

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

Patrick Roberts^{1*}, Mathew Stewart^{2*}, Abdulaziz N. Alagaili³, Paul Breeze⁴, Ian Candy⁵, Nick Drake⁴, Huw S. Groucutt^{6,1}, Eleanor M.L. Scerri^{6,1}, Julia Lee-Thorp⁶, Julien Louys⁷, Iyad S. Zalmout⁸, Yahya S. A. Al-Mufarreah⁸, Jana Zech¹, Abdullah M. Alsharekh⁹, Abdulaziz al Omari¹⁰, Nicole Boivin¹, Michael Petraglia^{1,11*}

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

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

³Mammals Researches Chair, Zoology Department, King Saudi University, Riyadh, Saudi Arabia.

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

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

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

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

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

⁹King Saud University, Saudi Arabia.

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

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

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

Abstract:

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

Introduction

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

In spite of its crucial geographic position at the interface of Africa and Eurasia, the Arabian Peninsula has remained remarkably absent from adaptive models of Pleistocene hominin expansions until relatively recently, owing to a lack of well-constrained archaeological and palaeoecological data. Climate modeling¹⁰, speleothem records¹¹, palaeontological findings¹²⁻¹⁵, and geomorphological studies of palaeolake records¹⁶⁻¹⁷ have been used to argue that at intervals in the past, notably during interglacials, the harsh, hyper-arid deserts that cover much of Arabia today were replaced by 'moister' and 'greener' conditions more hospitable to foraging occupation¹⁸⁻¹⁹. Furthermore, the find of a *H. sapiens* phalanx, in association with Middle Palaeolithic stone tools, at the site of Al Wusta dated to c. 90 ka provides definitive evidence for the early presence of our species in the interior of the Arabian Peninsula²⁰. There have also been suggestions that stone tools in the Arabian interior are associated with an earlier period of Middle Pleistocene hominin dispersal²¹⁻²⁴. However, despite the significance of climate and environmental change for hominin dispersal into the region, there has been no direct means of determining what 'wetter' represents in the context of regional ecology nor definitive identification of Middle Pleistocene hominin presence.

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

There has also been no way of analyzing, in detail, the vegetation and relative aridity associated with the Middle Pleistocene fossil assemblage, and potential hominin presence, at 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 diets²⁵⁻²⁷. Most terrestrial plants, including trees,
93 herbs, shrubs, and shade-loving grasses follow the C_3 photosynthetic pathway²⁸. C_4
94 photosynthesis is followed by most arid-adapted grasses and some sedges²⁹. C_3 and C_4 plants
95 have distinct and non-overlapping $\delta^{13}\text{C}$ values³⁰ 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 Arabia¹². In faunal diets, prior to the impact of significant
98 fossil fuel emission, average herbivore $\delta^{13}\text{C}$ values for C_3 and C_4 reliance are c. -12‰ and ~
99 0‰, respectively²⁵⁻²⁷ (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 time¹⁰. 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}O -enriched. This effect is even stronger in plants
107 due to the process of evapo-transpiration³²⁻³³. 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 palaeoaridity³⁴⁻³⁵ 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 formation³⁶. The preservation of all
115 samples was also checked using FTIR as per³¹ (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 basin¹⁴ (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 Nefud¹⁸⁻²⁰. At the MIS 5
129 site of Al Wusta, 3km from Ti's al Ghaddah, similar lacustrine chert was the main raw
130 material used by hominins²⁰. 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 alteration³⁷. The direction and location of the markings is consistent with cut marks
141 produced during filleting of meat from around the rib³⁸. 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 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 system¹⁰. The
154 uniformity of C_4 consumption by all animals suggests the presence of extensive, productive
155 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^{34-35,39-40}. 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 $n=5$)³⁵ (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 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 C_4 vegetation in the western Nefud Desert or animal movements tracking
184 seasonal availability of 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

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

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

Discussion

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

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

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

The data presented here highlight the presence of abundant C₄ grasslands and aridity levels somewhat similar to those found in East Africa today. The comparison of obligate and non-obligate drinker stable oxygen isotopes has been little-developed beyond Africa, yet we hope to have shown here that this methodology could and should be applied to other parts of Asia, such as the Thar Desert, central Asia, and eastern Asia in order to develop more detailed understandings of hominin adaptations to semi-arid and arid environments in these parts of the world. The data reported here also fits with palaeoecological reconstructions based on the fossil taxa identified at Ti's al Ghadah¹²⁻¹⁵ (Supplementary Table 2). The presence of various grassland taxa (*Palaeoloxodon* and an alcelaphine), fish and birds with strong affinities toward water (e.g. *Anas* and *Tachybaptus*) imply the presence of expansive grasses and large perennial water sources¹²⁻¹⁵ (Supplementary Figure 3; Supplementary Table 2). The presence of a large felid (*Panthera gombaszoegensis*) and hyena indicate that the western Nefud Desert was also host to a substantial prey-biomass¹³⁻¹⁴. Alongside evidence from sequential isotopic analysis of the wide-ranging *Palaeoloxodon recki* reported here, attainment of lake sequences should also help to clarify wider, regional environmental trends during the earliest arrival of hominins into Arabia. Overall, however, Early and Middle Pleistocene hominin populations would seemingly have been able to extend not only into the Levant, but also deep into the Arabian Peninsula, potentially making use of access to a combination of African and Eurasian medium and large sized mammals, as well as similar grassland habitats^{4,15,45}.

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

Methods

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 protocols⁵¹.

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. ⁵²⁻⁵³). Cut marks are defined as V-shaped grooves
291 and are often accompanied with features such as shoulder effect, flaking and microstriations⁵⁴,
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)⁵². 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 Blumenschine⁵² and notches were compared to those generated by carnivores, un-modified
301 hammerstones, and modified hammerstones under experimental settings^{52,55} (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

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

All enamel powder was pretreated to remove organic or secondary carbonate contaminants. This consisted of a series of washes in 1.5% sodium hypochlorite for 60 minutes, followed by three rinses in purified H₂O and centrifuging, before 0.1M acetic acid was added for 10 minutes, followed by another three rinses in purified H₂O (as per.⁵⁶⁻⁵⁷). Following reaction with 100% phosphoric acid, gases evolved from the samples were analyzed to stable carbon and oxygen isotopic composition using a Thermo Gas Bench 2 connected to a Thermo Delta V Advantage Mass Spectrometer at the Department of Archaeology, Max Planck Institute for the Science of Human History. Carbon and oxygen isotope values were compared against international standards (NBS 19, MERCK) registered by the International Atomic Energy Agency. Replicate analysis of OES standards suggests that machine measurement error is *c.* $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.2\text{‰}$ for $\delta^{18}\text{O}$. Overall measurement precision was studied through the measurement of repeat extracts from a bovid tooth enamel standard ($n=20$, $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.3\text{‰}$).

