Earliest isotopic evidence of high reliance on plant food in the Late Pleistocene hunter-gatherer population (Taforalt, Morocco)

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Article

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Abstract

The transition from hunting-gathering to agriculture stands as one of the most significant 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 first isotopic evidence of pronounced plant reliance among Late Pleistocene hunter-gatherers from North Africa, predating the advent of agriculture by several millennia. Employing a comprehensive multi-isotope approach, we conducted zinc ($\delta^{66}Zn$) and strontium ($^{87}Sr/^{86}Sr$) analysis on dental enamel, carbon ($\delta^{13}C$), and nitrogen ($\delta^{15}N$) isotope analysis on dentin and bone collagen, alongside single amino acid analysis on humans and fauna 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. Additionally, it 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 novel insights into the complexities of human subsistence strategies across different regions.

Introduction

The transition from hunting-gathering economies to agricultural-based ones, also known as "Neolithisation", is one of the biggest dietary revolutions in human history[1,2]. More than a revolution, a progressive intensification of plant consumption is believed to have begun long before domestication in the Neolithic[3,4]. Although the term Neolithic is still ambiguous and happened at different chronological periods across the world, it generally implies the domestication of wild animals and plants as well as the adoption of sedentary settlements[5]. The earliest known example of this economic transformation started with the Natufian, 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)[6]. One of the most significant dietary transitions that occurred in this period was the shift towards an increased reliance on plant foods[6–8], likely 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[9]. Natufian hunter-gatherers also engaged in early forms of plant cultivation, such as the intentional planting and harvesting of wild cereals. This practice likely paved the way for the development of agriculture in the region[10,11].

If the preconditions of the transition to food production in the Levant are deeply rooted in the Late Pleistocene Natufian hunter-gatherers, this transition is still a poorly understood and complex phenomenon in northwest Africa. 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 (7600 BP)[12–14]. In recent years, scholars have become increasingly interested in whether the Iberomaurusian period, a human population genetically similar to the Natufians[15], exhibited changes that preceded the transition to farming in North Africa[16,17].

Recent investigations of the site of Taforalt, Morocco, suggested an 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[17].

The Iberomaurusian hunter-gatherer groups that inhabited North Africa between the Late Pleistocene and early Holocene (25,000–11,000 cal BP) were characterized by the production of blade and bladelet stone technology[18–20]. Two key areas of interest are the domestication of plant and animal species, a crucial step in the development of agriculture, and sedentary behavior, which is often associated with the cultivation of plants. Although there is no evidence of local domestication during the Iberomaurusian period, it has been suggested that some behaviors indicative of a changing subsistence economy towards sedentism were present among these hunter-gatherers. For example, at the Iberomaurusian site of Taforalt (Fig. 1), some wild plant species were selectively harvested and possibly stored in baskets, and a high prevalence of tooth decay in human burials suggests a diet rich in starchy plants[17]. Currently, our knowledge of the Iberomaurisian diets is mostly derived from zooarchaeological evidence. Studies reveal that the Iberomaurusians relied primarily on ungulates, mainly represented by the Barbary sheep (*Ammotragus lervia*), in addition to snails[21–23]. These conclusions are also supported by an isotopic study conducted on the bulk collagen, which found a predominance of meat in the diet of the Taforalt humans[24]. Studies on the exploitation of marine resources for food are scarce despite both the proximity of Iberomaurisan sites to the coast[25] and the recovery of marine molluscs from various Iberomaurusian sites, where they appear to have been used for ornamental purposes[25].

However, it is important to note that the faunal remains may not accurately represent the entire range of foods consumed as plant remains do not preserve as well as bones in the archaeological record or may not be adequately recovered and identified as frequently as animal bones[26–28]. In addition, plant consumption is also easily overprinted by meat consumption when traced by nitrogen isotopes[29]. In terms of settlement patterns, while there is no evidence of stone-built structures as in the Natufians settlements[6], the existence of large Iberomaurusian cemeteries in caves that were repeatedly reused between 15,000 and 13,000 cal. BP (Taforalt, Tamar Hat, Afalou)[30,31]is interpreted as evidence of sedentarism[21].

