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Sexual dimorphism and morphometric variability of cheek teeth of the cave bear (*Ursus spelaeus*)

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ABSTRACT. The sexual dimorphism and the morphometric variability of the cheek teeth in *Ursus spelaeus* from six geographically well-separated localities dating from the Middle Weichselian were studied. The sexual dimorphism of the canines and of the lower carnassials (m1) of the cave bear are as much or more expressed than the dimorphism of these teeth in the Recent brown bear. The examined cave bear assemblages are rather similar in tooth size and proportions. The differences between the assemblages were presumably influenced by the ratio of male to female bears. The posterior cheek teeth M2 and m3 allowed us to divide more northern (Goyet in Belgium, Niedzwiedzia in Poland, and Medvezhiya Cave in European Russia) from more southern (Eirós in Spain, Arcy-sur-Cure in France, and Odessa in Ukraine) sites. These grouping suggest a difference in the diet of the cave bears in the northern and southern parts of the species distribution range, at least during the time segments studied.

KEY WORDS : *Ursus spelaeus*, cheek teeth, morphometric variability, sexual dimorphism, geographical variability

INTRODUCTION

During the Last Glacial, the cave bear (*Ursus spelaeus* Rosenmüller, 1794) was widely spread in Europe from the Atlantic coast to the Ural Mountains. The nature of its geographical variability is not clear. According to Vereshchagin & Baryshnikov (1984), every karst region possessed its own local population of *U. spelaeus*. The cheek teeth from successive stratigraphic levels are suitable for elaborating a model of the evolution of the dental system (Rabeder, 1983, 1999; Baryshnikov, 1998). However, are cheek teeth appropriate for the analysis of the geographic variation of *U. spelaeus*? Does the sexual dimorphism vary in different cave bear groups? We have raised these questions in studying the dental collections from several sites.

LOCALITIES, MATERIAL AND METHODS

Cave localities and collections :

AsC : Arcy-sur-Cure, France (c. 37,5-31,8 Ka BP, Girard et al., 1990), collections of Institut de Paléontologie, Paris, France

CE : Cova Eiros, Spain (c. 28,2 Ka BP, Grandal d'Anglade, 1993), collections of Instituto Universitario de Xeoloxia, Universidade da Coruña, Spain

GB4 : Goyet, Belgium, assemblage B4 (c. 35,5 Ka BP, Germonpre & Sablin, 2001), collections of the Royal Belgian Institute of Natural Sciences, Brussels, Belgium

Ni : Niedzwiedzia, Poland (< 30 Ka BP, Nadachowski et al., 1989), collections of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow, Poland

Me : Medvezhiya, Russia (cultural layers : c. 12,0 Ka BP, Sinitsyn & Praslov, 1997; cave bear bone : > 48,6 Ka BP, Rabeder, personal communication), collections of the Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia

Od : Odessa, Ukraine (c. 26,9 Ka BP, Kurtén, 1969), collections of the Zoological and Geological Museum, University Helsinki, Finland; the Zoological Institute, Russian Academy of Sciences, Saint-Petersburg, Russia; the Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia

Three sites are located near the northern limit of the cave bear range : Goyet in Belgium, Niedzwiedzia in Poland and Medvezhiya in the Ural Mountains (Russia). Three others occur markedly to the south : Cova Eirós in Spain, Arcy-sur-Cure in France and Odessa in Ukraine. The morphometrical data on the cheek teeth from Arcy-sur-Cure were published earlier (Baryshnikov & David, 2001). The collection from Arcy-sur-Cure here studied is from the Upper Palaeolithic layers of grotto Renne.

The cave bear teeth were measured using the scheme published earlier (Baryshnikov, 1998; Baryshnikov & David, 2000). The measurements were taken with dial calipers with accuracy up to 0.1 mm. Heavily worn teeth were not measured. The data were processed by Cluster Analysis from STATISTIKA 6.0 (> 1999 edition).

LIST OF ABBREVIATIONS

BL : basal length,
CBL : condylobasal length,

CV : coefficient of variation,
DtC : transversal diameter canine,
F : Female,
Fm : Female mean,
GL : greatest crown length,
Gln : greatest length of nasals,
GWocc. : greatest width of the occipital condyles,
GW : greatest crown width,
LaLTa : labial length of talonid,
LaLTr : labial lenght of trigonid,
Lcp : length of caudal part,
LE1 : Length of entoconid 1,
LE2 : length of entoconid 2,
Lfp : length of frontal part,
LiLTa : lingual length of talonid,
LiLTr : lingual length of trigonid,
LMe : length of metacone,
LP4-M2 : length of maxillary tooth row P4-M2,
LPa : length of paracone,
LTa : length of talonid,
LTr : length of trigonid,
M : male,
Mm : male mean,
m : mean,
MLPC : minimal length between frontal ridge of protocone and caudal side of crown,
MW : minimal width,
Mws : minimal width of the skull,
OR : observed range,
P : level of reliability
SD : standard deviation,
t : t-test, Student criterium of reliability,
W C : width at the canine,
Why : width of tooth through hypocone,
WTa : width of talonid,
WTr : width of trigonid,
WZ : zygomatic width,

SEXUAL DIMORPHISM

As demonstrated by Kurtén (1955, 1976), the sexual dimorphism of cave bears is well marked in the size of the upper and lower canines, and cave bear males were considerably larger than females. Therefore, differences in canine and bone mean dimensions from various sites may depend on the different ratio between males and females. The cave bear assemblage B4 from Goyet contains several skull fragments of which more than half belong to males. Measurements of the skulls are given in Table 1.

