BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN

SCIENCES DE LA TERRE, 71: 209-233, 2001
AARDWETENSCHAPPEN, 71: 209-233, 2001

The cave bear (*Ursus spelaeus*) from Goyet, Belgium
The bear den in Chamber B (bone horizon 4)

by Mietje GERMONPRÉ & Mikhail V. SABLIN

GERMONPRÉ, M., & SABLIN, M. V., 2001. – The cave bear (*Ursus spelaeus*) from Goyet, Belgium. The bear den in Chamber B (bone horizon 4). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre,* **71** : 209-233, 3 pls., 10 figs.,10 tables, Bruxelles-Brussel, May 15, 2001. – ISSN 0374-6291.

Abstract

The Dupont collections curated at the Royal Belgian Institute of Natural Sciences contain a large bone assemblage from Chamber B, horizon 4 of the third cave of Goyet (Belgium). This assemblage dates from the Weichselian (AMS date: 35.470 +780-710 years BP). Ninety eight percent of the remains are from *Ursus spelaeus*. The presence of several skeletons and articulated body parts, and the low frequency of gnawing traces and charriage-à-sec indicate that the carcasses were only slightly disturbed. Based on the eruption sequence of the teeth, cubs perished at or soon after birth, at an age of two and a half months and at an age of six-seven months old, when they were leaving the cave at the end of the winter rest. In Belgium, the timing and length of the dormancy period and the birth season varied according to the climatic conditions of the ice age. At Goyet, Chamber B, horizon 4, female cave bears probably began their winter rest in October, gave birth in November or December and left the cave in June.

Key-words: *Ursus spelaeus*, Weichselian, dormancy, dentition, age determination, mortality

Résumé

La collection Dupont de l'Institut royal des Sciences naturelles de Belgique contient un important assemblage osseux provenant de Goyet en Belgique (troisième caverne, Chambre B, niveau 4). Cet assemblage est daté du Weichselien (datation AMS: 35.470+780-710 ans BP). 98 % des restes appartiennent à *Ursus spelaeus*. La présence de plusieurs squelettes et d'ossements articulés de même que le peu de traces de morsures par des carnassiers ou de charriage-à-sec montrent que les cadavres ont été peu dérangés. La séquence de remplacement des dents indique que les oursons sont morts à la naissance ou juste après, quand ils avaient deux mois et demi et à la fin du repos hivernal quand ils avaient six-sept mois. En Belgique, le calendrier, la durée de l'hibernation et la période des naissances variaient en fonction des conditions climatiques de l'âge glaciaire. A Goyet (Chambre B, horizon 4) les femelles de l'ours des cavernes commençaient probablement leur hibernation en octobre, accouchaient en novembre ou en décembre et quittaient leur abri hivernal en juin.

Mots-clefs: *Ursus spelaeus*, Weichselien, hibernation, dentition, détermination d'age, mortalité

Introduction

At Goyet (50°26'44"N, 5°00'48"E) several caves are present which were excavated in 1868 and 1869 by Edouard Dupont. These caves are situated at an altitude of 130 m in a Carboniferous limestone cliff on the right bank of the river Samson close to the confluence with the river Strouvia (DUPONT, 1869, 1873, VAN DEN BROECK *et al.*, 1910; GERMONPRÉ, 1996, 1997) (Fig. 1). Cave number three, the richest one, is located 15 m above the Samson and oriented to the southwest. The cave is connected with the other caves by transverse galleries (DUPONT, 1873; RAHIR, 1908). An extensive historic overview of the research at the Goyet caves is given in ULRIX-CLOSSET (1975), OTTE (1979) and DEWEZ (1987).

Stratigraphy

DUPONT (1873) subdivided the cave in three parts: chamber A, B and C (Fig. 2). He described in total five bone bearing horizons inside the cave. The bones occur in clayey-sandy loam which DUPONT (*ibid.*) called "limon fluvial". The fossil yielding horizons are separated by sterile sediments. Fossil bones are present near the entrance as well as deeper in the cave. Mousterian and Upper Palaeolithic artefacts were found (ULRIX-CLOSSET, 1975). However, no detailed information on the stratigraphy was published by DUPONT (*ibid.*). The total thickness of the excavated layers is more or less 2 to 2.5 m as deduced from the sediment remains on the walls of the cavern.

Chamber A is about 26 m deep, 5 m wide and 3.8 m high. The entrance has a width of 3.8 m. The twilight zone stretches to the back of the chamber. DUPONT (1873) distinguishes four bone bearing horizons in this chamber. The lower one ("*le quatrième niveau ossifère*") is well developed only in the back of Chamber A, palaeolithic artefacts are lacking. The upper three bone horizons are concentrated near the entrance of Chamber A, and contain bones from human refuse and Upper Palaeolithic artefacts dating from the Aurignacian, Gravettian and Magdalenian (OTTE, 1979; LOPEZ BAYON *et al.*, 1997). However, the bear and hyena assemblages from these horizons were probably located more to the back of the chamber and have a different origin (GERMONPRÉ, 1996). It is not clear how the carnivores assemblages from these three horizons are interrelated. Chamber A was used by a population of cave bear at 38,770 years BP ago; cave hyenas occupied Chamber A at least during two phases at 35,000 years BP and 27,230 years BP (Table 1; GER-

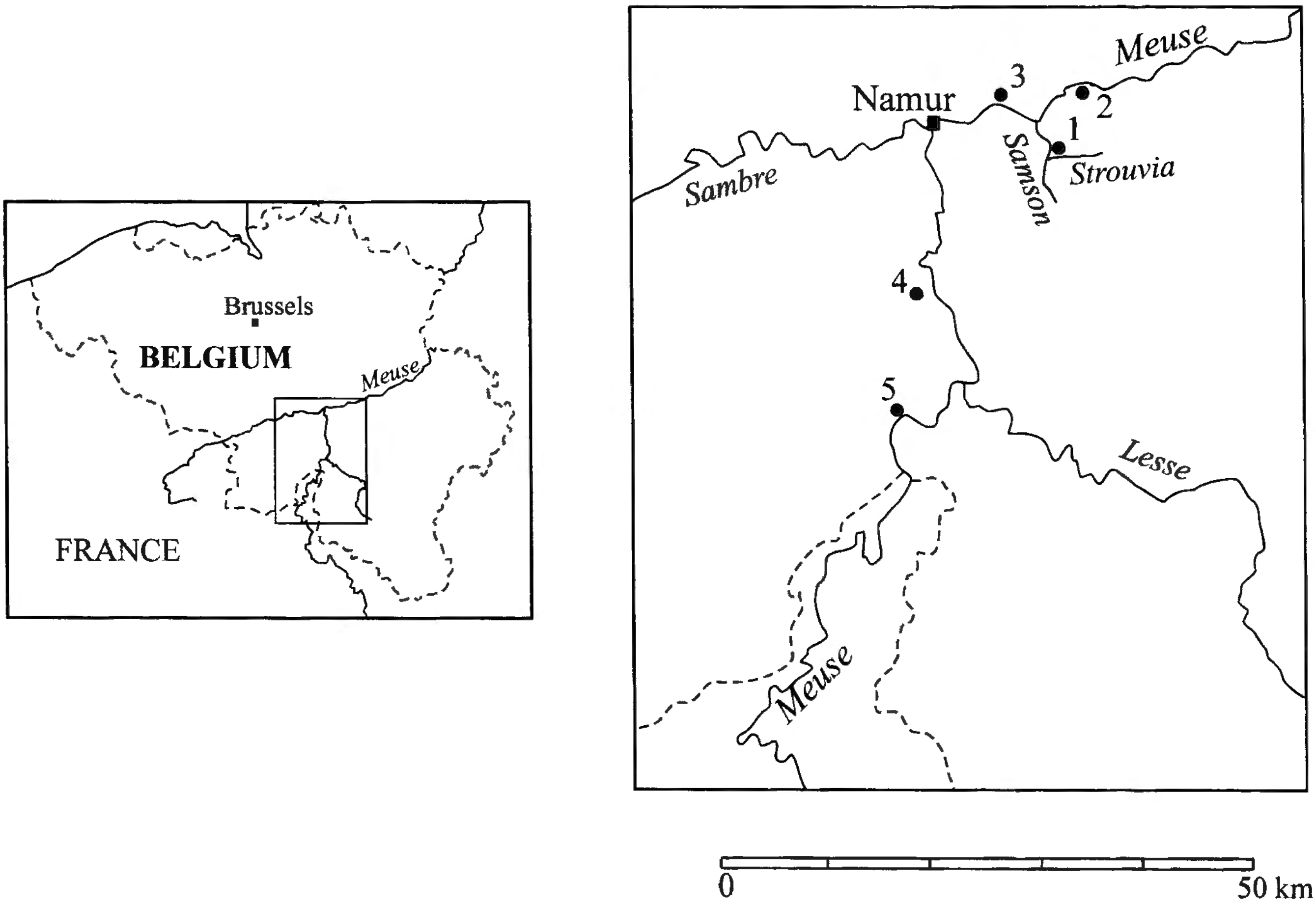


Fig. 1 — Location of the Belgian sites discussed in the text: 1: Goyet, 2: Sclayn, 3: Marche-les-Dames, 4: Montaigle, 5: Hastière.

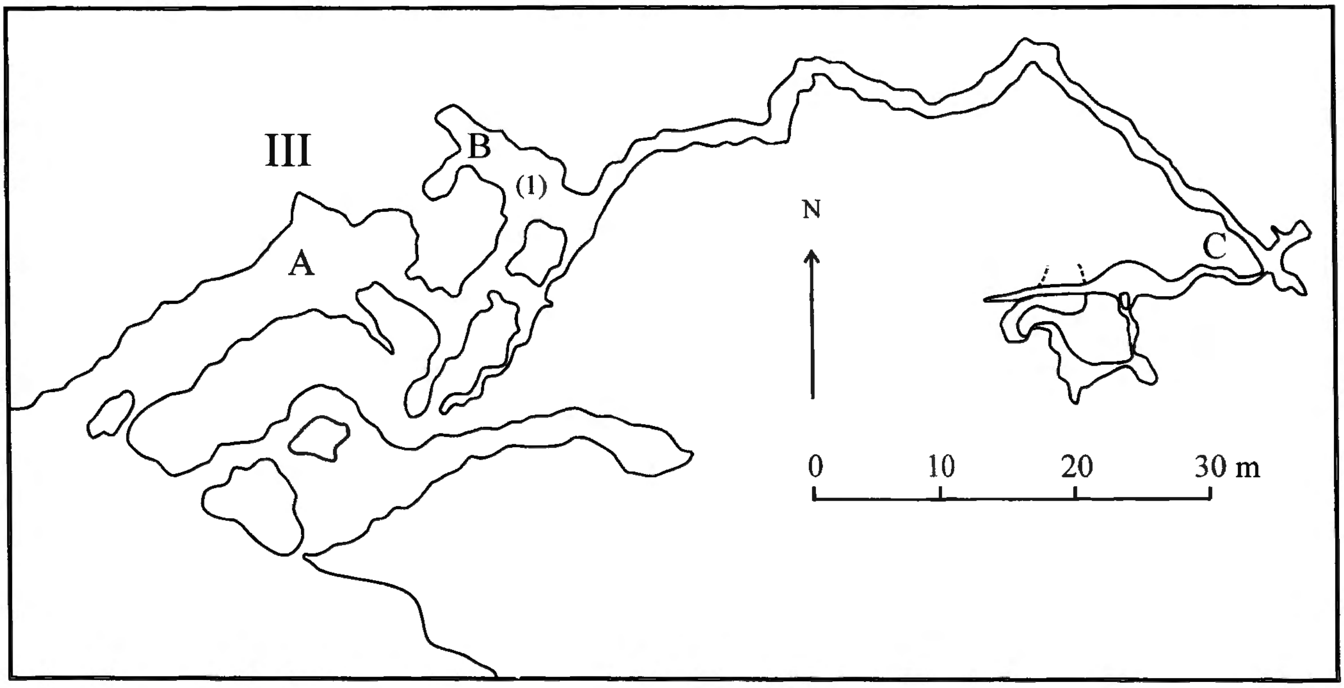


Fig. 2 — Map of Chambers A, B and C of the third cave of Goyet, modified after Rahir (1908), (1): excavation of a Magdalenian horizon by the Musées royaux du Cinquantaire in 1907.

Table 1 — AMS dates in years BP of carnivores from Goyet, Chamber A, bone horizon 1 (H1) and from Chamber B, bone horizon 4 (H4).

AMS (BP)	Chamber A	Chamber B
Ursus spelaeus		
GrA-9606 (H4)		35.470 +780-710
GrA-9605 (H1)	38.770 +1180-1030	
Crocuta crocuta		
GrA-2812 (H1)	27.230 +/- 260	
UtC 8958 (H1)	35.000 +/- 400	

MONPRÉ, 1997; Van Strydonck *et al.*, *in prep.*). AMS dates on Lateglacial mammals from horizon 1 are discussed in Germonpré (1997).

Chamber B lies behind Chamber A and is connected to it by two narrow perpendicular galleries, which are blocking the light, and has a length of circa 13 m. Here, Dupont (1873) found two bone horizons, which he called from bottom to top bone horizon 5 and bone horizon 4. Bone horizon 5 is only present in Chamber B and yielded remains from cave bear and cave lion. Dupont (*ibid.*) does not mention how and why he correlated bone horizon 4 in Chamber B with the ones in Chamber A and Chamber C. The majority of the bones from bone horizon 4 derive from cave bears (Dupont, *ibid.*). Other species present are brown bear, polar fox, and stoat. It is not clear if Dupont also excavated the narrow galleries. Here the sediments have also been removed and in the 1970's the owners of the cave dug deeper and found a partly articulated cave bear skeleton together with an articulated hind limb of a cave lion (D. Kindt, pers. comm), an association like the one noted by Dupont (*ibid.*) in horizon 5. Furthermore, the exact position of the Magdalenian excavated by Rahir (1908) remains doubtful.

A metacarpal of a cave bear from horizon 4 in Chamber B has an AMS age of 35,470+780-710 years BP (Table 1). At two standard deviations the result gives a chronological range of between 37,000 and 34,000 years BP. According to Van der Hammen (1995), the Hengelo interstadial (38-36,500 BP) was followed by the Hengelo/Huneborg stadial, the Huneborg I interstadial (36-35,000 BP) and the Huneborg stadial (35-33,500 BP), the latter three periods are integrated in the Huneborg interval. In the Netherlands, the summer temperatures remained in this period slightly lower than 10°C and the mean annual temperature was around 0°C. The vegetation is described as a shrub tundra (Ran, 1990; Ran & Van Huissteden, 1990). Pleniglacial interstadials persisted from 500 to 2,000 years; they began abruptly but terminated gradually (Johnsen *et al.*, 1992). According to Kasse *et al.* (1995), the Hengelo interstadial lasted from 38,700 to 36,900 years BP. They correlate this latter interstadial with interstadial number 12 in isotopic stage 3 of Dansgaard *et al.* (1993). However, according to Van der Hammen (1995) the Hengelo interstadial may rather coincide with interstadial number 8 of isotopic stage 3. The climatic optimum of the Hengelo interstadial was reached early in the sequence, with a mean summer temperature of about 13°C, and was of short duration (Kasse *et al.*, 1995). The summer temperature could possibly even have reached 15°C (Kolstrup & Wijmstra, 1977). Kasse *et al.* (*ibid.*) found at the end of the Hengelo interstadial indications for a distinct cooling, with a temperature drop of at least 3°C. A prolonged snow cover during winter existed between 36,900 and 35,500 years BP. The cave bear from Chamber A, horizon 1 (38,770 y BP, Table 1) can be placed in the very beginning of the Hengelo interstadial. The cave bear from Chamber B, horizon 4 (35,470 y BP, Table 1), would rather fall in the beginning of the Huneborg interval, following the Hengelo interstadial. According to Otte & Straus (1995) the oldest Aurignacian presence in Belgium dates from c. 38,000 BP. However, Jacobi & Pettitt (2000) are convinced that the Aurignacian in northwest Europe is not earlier than c. 34,000 BP.

Chamber C is at a distance of 120 m from the cave entrance (Dupont unpublished note April 1906) and only one bone horizon occurred, assigned by Dupont (1873) to bone horizon 4.

Faunal Analysis

The bone material collected by Dupont, curated in the Section of Fossil Vertebrates of the Royal Belgian Institute of Natural Sciences, is organized on trays and is

Table 2 — Species present in Goyet, bone horizon 4 (NISP: number of identified specimens, MNI: minimum number of individuals).

