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Cave bear's diet: a new hypothesis based on stable isotopes

La dieta del Oso de las Cavernas: nueva hipótesis basada en isótopos estables

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ABSTRACT

The *Ursus spelaeus* diet has always been a controversial topic in Paleontology. Both, morphometric and isotopic studies, have raised the hypothesis of herbivorism for this extinct ursid that belongs to the order Carnivora. However, the specific composition of its diet is still in doubt. In this paper, and dealing with stables isotopes of ^{13}C and ^{15}N in bone collagen, we point out the possibility of *Ursus spelaeus* feeding basically on nitrogen fixing plants, because of its low $\delta^{15}N$ signature, the lowest one among the published data from other Pleistocene herbivores.

Key words: *Ursus spelaeus*, $\delta^{15}N$, bone collagen, diet, nitrogen-fixing plants.

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INTRODUCTION

The cave bear presents a specific tooth morphology with wide grinding surfaces, and muscle insertions in the skull and the jaw which show a great biting power, which is the reason why it is thought to follow a basically herbivorous diet (KURTÉN, 1976). In recent years, different approaches have been followed as to the reconstruction of this species´ diet through the analysis of stable isotopes, usually ^{13}C and ^{15}N, preferably in bone collagen and in dentine collagen and hydroxyapatite (BOCHERENS *et al*., 1994; BOCHERENS *et al*., 1997; FERNÁNDEZ MOSQUERA, 1998; NELSON *et al*., 1998; LIDÉN & ANGERBJÖRN, 1999; VILA TABOADA *et al*., 1999). The results derived from these studies can be summed up in the following points:

a) Preferably herbivorous diet based on C_3 plants.

b) Marked lactation effect, which causes an increase in $\delta^{15}N$ values in bone collagen of young individuals, and in dentine values of young and adult individuals, the latter of which maintain the lactation signature due to non- renewing of dentine collagen after weaning.

c) In some cases, there is a hint of a possible influence of winter dormancy on isotopic signatures (BOCHERENS *et al*., 1997; FERNÁNDEZ MOSQUERA, 1998; VILA TABOADA *et al.* 1999). This fact has been confirmed in Fernández Mosquera *et al*. (2001).

It is know that isotopic analysis of animal nitrogen can also be used to reconstruct aspects of the diet when potential food resources had different $^{15}N/^{14}N$ ratios (AMBROSE & DE NIRO, 1989). Isotopic ratios for nitrogen and carbon are presented as δ values where $\delta=(R_{sample}/R_{standard})-1 \times 1000$, being $R={}^{15}N/{}^{14}N$ and $^{13}C/{}^{12}C$, respectively.

The relative amount of both nitrogen stable isotopes (^{15}N y ^{14}N) vary in soils and tissues, due to the fact that their isotopic compositions depend on the ^{15}N inputs into the system as well as on the fractionations of each physic and/or physiologic process. Nevertheless, it can be noticed a clear enrichment in ^{15}N as we get higher trophic levels. This enrichment ranges from 2.8 up to 5.7‰ for terrestrial ecosystems (BOCHERENS *et al*., 1997). It is assumed, as typical fractionation, the value 3 ‰ (KOCH *et al*., 1994), which is added to every step of the trophic chain (figure 1).

Nitrogen isotopes distinguish plants, such as legumes, that have symbioses with atmospheric nitrogen-fixing bacteria from those that do not. The $\delta^{15}N$ values of fixing plants average around 0‰ whilst other plants have higher average $\delta^{15}N$ values (SCHOENINGER & DE NIRO, 1984), although some of the variation in plant $\delta^{15}N$ values may be due to variation in soil $\delta^{15}N$ values. The biological nitrogen fixation causes a decrease in ^{15}N in the tissues of fixing-plants related to those from no fixing (KOCH *et al*., 1994). In this process of fixation, the atmospheric nitrogen is enzymatically converted into organic nitrogen, included in aminoacids, nucleotides and other molecules. Fixation may be caused by a symbiosis of nodules in the roots of several plants (for instance, the family Fabaceae) with some bacteria of

