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Osteometry, Variability, Biomechanics and Locomotion Pattern of the Cave Bear Limb Bones from Croatian Localities

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Key words: Cave bear, Limb bones, Rtg-osteometry, Variability, Biomechanics, Locomotion, Pleistocene, Vindija, Velika pećina, Veternica, Cerovačke pećine, Croatia.

Ključne riječi: spiljski medvjed, kosti udova, Rtg-osteometrija, varijabilnost, biomehanika, lokomotorika, pleistocen, Vindija, Velika pećina, Veternica, Cerovačke pećine, Hrvatska.

Abstract

The estimated stylo- and zeugopodial bone index is lower for the cave bears from the mountainous region (Cerovačke pećine caves) than the bone index from the hilly-lowlands caves (Vindija, Velika pećina, Veternica) and indicates that limb loading depends on the body mass and palaeoenvironment. The type of movement was similar to the locomotion of the recent brown bear but with somewhat more expressed plantigrady on the hind limbs. At the same time, the sex ratio of the studied material depends firstly on the site morphology (endogene or exogene cave), i.e. its function (dense or periodically visited shelter), and also on geological processes and human activity.

Sažetak

Analize dugih kosti udova (stilopodija i zeugopodija) spiljskih medvjeda iz pleistocenskih naslaga spilja Hrvatske pokazale su niže vrijednosti indeksa kostiju za medvjede koji su obitavali u visokogorskom području (Cerovačke pećine) u usporedbi s medvjedima brežuljkastog tipa nalazišta (Vindija, Velika pećina, Veternica). Takvi rezultati dovode do zaključka da način opterećenja udova ovisi kako o masi tijela tako i o okolišu. Način kretanja spiljskih medvjeda sličan je načinu kretanja recentnih medvjeda s nešto jače izraženom plantigradnošću stražnjih ekstremiteta. Istodobno omjer spolova na obrađenim lokalitetima prvenstveno ovisi o morfologiji terena i samog nalazišta (egzogena ili endogena spilja), njegovoj funkciji (brlog ili povremeno sklonište) te o geološkim procesima i ljudskoj aktivnosti.

1. INTRODUCTION

Previously, biomechanical analyses have been widely applied in anthropology and primatology and sporadically in the study of caviomorph rodents. Recently, because of the rich fossil record and contemporaneous presence of similarly designed, yet differently adapted forms, KUNST (1996) applied biomechanical analyses on femora of Pleistocene European bears. Along with other skeletal traits, femoral cross-sectional shape was interpreted in *Ursus spelaeus* as being indicative of limb bone structure designed primarily for static stability. Therefore, the previous study of the cave bear limb bones from Croatian sites based on the variability of bone lengths, width of epiphysis and diaphysis (KRKLEC, 1997; JAMBREšIć et al., 2000) is now extended to the analysis of the inner structure, because the internal bone structure yields some information on bone loading which can be analyzed and interpreted in biomechanical terms. Thus, the aim of this paper is to test a hypothesis of convergent adaptation that was registered on the metapodial bones from Mixnitz (SIVERS, 1931).

2. MATERIAL AND METHODS

The sample of 1328 limb bones of adult cave bears comprises 147 humeri, 392 radii, 218 ulnae, 160 femora, 343 tibiae, and 58 fibulae originating from different Middle and Late Pleistocene levels (oxygen isotope stages 6-2) of the Vindija, Velika pećina, and Veternica (NW Pannonian Croatia) and Cerovačke pećine caves (E Central Croatia) (Table 1).

The results are analysed together for each site because of the low statistical frequency of bones in stratigraphically different levels (Table 1).

Different lengths and widths were measured after DRIESCH (1976) and TSOUKALA & GRANDAL D'ANGLADE (1997) with a digital calliper. The data obtained were compared and also used for computation of the robusticity index (Ir), representing the ratio of the mean value of the smallest diaphysis diameter and maximal bone length, and bone index (BI) representing the

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Site	Level	humerus	radius	ulna	femur	tibia	fibula
Vindija	E, F	8	36	17	8	21	
	G	17	67	26	13	30	
	H	3	40	15	4	58	
	I	9	9		5	12	
	J	4	27	30	7	50	
	K		27		4	24	
	L	7	35	11	13	46	
	M	1			3	1	
Veternica	d-j	29	36	33	27	39	11
Cerovačke	c	62	62	63	67	52	13
Velika p.	d, e, f		10			1	1
	g, h, i	6	34	14	2	12	20
	j, k		17	8	2		13

Table 1 Frequency of the limb bones found in Pleistocene levels of the Vindija, Veternica, Cerovačke pećine and Velika pećina caves.

ratio of the mean value of the smallest diaphysis diameter and diaphyseal length. Diaphyseal length is the maximal length of a central axis which is defined as passing through two reference points. These reference points are different for each bone:

- femur (Fig. 1): proximal point lies on the superior face, in the middle between the femoral head and the greater trochanter, while the distal one is the most projecting point of the central trochlea;
- humerus: proximal point is located on the caput humeri and the distal one on the condylus humerii between the trochlea humerii and capitulum humerii;
- radius: proximal point is situated on the caput radii and distal one on the facies articularis carpea.

