

## Femoral morphology of some Quaternary bears

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**Abstract.** Cross-sectional geometric properties (areas, second moments of area) of ursid femoral diaphyses were calculated using formulae for a hollow ellipse. Inner bone contours were obtained from biplanar radiographs. The species included are *Ursus spelaeus*, *Ursus arctos*, *Ursus deningeri* and *Ursus* sp. from Deutsch-Altenburg 4B. Midshaft femoral bending rigidity is markedly increased in the mediolateral plane in *U. spelaeus*, while it is more equally distributed in *U. arctos*. This relationship is not correlated with size. The Early and Middle Pleistocene species investigated exhibit intermediate properties. Along with other skeletal traits, femoral cross-sectional shape in *U. spelaeus* is interpreted as being indicative of a limb structure designed primarily for static stability.

**Key words:** Ursidae, Quaternary, biomechanics, femur, cross-sectional morphology.

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### I. INTRODUCTION

From a biomechanical viewpoint, mammalian long bones can be modeled as hollow beams and analyzed by means of engineering beam theory. Since the late seventies, this approach has been widely applied in physical anthropology and primatology in a variety of different contexts (see RUFF 1989 for a recent review). Most important in this respect are the geometric properties (areas, moments of area) of cross sections. These properties are highly indicative of the way in which an animal uses its limbs and may reflect certain types of limb loading, posture and locomotory patterns. This correlation has been well established for primates, including different human groups, and only recently for caviomorph rodents (BIKNEVICIUS 1993). The cross-sectional shape of fossil long bones may provide valuable clues to behavioural patterns of extinct animals. Given the rich fossil record and contemporaneous presence of similarly designed, yet differently adapted forms, the case of Pleistocene European bears seems well suited for such an analysis.

The femur was chosen for several reasons. It represents a single weight-bearing element in a skeletal link; the hindlimb is generally more directly related to locomotor behavior than the forelimb, and the cross section of its diaphysis is regular enough to be estimated by a simple geometric model. The primary focus of this study is a comparative analysis of the mechanical properties of the femoral shaft of the cave bear (*Ursus spelaeus* ROSENMÜLLER, 1794) and the brown bear (*Ursus arctos* LINNAEUS, 1758). As a rule, the extinct cave bear is identified on the

basis of features differentiating it from the latter species, presumed by many to be its closest living relative. Thus, the cave bear is generally known as a robust animal with graviportal limbs and shortened distal limb segments. In order to test the taxonomic potential of beam analysis, some Early and Middle Pleistocene bears (*Ursus deningeri* REICHENAU, 1906 and *Ursus etruscus* CUVIER, 1823) are also included in the study. The phylogenetic relationships of Pleistocene European bears are still a matter of debate. A tooth-orientated paradigm is present in most studies, and postcranial material usually plays a minor role in taxonomic considerations. Quite often, however, metapodial proportions are used for demonstration of the *U. deningeri-U. spelaeus* morphocline (e. g., KURTÉN & POULIANOS 1977).

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## II. MATERIAL AND METHODS

Geometrical properties for a total of 16 femoral shafts were calculated, including the following species and specimens:

*Ursus spelaeus*, cave bear. Given the marked sexual dimorphism and considerable individual variation in this species, both male and female, slender and robust specimens were selected for study. In order to test the possible impact of body size on diaphyseal shape, the male and female subsamples were treated separately. Cave bear material should always be sexed before any further metric or morphologic analysis is carried out (KURTÉN 1955). Due to the bimodal distribution of metric traits, sexing represents a minor problem if samples are sufficiently large. The female femora are from the Salzofen skeleton (Upper Austria; EHRENBURG 1942), Cunturines cave (B.C.295, Italy, RABEDER 1991) and Apollo cave (AP-P-3S, Switzerland). The last mentioned specimen may belong to a so-called Alpine dwarfed population, but it is still within the normally observed female size range. Two male femora are from Herdengel cave (HD 60-1 and HD 339-6, Lower Austria, LEITNER-WILD et al. 1994) and one from the nearby Schwabenreith cave (SW 743). All bones are of Late Pleistocene or possibly late Middle Pleistocene age.

*Ursus arctos*, brown bear. Both Late Pleistocene and Recent European specimens were studied. Morphologic variability in *U. arctos* was also found to be important, but no consistent diachronic or size-related trend could be detected and fossil and recent bones are pooled. The fossil specimens are a very large fragmentary diaphysis from Herdengel cave (HD356) and a smaller one from Gamssulzen cave (GS 411, Upper Austria). The recent subsample includes wild European animals: Nr.1312 (Bulgaria) and one specimen each from Slovakia and Croatia. The latter two are from the collection of the Institute of Anatomy of the Veterinarian University of Vienna.