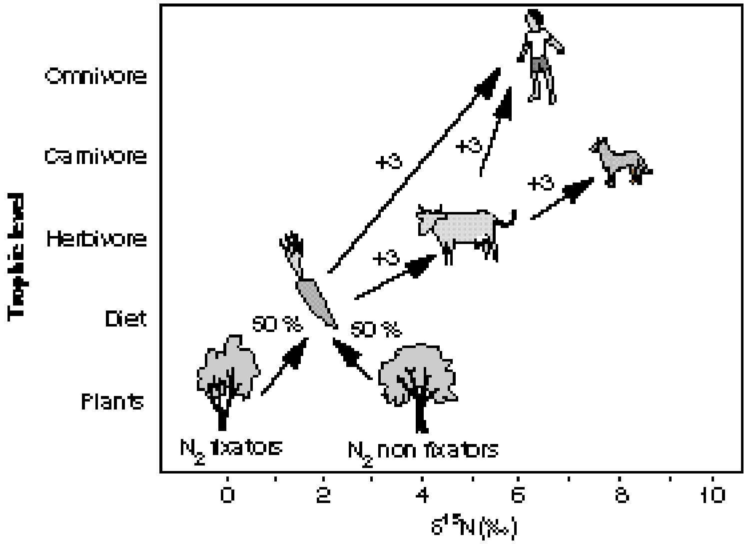

Figure 1. Relationship between different trophic levels and $\delta^{15}N$ in terrestrial trophic chains (Adapted from KOCH *et al*., 1994).

the genus *Rhizobium*, although it may also be a non symbiontic fixation, carried out by aerobic bacteria as *Azotobacter*, by Cianobacteria and there is also a fixation due to the rain (STRASBURGER *et al*., 1994).

Regarding the $\delta^{13}C$ signature, it mainly reflects the type of photosynthetic plants which are primery producers in the food web. Herbivore's $\delta^{13}C$ bone collagen allow us to estimate the amount of C_3 and C_4 plants in the diet because of their very different isotopic signals. Herbivores feeding on C_3 plants, which are all the trees and herbaceous plants from cold and temperate climates, will show $\delta^{13}C$ values around -20‰. On the other hand, herbivores feeding on C_4 plants, which are tropical herbaceous plants, will show $\delta^{13}C$ values around -8‰. As the fractionation step is larger between plants and herbivores than between herbivores and the rest of trophic levels, the $\delta^{13}C$ signature provides little information about the diet of omnivores and carnivores.

PLEISTOCENE HERBIVORE'S ISOTOPIC SIGNATURES

We have assembled published isotopic carbon and nitrogen data from bone collagen of fossil European Pleistocene herbivores. Only adult individuals have been taken into account. We have no used data from present specimens because most of the papers do not specify anything about diet, so it could be no natural. Thus, a preliminary plot would be:

In figure 2 we have assembled data from the following papers: *Bos primigenius* (n=36) from Marillac (BOCHERENS *et al*., 1991) and from Paglicci cave

(IACUMIN *et al*., 1997); *Equus caballus* (n=22) from Paglicci cave (IACUMIN *et al*., 1997); *Mammuthus primigenius* (n=10) from Yakutia (BOCHERENS *et al*., 1996); *Coelodonta* sp. i.e.: woolly rhinoceros (n=5) from Kent Cavern (BOCHERENS *et al*., 1995); *Rangifer tarandus* (n=5) from Marillac (BOCHERENS *et al*., 1991); *Ursus spelaeus* (n=20) from Liñares (VILA TABOADA *et al*., 1999); *Ursus spelaeus* (n=12) from Alpine sites (FERNÁNDEZ MOSQUERA *et al*., 2001); *Ursus spelaeus* (n=12) from Divje Babe (NELSON *et al*., 1998); *Ursus spelaeus* (n=8) from Eirós (FERNÁNDEZ MOSQUERA, 1998); *Cervus elaphus* (n= 32) from Paglicci cave (IACUMIN *et al*., 1997) and Liñares (VILA TABOADA *et al*., 1999, 2001). Other published data of *Ursus spelaeus* have not been plotted to improve the clarity of the graphic, since they show comparable values to the plotted ones.

