

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

3
4 Patrick Roberts^{1*}, Mathew Stewart^{2*}, N Aziz³, Paul Breeze⁴, Ian Candy⁵, Nick Drake⁴, Huw
5 S. Groucutt^{6,1}, Eleanor M.L. Scerri^{6,1}, Julia Lee-Thorp⁶, Julien Louys⁷, Iyad S. Zalmout⁸,
6 Yahya S. A. Al-Mufarreah⁸, Jana Zech¹, Abdullah M. Alsharekh⁹, Abdulaziz al Omari¹⁰,
7 Nicole Boivin¹, Michael Petraglia^{1,11*}

8 ¹Department of Archaeology, Max Planck Institute for the Science of Human History, Germany.

9 ²Palaeontology, Geobiology and Earth Archives Research Centre, School of Biological, Earth and
10 Environmental Science, University of New South Wales, Australia.

11 ³Geological Survey of the Government of Saudi Arabia, Saudi Arabia.

12 ⁴Department of Geography, King’s College London, University of London, United Kingdom.

13 ⁵Department of Geography, Royal Holloway, University of London, United Kingdom.

14 ⁶Research Laboratory for Archaeology and the History of Art, School of Archaeology, University of
15 Oxford, United Kingdom.

16 ⁷Environmental Futures Research Institute, Griffith Sciences - Centres and Institutes, Griffith
17 University, Australia.

18 ⁸Department of Paleontology, Saudi Geological Survey, Jeddah, Saudi Arabia.

19 ⁹King Saud University, Saudi Arabia.

20 ¹⁰Saudi Commission for Tourism and National Heritage, Saudi Arabia.

21 ¹¹Human Origins Program, National Museum of Natural History, Smithsonian Institution,
22 Washington, D.C., USA

23
24 *correspondence to: Patrick Roberts, Mathew Stewart, and Michael Petraglia
25 email: roberts@shh.mpg.de, ms231@uowmail.edu.au, petraglia@shh.mpg.de

26
27
28 **Introductory paragraph**
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

45 Introduction

46

47 Studies of Pleistocene hominin dispersals beyond Africa are important for understanding the
48 course of global human evolution and prehistory. In particular, analysis of the environmental
49 context under which members of the genus *Homo* moved into Europe and Asia in the Early
50 and Middle Pleistocene (2.6 Ma to 126 ka) relative to that of *Homo sapiens* populations
51 expanding around the globe in the Late Pleistocene (126-12 ka) can provide insight into the
52 potential ecologically unique nature of our species¹⁻³. It has recently been highlighted that our
53 species occupied and utilized a diversity of extreme environments, including deserts, tropical
54 rainforests, palaeartic, and high-altitude settings, around the world during the Late
55 Pleistocene³. By contrast, the dispersals of other earlier and contemporaneous *Homo* species
56 into Europe and Asia appear to be best associated with generalized utilization of different
57 forest and grassland mosaics proximate to riverine and lacustrine settings^{2,4}. Yet, a paucity of
58 associated palaeoenvironmental information has made it difficult to systematically test this
59 distinction and many hold that non-*H. sapiens* members of the genus *Homo* demonstrate
60 significant cultural⁵⁻⁶ and ecologically adaptive⁷⁻⁹ flexibility.

61 In spite of its crucial geographic position at the interface of Africa and Eurasia, the Arabian
62 Peninsula has remained remarkably absent from adaptive models of Pleistocene hominin
63 expansions until relatively recently, owing to a lack of well-constrained archaeological and
64 palaeoecological data. Climate modeling¹⁰, speleothem records¹¹, palaeontological findings<sup>12-
65 15</sup>, and geomorphological studies of palaeolake records¹⁶⁻¹⁷ have been used to argue that at
66 intervals in the past, notably during interglacials, the harsh, hyper-arid deserts that cover
67 much of Arabia today were replaced by 'moister' and 'greener' conditions more hospitable to
68 foraging occupation¹⁸⁻¹⁹. Furthermore, the find of a *H. sapiens* phalanx, in association with
69 Middle Palaeolithic stone tools, at the site of Al Wusta dated to *c.* 90 ka provides definitive
70 evidence for the early presence of our species in the interior of the Arabian Peninsula²⁰.
71 There have also been suggestions that stone tools in the Arabian interior are associated with
72 an earlier period of Middle Pleistocene hominin dispersal²¹⁻²⁴. However, despite the
73 significance of climate and environmental change for hominin dispersal into the region, there
74 has been no direct means of determining what 'wetter' represents in the context of regional
75 ecology nor definitive identification of Middle Pleistocene hominin presence.

76 We undertook renewed archaeological and taphonomic analysis of fossil fauna found at the
77 Middle Pleistocene (*c.* 500-300 ka) fossil locality of Ti's al Ghadah in the Nefud Desert of
78 Saudi Arabia (Fig. 1; SI Text 1 and 2; Figs. S1-S2) and report, for the first time at the site,
79 lithic artefacts in direct stratigraphic association with the fossil fauna. Ti's al Ghadah is one
80 of the most important palaeontological sites in the region, representing the only dated faunal
81 assemblage recovered from Middle Pleistocene Arabia¹²⁻¹⁴. Previous analyses have identified
82 a suite of terrestrial and aquatic animals, including extinct elephants (*Palaeoloxodon* sp.),
83 horses (*Equus hemionus*), and water birds (*Tachybaptus* sp. and *Anas* sp.)¹²⁻¹⁴ (Table S2), that
84 have been used to argue the western Nefud Desert was significant less arid at times during
85 the Middle Pleistocene than it is today. 'Middle Palaeolithic' artefacts of unknown age have
86 also been recovered from the surface of the basin²⁴. Yet, the lack of taphonomic analysis and
87 scarcity of anthropogenic remains has made evaluating the relationship between hominins
88 and fossil fauna difficult.

