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Cave bear (*Ursus spelaeus*) from Chamber B of the Goyet Cave in Belgium

Gennady F. Baryshnikov, Mietje Germonpré & Svetlana V. Baryshnikova

ABSTRACT. The morphometric characteristic of skulls and cheek teeth is given for the cave bear (*Ursus spelaeus*) from the Late Pleistocene cave locality Goyet (Chamber B) in Belgium. The sexual distribution of the adult skulls shows them to belong to females; at the same time, data on the upper canines demonstrates approximately equal number of males and females. The gender analysis of the lower canines reveals almost double predominance of females against males. The study of the canine dimensions indicates that males were nearly 30% as large as females, which markedly exceeds the difference in size between genders in the brown bear (*U. arctos*). The mortality profile demonstrates prevalence of young and old individuals. Measurements of cheek teeth in the young and subadult bears exceed, on the average, those in adults, suggesting that predominantly males died in the younger age groups. The analysis of cheek teeth from the Goyet Cave reveals peculiarity of the sample in upper teeth P4 and M2, which resemble in the parameters those of the dentally less specialized ancestral species *U. deningeri*. This peculiarity may be explained by the diet of *U. spelaeus* in this region situated near the Pleistocene Ice Sheet, where poor vegetation provoked more consumption of animal food, probably shortly before entering hibernation.

KEY WORDS: *Ursus spelaeus*, Belgium, Late Pleistocene, morphometry, sexual composition, diet.

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Пещерный медведь (*Ursus spelaeus*) из зала Б пещеры Гойе в Бельгии

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РЕЗЮМЕ. Дана морфометрическая характеристика черепов и щечных зубов пещерного медведя (*Ursus spelaeus*) из позднеплейстоценового пещерного местонахождения Гойе (зал Б) в Бельгии. Распределение черепов взрослых животных по полу показало принадлежность их к самкам, в то время как данные по верхним клыкам дали приблизительно равное количество самцов и самок. Гендерный анализ нижних клыков открыл почти двукратное преобладание самок над самцами. Размеры клыков показали, что самцы пещерных медведей были примерно на 30% крупнее, чем самки, что заметно превышает разницу в размерах между полами у бурого медведя (*U. arctos*). Профиль смертности продемонстрировал преобладание молодых и старых особей. Размеры щечных зубов молодых и полувзрослых медведей в среднем превысили таковые взрослых медведей, что интерпретируется как гибель в ранних возрастных группах преимущественно самцов. Анализ щечных зубов из пещеры Гойе выявил своеобразие выборки по верхним зубам P4 и M2, которые напоминают по метрическим показателям таковые менее специализированного предкового вида *U. deningeri*. Эта особенность может объясняться диетой *U. spelaeus* в регионе, располагавшемся вблизи от плейстоценового ледникового щита, где сложились условия, определившие преобладание в питании пещерных медведей животных кормов, в первую очередь непосредственно перед зимней спячкой.

КЛЮЧЕВЫЕ СЛОВА: *Ursus spelaeus*, Бельгия, поздний плейстоцен, морфометрия, половой состав, питание.

Introduction

The cave bear (*Ursus spelaeus* Rosenmüller, 1794) was widely distributed in the Late Pleistocene of Europe, occurring in various plain and mountain forest, meadow-forest, and forest-steppe biotopes. Its fossil remains are especially frequent in areas where billowy relief provided diversity of landscapes, variety of food sources, and shelters suitable for winter dens. Periglacial conditions in the north of Europe were not favorable for the cave bear causing its absence or extremely scarce occurrence throughout the greater part of the East European Plain as well as in the British Isles. Therefore the data on the *U. spelaeus* from the caves of Belgium, which territory was adjacent to the south margin of the ice shield coming from Scandinavia in the Late Pleistocene, are of special interest.

The Goyet cave is situated in a limestone cliff in the valley of the Samson, a tributary of the Meuse River. The cave was excavated by Edouard Dupont in the 1860s. Unfortunately not much information is available on the stratigraphy and spatial distribution of the faunal remains. The Goyet Cave consists of a branching system of corridors and several chambers. Dupont (1873) subdivided the cave in three parts: Chamber A, B, and C. Chamber B lies behind Chamber A and is about 13 m long. According to Dupont (1873) only two bone horizons were present in Chamber B, with Horizon 4 occurring on top of Horizon 5. AMS radiocarbon dates available for these horizons indicate that they were formed during the Pleniglacial (Peigné *et al*., 2009). The cave bear assemblages from Goyet resulted from the accumulations of remains from bears that died in the cave during successive hibernations. These hibernations could have occurred yearly or were separated by varying time spans, during which occupations by humans or other carnivores could have taken place. It can be presumed that the formation of the cave bear assemblages at Goyet took at least several centuries and probably several thousands of years. Cave bear assemblages from Chamber B, Horizons 4 (B4) and 5 (B5) contain several articulated skeletal parts, high frequencies of complete postcranial bones and a large number of remains of cubs of less than one year old. These characteristics can, at least partly, be explained by the more protected position of Chamber B, which is located deeper inside the cave. The assemblage B4 is a male dominated assemblage, with a high frequency of remains from prime aged males, based on the presence of unworn male canines. Cave bear assemblage B5 is a female dominated assemblage. In both assemblages gnawing marks of the bear bones by carnivores are rare, but several large puncture marks on cave bear bones can be ascribed to bears (Germonpré & Sablin, 2001; Germonpré, 2004).

