modern baseline estimate of aridity in Saudi  
309 Arabia for these taxa,  $\delta^{18}\text{O}$  measurements were made on modern equids (*Equus caballus*)  
310 (n=4) and camels (*Camelus dromedarius*) (n=2) reliant on oasis water and compared to the  
311  $\delta^{18}\text{O}$  of modern samples of Arabian oryx (*Oryx leucoryx*) (n=7) from the same region  
312 (Supplementary Text 2; Supplementary Table 4). Sequential  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  was also  
313 measured on two extinct elephant molars, three equids, and five *Oryx* sp. fossil teeth  
314 (Supplementary Texts 1 and 2). Fourier Transform Infrared Spectroscopy (FTIR) was used to  
315 assess enamel preservation (Supplementary Text 3).

316 21 samples were selected for stable carbon and oxygen isotope analysis of tooth enamel from  
317 the available fossil material from Unit 5 at Ti's al Ghadah. All teeth that could be confidently  
318 identified from excavations by the Palaeodeserts team between 2013 and 2014, as well as  
319 excavations by the Saudi Arabian Geological Survey in 2011 (Supplementary Table 3), were  
320 sampled. We selected 5 *Oryx* sp., 3 *Equid* sp. and 2 *Palaeoloxodon recki* teeth for additional,  
321 sequential analysis based on their completeness and robustness to endure additional sampling  
322 (Supplementary Table 3, Supplementary Tables 5-7). The 5 fossil *Oryx* sp. were, in turn,  
323 compared to 1 modern *Oryx* sp. (Supplementary Tables 4 and 8) in order to provide a modern  
324 baseline for seasonal changes in  $\delta^{18}\text{O}$  in this non-obligate drinker.

325 All teeth or teeth fragments were cleaned using air-abrasion to remove any adhering external  
326 material. Enamel powder for bulk analysis was obtained using gentle abrasion with a



327 diamond-tipped drill along the full length of the buccal surface in order to ensure a  
328 representative measurement for the entire period of enamel formation. For sequential  
329 samples, each sample was a 1–2 mm-wide groove perpendicular to the tooth growth axis,  
330 through the thickness of the enamel layer. The distance of the base of each sample groove  
331 from the enamel/root junction from the furthest sample margin was recorded.

332 All enamel powder was pretreated to remove organic or secondary carbonate contaminants.  
333 This consisted of a series of washes in 1.5% sodium hypochlorite for 60 minutes, followed by  
334 three rinses in purified H<sub>2</sub>O and centrifuging, before 0.1M acetic acid was added for 10  
335 minutes, followed by another three rinses in purified H<sub>2</sub>O (as per.<sup>56-57</sup>). Following reaction  
336 with 100% phosphoric acid, gases evolved from the samples were analyzed to stable carbon  
337 and oxygen isotopic composition using a Thermo Gas Bench 2 connected to a Thermo Delta  
338 V Advantage Mass Spectrometer at the Department of Archaeology, Max Planck Institute for  
339 the Science of Human History. Carbon and oxygen isotope values were compared against  
340 international standards (NBS 19, MERCK) registered by the International Atomic Energy  
341 Agency. Replicate analysis of OES standards suggests that machine measurement error is *c.* ±  
342 0.1‰ for δ<sup>13</sup>C and ± 0.2‰ for δ<sup>18</sup>O. Overall measurement precision was studied through the  
343 measurement of repeat extracts from a bovid tooth enamel standard (n=20, ± 0.2‰ for δ<sup>13</sup>C  
344 and ± 0.3‰).

345 The relationship between δ<sup>18</sup>O and Site and Group (obligate and non-obligate drinkers) was  
346 determined using a mixed Site\*Group ANOVA comparative test, followed by post-hoc  
347 Tukey pair-wise comparisons. Statistical regression analyses were undertaken to discern the  
348 statistical correlation between δ<sup>13</sup>C and δ<sup>18</sup>O at Ti's al Ghadah. All statistical analyses were  
349 conducted using the free program R software<sup>58</sup>.

#### 350 **Data availability**

351 All data generated or analysed during this study are included in the published article and its  
352 supplementary information files.

