1   **Pleistocene and Holocene palaeoclimates in the Gebel Akhdar (Libya) estimated using**

2   **herbivore tooth enamel oxygen isotope compositions**

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Abstract

The palaeoclimate of the Gebel Akhdar massif, in Cyrenaica, northeast Libya, is investigated using the stable oxygen isotope ratio ($\delta^{18}O$) of herbivore tooth enamel from the archaeological faunal assemblages of the Haua Fteah and Hagfet ed Dabba caves. Samples accumulated through human activity at the sites, thus climatic interpretations are in direct chronological association with periods of human presence in the local landscape. Wild *Ammotragus lervia* (Barbary sheep) and *Bos* sp. (auroch), and domestic *Ovis* sp. and *Capra* sp. from the Levalloiso-Mousterian (≥73.3 to 43.5 ka) to the Neolithic (~9.3. to 5.4 ka) cultural phases are analysed. Results indicate that the most arid environment represented by the samples occurred at ~32ka, when populations associated with Dabban lithic assemblages were present within the region. Climatic instability increased during oxygen isotope stage 2. Consistent with other palaeoenvironmental investigations in the Gebel Akhdar, there is no evidence for hyper-arid events during the last glacial and surface water, most probably in the form of local springs, was available throughout the time periods considered. Overall, results indicate that different cultural groups occupied the Gebel Akhdar landscape under different climatic conditions, but that climate variations appear to have been of lower magnitude than those that occurred at inland North African locations. These reconstructions provide further support to the theory that the Gebel Akhdar may have served as a *refugium* for human populations in North Africa during times of global climatic extremes.

Key words: Haua Fteah; North Africa; stable isotopes; *refugium*; caprid

1. Introduction

Climate plays a key role in determining human biogeography through influencing the distribution and composition of floral and faunal communities within a region, and in turn the food, water and raw material resources available to human populations (Cox et al., 1988; Eeley et al., 1999; Snyder and Tartowski, 2006). While it is well evidenced that the millennial-scale climatic oscillations that occurred throughout the last glacial cycle manifested as wet-dry alternations in the North African environment (e.g. Pachur and Rottinger, 1997; Ghoneim et al., 2007; Drake et al., 2011), variations that occurred at resolutions relevant to human resource exploitation (sub-annual to decadal) are less well understood. This is particularly the case for the North African coast where there is a notable deficit in high-resolution terrestrial climate information.

Understanding the climate of North Africa is important when considering the history of human populations in the region. Archaeological archives from across the continent indicate variations in population densities and distributions, subsistence strategies, and technological and cultural practices during the late Pleistocene and Holocene, which may have occurred in step with climatic variations (Cremaschi and di Lernia, 1999; Garcea, 2006; Bouzouggar et al., 2007; Scerri, 2013). Following the widespread distribution throughout North Africa of Middle Palaeolithic/Middle Stone Age hunter-gatherer groups during and immediately after oxygen isotope stage (OIS) 5, during OIS 3 and 2 there appears to have been considerable depopulation of the continental interior potentially in response to increasing aridity (Petit-Maire, 1991; Cremaschi et al., 1998; Castañeda et al., 2009; Cancellieri and di Lernia, 2013). This broadly coincided with an increased human presence in some North African coastal regions, and technological changes dating to this time period (termed the Iberomaurusian/Oranian) have been interpreted as possible adaptations to aridity (Irish, 2000; Barton et al., 2007; Bouzouggar et al., 2008). As the climate became increasingly less arid during the late glacial and early Holocene, populations spread further into the North

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59   African continent once more and there is evidence for wild plant exploitation and the

60   management of wild animals in the central Sahara, an increase in marine resource

61   exploitation along the coast, and later the appearance of domestic caprids and bovids

62   throughout the region (Cremaschi and di Lernia, 1999; di Lernia, 2001; Kuper and Kröpelin,

63   2006; di Lernia et al., 2012).

64   However, while many of these changes have been interpreted as responses to

65   variations in climate, there are few archives from which palaeoclimatic conditions in direct

66   chronological association with human activities can be established. The Gebel Akhdar in

67   northeastern Libya presents one such opportunity. The region's archaeological record

68   indicates people were present in the region during each of the OISs of the last glacial-

69   interglacial cycle, albeit likely in varying numbers and not necessarily continuously

70   (McBurney, 1967; Barker et al., 2007; 2008; 2009; 2010; 2012; Jones et al., 2011; Douka et al.,

71   2014). This raises questions of whether favourable environmental conditions in the Gebel

72   Akhdar made the region attractive for occupation and a *refugium* during periods when other

73   areas of North Africa appear to have been largely abandoned, and whether variations in the

74   technologies and subsistence strategies that occurred within the Gebel Akhdar were

75   influenced by the local climatic characteristics.

76   This paper provides palaeoclimatic data for the Gebel Akhdar between approximately

77   73 and 5 ka, which are directly associated with the archaeological record. The oxygen isotope

78   composition ($\delta^{18}O$) of herbivore tooth enamel carbonate is analysed and results are

79   principally used to infer past aridity. Samples come from two caves, the Haua Fteah and

80   Hagfet ed Dabba, that contain extensive archaeological deposits. The analysed material comes

81   from the major prey species found at the two sites and was excavated from spits/levels that

82   also contained other archaeological materials (predominately lithics) (McBurney, 1967;

83   McBurney and Hey, 1955).

2. Background

2.1 Environmental Context

The Gebel Akhdar massif (maximum elevation ~780m) is situated in Cyrenaica, northeast Libya, on the Mediterranean coast (Fig. 1). Present day mean annual temperatures range from 16 to 21°C and mean annual precipitation, which typically occurs between October and April each year, ranges from ~200-600 mm (Elfadli, 2009; El Kenawy et al., 2009; Ageena et al., 2014). Surrounded by the Sahara Desert to the south and east, and by the Mediterranean Sea to the north and west, there is high ecological diversity and notable endemism in the floral communities within the region (El-Darier and El-Mogaspi, 2009). Such endemism is characteristic of prolonged isolation, suggesting that the Gebel Akhdar's climate may have differed to adjacent regions over an extended period of time. This climatic setting is therefore of interest when considering the late Pleistocene and Holocene human populations that inhabited the region, and their connections to/isolation from other areas in North Africa.

Today the region sits at the southern extent of the mid-latitude Mediterranean climate system, which is typified by hot dry summers and mild wet winters, influenced by North Atlantic ocean-atmosphere circulation and Mediterranean cyclone activity (Alpert et al. 1990; Lionello et al., 2006). To the south, beyond the Sahara Desert, seasonal temperature fluctuations are lower in magnitude, and summer rainfall is the predominant source of moisture, driven by monsoonal circulation patterns and the seasonal movement of the Inter-Tropical Convergence Zone (ITCZ) across the region (Camberlin et al., 2001; Pomposi et al., 2014). While the maximum southward and northward extents of these two rainfall regimes have varied in the past, throughout the time period considered in this study, the dominant source of moisture to the northern African coastline has consistently been from North Atlantic and Mediterranean sources (Yan and Petit-Maire, 1994; Sultan et al., 1997; Abouelmagd et al., 2012).

109   To date, only a limited amount of palaeoenvironmental data from the Gebel Akhdar are

110   available. These data suggest that the variations in temperatures and rainfall amounts that

111   occurred over the last ~100,000 were less extreme than elsewhere in North Africa (Inglis,

112   2012; Prendergast, 2013). Alluvial, tufa and dune deposits are all found within the region

113   indicating variations in the amount of moisture available in the landscape varied with time,

114   but a lack of precise chronological understanding of these deposits hinders comparisons with

115   the archaeological record (McBurney and Hey, 1955). Mollusc isotope data from the Haua

116   Fteah cave suggest a more arid phase during OIS 2 (Prendergast et al., submitted). The Haua

117   Fteah cave sediments also highlight periods of increased landscape instability during OIS 3,

118   although taphonomic processes complicate climatic interpretations from these archives

119   (Barker et al., 2010; Hunt et al., 2010; Inglis, 2012). Thus there remains a need to gain further

120   local palaeoenvironmental information from additional archives that are directly linked to the

121   archaeological record.

122   *2.2 Archaeological Context*

123   To infer past climate in the Gebel Akhdar during periods of human activity, we

124   consider the oxygen isotope compositions of tooth enamel from the main prey species found

125   within the zooarchaeological assemblages from two cave sites, the Haua Fteah and Hagfet ed

126   Dabba. The Haua Fteah (32.90°N, 22.05°E, ~50m asl, Fig. 1) is a large rock shelter situated

127   ~1km from the coast on the northward facing lower escarpment of the Gebel Akhdar. The

128   cave was first excavated by Charles McBurney during the 1950s and its re-excavation has

129   been a central part of a renewed programme of archaeological investigation taking place in

130   the region since 2007 (McBurney, 1967; Barker et al., 2007; 2008; 2009; 2010; 2012; Rabett

131   et al., 2013; Farr et al., 2014). From the original excavations McBurney (1967) described an

132   archaeological sequence containing (using his terminology) Middle Palaeolithic (Pre-

133   Aurignacian and Levalloiso-Mousterian), Upper Palaeolithic (Dabban and Oranian), Mesolithic

134   (Libyco-Capsian), Neolithic (of Capsian tradition), Graeco-Roman and post-Classical deposits

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(McBurney, 1967). In brief, the Pre-Aurignacian and Levalloiso-Mousterian phases are characterized by blades and burins, while chamfered blades and wide bladelets are typical of Dabban assemblages (McBurney, 1967; Barker et al., 2010; 2012). Use of the cave (or at least the area excavated) appears to have intensified during the Oranian phase, with evidence for *in situ* blade production and re-touching, trampling, and the year-round shellfish exploitation (Barker et al., 2010; 2012, Prendergast et al., accepted). The Capsian assemblage is characterized by backed bladelets, microliths and bone and shell artefacts, with evidence for an increase in shellfish and wild plant exploitation (McBurney, 1967; Barker et al., 2010). In the Neolithic phase there is evidence for further intensification in the exploitation and management of floral and faunal resources, with evidence of grinding implements, domestic caprids, and pottery, but no evidence for cereal cultivation (McBurney, 1967; Barker et al., 2012).

The 2007-onwards re-excavation and re-dating of the Haua Fteah sequence, combined with the reanalysis of the McBurney archive, are examining if these cultural divisions and terminologies remain appropriate, but as this work is ongoing, McBurney's divisions and terminology are used in this paper. Chronological age estimates for McBurney's cultural phases are displayed in Table 1 (Douka et al., 2014). These age brackets indicate the most probable upper and lower date for the phases; they do not imply that the phase lasted the duration of the age bracket, nor indicate whether single or multiple periods of occupation occurred within each phase.

The Hagfet ed Dabba (32.68°N, 21.56°E, ~360m asl, Fig. 1) is a smaller cave located ~60km from the Haua Fteah and ~15km from the present day coast. Situated on a dry tributary of Wadi Kuf (today the main watershed of the Gebel Akhdar), the cave was excavated in 1947 and 1948 by Charles McBurney, with an additional small test-pit made in 2008 (McBurney and Hey, 1955; Barker et al., 2008). The 1940s excavations revealed stratified deposits containing Dabban lithics (Layers VI to II) and a loose sub-surface layer

161 (Layer I) containing Roman pottery (McBurney and Hey, 1955). No absolute chronological age

162 determinations are available for Hagfet ed Dabba.