The focus of the present study lies in the description of the skull and dental remains from cave bear assemblage B5. The material is housed in the Department of Paleontology, Royal Belgian Institute for Natural Sciences in Brussels (RBINS).

Material and methods

For this study, 11 skulls, 5 mandibles, 39 canines, and 198 cheek teeth of cave bears from Chamber B, Horizon 5 of Goyet Cave, were metrically examined. The cranial material from Chamber B, Horizon 4 of this cave was also studied. As a reference material, the data on teeth of the cave bear from the Late Pleistocene cave sites in Germany: Höhlenstein, Charlotten, and Sibyllen (coll. Staatliches Museum für Naturkunde, Stuttgart), Steeden (coll. Naturwissenschaftliche Sammlung, Museum Wiesbaden), Zoolithen (coll. Institut für Paläontologie, Erlangen), and Rübeland (coll. Museum für Naturkunde, Humbold-Universität, Berlin), and in Poland: Wierzchowska Górna, Nietoperzowa, and Niedźwiedzia (coll. Institute of Systematics and Evolution of Animals, Krakow) were used. Each sample includes as many as 10 specimens.

The skulls and teeth were measured with calipers to 0.5 mm precision according to published schemes (Baryshnikov *et al*., 2005; Baryshnikov, 2006, 2007).

Kurtén (1955) revealed that cave bears were highly sexually dimorphic and this dimorphism is particularly apparent in the dimensions of the canines. He argued that lower canine breadths in cave bears from cave sites of Mixnitz and Odessa were bimodal with modes at 16–17 mm and 21–22 mm, and with a little overlap between these distributions. Debeljak (2004, 2007) also obtained for Potočka zijalka and Mokriška jama in Slovenia a bimodal distribution of upper and lower canine breadths and on the basis of this distribution classified specimens smaller than 18 mm as female and those larger than 18.5 mm as male. Canines from the Krapina rockshelter in Croatia were attributed to males, having breadth greater than 17 mm and length greater than 23 mm (Miracle, 2011). Modes and extent of the development of sexual dimorphism can vary in different populations of cave bear (Grandal d'Anglade & López-González, 2005).

The reliable criterion for the sexing of canines is their width at the level of the lower margin of enamel. In the upper canines, when the crown width exceeds 19.0 mm, the teeth are assigned to males. Upper canines with a crown width less than 17.0 mm are ascribed to females. Lower canines with a width less than 17.0 mm are referred to females; those with a width of more than 18.0 mm are considered to belong to males.

The age distribution of the cave bear material was based on the wear pattern and the development of the root of each cheek tooth. The teeth were subdivided with regard to these characteristics into four age groups: I) juvenile: tooth rootless or roots with open pulp canals; II) subadult: tooth unworn and root canals close; III) prime adult: tooth inconspicuously or moderately worn; IV) old adult: tooth heavily worn. The attribution of the two latter groups is provisional, since the extent of the tooth crown wear is determined not only by the

Table 1. Size of female skulls from Goyet Cave, assemblage B5.

Measurements, mm	Chamber B5						
	2167, ad.	2168, sen	2169, sen	2172, ad	2173, ad	2174, sen	2175, ad
1	413	412	422	398		405	412
2			390	371			
3			365.5	ca347.5			
4	225		235.6	217.2		204.8	231
5	210.1		208.6	199.7	216.4	200.7	204.1
6			162.4	146.6	158	152.5	156.2
7						202	
8	149	142.4	154	153.1	158.4	150.7	150.7
9	84.2	87.4	81.0	84.0	83.7	86.8	83.6
10	250		ca244.5				231.4
11	111		105				98
12	88.2		84.0		80.2	86.3	79.9
13		93	104.6	ca93.5	102.4	98.7	97.2
14			78.8	82.5			
15			187.4				
16			47.1			43.2	
17		106.6	99.3	99.6		103.9	96.5
18	86	89	94.4	87.2		93.5	88.5
19			48.1	50.4	49.2		
20			115	116.5			
Canine							
C1 length	16.7	18.1	18.9	18.5	18.8	19.7	19.4
C1 width	14.4	15.3	15.7	14.2	15.4	15.7	16.2

Legend to measurements: 1 — total length, 2 — condylobasal length, 3 — basal length, 4 — upper neurocranium length, 5 — facial length, 6 — "snout" length, 7 — median palatal length, 8 — length of teeth row C1–M2, 9 — length of cheek teeth row P4-M2, 10 — zygomatic breadth, 11 — greatest neurocranium breadth, 12 — least breadth of skull, 13 — least breadth between the orbits, 14 — greatest breadth of the occipital condyles, 15 — greatest mastoid breadth, 16 — palatal breadth near choana, 17 — greatest palatal breadth, 18 — breadth at the canine alveoli, 19 — greatest inner height of the orbit, 20 — skull height.

individual age of the animal but also by the peculiarities of the consumed food.

Results

Skull. Skulls and cranial fragments from assemblage B5 and B4 of Goyet Cave belong to cave bears of both sexes and different individual age. Three skulls from assemblage B4 are ascribed to adult males (total length exceeds 470 mm; C1 width exceeds 22.5 mm), whereas there are no such specimens in assemblage B5. Skulls of adult females were found in both assemblages: two in B4 (total length less than 430 mm; C1 width less than 16.7 mm) and seven in B5 (total length less than 422 mm; C1 width less than 16.2 mm). Thus, assemblage B4 contains skulls of both males and females (sex ratio 3:2), whereas assemblage B5 incorporates only adult females (sex ratio 0:7). Dimensions of the specimens sexed demonstrate no difference from those of *U. spelaeus* in Zoolithen Cave in Germany (Baryshnikov, 2007) (Tables 1, 2).