#### 354 **Acknowledgments**

356 The authors declare no conflict of interest.

357  
358 For permission to conduct this study, we thank HRH Prince Sultan bin Salman, President of  
359 the Saudi Commission for Tourism and National Heritage (SCTH) and Vice Presidents A.  
360 Ghabban and J. Omar. This project was funded by the ERC (Grant no. 295719 to MDP), the  
361 Max Planck Society and the SCTH. Z. Nawab, former President of the Saudi Geological  
362 Survey, provided research support. We thank Andrew Gledhill, University of Bradford  
363 assistance with the stable isotope analysis. HSG and EMLS acknowledge the British  
364 Academy for funding.

#### 366 **Author contributions:**

367 PR, MS, and MP, planned the project. PR, MS, NA, PB, HSG, EMLS, JLT, JL, JZ, and ISZ  
368 performed the experiments. PR, MS, NA, PB, HSG, EMLS, JLT, JL, JZ, and ISZ performed  
369 data analysis. All authors interpreted the data. All authors wrote and provided comment on  
370 the paper.

371

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513 **List of Figures:**

514 **Figure 1.** Maps showing A) the position of the Ti's al Ghadah fossil site and the Mahazat as-  
515 Sayd Protected Area in the context of Saudi Arabia and B) A view of the Ti's al Ghadah  
516 basin showing in blue the extent of the lacustrine deposit overlying the main fossil faunal  
517 deposit.

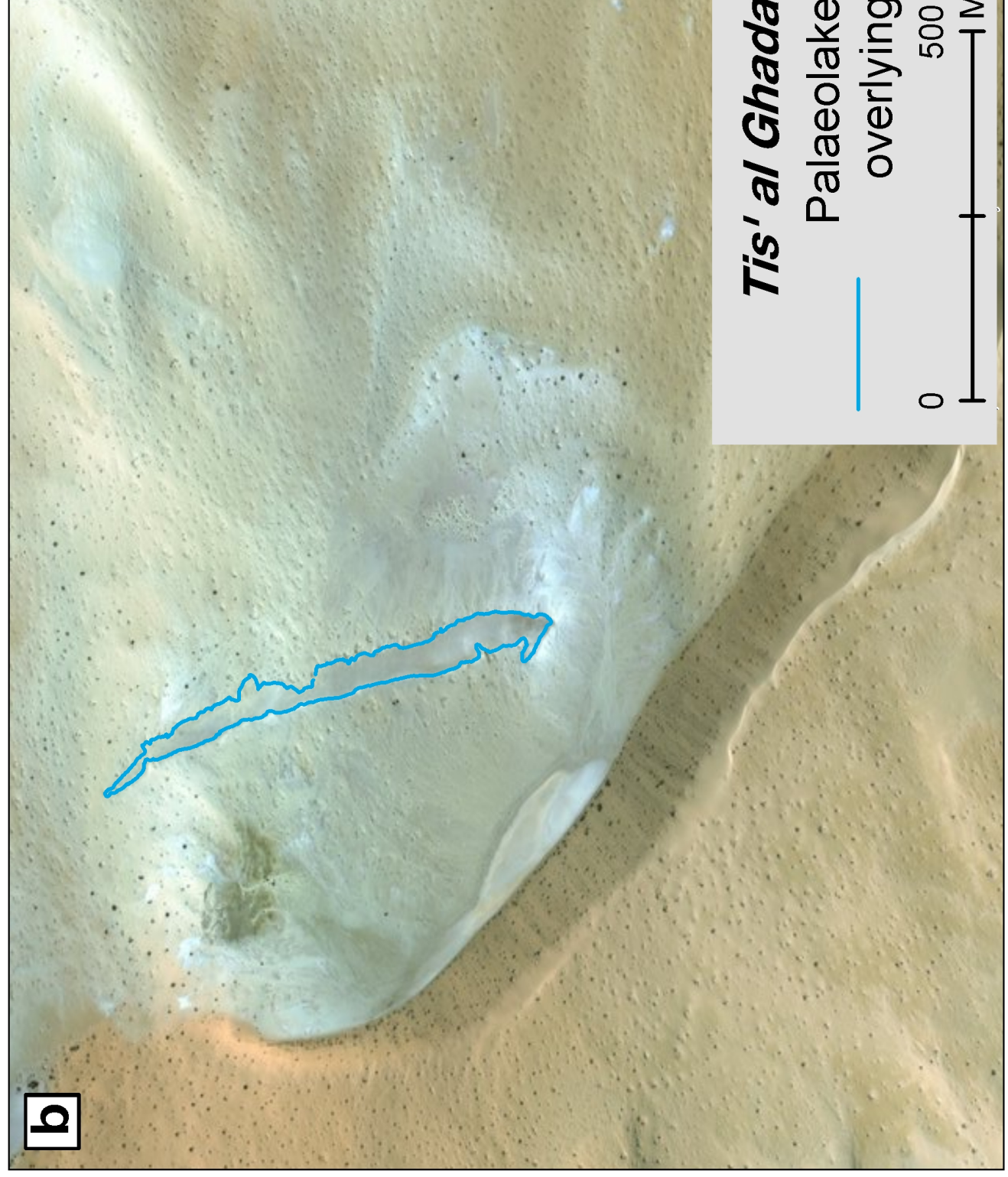
518 **Figure 2.** A) chert flakes with dihedral striking platforms (i, iii and iv) and a side retouched  
519 flake (ii). B) medium-sized bovid proximal metacarpal (TAG14/121) in cortical (i) and  
520 medullary (ii and iii) view. In the inset a wide striae field (white box) is visible adjacent the  
