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Review of the Results of Morphometric and Morphogenetic Analyses of Early Pleistocene Micromammals and Upper Pleistocene Cave Bears in Croatia

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Key words: Morphometry, Morphogenesis, Microevolution, Stratigraphy, Cave bear, Micromammals, Pleistocene, Croatia.

Abstract

Due to the large number and visible morphological variability of skeletal parts of the Early Pleistocene micromammals and Upper Pleistocene ursids we utilised morphometric, morphogenetic and statistical analyses in order to determine and process the material. The results indicate rapid microevolutionary processes which are reflected both in variations of the characteristic parameters of particular skeletal parts, and their morphology.

The Early Pleistocene age of the bone-breccias discovered along the Adriatic coast was confirmed by the morphogenetic analyses of micromammals, with reference to geochronologically important arvicolids: the fauna from Razvode near Knin comprises arvicolids characteristic of the Lower Early Pleistocene, the fauna from Tatinja draga near Karlobag comprises species typical for the Middle Early Pleistocene, while the fauna from Podumci near Unešić is of Late Early Pleistocene age.

The results of the analyses of teeth and metapodial bones of the cave bears from the Upper Pleistocene deposits in Vindija cave, Velika pećina and Veternica cave (NW Croatia) are expressed as morphodynamic indices, namely, the frequency of the morphotypes occurrence indicates the existence of an intermediate type (?subspecies) within the phyletic lineage *Ursus deningeri - Ursus spelaeus*, which appeared during the Riss glacial and Riss/Würm interglacial, and a lack of deposits of that particular age in Veternica cave and Velika pećina.

Ključne riječi: morfometrija, morfogeneza, mikroevolucija, stratigrafija, spiljski medvjed, mikrosisavci, pleistocen, Hrvatska.

Sažetak

Zbog brojnosti i uočene morfološke varijabilnosti skeletnih dijelova donjopleistocenskih mikrosisavaca, odnosno gornjopleistocenskih ursida, prilikom determinacije i obrade materijala korištene su morfometrijske, morfogenetske i statističke analize. Rezultati su ukazali na brze mikroevolucijske procese koji su se odrazili kako u promjenama mjerenih karakterističnih parametara pojedinih skeletnih dijelova tako i na njihovu morfologiju.

Pretpostavljena donjopleistocenska starost koštanih breča koje su nađene duž obale Jadrana potvrđena je morfogenetskim analizama fauna mikrosisavaca u kojima dominiraju geokronološki važni arvikolidi: fauna iz Razvoda kod Knina sadrži arvikolide karakteristične za rani donji pleistocen, ona iz Tatinje drage kod Karlobaga vrste tipične za srednji donji pleistocen, dok je fauna iz Podumaca kod Unešića kasno donjopleistocenske starosti.

Rezultati analiza zuba i metapodija spiljskih medvjeda iz gornjopleistocenskih naslaga spilja Vindija, Velika pećina i Veternica (SZ Hrvatska) izraženi morfodinamskim indeksima odnosno učestalostima pojava morfotipova ukazuju na postojanje prijelaznog varijeteta (?podvrste) u razvojnom nizu *Ursus deningeri - Ursus spelaeus* koji se javlja tijekom glacijala Riss i interglacijala Riss/Würm, odnosno nedostatak naslaga ove starosti u spiljama Veternica i Velika pećina.

1. INTRODUCTION

For large quantities and variability of fossil material the multifarious options for data processing provided by computer technology has helped to make morphometry a very commonly used method in the palaeontological analysis of vertebrates. Additional morphogenetic studies which also enable the determination of relative geological age of the material and microevolutionary trends, have been carried out for many assemblages, namely families and/or taxa. In Croatia, such investigations have intensified in the 1980's, when processing of the Upper Pleistocene bears from Vindija cave, then Veternica cave and Velika pećina (NW Croatia) began as well as analysis of the Early Pleistocene bone-breccias at Razvode, Tatinja draga and Podumci (S Croatia).

The large quantity and variability of the studied material has so far enabled the establishment of morphogenetical schemes for particular taxa (e.g. *Ursus spelaeus*, *Microtus*), thus also allowing a relative dating of the rest of the vertebrates from deposits of undefined or questionable age with respect to the method "counting from the top".

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2. LOCALITIES

2.1. EARLY PLEISTOCENE

The Early Pleistocene bone-breccias are located in karstic fissures along the Adriatic coast: at Tatinja draga near Karlobag, Razvođe near Knin, and Podumci near Unešić (Fig. 1).