In assemblage B5 three skulls are present from subadult bears. Of these, two skulls are from males (RBINS 2170, 2178) with C1 width equal to 21.5 mm and one with undetermined sex (RBINS 2176) (Table 3). Cranial sutures in RBINS 2170 (Fig. 1) are not fully obliterated, the mastoid processes are weakly developed, and the alveoli of the P1 are present, which is rarely observed in *U. spelaeus*. These characteristics are comparable to those of recent brown bears (*Ursus arctos*) of about 4–5 years old. The apices of lingual tubercles of M1 in RBINS 2170 are worn (Fig. 2); at the same time, these tubercles in brown bears of similar individual age are not so markedly erased. In RBINS 2178, this tooth is also worn along the lingual margin, although other cheek teeth of this specimen show no clear facets of wear.

One skull from assemblage B5 and three skulls from assemblage B4 belong to juveniles whose sex is difficult to establish (Table 3). RBINS 2210 and RBINS 2193 have canines and upper molars M2 that are not yet fully erupted. The specimen RBINS 2208 is somewhat younger, preserving deciduous canine alveoli and having apices of permanent canines not yet erupting.

Mandibles. Three adult mandibles from assemblage B5 (RBINS 2168, 2172 left and 2172 right) can be ascribed to females (length p4–m3 varies from 87.8 mm to 94.8 mm, c1 width less than 15.0 mm) (Table 4), while in the assemblage B4, all adult mandibles seem to belong to males (length p4–m3 varies from 103.0 mm to 114.6 mm, c1 width more than 22.2 mm). This result

Table 2. Size of skulls from Goyet Cave, assemblage B4.

Measurements, mm	Males			Females	
	2195, sen	2201, ad	2207, sen	2192, sen	2200, sen
1		477	ca470		430
2		442		394	400
3				372	
4		255.5	232		222.3
5		237.2	260	211.3	225.1
6		178.8	182.3	158.8	165.6
7		239.1	266	223	232.8
8	174.3	161.2	184	154	169.2
9	98.7	95.8	98.1	81.3	96.5
10			330		ca250
11		118.9		104.5	105.5
12		85.8		75.5	82.7
13		107.2	118.9	105.4	85.8
14				78.6	76
15			ca287	185.3	178
16		45	59.8		44.5
17	112.7	106.9	115.9	107.4	109.1
18	108		124	98.8	103.3
19				50.1	43.5
20				127	121.4
Canine					
C1 length	27.0		26.8	19.7	23.6
C1 width	22.6		22.8	15.8	16.7

Table 3. Size of immature cave bear skulls from Goyet Cave.

Measurements, mm	Subadults			Juveniles			
	Assemblage B5			Assemblage B5	Assemblage B4		
	2170	2176	2178	2177	2193	2208	2210
1	405						280
2	396						
3	368						
4	207.5	213.5			147	128.1	139
5	222.3		237.8	187.5			161.5
6	164		166.9	137.0			124
7	213.6		224.4	180.3			151.5
8	158.1		153				121.7
9	99.0		89.1				91.2
10	218.8				ca165		
11	109.2	106.4		105.6	105.3	99.8	103.3
12	77.0	73.9		72.7	71.7	68.3	71.5
13	79.8	76.4		64	58.9	52.7	61.7
14	86.7						
15	174.1				116.5	102	
16	42.9	42.6	49.3			78.4	32.4
17	103.3		113.5				
18	94.5		99.5	ca83			
19	50.8				40.5		
20	115.5					74.6	
Canine							
C1 length	27.6		25.7				
C1 width	21.5		21.5				

Figure 1. *Ursus spelaeus*, skull (RBINS 2170), from Goyet Cave, assemblage B5; lateral (A) and basal (B) views.

confirms the sex ratio in both horizons, which was established on the basis of cranial material.

The left mandible RBINS 2170 is referred to the same male subadult individual as the skull, being marked with the same number (Fig. 3). Its horizontal portion is low and its cheek teeth unworn (Fig. 4); the alveolus of the p1 is absent. The right mandible RBINS 2170, on the contrary, is characterized with a shorter tooth row, allowing its attribution to another individual. Both mandibles of specimen RBINS 2172 (right and left) are referred to the same individual as the skull, marked by the same number.

Sexual composition. As noted above, the examination of the cranial material revealed the presence of remains from adult females in assemblage B5. Males are represented only by subadult individuals. These data may be supplemented by the results of the crown width of the canines (isolated as well as preserved in jaws).

The sample of upper canines is rather small (n=15). In eighth specimens, the width exceeds 19 mm, suggesting that these teeth belong to males. The seven canines that have a width less than 17 mm are ascribed to females. Therefore, judging by the size of the upper canines, the number of females is nearly equal to that of males, which is pronouncedly different from the sexual ratio calculated on the basis of cranial fragments. This implies the skulls of females and subadults to be preserved in the assemblage B5, whereas skulls of adult males were destroyed. The explanation of this state may be that females and juveniles were the last to perish in the cave, while skulls of males that died earlier were trampled.