Taforalt is one of the two largest known Iberomaurusian cemeteries and the only site from this period where plant remains have been recovered and, as such, is of critical importance for the archaeology of the region and period. In addition, it contains the longest and most well-dated occupation sequence for the Iberomaurusian period [18,20,32] To date, it is the oldest cemetery 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[17], which coincides with a rapid warming period during the Last Glacial Maximum (LGM)[33]. It is a key site for studying human dietary behavior during the Late Pleistocene in North Africa and offers an exceptional opportunity to investigate human dietary behaviors at the end of the Late Pleistocene and before the spread of farming practices in the region. In addition, we have at this site contradicting evidence of meat (faunal remains, C and N isotopes[24,34]) and plant consumption (plant remains, tooth caries[17]). A plant-based consumption combined with an economic intensification could indicate a transitional subsistence strategy towards sedentism. By combining previously used isotope tracers and novel ones that are more sensitive to plant consumption, we aim here to investigate the dietary habits and the mobility patterns of pre-Neolithic hunter-gatherers in North Africa at Taforalt. In particular, we want to investigate whether this population was relying on local foods, and the proportion of plant foods in their diet.

To accomplish this, we evaluate the bulk stable isotope compositions of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in bone and dentine collagen to reconstruct dietary patterns of specific individuals rather than to determine the presence/absence of food products in the diet of a population (See Supplementary Information). However, these bulk isotopic results can be impacted by baseline variations[29,35,36]. 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 $\delta^{15}N$ results of two amino acids: Phenylalanine (Phe) and Glutamic acid (Gl). In addition, $\delta^{13}C$ analysis of amino acids such as Phe and Valine (Val) can effective distinguish between four main dietary groups (C_3, C_4, marine, freshwater) [37].

While these organic isotopic proxies are powerful for dietary reconstruction, their use in Africa is usually hindered because of the limited collagen preservation collagen in fossil remains in arid environments[38]. Thus we also analyzed zinc isotope ratios ($\delta^{66}Zn$) from tooth enamel, a method recently shown to reliably record trophic levels[39–43] even in Pleistocene and older remains that lack collagen preservation[42,44–46]. $\delta^{66}Zn$ and $\delta^{15}N$ measurements have an inverse relationship with lower $\delta^{66}Zn$ values reflecting an increase in trophic position. As baseline effects can impact $\delta^{66}Zn$ values [44–46], precautions to ensure viable comparison were taken by also performing analyses of some commonly-used mobility indicators, such as strontium ($^{87}Sr/^{86}Sr$) and/or sulphur ($\delta^{34}S$) isotopes[47,48]. All details on these isotopic tracers are provided in Supplementary Information 2.

We analysed the human remains and associated fauna from the Iberomaurusian burials recovered from sector 10 at Taforalt (Supplementary Information 1). In order to preserve morphometric information, all samples were CT-scanned, and we took this opportunity to document the presence or absence of hypoplasia and caries (Supplementary Information 3). Samples consisted of 25 human teeth (permanent and deciduous) and 7 bone samples belonging to 7 identified and 10 unassigned individuals (**Table S3.2)**. We also included several teeth and bones from different species of the associated fauna (n = 20): Barbary sheep (*Ammotragus Lervia*), Equidae (*Equus* sp.), hare (*Lepus* sp.), Hartebeest (*Alcelaphus buselaphus*), Gazelle (*Gazella* sp.), Rhinocerotidae and Canidae (*Canis* sp). The animal species were identified using traditional zooarchaeological methods[34] and ZooMS[49,50].Through the use of these isotopic proxies, the focus of this work is to quantify this population's reliance on plants and whether their transition to a more plant-based diet mirrors that of the Levantine Natufian.

Results and discussion

The measured δ^{66}Zn, δ^{13}C, δ^{15}N (bulk collagen and amino acids), ^{87}Sr/^{86}Sr, and δ^{34}S for the humans and animals from Taforalt are presented in Supplementary Information 4. The discussion of the fauna's diets is given in Supplementary Information 4.

All the fauna remains from Taforalt exhibit similar ^{87}Sr/^{86}Sr enamel values to the humans, which are close to the modern seawater value (~ 0.7092)[47]. Since the herbivores also exhibit this seawater value, it is unlikely that the similar values in the humans indicate marine food consumption but rather reflects the values of the local geology, which is dominated by calcareous bedrocks[21] (usually between 0.707–0.709 in literature)[47] (Fig. 2B).

All of the other proxies used in this study (δ^{15}N, δ^{13}C, δ^{34}S of bulk collagen as well as δ^{15}N, δ^{13}C of amino acids) suggest the absence of regular aquatic food consumption (Supplementary Information S4). In addition, our isotopic results contrast with previous isotopic research which found diets rich in meat in other pre-agricultural sites [51–54].

