

# Intra-specific morphological variability in the cave bear *Ursus spelaeus* (Mammalia, Carnivora, Ursidae) from the Trou du Sureau (Montaigle caves, Belgium) using an outline analysis

Hélène GOUBEL  
Patrick AUGUSTE  
Catherine CRÔNIER

Université Lille 1, UMR 8217 – CNRS, Géosystèmes, Sciences de la Terre,  
Bâtiment SN5, F-59655 Villeneuve d'Ascq cedex (France)

[hgoubel@gmail.com](mailto:hgoubel@gmail.com)  
[patrick.auguste@univ-lille1.fr](mailto:patrick.auguste@univ-lille1.fr)  
[catherine.cronier@univ-lille1.fr](mailto:catherine.cronier@univ-lille1.fr)

Mietje GERMONPRÉ

Royal Belgian Institute of Natural Sciences, Department of Paleontology,  
Vautier street 29, B-1000 Brussels (Belgium)

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

---

Goubel H., Auguste P., Crônier C. & Germonpré M. 2012. — Intra-specific morphological variability in the cave bear *Ursus spelaeus* (Mammalia, Carnivora, Ursidae) from the Trou du Sureau (Montaigle caves, Belgium) using an outline analysis. *Geodiversitas* 34 (4): 961-975. <http://dx.doi.org/10.5252/g2012n4a13>

## ABSTRACT

The first lower molars of the cave bear *Ursus spelaeus* Rosenmüller, 1794 exhibit a high variability in size and shape. An outline analysis *via* the elliptic Fourier transform has been performed on a population from the oldest archaeological deposit (Level 4, Upper Pleistocene) of the Trou du Sureau (Montaigle caves, Belgium) in order to quantify the intra-specific morphological plasticity. The size and shape descriptors were extracted and results were compared to traditional measurements of length, mesial width, distal width and height. We determined a few individual parameters, such as the individual age, the laterality and a few Rabeder's morphotypes and we tested their effect on the morphological variability. Results indicate no significant relationship between the shape variability and the individual parameters, except for the metastylid conformation and the laterality. The metastylid would induce a decoupling in the evolution of the size and the shape, maybe related to differences in the evolutionary patterns. The effect of the laterality could not be clearly established because it seems closely linked to the distribution of the metastylids in our sample. A marked polymorphism could be interpreted as a sexual dimorphism or could more probably correspond to two distinct cave bear sub-populations. Finally, our analysis demonstrates the feasibility of the outline analysis on ursid dental elements and provides a preliminary step before applying this method at an inter-specific level.

## KEY WORDS

Cave bear,  
first lower molar,  
occlusal surface,  
intra-specific variability,  
outline analysis,  
geometric  
morphometrics.

## RÉSUMÉ

*Variabilité morphologique intra-spécifique chez l'ours des cavernes Ursus spelaeus (Mammalia, Carnivora, Ursidae) du Trou du Sureau (Grottes de Montaigle) par une analyse des contours.*

Les premières molaires inférieures de l'ours des cavernes *Ursus spelaeus* Rosenmüller, 1794 montrent une importante variabilité de taille et de forme. Une analyse des contours *via* la transformée de Fourier elliptique a été appliquée sur une population provenant du dépôt archéologique le plus ancien (Niveau 4, Pléistocène supérieur) du Trou du Sureau (Grottes de Montaigle, Belgique) afin de quantifier la plasticité morphologique intra-spécifique. Les descripteurs de taille et de forme ont été extraits et les résultats ont été comparés avec les mesures traditionnelles de longueur, largeurs mésiale et distale et hauteur. Nous avons déterminé quelques paramètres individuels, tels que la latéralité, l'âge individuel et les morphotypes définis par Rabeder et testé leur effet sur la disparité morphologique. Les résultats n'indiquent pas de relation significative entre la variabilité morphologique et les paramètres individuels, excepté pour la conformation du métastylide et la latéralité. Le métastylide induirait un découplage dans l'évolution de la taille et de la forme, peut-être lié à des différences dans les patrons évolutifs. L'effet de la latéralité ne peut pas être clairement établi car il semble étroitement lié à la distribution des métastylides dans notre échantillon. Un polymorphisme marqué pourrait être interprété comme du dimorphisme sexuel ou correspondrait plus probablement à deux sous-populations distinctes d'ours des cavernes. Enfin, notre analyse démontre la faisabilité de l'analyse des contours sur les éléments dentaires d'Ursidae et constitue une première étape préliminaire nécessaire avant d'appliquer cette méthode au niveau inter-spécifique.

## MOTS CLÉS

Ours des cavernes,  
première molaire  
inférieure,  
surface occlusale,  
variabilité intra-spécifique,  
analyse des contours,  
morphométrie  
géométrique.

## INTRODUCTION

The cave bear (Mammalia, Carnivora, Ursidae Fischer, 1817) is often found in abundance in the Middle to Upper Pleistocene fossil records, notably in the cave deposits. Along the cave bear lineage, the Upper Pleistocene cave bear *Ursus spelaeus* Rosenmüller, 1794 succeeded to the Middle Pleistocene *Ursus deningeri* Von Reichenau, 1904. Some sub-specific intermediate forms between the typical *U. deningeri* and *U. spelaeus* were also described, notably *U. spelaeus deningeroides* Mortl, 1964 (Argant 1991; Auguste 1995). Numerous non-metrical and metrical features illustrate the gradual evolution from the archaic to evolved cave bear along the lineage (Kurtén 1976). The anatomical features of cave bear's skull, dental elements and limb bones have been frequently interpreted as an increasingly herbivorous feeding behav-

ior (Kurtén 1976), which was widely supported by isotopic analyzes (Bocherens *et al.* 1997). The main dental modifications that can be observed induce an increase of the occlusal efficiency, implying a growth of the crown dimensions, a duplication of the main cusps and a multiplication of secondary cusps, crests, ridges and pillars of enamel (Kurtén 1976; Prat & Thibault 1976). Some of these morphological features were defined as morphotypes and classified *a priori* in accordance to their evolutionary relevance (Rabeder 1983, 1999; Paunović 1988; Argant 1995; Grandal d'Anglade & López-González 2004). Nevertheless, recent studies based on dental microwear (Peigné *et al.* 2009), isotopic analyzes (Richards *et al.* 2008) and geometric morphometrics (landmarks) applied on cave bear's skull and mandible (Figueirido *et al.* 2009) have demonstrated that this statement should be nuanced. Indeed, these data suggest a more

omnivorous or even carnivorous feeding behavior for cave bears.

The cave bear cheek teeth also illustrate interesting examples of polymorphism even at the scale of a single population. A part of this intra-specific size and shape variability remains difficult to explain with traditional measurements which are usually sufficient for a specific determination. Moreover, because linear distance, these indicators are usually correlated with the body size (Bookstein *et al.* 1985). In our study, we quantified the morphology of the crown of first lower molars in occlusal view. For this, we used an outline analysis *via* the elliptic Fourier transform in order to assess the intra-specific variability of the first lower molars. We tested a cave bear population found in the oldest archaeological deposit Level 4 of the Trou du Sureau (Montaigle caves, southern Belgium). Then, we performed comparisons with traditional measurements of length, distal width, mesial width and height. Finally, we determined the laterality and the complexity of the occlusal surface using the morphotypes defined by Rabeder (1999) and we evaluated the individual age on the basis of the age classes defined by Stiner (1998) before testing the effect of such individual parameters on the size and shape variability.

## MATERIAL AND METHODS

Located in southern Belgium, in the valley of the Molinee (Fig. 1), the Trou du Sureau (Montaigle caves) was first prospected in the nineteenth century (Dupont 1868). The material studied here was excavated by Dupont in 1867 (Dupont 1868) and is stored in the Royal Belgian Institute of Natural Sciences. Dupont recognised twelve sedimentary layers. Six of them yielded archaeological objects and faunal remains. The finds from the sedimentary layers 12, 11 and 10 were each attributed to one archaeological level. However, Dupont grouped the finds from sedimentary layers 8, 7 and 6 in one archaeological level, the so-called "Niveau 4". The cave bear teeth analyzed in our study are all from this Level 4, and were thus found in three different sedimentary units (Dupont 1873; Otte 1979).

