Pleistocene and Holocene herbivore diets and palaeoenvironments in the Gebel Akhdar (Libya): implications for past human populations

Hazel Reade*[1,3], Rhiannon E. Stevens[1,3], Tamsin C. O'Connell[1,2], and Graeme Barker[1,2]

[1] McDonald Institute for Archaeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, UK
[2] Department of Archaeology and Anthropology, University of Cambridge, Downing Street, CB2 3DZ, UK
*Corresponding author's e-mail: h.reade@ucl.ac.uk
[3]Present address: UCL Institute of Archaeology, 31-34 Gordon Square, London WC1H 0PY, UK

Abstract

The Gebel Akhdar massif in Cyrenaica, northeast Libya, has yielded a long record of human occupation going back at least 100,000 years. To date, there is only a limited understanding of how the landscape of the region varied in response to the climatic fluctuations of the last glacial-interglacial cycle, and the implications of these changes for local human populations remain largely unexplored. This study provides an isotope-based interpretation of past environments directly linked to the archaeological record. Tooth enamel stable carbon isotope ratios ($\delta^{13}C$) from herbivore species hunted by past human populations are used to infer the isotopic characteristics of past diet and vegetation, and in turn the likely environmental conditions that prevailed during periods when humans were active within the landscape. To provide a baseline from which to interpret the archaeological $\delta^{13}C$ data, modern samples are considered in relation to their diet and environmental origin. Archaeological samples come from 2 cave sites, Haua Fteah and Hagfet ed Dabba, and span a period from oxygen isotope stage 4 to the mid-Holocene. While results indicate a more arid environment in the Pleistocene and an increase in humidity at the onset of the Holocene, the overall picture is one of relative environmental stability. The biggest landscape change observed in the data occurs during the mid-Holocene Neolithic, when C_4 plant species become evident in the herbivore diet for the first time. There is little evidence to suggest that this occurred at a time of any large-scale climate variation, and thus the contribution of anthropogenic influences to vegetation change is considered likely.

Key words:

Haua Fteah; carbon isotopes; North Africa; tooth enamel; C4 vegetation; human occupation

Highlights

- We study caprid and bovid tooth enamel carbon isotopes to infer diet and vegetation
- Archaeological samples from Haua Fteah and Hagfet ed Dabba are analysed
- Palaeoenvironmental interpretations for the Gebel Akhdar (Libya) are made
- The environment was relatively stable from OIS 4 to the mid Holocene
- An increase in C_4 plant species in the Neolithic is demonstrated

1. Introduction

The Gebel Akhdar massif in Cyrenaica, northeast Libya (Fig. 1), possesses an archaeological record that extends back to at least oxygen isotope stage (OIS) 5 (ca. 128 – 74 ka) (McBurney, 1967; Barker et al., 2007; Douka et al., 2014) and likely to OIS 6 (ca. 195 – 128 ka) on the evidence of unpublished OSL dates from the Haua Fteah cave (pers. comm. Z. Jacobs). Across this time period numerous oscillations in climate occurred at a wide range of spatial and temporal scales, which in North Africa were predominately manifested as shifts between wetter and drier conditions (Cacho et al., 2000; Sierro et al., 2005; Enzel et al., 2008; Kwiecien et al., 2009; Castañeda et al., 2010; Sprovieri et al., 2012). Concurrently, archaeological archives from across the region appear to display varying periods of population expansions and contractions, some of which occurred in step with environmental changes (Hoelzmann et al., 2001; Garcea, 2006; 2012a; Castañeda et al., 2009; Scerri, 2013). In particular, people appear to have been absent from many areas within North Africa during times when hyper-arid conditions prevailed across much of the region (Clark, 1980; Petit-Maire, 1991; Cremaschi et al., 1998; Cancellieri and di Lernia, 2013; Foley et al., 2013). In contrast, the archaeology of the Gebel Akhdar, a coastal area of varied topography (Fig. 1), alludes to a different population history, with people being present in the region during each OIS of the last interglacial-glacial cycle, albeit likely in varying numbers and not necessarily continuously (McBurney, 1967; Barker et al., 2010; 2012; Jones et al., 2011). This raises the question of whether favourable environmental conditions in the Gebel Akhdar made the region attractive for occupation during periods when other areas of North Africa appear to have been largely abandoned.

Rising to a maximum elevation of ~780m the Gebel Akhdar is today cooler and more humid than the surrounding desert regions (El-Darier and El-Mogaspi, 2009). Local mean annual precipitation ranges from <250mm to >600mm and mean annual temperatures from 16 to 21°C (Elfadli, 2009; El Kenawy et al., 2009; Ageena et al., 2014). Presently, the area has the richest vegetation and highest floral diversity of any area in Libya. Maquis scrubland dominates the local vegetation, with common species including *Juniperus phoenicea, Quercus coccifera, Pistacia lentiscus*, and *Ceratonia siliqua,* while steppe species such as *Sarcopoterium spinosum*, and *Artemisia* sp. are also common (Al-Sodany et al., 2003; El-Darier & El-Mogaspi, 2009). A high degree of floral endemism suggests that the Gebel Akhdar may have been biogeographically isolated for an extended period of time (Hegazy et al., 2011), and combined with its geographical setting may indicate that in the past, as is the case today, the Gebel Akhdar provided an environment notably different from adjacent more desertic regions of North Africa.

Palaeoenvironmental research to date has indicated that the Gebel Akhdar experienced relatively low magnitude variations in temperatures and rainfall amounts over the last ~100,000 years (Inglis, 2012; Reade et al., 2015a; Prendergast, et al., submitted). Alluvial, tufa, and dune deposits are all found within the region suggesting the amount of moisture in the landscape varied with time, but a lack of precise chronological understanding of these deposits hinders comparisons with the archaeological record (Hey, 1955). Sediments in the Haua Fteah cave, which contain archaeological material, indicate periods of increased climate instability, particularly during OIS 3 (ca. 59 – 24 ka) (Inglis, 2012). However, while these archives are sensitive to landscape-scale environmental conditions they are also heavily influenced by sedimentary and taphonomic processes within the cave, making environmental interpretations complex (Hunt et al., 2010; Inglis, 2012). Mollusc isotope data from the cave suggests an increase in aridity during OIS 2 (ca. 24 – 12 ka) (Prendergast et al., submitted). There is currently only a limited understanding of the impacts of these climatic variations on the local landscape. Differences in the species composition of mammalian and molluscan assemblages in the Haua Fteah and other archaeological sites have been use to infer shifts in the composition of woodland/steppic environments, although as these assemblages are the result of human procurement, the sensitivity of the archives to natural variations may be reduced (Higgs, 1967; Klein and Scott, 1986; Hunt et al., 2011). Thus there remains a need to gain further palaeoenvironmental insights from archives, which are linked to, but not directly influenced by, human activity.

Here we focus on estimating past vegetation and environmental conditions in the Gebel Akhdar through stable isotope analysis of mammalian faunal remains from two cave sites, Haua Fteah and Hagfet ed Dabba. The carbon isotope ($\delta^{13}C$) composition of tooth enamel apatite is used to infer the $\delta^{13}C$ of past herbivore diet, and in turn to isotopically characterise local vegetation. From this, the types of plants present within the region and the climatic conditions under which they grew can be approximated. The samples used in this study come from archaeological contexts and accumulated through human activities, so provide data temporally tied to periods when people were present within the local landscape. Analysed samples from Pleistocene-aged deposits come exclusively from wild herbivore species (*Ammotragus lervia* and *Bos* sp.), while Holocene-aged samples consist of both wild and domestic species (*A. lervia* and *Capra* sp. and *Ovis* sp.). In addition to palaeoenvironmental insights, comparing Holocene wild and domestic caprids provides the means to explore whether differences in ‘natural’ and ‘anthropogenic’ influences on herbivore diet can be identified. This contributes to investigations into human exploitation of local plant and animal resources, a topic of particular interest in understanding the development of the Neolithic in this region of North Africa (Lucarini et al., 2015). To provide a baseline from which to interpret the archaeological data, samples from modern herbivore species are also analysed.

2. Background

2.1 Archaeological context

Several caves have been excavated in the Gebel Akhdar revealing stratified sediments containing archaeological material. These place humans in the landscape at least as early as OIS 5 (ca. 128 – 74 ka) (Douka et al., 2014). By far the most significant site is the Haua Fteah (32.90˚N, 22.05˚E, ~50m asl, Fig. 1), a large rock shelter situated ~1km from the present day coastline on the northward facing lowest escarpment of the Gebel Akhdar. The cave was first excavated during the 1950s and its re-excavation has been a central part of a renewed programme of archaeological investigation in the region since 2007 (McBurney, 1967; Barker et al., 2007; 2008; 2010; 2009; 2012; Rabett et al., 2013; Farr et al., 2014). From the original excavations McBurney (1967) described an archaeological sequence containing (using his terminology) Middle Palaeolithic (Pre-Aurignacian and Levalloiso-Mousterian), Upper Palaeolithic (Dabban and Oranian), Epipaleaolithic (Libyco-Capsian), Neolithic (of Capsian tradition), Graeco-Roman, and post-Classical deposits (McBurney, 1967). The ongoing re-excavation of the cave and the reanalysis of the archive of material from the McBurney excavations are examining whether these divisions and terminologies remain appropriate. All samples selected for isotope analysis reported in this study are from the McBurney archives and data is discussed using the McBurney cultural determinations. Chronological age estimates for the cultural phases are displayed in Table 1 (Douka et al., 2014). These are the most probable upper and lower dates for each phase; 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.

Isotope investigations of archaeological fauna from a smaller cave in the Gebel Akhdar, the Hagfet ed Dabba (32.68˚N, 21.56˚E, 365m asl, Fig. 1), are also presented. The cave is located ~15km from the present-day coast and ~60km from the Haua Fteah. Situated on a south-facing slope of a tributary of Wadi Kuf (today the main watershed of the Gebel Akhdar), the site was excavated in 1947 and 1948 by McBurney, with an additional small test-pit being made in 2008 (McBurney and Hey, 1955; Barker et al., 2008). As with the Haua Fteah, the Hagfet ed Dabba samples used in this study come solely from the McBurney excavations, which revealed stratified deposits containing Upper Palaeolithic Dabban lithics (Layers VII to II) and a loose sub-surface layer (Layer I) containing Roman pottery (McBurney and Hey, 1955). The Hagfet ed Dabba sequence remains undated, and the site's chronological context can only be inferred through correlation with the lithic assemblage at the Haua Fteah and the dates associated with these layers. In particular, McBurney suggested that a change in lithic technology occurring between layers VI and III at the Hagfet ed Dabba was similar to a change that occurs within layer XX at the Haua Fteah (McBurney and Hey, 1955; McBurney, 1967, pp. 170). Layer XX at the Haua Fteah has been dated to ca. 32 ka (Douka et al., 2014) . It is unclear what duration or frequency of occupation the Hagfet ed Dabba archaeological sequence represents.

2.2 Enamel isotopes in environmental studies

The stable carbon isotope composition of herbivore tooth enamel ($\delta^{13}C_{enamel}$) from archaeological sites is used to estimate herbivore diets and, in turn, local vegetation through a known enamel-diet $\delta^{13}C$ offset. Plant $\delta^{13}C$ is primarily determined by photosynthetic pathway (C_3, C_4, or Crassulacean acid metabolism (CAM)), but is also influenced by species physiology, atmospheric carbon and, in C_3 plants in particular, by climatic conditions (O'Leary, 1988; Farquhar et al., 1989; Ehleringer et al., 1997; Dawson et al., 2002; Marshall et al., 2007). Globally, around 85% of plants use the C_3 photosynthetic pathway (including trees, herbs and most temperate grasses) and display $\delta^{13}C$ values ranging from -38‰ to -22‰

(O'Leary, 1988; Still et al., 2003). C_3 plant $\delta^{13}C$ is sensitive to changes in water availability, which is a function of temperature, precipitation and relative humidity, as well as local environmental parameters such as soil type and topography (Dawson et al., 2002; Seibt et al., 2008). Typically, C_3 plants in open, more arid environments have higher $\delta^{13}C$, while plants in humid, dense canopy environments possess lower $\delta^{13}C$ (Seibt et al., 2008; Cernusak et al., 2009; Gebrekirstos et al., 2009; Kohn, 2010). At a global scale there is a negative relationship between C_3 plant $\delta^{13}C$ and mean annual precipitation, with $\delta^{13}C$ values >-25.5‰ restricted to regions where mean annual precipitation is <500mm (Kohn, 2010). Seasonal variation in $\delta^{13}C$ within C_3 species has been shown to be in the order of 1‰-3‰, with higher values typically occurring in the driest season (Ehleringer et al., 1992; Li et al., 2007). Such conditions most commonly summer, when temperatures are high, and in many temperate environments, rainfall low. In contrast, C_4 plant species are dominated by warm-/arid-adapted grasses with $\delta^{13}C$ values between -16‰ and -9‰ (O'Leary, 1988; Coplen et al., 2002). CAM photosynthesis is predominately restricted to succulent plants that are adapted to very arid conditions and display $\delta^{13}C$ values that can span much of the range observed in C_3 and C_4 species (O'Leary, 1981; Luttge, 2004; Marshall et al., 2007). CAM plants make up only a small proportion of total vegetation globally, and are unlikely to make a significant contribution to herbivore diet in most habitats.

Studies of modern herbivore populations have demonstrated that $\delta^{13}C_{enamel}$ reflects dietary $\delta^{13}C$ with a diet-enamel isotopic offset of ~14.1 ± 0.5 ‰ in medium to large herbivores (Cerling and Harris, 1999; Passey et al., 2005). Variations in $\delta^{13}C_{enamel}$ are linked to the proportion of different plant species in the diet and to the environmental conditions in which the plants grew (e.g. Lee-Thorp et al. 1989; Hoppe et al. 2004; 2006; Balasse et al. 2005; Fraser et al. 2008). When applied to archaeological/palaeontological assemblages, this relationship has been used to infer palaeodietary/palaeoenvironmental parameters, typically using either 'bulk' or 'intra-tooth' sampling approaches (e.g. Merceron et al. 2006; Lee-Thorp et al. 2007; Bedaso et al. 2010; Boardman and Secord, 2013; Kita et al., 2014). Bulk enamel samples are used to estimate average dietary $\delta^{13}C$ over the period of tooth formation and have been used to infer average environmental conditions/vegetation structures (e.g. Forbes et al. 2010; Nunez et al. 2010). Intra-tooth $\delta^{13}C_{enamel}$ variation has been shown to preserve a signal of seasonal dietary and environmental oscillations in modern populations, and has been used to estimate a range of palaeo-seasonality parameters in fossil samples (e.g. Zazzo et al., 2002; Balasse et al., 2006; Fraser et al., 2008; Brookman and Ambrose 2012).

Using the known ranges in C_3 and C_4 plant $\delta^{13}C$ and a diet-enamel offset of +14.1 ± 0.5‰ (O'Leary 1988; Cerling and Harris 1999; Coplen et al. 2002; Still et al. 2003), the theoretical *maximum* $\delta^{13}C_{enamel}$ value of a herbivore consuming a C_3-only diet is approximately -8‰ and the theoretical *minimum* $\delta^{13}C_{enamel}$ of a herbivore consuming a C_4-only diet is approximately -2‰. In most environments, where C_3 $\delta^{13}C$ is not at the maximum of its potential range, and C_4 $\delta^{13}C$ is not at the minimum of its potential range, the difference between a C_3- and C_4- dominated $\delta^{13}C_{enamel}$ signature will be greater. In fossil samples from the last glacial and the pre-industrial Holocene, $\delta^{13}C$ values are ca. 0.5–1.5‰ higher than present day owing to differences in atmospheric $\delta^{13}C$ and CO_2 concentration (Marino et al., 1992; Koch, 1998; Tipple et al., 2010).

3. Materials and methods

The most common medium and large herbivores found in the faunal assemblages of the Haua Fteah and Hagfet ed Dabba were selected for analysis: wild *Ammotragus lervia* (Barbary sheep), wild *Bos* sp. (most likely aurochs), and domestic *Capra* sp. (goat) and *Ovis* sp. (sheep) (hereafter referred to as domestic caprids, as morphologically they can be difficult to distinguish in fragmentary archaeological material). To further our understanding of the species' $\delta^{13}C_{enamel}$ signature in relation to diet, climate, and environment, samples from modern populations of wild *A. lervia*, wild *Ovis orientalis musimon* (mouflon), and domestic *Capra hircus* and *Ovis aries* were also analysed.

Sample selection from the archaeological caprids was restricted to third molars (M3s), which are morphologically distinct and easily distinguished from the other cheek teeth in the studied species. Teeth with the best level of preservation, highest crown height, and most robust stratigraphic provenance were preferentially selected. For the archaeological bovids both M3s and M2s were analysed. All modern caprids had their mandibular M3 sampled. Where further dentition was available, the second (M2) and first (M1) molars were also sampled. Including the additional molars in the modern study provides the means to assess intra-tooth $\delta^{13}C$ variability over a greater period of time.