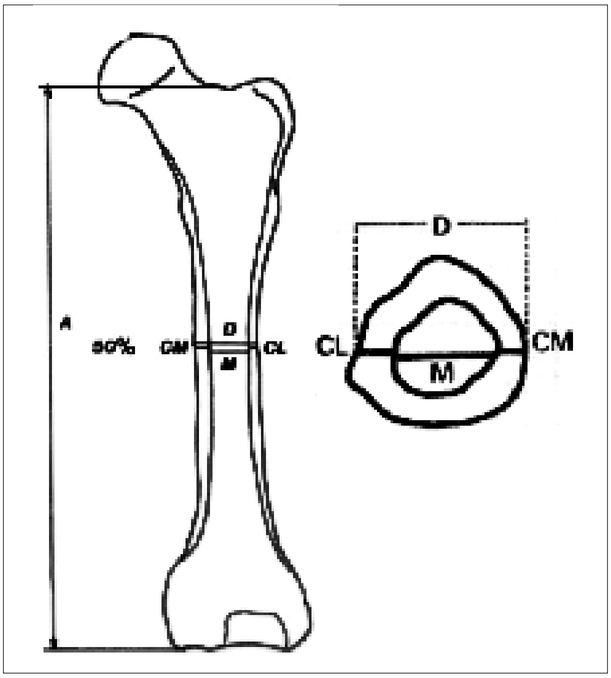

Fig. 1 Measuring points for radiograph analyses.

Diaphyseal length of ulna, fibula and tibia correspond to the maximal bone length.

For selected bones from each site radiographs were taken with the aim of measuring outer diameter (D), inner diameter (M), lateral cortical thickness (CL), and medial cortical thickness (CM) at 50% of the diaphyseal length from the distal end and perpendicular to the central axis (Fig. 1). These parameters have been used for calculation of the general cortical index (CI), medial cortical index (CIM), lateral cortical index (CIL) and cortical area (CA).

$$CI=((CM+CL)/D)\times 100,$$
$$CIM=(CM/D)\times 100,$$
$$CIL=(CL/D)\times 100,$$
$$CA=D^2-M^2$$

Data were analysed with “K-means clustering” and the “Hierarchical Joing (tree clustering)” method (ROHLF, 1992).

To test our results, comparisons were made with relevant data obtained from the material of the Conturines, Herdengel, and Gamssulzen (REISINGER & HOHENEGGER, 1998), Azé and Berzé (ARGANT, 1991), Cova Eiros (GRANDAL D’ANGLADE, 1993) caves and 38 other caves from Spain (TORRES PEREZ-HIDALGO, 1988).

3. STRATIGRAPHY AND PALAEOGEOGRAPHY

The present analysis was performed in order to try to confirm the hypothesis that the difference in morphology of the cave bear limb bones, opposite to the variability registered on the teeth, reflects distinct environmental conditions and not different geological age. Namely, considering the age, the studied material was found in levels ranging from the OIS 7 or 6 to the OIS 2. Thus,

Cave	Layer	Age	Method
Vindija	E	18,500	^{14}C
	F/d/d	26,000	^{14}C
	G1	28,020	AMS
	G1	29,080	AMS
	G1	27,010	U/Th
	G1	33,100	U/Th
	G1	33,000	AMS
	G3	41,000	U/Th
	G3	42,000	Amino acids
	G3	>42,000	AMS
	H	90,500	U/Th
	I/J	168,400	U/Th
	J	171,200	U/Th
	K	245,600	U/Th
Velika pećina	e	26,450	^{14}C
	g	31,168	^{14}C
	i	33,850	^{14}C
Veternica	c	13,660	^{14}C
	i	>43,200	^{14}C
Cerovačke	c	>40,000	^{14}C
Conturines	Surface	17,900	U-series
	GSt4	44,500	U-series
	Spelaeothem under the bones	>257,000	U-series
Gamssulzen	Fossiliferous layer	38,000	^{14}C
	Fossiliferous layer	25,000	^{14}C
	Fossiliferous layer	25,250	U-series
	Fossiliferous layer	27,250	U-series
Herdengel	Upper complex	37,000	^{14}C
	Main fossiliferous layer	45,000	U-series
	Main fossiliferous layer	65,800	U-series
	Main fossiliferous layer	66,400	U-series
	Basal complex	126,900	U-series
	Basal complex	135,200	U-series

Table 2 Radiometric dates from the Vindija, Velika pećina, Veternica, Cerovačke pećine, Conturines, Gamssulzen and Herdengel caves (after WILD et al., 2001, and LEITNER-WILD & STEFFAN, 1993).

for better understanding of the problem, the stratigraphy of the investigated material must be reconsidered.