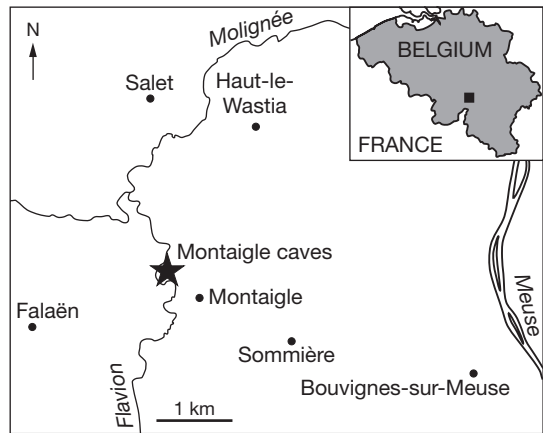


Fig. 1. — Location of the Montaigle caves, southern Belgium.

The problematic attribution of the chronological and palaeoenvironmental context was summarised by Otte (1979). The definition of the chronological context of the Level 4 was based on the lithic record: a dominant "Mousterien Charentien de type Quina" industry (Middle Palaeolithic) associated with a few Aurignacian lithics (Upper Palaeolithic) would mainly indicate an Upper Pleistocene deposit (Ulrix-Closset 1968). The palaeoenvironmental context of the Level 4 was defined on the basis of the faunal assemblage. The development of a *Mammuthus-Coelodonta* faunal complex as described by Kahlke (1999) with the characteristic *Alopex lagopus* (Linnaeus, 1758) (polar fox), *Rangifer tarandus* (Linnaeus, 1758) (reindeer), *Mammuthus primigenius* (Blumenbach, 1799) (woolly mammoth), *Coelodonta antiquitatis* (Blumenbach, 1807) (woolly rhinoceros) and *Bison priscus* Bojanus, 1827 (steppe bison) would indicate a cold, dry and open palaeoenvironment. However, the presence of *Capreolus capreolus* (Linnaeus, 1758) (roe deer), *Cervus elaphus* Linnaeus, 1758 (red deer) and *Sus scrofa* Linnaeus, 1758 (wild boar) would notice a more temperate and woody landscape (Dupont 1873; Otte 1979).

The fossil bear from the Level 4 is mainly assigned to a typical cave bear *U. spelaeus* and is represented by more than 1 700 remains, in majority limb bones and teeth (Ehrenberg 1935). A few remains of brown bear *U. arctos* Linnaeus, 1758 were also found in

TABLE 1. — Database of 37 *U. spelaeus* Rosenmüller, 1794 first lower molars from Trou du Sureau, Belgium. Abbreviations: **L**, length; **DW**, distal width; **MW**, mesial width; **PrdH**, protoconid height (all in mm); **A**, area (in cm<sup>2</sup>); **P**, perimeter (in cm) and principal component axes **PC1**, **PC2** and **PC3** extracted from the ACP. Individual parameters: **Lat**, laterality (right and left); **AC**, age class (Juvenile and Prime Adult); **Ed**, entoconid (B2 to B4); metastylid + **Mslid** (I to IV); **Prd**, protoconid (1 to 2); **EHyd**, enthyppoconid (A to D) and **EdP**, entoconid pillars (A to E). Morphotypes Ed, Mslid, EHyd and EdP determined according to Rabeder's encoding (1999). Collection: Montaigne, Trou du sureau, quatrième niveau ossifère (Dét Ehrenberg), Âge du mammoth, plate 2872.

N°	Morphometrical database									Individual parameters						
	Traditional morphometrics			Outline analysis						Morphotypes						
	L	DW	MW	PrdH	A	P	PC1	PC2	PC3	AC	Lat	Ed	Mslid	Prd	EHyd	EdP
1	30.5	14.6	11.1	11.6	3.25	7.93	-0.55	-0.58	1.41	J	R	B3	II	2	D	E
2	30.9	14.3	11.5	11.1	3.53	8.24	1.05	-0.16	0.95	J	R	B2	II	2	D	E
3	29.9	14.4	12	12.3	3.64	8.19	0.92	1.21	-0.06	J	R	B3	II	2	A/B	A
4	34.8	16.7	13.2	14.4	4.51	9.19	-0.94	0.85	0.46	J	R	B4	III	2	D	E
5	31.6	14.2	11.6	13.1	3.66	8.50	-0.19	-1.26	1.45	J	R	B3	III	2	D	E
6	31.7	15.2	12.2	13.7	3.91	8.58	0.38	-0.02	-0.07	J	R	B3	I	2	D	E
7	32.6	15.9	12.6	14.2	4.20	8.79	0.77	2.10	-0.01	J	R	B2	II	2	C	E
8	31.5	16	12.4	12.7	4.03	8.60	-0.06	2.07	0.72	J	R	B3	III	2	D	C
9	34.4	16.1	12.5	14.0	4.79	9.57	0.12	0.19	0.13	J	R	B3	IV	2	D	C
10	31.4	14.8	10.9	13.7	3.72	8.52	1.63	-0.16	1.88	J	R	B4	II	2	C	C
11	32.2	15.7	11.7	12.3	4.27	9.01	0.68	1.39	0.98	J	R	B3	II	2	D	D
12	32.6	15.1	12.4	-	4.05	8.67	0.94	-0.30	-0.41	J	R	B4	II	2	D	D
13	33.4	16.3	12.6	14.5	4.34	9.11	-1.09	0.46	1.07	J	R	B3	III	2	D	C
14	32.1	14.4	11.9	13.4	4.06	8.89	-1.09	-0.26	0.99	J	R	B3	III	2	D	E
15	31.9	16.1	13.2	14.0	4.26	8.78	-1.09	1.65	-0.85	J	R	B4	II	2	D	D
16	32.0	14.3	11.1	13.2	3.73	8.58	0.42	-1.88	-0.34	J	R	B2	III	2	D	B
17	28.1	13.0	10.4	11.5	2.92	7.55	0.04	-1.36	1.35	J	R	B4	II	2	D	D
18	31.6	15.2	12.0	13.7	3.91	8.67	-1.29	-0.02	0.06	J	R	B3	II	1	C	D
19	30.1	13.5	10.6	13.5	3.55	8.35	-1.75	-1.11	-0.21	J	R	B4	II	2	C	B
20	29.0	14.7	11.9	12.8	3.32	8.04	-0.86	-0.55	0.46	J	R	B2	II	2	C	D
21	32.2	16.2	13.1	14.9	4.19	8.77	0.56	0.56	-0.27	J	R	B3	II	2	D	E
22	30.1	14.2	11.1	12.7	3.40	8.08	-0.75	-0.20	0.75	J	R	B2	III	2	D	E
23	30.2	15.3	12.2	-	3.86	8.44	-1.42	1.24	-0.39	J	R	B3	I	1	D	E
24	30.0	14.2	11.6	-	3.52	8.25	-0.12	-0.44	-0.14	J	R	B3	II	2	D	E
25	29.8	14.0	11.3	-	3.53	8.14	1.78	-0.32	0.18	J	R	B3	III	2	D	E
26	30.4	14.6	11.6	-	3.42	8.08	-0.26	0.34	-0.77	PA	R	B2	II	2	D	D
27	30.3	13.6	10.5	-	3.22	7.98	-0.20	-1.11	0.31	J	R	B2	II	2	D	D
28	30.8	14.5	11.9	-	3.67	8.30	-0.24	0.63	0.04	PA	R	B2	III	1	D	D
29	32.2	14.7	11.5	12.5	3.86	8.72	-0.38	-1.15	0.19	J	L	B4	II	2	D	D
30	30.4	13.6	10.6	11.7	3.47	8.19	0.05	-0.76	-0.43	J	L	B3	II	2	D	E
31	30.8	14.7	11.8	12.2	3.57	8.23	0.94	-0.12	-2.09	J	L	B2	I	2	D	D
32	30.0	13.6	10.6	12.9	3.28	7.98	-0.95	-1.01	-0.97	J	L	B3	I	2	D	D
33	30.5	15.9	12.8	-	3.96	8.57	-1.03	1.20	-1.84	J	L	B2	III	2	C	C
34	28.0	13.5	10.8	11.8	2.77	7.28	-0.07	-1.53	-3.03	J	L	B3	I	2	D	C
35	31.1	15.3	11.4	12.9	3.82	8.51	2.92	-0.14	-0.75	J	L	B2	II	2	D	D
36	29.8	13.8	10.4	-	3.24	7.91	1.05	-0.15	-0.21	J	L	B3	III	2	D	E
37	31.1	15.2	11.7	-	3.68	8.37	0.11	0.68	-0.55	PA	L	B2	I	2	-	-
<b>N</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>27.0</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>36</b>	<b>36</b>

the fossil record. In our study, we focused on the first lower molar because of its diagnostic character (Mazza & Rustioni 1994) and its evolutionary and ecological interests (Legendre 1988). We selected the best-preserved first lower molars for a total of 37 teeth which details are listed in Table 1.

