From hunter-gathering to food production: isotopic insights on human diet from the later stone age to Neolithic in Northwest Africa, Morocco

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5 CHAPTER 5: DIET OF THE IBEROMAURUSIAN HUNTER-GATHERERS FROM TAFORALT (*PUBLISHED*)

This chapter present the published multi-isotopic results obtained from the archaeological site of Taforalt, Morocco. Through the examination of stable isotopes, it aims to investigate the dietary patterns and the subsistence strategies of the Iberomaurusian hunter-gatherers who lived there during the Later Stone Age. By using carbon, nitrogen, and sulphur analysis in bulk collagen and amino acids, as well as zinc and strontium in tooth enamel from human and faunal remains, the study provides insights into their food choices. These results were published in Nature Ecology and Evolution. Ultimately, this research helps understanding how human groups in Northwest Africa adapted to their environment during the Later Stone Age.

5.1 Isotopic evidence of high reliance on plant food among Later Stone Age hunter-gatherers at Taforalt, Morocco

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*Contribution: Research design, sampling, data analyses, data interpretation, article writing.

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Abstract

The transition from hunting-gathering to agriculture stands as one of the most important dietary revolutions in human history. Yet, due to a scarcity of well-preserved human remains from Pleistocene sites, little is known about the dietary practices of pre-agricultural human groups. Here we present the isotopic evidence of pronounced plant reliance among Late Stone Age hunter-gatherers from North Africa (15,000–13,000 cal BP), predating the advent of agriculture by several millennia. Employing a comprehensive multi-isotopic approach, we conducted zinc (δ^{66}Zn) and strontium (^{87}Sr/^{86}Sr) analysis on dental enamel, bulk carbon (δ^{13}C) and nitrogen (δ^{15}N) and sulphur (δ^{34}S) isotope analysis on dentin and bone collagen, and single amino acid analysis on human and faunal remains from Taforalt (Morocco). Our results unequivocally demonstrate a substantial plant-based component in the diets of these hunter-gatherers. This distinct dietary pattern challenges the prevailing notion of high reliance on animal proteins among pre-agricultural human groups. It also raises intriguing questions surrounding the absence of agricultural development in North Africa during the early Holocene. This study underscores the importance of investigating dietary practices during the transition to agriculture and provides insights into the complexities of human subsistence strategies across different regions.

5.2 Introduction

While the term ‘Neolithic’ remains ambiguous and this period occurred at different times worldwide, it generally implies the domestication of wild animals and plants, as well as the adoption of sedentary settlements (D. Q. Fuller et al., 2018; Svizzero, 2017). The transition from hunting-gathering economies to agriculture-based ones, also known as Neolithization, is one of the most important dietary revolutions in human history (Barker & Goucher, 2015; Larsen, 1995). Beyond being a revolution, a progressive intensification of plant consumption is believed to have begun long before domestication in the Neolithic (D. Q. Fuller et al., 2018; E. Weiss et al., 2004). Evidence of an early shift to grain-based resources is demonstrated by the discovery of a substantial archaeobotanical assemblage in the Upper Palaeolithic site of Ohalo II, in the Near East, dated to approximately 23,000 cal BP (E. Weiss et al., 2004) (Figure 5:1). This transformation intensified with the Natufians, a hunter-gatherer group that inhabited the Near East during the Late Pleistocene and the beginning of the Holocene (14,600–11,500 cal BP) (Simmons, 2015). A shift towards an increased reliance on plant foods occurred during this period (Arranz-Otaegui et al., 2018; Bar-Yosef, 1998; Simmons, 2015), probably driven by several factors, including the depletion of large game species and the availability of a wider range of edible plants in the environment, which led to the adoption of a broad-spectrum diet (Eitam & Schoenwetter, 2020). Natufian hunter-gatherers also engaged in early forms of plant cultivation, such as the intentional planting and harvesting of wild cereals. This practice probably paved the way for the development of agriculture in the region (Stiner, 2001; E. Weiss et al., 2006).

Figure 5:1 Location of the Taforalt site in Morocco and the other sites mentioned in the text. The circles indicate Iberomaurusian sites, the squares indicate European Upper Palaeolithic sites, the triangle indicates the Natufian site and the star indicates the Neolithic site in the Levant.

The preconditions of the transition to food production in the Levant are deeply rooted in the Natufian hunter-gatherers, but this transition is still a poorly understood and complex phenomenon in northwest Africa (Simões et al., 2023). In this region, a shift towards a reliance on plant resources in the diet was thought to be a relatively late phenomenon, which started with the spread of domesticated species from the Near East into this region during the Neolithic (~7,600 BP) (Linstädter et al., 2018; Morales et al., 2013; Simões et al., 2023). In recent years, scholars have become increasingly interested in whether the Iberomaurusians, a population with some genetic connections with the Natufians (Van de Loosdrecht et al., 2018), exhibited changes that preceded the transition to farming in North Africa (Barton et al., 2021; Humphrey et al., 2014). Recent investigations at the site of Taforalt (Figure 5:1), Morocco have suggested early consumption of carbohydrate-rich plants associated with the

Iberomaurusian culture. This has been attested by the high number of wild plant taxa along with the prevalence of tooth caries among the human burials (Humphrey et al., 2014).