The bone-breccia matrix from Tatinja draga and Podumci is reddish-brown in colour, reflecting a temperate climate during the deposition, while the yellowish-green sandy clay matrix from Razvođe was deposited under colder climate conditions. The faunal assemblages are typical for the Early Pleistocene and there are no signs of sedimentary recording of fossils transportation (see: MALEZ & RABEDER, 1984; PAUNOVIĆ & RABEDER 1996).

2.2. UPPER PLEISTOCENE

The Vindija cave is located near Varaždin (Fig. 1) in the semi-mountainous terrain of Hrvatsko Zagorje. The cave entrance lies at an altitude of 275 m above sea level on the slopes of Mt. Ravna gora, and is a single large chamber, 50 m long, 28 m wide, and more than 20 m high. Approximately 12 m of stratified deposits were investigated and divided into 13 distinct stratigraphic units designated A (youngest) to M (oldest). The layers M and L appear to date to the Riss Glacial, unit K correlates with the Riss Interglacial (Eemian), layers J-D encompass the Last Glacial (Würm=Weichselian), while the upper three layers (C-A) are post-Pleistocene (see: PAUNOVIĆ, 1988). All Pleistocene faunal assemblages found at Vindija cave are dominated by cave bear remains.

The Velika pećina near Varaždin (Fig. 1) is divided into three separate chambers. Of these the first chamber is the largest measuring 18 m in breadth, and approximately 3 m in high, while the other two chambers are much smaller. The Quaternary sediments are over 12 m thick and separated into 16 levels (a-p). After MALEZ (1986) the layers o-l are correlated to the Riss/Würm Interglacial (Eemian), layers k-e encompass the Last Glacial (Würm - Weichselian), and the upper four (d-a) are post-Pleistocene. All the strata contain skeletal remains of Quaternary mammals, with a predominance of cave bear.

The Veternica cave near Zagreb (Fig. 1) is the longest cave in NW Croatia with over 10 km of passageways and canals. The entrance chamber is about 15 m long, 7 m wide and 5-8 m high. Beginning from the NW corner of the entrance chamber, the "left hall" extends for 14 m and is 3-7 m wide. Quaternary sediments were excavated in the entrance chamber and "left hall". In the most complete profiles, 11 geological layers were identified (a-k) which were deposited from the Riss Glacial period until the Holocene. After MALEZ (1965) the lowest layer k did not contain any palaeontological or archaeological remains. The layer j was dated as Riss/Würm Interglacial, the layers i-e as Glacial Würm, and the upper four layers (d-a) as post-Glacial. All Pleistocene faunal assemblages found at the Veternica cave are dominated by cave bears.

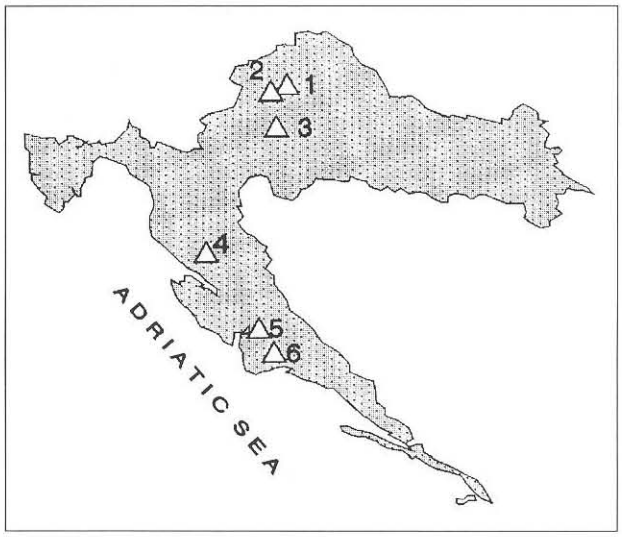

Fig. 1 Location map. Upper Pleistocene localities: 1) Vindija; 2) Velika pećina; 3) Veternica. Early Pleistocene localities: 4) Tatinja draga; 5) Razvođe; 6) Podumci.

3. METHODS

In the process we applied morphometric and morphogenetic methods described in the literature (e.g. CHALINE, 1972; RABEDER, 1983; MALEZ & RABEDER, 1984; PAUNOVIĆ, 1988; KRKLEC, 1995) in accordance with the basic conditions necessary for the reconstruction of functional-morphological changes in microevolutionary trends (CARROLL, 1988; BOULARD, 1993).