Trophic level information from was determined using three isotopic tracers: δ^{66}Zn, bulk collagen δ^{15}N and the TP (C3) equation of the $\delta^{15}N_{phe}$ and $\delta^{15}N_{Glu}$ values[36,55] (Fig. 3) (Supplementary Information S2). For δ^{66}Zn, the trophic level spacing ($TLS_{herbivore-carnivore}$) at Taforalt for all individuals is similar (+ 0.62‰) to that of Late Pleistocene sites in Laos (+ 0.63‰)[44,45] but higher than in a modern food web in Kenya (+ 0.40‰)[41]. However, when only considering human teeth formed after weaning, we find elevated adult human δ^{66}Zn values which indicates a low trophic level (0.79 ± 0.07‰, n = 22), and these results are close to the herbivores from Taforalt ($TLS_{human-herbivore}$ = 0.36‰). In addition, there is only a small offset (0.24‰) between these humans and the Barbary sheep, the primary source of game at Taforalt[34], which also suggests decreased consumption of meat. In contrast, this isotopic spacing is much higher at other Late Pleistocene sites such as Tam Pà Ling and Nam Lot II ($TLS_{human-herbivore}$ = + 0.48‰) in in Laos[44,45] and Gabasa ($TLS_{human-herbivore}$ = + 0.85‰) in Spain[46], and the medieval site of Rennes ($TLS_{human-herbivore}$ = + 0.63‰) in France[39]. Further, the δ^{66}Zn results of the Taforalt humans overlap with those of populations with historically-documented cereal-based diets and not with populations that regularly consumed meat [39], although this comparison does not take into account baseline effects (Supplementary Information 4). As dietary Zn is presumably absorbed preferentially from animal foods[56,57], the low $TLS_{human-herbivore}$ isotopic offsets and the high δ^{66}Zn results of the Taforalt Iberomaurusians is strong evidence for the substantial consumption of plants.

This δ^{66}Zn interpretation is also supported by the trophic level estimations obtained from the isotopic analyses of amino acids. The TP of adult humans was found to vary between 2.2 to 2.7 with an average of 2.5 ± 0.2, (n = 10). Thus for 60% of the individuals at Taforalt, most of the dietary proteins came from plant resources. This is the first time that such a substantial consumption of plant protein has been found for a pre-agriculturist human population[58,59] (Supplementary Information 6, Figure SI 6.3). In particular, these TP values at Taforalt are similar to the TP values of Neolithic farmers from the Levant[60].

Evidence for substantial plant consumption has also be found for two early modern humans (TP: 2.5 and 2.6) at the Palaeolithic site of Buran Kaya in Crimea and this was similar to most of the associated canids at the site[58]. However, here at Taforalt, the canids have higher TP values than the humans, which is additional evidence for a low reliance on animal protein, and in some cases (individual 1 and the unassigned tooth) actually have nearly identical TP results as the herbivores (Fig. 3).

In addition to the small $TLS_{humans-herbivores}$ values for $\delta^{66}Zn$ (0.37‰) and the low TP calculated by CSIA-AA,the $\delta^{15}N_{bulk}$ values between the humans and herbivores ($\Delta^{15}N$=2.4‰) are small when compared to other Upper Paleolithic sites in Europe and Asia where animal proteins were the main dietary component (e.g. Buran Kaya [$\Delta^{15}N$ = 6.2‰]), Tianyuan [$\Delta^{15}N$ = 6.4‰], Oase [$\Delta^{15}N$ = 10.8‰], Brno-Francouzska [$\Delta^{15}N$ = 7.1‰])[54,58,61]. Interestingly, our results on the trophic level spacing between humans and herbivores are different from the $\Delta^{15}N$ (TLS) observed by Lee Thorp et al[24] (+ 4.2‰) for Taforalt. While their study focused on the Barbary sheep, the primary hunted animal at the site, it is important to consider that this species had a flexible diet[62], 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 $\delta^{15}N_{bulk}$ values while having a trophic level of 2.1 ± 0.0, based on $\delta^{15}N$ values of single amino acids (Supplementary Information 4). In addition, Hedges and Reynard[29] found that $\delta^{15}N$ 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 $\delta^{15}N$ interpretation. This conclusion is supported by the association of a TLS of + 3‰ with a plant intake of 50%[63], and a TLS of + 4‰ among European Neolithic farmers with a meat intake of 40% [64]. As cereals and seeds are more enriched in $\delta^{15}N$ than forage plants by 1-1.25‰ [29], their consumption can explain higher $\delta^{15}N$ values among humans compared to other animals for a similar TP. Therefore, the TLS estimations for Taforalt based on $\delta^{15}N_{bulk}$ of + 4.2‰ and + 2.4‰ (this study) fall within the range observed among Neolithic populations [29] and suggests a plant food intake of about 50% in the Taforalt human diets. This is in agreement 1) with our conclusions based on Zn isotope ratios and CSIA-AA, 2) presence of a variety of wild plants at the site[17], and 3) 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[2,17,65]. However, it must be stressed that the Taforalt humans studied here were not strict vegetarians as isotopic offsets between the $\delta^{15}N$ and $\delta^{66}Zn$ herbivore and human values and zooarchaeological data indicate that animal protein was consumed. In particular, the cut marks observed on the faunal assemblage show that the Barbary sheep was the most exploited taxa during this time period[34].