Prior to sampling, the outer surface of each tooth was thoroughly cleaned by abrasion to prevent inclusion of surface contamination in the subsequent enamel sample. Powdered enamel samples (5-10 mg) were collected using a diamond coated drill bit mounted on a variable-speed handheld drill. All teeth were 'bulk' sampled. Bulk enamel samples, which provide a homogenised sample that spans the length of the tooth, were taken to infer average dietary composition over the period of formation. For bulk samples the enamel was abraded evenly down the tooth until sufficient powder was collected for analysis. Each caprid tooth sampled is predicted to have mineralized over approximately 1 year (Weinreb and Sharav, 1964; Ogren, 1965) although the time represented in each sample may be less as the full enamel depth was not sampled (see Reade et al., 2015b). A subset of the modern and archaeological teeth was then selected for serial sampling. Serial samples were taken down the same transect as the bulk sample at approximately 3 mm intervals, using a 1 mm-diameter cylindrical drill bit held perpendicular to the sampling axis. Between 7 and 16 samples were collected per tooth, as determined by crown height.

Powdered enamel was chemically pre-treated to remove organic and secondary carbonate material following the method described by Balasse et al. (2002). The treated powder was isotopically analysed at the Godwin Laboratory, Department of Earth Sciences, University of Cambridge. Samples were analysed on an automated Gasbench interfaced with a Thermo Finnigan MAT 253 isotope ratio mass spectrometer, being reacted with 100% orthophosphoric acid for 2 hours at 70°C in individual vessels. Results are reported with reference to the international standard VPDB calibrated through the NBS19 standard (Coplen, 2011). The long-term analytical precision for $^{13}C/^{12}C$ is better than ±0.08‰. Statistical analysis was performed using SPSS v.22 (Statistical Package for Social Sciences) and statistical significance was accepted at $p<0.05$.

4. Modern caprid diets and environments

4.1 Study design and sample collection

Modern wild and domestic caprids from semi-arid/arid environments are analysed. The study investigates the relationship between $\delta^{13}C_{enamel}$ and that of diet/vegetation, and the relationship between this signal and the local climate. The temporal character of the $\delta^{13}C_{enamel}$ signature in relation to these parameters, and the potential influence of human animal-management practices are also considered. Modern populations of wild *Ammotragus lervia*, wild *Ovis orientalis musimon* (mouflon), and domestic *Capra hircus* and *Ovis aries,* are analysed.

While *A. lervia's* natural range once extended across North Africa, today the species is locally extinct in many areas of the continent and it is currently listed as vulnerable on the IUCN Red List of Threatened Species (Manlius et al., 2003; Cassinello et al., 2008). Therefore, the only population of wild *A. lervia* available to this study was acquired from an introduced population, located on a private range near the White Sands Missile Range, New

Mexico, USA. Sampling of this population was only possible as it is considered invasive and hunting is consequently permitted. Geographical and political circumstances also prevented the collection of other wild caprid samples from North Africa. As such, the second wild caprid included in this study is *O. o. musimon* from Mount Tiede, Tenerife, off the west coast of North Africa.

Domestic caprids were collected from three populations in North Africa, two from the Gebel Akhdar and one from Cairo, Egypt. Sample collection sites in the Gebel Akhdar centred on two different areas, separated by ~150km: the central/eastern Gebel Akhdar escarpments and the El Marj basin in the western Gebel Akhdar. These samples were collected in the landscape and their level of preservation indicates that the animals died within approximately the last 5 years. The domestic caprid samples from Cairo were obtained from a butcher, with no further provenance information available. Although this study compares different caprid species, caprid physiology is similar enough across the species included so as not to introduce any additional uncertainty to interpretations.

The total number of samples, species attribution, and geographic origin (including local plant δ^{13}C where available, and key climatic characteristics) are detailed in Table 2. Results from bulk and intra-tooth sampling of these modern specimens are displayed in Table 2 and Figure 2, respectively. Where multiple teeth from an individual animal were sampled bulk-tooth $\delta^{13}C_{enamel}$ values were used to calculate an animal-mean $\delta^{13}C_{enamel}$ value. Full results are available in the online supplementary data file.

4.2 Wild caprid $\delta^{13}C_{enamel}$, diet, and local vegetation

Behaviourally, *A. lervia* and *O. o. musimon* are generalist feeders with non-selective, availability-mediated diets (Ogren, 1965; Ramsey and Anderegg, 1972; Rodriguez Piñero et al., 1987). Therefore, in the wild these animals likely have diets representing a homogenised average of local vegetation available within a region. Although both species vary their range size by tens of kilometres throughout the year, neither undertakes long-distance seasonal migrations (Hampy, 1978; Ciuti et al., 2009). Therefore, their $\delta^{13}C_{enamel}$ signatures are expected to represent plant $\delta^{13}C$ local to the site of sample collection.

A. lervia animal-mean $\delta^{13}C_{enamel}$ results range from -10.2‰ to -6.3‰ (mean = -8.1 ± 1.4‰ (n=7)). Using the diet-enamel offset of +14.1 ± 0.5‰ proposed by Cerling and Harris (1999), average *A. lervia* dietary $\delta^{13}C$ in the New Mexico samples is estimated to vary from -24.3 ± 0.5 ‰ to -20.4 ± 0.5‰ (Table 2). These values indicate a mix of C_3 and C_4 plant species in the *A. lervia* diet, consistent with the mixed C_3-C_4 vegetation in their habitat in New Mexico. Mean local C_3 and C_4 plant $\delta^{13}C$ signatures have been measured to be -25.6 ± 0.7‰ and -14.5 ± 0.7‰, respectively (Hoppe et al., 2004).

O. o musimon animal-mean $\delta^{13}C_{enamel}$ results range from -13.5‰ to -12.9‰ (mean = -13.2 ± 0.3 (n=4)), equating to an estimated mean dietary $\delta^{13}C$ intake ranging from -27.6 ± 0.5‰ to -27.0 ± 0.5‰ (Table 2). The vegetation in the local Tenerife environment is composed only of C_3 plant species, with $\delta^{13}C$ ranging from -25.3 ± 1.5‰ to -26.2 ± 2.0‰ (Yanes et al., 2009).

These results show that in both environments the wild caprids' $\delta^{13}C_{enamel}$ approximates an average of local vegetation $\delta^{13}C$, modified through a diet-enamel offset. However, greater inter-individual variation is observed in the environment where a greater variation in plant $\delta^{13}C$ is available. This demonstrates the influence of individual animal behaviour on the $\delta^{13}C_{enamel}$ signature and highlights the need to sample multiple individuals in order to estimate an average for that population, and to assess the variation within it.

Intra-tooth $\delta^{13}C_{enamel}$ profiles show temporal variability in dietary $\delta^{13}C$ (Fig. 2), likely linked to varying proportions of different plants in the diet at different times of the year and/or to plant $\delta^{13}C$ responses to seasonal variations in climate. For *A. lervia*, the combined M2-M3 intra-tooth profiles represent dietary intake over approximately 18-24 months, and assuming a spring birth (Ogren, 1965), should record a signal from the animal's first autumn/winter at the top of the M2 to the animal's third summer at the bottom of the M3. However, there is no consistent pattern of intra-tooth variation between the sampled individuals. While all animals display intra-tooth ranges (2.7‰ to 5.1‰) notably greater than the local mean seasonal range in C_3 $\delta^{13}C$ (1.0 ± 0.2‰) and C_4 $\delta^{13}C$ (0.6 ± 0.2‰) (Hoppe et al., 2004), indicating the relative contribution of C_3 and C_4 plant species in the diet likely varied seasonally, differences in dietary behaviour between individuals is apparent (Fig. 2). For example, some animals indicate a diet consistently dominated by C_3 plant species (NM7), some a diet where the proportion of C_3 and C_4 plants varies seasonally (NM5), and some a diet that has a relatively consistent mix of C_3-C_4 plants throughout the year (NM6). The lack of a consistent pattern between different individuals from the same environment could be produced by differences in the season of birth, variations in the timing of tooth formation (formation of the M3 has been shown to be particularly variable (Ogren, 1965)), year-to-year climate-mediated variations in local vegetation, and/or variations in individual animal behaviour. This again highlights the importance of analysing multiple individuals from the same population to capture the amount of $\delta^{13}C$ variation in the local vegetation. It also shows that while intra-tooth profiles can be used to explore sub-annual variations in diet, at least in this example, there are difficulties in using intra-tooth profiles to infer the timing of seasonal change.

The *O. o. musimon* samples from Tenerife appear to show more consistent intra-tooth $\delta^{13}C_{enamel}$ results than the *A. lervia* examples (Fig. 2). This is likely the result of less variation in plant $\delta^{13}C$ in the local environment. Intra-individual variation ranged from 0.7‰ to 2.0‰ (mean=1.3 ± 0.6‰, n=3). With the exception of sample TF4, whose profile is relatively short, a sinusoidal pattern of variation is recorded in the samples, probably reflecting seasonal variations in climate and/or plant species composition in the diet/local environment. Again, there is some variation in the timing of the recorded signal, but it is difficult to make further interpretations based on the small number of samples analysed.

4.3 Domestic caprid $\delta^{13}C_{enamel}$ and the influence of humans

Unlike the wild caprids analysed, for the domestic species the proportion of local versus imported vegetation (e.g. purchased animal feed) in the diet is unknown, as is the level of human management in the animals' access to specific food resources. Here we use $\delta^{13}C_{enamel}$ to infer likely diet, and consider the potential influence of human animal-management strategies.

Bulk-tooth $\delta^{13}C_{enamel}$ from the central/eastern Gebel Akhdar ranges from -12.2‰ to -10.5‰ (mean = -11.3 ± 0.8‰ (n=5)). Intra-tooth profiles (n=2) show little down-tooth variation (<1‰) and lack a clear pattern of variation (Fig. 2). Mean dietary estimates range from -26.3 ± 0.5 ‰ to -24.6 ± 0.5‰ and indicate a C_3-dominated diet (Table 2). This estimate is within the range of plant $\delta^{13}C$ measured from the region, but does not approximate the mean local value (Prendergast et al., 2015). In comparison, animal-mean $\delta^{13}C_{enamel}$ from El Marj ranges from -12.3‰ to -8.8‰ (mean -9.7 ± 1.1‰ (n=8)). With the exception of one result (-12.3‰), all other El Marj samples have $\delta^{13}C$ values ≥-9.9‰, yielding mean dietary estimates ranging from -24.0 ± 0.5 ‰ to -21.4 ± 0.5 ‰ (this range is extended to -26.4 ± 0.5 ‰ if the -12.3‰ $\delta^{13}C_{enamel}$ value is used). This estimate is at the boundary between what could be expected for animals that have a diet comprised solely of C_3 plants in water-poor environments, and those that have a diet containing both C_3 and C_4 plant species. The single intra-tooth profile from the El Marj samples displays a down-tooth variation of 3.0‰ and $\delta^{13}C_{enamel}$ values that suggest this is unlikely to be a result of a significant seasonal intake of C_4 plants (Fig. 2). No plant isotope data is available for El Marj, but the natural vegetation of the region is dominated by C_3 species (Gimingham and Walton, 1954; Still et al., 2003). It therefore seems probable that the El Marj caprids had little or no access to a C_4 dietary component, although it cannot be ruled out. Within the Gebel Akhdar, domestic caprids are often allowed to graze in the landscape during the day, being penned at night, and it is likely that the measured difference between dietary and mean plant $\delta^{13}C$ in the central/eastern Gebel Akhdar is produced by human-mediated access to specific plant resources, and/or the inclusion of extra-local supplementary feed in the diet. The difference between the central/eastern Gebel Akhdar and El Marj caprids may relate to different feeding practices, but could also be produced by climatic differences between the two regions (see section 4.4).

Mean bulk-tooth $\delta^{13}C_{enamel}$ for the Egyptian caprids is -8.5 ± 2.2‰ (n=11, range=6.3‰), which produces mean dietary $\delta^{13}C$ estimates of between -24.9 ± 0.5‰ and -18.6 ± 0.5‰ (Table 2). This predicts a mixed C_3-C_4 diet, which is consistent with local vegetation (Ziegler et al., 1981). While intra-tooth $\delta^{13}C_{enamel}$ variation ranges from 2.5‰ to 7.3‰ (n=5) between different animals, in all samples that have a crown height >20mm (n=3) the range is >7.0‰. Below 20mm intra-tooth $\delta^{13}C_{enamel}$ range decreases with crown height, suggesting the overall amplitude of variation in these samples had been truncated by wear (Fig. 2). It is therefore likely that ~>7.0‰ indicates the true typical variation in $\delta^{13}C_{enamel}$ in this population, indicative of considerable seasonal variation in the proportion of C_3 and C_4 plants in the diet. Four out of the five intra-tooth profiles show very similar patterns of $\delta^{13}C_{enamel}$ variations, with minimum $\delta^{13}C_{enamel}$ values occurring between 5.0mm and 6.7mm from the enamel-root junction. This is characteristic of a $\delta^{13}C_{enamel}$ signal produced by human-managed rearing and feeding practices (Balasse et al. 2003; 2012; Frémondeau et al. 2012), and suggests a narrow birth season and similar diets in the Egyptian animals. In domestic caprids the M3 begins to form when the animal is approximately 15-18 months old (Weinreb and Sharav, 1964). High $\delta^{13}C_{enamel}$ values, which are recorded at the top of the profiles (Fig. 2), indicate a C_4-dominated diet. Such a diet is consistent with animals inhabiting an arid environment. In Egypt the yearly dry season occurs from approximately May to October and the landscape is most water-poor in the late summer/early autumn (WMO, 2016). Therefore, this pattern of intra-tooth variation suggests a spring birth season, and an M3 signal that records summer maximum $\delta^{13}C_{enamel}$ values at the top of the crown and winter/spring minimum $\delta^{13}C_{enamel}$ values at the enamel root junction. One sample (EG21) shows a similar pattern of variation but is out of phase with the other samples ($\delta^{13}C$ minimum at 16.5 mm), which could indicate that this animal was born later in the year, although variations related to tooth formation timings can not be ruled out.

The results from the modern wild caprids suggested that the range of $\delta^{13}C_{enamel}$ values within a population provided a good indication of the range of plant $\delta^{13}C$ in the local environment. Despite uncertainty concerning how humans are modifying the diets of the modern domestic caprids, as in the case of the wild caprids, domestic $\delta^{13}C_{enamel}$ values appear to reflect feeding regimes based at least partly on local vegetation. When C_4 plants are present in the landscape relatively high inter-individual $\delta^{13}C_{enamel}$ variations are observed in both the wild and domestic caprids. Conversely, a relatively narrow range in inter-individual $\delta^{13}C_{enamel}$ is seen in both wild and domestic caprids in C_3-dominated environments. Intra-individual $\delta^{13}C_{enamel}$ profiles can further allude to the proportion of C_3-C_4 species within the diet, and the seasonal utilisation of these resources. The greatest observed difference between wild and domestic caprid $\delta^{13}C_{enamel}$ is in the consistency, or lack thereof, of the intra-tooth profiles, where domestic caprids from the same environment display very similar patterns of intra-tooth variation, and wild caprids from the same environment display greater inter-individual variation. We interpret this difference as indicative of human influence on the domestic caprid diet and breeding cycle. Such differences, if identified in wild and domestic archaeological samples of the same age, could be used to infer human management of the domestic animals' diets and breeding cycle.

4.4 Relationship to local climate

If the caprid diets are based on local vegetation, a relationship between $\delta^{13}C_{enamel}$ and local climate should exist. However, quantitative interpretation of $\delta^{13}C_{enamel}$ relative to climatic variables is complex, not least when both C_3 and C_4 plant species are present in the diet in unknown quantities. However, the *presence* of a C_4 dietary component can itself be indicative of climate, with C_4 plant species typically occurring in greater abundance in more arid environments. Indeed, the two sites that show evidence of C_4 plants in the caprid diets (Egypt and New Mexico) are the two sites with the lowest mean annual precipitation (Table 2). In the locations where the data indicates a C_3-dominated diet (El Marj, central/eastern Gebel Akhdar, and Tenerife) $\delta^{13}C_{enamel}$ is higher at sites with higher mean annual temperatures and lower mean annual precipitation amounts (Fig. 3). Sample size here is too small to facilitate quantitative analysis of this apparent trend confidently, however the pattern of decreasing $\delta^{13}C$ values with increasing rainfall is consistent with published studies of C_3 plant $\delta^{13}C$ values (Kohn, 2010).