163 *2.3 Enamel isotopes in climate studies*

164   This study analyses the oxygen isotope composition of the tooth enamel carbonate

165 ($\delta^{18}O_{enamel}$) from samples from the Haua Fteah and Hagfet ed Dabba caves. The carbon isotope

166 composition of the samples has also been measured and is submitted for publication

167 elsewhere (Reade et al., submitted). In mammals, $\delta^{18}O_{enamel}$ is determined by the animal's

168 body water $\delta^{18}O$ ($\delta^{18}O_{bw}$) during the period of mineralization; $\delta^{18}O_{bw}$ closely reflects ingested

169 water $\delta^{18}O$ ($\delta^{18}O_{iw}$) and is influenced by the animal's ecology and physiology (Longinelli,

170 1984; Luz et al., 1984; Luz and Kolodny, 1985; Bryant and Froelich, 1995; Kohn, 1996).

171 Enamel mineralization is a process that typically spans several months, and in medium and

172 large ruminants a whole tooth forms over approximately a full year (Brown et al., 1960;

173 Weinreb and Sharav, 1964; Suga, 1982; Aoba, 1996). $\delta^{18}O_{enamel}$ reflects an average of the

174 $\delta^{18}O_{iw}$ over an equivalent period, although the exact temporal character of the signal will

175 depend on sampling geometry and the species-specific pattern of minerlization (Passey and

176 Cerling, 2002; Balasse, 2003; Zazzo et al., 2005).

177   For terrestrial mammals ingested water is largely acquired, either directly or

178 indirectly, from meteoric water, which has a $\delta^{18}O$ composition dependent on climatic (e.g.

179 temperature, rainfall, and humidity) and geographical (e.g. distance from the

180 ocean/precipitation source and altitude) factors (Dansgaard, 1964; Rozanski et al., 1992). If

181 an animal migrates both climatic and geographical factors will be represented in the

182 $\delta^{18}O_{enamel}$. Sources of ingested waters can include surface water, groundwater, water

183 contained in the diet, and dew. Obligate drinkers typically consume water from surface

184 sources, which have a $\delta^{18}O$ similar to precipitation $\delta^{18}O$ ($\delta^{18}O_{precip}$) in environments where

185 evaporation is limited; in evaporative environments surface water is enriched in ^{18}O relative

186 to precipitation (Dansgaard, 1964; Longinelli, 1984; Luz and Kolodny, 1985; Rozanski et al.,

187 1992). Non-obligate drinkers principally acquire water from dietary sources (i.e. plant water

188 for herbivores) (Ayliffe and Chivas, 1990; Luz et al., 1990; Delgado Heurtas et al., 1995;

189 Murphy et al., 2007). Plant water is derived from recent precipitation and/or groundwater

190 and has a $\delta^{18}O$ signature indirectly linked to $\delta^{18}O_{precip}$, potentially being modified by input

191 from other water pools, through evaporation at the surface, and transpiration from the leafs

192 (which is mediated by water availability, temperature and humidity) (Dongmann et al., 1974;

193 Ehleringer and Dawson, 1992; Barbour, 2007). A number of studies have shown a strong

194 relationship between relative humidity and skeletal $\delta^{18}O$ from non-obligate drinking animals,

195 with higher $\delta^{18}O$ values occurring in lower humidity environments (Ayliffe and Chivas, 1990;

196 Delgado Huertas et al., 1995; Murphy et al., 2007). Skeletal $\delta^{18}O$ in obligate drinkers most

197 commonly relates to $\delta^{18}O_{precip}$ and temperature (e.g. Longinelli, 1984; Hoppe et al., 2006).

198 **3. Material and methods**

199 79 *Ammotragus lervia* teeth from the Haua Fteah and 50 from Hagfet ed Dabba were

200 sampled for oxygen isotope analysis. Additionally, 21 *Bos* sp. and 12 domestic caprid (*Ovis* sp.

201 and *Capra* sp.) teeth from Haua Fteah were also analysed. All samples are from the McBurney

202 excavations at the two sites. Samples from the Haua Fteah are curated in the Museum of

203 Archaeology and Anthropology, University of Cambridge. Samples from the Hagfet ed Dabba

204 are curated in the Natural History Museum, London. The teeth do not show direct evidence of

205 human manipulation (e.g. cut marks, burning, fracturing), but examples of such modifications

206 have been identified on other skeletal elements from the same species found within the same

207 contexts at the sites, albeit at relatively low frequencies (Klein and Scott, 1986). This,

208 combined with the large quantity of lithic and other archaeological material excavated from

209 the same spits/layers as the samples, we judge to indicate that the samples are the result of

210 human activity within the caves, and thus are temporally tied to periods when people were

211 present within the Gebel Akhdar landscape.

The species analysed in this study are a mix of obligate (*Bos* sp.), non-obligate (*A. lervia*) and 'intermediary' drinkers (domestic caprids). Domestic caprids cannot survive without drinking water indefinitely but desert-adapted breeds can tolerate arid, water-stressed environments with little or no access to water over short time periods (El-Nouty et al., 1988). Bovids have higher water requirements, and while arid-adapted species/breeds can survive with less water than those from more humid environments, the required volume and frequency of access to drinking water is far greater than for caprids (King, 1983). *A. lervia* is a non-obligate drinker and can meet its water requirements solely through water contained in the diet (Ogren, 1965). Therefore, we predict that *Bos* sp. $\delta^{18}O_{enamel}$ will most likely reflect the $\delta^{18}O$ of surface waters, potentially enriched relative to $\delta^{18}O_{precip}$ through evaporation, *A. lervia* $\delta^{18}O_{enamel}$ will most likely reflect $\delta^{18}O_{plant}$, and may be influenced by relative humidity, and domestic caprid $\delta^{18}O_{enamel}$ may represent an intermediary signal. None of the wild species analysed in this study are thought to undertake long distance seasonal migrations in the context of the Gebel Akhdar's geographical setting, thus the data presented here will reflect a signal local to the Gebel Akhdar. This also implies that year-round surface water must have been available within the region during the time periods where *Bos* sp. are present.

3.1 Chronological association of the samples

Samples analysed in this study from the Haua Fteah come from layers that are associated with the McBurney-defined cultural phases of the Levalloiso-Mousterian, Dabban, Oranian, Capsian and Neolithic, covering a period from OIS 4 to the mid Holocene (McBurney, 1967; Douka et al., 2014). McBurney excavated the site in a series of overlapping spits, which often spanned multiple stratigraphic layers (McBurney, 1967). As such, a large proportion of the samples cannot be attributed to a stratigraphic context more resolved than the cultural phase from which they came. Where samples can be attributed to spits that were either entirely contained within a single stratigraphic layer, or that span 2-3 layers but do not overlap with other spits, narrower chronological estimations are made (Table 1).

238   Samples from Hagfet ed Dabba come from Layers VI to I. So far, the site is undated and

239   its chronological context can only be inferred through correlation with the lithic assemblage

240   at Haua Fteah, and the dates associated with these Layers. In particular, McBurney suggested

241   that a change in lithic technology occurring between Layer VI and III at Hagfet ed Dabba was

242   similar to a change that occurs within Layer XX at Haua Fteah (McBurney and Hey, 1955;

243   McBurney, 1967). Layer XX at Haua Fteah has been dated to ~32 ka (Douka et al., 2014). The

244   duration and frequency of occupation represented in the Hagfet ed Dabba archaeological

245   sequence are unclear.

246   *3.2 Enamel sampling and isotopic analysis*

247   Sampling was restricted to third molars (M3s) in the caprid samples to ensure an *in

248   utero*/pre-weaning signal was avoided. M2s and M3s were sampled for the bovids. Bulk-tooth

249   samples were taken to infer average $\delta^{18}O_{iw}$ over the period of tooth formation. Each tooth

250   sampled is predicted to have mineralized over approximately 1 year (Brown, 1960; Ogren,

251   1965) although the time represented in each sample may be less as the full enamel depth was

252   not sampled (see Reade et al., 2015). Each tooth selected for analysis was thoroughly cleaned

253   prior to sampling. Using a diamond coated drill bit mounted on a variable-speed handheld

254   drill, powdered enamel was collected (10-15 mg) evenly along a transect that spanned the

255   length of the tooth from the occlusal surface to the enamel-root junction. A 5-7mg sub-sample

256   was then chemically pre-treated following the method described by Balasse et al. (2002) to

257   remove organic and secondary carbonate material. The treated powder was isotopically

258   analysed at the Godwin Laboratory, Department of Earth Sciences, University of Cambridge.

259   The carbonate phase of the samples were analysed on an automated Gasbench interfaced with

260   a Thermo Finnigan MAT253 isotope ratio mass spectrometer, being reacted with 100%

261   orthophosphoric acid for 2 hours at 70°C in individual vessels. Each run was accompanied by

262   10 reference carbonates (Carrara Z, $\delta^{18}O$ = -1.27‰), two control samples (Fletton Clay, $\delta^{18}O$ =

263   -0.3‰) and in-house enamel reference samples (STD1 ($\delta^{18}O$ = -4.3‰) and STD4 ($\delta^{18}O$ =

264 -6.1‰)), which were pre-treated following the same method used for the archaeological

265 samples (n=4 for every 20 archaeological samples analysed). Carrara Z has been calibrated to

266 VPDB using the IAEA NBS19 standard. Results are reported on the delta scale in units of per

267 mil with reference to the international standard VPDB. The machine precision for $^{18}O/^{16}O$ is

268 better than ±0.1‰ based on replicate analyses of laboratory standards. Reproducibility on

269 the in-house enamel references is ±0.2‰. Reproducibility on the Fletton Clay control sample

270 is ±0.8‰. Statistical analysis was performed using SPSS v.19 (Statistical Package for Social

271 Sciences) and statistical significance was accepted at $p<0.05$.

272 **4. Results**

273 A summary of results from the Haua Fteah and Hagfet ed Dabba is displayed in Table 2.

274 Full results are available in Appendix A.

275 *4.1 Haua Fteah*

276 Considered by cultural phase, *A. lervia* mean $\delta^{18}O_{enamel}$ from the Haua Fteah is highest

277 in the Dabban (1.2 ± 0.5‰, n=5, range=1.3‰) and lowest in the Neolithic (-0.9 ± 0.9‰,

278 n=29, range=3.4‰) (Table 2, Fig. 2), varying significantly through the sequence (Kruskal

279 Wallis, $H(4)$=20.967, $p<0.05$). Inter-individual variation within each cultural phase is higher

280 (≥3.4‰) in the Levalloiso-Mousterian (n=8), Oranian (n=30) and Neolithic (n=29) than in the

281 Dabban (n=5) and Capsian (n=7) (≤1.4‰). While this may partly be an effect of different

282 sample sizes, the notable difference in the spread of the data between the Levalloiso-

283 Mousterian and the Dabban and Capsian (Table 2, Fig. 2), despite relatively little difference in

284 sample size, suggests that the reduced variation observed in the Dabban and Capsian samples

285 may be a true reflection of $\delta^{18}O$ variability during these time periods.

286 Mean $\delta^{18}O_{enamel}$ and inter-individual variation in the Neolithic domestic caprids (-0.7 ±

287 0.8‰, n=12, range=3.0‰) cannot be distinguished from the wild Neolithic *A. lervia* samples

288 (-0.9 ± 0.9‰, n=29, range=3.4‰) (Mann Whitney, U=178, z=0.115, $p>0.05$), indicating that

289 the animals had isotopically similar sources of water. *Bos* sp. mean $\delta^{18}O_{enamel}$ does not vary

290 between cultural phase (Kruskal Wallis, $H(2)=0.440$, $p>0.05$), and is indistinguishable from *A.*

291 *lervia* $\delta^{18}O_{enamel}$ in the Capsian (Mann Whitney, $U=6.0$, $z=-1.512$, $p>0.05$), but significantly

292 different in the Oranian (Mann Whitney, $U=66.0$, $z=-3.828$, $p<0.05$). The two Dabban *Bos* sp.

293 samples are 2.1‰ and 2.4‰ lower than the mean Dabban *A. lervia* $\delta^{18}O_{enamel}$ (1.2 ± 0.5 ‰,

294 n=5). This suggests the two species were consuming isotopically different waters in the

295 Oranian and Dabban. The highest within-phase inter-individual variation in the *Bos* sp. data

296 occurs in the Oranian (2.2‰), although this may be influenced by the relatively large sample

297 size, in comparison to the Capsian and Dabban (Table 2).