	Chamber					
	A		B		C	
	NISP	MNI	NISP	MNI	NISP	MNI
Carnivora						
Canis lupus	18	4			17	1
Alopex lagopus	22	3	6	3		
Vulpes vulpes	37	7				
Ursus spelaeus	2	1	2173	88	38	5
Ursus arctos			26	3		
Mustela erminea			1	1		
C. crocuta spelaea	113	12			26	7
Lynx lynx	38	1				
Proboscidea						
M. primigenius	6	2			2	2
Perissodactyla						
C. antiquitatis	3	1			9	2
Equus germanicus	6	1			66	3
Equus hydruntinus					2	1
Artiodactyla						
Cervus elaphus	18	8			10	1
Rangifer tarandus	262	49			120	27
Bison priscus	51	3			1	1
Ovibos moschatus					5	1
Rupicapra rupicapra	8	1			4	1
Capra ibex	5	1			10	2
	589	94	2206	95	310	54

Table 3 — Frequency distribution of the skeletal elements of *Ursus spelaeus* and *Ursus arctos* from Goyet, Chamber B, bone horizon 4 (NISP: number of identified specimens, MNI: minimum number of individuals, MNIe: minimum number of individuals for each skeletal element, max: maxilla, mand: mandibula, Mc: metacarpus, Mt: metatarsus).

Ursus spelaeus	NISP		MNIe
cranium	23		21
maxilla	7		5
mandibula	67		52
I1 max	21		13
I1 mand	8		5
I2 max	22		14
I2 mand	9		5
I3 max	50		28
I3 mand	32		18
C max	76		45
C mand	78		44
P4 max	19		16
P4 mand	16		11
M1 max	32		21
M1 mand	47		33
M2 max	40		27
M2 mand	43		28
M3 mand	30		24
dentes indet.	18		
hyoid	4		2
os costa	229		11
vertebrae	221		
atlas		16	16
axis		12	12
cervical		41	12
thoracic		88	11
lumbar		54	12
sacrum		7	7
caudal		6	3
sternum	5		3
scapula	32		19
humerus	60		41
ulna	59		33
radius	59		44
carpalia	64		
scapholunare		21	14
Mc I	20		10
Mc II	19		10
Mc III	55		23
Mc IV	19		11
Mc V	26		16
pelvis	38		22
baculum	10		10
femur	57		32
patella	13		8

Ursus spelaeus continued	NISP		MNIe
tibia	50		40
fibula	18		9
tarsalia	73		
astragalus		27	15
calcaneum		28	17
Mt I	12		6
Mt II	26		16
Mt III	31		19
Mt IV	38		23
Mt V	33		18
Mp	3		
sesam	4		1
phalanx I	117		9
phalanx II	58		5
phalanx III	82		6
Total NISP	2173		
Total MNI	88		

Ursus arctos	NISP	MNIe
maxilla	1	1
mandibula	3	2
C mand	1	1
P4 mand	5	3
M1 mand	2	1
humerus	1	1
radius	4	3
McIV	1	1
femur	2	1
tibia	3	3
astragalus	1	1
Mt I	1	1
Mt II	1	1
Total NISP	26	
Total MNI	3	

accompanied by notes, signed by Dupont, dating from July 1905, April 1906 and May 1906. These unpublished notes contain more detailed information than his publications on the Goyet caves on the provenance and composition of the faunal assemblages. Furthermore, six mounted skeletons exists: two (2724, 2730) are on display in the museum of the Royal Belgian Institute of Natural Sciences, two (2726, 2725) are stored in the collections of the Institute, one is shown in the Schoolmuseum (2164) in Ghent and the last one is the museum of Trou de l'Abîme (2729) at Couvin.

Dupont mentions following locations: "*galleries voisines de l'entrée*", corresponding to the back of chamber A as described in 1873 (tray numbers 2735, 2737, 2842, 2860). Dupont (unpublished notes) lists bones of following mammals: woolly rhinoceros, horse, mammoth, bison, reindeer, red deer, ibex, chamois, bear, lynx and cave hyena. Of the latter also coprolites were found.

The main part of the collection, composed almost entirely of cave bear bones, is attributed to Chamber B (numbers 2732, 2739, 2742, 2743, 2745, 2834, 2835, 2836, 2837, 2838, 2839, 2854, 2855, 2856, 2857). To the cave bear material from Chamber B also belongs the unnumbered "collections d'étude" (note 2743, May 1906). However, all the bones with number 2855 have labels mentioning "4e niv. Extr", abbreviation for "*Galleries de l'extrémité*". These bones have in general a darker colour and many show root traces, excluding an origin from Chamber B, situated deeper in the cave. The species on this tray (mammoth, reindeer) were only found in Chamber A and C. All this points to a provenance from Chamber C for this tray.

The "*Galleries de l'extrémité*", corresponding to Chamber C (numbers 2746, 2861 + 2855), is farthest away from the southwest entrance. Dupont (unpublished notes April 1906) identified following mammals: woolly rhinoceros, mammoth, chamois, reindeer, roe deer, red deer, horse, wild boar, man, wolf, cave hyena (bones and coprolites).

A first analysis of the species from bone horizon 4 present in each chamber makes it clear that the assemblages in the chambers have a different taphonomic origin (Table 2). The analysis of the bone material includes calculation of the Number of Identified SPecimens per species (NISP) and of the Minimum Number of Individuals (MNI). Table 3 gives the NISP and the MNI of *Ursus spelaeus* and *Ursus arctos*. MNIe (MNI for each skeletal element) were established by matching left and right elements; the final MNI of the cave bear is based on aged and sexed canines, skulls, lower jaws and postcranial material. In what follows only the cave bear remains from Chamber B, horizon 4, which can be described as a typical cave bear den, will be discussed.

Ursus spelaeus

Cave bear (*Ursus spelaeus*) is the dominant species in bone horizon 4 with 2173 bones identified and with a MNI of 88 (NISP: 98%, MNI: 93%). The bones are in an excellent state of preservation. More than 85% of the postcranial material is complete or almost so compared to 15% complete postcranial bones in the Magdalenian assemblage from Chamber A, horizon 1. The colour of the bones from Chamber B varies from beige-whitish-yellowish to light brown. Most of the bones have not weathered to slightly weathered surfaces. Skeletal parts of *Ursus spelaeus* were often found in anatomical connection: "*les ossements d'ours sont souvent agglomérés dans leurs connexions normales*" (DUPONT, 1873: p.

Table 4 — Overview of associated skeletal parts of *Ursus spelaeus* from Goyet, Chamber B, bone horizon 4.

Number	Description	NISP involved	% complete	remarks
2726	mounted skeleton cub	36	17%	neonate, described in DUPONT (1873), Plate 1
2725	mounted skeleton cub	66	30%	2,5 months old cub, described in DUPONT (1873); Plate 1
2724	mounted skeleton cub	108	50%	7 months old cub, described in DUPONT (1873)
2729	mounted skeleton subadult	159	73%	subadult, probably male, described in DUPONT (1873); dentition: STINER's cohort IV (1998)
2164	mounted skeleton adult	135	62%	adult female, without skull & lower jaw, described in DUPONT (1873)
2730	mounted skeleton adult	127	?	adult male, composed from several individuals, described in DUPONT (1873)
2210	skull & lower jaws female	3	1%	young female 12- 14 months old
2209	skull & lower jaws male	3	1%	young male > 18 months old
2201	skull & lower jaws male	3	1%	adult male
2856-3	cervical vertebra 3 juvenile	3	1%	vertebra 5 has two canine punctures in opposition
2856-5	cervical vertebra 4 juvenile			
2856-4	cervical vertebra 5 juvenile			
2732-8	thoracic vertebra 13 adult	10	5%	DUPONT's unpublished note of May 1906
2732-9	thoracic vertebra 14 adult			
2732-10	lumbar vertebra 1 adult			
2732-11	lumbar vertebra 2 adult			
2732-12	lumbar vertebra 3 adult			
2732-13	lumbar vertebra 4 adult			
2732-14	lumbar vertebra 5 adult			
2732-15	lumbar vertebra 6 adult			
2732-17	sacrum adult			
2732-16	pelvis adult			
2856-36	lumbar vertebra 3 adult	4	2%	
2856-39	lumbar vertebra 4 adult			
2856-40	lumbar vertebra 5 adult			
2856-41	lumbar vertebra 6 adult			
G3.4.85	left scapula subadult	2	1%	
G3.4.86	right scapula subadult			
G3.4.62	left radius cub	2	1%	6-7 months cub
G3.4.63	right radius cub			
G3.4.70	left radius cub	2	1%	cub third winter, label "gauche O"
G3.4.71	right radius cub			cub third winter, label "droit O"
2743-39	right radius adult	2	1%	
2743-10	left radius adult			
G3.4.104	right ulna subadult	2	1%	
G3.4.109	left ulna subadult			
G3.4.106	right ulna subadult	2	1%	cub third winter or older, label "droit C"
G3.4.105	left ulna subadult			cub third winter or older, label "gauche C"
	Total	669		

111). Six skeletons of cave bear from horizon 4 were mounted and displayed in the museum (Dupont, *ibid.*): a newborn, a cub of two and a half months, a seven months old cub, a subadult male, an adult female and an adult male (Table 4). Dupont (*ibid.*, p. 109) writes the following of the female skeleton: "*Les ossements d'un individu ... y étaient réunis dans leurs rapports anatomiques et consitutent un spécimen presqu'intact de cette espèce éteinte.*" Furthermore, three skulls with their lower jaws were also mounted. In addition ten more or less complete skulls are preserved as well as several series of articulated vertebrae. The vertebral column described in Bürgl (1938: fig.5 & plates VII & VIII) could not be retrieved; it is not excluded that it originates from horizon 5.

Cave bear fossils of Weichselian age have been

Table 5 — *Ursus spelaeus*: osteometry of the limb bones from Goyet, bone horizon 4 (GL: Greatest Length, Bp: transversal diameter proximal epiphysis, KD: transversal diameter diaphysis, Bd: transversal diameter distal epiphysis; stdev: standard deviation, cv: coefficient of variation).

Humerus

female	GL	Bp	KD	Bd
n	2	2	9	8
min	333	70,6	32,3	102,5
max	382	71,7	40,2	110,5
average	358	71,2	37,0	106,7
stdev			26,6	3,5
cv			6,9	3,3

male	GL	Bp	KD	Bd
n	1	2	2	2
min	430	85,6	45,2	125,5
max		89,2	46,2	129,7
average		87,4	45,7	127,6

Radius

female	GL	Bp	Kd	Bd
n	4	3	7	5
min	278	36,8	26,8	64,2
max	294	43,0	33,5	68,4
average	286	40,9	29,0	66,4
stdev	6,6	3,6	2,5	1,7
cv	2,3	8,7	8,7	2,6

male	GL	Bp	Kd	Bd
n	5	6	7	6
min	302	51,2	33,5	69,2
max	345	59,0	40,5	82,8
average	325	55,5	36,7	77,1
stdev	17,7	3,0	2,4	5,9
cv	5,5	5,4	6,5	7,6

Ulna

female	GL	BPc
n	5	6
min	313	56,1
max	342	59,3
average	324	57,8
stdev	10,9	1,3
cv	3,4	2,3

male	GL	BPc
n	3	8
min	353	62,3
max	385	69,8
average	365	66,3
stdev	17,4	3,1
cv	4,8	4,7

Femur

female	GL	Bp	KD	Bd
n	3	2	4	4
min	385	108	39,1	88,4
max	411	112	43,2	89,5
average	402	110	40,9	89,0
stdev	14,7		2,0	0,5
cv	3,7		4,8	0,6

male	GL	Bp	KD	Bd
n	5	4	5	4
min	440	118,0	47,5	105,3
max	485	130,0	50,9	111,5
average	466	125,5	48,6	108,7
stdev	16,7	5,5	1,4	2,8
cv	3,6	4,4	2,8	2,5

Tibia

female	GL	Bp	Kd	Bd
n	6	6	6	6
min	246	80,5	26	36,7
max	269	89,5	29,4	71,1
average	257	86,6	28,0	67,5
stdev	10,2	3,2	1,5	2,4
cv	4,0	3,7	5,2	3,6

male	GL	Bp	Kd	Bd
n	7	7	8	8
min	290	92,5	30,9	66,6
max	308	108,7	36,7	89,4
average	296	102,3	34,3	81,4
stdev	6,7	6,7	2,1	6,8
cv	2,3	6,5	6,1	8,4

encountered in caves in the Pyrenees, Alps, Carpathian Mountains, Caucasus, the Crimea and the Ural. South Belgium with its limestone caves, is their most northwestern outpost. Cave bears were more numerous during Weichselian interstadials and preferred a forest-steppe environment with a relatively mild climate (Baryshnikov, 1991; Musil, 1980). According to Cordy (1988), cave bears were particularly abundant in Belgium during the Hengelo interstadial. They have been described as herbivorous, based on the morphology of their jugal teeth and skull (Kurten, 1958). Isotopic analysis on cave bear bones from Divje Babe cave, Slovenia confirmed that they were eating a C3-based terrestrial diet (Nelson *et al.* 1998). Also in the cave Scladina at Sclayn, a site situated some 5 km north of Goyet, isotopic analysis of 40,000 year old bones and teeth indicate that cave bears had a strictly vegetarian diet (Bocherens *et al.* 1997). The shrub-tundra from the Huneborg interval probably was an extreme habitat for them, although it is likely that the protected valleys in the Ardennes harboured a richer vegetation.

The osteometry of the limb bones of *Ursus spelaeus* is presented in Table 5. The measurements, expressed in mm, were taken following the procedures indicated by von den Driesch (1976). The isolated limb bones are compared to those of the sexed skeletons, furthermore their measurements were plotted and the bivariate distribution is used to attribute them to the male or female group (Fig. 3). A detailed osteometric analysis will be presented in a forthcoming paper.

Distribution of the skeletal elements

An inventory of the skeletal elements of *Ursus spelaeus* is given in Table 3. Robust elements such as mandibles and canines are very well represented, followed by most of the limb bones. The weaker elements such as vertebrae, ribs, hyoid, sternum and fibula have a much lower frequency. Isolated milk teeth are absent. This could be due to an uncomplete recovery of small elements during the excavation or because the box with isolated milk teeth was lost since the days of Dupont.

The mounted skeletons, the articulated body parts, the remarkable preservation of the skulls, the good representation of all skeletal elements, the low incidence of gnawing traces and charriage-à-sec (see further) indicate that little disturbance of the carcasses occurred. According to Fosse *et al.* (1997), the high frequency of complete long bones could indicate a rapid fossilisation.

Table 3 gives also the elements of *Ursus arctos* found

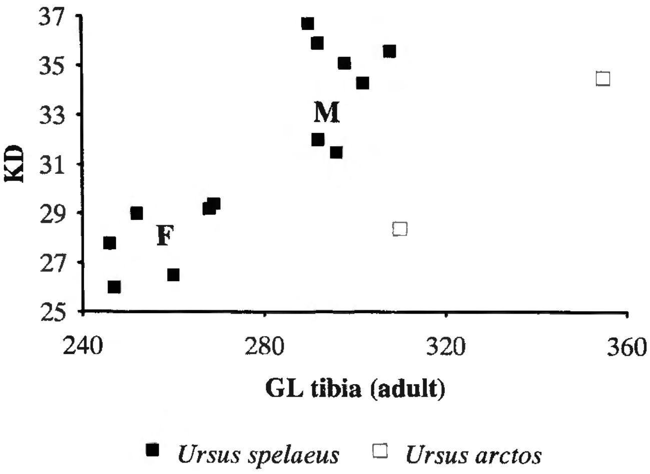


Fig. 3 — *Ursus spelaeus* and *Ursus arctos* from Goyet, Chamber B, bone horizon 4: tibia: the greatest length (GL) versus the transversal diameter of the diaphysis (KD).

in Chamber B. The bones of the two species are identified following DE TORREZ PEREZ-HIDALGO (1988a, b, c, d, e, f). The brown bear bones are from one subadult and two adults, one male and one female. Remains of brown bears are regularly found in the company of cave bear bones, although in small amounts (KURTEN, 1995; STINER, 1998). At Goyet, Chamber B, they constitute 1,2% of the total bear assemblage from horizon 4. According to MUSIL (1980), cave bear and brown bear occupied different econiches. The brown bears and cave bears from the cave Scladina had different carbon and nitrogen isotopic values, proving a more omnivorous diet, with an animal component for the brown bear (BOCHERENS *et al.*, 1997).

AGEING

Several authors reconstructed the age distribution of fossil bears based on the eruption sequence and wear of their jugal teeth compared with those of the recent brown (*Ursus arctos*) and black bear (*Ursus americanus*) (KURTEN, 1958; ANDREWS & TURNER, 1992; DEBELJAK, 1996; STINER, 1998). These two modern species are similar in several aspects of their biology and behaviour (KURTEN, 1995). Their hibernation habits and reproductive cycle probably also apply to the extinct cave bear *Ursus spelaeus* (STINER, 1998).