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

92 of 21 fossil fauna recovered from the site. $\delta^{13}\text{C}$ analysis of faunal tooth enamel is used to
93 assess different types of biomass in animal diets²⁵⁻²⁷. Most terrestrial plants, including trees,
94 herbs, shrubs, and shade-loving grasses follow the C_3 photosynthetic pathway²⁸. C_4
95 photosynthesis is followed by most arid-adapted grasses and some sedges²⁹. C_3 and C_4 plants
96 have distinct and non-overlapping $\delta^{13}\text{C}$ values³⁰ that are passed into faunal consumers
97 allowing reliance on tree and shrub versus grassland biomass to be determined in global
98 ecosystems, including those of Arabia¹². In faunal diets, prior to the impact of significant
99 fossil fuel emission, average herbivore $\delta^{13}\text{C}$ values for C_3 and C_4 reliance are *c.* -12‰ and ~
100 0‰, respectively²⁵⁻²⁷ (Fig. 3).

101 $\delta^{18}\text{O}$ data from fossil herbivore tooth enamel reflect precipitation source, humidity,
102 temperature, and also plant water. These multiple influences can often make faunal enamel
103 $\delta^{18}\text{O}$ difficult to interpret as a past environmental signal. This is particularly the case in areas
104 like the Arabian Peninsula where the source water, and therefore $\delta^{18}\text{O}$, for precipitation may
105 have changed over time¹⁰. Evaporation exerts a positive effect on $\delta^{18}\text{O}$, particularly in arid
106 desert regions such as the centre of the Arabian Peninsula, so that continental water bodies
107 and soils in areas with a water deficit are ^{18}O -enriched. This effect is even stronger in plants
108 due to the process of evapo-transpiration³²⁻³³. The difference between the $\delta^{18}\text{O}$ from tooth
109 enamel of obligate drinkers such as equids (that must drink from open water sources) and
110 non-obligate drinkers such as *Oryx* spp. (that can meet their water requirements through the
111 consumption of plants) will be strongly influenced by palaeoaridity³⁴⁻³⁵ at a given locale, and
112 will not be effected by changes in the precipitation or source water baseline (SI Text 2).
113 Finally, due to the fact that tooth enamel forms incrementally, sequential $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$
114 analysis of animal tooth enamel can be used to look at temporal changes in vegetation and
115 water source during the period of tooth enamel formation³⁶. The preservation of all samples
116 was also checked using FTIR as per³¹ (SI Text 3).

117 **Results**

118
119 The fossil faunal remains and newly-discovered stone tools analysed in this study were
120 recovered from a sandy horizon ('Unit 5') directly beneath a palaeolake deposit in the Ti's al
121 Ghadah basin¹⁴ (Fig. 2). The lithic artefacts, coupled with new taphonomic evidence
122 suggestive of anthropogenic accumulation of bones on-site, confirm a hominin presence in
123 association with the faunal remains analysed here (Fig. 2; see also SI Text 4). These findings
124 represent the oldest radiometrically dated hominin presence in the Arabian Peninsula, as well
125 as the first anthropogenically modified faunal assemblage from the Pleistocene. In total, six
126 unretouched flakes and one retouched flake were recovered from Unit 5. A further six chunks
127 were recovered with the artefacts and likely represent highly fragmented debitage. The lithics
128 and debitage fragments are made on a brown coloured lacustrine chert, and this material is
129 known from lakebeds across the Nefud¹⁸⁻²⁰. At the MIS 5 site of Al Wusta, 3km from Ti's al
130 Ghaddah, similar lacustrine chert was the main raw material used by hominins²⁰. Despite
131 difficulties in knapping such material, the artefacts are finely made and similar to one another
132 in terms of technology (Fig. 2A). The lithics consist of small flakes struck from prepared
133 cores and a side-retouched flake ('side scraper').

