

# The Pleniglacial cave bears from Goyet, Belgium taphonomic and palaeobiological characteristics

by Mietje GERMONPRE

GERMONPRÉ, M. 2004. – The Pleniglacial cave bears from Goyet, Belgium: taphonomic and palaeobiological characteristics. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique, Sciences de la Terre*, 74: 213-229, 1 pl., 1 fig., Bruxelles-Brussel, December 15, 2004. – ISSN 0374-6291.

## Abstract

Five Pleniglacial cave bear assemblages from the cave of Goyet (Condroz, Belgium) were studied. The assemblages display different distributions of the skeletal elements, divergent proportions of broken bones, worn canines, carnivore gnawed bones and juvenile remains, and different sex ratios of the canines, indicating that most assemblages can be considered as different groups. The Pleniglacial climatic fluctuations had probably a substantial influence on the cave bear populations from the Condroz. Cave bear assemblage B4 is the only male dominated assemblage, with a high frequency of remains from young and prime aged males and from cubs of less than one year old. In cave bear assemblage A2 the proportion of remains of old males is high, while the frequency of juvenile remains is relatively low. Also in cave bear assemblage A3 the frequency of old males was rather high. Cave hyaenas preyed heavily on the bears from this assemblage. The preliminary data of assemblage B5 indicate that this female dominated assemblage yielded also an elevated number of juvenile remains. The data of assemblage A1 do not permit to give detailed conclusions.

**Keywords:** cave bear, Pleniglacial, taphonomy, mortality, sexual segregation

## Résumé

Cinq assemblages d'ours de caverne datant du Pléniglaciaire et provenant de la caverne de Goyet (Condroz, Belgique) ont été étudiés. Les assemblages diffèrent dans la distribution des éléments squelettiques, la fréquence des os casés, la quantité de canines usées, la fréquence des os rongés par des carnivores, le nombre des restes juvéniles et la proportion des mâles et femelles, indiquant que ces assemblages peuvent pour la plupart être considérés comme des groupes différents. Les fluctuations climatiques du Pléniglaciaire ont eu une influence substantielle sur les populations d'ours du Condroz. L'assemblage d'ours de caverne B4 est la seule où les restes des mâles dominent, avec une grande fréquence de restes de mâles jeunes-adultes et d'oursons de moins d'un an. Dans l'assemblage A2 la proportion des restes de ours mâles âgés est haute et la fréquence des restes juvéniles est moindre. Dans l'assemblage A3, la fréquence de mâles âgés est aussi élevée. Beaucoup de cadavres des ours de cet assemblage ont été la proie des hyènes de caverne. Les données préliminaires concernant l'assemblage B5 indiquent que cet assemblage est dominé par des restes de femelles et contient aussi une grande quantité de restes juvéniles. Les données concernant l'assemblage A1 ne permettent pas de tirer des conclusions détaillées.

**Mots-clés:** ours de caverne, Pléniglaciaire, taphonomie, mortalité, ségrégation sexuelle

## Introduction

Since the 19<sup>th</sup> century many cave bear fossils have been discovered in Belgian cave sites (SCHMERLING, 1833; DUPONT, 1869, 1873; EHRENBURG 1935a, 1935b, 1966; SIMONET, 1992). Cave bear assemblages result from the accumulations of remains from bears that died in the cave during successive hibernations. These hibernations could have occurred yearly or were separated by varying time spans, during which occupations by humans or other carnivores could have taken place. The cave of Goyet (50°26'40''N, 5°00'46''E) yielded five cave bear assemblages (DUPONT, 1873). This cave lies in the Condroz, a region south of the Sambre and Meuse valleys in Belgium. The landscape is made of steep-sided valleys cutting through high plateaux of relatively constant altitudes, locally reaching 350 m (PEETERS *et al.*, 2003). The cave site has an interesting topographic position. It is situated at an altitude of 130 m in a limestone cliff 15 m above the river Samson (DUPONT 1873), near the confluence of the Strouvia with the latter. The valley of the Samson has a length of about 15 km. After a sinuous course the Samson joins the river Meuse some 3 km north of Goyet.

## Material and Stratigraphy

The palaeontological collection of the cave of Goyet is since its excavation by Edouard Dupont in the 1860's stored at the Royal Belgian Institute of Natural Sciences (DUPONT, 1873). Unfortunately not much information is available on the stratigraphy and spatial distribution of the remains and artefacts. DUPONT (1873) subdivided the cave of Goyet in three parts: Chamber A, B and C (Fig. 1). Only the bones from Chamber A and B are studied here. Most of the bones carry a number, assigning them to a bone horizon. He described in total five bone bearing horizons inside the cave. In his unpublished notes on the cave of Goyet dating from 1905 and 1906 DUPONT wrote: "Elle possédait cinq riches niveaux ossifères étagés dans des amas d'argile jaune blocailleux. Ils sont numérotés à partir du niveau supérieur". Fossil bones are present near the entrance as well as deeper in the cave.

Chamber A has a length of about 26 m and is 4-5 m wide. The total thickness of the excavated layers at the entrance is more or

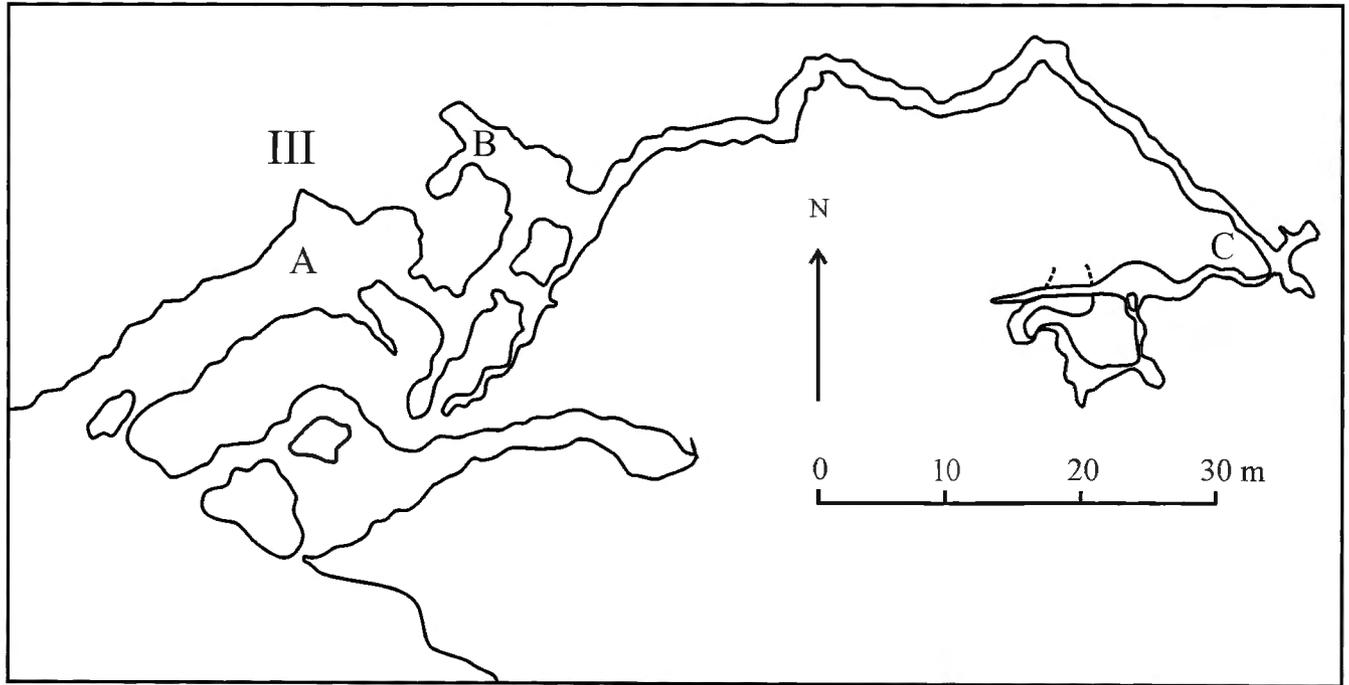


Figure 1 — Map of Chambers A, B and C of the third cave of Goyet modified after Rahir (1908).

less 1.5 m as deduced from the sediment remains on the walls of the cavern, while at the back of the chamber the thickness was around 1.2 m. DUPONT (1873) distinguished four bone and artefact bearing horizons in this chamber, numbered from top to bottom. The Palaeolithic artefacts date from the Mousterian, Aurignacian, Gravettian and Magdalenian. Unfortunately it is not always clear from which horizon they originated. In the lower one, Palaeolithic artefacts were apparently lacking. Aurignacian ivory beads were discovered in Horizon 3. Other spectacular finds include “batons de commandement”, teeth and shell necklaces from the Magdalenian (Horizon 2 and 1) and a bone harpoon (Horizon 1) (DUPONT, 1873; ULRIX-CLOSET, 1975; OTTE, 1979; DEWEZ, 1987; LOPEZ BAYON *et al.*, 1997). The upper three bone horizons contained bones from human refuse. The remains are among others from horse, reindeer, bison, ibex, muskox, mammoth, rhinoceros, wolf and polar fox (GERMONPRÉ, 1996), but include also some Holocene intrusive materials (domesticated animals, badgers) (GERMONPRÉ, 2001; GERMONPRÉ & SABLIN, 2002). In these three horizons the bones from herbivores were often fractured for marrow extraction, have cut marks or ochre stains. Bone horizon 3 was found at the entrance of the cave: “...ce niveau renfermait en effet une grande quantité d’ossements... il renfermait aussi beaucoup de S. taillés, des objets de parure, des os carbonisés; le tout particulièrement vers l’entrée, c’est à dire la partie éclairée du souterrain” (DUPONT, unpublished notes). A sterile clay horizon separated the third and second bone horizon: “Au 3<sup>e</sup> niveau ossifère en était superposé un autre, le 2<sup>e</sup>. Une couche stérile, épaisse de 20 à 80 cm et formée d’argile jaune et de blocailles détachées des parois de la Caverne, les séparait.” The second and first bone horizon were also separated by a sterile horizon: “Une nouvelle couche stérile d’argile jaune blocailleuse, épaisse de 1 à 15 cm, s’étendait sur le 2<sup>e</sup> niveau ossifère et servait de base à un autre, le 1<sup>er</sup>. C’est encore un niveau troglodytique”.