Dentition of lower jaw

ADOLF (1949) and DITTRICH (1961) described the progress of eruption of the deciduous and permanent teeth of brown bear and assigned an age for each erupting tooth (Table 6). The work of ADOLF (*ibid.*) is based on twelve bear cubs, six from the Moscow zoo and six wild ones. DITTRICH (*ibid.*) examined seventeen bear cubs born in the zoo of Leipzig and nine cubs preserved in formol and several skulls. According to these authors, the milk dentition is complete at three months. The earliest permanent teeth to appear are the first molars followed by the first and second incisors, the second molars, the premolars the third incisors, the third molars and finally the canines at an age of 12 to 14 months. The canines are at their definitive position between 17 and 18 months. Authors such as KOBY (1952), COUTURIER (1954) and RADULESCU & SAMSON (1959) give a different age for the eruption of some permanent teeth. In this analysis these ages are not used as we prefer the data from ADOLF (*ibid.*) and DITTRICH (*ibid.*) based on extensive samples. The eruption sequence of DITTRICH (*ibid.*) is also followed by ANDREWS & TURNER (1992) for the Deninger's bear

Table 6 — *Ursus spelaeus*: age distribution of the lower jaws from Goyet, Chamber B, horizon 4, based on the eruption of the deciduous and permanent teeth following ADOLF (1949), DITTRICH (1960), KURTEN (1958) and STINER (1998) (M: male, F: female).

Months	**ADOLF (1949) & DITTRICH (1960)** ***Ursus arctos***	**age cohorts**		**Goyet, Ch. B, H. 4: *U. spelaeus***				
		KURTEN (1958) ***U. spelaeus***	**STINER (1998)** ***Ursus***	**NISP**				**MNI**
				Total	**M/F**	**M**	**F**	
0-2	milk dentition: bud or erupting	a, b		9	9			7
3-5	milk dentition complete eruption M1		I					
6-8	eruption M2 eruption I1,I2 eruption P4	I, II	I, II	12	12			10
9-11	+/- erupted M2 unerupted C							
12-14	eruption C, M3	II	II, II-III	8	3	3	2	6
15-17/18	erupting C							
>18	permanent dentition complete	III	III	8		6	1	6
		III	IV	4		2	2	3
		IV	V	4		3	1	3
		V	VI	3		2	1	2
		VI	VII	4			4	3
		VI	VII-VIII	3	2	1		2
		VI	VIII	3		2	1	3
		VI	IX	2			2	2
	adult jaw without jugal dentition			8	4	2	2	5
				68	30	21	16	52

Table 7 — *Ursus arctos*: overview of some ethological characteristics; *Ursus spelaeus*: estimation of some ethological characteristics based on two cave bear populations from Goyet: Chamber B, bone horizon 4 and Chamber A, bone horizon 3 (M: males, PFN: (pregnant) females with new born cubs).

Ursus arctos	**rut**	**gestation period**	**dormancy period**	**birth season**	**number of cubs**
Koryak Mountains, Northeast Siberia (REVENKO, 1993)	May - June		PFN: early October - early June (c. 8 months) M: mid-November - early May (c. 5.5 months)		
South Kamchatka (REVENKO, 1993)	May - June		PFN: late October - early May (c. 6.5 months) M: late December - late March (c. 3 months)		
Western Caucasus (KUDATKIN & CHESTIN, 1993)	late May - early July	6 - 7 months	PFN: ? - early April M: mid-December - mid-March (c. 3 months)	December	
Foothills of Caucasus (HEPTNER et al.,1974)			PFN: ? - end March M: early January - mid-March (c. 2.5 months)		
Russia (general) (HEPTNER et al.,1974)	mid-May - mid-July	6 - 8 months		December - April	2 (1-3)
French Pyrenees (COUTURIER, 1954)	June - July	7 - 8 months	PFN: December - early June M: December - April	mid-January - mid-February	1-2
Europe (JAKUBIEC, 1993)	May - early June	7 - 8 months	December - late March	December - Januari	1 - 4
Alaska (MURIE, 1985)	mid-May - mid-July	7 months	late October - April	January - February	1.85 (1-3)
North America (BANFIELD, 1974)	late June - early July	7.5 -8.5 months	mid-November - April	mid-January - early March	2 (1-4)

Ursus spelaeus	**rut**	**gestation period**	**dormancy period**	**birth season**	**number of cubs**
Goyet, Belgium Chamber B, Horizon 4 (Weichselian, c. 35,500BP)	late May - June	5 - 6 months	PFN: October - June (c. 7.5-8.5 months) M: October? - May (c. 6.5-7.5 months?)	November-December	2
Goyet, Belgium Chamber A, Horizon 3 (Weichselian)	late May - June	7 months	PFN: mid-November - late April (c. 5.5 months) M: mid-November? - late March (c. 4.5 months?)	early January	2

(*Ursus deningeri*) of Westbury and by DEBELJAK (1996) for the cave bear from Divje Babe I cave in Slovenia. On basis of the sequence of the eruption of the different teeth described by DITTRICH (*ibid.*) and ADOLF (*ibid.*) for the recent brown bear, six age classes of three months each were established until an age of 18 months; the cave bear material from Goyet is split up following these classes (Table 6). KURTEN (1958) studied the cave bear material from Odessa. He organised the material in discrete growth stages one year apart, based on tooth replacement, deposition of dentine, closing of the root and wear of the tooth crowns and concluded that these caves were inhabited every winter for hibernation. Table 6 includes his age cohorts. STINER (1998) proposed nine age cohorts based on isolated teeth of *Ursus*; these cohorts are also added in Table 6.

The age distribution of the cave bear of horizon 4, Chamber B, based on the lower dentition, is given in Fig. 4 and Table 6. The left side of Fig. 4 and the upper part of Table 6 show the young specimens grouped according to ADOLF (*ibid.*) and DITTRICH (*ibid.*); the right side of Fig. 4 and lower part of Table 6 follow the grouping proposed by KURTEN (*ibid.*) and STINER (*ibid.*) for the specimens with a completely erupted permanent dentition.

Twenty-nine lower jaws have milk teeth or erupting permanent teeth. This material can be placed in three of the six age classes proposed in Table 6. The cave bear cubs of Goyet experienced in their first 18 months three difficult periods: at or soon after birth, at the age of six to seven months and when they were about one year or a bit older.

The following summary of the reproduction cycle and dormancy of brown and black bears is based on BANFIELD (1974), CHURCHER (1999), COUTURIER (1954), CRAIGHEAD & CRAIGHEAD (1972), HEPTNER *et al.* (1974), JACUBIEC (1993), MURIE (1985), REVENKO, (1993), ROGERS (1987, 1999), SHUBIN (1993), ZAVATZKIY (1993). Table 7 gives an overview of period of rut, dormancy etc. for recent brown bears from North America and Eurasia. The behavioural and physiological cycle of omnivorous bears is clearly linked to the annual cycle of plant growth and fruiting, and hibernation is an adaptation for survival through cold seasons of food scarcity. Bears need to accumulate fat during summer and autumn in order to enter dormancy and survive the winter. Brown bears are mostly solitary except for females with cubs or when breeding. The mating season extends in general from mid-May to June, before the fruit and berries are ripe. The implantation of the blastocyst, which is delayed for several months, occurs when the females enters winter sleep, and the gestation continues for at least six weeks. Also female polar bears show delayed implantation and enter dens at about the time of implantation (RAMSAY & STIRLING, 1988). The cubs are born during the dormancy period of their mother, mostly in the first half of January (see also Table 7). The birth during the winter sleep occurs at a time that does not interfere with feeding. Of all placental mammals, bears give birth to the smallest young relative to the body weight of the mother. The strong contribution of lipids in the energetic metabolism during hibernation hampers the growth of the fetuses in utero and an early birth permits the mother to nourish the nonhibernating cubs with milk. The dormancy period of brown bears can start as early as October or as late as December and end as early as March or as late as June depending on the geographical region: the more severe the climate, the earlier dormancy begins and the longer its duration. In the same region the length of the denning period can fluctuate with one month according to the weather conditions and food abundance. The retreat of brown bears to their winter quarters is often associated with heavy snowstorms and low temperatures. Male and female brown bears often gain their winter den simultaneously, especially just before or during snowfall which conceals tracks that could possibly reveal the den locations. When the weather is better and the food abundant, the male bears go later to their den than the pregnant females. In the region of Krasnoyarsk (Central Siberia) the winter rest can begin at the end of September. In the Koryak Mountains (Northeast Siberia), the dormancy period for pregnant female brown bears, that gave birth during that season, can take up to circa 8 months. In Kamchatka and the Koryak Mountains, female brown bears with older cubs go to the den two-three weeks later than pregnant females, prime males enter the den at least one month later than the pregnant females. However, the late retreat of the males and non-pregnant females in these regions could be related to the spawning salmon in the rivers. After the winter rest, the males and non-breeding females appear at first, when the heavy snow begin to melt. Lactating female brown bears abandon their den at the start of the growth season. Recent bears gradually switch from a winter to a spring life style, this can take up more than two weeks during which they return regularly to the den. At first, the mother bears leave their newborns alone in the cave for several hours when they are looking for food. During that time the cubs can be killed by wolves or lynxes. Later the mothers slowly bring out their young and teach them to search for food. In the Pyrenees, north Kamchatka and the Koryak Mountains, the family leaves the den only at the end of May or even in the beginning of June. Prime males come out at least one month earlier than females with newborns. Mother bears with cubs leave the den three to four weeks before the females with new born cubs. Also for their second winter the cubs stay with their mother. The young gradually gain independence during the following spring. At the time of rut, in the late spring or early summer, they are chased away by their mother. However, brown bear cubs in Alaska often continue to live with their mother until their third year. Motherless siblings stay together for their third winter and prefer a den near their place of birth. Brown bears have few natural enemies. Wolves and male bears can be dangerous for cubs. In the Primorje region, tigers are known to attack bears during winter.

The birth season, the timing and length of the dormancy period, and the abandon of the winter shelter of *Ursus spelaeus* depended no doubt on the geographical region and the climatic conditions of the ice age. LIDEN & ANGERBJORN (1999) studied the carbon and nitrogen isotopes of cave bear cubs and concluded that the cubs were fully lactated during their first winter, they received 50% lactation during the first summer, their diet being completed with 50% solids. During the second winter

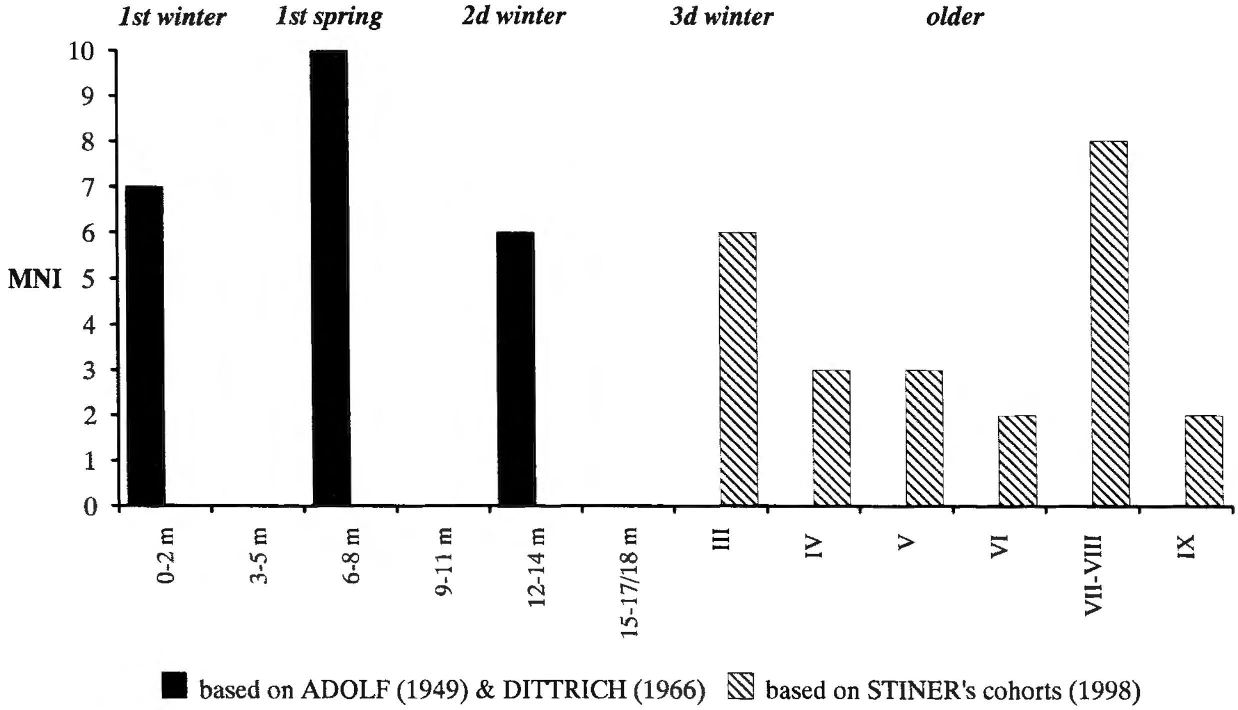


Fig. 4 — *Ursus spelaeus* from Goyet, Chamber B, bone horizon 4: age distribution of the lower jaws, based on the eruption of the teeth, left side following age attribution of brown bears by Adolf (1949) and Dittrich (1961), right side following Stiner's cohorts (1998) for bears of the genus *Ursus*.

they again received 100 % lactation and were finally weaned in their second spring. These data are in accordance with the behaviour of brown bear cubs during their first years.

At Goyet (Chamber B, horizon 4), the first peak in the age profile corresponds to the death of newborns to cubs of less than three months old (Fig. 4). Many died soon after birth. At Odessa, Kurten (1958) blames the death of very young cubs to hereditary diseases, but selective removal of weaker cubs because of the undernourishment of the lactating mother bears can explain these early deaths. Skeleton 2725 (Plate 1) is assigned to this age group. In the upper jaw part of the enamel cap of a jugal tooth, probably M1, of about 0.3 mm thin is preserved. In the lower jaw the deciduous teeth are missing and the crown of the M1 is already formed as is the tip of the crown of the canine. A furrow exists for the future eruption of the M1. According to Dittrich (1961: p. 88) and plate 3 of Debeljak (1996) this cub can be attributed an age of around two and a half months.

The second peak (Fig. 4) is separated from the first by an absence of cubs aged between three months to six months. In Chamber B at Goyet, the healthy mothers and cubs carried on, as those with problems were already eliminated during the first three months of the winter rest.

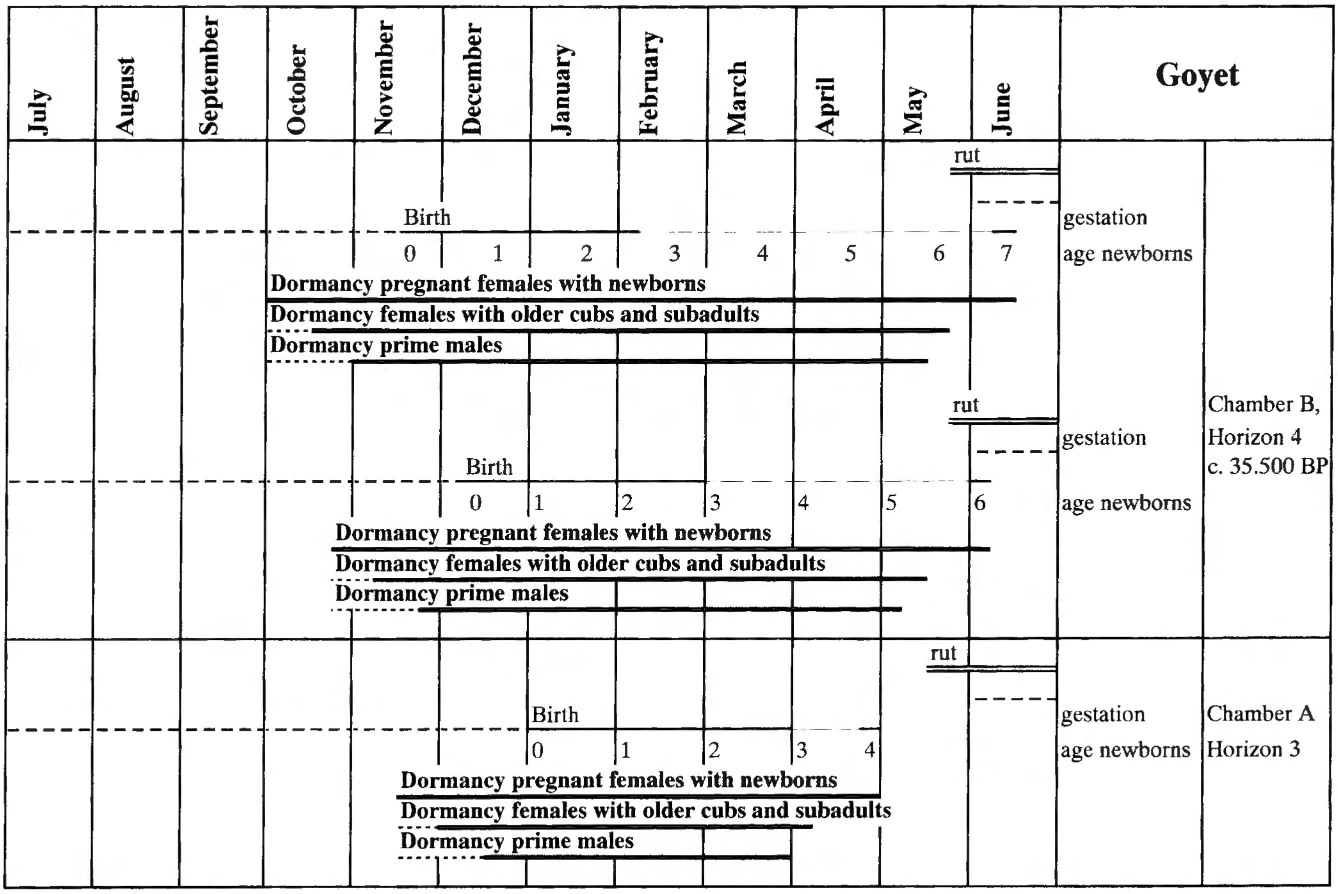
At Chamber B, the erupting stage of the dentition of the jaws in age class 6-8 months can be detailed as follows: the lower jaws have the M1 in permanent position. A few tiny wear facets on the fully erupted first molar can be observed under magnification. The P4 and the anterior part of the M2 are emerging, the M3 is still turned lingually in the ascending ramus and the germ of the canine is present in the jaw. The enamel of the latter two teeth is not whitish grey, as in the erupted teeth, but brown. The second incisor is erupting, the third incisor is present as a germ. In some jaws the tip of the P4 is just emerging while in others the P4 is half erupted (Plate 2, Fig. 3 & 4). Based on Dittrich (*ibid.*: p. 89) and Debeljak (*ibid.*: plate 5 & 6), we assign this sequence a more detailed age of six to seven months. Goyet skeleton 2724 fits in this age group. In the right lower jaw the jugal teeth are missing, but the germ of the canine is present; the left mandible is missing and has been replace by one from another individual. In the upper jaw P4 and M1 have erupted, the M2 is erupting and the milk molar dP3 is still present in front of the P4, pointing to an age of about seven months (Dittrich, *ibid.*: p. 89).