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

139 is apparent, the latter in the form of Hertzian cones. No internal microstriations were
140 observed, although fine-scale features, such as microstriations, are quickly removed during
141 chemical alteration³⁷. The direction and location of the markings is consistent with cut marks
142 produced during filleting of meat from around the rib³⁸. Notches with a broad arcuate
143 planform and conchoidal medullary flake scar, reminiscent of notches produced during
144 hammerstone percussion, were also identified and suggest hominins may have broken open
145 long bones to exploit marrow (SI Text 4; Figs 2B and S12). Together with the evidence of the
146 newly-identified associated lithics, this makes Ti's al Ghadah the first, at least partially
147 anthropogenic faunal assemblage from the Arabian 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 C_4 vegetation in the diets of herbivores ($\delta^{13}\text{C}$ range = -0.8 to 3.3‰), (Fig. 3)
151 (Table S5), and suggests that rainfall occurred during the warm season. The $\delta^{13}\text{C}$ evidence
152 also fits with climate simulations suggesting that the periodic amelioration of Arabian
153 environments reflects the incursion of the African monsoon system¹⁰. The uniformity of C_4
154 consumption by all animals suggests the presence of extensive, productive C_4 grasslands in
155 the vicinity of the palaeolake. The $\delta^{18}\text{O}$ range of fauna from Ti's al Ghadah is high ($\delta^{18}\text{O}$
156 range = -5.6 to 6.2‰) – though not higher than Pliocene, Pleistocene, and contemporary
157 African ecosystems^{34-35,39-40}. Differences in $\delta^{18}\text{O}$ between obligate drinking equids,
158 hartebeest, and elephants and non-obligate drinking *Oryx* sp. allow more detailed estimations
159 of relative environmental aridity to be made (SI 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 $n=5$)³⁵ (Fig.
166 4) (SI Text 2; Table S9). While caution is warranted given that taxon-specific habits could
167 vary through time, when the difference between obligate and non-obligate drinker $\delta^{18}\text{O}$ from
168 Ti's al Ghadah is compared to that of modern day Tsavo (1.7‰) and Laikipia (1.3‰),
169 Middle Pleistocene ecological conditions in the interior of Arabia appear to approximate that
170 of a relatively humid African savanna today (Fig. 4) (SI Text 2). Such a reconstruction is
171 supported by the results of a mixed ANOVA performed to compare the difference between
172 obligate drinkers and non-obligate drinkers at each site (Tables S10-S11). While Tsavo and
173 Laikipia show no significant difference between these 'drinker' groups, there is a significant
174 difference found between these groups at Ti's al Ghadah.

175 There is no correlation between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values in the Ti's al Ghadah fossil dataset
176 (Multiple R-squared=0.04, $p<0.01$, adjusted R-squared=-0.01, $p<0.01$), indicating that access
177 to vegetation was independent of factors affecting faunal $\delta^{18}\text{O}$. This is also borne out in
178 sequential $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analyses of selected fossil teeth that enables the identification of
179 potential environmental seasonality or mobility. The sequential $\delta^{13}\text{C}$ data, from all taxa,
180 document a homogeneous source of lush C_4 vegetation, likely in the form of grasses, at Ti's
181 al Ghadah (Figs. 5-6, Tables S5-S7). This could either be linked to the persistence of C_4
182 vegetation in the western Nefud Desert or animal movements tracking seasonal availability of
183 C_4 resources. Sequential $\delta^{18}\text{O}$ provided more insights in this regard and *Oryx* sp. $\delta^{18}\text{O}$
184 documents clear, sigmoidal fluctuations usually associated with seasonal variations in
185 regional environmental conditions rather than use of different water sources^{36,40} – in this case
186 seasonal variation in the evaporative stresses placed on plants consumed (Fig. 5). Similar,

187 although dampened, sigmoidal curves can also be seen in the equid individuals sampled,
188 suggesting seasonal changes in the level of evaporation affecting the drinking water imbibed
189 by these individuals (Fig. 6). These results are consistent with environmental seasonality in
190 ranges covered by the two taxa sampled. Furthermore, the difference in the degree of
191 acuteness of these seasonal changes between the *Oryx* sp. and equids further highlights the
192 validity of using the relative magnitude $\delta^{18}\text{O}$ distinctions between non-obligate and obligate
193 drinking taxa as a palaeoaridity indicator.

194 The two *Palaeoloxodon recki* specimens demonstrate very little variation in either $\delta^{13}\text{C}$ or
195 $\delta^{18}\text{O}$ through the formation of the tooth, suggesting reliable access to stable water bodies and
196 C_4 grasses (Fig. 6). Given documentation of seasonal patterns in $\delta^{18}\text{O}$ in *Oryx* sp. and equids
197 with more limited ranges, the fact that *Palaeoloxodon recki* documents limited changes
198 suggests that these animals were migrating over much larger distances, perhaps following
199 lake and river systems with relatively similar $\delta^{18}\text{O}$ values. Furthermore, geomorphological
200 insights have also suggested that the T'is al Ghadah palaeolake would have been relatively
201 shallow (SI Text 1), further suggesting that *Palaeoloxodon recki* had to range to obtain
202 enough water throughout the year. The potential undertaking of significant, long-distance
203 migrations in search of water and vegetation would fit with the behaviours documented
204 among African elephants today⁴¹. Furthermore, such results are also compatible with
205 suggestions based on palaeolake and palaeoriver modeling, using Geographical Information
206 Systems, that indicate that Ti's al Ghadah was not an isolated oasis, but rather part of a
207 broader, often interconnected, chain of palaeolakes during wet intervals¹⁹.

208

209 Discussion

210 The recovery of unambiguous hominin-produced lithic material, in association with evidence
211 from the fossil record suggestive of hominin butchery activities, reported here and dated to c.
212 500-300 ka, represents the oldest dated hominin occupation in Arabia. While the small
213 sample size makes detailed descriptions of the assemblage's lithic technology and cultural
214 attributions currently difficult, they demonstrate a Middle Pleistocene hominin presence in
215 Arabia. It is considerably older than the previously oldest site of Jebel Qattar-1 at c. 210 ka²³
216 and, alongside recent research⁴², highlights the benefits of systematic, detailed taphonomic
217 study of fossil material when exploring hominin arrival in different parts of the world. In
218 addition to recent finds of *H. sapiens* in the Arabian interior c. 90 ka²⁰, the Ti's al Ghadah
219 evidence highlights that focus on Pleistocene *Homo* expansions should not solely be limited
220 to Eurasia, Africa, and the Levant. The identification of Afro-tropical, Saharao-Arabian, and
221 Palearctic fauna¹²⁻¹⁵ in association with hominin presence also highlights the possibility of
222 Middle, and perhaps also Early, Pleistocene hominin migrations into the Arabian Peninsula
223 from Africa and Eurasia. Future systematic survey and excavation will help to further
224 constrain the chronology and nature of hominin dispersal into this part of the world.