The sample from the Vindija cave derives from deposits divided into 13 stratigraphic levels: the levels M and L appear to date to the OIS 7 or 6, unit K was previously correlated with the Eemian (OIS 5e), levels J-D encompass the Last Glacial (OIS 5d-2), while the upper three levels are Holocene (PAUNOVIĆ et al., 2001). The cave bears from the Velika pećina cave were found in level k (probably stadial phase of the Middle Würm), but also in levels j-i (interstadial phase of the Middle Würm), e-h (Late Würm), and d (Last Glacial Maximum). In the Cerovačke pećine cave (PAUNOVIĆ et al., 2001) only one fossiliferous level was registered and dated to the Last Glacial, i.e. to the OIS 3. Supported by palaeontological evidence the uppermost Pleistocene levels d and e from the Veternica cave are ascribed to the OIS 2, and the levels f, g and h to the OIS 3 (PAUNOVIĆ et al., 2001).

Also, the radiometrical data (Table 2) obtained from Croatian sites (WILD et al., 2001), as well as from Austrian and Italian caves (LEITNER-WILD & STEFFAN, 1993) show clearly the different ages of analysed populations.

At the same time, considering the geographical characteristics of the investigated sites, the analysed material was found in the caves belonging to: (1) the hilly-lowlands part of NW Pannonian Croatia (Vindija, Velika pećina, Veternica) and (2) the Dinarides - mountainous part of E Central Croatia (Cerovačke pećine). During the Last Glacial the northwestern part of Croatia was quite near to the ice cover of the Alps, while the northeastern area was part of huge steppe areas of the Pannonian Basin which featured a different vegetation, and was characterised by the dominance of sand steppe meadows, grassy steppes, riparian forests, and mixed deciduous and coniferous forests in the hilly regions. At

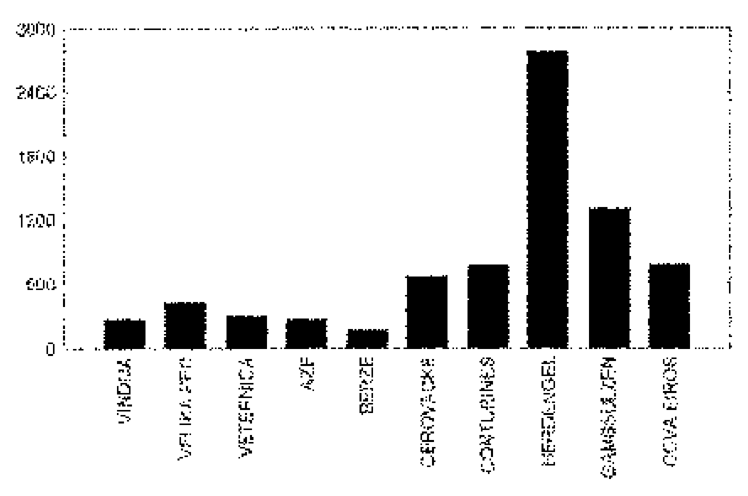

Fig. 2 Absolute altitude (msl) of the studied caves.

the same time, the Dinarides (as the southern extension of the Alps) played the role of a physiographic barrier between north and south. Although not glaciated today, they have supported isolated glaciers and were characterised by high mountain (?alpine) vegetation developed on a karstic relief.

Considering their palaeogeographical characteristics, i.e. the climate and altitude, the caves from Austria (Conturines, Gamssulzen, Herdengel), France (Azé, Berzé) and Spain also belong to these two main environmental types (Fig. 2).

4. RESULTS

4.1. Sexual dimorphism

The first step in recognizing the problem of expressed sexual dimorphism registered among bears (PERKINS, 1973; STIRLING, 1993; REISINGER & HOHENEGGER, 1998), required separation of the limb bones samples into those representing males and females.

The histograms and dendrograms (Fig. 3) showed a clear bimodal distribution for all bones - especially in the case of greatest and physiological length - in each site.

Thus, the differences in sex ratio obtained by cluster analysis strengthen the clear differentiation into sexes obtained by univariate analyses. While in the investigated 6 limb bone elements from Velika pećina the ratio is ♂3 : ♀1, in all other sites it is approximately ♂1 : ♀1.