521 flake scar (dashed line). A adhering bone flake (arrow) and conchoidal flake scar (dashed  
522 line) are visible from the medullary. The refitted piece (iii) exhibits a smooth, oblique  
523 fracture pattern indicating the bone was broken while fresh. C) a tibia shaft fragment  
524 (TAG14/9235) in cortical (i) and medullary (ii) view. An indeterminate narrow, V-shaped  
525 groove with a forked end (arrows) runs parallel to the long axis of the bone. A conchoidal  
526 flake scar is present on the medullary surface (dashed line). D) dorsal view (i) of a medium-  
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528 to the long axis of the rib. Shoulder effect (arrows) is clearly visible in the SEM image (ii). E)  
529 a medium-sized mammalian rib fragment (TAG13/133) with multiple parallel grooves  
530 running perpendicular to the long axis of the bone and shoulder effect in the form of Hertzian  
531 cones (triangles) that are clearly visible in the SEM image (ii). F) a medium-sized bovid  
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533 multiple opposing notches and conchoidal flake scars (dashed lines), and numerous carnivore  
534 tooth scores (arrows), suggesting the bone was broken open by a large carnivore. G) medium-  
535 size mammalian shaft bone flake (TAG13/9134) in medullary (i) and cortical (ii) view.  
536 Smooth and oblique fracture pattern indicates the bone was broken while fresh and likely by  
537 a dynamic force. The surface exhibits pitting (arrows) and the bone flake has tentatively been  
538 attributed to be the result of hammerstone percussion. Solid scale bar = 20 mm. Dashed scale  
539 bar = 0.5 mm.