We attribute the second mortality peak at Chamber B of Goyet to the period during which the cave bears were gradually leaving the cave at the end of the winter. According to Rogers (1999), some black bear cubs starve following emergence in spring. At Goyet, it seems that the cave bear cubs were very vulnerable during the few weeks when they were switching from a full milk diet to a mixed milk/plant diet. Small wear facets on the erupted M1 suggest that the cubs were already chewing some hard food outside the cave, where they could catch infections or suffer accidents. In Westbury, Andrews & Turner (1992: p. 174) concluded that cubs died in spring inside the cave, after venturing outside to feed on plants, based on the slight wear on some teeth. The young bears of Goyet could also be killed inside the cave by wolves, cave hyenas and adult male bears while their mother was foraging outside. Remains of this age group are more damaged by carnivores than the younger and older cubs (see further).

We suppose that 35,500 years ago, the six to seven months old cubs and their mothers gradually left the cave of Goyet in June, as nowadays brown bear cubs in the Pyrenees or the Koryak Mountains. If the cave bears abandoned their winter shelter later in summer, they would not have had enough time to find ample green for fat accumulation. If the cubs were six months in June, they must have been born in December; if they were seven months in June, they had to be born in November, earlier than is the case for recent brown bear. However, JACUBIEC (1993) remarks that exceptionally brown bear females can give birth in November. In that case, dormancy for the pregnant female cave bears should have started in early October. Such an early start of the hibernation was necessary for a postimplantation gestation of the blastocyst of at least six weeks, as in the recent brown bear (CHURCHER, 1999), leading to parturition in November. The total length of the dormancy period for pregnant female cave bear, including the transition from cave to outdoors in spring, would then have been between seven and a half to eight and a half months, ranging from October to June, which is at the limit of the range of dormancy in modern brown bears. During the Pleniglacial in Belgium there is little evidence for nut accumulation from beech, oak or hazel, which can be preserved through the winter into the next spring, and constitute a food resource after or before the growth season. The few pollen from these plants that were found in sediments dating from the Pleniglacial in Belgian caves, are contaminations (Damblon, pers. comm.).Therefore, we assume that the dormancy period of the male cave bears in Chamber B of Goyet started simultaneously with the hibernation of the pregnant females. However it is not excluded that hibernation of the male cave bears could begin later if plant food, like berries, was very abundant in autumn. Just as for the recent brown bear we suppose that the male dormancy probably ended one month earlier than the winter rest of lactating female cave bears, corresponding to a long winter season. Cave bear females with older cubs probably also abandoned the cave in May, so the rut in all likelihood took place at the end of May or in June, as for most recent brown bears. With a birth in November or December this gives a gestation period of five to six months, somewhat shorter than for the modern brown bear (Table 7). However, STEINBACHER (1963) mentions an exceptional short gestation period of around four months for a female brown bear in the zoo of Augsburg, Germany. An overview with the estimations of the length and timing of the dormancy, gestation and birth of the cave bears from Goyet is given in Table 8.

At Goyet, a hiatus follows of cubs aged between 8 and

Table 8 *Ursus spelaeus*: estimations of the reproduction cycle and the dormancy period of the cave bear from Goyet, Chamber B (horizon 4) and Chamber A (horizon 3).



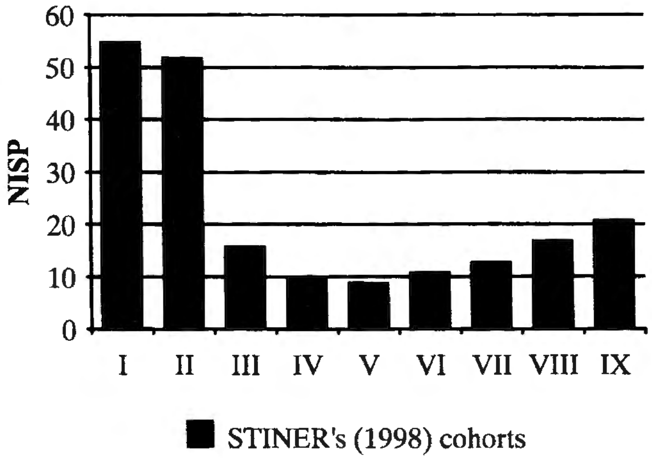


Fig. 5 — *Ursus spelaeus* from Goyet, Chamber B, bone horizon 4: frequency of the occlusal wear stages on the isolated P4, M1, M2, M3 grouped according to Stiner's cohorts (1998) for bears of the genus *Ursus*.

12 months (Fig. 4). We believe that this hiatus corresponds to the summer and autumn months, the period in which the cave bears spent outside.

The specimens of the third peak in the age profile of Goyet, Chamber B, with the tip of the canine one to two cm above the alveolus and the posterior part of the M3 not yet completely erupted are, based on Adolf (*ibid.*) and Dittrich (*ibid.*), 12-14 months old (Plate 3). Very slight wear occurs on the fourth premolar and the first and second molar. After a summer and autumn, during which the cubs fed on solids and on milk, they went with their mothers to the cave for their second winter dormancy. Bad summers soon took their toll and many cubs perished between November and January, as a result of infections, deficient fat accumulation or the undernourishment of their mother.

In the period of 14 to 18 months the permanent dentition, and more especially the canines, take their definite place. In Chamber B no mandibles of this stage are present.

The age attribution in the right side of the diagram (Fig. 4) is less detailed. A fourth peak of young individuals, cohort III of Stiner (1998), contains individuals more than 18 months old, which on the basis of the foregoing attributions died in their third winter. All teeth are completely erupted and have only slight wear. Young and prime adults (Stiner's cohorts IV, V, VI) are less well represented; they had gained strength and experience and escaped death more easily. Old animals occur in higher numbers (Stiner's cohort VII-VIII, IX) (Fig. 4). They perished in the cave from various causes: undernourishment, diseases, accidents, old age, etc.

In the cave of Princesse Pauline at Marche-les-Dames, Belgium, remains of cave bear were associated with Aurignacian artefacts. Several jaws of very young cubs

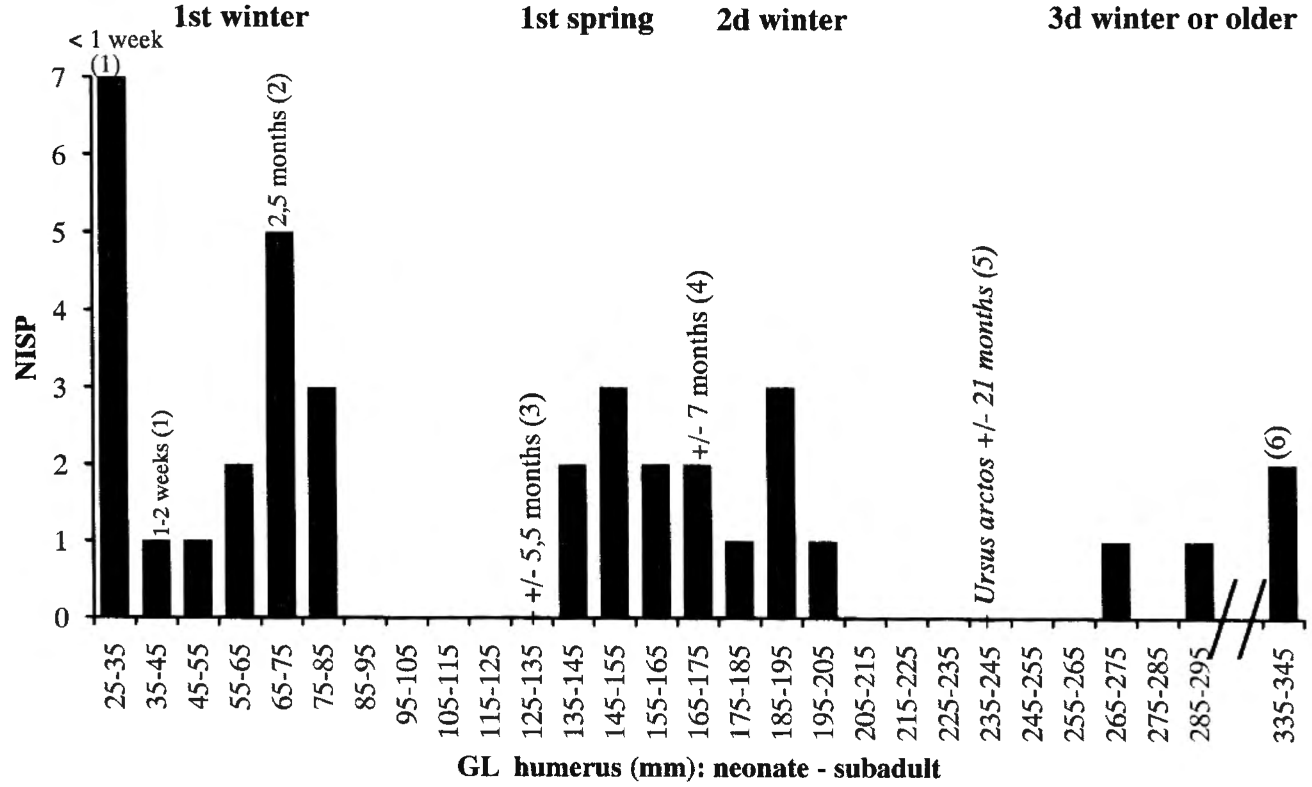


Fig. 6 — *Ursus spelaeus* from Goyet, Chamber B, bone horizon 4: immature humeri: (1) age of this size class based on Ehrenberg (1931, 1935), (2) skeleton 2725, dental age c. two and half months, (3) age of this size class based on Ehrenberg (1964), (4) skeleton 2724, dental age c. seven months, (5) humerus with fused distal epiphysis of recent subadult *Ursus arctos* of c. 21 months, (6) humerus with distal epiphysis fused (skeleton 2729), dental age: Stiner's cohort (1998) IV (GL: greatest length).

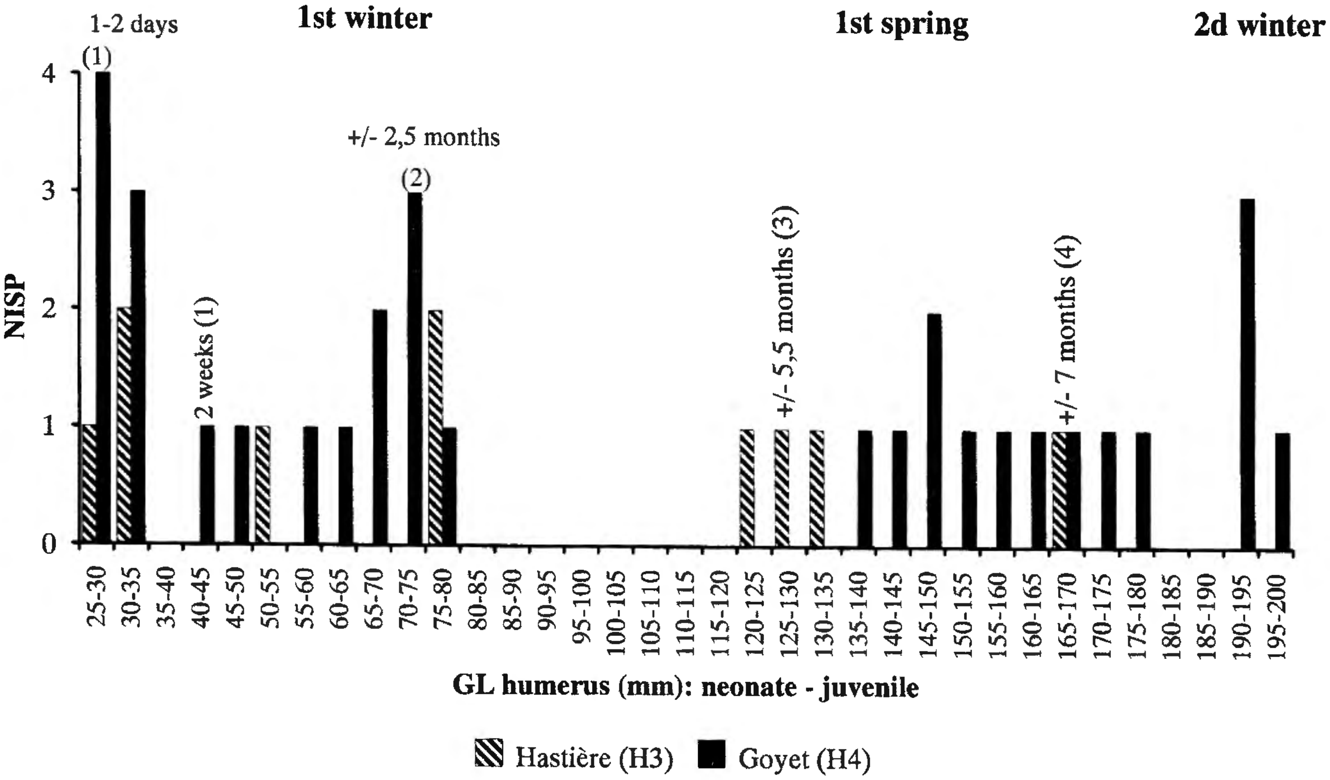


Fig. 7 — *Ursus spelaeus* from Goyet, Chamber B, bone horizon 4 (H4) and from Hastière, bone horizon 3 (H3): immature humeri: (1) age of this size class based on Ehrenberg (1931, 1935), (2) skeleton 2725, dental age c. two and half months, (3) age of this size class based on Ehrenberg (1964), (4) skeleton 2724, dental age c. seven months (GL: greatest length).

(< 3 months) were identified by Cordy (1974). Also jaws from the cave Trou du Sureau (bone horizon 4) at Montaigle, Belgium and from the cave of Hastière (horizon 3), Belgium, can be placed in this age group (Ehrenberg, 1935a, b), indicating a difficult period at birth and when the cubs were around two months displaying risky behaviour (see further). Bone horizon 4 of Trou du Sureau contained Aurignacian and Mousterian artefacts, horizon 3 from Hastière yielded Mousterian material (Otte, 1979).

Preliminary results on the cave bears of Chamber A, bone horizon 3 from Goyet indicate a different timing of the winter rest. Here, cave bear jaws were found with the germ of the P4 enclosed in the jaw and with the protoconide and metaconide of the M1 above the rim of the alveolus, which based on Dittrich (*ibid.*: 88-89) are from cubs of circa four months old (Plate 2, Fig. 2). We correlate the high mortality of this age group with the end of the winter rest, pointing to a dormancy period of about five and a half months for the pregnant females that gave birth during that winter (Table 8). The cave of Princesse Pauline yielded cub remains of about five months old (Cordy, 1974).The skeleton described by Ehrenberg (1964) from the Hartlesgraben cave, Austria, is slightly older: in the upper jaw the P4 is not completely erupted, the upper first molar is completely erupted while the M2 germ is present. In the lower jaw, the I1 and I2 are erupting, the germs of P4 and M2 are present and M1 has erupted. Based on Dittrich (*ibid.*: p. 89) this points to an age of about 5,5 months.

The cave Trou du Sureau at Montaigle (horizon 4) and the horizon 3 in the cave of Hastière also contained bear material of about seven months as we can deduce from the description in Ehrenberg (1935a, b).