4.2. Biometric analyses

Because of the danger of allometric effects, i.e. size dependence of proportions which is especially relevant in materials representing variability in size and distributions (sex ratio), the frequency distribution for each bone from each site was estimated (Fig. 4). It appears that all samples exhibit the same allometry, that the deviations from the regression are a result of modification, and that the single change deduced from the present data is size difference between geographically different populations.

The Hierarchical Joing (tree clustering) method showed the size variability of all limb elements, and a similar disposition for both sexes within the cluster of higher values for Vindija, Velika pećina and Veternica, and the cluster of lower values for Cerovačke pećine, Conturines, Herdengel and Gamssulzen (Fig. 5).

A robusticity index, ratio of the mean value of smallest diaphysis diameter and maximal bone length, was calculated for both sexes together, by reason of comparison with relevant but unsexed data from some European localities.

Calculated and compared robusticity index - Ir (Table 3) indicates the highest values for humeri (10.2-11.7) and tibiae (10.6-12.5). The Ir of femora varies from 9.0 to 10.6, of radii from 7.5 to 11.0, of ulnae from 6.7 to 8.9, and of fibulae from 4.6 to 5.3.

The strongest bones are the humerus and tibia. At the same time, the Ir of femora most probably indicates different types of locomotory and loading pattern: values higher than 10.0 are registered among material from Veternica, Vindija, Velika pećina and are similar to the indices from Azé, Berzé and the Iberian caves. On the other hand values lower than 10.0 are characteristic for bones from Cerovačke pećine, Conturines, Herdengel and Gamssulzen (Fig. 6).

Thus, biometric analyses, including robusticity index as an indicator of body size, show variability of the limb bones and the difference in body mass between geographically distinct populations of the cave bear.

4.3. Biomechanical and locomotory analysis

The analysis consists of calculation and comparison of the bone index (BI), cortical index (CI) and cortical area (CA).

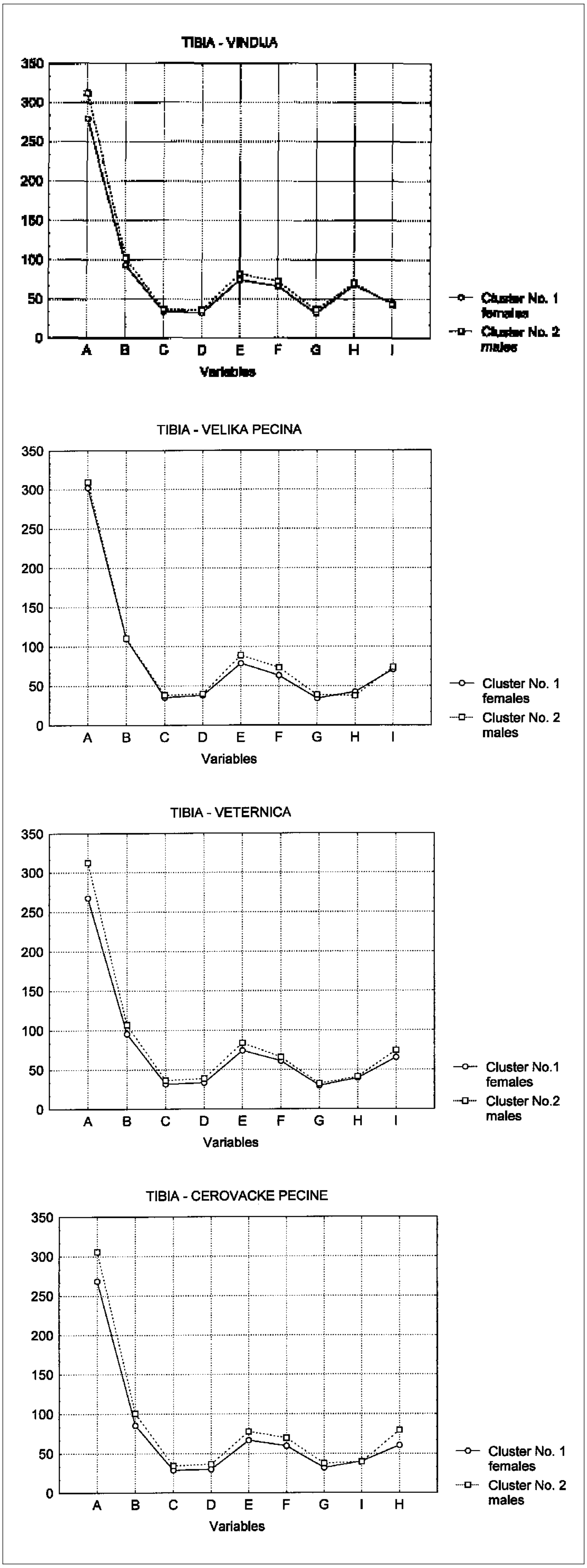

Fig. 3 Examples of sex separation by K-means clustering method.