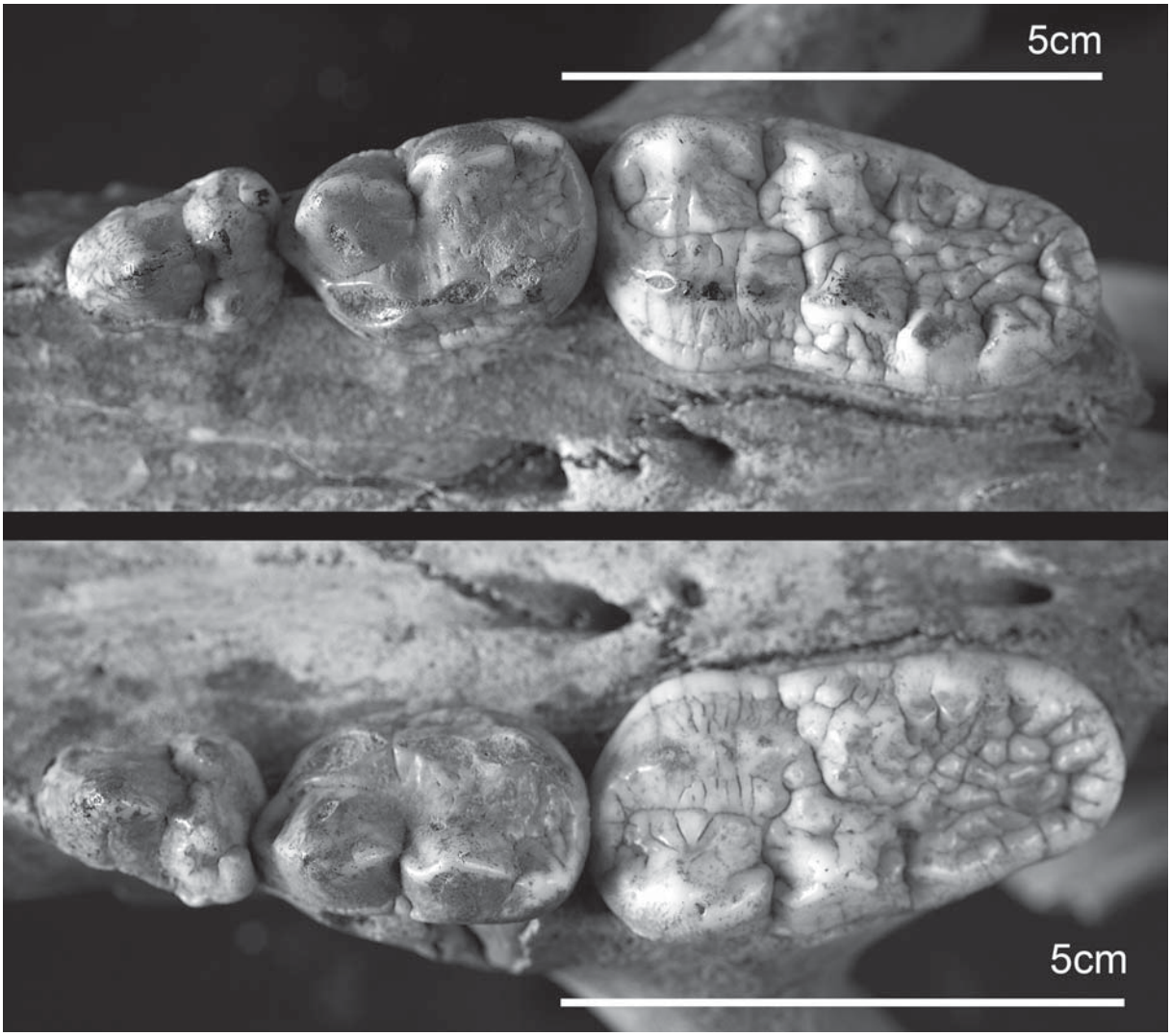

Figure 2. *Ursus spelaeus*, left (above) and right (below) upper cheek teeth rows, left and right (RBINS 2170), from Goyet Cave, assemblage B5; occlusal view.

Table 4. Size of mandibles from Goyet Cave.

Measurements, mm	Assemblage B5					Assemblage B4			
	Females			Subadults		Males			Subadults
	2168, ad	2172, sin	2172, dex	2170, sin	2170, dex	2201, ad	2835, sen	2207, sen	2210
21	272.1			279			360	238	210.5
22	275.9	279		276.1			335	232	208
23	160	169.7	167.4	172.5	155.5	197.5	207	200	145.3
24	87.8	94.8	93.0	105.9	101.1	114.6	110.4	103	103.9
25		126.4	126.5		117.8			145	
26	52.7	62.8	59.9	53.3	53.9	65.1	74.5	73.5	38.1
27	49.7	59.0	59.8	58.6		67.7	72.6	62	47.2
Canine									
c1 length		20.8	19.1	25.4		31.9	29.6	27.1	24.1
c1 width		14.6	15.0	20.0		24.6	23.9	22.2	

Legend to measurements: 21 — total length, 22 — length between the angular process and infradentale, 23 — length of c1–m3 row, 24 — length of p4–m3 row, 25 — height of the vertical ramus, 26 — height of the mandible behind m1, 27 — height of the mandible in diastema.