In the cave of Princesse Pauline (Cordy, *ibid.*) and of Goyet, Chamber A (horizon 3) remains of cubs with an age of 14 months also occur, dying in their second winter rest.

The dentition from the upper jaw will not be discussed in detail here. However, in general the data for the upper jaw are comparable to those of the lower jaw.

Isolated teeth

Stiner (1998) studied the *Ursus deningeri* remains from the Middle Pleistocene deposits in Yarimburgaz cave, Turkey. She divided the permanent cheek teeth into nine age cohorts, based on the development of the jugal teeth and the rate of wear of the crown. Stiner (*ibid.*) concluded that the bear remains in this cave resulted primarily from non-violent mortality in a hibernation den.

The same excercise on the isolated teeth of Goyet, Chamber B was performed (Fig. 5). Cohorts I and II are clearly predominant. There is a sharp decline after cohort II. Prime adult bears are under represented followed by a soft rising to a second maximum at cohorts VIII and IX of very old bears with extremely worn teeth. Juveniles (cohorts I-III) represent 60%, prime adults 21% and old adults 19% of the isolated jugal teeth. There is a slight difference with the diagram for the Deninger's bear from Yarimburgaz cave where the first peak occurs in cohort III. According to Stiner (1998), this points to a higher death rate for the young bears during their first winter without their mother. Mortality in Goyet was higher in cohorts I and II than in the Yarimburgaz cave. Probably climatic conditions were at c. 35,500 year ago more severe in Goyet than during the Middle Pleistocene in Yarimburgaz, Turkey, and the mother bears in Goyet had to cope with harder conditions, resulting in a higher mortality rate for younger cubs. The frequency distribution of the STINER's age cohorts from Goyet, Chamber B is comparable to the one of cave bear teeth from the Bärenhöhle-Hohlenstein in the Swabian Alb, Germany (WEINSTOCK, 2000).

Postcranial skeletal elements

The dental age groups can be found in the postcranial material as well. In what follows the humerus and radius are treated in detail since specimens of these bones of varying age are well represented.

Humerus

Figure 6 gives the distribution of the total length of humeri from neonates to subadult cave bears from Goyet, Chamber B, horizon 4. Five sequences can be distinguished: from 25 mm to 35, from 65 to 85 mm, from 135 mm to 205 mm, from 265 mm to 295 mm and from 335 to 345 mm.

The first sequence contains neonates and very young cubs. According to plates 115, 116 and 117 of EHRENBERG (1931) and figures 3 and 4 of EHRENBERG (1935c), for recent brown bear and cave bear cubs, dimensions between 25 mm to 35 mm corresponds with bears from a few days to one week old. Probably the large number of humeri in this age group reflects difficulties at birth. Humeri with a length of 35 to 45 mm can be attributed an age of about one to two weeks.

A second mortality peak is indicated by humeri with a length from 65 to 85 mm, including the humerus of cub 2725, with a dental age of two and a half months. Brown bear cubs start to become active at around two months of age. They explore their environment in a playful and adventurous way, but they are not yet very strong and well coordinated enough and can have difficulties to find their way back to their mother (PAZHETNOV *et al.*, 1998). This behaviour probably also occurred in cave bears of the same age: the cubs took too many risks and got lost in the cave or hurt themselves and died. Furthermore, according to ADOLF (1949), the fastest growth rate during the first year happens when the cubs are between two to fourth months. This accelerated growth rate could have diminished the survival changes of the cubs. After the fourth month the growth rate gradually decreases. Possibly this slowing down correlates with better survival changes. At the same time the cubs were becoming stronger and smarter and were able to return to their mother.

The first part (135-175 mm) of the following mortality peak is comparable with the second peak in the age graph of the mandibles, with remains of cubs of between six and seven months, that died in their first spring. The mounted juvenile (2724) with a dental age of seven months has an estimated humerus length of 170 mm. The metacarpals II to V (MC I is missing) in this individual have their proximal epiphyses in the process of fusion, the distal epiphyses are lacking; the phalanges of this individual have fused distal epiphyses with the suture visible, the proximal epiphyses are not present. According to MARKS & ERICSON (1966: 402-403) this stage corresponds in the black bear with an age between 7,5 and 8 months, confirming the dental age. Skeleton 2724 is larger than the one described from the Hartlesgraben cave in Austria by EHRENBERG (1964), which has an estimated dental age of five and a half months (see above).

We assume that the last part of the second sequence corresponds to cubs in their second winter. According to MURIE (1985, p. 17) writing about the brown bears in Alaska: "*The yearlings in spring are about the size of the spring cubs in autumn.*" Apparently cave bear cubs that died in their second winter were not much larger than cubs in their first spring and therefore the length of the humeri do not show a clear "summer-autumn" hiatus. However, if we look into detail to this distribution (Fig. 7), a small hiatus can be observed between first spring and second winter (180-190 mm). In this graph we also added the humeri from bone horizon 3 of the cave of Hastière (own measurements). Here also neonates and cubs of two-three months are well represented. Three humeri are comparable to the humerus from the Hartlesgraben skeleton (EHRENBERG, 1964) with a dental age of 5,5 months (see above). One humerus is much larger and probably has an age of seven months. Also in the mandibles this latter age group is present. This indicates that the bear assemblage from Hastière (horizon 3) is not homogenous and has two components: one with a first spring mortality of the cubs at circa five and a half months and another one with a mortality at circa seven months.

The two humeri with lengths between 265 and 295 mm, without their proximal and distal epiphyses, are from subadult animals (Fig. 6). A recent female brown bear in the collection of Recent Vertebrates in the Royal Belgian Institute of Natural Sciences with an age of around 21 months has humeri with the distal epiphyse attached. The epiphyses in female black bear fuse earlier than in the males (MARKS & ERICSON, 1966). The same can be supposed for cave bears. These subadult humeri might represent males that died in their third winter (+/- 24 months or slightly older). The subadult humeri with a length of 340 mm and their distal epiphysis fused are from the mounted subadult 2729, which likely is a male. This animal probably perished in its fourth winter or even in a later winter season.

Radius

Figure 8 gives the size distribution of the radius from young cave bear cubs to subadults. Four sequences can be distinguished: first winter, first spring, second winter and third winter and/or older. Figure 8 includes the radii from Hastière (horizon 3) as well. Again, material with an age of circa five and a half months and of seven months is present. We also added the female brown bear from the collection of recent vertebrates of the RBINS. The radius of this bear of about 21 months has a fused proximal epiphysis. All the radii of the subadult cave bears, except one, have also the proximal epiphysis fused, while the distal epiphysis is lacking, indicating an age of at least 21 months and more. According to MARKS & ERICSON (1966) the fusion of the distal epiphysis of the radius occurs in female black bears at an age of five and a half

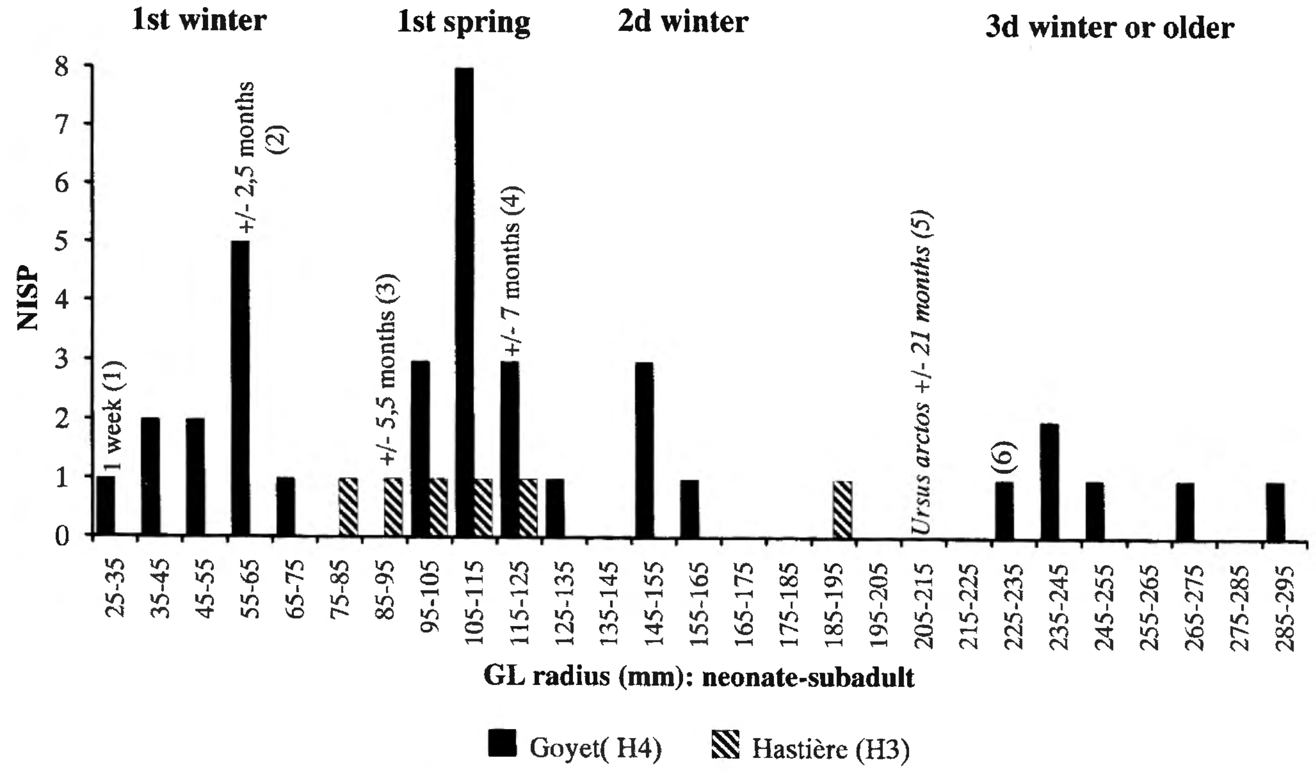


Fig. 8 — *Ursus spelaeus* from Goyet, Chamber B, bone horizon 4 (H4) and from Hastière, bone horizon 3 (H3): immature radii: (1) age of this size class based on EHRENBERG (1931, 1935), (2) skeleton 2725, dental age c. two and half months, (3) age of this size class based on EHRENBERG (1964), (4) skeleton 2724, dental age c. seven months, (5) radius with fused proximal epiphysis of recent subadult *Ursus arctos* of c. 21 months, (6) subadult radius without epiphyses fused (GL: greatest length).

years and in male black bears at an age of six years and seven months. We can conclude that the third sequence contains cave bears in the age category of two years (third winter) until six or seven years.

SEX RATIO

Based on the dimensions of the third incisor and the canine almost 70% of the adult teeth are male, both in NISP and MNI (Table 9, Fig. 9 & 10). The chance that a bear dies inside its den is partly related to the length of time it resides in the hide-out. Pregnant female bears must hibernate for many months in order to allow their cubs to develop (ROGERS, 1987). The winter rest of the males depends mostly on the availability of food. For the herbivorous cave bear the food supply is strongly related to the growth season. According to STINER *et al.* (1998), the longer the plant food is lacking, the more the length of the winter rest of adult males will approach that of the pregnant females and the higher the number of males that can perish inside the cavern. Brown bear females outside the breeding season avoid as much as possible male bears and prefer to select hide-outs where they are save from males (MURIE, 1985). If the hibernation period of the male and female cave bears started simultaneously, the female cave bears were at a disadvantage in selecting a den and the males had the opportunity to chose the most favourable caves, as the one of Goyet with its interesting location at the confluence of the Samson and the Strouvia. The large frequency of male bears in Goyet, Chamber B, horizon 4 might indeed indicate that the males started to look for a den at the same time as the females, who avoided the occupied cave and went else-

Table 9 *Ursus spelaeus*: frequency distribution of sexed third incisors (I3), canines (C), lower jaws and skulls from Goyet, Chamber B, bone horizon 4 (mand: mandibula, NISP: number of identified specimens, MNI: minimum number of individuals).

	maxilla		mandibula		mand.	skull	aver.
NISP	I3	C	I3	C			
n							
male	41	49	24	56	17	5	
female	9	28	8	22	16	2	
%							
male	82	64	75	72	52	71	**69**
female	18	36	25	28	48	29	**31**

	maxilla		mandibula		mand.	skull	aver.
MNI	I3	C	I3	C			
n							
male	21	30	30	33	17	5	
female	7	16	15	11	16	2	
%							
male	75	65	67	75	52	71	**67**
female	25	35	33	25	48	29	**33**

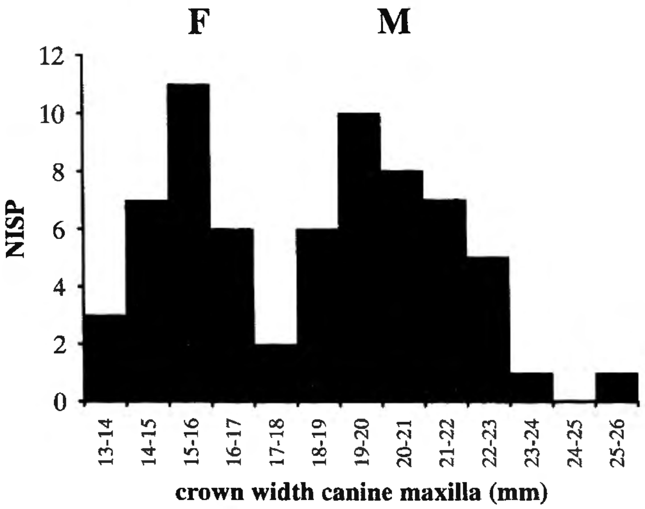


Fig. 9 — *Ursus spelaeus* from Goyet, Chamber B, bone horizon 4: frequency distribution of the crown width (mm) of the upper canine.

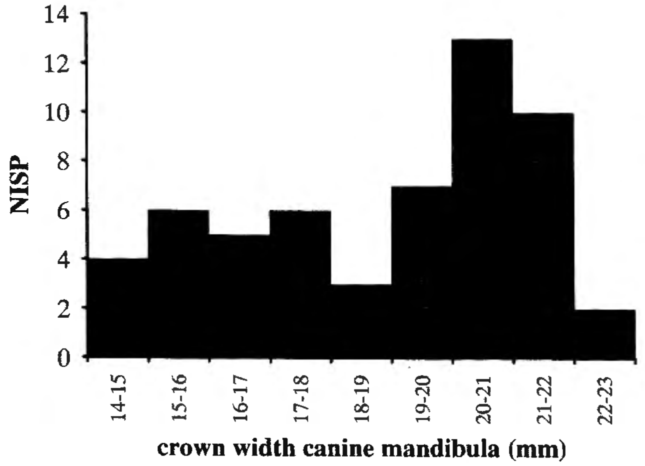


Fig. 10 — *Ursus spelaeus* from Goyet, Chamber B, bone horizon 4: frequency distribution of the crown width (mm) of the lower canine.

where. The preponderance of male cave bears in an assemblage from a site with an interesting ecological location could therefore imply an early start of the winter season. Also REISINGER & HOHENEGGER (1998) found a correlation between the sex ratio of the cave bears in Alpine sites and the location of their dens. Caves in an ecologically extreme area (high altitude) are female biased as a result of the need of the females to protect their cubs from male intruders.

According to EHRENBERG (1935b), in the Trou du Sureau at Montaigle male bears also dominate the assemblage, and as for Goyet, Chamber B, the cubs were, when they emerged for the first time out of the cave, probably about seven months old, implicating a long winter season. At the cave of Hastière, EHRENBERG (1935a) found a more equal ratio between male and female bears. The postcranial material indicates that at least part of the bears abandoned the cave earlier, when the cubs were around five and a half months old. At Chamber A (horizon 3) of Goyet, preliminary results indicate a preponderance of female individuals (c. 70% of the isolated canines) and a short dormancy period for the pregnant females of about five and a half months (see above). This suggests a milder climate which could induce the male cave bears to feed longer during autumn than the pregnant females, who retired earlier to the cave. The males started then to select their den later and had to be content with less interesting caves since the better ones were already taken.

PATHOLOGIES

Eight cave bear bones show traces of pathologies, giving a total of only 0.4% of the cave bear assemblage afflicted. According to EHRENBERG (1935a), the cave bears from Hastière were also healthy. In the bear assemblage from Goyet, Chamber B, two cases of fusion between adjacent bones are present: a central tarsal bone is fused with a first tarsal bone and a incomplete metapodial is fused with a first phalanx. One Mt IV has several bony outgrowths (periostitis ossificans). A fibula displays at it distal end bony outgrowths with an outlet which, based on BREUER (1931a) could be osteomyelitis caused by a bacterial infection. A tibia from a female and a femur from a cub of six-seven months show a periostitis ossificans with clear boundaries comparable to the one described by BREUER (1931b, plate 106) on a cave bear radius. According to this author such a periostitis is caused by trauma. One thoracic vertebra show bony excrescences on the vertebral body. A remarkable upper jaw of a cub of 12-14 months has, between the erupted first molar and the erupting second molar, a supplementary abnormal tooth, carrying two crowns on one root (Plate 3, Fig. 1). BREUER (1931b, plate 91) also found surnumerous teeth in the skull of a cave bear that died at the age of one year in the Drachenhöhle, Austria.