The bear, lion and hyaena assemblages from Horizon 1, 2 and 3 appear not to be related to the human refuse assemblages in the front of Chamber A (GERMONPRÉ 1996, 2001). In his unpublished notes Dupont mentions that the bear and hyaena remains from Horizon 2 were found deep in the cave: “...ces restes de l’Hyène et de l’Ours se trouvaient dans la partie obscure de la Caverne”. Recently some unpublished notes of VINCENT, a collaborator of DUPONT, were discovered in the archives of the Royal Belgian Institute of Natural Sciences. They were interpreted as schematic representations of the spatial distribution of the bones from Chamber A (GERMONPRÉ, 2001). From this it can be deduced that the bulk of the cave bear material probably originated from the back of the chamber, while bones manipulated by Palaeolithic people were apparently discovered near the entrance. Furthermore, plant root traces are very rare on the bear bones. Plant growth can only occur where daylight is present, i.e. close to the cave entrance. Only 2.6% of the cave bear remains from Horizon 1 carrying root traces, 0.6% of the bear bones from Horizon 3 have root marks and no bear bones from Horizon 2 show this type of traces. On the other hand, 15% of the horse bones and 10% of the reindeer bones from Horizon 1 have root traces. The observed frequency of root marks strengthens the suggested spatial distribution of the bear remains. In the late Pleistocene deposits of Denisova cave, Altai, bone fragments with root marks were also only found at the cave entrance (GERMONPRÉ, 1993).

Chamber B lies behind Chamber A and has a length of circa 13 m. Bone horizon 5 yielded remains from cave bear, brown bear and cave lion. This horizon has only been partly studied so far. According to Dupont (unpublished notes), this horizon had a wide extension: “Le cinquième, qui est par conséquent l’inférieur, fut d’abord un repaire de Lion, dans l’anfractuosité B. Animaux craintifs, ils en furent chassés par les grands Ours, animaux de tempérament turbulent qui avaient la coutume

d'expulser les autres fauves de leurs antres, lorsque ceux-ci lui convenaient... Outre le fait de l'évincement du Lion par ce fauve moins jouissant mais plus turbulent et l'autre fait que plusieurs générations d'Ours se succédèrent à ce niveau, il faut noter que, tandis que le Lion se tenait dans les premières galeries obscures (en B), l'Ours occupait la Caverne jusque dans ses parties les plus reculées, même à 100 m et plus de l'entrée". Dupont (unpublished notes) assigns horizon 4 mainly to Chamber B: "Déjà assez développé au fond de la salle d'entrée A, il était surtout en B". The majority of the bones from horizon 4 derives mainly from cave bears, but include also remains from horse, reindeer, bison, hyaena and other species (GERMONPRÉ & SABLIN, 2001). Only 0.7% of the bear bones from this horizon carries root marks.

#### AMS dates

Table 1 summarises the AMS dates of cave bear, cave hyaena, reindeer and horse finds from Goyet (VAN STRYDONCK *et al.*, 2001; *in prep.*). The reindeer and horse bones were manipulated by prehistoric people (ochre coloured, cut marked and/or broken for marrow extraction). The table does not include the dates on cave bear bones with ochre stains, which will be discussed in detail in a forthcoming paper (GERMONPRÉ & HÄMÄLÄINEN, *in prep.*). The dated cave bear bones from Goyet can all be assigned to the Pleniglacial.

The Netherlands is the classic area for describing the interstadials of the last glacial. Furthermore this area is relatively close to the Condroz, that is situated about 250 km south of the Dinkel Valley, where many interstadial deposits were found. During the Pleniglacial the climate changed in the Netherlands from relatively mild during the interstadials to more severe during the stadials and the vegetation varied from shrub tundra to tundra (RAN & VAN HUISSTEDEN, 1990). Probably in the small, protected valleys of the Condroz in Belgium, willows, alders and poplars could grow during the Pleniglacial as well as several types of berries (*Vaccinium*) (DAMBLON, personal communication). The Hengelo Interstadial lasted from 38,700 to 36,900 years BP (KASSE *et al.*, 1995). This Interstadial was followed by the Huneborg Interval (RAN & VAN HUISSTEDEN, 1990). In Northwestern Europe, the mean temperature of the warmest month during the Huneborg Interval was about 10°C, the mean temperature of the coldest month is estimated between -12 and -20°C (HUIJZER & VANDENBERGHE, 1998). The Hu-

neborg Interval is succeeded by the Denekamp Interstadial Complex (c. 32-27,000 BP) (RAN, 1990).

In the ice-core record of Greenland, abrupt climatic shifts, the so-called Dansgaard-Oeschger (D/O) events, occurred repeatedly during the Pleniglacial. These abrupt changes started with a rapid warming taking a few decades, followed by a plateau phase with slow cooling lasting several centuries, succeeded finally by a more rapid decrease to cold stadial conditions. Two types of D/O events exist: short D/O events and long ones. The long events coincide with large N<sub>2</sub>O amplitudes (FLÜCKIGER *et al.*, 2004). In Belgium at least five warm-cold cycles are recorded between about 41 and 27 ka (VANDENBERGHE *et al.*, 1998).

All AMS dates in Table 1 were calibrated with the CalPal programme ([www.calpal.de](http://www.calpal.de), authors: WENIGER, JÖRIS & DANZEGLOCKE). The AMS date of 38,770 y BP (Table 1) from a cave bear bone from Chamber A, Horizon 1 (cave bear assemblage A1) resulted in a Calendric Age calBP of 42,013 +/- 580 with a 68% range calBP of 41,432-42,593. In the new age scale for the GRIP and GISP2 Greenland ice cores proposed by SHACKLETON *et al.* (2004), the D/O event 10 started 42,100 years ago. This event had a duration of about 750 years (FLÜCKIGER *et al.* 2004). The Calendric Age of the cave bear date imply that this assemblage was formed shortly before or during D/O event 10. Cave bear assemblage A1 has been tentatively placed in the beginning of the Hengelo interstadial. Goyet was used as a den by cave bears from this assemblage for at least 50 years (GERMONPRÉ, 2004). Two hyaena bones that originated according to DUPONT (unpublished notes) from the same horizon have different AMS ages (Table 1), pointing to the mixed nature of this horizon.

In Table 1 two AMS dates are given for cave bear bones from Chamber B, Horizon 4 (cave bear assemblage B4). The date of 36,500 +/- 1040 y BP has a Calendric Age calBP of 40,518 +/- 822 (68% range calBP: 39,695-41,340), the second date of 35,470 +/- 780 gives a Calendric Age calBP of 40,087 +/- 828 (68% range calBP: 39,258-40,915). The AMS dates could imply that these bears were present in the beginning of the Huneborg interval (GERMONPRÉ & SABLIN, 2001), probably in the Hengelo/Huneborg Stadial, which according to VAN DER HAMMEN (1995) lasted from 36,500 until 36,000 y BP. In the Netherlands a chinophilous shrub tundra vegetation was present between 36,900 and 35,500 y BP, when prolonged snow covers

Table 1 — AMS dates in years BP of *Ursus spelaeus*, *Crocota crocuta*, *Equus ferus* and *Rangifer tarandus* from Goyet, Chamber A, Horizon 1 (A1); Chamber A, Horizon 2 (A2), Horizon 3 (A3) and from Chamber B, Horizon 4 (B4) (Van Strydonck *et al.*, 2001; *in prep.*; \*Groningen: Centre for Isotope Research)

| AMS (y BP)<br>assemblage | Chamber A<br>entrance<br><i>Equus ferus</i> | Chamber A<br>entrance<br><i>Rangifer tarandus</i> | Chamber A<br>back<br><i>Ursus spelaeus</i> | Chamber A<br>back<br><i>Crocota crocuta</i> | Chamber B<br><i>Ursus spelaeus</i>     |
|--------------------------|---|---|--|---|--|
| B5                       |   |   |  |   | 20,780 +/- 140<br>28,160 + 370-360     |
| A3                       |   | 27,590 +/- 70                                     | 27,440 +/- 165                             |   |  |
| A2                       |   |   | 34,920 + 330-320                           |   |  |
| B4                       |   |   |  |   | 35,470 + 780-710*<br>36,500 + 1040-920 |
| A1                       | 12,560 +/- 50<br>12,770 +/- 90*             |   | 38,770<br>+1180-1030*                      | 27,230 +/- 260*<br>35,000 +/- 400           |  |

could last and accumulate because of low winter temperatures (KASSE *et al.* 1995). The Calendric Ages calBP of the AMS dates could indicate that the cave was utilised by cave bears around the O/D event 9, which according to SHACKLETON *et al.* (2004) started 40,830 years ago. Event 9 was very short with a length of about 250 years (FLÜCKIGER *et al.*, 2004). However, in the stalagmite record of the Villars cave, France, the D/O event 10 is placed between 40,400 and 41,500 years ago (GENTY *et al.*, 2003), which could imply that the cave was used shortly after D/O 10. Chamber B was probably occupied during at least 350 years by cave bears when assemblage B4 was formed (GERMONPRÉ & SABLIN, 2001).

A dated cave bear bone from Horizon 2 (cave bear assemblage A2) has an AMS age of c.35,000 y BP (Table 1). Its Calendric Age calBP is 39,997  $\pm$  680 (68% range calBP: 39,319–40,677). According to Van der Hammen (1995), the Huneborg I interstadial, which belongs to the Huneborg interval, lasted from 36,000 y BP to 35,000 y BP. The calibrated Calendric Age suggests that this bear lived during or shortly after the D/O event 9, that began 40,830 years ago (SHACKLETON *et al.*, 2004). The bears used the cave as a den for at least 150 years during the accumulation of this assemblage (GERMONPRÉ, 2004).

A cave bear canine from Horizon 3 from Chamber A (cave bear assemblage A3) has an AMS date of 27,440 y BP (Table 1), with a Calendric Age calBP of 30,809  $\pm$  407 (68% range calBP: 30,402–31,216). Cave bear assemblage A3 was formed over a period of at least two centuries. So far this assemblage has been assigned to the Denekamp interstadial (GERMONPRÉ, 2004). However, the new data available in SHACKLETON *et al.* (2004) make this improbable. The Calendric Age of the AMS date rather assign the accumulation of this cave bear assemblage to the cold interval between the O/D5 and O/D4 event, that are resp. timed at 33,440 and 30,060 years ago (SHACKLETON *et al.*, 2004).

The AMS dates available so far show that the bears from Chamber B, Horizon 5 (cave bear assemblage B5) seems to be the youngest one at Goyet. The two AMS dates gave a Calendric Age calBP of resp. 24,139  $\pm$  440 (68% range calBP: 23,698–24,579) and 31,720  $\pm$  796 (68% range calBP: 30,923–32,516). More AMS dates are necessary to decide if the assemblage has a duration of several millennia or if one of the two dates is an outlier indicating that the formation of the assemblage can be assigned to a shorter time span. The long interval covered by both dates overlaps the O/D4, O/D3 and O/D2 events and the cold intervals in between.