4. RESULTS

4.1. MICROMAMMALS FROM EARLY PLEISTOCENE BONE-BRECCIAS

The determination of micromammals from Early Pleistocene bone-breccias that were considered not to be synchronous, yielded a large number of endemic taxa in the fauna of southern Croatia (Tatinja draga, Razvođe, Podumci) and also geochronologically important arvicolids (Tables 1-3).

From Podumci near Unešić, a site known since 1930 (see: MALEZ & RABEDER, 1984), extensive material discovered by Malez led to new knowledge of the genera *Episoriculus*, *Microtus*, *Pliomys*, *Lagurus* and *Dinaromys*, as well as to the stratigraphic classification of the Podumci fauna as being of late Lower Pleistocene age (op.cit.). Four new taxa were established: *Episoriculus thenii*, *Reteliomys podumcensis*, *Microtus thenii* and *Lagurus arankae podumcensis*

Mammalia	Localities		
	Razvođe	Tatinja draga	Podumci
Talpa minor	+	+	+
Talpa europaea	-	+	-
Sorex runtonensis	+	+	+
Episoriculus thenii	+	+	+
Beremendia fissidens	+	+	+
Crocidura kornfeldi	+	+	+
Rhinolophus ferrumequinum	-	-	+
Myotis bechsteini	-	-	+
Myotis blythi	-	-	+
Hypolagus brachygnathus	-	-	+?
Lepus sp.	+	+	+
Marmota sp.	-	+	+
Sciurus sp.	+	-	+
Glis sackdillingensis	+	+	+
Reteliomys podumcensis	-	-	+
Allocricetus	*croaticus*	*bursae*	*bursae*
Microtus	*praehintoni*	*ratticeps*	*thenii*
Mimomys malezi	+	+	+
Mimomys savini	+	+	+
Mimomys pusillus	+	+	+
Dinaromys dalmatinus	+	+	+
Pliomys cf. *schernfeldensis*	+	-	-
Pliomys	*simplicior*	*bolkayi*	*bolkayi*
Pliomys cf. *hollitzeri*	-	+	+
Lagurus arankae	+	+	*podumcensis*
Apodemus cf. *sylvaticus*	+	+	+
Apodemus mystacinus epimelas	+	+	+

Table 1 List of Lower Pleistocene fossil mammals (after PAUNOVIĆ & RABEDER, 1996).

(MALEZ & RABEDER, 1984). According to CHALINE (1972), RABEDER (1981), KOWALSKI (1992) and the presence of successive stages of the evolutionary lineage of the *Microtus*-species can be interpreted as local evolutionary trends and therefore the new established Montepeglian *Microtus-thenii*-zone is also of local significance (MALEZ & RABEDER, 1984).

The fauna of Razvođe near Knin contains arvicolids (*Microtus* cf. *praehintoni*, *Pliomys simplicior/hollitzeri*, *Mimomys pusillus*) which indicate an Early Pleistocene age. A new species of hamster (*Allocricetus croaticus*) is to be emphasized (PAUNOVIĆ & RABEDER, 1996). The fauna of Tatinja draga near Karlobag contains many more individuals and is also dominated by arvicolids (*Lagurus arankae*, *Pliomys bolkayi*, *Pliomys hollitzeri*, *Dinaromys dalmatinus*, *Mimomys savini*, *M. pusillus*). Among these remains a new species *Microtus eoratticeps* was determined (PAUNOVIĆ & RABEDER, 1996).

From these results the following conclusions may be drawn:

- three species of the genus *Microtus* obviously belong to the Lower Pleistocene ancestral group (MALEZ & RABEDER, 1984).
- the lower evolutionary level of the majority of determined taxa is also confirmed by indices and the frequency of morphotypes (MALEZ & RABEDER, 1984; PAUNOVIĆ & RABEDER, 1996).

Taxa	Razvođe	Tatinja draga	Podumci
Allocricetus	31	3	4
Mimomys	3	4	1
Pliomys	14	5	36
Dinaromys	0	1	6
Lagurus	0.1	76	21
Microtus	31	7	29
Apodemus	20	4	3
others	1	0	0
Total	**166**	**877**	**868**

Table 2 Frequencies of rodent taxa (mostly after M_1) in % (after PAUNOVIĆ & RABEDER, 1996).