540 **Figure 3.**  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements from the tooth enamel of fossil fauna from Ti's al  
541 Ghadah, Saudi Arabia analyzed in this study. VPDB, Vienna PeeDee Belemnite.

542 **Figure 4.**  $\delta^{18}\text{O}$  values for non-obligate and obligate drinking taxa at the East African  
543 localities of Laikipia (Kenya) and Tsavo (Kenya) reported by Blumenthal et al.<sup>35</sup>, for modern  
544 Saudi Arabia, and for the Middle Pleistocene Ti's al Ghadah (TAG) (Saudi Arabia)  
545 assemblage. Boxes show the median and the lower (25%) and upper (75%) quartiles;  
546 whiskers encompass all data points within  $1.5 \times$  the interquartile range of the box. VPDB,  
547 Vienna PeeDee Belemnite.

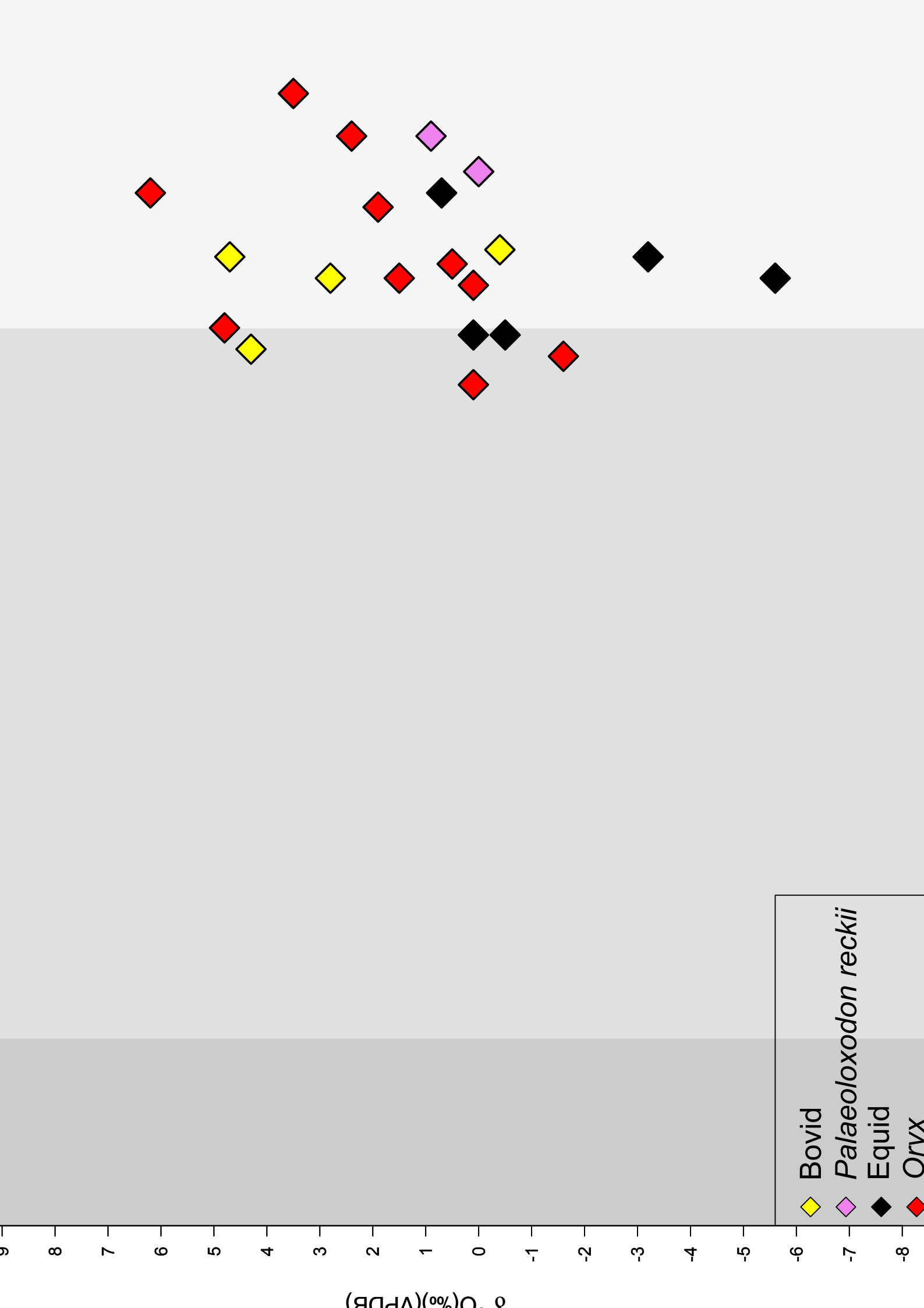
548 **Figure 5.** Sequential  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements for *Oryx* sp. samples TAG 1551, TAG  
549 1541, TAG 149, TAG 942, and TAG 944 from the Middle Pleistocene levels of T'is al  
550 Ghadah and one modern *Oryx* sp. sample from the Mahazat as-Sayd Protected Area. VPDB,  
551 Vienna PeeDee Belemnite.

552 **Figure 6.** Sequential  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  measurements for equid samples SGS180, SGS57 and  
553 SGS1094 and *Palaeoloxodon reekii* samples TAG14 301 and TAG14 129 from the Middle  
554 Pleistocene levels of T'is al Ghadah. VPDB, Vienna PeeDee Belemnite.