298 When considering the subset of data for which more discrete stratigraphic

299 provenances can be determined (n=59), and where n≥3 (Fig. 3), the highest $\delta^{18}O_{enamel}$ for *A.*

300 *lervia* (1.5 ± 0.2‰, n=3) occurs in Dabban Layer XX, which is dated to ~32 ka (Douka et al.,

301 2014). The Oranian Layers XIV, XV (~16.6-14.7 ka) display the widest intra-layer variability

302 (3.4‰), being only 0.9‰ less than the total variation observed across the whole of the Haua

303 Fteah sequence for *A. lervia*. *Bos* sp. $\delta^{18}O_{enamel}$ shows lower values and higher variation within

304 Oranian Layer XII (~15.0-13.5 ka) than in the preceding Oranian Layer XIII, XIV or

305 subsequent Capsian Layer X (~12.6-7.9 ka), although differences are small in comparison to

306 the *A. lervia* data (Fig. 3).

307 *4.2 Hagfet ed Dabba*

308 Only *A. lervia* samples were available for analysis from Hagfet ed Dabba. Mean

309 $\delta^{18}O_{enamel}$ shows little variation between Layers IV and I (Fig. 4), ranging from 0.0 ± 0.4‰

310 (n=6, range=1.0‰) in Layer III to 0.3 ± 1.3‰ in Layer I (n=8, range=3.8‰)(Table 2). The

311 lack of between-layer difference includes the samples from Layer I, from which Roman

312 ceramic material was recovered. It is not clear whether teeth from Layer I are Dabban in age

313 but have become mixed with Roman accumulations, or are contemporaneous with the Roman

314 pottery, or date to an intervening period. Inter-individual variation is 3.8‰ in Layer I. This is

315 similar to the variation observed within some layers in the Haua Fteah assemblage but is

316 greater than the range seen in the other Hagfet ed Dabba layers, which do not exceed 2.5‰.

317 Across the whole sequence (Layers VI-I, excluding Layer V) there is a significant inter-layer

318 difference in mean $\delta^{18}O_{enamel}$ (Kruskal Wallis, $H(5)=17.417$, $p<0.05$), with lower values in

319 Layer VI (-0.9 ± 0.7‰, n=12, range=1.9‰) than Layers IV-I (Table 2). Sample size for Layer V

320 (n=2) is too small to facilitate statistical comparison to the other layers.

321 Although the $\delta^{18}O$ results from the Haua Fteah Dabban samples are within the range

322 seen at Hagfet ed Dabba, there is a significant difference between the mean $\delta^{18}O$ from Hagfet

323 ed Dabba (n=50) and that of the Dabban Haua Fteah samples (n=5) (Mann-Whitney, $U=228$,

324 $z=3.016$, $p<0.05$). This difference appears to be slightly reduced (Mann-Whitney, $U=142$,

325 $z=2.579$, $p<0.05$) when only the Haua Fteah samples from Layer XX (n=3) are considered,

326 which is the layer thought to be most chronologically similar to the Hagfet ed Dabba

327 assemblage (McBurney and Hey, 1955; McBurney, 1967). However, the very large

328 discrepancy in sample size between the two sites should be noted.

329 **5. Discussion**

330 Data here are derived from non-obligate drinking *A. lervia*, obligate drinking *Bos* sp.,

331 and domestic caprids. Domestic caprids and wild *A. lervia* are isotopically indistinguishable.

332 Lower *Bos* sp. $\delta^{18}O_{enamel}$ values most probably reflect a larger intake of drinking water

333 compared to the caprids, for whom plant water would have constituted a greater component.

334 It is interesting to note that the largest differences between *Bos* sp. and *A. lervia* occur in the

335 late Pleistocene Dabban and Oranian samples. The Holocene Capsian *Bos* sp. and *A. lervia*

336 samples follow a similar pattern to the Holocene Neolithic *A. lervia* and domestic caprid

337 samples, being statistically indistinguishable. This could suggest that there was less difference

338 in $\delta^{18}O$ between surface waters and plant waters during the Holocene than the Pleistocene, an

339 effect that would be produced under more humid conditions.

340 While the water sources vary, ultimately all originate from local precipitation, which is

341 derived from the global oceans. As glacial ocean $\delta^{18}O$ was ~1‰ higher than today

14

(Shackleton, 1987; Schrag et al., 2002), some of the temporal variation that occurs in our data is likely the product of this change. However, accounting for this variation is not straightforward as glacial-interglacial ocean $\delta^{18}O$ change appears to have been geographically and temporally variable (Elderfield and Ganssen, 2000; Paul et al., 2001; Duplessy et al., 2002). Accounting for variations in the source composition is further complicated if the source area from which local precipitation is derived also changes. Comparison of modern $\delta^{18}O_{precip}$ to Saharan fossil groundwater suggests precipitation during the late Pleistocene and early Holocene was derived from mid-latitude climate systems, and particularly palaeo-westerlies of Atlantic origin (Sultan et al., 1997; Abouelmagd et al., 2012). However, these groundwaters are located to the south of the Gebel Akhdar, and may not reflect the situation in coastal locations. In comparison, precipitation along the Levantine coast to the northeast of the Gebel Akhdar, is heavily influence by Mediterranean cyclone activity (Alpert et al., 1990). Given the Gebel Akhdar's topography and promontory position jutting out into the eastern Mediterranean Sea it is probable that this region received rainfall from Mediterranean sources in addition to those from the Atlantic across the time period considered.

The highest *A. lervia* $\delta^{18}O_{enamel}$ values in the Haua Fteah sequence occur in the Dabban, and in particular in Layer XX, which is dated to ~32 ka (Douka et al., 2014). We interpret this as representing the most arid environment of the time periods considered in this study. However, overall variation in aridity appears to be of a relatively small magnitude: the difference between the 'most humid' and 'most arid' cultural phase at the Haua Fteah is represented by a difference in mean $\delta^{18}O_{enamel}$ of only 2.1‰. High $\delta^{18}O$ values are also seen in terrestrial molluscs from Dabban layers in the Haua Fteah (Prendergast et al., submitted). At a more regional scale this arid episode could correlate chronologically with Heinrich event 3, which was marked by a widespread reduction of moisture availability (Bartov et al., 2003).

Quantitative palaeoaridity estimates are currently beyond the scope of this study. The precise relationship between skeletal $\delta^{18}O$ and the external environment is determined by

species-specific physiological processes such as metabolism, respiration and water turnover rate (Luz et al., 1984; Bryant and Froelich, 1995; Kohn, 1996). No studies that characterize this relationship in modern *A. lervia* populations, or other in non-obligate drinking caprids, currently exist, and the protected status of the species (Cassinello et al., 2008) makes conducting such a study presently unfeasible. In the meantime, our results can be given some context by considering what is known of $\delta^{18}O$ variation from comparable modern populations and environments.

Globally, wild goat (*Capra ibex*), mouflon (*Ovis ammon musimon*) and roe deer (*Capreolus capreolus*) display an average decrease of ~0.88‰ in bone phosphate $\delta^{18}O$ ($\delta^{18}O_{phos}$) for every ~1‰ decrease in local $\delta^{18}O_{precip}$ (Delgado Huertas et al., 1995). While *A. lervia* physiology may be similar to these species, ingested water for *A. lervia* is only indirectly linked to precipitation, through plant water (Ogren, 1965). The degree of enrichment in $\delta^{18}O_{plant}$ relative to $\delta^{18}O_{precip}$ is highly variable and depends on the exact sources of the plant's water, the amount of evaporation that these sources have been subject to, plant physiology, and plant transpiration rates, which are strongly influenced by relative humidity (Ehleringer and Dawson, 1992; Barbour, 2007). Considering other herbivore species consuming water largely or solely from plants, a ~1‰ change in $\delta^{18}O_{phos}$ has been observed to correspond to a ~3% change in mean annual relative humidity in macropods (Ayliffe and Chivas, 1990). White tailed and mule deer (*Odocoileus* sp.) $\delta^{18}O_{phos}$ has been shown to vary by 9.65‰ between environments where $\delta^{18}O_{precip}$ differs by 1.2‰, relative humidity by 44% and temperature by 14°C (Luz et al., 1990). More recently, the interactive effect of temperature and relative humidity on macropod tooth enamel carbonate $\delta^{18}O$ has also been demonstrated (Murphy et al., 2007). It is not possible to estimate the effect of these different parameters on the archaeological *A. lervia* $\delta^{18}O_{enamel}$ without comparative studies of modern populations and palaeotemperature estimates from additional independent proxies in the Gebel Akhdar.

393   However, with reference to the other studies discussed, a 2.1‰ change in *A. lervia* $\delta^{18}O_{enamel}$

394   is likely to indicate a relative small climatic change, most likely in relative humidity.

395   In the Mediterranean environment, $\delta^{18}O_{precip}$ is influenced by both temperature and

396   rainfall amount (Gourcy, 2005). At the Soreq cave site (Israel, 31.45°N, 35.03°E) rainfall was

397   found to be the dominant factor, with weighted annual average $\delta^{18}O_{precip}$ being 1.02 ± 0.11‰

398   higher per 100mm decrease in annual precipitation amount (Bar-Matthews et al., 2003).

399   Rainfall amount was also found to be the dominant factor in northwest African gerbil

400    $\delta^{18}O_{enamel}$ when mean annual precipitation (MAP) is <600mm, with a 3.7‰ increase in

401    $\delta^{18}O_{enamel}$ corresponding to a MAP decrease from 600 to 200 mm (Jeffery et al., 2015).

402   However, small mammal's body water may be subject to greater evaporative enriched than in

403   large mammals, so direct comparison between the magnitude of change in gerbil and

404   caprid/bovid $\delta^{18}O_{enamel}$ cannot be made. It is therefore likely that our results indicate a change

405   in environmental aridity/humidity, controlled largely by the amount of rainfall. However, the

406   amount of variation observed in the data , compared to the magnitude a variation seen in

407   other data sets, suggests this would not have resulted in major ecological changes in the local

408   environment.

409   The samples from Hagfet ed Dabba are most likely of a similar age to the Dabban phase

410   at Haua Fteah. The $\delta^{18}O_{enamel}$ values from Layers IV-I, while lower than the corresponding

411   Dabban samples from Haua Fteah, are still higher than elsewhere in the Haua Fteah sequence.

412   The $\delta^{18}O_{enamel}$ values from Layers VI and V are lower and fall within the ranges seen during

413   the earlier and later cultural phases at the Haua Fteah. Differences between the two sites may

414   in part relate to differences in sample size and/or chronological association, but could also in

415   part be explained by altitudinal differences, which would produce both higher amounts of

416   precipitation and lower $\delta^{18}O$ at the Hagfet ed Dabba (Dansgaard, 1964; Poage and

417   Chamberlain, 2001).

418   In relation to the archaeological record, the increased aridity between the Levalloiso-

419   Mousterian and Dabban samples recorded here broadly correlates with a notable decrease in

420   the distribution of archaeological sites in the pre-desert regions immediately south of the

421   Gebel Akhdar between the Middle Stone Age (MSA) and Later Stone Age (LSA) (which are

422   roughly comparable to McBurney's (1967) Levalloiso-Mousterian and Dabban phases), and a

423   corresponding increase in sites between the MSA and LSA within Gebel Akhdar (Barker et al.,

424   2010; 2009; Jones et al., 2011). These events also broadly correspond to a period of increased

425   aridity and depopulation in the wider Saharan region (Castañeda et al., 2009; Cancellieri et al.,

426   2013). The observed increase in population distribution/density within the Gebel Akhdar,

427   and the corresponding decrease elsewhere, could have been in response to the climatic

428   changes reported here, where the Gebel Akhdar, although following the regional trend

429   towards more arid conditions, provided a relatively more humid environment than adjacent

430   regions. Within the Gebel Akhdar, the persistence of more humid conditions is likely to have

431   occurred particularly in more inland areas, such as in the Wadi Kuf and Hagfet ed Dabba

432   region, where the higher elevation is likely to have resulted in higher rainfall amounts. This

433   suggestion is consistent with archaeological site distribution patterns, which show sites

434   dating to this time period were most common in higher elevation areas (Jones et al., 2011).