- the determination of the genera *Lagurus* (type *arankae*) and *Mimomys* (species *pusillus* and *savinii*) favour a Lower Pleistocene age. At the same time the metrical data and molar morphotypes of the genus *Lagurus* (Fig. 2), as well as the genus *Pliomys* (Fig. 3) indicate that the fauna from Razvođe (Lower Early Pleistocene) is older than the fauna from Tatinja draga (Middle Early Pleistocene), which is somewhat older than the fauna from Podumci (Late Early Pleistocene) (Table 3; PAUNOVIĆ & RABEDER, 1996).

Taxa	Early Pleistocene Lower Razvođe	Middle Tatinja draga	Late Podumci	recent Balkan peninsula
Episoriculus	*thenii*	*thenii*	*thenii*	-
Reteliomys	-	-	*podumcensis*	-
Allocricetus	*croaticus*	(*bursae*)-	(*bursae*)-	-
Apodemus mystacinus	*epimelas*	*epimelas*	*epimelas*	*epimelas*
Microtus	(cf. *praehintoni*)	*eoratticeps*	*thenii*	(div.sp)
Mimomys	*malezi*	*malezi*	*malezi*	-
Dinaromys	-	*dalmatinus*	*dalmatinus*	*bogdanovi*
Pliomys	(*simplicor*)	*bolkayi*	*bolkayi*	-

Table 3 Geochronological dispersal of endemic taxa (after PAUNOVIĆ & RABEDER, 1996).

4.2. TEETH AND METAPODIAL BONES OF THE CAVE BEARS (*Ursus spelaeus* ROSENM. & HEINROTH)

In contrast to the uniform incisors, the premolars and molars (4787 from Vindija, 4356 from Velika pećina and 1682 from Veternica) of a cave bear clearly showed in preliminary analyses a great variability in crown morphology, particularly the repetition of similar or the same elements, morphotypes that appear with variable frequency in deposits of different ages. Such morphological changes can be traced from simple (primitive) morphotypes which predominate in older deposits to distinctly complicated (evolved, specialised) morphotypes predominating in younger sediments. This, together with differences from premolars which show characteristic molarisation processes (RABEDER, 1983), the molars show the reduction of the primary elements of the crown followed by multiplication of secondary ones (PAUNOVIĆ, 1988).

The analyses of odontological material from deposits in the Vindija cave yielded data on rapid functional-morphological (microevolutionary) changes which are visible in growth of lenght parameters (Fig. 4), namely the ever increasing percentage of evolved morphotypes (Fig. 5) in the younger sediment sequences. In the oldest complex (Riss, Riss/Würm) there is variation with a high percentage of more primitive (deningeroid) characteristics that probably represents a transitional form in a phyletic lineage *Ursus deningeri* - *Ursus spelaeus* while the typical representative of the *spelaeus*-group is characteristic for deposits of Würmian age (PAUNOVIĆ, 1988).

The morphogenetic schemes of premolar-molar teeth series of the cave-bear from Velika pećina, found in the depositional sequence interpreted as representing the Interglacial Riss/Würm (MALEZ, 1986), are characterised by a low percentage of primitive (deningeroid) morphotypes (Fig. 5). These sediments were probably deposited during the Würm (Early Würm), as the rest of the fauna from this sequence does not show any distinct characteristics of an interglacial period (PAUNOVIĆ, 1988).

Similar results were obtained from the material from Veternica cave with a predomince of more evolved morphotypes and dimensions larger than the average values of the typical *Ursus spelaeus*. Considering that the frequency of the appearance of higher evolved morphotypes (Fig. 5) corresponds to the frequency from younger sequences of Vindija cave and also to the morphotype schemes from Velika pećina, these results indicate that the oldest deposits in Veternica cave were laid down during the Early Würm, but not during the Interglacial Riss/Würm (PAUNOVIĆ, 1991). This assumption was confirmed by the results of the revision of the ungulate fauna (MIRACLE & BRAJKOVIĆ, 1992).

