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What size were *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)?

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Body masses of the giant short-faced bear (*Arctodus simus* Cope) and the cave bear (*Ursus spelaeus* Rosenmüller & Heinroth) were calculated with equations based on a long-bone dimensions:body mass proportion ratio in extant carnivores. Despite its more long-limbed, gracile and felid-like anatomy as compared with large extant ursids, large *Arctodus* specimens considerably exceeded even the largest extant ursids in mass. Large males weighed around 700–800 kg, and on rare occasions may have approached, or even exceeded one tonne. *Ursus spelaeus* is comparable in size to the largest extant ursids; large males weighed 400–500 kg, females 225–250 kg. Suggestions that large cave bears could reach weights of one tonne are not supported.

1. Introduction

The giant short-faced bear (*Arctodus simus* Cope, Ursidae: Tremarctinae) from North America, and the cave bear (*Ursus spelaeus* Rosenmüller & Heinroth, Ursidae: Ursinae) from Europe were among the most massive mammalian carnivorans ever to have lived. Both appear to have become extinct at the end of the Pleistocene along with most of the megafauna (Osborn 1910, Kurtén & Anderson 1980). It has been established that *Arctodus simus* still existed as recently as 11 500 B.P. (Richards & Turnbull 1995). Among extinct mammalian carnivores only certain creodonts, the huge Eocene mesonychid *Andrewsarcus* (Osborn 1924), the Miocene hyaenodont *Megistotherium* (Savage 1973), and perhaps the North American lion (*Panthera atrox*) (Anyonge 1993), appear to have equalled the largest ursids in size.

Extant ursids vary markedly in size from the small, partly arboreal Malayan sunbear (*Ursus malayanus*), which reaches a body mass of only 27–65 kg (Nowak 1991), to the Kodiak bear (*U. arctos middendorffi*), and polar bear (*U. maritimus*). Body masses of around 500 kg are not unusual for large males (Lyneborg 1970, Banfield 1974, Wood 1981, Nowak 1991), but the world records are considerably higher.

According to Wood (1981), the largest recorded wild Kodiak bear was a 750-kg male shot at the English Bay on Kodiak Island in 1894. The largest polar bear was a huge male, alledgedly weighing 1 002 kg, shot at the Kotzebue Sound in northwestern Alaska in 1960 (Wood 1981); this