The relationship between $\delta^{18}\text{O}$ and Site and Group (obligate and non-obligate drinkers) was determined using a mixed Site*Group ANOVA comparative test, followed by post-hoc Tukey pair-wise comparisons. Statistical regression analyses were undertaken to discern the statistical correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ at Ti's al Ghadah. All statistical analyses were conducted using the free program R software⁵⁸.

Data availability

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

Acknowledgments

The authors declare no conflict of interest.

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

Author contributions:

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

372 **References:**

- 373
- 374 1. Gamble, C. *Timewalkers: The prehistory of global colonization* (Alan Sutton Press, 1993).
- 375 2. Gamble, C. *Settling the earth: the archaeology of deep human history* (Cambridge
- 376 University Press, 2013).
- 377 3. Roberts, P., Stewart, B.A. (2018). Defining the ‘generalist-specialist’ niche for Pleistocene
- 378 *Homo sapiens*. *Nature Human Behaviour*.
- 379 4. Dennell, RW, Roebroeks, W. Out of Africa: An Asian perspective on early human
- 380 dispersal from Africa. *Nature* **438**, 1099-1104 (2005).
- 381 5. Joordens, JCA. et al. *Homo erectus* at Trinil on Java used shells for tool production and
- 382 engraving. *Nature* **518**, 228-231 (2016).
- 383 6. Hoffman, DL. Et al. U-Th dating of carbonate crusts reveals Neandertal origin of Iberian
- 384 cave art. *Science* **359**, 912-915 (2018).
- 385 7. Morwood, M.J. et al. Fission track age of stone tools and fossils on the east Indonesian
- 386 island of Flores. *Nature* **392**: 173-176.
- 387 8. Zhu, RX. et al. Early evidence of the genus *Homo* in East Asia. *J Hum Evol* **55**, 1075-1085
- 388 (2008).
- 389 9. Parfitt, SA. et al. Early Pleistocene human occupation at the edge of the boreal zone in
- 390 northwest Europe. *Nature* **466**, 229–233 (2010).
- 391 10. Jennings, RP. et al. The greening of Arabia: Multiple opportunities for human occupation
- 392 in the Arabian Peninsula during the Late Pleistocene inferred from an ensemble of climate
- 393 model simulations. *Quat Int* **205**, 181-199 (2015).
- 394 11. Fleitmann, D, Burns, SJ, Neff, U, Mangini, A, Matter, A. Changing moisture sources over
- 395 the last 333,000 years in Northern Oman from fluid-inclusion evidence in speleothems. *Quat*
- 396 *Res* **60**, 223-232 (2003).
- 397 12. Thomas, H. et al. First Pleistocene faunas from the Arabian peninsula: an Nefu desert,
- 398 Saudi Arabia. *Compte Rendus* **326**, 145-152 (1998).
- 399 13. Stimpson, CM. et al. Stratified Pleistocene vertebrates with a new record of a jaguar-sized
- 400 pantherine (*Panthera* cf. *gombaszogensis*) from northern Saudi Arabia. *Quat Int* **382**, 168-
- 401 180 (2015).
- 402 14. Stimpson, CM. et al. Middle Pleistocene vertebrate fossils from the Nefud Desert, Saudi
- 403 Arabia: implications for biogeography and palaeoecology. *Quat Sci Rev* **143**, 13-36 (2016).
- 404 15. Stewart, M. et al. Middle and Late Pleistocene mammal fossils of Arabia and surrounding
- 405 regions: Implications for biogeography and hominin dispersals. *Quat Int*,
- 406 <https://doi.org/10.1016/j.quaint.2017.11.052> (2017).
- 407 16. Rosenberg, TM. et al. Middle and Late Pleistocene humid periods recorded in palaeolake
- 408 deposits of the Nafud desert, Saudi Arabia. *Quat Sci Rev* **70**, 109-123 (2013).
- 409 17. Parton, A. et al. Alluvial fan records from southeast Arabia reveal multiple windows for
- 410 human dispersal. *Geology* **43**, 298 (2015).

18. Groucutt, HS. et al. Human occupation of the Arabian Empty Quarter during MIS 5: evidence from Mundafan Al-Buhayrah, Saudi Arabia. *Quat Sci Rev* **119**, 116-135 (2015).
19. Breeze, PS. et al. Palaeohydrological corridors for hominin dispersals in the Middle East ~250-70,000 years ago. *Quat Sci Rev* **144**, 155-185 (2016).
20. Groucutt, HS. et al. *Homo sapiens* in Arabia by 85,000 years ago. *Nat Ecol Evol*, doi: 10.1038/s41559-018-0518-2
21. Armitage, SJ. et al. The southern route “out of Africa”: evidence for an early expansion of modern humans into Arabia. *Science* **331**, 453-456 (2011).
22. Petraglia, M. et al. Middle Paleolithic occupation on a Marine Isotope Stage 5 lakeshore in the Nefud Desert, Saudi Arabia. *Quat Sci Rev* **30**, 1555-1559 (2011).
23. Petraglia, M. et al. Hominin Dispersal into the Nefud Desert and middle palaeolithic settlement along the Jubbah Palaeolake, Northern Arabia. *PLoS One* **7**: e49840. <https://doi.org/10.1371/journal.pone.0049840> (2012).
24. Scerri, E.M.L. et al. Middle to late Pleistocene human habitation in the Nefud Desert, Saudi Arabia. *Quat Int* **382**, 200-214 (2015).
25. Lee-Thorp, JA, Sealy, JC, van der Merwe, NJ. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. *J Arch Sci* **16**, 585-599 (1989).
26. Lee-Thorp, J.A., van der Merwe, N.J., Brain, C.K. Isotopic evidence for dietary differences between two extinct baboon species from Swartkrans (South Africa). *J Hum Evol* **18**, 183-190 (1989).
27. Levin, N.E., Simpson, S.W., Quade, J., Cerling, T.E., Frost, S.R. 2008. Herbivore enamel carbon isotopic composition and the environmental context of *Ardipithecus* at Gona, Ethiopia. In J.Quade, J.G. Wynn (eds.). *The Geology of Early Humans in the Horn of Africa*. Boulder, Colorado: Geological Society of America Special Paper 446. Pp. 215-234.
28. Calvin, M., Benson, A.A. The path of carbon in photosynthesis. *Science* **107**, 476-480 (1948).
29. Hatch, M., Slack, C., Johnson, H. Further studies on a new pathway of photosynthesis carbon dioxide fixation in sugarcane and its occurrence in other species. *Biochemical Journal* **102**, 417-422 (1967).
30. Tieszen, L.L. Natural variations in the carbon isotopes of plants: implications for archaeology, ecology and paleoecology. *J Arch Sci* **18**, 227-248 (1991).
31. Roberts, P. et al. Fruits of the forest: Human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene (~ 36 to 3 ka) Sri Lanka. *J Hum Evol* **106**, 102-118 (2017).
32. Flanagan, L.B., Comstock, J.P., Ehleringer, J.R. Comparison of modelled and observed environmental influences on the stable oxygen and hydrogen isotope composition of leaf water in *Phaseolus vulgaris* L. *Plant Physiol* **96**, 588-596 (1991).
33. Barbour, M.M. Stable oxygen isotope composition of plant tissue: a review. *Funct Plant Biol* **34**, 83-94 (2007).