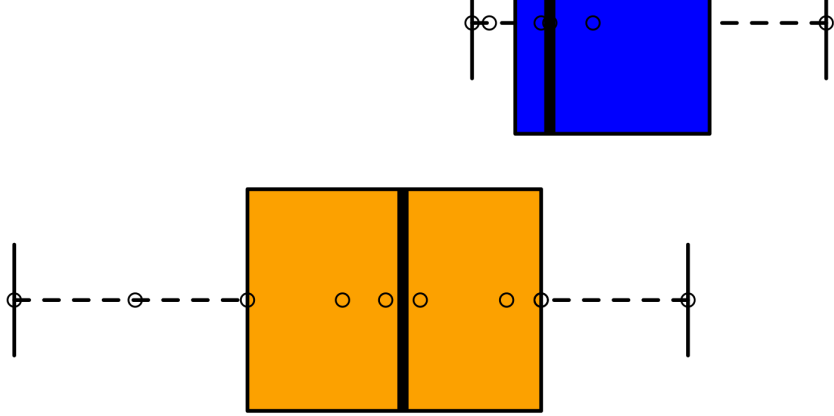




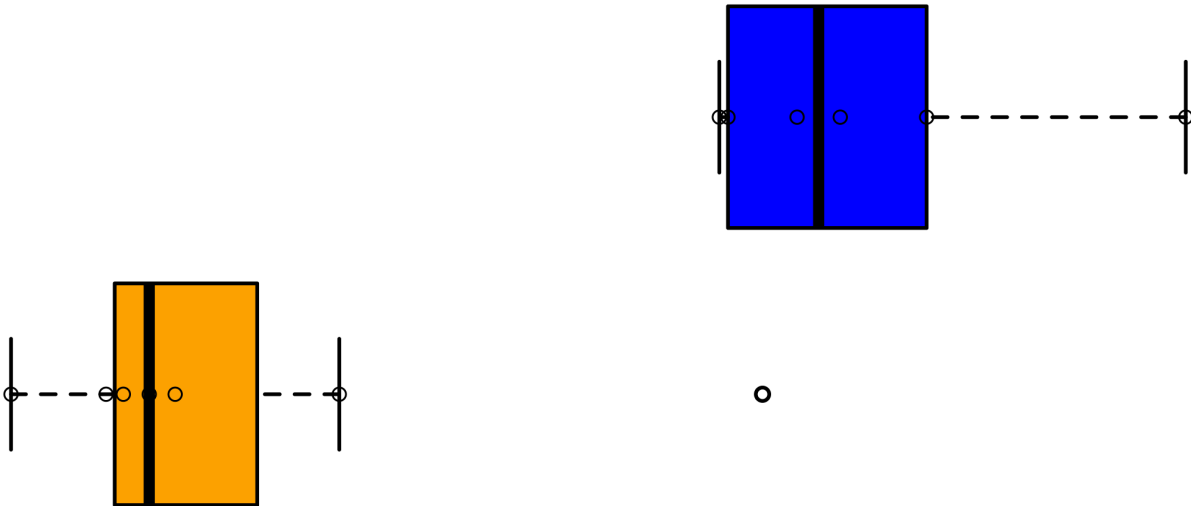




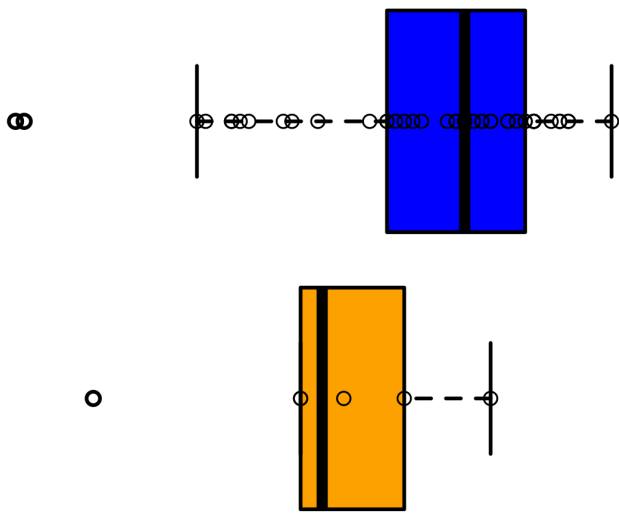
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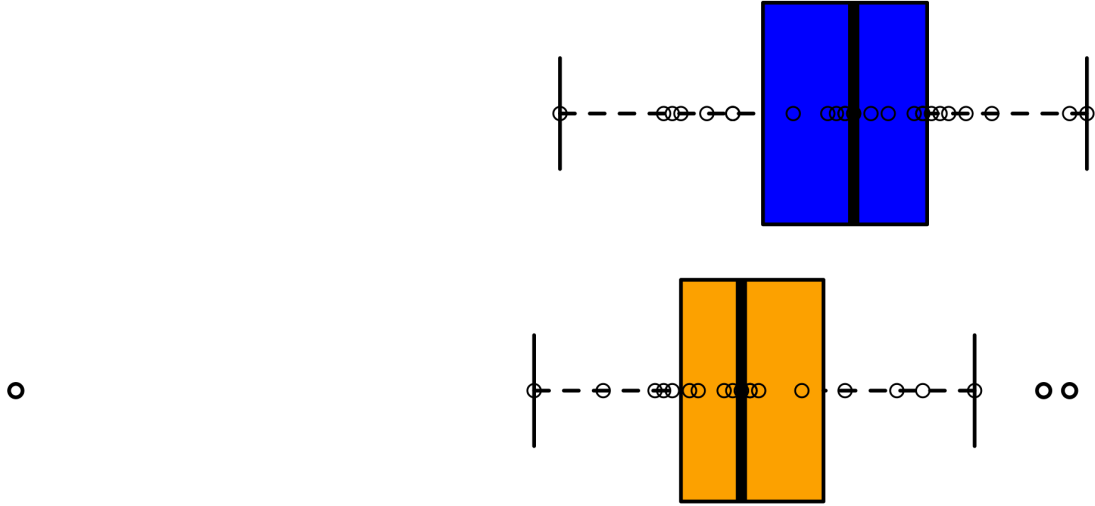
Modern Arabia

