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First insights into the diet of the Atlas brown bear: evidence from Ifri Oussaïd Cave (Middle Atlas, Morocco)

Primeros datos sobre la dieta del oso pardo del Atlas: hallazgos en la cueva de Ifri Oussaïd (Atlas Medio, Marruecos)

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Abstract
This study presents the first isotopic evidence of the palaeodiet of the extinct Atlas bear, based on remains recovered from Ifri Oussaïd cave in the Middle Atlas Mountains of Morocco. Comparative isotopic analysis with Holocene brown bears from Europe suggests an omnivorous diet with a notable intake of animal protein, in contrast to more herbivorous populations such as Holocene Cantabrian bears, although these conclusions should be taken with caution, as there is no local baseline with which to compare. This bear likely inhabited a closed, humid forest environment, with C3 plants at the base of the trophic chain. The calibrated radiocarbon dating places this individual shortly after the 8.2 kyr BP cooling event, during a period characterised by slightly warmer

temperatures and greater arboreal vegetation compared to present-day conditions in the area.

Key words: Atlas bear, *Ursus arctos*, stable isotopes, paleodiet, Morocco

Resumen
Este estudio presenta el primer análisis isotópico sobre la paleodieta del extinto oso del Atlas, basada en restos recuperados de la cueva de Ifri Oussaïd, en las Montañas del Atlas Medio de Marruecos. La comparación con los valores isotópicos de osos pardos holocenos de Europa sugiere una dieta omnívora con una notable ingesta de proteína animal, en contraste con poblaciones más herbívoras, como los osos pardos cantábricos del Holoceno, aunque estas conclusiones deben tomarse con cautela, ya que no existe una referencia local con la que comparar. Este oso probablemente habitaba un entorno boscoso cerrado y húmedo, con plantas C3 en la base de la cadena trófica. La datación por radiocarbono calibrada sitúa a este individuo poco después del evento frío de 8,2 ka BP, en un período caracterizado por temperaturas ligeramente más cálidas y una vegetación arbórea más abundante en comparación con las condiciones actuales de la región.

Palabras clave: oso del Atlas, *Ursus arctos*, isotopos estables, paleodieta, Marruecos

1. INTRODUCTION

1.1. The Atlas brown bear

The brown bear (*Ursus arctos*) is widely distributed across the Northern Hemisphere, occupying diverse habitats from the boreal forests of North America and Eurasia to parts of the temperate zones. In North America, its populations are primarily found in Alaska, western Canada, and parts of the northwestern United States, particularly within protected areas. In Europe, significant populations are present in the Carpathian Mountains, the Alps, the Cantabrian Mountains, and parts of Scandinavia, though habitat fragmentation has reduced their continuous range. In Asia, the brown bear is found throughout Russia, with notable populations in Siberia, and extends southward to regions in Japan and isolated areas in the Himalayas (PASITSCHNIAK-ARTS, 1993).

Historically, brown bears inhabited parts of North Africa; however, their presence in this region has become extinct, probably due to habitat loss, human encroachment, or hunting pressures. Limited fossil evidence and historical records suggest the Atlas Mountains in Morocco as their southernmost range. The origin of the Atlas brown bear remains uncertain, as it is unclear whether it descended from ancient African populations or if its presence in North Africa resulted from a later migration from Asia or even Europe. Fossil data are limited and do not provide sufficient evidence to determine whether this subspecies evolved locally in the Maghreb or was introduced subsequently through migratory currents from other regions. Additionally, the scarcity of records complicates the reconstruction of its evolutionary history. The few genetic studies conducted on African bears have not resolved the question (CALVIGNAC *et al*., 2008; 2009), yielding controversial results that could support both hypotheses for an African and non-African origin of these populations.