- 451 34. Levin, NE, Cerling, TE, Passey, BH, Harris, JM, Ehleringer, JR. A stable isotope aridity
452 index for terrestrial environments. *PNAS* **103**, 11201-11205 (2006).
- 453 35. Blumenthal, SA. et al. Aridity and hominin environments. *PNAS* **14**, 7331-7336 (2017).
- 454 36. Balasse, M. Reconstructing dietary and environmental history from enamel isotopic
455 analysis: Time resolution of intra-tooth sequential sampling. *Int J Osteoarch* **12**, 155-165
456 (2002).
- 457 37. Pineda, A. et al. Trampling *versus* cut marks on chemically altered surfaces: an
458 experimental approach and archaeological application at the Barranc de la Boella site (la
459 Canonja, Tarragona, Spain). *J Archaeol Sci* **50**, 84-93 (2014).
- 460 38. Pickering, T.R. et al. Taphonomy of ungulate ribs and the consumption of meat and bone
461 by 1.2-million-year-old hominins at Olduvai Gorge, Tanzania. *J Arch Sci* **40**, 1295-1309
462 (2013).
- 463 39. Sponheimer, M, Lee-Thorp, JA. Isotopic evidence for the diet of an early hominid,
464 *Australopithecus africanus*. *Science* **283**, 368-370 (1999).
- 465 40. Sponheimer, M, Lee-Thorp, JA. The oxygen isotope composition of mammalian enamel
466 carbonate from Morea Estate, South Africa. *Oecologia* **126**, 153-157 (2001).
- 467 41. Cerling, TE. et al. Stable isotopes in elephant hair document migration patterns and diet
468 changes. *PNAS* **103**, 371-373 (2006).
- 469 42. Ingicco, T. et al. Earliest known hominin activity in the Philippines by 709 thousand
470 years ago. *Nature* **557**, 233-237 (2018).
- 471 43. Parker, A. Pleistocene climate change in Arabia: Developing a framework for hominin
472 dispersal over the last 350 ka. In M.D. Petraglia, J. Rose (e.ds). *The Evolution of Human*
473 *Populations in Arabia*. Dordrecht: Springer. Pp. 39-49 (2010).
- 474 44. Drake, N.A., Breeze, P., Parker, A.G. Palaeoclimate in the Saharan and Arabian Deserts
475 during the Middle Palaeolithic and the potential for hominin dispersals. *Quat Int* **300**, 48–61.
476 doi:10.1016/j.quaint.2012.12.018 (2013)
- 477 45. Martínez-Navarro, B. Hippos, pigs, bovids, saber-toothed tigers, monkey, and hominids:
478 dispersals through the Levantine corridor during Late Pliocene and Early Pleistocene. In N
479 Goren-Inbar, JD. Speth. Eds. *Human Palaeoecology in the Levantine Corridor* (Oxbow
480 Books, Oxford, 2004). Pp. 37-52.
- 481 46. Potts, R. Hominin evolution in settings of strong environmental variability. *Quat Sci Rev*
482 **73**, 1-13 (2013).
- 483 47. Delagnes, A. et al. Inland human settlement in southern Arabia 55,000 years ago. New
484 evidence from the Wadi Surdud Middle Paleolithic site complex, western Yemen. *J Hum*
485 *Evol* **63**, 452-474 (2012).
- 486 48. Breeze, P. et al. Prehistory and palaeoenvironments of the western Nefud Desert, Saudi
487 Arabia. *Archaeol Res Asia* **10**, 1-16.
- 488 49. Nash, D. et al. Going the distance: mapping mobility in the Kalahari Desert during the
489 Middle Stone Age through multi-site geochemical provenancing of silcrete artefacts. *J Hum*
490 *Evol* **96**, 113–133 (2016).