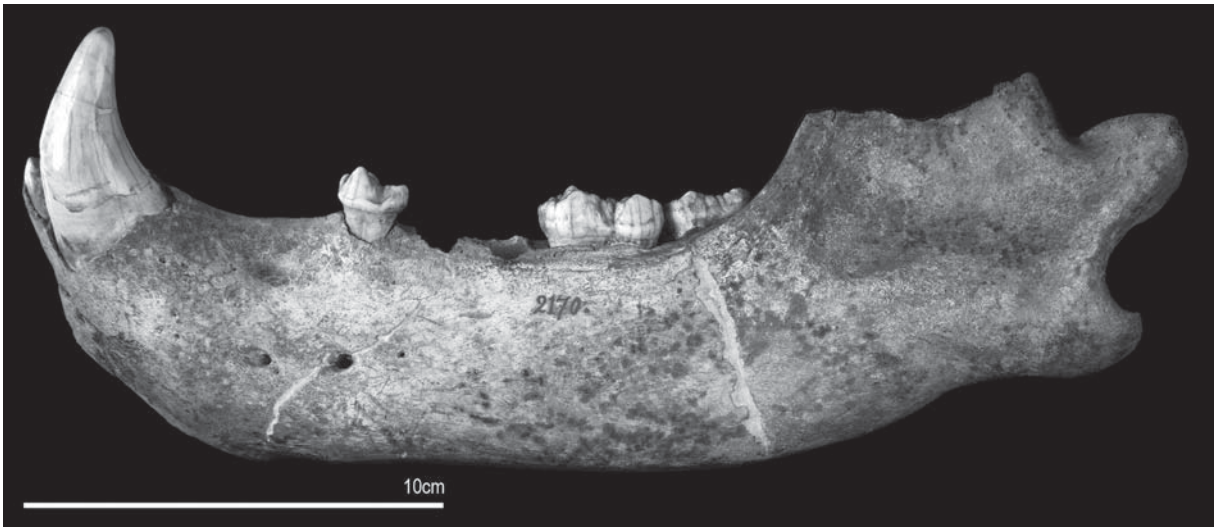

Figure 3. *Ursus spelaeus*, left mandible (RBINS 2170), from Goyet Cave, assemblage B5; lateral view.

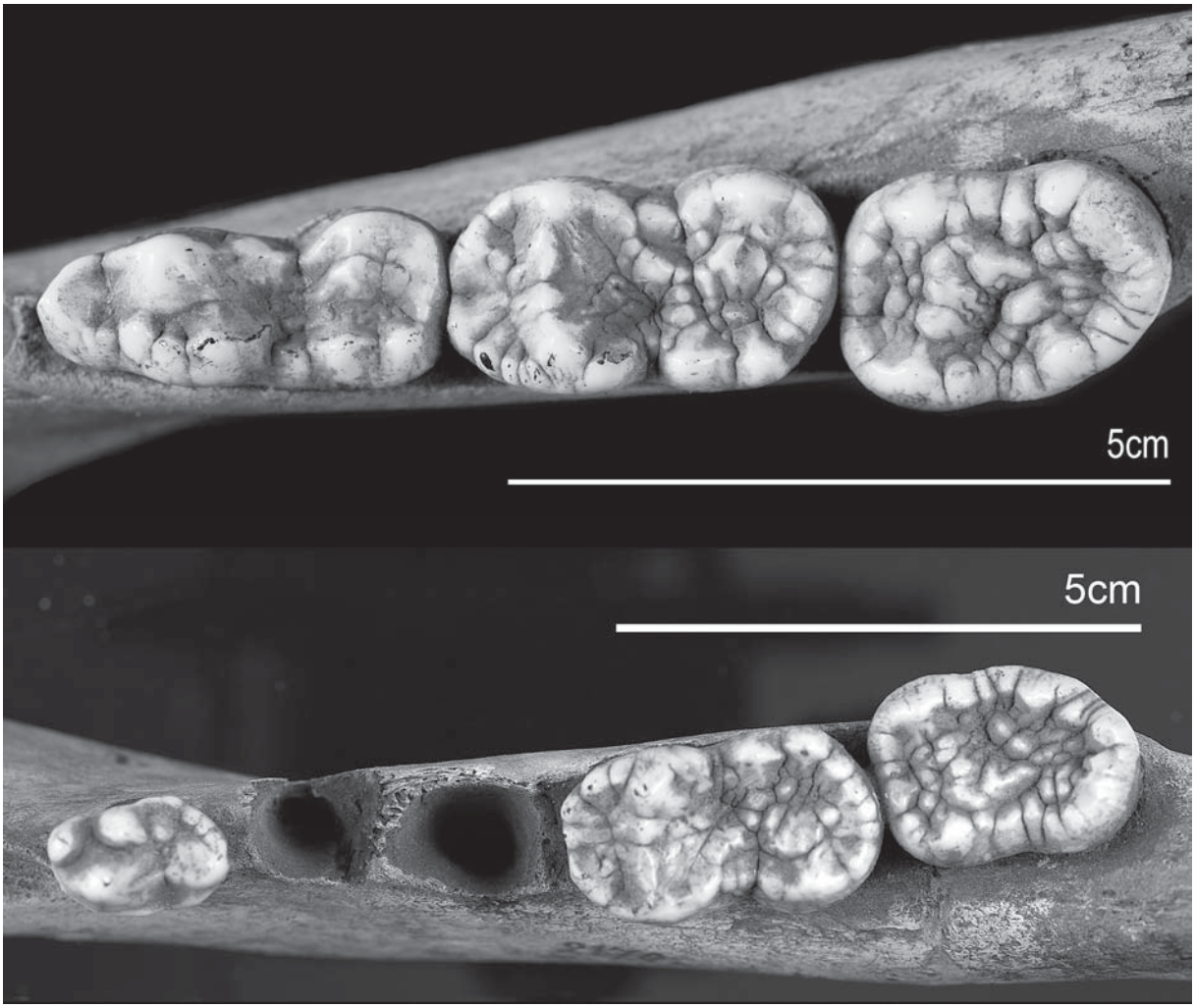

Figure 4. *Ursus spelaeus*, right (above) and left (below) lower cheek teeth rows (RBINS 2170), from Goyet Cave, assemblage B5; occlusal view.