Ecologically, we also lack understanding of the role played by the Atlas brown bear within the North African faunal community. Unlike postglacial Europe, where large carnivores were already extinct by the onset of the Holocene, in North Africa these brown bear populations coexisted with prominent predators like lion (*Panthera leo*) and leopard (*Panthera pardus*), which endured in the region until historical times, or the spotted hyena (*Crocuta crocuta*), which is present in several Moroccan Holocene sites (OUCHAOU & BOUGARIANE, 2015; OUCHAOU *et al.,* 2017). This coexistence suggests that the Atlas brown bear may have occupied a specific niche, though the exact interactions and its impact on the ecosystem remain unknown. The lack of detailed studies limits our understanding of its ecology and its contribution to the historical biodiversity of the region.

Today, no extant populations remain in this region, although the exact time of the Atlas brown bear's extinction in North Africa is uncertain. Brown bear presence has been reported at least in ten Holocene sites in the Atlas Mountains (OUCHAOU, 2008; OUCHAOU *et al.,* 2017). However, in most of these sites, skeletal remains are scarce, partially represented, and often fragmented. Many of these remains come from older excavations with limited knowledge of the stratigraphic context. Furthermore, chronological attribution is often imprecise, except for certain sites that have been more extensively studied in recent years due to their archaeological interest.

An exception is the Ifri Oussaid site, located in the Middle Atlas in the Boulmane region of Morocco (Figure 1). In this cave, brown bear skeletal remains are the most abundant among the recovered fauna (OUCHAOU *et al.,* 2007; BENABDELHADI *et al*., 2008, FONTUGNE *et al.,* 2012). In this paper we report and discuss the results of a stable isotope analysis of brown bear bone collagen from this cave in order to determine, if possible, the type of diet of brown bears in this area, which is probably the southernmost area of brown bear distribution during the Holocene.

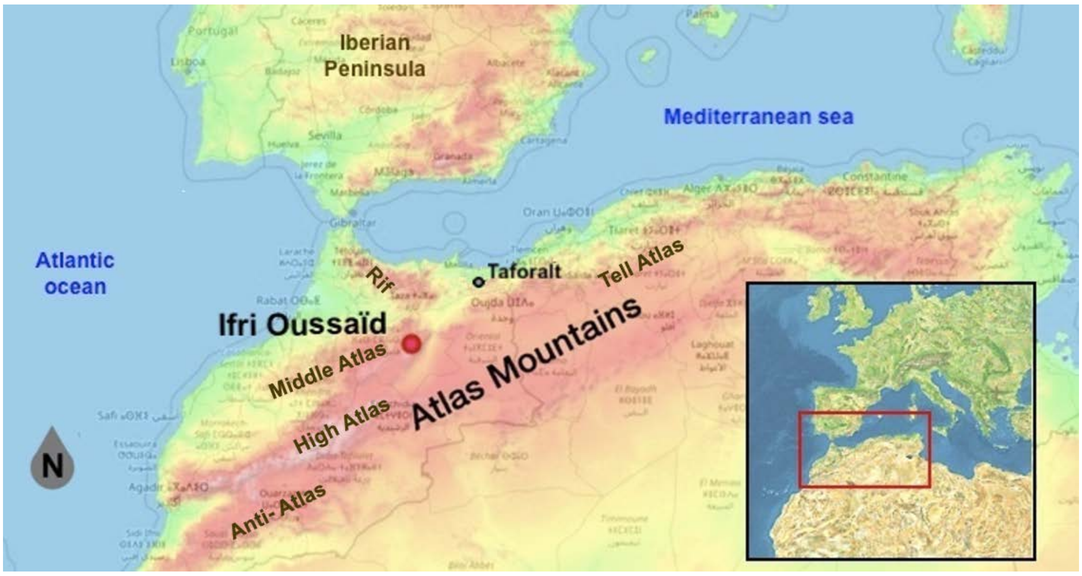

Figure 1. Map of North Africa showing the location of the main mountain ranges and the Ifri Oussaïd cave in the Middle Atlas. The Taforalt cave, that was used for comparative purposes, is also shown.