- 491 50. Dewar, G, Stewart, BA. Paleoenvironments, sea levels and land use in Namaqualand,
 492 South Africa, during MIS 6-2. In S. C. Jones, B. A. Stewart (eds.). *Africa from MIS 6-2:
 493 Population dynamics and paleoenvironments* (Dordrecht: Springer, 2016) Pp. 195-212.
- 494 **Method references**
- 495 51. Scerri, EML, Drake, NA, Jennings, R, Groucutt, HS. Earliest evidence for the structure of
 496 Homo sapiens populations in Africa. *Quat Sci Rev* **101**, 207-216 (2014).
- 497 52. Capaldo, SD, Blumenschine, RJ. A quantitative diagnosis of notches made by
 498 hammerstone percussion and carnivore gnawing on bovid long bones. *Am Antiq* **59**, 724-748
 499 (1994).
- 500 53. Fisher, JW. Bone surface modifications in zooarchaeology. *J Archaeol Method Th.* **2**, 7-
 501 68 (1995).
- 502 54. Domínguez-Rodrigo, M, de Juana, S, Galán, AB, Rodríguez, M. A new protocol to
 503 differentiate trampling marks from butchery cut marks. *J Archaeol Sci.* **26**, 2643-2654 (2009).
- 504 55. Galán, AB, Rodríguez, M, de Juana, S, Domínguez-Rodrigo, M. A new experimental
 505 study on percussion marks and notches and their bearing on the interpretation of
 506 hammerstone-broken faunal assemblages. *J Archaeol Sci* **36**, 776-784 (2009).
- 507 56. Sponheimer, M. et al. Hominins, sedges, and termites: new carbon isotope data from the
 508 Sterkfontein valley and Kruger National Park. *J Hum Evol.* **48**, 301-312 (2005).
- 509 57. Lee-Thorp, JA. et al. Isotopic evidence for an early shift to C4 resources by Pliocene
 510 hominins in Chad. *PNAS* **109**, 20369 (2012).
- 511 58. R Core Team. 2013. R: A language and environment for statistical computing. R
 512 Foundation for Statistical Computing, Vienna, Austria.

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.

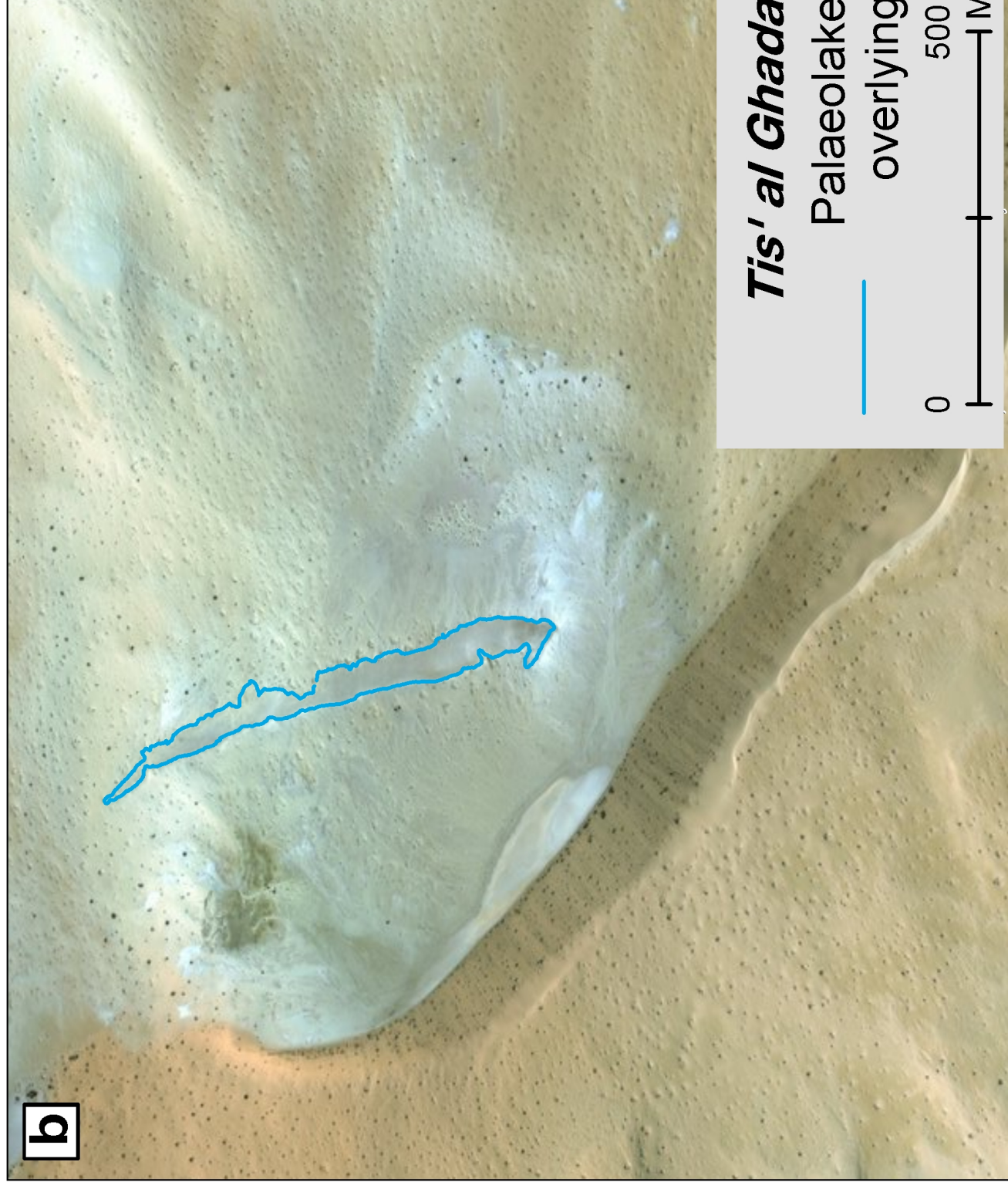
518 **Figure 2.** A) chert flakes with dihedral striking platforms (i, iii and iv) and a side retouched
519 flake (ii). B) medium-sized bovid proximal metacarpal (TAG14/121) in cortical (i) and
520 medullary (ii and iii) view. In the inset a wide striae field (white box) is visible adjacent the
521 flake 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-
527 sized mammalian rib fragment (TAG13/900) with two probable cut marks that run obliquely
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
532 metapodial shaft fragment (TAG14/9257) in cortical (ii) and medullary (ii) view with
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.