435   Evidence for less arid conditions than in adjacent regions provides further support to the

436   theory that the Gebel Akhdar may have served as a *refugium* for humans in North Africa

437   during times of global climatic extremes (Barker et al. 2012; Prendergast et al. submitted;

438   accepted; Reade et al., submitted).

439   The large variation in *A. lervia* and *Bos* sp. $\delta^{18}O_{enamel}$ that occurs during the late glacial

440   Oranian likely reflects a variable climate during this time period, where relatively high-

441   magnitude changes occurred on sub-millennial timescales across the Mediterranean basin

442   (Bartov et al., 2003; Combourieu Nebout et al., 2009). At this time human activity at Haua

443   Fteah appears to have intensified (at least in the area excavated) and potentially occurred

year round, with the density of lithic and faunal remains increasing, and evidence for *in situ* processing of lithics and an increase in marine and terrestrial mollusc exploitation (McBurney, 1967; Klein and Scott, 1986; Barker et al., 2010; 2012; Prendergast et al., accepted). Such activities have been suggested as possible indications of increased population density, changing landscape use, or increased resource pressure/dietary stress (Hunt et al., 2011; Prendergast et al., accepted). If the climate at this time was increasingly less stable it could have resulted in a more variable landscape with less predictable access to specific plant and animal resources on a year-to-year basis.

Capsian and Neolithic cultural phases in the Gebel Akhdar occurred in a more humid environment than earlier cultural phases. Little between-layer variation in mean $\delta^{18}O_{enamel}$ is apparent (Fig. 3), but an increase in intra-layer variation with time may indicate that after a period of relative stability in the early Holocene, the climate once again became less stable by the mid-Holocene. However, this change coincides with the first evidence of domestic animals in the region, as well as evidence of a change in local vegetation structure (McBurney, 1967; Klein and Scott, 1986; Reade et al., submitted), and it is possible that some variation may be caused by increased human influence on the local landscape and its local animal populations. The increase in humidity is consistent with archives from elsewhere in North Africa which attest to increased fluvial activity in the early Holocene, related to an increase in Mediterranean precipitation and/or enhanced monsoonal circulation (Pachur and Rottinger, 1997; Kuper and Kröpelin, 2006). The later Neolithic samples from the Gebel Akhdar, which date to ~7-6 ka, may be contemporaneous with a period of short-term climatic instability seen elsewhere in the Mediterranean, as well as a trend towards more arid conditions in the Sahara (Cremaschi and di Lernia, 1999; De Rijk et al., 1999; Baioumy et al., 2011). In the Sahara this resulted in an increase in human mobility (Tafuri et al., 2006; Stojanowski and Knudson, 2014). In contrast, the appearance domesticated animals, pottery, and grinding implements in the Neolithic layers at Haua Fteah (McBurney, 1967), could be taken to indicate

470 a less mobile population, which presumably would indicate a favourable year-round

471 environment in the region.

472   *Bos* sp. samples were analysed for the Dabban, Oranian and Capsian periods. Bovids

473 are present in the Levalloiso-Mousterian and Neolithic faunal assemblages but no suitable

474 skeletal elements were available for inclusion in this study (McBurney, 1967; Klein and Scott,

475 1986). Given the variations in aridity inferred from the *A. lervia* samples across the Dabban-

476 Oranian-Capsian, the relatively stable *Bos* sp. $\delta^{18}O_{enamel}$ values are intriguing, particularly as

477 these samples span the time period when changes in global ocean $\delta^{18}O$ would have influenced

478 local $\delta^{18}O_{precip}$, irrespective of other climatic variation. For *Bos* sp. to be present in the

479 landscape there must have been year-round drinking water available, but the lack of variation

480 in the data would indicate that the source water $\delta^{18}O$ did not vary significantly. One possible

481 explanation is the contribution of groundwater to the bovid's drinking water. Today in the

482 Gebel Akhdar precipitation is highly seasonal and year-round surface water is relatively rare,

483 with no large river networks or other permanent large bodies of surface water being present

484 (Hamad, 2009). Natural springs occur in the region and these are supplied by highly localized,

485 relatively shallow groundwater, which is recharged from local precipitation (Hamad, 2009). It

486 is likely that these springs were also present during the last glacial, and it is possible that

487 these were an important source of drinking water for the local bovid population. As

488 groundwater $\delta^{18}O$ typically reflects a signal homogenized over many years to millennia

489 (Darling, 2004) the relative lack of variation in the *Bos* sp. data could be explained by at least

490 part of the animal's water being derived from such sources.

491   Using a conversion equation derived from modern bovid (*Bison bison*) tooth enamel

492 carbonate in North America the mean *Bos* sp. $\delta^{18}O_{enamel}$ from Haua Fteah produces a $\delta^{18}O_{iw}$

493 estimate of -0.6 ± 2.0‰ (n=21) (Hoppe et al., 2006; Pryor et al., 2014). No comparative

494 groundwater $\delta^{18}O$ data are available from the Gebel Akhdar, but the estimated value is higher

495 than present day local $\delta^{18}O_{precip}$ (~-4.5‰) (IAEA, 2015), suggesting that the ingested water

496   may have been enriched relative to its source through evaporative processes in the surface

497   environment. The estimated $\delta^{18}O_{iw}$ is considerably higher than groundwater $\delta^{18}O$ from the

498   Western Desert in Egypt ($\sim$-11‰), which likely indicates differing sources of precipitation

499   between the two regions (Sultan et al., 1997). However, we have not tested modern samples

500   to establish whether the Hoppe et al. (2006) correlation is valid for the bovid species analysed

501   or environmental context considered here.

502   **6. Conclusion**

503   Overall, the data presented in this paper indicate that the Gebel Akhdar did not

504   experience climatic variation of a magnitude comparable to more continental areas of North

505   Africa. The region was more arid during the last glacial than during the early/mid Holocene,

506   with the most arid phase identified dating to $\sim$32ka, but no hyper-arid periods are evident in

507   the data and the region was overall more humid than adjacent regions. This finding provides

508   further support to the theory that the Gebel Akhdar may have served as a *refugium* for

509   humans in North Africa during times of global climatic extremes (Barker et al. 2012;

510   Prendergast et al. submitted; accepted; Reade et al submitted). The most humid phase

511   identified in the record dates to $\sim$9-5ka. Climate instability may have been greater in the late

512   glacial, and to a lesser extent the mid-Holocene, than during other periods.

513   In relation to the archaeology of the Gebel Akhdar, differences in climates during

514   different cultural units are observed. While Dabban populations inhabited a relatively arid

515   landscape, the climatic conditions were likely to have been relatively stable. Data from the

516   Hagfet ed Dabba suggest upland/inland areas within the Gebel Akhdar could have provided

517   less arid environments than on the coast, which is consistent with the distribution of known

518   archaeological sites across the region at this time period (Jones et al., 2011). Oranian

519   populations living in the region during the late glacial would likely have experienced much

520   greater climate instability than in other time periods, and this instability may have

521   contributed to the increased intensity of human activity and possible change in resource

522 exploitation evident in the archaeological record (Barker et al., 2010; Prendergast et al.,

523 accepted). The Capsian and Neolithic phases occurred within a more humid environment,

524 which would have increased the potential to exploit a variety of floral, faunal and water

525 resources within the landscape.

526   The results of this study show that the environment of the Gebel Akhdar did not

527 remain stable and the landscape in which human populations operated was dynamic.

528 However, in the wider context of North Africa, the Gebel Akhdar most likely provided

529 relatively consistent opportunities for resource exploitation in comparison with adjacent

530 areas. The corollary of this finding is that it is unlikely that the technological and cultural

531 changes evident in the archaeological record occurred as a direct response to local climate

532 variations.

540

541   **References:**

542   Abouelmagd, A., Sultan, M., Milewski, A., Kehew, A.E., Sturchio, N.C., Soliman, F.,

543   Krishnamurthy, R.V., Cutrim, E., 2012. Toward a better understanding of palaeoclimatic

544   regimes that recharged the fossil aquifers in North Africa: Inferences from stable isotope

545   and remote sensing data. Palaeogeography, Palaeoclimatology, Palaeoecology 329-330,

546   137–149. doi:10.1016/j.palaeo.2012.02.024

547   Ageena, I., Macdonald, N., Morse, A.P., 2014. Variability of maximum and mean average

548   temperature across Libya (1945–2009). Theoretical and Applied Climatology 117, 549–

549   563. doi:10.1007/s00704-013-1012-z

550   Alpert, P., Neeman, B.U., Shay-el, Y. 1990. Climatoligcal analysis of Mediterranean cyclone

551   using ECMWF data. Tellus 42A, 65-77.

552   Aoba, T., 1996. Recent observations on enamel crystal formation during mammalian

553   amelogenesis. The Anatomical Record 245, 208–218.

554   Ayliffe, L.K., Chivas, A.R., 1990. Oxygen isotope composition of the bone phosphate of

555   Australian kangaroos: potential as a palaeoenvironmental recorder. Geochimica et

556   Cosmochimica Acta 54, 2603–2609.

557   Baioumy, H., Kayanne, H., Tada, R., 2011. Record of Holocene aridification (6000-7000 BP) in

558   Egypt (NE Africa): Authigenic carbonate minerals from laminated sediments in Lake

559   Qarun. Quaternary International 245, 170–177. doi:10.1016/j.quaint.2010.05.021

560   Balasse, M., Ambrose, S.H., Smith, A.B., Price, T.D, 2002. The seasonal mobility model for

561   prehistoric herders in the south-western Cape of South Africa assessed by isotopic

562   analysis of sheep tooth enamel. Journal of Archaeological Science 29, 917–932.

563   Balasse, M., 2003. Potential biases in sampling design and interpretation of intra-tooth isotope

564   analysis. International Journal of Osteoarchaeology 13, 3–10.

565   Bar-Matthews, M., Ayalon, A., Gilmour, M., Matthews, A., Hawkesworth, C., 2003. Sea-land

566   oxygen isotopic relationships from planktonic foraminifera and speleothems in the

567   Eastern Mediterranean region and their implication for paleorainfall during interglacial

568   intervals. Geochimica et Cosmochimica Acta 67, 3181–3199.

569   Barbour, M.M., 2007. Stable oxygen isotope composition of plant tissue: a review. Functional

570   Plant Biology 34, 83-94. doi:10.1071/FP06228

571   Barker, G., Antoniadou, A., Armitage, S., Brooks, I., Candy, I., Connell, K., Douka, K., Drake, N.,

572   Farr, L., Hill, E., Hunt, C., Inglis, R., Jones, S., Lane, C., Lucarini, G., Meneely, J., Morales, J.,

573   Mutri, G., Prendergast, A., Rabett, R., Reade, H., Reynolds, T., Russell, N., Simpson, D., Smith,

574   B., Stimpson, C., Twati, M., White, K., 2010. The Cyrenaican Prehistory Project 2010: the

575   fourth season of investigations of the Haua Fteah cave and its landscape, and further

576   results from the 2007–2009 fieldwork. Libyan Studies 41, 23–49.