1.2. Stable isotopes and Brown bear diet

Stable isotope analysis of carbon (C) and nitrogen (N) in bone collagen is a powerful tool for reconstructing the diet of animals, as it provides direct insight into the types of plants and prey consumed. Carbon isotopes reflect the types of plants at the base of the food chain, such as C3 or C4 plants (KÖRNER *et al.,* 1991). Nitrogen isotopes, meanwhile, are valuable in determining trophic level, as higher nitrogen values are typically associated with carnivorous diets, while lower values indicate herbivory (SCHOENINGER & DENIRO, 1984).

Isotopic values are also influenced by climatic factors, which affect plant distribution, photosynthetic pathways, and nutrient availability. For example, warm climates often result in higher nitrogen isotope values in plants, which then translate to elevated $\delta^{15}N$ values in herbivores and predators in those regions (CHENG *et al.,* 1964, AMUNDSON *et al.,* 2003). The carbon isotopic signature is also influenced by temperature, humidity, altitude (HEATON, 1999; KOHN, 2010), and the thickness of the tree canopy (HARE *et al.*, 2018) Thus, climatic factors can either add up or counterbalance, generating different baseline values depending on the geographical region and time period.

In turn, diet is the main determinant of an individual's collagen isotopic values. Brown bears are omnivores with remarkable dietary flexibility, adapting their feeding habits to seasonal and geographical variations in food availability. Their diet includes a diverse mix of plant material, terrestrial animals (such as insects, small mammals, and ungulates), fish (particularly anadromous salmonids), fungi, honey, and even unconventional resources like soil and bones (COUTURIER, 1954; CLEVENGER, 1991; MATTSON, 1997, 2001, 2002; MATTSON *et al*., 1999, 2002a, 2002b; NOMURA AND HIGASHI, 2000; GENDE *et al*., 2001; WALD, 2011).

Changes in diet can be detected through isotopic data, providing indirect evidence of shifts in animal behavior and/or their environment. For example, Pleistocene and Holocene brown bears in the Cantabrian region show consistent isotopic values over time, indicating minimal dietary changes despite environmental shifts. Comparisons with cave bears and red deer from the same region show that brown bears exploited different ecological niches, inhabiting higher, less forested areas—a pattern that continued into the Holocene, likely driven by increasing human activity (GARCÍA-VÁZQUEZ *et al*., 2011, 2018). On the contrary, in Central Europe, the carnivorous brown bears of the Late Pleistocene contrast with the primarily herbivorous brown bears of the Holocene, which lived in open landscapes. This shift in diet likely reflects an ecological niche similar to that of the herbivorous cave bears and may also indicate an adaptation to the cold climate of the period (BOCHERENS, 2015; DÖPPES *et al.* 2008; ERSMARK *et al*., 2019; MÜNZEL *et al.*, 2011).

2. MATERIAL AND METHODS

2.1. The brown bear from Ifri Oussaïd cave

The Ifri Oussaïd cave is located in the Chaabat el-Melha valley, in the rural commune of Essaf in the province of Boulemane. The cave stands at an altitude of 2,075 m and opens out towards the south-east onto the Middle Atlas plateau (BENABDELHADI *et al.,* 2008).

From 2005 to 2007, a test pit of 2 m^2, approximately 30 cm deep, provided micro and macrovertebrate bone remains that were found under two stalagmitic floors. A total of 156 brown bear remains were recovered, including a damaged skull and several connected pieces of appendicular skeleton. The minimum number of individuals is five: one juvenile, three young and one adult (BENABDELHADI *et al.,* 2008). Other fauna recovered include *Vulpes vulpes* (37 remains), *Equus asinus* (2 remains), *Sus scrofa* (2 remains) and Bovidae (33 remains) with the presence of *Alcelaphus buselaphus*, *Bos primigenius*, *Ammotragus lervia*, *Ovis aries*, *Capra hircus* and *Gazella* sp. (OUCHAOU *et al.,* 2007). Several microvertebrate remains such as insectivores, rodents, chiropterans, amphibians, etc. (OUCHAOU, 2008) were recovered by sieving. At the base of this sequence, a bear radius was used for dating.