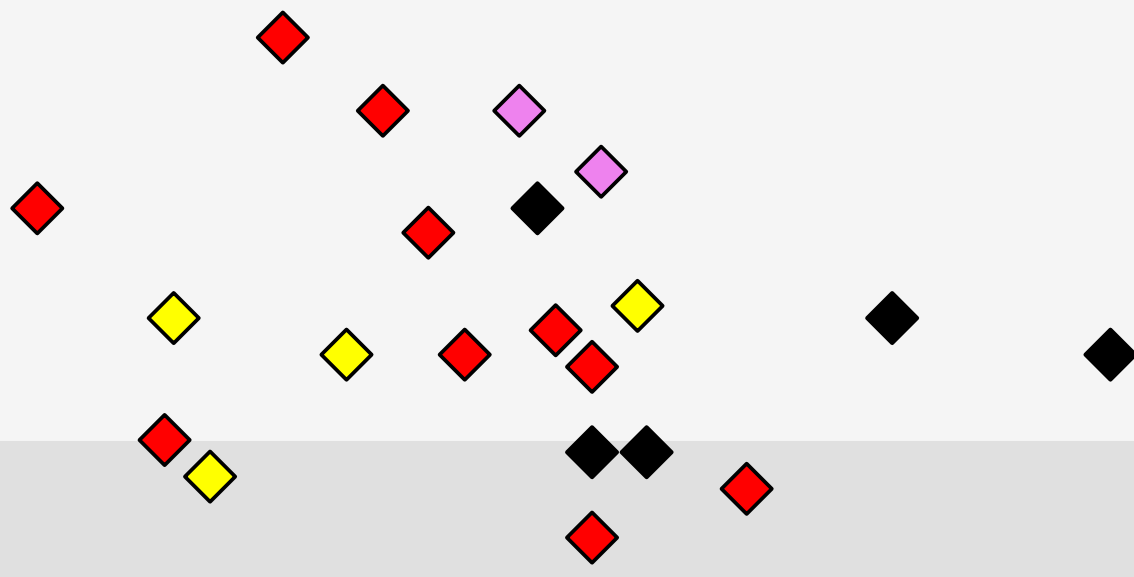
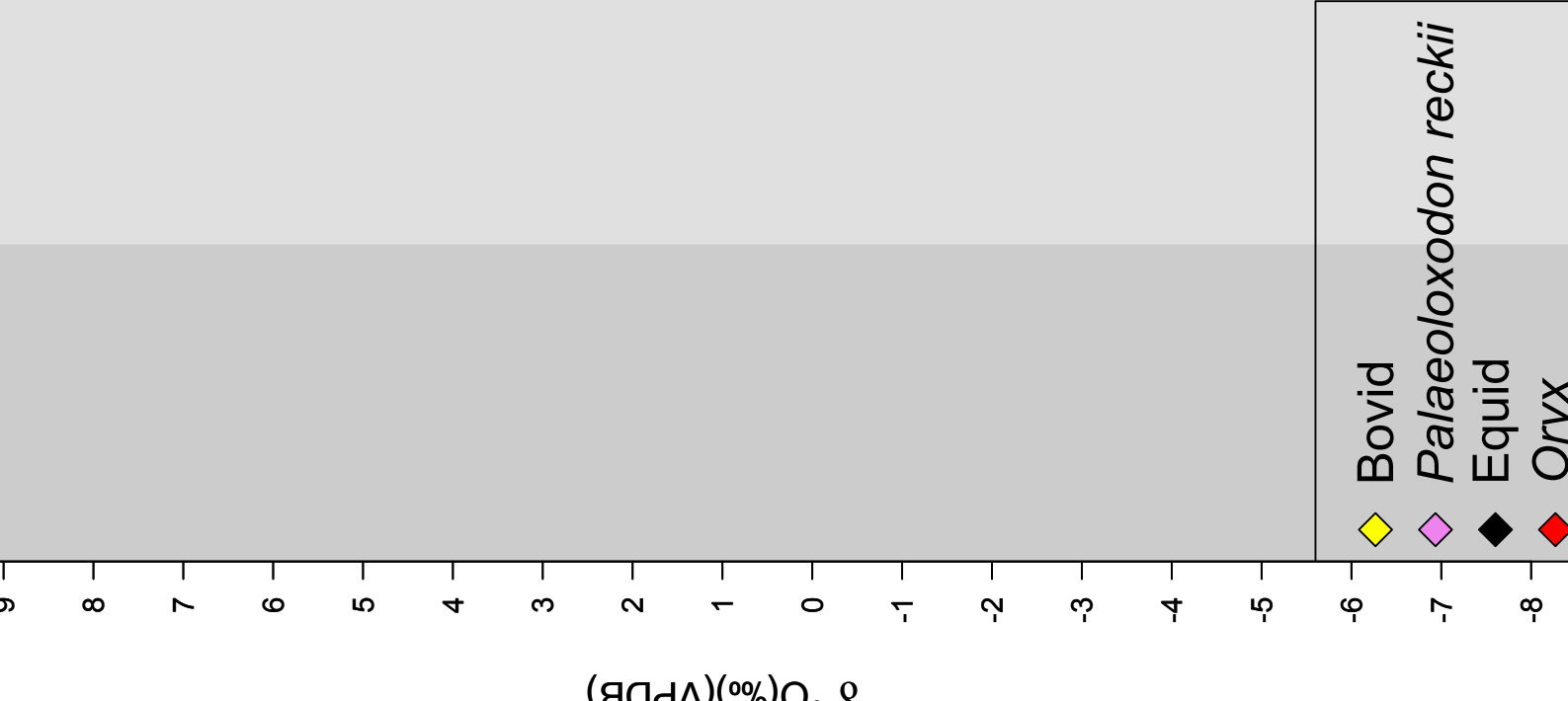
542 **Figure 4.** $\delta^{18}\text{O}$ values for non-obligate and obligate drinking taxa at the East African
543 localities of Laikipia (Kenya) and Tsavo (Kenya) reported by Blumenthal et al.³⁵, for modern
544 Saudi Arabia, and for the Middle Pleistocene Ti's al Ghadah (TAG) (Saudi Arabia)
545 assemblage.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