The Iberomaurusian hunter-gatherers, characterized by bladelet-based technology, inhabited North Africa during the Late Pleistocene. The first evidence of this culture, found in Tamar Hat (Figure 5:1), dates back to 25,000 cal BP (Close, 1981; Sari, 2014). The timing of its end remains uncertain, with some evidence suggesting the possibility of its persistence into the Holocene after 11,000 cal BP (Barton et al., 2008; Hogue, 2014).

Two key areas of interest are the domestication of plant and animal species, a crucial step in agricultural development, and the adoption of a sedentary lifestyle, often associated with plant cultivation. While there is no evidence of local domestication during the Iberomaurusian period (Klein & Scott, 1986; Merzoug & Sari, 2008; Turner, 2020), some behaviours suggestive of a shift towards sedentism in the subsistence economy were present among these hunter-gatherers. For example, at the Iberomaurusian site of Taforalt (Figure 5:1), evidence points to the selective harvesting and possible storage of some edible plant species (Humphrey et al., 2014). This is documented by the presence of fragments of alfa grass (*Stipa tenacissima*), which would have been used to make baskets. Wild plants have been recovered from other Iberomaurusian sites and could have been collected for the purpose of consumption, such as at Tamar Hat, Algeria (Saxon et al., 1974), and Ifri el Baroud, Morocco (Figure 5:1) (Potì et al., 2019).

Currently, our knowledge of the Iberomaurusian diets is mostly derived from zooarchaeological evidence. Studies have revealed that the Iberomaurusians relied primarily on ungulates, mainly represented by the Barbary sheep (*Ammotragus lervia*), in addition to snails (Taylor et al., 2011; Turner, 2020). These conclusions find further support in an isotopic study conducted on bulk collagen, which identified a predominance of meat in the diet of the Taforalt humans Thorp (Lee-Thorp et al., 2020). Studies on the exploitation of marine resources for food are scarce despite both the proximity of Iberomaurusian sites to the coast (Campmas et al., 2016) and the recovery of marine mollusc shells from various Iberomaurusian sites, where these shells appear to have been used for ornamental purposes (Campmas et al., 2016).

However, it is worth noting that the faunal remains may not fully represent the entire spectrum of the foods consumed. This limitation arises because plant remains are less likely to preserve well in the archaeological record, and their recovery and identification may not be as frequent as that of animal bones (D. Q. Fuller, 2007; Hastorf, 1999; Miller et al., 2020). Furthermore, the detection of plant consumption can be easily overprinted by the presence of meat consumption when assessed using nitrogen isotopes on bulk collagen (Hedges & Reynard, 2007). In terms of settlement patterns, while no stone-built structures similar to those in Natufian settlements are evident (E. Weiss et al., 2004), the presence of large Iberomaurusian cemeteries (such as Taforalt and Afalou; Figure 5:1) in frequently reused sheltered sites—from 15,000 to 13,000 cal BP (Figure 5:1) (Hachi et al., 2002; Humphrey et al., 2014) —is interpreted as evidence of sedentarism (Barton et al., 2020).

Taforalt is one of the two largest known Iberomaurusian cemeteries. This site has yielded substantial amounts of recovered plant remains. In addition, it contains the longest and best-dated occupation sequence for the Iberomaurusian period (Barton et al., 2013, 2020; Hogue & Barton, 2016). To date, it is one of the oldest cemeteries in North Africa, with the largest number of human burials (including adults, adolescents and infants). The human remains were directly dated to 15,077 to 13,892 cal BP (Humphrey et al., 2014), which coincides with a rapid warming period following the Last Glacial Maximum (Potì et al., 2019). It is a key site for studying human dietary behaviour during the Late Pleistocene in North Africa and offers an exceptional opportunity to investigate human dietary behaviours at the end of the Late Pleistocene and before the spread of farming practices in the region. In addition, we have at this site contradictory evidence of dietary reliance on meat (faunal remains (Turner, 2020), C and N isotopes (Lee-Thorp et al., 2020)) and plant foods (plant remains, tooth caries (Humphrey et al., 2014)). A plant-based diet combined with economic intensification could indicate a transitional subsistence strategy towards sedentism. By combining previously used isotope tracers and new ones that are more sensitive to plant consumption, we aimed here to investigate the dietary habits and the mobility patterns of pre-Neolithic hunter-gatherers in North Africa at Taforalt. In particular, we investigated the proportion of plants in their diet and whether this population was relying on local foods.