One of these skulls (no. 2201), judging from its basal length, approaches the maximum size known for *U. spelaeus* (Cordy, 1972). The preponderance of male bears was also observed in the length of the mandibular tooth row p4-m3 and in the distribution of the canines (Germonpre & Sablin, 2001). In five male mandibles the length of the p4-m3 ranges between 107.2 and 115.5 mm with an average of 110.8 mm, in three female specimens the range is : 92.2-102.0 mm, and the average is : 97.5 mm.

The sexual dimorphism of the width of the lower canine was calculated as the ratio of male mean to female mean (Van Valkenburgh & Sacco, 2002). The dimorphism obtained for isolated canines from Goyet B4 is 1.28 (n M : 34, n F : 22; Germonpré, unpublished data), the mean for Odessa, based on the mean of female and male canine width given in Kurtén (1976), is 1.29. Both

TABLE 1

Measurements of the skulls of *Ursus spelaeus* from Goyet (assemblage B4), Belgium

Male					
	n	OR	m		
BL	3	409.0-445.0	428.0		
GLn	2	98.0-121.0	109.5		
LP4-M2	3	90.8-94.9	93.2		
GWocc	1	76.2	-		
WZ	-	-	-		
MW	1	98.7	-		
W C	2	102.8-114.8	108.8		
Female					
	n	OR	m	SD	CV
BL	2	372.0-390.0	381	-	-
GL n	1	80.9	-	-	-
L P4-M2	4	83.3-93.1	88.8	4.08	4.60
GW occ	2	79.3-84.8	82.5	-	-
WZ	1	206.0	-	-	-
MW	1	72.6	-	-	-
W C	2	83.0-99.0	91.0	-	-

are much higher than the mean of 1.13 for recent brown bear and are comparable to the mean of 1.25 for recent lion and 1.24 for recent leopard (data from Gittleman & van Valkenburg, 1997). According to these authors, dimorphism in canine size is related to severe male-male competition and frequent incidence of infanticide in polygynous species. These behaviours were therefore probably at least as much pronounced in cave bear as in Recent brown bear. According to Kurtén (1955), sexual dimorphism is stronger in cave bears than in Recent brown and polar bear. Furthermore, the dimorphism becomes more accentuated with increasing size.

The carnassials of bears show a weak dimorphism. The mean sexual dimorphism of the lower carnassial for brown bear equals 1.04 (Gittleman & van Valkenburg, 1997). The same ratio is obtained for two Russian subspecies of the brown bear : *Ursus arctos arctos* Linnaeus, 1758 from the north of European Russia and *Ursus arctos piscator* Pucheran, 1855 from Kamchatka (Table 2). However, in the subspecies *Ursus arctos pruinosus* (Blyth, 1854) from Tibet, the sexual dimorphism of the carnassial is much more expressed with a value of 1.09. Our data indicate that male and female brown bears reliably differ in means of the m1 length. The values of t-test change from 1.95 in *Ursus arctos arctos* ($P<0.05$) to 5.78 in *Ursus arctos pruinosus* ($P< 0.001$) (Table 2). The difference between male and female carnassial length is more pronounced for those brown bears that possess larger teeth, as shown by the Tibet sample. Although the first molar from the Kamchatka bears is quite large, sexual dimorphism remains small. Possibly the feeding by both males and females of these bears on soft and nutritious food, containing a large amount of salmon (Revenko, 1993) does not require tooth enlargement, even in large males. Presumably the sexual dimorphism in cheek teeth size in bears is allometric in nature and is revealed only when the tooth size exceeds a threshold level. This is probably reached in the Tibet bears, which

TABLE 2

Greatest crown length of the lower carnassial of male and female Recent *Ursus arctos* and of the lower carnassial in sexed jaws from *Ursus spelaeus* from Goyet (assemblage B4)

Samples	sex	n	OR	m	t	P	SD	sex dimor.	Mm-Fm	MSD/FSD
Ursus a. arctos										
European Russia	M	21	20,9-26,4	23.41	-	-	1.50	-	-	-
	F	18	20,5-25,0	22.55	-	-	1.26	-	-	-
	M+F	50	20,5-26,4	22.97	1.95	<0,05	1.43	1.04	0.86	1.19
Ursus a. piscator										
Kamchatka	M	15	24,1-27,9	25.89	-	-	1.23	-	-	-
	F	13	23,5-25,8	24.80	-	-	0.64	-	-	-
	M+F	30	22,8-27,9	25.28	2.99	<0,01	1.19	1.04	1.09	1.92
Ursus a. pruinosus										
Tibet	M	16	25,1-28,1	26.41	-	-	0.83	-	-	-
	F	7	23,4-25,9	24.14	-	-	0.88	-	-	-
	M+F	23	23,4-28,1	25.72	5.78	<0,001	1.35	1.09	2.27	0.94
Ursus spelaeus										
Goyet B4	M	10	28,7-32,6	30.92	-	-	1.23	-	-	-
m1 in sexed jaw	F	8	27,3-29,6	28.29	-	-	0.90	-	-	-
	M+F	18	27,3-32,6	29.75	5.23	<0,001	1.72	1.09	2.63	1.37