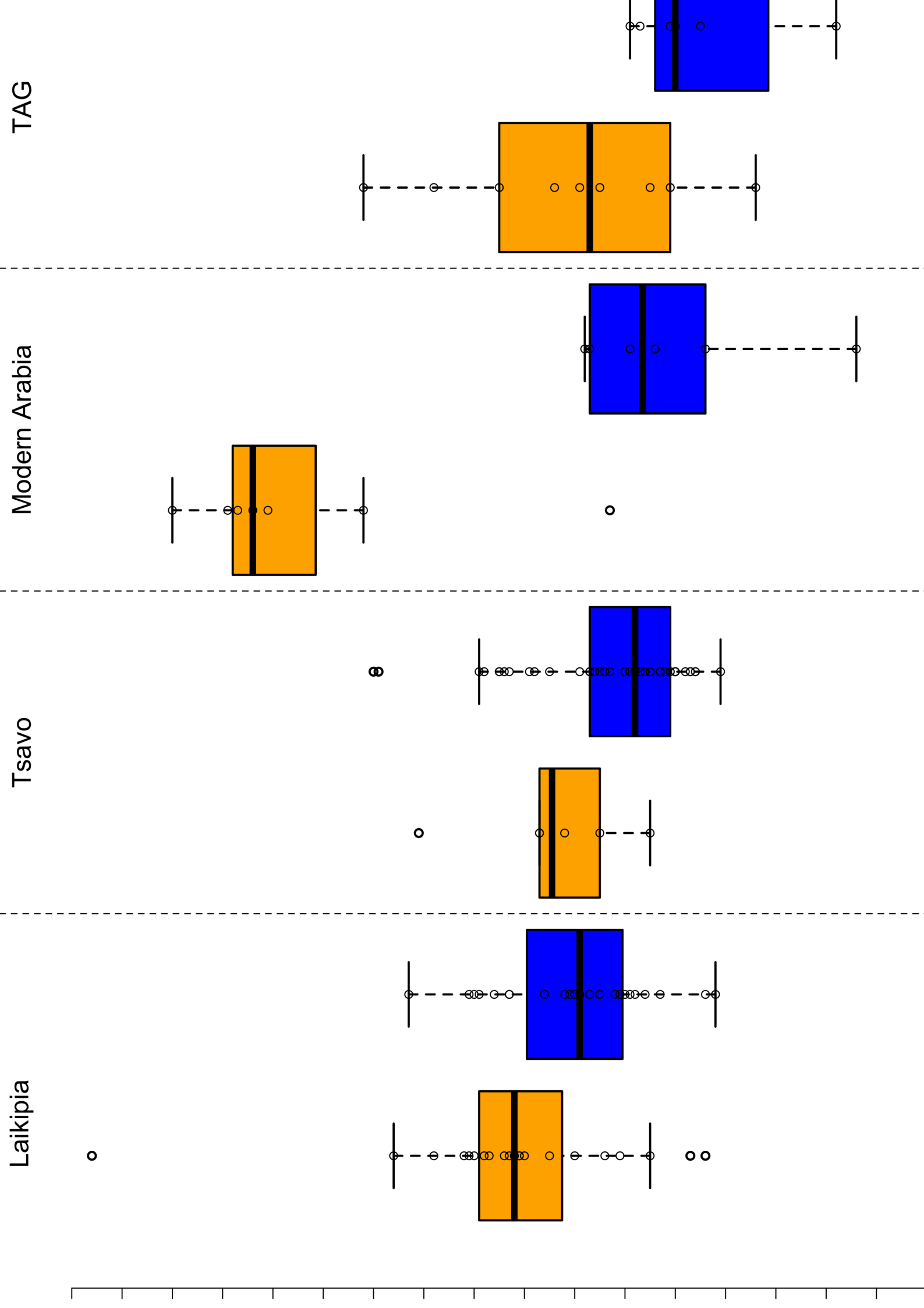
548 **Figure 5.** Sequential $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements for *Oryx* sp. samples TAG 1551, TAG
549 1541, TAG 149, TAG 942, and TAG 944 from the Middle Pleistocene levels of T'is al
550 Ghadah and one modern *Oryx* sp. sample from the Mahazat as-Sayd Protected Area. VPDB,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