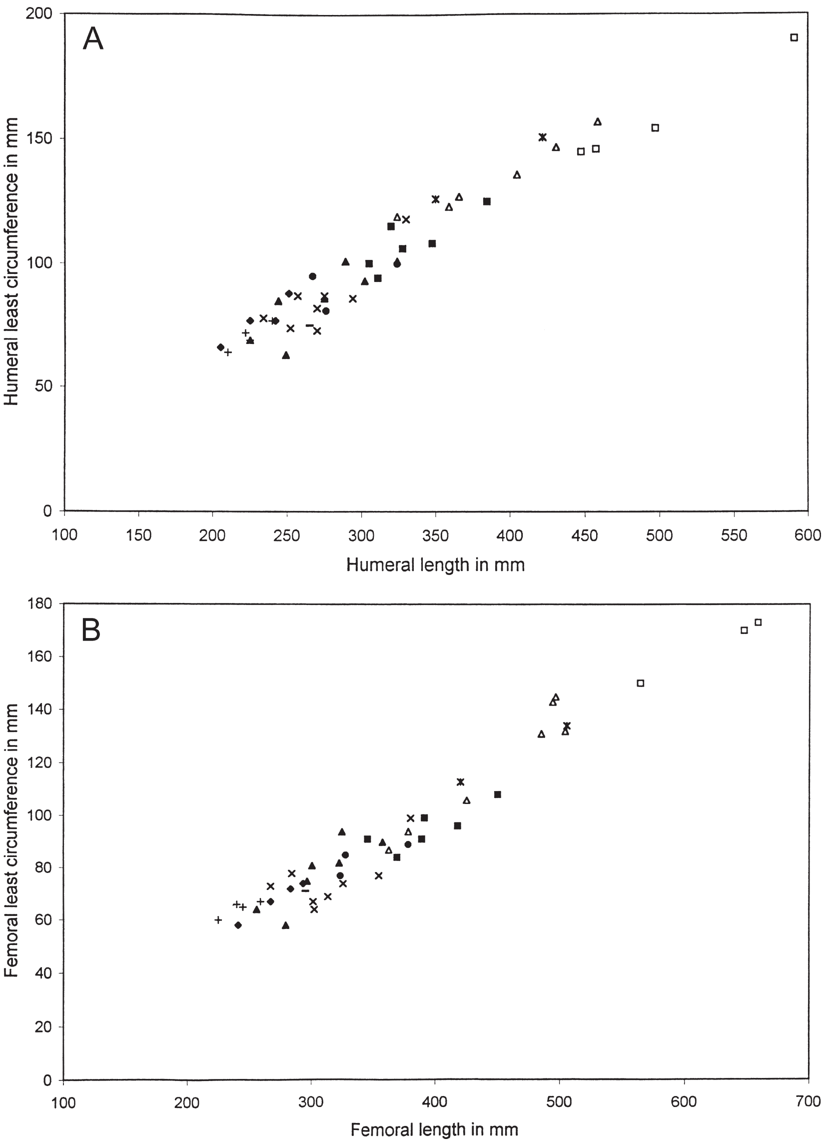

Fig. 1. Linear dimensions of the propodial bones in extant ursids, *Arctodus simus* and *Ursus spelaeus*. ●: *Ursus americanus*; ■: *U. maritimus*; ▲: *U. thibetanus*; ◆: *U. ursinus*; ×: *U. arctos*; ✳: *U. arctos middendorffi*; +: *U. malayanus*; –: *Tremarctos ornatus*; □: *Arctodus simus*; △: *Ursus spelaeus*.

figure, however, appears somewhat excessive and possibly needs verification. As compared to even the largest extant ursids, the linear dimensions of *Arctodus simus* are impressive (Fig. 1A and B). The humeri of *Ursus spelaeus* appear comparable in size to those of polar bears (Fig. 1A), as do the femora of females (Fig. 1B), whereas the male femora are of similar size to that of the almost 500-kilogram *Ursus arctos middendorffi* male (*see* also Table 1).

Arctodus simus appears to have been distinctly more long-limbed, possibly even with a more digitigrade stance than the extant plantigrade ursids, shorter-bodied, and probably more gracile than large extant ursids (Kurtén 1967, Kurtén & Anderson 1980). The metapodials also appear to have been less medially directed during locomotion than in extant ursids, and metapodial limb action more parasagittal (Kurtén 1967, Kurtén & Anderson 1980). The skull is also shorter and broader than those of extant ursids; it has a wide and shortened rostrum, giving it a more felid-like appearance (Kurtén 1967, Kurtén & Anderson 1980, Richards & Turnbull 1995). The dentition, particularly well-developed carnassials, also pointed to more felid-like feeding ecology (Kurtén 1967).

Certain myological aspects of the appendicular skeleton also indicate that this species was better adapted to fast locomotion than extant ursids (Kurtén 1967).

Ursus spelaeus appears to have been anatomically more comparable to large extant ursids, albeit possibly somewhat heavier in overall build (Osborn 1910, Kurtén 1967, 1971, 1976). The dental cusps are rather blunt, the anterior premolars greatly reduced, and, along with the anterposteriorly elongated, rather planar and bunodont molars, indicate a primarily herbivorous diet (Osborn 1910, Kurtén 1971, Vereshchagin & Baryshnikov 1984). Such a lifestyle would also relax the constraints on axial and appendicular morphology for fast locomotion. However, the appendicular skeleton might have been subjected to substantial torsional and bending forces as the behaviour of the cave bear appears to have included mountain climbing (Ehrenberg 1962, Kurtén 1976). This is also indicated by the rather wide diaphysial diameters of its long bones as compared with those of extant ursids (Viranta 1994).

Kurtén (1967) estimated the mass of a large, lean *Arctodus* male, comparable in size to some of the specimens used in this analysis, at 470–500 kg and 590–630 kg; his calculations were based on the body length and cross-sectional area of the femoral diaphysis, respectively. Nelson and Madsen (1983) estimated that a large *Arctodus* weighed 620–650 kg. Richards and Turnbull (1995) considered the specimen PM 24880 (the most complete specimen used in this analysis) to have weighed 766 kg. Their estimate was based on the combined diaphysial cross-sectional area of humerus and femur.