225 The stable isotope data from fauna directly associated with these traces of hominin activity at
226 Ti's al Ghadah provide detailed insights into palaeoaridity and palaeovegetation in this part
227 of Arabia during periods of hominin migration. A substantial corpus of environmental data
228 exists for the Late Pleistocene (from MIS7 onwards) documenting recurrent humid
229 episodes^{17,19,43-44} (SI Text 5), although generally deficient knowledge of evapotranspiration
230 and insufficient on-the-ground testing of the results of climate change models has led to
231 limited understanding as to what 'wetter' represents in the context of regional vegetation and
232 biomass. Meanwhile, modern Arabian landscapes, to which we might look for analogues,
233 have been heavily modified by Holocene anthropogenic activity. The situation is even worse
234 for the Middle Pleistocene (pre-MIS6 on the MIS stage of the date mean). As Table S13

235 shows (SI Text 5), the majority of these three proxies from from three locales (the Hoti and
236 Al Mukalla caves in Oman and Yemen, and the alluvial fan complexes of the Hajar
237 mountains. Only a few exist for northern Arabia, demonstrating the importance of the Ti's al
238 Ghadah assemblage for studying environmental conditions associated with hominin
239 incurrences

240 The data presented here highlight the presence of abundant C₄ grasslands and aridity levels
241 somewhat similar to those found in East Africa today. The comparison of obligate and non-
242 obligate drinker stable oxygen isotopes has been little-developed beyond Africa, yet we hope
243 to have shown here that this methodology could and should be applied to other parts of Asia,
244 such as the Thar Desert, central Asia, and eastern Asia in order to develop more detailed
245 understandings of hominin adaptations to semi-arid and arid environments in these parts of
246 the world. The data reported here also fits with palaeoecological reconstructions based on the
247 fossil taxa identified at T'is al Ghadah¹²⁻¹⁵(Table S2). The presence of various grassland taxa
248 (*Palaeoloxodon* and an alcelaphine), fish and birds with strong affinities toward water (e.g.
249 *Anas* and *Tachybaptus*) imply the presence of expansive grasses and large perennial water
250 sources¹²⁻¹⁵ (Fig. S3; Table S2). The presence of a large felid (*Panthera gombaszoegensis*)
251 and hyena indicate that the western Nefud Desert was also host to a substantial prey-
252 biomass¹³⁻¹⁴. Alongside evidence from sequential isotopic analysis of the wide-ranging
253 *Palaeoloxodon recki* reported here, attainment of lake sequences should also help to clarify
254 wider, regional environmental trends during the earliest arrival of hominins into Arabia.
255 Overall, however, Early and Middle Pleistocene hominin populations would seemingly have
256 been able to extend not only into the Levant, but also deep into the Arabian Peninsula,
257 potentially making use of access to a combination of African and Eurasian medium and large
258 sized mammals, as well as similar grassland habitats^{4,15,45}.

259 The identification of Late Pleistocene *H. sapiens* and Middle Pleistocene hominins in the
260 interior of the Arabian Peninsula opens up the possibility of exploring the adaptive capacities
261 of different hominin taxa in what is, today, an extreme environment. The proto-global
262 distribution of non-*H. sapiens* Middle Pleistocene *Homo*, as well as growing evidence for its
263 cultural capacity⁵⁻⁶, have been argued to represent a potential adaptive threshold,
264 demonstrating the exploitation of new environments (e.g.^{7,46}). In line with previous
265 suggestions⁴⁻¹⁵, we demonstrate that Middle Pleistocene hominin expansions into this region
266 would not necessarily have required new innovations or adaptations to harsh desertic aridity
267 and imply a range expansion similar to other large and medium sized mammal populations
268 moving between Africa, the Levant, and Eurasia¹⁵. By contrast, although our own species
269 was also reliant on periods of increased precipitation to access the Arabian Peninsula²⁰, it
270 appears to have had a wide geographic spread^{20-21,47}, penetrating further into the dunefields
271 and living under conditions that were perhaps harsher than their Middle Pleistocene
272 predecessors^{16,48}. Recent research in the Kalahari and Namib Deserts of southern Africa has
273 also highlighted that our species was potentially uniquely able to occupy arid regions during
274 periods of limited surface water in the Late Pleistocene⁴⁹⁻⁵⁰. Future work, and the application
275 of palaeoenvironmental methodologies akin to that developed here, should enable further
276 testing as to whether our species is ecologically unique within the genus *Homo*.

277 278 **Acknowledgments**

279
280 The authors declare no conflict of interest.
281

282 For permission to conduct this study, we thank HRH Prince Sultan bin Salman, President of
283 the Saudi Commission for Tourism and National Heritage (SCTH) and Vice Presidents A.
284 Ghabban and J. Omar. This project was funded by the ERC (Grant no. 295719 to MDP), the
285 Max Planck Society and the SCTH. Z. Nawab, former President of the Saudi Geological
286 Survey, provided research support. We thank Andrew Gledhill, University of Bradford
287 assistance with the stable isotope analysis. HSG and EMLS acknowledge the British
288 Academy for funding.
289

290 **References:**

291

292 1. Gamble, C. *Timewalkers: The prehistory of global colonization* (Alan Sutton Press, 1993).