577   Barker, G., Antoniadou, A., Barton, H., Brooks, I., Candy, I., Drake, N., Farr, L., Hunt, L., Ibrahim,

578   A., Inglis, R., Jones, S., Morales, J.I., Mutri, G., Rabett, R., Reynolds, T., Simpson, D., Twati, M.,

579   White, K., 2009. The Cyrenaican Prehistory Project 2009: the third season of

580   investigations of the Haua Fteah cave and its landscape, and further results from the

581   2007-2008 fieldwork. Libyan Studies 40, 1–42.

582   Barker, G., Basell, L., Brooks, I., Burn, L., Cartwright, C., Cole, F., Davison, J., Farr, L., Grun, R.,

583   Hamilton, R., Hunt, C.R., Jacobs, Z., Leitch, V., Morales, J., Morley, I., Morley, M., Pawley, S.,

584   Pryor, A., Rabett, R., Reynolds, E.-R.H., Roberts, R., Simpson, D., Stimpson, C., Touati, M.,

585   van der Veen, M., 2008. The Cyrenaican Prehistory Project 2008: the second season of

586   investigations of the Haua Fteah cave and its landscape, and further results from the

587   initial (2007) fieldwork. Libyan Studies 39, 175–221.

588   Barker, G., Bennett, P., Farr, L., Hill, A., Hunt, C., Lucarini, G., Morales, J., Mutri, G., Prendergast,

589   A., Pryor, A., Rabett, R., Reynolds, T., Spry-Marques, P., Twati, M., 2012. The Cyrenaican

590   Prehistory Project 2012: the fifth season of investigations of the Haua Fteah cave. Libyan

591   Studies 43, 115–136.

592   Barker, G., Hunt, C., Reynolds, T., 2007. The Haua Fteah, Cyrenaica (Northeast Libya): renewed

593   investigations of the cave and its landscape, 2007. Libyan Studies 38, 1–22.

594 Barton, R.N.E., Bouzouggar, A., Bronk-Ramsey, C., Collcutt, S.N., Higham T.F.G., Humphrey, L.T.,

595   Parfitt, S., Rhodes, E.J., Schwenninger, J.L., Stringer, C.B., Turner, E., Ward, S., 2007. Abrupt

596   climate change and chronology of the Upper Palaeolithic in northern and eastern

597   Morocco. In: Mellars, P., Boyle, K., Bar-Yosef, O., Stringer, C. (Eds.), Rethinking the Human

598   Revolution: New Behavioural & Biological Perspectives on the Origins and Dispersal of

599   Modern Humans. McDonald Institute for Archaeological Research, Cambridge, pp. 177–

600   186.

601 Bartov, Y., Goldstein, S.L., Stein, M., Enzel, Y., 2003. Catastrophic arid episodes in the Eastern

602   Mediterranean linked with the North Atlantic Heinrich events. Geology 31, 439-442.

603 Bouzouggar, A., Barton, N., Vanhaeren, M., d'Errico, F., Collcutt, S., Higham, T., Hodge, E.,

604   Parfitt, S., Rhodes, E., Schwenninger, J-L., Stringer, C., Turner, E., Ward, S., Moutmir, A.,

605   Stambouli, A., 2007. 82,000-year-old shell beads from North Africa and implications for

606   the origins of modern human behavior. Proceedings of the National Academy of Sciences

607   104, 9964-9969. doi: ☐10.1073/PNAS.0703877104

608 Bouzouggar, A., Barton, R.N.E., Blockley, S., Bronk-Ramsey, C., Collcutt, S., Gale, R., Higham, T.,

609   Humphrey, L.T., Parfitt, S., Turner, E., Ward, S., 2008. Reevaluating the age of the

610   Iberomaurusian in Morocco. African Archaeological Review 25, 3–19. doi:

611   0.1007/s10437-008-9023-3

612 Brown, W.A.B., Christofferson, P.V., Massler, M., Weiss, M.B., 1960. Postnatal tooth

613   development in cattle. American Journal of Veterinary Research 21, 7–34.

614 Bryant, J.D., Froelich, P.N., 1995. A model of oxygen isotope fractionation in body water of

615   large mammals. Geochimica et Cosmochimica Acta 59, 4523–4537.

616 Camberlin, P., Janicot, S., Poccard, I., 2001. Seasonality and atmospheric dynamics of the

617   teleconnection between African rainfall and tropical sea-surface temperature: Atlantic vs.

618   ENSO. International Journal of Climatology 21, 973–1005. doi:10.1002/joc.673

619   Cancellieri, E., di Lernia, S., 2013. Middle Stone Age human occupation and dispersals in the

620   Messak plateau (SW Libya, central Sahara) Quaternary International 300, 142–152.

621   doi:10.1016/j.quaint.2012.08.2054

622   Cassinello, J., Cuzin, F., Jdeidi, T., Masseti, M., Nader, I. & de Smet, K. 2008. Ammotragus lervia.

623   The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Last

624   accessed on 14 April 2015.

625   Castañeda, I.S., Mulitza, S., Schefuβ, E., dos Santos, R.A.L., Sinninghe Damste, J.S., Schouten, S.,

626   2009. Wet phases in the Sahara/Sahel region and human migration patterns in North

627   Africa. Proceedings of the National Academy of Sciences 106, 20159–20163.

628   doi:10.1073/PNAS.0905771106

629   Combourieu Nebout, N., Peyron, O., Dormoy, I., Desprat, S., Beaudouin, C., Kotthoff, U., Marret,

630   F., 2009. Rapid climatic variability in the west Mediterranean during the last 25 000 years

631   from high resolution pollen data. Climate of the Past 5, 503–521.

632   Cox, J.R., Martin-R, M.H., Ibarra-F, F.A., Fourie, J.H., Rethman, J.T.G., Wilcox, D.G., 1988. The

633   influence of climate and soils on the distribution of four African grasses. Journal of Range

634   Management 41, 127–139.

635   Cremaschi, M., di Lernia, S., 1999. Holocene climate changes and cultural dynamics in the

636   Libyan Sahara. African Archaeological Review 16, 211–238.

637   Cremaschi, M., di Lernia, S., Garcea, E., 1998. Some insights on the Aterian in the Libyan

638   Sahara: chronology, environment, and archaeology. African Archaeological Review 15,

639   261–286.

640   D'Angela, D., Longinelli, A., 1990. Oxygen isotopes in living mammal's bone phosphate: further

641   results. Chemical Geology 86, 75–82.

642   Dansgaard, W., 1964. Stable isotopes in precipitation. Tellus 16, 436–468.

643   Darling, W.G., 2004. Hydrological factors in the interpretation of stable isotopic proxy data

644   present and past: a European perspective. Quaternary Science Reviews 23, 743–770.

645   doi:10.1016/j.quascirev.2003.06.016

646 De Rijk, S., Hayes, A., Rohling, E.J., 1999. Eastern Mediterranean sapropel S1 interruption: an

647   expression of the onset of climatic deterioration around 7 ka BP. Marine Geology 153,

648   337–343.

649 Delgado Huertas, A., Iacumin, P., Stenni, B., Sánchez Chillón, B., Longinelli, A., 1995. Oxygen-

650   isotope variations of phosphate in mammalian bone and tooth enamel. Geochimica et

651   Cosmochimica Acta 59, 4299–4305.

652 di Lernia, S., 2001. Dismantling dung: Delayed use of food resources among early Holocene

653   foragers of the Libyan Sahara. Journal of Anthropological Archaeology 20, 408–441.

654 di Lernia, S., N'siala, I.M., Mercuri, A.M., 2012. Saharan prehistoric basketry. Archaeological

655   and archaeobotanical analysis of the early-middle Holocene assemblage from Takarkori

656   (Acacus Mts., SW Libya). Journal of Archaeological Science 39, 1837–1853.

657   doi:10.1016/j.jas.2012.01.026

658 Dongmann, G., Nürnberg, H.W., Förstel, H., Wagener, K., 1974. On the enrichment of $H_2^{18}O$ in

659   the leaves of transpiring plants. Radiation and Environmental Biophysics 11, 41–52.

660 Douka, K., Jacobs, Z., Lane, C., Grün, R., Farr, L., Hunt, C., Inglis, R.H., Reynolds, T., Albert, P.,

661   Aubert, M., Cullen, V., Hill, E., Kinsley, L., Roberts, R.G., Tomlinson, E.L., Wulf, S., Barker, G.,

662   2014. The chronostratigraphy of the Haua Fteah cave (Cyrenaica, northeast Libya).

663   Journal of Human Evolution 66, 39–63. doi:10.1016/j.jhevol.2013.10.001

664 Drake, N.A., Blench, R.M., Armitage, S.J., Bristow, C.S., White, K.H., 2011. Ancient watercourses

665   and biogeography of the Sahara explain the peopling of the desert. Proceedings of the

666   National Academy of Sciences 108, 458–462.

667 Duplessy, J-C., Labeyrie, L., Waelbroeck, C., 2002. Constraints on the ocean oxygen isotopic

668   enrichment between the Last Glacial Maximum and the Holocene: Paleoceanographic

669   implications. Quaternary Science Reviews 21, 315–330.

670 Eeley, H.A.C., Lawes, M.J., Piper, S.E., 1999. The influence of climate change on the distribution

671   of indigenous forest in KwaZulu-Natal, South Africa. Journal of Biogeography 26, 595–617.

672   Ehleringer, J.R., Dawson, T.E., 1992. Water uptake by plants: perspectives from stable isotope

673   composition. Plant, Cell and Environment 15, 1073–1082.

674   El-Darier, S.M., El-Mogaspi, F.M., 2009. Ethnobotany and relative importance of some endemic

675   plant species at El-Jabal El-Akhdar Region (Libya). World Journal of Agricultural Sciences

676   5, 353–360.

677   El-Nouty, F.D., Hassan, G.A., Taher, T.H., Samak, M.A., Abo-Elezz, Z., Salem, M.H., 1988. Water

678   requirements and metabolism in Egyptian Barki and Rahmani sheep and Baladi goats

679   during spring, summer and winter seasons. Journal of Agricultural Science, Cambridge

680   111, 27–34.

681   Elderfield, H., Ganssen, G., 2000. Past temperature and $\delta^{18}O$ of surface ocean waters inferred

682   from foraminiferal Mg/Ca ratios. Nature 405, 442–445.

683   Elfadli, K.I., 2009. Precipitation Data of Libya. Libyan National Meteorological Center (LNMC).

684   El Kenawy, A.M., López-Moreno, J.I., Vicente-Serrano, S.M., Mekld, M.S., 2009. Temperature

685   trends in Libya over the second half of the 20th century. Theoretical and Applied

686   Climatology 98, 1–8.

687   Farr, L., Lane, R., Abdulazeez, F., Bennett, P., Holman, J., Marasi, A., Prendergast, A., Al-Zweyi,

688   M., Barker, G., 2014. The Cyrenaican Prehistory Project 2013: the seventh season of

689   excavations in the Haua Fteah cave. Libyan Studies 45, 163–173. doi:10.1017/lis.2014.2

690   Garcea, E.A.A., 2006. Semi-permanent foragers in semi-arid environments of North Africa.

691   World Archaeology 38, 197–219.

692   Ghoneim, E., Robinson, C., El-Baz, F., 2007. Radar topography data reveal drainage relics in the

693   eastern Sahara. International Journal of Remote Sensing 28, 1759–1772.

694   Gourcy, L., 2005. Isotopic composition of precipitation in the Mediterranean Basin in relation

695   to air circulation patterns and climate. IAEA, Vienna.

696   Hamad, S., 2009. Geostatistical analysis of groundwater levels in the south Al Jabal Al Akhdar

697 area using GIS. GIS Ostrava 25-28, 1–10.