Based on multiple isotope proxies, we can also document an early weaning age for an infant (Ind.6) at Taforalt (Fig. 3 and Supplementary Information 5). The clear decrease in the TP calculated from the $\delta^{15}N$ on single amino acids between the tissues formed at the beginning of his first year (di^2 and long bone) and the one formed shortly before his death (rib bone ~ 6–12 months) suggest a rapid introduction of adult foods into his diet (Fig. 3). This is evidence that weaning was initiated before one year of his age and possibly with plant-based foods since we observed a clear decrease in his TP (2.8 to 2.5). Unlike other sites[66], we do not see a clear weaning pattern in the $\delta^{66}Zn$ results when comparing different teeth of a single individual or at the population level (Supplementary information 5). This observation may be due to a sample bias as the limited sample size per individual prevented the tracing of potential weaning patterns. Alternatively, it is possible that 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[67]. This contrasts with hunter-gatherer societies, where extended breastfeeding periods are the norm due to the limited availability of suitable weaning foods[2,68]. These observations suggest that changes in diet and lifestyle in the Iberomaurusians from Taforalt might have had significant impacts on infant feeding practices. However, it is clear that additional detailed analyses are needed to fully understand this pattern.

According to broad-spectrum and dietary breadth models, a reduction in the availability of higher-ranking foods would generally lead to a greater concentration of foraging for lower-ranking resources[9,69]. 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[17]. The prevalence of caries in the teeth of humans in burials also suggests a significant reliance on highly cariogenic wild plant foods such as sweet acorns and pine nuts. 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 a flour or meal, requiring significant processing[21]. Our $\delta^{13}C$ amino acid results indicate that most of the humans and herbivores consumed C_3 plants (Supplementary Information 4), which is the photosynthetic pathway of all the edible plant species found at Taforalt. The presence of Alfa grass (*Stipa tenacissima*) suggests that the plants were collected and stored in baskets[13,17]. It is likely that the inhabitants of the site practiced both harvesting and storing of wild plants as a means of ensuring a food staple throughout the year. Most of these plant taxa reach maturity in the autumn, and only a few in spring to late summer. Overall, these findings could suggest that the population of Taforalt increased their reliance on plant resources due to changes in the availability of higher-ranking foods and the abundance of plant resources in their environment. The consumption of wild plant resources (such as acorn) 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 in order to confirm this hypothesis.

Concluding remarks

Our study highlights the importance of the dietary reliance on plants of the Taforalt population while animal resources were consumed in a lower proportion compared to 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 comprehend 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, which developed cultivation and became one of the earliest agriculturists. In that region, it is believed that the Younger Dryas (YD) climatic deterioration in the early Holocene (11,000–10,300 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[6,70]. Although the Natufian and Iberomaurusian populations had broad similarities regarding the preconditions for the emergence of food production (intensive plant consumption, increased sedentism) and genetic connections (63% of shared genes between Natufian and Iberomaurusian individuals)[15], it 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 late Pleistocene. 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 [18].

Declarations

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Figures

Figure 1

Location of Taforalt cave in Morocco, North Africa as well as other Iberomaurusian sites mentioned in the text.