Seasonal climate interpretations from the intra-tooth data are difficult. While the wild samples display $\delta^{13}C_{enamel}$ variation that could relate to seasonal climate variations, any sub-annual climate signal appears to be obscured by variations introduced by differences in dietary behaviour, tooth formation rates, and/or season of birth between individuals. The pattern of $\delta^{13}C_{enamel}$ variation in the Egyptian samples is typical of sinusoidal seasonal climate fluctuations, which characterise the local climate (WMO, 2016). However, quantification of this pattern in relation to climatic parameters is prohibited by a lack of dietary information for the animals. The proportion of C_3 and C_4 plants in the diet, and how it varies throughout the year is not known, nor is the proportion of local versus extra-local plants in the animals' diets. In sum, while our data indicates intra-tooth variation is most likely influenced by seasonal fluctuations in climate there is no clear relationship between the shape or phase of the signal and climate. Thus, there may be limited scope to make inferences of climate seasonality from the archaeological samples.

5. Archaeological diets and environments

5.1 Sample selection

79 *Ammotragus lervia* teeth from the Haua Fteah and 50 from the Hagfet ed Dabba, together with 21 *Bos* sp. and 12 domestic caprid teeth from the Haua Fteah, were selected for bulk sampling. From these, a subset of 37 *A. lervia*, 6 *Bos* sp., and 5 domestic caprid teeth were selected for serial sampling. Details of samples and their provenance are given in summary in Table 3 and in full in the online supplementary data file. The sampled teeth from the Haua Fteah are curated in the McBurney Haua Fteah archive in the Museum of Archaeology and Anthropology, University of Cambridge. The sampled teeth from the Hagfet ed Dabba are curated in the Natural History Museum, London.

The archaeological tooth samples in this study do not show direct evidence of human manipulation such as cut marks, burning, or fracturing, but examples of such modifications have been identified on other skeletal elements from the same species found within the same archaeological contexts, albeit at relatively low frequencies (Klein and Scott, 1986). This, combined with the large quantity of lithic and other archaeological material found in the associated deposits, we judge to indicate that the samples are the result of human activity within the caves, and thus are temporally tied to periods when people were present within the local landscape.

Samples from the Haua Fteah come from the McBurney Levalloiso-Mousterian, Dabban, Oranian, Capsian and Neolithic cultural phases, and cover a period from ca. 74 – 5 ka (McBurney, 1967; Douka et al., 2014). As McBurney excavated the deposits in a series of overlapping spits, which often spanned multiple stratigraphic layers, a large proportion of the samples cannot be attributed to a stratigraphic context more resolved than the cultural phase from which they came (McBurney, 1967). However, a small proportion of samples come from spits that were either entirely contained within a single stratigraphic layer, or that spanned 2-3 layers but did not overlap with other spits. Age estimates for the Haua Fteah sequence and for these layers are detailed in Table 1. Samples from the Hagfet ed Dabba are thought to be most similar in age to those from Layer XX from the Haua Fteah (McBurney, 1967).

Bulk-tooth $\delta^{13}C_{enamel}$ results from all archaeological samples are summarised in Table 3 and Figure 4. Intra-tooth profiles are displayed in Figure 5. Full results are available in the online supplementary data file. Where results from the modern caprids from Libya are displayed alongside the archaeological results, the modern data have been corrected to account for the ~1.5‰ decrease in atmospheric $\delta^{13}C$ since the start of the industrial revolution (Long et al., 2005).

5.2 Caprid and bovid palaeodiet at Haua Fteah

The *A. lervia* samples provide the greatest temporal span over which to evaluate diet. At Haua Fteah *A. lervia* bulk-tooth $\delta^{13}C_{enamel}$ values ranges from -12.3‰ to -4.9‰ indicating considerable dietary variation across the sampled animals. Averaged by cultural unit, mean *A. lervia* bulk-tooth $\delta^{13}C_{enamel}$ remains relatively similar throughout the sequence (Table 3). The exception is the Neolithic samples, which are significantly different to that of the preceding cultural units (Kruskal Wallis, $H(4)=25.923$, $p<0.001$). Post-hoc pair-wise comparisons using Mann-Whitney tests with a Bonferroni correction identify the largest differences occur between the Oranian and Neolithic ($U=26.439$, $z=4.424$, $p>0.05$) and the Capsian and Neolithic ($U=-33.601$, $z=-3.477$, $p>0.05$). Dietary estimates for the Haua Fteah *A. lervia* indicate a C_3-dominated diet through most of the sequence (Table 3). While C_4 plants may have been present in the diet in small quantities throughout the time period considered, it is only in the Neolithic where they make a notable contribution to the diets of some animals. A C_4 dietary component is also detected in some of the Neolithic domestic caprids (Table 3). There is no significant difference between wild and domestic caprid $\delta^{13}C_{enamel}$ in the Neolithic (Mann-Whitney, U=163, z=-0.315, p>0.05, Fig. 4), indicating that the animals had access to the same range (at least isotopically) of dietary resources.

A C_3-dominated diet prior to the Neolithic is also evident in the *Bos* sp. bulk-tooth $\delta^{13}C_{enamel}$ (Table 3). There is no significant difference between wild *A. lervia* and *Bos* sp. $\delta^{13}C_{enamel}$ in any of the archaeological units in which they both are present (Dabban (U=1.0, z=-1.549, p<0.05), Oranian (U=305.5, z=1.938, p<0.05) and Capsian (U=21.0, z=1.326, p<0.05), Fig. 4). Given that the two species display different dietary behaviours (*A. lervia* is a mixed feeder and *Bos* sp. a grazer), they are likely to have had diets composed of different plants species. The lack of isotopic difference between the two suggests an isotopic homogeneity in the Gebel Akhdar vegetation during these time periods.

In comparison to the modern samples from C_3-dominated environments, there is a larger inter-individual variation in the archaeological samples from Haua Fteah, including between those interpreted as having a C_3-dominated diet. This is likely the result of the significantly greater time spans represented in the archaeological cultural units in comparison to the modern samples, resulting in data averaging across potentially more variable environments. In the Oranian and Neolithic samples inter-individual variation is similar to that observed in the modern caprids from mixed C_3-C_4 environments (being 4.2‰ and 7.3‰, respectively in the archaeological samples, Table 3). However, absolute $\delta^{13}C_{enamel}$ values from the Oranian samples do not indicate a notable contribution of C_4 to the animals' diet. Only in the Neolithic is the range (7.3‰) of a magnitude that can confidently be attributed to animals' consuming diets composed of notable proportions of both C_3 and C_4 plant species, a conclusion further supported by the intra-tooth data (Fig 5).

Considering the seasonal consumption of different dietary components, intra-tooth data show a change with time (Fig. 5). *A. lervia* intra-tooth $\delta^{13}C_{enamel}$ ranges do not exceed 1.0‰ in the Levalloiso-Mousterian (ca. 68.1 – 48.7 ka) and range from 0.8‰ to 2.3‰ in the Dabban (ca. 40.0 – 18.1 ka) and Oranian (ca. 16.1 - 13.1 ka). In the Capsian (ca. 12.3 – 9.3 ka) greater variation between different *A. lervia* individuals is observed, with the largest recorded intra-tooth $\delta^{13}C$ range being 3.3‰ (HR33). A corresponding increase in intra-tooth variation is not seen between the Oranian and Capsian *Bos* sp. samples (Fig. 5), with the mean range in each group being 1.3 ± 0.4‰ and 1.1 ± 0.6‰, respectively. Variation further increases in the Neolithic samples, with intra-tooth ranges between 0.6‰ and 5.7‰ recorded in the *A. lervia* samples, and 0.7‰ and 4.0‰ in the domestic caprid samples.

In the absolute $\delta^{13}C_{enamel}$ values recorded in the intra-tooth profiles, all teeth analysed display values consistent with a diet dominated by C_3 plant species for at least part of the year (intra-tooth minimums range between individuals from -13.1‰ to -9.3‰). In the Levalloiso-Mousterian, Dabban and Oranian samples intra-tooth maximum values do not exceed -8.8‰ for *A. lervia* and -9.9‰ for *Bos* sp., indicating a year-round C_3-dominated diet for all individuals sampled. Sinusoidal patterns of variation, characteristic of a seasonal cycle, are present in some teeth, but, as with the modern samples analysed, no consistent pattern of variation between different individuals from the same cultural units is observed.

In the Capsian samples intra-tooth maximum values range from -11.0‰ to -9.5‰ in all *A. lervia* and *Bos* sp. samples, with the exception of one *A. lervia* sample (HR33). In this one tooth, a $\delta^{13}C_{enamel}$ maximum of -7.7‰ is recorded and a sinusoidal pattern is evident. While this indicates clear seasonal variation in the diet, the absolute $\delta^{13}C_{enamel}$ values and the magnitude of intra-tooth variation are within the range that could occur in a C_3 only environment. Equally, such results could indicate a seasonally variable diet composed of both C_3 and C_4 plants. When evaluated alongside the other Capsian samples, which all display lower $\delta^{13}C$ values, we argue that it is unlikely that C_4 plant species were present in the local environment in significant proportions during this time period, although it cannot be ruled out.

The pattern changes in the Neolithic (ca. 7.7 – 6.2 ka), where higher seasonal variation, and a higher proportion of C_4 plant species in some, but not all caprid diets, becomes apparent (Fig. 5). This pattern is observed in samples from both wild and domestic caprids. The presence of a C_3-dominated diet in some samples, and a seasonally mixed C_3-C_4 in others, could indicate that different animals were utilising different grazing sites seasonally. However, we observed a similar pattern in our modern *A. lervia* samples, from animals that are known not to undertake long distance seasonal migrations (Hampy, 1978). Thus, while we cannot rule out the possibility of some animals from the archaeological samples moving over long distances, we suggest it is more probable that they were feeding on different plant species available locally. These would have likely been available in different proportions in different microenvironments within the Gebel Akhdar. The similarity between wild and domestic samples, which would not display the same migratory behaviour, adds further support to this interpretation.

5.3 Caprid palaeodiet at Hagfet ed Dabba

At Hagfet ed Dabba, *A. lervia* bulk-tooth $\delta^{13}C_{enamel}$ values range from -12.0‰ to -9.4‰ (n=50, Fig. 6, Table 3), indicating considerable dietary similarity across the sampled animals. There is no significant between-layer difference in $\delta^{13}C_{enamel}$ within the Hagfet ed Dabba sequence (Kruskall Wallis, $H(5)=3.6, p>0.05$). The lack of between-layer difference includes the samples from Layer I, which also contained Roman ceramic material. It is not clear whether the *A. lervia* samples from Layer I are contemporaneous with the Roman pottery, whether the Roman pottery and Dabban accumulations have become mixed, or whether the material dates to an intervening period. Dietary estimates indicate a C_3-dominate diet throughout the sequence (Table 3).

Intra-tooth samples from the Hagfet ed Dabba were analysed from Layers II, IV and VI, and have $\delta^{13}C$ ranges varying from 1.1‰ to 1.8‰ (Fig. 7), similar to the intra-tooth ranges observed in the modern caprids from C_3 environments. Similar absolute values and patterns of within-tooth $\delta^{13}C$ variation are recorded in each sample, and within-layer differences between animals are as large as the differences between animals from different layers.

Overall, results from the Hagfet ed Dabba indicate a C_3-dominated environment with no notable variation over time. However, the scope to make further environmental or climate interpretations is limited given the uncertainty surrounding the absolute age and time span represented in the assemblage.

While this interpretation is consistent with that made from the Dabban-aged samples at Haua Fteah, there is a significant difference between the $\delta^{13}C_{enamel}$ results from Hagfet ed Dabba (n=50) and the Dabban Haua Fteah samples (n=5) (Mann-Whitney, U=197, z=2.108, p<0.05). No significant difference is present when the comparison is limited to the Haua Fteah samples from Layer XX (Mann-Whitney, U=101, z=1.001, p>0.05), the layer that McBurney suggested might be contemporaneous with the Hagfet ed Dabba (McBurney and Hey, 1955; McBurney, 1967, pp. 168-170). However, the large discrepancy in sample size between the two sites should be noted (Table 3).

5.4 Climatic and environmental interpretations

Bulk and intra-tooth data from the Haua Fteah and Hagfet ed Dabba provide strong evidence that the Gebel Akhdar landscape was dominated by C_3 plant species throughout the last glacial period and in the early Holocene (Levalloiso-Mousterian to Capsian), with C_4 plant species only becoming apparent in the mid-Holocene (Neolithic).

The relative lack of variation recorded in $\delta^{13}C_{enamel}$ throughout much of the sequence, and the persistence of a C_3-dominate landscape, supports other palaeoenvironmental and archaeological interpretations that human occupation of the Gebel Akhdar occurred under relatively stable environmental conditions (Inglis, 2012; Prendergast et al., submitted). Given the complexities in making environmental interpretations from $\delta^{13}C_{enamel}$ values where C_4 plant species could be present in the diet in a significant but unknown proportion, the mid-Holocene Neolithic samples will be discussed separately (section 5.5).

From the Levalloiso-Mousterian to the Capsian (ca. 74 - 7.9 ka) there is an overall trend towards lower bulk-tooth $\delta^{13}C_{enamel}$ values in the *A. lervia* data (Fig. 4) and a corresponding increase in intra-tooth variability (Fig. 5). Grouping the samples by cultural unit introduces significant time averaging to the dataset. This can be reduced by considering only those samples attributed to more discrete stratigraphic provenances. Following this approach, while the overall temporal trend towards lower bulk-tooth $\delta^{13}C_{enamel}$ through time is preserved, greater variation is identified (Fig. 8).

Overall, the higher $\delta^{13}C_{enamel}$ values in samples that pre-date the LGM suggest that the environment of the Gebel Akhdar during the last glacial period (during the Levalloiso-Mousterian and Dabban phases of occupation) was drier than in later periods. Based on palaeoenvironmental records from elsewhere in North Africa (Armitage et al., 2007; Castañeda et al., 2009), this was likely the result of lower amounts of precipitation rather than higher temperatures. Results indicate that the Gebel Akhdar environment was likely also less variable, both intra- and inter-annually. The indication of increased aridity is consistent with that identified in other palaeoenvironmental archives from within the region, although none of these show evidence for hyper-arid periods (Inglis, 2012; Prendergast et al., submitted). Analysis of the Haua Fteah cave sediments found evidence that local environmental conditions during OIS 3 (ca. 59 – 24 ka) were less stable than our data suggests (Inglis, 2012). These disparities require further investigation but may reflect differences in the spatial and/or temporal resolution of the two different archives.

The most arid period identified in our samples dates to ca. 43 ka (Fig. 8), during the later Levalloiso-Mouterian occupation phase, although extreme aridity is not likely to have occurred. While no *Bos* sp. from this level were available for analysis, other skeletal elements of *Bos* sp. have been identified from the assemblage. The presence of *Bos* sp., an obligate drinker, in the faunal assemblage indicates that there must have been sources of surface waters available in the region at this time. This arid episode appears to correspond to a period of reduced tree cover and possibly cooler temperatures in the southeastern Mediterranean region (Bar-Matthews et al., 1999; Langgut et al., 2011). In the Sahara, most areas prone to palaeolake formation during periods of humidity also suggest arid conditions prevailing at this time, with the potential exception of Shati Cardium in southeastern Libya (Gaven et al., 1981; Szabo et al., 1995; Armitage et al., 2007). Archaeologically this time period corresponds to the widespread decline in the Aterian across North Africa (Garcea, 2012b; Richter et al., 2012; Spinapolice and Garcea, 2014). If other areas of North Africa where becoming uninhabitable due to aridity, the Gebel Akhdar environment by comparison may have provided an attractive refuge at this time.

Layer XVII (ca. 22.6 – 20.0 ka), associated with the later Dabban occupation phase, is the sample group closest in age to the LGM. While $\delta^{13}C_{enamel}$ is higher in this layer than in following periods, the data does not indicate that the hyper-arid conditions that prevailed elsewhere in North Africa at the LGM were present within the Gebel Akhdar. Following the LGM, data indicate that climatic instability increased in the late glacial (ca. 16.6 – 14.7 ka), and continued into the early Holocene Capsian (ca. 12.3 – 9.3 ka). While there is a long-term decrease in *A. lervia* $\delta^{13}C_{enamel}$ from the LGM to the early Holocene (Fig. 8), within this time period $\delta^{13}C_{enamel}$ values oscillate, with a return to higher values similar to those of the LGM between ca. 15.0 and 13.5 ka. This is a different pattern to that observed in local land snail $\delta^{13}C$ (Prendergast et al., submitted) and in plant and animal $\delta^{13}C$ archives from other regions (e.g. Bump et al., 2007). These typically show a consistent decrease in $\delta^{13}C$ from the LGM to the Holocene of 1-4‰, which coincides with an increase in atmospheric CO_2 concentrations (Neftel et al., 1988; Marino et al., 1992; Smith et al., 1999; Stevens and Hedges, 2004; Bump et al., 2007; Drucker et al., 2008).