To accomplish this, we evaluated the bulk stable isotope compositions of carbon ($\delta^{13}C_{collagen}$) and nitrogen ($\delta^{15}N_{collagen}$) in bone and dentine collagen to reconstruct dietary patterns of both human individuals and coexisting fauna rather than to determine the presence/absence of food products in the diet of a population (Supplementary Information Section 2 and Supplementary Fig. 1 in the Appendix for the Chapter 5). However, these bulk isotopic results can be impacted by baseline variations related to environmental parameters such as aridity, essential element availability or the nature of local mycorrhizae (Chikaraishi et al., 2010; Metcalfe, 2021; Szpak et al., 2013). To overcome this issue, compound-specific isotope analysis of single amino acids (CSIA-AA) is used to determine more precisely the trophic position (TP) of an organism independent of environmental factors using the δ^{15}N results for two amino acids: Phe and Glu (Chikaraishi et al., 2010). In addition, δ^{13}C analysis of amino acids such as Phe and Val can effectively distinguish between four main dietary groups (C_3, C_4, marine and freshwater) (Supplementary Information Section 2) (Honch et al., 2012).

While organic isotopic proxies are powerful for dietary reconstruction, their application in Africa often faces challenges due to limited collagen preservation in fossil remains from arid environments (Van Klinken, 1999) . Hence, we enhanced our analysis by investigating zinc isotope ratios (δ^{66}Zn) in tooth enamel, a method that has been proved to reliably document trophic levels (Jaouen et al., 2018, 2022; McCormack et al., 2021) even in the absence of collagen preservation (Bourgon et al., 2021; Jaouen et al., 2022). Zinc and nitrogen isotope ratios have an inverse relationship, wherein lower δ^{66}Zn values reflect an elevation in the TP. Given that baseline effects related to geological and environmental parameters can influence δ^{66}Zn values (Bourgon et al., 2020, 2021; Jaouen et al., 2022), we ensured valid comparisons by also conducting analyses of commonly used mobility indicators, including strontium (^{87}Sr/^{86}Sr) and sulphur (δ^{34}S) isotope ratios (Bentley, 2006; Nehlich, 2015). All details on these isotopic proxies are provided in Supplementary Information Section 2.

We analysed the human remains from the Iberomaurusian burials recovered from sector 10 and associated fauna at Taforalt (Supplementary Information Section 1 and Supplementary Tables 1–3). Human samples consisted of 25 teeth (permanent and deciduous) and seven bone samples belonging to seven identified and ten unassigned individuals (Supplementary Tables 3, 14 and 23). The tissues sampled record different periods of the lives of the individuals, including the breastfeeding period (Supplementary Table 15). Special attention was therefore paid to the potential impact of breastmilk consumption on the isotope ratios throughout the text and figures (Figure 5:2, Figure 5:3 and Supplementary Information Section 5). To preserve morphometric information, the human teeth samples were CT-scanned, and we took this opportunity to document the presence or absence of hypoplasia and caries (Supplementary Information Sections 3 and 7 and Supplementary Table 4). We selected several teeth and bones from various species of associated faunal taxa (sectors 8 and 10) that were exploited by humans to reconstruct the isotopic baseline for Taforalt (Turner, 2020) ($n_{\mathrm{samples}} = 20$; Supplementary Fig. 1 and Supplementary Table 13): Barbary sheep (*Ammotragus lervia*), Equidae (*Equus* sp.), hare (*Lepus* sp.), hartebeest (*Alcelaphus buselaphus*), gazelle (*Gazella* sp.) and Rhinocerotidae. We also analysed two canid specimens (*Canis* sp. and *Vulpes vulpes*) to evaluate isotope values associated with a meat-based diet (Wilman et al., 2014). The faunal taxa were identified using traditional zooarchaeological methods (Turner, 2020) and zooarchaeology by mass spectrometry (ZooMS) (Buckley et al., 2009; Welker et al., 2016) (Supplementary Information Section 3 and Supplementary Table 2). Through the use of these isotopic proxies, the focus of this work is to quantify this population's reliance on plants and determine whether their transition to a more plant-based diet mirrors that of the Levantine Natufian.