By taking into account that the typical fractionation is 3‰ and that the interval of *Ursus spelaeus* values is [0.81-5.53], it could be inferred that the basis of the trophic chain would show a negative $\delta^{15}N$, corresponding to that of N_2 fixing plants, from -1 up to +2, whereas the $\delta^{15}N$ of non fixing ones ranges from +3 up to +6 (LAJTHA & MARSHALL, 1994).

As the isotopic studies are from different geographical locations: NW Spain (FERNÁNDEZ MOSQUERA, 1998, VILA TABOADA *et al*., 1999), Central Europe (NELSON *et al*., 1998, FERNÁNDEZ MOSQUERA *et al*., 2001), Pyrenees sites (BOCHERENS *et al*., 1991, BOCHERENS *et al*., 1994), Belgium (BOCHERENS *et al*., 1997, BOCHERENS *et al*., 1999), we do not

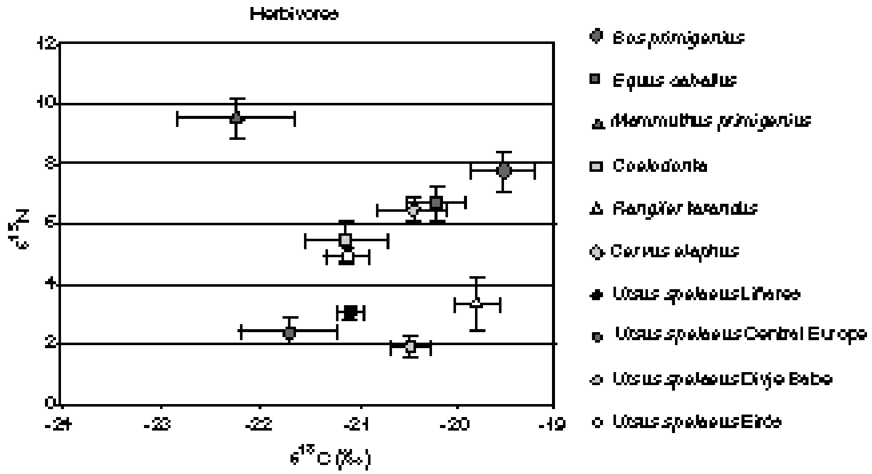

Figure 2. $\delta^{15}N$ versus $\delta^{13}C$ from different fossil herbivores. Notice that *Ursus spelaeus* $\delta^{15}N$ values are clearly lower that the rest of herbivores, but data from reindeer (*Rangifer tarandus*). See Discussion for further explanation.

have to take into account specifically site factors as soil, altitude or endemic vegetation. Thus, even the highest $\delta^{15}N$ cave bear values, which are related to the dormancy length (FERNÁNDEZ MOSQUERA, *et al*., 2001) are always lower than those from other herbivores, but the reindeer (*Rangifer tarandus* L.)

DISCUSSION

Coeval isotopic signatures from different species have been preserved in the fossil remains from Liñares site (Lugo, Galicia, NW Iberian Peninsula). Liñares (GRANDAL d'ANGLADE & LÓPEZ GONZÁLEZ, 1998) has provided with contemporary specimens of both species: *Cervus elaphus* and *Ursus spelaeus* {37,865 ± 2,070 years Before Present [yBP]; 37,690 ± 1,955 yBP and >38,000 yBP for red deer (LÓPEZ GONZÁLEZ *et al*., 1997) and 35,220 ± 1,440 yBP and >38,000 yBP for cave bears (GRANDAL d'ANGLADE & LÓPEZ GONZÁLEZ, 1998)}. Then, they are supposed to feed on the same ecosystem, i.e: they are members of trophic chains based on the same soil. By comparing adult specimens of the same site and same time-span we can remove the influence of soil $\delta^{15}N$ variation.