For the present biogeochemical analysis, a brown bear ulna of the adult individual from

Ifri Oussaïd was selected (laboratory ID: IFRI-1). The sampling was performed at the *Institut National des Sciences de l'Archéologie et du Patrimoine* (Rabat, Morocco), using a Dremel tool fitted with a diamond circular saw. A piece of about 1 g of bone was cut apart from the most distal area of an already fragmented diaphysis, in order to avoid further damage or spoil any measurable landmark (Figure 2).

Figure 2. Sampled ulna of adult brown bear from Ifri Oussaïd cave. The rectangle marks the area where the bone sample IFRI-1 was taken.

2.2. Purification and isotopic analysis of bone collagen

The purification of collagen from the bone sample was carried out at the Laboratory of Molecular Palaeontology of the University Institute of Geology, in the University of A Coruña (Spain). First, the bone fragment was cleaned following a standardised procedure. This consisted of subjecting the fragment to at least 12 cycles of ultrasonic bath washing, each lasting 5 minutes and alternating between acetone and distilled water until no turbidity was detected. The sample was then left to dry at room temperature for a duration of 48 to 72 hours. Approximately 1 g of bone was ground using an agate mortar and pestle until it was reduced to particles smaller than 0.3 mm. An aliquot of 10 mg from the obtained bone powder was taken for elemental analysis (% C and % N). This analysis is intended as a reference, as it helps to evaluate the preservation level of the bone collagen (BOCHERENS *et al.*, 2005; IACUMIN *et al.*, 1996).

Approximately 300 mg of bone powder were used for collagen extraction, following a procedure based on BOCHERENS *et al.* (1997). The pulverised sample undergoes successive digestions in HCl and NaOH to eliminate the mineral fraction of the bone and any potential contaminating organic material. Each digestion is followed by microfiltration using 5 µm filters to remove disposable residues. This microfiltration process enables the removal of dissolved inorganic matter, soluble organic acids, and bone organic components other than well-preserved collagen, including degraded collagen.

Finally, the collagen is solubilized by incubation in a mild acid solution at 90 °C for 17 hours, lyophilised, and subjected to combustion analysis using an isotopic ratio mass spectrometer (IRMS) at the Unit of Instrumental Techniques of Analysis of the Reserch

Support Facilites (SAI), in the University of A Coruña, using a Finnigan Mat Delta Plus coupled with a Carlo-Erba 1108 elemental analyser. The following secondary standards were employed: USGS 40 (−4.52‰), USGS41a (+47.55‰), IAEAN-1 (+0.4‰), IAEA-N-2 (+20.3‰) and USGS-25 (−30.4‰) for $\delta^{15}N$, and USGS 40 (−26.39‰), USGS41a (+36.55‰) NBS 22 (−30.031‰), IAEA-CH-6 (−10.449‰) and USGS 24 (−16.049‰) for $\delta^{13}C$. Acetanilide was employed as an internal standard to test for precision. Reproducibility resulted in ± 0.15‰ (n = 10). Acetanilide was used as the internal standard, and quantifications were performed in duplicate. The results are presented using delta (δ) notation, which reflects the ratio between both isotopes in the sample relative to the proportions in an international standard (Vienna Pee Dee Belemnite (VPDB) for carbon and atmospheric air (AIR) for nitrogen), as illustrated in the following equation: $\delta X(‰)=(R_{sample}/R_{standard}-1)\times1000$, where X represents the heavier isotope and R denotes the $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratio.

2.3. Radiocarbon date calibration

To determine the age of the brown bear remains from this cave, FONTUGNE *et al*. (2012) carried out a 14C dating on an adult bear radius. We can assume that this dating also corresponds to the ulna analysed in this work since only one adult bear was identified at the site. The age obtained was 7300 ± 40 y BP (GifA-80184/SacA12263), which calibrated using CALIB 5.1 (Stuiver & Reimer, 1993) yielded a range between 8019-8180 y cal BP. In this work, we applied the software OxCal 4.4 (Bronk Ramsey, 2009) and the IntCal20 calibration curve from Reimer *et al.* (2020) to adjust the age calibration obtained by the aforementioned authors.