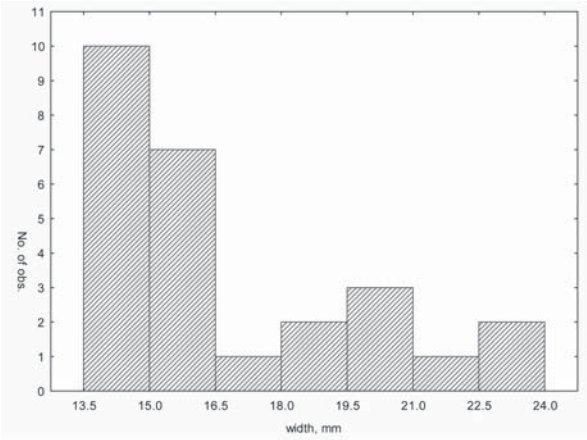

Figure 5. Frequency distribution of lower canine width of *Ursus spelaeus* in Goyet Cave, assemblage B5.

The distributional frequency of width of the lower canine (n=26) is bimodal (Fig. 5). Most specimens possess a width less than 16.5 mm and are therefore referred to females (n=17). Three robust canines whose width exceeds 18 mm were considered to belong to males. One specimen could not be sexed. Therefore, the analysis of the dimensions of the lower canine revealed that females are approximately twice as numerous as males.

Thus the morphometric data permit to attribute the fossil remains of the adult cave bears from assemblage B5 predominantly to females.

The ratio between average values of the width of lower canine in males and females of *U. spelaeus* from assemblage B5 constitutes 1.35 (n=24), which is comparable to that in the cave bear from Zoolithen Cave in Germany (1.34, n=25). It may be, therefore, hypothesized that males of cave bear were approximately 30% as large as females. In the extant brown bear *U. arctos*, this index is markedly lower (1.19, n=158), i.e. difference in size between sexes in cave bear was more pronounced than in the brown bear.

Mortality composition. To establish the mortality profile of the cave bear in the assemblage B5, following permanent teeth: the upper molar M2 and the lower molar m2, which dominate in the samples of upper and lower cheek teeth respectively, were examined. The M2 teeth were distributed into following age groups: I: 13; II: 6; III: 8; IV: 15. This distribution indicates a predominance of juveniles and old adults, whereas subadults and prime adults constitute only one third of the sample. A different distribution is found in the lower m2 teeth: I: 12; II: 9; III: 7; IV: 4. This sample consists mainly of the teeth of immature bears that represent two thirds of the m2 sample. Nevertheless, the data on both molars indicate that a considerable number of juveniles died in the Chamber B, Horizon 5 during their second overwintering.

On the basis of aforementioned subdivision, we are able to hypothesize the gender of the immature animals. For this purpose, means of M2 and m2 length were calculated for each age group, except for the group of the old adults that possess heavily worn teeth. The average length in the different age groups is as follows: I: 42.7 mm; II: 45.8 mm; III: 42.2 mm for the M2 and I: 29.8 mm; II: 29.5 mm; III: 26.7 mm for the m2. In both cases, the molars in the juvenile and subadult groups are longer than those in the prime adults (with exception of the group I for M2). Since cheek teeth of males are on the average longer than those of females (Baryshnikov *et al*., 2003), the obtained data allow to suggest that perished young animals from the age groups I and II were predominantly males.

Dentition. The metric data of the upper (P4, M1, M2) and lower (p4, m1, m2, m3) cheek teeth from assemblage B5 are shown in Tables 5–11. These dimensions were compared with tooth measurements of *U. spelaeus* from assemblage B4, as well as with those from the caves of Germany (Höhlenstein, Charlotten, Sibyllen, Steeden, Zoolithen, and Rübeland) and Po-

Table 5. Size of upper premolar P4 from Goyet Cave, assemblage B5.

Measurements, mm	Greatest length	Length of paracone	Greatest width	Least distance between frontal ridge of protocone and caudal side of crown
n	24	23	24	24
min	16.7	10.3	11.3	12.6
max	22.0	14.3	16.1	18.2
M	18.42	11.96	13.26	14.73
SD	1.47	1.14	1.36	1.44

Table 6. Size of upper molar M1 from Goyet Cave, assemblage B5.

Measurements, mm	Greatest length	Length of frontal part	Length of caudal part	Length of paracone	Length of metacone	Greatest width
n	35	35	35	35	35	35
min	24.5	11.8	12.0	8.9	8.2	16.9
max	30.2	14.9	15.9	11.6	10.9	20.7
M	26.86	13.28	13.47	10.09	9.39	18.70
SD	1.29	0.73	0.80	0.63	0.66	1.07

Table 7. Size of upper molar M2 from Goyet Cave, assemblage B5.

Measurements, mm	Greatest length	Length of paracone	Length of metacone	Greatest width	Width through hypocone
n	41	41	41	41	41
min	37.4	11.4	9.2	18.9	15.6
max	49.5	14.8	13.5	24.7	23.4
M	42.55	12.99	11.04	21.39	18.77
SD	2.69	0.87	1.22	1.33	1.58

Table 8. Size of lower premolar p4 from Goyet Cave, assemblage B5.

Measurements, mm	Greatest length	Greatest width	Distance between peak of paraconid and peak of metaconid
n	14	14	14
min	12.8	8.4	2.9
max	17.2	11.6	5.2
M	14.30	9.43	4.13
SD	1.26	0.83	0.76

Table 9. Size of lower molar m1 from Goyet Cave, assemblage B5.