293 2. Gamble, C. *Settling the earth: the archaeology of deep human history* (Cambridge
294 University Press, 2013).

295 3. Roberts, P., Stewart, B.A. (2018). Defining the ‘generalist-specialist’ niche for Pleistocene
296 *Homo sapiens*. *Nature Human Behaviour*.

297 4. Dennell, RW, Roebroeks, W. Out of Africa: An Asian perspective on early human
298 dispersal from Africa. *Nature* **438**, 1099-1104 (2005).

299 5. Joordens, JCA. et al. *Homo erectus* at Trinil on Java used shells for tool production and
300 engraving. *Nature* **518**, 228-231 (2016).

301 6. Hoffman, DL. Et al. U-Th dating of carbonate crusts reveals Neandertal origin of Iberian
302 cave art. *Science* **359**, 912-915 (2018).

303 7. Morwood, M.J. et al. Fission track age of stone tools and fossils on the east Indonesian
304 island of Flores. *Nature* **392**: 173-176.

305 8. Zhu, RX. et al. Early evidence of the genus *Homo* in East Asia. *J Hum Evol* **55**, 1075-1085
306 (2008).

307 9. Parfitt, SA. et al. Early Pleistocene human occupation at the edge of the boreal zone in
308 northwest Europe. *Nature* **466**, 229–233 (2010).

309 10. Jennings, RP. et al. The greening of Arabia: Multiple opportunities for human occupation
310 in the Arabian Peninsula during the Late Pleistocene inferred from an ensemble of climate
311 model simulations. *Quat Int* **205**, 181-199 (2015).

312 11. Fleitmann, D, Burns, SJ, Neff, U, Mangini, A, Matter, A. Changing moisture sources over
313 the last 333,000 years in Northern Oman from fluid-inclusion evidence in speleothems. *Quat*
314 *Res* **60**, 223-232 (2003).

315 12. Thomas, H. et al. First Pleistocene faunas from the Arabian peninsula: an Nefu desert,
316 Saudi Arabia. *Compte Rendus* **326**, 145-152 (1998).

317 13. Stimpson, CM. et al. Stratified Pleistocene vertebrates with a new record of a jaguar-sized
318 pantherine (*Panthera cf. gombaszogensis*) from northern Saudi Arabia. *Quat Int* **382**, 168-
319 180 (2015).

320 14. Stimpson, CM. et al. Middle Pleistocene vertebrate fossils from the Nefud Desert, Saudi
321 Arabia: implications for biogeography and palaeoecology. *Quat Sci Rev* **143**, 13-36 (2016).

- 322 15. Stewart, M. et al. Middle and Late Pleistocene mammal fossils of Arabia and surrounding
323 regions: Implications for biogeography and hominin dispersals. *Quat Int*,
324 <https://doi.org/10.1016/j.quaint.2017.11.052> (2017).
- 325 16. Rosenberg, TM. et al. Middle and Late Pleistocene humid periods recorded in palaeolake
326 deposits of the Nafud desert, Saudi Arabia. *Quat Sci Rev* **70**, 109-123 (2013).
- 327 17. Parton, A. et al. Alluvial fan records from southeast Arabia reveal multiple windows for
328 human dispersal. *Geology* **43**, 298 (2015).
- 329 18. Groucutt, HS. et al. Human occupation of the Arabian Empty Quarter during MIS 5:
330 evidence from Mundafan Al-Buhayrah, Saudi Arabia. *Quat Sci Rev* **119**, 116-135 (2015).
- 331 19. Breeze, PS. et al. Palaeohydrological corridors for hominin dispersals in the Middle East
332 ~250-70,000 years ago. *Quat Sci Rev* **144**, 155-185 (2016).
- 333 20. Groucutt, HS. et al. *Homo sapiens* in Arabia by 85,000 years ago. *Nat Ecol Evol*, doi:
334 10.1038/s41559-018-0518-2
- 335 21. Armitage, SJ. et al. The southern route “out of Africa”: evidence for an early expansion
336 of modern humans into Arabia. *Science* **331**, 453-456 (2011).
- 337 22. Petraglia, M. et al. Middle Paleolithic occupation on a Marine Isotope Stage 5 lakeshore
338 in the Nefud Desert, Saudi Arabia. *Quat Sci Rev* **30**, 1555-1559 (2011).
- 339 23. Petraglia, M. et al. Hominin Dispersal into the Nefud Desert and middle palaeolithic
340 settlement along the Jubbah Palaeolake, Northern Arabia. *PLoS One* **7**: e49840.
341 <https://doi.org/10.1371/journal.pone.0049840> (2012).
- 342 24. Scerri, E.M.L. et al. Middle to late Pleistocene human habitation in the Nefud Desert,
343 Saudi Arabia. *Quat Int* **382**, 200-214 (2015).
- 344 25. Lee-Thorp, JA, Sealy, JC, van der Merwe, NJ. Stable carbon isotope ratio differences
345 between bone collagen and bone apatite, and their relationship to diet. *J Arch Sci* **16**, 585-599
346 (1989).
- 347 26. Lee-Thorp, J.A., van der Merwe, N.J., Brain, C.K. Isotopic evidence for dietary
348 differences between two extinct baboon species from Swartkrans (South Africa). *J Hum Evol*
349 **18**, 183-190 (1989).
- 350 27. Levin, N.E., Simpson, S.W., Quade, J., Cerling, T.E., Frost, S.R. 2008. Herbivore enamel
351 carbon isotopic composition and the environmental context of *Ardipithecus* at Gona, Ethiopia.
352 In J.Quade, J.G. Wynn (eds.). *The Geology of Early Humans in the Horn of Africa*. Boulder,
353 Colorado: Geological Society of America Special Paper 446. Pp. 215-234.
- 354 28. Calvin, M., Benson, A.A. The path of carbon in photosynthesis. *Science* **107**, 476-480
355 (1948).
- 356 29. Hatch, M., Slack, C., Johnson, H. Further studies on a new pathway of photosynthesis
357 carbon dioxide fixation in sugarcane and its occurrence in other species. *Biochemical Journal*
358 **102**, 417-422 (1967).
- 359 30. Tieszen, L.L. Natural variations in the carbon isotopes of plants: implications for
360 archaeology, ecology and paleoecology. *J Arch Sci* **18**, 227-248 (1991).
- 361 31. Roberts, P. et al. Fruits of the forest: Human stable isotope ecology and rainforest