In contrast, the *Bos* sp. data show no change in mean bulk-tooth $\delta^{13}C$ across the same time period (Fig. 5), which would most likely indicate environmental and climatic stability and is consistent with the pattern observed in local land snail $\delta^{13}C$ (Prendergast et al., submitted). However, this masks the variability observed within each layer grouping. Inter-individual variation in bulk-tooth $\delta^{13}C_{enamel}$ in both *A. lervia* and *Bos* sp. is highest in the late glacial, which could be interpreted as indicating a more rapidly fluctuating, and therefore less stable environment during this time period.

The most humid environmental conditions are recorded in the Capsian samples, which date to ca. 12.3 – 9.3 ka (Fig. 8). This coincides with the early Holocene humid phase that occurred across North Africa (deMenocal et al., 2000; Pachur and Hoelzmann, 2000; Renssen et al., 2006; Lézine et al., 2011).

In conclusion, while the climate of the Gebel Akhdar appears to have followed regional-scale trends in aridity/humidity, no extreme climatic events are identified. This likely produced a relatively stable environment, with somewhat predictable animal and plant resources available for human exploitation. Such conditions could have made the Gebel Akhdar an attractive option to local human populations in comparison to more variable environments in adjacent regions.

5.5 The 'Neolithic' appearance of C_4 plant species

While C_4 plants may have been present in the Gebel Akhdar throughout the time period covered by our data, they only make a notable contribution to caprid diet in the samples assigned to the Neolithic cultural phase. Both C_3 and C_4 plant species have been identified in the plant macrofossil remains contained in the Holocene-aged sediments at Haua Fteah (Barker et al., 2008; 2010). However, the number of macrofossil samples is limited, and spatial patterning of accumulation and taphonomic processes influence the archive (Barker et al., 2009). Therefore it is not possible to use this record to assess the proportion of different plant species present in the location environment. In comparison to the caprid data, a study of land snail $\delta^{13}C$ from the same region found no evidence for C_4 plant species during the mid-Holocene (Prendergast et al., submitted). This difference could be related to the differences in the spatial resolution of data provided by each sample type, and/or to the different feeding behaviours of the two species.

For caprid diet, the C_4 signal is present in some, but not all, of both the wild and domestic animals. A similar pattern was recorded in our modern sample of wild caprids from mixed C_3-C_4 environments, where a C_4 plant signal was recorded in some, but not all of the animals sampled. As the signal is see in both wild and domestic archaeological caprids, we do not interpret the signal as indicative of seasonal migratory behaviour. If it were we would expect to see differences between the wild and domestic samples, and likely greater similarity between the animals within each group. We therefore interpret the appearance of dietary C_4 in the archaeological samples as representing the appearance/significant increase in abundance of C_4 plant species available to the animals, indicating change in vegetation composition within the local Gebel Akhdar landscape.

There is no evidence to suggest that C_4 plants were present in any notable abundance prior to this period; the signal is largely absent in samples dated to ca. 12.3 – 9.3 ka and present in samples dating to ca. 7.4–6.9 ka (Fig. 8). This places the appearance/increase of C_4 plants in the Gebel Akhdar landscape sometime during the early-mid Holocene. It is possible that this change in local vegetation structure reflects a change in the natural distribution of C_4 species in response to environmental changes, or that our data record an anthropogenic influence on the local vegetation/herbivore diet, or both.

Increased fluvial activity in North Africa, related to an increase in Mediterranean precipitation and/or enhanced monsoonal circulation, has been recorded in early Holocene archives (Pachur and Rottinger, 1997; Armitage et al., 2007; Cremaschi et al., 2010). In the mid Holocene the climate became more arid, beginning between 8 and 7 ka; in the Sahara this decline appears to be the start of a long-term trend to more arid conditions, whereas in the Mediterranean region it appears to have been a relatively short-term perturbation (Hassan, 1997; Cremaschi and di Lernia, 1999; De Rijk et al., 1999; Triantaphyllou et al., 2009; Baioumy et al., 2011). Aridification is therefore one potential explanation for the C_4 plant expansion in the Gebel Akhdar between the Capsian and Neolithic. However, there is no other evidence for a major climatic shift during this period within the Gebel Akhdar, nor in palaeoenvironmental archives from adjacent coastal regions (Giraudi et al., 2013; Reade 2015a; Prendergast et al., submitted). We also observed no evidence for an increase in C_4 plant abundance within the Gebel Akhdar during earlier time periods that coincide with older regional-scale arid events, suggesting that an exclusively climate-mediated explanation is unlikely.

An alternative hypothesis relates to human activity both within the Gebel Akhdar and in the wider North African region. During the early Holocene humid phase human populations expanded into previously unoccupied areas of North Africa and there is evidence for increased sedentism, management of wild animals, and wild cereal exploitation and storage in the Sahara (Cremaschi and di Lernia, 1999; di Lernia, 2001; Kuper and Kröpelin, 2006; Mercuri, 2008a; 2008b; di Lernia et al., 2012). The subsequent climatic aridification appears to have resulted in increased human mobility and a shift to pastoral practices (Cremaschi and di Lernia, 1999; Biagetti and di Lernia, 2013; Stojanowski and Knudson, 2014). Barich (2014) speculates that the North African coast may have provided an attractive environment for pastoral populations from the central Sahara during the mid Holocene, when more southerly regions were becoming increasingly desiccated. If this were the case then it is possible that these populations, who were using wild C_4 plant resources while in the central Sahara, brought with them the plants and/or the knowledge of how to exploit them. While there is no evidence of Neolithic plant cultivation/domestication in the Gebel Akhdar's archaeological sequences (Barker et al., 2010; Lucarini et al., 2015), it is possible that an increased focus on the exploitation of wild C_4 plants, which may have always been present in the Gebel Akhdar region in abundances too low to be recorded in the wild herbivore diet, was enough to increase their abundance in the Neolithic landscape to levels where they could become a significant component of some caprid diets. This could explain why a C_4 signal is seen in some caprids, both wild and domestic, but not in others. If the C_4 signal was indicative of specific human-regulated animal feeding regimes, it could be expected that all domestic animals would display a similar $\delta^{13}C$ signature, which would be different to wild caprid $\delta^{13}C$. The pattern observed in our data, where wild and domestic animals cannot be distinguished, strongly suggests that the dietary changes were the result of changes to the wild vegetation structure, be they naturally or anthropogenically driven.

6. Conclusion

The analysis of modern wild and domestic caprids from C_3 and mixed C_3-C_4 arid and semi-arid environments facilitates the interpretation of data from the archaeological records of the Gebel Akhdar. The generalist nature of caprid dietary behaviour is shown to capture the range of plant types present in the local vegetation. This indicates that applying such an approach to caprids from the archaeological/palaeontological record is a valid means of estimating past isotopic variation in the local vegetation cover. However, the influence of individual animal behaviour is also apparent in our results from the wild samples. In contrast, difference in dietary behaviour in modern domestic caprids is low, presumably because humans control their food intake. This highlights how human animal-management strategies can be identified in the fossil record. Intra-tooth analysis can be used to further explore the temporal role of different plant types in the diet, and assess whether patterns of variation are linked to seasonal climatic/environmental changes.

Results from the archaeological wild samples show that for the whole of the last glacial period and the early Holocene, the Gebel Akhdar was a landscape dominated by C_3 vegetation. The region appears to have experienced similar but less extreme climatic shifts to other areas of North Africa. Though we recognise that our data only provide temporal ‘snap shots’ from when people were active within the landscape, overall our results suggest a largely stable environment. Our findings provide support to the theory that the Gebel Akhdar may have provided an unusually favourable environment to human populations during periods when increased aridity produced less favourable conditions in adjacent regions. In particular, environmental stability is likely to have resulted in somewhat predictable access to animal and plant resources. This would likely have made the Gebel Akhdar an attractive option to local human populations, when resources in other regions were under increasing stress from changing climates.

The appearance of a notable proportion of C_4 plants in the Gebel Akhdar landscape coincides with the first evidence for domestic animals in the region. Our results suggest that the increase in C_4 abundance most likely occurred within the natural vegetation, rather than being indicative of domestic plant cultivation. We cannot determine whether this C_4 signal reflects a change in the natural distribution of C_4 plant species in response to environmental changes, or if it indicates human influence on the local vegetation. However, for a natural shift in vegetation structure to occur, a corresponding shift in local climate would also be expected. As there is no evidence of such climatic variability occurring at this time within the Gebel Akhdar, we favour the conclusion that the appearance of a C_4 signal in the region was linked, at least in part, to human influences on the natural landscape.

Acknowledgements

The authors wish to thank Patrick Morrow, Dr. Louise Bertini, Dr, Jacob Morales, Dr. Matilde Arnay, the National Park of Las Cañadas del Teide, Tenerife, and TRANS-NAP project members for assistance with modern sample collection. The late Prof. Anthony Legge identified all of the archaeological samples from the Haua Fteah included in this study. We are grateful to the Museum of Archaeology and Anthropology, University of Cambridge and the Natural History Museum, London for providing access to the archaeological samples. We thank James Rolfe, Mike Hall, Louise Butterworth, Catherine Kneale and Charlotte Ridding for assistance with stable isotope analysis. This research was funded by a European Research Council Advanced Investigator Grant 230421 (to GB, from which HR was funded). RES was funded by the Royal Society, Grant 502008.K518/SLB.

References

Ageena, I., Macdonald, N., Morse, A.P., 2014. Variability of maximum and mean average temperature across Libya (1945–2009). Theor Appl Climatol 117, 549–563. doi:10.1007/s00704-013-1012-z

Al-Sodany, Y.M., Shehata, M.N., Shaltout, K.H., 2003. Vegetation along an elevation gradient in Al-Jabal Al-Akhdar, Libya. Ecologia Mediterranea 29, 125–138.

Armitage, S.J., Drake, N.A., Stokes, S., El-Hawat, A., Salem, M.J., White, K., Turner, P., McLaren, S.J., 2007. Multiple phases of North African humidity recorded in lacustrine sediments from the Fazzan Basin, Libyan Sahara. Quat Geochronol 2, 181–186. doi:10.1016/j.quageo.2006.05.019

Baioumy, H., Kayanne, H., Tada, R., 2011. Record of Holocene aridification (6000-7000 BP) in Egypt (NE Africa): Authigenic carbonate minerals from laminated sediments in Lake Qarun. Quatern Int 245, 170–177. doi:10.1016/j.quaint.2010.05.021

Balasse, M., Ambrose, S.H., Smith, A., Price, T., 2002. The seasonal mobility model for prehistoric herders in the south-western Cape of South Africa assessed by isotopic analysis of sheep tooth enamel. J Archaeol Sci 29, 917–932.

Balasse, M., Obein, G., Ughetto-Monfrin, J., Mainland, I., 2012. Investigating seasonality and season of birth in past herds: a reference set of sheep enamel stable oxygen isotope ratios. Archaeometry 54, 349–368. doi:10.1111/j.1475-4754.2011.00624.x

Balasse, M., Smith, A., Ambrose, S.H., Leigh, S., 2003. Determining sheep birth seasonality by analysis of tooth enamel oxygen isotope ratios: the Late Stone Age site of Kasteelberg (South Africa). J Archaeol Sci 30, 205–215.

Balasse, M., Tresset, A., & Ambrose, S.H. 2006. Stable isotope evidence ($\delta^{13}C$, $\delta^{18}O$) for winter feeding on seaweed by Neolithic sheep of Scotland. Journal of Zoology 270(1), 170–176.

Balasse, M., Tresset, A., Dobney, K., & Ambrose, S.H. 2005. The use of isotope ratios to test for seaweed eating in sheep. Journal of Zoology 266, 283–291.

Bar-Matthews, M., Ayalon, A., Kaufman, A., Wasserburg, G.J., 1999. The Eastern Mediterranean paleoclimate as a reflection of regional events: Soreq cave, Israel. Earth and Planetary Science Letters 166, 85–95.

Barich, B.E., 2014. Northwest Libya from the early to late Holocene: New data on environment and subsistence from the Jebel Gharbi. Quatern Int 320, 15–27. doi:10.1016/j.quaint.2013.09.007

Barker, G., Antoniadou, A., Armitage, S., Brooks, I., Candy, I., Connell, K., Douka, K., Drake, N., Farr, L., Hill, E., Hunt, C., Inglis, R., Jones, S., Lane, C., Lucarini, G., Meneely, J., Morales, J., Mutri, G., Prendergast, A., Rabett, R., Reade, H., Reynolds, T., Russell, N., Simpson, D., Smith, B., Stimpson, C., Twati, M., White, K., 2010. The Cyrenaican Prehistory Project 2010: the fourth season of investigations of the Haua Fteah cave and its landscape, and further results from the 2007–2009 fieldwork. Libyan Studies 41, 23–49.

Barker, G., Antoniadou, A., Barton, H., Brooks, I., Candy, I., Drake, N., Farr, L., Hunt, L., Ibrahim, A., Inglis, R., Jones, S., Morales, J.I., Mutri, G., Rabett, R., Reynolds, T., Simpson, D., Twati, M., White, K., 2009. The Cyrenaican Prehistory Project 2009: the third season of investigations of the Haua Fteah cave and its landscape, and further results from the 2007-2008 fieldwork. Libyan Studies 40, 1–42.

Barker, G., Basell, L., Brooks, I., Burn, L., Cartwright, C., Cole, F., Davison, J., Farr, L., Grun, R., Hamilton, R., Hunt, C.R., Jacobs, Z., Leitch, V., Morales, J., Morley, I., Morley, M., Pawley, S., Pryor, A., Rabett, R., Reynolds, E.-R.H., Roberts, R., Simpson, D., Stimpson, C., Touati, M., van der Veen, M., 2008. The Cyrenaican Prehistory Project 2008: the second season of investigations of the Haua Fteah cave and its landscape, and further results from the initial (2007) fieldwork. Libyan Studies 39, 175–221.

Barker, G., Bennett, P., Farr, L., Hill, A., Hunt, C., Lucarini, G., Morales, J., Mutri, G., Prendergast, A., Pryor, A., Rabett, R., Reynolds, T., Spry-Marques, P., Twati, M., 2012. The Cyrenaican Prehistory Project 2012: the fifth season of investigations of the Haua Fteah cave. Libyan Studies 43, 115–136.

Barker, G., Hunt, C., Reynolds, T., 2007. The Haua Fteah, Cyrenaica (Northeast Libya): renewed investigations of the cave and its landscape, 2007. Libyan Studies 38, 1–22.

Barrett, R.H., 1967. Exotic big game on the Rancho Piedra Blanca. California-Nevada Section TWS Transactions 1–16.

Bedaso, Z., Wynn, J.G., Alemseged, Z., & Geraads, D. 2010. Paleoenvironmental reconstruction of the Asbole fauna (Busidima Formation, Afar, Ethiopia) using stable isotopes. Geobios 43(2), 165–177.

Biagetti, S., di Lernia, S., 2013. Holocene deposits of Saharan rock shelters: the case of Takarkori and other sites from the Tadrart Acacus Mountains (Southwest Libya). African Archaeological Review 30, 305–338. doi:10.1007/s10437-013-9138-z

Boardman, G. S., Secord, R. 2013. Stable isotope paleoecology of White River ungulates during the Eocene–Oligocene climate transition in northwestern Nebraska. Palaeogeography, Palaeoclimatology, Palaeoecology 375, 38-49.

Brookman, T.H., & Ambrose, S.H. 2012. Seasonal variation in kangaroo tooth enamel oxygen and carbon isotopes in southern Australia. Quaternary Research 78(2), 256–265.

Bump, J.K, Fox-Dobbs, K., Bada, J.L., Koch, P.L., Peterson, R.O, Vucetich, J.A. 2007. Stable isotopes, ecological integration and environmental change: wolves record atmospheric carbon isotope trend better than tree rings. Proceedings of the Royal Society B: Biological Sciences 274(1624), 2471-2480. doi: 10.1098/rspb.2007.0700

Cacho, I., Grimalt, J.O., Sierro, F.J., Shackleton, N.J., Canals, M., 2000. Evidence for enhanced Mediterranean thermohaline circulation during rapid climatic coolings. Earth and Planetary Science Letters 183, 417–429.

Cancellieri, E., di Lernia, S., 2013. Middle Stone Age human occupation and dispersals in the Messak plateau (SW Libya, central Sahara). Quatern Int 300, 142–152. doi:10.1016/j.quaint.2012.08.2054

Cassinello, J., Cuzin, F., Jdeidi, T., Masseti, M., Nader, I. & de Smet, K. 2008. Ammotragus lervia. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 14 April 2015.

Castañeda, I.S., Mulitza, S., Schefuβ, E., dos Santos, R.A.L., Sinninghe Damste, J.S., Schouten, S., 2009. Wet phases in the Sahara/Sahel region and human migration patterns in North Africa. PNAS 106, 20159–20163. doi:10.1073/pnas.0905771106

Castañeda, I.S., Schefuβ, E., Pätzold, J., Sinninghe Damsté, J.S., Weldeab, S., Schouten, S., 2010. Millennial-scale sea surface temperature changes in the eastern Mediterranean (Nile River Delta region) over the last 27,000 years. Paleoceanography 25, PA1208. doi:10.1029/2009PA001740

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363.