*Ursus deningeri*, Hundsheim (Lower Austria). The bear remains from this locality have been extensively described by ZAPFE (1946). Apart from one femur belonging to a partial skeleton, two additional adult specimens (labeled 1 and 3.724) were included in the cross-sectional analyses. A larger, subadult specimen (A 146) was used for the comparison of external breadth ratios only. According to RABEDER (1981) the stratigraphic position of the Hundsheim fissure filling is early Middle Pleistocene.

*Ursus* sp., Deutsch Altenburg (Lower Austria). Two fragmentary femoral diaphyses are present at locality 4B of the limestone quarry of Deutsch-Altenburg, labelled DA 4B-1 and DA 4B-2 in this study. The bear remains from this locality are not yet published in detail, but in the faunal list given by MAIS & RABEDER (1984) both *U. etruscus* and *U. deningeri* are indicated for locality 4B. The more fragmentary specimen DA 4B-2 allowed only the determination of the two central section locations, and its values are therefore not included in Figs. 3 and 4. The stratigraphic position is Early Biharian (RABEDER 1981, see also FLADERER & REINER 1996).

Unless otherwise indicated, all materials are housed in the Institute of Palaeontology, University of Vienna. For the simple comparison of midshaft external breadths, all available femora of *U. spelaeus* from the sites mentioned above (altogether 120 specimens) were measured, thus providing a broad data base of the Late Pleistocene Alpine cave bear. Published data for *Ursus arctos* were taken from BALLELIO (1983), and for *U. etruscus* from MAZZA & RUSTIONI (1992).

The determination of section locations roughly follows the method given by RUFF & HAYES (1983), but was somewhat modified according to ursid femoral morphology. Cross sectional analysis requires a standardized orientation of the bone under study (Fig. 1). A central axis was defined as passing through two reference points, a proximal point lying on the superior face, midway between the femoral head and the greater trochanter, the other distally at the distalmost projecting point of the central trochlea, just anterior to the intercondylar notch. The bones were then placed on an osteometric board with the posterior side down, and the proximal end was raised until both reference points were brought to same height. The frontal plane was defined as parallel to the resting surface and the sagittal plane as perpendicular to it. Both planes intersect along the central axis.

The distance between the two reference points was defined as diaphyseal length ('length'). Sections were located at 20, 35, 50, and 65% of diaphyseal length, measured from the distal end, perpendicular to the central axis. The 80% section used by RUFF & HAYES (1983) could not be used because it is to varying degrees infringed upon by the gluteal tuberosity. In incomplete specimens, section locations and orientations had to be estimated. The external (subperiosteal) bone contours were traced with lead wire of one mm thickness and then transferred to graph paper. Inner bone (endosteal) contours and cortical thickness were estimated using biplanar radiographs (RUNESTAD et al. 1993).

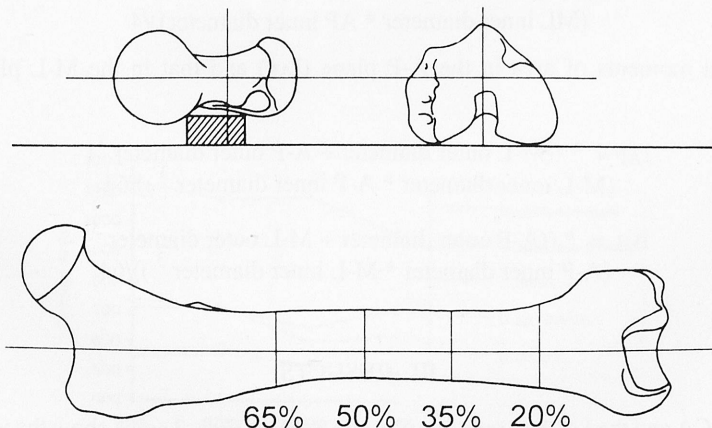


Fig. 1. Reference axes and cross section locations on the femur.