698 Hoppe, K.A., 2006. Correlation between the oxygen isotope ratio of North American bison

699 teeth and local waters: Implication for paleoclimatic reconstructions. Earth and Planetary

700 Science Letters 244, 408–417. doi:10.1016/j.epsl.2006.01.062

701 Hunt, C.O., Davison, J., Inglis, R., Farr, L., Reynolds, T., Simpson, D., el-Rishi, H., Barker, G., 2010.

702 Site formation processes in caves: The Holocene sediments of the Haua Fteah, Cyrenaica,

703 Libya. Journal of Archaeological Science 37, 1600–1611. doi:10.1016/j.jas.2010.01.021

704 Hunt, C.O., Reynolds, T.G., El-Rishi, H.A., Buzaian, A., Hill, E., Barker, G., 2011. Resource

705 pressure and environmental change on the North African littoral: Epipalaeolithic to

706 Roman gastropods from Cyrenaica, Libya. Quaternary International 244, 15–26.

707 doi:10.1016/j.quaint.2011.04.045

708 IAEA/WMO 2015. Global Network of Isotopes in Precipitation. The GNIP Database.

709 <http://www.iaea.org/water>.

710 Inglis, R., 2012. Human occupation and changing environments during the Middle to Later

711 Stone Ages: soil micromorphology at the Haua Fteah, Libya. PhD Thesis, University of

712 Cambridge, United Kingdom.

713 Irish, J., 2000. The Iberomaurusian enigma: North African progenitor or dead end? Journal of

714 Human Evolution 39, 393–410. doi:10.1006/jhev.2000.0430

715 Jeffrey, A., Denys, C., Stoetzel, E., Lee-Thorp, J.A. 2015. Influences on the stable oxygen and

716 carbon isotopes in gerbillid rodent teeth in semi-arid and arid environments: Implications

717 for past climate and environmental reconstruction. Earth and Planetary Science Letters

718 428, 84-96.

719 Jones, S., Farr, L., Barton, H., Drake, N., White, K., Barker, G., 2011. Geoarchaeological patterns

720 in the pre-desert and desert ecozones of northern Cyrenaica. Libyan Studies 42, 11–19.

721 King, J.M., 1983. Livestock water needs in pastoral Africa in relation to climate and forage.

722 International Livestock Centre for Africa Researh Report No. 7.

723 Klein, R.G., Scott, K., 1986. Re-analysis of faunal assemblages from the Haua Fteah and other

724   Late Quaternary archaeological sites in Cyrenaican Libya. Journal of Archaeological

725   Science 13, 515–542.

726 Kohn, M.J., 1996. Predicting animal $\delta^{18}O$: Accounting for diet and physiological adaptation.

727   Geochimica et Cosmochimica Acta 60, 4811–4829.

728 Kuper, R., Kröpelin, S., 2006. Climate-controlled Holocene occupation in the Sahara: Motor of

729   Africa's evolution. Science 313, 803–807.

730 Lionello, P., Malanotte-Rizzoli, P., Boscolo, R., Alpert, P., Artale, V., Li, L., Luterbacher, J., May,

731   W., Trigo, R., Tsimplis, M., Ulbrich, U., Xoplaki, E., 2006. The Mediterranean climate: an

732   overview of the main characteristics and issues. In: Lionello, P., Malanotte-Rizzoli, P.,

733   Boscolo, R. (Eds.), Mediterranean Climate Variability. Elsevier, London.

734 Longinelli, A., 1984. Oxygen isotopes in mammal bone phosphate: a new tool for

735   paleohydrological and paleoclimatological research? Geochimica et Cosmochimica Acta

736   48, 385–390.

737 Luz, B., Cormie, A.B., Schwarcz, H.P., 1990. Oxygen isotope variations in phosphate of deer

738   bones. Geochimica et Cosmochimica Acta 54, 1723–1728.

739 Luz, B., Kolodny, Y., 1985. Oxygen isotope variations in phosphate of biogenic apatites, IV.

740   Mammal teeth and bones. Earth and Planetary Science Letters 75, 29–36.

741 Luz, B., Kolodny, Y., Horowitz, M., 1984. Fractionation of oxygen isotopes between mammalian

742   bone-phosphate and environmental drinking water. Geochimica et Cosmochimica Acta 48,

743   1689–1693.

744 McBurney, C.B.M., 1967. The Haua Fteah (Cyrenaica) and the Stone Age of the South-East

745   Mediterranean. Cambridge University Press, Cambridge.

746 McBurney, C.B.M., Hey, R.W., 1955. Prehistory and Pleistocene geology in Cyrenaican Libya.

747   Cambridge University Press, Cambridge.

748 Murphy, B.P., Bowman, D.M.J.S., Gagan, M.K., 2007. The interactive effect of temperature and

749   humidity on the oxygen isotope composition of kangaroos. Journal of Ecology 21, 757–
750   766.

751   Ogren, H.A., 1965. Barbary sheep. New Mexico Department of Fish and Game Bulletin, Vol. 13.

752   Pachur, H., Rottinger, F., 1997. Evidence for a large extended paleolake in the eastern Sahara
753   as revealed by spaceborne radar lab images. Remote Sensing of the Environment 61, 437–
754   440.

755   Passey, B.H., Cerling, T.E., 2002. Tooth enamel mineralization in ungulates: implications for
756   recovering a primary isotopic time-series. Geochimica et Cosmochimica Acta 66, 3225–
757   3234.

758   Paul, H.A., Bernasconi, S.M., Schmid, D.W., McKenzie, J.A., 2001. Oxygen isotopic composition
759   of the Mediterranean Sea since the Last Glacial Maximum: constraints from pore water
760   analyses. Earth and Planetary Science Letters 192, 1–14.

761   Petit-Maire, N., 1991. Recent Quaternary climatic change and man in the Sahara. Journal of
762   African Earth Sciences 12, 125–132.

763   Poage, M.A., Chamberlain, C.P., 2001. Empirical relationships between elevation and the stable
764   isotope composition of precipitation and surface waters: considerations for studies of
765   paleoelevation change. American Journal of Science 301, 1–15.

766   Pomposi, C., Kushnir, Y., Giannini, A., 2014. Moisture budget analysis of SST-driven decadal
767   Sahel precipitation variability in the twentieth century. Climate Dynamics.
768   doi:10.1007/s00382-014-2382-3

769   Prendergast, A., 2013. Late Pleistocene to Holocene human-environment interaction in the
770   southeastern Mediterranean: Stable isotope analysis of mollusc shells from Haua Fteah,
771   Libya and Ksar Akil, Lebanon. PhD Thesis, University of Cambridge, United Kingdom.

772   Prendergast, A. L., Stevens, R. E., O'Connell, T. C., Hill, E., Hunt, C., and Barker, G. W. submitted.
773   A late Pleistocene refugium in North Africa? Palaeoenvironmental reconstruction from
774   stable isotope analysis of land snail shells (Haua Fteah, Libya), Quaternary Science

775   Reviews.

776   Prendergast, A. L., Stevens, R. E., O'Connell, T. C., Fadlalak, A., Touati, M., Al Muzeni, A., Schöne,

777   B. R., Hunt, C., and Barker, G. W. accepted. Changing patterns of eastern Mediterranean

778   shellfish exploitation in the Late Glacial and Early Holocene: oxygen isotope evidence

779   from gastropod in Epipaleolithic to Neolithic human occupation layers at the Haua

780   Fteah, Libya. Quaternary International

781   Pryor, A.J.E., Stevens, R.E., O'Connell, T.C., Lister, J.R., 2014. Quantification and propagation of

782   errors when converting vertebrate biomineral oxygen isotope data to temperature for

783   palaeoclimate reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 412,

784   99–107. doi:10.1016/j.palaeo.2014.07.003

785   Rabett, R., Farr, L., Hill, E., Hunt, C., Lane, R., Moseley, H., Stimpson, C., Barker, G., 2013. The

786   Cyrenaican Prehistory Project 2012: the sixth season of excavations in the Haua Fteah

787   cave. Libyan Studies 44, 113–125. doi:10.1017/S0263718900009717

788   Reade, H., Stevens, R.E., Barker, G., O'Connell, T.C., 2015. Tooth enamel sampling strategies for

789   stable isotope analysis: Potential problems in cross-method data comparisons. Chemical

790   Geology 404, 126–135. doi:10.1016/j.chemgeo.2015.03.026

791   Reade, H.R. Stevens, R. E., O'Connell, T. C. and Barker, G. W. submitted. Pleistocene and

792   Holocene herbivore diets and palaeoenvironments in the Gebel Akhdar (Libya):

793   implications for past human populations. Palaeogeography, Palaeoclimatology,

794   Palaeoecology

795   Rozanski, K., Araguás-Araguás, L., Gonfiantini, R., 1992. Relation between long-term trends of

796   oxygen-18 isotope composition of precipitation and climate. Science 258, 981–985.

797   Scerri, E.M.L., 2013. The Aterian and its place in the North African Middle Stone Age.

798   Quaternary International 300, 111–130. doi:10.1016/j.quaint.2012.09.008

799   Schrag, D., Adkins, J., McIntyre, K., Alexander, J.L., Hodell, D., Charles, C.D., McManus, J., 2002.

800   The oxygen isotopic composition of seawater during the Last Glacial Maximum.

801   Quaternary Science Reviews 21, 331–342.

802   Shackleton, N.J., 1987. Oxygen isotopes, ice volume and sea level. Quaternary Science Reviews

803   6, 183–190.

804   Snyder, K.A., Tartowski, S.L., 2006. Multi-scale temporal variation in water availability:

805   Implications for vegetation dynamics in arid and semi-arid ecosystems. Journal of Arid

806   Environments 65, 219–234. doi:10.1016/j.jaridenv.2005.06.023

807   Stojanowski, C.M., Knudson, K.J., 2014. Changing patterns of mobility as a response to climatic

808   deterioration and aridification in the middle Holocene southern Sahara. American Journal

809   of Physical Anthropology 154: 79-93. doi:10.1002/ajpa.22474

810   Suga, S., 1982. Progressive mineralization pattern of developing enamel during the

811   maturation stage. Journal of Dental Research 61, 1532–1542.

812   Sultan, M., Sturchio, N., Hassan, F., Hamdan, M., Mahmood, A., El Alfy, Z., Stein, T., 1997.

813   Precipitation source inferred from stable isotopic composition of Pleistocene

814   groundwater and carbonate deposits in the Western Desert of Egypt. Quaternary

815   Research 48, 29–37.

816   Tafuri, M.A., Bentley, R.A., Manzi, G., di Lernia, S., 2006. Mobility and kinship in the prehistoric

817   Sahara: Strontium isotope analysis of Holocene human skeletons from the Acacus Mts.

818   (southwestern Libya). Journal of Anthropological Archaeology 25, 390–402.

819   doi:10.1016/j.jaa.2006.01.002

820   Weinreb, M.M., Sharav, Y., 1964. Tooth development in sheep. Journal of Veterinary Research

821   25, 891–908.

822   Yan, Z.W., Petit-Maire, N., 1994. The last 140-ka in the Afro-Asian arid semiarid transitional

823   zone. Palaeogeography, Palaeoclimatology, Palaeoecology 110, 217–233.

824   Zazzo, A., Balasse, M., Patterson, W.P., 2005. High-resolution δ^{13}C intratooth profiles in bovine

825   enamel: implications for mineralization pattern and isotopic attenuation. Geochimica et

826   Cosmochimica Acta 69, 3631–3642. doi:10.1016/j.gca.2005.02.031

Figure captions

829 Figure 1. Map of the Gebel Akhdar showing the position of the Haua Fteah and Hagfet ed
830 Dabba caves. Grey areas represent areas of higher elevation (*Drawing: D. Kemp*).

831 Figure 2. Bulk-tooth δ^{18}O results from all samples, displayed by species. Each circle (top
832 graph) represents an individual animal. Boxplots (bottom graph) represent the median and
833 interquartile ranges for each group. Haua Fteah samples are grouped by cultural
834 attribution. Hagfet ed Dabba samples have an uncertain chronological association (both
835 within site and with Haua Fteah), but are thought to be most likely associated with the
836 Dabban at Haua Fteah. All samples from Hagfet ed Dabba are plotted as a single
837 population.