The traditional measurements (Table 1) detailed in Von den Driesch (1976) were performed on the dental crown: length L, distal width DW corresponding to the talonid breadth and mesial width MW corresponding to the trigonid breadth (Fig. 2). We also measured the protoconid height PrdH (Prat &

Thibault 1976; Argant 1991) on 27 teeth with wearing pattern corresponding to stages I and II of Stiner (1998). All traditional measurements are reported in mm. Maximum and minimum values, averages, standard deviations and coefficients of variation were summarised in Table 2. Ehrenberg's maxima and minima (Ehrenberg 1935) were also reported for comparison.

Geometric morphometrics are powerful tools to quantify and describe the morphology of any object (Rohlf 1990; Rohlf & Marcus 1993; Adams *et al.* 2004). When the material is poor-landmark, an outline analysis using an elliptic Fourier transform can be performed. It has been applied successfully on many invertebrates (Foote 1989; Cr n nier *et al.* 1998, 2005) and vertebrates, notably on rodent and pig molars (Renaud 1999; Cucchi *et al.* 2009) but has not yet been performed on ursid cheek teeth. After positioning the tooth in a reference grid, we took a picture of the occlusal surface using a numeric camera with focus at the crown maxima. The *x*- and *y*- coordinates of 64 points equally spaced along the outline have been automatically extracted using the optical image analyzer Optimas v.6.5 (Fig. 2). Before standardizing the size, we calculated the area (*A*) in cm<sup>2</sup> and the perimeter (*P*) in cm and applied elementary statistics (Table 2). Then, the sets of coordinates were expanded in 64 Fourier series (or harmonics) *via* an elliptic Fourier transform (Kuhl & Giardina 1982; Ferson *et al.* 1985) using the software NTSYS-pc v.1.8 (Rohlf 1973). Each harmonic describes an ellipse and is defined by a set of four Fourier coefficients. Since most of the morphology can be described by the first few harmonics, we calculated the average cumulative Fourier power and selected the first six harmonics corresponding to the first 24 Fourier coefficients (Fig. 3).

A principal component analysis (PCA) was performed on the sets of Fourier coefficients and the first three axes PC1, PC2 and PC3 were extracted. The shape descriptors PC1, PC2 and PC3 provide respectively 24.20%, 20.02% and 13.82% of the total variance. Pearson's coefficients of correlation *r* and the associated significance level *p* were calculated between size and shape (Table 3). We performed univariate analyses of variance (ANOVA) on the

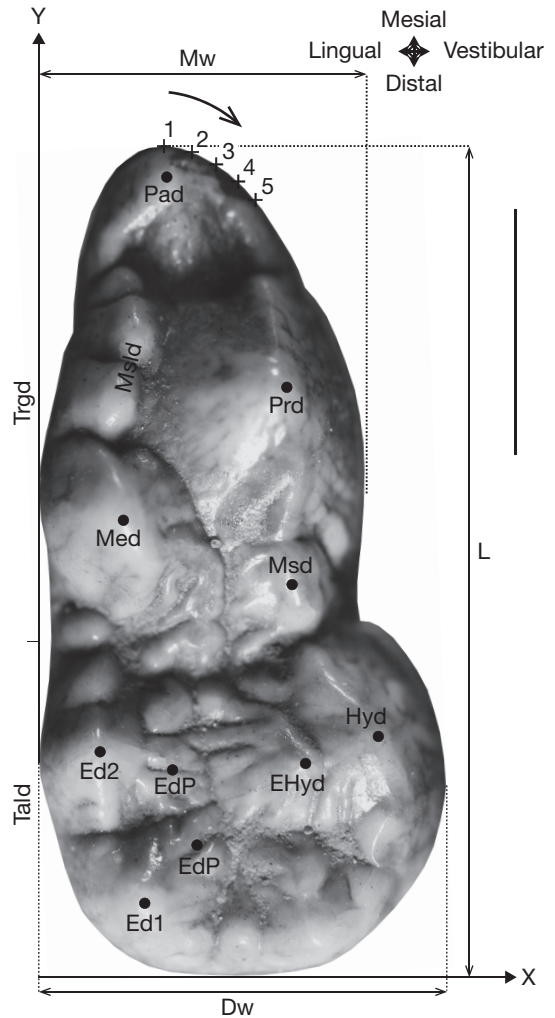


FIG. 2. — Traditional morphometrics performed on the dental crown. Location of the first five points equally spaced along the outline and positioned over a reference grid. Abbreviations: **DW**, distal width; **Ed**, entoconid; **EdP**, entoconid pillars; **EHyd**, Entoconid; **Hyd**, Hypoconid; **L**, length; **Med**, metaconid; **Msd**, mesoconid; **Mslid**, metastylid; **MW**, mesial width; **Pad**, paraconid; **Prd**, protonid; **Tald**, talonid; **Trgd**, Trigonid. Scale bar: 1 cm.

linear distance measurements and calculated the Fischer's test *F* and the associated significance level *p* (Table 4). Mean outlines were reconstructed to visualize the shape variability using an inverse elliptic Fourier transform performed on the sets of Fourier coefficients. We checked the normality of the size and shape distributions using a Shapiro-Wilk's test.



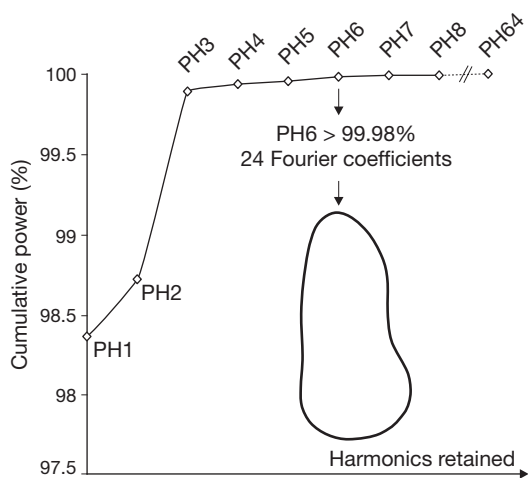


Fig. 3. — Average cumulative Fourier power spectrum calculated from the Fourier coefficients. Cumulative power is above 99.98% for the first six harmonics corresponding to the first 24 Fourier coefficients. A reconstructed mean outline calculated from the sets of Fourier coefficients is included.

Finally, the individual age was estimated using the wear stage of the occlusal surface after determining the laterality (Lat). The juvenile (J) and prime adult (PA) age classes (AC) correspond respectively to the wear stages I to III and IV to VII (Stiner 1998). We also determined the conformation of some features on the occlusal surface using the morphotypes defined by Rabeder (1999), which details were not reported here. The entoconid Ed (from B2 to B4) and the metastylid Msl (from I to IV corresponding to the number of cusplets) are located on the lingual side of respectively the talonid and the trigonid. On the central part of the talonid, the enthyoconid EHyd (from A to D) is situated near the hypoconid and the entoconid enamel pillars EdP (from A to E) near the entoconid. In addition, we tested the absence or the presence of the mesoconid defined as a secondary cusp of the protoconid (Prd from 1 to 2) located on the vestibular side of the trigonid (Fig. 2).

In order to assess measurement error, five specimens have been selected randomly and replicated in ten series following the same data acquisition procedure. Then, ANOVAs have been performed on both individual and replication series. Results indicate a significant difference between the five

individual series ( $p < 0.001^{***}$ ) whereas these results indicate no significant difference between the ten replication series ( $p > 0.05$  NS). Thus, measurement error that could occur during the data acquisition can be considered as negligible.

## RESULTS

The mean values of traditional measurements (see Tables 1 and 2) obtained in our analysis exhibit long, wide and high crowns. Our maxima and minima are similar to Ehrenberg's (1935). In our sample, the dispersions of the mesial width, distal width and protoconid height are similar. The minimal dispersion is observed for the length. The mean area and perimeter equal respectively 3.73 cm<sup>2</sup> and 8.42 cm (Table 2). Size descriptors and traditional measurements are highly correlated. The strongest positive correlations were calculated between area, perimeter and length (Table 3). The scatter diagram of length plotted with the distal width, mesial width, protoconid height, perimeter and area exhibits isometric distributions (Fig. 4). The second shape axis PC2 is correlated to the size, notably the distal and mesial widths. The first and third shape axes PC1 and PC3 show no correlation with size (Table 3).