## Methods

During the excavation of the Goyet cave DUPONT and his workmen collected not only the complete bones, but also thousands of small bone fragments (lengths c. 1 cm). It is clear from the AMS dates of Horizon 1, that DUPONT did not recognise all stratigraphic units. In his opinion (DUPONT, 1873 and unpublished notes) the horizons from Chamber A cover the whole floor of this chamber from the entrance to the back, although he pointed out the different origins of the bones: human-accumulated at the entrance and carnivore-accumulated at the back. In order to evaluate the depositional integrity of the cave bear assemblages from Goyet, the frequency of mutually exclusive taphonomic features in each of the assemblages was compared. The null hypothesis is that the proportion of bones per taphonomic attribute in the assemblages is identical (or not associated). Some dental measurements are compared as well. The null hypothesis is that the assemblages have identical means. The taphonomic characteristics of the cave bear assemblages were statistically analysed with the chi-square test. A few

analyses include cave bear assemblage B5, for which at the moment some preliminary results are available, and the small assemblage A1. For some features, the assemblages were compared pairwise by Fisher's exact test. The comparisons of the dental measurements are based on t-test (two-tailed) or one-way ANOVA. For all statistic tests Graph Pad InStat version 3.00 for Windows 95, GraphPad Software, San Diego California USA ([www.graphpad.com](http://www.graphpad.com)) was used. The level of significance was set at  $\alpha < 0.05$ .

## Results

### Skeletal element representation

Table 2 gives the distribution of the cranial, dental and postcranial remains of cave bear assemblages A3, A2, A1 and B4. Cranial elements, including lower jaw fragments, are in all assemblages the least represented group. Teeth are the most frequent elements in the assemblages of Chamber A: in assemblage A3 61% of the remains are teeth, in assemblage A2 53% and in assemblage A1 65%. Teeth constitute only 25% of the remains in assemblage B4. Postcranial bones are the most frequent in assemblage B4 (71%). The chi-squared test gives a value of  $P < 0.0001$  ( $\chi^2 = 485.16$ ,  $df = 6$ ), indicating that the null hypothesis can be rejected and that the proportions of the three types of skeletal elements in assemblages A3, A2, A1 and B4 are different (associated).

### Complete bones

In assemblage B4 83% of the postcranial remains is complete (Table 3). Furthermore, skeletal parts were often found in anatomical connection. DUPONT (1873) mentions the remains of six articulated skeletons. The associated skeletal parts are discussed in GERMONPRÉ & SABLIN (2001). Also in assemblage B5 many skeletal parts were articulated and most bones are complete (DUPONT, unpublished notes; GERMONPRÉ, preliminary data). In Chamber A more or less half of the bear bones is broken (Table 3) and no articulated remains were collected. The bones were broken due to trampling, carnivore gnawing, rock fall or pressure caused by sediment load. Spiral fractures are extremely rare.

The results of the chi-squared test ( $\chi^2 = 240.29$ ,  $df = 3$ ,  $P < 0.0001$ ) for assemblages A3, A2, A1 and B4 confirm that the numbers of broken and unbroken postcranial bones in the assemblages are different. Furthermore, also the completeness of the long bones differ significantly between the assemblages A3, A2 and B4 ( $\chi^2 = 125.25$ ,  $df = 2$ ,  $P < 0.0001$ ). For these group of skeletal elements again assemblage B4 has the highest frequency of unbroken bones with 80%, followed by A2 (42%) and A3 (16%) (Table 3). The compact metapodial bones are much more complete in the assemblages than the long bones: assemblage B4: 98%, assemblage A2: 86% and assemblage A3: 73% (Table 3). Again the differences between the three assemblages are significant ( $\chi^2 = 56.398$ ,  $df = 2$ ,  $P < 0.0001$ ). Assemblage A1 was not included in the latter two calculations due to its low numbers of long bones and metapodials.

Table 2 — *Ursus spelaeus*: comparison of the numbers of dental, cranial and postcranial elements of the cave bear assemblages from Chamber A, Horizon 3 (A3), Horizon 2 (A2), Horizon 1 (A1) and Chamber B, Horizon 4 (B4) (NISP: number of identified specimens, MNI: Minimum Numbers of Individuals)

| Goyet<br>cave bear assemblage<br>AMS date | Chamber A          |                    |                    | Chamber B          |
|---|--------------------|--------------------|--------------------|--------------------|
|   | A3<br>c. 27,500 BP | A2<br>c. 34,900 BP | A1<br>c. 38,800 BP | B4<br>c. 36,000 BP |
| cranial elements                          | 32                 | 23                 | 12                 | 97                 |
| dental elements                           | 588                | 227                | 127                | 541                |
| postcranial elements                      | 348                | 182                | 54                 | 1546               |
| vertebrae                                 | 25                 | 6                  | 2                  | 221                |
| ribs                                      | 6                  | 26                 | 5                  | 229                |
| long bones                                | 87                 | 43                 | 5                  | 303                |
| scapula                                   | 6                  | 2                  | 0                  | 32                 |
| pelvis                                    | 6                  | 1                  | 0                  | 38                 |
| baculum                                   | 6                  | 6                  | 2                  | 10                 |
| carpalia/tarsalia                         | 27                 | 18                 | 4                  | 137                |
| metapodia                                 | 90                 | 49                 | 19                 | 282                |
| phalanges                                 | 77                 | 19                 | 17                 | 257                |
| other                                     | 18                 | 12                 | 0                  | 37                 |
| NISP                                      | 968                | 432                | 193                | 2184               |
| MNI                                       | 62                 | 30                 | 14                 | 89                 |
| juvenile                                  | 17                 | 5                  | 6                  | 29                 |
| subadult                                  | 4                  | 2                  | 1                  | 5                  |
| adult (male/female)                       | 41 (15/26)         | 23 (12/11)         | 7 (4/3)            | 55 (37/18)         |

#### Sex ratio

The majority of the canines of the cave bears of the different assemblages were sexed based on the bimodal distribution of their crown width (not shown). According to KURTÉN (1955) more than 99% of the canines of cave bears can be sexed accurately. Based on the size of the canines, the cave bear assemblages from Goyet can be split up according to the sex ratio (Tab. 4). In assemblage B4 the observed numbers of the male and female upper and lower canines differ significantly from the expected 50:50 ratio, with a dominance of the male canines. Cave bear assemblage B5 is female dominated based on both upper and lower canine frequencies. The lower canines of cave bear assemblage A3 indicates that it is a female dominated assemblage. For the assemblages A2 and A1 the distribution between male and female upper and lower teeth do not differ statistically from the 50:50 ratio.

#### Canine size and sexual dimorphism

Table 5 compares the crown widths of the upper and lower canines from the five cave bear assemblages from Goyet. The male upper (ANOVA,  $F_{4,68}=0.7167$ ,  $P=0.58$ ) and lower (ANOVA,  $F_{4,83}=0.7168$ ,  $P=0.58$ ) canines do not differ among the five assemblages. However, there is a significant difference between the mean crown widths of the female upper canines (ANOVA,  $F_{3,90}=10.599$ ,  $P<0.0001$ ). Pairwise comparisons (Tukey-Kramer post hoc test for unequal sample size) show

that the mean crown width of the female bears from assemblage A3 is significantly different from that of both assemblage B4 ( $P<0.001$ ) and assemblage B5 ( $P<0.001$ ). Also the lower female canine width differs notably among the five assemblages (ANOVA,  $F_{4,105}=12.819$ ,  $P<0.0001$ ). Pairwise comparison (Tukey-Kramer post hoc test) indicates that the female canines of assemblage B5 are significantly different from those of all the other assemblages: B4 ( $P<0.01$ ), A2 ( $P<0.001$ ), A3 ( $P<0.001$ ), A1 ( $P<0.001$ ). The same pattern is repeated with the crown lengths of the first carnassial from the lower jaws (Table 5). The jaws were sexed based on the size of the canines. The molar length of the male bears seems to remain stable among assemblages B5 and B4 (t-test,  $t=0.74$ ,  $df=11$ ,  $P=0.48$ ). The mean length of the carnassial of female bears from assemblage B5 is significantly smaller than that of assemblage B4 (t-test,  $t=3.730$ ,  $df=15$ ,  $P=0.002$ ) (Table 5).

The sexual dimorphism of the width of the upper and lower canines was calculated as the ratio of male mean to female mean (VAN VALKENBURGH & SACCO, 2002). The dimorphism ranges for the upper canines teeth from 1.23 to 1.33 and for the lower teeth from 1.21 to 1.36 (Tab. 5). The dimorphism is most expressed in the bears of assemblage B5, due to the small size of the female dentition, and is also quite high in assemblage B4, especially for the upper canines. The sexual dimorphism of the lower first

Table 3 — *Ursus spelaeus*: comparison of the numbers of broken and complete postcranial bones of the cave bear assemblages and details of the long bones and metapodial (MC+MT) bones from Chamber A, Horizon 3 (A3), Horizon 2 (A2), Horizon 1 (A1) and Chamber B, Horizon 4 (B4)

| Goyet                            | Chamber A          |                    |                    | Chamber B          |
|----------------------------------|--------------------|--------------------|--------------------|--------------------|
| cave bear assemblage<br>AMS date | A3<br>c. 27,500 BP | A2<br>c. 34,900 BP | A1<br>c. 38,800 BP | B4<br>c. 35,500 BP |
| broken postcranial bones         | 149                | 109                | 26                 | 263                |
| complete postcranial bones       | 199                | 73                 | 28                 | 1283               |
| postcranial bones (total)        | 348                | 182                | 54                 | 1546               |

| Goyet                            | Chamber A          |                    |                    | Chamber B          |
|----------------------------------|--------------------|--------------------|--------------------|--------------------|
| cave bear assemblage<br>AMS date | A3<br>c. 27,500 BP | A2<br>c. 34,900 BP | A1<br>c. 38,800 BP | B4<br>c. 35,500 BP |
| broken long bones                | 73                 | 25                 | 4                  | 62                 |
| complete long bones              | 14                 | 18                 | 1                  | 241                |
| long bones (total)               | 87                 | 43                 | 5                  | 303                |

| Goyet                            | Chamber A          |                    |                    | Chamber B          |
|----------------------------------|--------------------|--------------------|--------------------|--------------------|
| cave bear assemblage<br>AMS date | A3<br>c. 27,500 BP | A2<br>c. 34,900 BP | A1<br>c. 38,800 BP | B4<br>c. 35,500 BP |
| broken MC + MT                   | 24                 | 7                  | 8                  | 5                  |
| complete MC + MT                 | 66                 | 42                 | 11                 | 277                |
| Mc + MT (total)                  | 90                 | 49                 | 19                 | 282                |

molar of assemblage B5 (1.14) is again higher than that of assemblage B4 (1.09) (Table 5).