838 Figure 3. Bulk-tooth δ^{18}O from Haua Fteah *A. lervia* and *Bos* sp. for samples that can be
839 attributed to specific stratigraphic layers/layer groupings, where n≥3. Where possible, age
840 estimates for each group are provided in table 1. Each circle (top graph) represents and
841 individual animal. Boxplots (bottom graph) represents the median and interquartile ranges
842 for each group.

843 Figure 4. Bulk-tooth δ^{18}O from Hagfet ed Dabba, grouped by stratigraphic layer. Each
844 circle (top graph) represents and individual animal. Boxplots (bottom graph) represents the
845 median and interquartile ranges for each group.

846 **Table captions**

847 Table 1: The chronology of the Haua Fteah archaeological sequence according to
848 McBurney (1967) and the Bayesian statistical model from Douka et al. (2014) at 68.2%
849 and 95.4% confidence. Age estimations from specific layers/layer groupings from which
850 samples analysed in this study come from are also provided. The listed age estimates
851 presented are made using dates published in Douka et al. (2014) with correlations in site
852 stratigraphy made between the McBurney excavations and the recent TRANS-NAP
853 excavations. Dates with a * are based on a single sample, dates in italics are from
854 Bayesian model estimates, all others are determinations from multiple radiocarbon
855 samples.

856 Table 2: Summary of δ^{18}O tooth enamel data from Haua Fteah and Hagfet ed Dabba,
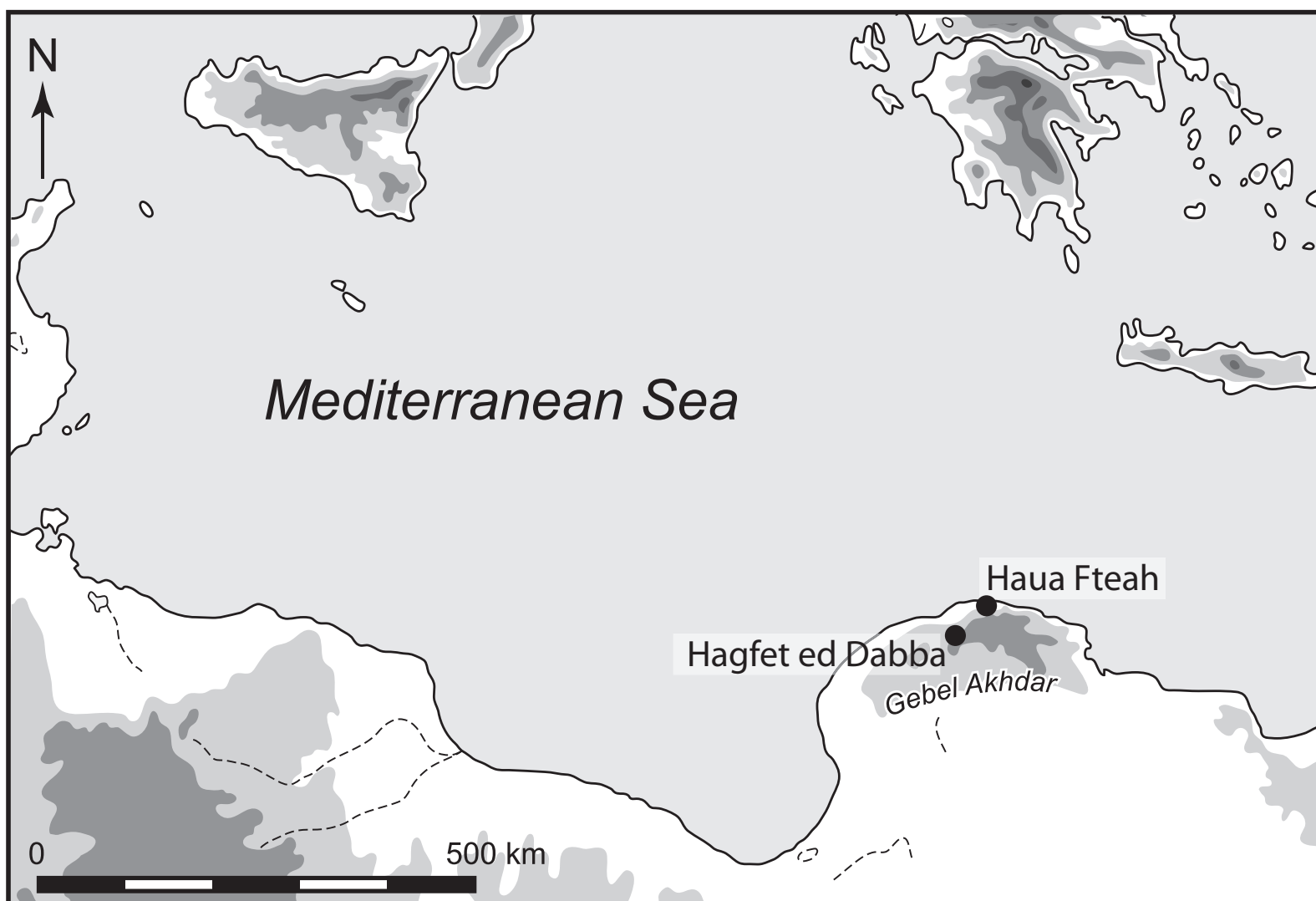857 divided by cultural phase. A full list of results is available in Appendix A.
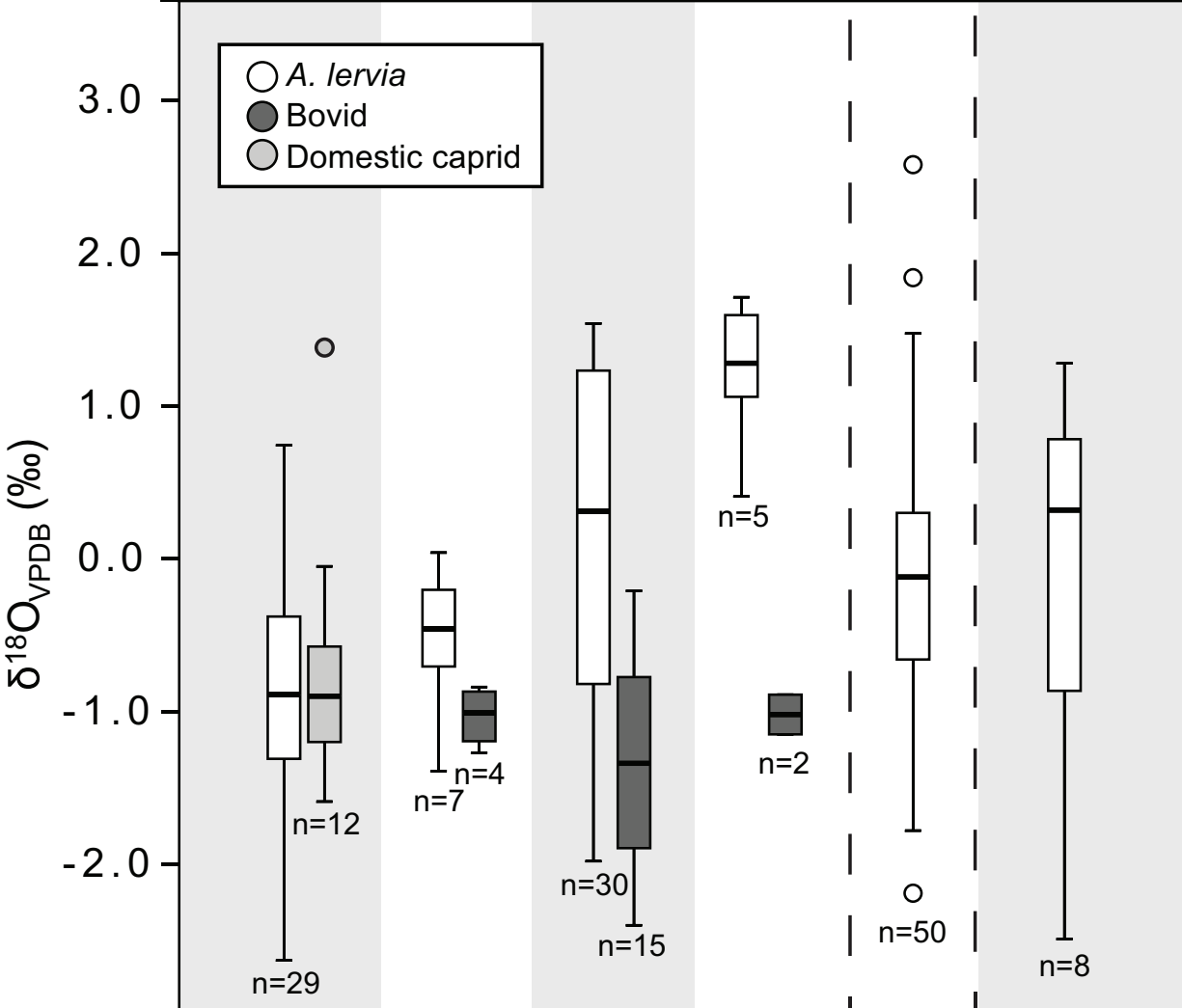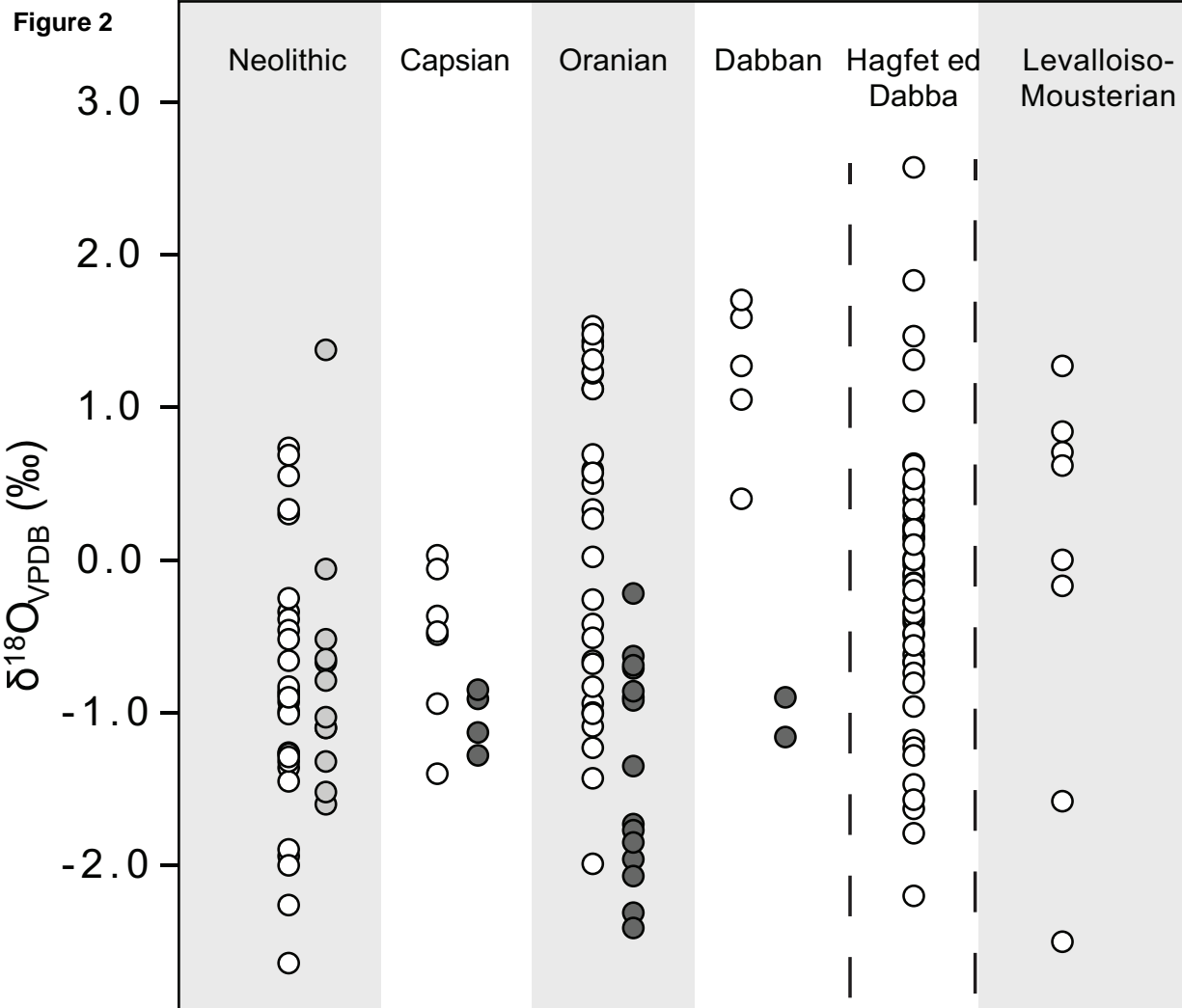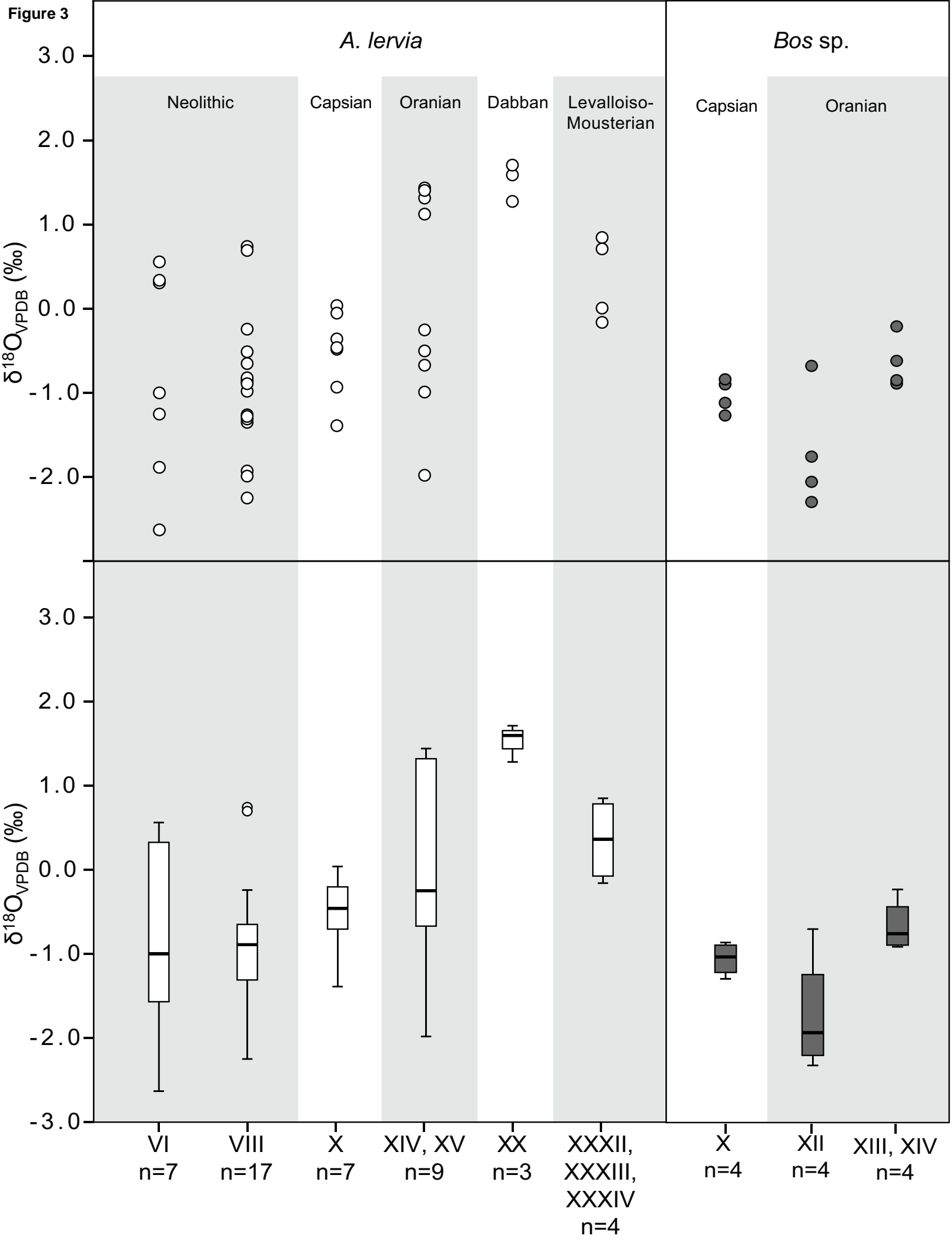
Figure 1
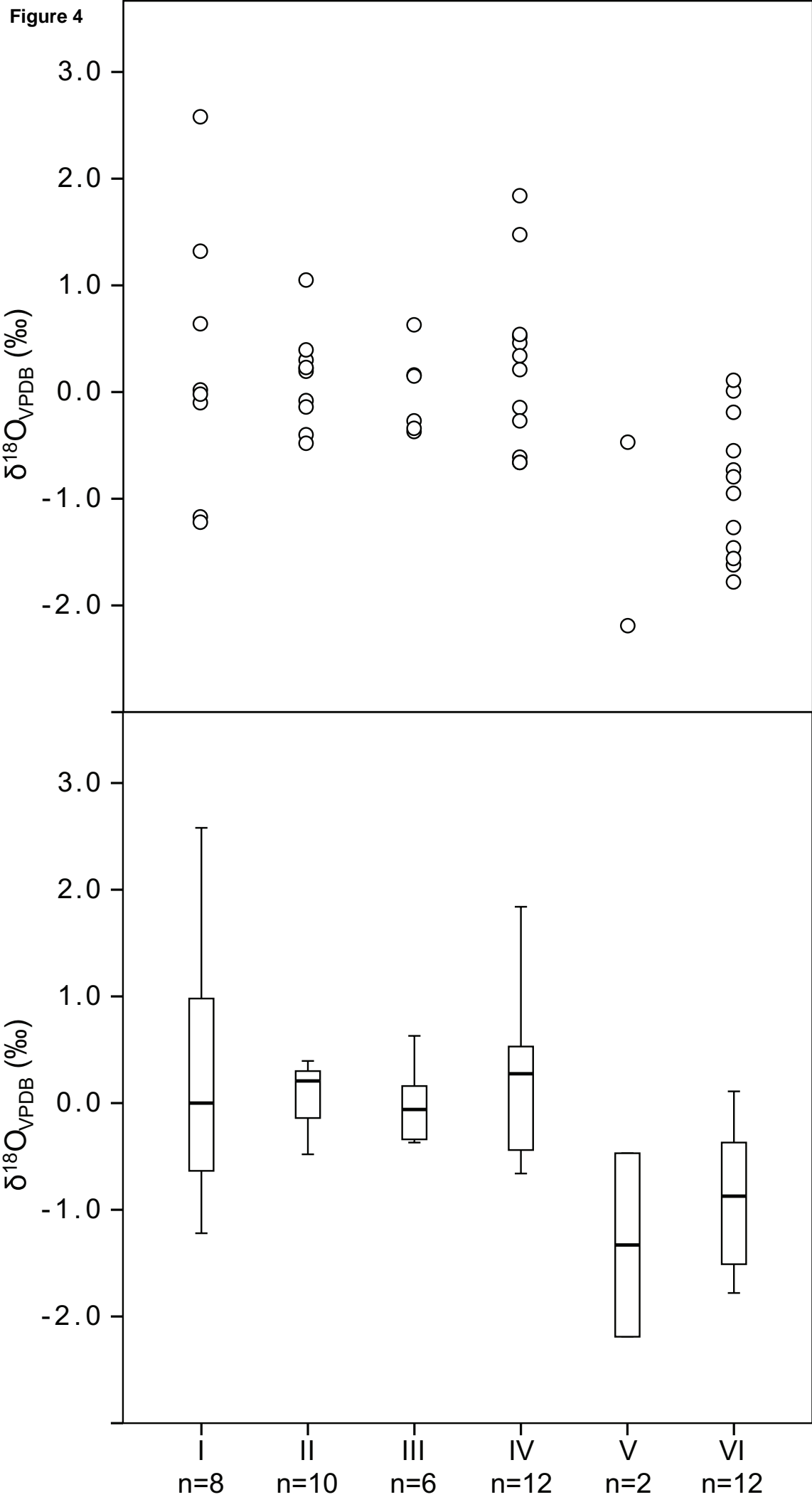
Figure 2