Using the cross-sectional area of the femoral diaphysis, Kurtén (1967) assessed that a large *Ursus spelaeus* male would have had a mass of 410–440 kg. Later, he (Kurtén, 1976) considered that males may have weighed 400–450 kg under normal conditions, but considerably more just prior to hibernation, as in extant hibernating ursids. Using long-bone dimensions, Viranta (1994) estimated the mass of male cave bears at 224–1 316 kg, whereas the masses of females varied between 142 and 986 kg. The high variation was due to the great diaphysial width of cave bear long bones, especially the humerus, as opposed to the other long-bone dimensions. Viranta (1994) tentatively suggested that males may have had an average body mass of 319 kg and females 244 kg. Vereshchagin and Baryshnikov (1984), on the other hand, suggested that large cave bear males may have reached, or even exceeded, body masses of no less than 1 000 kg.

Table 1. List of species used in the analysis. All species are from the mammal collection of the Zoological Museum in Copenhagen.

Species	Mass (kg)
Canidae	
Arctic fox (*Aloplex lagopus*)	4.4
Golden jackal (*Canis aureus*)	9.2
Domestic dog (*Canis familiaris*)	29
Gray wolf (*Canis lupus*)	35
Fennec fox (*Fennecus zerda*)	1.2
Hoary fox (*Lycaloplex vetulus*)	4.2
Red fox (*Vulpes vulpes*)	5.5
Felidae	
Cheetah (*Acinonyx jubatus*)	39
Puma (*Felis concolor*)	45.7
Lynx (*Felis lynx*)	6.7
Ocelot (*Felis pardalis*)	13.9
Lion (*Panthera leo*)	170
Jaguar (*Panthera onca*)	67.4
Leopard (*Panthera pardus*)	51
Indian tiger (*Panthera tigris*)	145
Snow leopard (*Panthera uncia*)	34.8
Hyaenidae	
Striped hyaena (*Hyaena hyaena*)	32
Mustelidae	
Wolverine (*Gulo gulo*)	12
European river otter (*Lutra lutra*)	6.2
Old world badger (*Meles meles*)	10
Stone marten (*Martes foina*)	1.4
Procyonidae	
Lesser panda (*Ailurus fulgens*)	4.4
Coatimundi (*Nasua nasua*)	3.4
Viverridae	
Falanouc (*Eupleres goudotii*)	2.6
Palm civet (*Paradoxurus hermaphroditus*)	2.2
Suricate (*Suricata suricatta*)	0.7
Ursidae	
American black bear (*Ursus americanus*)	105
Kodiak bear (*Ursus arctos middendorffi*)	496
Polar bear (*Ursus maritimus*)	175
Asiatic black bear (*Ursus thibetanus*)	98

2. Materials and methods

For predicting the body masses of *Arctodus simus* and *Ursus spelaeus,* a data set of 30 species of extant terrestrial carnivorans were used (Table 1). This sample was a subsample of the data set used by Christiansen (1999a) in the study of long-bone allometry. However, a few species were omitted in this study, and additional osteological parameters were introduced (femoral distal articular surface area and humeral distal epiphysial width). Unlike in most studies of bone allometry or studies predicting the body mass of extinct animals, the body masses used were the recorded masses of the specimens, not averages from literature. This offers a greater degree of accuracy in relating osteological parameters to body mass as also concluded by Van Valkenburg (1990).

Limb bone proportions are affected by the mass of an animal, since the limbs are directly responsible for support of mass and locomotion. The proportions of the upper long bones (humerus and femur) usually show a stronger correlation with body mass than proportions of the distal long bones (e.g., Biewener 1983, Christiansen 1999a). Especially the circumferences of the proximal long bones show good correlation with body mass (Christiansen 1999a). Thus, I decided to predict masses of the two extinct ursids by using a combination of features, such as bone length, circumference and geometric properties of the distal epiphysis of the two proximal long bones. Bone lengths are given as the greatest length of a bone. For humerus and femur, this was the vertical distance from the caput to the trochlea and distal condyles, respectively. Circumference is given as the least circumference of the diaphysis, located roughly at midshaft. Distal humeral epiphysial width is the width of the distal epiphysis perpendicular to the long (vertical) axis of the bone. All the measurements are in millimetres. The femoral distal condylar area (in mm^2) is the combined surface area of the medial and lateral femoral condyles (*see* Ruff 1990). Ruff (1990) and Anyonge (1993) found that circumferences and distal articular surface areas usually constitute good parameters for predicting body mass, as compared with bone lengths. All measurements were taken with callipers, except least circumferences, which were measured using a measuring tape.