2.4. Bioinformatics

Statistic calculations and plots were made using RStudio 2022.07.0 + 548 (R CORE TEAM, 2023).

2. RESULTS

Table 1 and Figure 3 show the newly calibrated ^{14}C date, nearly identical to those provided by FONTUGNE *et al.* (2012) using the previous calibration curve.

Table 1. Calibrated dating and isotopic results of IFRI-1.

Lab ID	Radiocarbon date		Bone powder		Bone collagen				
	^{14}C y BP	^{14}C y Cal BP (Intcal 2020)	% N	%C	% N	$\delta^{15}N$	%C	$\delta^{13}C$	C:N
IFRI-1	7300 ± 40	8104 ± 49	1.5	7.2	10.3	5.5	27.1	-20.8	3.1

The results of the isotopic analysis are summarised in Table 1 and visualised in Figure 4. The threshold for collagen preservation is 0.4% nitrogen in bone powder (BOCHERENS *et al.*, 2005). The value obtained for IFRI-1 was 1.5%, confirming that the collagen was well preserved. The extracted collagen met the quality criteria established by AMBROSE

(1990), with %C in bone collagen exceeding 13% and %N greater than 5%, as well as the standards set by DeNiro (1985), with a C:N atomic ratio ranging between 2.9 and 3.6

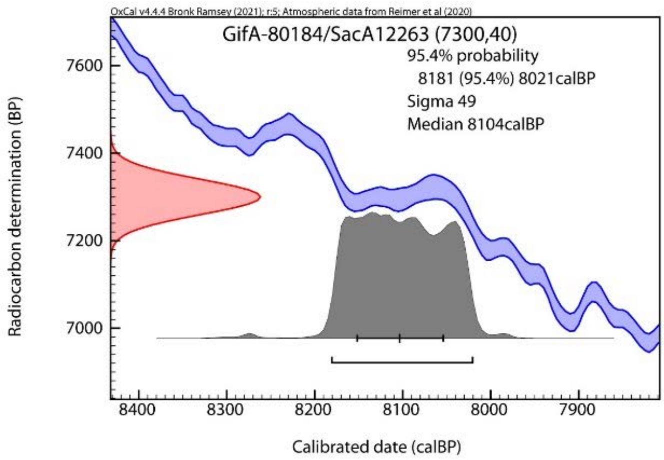

Figure 3. Calibration date obtained using OxCal v4.4.4.

3. DISCUSSION

The calibrated ^{14}C dating of IFRI-1 places the cave occupation shortly after the global cooling episode of 8.2 ky BP. Based on pollen data from sedimentary fills of a similar age at lake Tigalmamine, located 40 km southwest of Ifri Oussaïd at an altitude of 1600 m above the sea level, FONTUGNE *et al.* (2012) suggested a slightly more temperate climate for the region compared to today, with temperatures 1 to 2.5 ºC higher, slightly reduced rainfall, and more arboreal vegetation dominated by evergreen oaks (*Quercus ilex* and/or *Quercus rotundifolia*). Cedar and pine were almost absent, while grasses dominated the herbaceous vegetation over sagebrush (LAMB & VAN DER KAARS, 1995; FONTUGNE *et al.,* 2012). In this environment, despite the high altitude, the brown bear could have found a suitable habitat. According to the same authors, the deforestation observed in the region today began much more later, around 1300 years BP, because of anthropic exploitation (LAMB & VAN DER KAARS, 1995).

The carbon isotopic signature of the Ifri Oussaïd bear indicates that its food chain was based on C3 plants, with no significant consumption of C4 plants, which would otherwise result in elevated $\delta^{13}C$ values (EHLERINGER & CERLING, 2002). However, interpreting the isotopic values of the Ifri Oussaïd bear requires a reference framework. For the time being, there are no other isotopic data for African brown bears. For an initial comparison test, isotopic data from Holocene brown bears across several European regions were used: Spain (GARCÍA-VÁZQUEZ *et al.,* 2018; ERSMARK *et al.,* 2019), Austria (DÖPPES *et al*., 2008), Hungary, Bulgaria, Estonia, Sweden and the Netherlands (ERSMARK *et al*., 2019). These data cover a time span of approximately 2000 years before and after the radiocarbon date of the bear sample from Ifri Oussaïd.