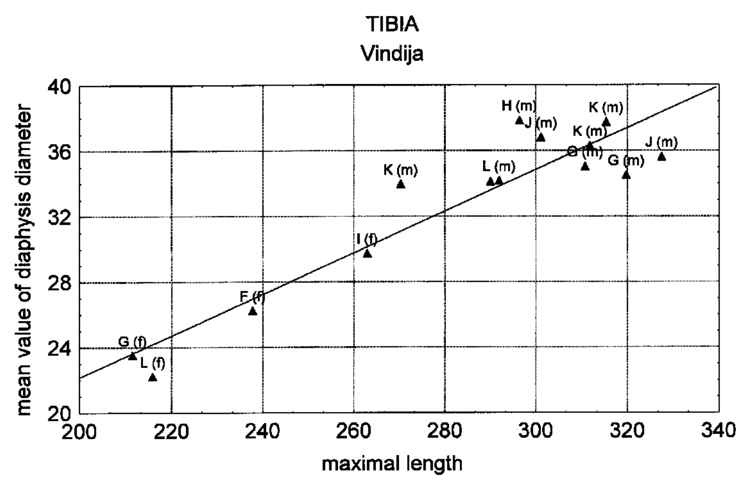

Fig. 4 Example of distribution around intermediate regresion.

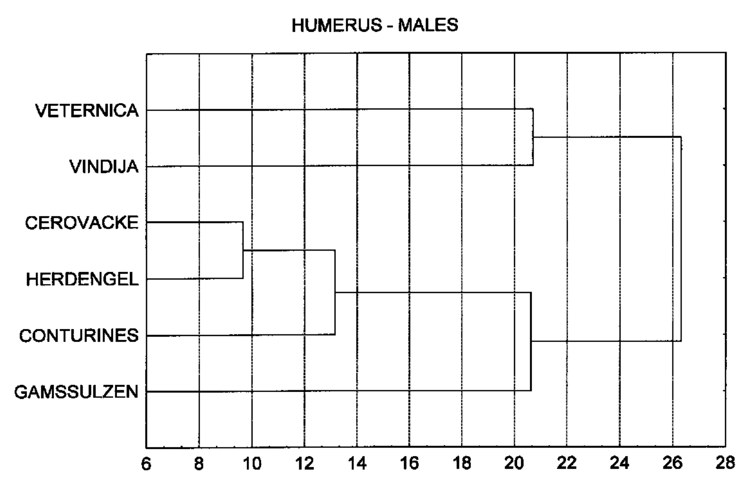

Fig. 5 Example of size variability based on metric parameters for material from the caves Veternica, Vindija, Cerovačke pećine, Herdengel, Conturines and Gamssulzen by Joing tree clustering method.

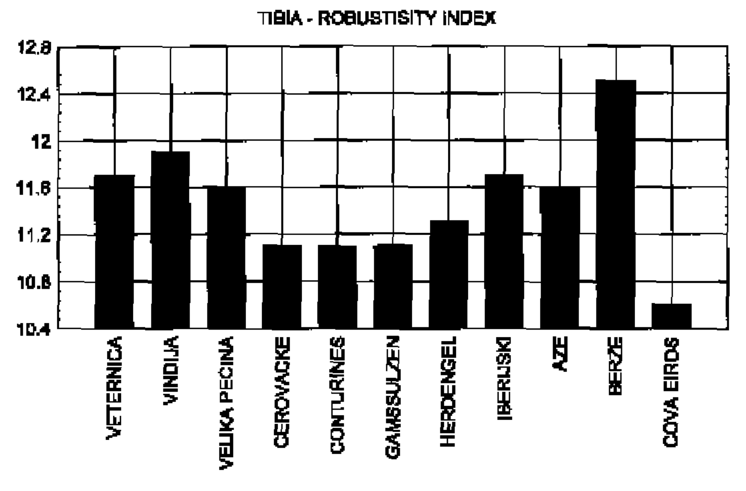

Fig. 6 Example for values of robusticity index (Ir) calculated for material from the caves Veternica, Vindija, Velika pećina, Cerovačke pećine, Herdengel, Conturines and Gamssulzen, Azé, Berzé, Cova Eiros and Iberian caves.

The bone index (BI) reflects the ratio between the mean value of the smallest diaphysis diameter and diaphyseal length. Unlike the maximal length (used in Ir), representing linear distance between two punctuate points on the epiphyses, diaphyseal length strictly connote maximal length of a central axis and therefore represent the length of the most laden part of the bone. Accordingly BI could indirectly reflect a type of bone loading.