The data were logarithmically transformed and regression lines were calculated by means of least squares regression analysis. The results are expressed as a standard power function:

$$Y = aX^b,$$

which describes an allometric relationship (Gould 1966). Regression lines were calculated for all species, and also for the families Felidae (9 species) and Ursidae (4 species) separately. These were chosen as they comprise all the large extant, terrestrial carnivore species. *Arctodus simus* and *Ursus spelaeus* are ursids, but the skeleton of the former in many respects resembles that of a hypothetical huge felid, as mentioned above. Pearsons product moment correlation coefficient and confidence limits for the slope (95% CI) were computed for the samples. Slopes were also tested for significant departure from isometry.

If a sample is fairly large, spans a large size range and has a slope far from zero, as in this analysis, the correlation coefficient tends to be high, regardless of whether or not the residuals are fairly high as well (Smith 1981, 1984, Van Valkenburg 1990). Thus, it is often important to examine the residuals of the data sets to evaluate the true goodness of fit, and the predictive value of the equations (Smith 1981, 1984, Sokal & Rohlf 1981). Even high correlation coefficients do not *per se* guarantee that the equation has strong predictive power in all cases (Smith 1981, 1984). In large data sets, underlying factors such as curvilinearity can be present even in samples with high correlation coefficients (Bertram & Biewener 1990, Christiansen 1999b). Thus, for all these equations, the percent prediction error (%PE), and the percent standard error of the estimate (%SEE) were also computed. In addition to the correlation coefficient, they give information about the predictive value of the equations (Smith 1981, 1984, Van Valkenburg 1990, Anyonge 1993). The percent prediction error gives an indication of the average percent difference between the actual mass and the mass predicted by the equation for each species. The percent standard error of the estimate gives an indication of the reliability of the equation to predict the actual mass of a specimen. For example, for %SEE = 25, assuming a normal distribution, 68% of the actual mass values would be expected to fall within ± 25% of the estimated value.

The calculated equations were used to predict the body masses of *Arctodus simus* and *Ursus spelaeus*. The material used of *Arctodus simus* consists of 4 humeri and 3 femora (Fig. 1) (at the Field Museum of Natural History in Chicago and the Los Angeles County Museum). None had been sexed, but their general large size would indicate that they were males. From *Ursus spelaeus*, 3 humeri and 3 femora were used from females, and 3 humeri and 4 femora from males (at the Zoological Museum in Copenhagen, and the Museum National d' Histoire Naturelle in Paris).

3. Results

The results are shown in Table 2 and Figs. 2 and 3. A few slopes departed from isometry and these were all from the total sample (Table 2). Elastic similarity predicts circumference = $M^{2.67}$(*sensu* McMahon 1973), very similar to the value of $M^{2.604}$ ($0.50 > p > 0.40$) obtained for the humeral circumference. Femoral distal condylar area and femoral circumference also diverged from isometry, and again the circumference was elastically similar ($0.20 > p > 0.10$). The correlation coefficients were high for all samples, implying that regression equations calculated with model-II analyses would be very similar.

In many cases, the regressions for felids and ursids have slopes that visually appear to diverge markedly from the predicted value of isometry (e.g., humeral length). However, the regressions for felids always display the lowest correlation coefficients of the samples, and in the case of distal humeral epiphysial width and femoral length, the correlation is rather poor (Table 2). This, of course, implies high residual variances of the samples, making a rejection of the null hypothesis more difficult. This is further corroborated by the substantially lower sample size as compared with the overall sample. In the case of ursids, the correlation coefficients are very impressive, but in this case it is a very small sample size of just four that makes a rejection of the null hypothesis difficult, as the required table value for significance gets progressively higher as the sample size decreases. This is particularly the case for samples with five or fewer data points (e.g., Campbell 1990).