#### Mortality based on canines

A number of the permanent canines from the cave bear assemblages are heavily worn (Table 6, Plate 1). Some show clear wear facets, in others these facets are combined with a band of lost enamel at the base of the crown and in some only the band of worn enamel occurs. These wear facets are caused by the attrition between the lower and upper canines and contacts with the third incisors (Koby, 1940). Probably grasses or roots that became recurrently entangled around the canines caused the wear bands. Examination of the lower jaws and skulls from assemblage B4 indicates that the canines from the lower jaw show more rapidly wear bands and facets than the ones of the upper jaw. The youngest female lower jaws with this wear are in STINER's (1998) age cohort IV, the youngest male lower jaws are in cohort VIII. One female skull from assemblage B5 has wear facets on the canines and extremely worn jugal teeth (cohort IX). It seems that

for an estimation of the number of very old individuals, based on damaged canines, it is better to use the upper ones which seems to be less sensitive to this type of wear. Based on the maxillary dentition, heavy wear on the upper canines corresponds with STINER's cohorts IX on the jugal teeth. Furthermore, it appears that canines of the females erode quicker; maybe because the smaller canines are more easily abraded or because the female cave bears used their canines in a slightly different way than the males. According to BARYSHNIKOV (1999), polished vertical traces of wear on canines were observed on skulls of old brown bears from Kamchatka. DEBELJAK (2002) describes seven age classes for cave bear canines from unerupted, uncomplete canines (class I) to canines with heavily worn crowns (classes VI & VII). The worn canines from Goyet correspond with DEBELJAK (2002) classes VI and VII.

In cave bear assemblages A3, A2 and B5 c. 50% of the adult maxillary canines display wear, indicating a high frequency of old individuals (Table 6). In assemblage B4, around 21% of the upper canines derives from old bears

Table 4 — *Ursus spelaeus*: comparison of the numbers of observed and expected canines: (1): male dominated, (2): female dominated, cave bear assemblages from Chamber A, Horizon 3 (A3), Horizon 2 (A2), Horizon 1 (A1) and Chamber B, Horizon 4 (B4) and Horizon 5 (B5) (C max.: maxillary canines, C mand.: mandibular canines); the numbers of canines in this table can be different from those in Table 5 and include also specimens that could not be measured.

| Comparing observed and expected (50/50) counts |            |        |
|--|------------|--------|
| C max. (male/female)                           | chi-square | P      |
| A3 (15/16)                                     | 0,06       | 1,0000 |
| A2 (11/7)                                      | 0,94       | 0,3428 |
| A1 (3/3)                                       | 0,00       | 1,0000 |
| B4 (50/31) (1)                                 | 4,47       | 0,0339 |
| B5 (8/40) (2)                                  | 21,35      | 0,0001 |

| Comparing observed and expected (50/50) counts |            |        |
|--|------------|--------|
| C mand. (male/female)                          | chi-square | P      |
| A3 (18/39) (2)                                 | 7,75       | 0,0053 |
| A2 (20/12)                                     | 2,03       | 0,1573 |
| A1 (3/6)                                       | 1,11       | 0,2943 |
| B4 (56/22) (1)                                 | 14,83      | 0,0001 |
| B5 (12/32) (2)                                 | 9,11       | 0,0026 |

(GERMONPRÉ, 2004). The statistical analysis of the number of worn and unworn upper canines from these assemblages indicates that the variables are significantly associated ( $\chi^2 = 15.931$ ,  $df = 3$ ,  $P = 0.0012$ ). Furthermore, the number of worn and unworn male and female canines across the five assemblages were analysed separately. The proportions of the female canines do not differ significantly across the studied assemblages (results not shown). Statistically, the calculated chi-squared test ( $\chi^2 = 24.261$ ,  $df = 3$ ,  $P < 0.0001$ ) confirms that the number of worn and unworn male canines in the assemblages are not identical. Moreover, the Fisher's exact test demonstrates that the frequencies of the worn and unworn male canines of assemblage B4 differ significantly from that of assemblage A3 ( $P < 0.0001$ ) ( $\alpha < 0.0083$  after Bonferroni adjustment). All other assemblages do not differ amongst each other: B4 vs A2 ( $P = 0.11$ ), B4 vs B5 ( $P = 0.34$ ), A2 vs A3 ( $P = 0.04$ ), B5 vs A3 (0.03), B5 vs A2 ( $P = 1.00$ ).

#### Mortality based on jugal 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 teeth and

the wear of the crown. In order to work also with small samples the data can be collapsed in three age stages: juvenile (I-III), prime adult (IV-VII) and old adult (VIII-IX) (Table 7). The chi square test shows that the numbers are not significantly different among these assemblages ( $\chi^2 = 7,641$ ,  $df = 6$ ,  $P = 0.2656$ ). The mortality pattern in these assemblages can be described as normal non-violent attrition, affecting mostly young and old individuals that died during hibernation primarily from starvation and other attritional factors.

The juvenile mortality can be more detailed. The minimal mortality rate of the cubs can be considered as the minimal rate accounting for the number of dead cubs younger than one year found in a cave bear assemblage. It is calculated on basis of the estimated number of cubs born and the actually number found dead (GERMONPRÉ, 2004). The estimated number of new born cubs is obtained by using the reproductive rate of 0.46 for recent brown bears from Kananaskis, Alberta, a region with a continental climate (WIELGUS & BUNNELL, 2000). The minimal mortality rate includes only offspring that died inside the den during or shortly after hibernation when the cubs remained in or around the den. This rate does not incorporate cubs of less than one year that died in summer or autumn, after leaving the cave area. Although the rate will be different if another reproductive rate is accepted, trends can be compared. Furthermore, the taphonomic characteristics of the assemblage and the collecting biases of the excavation also influence this rate. KURTÉN (1958, p. 34) obtained a mortality rate of about 17% for mother cave bears from Odessa. BUNNELL & TAIT (1985) give an apparent annual mortality rate for North American female brown bear of 16.8%. Based on such mortality rates at least 170 female bears must have hibernated in the cave to give a harvest of 29 dead females (the minimal number of individuals (MNI) of the female upper canines) found in cave bear assemblage B5. These females gave ideally birth to 78,2 cubs. The B5 assemblage yielded 74 juvenile humeri (greatest length < 180 mm), combining into 40 individuals of less than eight months old (GERMONPRÉ, 2003). The age attribution of juvenile humeri is detailed in GERMONPRÉ & SABLIN (2001). Consequently, the minimal mortality rate of the cubs, from birth until the abandoning of the den, in assemblage B5 amounts to 51%. This mortality rate includes three periods during which the cubs of the year died more frequently: at birth, at an age of around three months, when the cubs become active, and at the end of the hibernation period (GERMONPRÉ & SABLIN, 2001). For assemblages A1, A2, A3 and B4 a minimal mortality rate for the cubs of reps. 23%, 20%, 19% and 51% is obtained (GERMONPRÉ, 2004). The minimal mortality rate of assemblage B4 is comparable with the figure for assemblage B5.

Since postcranial bones are rare in Chamber A, the lower carnassial was chosen for statistic comparison. Table 7 shows the proportions of the lower carnassial from cubs (STINER's 1998 age cohorts I+II) and older juveniles (STINER's 1998 age cohorts III). The chi square test indicates that the numbers are significantly different

Table 5 — *Ursus spelaeus*: comparison of the crown widths of the canines and of the crown lengths of the lower carnassial (M/1) of the cave bear assemblages from Chamber A, Horizon 3 (A3), Horizon 2 (A2), Horizon 1 (A1), and Chamber B, Horizon 4 (B4), Horizon 5 (B5) (C max.: maxillary canines, C mand.: mandibular canine, cw: crown width, cl: crown length, OR: observed range: minimum and maximum observed values, sd: standard deviation, sex. dim.: sexual dimorphism)

| Cmax.  | n  | mean cw | sd cw | OR cw     |  | Cmax.  | n  | mean cw | sd cw | OR cw     | sex. dim. |
|--------|----|---------|-------|-----------|--|--------|----|---------|-------|-----------|-----------|
| A3 M   | 15 | 21,27   | 1,48  | 19,4-23,5 |  | A3 F   | 15 | 17,37   | 1,19  | 15,0-18,5 | 1,23      |
| A2 M   | 11 | 20,70   | 0,92  | 19,6-22,4 |  | A2 F   | 7  | 16,87   | 1,56  | 14,1-18,4 | 1,25      |
| A1 M   | 3  | 20,27   | 0,35  | 19,9-20,6 |  | A1 F   | 2  | 17,90   | —     | 17,7-18,1 | —         |
| B4 M   | 36 | 20,63   | 1,49  | 18,5-25,4 |  | B4 F   | 31 | 15,64   | 1,32  | 13,4-18,6 | 1,32      |
| B5 M   | 8  | 20,79   | 1,05  | 19,0-22,2 |  | B5 F   | 40 | 15,61   | 0,95  | 14,0-18,0 | 1,33      |
| Cmand. | n  | mean cw | sd cw | OR cw     |  | Cmand. | n  | mean cw | sd cw | OR cw     | sex. dim. |
| A3 M   | 18 | 20,82   | 0,97  | 19,1-22,8 |  | A3 F   | 39 | 16,15   | 1,03  | 14,5-18,5 | 1,29      |
| A2 M   | 20 | 20,73   | 0,87  | 19,1-22,4 |  | A2 F   | 12 | 16,79   | 0,80  | 15,6-18,0 | 1,23      |
| A1 M   | 3  | 20,13   | 0,95  | 19,2-21,1 |  | A1 F   | 6  | 17,05   | 0,40  | 16,4-17,5 | 1,21      |
| B4 M   | 35 | 20,58   | 0,99  | 18,6-22,3 |  | B4 F   | 21 | 16,03   | 1,17  | 14,4-17,9 | 1,28      |
| B5 M   | 12 | 20,37   | 0,77  | 19,1-21,9 |  | B5 F   | 32 | 14,98   | 0,83  | 13,5-16,6 | 1,36      |
| M/1    | n  | mean cl | sd cl | OR cl     |  | M/1    | n  | mean cl | sd cl | OR cl     | sex. dim. |
| B4 M   | 10 | 30,92   | 1,23  | 28,7-32,6 |  | B4 F   | 8  | 28,29   | 0,90  | 27,3-29,6 | 1,09      |
| B5 M   | 3  | 30,30   | 1,45  | 28,9-31,8 |  | B5 F   | 9  | 26,59   | 0,97  | 24,8-27,9 | 1,14      |

among the assemblages A3, B4 and B5 ( $\chi^2=20.892$ ,  $df=2$ ,  $P<0.0001$ ).