The estimated BI for Cerovačke pećine and Conturines, Herdengel and Gamssulzen caves are very similar, while the BI of the bears from the Veternica and

	humerus	radius	ulna	femur	tibia	fibula
Vindija	10.8	8.6	7.6	10.2	11.9	
Velika pećina		8.0	8.9	10.6	11.6	5.0
Veternica	10.4	7.5	7.8	9.9	11.7	4.6
Cerovačke	10.2	6.7	6.7	9.7	11.1	4.8
Conturines	10.2	6.8	7.3	9.6	11.1	
Gamssulzen	10.6	7.0	7.4	9.8	11.1	
Herdengel	10.3	6.9	7.5	9.8	11.3	
Iberian caves	11.5	10.9		10.4	11.7	
Azė	10.5	10.0		9.9	11.6	4.3
Berzė	11.7	9.1		10.5	12.5	
Cova Eiros	10.4	11.0		10.2	10.6	5.3

Table 3 Robusticity index (Ir) calculated for the material from the Veternica, Vindija, Velika pećina, Cerovačke pećine, Herdengel, Conturines, Gamssulzen, Azé, Berzé, Cova Eiros and Iberian caves.

	humerus	radius	ulna	femur	tibia	fibula
Males						
Vindija	12.0	7.9	7.7	9.2	11.6	
Velika pećina		8.6	9.8		12.5	5.8
Veternica	12.0	8.2	9.2	9.5	12.0	5..5
Cerovačke	11.4	7.2	8.2	9.0	11.6	
Conturines	11.6	7.9	8.7	9.1	11.4	
Gamssulzen	11.3	7.9	8.6	8.8	10.9	
Herdengel	11.4	8.0	8.9	9.0	11.5	
Females						
Vindija	12.7	8.5	6.9	9.0	11.8	
Velika pećina		8.6	9.8		12.5	5.8
Veternica	12.3	8.0	8.6	9.0	12.1	5.4
Cerovačke	10.8	7.4	7.1	8.7	10.9	
Conturines	11.3	7.2	8.1	8.7	11.1	
Gamssulzen	11.6	7.6	7.9	8.7	11.3	
Herdengel	10.7	7.0	7.2	8.6	11.3	

Table 4 Bone index (BI) calculated for the material from the Veternica, Vindija, Velika pećina, Cerovačke pećine, Herdengel, Conturines and Gamssulzen caves.

Velika pećina caves are higher, approximately 5-10% for males and 10-12% for females (Table 4, Fig. 7).

Calculated general cortical index (CI), medial cortical index (CIM), lateral cortical index (CIL) and cortical area (CA), which also reflect the limb loading type, posture and locomotory pattern (Table 5), were examined by the Hierarchical Joing (tree clustering) method. The dendrograms clearly show two main clusters con-

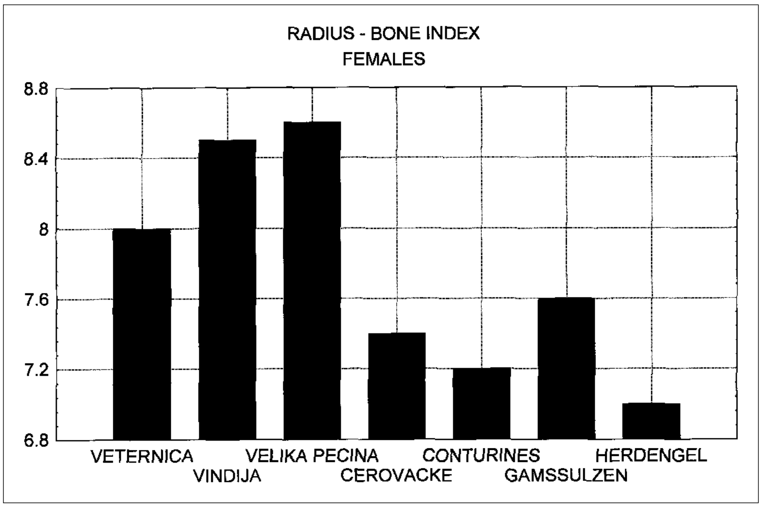

Fig. 7 Example for values of bone index (BI) calculated for material from the caves Veternica, Vindija, Velika pećina, Cerovačke pećine, Herdengel, Conturines and Gamssulzen.