feed on rough plant material (ZHIRYAKOV & GRACHEV, 1993). The sexual dimorphism of the Recent brown bears vary in the different geographical groups of the brown bear. Since the teeth of the cave bear from Goyet are larger than those of the modern brown bear, the difference in mean tooth lengths between males and females might be more considerable than in the Recent brown bear. The sexual dimorphism of the crown length of lower carnassials from the cave bears of Goyet was calculated, based on the carnassials in the sexed jaws (Table 2). The jaws were defined as male or female judged on the size of the canine. The sexual dimorphism of the sexed sample is 1.09, comparable with the dimorphism of the Tibet brown bears, and larger than that of the other brown bears. The value of the t-test is 5.23, the two-tailed P-value is less than 0.001, the difference between the male and female carnassial length from Goyet is extremely statistically significant (Table 2). The sexual dimorphism of the m1 of the cave bears from Mixnitz, Austria, is comparable with a value of 1.08 (data from KURTÉN, 1955, table 8). Furthermore, the fact that the dimorphism of the canine is larger than that of the carnassial indicates the influence of the breeding system on the canine size rather than that of the feeding process (GITTLEMAN & VAN VALKENBURG, 1997).

The carnassial mean length of the sexed subsample from Goyet (m1 in situ) is 29.75 mm. This subsample is probably more balanced (n M : 10, n F : 8 - males : 56%) than the total sample from Goyet. The mean male frequency of the Goyet assemblage is 69%, based on the third incisors, canines, skulls and lower jaws present in assemblage B4 (GERMONPRÉ & SABLIN, 2001). However, this mean is based on adult and subadult specimens and the frequency of the males could be different in the sample of the lower carnassials as it contains a large frequency of young animals (GERMONPRÉ, in press). The mean of the more balanced subsample is much smaller than the mean crown length of all lower carnassials, isolated and attached in the lower jaw, from Goyet, which is 30.95 mm, and than the mean crown length of the other studied assemblages as well (Table 3) (Tables 3-9 : see appendix). Different causes may explain the discrepancy between the mean lengths of the lower carnassials from all studied assemblages, all being assigned to the Pleniglacial. The variation among the crown length means is statistically significant (P=0.0373).

The discrepancy may be due to :

1. The different ratio between the males and females in the assemblages
2. Individual peculiarities of the samples. They may depend on : (a) the number of specimens in each sample, which could be too small to show a real mean, (b) the individual variability of cave bears, (c) the individual age of the specimens as natural selection might accumulate unsuccessful variants among young animals, etc.
3. Different diet of the populations (see further)
4. Different system of taking measurements.

According to GRANDAL D'ANGLADE (2001), a predominance of males in a cave bear population would lead to an increment in the average values of the cheek teeth, while a preponderance of females would decrease the average. The large frequency of males in assemblage B4 from Goyet is explained by sexual segregation (GERMONPRE, *in press*). According to the frequency distribution of the lower canines, the assemblage from Odessa shows almost the same presence of males and females (KURTÉN, 1976). The caves of Arcy-sur-Cure, Eirós, Niedzwiedzia and Medvezhiya Cave were probably used as dens predominantly by females. The abundance of deciduous bear teeth and the larger frequency of female canines in Arcy-sur-Cure (BARYSHNIKOV & DAVID, 2001) confirms this. In Eirós a slight predominance of females is observed (LOPEZ-GONZALES & GRANDAL D'ANGLADE, 2001). In our opinion, the mean value of the lower carnassial length is strongly influenced by the sex ratio of the assemblage, although other factors, mentioned above, may play a role as well.

According to RABEDER (2001), the mean dimensions of cheek teeth of cave bears are not influenced by the sex ratio, but by geological age and phylogenetic position of the assemblage. He further considers that the distribution of the dimensions corresponds to a unimodal Gauss curve as shown in his figure 6 of the greatest crown length of the m1 from the Ramesch-Knochenhöhle; the mean of this assemblage is 29.26 mm. However, according to GODFREY et al. (1993), a mixture of male and female subsamples does not show a bimodality if the means of the males and females are separated by less than two subsample standard deviations, for subpopulation standard deviaton ratios of between 0.4 and 2.5, even if the mixing proportions of the males in the sample fluctuates between 20-80%. The distribution becomes progressively bimodal as the separation of the means increases. In the samples of brown bears from European Russia and Kamchatka the difference between the male and female means is less than two male and female standard deviations (Table 2). Only the brown bear sample from Tibet could indicate a trend to bimodal distribution as the difference between the male and female mean is larger (2.27 mm) than two male or female standard deviations.