Judging by the %SEE and %PE values, the best predictors of body mass for the total sample is femoral least circumference, followed by humeral least circumference and femoral distal condylar area. Humeral distal epiphysial width appears less reliable (Table 2). As also found by Anoynge (1993), bone lengths are not as good predictors of body mass as circumferences, although the differences appear modest. Both %SEE and %PE are high for most of the regressions for felids, and apart from humeral and femoral least circumferences, no equations for felids appear to be as good predictors of body mass as the regressions based on the total sample. In contrast, the %SEE and %PE are so low for all the regressions for ursids, and particularly impressive in the case of femoral distal condylar area (Table 2), that all

Table 2. Regression equations, given as $Y = aX^b$, relating body mass with long-bone dimensions in extant mammals. In all cases, body mass constitutes the dependent variable. One, two or three asterisks after the slope indicate significance from isometry at the level of 5%, 1% and 0.1%, respectively, and ns indicates $p > 0.05$.

Measure	Group	*n*	*a*	*b* + 95% CI	*r*	%SEE	%PE
HL	All	30	9×10^{-6}	2.881 ± 0.245ns	0.977	45	28
	Felidae	9	7×10^{-7}	3.325 ± 1.220ns	0.925	51	30
	Ursidae	4	1×10^{-7}	3.682 ± 1.302ns	0.993	11	6
HC	All	30	1×10^{-3}	2.604 ± 0.173***	0.986	34	23
	Felidae	9	1×10^{-3}	2.605 ± 0.720ns	0.955	38	25
	Ursidae	4	9×10^{-4}	2.645 ± 1.061ns	0.991	13	7
HW	All	30	2×10^{-3}	2.511 ± 0.247***	0.969	53	32
	Felidae	9	3×10^{-3}	2.427 ± 1.140ns	0.885	66	37
	Ursidae	4	3×10^{-5}	3.479 ± 1.527ns	0.990	14	8
FL	All	30	7×10^{-6}	2.860 ± 0.228ns	0.979	41	22
	Felidae	9	5×10^{-7}	3.318 ± 1.396ns	0.905	59	32
	Ursidae	4	1×10^{-6}	3.184 ± 1.611ns	0.986	16	9
FC	All	30	5×10^{-4}	2.808 ± 0.185*	0.986	33	22
	Felidae	9	2×10^{-4}	2.945 ± 0.816ns	0.955	38	22
	Ursidae	4	3×10^{-4}	2.956 ± 1.312ns	0.990	14	8
FA	All	30	4×10^{-3}	1.371 ± 0.102*	0.982	38	22
	Felidae	9	4×10^{-3}	1.346 ± 0.515ns	0.919	54	31
	Ursidae	4	5×10^{-3}	1.376 ± 0.243ns	0.998	5	3

Abbreviations: HL, humeral length; HC, humeral least circumference; HW, humeral distal epiphysial width; FL, femoral length; FC, femoral least circumference; FA, femoral distal condylar area.