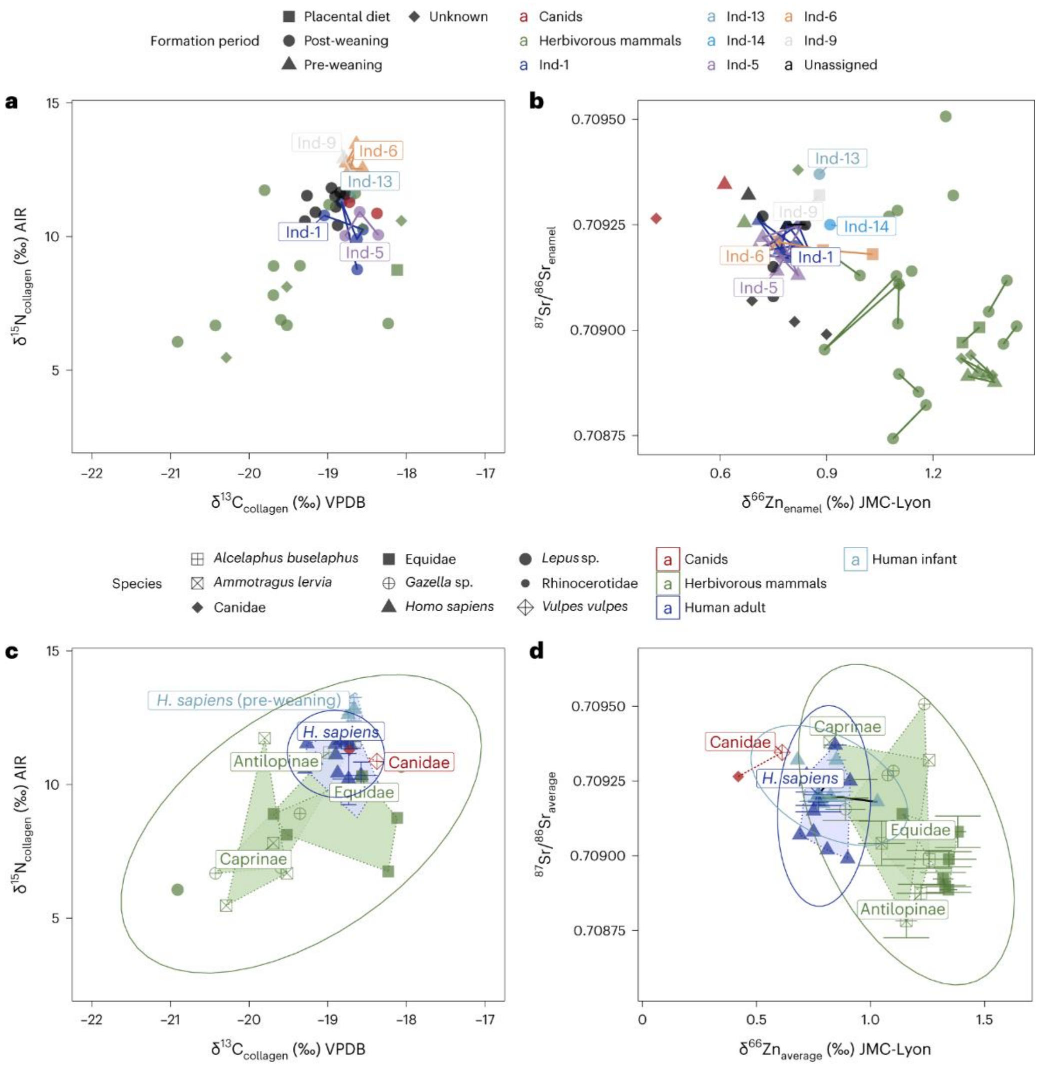

Figure 5:2 Isotopic ratios of various elements from the human and faunal teeth/ bone of Taforalt. a, Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic ratios from bulk collagen of dentine and bone samples. Each point corresponds to a sample; samples from the same individual are connected with a line. The typical analytical error is 0.1‰ for the two isotope systems. VPDB, Vienna PeeDee Belemnite; AIR, atmospheric N2; Ind, individual. b, Zinc (δ^{66}Zn) and strontium (^{87}Sr/^{86}Sr) isotopic ratios from enamel bioapatite. Each point corresponds to a sample; samples from the same individual are connected with a line. The typical analytical error is 0.05‰ for δ^{66}Zn and 7 × 10−6 for ^{87}Sr/^{86}Sr. c, Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic ratios from bulk collagen of dentine and bone samples with associated 95% confidence ellipses. Each point corresponds to the average value of all samples coming from a single individual (nindividual = 33; 44 samples in total); the error bars give the standard deviation for all the values from the same individual. d, Zinc (δ^{66}Zn) and strontium (^{87}Sr/^{86}Sr) isotope ratios from enamel bioapatite with associated 95% confidence ellipses. Each point corresponds to the average value of all samples coming from a single individual (nindividual = 33; 41 samples in total); the error bars give the standard deviation for all the values from the same individual.

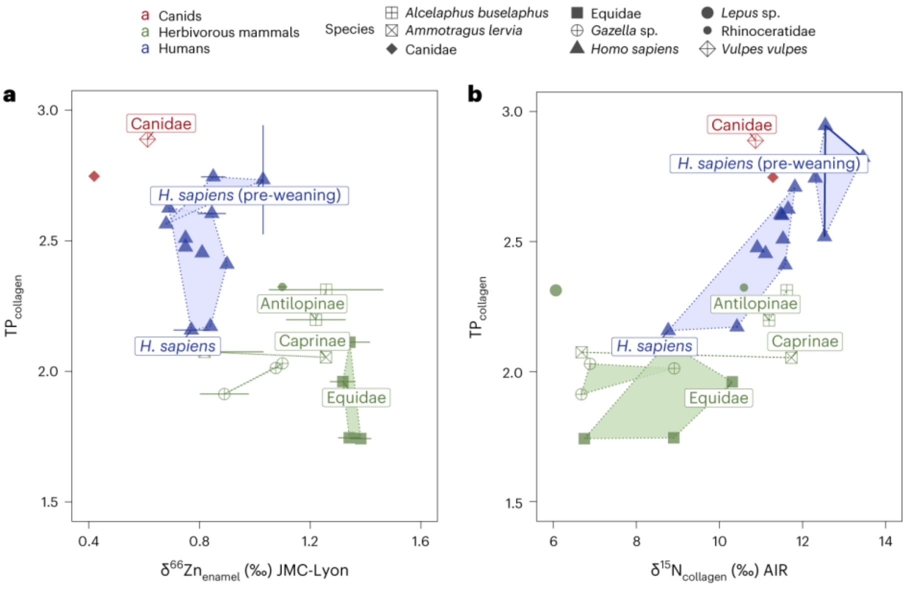

Figure 5:3 Zinc and nitrogen isotope values versus TP. a, Zinc (δ^{66}Zn) isotope values versus the TP obtained from single amino acids (Supplementary Information Section 4). b, Nitrogen (δ^{15}N) isotope values from bulk collagen versus the TP obtained from single amino acids. The TP was estimated from $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Glu}$ values (Supplementary Information Section 2). Samples from the same human individual are connected with a line.