It is possible that also in cave bear populations the sexual dimorphism of the carnassials fluctuated. In the Goyet sample, the separation between the female mean and the male mean (2.63 mm) is larger than two male standard deviations or female standard deviations (Table 2). In this sample and in our brown bear samples the male / female standard deviation ratio is larger than 0.4 and smaller than 2.5 (Table 2). RABEDER (2001) does not give the male or female mean of the Ramesch-Knöchenhöhle m1 mixture. However, it is possible that the lower carnassial of the small-sized Alpine cave bears was less sexually dimorphic than that of the large-sized cave bears from Goyet or Mixnitz. Also according to GRANDAL D'ANGLADE (2001), the different degree of sexual dimorphism in different cave bear populations is well marked, especially in the lower jaw.

MORPHOMETRICAL VARIABILITY

In the assemblages from Goyet and Odessa, the mean lengths of the P4, M2, p4, m1 and m3 are larger than from the other assemblages, with the exception of the lower carnassial from Eiros (Tables 3, 4, 6, 7, 9). Eiros has the smallest mean length for the M1 and Medvezhiya for the m2 (Tables 5, 8).The posterior jugal teeth can be grouped according to the geographical position of the assemblages. The greatest average length of the M2 is found in the Odessa assemblage, the largest tooth size occurs in Goyet. The smallest average tooth length occurs at Medvezhiya Cave. In Goyet, Niedzwiedzia and Medvezhiya, the metacone of this tooth is larger than in the other sites (Table 6). The mean metacone index (Lme/GL*100) for the latter sites is larger than 25 (GB4 : 26.1, Ni : 28.0, Me : 25.3), this index from the other sites is smaller than 25 (Od : 24.6, AsC : 22.9, CE : 22.7). According to KURTÉN (1958), juveniles from Odessa with a large paracone had a higher mortality rate than those with a small paracone, due to a less-well-functioning occlusion. It is not clear from our studies if the posterior metacone posed a comparable problem. The cluster analysis in Figure 1, based on the greatest length, length of paracone, length of metacone, greatest width and width across hypocone, shows an interesting subdivision into two groups. The first group unites Goyet, Niedzwiedzia and Medvezhiya, which are situated near the northern border of the distributional range of the cave bear. The second group is constituted by the southern localities (Eiros, Arcy-sur-Cure, Odessa). The differences between these groups are rather small (squared Mahalanobis distances less than 6.1).

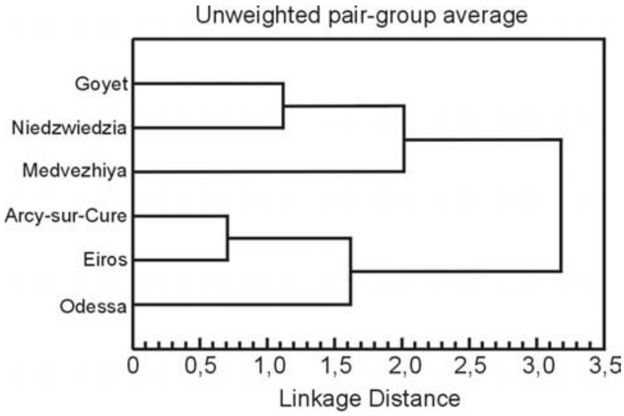

Fig. 1. – Hierarchical tree plot for M2 of *Ursus spelaeus* according to squared Malalanobis distances

The m3 from Goyet are the longest in average. The third molars from Medvezhiya Cave are extremely small. The assemblages of Goyet, Niedzwiedzia and Medvezhiya are characterized by a long talonid (> 14 mm, Table 9). The talonid index (LTa/GL*100) amounts to 51.5 for Goyet, to 52.8 for Niedzwiedzia and reaches the extreme value of 63.8 for Medvezhiya. This index remains below 50 for the other sites (Od : 47.1, AsC : 45.9, CE : 45.8). The cluster analysis given in Figure 2 is based on four measurements (greatest length, length of talonid, greatest width and width of talonid). The analysis subdivides the sites into two groups. The first group includes Medvezhiya Cave, being well-distanced from the second one (squared Mahalanobis distances from 9.20 to 25.17). Within the second group, there are two clusters, one involving more northern sites (Goyet, Niedzwiedzia) and the other uniting the sites located in the south of the distributional range for *U. spelaeus* (Eirós, Arcy-sur-Cure, Odessa).-

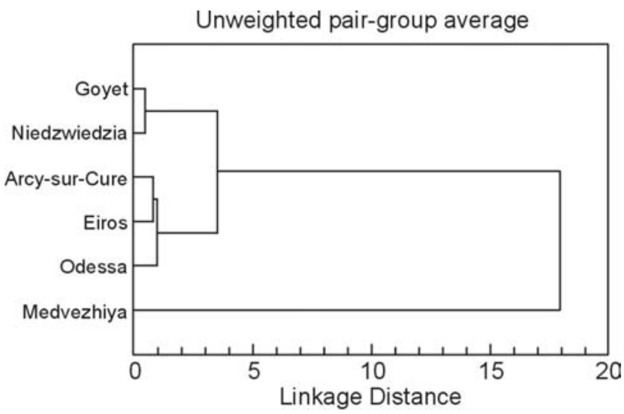

Fig. 2. – Hierarchical tree plot for m3 of *Ursus spelaeus* according to squared Malalanobis distances