It should be pointed out that the red deer (*Cervus elaphus*) is a ruminant (KOWALSKI, 1981) and this kind of herbivores have rather low $\delta^{15}N$ values whereas the non-ruminant herbivores, specially mammoth (*Mammuthus primigenius*), present high $\delta^{15}N$ values (BOCHERENS *et al*. 1996 *and included references*).

As we have proposed before and considering that: i) the typical frationation is around 3‰, ii) $\delta^{15}N$ values of *Cervus elaphus* from Liñares are [5.71-7.42] (n=8, mean: 6.33, standard deviation: 0.53) and iii) *Ursus spelaeus* $\delta^{15}N$ values from Liñares are included into the interval [2.11-3.61] (n= 20, mean 3.03, standard deviation: 0.44), there is a difference of 3.3‰ between the red deer and the cave bear $\delta^{15}N$ average.

This difference could correspond to the one between fixing N_2 fixing plants, whose $\delta^{15}N$ ranges from -1 up to +2, and non fixing plants, which range from +3 up to +6 (LAJTHA & MARSHALL, 1994). It could be possible that cave bears

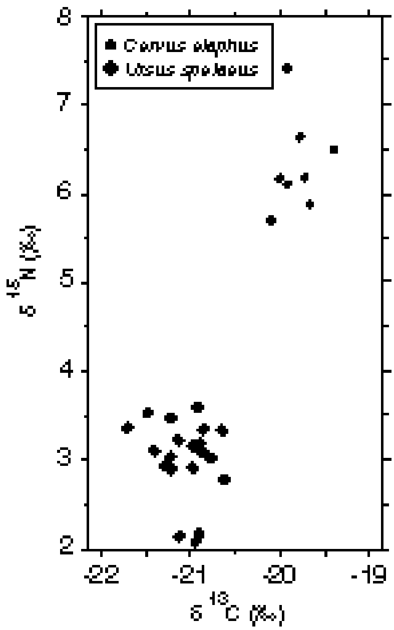

Figure 3. Isotopic data of *Cervus elaphus* and *Ursus spelaeus* from Liñares site. Data from VILA TABOADA *et al*. 1999 and VILA TABOADA *et al*. 2001.

from Liñares ($\delta^{15}N$ mean: 3.03‰) fed on fixing plants whose $\delta^{15}N$ was around 0‰. Red deer would feed, mainly, on non fixing plants as it makes, at present time, and this differentiation in their diet could explain such a difference in $\delta^{15}N$ of both herbivorous.

In addition some other issues lead us to wonder about the possibility of cave bears feeding on N_2 fixing plants.

I.- Vegetation

Our hypothesis of feeding on nitrogen-fixing plants (not only on Fabaceae) is reliable because they are taxonomically diverse trees, herbs and shrubs, occurring in eight families and 23 genera (SALISBURY & ROSS, 1992) including, for instance, the genus *Alnus*, pollen from which has been positively found in the Ramesch site, Austrian Alps (FRANK & RABEDER, 1997). This means that feeding on N_2 fixing plants would not be a restricted diet, because they range a wide variability of forms, climates and conditions. There are no pollen records published for the best isotopically known sites: Eirós or Liñares.

II.- Nutritional value

The nutritive value of nitrogen-fixing plants is fairly rich, as much as Graminaceae (cereals), and without the problem of Silicium nodules, which many Graminaceae (=Poaceae) show, and cause a strong abrasion in the herbivore teeth. It should be noted that the family of fixing plants Fabaceae (legumes) provides with a significantly higher amount of the essential aminoacid Lysine (GONZÁLEZ MONTERO, 1995).