Based on the sets of 24 Fourier coefficients, a mean outline of the 37 first lower molars was reconstructed (Fig. 3). The global shape of this mean first lower molar is massive, broad and almost rectangular. The trigonid seems well developed and longer than the talonid. The trigonid and the talonid are delimited by a slight concavity on the lingual side and a pronounced angle on the vestibular side. The paraconid is broad and not clearly delimited from the metaconid and the protoconid. The entoconid and the protoconid can be clearly located. The hypoconid is well developed and exceeds the protoconid in breadth.

The individual parameters (see Table 1) were determined and compared to the intra-specific variability using ANOVAs (Table 4). We discriminated 28 right teeth, 9 left teeth, 34 juvenile and 3 prime adults. On the basis of Rabeder's encoding, we recognized four metastylid con-

TABLE 2. — Maximum, minimum and mean values of the first lower molar; **L**, standard deviation and coefficient of variation calculated for length; mesial and distal width respectively **MW** and **DW**; **PrdH**, protoconid height (in mm); **PrdHi**, protoconid height index; **A**, area (in cm<sup>2</sup>) **P**, perimeter (in cm). Ehrenberg's results (Ehrenberg 1935) reported below (last two lines) for comparison.

	<b>L</b>	<b>DW</b>	<b>MW</b>	<b>PrdH</b>	<b>PrdHi</b>	<b>A</b>	<b>P</b>
Max	34.8	16.7	13.2	14.9	46.2	4.79	9.57
Min	28.0	13.0	10.4	11.1	36.0	2.77	7.28
Mean	31.1	14.8	11.7	13.0	41.6	3.73	8.42
Standard deviation	1.46	0.94	0.80	0.99	2.3	0.43	0.45
Coefficient variation	4.70	6.36	6.82	7.65	5.6	11.56	5.36
Max	35.0	16.9					
Min	28.0	12.9					

TABLE 3. — Pearson's coefficients of correlation *r* (top right) and associated significance level (*p*) (bottom left) between length (**L**); **MW**, mesial width; **DW**, distal width; **PrdH**, protoconid height (all in mm); **A**, area (in cm<sup>2</sup>); **P**, perimeter (in cm). **Bold**, significant correlation; \*, probability:  $p < 0.05$  (*p*\*);  $p < 0.01$  (*p*\*\*);  $p < 0.001$  (*p*\*\*\*)

	<b>L</b>	<b>DW</b>	<b>LW</b>	<b>PrdH</b>	<b>PC1</b>	<b>PC2</b>	<b>PC3</b>	<b>A</b>	<b>P</b>
<b>L</b>		<b>0.759</b>	<b>0.651</b>	<b>0.680</b>	-0.008	<b>0.370</b>	0.250	<b>0.908</b>	<b>0.932</b>
<b>DW</b>	<i>p</i> ***		<b>0.894</b>	<b>0.676</b>	-0.032	<b>0.747</b>	0.044	<b>0.871</b>	<b>0.797</b>
<b>LW</b>	<i>p</i> ***	<i>p</i> ***		<b>0.667</b>	-0.156	<b>0.713</b>	-0.057	<b>0.806</b>	<b>0.707</b>
<b>PrdH</b>	<i>p</i> ***	<i>p</i> ***	<i>p</i> ***		-0.198	0.376	0.051	<b>0.726</b>	<b>0.704</b>
<b>PC1</b>	NS	NS	NS	NS		0	0	-0.050	-0.071
<b>PC2</b>	<i>p</i> *	<i>p</i> ***	<i>p</i> ***	NS	NS		0	<b>0.601</b>	<b>0.469</b>
<b>PC3</b>	NS	NS	NS	NS	NS	NS		0.160	0.250
<b>A</b>	<i>p</i> ***	<i>p</i> ***	<i>p</i> ***	<i>p</i> ***	NS	<i>p</i> ***			<b>0.976</b>
<b>P</b>	<i>p</i> ***	<i>p</i> ***	<i>p</i> ***	<i>p</i> ***	NS	<i>p</i> **	<i>p</i> ***		

TABLE 4. — Fisher's test (**F**) and associated significance level (*p*) extracted from ANOVAs based on length (**L**); **MW**, mesial width; **DW**, distal width; **PrdH**, protoconid height (all in mm); **A**, area (in cm<sup>2</sup>); **P**, perimeter (in cm) and the axes PC1, PC2 and PC3. Groups defined with: **Lat**, laterality; **AC**, age class; **Ed**, entoconid; **Mslid**, metastylid; **Prd**, protoconid; **EHyd**, enthyoconid; **EdP**, entoconid pillars. **Bold**, significant correlation; \*, probability:  $p < 0.05$  (*p*\*);  $p < 0.01$  (*p*\*\*);  $p < 0.001$  (*p*\*\*\*)

	<b>Lat</b>		<b>AC</b>		<b>Ed</b>		<b>Mslid</b>		<b>Prd</b>		<b>EHyd</b>		<b>EdP</b>	
	<b>F</b>	<b>p</b>	<b>F</b>	<b>p</b>	<b>F</b>	<b>p</b>	<b>F</b>	<b>p</b>	<b>F</b>	<b>p</b>	<b>F</b>	<b>p</b>	<b>F</b>	<b>p</b>
<b>L</b>	2.344	NS	0.168	NS	0.627	NS	<b>3.087</b>	<i>p</i> *	0.080	NS	0.475	NS	0.371	NS
<b>DW</b>	1.321	NS	0.003	NS	0.018	NS	0.855	NS	0.142	NS	0.172	NS	1.317	NS
<b>MW</b>	3.480	NS	0.001	NS	0.024	NS	0.583	NS	0.577	NS	0.086	NS	0.827	NS
<b>PrdH</b>	3.739	NS	—	—	0.460	NS	1.033	NS	0.526	NS	0.390	NS	0.408	NS
<b>PC1</b>	1.009	NS	0.054	NS	0.549	NS	0.343	NS	3.371	NS	1.159	NS	0.410	NS
<b>PC2</b>	1.318	NS	0.988	NS	0.212	NS	0.083	NS	1.258	NS	0.899	NS	1.896	NS
<b>PC3</b>	<b>21.660</b>	<i>p</i> ***	0.578	NS	1.093	NS	<b>4.293</b>	<i>p</i> *	0.028	NS	0.221	NS	0.547	NS
<b>A</b>	3.127	NS	0.351	NS	0.601	NS	<b>3.300</b>	<i>p</i> *	0.109	NS	0.047	NS	0.418	NS
<b>P</b>	3.149	NS	0.471	NS	0.602	NS	<b>3.957</b>	<i>p</i> *	0.035	NS	0.137	NS	0.371	NS

formations (6 Mslid I, 19 Mslid II, 11 Mslid III and 1 Mslid IV), three entoconid conformations (12 B2, 18 B3 and 7 B4), three enthyoconid conformations (1 A/B, 6 C and 29 D) and five entoconid pillars conformations (1 A, 2 B, 6 C, 13 D and 14 E). In addition, we noticed 34

mesoconid occurrences. The ANOVAs reveal no significant effect of such parameters on the variability, except for the laterality and the conformation of the metastylid (Table 4). The laterality is well differentiated on the third shape axis PC3. The conformation of the metastylid is slightly

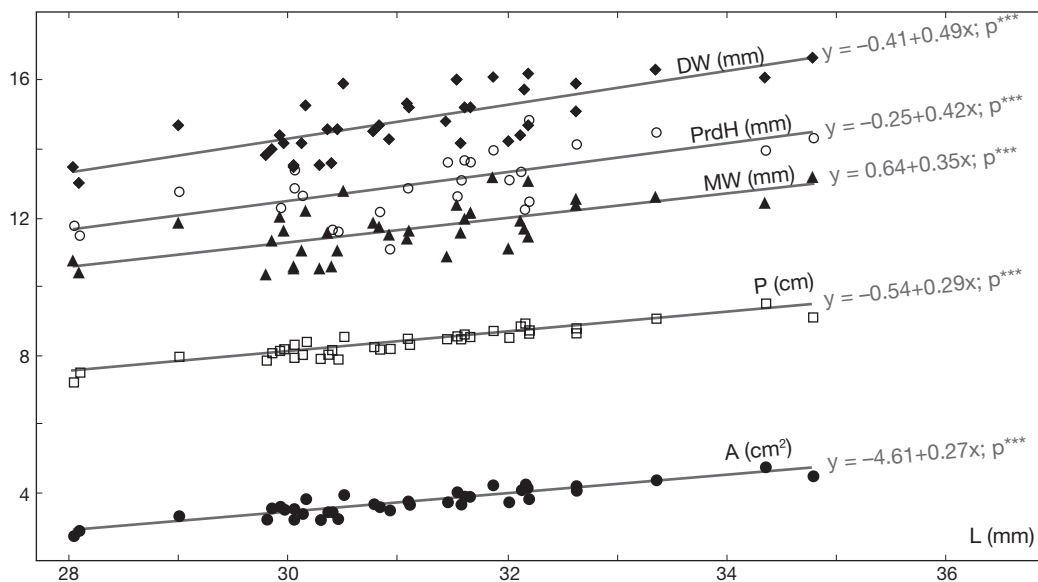


Fig. 4. — Scatter diagram of length (L) plotted with distal width (DW), mesial width (MW), protoconid height (PrdH) (all in mm), area A (in cm<sup>2</sup>) and perimeter (P) (in cm).