- 362 adaptations in Late Pleistocene and Holocene (~ 36 to 3 ka) Sri Lanka. *J Hum Evol* **106**, 102-
363 118 (2017).
- 364 32. Flanagan, L.B., Comstock, J.P., Ehleringer, J.R. Comparison of modelled and observed
365 environmental influences on the stable oxygen and hydrogen isotope composition of leaf
366 water in *Phaseolus vulgaris* L. *Plant Physiol* **96**, 588-596 (1991).
- 367 33. Barbour, M.M. Stable oxygen isotope composition of plant tissue: a review. *Funct Plant*
368 *Biol* **34**, 83-94 (2007).
- 369 34. Levin, NE, Cerling, TE, Passey, BH, Harris, JM, Ehleringer, JR. A stable isotope aridity
370 index for terrestrial environments. *PNAS* **103**, 11201-11205 (2006).
- 371 35. Blumenthal, SA. et al. Aridity and hominin environments. *PNAS* **14**, 7331-7336 (2017).
- 372 36. Balasse, M. Reconstructing dietary and environmental history from enamel isotopic
373 analysis: Time resolution of intra-tooth sequential sampling. *Int J Osteoarch* **12**, 155-165
374 (2002).
- 375 37. Pineda, A. et al. Trampling *versus* cut marks on chemically altered surfaces: an
376 experimental approach and archaeological application at the Barranc de la Boella site (la
377 Canonja, Tarragona, Spain). *J Archaeol Sci* **50**, 84-93 (2014).
- 378 38. Pickering, T.R. et al. Taphonomy of ungulate ribs and the consumption of meat and bone
379 by 1.2-million-year-old hominins at Olduvai Gorge, Tanzania. *J Arch Sci* **40**, 1295-1309
380 (2013).
- 381 39. Sponheimer, M, Lee-Thorp, JA. Isotopic evidence for the diet of an early hominid,
382 *Australopithecus africanus*. *Science* **283**, 368-370 (1999).
- 383 40. Sponheimer, M, Lee-Thorp, JA. The oxygen isotope composition of mammalian enamel
384 carbonate from Morea Estate, South Africa. *Oecologia* **126**, 153-157 (2001).
- 385 41. Cerling, TE. et al. Stable isotopes in elephant hair document migration patterns and diet
386 changes. *PNAS* **103**, 371-373 (2006).
- 387 42. Ingicco, T. et al. Earliest known hominin activity in the Philippines by 709 thousand
388 years ago. *Nature* **557**, 233-237 (2018).
- 389 43. Parker, A. Pleistocene climate change in Arabia: Developing a framework for hominin
390 dispersal over the last 350 ka. In M.D. Petraglia, J. Rose (e.ds). *The Evolution of Human*
391 *Populations in Arabia*. Dordrecht: Springer. Pp. 39-49 (2010).
- 392 44. Drake, N.A., Breeze, P., Parker, A.G. Palaeoclimate in the Saharan and Arabian Deserts
393 during the Middle Palaeolithic and the potential for hominin dispersals. *Quat Int* **300**, 48-61.
394 doi:10.1016/j.quaint.2012.12.018 (2013)
- 395 45. Martínez-Navarro, B. Hippos, pigs, bovids, saber-toothed tigers, monkey, and hominids:
396 dispersals through the Levantine corridor during Late Pliocene and Early Pleistocene. In N
397 Goren-Inbar, JD. Speth. Eds. *Human Palaeoecology in the Levantine Corridor* (Oxbow
398 Books, Oxford, 2004). Pp. 37-52.
- 399 46. Potts, R. Hominin evolution in settings of strong environmental variability. *Quat Sci Rev*
400 **73**, 1-13 (2013).