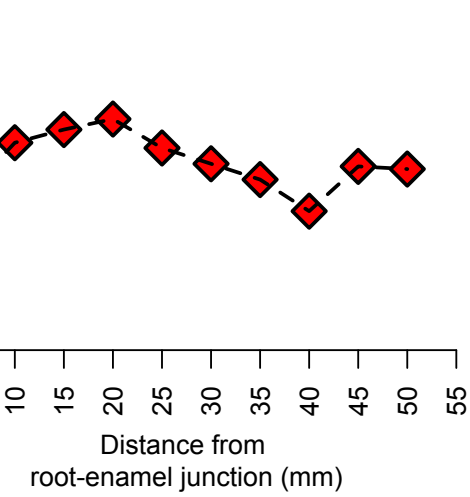
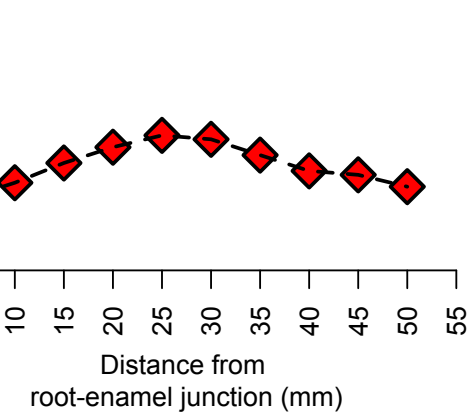


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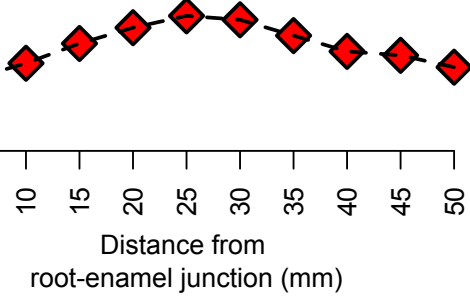


Laikipia

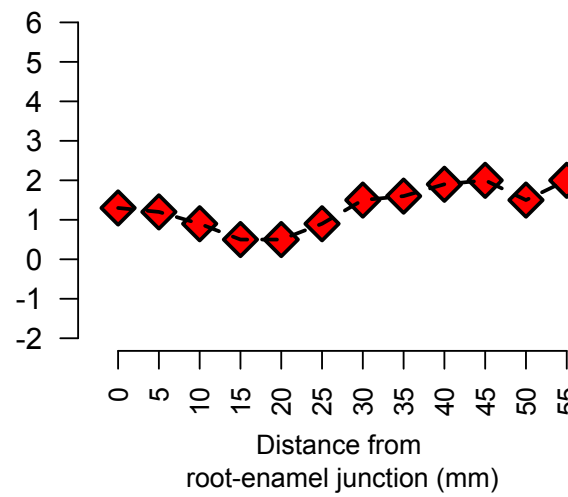




**TAG 942**



**TAG 944**



**Moder**