Humerus ♂	**CA CAKa**	**CI**	**CIL**	**CIM**	**%**	**Humerus** ♀	**CA**	**CI**	**CIL**	**CIM**	**%**
Vindija	2816	53.3	28.3	25.0	11.6	Vindija	2541	60.0	30.9	29.0	6.1
Veternica	2573	50.8	29.8	24.5	17.8	Veternica	1525	55.8	30.2	27.9	7.6
							2176	60.0	32.0	32.0	0
							2400	54.5	29.0	25.4	12.4
Cerovačke	1365	48.8	27.9	20.9	25.1	Cerovačke	1071	45.0	22.5	20.0	11.1
							1365	41.8	23.2	18.6	19.8
Recent						Recent	522	41.3	17.2	24.1	28.6
Radius ♂	**CA**	**CI**	**CIL**	**CIM**	**%**	**Radius** ♀	**CA**	**CI**	**CIL**	**CIM**	**%**
Vindija	1113	56.7	29.7	27.0	9.1	Vindija	1008	48.6	27.0	21.6	20.0
	1475	59.5	30.9	28.5	7.8						
Velika pećina	1276	55.0	30.0	25.5	17.0	Velika pećina	616	48.2	27.5	20.6	25.0
	1200	64.8	35.1	29.7	15.4						
Veternica	1200	45.0	30.0	20.0	33.4	Veternica	800	48.4	27.2	21.2	22.0
	1357	56.0	31.7	24.3	23.4						
Cerovačke	1008	48.6	27.0	21.6	20.0	Cerovačke	440	37.0	22.2	14.8	33.3
	960	58.8	35.2	23.5	33.3						
Recent	731	42.8	36.6	20.0	45.4	Recent					
Ulna ♂	**CA**	**CI**	**CIL**	**CIM**	**%**	**Ulna** ♀	**CA**	**CI**	**CIL**	**CIM**	**%**
Vindija	864	63.6	33.3	27.2	9.0	Vindija	465	63.6	33.3	30.4	8.7
Velika pećina	1525	58.1	30.2	30.3	7.6	Velika pećina					
	1160	47.4	26.7	25.6	4.1						
Veternica	1088	53.4	37.5	22.5	40.0	Veternica	825	42.8	25.7	17.1	33.4
	1449	60.4	30.2	23.2	23.2						
	1365	52.3	23.8	23.8	0						
Cerovačke	1056	60.0	31.4	28.5	9.2	Cerovačke	585	55.5	29.6	25.9	12.5
							362	54.0	31.8	27.2	14.4
Recent						Recent	528	53.3	25.0	17.8	28.8
Femur ♂	**CA**	**CI**	**CIL**	**CIM**	**%**	**Femur** ♀	**CA**	**CI**	**CIL**	**CIM**	**%**
Vindija	2059	58.0	28.0	30.0	6.6	Vindija	1375	62.5	30.0	32.5	7.6
							1525	58.1	27.9	30.2	7.6
Velika pećina	2241	49.0	23.6	25.4	7.0	Velika pećina					
	2080	49.0	22.6	26.4	14.3						
Veternica						Veternica	1407	47.7	22.7	25.0	9.2
							1452	51.1	22.7	27.2	16.5
							1408	50.0	23.2	27.9	16.8
Cerovačke	1860	65.2	30.4	34.7	12.3	Cerovačke	1197	56.4	25.6	28.2	11.1
							825	44.2	20.0	22.8	12.2
Recent						Recent	473	38.3	18.5	22.2	16.6
Tibia ♂	**CA**	**CI**	**CIL**	**CIM**	**%**	**Tibia** ♀	**CA**	**CI**	**CIL**	**CIM**	**%**
Vindija	611	43.0	20.0	23.3	14.1	Vindija					
	1225	67.5	32.4	35.1	7.6						
	1045	54.3	24.3	27.0	10.0						
Velika pećina	1161	74.2	37.1	40.0	7.2	Velika pećina	1121	48.7	23.0	25.6	10.1
							945	63.6	30.3	33.3	9.0
Veternica						Veternica	1710	60.0	28.8	31.1	7.3
							1081	65.7	31.4	34.2	8.1
							741	65.5	31.0	34.4	9.0
Cerovačke	1196	53.8	25.6	28.2	9.2	Cerovačke					
	633	60.7	28.5	32.1	11.2						
	800	63.6	21.2	27.2	22.0						
Recent	319	60.0	25.0	30.0	16.6	Recent					

Table 5 General cortical index (CI), medial cortical index (CIM), lateral cortical index (CIL) and cortical area (CA) estimated for the cave bear long bones from the Veternica, Vindija, Velika pećina, Cerovačke pećine caves and the long bones of the recent brown bear.