size and shape differentiated on the length, area and perimeter and on the third axis PC3. Additionally, we plotted the perimeter *versus* PC3 to visualize the size and shape trajectories for each metastylid conformation (Fig. 5A). Then, the mean perimeter and PC3 were calculated for each Rabeder's morphotype for comparison (Fig. 5B). The evolution of the perimeter shows a progressive size increase from Mslid I to Mslid III followed by a main size increase between Mslid III and Mslid IV, also underlined by the ANOVA. Conversely, the evolution of the shape shows a main change occurring between Mslid I and Mslid II followed by a rather constant shape change. The mean outlines reconstructed for each metastylid conformation indicate a smoothing of the lingual side of the trigonid (metastylid and metaconid) and a broadening of the vestibular side of the paraconid from Mslid I to Mslid IV.

Finally, we plotted the distal width *versus* PC2 (Fig. 6A) to visualize the correlation between the size and the shape (see Table 3). We included reconstructed mean outlines (Fig. 6A) and performed a tree clustering analysis (in Euclidian distance) using the Ward's aggregation (Fig. 6B). The cluster

analysis exhibits two morphogroups (Morphogroup I and II) clearly differentiated in both size and shape. We calculated the mean length, mesial width, distal width and height (Table 5) which reveal strong gap values between these two morphogroups. Crowns are short, narrow and low for Morphogroup I whereas they are long, wide and high for Morphogroup II. The differences in crown proportions between Morphogroup I and II were calculated after the index of the mesial width, distal width and protoconid height (respectively MWi, DWi and PrdHi) corresponding to  $MW^*100/L$ ,  $DW^*100/L$  and  $PrdH^*100/L$ . The mean distal and mesial widths index show strong differences (Table 5). The reconstructed mean outlines (Fig. 6A) indicate main shape differences affecting the vestibular side of the crown, notably on the protoconid and hypoconid and on the limit trigonid/talonid (see arrows). Therefore, Morphogroup I and II appear clearly different in size (absolute dimensions) and shape (proportions and outline of vestibular side). Nevertheless, no correlation can be observed between this marked polymorphism and the individual parameters (individual age, laterality and Rabeder's morphotypes).



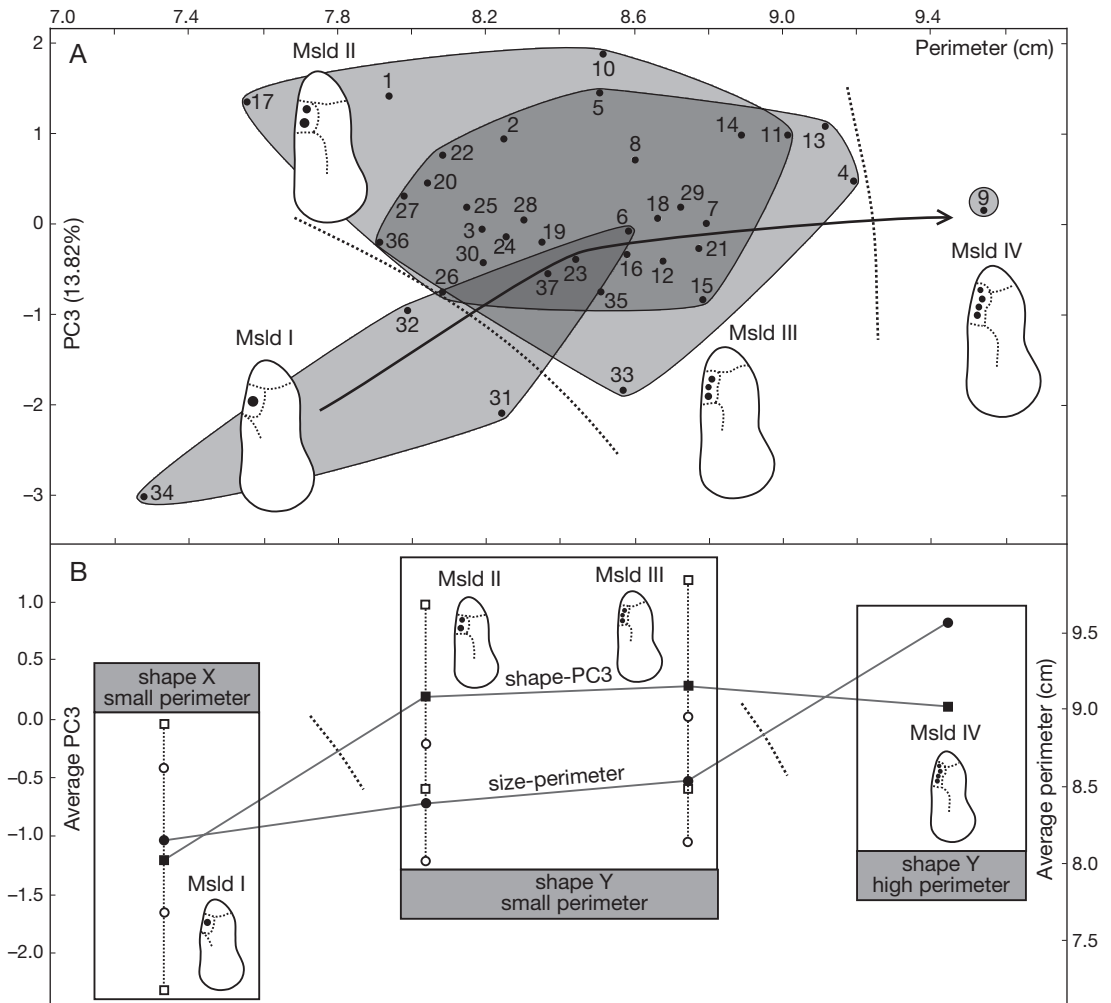


FIG. 5. — **A**, Scatterplot of size defined by the perimeter (in cm) versus shape defined by PC3 (13.82% of the total variance); **B**, evolution of the mean perimeter and PC3 (black symbols) and associated standard deviations (white symbols). The mean outlines were reconstructed for each metastyloid conformation Mslid I, II, III and IV.

## DISCUSSION

The length, width and height measured on the fossil bear of Level 4 correspond to a typical cave bear *U. spelaeus*. The mean outline (Fig. 3) also exhibits a typical *U. spelaeus* with well-developed trigonid and talonid. Because it is said that the occlusal surface of cave bear's teeth increases in complexity with time (Kurtén 1976), this assignation to *U. spelaeus* is confirmed by the presence of numerous secondary cusplets leading

to complicated metastyloid conformations (see Table 1). The main part of the size variability is explained by the development of the trigonid and talonid in breadth, as indicated by the dispersion of the mesial and distal widths. The area and the perimeter seem informative and could be considered as relevant size indicators. However, the maximal dispersion observed for the area would be related to its squared function. Thus, further analyses will be limited in extracting and comparing the perimeter only.

TABLE 5. — **L**, mean and gap values of length of the first lower molar; **DW**, distal width; **MW**, mesial width; **PrdH**, protoconid height; **A**, area; **P**, perimeter and the normalized index of mesial and distal width (**MWi** and **DWi**) and protoconid height (**PrdHi**) calculated for Morphogroup I and II.

	Morph I	Morph II	Gap
L	30.6	32.6	2.0
MW	11.4	12.7	1.3
DW	14.4	16.1	1.7
PrdH	12.7	13.9	1.2
A	3.6	4.3	0.7
P	8.3	8.9	0.6
MWi	37.2	38.9	1.7
DWi	47.0	49.5	2.4
PrdHi	41.4	42.2	0.8

We have demonstrated significant relationships between the morphological variability and a few individual parameters. On the third shape axis PC3, a part of the variability would be explained by the conformation of the metastylid. This corresponds to the multiplication of several secondary cusplets on the lingual side of the trigonid. In addition, the evolutionary patterns show uncoupled trajectories of size and shape. Indeed, our results show a progressive size increase according to the complexity of the metastylid with a main size increase occurring for metastylid with four cusplets (recognized here on a single tooth). Conversely, the shape trajectory shows a main shape change occurring between the metastylids with one and two cusplets, followed by a rather constant shape change.

