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# Isotopic biogeochemistry and the evolution of cave bear ecology during Marine Oxygen Isotopic Stage 3 in Western and Central Europe

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The last few years have witnessed impressive new developments in our understanding of the evolution of cave bears in Europe during the Marine Oxygen Isotopic Stage 3, from around 65,000 to 25,000 years BP. This is mainly due to the contribution of new approaches, such as the palaeogenetical investigations of fossil remains (e.g. Hofreiter et al., 2002, 2004, 2007; Orlando et al., 2002), the direct radiocarbon dating of cave bear remains (e.g., Bocherens et al., 2006), and the improvement of morphometric approaches (e.g. Rabeder, 1999; Baryshnikov et al., 2003). These new results show that more than! one type (species?) of cave bear was present in Western and Central Europe during this period, and that climatic and possibly human factors impacted on the evolution of this (these?) species.

What are the links between changes in ecology and cave bear evolution? Isotopic biogeochemistry of fossil tissues can provide a direct link between some aspects of the life history of individual cave bears and their environment. Indeed, isotopic biogeochemistry is a powerful tool that is used more and more in mammal ecology to decipher trophic relationships and environmental impact on modern populations, in particular for bears. Stable isotope ratios of light elements such as carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$) and oxygen ($^{18}O/^{16}O$) in an animal tissues reflect the signature in the food and drinking water ingested by these animals (e.g. recent review in Bocherens and Drucker, 2007). This allows the distinction of plant *versus* meat feeders, the contribution of aquatic resource in the diet, and the evaluation of ancient temperatures. The use of this approach on modern bear populations, especially in North America, has yielded important results on the current diet of grizzly bears, black bears and polar bears, as well as on the dietary competition or niche partitioning of coeval bear species or populations (e.g., Ramsay and Hobson, 1991; Jacoby et al., 1999; Hobson et al., 2000). The preservation of carbon and nitrogen isotopic ratios in bone collagen, and those of oxygen in bone apatite, allows the of this approach to Late Pleistocene bear populations. It is therefore possible to compare the dietary and environment preferences of cave bears in different regions, to test hypotheses of dietary competition or niche partitioning with other carnivores, including other bear species (i.e. brown bear *Ursus arctos*), and to analyse the dietary differences between different genetic types of cave bears, when they coexist and when they change through time in a given region.

Cave bear material comes from sites in Belgium (Goyet and Scladina Cave), Germany (Geissenklösterle), France (Chauvet, Aldčne, Mialet, Font de Gaume), and Austria (Ramesch, Gamssulzen), ranging in age from around 25,000 to more than 45,000 years BP. Most of the studied material was directly dated by radiocarbon, the rest being dated indirectly according to their stratigraphic origin. The genetic type of most of the studied material was determined by sequencing of ancient mitochondrial DNA. Bone collagen was purified and the carbon and nitrogen isotopic measurements were performed according to Bocherens et al. (1997) and phosphate preparation and oxygen isotopic measurements according to Tütken et al. (2006). Only bones from adult animals were considered, except for the bears from Geissenklösterle, where teeth were used. Since the tooth $\delta^{13}C$ and $\delta^{15}N$ values are consistantly shifted compared to those of bone from the same individual, due to the impact of metabolic changes during hibernation recorded in tooth dentine but not in bones (Bocherens, 2004), a correction could be applied to compare these dentine isotopic values to bone isotopic values ($\delta^{13}C_{bone} = \delta^{13}C_{dentine} + 0.9$ ‰, $\delta^{15}N_{bone} = \delta^{15}N_{dentine} - 2.2$ ‰). In most cases, ungulate bones from each stratum (large bovids, horse, reindeer) were studied in parallel to cave bear material to provide a baseline of isotopic variation for pure herbivorous grazers.

The first isotopic studies on cave bears have shown that these carnivores exhibited low $\delta^{15}N$ values, which pointed to a vegetarian diet (e.g. Bocherens et al., 1994). Our new isotopic results show that this pattern is present in many sites in Western and Central Europe, and confirms the conclusions based on tooth morphology. When brown bears could be found in the same sites, as in Belgium and Austria, these bears exhibit isotopic signatures pointing to a much more carnivorous diet, sometimes similar to that of hyaenas. This suggests a niche partitioning between *U. arctos* and *U. spelaeus* in Late Pleistocene Europe, with brown bears on the carnivorous side and cave bears on the vegetarian side of the food spectrum available to bears.