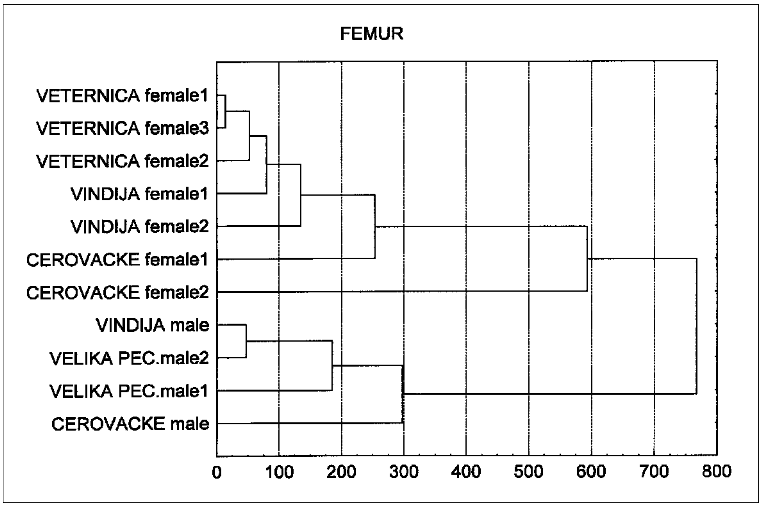

Fig. 8 Example of radiograph analysis performed on material from the caves Veternica, Vindija, Velika pećina and Cerovačke pećine by Joing tree clustering method.

sisting of males and females, and within each of them a disctinct sub-cluster of the Cerovačke pećine cave (Fig. 8).

The analysis of the CIM and CIL calculated for the cave bear bones and of CIM and CIL of the recent brown bear sample, shows that there is a difference in the loading pattern of limbs: on the forelimbs loading is stronger laterally, and medially on the hind limbs. But, there is no distinction between various populations of the cave bear as well as between these two species.

5. DISCUSSION

Because the vertebrate body is defined by dimensions, weight, constitution, and proportions, its characteristics are closely related to the configuration, geometry and distribution of the mass, thus with inner mechanical forces deriving from the activity of the organism and/or caused by external forces connected with the environmental conditions (NIKOLIĆ & HUDEC, 1988). For example, performed anthropological studies (ŠEĆEROV, 1973) showed differences between the mountain and lowland populations expressed in the different width of the cortical bone and robusticity of the skeletal elements. These differences were explained with the subsistence and activity pattern of investigated human groups in different surroundings. The investigations of the human long bones were performed using, among other characteristics, the fact that the diaphyseal cross-section is non-homogeneous, and that the stress and tension is stronger on the outer contour of the bone than near the medullar cavity.

Thus, using the actualistic theory, we have applied the same methods to study the biomechanical and locomotory pattern of the fossil sample, especially because the cave bear was previously treated as a plantigrad animal, and the obtained results showed a clearly different pattern of ecologically different populations.

Therefore, if external mechanical forces depend on the activity of the organism, but in the first place reflect the ecological influences, the present study leads to the following conclusions:

- The statement that large sized males are numerous at low altitudes, while females seem to be more abundant in higher regions (REISINGER & HOHENEGGER, 1998) must be reconsidered. Our oppinion is that the sex ratio of the cave bears depends in the first place on the site morphology (exogene or endogene cave), i.e. its function (dense or periodically visited shelter), geological processes and human activity.
- The estimated bone index is lower for the material from the mountainous Cerovačke pećine caves than the bone index for hilly-lowland sites Vindija, Velika pećina and Veternica indicating that limb loading was caused by the smaller body mass, i.e. the type of movement was similar to the locomotion of the recent brown bear.
- The RTG-osteometry of the studied bones showed the biggest difference in a cortical area (amount of cortical bone that is proportional to the axial rigidity, i.e. closely related to the body weight) indicating that the hilly-lowland forms from Vindija, Velika pećina and Veternica were heavier and bigger and therefore featured clumsier locomotion.
- Comparison of medial and lateral cortical indices of all samples leads to the conclusion that plantigrady (sensu DENDALETCHE, 1986) described by PRAT & THIBAUT (1976) and CHAGNEAU (1986) is not a characteristic of the cave bears. From the obtained results it is obvious that the cave bear, similarly to the recent brown bears, was a semiplantigrad with somewhat more expressed plantigrady on the hind limbs.

Thus, because differences in biometry and biomechanical characteristics between geologically older and younger populations were not registered, the obtained results confirmed only the discrepancy between the hilly-lowlands- and mountain-populations of the cave bear, and coinciding with the study of VIRANTA (1994) indicated different limb loading and locomotory patterns. The smaller and more intensively movable forms (?cursorial) of the cave bear were adapted to harsher environmental conditions with insufficient food sources.

Still, a more integrated approach, i.e. careful morphological (not only metrical) analysis (e.g. articular shape, cross-sectional morphology, muscular scars, etc.) of skeletal elements, especially of the distal elements, is required for future studies of the cave bear because the effects of altitude, local morphology, pleistocene climate and fodder quality upon bear size/morphology remain only partially understood and not straightforward.

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