Measurements, mm	Greatest length	Length of trigonid	Length of entoconid 1	Length of entoconid 2	Width of trigonid	Width of talonid	Least width in middle part
n	24	24	22	22	24	24	24
min	25.2	15.7	3.7	3.7	9.9	12.4	9.5
max	32.3	20.7	6.5	6.5	13.1	15.5	13.0
M	28.77	18.14	4.85	4.90	11.43	13.86	11.23
SD	1.68	1.20	0.77	0.67	0.91	0.89	0.90

Table 10. Size of lower molar m2 from Goyet Cave, assemblage B5.

Measurements, mm	Greatest length	Labial length of trigonid	Lingual length of trigonid	Labial length of talonid	Lingual length of talonid	Width of trigonid	Width of talonid
n	32	32	32	32	32	32	32
min	25.2	14.0	11.7	9.0	9.6	14.8	14.3
max	35.4	18.8	17.9	14.9	15.3	21.1	23.2
M	28.82	16.69	14.71	11.03	12.19	16.99	17.51
SD	1.98	1.11	1.12	1.05	1.16	1.21	1.58

Table 11. Size of lower molar m3 from Goyet Cave, assemblage B5.

Measurements, mm	Greatest length	Length of talonid	Greatest width	Width of talonid
n	28	28	28	28
min	21.8	8.3	16.2	15.0
max	30.5	13.5	20.0	19.9
M	24.97	11.23	18.02	17.33
SD	1.72	1.47	0.99	1.25

land (Wierzchowska Górna, Nietoperzowa, and Niedźwiedzia).

The morphology of the cheek teeth in assemblage B5 (Fig. 2, 4) is characteristic of *U. spelaeus* (Rabeder, 1999). For example, the metaconid of the lower carnassial tooth m1 consists of two or three cusps of different size, whereas the entoconid of this tooth is most often formed by two robust and well defined cusps (Fig. 6).

Baryshnikov (2006) carried out morphometric analysis of the cave bear cheek teeth from various localities of Europe and Caucasus, which provided a possibility for distinguishing *U. spelaeus* and *U. deningeri*. These analyzed measurements were supplemented by the material from assemblage B5 and B4 in Goyet, which made it possible to run a discriminant analysis for the combined sample. As a result, the lower cheek teeth

Figure 6. *Ursus spelaeus*, lower carnassial tooth m1 from Goyet Cave, assemblage B5 (coll. RBINS); lingual view.

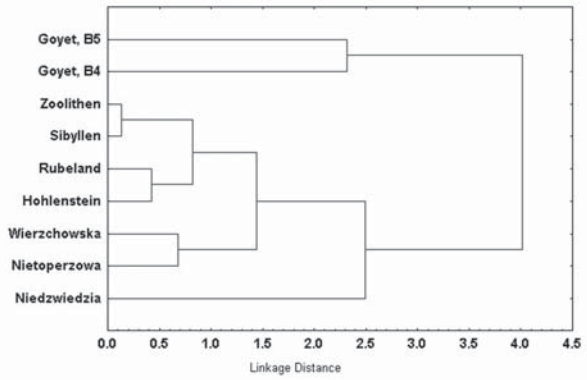

Figure 7. Hierarchical tree plot for P4 of *Ursus spelaeus* from different localities according to squared Mahalanobis distances.

(p4, m1, m2, m3) and upper molar M1 from Goyet were referred to *U. spelaeus*, whereas the teeth P4 and M2 were placed within the ancestral species *U. deningeri*.

The dendrogram of similarity, built on the basis of the dimensions of upper premolar P4 from Goyet Cave and from localities of southern Germany and Poland, shows that samples from both horizons of Goyet form a single cluster, which is well differentiated from another cluster (Fig. 7). Their divergence is based on the paracone length. The average value of this parameter constitutes 11.96 mm (n=23) for the assemblage B5 and 12.17 mm (n=27) for the assemblage B4, which corresponds to that in *U. deningeri* (11.94 mm, n=159) (Baryshnikov, 2006). Other examined samples of *U. spelaeus* were found to have markedly longer paracone: 13.19 mm (n=37) in Rübeland and 13.23 mm (n=62) in Zoolithen Cave in Germany, and 13.45 mm (n=30) in Nietoperzowa Cave in Poland.

The analysis of variance (ANOVA/MANOVA) carried out for four measurements of P4 indicates that samples from assemblages B5 and B4 in Goyet Cave,

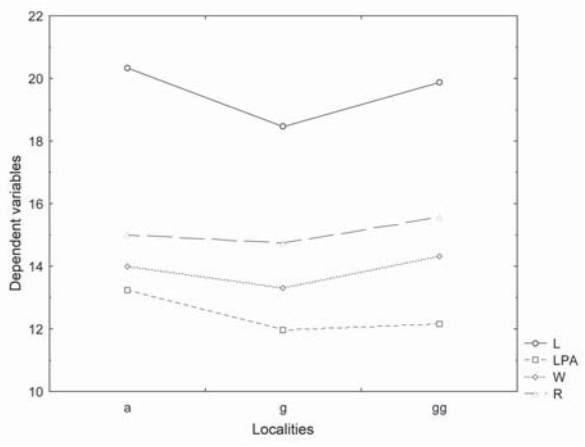

Figure 8. Plot of means for four measurements of upper premolar P4.
L — greatest length, LPA — length of paracone, W — greatest width, R — least distance between frontal ridge of protocone and caudal side of crown.
Samples: a — localities of southern Germany and Poland; g — Goyet Cave, assemblage B5; gg — Goyet Cave, assemblage B4.

being similar to each other, are distinctly different from the samples from localities of southern Germany and Poland by average value of the paracone length (Fig. 8). The use of criterion Tukey HSD for unequal N (Spjøtvoll-Stoline test) revealed reliable differences between samples from Germany/Poland and assemblage B5 ($p< 0.000036$) and assemblage B4 ($p< 0.000120$). At the same time, a difference in the tooth greatest length is observed only in the sample from assemblage B5 ($p< 0.000055$). The sample from assemblage B4 has no difference from those of Germany and Poland, being reliably distinguished from the sample from assemblage B5 ($p< 0.002826$).