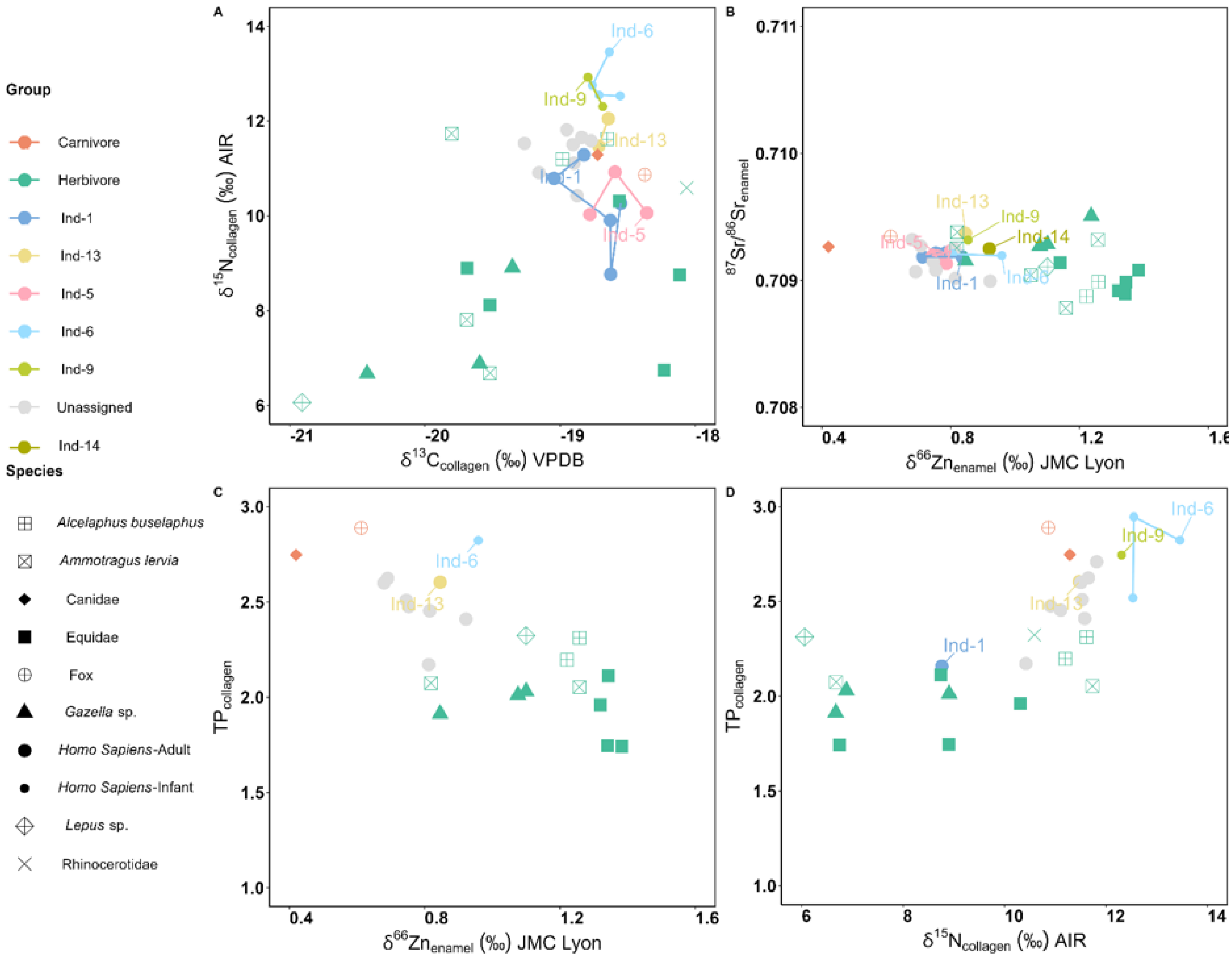

Figure 2

Isotopic ratios of various elements from the human and animal teeth of Taforalt: A) Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic ratios from bulk collagen of dentine and bone samples, B) Zinc (δ^{66}Zn) and strontium (^{87}Sr/^{86}Sr) isotopic ratios from enamel bioapatite, C) Zinc (δ^{66}Zn) versus the trophic position (TP) obtained from amino acids (Supplementary Information 4), D) Nitrogen (δ^{15}N) isotopic ratios from bulk collagen versus the trophic position obtained from amino acids. The TP was estimated from $\delta^{15}N_{phe}$ and $\delta^{15}N_{Glu}$values. Each point corresponds to the average value of a single tooth or bone sample**.** The samples from the same individual are connected with a line.