Cernusak, L.A., Winter, K., Turner, B.L., 2009. Physiological and isotopic ($\delta^{13}C$ and $\delta^{18}O$) responses of three tropical tree species to water and nutrient availability. Plant Cell Environ 32, 1441–1455. doi:10.1111/j.1365-3040.2009.02010.x

Ciuti, S., Pipia, A., Grignolio, S., Ghiandai, F., Apollonio, M. 2009. Space use, habitat selection and activity patterns of female Sardinian mouflon (Ovis orientalis musimon) during the lambing season. European Journal of Wildlife Research 55, 589-595.

Clark, J.D., 1980. Human populations and cultural adaptations in the Sahara and Nile during prehistoric times, in: Williams, M.A.J., Faure, H. (Eds.), The Sahara and the Nile. A. A. Balkema, Rotterdam.

Coplen, T.B., 2011. Guidelines and recommended terms for expression of stable isotope ratio and gas ratio measurement results. Rapid Commun. Mass Spectrom. 25, 2538–2560. doi:10.1002/rcm.5129

Coplen, T.B., Hopple, J.A., Böhlke, J.K., Peiser, H.S., Rieder, S.E., Krouse, H.R., Rosman, K.J.R., Ding, T., Vocke, R.D., Révész, K.M., Lamberty, A., Taylor, P., de Bièvre, P., 2002. Compilation of minimum and maximum isotope ratios of selected elements in naturally occurring terrestrial materials and reagents (Water-Resources Investigations Report No. 01-4222). United States Geological Survey, Renston, Virginia.

Cremaschi, M., Di Lernia, S., 1999. Holocene climate changes and cultural dynamics in the Libyan Sahara. African Archaeological Review 16, 211–238.

Cremaschi, M., Di Lernia, S., Garcea, E.A.A, 1998. Some insights on the Aterian in the Libyan Sahara: chronology, environment, and archaeology. African Archaeological Review 15, 261–286.

Cremaschi, M., Zerboni, A., Spötl, C., Felletti, F., 2010. The calcareous tufa in the Tadrart Acacus Mt. (SW Fezzan, Libya). Palaeogeogr Palaeocl 287, 81–94. doi:10.1016/j.palaeo.2010.01.019

Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., Tu, K.P., 2002. Stable isotopes in plant ecology. Annu Rev Ecol Syst 33, 507–559. doi:10.1146/annurev.ecolsys.33.020602.095451

De Rijk, S., Hayes, A., Rohling, E.J., 1999. Eastern Mediterranean sapropel S1 interruption: an expression of the onset of climatic deterioration around 7 ka BP. Marine Geology 153, 337–343.

deMenocal, P., Ortiz, J., Guilderson, T., Adkins, J., Sarnthein, M., Baker, L., Yarusinsky, M.,

2000. Abrupt onset and termination of the African Humid Period: rapid climate responses to gradual insolation forcing. Quaternary Science Reviews 19, 347–361.

di Lernia, S., 2001. Dismantling dung: Delayed use of food resources among early Holocene foragers of the Libyan Sahara. Journal of Anthropological Archaeology 20, 408–441.

di Lernia, S., N'siala, I.M., Mercuri, A.M., 2012. Saharan prehistoric basketry. Archaeological and archaeobotanical analysis of the early-middle Holocene assemblage from Takarkori (Acacus Mts., SW Libya). J Archaeol Sci 39, 1837–1853. doi:10.1016/j.jas.2012.01.026

Douka, K., Jacobs, Z., Lane, C., Grun, R., Farr, L., Hunt, C., Inglis, R.H., Reynolds, T., Albert, P., Aubert, M., Cullen, V., Hill, E., Kinsley, L., Roberts, R.G., Tomlinson, E.L., Wulf, S., Barker, G., 2014. The chronostratigraphy of the Haua Fteah cave (Cyrenaica, northeast Libya). Journal of Human Evolution 66, 39–63. doi:10.1016/j.jhevol.2013.10.001

Drucker, D.G., Bridault, A., Hobson, K.A., Szuma, E., Bocherens, H., 2008. Can carbon-13 in large herbivores reflect the canopy effect in temperate and boreal ecosystems? Evidence from modern and ancient ungulates. Palaeogeogr Palaeocl 266, 69–82.

Ehleringer, J.R., Cerling, T.E., Helliker, B.R., 1997. C_4 photosynthesis, atmospheric CO_2, and climate. Oecologia 112, 285–299.

Ehleringer, J.R., Phillips, S.L., Comstock, J.P., 1992. Seasonal-variation in the carbon isotopic composition of desert plants. Funct Ecol 6, 396–404.

El-Darier, S.M., El-Mogaspi, F.M., 2009. Ethnobotany and relative importance of some endemic plant species at El-Jabal El-Akhdar Region (Libya). World Journal of Agricultural Sciences 5, 353–360.

El Kenawy,, A.M., López-Moreno, J.I., Vicente-Serrano, S.M., Mekld, M.S., 2009. Temperature trends in Libya over the second half of the 20th century. Theor Appl Climatol 98, 1–8.

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

Enzel, Y., Arnit, R., Dayan, U., Crouvi, O., Kahana, R., Ziv, B., Sharon, D., 2008. The climatic and physiographic controls of the eastern Mediterranean over the late Pleistocene climates in the southern Levant and its neighboring deserts. Global and Planetary Change 60, 165–192. doi:10.1016/j.gloplacha.2007.02.003

Farquhar, G.D., Ehleringer, J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40, 503–537.

Farr, L., Lane, R., Abdulazeez, F., Bennett, P., Holman, J., Marasi, A., Prendergast, A., Al-Zweyi, M., Barker, G., 2014. The Cyrenaican Prehistory Project 2013: the seventh season of excavations in the Haua Fteah cave. Libyan Studies 45, 163–173. doi:10.1017/lis.2014.2

Foley, R.A., Maíllo Fernández, J.M., Mirzaón Lahr, M., 2013. The Middle Stone Age of the Central Sahara: Biogeographical opportunities and technological strategies in later human evolution. Quatern Int 300, 153–170. doi:10.1016/j.quaint.2012.12.017

Forbes, M.S., Kohn, M.J., Bestland, E.A., & Wells, R.T. 2010. Late Pleistocene environmental change interpreted from δ^{13}C and δ^{18}O of tooth enamel from the Black Creek Swamp Megafauna site, Kangaroo Island, South Australia. Palaeogeogr Palaeocl 291(3-4): 319–327.

Fraser, R.A., Grün, R., Privat, K., & Gagan, M.K. 2008. Stable-isotope microprofiling of wombat tooth enamel records seasonal changes in vegetation and environmental conditions in eastern Australia. Palaeogeogr Palaeocl 269(1-2): 66–77.

Frémondeau, D., Cucchi, T., Casabianca, F., Ughetto-Monfrin, J., Horard-Herbin, M.P., Balasse, M., 2012. Seasonality of birth and diet of pigs from stable isotope analyses of tooth enamel (δ^{18}O, δ^{13}C): a modern reference data set from Corsica, France. J Archaeol

Sci 39, 2023–2035. doi:10.1016/j.jas.2012.04.004

Garcea, E.A.A., 2006. Semi-permanent foragers in semi-arid environments of North Africa. World Archaeology 38, 197–219.

Garcea, E.A.A., 2012a. Successes and failures of human dispersals from North Africa. Quatern Int 270, 119–128. doi:10.1016/j.quaint.2011.06.034

Garcea, E.A.A., 2012b. Modern Human Desert Adaptations: A Libyan perspective on the Aterian complex, in: Hublin, J.-J., McPherron, S.P. (Eds.), Modern Origins. a North African Perspective. Springer Netherlands, Dordrecht, pp. 127–142.

Gaven, C., Hillaire-Marcel, C., Petit-Maire, N., 1981. A Pleistocene lacustrine episode in southeastern Libya. Nature 290, 131–133.

Gebrekirstos, A., Worbes, M., Teketay, D., Fetene, M., Mitlöhner, R., 2009. Stable carbon isotope ratios in tree rings of co-occurring species from semi-arid tropics in Africa: Patterns and climatic signals. Global and Planetary Change 66, 253–260. doi:10.1016/j.gloplacha.2009.01.002

Gimingham, C.H., Walton, K., 1954. Environment and the structure of scrub communities on the limestone plateaux of Northern Cyrenaica. Journal of Ecology 42, 505–520.

Giraudi, C., Mercuri, A.M., Esu, D., 2013. Holocene palaeoclimate in the northern Sahara margin (Jefara Plain, northwestern Libya). The Holocene 23, 339–352. doi:10.1177/0959683612460787

Hampy, D., 1978. Home range and seasonal movement of Barbary sheep in the Palo Duro Canyon. Texas Tech University, Unpublished PhD Thesis.

Hassan, F.A., 1997. Holocene palaeoclimates of Africa. African Archaeological Review 14, 213–230.

Hegazy, A.K., Boulos, L., Kabiel, H.F., Sharashy, O.S., 2011. Vegetation and species altitudinal distribution in Al-Jabal Al-Akhdar landscape, Libya. Pakistan Journal of

Botany 43, 1885–1898.

Hey, R.W., 1955. Pleistocene geology, in: McBurney, C.B.M., Hey, R.W. (Eds.), Prehistory and Pleistocene Geology in Cyrenaican Libya. Cambridge University Press, Cambridge, pp. 15-137.

Higgs, E.S., 1967. Environment and chronology: evidence from mammalian fauna, in: McBurney, C.B.M. (Ed.), The Haua Fteah (Cyrenaica) and the Stone Age of the South-East Mediterranean. Cambridge University Press, Cambridge, pp. 16–44.

Hoelzmann, P., Keding, B., Berke, H., Kröpelin, S., Kruse, H.-J., 2001. Environmental change and archaeology: lake evolution and human occupation in the Eastern Sahara during the Holocene. Palaeogeogr Palaeocl 169, 193–217.

Hoppe, K.A., Amundson, R., Vavra, M., McClaran, M., Anderson, D.L., 2004. Isotopic analysis of tooth enamel carbonate from modern North American feral horses: implications for paleoenvironmental reconstructions. Palaeogeogr Palaeocl 203, 299–311.

Hoppe, K.A., Paytan, A., Chamberlain, C.P., 2006. Reconstructing grassland vegetation and paleotemperatures using carbon isotope ratios of bison tooth enamel. Geology 34, 649–652. doi:10.1130/G22745.1

Hunt, C., Davison, J., Inglis, R., Farr, L., Reynolds, T., Simpson, D., el-Rishi, H., Barker, G., 2010. Site formation processes in caves: The Holocene sediments of the Haua Fteah, Cyrenaica, Libya. J Archaeol Sci 37, 1600–1611. doi:10.1016/j.jas.2010.01.021

Hunt, C.O., Reynolds, T.G., El-Rishi, H.A., Buzaian, A., Hill, E., Barker, G., 2011. Resource pressure and environmental change on the North African littoral: Epipalaeolithic to Roman gastropods from Cyrenaica, Libya. Quatern Int 244, 15–26. doi:10.1016/j.quaint.2011.04.045

Inglis, R., 2012. Human occupation and changing environments during the Middle to Later Stone Ages: soil micromorphology at the Haua Fteah, Libya. Universiy of Cambridge, Unpublished PhD Thesis.

Jones, S., Farr, L., Barton, H., Drake, N., White, K., Barker, G., 2011. Geoarchaeological patterns in the pre-desert and desert ecozones of northern Cyrenaica. Libyan Studies 42, 11–19.

Kita, Z. A., Secord, R., Boardman, G. S. 2014. A new stable isotope record of Neogene paleoenvironments and mammalian paleoecologies in the western Great Plains during the expansion of C4 grasslands. Palaeogeography, Palaeoclimatology, Palaeoecology 399, 160-172.

Klein, R.G., Scott, K., 1986. Re-analysis of faunal assemblages from the Haua Fteah and other Late Quaternary archaeological sites in Cyrenaican Libya. J Archaeol Sci 13, 515–542.

Koch, P.L., 1998. Isotopic reconstruction of past continental environments. Annual Review of Earth and Planetary Sciences 26, 573–613.

Kohn, M.J., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. P Natl Acad Sci USA 107, 19691–19695. doi:10.1073/pnas.1004933107

Kuper, R., Kröpelin, S., 2006. Climate-controlled Holocene occupation in the Sahara: Motor of Africa's evolution. Science 313, 803–807.

Kwiecien, O., Arz, H.W., Lamy, F., Plessen, B., Bahr, A., Haug, G.H., 2009. North Atlantic control on precipitation pattern in the eastern Mediterranean/Black Sea region during the last glacial. Quaternary Res 71, 375–384. doi:10.1016/j.yqres.2008.12.004

Langgut, D., Almogi-Labin, A., Bar-Matthews, M., Weinstein-Evron, M., 2011. Vegetation and climate changes in the South Eastern Mediterranean during the Last Glacial-Interglacial cycle (86 ka): new marine pollen record. Quaternary Science Reviews 30, 3960–3972. doi:10.1016/j.quascirev.2011.10.016

Lee-Thorp, J.A., Sealy, J.C., van der Merwe, N.J., 1989. Stable carbon isotope ratio differences between bone collagen and bone apatite, and their relationship to diet. J Archaeol Sci 16, 585–599.

Lee-Thorp, J.A., Sponheimer, M., Luyt, J. 2007. Tracking changing environments using stable carbon isotopes in fossil tooth enamel: an example from the South African hominin sites. Journal of Human Evolution 53(5), 595–601.

Lézine, A.-M., Hély, C., Grenier, C., Braconnot, P., Krinner, G., 2011. Sahara and Sahel vulnerability to climate changes, lessons from Holocene hydrological data. Quaternary Science Reviews 30, 3001–3012. doi:10.1016/j.quascirev.2011.07.006

Li, S.-G., Tsujimura, M., Sugimoto, A., Davaa, G., Oyunbaatar, D., Sugita, M., 2007. Temporal variation of $\delta^{13}C$ of larch leaves from a montane boreal forest in Mongolia. Trees 21, 479–490. doi:10.1007/s00468-007-0142-2

Long, E.S., Sweitzer, R.A., Diefenbach, D.R., Ben-David, M., 2005. Controlling for anthropogenically induced atmospheric variation in stable carbon isotope studies. Oecologia 146, 148–156. doi:10.1007/s00442-005-0181-6

Lucarini, G., Radini, A., Barton, H., Barker, G. 2015. The exploitation of wild plants in Neolithic North Africa. Use-wear and residue analysis on non-knapped stone tools from the Haua Fteah cave, Cyrenaica, Libya. Quatern Int. http://dx.doi.org/10.1016/j.quaint.2015.11.109

Luttge, U., 2004. Ecophysiology of crassulacean acid metabolism (CAM). Annals of Botany 93, 629–652.

Manlius, N., Menardi-Noguera, A., Zboray, A., 2003. Decline of the Barbary sheep (Ammotragus lervia) in Egypt during the 20th century: literature review and recent observations. J Zool 259, 403–409.

Marino, B.D., McElroy, M.B., Salawitch, R.J., Spaulding, W.G., 1992. Glacial-to-interglacial variations in the carbon isotopic composition of atmospheric CO_2. Nature 357, 461–466.

Marshall, J., Brooks, J.R., Lajtha, K., 2007. Sources of variation in the stable isotopic composition of plants, in: Mitchener, R., Lajtha, K. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing, Oxford, pp. 22-60.

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

McBurney, C.B.M., Hey, R.W., 1955. Prehistory and Pleisticene geology in Cyrenaican Libya. Cambridge University Press, Cambridge.

Mercuri, A.M., 2008a. Human influence, plant landscape evolution and climate inferences from the archaeobotanical records of the Wadi Teshuinat area (Libyan Sahara). J Arid Environ 72, 1950–1967. doi:10.1016/j.jaridenv.2008.04.008

Mercuri, A.M., 2008b. Plant exploitation and ethnopalynological evidence from the Wadi Teshuinat area (Tadrart Acacus, Libyan Sahara). J Archaeol Sci 35, 1619–1642. doi:10.1016/j.jas.2007.11.003

Merceron, G., Zazzo, A., Spassov, N., Geraads, D., & Kovachev, D. 2006. Bovid paleoecology and paleoenvironments from the Late Miocene of Bulgaria: Evidence from dental microwear and stable isotopes. Palaeogeogr Palaeocl 241(3-4), 637–654.

Neftel, A., Oeschger, H., Staffelbach, T., Stauffer, B., 1988. CO_2 record in the Byrd ice core 50,000–5,000 years BP. Nature 331, 609–611.