In accordance with the assumption that microevolutionary changes also affected the postcranial skeleton, morphometric studies have been continued on 8,267

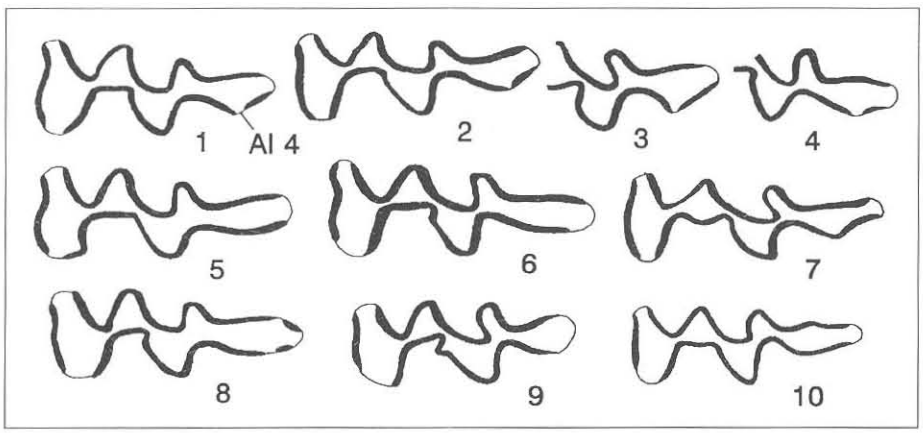

Fig. 2 Morphotypes of M^3 belonging to *Lagurus* from Podumci (from MALEZ & RABEDER, 1984, p. 477, Fig. 28): 1-4 Morphotype "*arankae*"; 5-7 Morphotype "*pannonicus*"; 8-10 rare particular forms

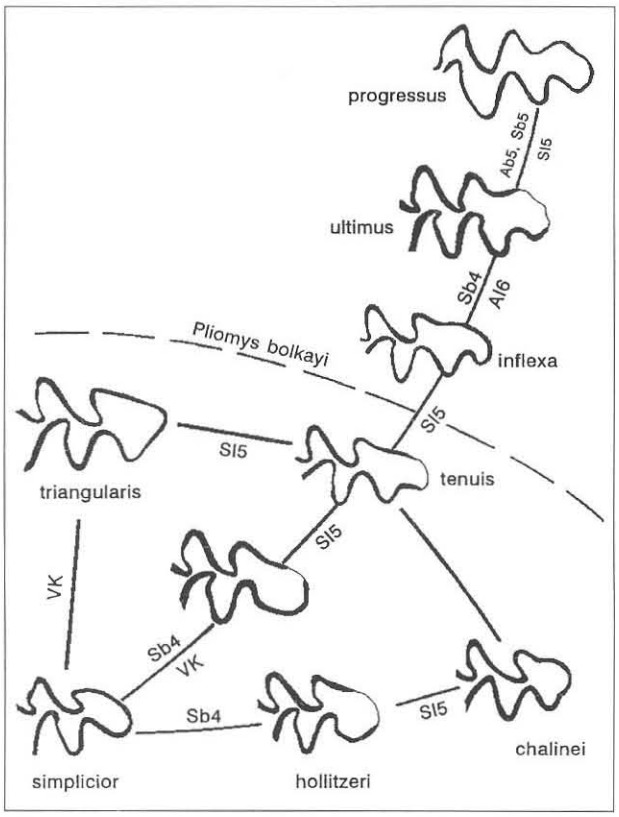

Fig. 3 Morphotypes of M_1 belonging to *Pliomys* from Podumci. Morphotypes *inflexa*, *ultimus*, *progressus*, *chalinei* defined by secondary elements (from MALEZ & RABEDER, 1984, p. 482, Fig. 32).

metapodial bones of cave bears from Vindija cave (Fig. 6). Morphogenetic studies showed that changes are the most distinct in the morphology of the proximal epiphysis of the first metacarpal, namely metatarsal bones and descriptive statistics showed that the most characteristic length and width parameters of the proximal joint surface is shorter and wider in older layers, and longer and narrower when found in younger levels (PAUNOVIĆ et al., 1997). Morphometric and morphogenetic study of the material from Velika pećina and Veternica caves is still in progress.

5. CONCLUSION

This short review of previously published results of morphometric and morphogenetic studies indicates the need for analyses of the Pleistocene vertebrates from other localities in Croatia, with the aim of determining changes in every studied population, species or fauna, and the causes of their occurrence and evolutionary processes. In other words, only the correlation of results of such investigations followed by geological, sedimentological and other various analyses shall enable the establishment of a uniform biostratigraphy of Pleistocene deposits in Croatia, and simultaneously solve the dilemma of which Quaternary subdivision to use in practice, especially for the Upper Pleistocene.