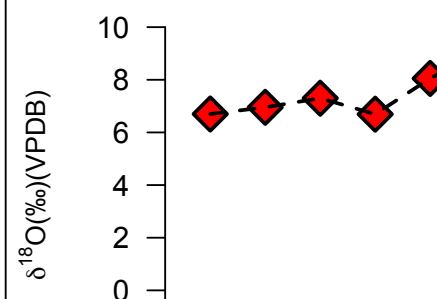
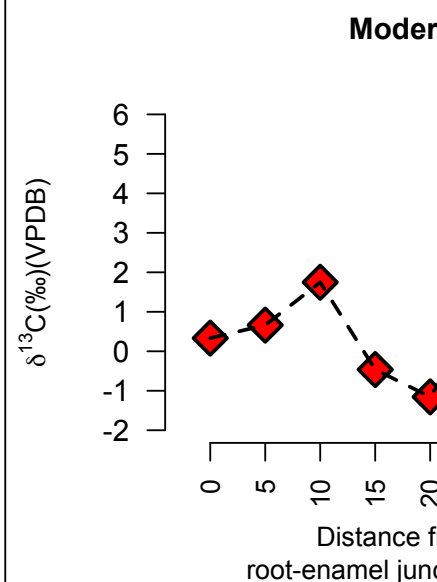
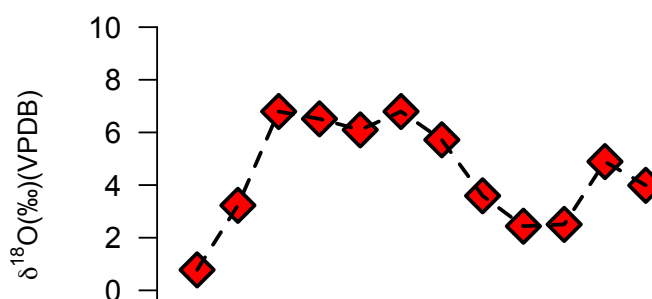
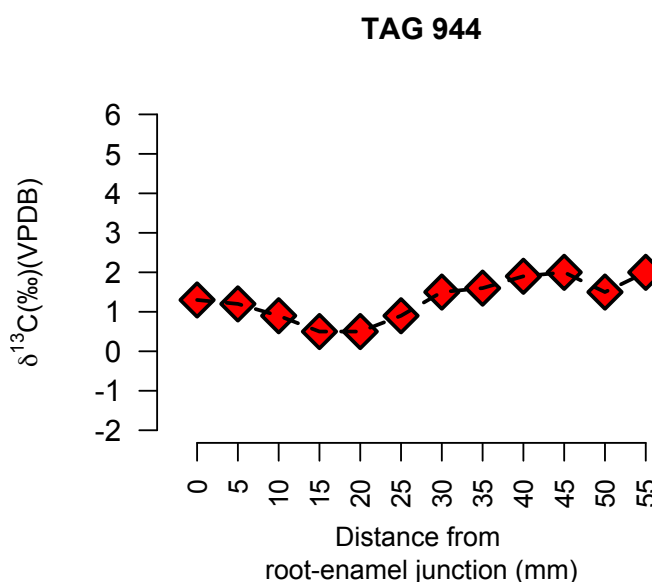
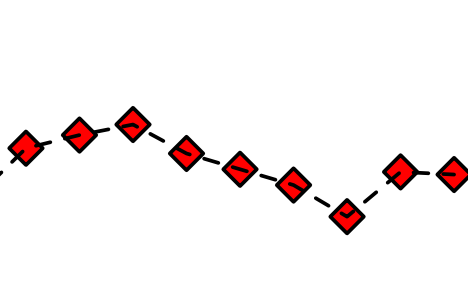
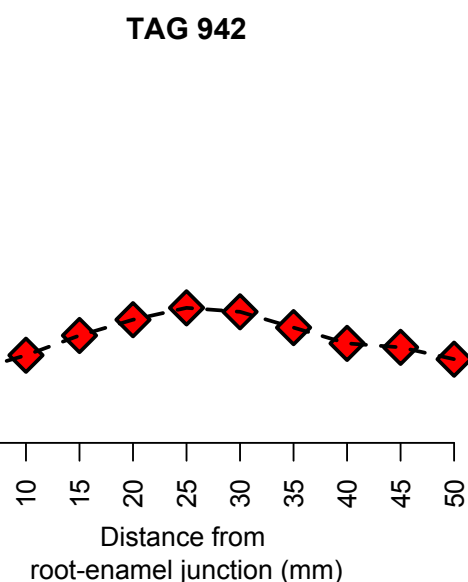
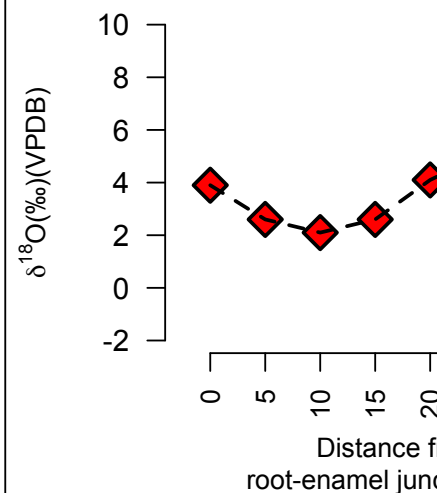
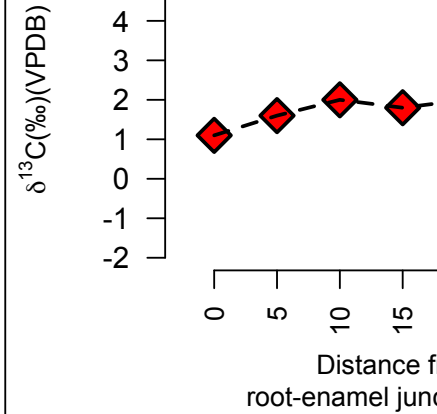
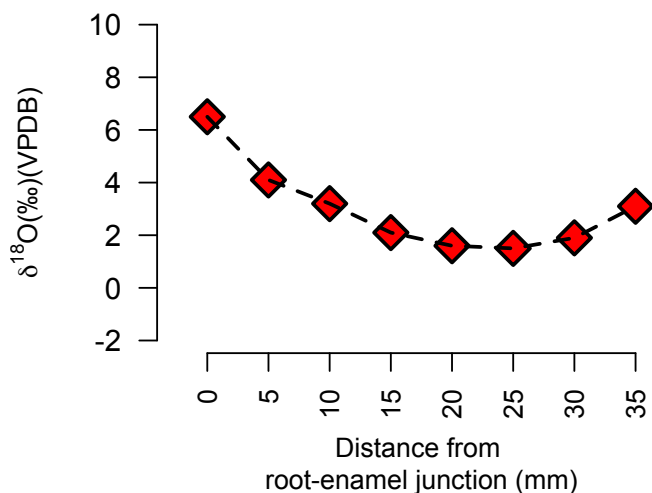
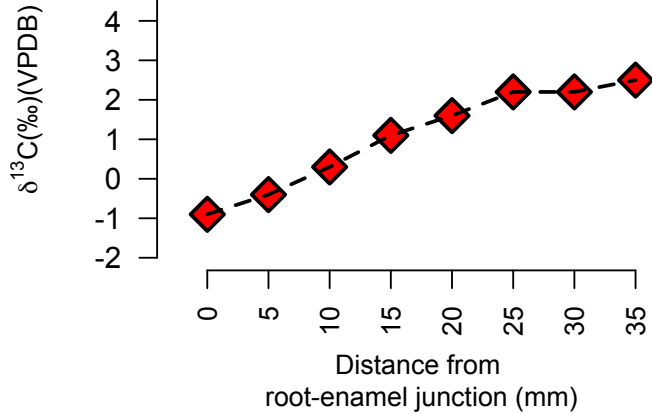
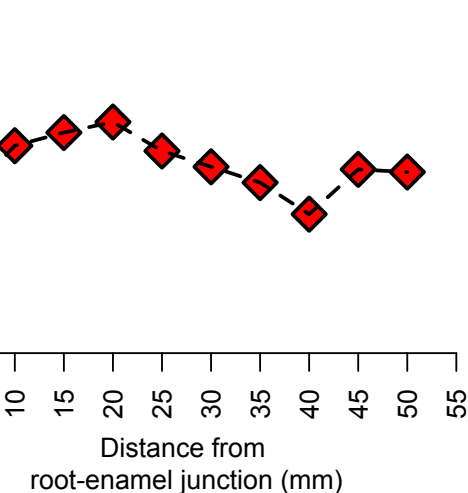
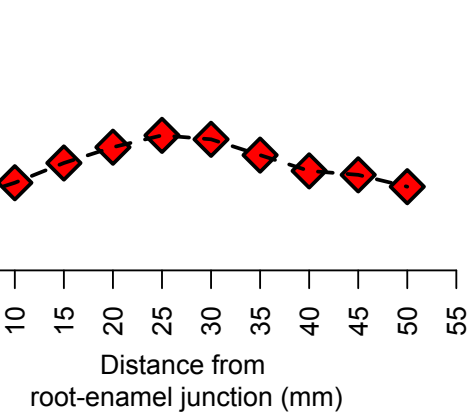
552 **Figure 6.** Sequential $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements for equid samples SGS180, SGS57 and
553 SGS1094 and *Palaoloxodon reckii* samples TAG14 301 and TAG14 129 from the Middle
554 Pleistocene levels of T'is al Ghadah. VPDB, Vienna PeeDee Belemnite.