Nunez, E.E., MacFadden, B.J., Mead, J.I., & Baez, A. 2010. Ancient forests and grasslands in the desert: Diet and habitat of Late Pleistocene mammals from Northcentral Sonora, Mexico. Palaeogeogr Palaeocl 297(2), 391–400.

O'Leary, M.H., 1988. Carbon isotopes in photosynthesis. Bioscience 38, 328–336.

O'Leary, M.H., 1981. Carbon isotope fractionation in plants. Phytochemistry 20, 553–567.

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

13.

Pachur, H.-J, Hoelzmann, P., 2000. Late Quaternary palaeoecology and palaeoclimates of the eastern Sahara. J Afr Earth Sci 30, 929–939.

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

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotope fractionation between diet, breath CO_2, and bioapatite in different mammals. J Archaeol Sci 32, 1459–1470. doi:10.1016/j.jas.2005.03.015

Petit-Maire, N., 1991. Recent Quaternary climatic change and man in the Sahara. J Afr Earth Sci 12, 125–132.

Prendergast, A.L., Stevens, R.E., Hill, E.A., Barker, G., Hunt, C., O'Connell, T.C., 2015. Carbon isotope signatures from land snail shells: Implications for palaeovegetation reconstruction in the eastern Mediterranean. Quatern Int 1–10. doi:10.1016/j.quaint.2014.12.053

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

Rabett, R., Farr, L., Hill, E., Hunt, C., Lane, R., Moseley, H., Stimpson, C., Barker, G., 2013. The Cyrenaican Prehistory Project 2012: the sixth season of excavations in the Haua Fteah cave. Libyan Studies 44, 113–125. doi:10.1017/S0263718900009717

Ramsey, C., Anderegg, M.J., 1972. Food habits of an aoudad sheep, Ammotragus lervia (Bovidae), in the Edwards Plateau of Texas. The Southwestern Naturalist 16, 267–280.

Reade, H., O'Connell, T.C., Barker, G., Stevens, R. E., 2015a. Pleistocene and Holocene palaeoclimates in the Gebel Akhdar (Libya) estimated using herbivore tooth enamel oxygen isotope compositions. Quatern Int 1-13. http://dx.doi.org/10.1016/j.quaint.2015.10.009

Reade, H., Stevens, R. E., Barker, G., O'Connell, T. C., 2015b. Tooth enamel sampling strategies for stable isotope analysis: Potential problems in cross-method data comparisons. Chemical Geology 404, 126-135

Renssen, H., Brovkin, V., Fichefet, T., Goosse, H., 2006. Simulation of the Holocene climate evolution in Northern Africa: The termination of the African Humid Period. Quatern Int 150, 95–102. doi:10.1016/j.quaint.2005.01.001

Richter, D., Moser, J., Nami, M., 2012. New data from the site of Ifri n'Ammar (Morocco) and some remarks on the chronometric status of the Middle Paleolithic in the Maghreb, in: Hublin, J.-J., McPherron, S.P. (Eds.), Modern Origins. a North African Perspective, Vertebrate Paleobiology and Paleoanthropology. Springer Netherlands, Dordrecht, pp. 61–78. doi:10.1007/978-94-007-2929-2_5

Rodríguez Piñero, J. C., Rodríguez Luengo, J. L., Domìnguez Casanova, F. 1987. Datos sobre la alimentación del muflón de Córcega (Ovís ammon musimon) (Bovidade) en Tenerife, Islas Canarias. Vieraea 17, 11-18.

Scerri, E.M.L., 2013. The Aterian and its place in the North African Middle Stone Age. Quatern Int 300, 111–130. doi:10.1016/j.quaint.2012.09.008

Seibt, U., Rajabi, A., Griffiths, H., Berry, J.A., 2008. Carbon isotopes and water use efficiency: sense and sensitivity. Oecologia 155, 441–454. doi:10.1007/s00442-007-0932-7

Sierro, F.A., Hodell, D.A., Curtis, J.H., Flores, J.A., Reguera, I., Colmenero-Hidalgo, E., Bárcena, M.A., Grimalt, J.O., Cacho, I., Frigola, J., Canals, M., 2005. Impact of iceberg melting on Mediterranean thermohaline circulation during Heinrich events. Paleoceanography 20, PA2019.

Smith, H.J., Fischer, H., Wahlen, M., Mastroianni, D., Deck, B., 1999. Dual modes of the carbon cycle since the Last Glacial Maximum. Nature 400, 248–250.

Spinapolice, E.E., Garcea, E.A.A., 2014. Aterian lithic technology and settlement system in the Jebel Gharbi, North-Western Libya . Quatern Int 350, 241–253. doi:10.1016/j.quaint.2014.07.062

Sprovieri, M., Di Stefano, E., Incarbona, A., Salvagio Manta, D., Pelosi, N., Ribera d'Alcalà, M., Sprovieri, R., 2012. Centennial-to millennial-scale climate oscillations in the Central-Eastern Mediterranean Sea between 20,000 and 70,000 years ago: evidence from a high-resolution geochemical and micropaleontological record. Quaternary Science Reviews 46, 126–135. doi:10.1016/j.quascirev.2012.05.005

Stevens, R., Hedges, R.E.M., 2004. Carbon and nitrogen stable isotope analysis of northwest European horse bone and tooth collagen, 40,000 BP–present: Palaeoclimatic interpretations. Quaternary Science Reviews 23, 977–991.

Still, C.J., Berry, J.A., Collatz, G.J., DeFries, R.S., 2003. Global distribution of C3 and C4 vegetation: Carbon cycle implications. Global Biogeochem Cy 17, 1006.

Stojanowski, C.M., Knudson, K.J., 2014. Changing patterns of mobility as a response to climatic deterioration and aridification in the middle Holocene southern Sahara. Am J Phys Anthropol 154, 79-93. doi:10.1002/ajpa.22474

Szabo, B.J., Haynes, C.V., Maxwell, T.A., 1995. Ages of Quaternary pluvial episodes determined by uranium-series and radiocarbon dating of lacustrine deposits of Eastern Sahara. Palaeogeogr Palaeocl 113, 227–242.

Tipple, B. J., Meyers, S. R., Pagani, M. 2010. Carbon isotope ratio of Cenozoic CO_2: A comparative evaluation of available geochemical proxies. Paleoceanography 25, PA3202, doi:10.1029/2009PA001851

Triantaphyllou, M.V., Antonarakou, A., Kouli, K., Dimiza, M., Kontakiotis, G., Papanikolaou, M.D., Ziveri, P., Mortyn, P.G., Lianou, V., Lykousis, V., Dermitzakis, M.D., 2009. Late Glacial-Holocene ecostratigraphy of the south-eastern Aegean Sea, based on plankton and pollen assemblages. Geo-Mar Lett 29, 249–267. doi:10.1007/s00367-009-0139-5

Weinreb, M. M., Sharav, Y. 1964. Tooth development in sheep. American Journal of Veterinary Research 25, 891-908.

WMO. 2016. World Meteorological Organization precipitation data. Accessed online: http://www.wmo.int/datastat/wmodata_en.html. January 2016.

Yanes, Y., Romanek, C.S., Delgado, A., Brant, H.A., Noakes, J.E., Alonso, M.R., Ibáñez, M., 2009. Oxygen and carbon stable isotopes of modern land snail shells as environmental indicators from a low-latitude oceanic island. Geochimica et Cosmochimica Acta 73, 4077–4099. doi:10.1016/j.gca.2009.04.021

Zazzo, A., Mariotti, A., Lecuyer, C., & Heintz, E. 2002. Intra-tooth isotope variations in late Miocene bovid enamel from Afghanistan: paleobiological, taphonomic, and climatic implications. Palaeogeogr Palaeocl 186(1-2), 145–161.

Ziegler, H., Batanouny, K.H., Sankhla, N., Vyas, O.P., Stichler, W., 1981. The photosynthetic pathway types of some desert plants from India, Saudi Arabia, Egypt, and Iraq. Oecologia 48, 93–99.

Table captions

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

Table 2: List of modern samples, including collection location, local mean annual temperature (MAT), mean annual precipitation (MAP) and plant $\delta^{13}C$, and summary of bulk-tooth enamel $\delta^{13}C$ results and estimated dietary $\delta^{13}C$. Temperature and precipitation data for New Mexico is 1990-2014 averages from White Sands National Monument weather station (National Climate Data Center (US). New Mexico plant $\delta^{13}C$ from Hoppe et al. (2004). Temperature and precipitation data for Tenerife is 1971-2000 average from Izaña weather station (Agencia Estatal De Meteorologia, Gobierno de España). Tenerife plant $\delta^{13}C$ from Yanes et al. (2009). Temperature and precipitation data for Cairo is 1961-1990 averages (Egyption Meteroloigcal Authority). Temperature and precipitation data for El Marj is 1943-2012 averages from the Benina weather station and for the central/eastern Gebel Akhdar is 1990-2011 averages from the Shahat weather station (Libyan National Meteorological Centre). Central/eastern Gebel Akhdar plant $\delta^{13}C$ from Prendergast et al. (2015). Dietary estimate in parentheses indicates estimate from outlier value.

Table 3: Summary of archaeological bulk-tooth enamel $\delta^{13}C$ results from Haua Fteah and Hagfet ed Dabba. Population averages are displayed by cultural phase (Haua Fteah) and stratigraphic layer (Hagfet ed Dabba).

Figure Captions

Figure 1. A: Map showing the position of the Gebel Akhdar (square) in the eastern Mediterranean. B: Map of northeast Libya showing the location of sites mentioned in the text, situated within the Gebel Akhdar.

Figure 2. Caprid intra-tooth $\delta^{13}C$ for modern samples. Each line represents an individual intra-tooth $\delta^{13}C$ profile. In locations where more than one tooth per individual were sampled, each individual's intra-tooth $\delta^{13}C$ profile is displayed on a separate graph.

Figure 3. Bulk-tooth $\delta^{13}C$ from modern samples, plotted against mean annual precipitation (top) and mean annual temperature (bottom). Each point indicates the group mean. Vertical bars indicate total range of recorded values. Source of climatic data as described for Table 2.

Figure 4. Bulk-tooth $\delta^{13}C$ from modern Libyan samples and all archaeological samples from Haua Fteah and Hagfet ed Dabba. Each circle (top graph) represents an individual animal. Boxplots (bottom graph) represent the median and interquartile ranges for each sample group. Haua Fteah samples have been grouped by cultural attribution. Hagfet ed Dabba samples have an uncertain chronological association (both within site and with Haua Fteah), but are thought to most likely be associated with the Dabban at Haua Fteah. All samples from Hagfet ed Dabba are plotted as a single population.

Figure 5. Caprid (top) and bovid (bottom) intra-tooth $\delta^{13}C$ profiles for Haua Fteah samples, divided by stratigraphic provenance. Age estimates for layer/layer groups are provided in table 1. Each line represents an individual intra-tooth $\delta^{13}C$ profile.

Figure 6. Bulk-tooth $\delta^{13}C$ from modern Libyan samples and archaeological samples from Hagfet ed Dabba and the Dabban layers at Haua Fteah. Each circle (top graph) represents an individual animal. Boxplots (bottom graph) represent the median and interquartile ranges for

each population. Haua Fteah samples have been grouped by layer attribution. Hagfet ed Dabba samples have an uncertain chronological association (both within site and with Haua Fteah), but are thought to most likely be associated with the Dabban at Haua Fteah.

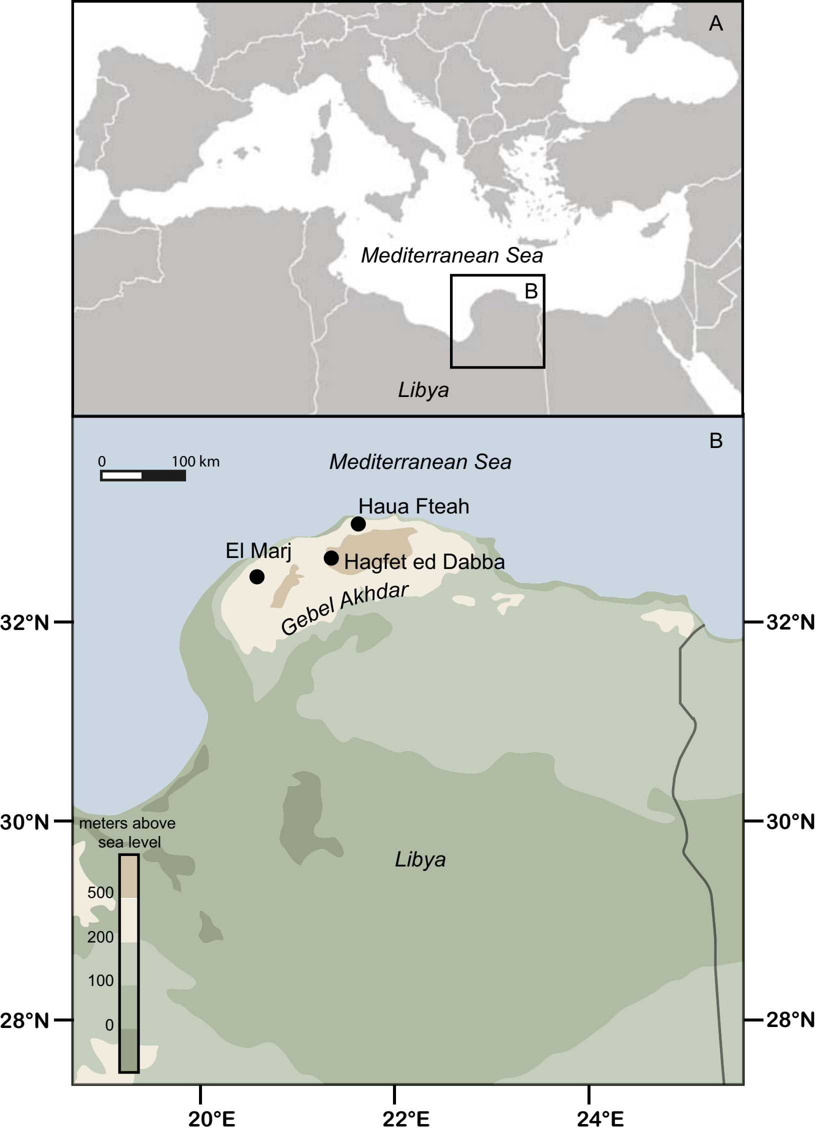
Figure 7. *A. lervia* intra-tooth $\delta^{13}C$ profiles for Hagfet ed Dabba layers II, IV and VI, and Haua Fteah Dabban layers XVII and XX. Each line represents an individual intra-tooth $\delta^{13}C$ profile.

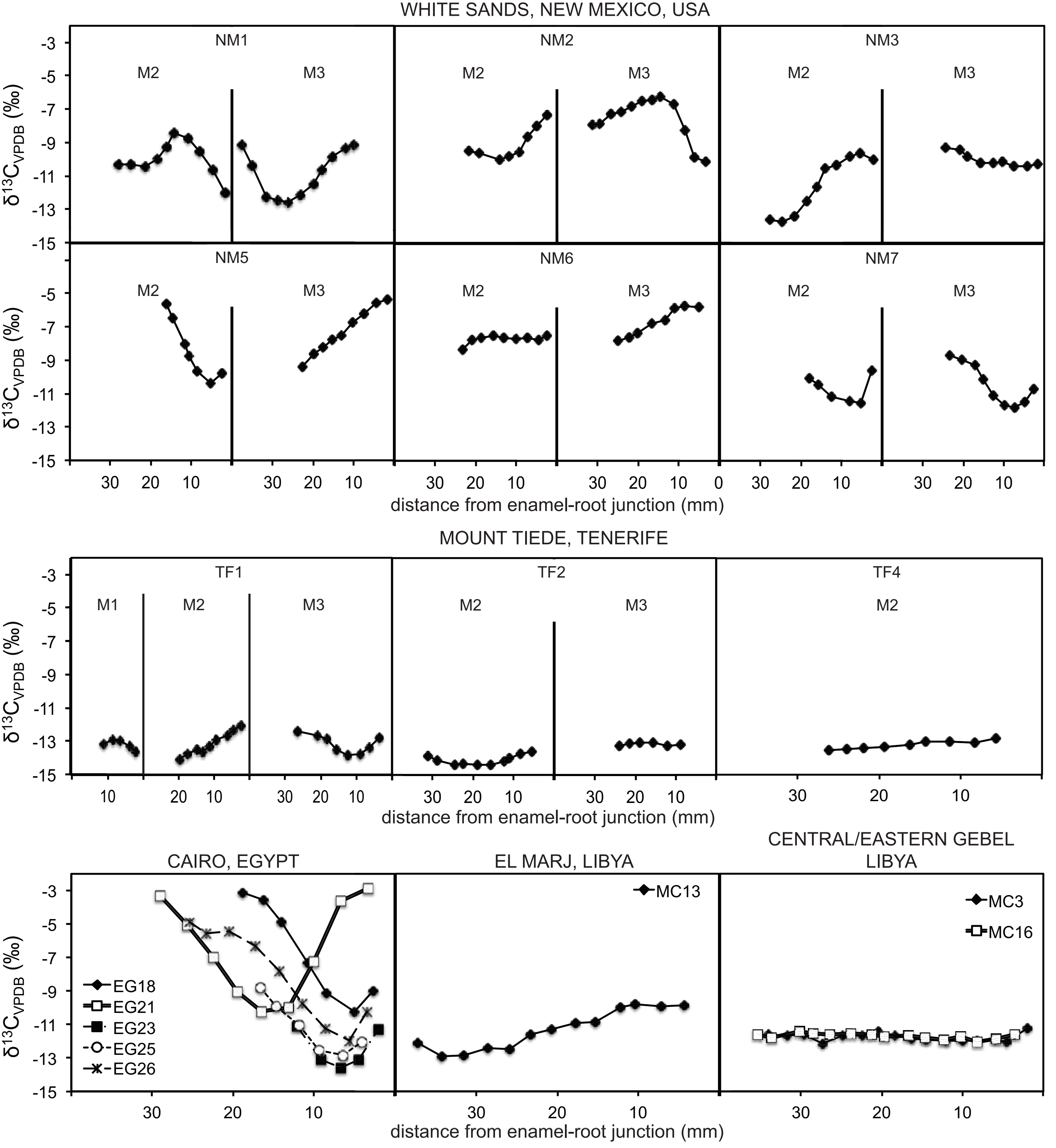
Figure 8. Bulk-tooth $\delta^{13}C$ from Haua Fteah *A. lervia*, for samples that can be attributed to a stratigraphic layer/group of discrete layers. Mean and range of each sample group is plotted against age estimates for layer/layer groups, as detailed in Table 1.