Detailed studies on the use of such morphotypes concluded on their disputable evolutionary value, *i.e.* some Rabeder's morphotypes may be correlated with time and thus be used as bio-chronological indicators (Rabeder 1999). It seems difficult to assign a strict evolutionary value to a single morphotype. As we can see in our sample (see Table 1), simple and complicated conformations can coexist on the same tooth due to the mosaic acquisition of features in ursid cheek teeth. Thus, the use of an index corresponding to the relative proportions of morphotypes is generally preferred. Such decoupling between the size and shape evolution has already been observed in other taxa such as small mammals (Renaud *et al.* 1996; Vianey-Liaud & Michaux 2003). If we admit

that the number of metastylid's cusplets increase with time, our results based on a quantitative and "objective"/"neutral" method suggest a shift in the resource allocations between size increase and shape change along evolution, *i.e.* in the energy being first allocated mainly to morphological changes, and then followed by size increase. These results are in contradiction with the Rabeders' encodings where its different morphotypes are defined "subjectively"/"artificially" according to the complexity of the conformation based on discrete features.

Additionally, our results indicate an effect of the laterality on the variability. However, the axis PC3 also indicates a shape differentiation related to the metastylid conformation Msl I. We can notice that most of the teeth showing this conformation were determined as left molars (see Table 1). Thus, we could assume an amplification of the effect of the laterality due to a bias in sampling, although a random selection was postulated. In fact, a few size and shape differences between teeth of opposite sides can occur (Garn *et al.* 1966; Corruccini & Potter 1981). However, this fluctuating dental asymmetry is supposed to be random in mammals (Black 1980). Additional statistics should be conducted at an inter-specific level to check the extent of this effect on the morphological variability and to determine if this effect can be considered as "noise" (Hillson 1986).

We also demonstrated no effect of the individual age using the age classes proposed by Stiner (1998). We performed an ANOVA on the size and shape using the corresponding wear stages (Stiner 1998) which were not reported here. Similarly, results indicate no effect of wear on both size and shape. Such results were in fact expected because no old individuals were selected in our sample. Indeed, the dental attrition mainly occurs on the occlusal surface due to the abrasive food and the opposing teeth corresponding to the upper fourth premolar and the upper first molar. Wear facets also often appear on the mesial and distal edges due to the contact with the neighboring teeth corresponding to the fourth lower premolar and the second lower molar, but occur in old bears only. Finally, the complexity of the entoconid, the protoconid, the enthyoconid and the entoconid pillars does not imply size and shape modifications.

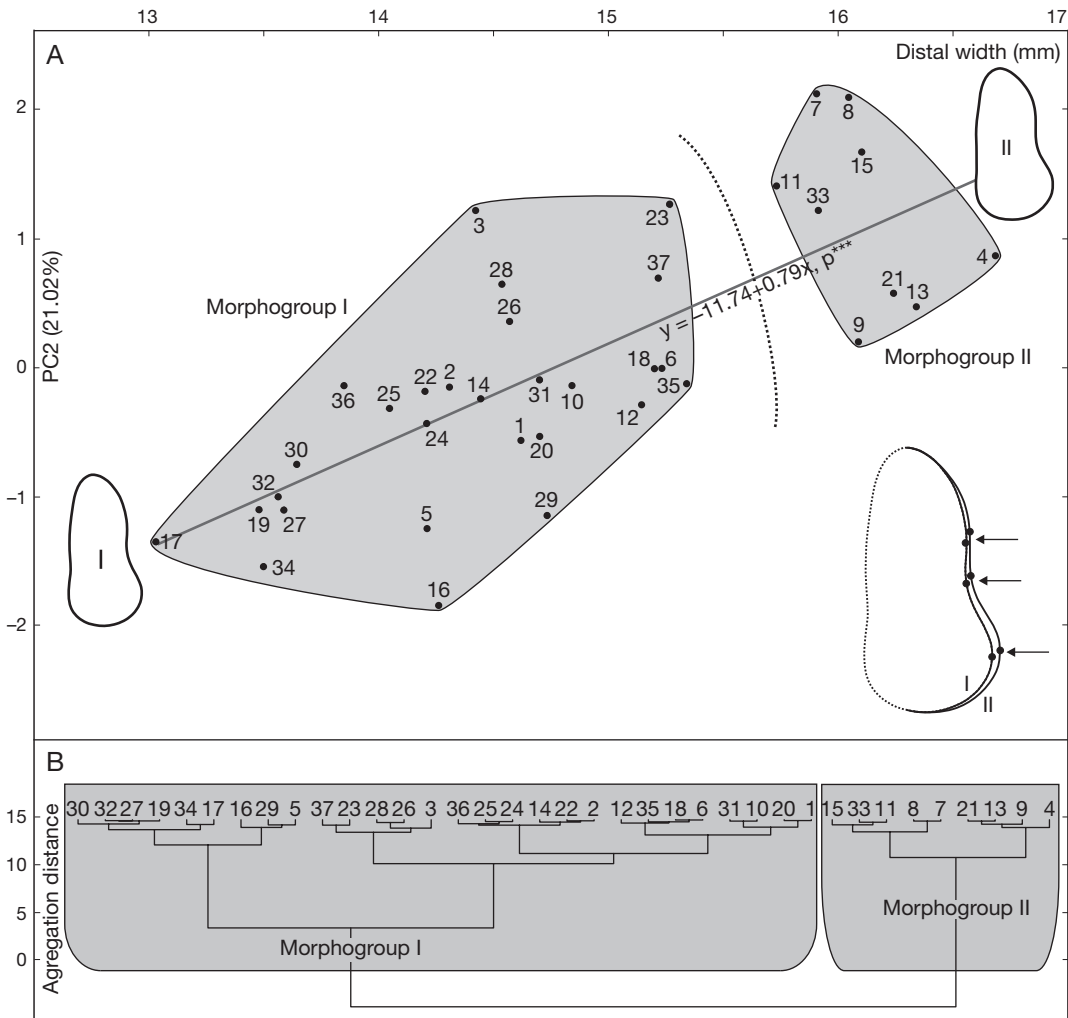


FIG. 6. — Scatterplot of size, defined by the distal width (in mm), versus shape, defined by PC2 (21.02% of the total variance): **A**, re-constructed mean outlines of Morphogroups I and II; **B**, Tree clustering analysis in Euclidian distance using Ward's aggregation.

Ehrenberg noticed in his study the occurrence of two morphologies of first lower molars (Ehrenberg 1935). He discriminated teeth with narrow and broad talonid on the basis of his distal width measurements. Ehrenberg interpreted this “distal” polymorphism as a sexual dimorphism. He estimated a sex ratio male/female in favor of males using the upper canines and the third upper incisors (respectively 10/4 and 59/35). In our study, if our two morphogroups correspond to females (Morphogroup I) and males (Morphogroup II), the

sex ratio is in favor of females (9/28) which is in contradiction with the observations of Ehrenberg. However, the age differences between the canines, including all age groups, and the selection of first molars, excluding the old, worn teeth, could partly explain this difference in sex ratio.

Nevertheless, the effect of sexual dimorphism in cave bear cheek teeth is still discussed. Many studies (Kurtén 1955; Torres 1984; Grandal d'Anglade 1993, 2001) concluded that no bimodal distribution related to sexual dimorphism can be observed

in cheek teeth, conversely to canines or incisors. Because of the high overlapping between male and female metric values, the sex determination is rarely carried out on isolated cheek teeth. This determination can only be done on teeth incorporated in the jaw that can be sexed on base of the canine size. However, Baryshnikov *et al.* (2003) demonstrated that in cave bears from Goyet, a cave some 30 km north of Montaigle, the length of the lower carnassials shows a clear dimorphism. This dimorphism is as strong as the dimorphism of this tooth in the recent *Ursus arctos pruinosus* Blyth, 1854, a subspecies of the brown bear that lives in Tibet and feed on rough plant material (Zhiryakov & Grachev 1993). In our study, only isolated first molars were analyzed, so at the moment it is neither possible to link the differences in size and shape between the morphogroups to sexual dimorphism nor to exclude it.