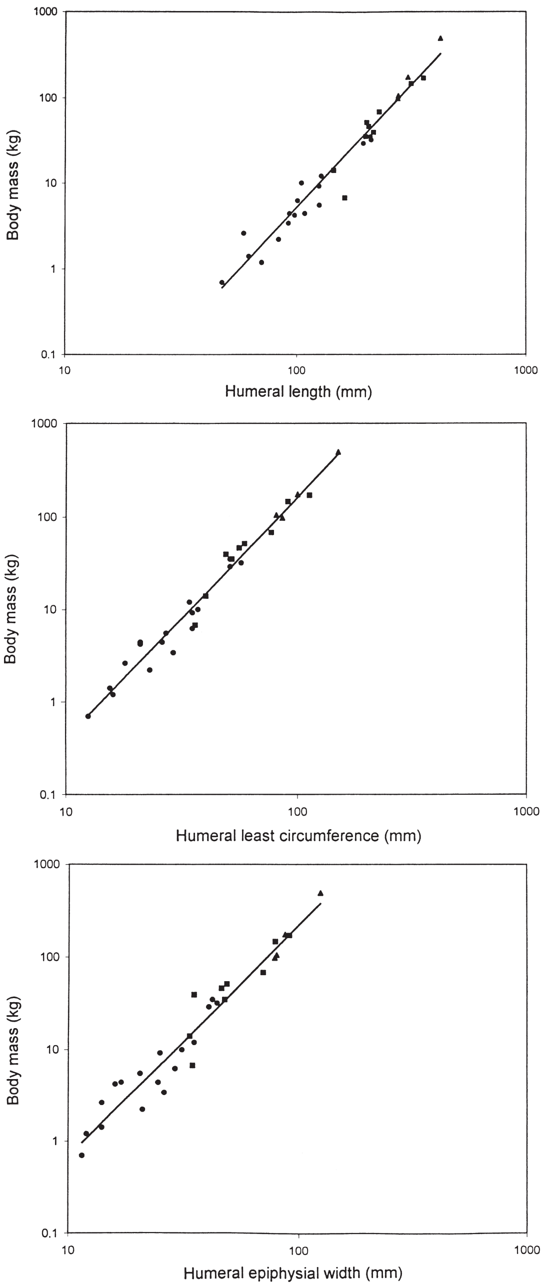

Fig. 2. Body mass to humeral dimension in 30 species of extant Carnivora. Regression line fitted to the data by means of least squares regression analysis. ▲: ursids (4 species); ■: felids (9 species); ●: other carnivores (17 species). *See* Table 1 for data.

these should be considered good predictors of body mass in extinct ursids.

U. spelaeus females appear to have had an average body mass of around 180–230 kg as esti-

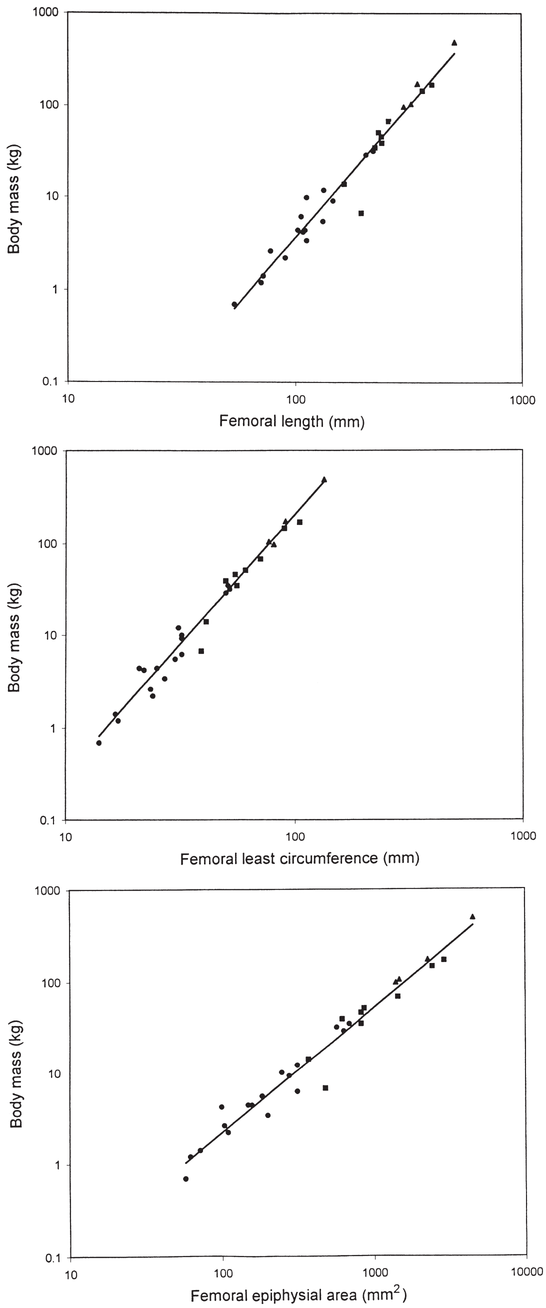

Fig. 3. Body mass to femoral dimension in 30 species of extant Carnivora. Regression line fitted to the data by means of least squares regression analysis. ▲: ursids (4 species); ■: felids (9 species); ●: other carnivores (17 species). *See* Table 1 for data.

mated from the bone lengths (Table 3), but perhaps even 300 kg when estimation was based on bone circumferences, lending support to the conclusions of Viranta (1994) that cave bear long bones tend to be rather more massive than in extant ursids. However, the femoral distal condylar area appears to be the best predictor of body mass in extant ursids, but masses calculated with this regression are considerably higher than those resulting from other regressions (Table 3). The average mass value predicted by this equation appears slightly excessive, unless the cave bear was markedly more robust in overall body morphology than large extant ursids are, which seems unlikely, particularly for species other than the polar bear. The average body mass of *U. spelaeus* females, when taking the average of the six mean values for the total sample from Table 3 is 225 kg, and 256 kg when calculated with the regressions for ursids; both values are very close to the 244 kg suggested by Viranta (1994).