TRACE FOSSILS

Root marks

A small number of bones (18) assigned by Dupont to Chamber B carry root traces. Most of these bones have a darker colour than the rest of the bones. Since roots can only develop in the lightened part of the cave (GERMONPRÉ, 1996), these bones were added inadvertently to the Chamber B assemblage.

Charriage-à-sec

Charriage-à-sec was described by KOBY (1941). He explained that bones found in bear dens maybe broken and abraded by being moved over the floor by walking bears. Twenty-seven bones (1,3%) from Chamber B show abrasion caused by charriage-à-sec. Most abraded bones are small: metapodials (63% of the damaged bones) and carpals and tarsals (26%); generally only the anterior surface is abraded perhaps suggesting abrasion in the most stable position. The low percentage of abraded bones indicates that the carcasses were not very much disturbed by bears or other animals. Possibly the cubs are responsible for the abrasion: maybe the big bones were to large for them to move, while the small metapodials and carpals and tarsals posed no problem. Brown bear cubs show play behaviour from an age of two months onwards (PAZHETNOV *et al.*, 1998). It is possible that Chamber B was used only during a relatively short period by the cave bears so that there was not a prolonged circulation during which the bones were moved to the side, being broken and abraded in the process.

The small amount of charriage-à-sec and broken bones could be explained by an biased excavation by Dupont. In general, the bone assemblage from horizon 4 in Chamber B is composed of unbroken bones, only 15% of the post-cranial material is broken. In the bone assemblage from the Magdalenian horizon 1 in Chamber A, several non-identifiable specimens were collected (36,5% of all the bones) as well as a lot of broken specimens (85% of the postcranial material). Also in bone horizons 2 and 3 large quantities of unidentifiable and broken remains were gathered. So the presence of only a few abraded and broken bones in horizon 4 is probably a consequence of the better preservation of the bones from this assemblage and not of a biased excavation.

Gnawing marks and etching

In Chamber B one cave bear humerus displays gnawing traces of a rodent. Predator or scavenger action on the cave bear bones is indicated by punctures and gnawing marks on a total of 109 bones (5,2%). This relatively small percentage is much lower than the frequency of gnawed bones observed in recent spotted hyena dens near Koobi Fora, Kenya (LAM, 1992) and near Syokimau Farm, Kenya (BUNN, 1983), with respectively 38% and 50.4% of the bones gnawed.

In general, the characteristics of the gnawing compare with those due to wolf (*Canis lupus*) and spotted hyena (*Crocuta crocuta*), as observed by HAYNES (1983). The punctures are conical and have mostly a diameter of 6 mm. One large rectangular puncture resembles that of an ursid as described by LYMAN (1994). A cervical vertebra from a co-articulating series of three, from a young animal, carries two punctures in opposition on the dorsal and ventral side. Both wolf and cave hyena were present in Chamber A, but lack in Chamber B (Table 1). Remains from cave hyena were also discovered further down the gallery (Dupont's unpublished notes).

Table 10 *Ursus spelaeus*: distribution of carnivore punctures, etching and gnawing marks from Goyet, Chamber B, bone horizon 4 (NISP: number of identified specimens, carn.dam: bones damaged by carnivores).

mandibula + limb bones	NISP	n carn. dam.	% carn. dam.
1st winter	61	1	1,6
1st spring	66	14	21,2
2d winter	32	4	12,5
subadult	62	9	14,5
adult	152	33	21,7
	373	61	

Pitting and dissolution of the bone surface by stomach acids occur on six bones (0,3%). The frequency of this phenomenon is very low. The carnivore responsible is probably the cave hyena. However, the rarity of the gnawing marks and etching indicates that the hyenas rarely met the cave bears; the latter probably abandoned the cave once the hyenas moved in. An AMS date for hyena remains from Chamber A is roughly contemporaneous (35,000 BP) with the one on the cave bear bone from Chamber B (Table 1).

Table 10 gives the distribution of all carnivore damage on the aged lower jaws and limb bones. All age groups are affected. However, cubs of the first spring show a higher percentage (21,2%), compared to first winter (1,6%) and second winter cubs (12,5%). Perhaps carnivores took advantage of the fact that the mothers left their young alone while they went out to look for food at the end of the winter rest. The high frequency of damaged adult bones can be expected since bones from this age group are much stronger and survive carnivore attack more easily.

Humanly induced traces

DUPONT (1873) points to the presence of ochre nodules in the three upper bone horizons of Chamber A. More than seven percent of all the bone fragments from horizon 1, dating from the Magdalenian, have traces of red ochre (GERMONPRÉ, 1996). Iron oxides had different functions in prehistoric life: they formed the basis for artistic techniques or were related to domestic activities such as the preparation of animal skins (COURAUD, 1988).

Three cave bear bones (0,1%) from Chamber B carry traces of ochre: a metatarsal and two rib fragments. These bones came in contact with spilt ochre or were manipulated by prehistoric people. Two cave bear bones (0,1%) with cut marks were recognised. Different stages of butchering can leave traces on bones: skinning, dismembering, removal of meat, removal of tendons. The marks on a pisiforme (dorsal part) from a female cave bear and a third metacarpal (dorsal part of distal epiphysis) of a male can be related to skinning. One cave bear tibia show a spiral fracture and one astragalus (0,1%) shows a conspicuously breakage, which could be caused by Palaeolithic visitors. In total, seven cave bear bones (0,3%) appear to be modified by prehistoric people.

Few documents exist on the utilisation of cave bear by prehistoric men. In the Aurignacian horizon of cave Princesse Pauline, situated five km northwest of Goyet, CORDY (1974) observed cut marks and traces of burning on the cave bear remains. A canine of an adult female is coloured by ochre. CORDY (*ibid.*) concluded that the Auriginacians hunted the bears during the hibernation. BARYSHNIKOV & DAVID (2000) mention cut marks on cave bear remains from Chatelperronian levels in the Grotte du Renne in Arcy-sur-Cure, France. At the Divje babe I cave in Slovenia, only few cut marks on cave bear bones were observed. A cave bear femur with holes has been interpreted as a Mousterian flute (TURK *et al.*, 1997; OTTE, 2000). But this interpretation is highly controversial (D'ERRICO *et al.*, 1998; CHASE & NOWELL, 1998).

Summing up the available data suggest that Palaeolithic people did not interfere much with cave bears.

USE OF CHAMBER B AS A DEN

Brown bears are rather choosy about their winter den. They prefer dry caves, often with a difficult access and hidden entrance. They like to close the entrance with branches of trees. Once they found an undisturbed cave, they like to return to it for several winters. However, they abandon it when bothered by hunters or tigers. Brown bears always hibernate alone except for the female with her cubs, and siblings their first winter alone (COUTURIER, 1954; HEPTNER *et al.*, 1974; MURIE, 1985).

The location of the third cave of Goyet in the small valley of the Samson near the valley of the Strouvia, must have been attractive for cave bears. In spring, they could forage in the valleys where, like modern brown bears, they probably were looking for plants with fleshy roots growing on the river banks. In summer, they could find grasses and berries in the valleys and on the slopes, and later in the season they could again forage for roots. According to MURIE (*ibid.*), grizzlies in Alaska tend to use the same ranges, with which they are thoroughly familiar, year after year. Families like to remain in a valley, although males cover larger areas.

Many cave bears visited the cave and at least 88 individuals (cubs, males and females) died in Chamber B. According to KURTEN (1958, p. 34) the mortality rate at Odessa for the mother bears with young is about 17%. We use the skeletal element with the highest MNIe (18 female upper canines: isolated and in the skull) to calculate the group size of mother bears needed to give a "harvest" of 18 dead females. We obtain a number of at least 106 female bears, passing winter in the cave of Goyet. Accepting a mean litter of two cubs and supposing that alle female bears were giving birth every three years (CHURCHER, 1999), 141 cubs were born during 106 winters. KURTEN (1995 p.117) gives a first-winter mortality rate of 19.1%. This figure agrees with a mortality of 30-40 % for brown bear cubs in their first year of life (BUNNELL & TAIT, 1985). MURIE (1985) gives a loss of cubs in their first year of 31%. The number of dead cubs aged from one day to seven months in Chamber B, following KURTEN (*ibid.*), should be around 27. Seventeen MNIe mandibles of cubs of this age group were collected by Dupont or 63% of the expected amount. This is a close match taking into account the preservation chances of fragile juvenile material and the possible sampling bias. The postcranial material in this age group gives even a better representation with 93% for the humerus (MNIe: 25); the MNIe for the radius, ulna, femur and tibia are resp. 22, 11, 18, 15 in this age group.

Six (MNIe) lower jaws from young bears in STINER cohort III are present (Table 6). According to the life table of KURTEN (1958, table 10) at average 23% of cubs died in their third winter, suggesting that at least 26 young bears of this age group had their den at Goyet. Since sibling pairs, after being chased by their mother, often stay together during their first winter alone, this could indicate a winter occupation by this age group for some 13 dormancy periods.

According to KURTEN (1958 p. 30) annual mortality for adults fluctuated around 17%. The MNIe of the lower canines of males is 37 (isolated and *in situ*), leading to a minimal of 218 male bears that occupied the cave as a winter residence. Since brown bears tend to hibernate alone (COUTURIER, 1954; HEPTNER *et al.*, 1974; MURIE, 1985) and Chamber B of the cave of Goyet is rather small, we assume that the cave bears preferred to overwinter here alone. Chamber B would then have been used by male bears, one after the other, for more than two centuries. Also the low frequency of broken bones and charriage-à-sec could indicate that Chamber B was not crowded. Since mothers with cubs, males and young motherless bears probably did not den together, the occupations in Chamber B by the different age groups of cave bears can be added up.

We conclude that somewhere in the range of 37-34,000 years ago the cave of Goyet (Chamber B, horizon 4) was used as a den exclusively by cave bears for at least three and a half centuries. Males occupied the cave more often than females with young. This male-biased sex ratio is probably induced by a simultaneously selecting of the caves by the male and female bears, causing the females to avoid the caves with an ecologically interesting location. This could point to an early ending of the autumn indicating a rather severe climate.

Conclusion

The cave bear material from bone horizon 4 in Chamber B at Goyet is very well preserved and all skeletal elements are represented. Most bones are more or less complete. Several articulated skeletons and body parts were discovered. Charriage à sec, which points to trampling of the remains, is very restricted. All this indicates that the carcasses remained relatively undisturbed until they were covered by sediment, although carnivores and prehistoric men sporadically had access to them, as shown by carnivore damage and the few bones modified by Palaeolithic people.

During the dormancy period the mortality rate of the cubs fluctuated: it was relatively high for newborn cubs, it diminished after a few weeks. It increased at an age of two-three months, probably because of adventurous behaviour without enough skills to return to their mothers, and/or an accelerated growth. At an age of three months the mortality rate decreased again. A new peak was reached when the cubs left their overwintering den for the first time at the start of the growth season. During consecutive years, these cubs succumbed at an age of six to seven months old, when adapting to a life outside the den. This indicates a precise timing of the abandoning of the den every year, implying a homogeneous climatic phase during which bone horizon 4 accumulated. The mortality rate was again relatively high in the first months of the second winter rest.

The total dormancy period for pregnant female cave bears in Chamber B at Goyet, which likely gave birth in November or December, lasted between seven and a half to eight and a half months. The male bears probably had a shorter dormancy of about six and a half to seven and a half months. The very long winter rest of the female cave bears of Goyet, Chamber B, horizon 4, indicates that these animals were living during a relatively severe climatic phase, with a long winter and a late start of spring. The preponderance of male bears points to a simultaneously retreat of the males and females to their den sites at the early start of the winter. The AMS date of circa 35,500 years BP places this population somewhere in the range of 37-34,000 years ago, at the beginning of the Huneborg interval. This period was in the Netherlands characterised by prolonged snow cover (KASSE *et al.*, 1995). Recent brown bears avoid snow (PAJETNOV, 1998) and the same probably applies to cave bears as well. The presence of a prolonged snow cover could be a supplementary necessity for the cave bears at Goyet, Chamber B, horizon 4 to have a long winter rest in order to shun the snow which could betray their whereabouts. Around 500 bears used the cave during minimally 350 years and at least 88 cubs, females and males died here. Many cubs typically died in spring, when they were switching from a residence in the cave to an outdoor life.

In Europe the season of birth and the timing of the winter rest of the cave bears no doubt varied according to the climatic conditions, just as is the case for recent brown bears. In Belgium, several cases of different lengths of winter rest have been found. In Chamber A, horizon 3 at Goyet, bears abandoned the cave when the cubs were around four months old. The dormancy period for the pregnant females probably lasted at this time five and a half months indicating a milder climate with a later birth season and an earlier spring for horizon 3 in Chamber A than for Chamber B, horizon 4. In the assemblage from horizon 3, remains of female bears are more frequent. This suggests a milder climate which could induce the male cave bears to feed longer during autumn than the pregnant females, which retired earlier to their den than the males. Later in autumn, the males probably selected an unoccupied cave elsewhere. A cave bear bone from Chamber A, horizon 1, can be placed in the Hengelo interstadial (Table 1). In the cave Princesse Pauline, CORDY (1974) recognised cubs from one month up to five months and from 14 months; he tentatively assigns this horizon to the Arcy-Kesselt interstadial. At Hastière, the Mousterian horizon 3 yielded cubs of about five and a half months. The frequency of male cave bears, based on the canines (EHRENBERG, 1935b) equals the female frequency, confirming the milder winter season. However, in the same general context cubs of seven months were collected, suggesting that the Hastière assemblage may not be homogeneous. The winter rest of the bears from bone horizon 4 at Trou du Sureau, Montaigle had a duration of about eight months, just as for the bears from Chamber B, horizon 4 in Goyet, and male bears clearly dominate.

It is hoped that further research on the Belgian cave bear populations will confirm a different timing for the birth season and the dormancy period for the *Ursus spelaeus* in its most northwestern outpost and correlate its winter rest with the changing climatic and ecological conditions of the Weichselian. In addition, the relation between cave bear and prehistoric man, which was not always one of total avoidance, can be clarified by looking into detail to well preserved cave bear dens.

Acknowledgements

The second author was invited in 1995 and 1996 by the Royal Belgian Institute for Natural Sciences (RBINS) to work on the Goyet material. A. Gautier, J.P. Brugal and A. Turner helped with the manuscript. M. Van Strydonck is thanked for a free AMS date. J. van der Plicht made the other AMS dates. D. Kindt gave access to the caves of Goyet. The Schoolmuseum, Mr Bron and G. Lenglet gave access to the bear material in their care. A. Wauters, W. Miseur and H. Depotter helped with the iconography.

References

ADOLF, T.A., 1949. Rost i razvitie medvejat po nablioudenijam v Moskovskom zooparke v 1940g. *Trudy Moskovskogo zooparka*, **4**: 78-91 (in Russian).

ANDREWS, P. & TURNER, A., 1992. Life and death of the Westbury bears. *Annales Zoologici Fennici*, **28**: 139-149.

BANFIELD, A.W.F., 1974. The mammals of Canada. National Museum Natural Sciences, University of Toronto Press, Toronto, 437 pp.

BARYSHNIKOV, G.F., 1991. *Ursus meditarraneus* v pleistocene Kavkaza i zametsanija po istorii melkich medvedei Evrazii. *Trudy Zoologiceckogo Instituta AN SSSR*, **238**:3-60 (in Russian).

BARYSHNIKOV, G. & DAVID, F., 2000. Les ours des cavernes à Arcy-sur-Cure (Yonne, France) - *Ursus (Spelearctos) spelaeus* ROSENMÜLLER et HEINROTH, 1794. *Quaternaire*, **11**: 65-79.

BOCHERENS, H., BILLIOU, D., PATOU-MATHIS, M., BONJEAN, D., OTTE, M. & MARIOTTI, A., 1997. Paleobiological implications of the isotopic signatures (^{13}C, ^{15}N) of fossil mammal collagen in Scladina cave (Sclayn, Belgium). *Quaternary Research* **48**: 370-380.

BREUER, R. 1931a. Zur Anatomie, Pathologie und Histologie der Zähne und der Kiefer von *Ursus spelaeus*. *In*: ABEL, O. & KYRLE, G. (Editors), Die Drachenhöhle bei Mixnitz. *Speläologische Monographien*, **VII-IX**: 581-610.

BREUER, R. 1931b. Pathologisch-anatomisch Befunde am Skelette des Höhlenbären. *In*: ABEL, O. & KYRLE, G. (Editors), Die Drachenhöhle bei Mixnitz. *Speläologische Monographien*, **VII-IX**: 611-623.

BUNN, H.T., 1983. Comparative analysis of modern bone assemblages form a San hunter-gatherer camp in the Kalahari Desert, Botswana, and from a spotted hyena den near Nairobi, Kenya. *In*: CLUTTON-BROCK, J. & GRIGSON, C. (Editors), Animals and archaeology, Volume 1, Hunters and their prey, *British Archaeological Reports, International Series* **163**: 143-162.