Furthermore, recent molecular data revealed clearly distinct haplogroups within the clade of cave bears (Hofreiter *et al.* 2004, 2007; Rabeder *et al.* 2008; Knapp *et al.* 2009). Since the taxonomic status of these forms is still discussed (subspecies or species), genetic analyses also suggest a sudden biodiversification of cave bears during the Upper Pleistocene, or even much earlier (Bon *et al.* 2008; Krause *et al.* 2008). In our study, the polymorphism observed within the Level 4 could be explained by the occurrence of two cave bear “lineages” genetically differentiated. However, a single cave bear “lineage” could be also admitted, the strong discrepancies representing an evolutionary divergence between two chronological cave bear forms. Indeed, our sample probably suffered from few taphonomic biases. Numerous sedimentary and post-depositional processes specific to cave deposits can lead to irregular and discontinuous fossil records. Bears also probably mixed and buried the sediments during their ecoethological activities in the cave, such as the digging of a den. In addition, the mixture of the three sedimentary layers within the Level 4 leads to uncertainties in the definition of the chronological and palaeoenvironmental contexts. The co-occurrence of two lithic industries (Mousterian and Aurignacian) and two faunal assemblages showing different ecological affinities

(temperate versus Mammuthus-Coelodonta faunal complex) indicate that the Level 4 recorded at least two human occupations, two contrasted climatic contexts and at least a significant time range. We can suggest that the bears occupied the cave several times, maybe under two contrasted climatic contexts. Recently, comparative dental microwear analyzes have been successfully performed on ursid dental elements (Pinto Llona 2006; Peigné *et al.* 2009). Such analyzes could be performed on our sample to quantify the diet differences between these forms in order to check this hypothesis.

## CONCLUSION

The outline analysis seems to be a powerful tool to quantify the morphological variability observed in ursid cheek teeth. We focused here the size and shape variability at an intra-specific level. Comparisons between traditional measurements and geometric descriptors provide access to additional information, which can be visualized using reconstructed mean outlines. A mean outline of the selected population has been extracted and described and will be compared with other cave bear populations in further analyzes. The main results indicate no clear relationship between the size and shape variability and the individual parameters, except for the metastylid conformation and the laterality. The metastylid complexity would induce a decoupling in the evolution of size and shape, maybe related to a shift in the resource allocations between the size and shape modifications, *i.e.* in the energy being first allocated to morphological change, and followed by size increase.

The effect of the laterality could not be clearly established because closely linked to the metastylid distribution in our sample. The study confirmed the polymorphism indicated by Ehrenberg (1935), which affects both the mesial and distal parts of the teeth. Because only isolated cheek teeth have been taken into account, it is neither possible at the moment to link this polymorphism with a sexual dimorphism nor to exclude it. Nevertheless, the hypothesis of two distinct cave bears would be favoured here because of the uncertain stratigraphical

context and the obvious mixed levels. Such morphological differences could be explained either by genetic differences from two distinct cave bear “lineages” or by evolutionary divergences within the same haplogroup. Finally, our study provided a preliminary step before applying an outline analysis at inter-specific and inter-generic levels.

### Acknowledgements

The authors thank the Royal Belgian Institute of Natural Sciences (Brussels) and especially E. Steurbaut, A. Folie and A. Dreze for permission and their kind assistance during the study of collections. This work benefited from the helpful and constructive suggestions made by the reviewers S. Peigné (Paris, France), P. Neige (Dijon, France) and A. Ohler (Paris, France). This is a contribution of UMR 8217 GEOSYSTEMES-CNRS.

### REFERENCES

- ADAMS D. C., ROHLF F. J. & SLICE D. E. 2004. — Geometric morphometrics: Ten years of progress following the “revolution”. *Italian Journal of Zoology* 71: 5-16.
- ARGANT A. 1991. — *Carnivores quaternaires de Bourgogne*. Thèse de Doctorat, Documents des Laboratoires de Géologie (115), Université Claude Bernard, Lyon, France, 301 p.
- ARGANT A. 1995. — Un essai de biochronologie à partir de l'évolution dentaire de l'ours des cavernes. Datations du site de Balme à Collomb (Entremont-le-Vieux, Savoie, France). *Quaternaire* 6: 139-149.
- AUGUSTE P. 1995. — *Cadres biostratigraphiques et paléocologiques du peuplement humain dans la France septentrionale durant le Pléistocène. Apports de l'étude paléontologique des grands mammifères du gisement de Biache-Saint-Vaast (Pas-de-Calais)*. Thèse de Doctorat inédite, Muséum national d'Histoire naturelle, Paris, France, 724 p.
- 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 (2): 111-119.
- BLACK T. K. 1980. — An exception to the apparent relationship between stress and fluctuating dental asymmetry. *Journal of Dental Research* 59: 1168-1169.
- BOCHERENS H., BILLIQUO D., PATOU-MATHIS M., BONJEAN D., OTTE M. & MARIOTTI A. 1997. — Paleobiological implications of the isotopic signatures ( $^{13}\text{C}$ ,  $^{15}\text{N}$ ) of fossil mammal collagen in Sceladina cave (Sclayn, Belgium). *Quaternary Research* 48 (3): 370-380.
- BON C., CAUDY N., DE DIEULEVEULT M., FOSSE P., PHILIPPE M., MAKSUD F., BERAUD-COLOMB E., BOUZAID E., KEFI R., LAUGIER C., ROUSSEAU B., CASANE D., VAN DER PLICHT J. & ELALOUF J.-M. 2008. — Deciphering the complete mitochondrial genome and phylogeny of the extinct cave bear in the Paleolithic painted cave of Chauvet. *Proceedings of the National Academy of Sciences of the USA* 105: 17447-17452.
- BOOKSTEIN F. L., CHERNOFF B., ELDER R. L., HUMPHRIES J. M., SMITH G. R. & STRAUSS R. E. 1985. — *Morphometrics in Evolutionary Biology: the Geometry of Size and Shape Change, with Examples from Fishes*. The Academy of Natural Sciences, Special Publication 15, 277 p.
- CORRUCCINI R. S. & POTTER R. H. Y. 1981. — Developmental correlates of crown component asymmetry and occlusal discrepancy. *American Journal of Physical Anthropology* 55: 21-31.
- CRÔNIER C., RENAUD S., FEIST R. & AUFRAY J.-C. 1998. — Ontogeny of *Trimeroccephalus lelieurei* (Trilobita, Phacopida) in relation to paedomorphosis: a morphometric approach. *Paleobiology* 24: 359-370.
- CRÔNIER C., AUFRAY J.-C. & COURVILLE P. 2005. — Diversity or disparity in the Jurassic (Upper Callovian) genus *Kosmoceras* (Ammonitina): a morphometric approach. *Journal of Paleontology* 79 (5): 944-953.
- CUCCHI T., FUJITA M. & DOBNEY K. 2009. — New insights into pig taxonomy, domestication and human dispersal in Island South East Asia: Molar shape analysis of *Sus* remains from Niah caves, Sarawak. *International Journal of Osteoarchaeology* 19: 508-530.
- DUPONT E. 1868. — Étude sur les cavernes du Bois de Foy à Montaigne. *Bulletin de l'Académie Royale des sciences, des lettres et des beaux-arts de Belgique*, 2e série 25: 199-224.
- DUPONT E. 1873. — *L'Homme pendant les âges de la pierre dans les environs de Dinant-sur-Meuse*. 2<sup>e</sup> édition. Bruxelles, 250 p.
- EHRENBERG K. 1935. — Die Pleistozänen Bären Belgiens. Teil II: Die Bären vom « Trou du Sureau » (Montaigne). *Mémoires du Musée royal d'Histoire naturelle de Belgique* 71: 1-97.
- FERSON S., ROHLF F. J. & KOEHN R. K. 1985. — Measuring shape variation of two-dimensional outlines. *Systematic Zoology* 34 (1): 59-68.
- FIGUEIRIDO B., PALMQVIST P. & PÉREZ-CLAROS J. A. 2009. — Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: an approach based on geometric morphometrics *Journal of Zoology* 277 (1): 70-80.
- FOOTE M. 1989. — Perimeter-based Fourier analysis: a new morphometric method applied to the trilobite cranidium. *Journal of Paleontology* 63 (6): 880-885.
- GARN S. M., LEWIS A. B. & KERESKY R. S. 1966. — Bilateral asymmetry and concordance in cusp number