TABLE 10

Condylobasal skull length and greatest crown length of the lower carnassial of male Recent brown bears

males	n	CBL	n	GL m1
Ursus a. arctos	24	332.21	20	23.44
Ursus a. piscator	52	370.88	15	25.89
Ursus a. pruinosus	21	340.37	13	26.48

DISCUSSION

The study shows that sexual dimorphism of the canines and of the lower carnassial of the cave bear is as much or more expressed than the dimorphism of these teeth in the Recent brown bear. The morphometry of the cheek teeth of *U. spelaeus* from the studied localities is rather similar. The largest average tooth size occurs in the samples from Odessa (p4, M1, M2) and Goyet (P4, m3). The teeth with the smallest average size were observed in the Medvezhiya Cave (M2, m1, m2, m3). The smaller dimensions may be associated with the dominance of female remains. The cave bears from North Urals were not dwarfed because several teeth found in the Medvezhiya Cave exhibit the maximum length for all the material examined. The lack of important morphological differences could indicate that an exchange of genetic material between adjacent cave bear populations took place. Ancient mitochondrial DNA analysis for the cave bear sometimes reveals difference between individual bears from closely-located caves (HOFREITER et al., 2002). These data may be in contrast with our evidence. However, the differences in mtDNA sequences are passed on via females. The analysis with use of nuclear microsatellite markers produced for modern Alaskan brown bears of insular populations has demonstrated that bears of the ABC Islands, which have previously been shown to undergo little or no female-mediated gene flow with mainland populations (TALBOT & SHIELDS, 1996), were found not to be genetically distinct from mainland bears (PAETKAU et al., 1998). Possibly this is associated with a different dispersal capability of male and female bears, the females being more phylopatric. Also ORLANDO et al. (2002) found that extensive gene flow seems to have connected European cave bear populations because two haplogroups cover wide geographic areas.

Most cheek teeth do not show characters useful for the creation of a model of geographical variability in *U. spelaeus*. The exceptions are the M2 and m3. These teeth are in contact in occlusion and are especially active in food processing. Based on these molars, the assemblages can be divided into two well-separated geographical groups. The first group includes the localities situated on the northern boundary of the cave bear's distributional range (Goyet, Niedzwiedzia and Medvezhiya Cave). The second group involves more southern localities (Eirós, Arcy-sur-Cure and Odessa). During the evolution of the genus *Ursus* the posterior cheek teeth were strongly modified, particularly in cave bears (*U. deningeri* Reichenau, 1904 - *U. spelaeus* Rosenmüller, 1794), as these teeth are functionally important for the processing of rough plant food (RABEDER et al., 2000). Therefore, the differences observed in the proportions of the M2 and the m3, in the M2 metacone index and in the m3 talonid index are interpreted as adaptive. The diet of cave bears inhabiting the north of their range might have differed from that in bears occupying more southern regions.

A similar tendency in geographical variability of cheek teeth is found in the recent *U. arctos* in Asia. The brown bears from Tibet demonstrate larger teeth than the animals from northern Siberia; bears from southern Siberia and Mongolia are intermediate (ARISTOV & BARYSHNIKOV, 2001). The southern brown bears have a more herbivorous diet than those from northern Siberia, whose diet includes a larger proportion of meat and fish (ZHIRYAKOV & GRACHEV, 1993, CHERNYAVSKIY et al., 1993, CHERNYAVSKIY & KRECHMAR, 2001). Furthermore, the size of the cheek teeth depends not only on the habitat but of the size of the animal as well. In Table 10 the crown length of the m1 from the males of three brown bear populations is compared with the condylobasal length of the skull. The largest m1 values are found both in the enormous bears from Kamchatka and in the moderate-sized bears of Tibet. Furthermore, sexual dimorphism seems to be larger in the latter group (Table 2). Size differences in Recent brown bear do not necessarily mean that the bears are genetically distinct. The difference in body size between the coastal brown bears of Alaska and those from the interior of Alaska, can be explained by ecological (abundant salmon resource) rather than genetic factors. These populations comprise a single subspecies (*Ursus arctos horriblis* (Ord)) (PAETKAU et al., 1998).

Cave bears are presumed herbivores, based on dental morphology and isotope signatures (KURTÉN, 1976; BOCHERENS et al., 1997). Probably the northern cave bear populations had to cope with harder plant food, which needed to be chewed longer; they adapted by modifying their posterior jugal molars. The cave bears from the Ural, due to their most northeastern location, show this adaptation in an extreme form. Furthermore, the moderate sexual dimorphism of the lower carnassial of the cave bears from Goyet could be a consequence of feeding on rough plant material, as the larger sex had to eat more abrasive food to sustain its greater mass. Stable isotope analyses of cave bears from distinct geographic regions confirms this difference in plant food. BOCHERENS et al. (1997) found significant differences between the $\delta^{13}C$ values in cave bears from layer 1A of the Belgian site of Sclayn, dating from the Middle Weichselian, and sites in southern France. During the Last Glacial, Belgium experienced more severe climatic conditions than southern Europe and the more ^{13}C-depleted collagen in cave bear bones from Sclayn is linked by the authors to the influence of the climatic conditions on plant photosynthesis ^{13}C fractionation. According to FERNANDEZ-MOSQUERA et al. (2001), depletion of $\delta^{13}C$ can also be caused by the high rate of bone renewal during dormancy. The length of the dormancy in cave bears depends not only on the climatic conditions, but furthermore differs between males and females (GERMONPRE & SABLIN, 2001). Thus, isotope signatures could also depend on the sex of the cave bear bones.