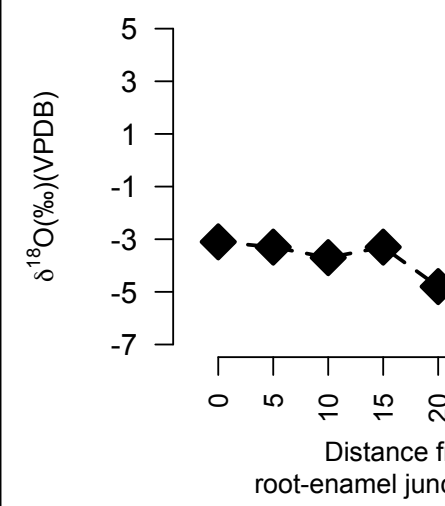
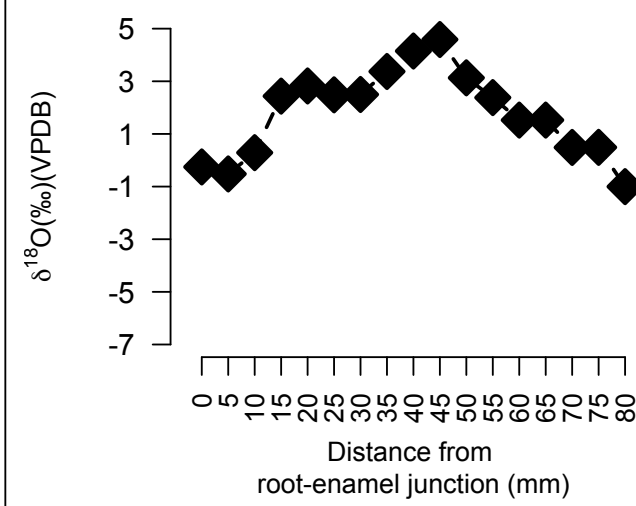
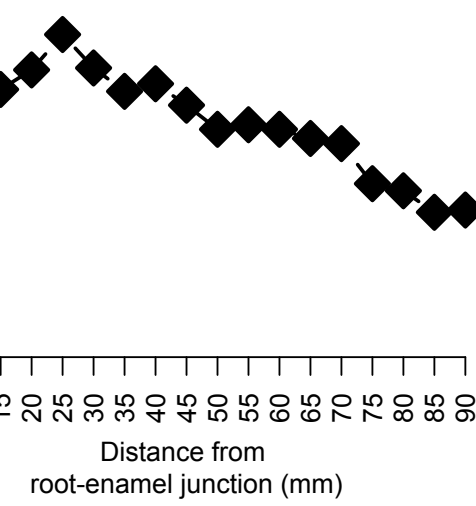
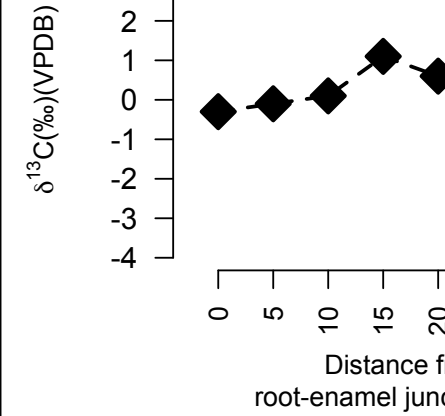
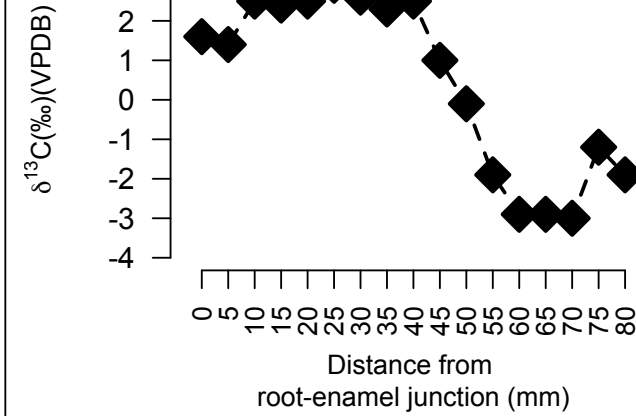
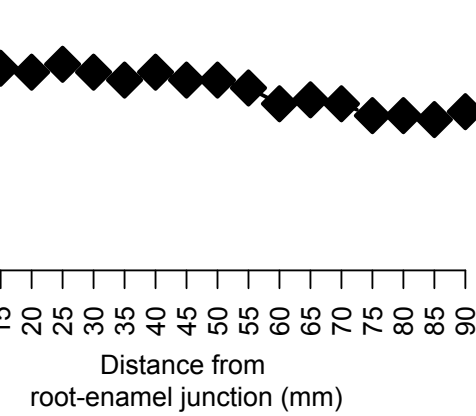






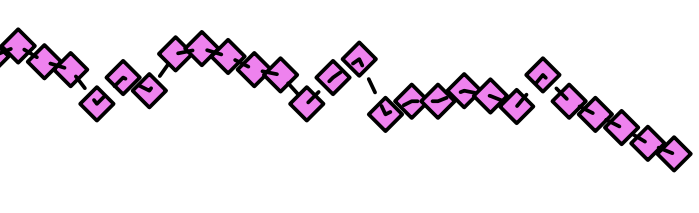
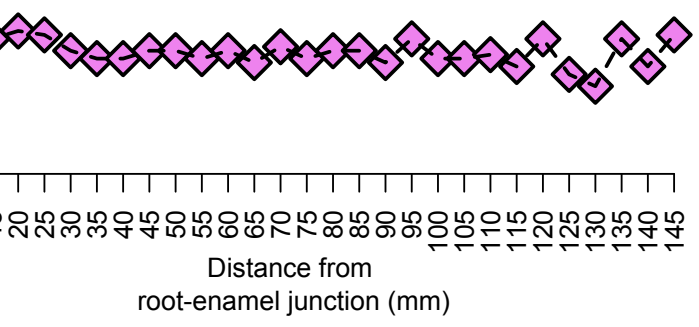






odon

TAG14 301



TAG14 129