- and crown morphology of the mandibular first molar. *Journal of Dental Research* 45: 1820.
- GRANDAL D'ANGLADE A. 1993. — Sexual dimorphism and interpopulational variability in the Lower Carnassial of the Cave bear, *Ursus spelaeus* Ros.-Hein. *Cuadernos do Laboratorio Xeológico de Laxe* 18: 231-239.
- GRANDAL D'ANGLADE A. 2001. — A review of the cave bear sex dimorphism. *Cuadernos do Laboratorio Xeológico de Laxe* 26: 399-405.
- GRANDAL D'ANGLADE, A. & LÓPEZ-GONZÁLEZ F. 2004. — A study of the evolution of the Pleistocene Cave Bear by a morphometric analysis of the lower carnassial. *Oryctos* 5: 83-94.
- HILLSON S. 1986. — *Teeth*. Press Syndicate of the University of Cambridge, New-York, 376 p.
- HOFREITER M., RABEDER G., JAENICKE-DESPRÉS V., WITHALM G., NAGEL D., PAUNOVIĆ M., JAMBRESIĆ G. & PÄÄBO S. 2004. — Evidence for reproductive isolation between cave bear populations. *Current biology* 14 (1): 40-43.
- HOFREITER M., MÜNZEL S., CONARD N. J., POLLACK J., SLATKIN M., WEISS G. & PÄÄBO S. 2007. — Sudden replacement of cave bear mitochondrial DNA in the Late Pleistocene. *Current Biology* 17 (4): R122-123.
- KAHLEKE R.-D. 1999. — *The History of the Origin, Evolution and Dispersal of the Late Pleistocene Mammuthus-Coelodonta Faunal Complex in Eurasia (large mammals)*. The Mammoth Site of Hot Springs, Rapid City, 219 p.
- KNAPP M., ROHLAND N., WEINSTOCK J., BARYSHNIKOV G., SHER A., NAGEL D., RABEDER G., PINHASI R., SCHMIDT H. A. & HOFREITER M. 2009. — First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. *Molecular ecology* 18 (6): 1225-1238.
- KRAUSE J., UNGER T., NOÇON A., MALASPINAS A.-S., KOLOKOTRONIS S.-O., STILLER M., SOIBELZON L., SPRIGGS H., DEAR P. H., BRIGGS A. W., BRAY S. C. E., O'BRIEN S. J., RABEDER G., MATHEUS P., COOPER A., SLATKIN M., PÄÄBO S. & HOFREITER M. 2008. — Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. *BMC Evolutionary Biology* 8 (220): 1-12.
- KUHL F. P. & GIARDINA C. R. 1982. — Elliptic Fourier features of a closed contour. *Computer Graphics and Image Processing* 18: 236-258.
- KURTÉN B. 1955. — Sex dimorphism and size trends in the cave bear, *Ursus spelaeus* Rosenmüller and Heinrich. *Acta Zoologica Fennica* 90: 1-48.
- KURTÉN B. 1976. — *The Cave Bear Story*. Columbia University Press, New-York, 163 p.
- LEGENDRE S. 1988. — Les communautés de mammifères du Paléogène (Éocène supérieur et Oligocène) d'Europe occidentale: structure, milieu et évolution. Thèse de Doctorat inédite, Université de Montpellier, 118 p.
- LINNAEUS C. 1758. — *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. I Regnum animale*. Laurentii Salvii, Stockholm, 824 p.
- MAZZA P. & RUSTIONI M. 1994. — On the phylogeny of eurasian bears. *Palaeontographica Abt. A* 230:1-38.
- MOTTL M. 1964. — Bärenphylogenese in Südost-Österreich. *Mitteilung des Museums für Bergbau, Geologie und Technik am Landesmuseum "Joanneum"* 26: 1-56.
- OTTE M. 1979. — *Le Paléolithique supérieur ancien en Belgique*. Monographies d'Archéologie Nationale. Vol. 5, Musées Royaux d'Art et d'Histoire, Bruxelles, 684 p.
- PAUNOVIĆ M. 1988. — Morphometrische und morphogenetische Untersuchungen der Ursidenzähne aus der Höhlen Nordwestkroatiens. *Palaeontologia Jugoslavica* 36: 1-40.
- PEIGNÉ S., GOILLOT C., GERMONPRÉ M., BLONDEL C., BIGNON O. & MERCERON G. 2009. — Predomancy omnivory in European cave bears evidenced by a dental microwear analysis of *Ursus spelaeus* from Goyet, Belgium. *Proceedings of the National Academy of Sciences of the USA* 106: 15390-15393.
- PINTO LLONA A. C. 2006. — Comparative dental microwear analysis of cave bears *Ursus spelaeus* Rosenmüller, 1794 and brown bears *Ursus arctos* Linnaeus, 1758. *Scientific Annals, School of Geology Aristotle University of Thessaloniki* 98: 103-108.
- PRAT F. & THIBAUT C. 1976. — *Le gisement de la Nauterie à la Romieu (Gers). Fouilles de 1967 à 1973. Nauterie I*. Mémoires du Muséum national d'Histoire naturelle, série C 35: 1-82.
- RABEDER G. 1983. — Neues vom Höhlenbären: Zur Morphogenetik der Backenzähne. *Die Höhle* 34 (2): 67-85.
- RABEDER G. 1999. — Die Evolution des Höhlenbärengebisses. *Mitteilungen der Kommission für Quartärforschung der Österreichischen Akademie der Wissenschaften* 11: 1-102.
- RABEDER G., DEBELJAK I., HOFREITER M. & WITHALM G. 2008. — Morphological responses of cave bears (*Ursus spelaeus* group) to high-alpine habitats. *Die Höhle* 59: 59-72.
- RENAUD S. 1999. — Size and shape variability in relation to species differences and climatic gradients in the African rodent *Oenomys*. *Journal of Biogeography* 26 (4): 857-865.
- RENAUD S., MICHAUX J., JAEGER J.-J. & AUFRAY J.-C. 1996. — Fourier analysis applied to *Stephanomys* (Rodentia, Muridae) molars: Nonprogressive evolutionary pattern in a gradual lineage. *Paleobiology* 22 (2): 255-265.
- RICHARDS M. P., PACHER M., STILLER M., QUILÈS J., HOFREITER M., CONSTANTIN S., ZILHAO J. & TRINKAUS E. 2008. — Isotopic evidence for omnivory among European cave bears: Late Pleistocene *Ursus spelaeus* from the Peștera cu Oase, Romania. *Proceedings of the National Academy of Sciences of the USA* 105: 600-604.



- ROHLF F. J. 1973. — Algorithm 76. Hierarchical clustering using the minimum spanning tree. *The Computer Journal* 16: 93-95.
- ROHLF F. J. 1990. — Fitting curves to outlines, in ROHLF F. J. & BOOKSTEIN F. L. (eds), *Proceedings of the Michigan Morphometrics Workshop*, Special Publication 2: 167-177.
- ROHLF F. J. & MARCUS L. F. 1993. — A revolution in morphometrics. *Trends in Ecology and Evolution* 8 (4): 129-132.
- ROSENMÜLLER J. C. 1794. — *Quaedam de Ossibus Fossilibus Animalis cuiusdam, Historiam eius et Cognitionem accuratorem illustrantia*. Ex Officina Sommeria, Leipzig, 34 p.
- STINER M. C. 1998. — Mortality analysis of Pleistocene bears and its paleoanthropological relevance. *Journal of Human Evolution* 34: 303-326.
- TORREST. 1984. — *Ursidos del Pleistoceno-Holoceno de la Peninsula Iberica*. PhD dissertation, Escuela Técnica Superior de Ingenieros de Minas de Madrid, 653 p.
- ULRIX-CLOSSET 1968. — Le site préhistorique de Montaigne (prov. de Namur) et l'industrie moustérienne du Trou du Sureau. *Bulletin de la Société Royale Belge d'Anthropologie et de Préhistoire* 79: 67-90.
- VIANEY-LIAUD M. & MICHAUX J. 2003. — Évolution « graduelle » à l'échelle géologique chez les rongeurs fossiles du Cénozoïque européen. *Comptes Rendus Palevol* 2: 455-472.
- VON DEN DRIESCH A. 1976. — *A Guide to the Measurement of Animal Bones from Archaeological Sites*. Peabody Museum of Archaeology and Ethnology, Harvard University, USA, 137 p.
- ZHIRYAKOV V. A. & GRACHEV Y. A. 1993. — [The Brown Bear. Central Asia And Kazakhstan] Buryi medved. Centralnoi Azii u Kazakhstana, in VAISFELD M. A. & CHESTIN I. E. (eds), [Bears: brown bear, polar bear, asian black bear. Distribution, ecology, use and protection] Medvedi: buryi medved, belyi medved, gimlanskii medved. Razmeshchenie zaposy, ekologiya, ispolzovanie i okhrana. *Nauka*: 170-206. (in Russian with English summary).

Submitted on 20 February 2011;  
accepted on 13 October 2011.