The following geometric section properties have been shown to be most relevant for biomechanical analysis. Cortical area (CA) is the amount of cortical bone in a cross section and is proportional to axial rigidity, i. e., it is closely related to body weight and may be used for body weight estimates. Second moments of area (I, also called area moments of inertia) describe the distribution of material in a plane about a defined axis. They are directly proportional to the bending rigidity about that axis. In our case,  $I_{AP}$  was calculated in the sagittal (anteroposterior) plane about a mediolateral axis, and  $I_{ML}$  defines the bending rigidity in the mediolateral (coronal) plane about an anteroposterior axis.  $I_{AP}/I_{ML}$  is the ratio of bending strength in the anteroposterior (A-P) plane relative to the mediolateral (M-L) plane and can be used as a shape index, since it reflects the relative distribution of bone about perpendicular axes. A ratio of 1.0 indicates an equivalent distribution of bone about the axes, while ratios greater or less than 1.0 indicate a direction of greater bending strength in the A-P or M-L planes, respectively (RUFF 1987; Fig. 2).

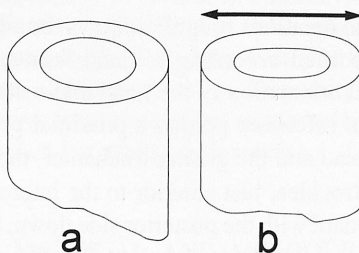


Fig. 2. Tubular bones can be modeled as hollow beams. In a), bending rigidity is equally distributed, whereas in b) it is increased in the direction indicated by the arrows.

The section contours and wall thicknesses of ursid femora were considered to be sufficiently regular to be amenable to a symmetrical elliptical hollow beam model. Outer (periosteal) and inner (endosteal) diameters were measured with a digital caliper from either the graph paper or radiograph images as maximum diameters in the defined directions. Values were entered into standard engineering formulae for cortical area and second moments of area (RUNESTAD et al. 1993).

$$CA = \pi ((M-L \text{ outer diameter} * A-P \text{ outer diameter}) - (M-L \text{ inner diameter} * A-P \text{ inner diameter}))/4$$

The second moments of area in the A-P plane ( $I_{AP}$ ) and that in the M-L plane ( $I_{ML}$ ) are calculated as:

$$I_{AP} = \pi ((M-L \text{ outer diameter} + A-P \text{ outer diameter})^3 - (M-L \text{ inner diameter} + A-P \text{ inner diameter})^3)/64$$

$$I_{ML} = \pi ((A-P \text{ outer diameter} + M-L \text{ outer diameter})^3 - (A-P \text{ inner diameter} + M-L \text{ inner diameter})^3)/64$$

### III. RESULTS

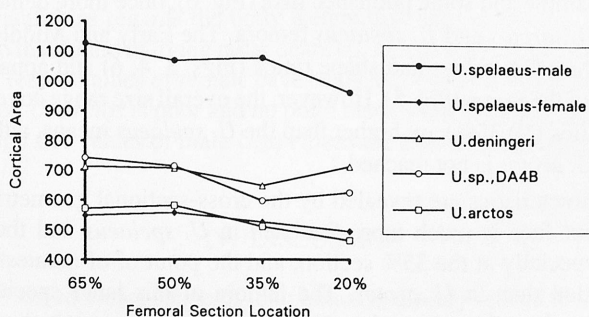
Values for CA and the  $I_{AP}/I_{ML}$  ratio are given in Table I. Figs. 3 and 4 show the variation along the femoral shaft for the subsample means of both values. It is clear from Fig. 3 that CA does not vary significantly with section location. If CA is taken as an indicator of body mass (RUFF 1989),