BUNNELL, F.L. & TAIT, D.E.N., 1985. Mortality rates of North American bears. *Arctic*, **38**: 316-323.

BÜRGL, H. 1938. Morphologische und funktionelle Analyse der Wirbelsäule des Höhlenbären I. *Palaeobiologica* **6**: 65-110.

CHASE, P.G. & NOWELL, A., 1998. Taphonomy of a suggested Middle Paleolithic bone flute from Slovenia. *Current Anthropology*, **39**: 549-553.

CHURCHER, C.S., 1999. Grizzly or brown bear. *In*: WILSON, D.E. & RUFF, S. (Editors). The Smithsonian Book of North

American Mammals, Smithsonian University Press, Washington D.C.: 160-163.

Cordy, J.-M., 1974. La faune aurignacienne de la grotte Princesse Pauline à Marche-les-Dames. *Bulletin de la Société royale belge d'Anthropologie et Préhistoire*, **85**: 243-252.

Cordy, J.-M., 1988. Apport de la paléozoologie à la paléoécologie et à la chronostratigraphie en Europe du Nord-Occidental. *In*: Laville, H. (Editor). L'Homme de Néandertal. Volume 2: L'environnement. *Etudes et Recherches Archéologiques de l'Université de Liège*, **29**:55-64.

Couraud, C., 1988, Pigments utilisés en préhistoire. Provenance, préparation, mode d'utilisation, *L'Anthropologie*, **92**: 17-28.

Couturier, M.A.J., 1954. L'ours brun. Grenoble, 904 pp.

Craighead, F.C. Jr. & Craighead, J.J., 1972. Grizzly bear prehibernation and denning activities as determined by radiotracking. *Wildlife Monographs*, **32**: 1-35.

Dansgaard, W., Johnsen, S.J., Clausen, H.B., Dahl-Jensen, D., Gundestrup, N.S., Hammer, C.U., Hvidberg, C.S., Sstreffensen, J.P., Sveinbjörnsdottir, A.E., Jouzel, J. & Bond, G., 1993. Evidence for general instability of past climate from a 250-kyr ice-core record. *Nature*, **364**: 218-220.

Debeljak, I., 1996. Ontogenetic development of dentition in the cave bear. *Geologija*, **39**: 13-77.

D'Errico, F., Villa, P., Pinto Llona, A.C. & Ruiz Idarraga, R., 1998. A Middle Palaeolithic origin of music? Using cave-bear bone accumulations to assess the Divje Babe I bone "flute". *Antiquity*, **72**: 65-79.

de Torrez Perez-Hidalgo, T. 1988a. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Iberico: I. Filogenia: Distribucion estratigrafica y geografica. Estudio anatomico y metrico del craneo. *Boletin geologico y minero*, **99**: 3-46.

de Torrez Perez-Hidalgo, T. 1988b. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Iberico (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmüller-Heinroth, *U. arctos* Linneo): II. Estudio anatomico y metrico de la mandibula, hioides, atlas y axis. *Boletin geologico y minero*, **99**: 220-249

de Torrez Perez-Hidalgo, T. 1988c. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Iberico (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmüller-Heinroth, *U. arctos* Linneo): III. Estudio anatomico y metrico del miembro toracico, carpo y metacarpo. *Boletin geologico y minero*, **99**: 356-412.

de Torrez Perez-Hidalgo, T. 1988d. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Iberico (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmüller-Heinroth, *U. arctos* Linneo): IV. Estudio anatomico y metrico del miembro pelviano, tarso, metatarso y dedos. *Boletin geologico y minero*, **99**: 516-577.

de Torrez Perez-Hidalgo, T. 1988e. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Iberico (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmüller-Heinroth, *U. arctos* Linneo): V. Denticion decidual, formula dentaria y denticion superior. *Boletin geologico y minero*, **99**: 660-714.

de Torrez Perez-Hidalgo, T. 1988f. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Iberico (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmüller-Heinroth, *U. arctos* Linneo): VI. Denticion inferior. *Boletin geologico y minero*, **99**: 886-940.

Dewez, M., 1987. Le Paléolithique Supérieur Récent dans les Grottes de Belgique. *Publications d'Histoire de l'Art et d'Archéologie de l'Université Catholique de Louvain,* **57**: 1-466.

Dittrich, L., 1961. Milchgebissentwicklung und Zahnwechsel beim Braunbären (*Ursus arctos* L.) und anderen Ursiden. *Gegenbaurs morphologisches Jahrbuch*, **101**: 1-141.

Dupont, E., 1869. (Note sur la découverte d'une caverne à Goyet). *Bulletin de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, **(2), 27**: 193.

Dupont, E., 1873. L'homme pendant les âges de la pierre dans les environs de Dinant-sur-Meuse. Deuxième édition, C. Muquardt, Bruxelles, 250 pp.

Ehrenberg, K., 1931. Über die ontogenetische Entwicklung des Höhlenbären. *In*: Abel, O. & Kyrle, G. (Editors), Die Drachenhöhle bei Mixnitz. *Speläologische Monographien*, **VII-IX**: 624-710.

Ehrenberg, K., 1935a. Die plistozaenen Baeren Belgiens. I Teil: Die Baeren von Hastière. *Mémoires du Musée royal d'Histoire Naturelle de Belgique*, **64**: 1-126.

Ehrenberg, K., 1935b. Die plistozaenen Baeren Belgiens. II Teil: Die Baeren vom "Trou du Sureau" (Montaigle). *Mémoires du Musée royal d'Histoire Naturelle de Belgique*, **71**: 1-97.

Ehrenberg, K., 1935c. Neue Untersuchungen über das Skelett von neugeborenen Braun- und Höhlenbären. *Verhandlungen der Zoologische-Botanischen Gesellschaft in Wien*, **85**: 5-13.

Ehrenberg, K., 1964. Ein Jungbärenskelett und andere Höhlenbärenreste aus der Bärenhöhle im Hartlesgraben bei Hieflau (Steiermark). *Annalen naturhistorischen Museums Wien*, **67**: 189-252.

Fosse, P., Morel, P. & Brugal, J.P., 1997. Taphonomie et paleoéthologie des ursidés pléistocènes. *In*: Tillet, T. & Binford, L. (Editors), L'homme et l'ours, Colloque international, Auberives-en-Royans, 1-29.

Germonpré, M., 1996. Preliminary results on the mammals of the Magdalenian upper horizon of Goyet (Belgium). *Notae Praehistoricae* **16**: 75-85.

Germonpré, M.,1997. The Magdalenian upper horizon of Goyet and the late Upper Palaeolithic recolonisation of the Belgian Ardennes. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique, Série Sciences de la Terre* **67**: 167-182.

Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. *Paleobiology,* **9**: 164-172.

Heptner, V.G., Naumov, N.P., Jürgenson, P.B., Sludski, A.A., Cirkova, A.F. & Bannikov, A.G., 1974. Band II: Seekühe und Raubtiere. *In*: Heptner, V.G. & Naumov, N.P. (Editors). Die Säugetiere der Sowjetunion. Gustav Fischer Verlag, Jena, 1006 pp.

Jacobi, R.M. & Pettitt, P.B., 2000. An Aurignacian point from Uphill Quarry (Somerset) and the earliest settlement of Britain by *Homo sapiens sapiens*. *Antiquity*, **74**: 513-518.

Jacubiec, Z., 1993. *Ursus arctos* Linnaeus, 1758 - Braunbär. *In*: Niethammer, J. & Krapp, F. (Editors). Handbuch der Säugetiere Europas. Band 5: Raubsäuger - Carnivora (Fissipedia) Teil I: Canidae, Ursidae, Procyonidae, Mustelidae 1 (Stubbe, M. & Krapp, F.), Aula-Verlag Wiesbaden: 254-300.

Johnsen, S.J., Clausen, H.B., Dansgaard, W., Fuhrer, K., Gundestrup, N., Hammer, C.U., Iversen, P., Jouzel, J., Stauffer, B. & Steffensen, J.P., 1992. Irregular glacial interstadials recorded in a new Greenland ice core. *Nature,* **359**: 311-313.

Kasse, C., Bohncke, S.J.P. & Vandenberghe, J., 1995. Fluvial periglacial environments, climate and vegetation during the Middle Weichselian in the northern Netherlands with special reference to the Hengelo Interstadial. *Mededelingen Rijks Geologische Dienst*, **52**: 387-414.

KOBY, F.E., 1941. Le "charriage à sec" des ossements dans les cavernes. *Eclogae Geologicae Helvetiae*, **34**: 319-320.

KOBY, F.E., 1952. La dentition lactéale d'*Ursus spelaeus*. *Revue suisse de zoologie*, **59**: 511-541.

KOLSTRUP, E. & WIJMSTRA, T.A., 1977. A palynological investigation of the Moershoofd, Hengelo, and Denekamp interstadials in the Netherlands. *Geologie en Mijnbouw*, **56**: 85-102.

KUDATKIN, A.N & CHESTIN, I.E., 1993. Buryi medved. Kavkaz. *In*: VAISFELD, M.A. & CHESTIN, I.E. Medvedi: buryi medved, belyi medved, gimalaiskii medved. Razmeshchenie zapasov, ekologiyia, ispolzovanie i okhrana. Nauka, Moskva: 136-170 (in Russian).

KURTEN, B., 1958. Life and death of the Pleistocene cave bear. A study in paleoecology. *Acta Zoologica Fennica*, **95**: 1-59.

KURTEN, B., 1995. The cave bear story. Life and death of a vanished animal. Columbia University Press, 163 pp.

LAM, Y.M., 1992. Variability in the behaviour of spotted hyaenas as taphonomic agents. *Journal Archaeological Science*, **19**: 389-406.

LIDEN, K. & ANGERBJÖRN, A., 1999. Dietary change and stable isotopes: a model of growth and dormancy in cave bears. *Proceedings Royal Society London*, **B**, **266**: 1779-1783.

LOPEZ BAYON, I, OTTE, M., LEOTARD, J.-M. & STRAUS, L.G., 1997. L'occupation des grottes au Paléolithique supérieur. *In*: CORBIAU, M.H. (Editor), Le patrimoine archéologique de Wallonie. Division du Patrimoine, Namur:114-116.

LYMAN, R.L., 1994. Vertebrate taphonomy. Cambridge manuals in archaeology, Cambridge University Press, 524 pp.

MARKS, S.A. & ERICKSON, A.W., 1966. Age determination in the black bear. *Journal of Wildlife Management*, **30**: 389-410.

MURIE, A., 1985. The grizzlies of Mount McKinley.University of Washington Press, 251 pp.

MUSIL, R., 1980. *Ursus spelaeus*. Der Höhlenbär. I-III, *Weimarer Monographien zur Ur- und Frühgeschichte*, 93 + 118 + 112 pp.

NELSON, D.E., ANGERBJÖRN, A., LIDEN, K. & TURK, I., 1998. Stable isotopes and the metabolism of the European cave bear. *Oecologia*, **116**: 177-181.

OTTE, M., 1979. Le paléolithique supérieur ancien en Belgique. *Monographies d'Archéologie Nationale*, **5**: 1-684.

OTTE, M. (2000). On the suggested bone flute from Slovenia. *Current Anthropology*, **41**: 271-272.

OTTE, M. & STRAUS, L.G., 1995. Conclusions et résumé. *In*: OTTE, M. & STRAUS, L.G. (Editors). Le Trou Magrite. Fouilles 1991-1992. *Etudes et recherches archéologiques de l'Université de Liège*, **69**: 229-238.

PAZHETNOV, V.S., 1998. Avec les ours. Actes Sud, Terres d'aventure, Arles: 235 pp.

PAZHETNOV, V.S., PAZHETNOV, S.V. & PAZHETNOVA, S.I., 1998. Postnatal development of sensory systems in the brown bear (*Ursus arctos*). *Zoologicheskii Zhurnal*, **77**: 1051-1057 (in Russian).

RADULESCU, C. & SAMSON, P., 1959. Contribution à la connaissance de la dentition lactéale d'*Ursus spelaeus*. *Eiszeitalter und Gegenwart*, **10**: 205-216.

RAHIR, E., 1908. Etude spéléologique des environs de Goyet et de Hotton (Belgique). *Spelunca*, **7**: 131-150.

RAMSEY, M.A. & STIRLING, I., 1988. Reproductive biology and ecology of female polar bears (*Ursus maritimus*). *Journal of Zoology*, **214**:601-634.

RAN, E.T.H., 1990. Dynamics of vegetation and environment during the middle Pleniglacial in the Dinkel valley (The Netherlands). *Mededelingen Rijks Geologische Dienst*, **44**: 141-199.

RAN, E.T.H. & VAN HUISSTEDEN, J., 1990. The Dinkel valley in the middle Pleniglacial: dynamics of a tundra river system. *Mededelingen Rijks Geologische Dienst*, **44**: 209-220.

REISINGER, C. & HOGENEGGER, J. 1998. Sexual dimorphism in limb bones of Late Pleistocene cave bear (*Ursus spelaeus*, Carnivora, Mammalia) from three caves in Eastern Alps (Austria and Italy). *Bollettino della Societa Paleontologica Italiana*, **37**: 99-116.

REVENKO, I.A. 1993. Buryi medved. Kamchatka. *In*: VAISFELD, M.A. & CHESTIN, I.E. Medvedi: buryi medved, belyi medved, gimalaiskii medved. Razmeshchenie zapasov, ekologiyia, ispolzovanie i okhrana. Nauka, Moskva: 380-403 (in Russian).

ROGERS, L.L., 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in Northeastern Minnesota. *Wildlife Monographs*, **97**: 1-72.

ROGERS, L.L., 1999. American black bear. *Ursus americanus*. *In*: WILSON, D.E. & RUFF, S. (Editors). The Smithsonian Book of North American Mammals, Smithsonian Institution Press, Washington D.C.: 157-160.

SHUBIN, N.G. 1993. Buryi medved. Zapadnaya Sibir. *In*: VAISFELD, M.A. & CHESTIN, I.E. Medvedi: buryi medved, belyi medved, gimalaiskii medved. Razmeshchenie zapasov, ekologiyia, ispolzovanie i okhrana. Nauka, Moskva: 206-214 (in Russian).

STEINBACHER, G., 1963. Zür Trächtigkeitsdauer beim Braunbären (*Ursus arctos*). *Säugetierkundliche Mitteilungen*, **19**: 20-21.

STINER, M.C., 1998. Mortality analysis of Pleistocene bears and its paleoanthropological relevance. *Journal of Human Evolution*, **34**: 303-326.

STINER, M.C.; ACHYUTHAN, H.; ARSEBÜK, G.; CLARK HOWELL, F.; JOSEPHSON, S.C.; JUELL, K.E.; PIGATI, J. & QUADE, J. 1998. Reconstructing cave bear paleoecoloy from skeletons: a cross-disciplinary study of middle Pleistocene bears from Yarimburgaz cave, Turkey. *Paleobiology*, **24**: 74-98.

TURK , I., DIRJEC, J. & KAVUR, B., 1997. A-t-on trouvé en Slovénie le plus vieil instrument de musique en Europe? *L'Anthropologie*, **101**: 531-540.

ULRIX-CLOSSET, M., 1975. Le paléolithique moyen dans le bassin mosan en Belgique. Wetteren, 221 pp.

VAN DEN BROECK, E., MARTEL, E.A. & RAHIR, E., 1910. Les cavernes et les rivières souterraines de la Belgique. Bruxelles, 2 volumes, 1751 pp.

VAN DER HAMMEN, T., 1995. The Dinkel valley revisited: Pleniglacial stratigraphy of the eastern Netherlands and global climatic change. *Mededelingen Rijks Geologische Dienst*, **52**: 343-355.

VAN STRYDONCK, M. *et alii*, in preparation. Royal Institute for Cultural Heritage - Radiocarbon dates XVII.

VON DEN DRIESCH, A., 1976. A guide to the measurement of animal bones from archaeological sites. *Bulletin Peabody Museum*, **1**: 129 pp.

WEINSTOCK, J. 2000. Cave bears from Southern Germany: sex ratios and age structure. A contribution towards a better understanding of the palaeobiology of *Ursus spelaeus*. *Archaeofauna*, **9**: 165-182.

ZAVATZKIY, B.P. 1993. Buryi medved. Centralnaya Sibir. *In*: VAISFELD, M.A. & CHESTIN, I.E. Medvedi: buryi medved, belyi medved, gimalaiskii medved. Razmeshchenie zapasov, ekologiyia, ispolzovanie i okhrana. Nauka, Moskva: 249-275 (in Russian).