- 401 47. Delagnes, A. et al. Inland human settlement in southern Arabia 55,000 years ago. New
402 evidence from the Wadi Surdud Middle Paleolithic site complex, western Yemen. *J Hum*
403 *Evol* **63**, 452-474 (2012).
- 404 48. Breeze, P. et al. Prehistory and palaeoenvironments of the western Nefud Desert, Saudi
405 Arabia. *Archaeol Res Asia* **10**, 1-16.
- 406 49. Nash, D. et al. Going the distance: mapping mobility in the Kalahari Desert during the
407 Middle Stone Age through multi-site geochemical provenancing of silcrete artefacts. *J Hum*
408 *Evol* **96**, 113–133 (2016).
- 409 50. Dewar, G, Stewart, BA. Paleoenvironments, sea levels and land use in Namaqualand,
410 South Africa, during MIS 6-2. In S. C. Jones, B. A. Stewart (eds.). *Africa from MIS 6-2:
411 Population dynamics and paleoenvironments* (Dordrecht: Springer, 2016) Pp. 195-212.
- 412 **Method references**
- 413 51. Scerri, EML, Drake, NA, Jennings, R, Groucutt, HS. Earliest evidence for the structure of
414 *Homo sapiens* populations in Africa. *Quat Sci Rev* **101**, 207-216 (2014).
- 415 52. Capaldo, SD, Blumenschine, RJ. A quantitative diagnosis of notches made by
416 hammerstone percussion and carnivore gnawing on bovid long bones. *Am Antiq* **59**, 724-748
417 (1994).
- 418 53. Fisher, JW. Bone surface modifications in zooarchaeology. *J Archaeol Method Th.* **2**, 7-
419 68 (1995).
- 420 54. Domínguez-Rodrigo, M, de Juana, S, Galán, AB, Rodríguez, M. A new protocol to
421 differentiate trampling marks from butchery cut marks. *J Archaeol Sci.* **26**, 2643-2654 (2009).
- 422 55. Galán, AB, Rodríguez, M, de Juana, S, Domínguez-Rodrigo, M. A new experimental
423 study on percussion marks and notches and their bearing on the interpretation of
424 hammerstone-broken faunal assemblages. *J Archaeol Sci* **36**, 776-784 (2009).
- 425 56. Sponheimer, M. et al. Hominins, sedges, and termites: new carbon isotope data from the
426 Sterkfontein valley and Kruger National Park. *J Hum Evol.* **48**, 301-312 (2005).
- 427 57. Lee-Thorp, JA. et al. Isotopic evidence for an early shift to C4 resources by Pliocene
428 hominins in Chad. *PNAS* **109**, 20369 (2012).
- 429 58. R Core Team. 2013. R: A language and environment for statistical computing. R
430 Foundation for Statistical Computing, Vienna, Austria.

431

432 **Methods**

433

434 *Lithic and faunal analysis*

435 Lithic artefacts were recovered from Unit 5 of trench 6. The lithic material and debitage was
436 measured, recorded, and drawn following previously published protocols⁵¹.

437 Fossil identification and analysis was conducted at the Australian National University (ANU)
438 and the University of New South Wales (UNSW), Australia, and facilitated by comparative
439 osteological material. Each specimen was examined by eye and hand-lens (10-20x) and at
440 different angles to identify fine-scale surface modifications that only become apparent at

441 certain angles of light exposure. Bone surface modifications, such as tooth and percussion
442 marks, were analyzed and recorded following standard methodologies for taphonomic
443 analysis of fossil faunal assemblages (e.g. ⁵²⁻⁵³). Cut marks are defined as V-shaped grooves
444 and are often accompanied with features such as shoulder effect, flaking and microstriations⁵⁴,
445 and were considered when analyzing modifications in this study. Markings suspected of
446 being cut marks were further inspected by Scanning Electron Microscopy (SEM) (SI Text 4).
447 Notches were defined as circular to semi-circular breaks in the edge of midshaft fragments
448 and are typically produced by both hominins and large carnivores when exploiting within
449 bone nutrients (i.e. marrow)⁵². Dynamic loading forces associated with hammerstone
450 percussion tend to produce notches that are wider and shallower than those generated by
451 carnivores, allowing notches to be quantitatively differentiated. Notch morphology was
452 determined following the protocol described in Capaldo and Blumenschine⁵² and notches
453 were compared to those generated by carnivores, un-modified hammerstones, and modified
454 hammerstones under experimental settings^{52,55} (Fig. S13) (SI Text 4).

455 *Stable isotope analysis*

456 Tooth enamel samples were selected from the available fauna from deposits at Ti's al Ghadah
457 dated to *c.* 300-500 ka (SI Texts 1 and 2, Table S3). Fossil equids, extinct elephants, and
458 hartebeest were targeted for stable oxygen isotope measurement as abundant obligate
459 drinkers, while *Oryx* sp. comprise the non-obligate drinker sample from the site (SI Text 2).
460 To provide a modern baseline estimate of aridity in Saudi Arabia for these taxa, $\delta^{18}\text{O}$
461 measurements were made on modern equids (*Equus caballus*) (n=4) and camels (*Camelus*
462 *dromedarius*) (n=2) reliant on oasis water and compared to the $\delta^{18}\text{O}$ of modern samples of
463 Arabian oryx (*Oryx leucoryx*) (n=7) from the same region (SI Text 2; Table S4). Sequential
464 $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was also measured on two extinct elephant molars, three equids, and five *Oryx*
465 sp. fossil teeth (SI Texts 1 and 2). Fourier Transform Infrared Spectroscopy (FTIR) was used
466 to assess enamel preservation (SI Text 3).

467 21 samples were selected for stable carbon and oxygen isotope analysis of tooth enamel from
468 the available fossil material from Unit 5 at Ti's al Ghadah. All teeth that could be confidently
469 identified from excavations by the Palaeodeserts team between 2013 and 2014, as well as
470 excavations by the Saudi Arabian Geological Survey in 2011 (Table S3), were sampled. We
471 selected 5 *Oryx* sp., 3 *Equid* sp. and 2 *Palaeoloxodon recki* teeth for additional, sequential
472 analysis based on their completeness and robustness to endure additional sampling (Table S3,
473 Tables S5-S7). The 5 fossil *Oryx* sp. were, in turn, compared to 1 modern *Oryx* sp. (Tables
474 S4, S8) in order to provide a modern baseline for seasonal changes in $\delta^{18}\text{O}$ in this non-
475 obligate drinker.