Table I

## Cross-sectional bone areas

Species			Cortical area (square-mm)				AP/ML Bending Rigidity			
	Cross section (%)		65	50	35	20	65	50	35	20
	specimen	length' (mm)								
<i>Ursus spelaeus</i> male	HD 60-1	393.0	1159.3	1043.4	1052.6	815.2	0.59	0.55	0.63	0.50
	HD 339-6	413.3	1016.4	956.3	1003.4	974.3	0.47	0.44	0.55	0.48
	SW743	436.0	1206.0	1200.7	1156.6	1078.5	0.67	0.65	0.66	0.52
Mean			1127.3	1066.8	1070.9	956.0	0.58	0.55	0.61	0.50
<i>Ursus spelaeus</i> female	BC.295	327.8	548.1	534.1	518.3	417.3	0.46	0.51	0.64	0.50
	Salzofen	355.3	604.7	625.8	617.7	577.5	0.50	0.51	0.64	0.57
	AP-P-3S	343.5	492.5	509.4	439.0	487.6	0.48	0.56	0.63	0.56
Mean			548.5	556.5	525.0	494.1	0.48	0.53	0.64	0.54
<i>Ursus deningeri</i> Hundsheim	skeleton	348.9	651.1	688.8	612.2	715.8	0.52	0.58	0.62	0.66
	1	339.3	974.8	681.2	659.1	642.0	0.53	0.65	0.68	0.40
	3.724	359.2	812.0	742.7	664.0	765.0	0.43	0.76	0.76	0.64
Mean			712.6	704.2	645.1	707.6	0.49	0.66	0.69	0.56
<i>Ursus</i> sp. Dt.-Altenbg.	DA4B-1	426.7	742.1	712.5	594.5	622.1	0.45	0.60	0.66	0.50
	DA4B-2			889.9	771.3			0.65	0.74	
<i>Ursus arctos</i>	HD356	466.7	865.7	884.1	758.5	579.8	0.68	0.79	0.82	0.49
	1312	318.0	464.1	481.7	417.9	401.0	0.66	0.87	0.76	0.43
	GS411-1	344.0	460.2	473.3	399.1	427.3	0.52	0.67	0.72	0.51
	Slovakia	370.0	657.6	642.7	580.7	508.0	0.58	0.65	0.66	0.47
	Croatia	319.0	410.6	418.0	390.9	404.9	0.60	0.75	0.74	0.62
Mean			571.6	580.0	509.4	464.2	0.61	0.74	0.74	0.51

Fig. 3. Changes in cortical area of the femoral shaft for sample means. Measurements in mm<sup>2</sup>.

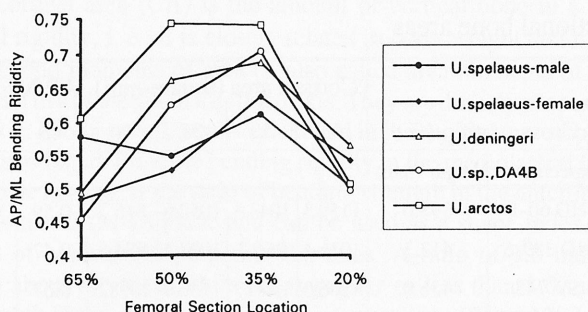


Fig. 4. Changes in the ratio of A-P/M-L bending rigidity (calculated as  $I_{AP}/I_{ML}$  ratio) of the femoral shaft for sample means.

the means for *U. arctos* and female *U. spelaeus* are comparable as to overall size. Furthermore, male cave bears may have weighed up to twice as much as females. The values and pattern of variation of the shape ratio  $I_{AP}/I_{ML}$ , however, show striking differences between species, especially for the midshaft sections (50 and 35%). They are less pronounced and consistent near the articulations, where the shaft is less amenable to modelling by beam theory (RUFF & HAYES 1983). These differences are clearly not size-related, as male and female cave bears follow a similar pattern, at least in the biomechanically most relevant midshaft region. As noted above, values near 1.0 stand for an equal distribution of bending rigidity, whereas values significantly above or below 1.0 indicate a preferred direction of increased bending rigidity. Although values are lower than 1.0 for all sections studied, the femora of *U. arctos* exhibit circular diaphyseal midshaft sections, while those of *U. spelaeus* are much more flattened antero-posteriorly, regardless of individual bone size. These conditions are equally obvious from the cross-sectional images themselves (Fig. 5). It should be noted that the specimens shown in 5c) and 5d) are outliers in terms of the circularity of the shaft, with the typical situation found in *U. spelaeus* largely corresponding to that seen in 5a) and 5b). As the orientation of greatest bending rigidity closely coincides with the M-L plane in most sections, the choice of anatomical axes for the calculation of second moments of area is well justified. Although external breadths are only a partial reflection of cross sectional geometric distribution, the same general patterns of variation should be expected for midshaft depth/width ratios as for the  $I_{AP}/I_{ML}$  ratio at the 50% section. This ratio is directly analogous to the pilasteric index used in anthropology (RUFF 1987). External breadths are easily measured and allow for the inclusion of a large sample and some published data (Fig. 6), once more demonstrating the shape differences between *U. arctos* and *U. spelaeus* femora. The Early and Middle Pleistocene ursids are intermediate in their CA values and shape ratios (Figs. 3, 4, 6) and apparently exhibit some distinct morphology of their own (Fig. 5). However, the overall size range covered is much smaller here. The  $I_{AP}/I_{ML}$  ratios (50,35%) are higher than the *U. spelaeus* means, although the degree of circularity found in *U. arctos* is not reached.