#### Carnivore traces

Punctures and tooth scratches on cortical bone, and gnawing furrows on cancellous tissue testify to predator or scavenger action on cave bear bones from Goyet. Since the cave bear teeth rarely show carnivore traces, the proportion of carnivore damaged bones is based on all remains excluding the teeth. Cave bear assemblage A3 shows the highest number of gnawed bones with 35% of all the skeletal elements, excluding the teeth, damaged (Table 8). Often only the shaft of the long bones remains and epiphyses are lacking (Plate 1). This type of modification is typical for spotted hyaena action (LYMAN 1994). Many tooth marks on cortical bone have a diameter of 4 to 7 mm. The characteristics of the gnawing are similar to those due to spotted hyaena (*Crocuta crocuta*) as observed by HAYNES (1983). In assemblages A2, A1 and B4 the frequency of carnivore damaged bones is less than 10% of the NISP, excluding the teeth. A frequency for assemblage B5 can not be given since the study of this assemblage is not yet finished. However, preliminary data show that gnawing marks of hyaenas are not frequently seen on the bear bones. However, several rectangular puncture marks on cortical bone surfaces have large diameters (> 6 mm) and were probably made by bears (Plate 1), as described by LYMAN (1994).

The statistical analysis ( $\chi^2=265.5$ ,  $df=3$ ,  $P<0.0001$ ) confirmed that the proportions of gnawed and undamaged bones in the assemblages are not identical. Fisher's exact test indicates that the proportion of carnivore damaged and undamaged bear bones from assemblage A3 differ significantly from the ones of assemblages B4 ( $P<0.0001$ ), A1 ( $P<0.0001$ ) and A2 ( $P<0.0001$ ) ( $\alpha<0.0083$  after Bonferroni adjustment). The frequency of gnawed bear bones from the assemblages A2, A1 and B4 do not differ among each other: A2 vs. B4 ( $P=0.07$ ), A1 vs. B4 ( $P=0.30$ ), A2 vs. A1 ( $P=1.00$ ).

#### Human hunting

Cave bear assemblages A3, A2, and B4 contain a few bones with cut marks and ochre staining. The cut marks on the bear bones are related to skinning and butchering, the ochre coloured skeletal elements could indicate symbolic behaviour of the prehistoric people towards the cave bears (GERMONPRÉ & SABLIN, 2001; GERMONPRÉ, 2004). According to BÄCHLER (1940) and HÖRMANN (1933) a cave bear cult existed during the Middle Palaeolithic. This cave bear cult was seen as part of a specialised culture based on cave bear hunting (PACHER, 1997, 2002). Many authors have contested this interpretation and have shown that the majority of bear bone accumulations in cave sites were the result of natural death during hibernation (KOBY 1940, 1941, 1943; KURTEN, 1958, 1976; PACHER, *ibid.*). The human modified cave bear

Table 6 — *Ursus spelaeus*: comparison of the numbers of worn and unworn upper canines from the cave bear assemblages from Chamber A, Horizon 3 (A3), Horizon 2 (A2), Horizon 1 (A1) and Chamber B, Horizon 4 (B4), Horizon 5 (B5)

| Goyet                            | Chamber A          |                    | Chamber B          |                    |
|----------------------------------|--------------------|--------------------|--------------------|--------------------|
|                                  | A3<br>c. 27,500 BP | A2<br>c. 34,900 BP | B4<br>c. 35,500 BP | B5<br>c. 24,000 BP |
| cave bear assemblage<br>AMS date |                    |                    |                    |                    |
| worn upper canines (all)         | 19                 | 10                 | 17                 | 23                 |
| unworn upper canines (all)       | 21                 | 8                  | 64                 | 25                 |
| canines (all)                    | 40                 | 18                 | 81                 | 48                 |

| Goyet                            | Chamber A          |                    | Chamber B          |                    |
|----------------------------------|--------------------|--------------------|--------------------|--------------------|
|                                  | A3<br>c. 27,500 BP | A2<br>c. 34,900 BP | B4<br>c. 35,500 BP | B5<br>c. 24,000 BP |
| cave bear assemblage<br>AMS date |                    |                    |                    |                    |
| worn upper canines (males)       | 13                 | 5                  | 9                  | 3                  |
| unworn upper canines (males)     | 2                  | 6                  | 41                 | 5                  |
| canines (males)                  | 15                 | 11                 | 50                 | 8                  |

| Goyet                            | Chamber A          |                    | Chamber B          |                    |
|----------------------------------|--------------------|--------------------|--------------------|--------------------|
|                                  | A3<br>c. 27,500 BP | A2<br>c. 34,900 BP | B4<br>c. 35,500 BP | B5<br>c. 24,000 BP |
| cave bear assemblage<br>AMS date |                    |                    |                    |                    |
| worn upper canines (females)     | 6                  | 5                  | 8                  | 20                 |
| unworn upper canines (females)   | 10                 | 2                  | 23                 | 20                 |
| canines upper (females)          | 16                 | 7                  | 31                 | 40                 |

Table 7 — *Ursus spelaeus*: comparison of the numbers of lower carnassial (M/1) from juvenile (STINER's 1998 age cohorts III-IV), prime (STINER's 1998 age cohorts IV-VII) and old (STINER's 1998 age cohorts VIII-IX) bears and details of STINER's 1998 age cohorts I-III; cave bear assemblages from Chamber A, Horizon 3 (A3), Horizon 2 (A2) and Chamber B, Horizon 4 (B4), Horizon 5 (B5)

| Goyet                              | Chamber A          |                    | Chamber B          |                 |
|------------------------------------|--------------------|--------------------|--------------------|-----------------|
|                                    | A3<br>c. 27,500 BP | A2<br>c. 35,000 BP | B4<br>c. 35,500 BP | B5<br>c. 24,000 |
| cave bear assemblage<br>AMS date   |                    |                    |                    |                 |
| M/1: Stiner's age cohorts juvenile | 23                 | 8                  | 30                 | 28              |
| M/1: Stiner's age cohorts prime    | 11                 | 2                  | 12                 | 14              |
| M/1: Stiner's age cohorts old      | 12                 | 3                  | 5                  | 4               |
| M/1 total                          | 46                 | 13                 | 47                 | 46              |

| Goyet                            | Chamber A          | Chamber B          |                 |
|----------------------------------|--------------------|--------------------|-----------------|
|                                  | A3<br>c. 27,500 BP | B4<br>c. 35,500 BP | B5<br>c. 24,000 |
| cave bear assemblage<br>AMS date |                    |                    |                 |
| M/1: Stiner's age cohorts I+II   | 4                  | 24                 | 20              |
| M/1: Stiner's age cohorts III    | 19                 | 6                  | 8               |
| M/1 juvenile                     | 23                 | 30                 | 28              |

Table 8 — *Ursus spelaeus*: comparison of the numbers of carnivore damaged and undamaged bones from the cave bear assemblages from Chamber A, Horizon 3 (A3), Horizon 2 (A2), Horizon 1 (A1) and Chamber B, Horizon 4 (B4) (ex. teeth: excluding teeth)

| Goyet                               | Chamber A          |                    |                    | Chamber B          |
|-------------------------------------|--------------------|--------------------|--------------------|--------------------|
| cave bear assemblage<br>AMS date    | A3<br>c. 27,500 BP | A2<br>c. 34,900 BP | A1<br>c. 38,800 BP | B4<br>c. 35,500 BP |
| carnivore damaged bones ex. teeth   | 133                | 20                 | 6                  | 108                |
| carnivore undamaged bones ex. teeth | 247                | 185                | 60                 | 1535               |
| all bones ex. teeth                 | 380                | 205                | 66                 | 1643               |

bones will be discussed in detail in a forthcoming paper (GERMONPRÉ & HÄMÄLÄINEN, *in prep.*).

### Discussion

The cave bear assemblages from Goyet display different distributions of the skeletal elements, divergent proportions of broken bones, worn canines, carnivore gnawed bones and juvenile remains, and different sex ratios of the canines. Furthermore dental measurements discriminate assemblages B5, B4 and A3. Since the examined taphonomic and osteometric characteristics differ among the studied assemblages, the null hypotheses can be rejected and most assemblages can be considered as separated groups, each with a different taphonomic history. Stable isotope analyses of the cave bear bones from all assemblages are currently being undertaken (BOCHERENS *in prep.*) in order to see if the assemblages differ also from a biogeochemical point of view.

The recent brown (*Ursus arctos*), polar bear (*U. maritimus*) and black bear (*U. americanus*) are similar in several aspects of their biology and behaviour (KURTÉN, 1976). Furthermore, all species in the subfamily Ursinae probably have the ability to crossbreed (CRAIGHEAD, 2000). The hibernation habits and reproductive cycle of the recent Ursinae probably also apply to the extinct cave bear (STINER, 1998). The results from the taphonomy and osteometry of the cave bears from Goyet and reference data on modern ursids are used to come to a reconstruction of the palaeobiology of *Ursus spelaeus* during the Middle Pleniglacial in Belgium.

#### Cave bear assemblage A1

Cave bear assemblage A1 is the oldest dated assemblage from Goyet so far and has a Calendric Age calBP of c. 42,000. This cave bear assemblage was found in Chamber A and is the smallest of Goyet (NISP: 193, MNI: 14). Two other AMS dates on hyaena bones from the same horizon have very different results (Tab. 1) and could point to the mixed nature of this horizon. The frequency of the dental material is high and most of the postcranial

bones are broken. The sex ratio seems not to be different from the expected one. The sexual dimorphism based on the lower canines is the lowest of all assemblages from Goyet (1.21), due to the large size of the female teeth and is comparable to the one of recent brown bear from Fennoscandia (KURTÉN, 1955). The minimal mortality rate of the cubs of the year is relatively low (c. 23%), although this is based on a very small sample size. This assemblage shows also a low proportion of carnivore damaged bones.