Whether cave bears ate fruits (more protein storage than leaves or stems), tubercules or other plant components is not important for our isotopic discussion. This is because the $\delta^{15}N$ values are no influenced by the amount of proteins, but by the ratio of the two nitrogen isotopes, which is similar in every vegetal tissue.

Thus, it is reasonable to think of cave bears feeding on nitrogen-fixing plants (no matter grazing, browsing or bitting) which are more nutritive than any other, and less negative than Poaceae for their Carnivora-structure teeth.

III.- Dental wearing

The Cave Bear, despite belonging to the Order Carnivora, is an hervivorous whose dental formula lacks the three first upper and lower premolars (in *U. deningeri* P^3 and/or P_1 are sometimes preserved) showing instead a long diastema. The cheek teeth show rounded cusps, frequently splitted into several cusplets, and broad occlusal surfaces often covered by tubercles, ridges and cusplets that enlarge the masticatory surface to the detriment of the cutting fuction of other carnivores molars.

This morphological feature that gives to the *Ursus spelaeus* cheek teeth a bunodont appearance, very similar to those of the omnivorous artiodactyl *Sus*, is not correlationated with the structure of the tooth enamel. The enamel of *Ursus spelaeus* does not differ basically from that in other carnivores. This vegetarian carnivore retains the typical enamel of its phylogenetic group (Von KOENIGSWALD, 1992).

As a direct consequence of such features, cave bears teeth show a low strength to the abrasion caused by a vegetarian diet. The high degree of wearing in adult teeth is a commpon characteristic in most sites os this species. (KURTÉN, 1976).

A diet based in N_2 fixing plants would cause a determined teeth wearing depending on the kind of plants and depending on which part of the plant. It is clear that a diet based on Poaceae, with siliceous stems and leaves, could cause a stronger abrasion.

However, there are no comparative studies about dental wearing among different time-span and/or location sites other than the presented in this volume (LÓPEZ & GRANDAL, 2001). Besides, there is not a study of the degree of wearing and the age in years of the individuals.

The current research on dental microwearing will hopefully clarify the *Ursus spelaeus* diet, as it has happened with other species (HAYEK *et al*., 1992).

IV.- Rangifer tarandus

We have noticed that the other fossil herbivore with such low $\delta^{15}N$ is the reindeer. This striking fact is very interesting if we bear in mind that current reindeer show a very restricted diet: the reindeer lichens (Genus *Cladonia*, Subgenus *Cladina*), which are are a good source of energy.

How is this related to cave bears and their diet if it is not possible to compare such a different animals about their physiology nor metabolism ?

On one hand we should remark that lichens are a symbiosis between a fungal member (Mycobiont) and an Green Algae (Eukariota) or Cianobacteria. Thus, some of them show the ability of fixing nitrogen.

Even though reindeers were thought to feed only on *Cladina* lichens (non N_2-fixing), recent studies on present American *Rangifer tarandus* (caribou) show that although it appears to be able to balance the low protein content of the reindeer lichens by including in its diet a portion of the nitrogen-fixing lichens of the genera *Stereocaulon* and *Peltigera* which have relatively high protein contents (KLEIN, 1982).

Thus, the explanation of the low $\delta^{15}N$ of the Pleistocene reindeer plotted in the figure 2 (BOCHERENS *et al.*, 1991) could be a lichen diet with a significant nitrogen-fixing component. Even though it is not a true neither reliable comparison, the low $\delta^{15}N$ of cave bears could also be due to feed basically on nitrogen-fixing organisms.

CONCLUSION

It is demonstrated that physiology and metabolism are two important factors when dealing with isotopic signatures. If *Cervus elaphus* from Liñares, which –as ruminant- is supposed to show low $\delta^{15}N$, and presents a $\delta^{15}N$ 3‰ higher than *Ursus spelaeus* from the same site and absolute age, we might infer that the extremely low $\delta^{15}N$ of cave bears could be due to feed on nitrogen fixing plants.

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