For a better view on the geographical variability of *U. spelaeus*, further research is needed, on well-dated cave bear assemblages, concerning the dental morphometry of sexed teeth as well as the isotope signatures in collagen from sexed skeletal elements.

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TABLE 3

Measurements of the m1 in *Ursus spelaeus*

m1	n	OR	m	SD	CV
Goyet B4					
GL	42	26.1-34.0	30.95	1.84	5.95
LTr	37	16.5-19.3	18.68	1.05	5.62
LE1	25	3.4-6.5	5.65	0.73	12.92
LE2	25	4.9-7.5	6.04	0.60	9.93
WTr	40	10.3-14.1	12.25	1.05	8.57
WTa	41	13.6-17.0	15.09	0.89	5.90
MW	41	9.6-13.6	11.82	0.90	7.61
Odessa					
GL	45	28.0-34.1	31.24	1.53	4.90
LTr	42	10.2-26.0	19.72	2.08	10.55
LE1	40	4.5-7.5	5.54	0.69	12.45
LE2	40	4.2-8.2	5.59	0.83	14.85
WTr	45	10.8-14.4	12.60	0.82	6.51
WTa	45	13.8-17.2	15.40	0.77	5.00
MW	45	10.9-14.1	11.98	0.64	5.34
Arcy-sur-Cure					
GL	25	27.3-32.5	30.70	1.39	4.53
LTr	25	17.2-20.7	19.33	0.90	4.66
LE1	24	3.4-6.3	5.26	0.72	13.69
LE2	24	3.8-7.1	5.72	0.60	10.49
WTr	25	10.7-13.9	12.34	0.75	6.08
WTa	25	13.1-16.4	14.97	0.53	3.54
MW	25	10.4-12.9	11.56	0.53	4.59
Eiros					
GL	25	27.7-34.0	31.32	1.48	4.73
LTr	25	17.3-21.1	19.42	0.94	4.84
LE1	25	4.3-7.0	5.34	0.86	16.10
LE2	25	3.8-7.2	5.36	0.77	14.37
WTr	25	10.4-13.1	11.67	0.69	5.91
WTa	25	13.4-16.0	14.81	0.76	5.13
MW	25	10.4-12.6	11.19	0.55	4.92
Niedzwiedzia					
GL	28	27.2-32.7	30.49	1.35	4.43
LTr	28	15.7-21.1	19.20	1.11	5.78
LE1	38	4.0-7.4	5.66	0.70	12.37
LE2	38	4.2-7.7	5.81	0.79	13.60
WTr	28	9.7-12.7	11.75	0.70	5.96
WTa	38	11.8-16.0	14.32	0.97	6.77
MW	38	9.1-13.0	11.42	0.79	6.92
Medvezhiya					
GL	24	26.9-33.9	30.11	1.68	5.58
LTr	24	17.3-21.5	19.24	1.15	5.98
LE1	24	4.8-9.6	6.04	1.06	17.55
LE2	24	4.0-6.4	5.14	0.63	12.26
WTr	24	10.8-12.4	11.73	0.58	4.94
WTa	24	12.8-16.2	14.36	0.96	6.69
MW	24	9.8-12.0	10.96	0.60	5.47

TABLE 4

Measurements of the P4 in *Ursus spelaeus*

P4	n	OR	m	SD	CV
Goyet B4					
GL	13	19.4-22.8	21.52	0.99	4.60
LPa	13	10.6-13.4	12.58	0.80	6.36
GW	13	14.9-17.4	15.56	0.74	4.76
MLPC	13	14.2-17.8	16.51	1.05	6.36
Odessa					
GL	50	18.2-24.0	21.30	1.49	7.00
LPa	50	10.3-16.4	13.66	1.18	8.64
GW	50	12.8-17.1	14.83	1.07	7.22
MLPC	50	9.9-18.5	14.80	1.64	11.08
Arcy-sur-Cure					
GL	22	18.9-23.3	20.94	1.33	6.35
LPa	22	11.6-15.3	13.47	0.94	6.98
GW	22	12.7-16.9	14.81	1.12	7.56
MLPC	22	13.3-17.3	15.25	1.28	8.39
Eiros					
GL	17	18.1-21.8	20.41	1.20	5.88
LPa	17	10.9-14.2	12.87	0.87	6.76
GW	17	12.5-16.0	14.38	1.10	7.65
MLPC	17	13.8-17.9	15.84	1.29	8.14
Niedzwiedzia					
GL	9	18.8-21.3	19.92	0.75	3.77
LPa	9	11.1-13.4	12.49	0.70	5.60
GW	9	10.5-14.7	13.14	1.25	9.51
MLPC	9	12.0-16.2	14.40	1.32	9.17
Medvezhiya					
GL	8	19.3-26.0	21.00	2.18	10.38
LPa	8	11.6-14.3	13.07	0.84	6.42
GW	8	13.4-15.1	14.10	0.60	4.26
MLPC	8	13.5-16.6	14.97	0.92	6.15