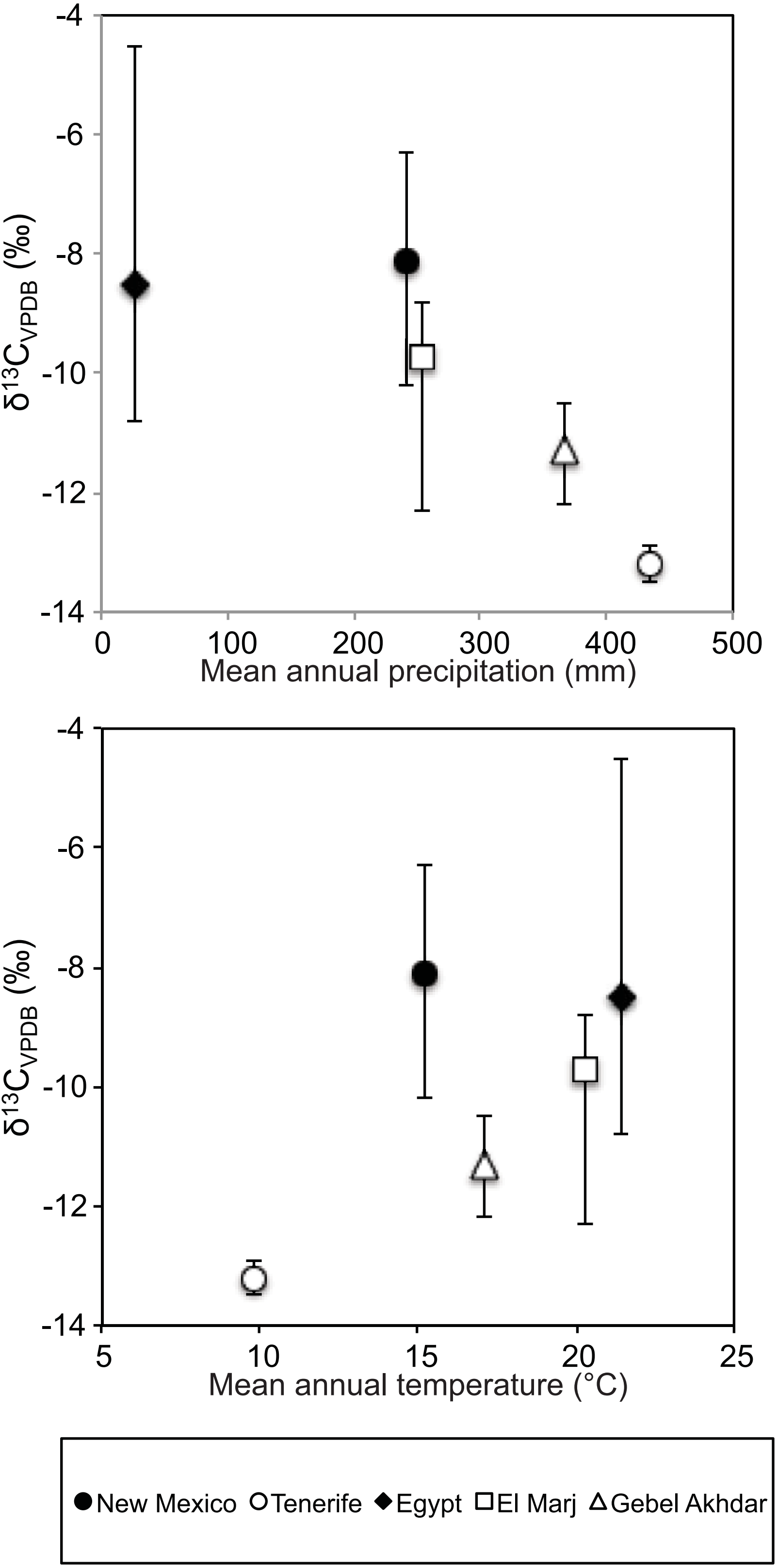
			Proposed Age (ka) for cultural phases			Age estimations for specific layers/layer groupings used in this study	
			McBurney (1967)	Douka et al. (2014)			
Phase	Layers (McBurney, 1967)	Oxygen Isotope Stage		68.2% probability	95.4% probability	Layer	Proposed Age (ka)
Levalloiso-Mousterian	XXXIV-XXV	4-3	65 - 40	68.1 -48.7	73.3 – 43.5	XXXII,XXXIII,XXXIV	*73.3 – 64.0*
						XXXVIII, XXIX	43.2 – 42.0*
Dabban	XXV-XVI	3 – 2 (including LGM)	40 - 15	40.0 -18.1	43.5 – 17.1	XX	32.8 – 31.0
						XVII	22.6 – 22.0*
Oranian	XV-XI	2	15 - 10	16.1 -13.1	17.2 – 12.5	XIV, XV	16.6 – 14.7
						XII	15.0 – 13.5
Capsian	X-IX	1	10 - 7	12.3 -9.3	12.7 – 7.9	X	*12.3 -9.3*
Neolithic	VIII-IV	1	7 - 4.7	7.7 - 6.2	9.3 – 5.4	VIII	7.4 – 6.9
						VI	6.4 - 6.2*

Location	Approx. Latitude/ Longitude	Altitude (m asl)	Sampled species	Number of individuals sampled	MAT	MAP	Mean local plant $\delta^{13}C$ (‰)		Bulk-tooth enamel $\delta^{13}C$ (‰)				Estimated dietary range of individuals sampled (±0.5‰ uncertainty)	
					(°C)	(mm)	C_3	C_4	Mean ± SD	Median	Maximum	Minimum	Maximum	Minimum
White Sands Missile Range, NM, USA	33°23′N 105°16′W	~1500	*A. lervia*	7	15.2	241	-25.6	-14.5	-8.1 ± 1.4	-7.6	-6.3	-10.2	-20.4	-24.3
Mount Tiede, Tenerife	28°16′N 16°38′W	>2000	*O. o. musimon*	4	9.8	434	-26.4	absent	-13.2 ± 0.3	-13.2	-12.9	-13.5	-27.0	-27.6
Cairo, Egypt	30°3′N 31°14′E	<100	Domestic caprids	11	21.4	26	No data	No data	-8.5 ± 2.2	-8.6	-4.5	-10.8	-18.6	-24.9
El Marj, Libya	32°35’N 20°57’E	~300	Domestic caprids	8	20.3	254	No data	No data	-9.7 ± 1.1	-9.7	-8.8	-12.3	-22.9	-24.0 (-26.4)
		~300	*B. taurus*	1					-12.6	n/a (single sample)				
Central/eastern Gebel Akhdar, Libya	32°46′N 22°38′E	<800	Domestic caprids	5	17.1	366	-25.7	No data	-11.3 ± 0.8	-11.1	-10.5	-12.2	-24.6	-26.3
		<800	*B. taurus*	1					-13.5	n/a (single sample)				

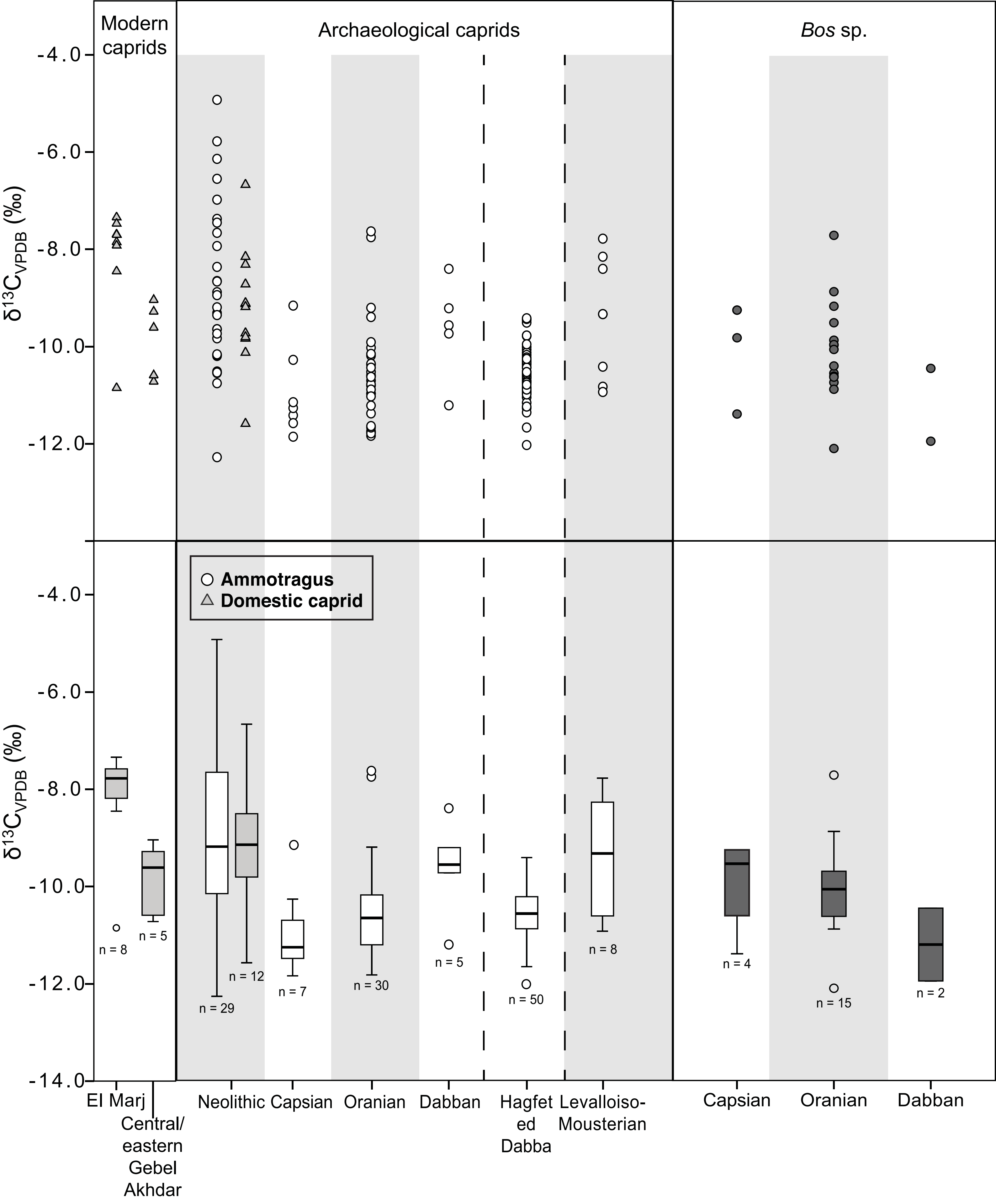
Site	Layer(s)	Cultural 'Phase'	Date range (ka,95.4% confidence from Douka *et al.,* 2014)	Sampled Species	Number of teeth sampled	Bulk-tooth enamel δ^{13}C (‰)					Estimated mean dietary δ^{13}C (‰) of individuals sampled (±0.5‰ uncertainty)	
						Mean ± SD	Median	Maximum	Minimum	Range	Maximum	Minimum
Haua Fteah	VIII-IV	Neolithic	9.3 – 5.4	*A. lervia*	29	-8.8 ± 1.7	-9.2	-4.9	-12.3	7.3	-19.0	-26.4
				Domestic caprid	12	-9.2 ± 1.2	-9.2	-6.7	-11.6	4.9	-20.8	-25.7
	X-IX	Capsian	12.7 – 7.9	*A. lervia*	7	-11.0 ± 0.9	-11.3	-9.2	-11.9	2.7	-23.3	-26.0
				Bos sp.	4	-9.9 ± 1.0	-9.5	-9.3	-11.4	2.1	-23.4	-25.5
	XV-XI	Oranian	17.2 – 12.5	*A. lervia*	30	-10.6 ± 1.0	-10.7	-7.6	-11.8	4.2	-21.7	-25.9
				Bos sp.	15	-10.1 ± 1.0	-10.1	-7.7	-12.1	4.4	-21.8	-26.2
	XXV-XVI	Dabban	43.5 – 17.1	*A. lervia*	5	-9.6 ± 1.0	-9.6	-8.4	-11.2	2.8	-22.5	-25.3
				Bos sp.	2	n/a (only two samples)		-10.5	-12	1.5	-24.6	-26.1
	XXXIV-XXV	Levalloiso-Mousterian	73.3 – 43.5	*A. lervia*	8	-9.4 ± 1.2	-9.3	-7.8	-10.9	3.2	-21.9	-25.0
Hagfet ed Dabba	I	Roman (?)	unknown	*A. lervia*	8	-10.6 ± 0.6	-10.5	-9.8	-11.6	1.9	-23.9	-25.7
	II	Dabban	unknown	*A. lervia*	10	-10.5 ± 0.6	-10.6	-9.5	-11.3	1.8	-23.6	-25.4
	III	Dabban	unknown	*A. lervia*	6	-10.5 ± 0.8	-10.8	-9.4	-11.4	1.9	-23.5	-25.5
	IV	Dabban	unknown	*A. lervia*	12	-10.4 ± 0.5	-10.4	-9.4	-11.2	1.7	-23.5	-25.3
	V	Dabban	unknown	*A. lervia*	2	n/a (only two samples)		-10.7	-12	1.3	-24.8	-26.1
	VI	Dabban	unknown	*A. lervia*	12	-10.5 ± 0.3	-10.5	-10	-11.2	1.3	-24.1	-25.3


A
Mediterranean Sea
B
Libya
B
0
100 km
Mediterranean Sea
Haua Fteah
El Marj
Hagfet ed Dabba
Gebel Akhdar
32°N
32°N
30°N
30°N
meters above sea level
500
200
100
0
Libya
28°N
28°N
20°E
22°E
24°E