#### Cave bear assemblage B4

The Calendric Ages calBP of c. 40,500 and 40,000 of the AMS dates (Table 1) of cave bear assemblage B4 could point to an occupation of the cave around the Dansgaard/Oeschger (D/O) event 9 about 40,830 years ago (SHACKLETON *et al.*, 2004). However, in the stalagmite record of the Villars cave, France, the D/O event 10 is placed between 41,500 and 40,400 years ago (GENTY *et al.*, 2003), which could imply that the cave was used shortly after D/O 10. In the Netherlands this period is characterised by prolonged snow covers, indicating low winter temperatures (KASSE *et al.*, 1995). Cave bears denned inside the cave for at least 350 years when assemblage B4 was formed (GERMONPRÉ & SABLIN, 2001). This minimal occupation time is based on the assumption that the cave bears preferred to hibernate alone or in families. Recent brown bears tend to hibernate alone (COUTURIER, 1954; HEPTNER *et al.*, 1974; MURIE, 2000). According to KURTÉN (1976), male cave bears could have denned together in large caves and females with cubs would have preferred small undisturbed caves. Also DEBELJAK (2002) proposed that female cave bears with cubs occasionally denned together. FOSSE (2001) also suggested that cave bears may have spent their winter rest together, as he found non-overlapping traces of their beds in caves of the Pyrenees. However, since Chamber A and Chamber B are quite small it is assumed here that the cave bears hibernated alone or in families (one female with her cubs).

Cave bear assemblage B4 was found mainly in Chamber B. It has a number of identified specimens (NISP) of 2184 and a minimal number of individuals (MNI) of 89.

This assemblage yielded several articulated skeletal parts and has a high frequency of unbroken postcranial bones. This can probably be explained by the more protected location of the deeper lying Chamber B where less traffic and trampling occurred than near the entrance of the cave.

The sexual dimorphism of the width of the canines was calculated as the ratio of the male mean to the female mean. The dimorphism for the canines from assemblage B4 is 1.32 (upper canines) and 1.28 (lower canines). The sexual dimorphism of the lower canines of the cave bears from Mixnitz, Austria, based on the data in KURTÉN (1955), is 1.30, the dimorphism of Spanish cave bears is 1.32 (data from DE TORRES PEREZ HIDALGO, 1988). The Mixnitz, Spanish and Goyet values are much higher than the mean of 1.20 for recent brown bear from Fennoscandia (data from KURTÉN, 1955) and are even bigger than the mean of 1.25 for recent lion (data from GITTLEMAN & VAN VALKENBURG, 1997). The sexual dimorphism of the first lower molar from assemblage B4 is 1.09, similar to the dimorphism of the lower carnassial of recent Tibet brown bears, and larger than that of two Russian subspecies, that both have a ratio of 1.04 (BARYSHNIKOV *et al.*, 2003). The dimorphism of the first lower molar of the cave bears from assemblage B4 is comparable to the ones of Mixnitz, Austria (data from KURTÉN, 1955) and Spain (data from DE TORRES PEREZ HIDALGO, 1988), the latter have both a value of 1.08. The pronounced dimorphism of the canines compared to the one of the first molar indicates the importance of the breeding system on the canine size, rather than that of the feeding process which generates a much weaker dimorphism on the cheek teeth (GITTLEMAN & VAN VALKENBURG, 1997). According to these authors, large dimorphism in canine size is related to severe male-male competition and frequent infanticide in polygenous species. The cubs of brown, black and polar bears are born during the dormancy period of their mother (BANFIELD, 1974; CHURCHER, 1999; ROGERS, 1999). After hibernation, female brown bears do not immediately leave the den area. The transition time after emergence from the den but before the abandonment of the den area can take two to four weeks (CRAIGHEAD & CRAIGHEAD, 1972; HEPTNER *et al.*, 1974; MURIE, 2000; ROLS, 1984) during which the female with her cubs can spend the nights in the hibernation den (ZAVATSKIY, 1993). Adult bears may be anorectic for up to three weeks after the emergence (MCLOUGHLIN *et al.*, 2002). This transition time can be a difficult period for the cubs. Recent grizzly males behave agonistically to other males and females not in oestrus. They frequently kill cubs, provoking the females to begin breeding sooner (CRAIGHEAD *et al.*, 1995). In Yakutia, adult bears kill cubs early in spring, before the beginning of the vegetation (MOROSOV, 1993). In Sweden, brown bear cubs are killed during the breeding season in May-June by immigrating young male brown bears (SWENSON *et al.*, 1997). According to ROGERS (1999), black bear cubs can starve following emergence from the winter den in spring. The most vulnerable period for polar bear cubs is just after leaving the maternity den when males can kill the young (TAYLOR

*et al.*, 1985). According to DEROCHE & WIIG (1999), infanticide in polar bear populations may be density-dependent. In areas that act as corridors, passing male bears can inspect dens and kill the cubs they find there. Possibly the Samson valley was such a corridor. Based on the large sexual dimorphism in the canines of the cave bears from B4, severe male-male competition and infanticide were probably at least as much pronounced in cave bear as in recent brown bear. In spring, after the winter sleep but before leaving the den area, several cubs of around seven months old died inside the cave (GERMONPRÉ & SABLIN, 2001); possibly they were fatally hurt by male cave bears. Furthermore not only cave bear was present, but in most assemblages a small fraction of brown bear remains is found as well (GERMONPRÉ & SABLIN, 2001; VAN TROOS, 2002-2003). In the Pyrenees, FOSSE (2001) and FOSSE *et al.* (2003) found a spatial segregation in the location of brown and cave bear dens. The cave bear dens were located at a lower altitude. This could suggest that the brown bears evaded the cave bears for denning, at least in the Pyrenees, possibly to avoid aggressive encounters. Unfortunately due to the scarcity of the brown bear material the sexual dimorphism of this bear from Goyet could not be calculated.

The more severe the climate, the longer recent bears hibernate (HEPTNER *et al.*, 1974). Environmental factors such as snowfall, temperature and scarcity of food influence the onset and duration of dormancy (MCLOUGHLIN *et al.*, 2002). Female bears, giving birth during their dormancy, must hibernate many months in order to allow their cubs to develop (ROGERS, 1987). Recent female grizzly bears in Canada's Central Arctic retreat earlier to the den than the male bears and the duration of the denning of the females is significantly longer than that of the males. Furthermore, older males den for shorter periods of time than subadult males (MCLOUGHLIN *et al.*, 2002). As in recent brown bears, the dormancy in both sexes of cave bear probably took longer when the winter season was harsher. An unbalanced sex ratio of a cave bear assemblage shows the main trend of selective occupation or selective mortality in the cave over an extended period of time, maybe as long as several centuries. Cave bear assemblage B4 is male dominated (Table 4). In the Condroz, during colder intervals, areas with a rich vegetation were more restricted than during the Pleniglacial interstadials. The small, protected valley of the Samson must have formed a relatively rich habitat for cave bears. During the formation of assemblage B4, males probably concentrated in this food-rich valley. Based on the high number of unworn canines many young and prime male bears died inside the cave during their dormancy. WIELGUS & BUNNELL (1995) found that in Alberta the selective hunting of large old brown bear males induces an immigration of young, potentially infanticidal males. The females evaded these young males and male-favoured habitats and abandoned the area. They restricted their activities to poorer habitats resulting in a sexual segregation (WIELGUS & BUNNELL, 2000). In Scandinavia female brown bears with cubs minimise their range size during

the mating season, probably to reduce the risk of infanticide (DAHLE & SWENSON, 2003). The same scenario might apply at Goyet during the formation of assemblage B4. Only 11% of all upper canines are worn male ones, while the total male frequency amounts to almost 62% of the upper canines. The high frequency of remains from young and prime males (51% of the upper canines) in this assemblage could point to an immigration of young aggressive males into the valley of the Samson. Maybe harsh ecological conditions promoted aggressive behaviour particularly among males, which accordingly died at a relative young age. The dominant males probably had priority in selecting the Goyet cave as a den site. They could have induced female bears from all age groups to search for a den elsewhere, resulting in a higher proportion of remains from male bears in the taphocoenosis.

The minimal mortality rate of the cubs reaches c. 51% while for the assemblages in Chamber A this rate remains below 25%. According to BUNNELL & TAIT (1985) North American brown bear cubs in their first year have a mortality rate of 30-40%. MURIE (2000) gives a loss of brown bear cubs of the first year of 31% in Denali Park, Alaska. This suggests that the mortality of the cave bear cubs could be relatively high in assemblages with high frequencies of young and prime males. In a recent black bear population, where male competition for mates is intense, a subset of old and large males contributes disproportionately to the production of offspring (KOVACH & POWELL, 2003). In grizzly bear populations only about half of the males are effective breeders and paternity is biased towards large and old males (CRAIGHEAD *et al.*, 1995). At Goyet, the young male cave bears, new to the area, probably had a reproductive advantage by killing the cubs since there was a large chance that they were fathered by another male. The influx of young males could in this way explain the elevated juvenile mortality at Goyet. Furthermore, the hibernation took about eight months during the formation of assemblage B4. Maybe after such a long winter rest the mother bears were not in a good condition and not very capable to look after their offspring (GERMONPRÉ & SABLIN, 2001). On the other hand, the minimal mortality rate of assemblage B4 could also be relatively high thanks to the deeper lying position of Chamber B, where less trampling of carcasses and bones occurred than in Chamber A, permitting a better preservation of the fragile juvenile remains.

Data on the size of dental remains (canines and lower carnassial) from male cave bears shows that the sizes of these elements do not differ among the several assemblages from Goyet. It is possible that intra- and intersexual selection maintained the large size of the male cave bears in these populations. However, the differences in size of some of the teeth from female cave bears are significant among the assemblages. The female bears from assemblage B4 have upper canines that are significantly smaller than those of assemblage A3 (Table 6). According to BADYAEV (1998) recent grizzly bears are less able to achieve large canines during stressful periods. Especially the developmental stability of the canines

from male grizzlies was responsive to environmental stress. It is possible that due to stress caused by the sexual segregation the cave bear females of assemblage B4 developed smaller canines than those of assemblage A3. The female lower canines from assemblage B4 are larger than those of assemblage B5, which could indicate more stressful conditions for this latter assemblage. However, it can not be excluded that a genetic difference between the populations can explain the differences in the female dental sizes. Mitochondrial DNA analyses of the cave bears from Goyet are being performed at the moment (HOFREITER *in prep.*).

The relatively high minimal mortality rate of the cubs, the high number of males, the low frequency of old individuals and the long hibernation period all indicate that this assemblage was formed during relatively severe conditions. For these reasons it is believed that the assemblage B4 was formed during a cold climatic interval. Based on the available AMS dates and their Calpal calibration, the bears used the cave as a den probably between D/O event 10 and 9.