5.3 Results and discussion

The measured $\delta^{66}Zn_{enamel}$, δ^{13}C, δ^{15}N (bulk collagen and amino acids), $^{87}Sr/^{86}Sr_{enamel}$ and $\delta^{34}S_{collagen}$ for the humans and fauna from Taforalt are presented in Figure 5:2, Figure 5:3, Figure 5:4, Extended Data Figs. 1–3, Supplementary Information Section 4 (Supplementary Figs. 3–12 and Supplementary Tables 5–12), Supplementary Tables 16–24 and Supplementary Fig. 16. The diets of the humans are discussed in Supplementary Information Section 5 (Supplementary Figs. 13–15 and Supplementary Table 13).

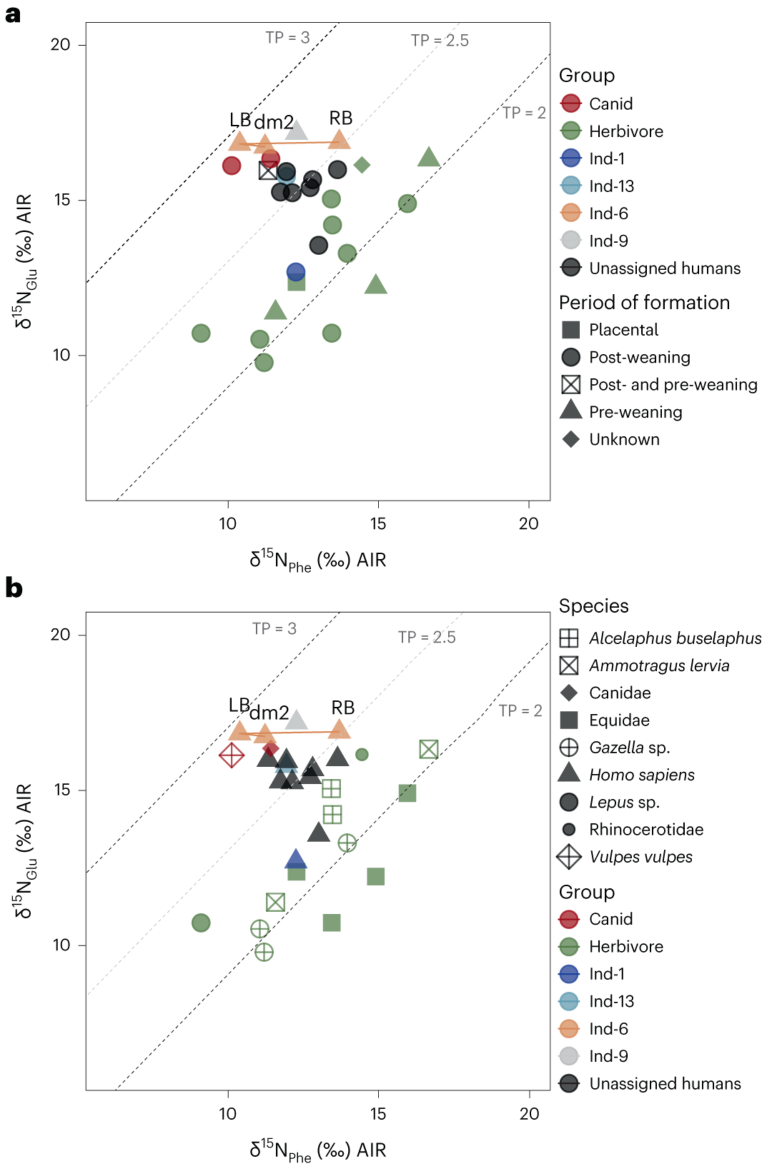

Figure 5:4 Measured $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Glu}$ values on human and faunal collagen from Taforalt. a, Values according to the formation time of the sample. b, Values according to the species. The dashed black lines indicate approximately the theoretical TP of herbivores (TP = 2) and carnivores (TP = 3). The dashed grey line is the intermediate (TP = 2.5). Samples from the same human individual are connected with a line. RB, rib bone; LB, long bone; dm2, deciduous second molar.