Among the set of isotopic signatures, the Atlas bear is in an intermediate position between bears with a highly plant-based diet, which was the majority among the Cantabrian brown bears which obtained less than 20% of their diet from animal matter (GARCÍA-VÁZQUEZ *et al*., 2018), and some much more carnivorous bears in some Central European sites (Figure 4). The large dispersion of values observed undoubtedly responds to the different trophic strategies followed by this versatile species also during the Holocene.

The intermediate $\delta^{15}N$ values indicate that the Ifri Oussaïd bear would have had an omnivorous diet, with a significant animal protein component. The $\delta^{13}C$ values are slightly negative, indicating not only that the food chain was based on C3 plants, but also that the habitat could be a closed and humid woodland (HARE *et al.,* 2018). However, the brown bears we have used as a comparative framework are very far from North Africa and the isotopic baselines may have been very different in each region, given the differences in temperature, rainfall, insolation, altitude, etc., as was already said.

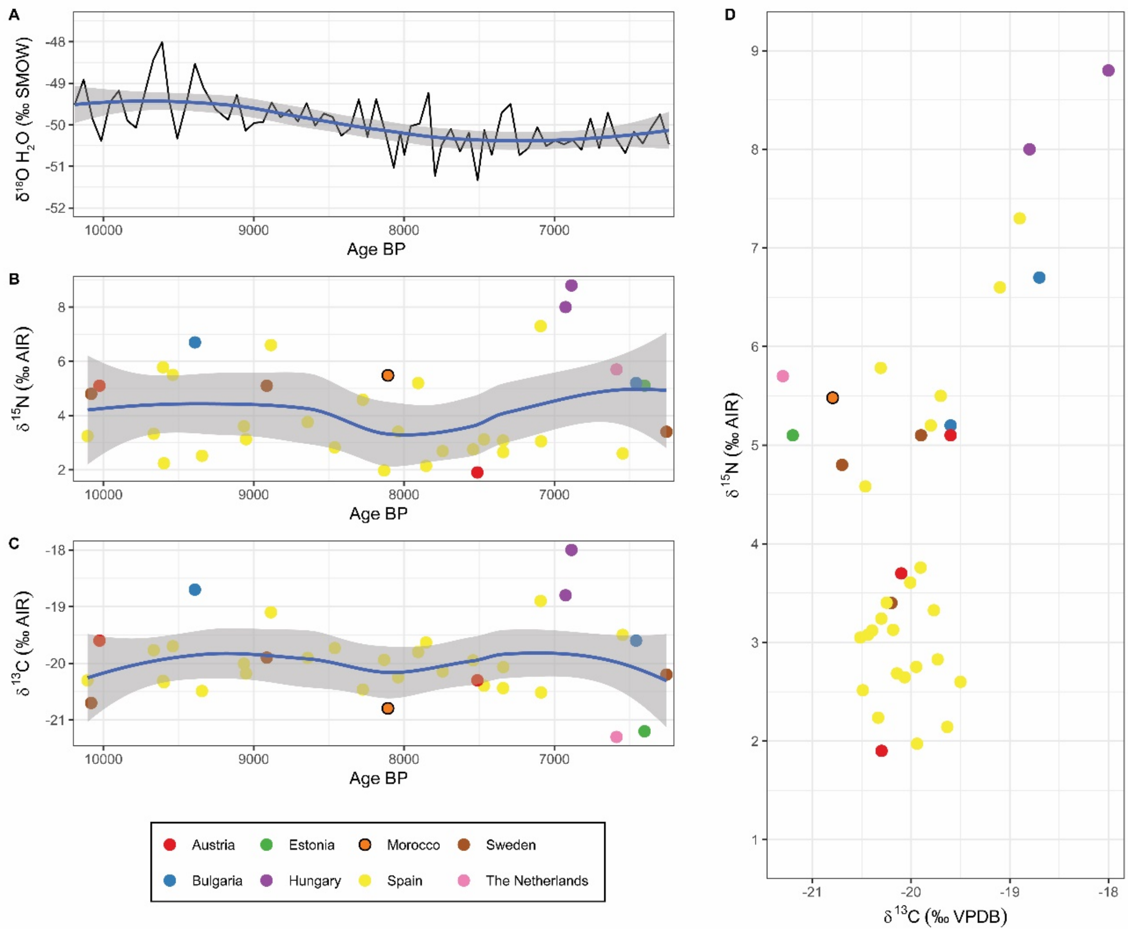

Figure 4. Comparison of the diet of the Ifri Oussaïd bear with isotopic data from several European Holocene brown bears (DÖPPES *et al*., 2008; ERSMARK *et al*., 2019; GARCÍA-VÁZQUEZ *et al*., 2018). A) Greenland Ice-Core climate curve (RASMUSSEN *et al*., 2023). B) Radiocarbon dates of brown bear remains (CalBP) in relation to their $\delta^{15}N$ values. C) Radiocarbon dates of brown bear remains (CalBP) in relation to their $\delta^{13}C$ values. D) Bivariate plot of $\delta^{13}C$ *versus* $\delta^{15}N$.

Ideally, the isotopic signature of the Ifri Oussäid bear should be compared with that of other contemporary bears in Morocco, but this is not possible as there are no studies of this type available yet. There are also no isotopic data for other faunas from contemporary or at least chronologically close sites. The only exception is the site of Taforalt or Grotte des Pigeons, a cave in the province of Berkane, possibly the oldest cemetery in North Africa with a group of Iberomaurusian gaves. In a recent study conducted to investigate the diet of these humans (MOUBTAHIJ *et al.,* 2024), some isotopic data from mammal faunas (herbivores and some carnivores, but no bears) were also offered. These data can be used as a framework to compare the isotopic signature of the Ifri Oussaïd bear (figure 5).