476 All teeth or teeth fragments were cleaned using air-abrasion to remove any adhering external
477 material. Enamel powder for bulk analysis was obtained using gentle abrasion with a
478 diamond-tipped drill along the full length of the buccal surface in order to ensure a
479 representative measurement for the entire period of enamel formation. For sequential
480 samples, each sample was a 1–2 mm-wide groove perpendicular to the tooth growth axis,
481 through the thickness of the enamel layer. The distance of the base of each sample groove
482 from the enamel/root junction from the furthest sample margin was recorded.

483 All enamel powder was pretreated to remove organic or secondary carbonate contaminants.
484 This consisted of a series of washes in 1.5% sodium hypochlorite for 60 minutes, followed by
485 three rinses in purified H₂O and centrifuging, before 0.1M acetic acid was added for 10

486 minutes, followed by another three rinses in purified H₂O (as per.⁵⁶⁻⁵⁷). Following reaction
487 with 100% phosphoric acid, gases evolved from the samples were analyzed to stable carbon
488 and oxygen isotopic composition using a Thermo Gas Bench 2 connected to a Thermo Delta
489 V Advantage Mass Spectrometer at the Department of Archaeology, Max Planck Institute for
490 the Science of Human History. Carbon and oxygen isotope values were compared against
491 international standards (NBS 19, MERCK) registered by the International Atomic Energy
492 Agency. Replicate analysis of OES standards suggests that machine measurement error is *c.* ±
493 0.1‰ for δ¹³C and ± 0.2‰ for δ¹⁸O. Overall measurement precision was studied through the
494 measurement of repeat extracts from a bovid tooth enamel standard (n=20, ± 0.2‰ for δ¹³C
495 and ± 0.3‰).

496 The relationship between δ¹⁸O and Site and Group (obligate and non-obligate drinkers) was
497 determined using a mixed Site*Group ANOVA comparative test, followed by post-hoc
498 Tukey pair-wise comparisons. Statistical regression analyses were undertaken to discern the
499 statistical correlation between δ¹³C and δ¹⁸O at Ti's al Ghadah. All statistical analyses were
500 conducted using the free program R software⁵⁸.

501 **List of Figures:**

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

506 **Figure 2.** A) chert flakes with dihedral striking platforms (i, iii and iv) and a side retouched
507 flake (ii). B) medium-sized bovid proximal metacarpal (TAG14/121) in cortical (i) and
508 medullary (ii and iii) view. In the inset a wide striae field (white box) is visible adjacent the
509 flake scar (dashed line). A adhering bone flake (arrow) and conchoidal flake scar (dashed
510 line) are visible from the medullary. The refitted piece (iii) exhibits a smooth, oblique
511 fracture pattern indicating the bone was broken while fresh. C) a tibia shaft fragment
512 (TAG14/9235) in cortical (i) and medullary (ii) view. An indeterminate narrow, V-shaped
513 groove with a forked end (arrows) runs parallel to the long axis of the bone. A conchoidal
514 flake scar is present on the medullary surface (dashed line). D) dorsal view (i) of a medium-
515 sized mammalian rib fragment (TAG13/900) with two probable cut marks that run obliquely
516 to the long axis of the rib. Shoulder effect (arrows) is clearly visible in the SEM image (ii). E)
517 a medium-sized mammalian rib fragment (TAG13/133) with multiple parallel grooves
518 running perpendicular to the long axis of the bone and shoulder effect in the form of Hertzian
519 cones (triangles) that are clearly visible in the SEM image (ii). F) a medium-sized bovid
520 metapodial shaft fragment (TAG14/9257) in cortical (ii) and medullary (ii) view with
521 multiple opposing notches and conchoidal flake scars (dashed lines), and numerous carnivore
522 tooth scores (arrows), suggesting the bone was broken open by a large carnivore. G) medium-
523 size mammalian shaft bone flake (TAG13/9134) in medullary (i) and cortical (ii) view.
524 Smooth and oblique fracture pattern indicates the bone was broken while fresh and likely by
525 a dynamic force. The surface exhibits pitting (arrows) and the bone flake has tentatively been
526 attributed to be the result of hammerstone percussion. Solid scale bar = 20 mm. Dashed scale
527 bar = 0.5 mm.

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

530 **Figure 4.** $\delta^{18}\text{O}$ values for non-obligate and obligate drinking taxa at the East African
531 localities of Laikipia (Kenya) and Tsavo (Kenya) reported by Blumenthal et al.³⁵, for modern
532 Saudi Arabia, and for the Middle Pleistocene Ti's al Ghadah (TAG) (Saudi Arabia)
533 assemblage.

534 **Figure 5.** Sequential $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements for *Oryx* sp. samples TAG 1551, TAG
535 1541, TAG 149, TAG 942, and TAG 944 from the Middle Pleistocene levels of T'is al
536 Ghadah and one modern *Oryx* sp. sample from the Mahazat as-Sayd Protected Area.

537 **Figure 6.** Sequential $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements for equid samples SGS180, SGS57 and
538 SGS1094 and *Palaeoloxodon reckii* samples TAG14 301 and TAG14 129 from the Middle
539 Pleistocene levels of T'is al Ghadah.