All the faunal remains from Taforalt exhibit similar $^{87}Sr/^{86}Sr_{enamel}$ values to the humans, which are close to the modern seawater value (~0.7092, Figure 5:2 (b)) (Bentley, 2006). Since the herbivores also exhibit this seawater value and given the $\delta^{13}C_{collagen}$ of human individuals, it is unlikely that the similar values in the humans indicate marine food consumption; rather, they probably reflect the values of the local geology, which is dominated by calcareous bedrocks (Barton et al., 2020) (expected to be between 0.707 and 0.709 (refs. (Bataille et al., 2020; Bentley, 2006)); Figure 5:2 (b)). All of the other proxies used in this study ($\delta^{15}N_{collagen}$,

$\delta^{13}C_{collagen}$, $\delta^{34}S_{collagen}$, $\delta^{15}N_{AA}$ and $\delta^{13}C_{AA}$) suggest the absence of regular aquatic food consumption (Supplementary Information Section 4).

Trophic level information was determined using three isotopic tracers: $\delta^{66}Zn_{enamel}$, $\delta^{15}N_{collagen}$ and the TP (C3) equation based on $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Glu}$ values (Chikaraishi et al., 2010; Ohkouchi et al., 2017) (Figure 5:3 and Supplementary Information Section 4). Given that the canids from Taforalt primarily have a meat-based diet (Wilman et al., 2014) and that the plant portion of their diet consists of fruits, a resource showing exceptionally low zinc concentrations (Murphy et al., 1975), their $\delta^{66}Zn_{enamel}$ values should be indicative of a carnivorous diet. For $\delta^{66}Zn_{enamel}$, the trophic level spacing ($TLS_{herbivores–canids}$) for all individuals is +0.62‰ and +0.70‰ if we consider only teeth formed post-weaning. This is close to that of Late Pleistocene sites in Laos (+0.63‰) (Bourgon et al., 2020, 2021) and higher than in a modern food web in Kenya (+0.40‰) (Jaouen,et al., 2016). However, the $TLS_{herbivores–canids}$ should be considered with precaution, given the small number of canid samples and the fact that the teeth might have been impacted by consumption of their mother's milk. When only considering human teeth formed after weaning, we found elevated adult human $\delta^{66}Zn_{enamel}$ values, which indicates a low trophic level (0.78 ± 0.07‰, $n_{samples} = 28$, $n_{individuals} = 12$), and these values are close to those of Taforalt herbivores ($n_{herbivores} = 7$, $n_{samples} = 20$, $TLS_{humans–herbivores} = +0.34$‰). The offset is 0.32‰ between the humans and the Barbary sheep, the primary source of game at Taforalt (Turner, 2020). In contrast, this isotopic spacing is much higher at other Late Pleistocene sites such as Tam Pà Ling ($TLS_{humans–herbivores} = +0.48$‰) in Laos (Bourgon et al., 2021, 2020), Gabasa ($TLS_{humans–herbivores} = +0.85$‰) in Spain (Jaouen et al., 2022) and the medieval site of Rennes ($TLS_{humans–herbivores} = +0.63$‰) in France (Jaouen et al., 2018). Furthermore, the $\delta^{66}Zn_{enamel}$ results from the Taforalt humans overlap with those from populations with historically documented cereal-based diets and not with those from populations that regularly consumed meat (Supplementary Fig. 17) (Jaouen et al., 2018), although this comparison does not consider baseline effects (Supplementary Information Section 4). As dietary zinc is likely to be primarily absorbed from animal sources (Davidsson et al., 1996; Sandström et al., 1980), the minimal isotopic differences between Taforalt Iberomaurusians and herbivores at low trophic levels ($TLS_{humans–herbivores}$) and the elevated $\delta^{66}Zn_{enamel}$ values provide compelling evidence of substantial plant consumption. This, in turn, affirms their meat intake as well.

This interpretation of $\delta^{66}Zn_{enamel}$ data is also supported by the trophic level estimations obtained from the isotopic analyses of amino acids. The TP of adult humans, in tissues formed post-weaning, was found to vary between 2.2 and 2.6 with an average of 2.4 ± 0.2 ($n_{\text{samples}} = 9$). Thus, for the majority of individuals, plant resources were the primary source of dietary proteins. This finding highlights a substantial consumption of plant protein in a pre-agriculturist human population (Drucker et al., 2017; Naito et al., 2013). In particular, these TP values at Taforalt are similar to the TP values of Neolithic farmers from the Levant (Tell El Kerkh) (Figure 5:1) (Itahashi et al., 2018). Evidence for substantial plant consumption has also been found for two early modern humans (TP values of 2.5 and 2.6) at the Palaeolithic site of Buran Kaya in Crimea (Fig. 1), and this was similar to most of the associated canids at this site (Drucker et al., 2017). While the canids at Taforalt may not be categorized as pure carnivores, their TP values remain notably high, especially in the case of the red fox (*Vulpes vulpes*) with a TP of 2.9. It is interesting to note that the canids' TP values surpass that of the humans, further supporting the idea that humans had a low reliance on animal protein. In particular, the TP results for individual 1 and an unassigned tooth closely resemble those of the herbivores (Figure 5:4).