Not all shape characteristics are revealed by the cross-sectional geometric values alone. For example, the posterior face is much more flattened in *U. spelaeus* and the Early and Middle Pleistocene bears, especially at the 35% section, and the point of of greatest M-L breadth has a more posterior position than in *U. arctos*. The femora of this latter species usually exhibit a prominent linea aspera along the postero-lateral edge of the diaphysis, which may contribute to the greater relative A-P bending strength. The widely assumed robusticity of cave bear long bones is

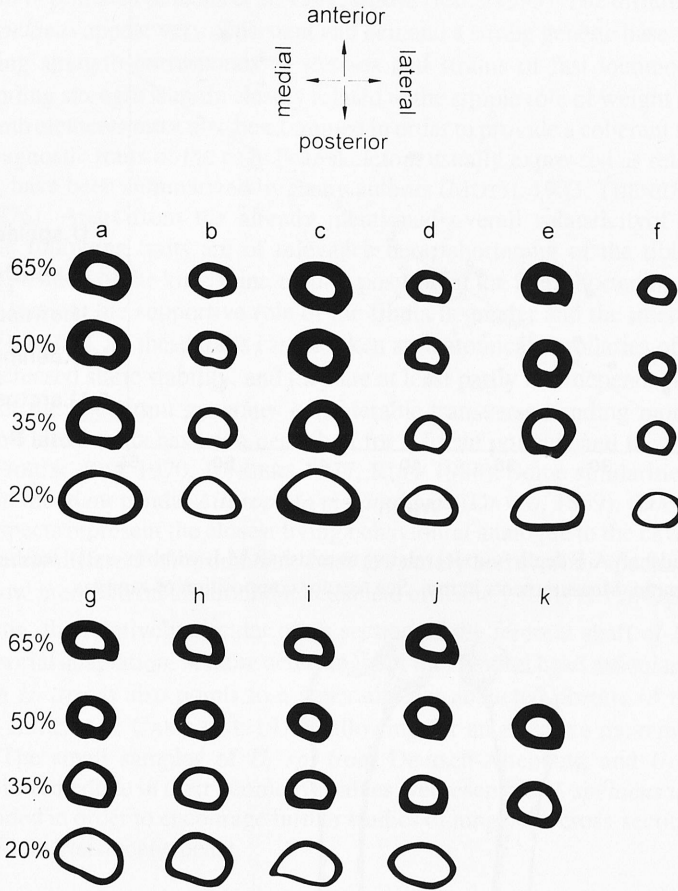


Fig. 5. Cross section outlines of selected specimens. a-d), *U. spelaeus*; e-f), *U. arctos*; g-i), *U. deningeri*, Hundheim; j-k), *U. sp.*, Deutsch-Altenburg 4B. a) and b) represent "typical", c) and d) "circular" shaped individuals of the cave bear.

possibly an artifact of conventional osteometric procedures taking transverse (M-L) linear measurements as representative for the whole cross section. Quite logically, body weight estimates for *U. spelaeus* appear as too high when based on transverse shaft widths (VIRANTA 1994). The assumption of this author as regards the body weight distribution among sexes in the cave bear being comparable to that found in living polar bears (*U. maritimus*), is largely borne out by the CA values of this study (equal values of female cave bears and extant European brown bears). As our sample of large-sized *U. arctos* is poor and no polar bears were included, it cannot be determined at this time if the high CA values of male *U. spelaeus* are ever reached by these species.

#### IV. DISCUSSION

Differences in cross-sectional shape of long bones in closely related animals can be seen as a mechanical response to habitual patterns of limb use and may be genetically or developmentally controlled. As noted previously, this relationship has been established for different mammalian