#### Cave bear assemblage A2

Assemblage A2 was found in Chamber A. Based on the a Calendric Age calBP of c. 40,000 this assemblage could have been formed around D/O event 9 that started c. 40,830 years ago (SHACKLETON *et al.*, 2004) or c. 39,500 years ago (GENTY *et al.*, 2003, fig. 2). This event had a duration of around 250 years (FLÜCKIGER *et al.*, 2004). The cave functioned as a den for at least 150 years during the accumulation of this assemblage (GERMONPRÉ, 2004). Less than 500 skeletal remains belong to this assemblage (NISP: 432, MNI: 30). The frequency of the dental material is high and most of the postcranial bones are broken. Probably in Chamber A traffic was higher than in Chamber B since the entrance to the cave is located at the front of this chamber. The carcasses and bones were more trampled upon and more easily fragmented than those of Chamber B. Also according to FOSSE *et al.* (2002), a high frequency of broken bones points to an intensive circulation by the bears inside the den. The sex ratio seems not to be different from the expected one. The sexual dimorphism of the canines is quite low (upper: 1.25; lower: 1.23). The minimal mortality rate of the cubs of the year is low (c. 20%). In assemblage A2 remains from old males are relatively frequent: 28% of the total number of upper canines are worn male teeth. Since this assemblage has several taphonomic characteristics that clearly differentiate it from the one of B4, although both are seemingly very close in age, it can be assumed that they were formed during a different climatic phase. It is possible that assemblage A2 accumulated during a warmer interval (D/O9?) than assemblage B4.

#### Cave bear assemblage A3

A cave bear canine from assemblage A3 from Chamber A has an AMS age of 27,440 y BP (Table 1). The Calendric Age calBP of c. 30,800 places this assemblage into the cold interval between D/O5 and D/O4. This cave bear

assemblage was formed over a period of at least two centuries (GERMONPRÉ, *in press*).

Cave bear assemblage A3 is the richest one from Chamber A with a NISP of 965 and a MNI of 62. A high frequency of the bear bones is broken. This can be explained by the location of Chamber A near the entrance.

During the formation of assemblage A3, sexual segregation was probably not very important, as demonstrated by the dominance of female remains (Table 4). According to MURIE (2000), grizzlies in Alaska use the same ranges, with which they are thoroughly familiar, year after year. Females with cubs like to remain in a valley, males can cover larger areas. The valley of the Samson, with a length of around 15 km and a width of around 500 m, resembles the valleys in Central Asia (ZHIRYAKOV & GRACHEV, 1993) and Alaska (MURIE, 2000) much frequented by recent brown bears. During the accumulation of assemblage A3 many cave bears reached an old age. The proportion of worn male canines of assemblage A3 amounts to 32% of the total number of the upper canines present (Table 6) and differs significantly from the proportion of the worn male canines in assemblage B4. The old male cave bears, that probably sired the majority of the cubs, could have protected the juvenile bears from aggressive young males. The minimal mortality rate of the cubs is around 19%. This low rate can maybe also be explained by a more pronounced destruction of the juvenile carcasses in Chamber A than in Chamber B.

The female cave bear canines from assemblage A3 are relatively large. Their size possibly indicate more stable environmental conditions than those during accumulation of assemblages B4 and B5, or point to a genetic difference. Sexual dimorphism, based on upper (1.23) and lower canines (1.29), is low compared to the ones of assemblage B5 (upper and lower canines) and B4 (upper canines only).

A relative high frequency of the cave bears bones is gnawed. The traces compare best to those made by hyaenas (Plate 1). This latter species is well represented in Horizon 3 with an NISP of 146. Remains from wolf, another possible predator, are less frequent (NISP: 58). Hyaenas were present at c. 27,500 y BP (Table 1) when they used the cave as a den as evidenced by remains of hyaena pups. Also prehistoric people were active in the cave at that time (Table 1).

#### Cave bear assemblage B5

The Calendric Ages calBP of the AMS dates, currently available for this assemblage, have a difference of more than 7000 years: c. 24,000 and c. 32,000 years BP. It is not clear yet if this assemblage was formed over several millennia or if one of the dates is not correct. According to DUPONT (1873, unpublished notes) bone horizon 5 was found in Chamber B, subjacent to bone horizon 4, and deeper in the gallery to a distance of more than 100 m from the entrance. This is in contradiction with the AMS dates that are older for assemblage B4 than for assemblage B5. More AMS dates might solve these problems. This cave bear assemblage is not yet completely studied.

Several cave bear skeletal parts in horizon B5 were found in anatomical connection. The size of the male canines does not differ from that of the other assemblages, but the female canines are the smallest from Goyet. The sexual dimorphism of the canines is high: 1.33 for the upper canines and 1.36 for the lower ones. Also the lower carnassial dimorphism is relatively high (1.14). This is due to the small size of the female dentition. The small canine size could point to stressful environmental conditions. The minimal mortality rate of cubs less than one year old is high with c. 51%, comparable to the rate in assemblage B4. However, it is also possible that the deeper lying position of Chamber B helped to protect the remains from the juvenile bears in contrast to the assemblages in Chamber A where carcasses and bones were more easily destroyed. Preliminary data indicate that gnawing marks of hyaenas are rare. However, bears probably made the large puncture marks on bone surfaces (Plate 1). Cave bear assemblage B5 is, in contrast with assemblage B4, clearly female dominated, suggesting a higher mortality for the female occupants of the cave and/or a higher preference of the female bears to select this cave as a den site.

#### Conclusion

The four dated cave bear assemblages from Goyet have AMS dates ranging from 38,770 y BP to 20,780 y BP assigning them to the Pleniglacial. The different proportions of several taphonomic and dental characteristics indicate that most of the studied cave bear assemblages can be considered as separated groups. The Pleniglacial climatic fluctuations probably had a substantial influence on the cave bear populations. The cave bears were present during the warmer Dansgaard/Oeschger events but also during the cold intervals. The data of cave bear assemblage A1 do not permit to give detailed conclusions and this assemblage has a mixed origin. Cave bear assemblage B4 formed in all likelihood under more extreme climatic conditions. It is the only male dominated assemblage, with a high frequency of remains from young males and from cubs. In assemblage A2 the frequency of the remains of old males is high, which could have protected the cubs from aggressive young males, while the proportion of juvenile remains is low. Cave bear assemblage A3 has again a high frequency of old males. Carnivores preyed heavily on the bears from this assemblage. Assemblage B5 yielded an elevated number of juvenile remains. The sizes of the female teeth are small compared to those of the other assemblages. Only a very small number of cave bear bones from assemblages B4, A2 and A3 were modified by prehistoric people.

#### Acknowledgements

Dr. Bultynck enabled me more than 20 years ago to launch my study of the collections of Pleistocene mammals in the Royal Belgian Institute

of Natural Sciences and made it possible for me to take up a job as a researcher a few years later. I would like to thank J.P. Brugal and M. Pacher for commenting on an earlier typescript. The discussions with P. Haesaerts and F. Damblon on Pleniglacial climate and calibration of AMS dates were greatly appreciated. Dr. J. Godefroid helped with the French résumé. W. Miseur, H. De Potter and A. Wauters helped with the iconography.

## References

- BÄCHLER, E. 1940. Das Alpine Paläolithikum der Schweiz. *Monographien zur Ur-und Frühgeschichte der Schweiz*, 2: 1-263.
- BADYAEV, A.V., 1998. Environmental stress and developmental stability in dentition of the Yellowstone grizzly bears. *Behavioral Ecology*, 9: 339-344.
- BANFIELD, A.W.F., 1974. The mammals of Canada. National Museum Natural Sciences, University of Toronto Press.
- BARYSHNIKOV, G., 1999. Bone assemblages from Acheulean and Mousterian levels in the Kudaro caves in the Caucasus Mountains. The role of early humans in the accumulation of European Lower and Middle Palaeolithic bone assemblages. *Römisch-Germanisches Zentralmuseum Monographien*, 42: 237-253.
- BARYSHNIKOV, G., GERMONPRÉ, M. & SABLIN, M., 2003. Sexual dimorphism and morphometric variability of cheek teeth of the cave bear (*Ursus spelaeus*). *Belgian Journal of Zoology*, 133: 111-119.
- BUNNEL, F.L. & TAIT, D.E.N., 1985. Mortality rates of North American bears. *Arctic*, 38: 316-323.
- 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.
- COUTURIER, M.A.J., 1954. L'ours brun. Grenoble, 904 pp.
- CRAIGHEAD, F.C.Jr. & CRAIGHEAD, J.J., 1972. Data on grizzly bear denning activities and behavior obtained by using wildlife telemetry. In: HERRERO, S. (Editor), *Bears, their biology and management*. *International UCN Publications New series* 23: 84-106.
- CRAIGHEAD, L. 2000. Bears of the world. Voyageur Press, Stillwater, 132 pp.
- CRAIGHEAD, L., PAETKAU, D., REYNOLDS, H.V., VYSE, E.R. & STROBECK, C., 1995. Microsatellite analysis of paternity and reproduction in Arctic grizzly bears. *Journal of Heredity*, 86: 255-261.
- DAHLE, B. & SWENSON, J.E., 2003. Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology*, 72: 660-667.
- DEBELJAK, I., 2002. Fossil population structure of the cave bear from Divje babe I site, Slovenia: preliminary results. In: ROSENDAHL, W., MORGAN, M. & LOPEZ CORREA, M. (Editors), *Cave bear researches/Höhlen Bären Forschungen*. *Abhandlungen zur Karst-und Höhlenkunde*, 34: 41-48.
- DEROCHER, A.E. & WIIG, O., 1999. Infanticide and cannibalism of juvenile polar bears (*Ursus maritimus*) in Svalbard. *Arctic*, 52: 307-310.
- 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.
- DE TORRES PEREZ-HIDALGO, T. 1988. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Iberico (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmüller-Heinroth, *U. arctos* Linneo): VI. Denticion inferior. *Boletín geológico y minero*, 99: 886-940.
- DUPONT, E., 1869. Note sur la découverte d'une caverne à Goyet. *Bulletin de l'Académie royale des Sciences, 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.
- 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., 1966. Die plistozaenen Baeren Belgiens. III Teil: Cavernes de Montaigle (Schluss), Cavernes de Walzin, caverne de Freyr, caverne de Pont-à-Lesse. *Mémoires de l'Institut royal des Sciences Naturelles de Belgique*, 155: 1-74.
- FLÜCKIGER, J., BLUNIER, T., STAUFFER, B., CHAPPELLAZ, J., SPAHNI, R., KAWAMURE, K., SCHWANDER, J., STOCKER, T.F. & JAHL-JENSEN, D. 2004. N<sub>2</sub>O and CH<sub>4</sub> variations during the last glacial epoch: insight into global processes. *Global Biogeochemical Cycles* 18, GB1020, doi 10.1029/2003GB002122.
- FOSSE, P., 2001. Ursidés pléistocènes des Pyrénées: éléments de paléontologie et de paléobiologie. *Bulletin de la Société pré-historique Ariège-Pyrénées*, 56: 103-138.
- FOSSE, P., BESSON, J.-P., LABORDE, H., CANTIE, T., CAZENAVE, G. & DELMASURE, M.-C., 2003. Denning behaviour of modern brown bear (*Ursus arctos* L.) in caves: biological and paleontological considerations from a french pyrenean site. Abstracts. 9<sup>th</sup> International Cave Bear Symposium, 25th-27th September 2003: 61.
- FOSSE, P., MOREL, P. & BRUGAL, J.P., 2002. Taphonomie et paléothologie des ursidés pléistocènes. In: Tillet, T. & Binford, L. (Editors), *L'homme et l'ours*, Colloque international, Auberives-en-Royans. *Études et Recherches Archéologiques de l'Université de Liège*, 100: 79-101.
- GENTY, D., BLAMART, D., OUAHDI, R., GILMOUR, M., BAKER, A., JOUZEL, J. & VAN-EXTER, S. 2003. Precise dating of Dansgaard-Oeschger climate oscillations in western Europe from stalagmite data. *Nature*, 421: 833-837.
- GERMONPRÉ, M. 1993. Preliminary results on the taphonomy of the Denisova cave 1992 excavation. *Altaica* 2: 11-16.
- GERMONPRÉ, M., 1996. Preliminary results on the mammals of the Magdalenian upper horizon of Goyet (Belgium). *Notae Praehistoricae*, 16: 75-85.