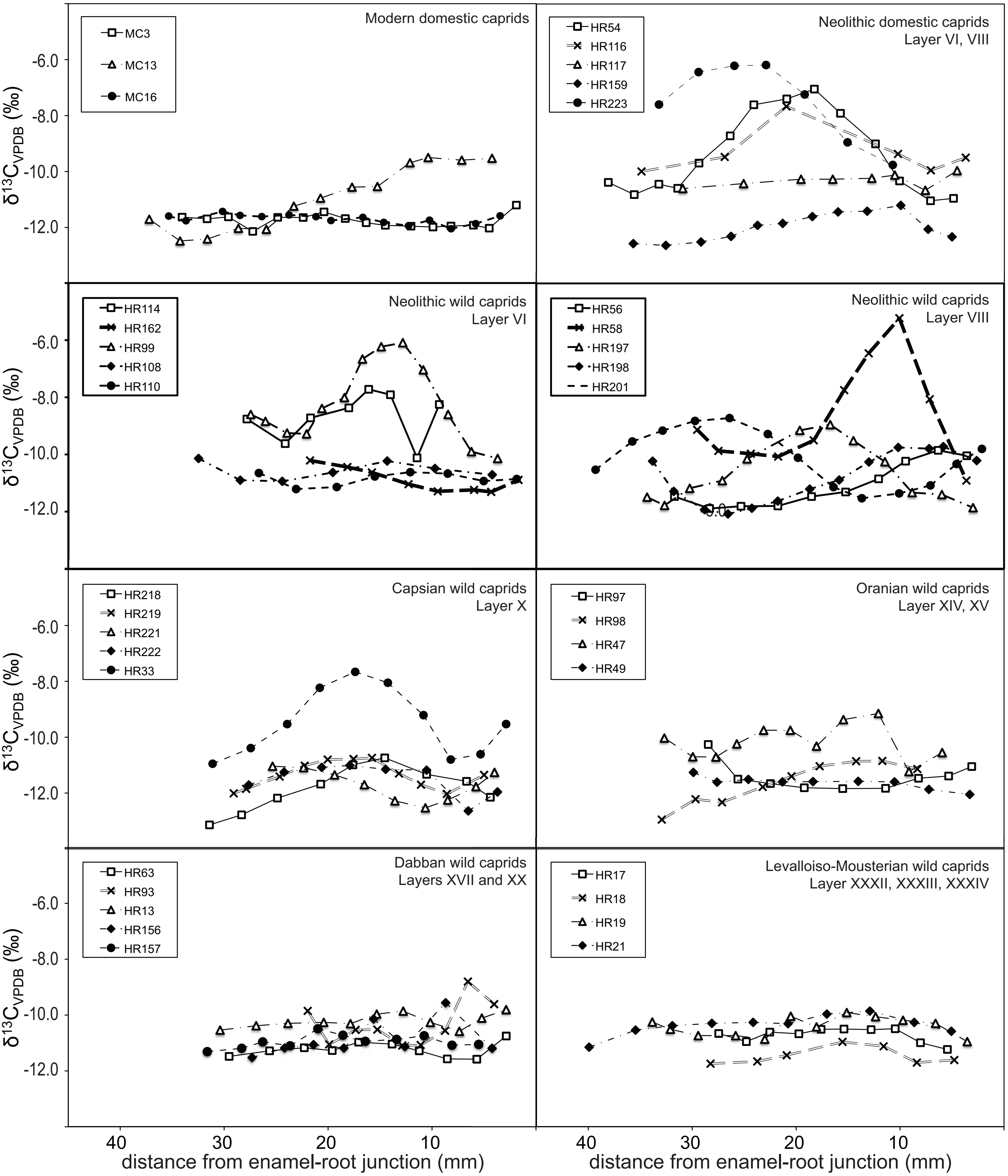

WHITE SANDS, NEW MEXICO, USA
NM1
NM2
NM3
NM5
NM6
NM7
M1
M2
M3
$\delta^{13}C_{VPDB}$ (‰)
-3
-5
-7
-9
-11
-13
-15
30
20
10
0
distance from enamel-root junction (mm)
MOUNT TIEDE, TENERIFE
TF1
TF2
TF4
CAIRO, EGYPT
EL MARJ, LIBYA
CENTRAL/EASTERN GEBEL LIBYA
EG18
EG21
EG23
EG25
EG26
MC13
MC3
MC16



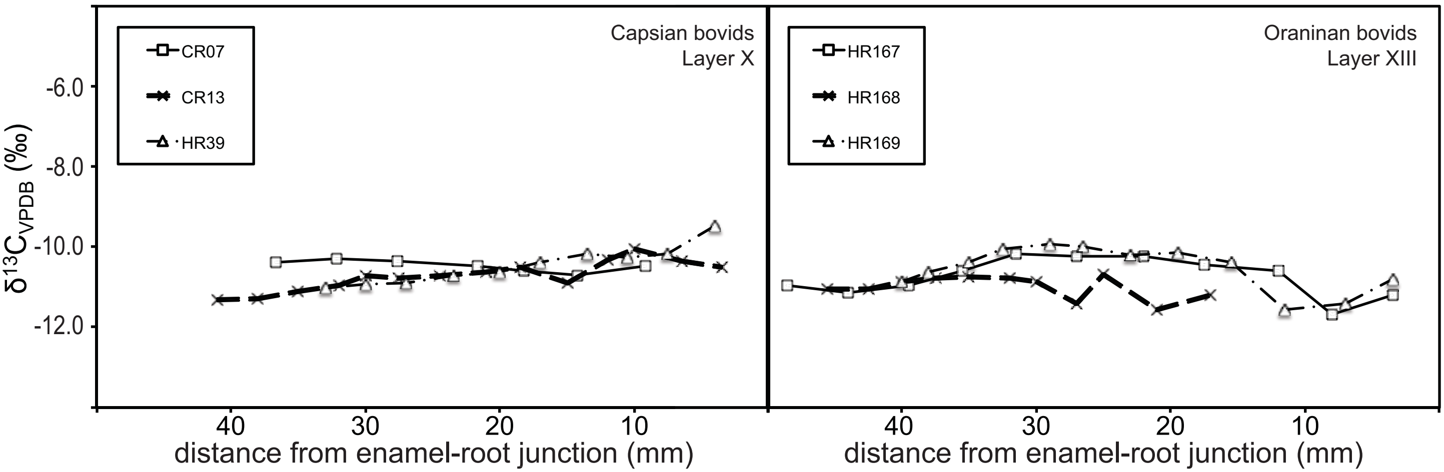
$\delta^{13}C_{VPDB}$ (‰)
-4
-6
-8
-10
-12
-14
0
100
200
300
400
500
Mean annual precipitation (mm)
$\delta^{13}C_{VPDB}$ (‰)
-4
-6
-8
-10
-12
-14
5
10
15
20
25
Mean annual temperature (°C)
● New Mexico
○ Tenerife
◆ Egypt
□ El Marj
△ Gebel Akhdar

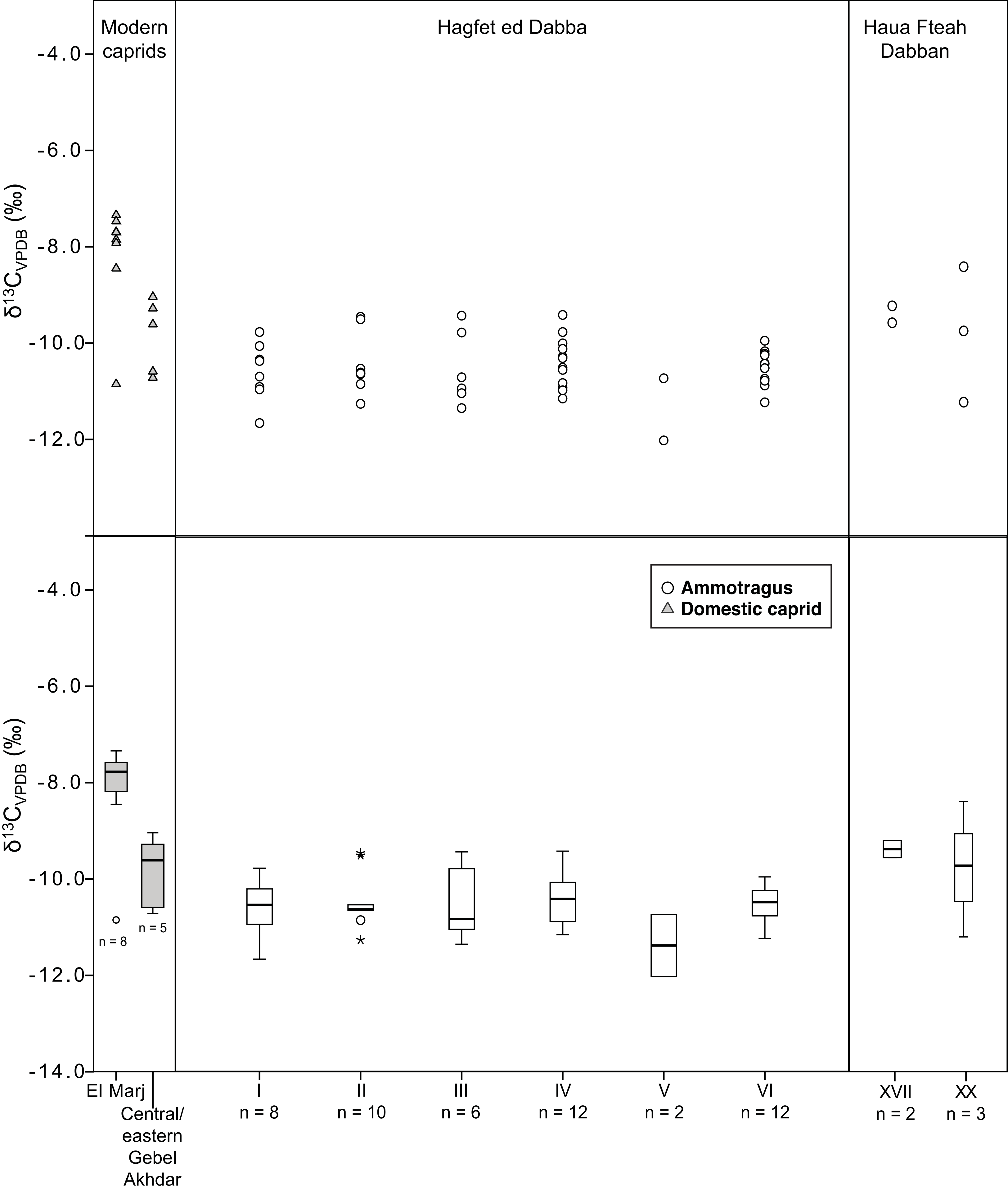

Modern caprids
Archaeological caprids
Bos sp.
δ13CVPDB (‰)
-4.0
-6.0
-8.0
-10.0
-12.0
-14.0
Ammotragus
Domestic caprid
n = 8
n = 5
n = 29
n = 12
n = 7
n = 30
n = 5
n = 50
n = 8
n = 4
n = 15
n = 2
El Marj
Central/ eastern Gebel Akhdar
Neolithic
Capsian
Oranian
Dabban
Hagfet ed Dabba
Levalloiso-Mousterian
Capsian
Oranian
Dabban

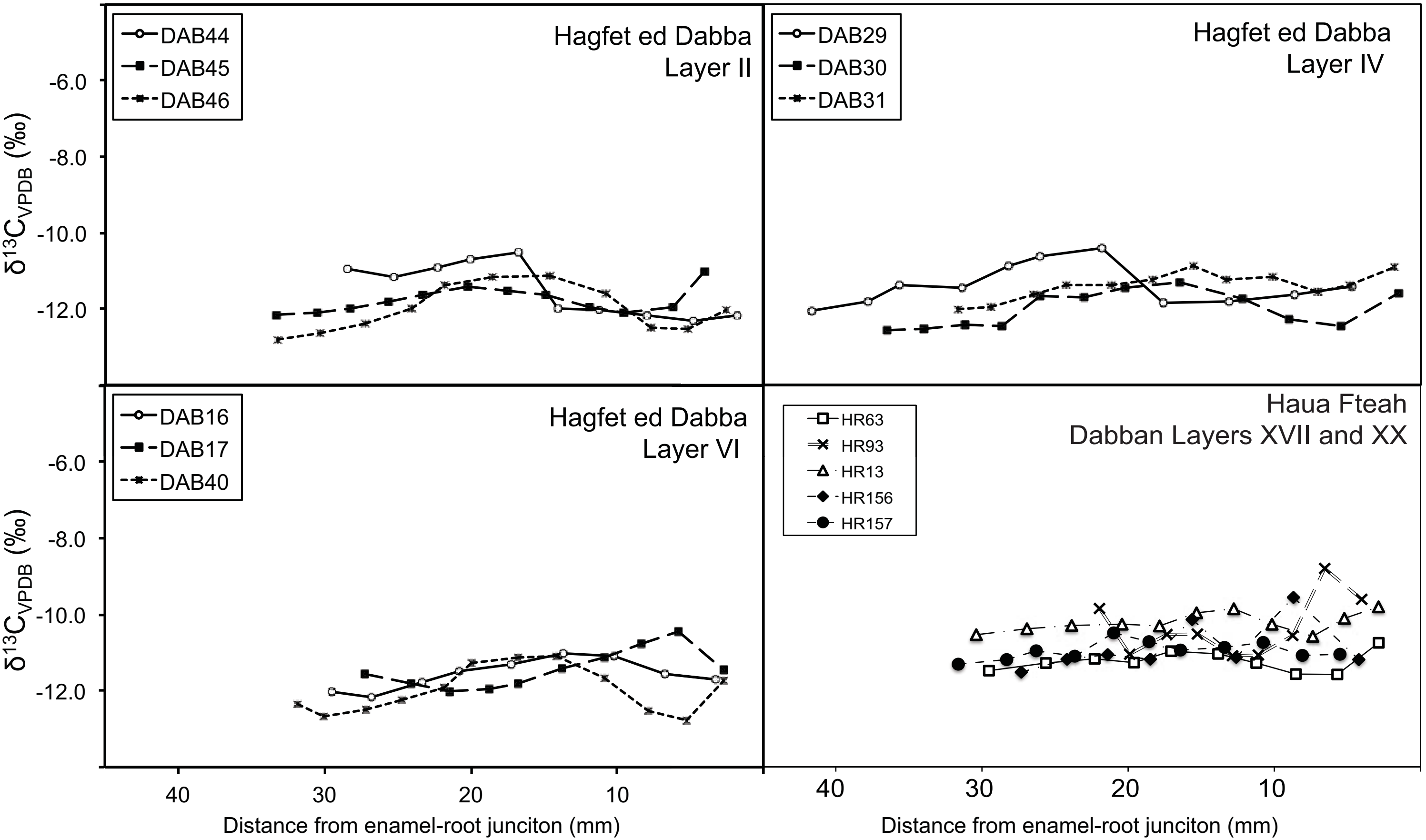
Caprids



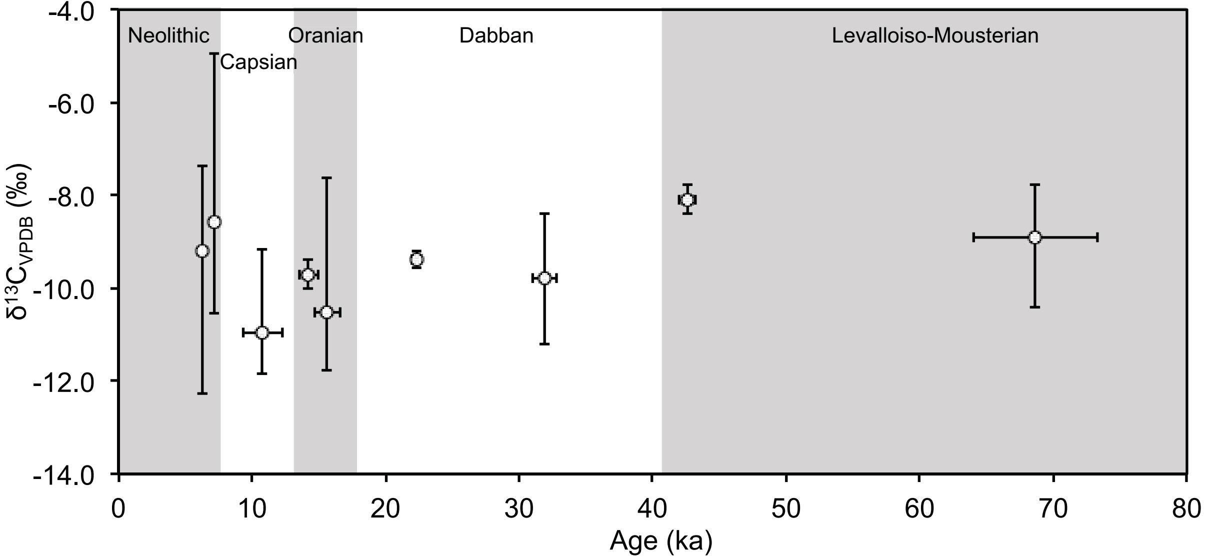
Bovids




Modern caprids
Hagfet ed Dabba
Haua Fteah Dabban
-4.0
-6.0
-8.0
-10.0
-12.0
-14.0
$\delta^{13}C_{VPDB}$ (‰)
○ Ammotragus
△ Domestic caprid
n = 8
n = 5
El Marj
Central/ eastern Gebel Akhdar
I n = 8
II n = 10
III n = 6
IV n = 12
V n = 2
VI n = 12
XVII n = 2
XX n = 3



Hagfet ed Dabba Layer II
DAB44
DAB45
DAB46
Hagfet ed Dabba Layer IV
DAB29
DAB30
DAB31
Hagfet ed Dabba Layer VI
DAB16
DAB17
DAB40
Haua Fteah Dabban Layers XVII and XX
HR63
HR93
HR13
HR156
HR157
$\delta^{13}C_{VPDB}$ (‰)
-6.0
-8.0
-10.0
-12.0
40
30
20
10
Distance from enamel-root junciton (mm)


Neolithic
Capsian
Oranian
Dabban
Levalloiso-Mousterian
-4.0
-6.0
-8.0
-10.0
-12.0
-14.0
$\delta^{13}C_{VPDB}$ (‰)
0
10
20
30
40
50
60
70
80
Age (ka)