In addition to the small TLS$_{\text{humans–herbivores}}$ values for $\delta^{66}\text{Zn}$ (0.34‰) and the low TP calculated by CSIA-AA, the $\delta^{15}\text{N}_{\text{collagen}}$ values between the humans and herbivores ($\Delta^{15}\text{N} = 2.5‰$) are smaller than those from other Upper Palaeolithic sites in Europe and Asia (Figure 5:1) where animal proteins were the main dietary component (for example, Buran Kaya ($\Delta^{15}\text{N} = 6.2‰$), Oase ($\Delta^{15}\text{N} = 10.8‰$), Brno-Francouzska ($\Delta^{15} = 7.1‰$) and Tianyuan ($\Delta^{15}\text{N} = 6.4‰$)) (Drucker et al., 2017; Richards & Trinkaus, 2009; Trinkaus et al., 2009). Our results on the TLS between humans and herbivores are different from the $\Delta^{15}\text{N}$ (TLS) observed by Lee-Thorp et al. (+4.2‰) for Taforalt (Supplementary Information Section 4 and Supplementary Table 10) (Lee-Thorp et al., 2020). While their study focused on the Barbary sheep, the primary hunted faunal species at the site (Turner, 2020), it is important to consider that this species has a flexible diet (Mimoun & Nouira, 2015), which might have influenced the accuracy of the TLS value due to potential differences in isotopic baselines. Our study demonstrates that this species had variable $\delta^{15}\text{N}_{\text{collagen}}$ values while having a stable trophic level of 2.1 ± 0.0 based on $\delta^{15}\text{N}_{\text{AA}}$ values (Supplementary Information Section 4). However, Lee-Thorp et al. (Lee-Thorp et al., 2020) observed an absence of aquatic food consumption, aligning with our conclusions. In addition, Hedges and Reynard (Hedges & Reynard, 2007) found that $\delta^{15}\text{N}_{\text{collagen}}$ bulk-based diet reconstructions tend to overestimate animal protein intake by 60–80% when a nitrogen isotopic ratio enrichment of 3‰ or more is applied using the standard model for $\delta^{15}\text{N}$ interpretation. This conclusion is supported by the association of a TLS of +3‰ with a plant intake of 50% (ref. (O'Connell et al., 2012)) and a TLS of +4‰ among European Neolithic farmers with a meat intake of 40% (ref. (Hamilton et al., 2013)). We should take into consideration that the plants eaten by humans could be more enriched in $\delta^{15}N$ than plants consumed by herbivores due to the effect of charring, which can increase their $\delta^{15}N_{collagen}$ by up to +1‰ (ref. (Fahy et al., 2017)). The $\delta^{15}N_{collagen}$ values observed in humans are probably affected by their consumption of these processed plants (Bogaard et al., 2007; Fraser et al., 2013) , compared with unprocessed forage plants consumed by herbivores. Our TLS estimations for Taforalt based on $\delta^{15}N_{bulk}$ of +4.2‰ and +2.5‰ could therefore suggest a plant food intake of about 50% in the Taforalt human diets. This is in agreement with our conclusions based on Zn isotope ratios and CSIA-AA, the presence of a variety of wild plants at the site (Humphrey et al., 2014) and the high prevalence of tooth caries and other periodontal diseases, which frequently exceeds those observed for hunter-gatherers, all suggesting a high consumption of fermentable starchy plants (Forshaw, 2014; Humphrey et al., 2014; Larsen, 1995). However, it must be stressed that the Taforalt humans studied here were not strict vegetalians, as isotopic offsets between the $\delta^{15}N$ and $\delta^{66}Zn$ herbivore and human values are documented and because zooarchaeological data indicate that animal protein was consumed. In particular, cut marks were observed on the faunal assemblage, mostly on Barbary sheep but also on gazelle, equid, large bovines and hartebeest (Turner, 2020). These cut marks provide evidence of butchery and processing of animal remains, which directly supports the notion that animal protein was an integral part of the Taforalt human diet.

On the basis of multiple isotope proxies, we can also document an early weaning age for an infant (Ind-6) at Taforalt (Figure 5:4 and Supplementary Information Section 5). The noticeable decline in TP, as calculated from the $\delta^{15}N$ values of single amino acids, among tissues with varying formation periods is particularly evident. The tissues, such as the deciduous second molar (TP = 2.8, formed over a span of approximately −0.34 to 1 year (AlQahtani et al., 2010; Humphrey et al., 2020)) and the long bone (TP = 2.9, formed over the first year (AlQahtani et al., 2010; Humphrey et al., 2020)), which have slower remodelling rates, exhibit higher TP values. In contrast, the rib bone, with its faster turnover rate (Fahy et al., 2017) and TP of 2.5, is likely to have recorded dietary information much closer to the time of the individual's death (6–12 months (Humphrey et al., 2020)) (Supplementary Information Sections 2–4). This pattern of decreasing TP values strongly suggests a rapid transition in the individual's diet, with the introduction of adult foods playing a substantial role in this dietary shift (B. T. Fuller et al., 2006) (Figure 5:4).