Figure 3

Figure 4

Table 1

Phase	Layers (McBurney, 1967)	Proposed Age (ka) for cultural phases			Age estimations for specific layers/layer groupings from which samples in this study came	
		McBurney (1967)	Douka et al. (2014)		Layer	Proposed Age (ka)
			68.2%	95.4%		
Levalloiso-Mousterian	XXXIV-XXV	65 - 40	68.1 -48.7	73.3 – 43.5	XXXII,XXXIII,XXXIV	*73.3 – 64.0*
Dabban	XXV-XVI	40 - 15	40.0 -18.1	43.5 – 17.1	XX	32.8 – 31.0
Oranian	XV-XI	15 - 10	16.1 -13.1	17.2 – 12.5	XIV, XV XII	16.6 – 14.7 15.0 – 13.5
Capsian	X-IX	10 - 7	12.3 -9.3	12.7 – 7.9	X	*12.6 – 7.9*
Neolithic	VIII-IV	7 - 4.7	7.7 -6.2	9.3 – 5.4	VIII VI	7.4 – 6.9 6.4 - 6.2*

Table 2

Site	Layer(s)	Cultural 'Phase'	Species	n	Enamel δ^{18}O (VPDB, ‰)				
					Mean ± Standard deviation	Median	Max	Min	Range
Haua Fteah	VIII-IV	Neolithic	*A. lervia*	29	-0.9 ± 0.9	-0.9	0.7	-2.6	3.4
			Domestic caprid	12	-0.7 ± 0.8	-0.9	1.4	-1.6	3.0
	X-IX	Capsian	*A. lervia*	7	-0.5 ± 0.5	-1.0	0.0	-1.4	1.4
			Bos sp.	4	-1.0 ± 0.2	-1.3	-0.8	-1.3	0.4
	XV-XI	Oranian	*A. lervia*	30	0.1 ± 1.1	0.3	1.5	-2.0	3.5
			Bos sp.	15	-1.3 ± 0.7	-1.3	-0.2	-2.4	2.2
	XXV-XVI	Dabban	*A. lervia*	5	1.2 ± 0.5	1.3	1.7	0.4	1.3
			Bos sp.	2			-0.9	-1.2	0.3
	XXXIV-XXV	Levalloiso-Mousterian	*A. lervia*	8	-0.1 ± 1.3	0.3	1.3	-2.5	3.8
Hagfet ed Dabba	I	Roman(?)	*A. lervia*	8	0.3 ± 1.3	0.0	2.6	-1.2	3.8
	II	Dabban	*A. lervia*	10	0.1 ± 0.4	0.2	1.1	-0.5	1.5
	III		*A. lervia*	6	0.0 ± 0.4	-0.1	0.6	-0.4	1.0
	IV		*A. lervia*	12	0.3 ± 0.8	0.3	1.8	-0.7	2.5
	V		*A. lervia*	2			-0.5	-2.2	1.7
	VI		*A. lervia*	12	-0.9 ± 0.7	-0.9	-0.1	-1.8	1.9