TABLE 5

Measurements of the M1 in *Ursus spelaeus*

M1	n	OR	m	SD	CV
Goyet B4					
GL	25	25.7-31.1	28.57	1.58	5.53
GW	25	18.6-21.8	20.14	0.99	4.92
Lfp	22	12.5-15.4	14.01	0.68	4.85
Lcp	22	13.3-16.5	15.05	0.88	5.85
LPa	21	10.0-12.8	11.43	0.78	6.82
LMe	21	9.5-11.5	10.51	0.65	6.18
Odessa					
GL	53	27.6-33.4	29.82	1.35	4.53
GW	52	18.5-23.6	20.83	0.98	4.70
Lfp	53	13.1-16.0	14.41	0.69	4.79
Lcp	53	13.9-18.0	15.59	0.91	5.84
LPa	53	9.9-12.4	11.08	0.60	5.42
LMe	53	9.2-11.8	10.37	0.50	4.82
Arcy-sur-Cure					
GL	19	24.9-32.0	28.92	1.98	6.85
GW	19	18.3-22.5	20.16	1.36	6.75
Lfp	19	11.5-15.2	13.69	1.00	7.30
Lcp	19	13.1-17.0	15.08	1.29	8.55
LPa	19	8.6-12.0	10.49	0.87	8.29
LMe	18	8.5-11.7	9.97	0.91	9.13
Eiros					
GL	26	26.0-30.8	28.43	1.32	4,464
GW	26	16.9-21.7	19.85	1.23	6.20
Lfp	26	12.0-14.6	13.56	0.69	5.09
Lcp	26	13.1-16.4	14.72	0.86	5.84
LPa	26	9.0-11.4	10.06	0.53	5.27
LMe	26	8.6-10.7	9.58	0.57	5.95
Niedzwiedzia					
GL	20	26.6-32.8	29.38	1.87	6.36
GW	20	17.8-21.2	19.59	1.17	5.97
Lfp	20	12.0-15.4	14.01	0.88	6.28
Lcp	19	13.2-16.6	14.84	1.07	7.21
LPa	16	10.4-12.2	11.27	0.58	5.15
LMe	16	9.4-11.5	10.72	0.62	5.78
Medvezhiya					
GL	22	26.4-32.6	29.31	1.54	5.25
GW	22	12.5-17.5	14.23	0.98	6.89
Lfp	22	12.9-17.7	15.25	1.20	7.87
Lcp	22	9.3-11.4	10.22	0.59	5.77
LPa	22	8.6-10.7	9.85	0.56	5.69
LMe	22	18.2-22.0	20.16	0.98	4.86

TABLE 6

Measurements of the M2 in *Ursus spelaeus*

M2	n	OR	m	SD	CV
Goyet B4					
GL	22	41.2-53.5	45.95	2.89	6.29
LPa	18	12.6-16.4	14.14	1.09	7.71
LMe	17	10.3-14.4	11.98	1.11	9.27
GW	22	21.1-25.1	23.19	1.09	4.70
WHy	22	18.1-23.3	20.60	1.33	6.46
Odessa					
GL	53	36.7-51.9	46.32	2.87	6.20
LPa	53	12.0-15.4	13.55	0.81	5.98
LMe	53	8.7-15.0	11.40	1.46	12.81
GW	52	19.9-27.1	23.73	1.61	5.81
WHy	53	16.0-23.0	20.42	1.53	7.49
Arcy-sur-Cure					
GL	18	38.5-48.7	45.43	2.53	5.57
LPa	18	12.0-14.8	13.24	0.92	6.95
LMe	18	8.9-12.8	10.40	1.12	10.77
GW	18	21.4-25.1	23.12	1.08	4.67
WHy	18	19.3-23.1	21.29	1.08	5.07
Eiros					
GL	25	41.4-47.1	44.71	1.52	3.40
LPa	25	11.0-14.7	12.96	0.92	7.10
LMe	25	7.6-12.1	10.22	1.05	10.27
GW	25	20.3-25.1	22.61	0.92	4.07
WHy	25	17.8-21.6	20.27	0.78	3.85
Niedzwiedzia					
GL	14	40.6-48.2	44.40	2.40	5.41
LPa	17	12.2-16.2	13.98	1.07	7.65
LMe	14	10.6-14.7	12.43	1.21	9.73
GW	17	19.5-26.4	22.91	1.89	8.25
WHy	14	18.3-21.1	19.55	0.94	4.81
Medvezhiya					
GL	21	39.1-52.6	44.10	3.14	7.12
LPa	21	11.3-18.4	13.03	1.48	11.36
LMe	21	10.1-14.4	11.71	1.07	9.14
GW	21	19.9-27.7	22.72	1.52	6.69
WHy	21	18.1-24.5	20.50	1.51	7.37

TABLE 7

p4	n	OR	m	SD	CV
Goyet B4					
GL	30	13.0-19.0	16.01	1.71	10.68
GW	30	8.4-13.7	10.86	1.27	11.69
Odessa					
GL	56	12.9-18.5	16.14	1.27	7.87
GW	56	9.5-13.0	11.24	0.83	7.38
Arcy-sur-Cure					
GL	28	13.9-17.6	15.44	0.95	6.15
GW	28	9.4-12.8	10.74	0.95	8.85
Eiros					
GL	17	11.3-17.8	15.52	1.63	10.5
GW	17	8.9-12.4	10.64	0.92	8.65
Medvezhiya					
GL	4	14.2-17.5	15.58	1.39	8.92
GW	4	9.4-12.5	10.80	1.33	12.31