The peculiarity of dentition in the cave bear from Goyet may be a result of a local adaptation substantiated by the difference in diet in animals belonging to geographically distanced populations of *U. spelaeus*. The similar peculiarities are observed in different subspecies of the recent *U. arctos*. For example, the mean length of paracone of omnivorous brown bear from Eastern Europe (*U. a. arctos*) constitutes 9.39 mm (n=51), whereas in the brown bear from Tibet (*U. a. pruinosus*) consuming abrasive matters (rough plants, picas and rodents excavated from the soil) the paracone of P4 is clearly longer (11.46 mm, n=23).

Discussion and Conclusion

The study of the cave bear assemblages B4 and B5 of the Goyet Cave revealed the accumulation of remains of animals that perished in the cave during hibernation. This may be concluded from the prevalence of females as well as from the presence of bones and teeth belonging to subadults and juveniles in the cave. Such gender and age compositions suggest that Chamber B was exploited as a winter den by females with cubs. The

robust tooth size in the immature groups suggest a male prevalence, based on the fact that the cheek teeth of males in the cave bears are on the average longer than those of females (Baryshnikov *et al*., 2003). Subadults from preceding litters might have hibernated with their mother with her younger cubs in order to escape predators, including adult male bears. Skull 2208 is presumably from an animal that perished in the cave during its second overwintering, as inferred from the presence of the alveoli of its deciduous canines. The associated finding of skulls and mandibles belonging to the same individual testifies that several of the cave bears perished and were buried in Chamber B, since the mandible detaches as a rule early from the skull during the decay of the carcass and is easily transported by water or removed by animals in the cave. The associated presence of skull and lower jaws indicates that only limited disturbance occurred after the animals expired, permitting the preservation of associated skeletal parts. Their skulls and mandibles were not trampled upon nor removed by cave visitors. This exceptional preservation probably can be explained by the protected location of Chamber B that probably limited the number of visitors in this part of the cave.

The long hibernation obviated the necessity to store big fat supplies; therefore, weakened individuals, accumulating not enough fat, perished in the cave by starvation. The ratios of nitrogen stable isotopes ($d^{15}N$) in bone collagen of adult cave bears from well dated sites point to a vegetarian diet for this species (Bocherens *et al*. 1994, 2007). It was earlier hypothesized (Baryshnikov *et al*., 2003) that the tooth proportions in *U. spelaeus* are correlated with peculiarities of its diet. In addition, the peculiarity of the reduced P4 paracone in the cave bear from Goyet Cave is explained, in our opinion, by its diet. In the periglacial conditions, not favorable for the cave bear, the local cave bears might have consumed more animal food, which did not obviate the necessity for developing a robust paracone for processing rough plants.

Hence, we propose that this structure of the upper premolar P4 can be considered to be an indicator of a lesser consumption of plant food by the cave bears from Goyet Cave, in comparison with cave bears in other parts of Europe. Furthermore, the very pronounced early wear of the M1 in several skulls testifies that these cave bears fed on more coarse food than recent brown bears, on the basis of a less marked wear in brown bears of a similar age. The Belgian cave bears could have relied on other food sources especially in the weeks just preceding the beginning of the hibernation. Such a change in diet has also been postulated on the basis of a microwear analysis (Peigné *et al*., 2009). In the severe conditions of the periglacial zone, cave bears probably turned to consuming nutritious animal food, similar to the strategy used by the recent brown bears inhabiting the tundra of Northeast Asia (Chernyavskiy & Krechmar, 2001), especially shortly before their retreat to their dens. In addition to the present study on morphometric characteristics, the diet of a large number of cave bear individuals from Goyet is being analyzed based on stable isotopes. Preliminary data suggest that a difference exists between cave bears from northern Europe (i.e. Belgium, including Goyet) and those from southern Europe (i.e. southern France), the former populations showing a more negative $d^{13}C$ values than those of coeval herbivores compared to southern populations; on the contrary, cave bears from southern France exhibit lower $d^{15}N$ values than coeval ungulates. The cave bears from southern Germany follow more closely the isotopic pattern of the cave bears from southern France (Bocherens *et al*., 2007).

The large sexual dimorphism based on the canines and skulls, indicates that a noticeable difference in body size existed between male and female *Ursus spelaeus*, just as in large bovids and cervids. These ungulates are polygamous, with males fighting vigorously against other males for females. Cave bears, like recent brown bears, lived alone or in families (female with cubs). However, behavior of brown bears changes when in heat. In the forests of Eastern Europe, males and females live in pairs in the mating period, active and larger males occupying extensive territories and forcing the opponents (Pazhetnov, 1990). In Caucasus, bears can form mating groups including a female and male, and several rival males that occasionally fight with each other (Kudaktin & Chestin, 1993). Cave bears, judging from the development of the sexual dimorphism in size, could form larger mating aggregations, which probably was accompanied with stronger antagonism between males.

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