- GERMONPRÉ, M., 2001. A reconstruction of the spatial distribution of the faunal remains from Goyet, Belgium. *Notae Praehistoricae*, 21: 57-65.
- GERMONPRÉ, M., 2003. The Pleniglacial cave bear from Goyet, Belgium. Abstracts. 9<sup>th</sup> International Cave Bear Symposium, 25th-27th September 2003: Entremont-le-Vieux, Savoie, France: 57-58.
- GERMONPRÉ, M., 2004. Influence of climate on sexual segregation and cub mortality in Pleniglacial cave bear. In: LAUWERIER, R.C.G.M. & PLUG, I. (Editors), *The Future from the Past: Archaeozoology in Wildlife Conservation and Heritage Management*. Proceedings of the 9th congress of the International Council of Archaeozoology, Oxford: Oxbow Books: 51-63.
- GERMONPRÉ, M., *in press*. Two cave bear assemblages from Goyet (Chamber A, horizon 1 and 3), Belgium. *Revue de Paléobiologie*.
- GERMONPRÉ, M. & SABLIN, M., 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, Série Sciences de la Terre*, 71: 209-233.
- GERMONPRÉ, M. & SABLIN, M., 2002. Preliminary results on the bovids of the Belgian Magdalenian. *Notae praehistoricae*, 22: 71-73.
- GITTLEMAN, J.L. & VAN VALKENBURG, B., 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *Journal of Zoology*, 242: 97-117.
- 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., A.F. & BANNIKOV, A.G., 1974. Die Säugetiere der Sowjetunion. Band II: Seekühe und Raubtiere. Gustav Fischer Verlag, Jena, 1006 pp.
- HÖRMANN, K., 1933. Die Petershöhle bei Velden in Mittelfranken, eine altpaläolithische Station. *Abhandlungen der Naturhistorischen Gesellschaft zu Nürnberg*, 23:1-70.
- HUIJZER, B. & VANDENBERGHE, J., 1998. Climatic reconstruction of the Weichselian Pleniglacial in northwestern and central Europe. *Journal of Quaternary Science*, 13: 391-417.
- 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., 1940. Les usures séniles des canines d'*Ursus spelaeus*. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 51: 76-95.
- KOBY, F.E. 1941. Le "charriage à sec" des ossements dans les cavernes. *Eclogae Geologicae Helvetiae*, 34: 319-320.
- KOBY, F. E. 1943. Les soi-disant instruments osseux du paléolithique alpin et la charriage à sec des os d'ours des cavernes. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 54: 59-94.
- KOVACH, A.I. & POWELL, R.A., 2003. Effects of body size on male mating tactics and paternity in black bears, *Ursus americanus*. *Canadian Journal of Zoology*, 81: 1257-1268.
- KURTÉN, B., 1955. Sex dimorphism and size trends in the cave bear, *Ursus spelaeus* Rosenmüller and Heinroth. *Acta Zoologica Fennica*, 90: 1-48.
- KURTÉN, B., 1958. Life and death of the Pleistocene cave bear. A study in paleoecology. *Acta Zoologica Fennica*, 95: 1-59.
- KURTÉN, B., 1976. The cave bear story. Life and death of a vanished animal. Columbia University Press.
- 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.
- MCLOUGHLIN, P.D., CLUFF, H.D. & MESSIER, F., 2002. Denning ecology of barren-ground grizzly bears in the central arctic. *Journal of Mammalogy*, 83: 188-198.
- MORDOSOV, I.I., 1993. Buryi medved. Yakutia. In: VAISFELD, M.A. & CHESTIN, I.E. (Editors), *Medvedi: buryi medved, belyi medved, himalaiskii medved*. Razmeshchenie zapasov, ekologiya, ispolzovanie i okhrana. Nauka, Moskva (in Russian with English summary): 301-318.
- MURIE, A., 2000. The grizzlies of Mount McKinley. University of Washington Press, 251 pp.
- OTTE, M., 1979. Le paléolithique supérieur ancien en Belgique. *Monographies d'Archéologie Nationale*, 5: 1-684.
- PACHER, M. 1997. Der Höhlenbärenkult aus ethnologischer Sicht. *Wissenschaftliche Mitteilungen Niederösterreichs Landesmuseum* 10: 251-375.
- PACHER, M. 2002. Polémique autour d'un culte de l'ours des cavernes. In: Tillet, T. & Binford, L. (Editors), *L'homme et l'ours*, Colloque international, Auberives-en-Royans. *Etudes et Recherches Archéologiques de l'Université de Liège*, 100: 235-246.
- PEETERS, M., FRANKLIN, A. & VAN GOETHEM, J.L., 2003. Biodiversity in Belgium. Royal Belgian Institute of Natural Sciences, Brussels, 416 pp.
- RAHIR, E., 1908. Etude spéléologique des environs de Goyet et de Hotton (Belgique). *Spelunca*, 7: 131-150.
- 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.
- 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 University Press, Washington D.C.:157-160
- ROLS, P.M.A., 1984. L'hibernation de l'ours. Ecole nationale vétérinaire de Toulouse, thèse 66.
- SCHMERLING, P.C., 1833. Recherches sur les ossements fossiles découverts dans les cavernes de la province de Liège. Liège, Collardin.
- SHACKLETON, N.J., FAIRBANKS, R.G., DHU, T.-C. & PARRENIN, F. 2004. Absolute calibration of the Greenland time scale: implications for Antarctic time scales and for d14C. *Quaternary Science Reviews* 23: 1513-1522.
- SIMONET, P., 1992. Les associations de grands mammifères du gisement de la grotte Scladina à Sclayn (Namur, Belgique). In *Recherches aux grottes de Sclayn? Volume 1, Le contexte*.

*Etudes et Recherches Archéologiques de l'Université de Liège* 27: 127-151.

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

SWENSON, J.E., SANDEGREN, F., SÖDERBERG, A., BJÄRVALL, A., FRANZÉN, R. & WABAKKEN, P., 1997. Infanticide caused by hunting of male bears. *Nature*, 386: 450-451.

TAYLOR, M., LARSEN, T. & SCHWEINSBURG, R.E., 1985. Observations of intraspecific aggression and cannibalism in polar bears (*Ursus maritimus*). *Arctic*, 38: 303-309.

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

VANDENBERGHE, J., HUIJZER, B. S., MÜCHER, H. & LAAN, W. 1998. Short climatic oscillations in a western European loess sequence (Kesselt, Belgium). *Journal of Quaternary Science*, 13: 471-485.

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., LANDRIE, M., HENDRIX, V., MAES, A., DAN DER BORG, K., DE JONG, A.F.M., ALDERLIESTEN, C. & KEPPENS, E., 2001. Royal Institute for Cultural Heritage, Radiocarbon dates. VIII. KIK, Brussels, 50 pp.

VAN TROOS, K., 2002-2003. Revisie van de Quartaire zoogdieren uit de vierde grot van Goyet, provincie Namen. Scriptie tot het verkrijgen van het diploma van Licentiaat in de Geologie, Faculteit Wetenschappen, Universiteit Gent, 89pp.

VAN VALKENBURG, B. & SACCO, T., 2002. Sexual dimorphism, social behaviour, and intrasexual competition in large Pleisto-

cene carnivores. *Journal of Vertebrate Palaeontology*, 22: 164-169.

WIELGUS, R.B. & BUNNELL, F.L., 1995. Tests of hypotheses for sexual segregation in grizzly bears. *Journal of Wildlife Management*, 59: 552-560.

WIELGUS, R.B. & BUNNELL, F.L., 2000. Possible negative effects of adult male mortality on female grizzly bear reproduction. *Biological Conservation*, 93: 145-154.

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

ZHIRYAKOV, V.A. & GRACHEV, Y.A. 1993. Buryi medved. Centralnoi Azii u Kazakhstana. In: VAISFELD, M.A. & CHESTIN, I.E. (Editors), *Medvedi: buryi medved, belyi medved, gimalaiskii medved. Razmeshchenie zapasov, ekologiya, ispolzovanie i okhrana*. Nauka, Moskva (in Russian with English summary): 170-206.

Mietje GERMONPRÉ

Departement Paleontologie

Koninklijk Belgisch Instituut voor Natuurwetenschappen

Vautierstraat 29

B-1000 Brussel

Belgium

[mietje.germonpre@naturalsciences.be](mailto:mietje.germonpre@naturalsciences.be)

Typescript submitted: 1 March 2004

Revised typescript received: 16 August 2004

#### Explanation of the Plate

Fig. 1 — *Ursus spelaeus*: lower canine with wear facet (assemblage B5: G3.5.5)

Fig. 2 — *Ursus spelaeus*: upper jaw fragment with worn canines (assemblage B4: 3226), arrow indicates band of worn enamel

Fig. 3 — *Ursus spelaeus*: two ilium fragments, arrows indicate punctures by bear? (assemblage B5: 2740-1 & 2740-2)

Fig. 4 — *Ursus spelaeus*: shaft fragment of a humerus showing hyaena-induced damage with extensive gnawing to both upper and lower margins (assemblage A3: 2800)