Mietje GERMONPRÉ
Departement Paleontologie
Koninklijk Belgisch Instituut
voor Natuurwetenschappen
Vautierstraat 29
B-1000 Brussel
Belgium
mietje.germonpre@kbinirsnb.be

Mikhail SABLIN
Zoological Institute
Russian Academy of Sciences
Universitetskaja nab. 1
199034 Sankt Peterburg
Russia
msablin@mail.ru

PLATE 1

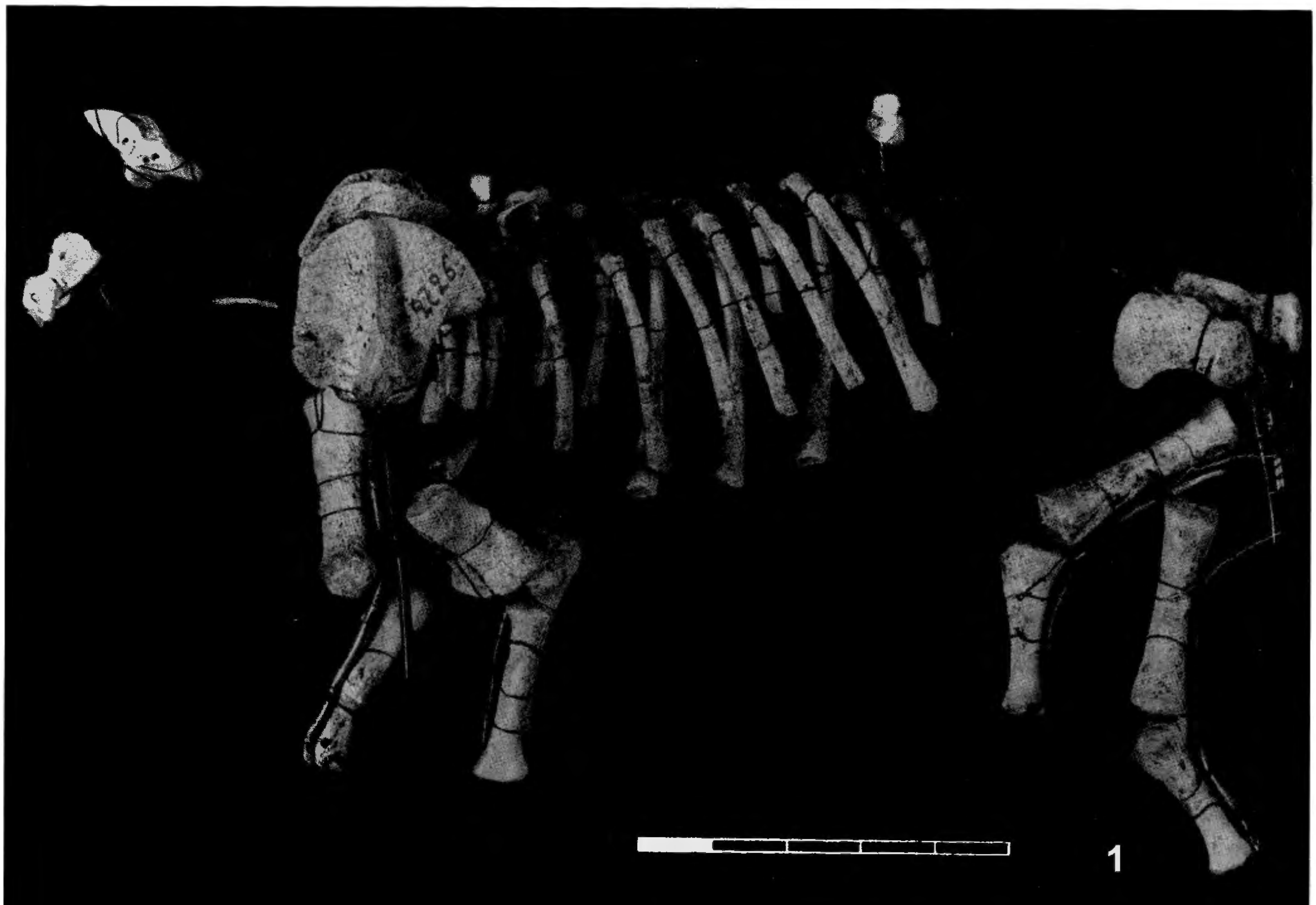
Fig. 1 — *Ursus spelaeus*: newborn cub (skeleton 2726).
Fig. 2 — *Ursus spelaeus*: cub of two and a half months old (skeleton 2725).

PLATE 2

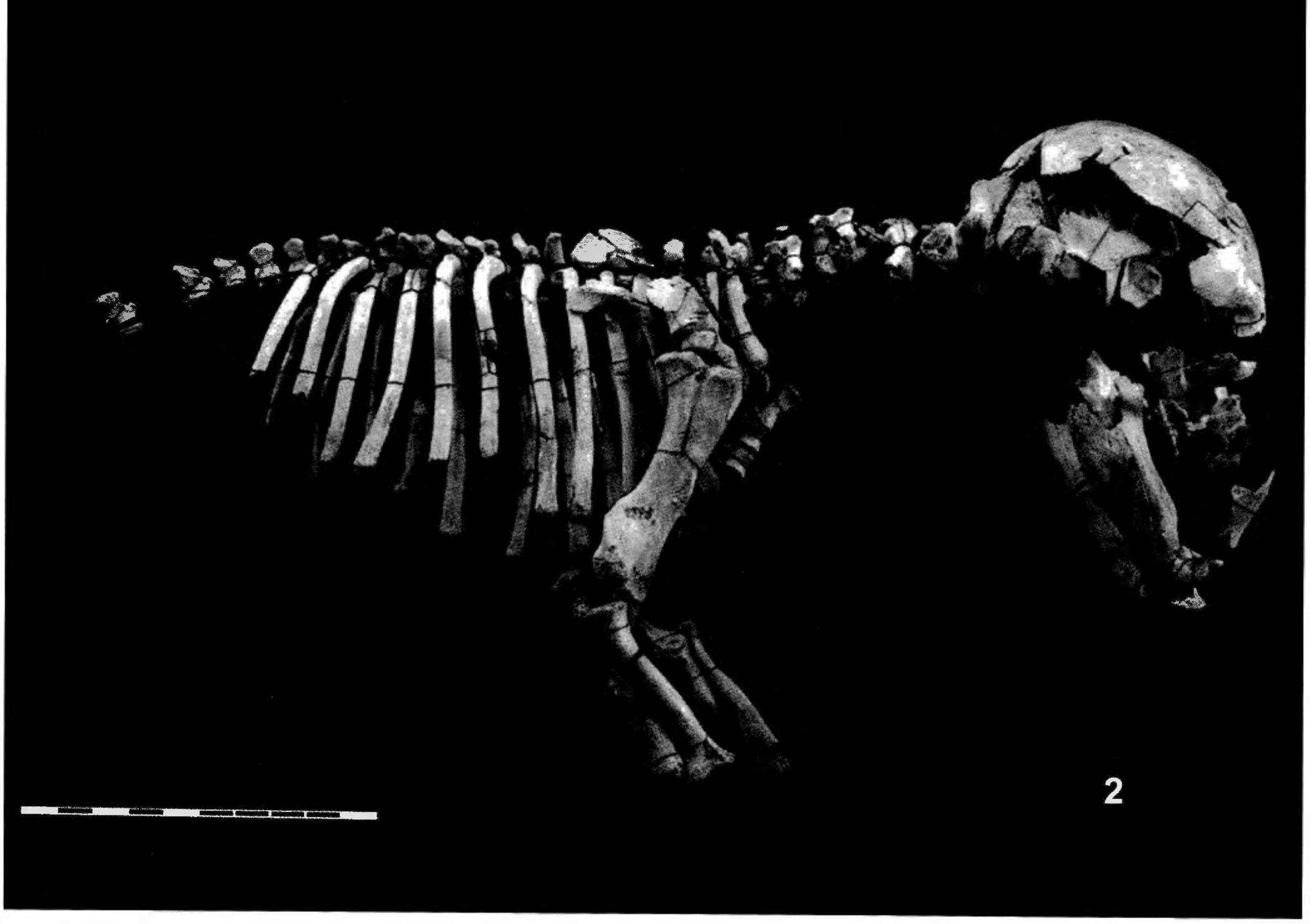
Fig. 1 — *Ursus spelaeus*, Chamber B, horizon 4: lower mandible 2725 of a cub of approximately 2,5 months old: milk canine present, alveolus for dp3 and dp4 present, fissure for M1 (germ in jaw).
Fig. 2 — *Ursus spelaeus*, Chamber A, horizon 3: lower mandible 2763-1 of a cub of approximately 4 months old: erupting M1 with the protoconide and metaconide just above the alveolus rim.
Fig. 3 — *Ursus spelaeus*, Chamber B, horizon 4: lower mandible 2835-3 of a cub of approximately 6 months old: I2 half erupted, emerging P4: protoconide just above alveolus rim, fully erupted M1, erupting M2, germ M3 in vertical ramus.
Fig. 4 — *Ursus spelaeus*, Chamber B, horizon 4: lower mandible 2835-6 of a cub of approximately 7 months old: germ canine present (not visible), P4 half erupted, M1 fully erupted, germ M3 in vertical ramus (not visible).

PLATE 3

Fig. 1 — *Ursus spelaeus*, Chamber B, horizon 4: maxilla of a cub of approximately 12-14 months old: supplementary tooth with double crown between M1 and M2.
Fig. 2 — *Ursus spelaeus*, Chamber B, horizon 4: lower mandible 2835-1 of a cub of approximately 12-14 months old: erupting canine 1-2 cm above alveolus rim, P4, M1 & M2 fully erupted, erupting M3.



1



2

PLATE 1

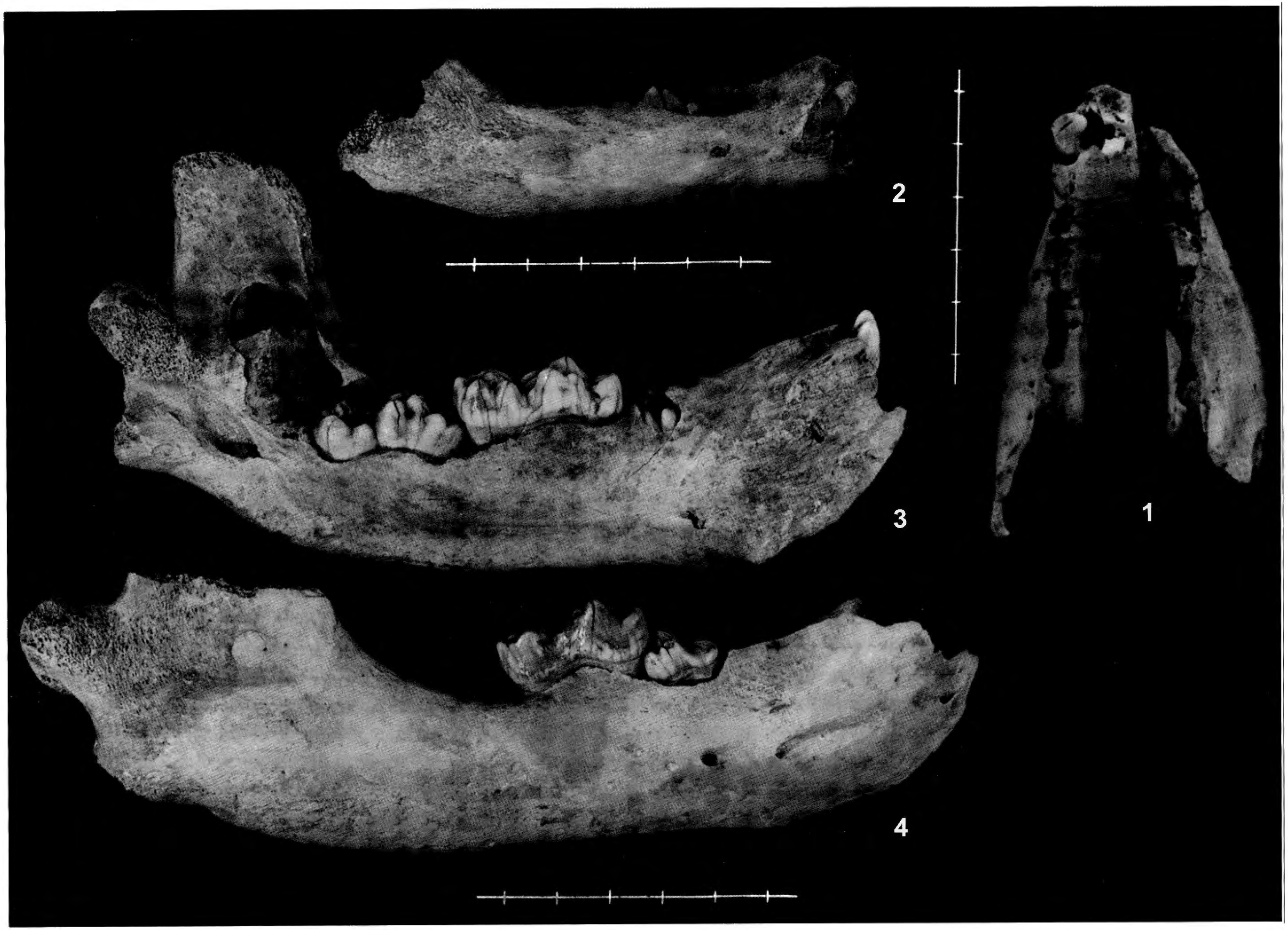


PLATE 2

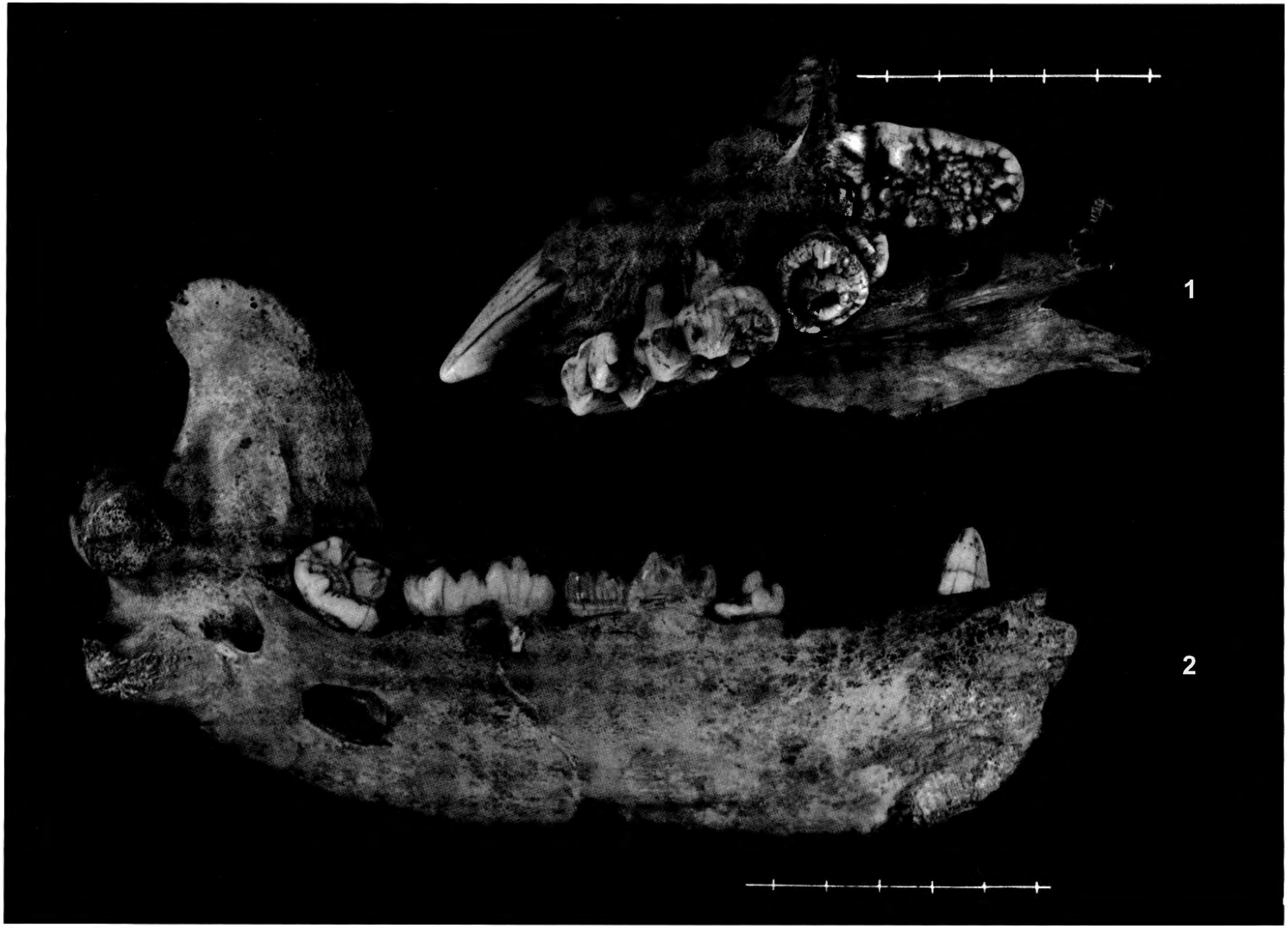


PLATE 3