This is evidence that weaning was initiated before 1 year of age and possibly with plant-based foods, since we observed a clear decrease in this individual's TP (2.8 to 2.5). Unlike at other sites (Jaouen et al., 2020), we do not see a clear weaning pattern in the δ^{66}Zn results when comparing different teeth of a single individual or at the population level (Supplementary information Section 5 and Supplementary Fig. 13). This observation may be due to a sample bias, as the limited sample size per individual prevented the tracing of potential weaning patterns. Alternatively, this could be attributed to the early introduction of solid foods in infant diets. The adoption of a starchy diet in Taforalt may have facilitated early weaning, a pattern commonly associated with the transition to agriculture due to the availability of soft and digestible foods such as cereals. However, early weaning can result in increased stress and mortality for infants (Ash et al., 2016). This contrasts with hunter-gatherer societies, where extended breastfeeding periods are the norm due to the limited availability of suitable weaning foods (Larsen, 1995; Veile & Miller, 2021). These observations suggest that changes in diet and lifestyle in the Iberomaurusians from Taforalt might have had important impacts on infant feeding practices. However, it is clear that additional detailed analyses are needed to fully understand this weaning pattern on a larger scale.

According to the broad-spectrum and dietary breadth models, a reduction in the availability of large to medium-sized game animals often leads to increased foraging for previously overlooked resources such as lagomorphs and small birds and an increased exploitation of wild plants (Flannery et al., 1969; Stiner, 2001). This hypothesis has been commonly applied to explain the emergence of farming in Southwest Asia, where the Natufian hunter-gatherers, initially reliant on small to medium-sized ungulates, adapted their subsistence strategy due to ecological pressure on these animals. As a result, they gradually diversified their diet by incorporating a broader range of food resources, including wild plants. This may have been the case for the Taforalt population, as evidenced by the high incidence and diversity of charred macrobotanical plant remains found in the Grey Series level (Humphrey et al., 2014). The prevalence of caries in the human teeth in burials also suggests a substantial reliance on highly cariogenic wild plant foods such as sweet acorns, pine nuts and some legumes. Furthermore, the presence of grinding stones in the same deposits suggests plant processing, which is possible evidence that the nuts and acorns were ground into flour or meal

(Humphrey et al., 2014). While the removal of the central upper incisors was a prevalent practice among 90% of the Taforalt population and is common among the Iberomaurusians (De Groote & Humphrey, 2016; Humphrey et al., 2014), it is important to note that this practice is not linked to oral pathology. Instead, it may have impacted the functional use of teeth for mastication (De Groote & Humphrey, 2016).

The $\delta^{13}C$ amino acid results presented here indicate that most of the humans and herbivores consumed C_3 plants (Supplementary Information Section 4), which is the photosynthetic pathway of all the edible plant species found at Taforalt. It is likely that most of the wild plants were collected during autumn, such as acorns, while pulses were harvested from late spring to summer (Humphrey et al., 2014). The inhabitants probably stored plants, which would have ensured consistent food staples throughout the year (Humphrey et al., 2014).

These findings suggest a notable increase in the reliance on plant resources by the Taforalt population. While there is no evidence of a decline in Barbary sheep (the main hunted species during the Iberomaurusian period (Turner, 2020)) at the site, it is plausible that the seasonal availability of these species and other ungulates at the site influenced the access to meat proteins through the year. The mortality age of Barbary sheep and gazelle points to hunting activities occurring between spring and early summer (Turner, 2020). Simultaneously, the increased abundance of wild plant resources in the inhabitants' environment may have played a role in their subsistence strategy behaviour. Land snails might have been consumed seasonally too (Taylor et al., 2011). The consumption of wild plant resources (such as acorns) may explain why most of the Iberomaurusian sites were located in the coastal Mediterranean forest regions of Northwest Africa. However, more Iberomaurusian sites need to be studied to confirm this hypothesis.

5.4 Conclusion

Our study highlights the importance of the Taforalt population's dietary reliance on plants, while animal resources were consumed in a lower proportion than at other Upper Palaeolithic sites with available isotopic data. The potential early weaning of infants at Taforalt reinforces the notion of a plant-based food focus for the population, potentially extending to the primary source of nutrition for infants. However, it is crucial to acknowledge that further comprehensive investigations are necessary to fully understand these findings and their implications. Evidence of intensive exploitation of wild plants at the end of the Late

Pleistocene is also documented in the Near East with the Natufian hunter-gatherers, who developed cultivation and became some of the earliest agriculturists. In that region, it is believed that the Younger Dryas climatic deterioration in the early Holocene (11,000–10,300 uncal BP) was the major trigger for systematic cultivation in response to the reduction of the vegetal cover and, consequently, the availability of exploited wild plants (Bar-Yosef, 1998; Weisdorf, 2005). Although the Natufian and Iberomaurusian populations had broad similarities regarding the preconditions for the emergence of food production (intensive plant consumption and increased sedentism) and genetic connections (63% of shared genes between Natufian and Iberomaurusian individuals) (Van de Loosdrecht et al., 2018), these factors did not lead in North Africa to a similar local development of agriculture and farming despite the high reliance on plants as a food staple during the Later Stone Age. While the origin of this dissimilarity is still open to debate, the Younger Dryas cooling phase might have reduced the abundance of plant resources, which could explain why Iberomaurusian sites became less occupied during the period (Bouzouggar et al., 2008).