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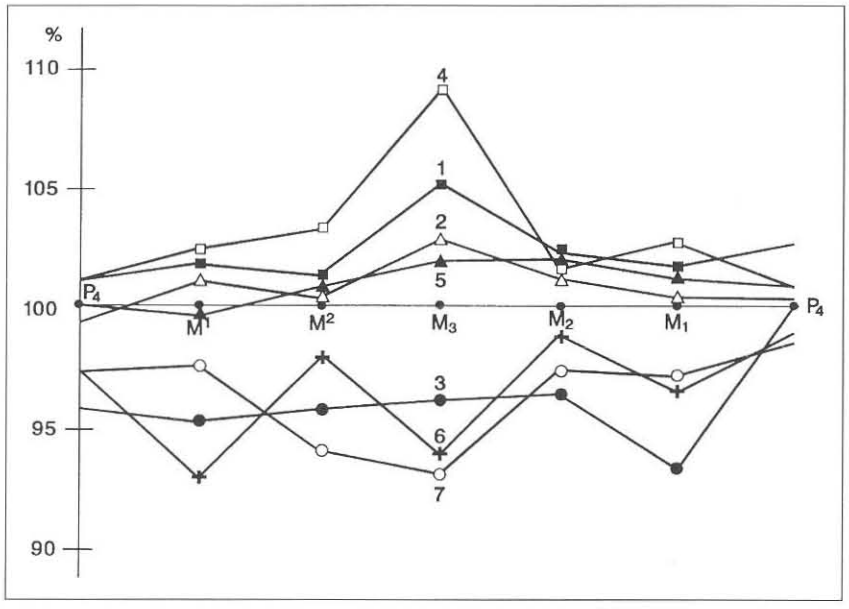

Fig. 4 Correlation of premolar-molar lengths (%) with mean values (100%) characteristic for typical *Ursus spelaeus* (after PAUNOVIĆ, 1988): 1) Velika Pećina; 2) Vindija J-D; 3) Vindija M-L-K; 4) Mixnitz; 5) Merkenstein; 6) Herdengehöhle; 7) Ramesch.

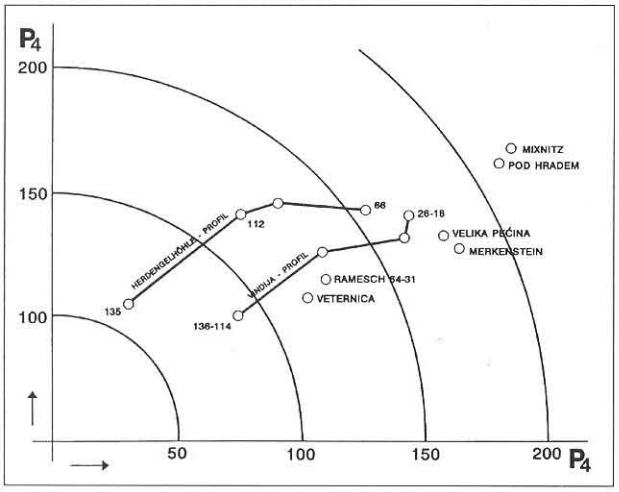

Fig. 5 Evolutionary scheme of cave bear premolars based on the morphodynamical index: I = Frequency of morphotype (%) x coefficient of evolution x 100 (after PAUNOVIĆ et al., 1997).

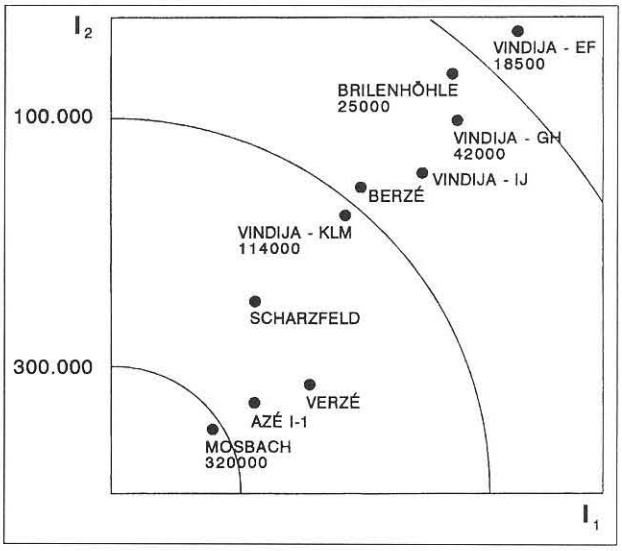

Fig. 6 Evolutionary scheme of the cave bear Mt3 based on the indices: I_1 = length x 100 / width of diaphysis, I_2 = length x 100 / width of distal end (after PAUNOVIĆ et al., 1997).

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