TABLE 8

Measurements of the m2 in *Ursus spelaeus*

m2	n	OR	m	SD	CV
Goyet B4					
GL	37	26.8-33.7	30.97	1.74	5.62
LaLTr	26	16.4-20.7	18.40	1.10	5.98
LiLTr	25	13.8-18.3	16.95	1.17	6.90
LaLTa	26	11.0-15.5	13.36	1.13	8.46
LiLTa	23	11.5-15.8	14.32	1.20	8.38
WTr	35	16.3-20.3	18.41	1.11	6.03
WTa	36	16.7-21.0	19.01	1.29	6.79
Odessa					
GL	89	27.5-35.7	31.26	1.64	5.25
LaLTr	89	16.4-21.9	18.73	1.28	6.83
LiLTr	89	13.5-19.6	16.44	1.29	7.85
LaLTa	89	9.9-15.2	12.74	1.21	9.50
LiLTa	89	10.8-18.0	13.99	1.54	11.01
WTr	89	16.4-20.9	18.44	1.01	5.48
WTa	89	17.1-22.1	19.30	1.09	5.65
Arcy-sur-Cure					
GL	23	28.1-32.2	31.51	1.76	5.59
LaLTr	23	17.3-20.6	18.61	0.90	4.84
LiLTr	23	14.7-19.2	16.57	1.13	6.82
LaLTa	23	9.6-13.9	11.84	1.04	8.78
LiLTa	23	10.1-15.3	12.69	1.27	10.01
WTr	23	16.4-21.0	18.23	1.16	6.36
WTa	23	16.0-21.4	18.94	1.31	6.92
Eiros					
GL	24	28.3-34.5	31.36	1.42	4.53
LaLTr	24	15.7-19.9	17.56	1.18	6.72
LiLTr	24	14.4-17.7	15.77	0.84	5.33
LaLTa	24	10.3-14.3	12.48	0.94	7.53
LiLTa	24	11.4-16.0	13.33	1.18	8.85
WTr	24	15.5-20.5	17.66	1.04	5.89
WTa	24	17.1-22.8	19.12	1.27	6.64
Niedzwiedzia					
GL	27	28.0-34.4	31.18	1.98	6.35
LaLTr	27	16.5-20.8	18.54	1.24	6.69
LiLTr	27	13.7-19.7	16.71	1.54	9.22
LaLTa	27	10.6-15.7	12.70	1.08	8.50
LiLTa	27	10.9-16.3	13.65	1.33	9.74
WTr	27	15.6-20.3	18.01	1.24	6.89
WTa	27	16.3-20.9	18.57	1.30	7.00
Medvezhiya					
GL	15	27.4-31.9	29.17	1.35	4.97
LaLTr	15	15.3-18.9	17.02	0.88	5.17
LiLTr	15	14.5-17.2	15.73	0.79	5.02
LaLTa	15	10.0-14.2	11.76	1.26	10.71
LiLTa	15	9.7-15.7	12.60	1.44	11.43
WTr	15	15.5-18.6	17.04	0.89	5.22
WTa	15	15.6-19.9	17.49	1.32	7.55

TABLE 9

Measurements of the m3 in *Ursus spelaeus*

m3	n	OR	m	SD	CV
Goyet B4					
GL	29	24.9-32.4	28.70	2.12	7.39
LTa	15	11.9-16.2	14.77	1.50	10.16
GW	26	17.2-22.1	19.87	1.27	6.39
WTa	27	15.6-21.2	18.66	1.57	8.41
Odessa					
GL	100	21.0-31.4	27.33	2.10	7.68
LTa	100	8.1-16.7	12.86	1.45	11.28
GW	99	17.5-22.7	19.91	1.24	6.23
WTa	99	14.1-22.0	18.79	1.48	7.88
Arcy-sur-Cure					
GL	21	23.8-29.5	27.13	1.47	5.42
LTa	21	10.0-14.7	12.44	1.25	10.05
GW	21	17.1-20.8	19.04	0.96	5.04
WTa	21	15.6-20.6	18.22	1.38	7.57
Eiros					
GL	12	25.2-30.1	27.20	1.78	6.54
LTa	12	10.6-14.6	12.45	1.40	11.24
GW	12	17.4-21.0	19.32	1.17	6.06
WTa	12	14.8-20.3	17.29	1.65	9.54
Niedzwiedzia					
GL	20	24.1-31.0	27.28	1.94	7.11
LTa	20	11.5-17.1	14.40	1.68	11.67
GW	20	17.5-21.2	19.32	1.05	5.43
WTa	19	16.8-20.5	18.23	1.08	5.92
Medvezhiya					
GL	21	21.5-29.7	25.31	2.17	8.57
LTa	21	10.4-20.2	16.15	1.92	11.89
GW	21	15.7-20.5	18.46	1.30	7.04
WTa	21	13.3-19.2	16.74	1.62	9.68

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