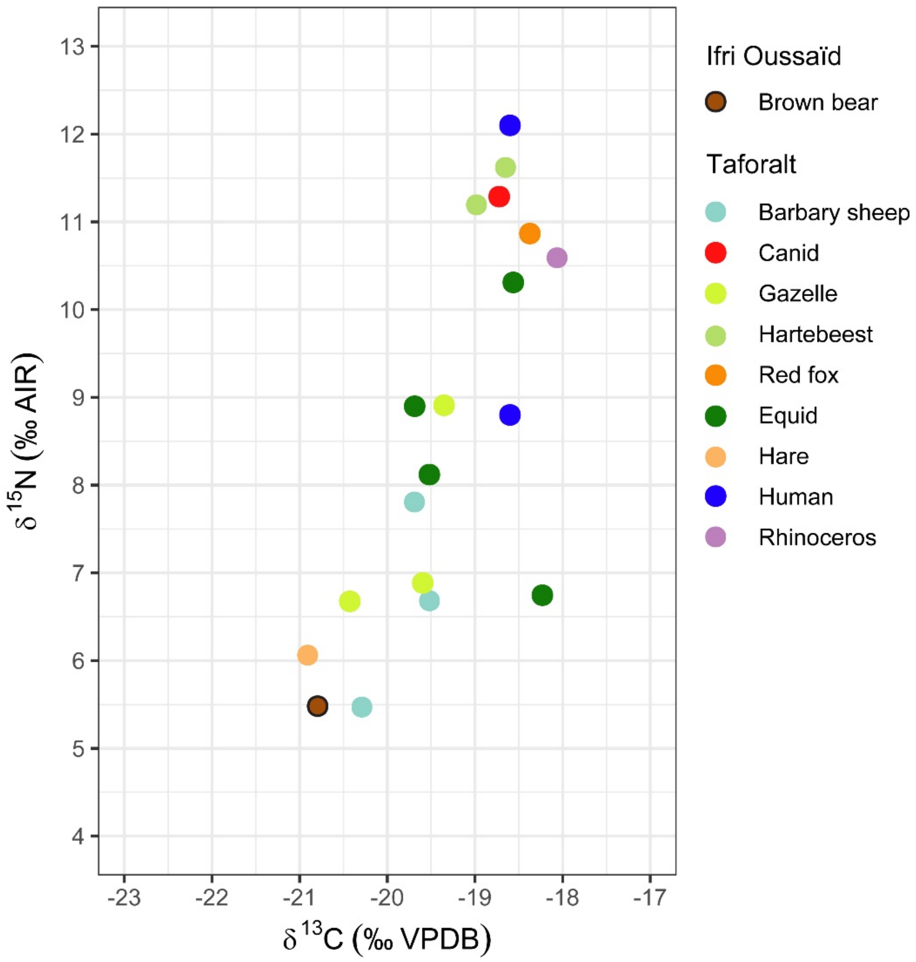

Figure 5. Isotopic data of humans and faunas from Taforalt (MOUBTAHIJ *et al.*, 2024) and the bear of Ifri Oussaïd.

Into this framework, the bear surprisingly shows a strong herbivore signature, in comparison with a varied group of herbivore ungulates. However, two fundamental factors must be considered. Firstly, the chronology of Taforalt (around 14000 to 15000 years cal BP, MOUBTAHIJ *et al.,* 2024) is several millennia older than that of Ifri Oussaïd. Therefore, the environmental conditions might have been very different at each site. Secondly, the altitude above sea level is also very different, since Taforalt is situated much lower respect to sea level (around 800 m asl) than Ifri Oussaïd, so there is a difference of more than 1000 metres in altitude between the two sites. This may have significantly influenced the relative position occupied by the bear in the isotopic landscape traced by the Taforalt fauna. Even if we hypothesise that the Ifri Oussaïd bears would have fed preferentially at lower altitudes than the cave itself, the Middle Atlas region is higher than the Taforalt location.

When comparing isotopic signatures of domestic herbivores, MÄNNEL *et al.* (2007) observed an increase in $\delta^{13}C$ values and a decrease in $\delta^{15}N$ values following an altitudinal gradient. These authors calculated increases of 1.1 ‰ in $\delta^{13}C$ and decreases of 1.6 ‰ in $\delta^{15}N$ for every 1000 m of altitude. Thus, only the effect of altitude could make the bear's $\delta^{15}N$ signal about 1.6 ‰ lower than that of animals with the same diet at Taforalt. Even so, the bear's diet would still be mainly herbivorous.