As in extant ursids, *U. spelaeus* males were evidently considerably larger than the females (Table 3). Average masses range from 354 kg, predicted from humeral length for the total sample, to 634 kg, if estimation was based on the femoral least circumference for the ursid sample (Table 3). Unlike in the females, humeral distal epiphysial width did not result in lower mass values than the other samples. On the contrary, for males, the humeral distal epiphysial width and femoral least circumference of the ursid samples actually resulted in considerably greater body mass predictions than was the case for any other equation (Table 3). Humeral least circumference did not produce excessive values, however.

This is somewhat in contrast to the results of Viranta (1994) who found very high mass values when estimation was based on humeral shaft width, but not on distal articular surface width of the humerus. The mean body mass of *U. spelaeus* males is 418 kg when estimated from the average of the six mean values of the total sample in Table 3, and 526 kg when calculated with the regressions for ursids. Both values are considerably higher than the average of 319 kg suggested by Viranta (1994).

It is evident that *Arctodus simus* was larger than the cave bear. The lowest mass values are

Table 3. Predicted body masses for *Ursus spelaeus*, female and male, and *Arctodus simus*. The ranges shown represent the lowest and highest values calculated for the species from the individual long bone dimensions and the value in parentheses is the mean. All values are in kilogrammes. Abbreviations as in Table 2.

		U. spelaeus (♀)	*U. spelaeus* (♂)	*Arctodus simus*
HL	All	154–219 (193)	293–420 (354)	392–871 (552)
	Felidae	–	–	457–1148 (687)
	Ursidae	175–274 (235)	398–630 (509)	576–1598 (913)
HC	All	254–301 (277)	360–523 (441)	425–859 (554)
	Felidae	–	–	428–865 (557)
	Ursidae	278–330 (304)	395–577 (486)	468–956 (612)
HW	All	147–210 (174)	335–469 (402)	210–380 (267)
	Felidae	–	–	211–374 (266)
	Ursidae	155–254 (196)	484–774 (628)	254–576 (359)
FL	All	146–231 (181)	337–376 (357)	518–806 (697)
	Felidae	–	–	673–1122 (952)
	Ursidae	140–234 (178)	356–402 (379)	576–940 (802)
FC	All	190–244 (222)	442–587 (511)	646–965 (843)
	Felidae	–	–	513–781 (679)
	Ursidae	224–291 (263)	543–734 (634)	811–1236 (1074)
FA	All	277–347 (304)	392–561 (440)	589–884 (762)
	Felidae	–	–	498–743 (642)
	Ursidae	325–407 (357)	460–659 (517)	692–1041 (896)

calculated from the humeral distal epiphysial width (Table 3), but *Arctodus* has more slender epiphyses than either *U. spelaeus* or large extant ursids, in this respect closely resembling large extant felids. A very high average value is calculated from the ursid sample of femoral least circumference. If, however, *Arctodus* was more fleet than extant ursids, which seems entirely likely, this is to be expected from the greater stress of fast locomotion, necessitating thicker diaphyses, particularly in a long-limbed animal. This would especially be true for the femur, which has a long diaphysis and does not display large crests extending down the diaphysis, and potentially acting as a mechanical support, such as the humeral deltopectoral crest. Nor does the femur have the large metaphysis of the humerus, extending a considerable distance dorsally, and with distinct epicondyles.

The average body mass of *Arctodus* is 613 kg when evaluated from the average of the six mean values for the total sample from Table 3, and 776 kg when calculated with the regressions for ursids. When omitting the very low value predicted from the humeral distal epiphysial width, the average value for the total sample is 682 kg. In the case of the ursid sample, when omitting the distal epiphysial width, and the two high values calculated from the humeral length and femoral least circumference, the mean body mass of *Arctodus* calculated with the remaining three regressions for ursids is 770 kg (859 kg if omitting just the humeral distal epiphysial width).