Moreover, more subtle distinctions can be revealed using geographic stable isotopic variations. For instance, Baryshnikov et al. (2003) have suggested, on the basis of morphometric variability in the cheek teeth of cave bears, that northern and southern cave bear populations exhibited differences in the upper second molars and lower third molars. The authors tentatively link this variability to differences in hardness of plant food, since these teeth are especially active in food processing They quote preliminary isotopic data as supporting this view. The increased corpus of isotopic data on cave bears and coeval fauna confirms differences in the pattern observed in northern populations, such as those from Belgium (Scladina, layer 1A, and Goyet) and those from southern France (Font de Gaume, Aldčne, Mialet, Chauvet). In the Belgian sites, cave bears exhibit $\delta^{13}C$ values significantly more negative than those of coeval ungulates, while their $\delta^{15}N$ values are in the same range. On the contrary, cave bear! s from southern France exhibit lower $\delta^{15}N$ values than coeval ungulates, while their $\delta^{13}C$ values are not as negative as in Belgium. Interestingly, the cave bears from southern Germany seem to follow an isotopic pattern more similar to that of cave bears from southern France than from Belgium. It is noteworthy that all these cave bears belong to the same genetic group.

Comparisons of isotopic patterns according to types defined by palaeogenetic studies yields valuable information about the ecological partitioning of cave bear populations. For instance, two genetically different types of cave bears coexisted in two caves only ten kilometres apart in Austria for at least 15,000 years (Hofreiter et al., 2004). These cave bears are even considered to belong to different species, *Ursus spelaeus eremus* in Ramesch and *Ursus ingressus*! in Gamssulzen (Rabeder et al., 2004). The carbon isotopic signatures of specimens from Ramesch and Gamssulzen differ significantly ($\delta^{13}C = -21.7\pm0.3$ ‰, n=7 and $\delta^{13}C = -20.9\pm0.2$ ‰, n=9, respectively) while their nitrogen isotopic signatures are similarly low and indicate a vegetarian diet for both types. It is noticeable that the phosphate $\delta^{18}O$ values are also significantly different between the two types of cave bears, supporting the view of animals foraging in different landscapes, possibly at different altitudes, rather than an ecological partitioning based on the exploitation of different plant food resources in the same area.

Palaeogenetic investigations have revealed unexpected replacements of cave bear populations in southwestern Germany around 28,000 years ago (Hofreiter et al., 2007). Collagen isotopic variations offer the possibility to test whether this change was linked to an ecological shift. This is not the case, since the isotopic signatures of cave bears before and after the genetic change do not differ significantly compared to those of coeval ungulates, suggesting a similar feeding strategy for the two types of cave bears, within landscapes that remained basically unchanged. The question is now whether the new genetic type displaced the older one through competition, or if the new type occupied the niche left vacant after the extinction of the old type of cave bear.

The high resolution palaeoecological investigations of cave bears permitted by using stable isotope biogeochemistry allows researchers to study the possible impact of prehistoric human populations on the evolution of Upper Pleistocene bears in Europe. Humans have the biological ability to exploit the same range of food resources as bears, leading to the possibility of dietary competition, a hypothesis that can be directly tested with collagen carbon and nitrogen isotopic abundance. The isotopic data available for Neanderthals and early Upper Palaeolithic modern humans show that these humans relied heavily on proteins from terrestrial large herbivores (e.g., Bocherens and Drucker, 2006), therefore avoiding direct competition with cave bears. However, humans could have disrupted cave bear ecology by other means, such as direct predation or competition for hibernation caves, and this could be reflected in changes of isotopic signatures coincident with changes in human activity patterns as documented by archaeology. Data from Southwestern Germany documents the presence of new hunting technology beginning in the Upper Palaeolithic ca 35,000 years BP. Archaeological analyses also point to increased population densities of modern humans versus neanderthals and higher levels of predation in the Upper Palaeolithic than in the Middle Palaeolithic (Münzel et al., 2001; Conard et al., 2006). Thus we argue that human impact on cave bear populations, at least in Southwestern! Germany, played a significant role in the demography and population genetics of Late Pleistocene cave bears.

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