Interestingly, in present-day brown bears from various mountain populations in Europe (Pyrenees, Apennines, Alps), GARCÍA-VAZQUEZ *et al.* (2023) observed that bears living at higher altitudes have a more carnivorous diet, which contrasts with the nitrogen isotopic values of the Ifri Oussaïd bear. Moreover, its carbon isotopic signature is not congruent with a herbivorous diet in a high mountain environment, as it should show a less negative value, as observed by MÄNNEL *et al.* (2017).

The reconstruction of the diet of an extinct animal by means of stable isotope analysis requires a baseline of data from other coeval taxa with which to make relative comparisons of isotopic values (CASEY & POST, 2011). In this case, we found no concordance between the combination of isotopic values characteristic of a particular diet or environment, and those shown by the brown bear studied. This seems to indicate that the reference frames used to establish the isotopic baseline, being the only ones available, are not adequate to determine what proportion of animal protein was included in the diet of the Ifri Oussaïd bear.

4. CONCLUSIONS

This study provides the first isotopic data on the bone collagen of the extinct Atlas brown bear, in an individual of Holocene age. Comparison of its isotopic values with those of Holocene bears from various European populations points to an omnivorous diet, with a significant proportion of animal protein, which contrasts with that of Holocene Cantabrian bears. The base of the food chain was composed of C3 plants, and carbon isotope values suggest that the bear probably inhabited a closed, moist forest environment.

However, for a more detailed reconstruction of the bear's diet, it would be essential to analyse isotopic data representative of the faunal assemblage recovered from the same site or a site of similar age and with comparable environmental conditions.

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