As *Arctodus* in many ways convergently resembles a large felid more closely than a large ursid, particularly in cranial and appendicular morphology, the regressions for felids were also used to predict body masses in this species (Table 3). The average value of the six means calculated with these regressions is 631 kg, and 703 kg when the very low value calculated from the humeral distal epiphysial width was omitted. In addition, this regression also had the lowest predictive power in the entire data set (Table 2).

4. Discussion

The average body mass predicted for *U. spelaeus* females in this analysis is very close to the average body mass suggested by Viranta (1994). The average body mass predicted for males is considerably higher than the value of 319 kg suggested by Viranta (1994). However, the *Ursus spelaeus* adult male's mean body mass of 319 kg calculated from the overall size and gross morphology may appear slightly too low. It is about as great as the average mass of polar bear males (Viranta 1994). The polar bear is a large ursid, but usually also more slender in overall build than the large subspecies of *U. arctos*, which do not hunt for a living to anywhere near the same extent (e.g., Nowak 1991). A mean body mass of 400–500 kg, however, would place the cave bear close to the mass range of large, but still normal-sized adult males of *U. arctos middendorffi*, a subspecies which appears to resemble *U. spelaeus* in feeding ecology and overall size and morphology more than *U. maritimus*.

The masses presented in Table 3 are averages for several specimens, but in this analysis *Arctodus simus* is represented by the specimen PM 24880, one of the largest and most complete specimens known (Richards & Turnbull 1995). If one takes the average value of the six means calculated for this particular animal from the total sample, the result is a mass of 780 kg, very close to the 766 kg calculated for the specimen by Richards and Turnbull (1995). The corresponding values for the regressions for felids and ursids are 822, and no less than 1 039 kg, respectively.

The above values indicate an animal markedly larger than even large *Ursus spelaeus* males; a conclusion also supported by the colossal overall dimensions of *Arctodus simus*. The value calculated with the regressions for felids is very close to the overall one. The regressions for ursids, however, probably give too high a mass, as *Arctodus* was more long-limbed than large extant ursids, with thicker diaphyses to go with the elongated long bones, most likely due to the greater locomotory capabilities of this species as compared with the other large ursids.

It is unlikely that the above mass values for *Arctodus simus* and *Ursus spelaeus* represent the extreme upper mass range of the two species. As in extant mammals, the rare giant specimens may have considerably extended the mass range upwards. Such "world record" specimens are always very rare, and are thus unlikely to appear in the fossil record, even in the case of species known from numerous individuals. The cave bear appears to have been rather similar in size to the polar bear and the large subspecies of the brown bear, and it, thus, appears likely that the mass of exceptionally large males may well have substantially exceeded 700 kg. *Arctodus* appears to have been the largest known ursid, and it is certainly probable that this species occasionally approached, perhaps even exceeded, one tonne in body mass. The constraints on body mass, however, may be greater in such a huge animal that probably, unlike most other large ursids, had to rely to a large extent on hunting for a living.

Ursus spelaeus appears to have been ecologically tied to mountain caves (Vereshchagin & Baryshnikov 1984). The heavy build, but especially the dentition, appears to indicate a primarily herbivorous species, although probably, as extant ursids, omnivorous to a certain extent. The distinctly more cat-like appendicular and cranial, and especially dental, anatomy of *Arctodus simus* have inspired most scholars to conclude that this species was primarily carnivorous, although a certain degree of omnivory is possible, if not probable (Kurtén 1967, 1971, Kurtén & Anderson 1980, Voorhies & Corner 1984).

Such a massive carnivore appears to constitute just as likely a candidate for predation on the megafauna as do the saber-toothed felids, as also suggested by Osborn (1910). *Arctodus* lived alongside another huge predator, the North American lion (*Panthera atrox*), which appears to have been much larger than any extant felid, perhaps as heavy as 500 kg (Anyonge 1993). It is probable that a species of such massive size also constituted a likely candidate for predation on the megafauna. Possibly the decline and ultimate extinction of the megafauna in North America at the end of the Pleistocene also brought about the extinction of the largest ursid, ecologically dependent on the availability of large, graviportal to subcursorial, and thus, only moderately fast-moving, prey species.

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