human

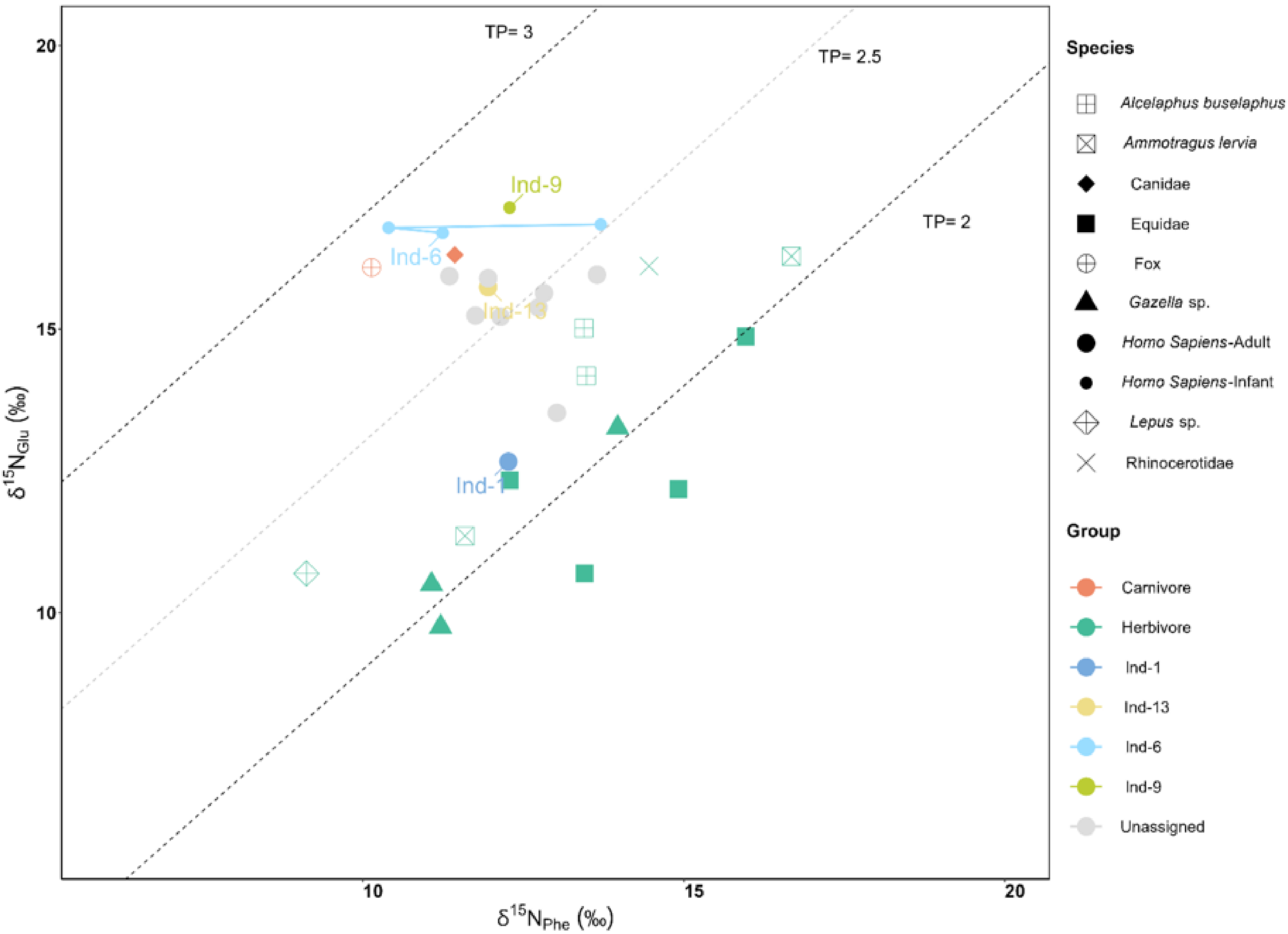

Figure 3

Measured $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Glu}$ values on humans and animals from Taforalt. Dashed black lines indicate the theoretical trophic position of herbivores (TP = 2) and carnivores (TP = 3). Dashed grey line is the intermediate (TP = 2.5). The samples from the same individual are connected with a line.

human

Supplementary Files

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