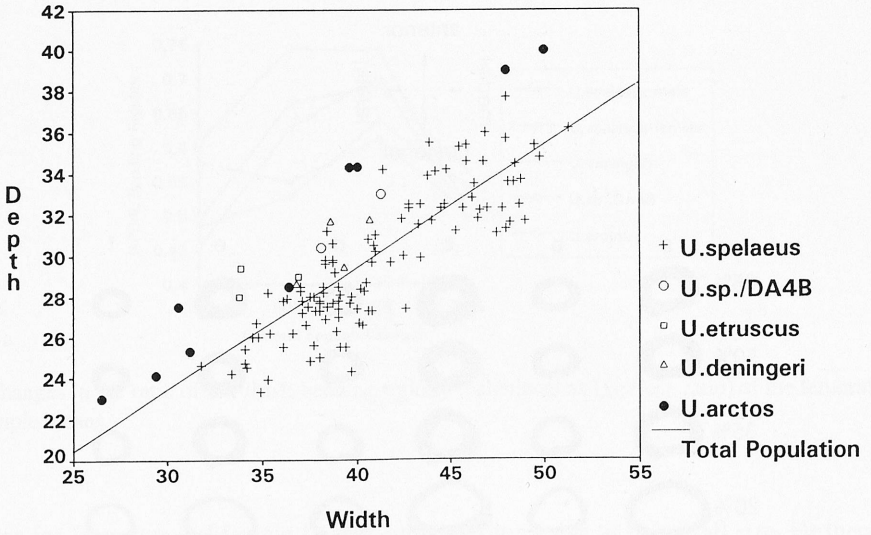


Fig. 6. Femoral midshaft A-P depth (y-axis) relative to midshaft M-L width (x-axis), least-squares regression line for total sample. Measurements in mm. See text for composition of samples.

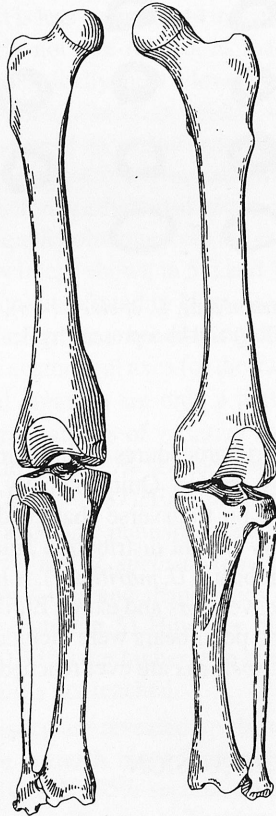


Fig. 7. Rearticulated long bones of the hindlimb of *U. arctos* (left; right limb) and *U. spelaeus* (right; left limb), anterior view, drawn to the same size.



groups, above all in primates (DEMES et al. 1991, BIKNEVICIUS 1993). The differences between *U. arctos* and *U. spelaeus* appear very consistent and demand a strong genetic base. Simply put, A-P (sagittal) bending strength corresponds to stresses and strains of fast locomotion, while M-P (transverse) bending strength is more closely related to the simple role of weight support. Clearly, the other hindlimb elements must also be examined in order to provide a coherent functional model (Fig. 7). The diagnostic traits of the cave bear skeleton, usually expressed as relative differences from *U. arctos*, have been summarized by many authors (MOTTL 1933, THENIUS 1951, KURTÉN 1976, PRAT 1976). Apart from the already mentioned overall robusticity of long bones and metapodials, the following traits are of relevance here: shortening of the tibia, tibial torsion, increased varus position of the knee joint, toed-in position of the feet, shortening of the first digit. Owing to tibial torsion, the supportive role of the fibula is greater and the interosseous space is widened (Fig. 7). In fact, all these traits can be taken as anatomical corollaries of a limb designed primarily for increased static stability, and they are at least partly interdependent. For example, a varus position of the knee joint generates considerable transverse bending moments. A similar combination of skeletal traits has been described for African pongids and the extinct prosimian *Megaladapis* (PREUSCHT 1970, JUNGERS 1977, RUFF 1988). Some similarities (tibial torsion) are also found in the giant panda, *Ailuropoda melanoleuca* (DAVID, 1869), (DAVIS 1964), which may in some respects represent the closest living behavioural analogue to the cave bear. Although living in completely different environments, both are purely herbivorous species whose adaptive niche places a low premium on all-around mechanical efficiency (DAVIS 1964, p. 123).

In comparison, the relatively circular cross section of the femoral shaft of *U. arctos* can be viewed as a cursorial adaptation. A more acute angle of the femoral head articular margin with the femoral shaft in *U. arctos* also points to a generally less abducted posture of the femur in this species (Fig. 7, JENKINS & CAMAZINE 1977), allowing for an effective movement closer to the sagittal plane. The small samples of *U. sp.* from Deutsch-Altenburg and *U. deningeri* from Hundsheim are intermediate in their geometric values, yet resemble *U. spelaeus* morphologically. They were included in order to encourage further studies of long bone cross-sectional morphology of Early and Middle Pleistocene bears.

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