# Evolutionary shifts in the first premolar pattern of *Hypolagus* beremendensis (PETÉNYI, 1864) (Lagomorpha, Mammalia) in the Plio-Pleistocene of Central Europe

Florian A. FLADERER and Gerhard REINER

Accepted for publication: 28 Feb., 1995

FLADERER F. A., REINER G. 1996. Evolutionary shifts in the first premolar pattern of *Hypolagus beremendensis* (PETÉNYI, 1864) (Lagomorpha, Mammalia) in the Plio-Pleistocene of Central Europe. Acta zool. cracov., **39**(1): 147-160.

Abstract. The abundant material of leporids from the karst infills near Deutsch-Altenburg, lower Austria, dating from the Middle Pliocene to the Early Pleistocene allowed us to study the variability of the first premolars ( $P^2$ ,  $P_3$ ) of *Hypolagus beremendensis*. The morphological variation shown by means of morphotypes, morphogenetic schemes and frequency diagrams is interpreted as the result of microevolutionary change. Biostratigraphic applicability is demonstrated by comparison with leporid remains from Polish, Czech, Slovakian and Hungarian sites. Some other morphological features of the cranial and postcranial skeleton also document the transition from the older *H. beremendensis beremendensis* (MN14 – lower part of MN 17) to the younger *H. beremendensis brachygnathus* (MN 17 – early Middle Pleistocene).

Key words: Pliocene, Pleistocene, Lagomorpha, Poland, Austria, Czech Republic, Slovakia, Hungary.

Florian A. FLADERER, Gerhard REINER, Institut für Paläontologie, Universität Wien, Universitätsstraße 7/II, A-1010 Wien, Austria.

### I. INTRODUCTION

Remains of the archaeolagine leporid genus *Hypolagus* DICE, 1917 of Plio-Pleistocene age are fairly well-known in Central Europe. Pioneer work on this taxon has been carried out on the rich material from the Carpathian basin by KORMOS (1934), closely followed by SCHREUDER (1937), who concentrated on the finds from the Tegelen clay in Western Europe. The first evidence in Central Europe comes from Lower Pliocene layers. Right up until its extinction in the lowermost Middle Pleistocene, remains of *Hypolagus* are regarded as belonging to *H. beremendensis* (PETÉNYI, 1864). The synonym *H. brachygnathus* KORMOS, 1934 is often used but is considered invalid (KRETZOI 1962; JÁNOSSY 1963).

The most detailed studies were carried out by Polish authors. Special attention was paid to the abundant remains of leporids from Węże 1, Rębielice Królewskie 1, Kadzielnia 1 and Kamyk, dating from the Middle Pliocene to Early Pleistocene (KOWALSKI 1958a, 1960; SULIMSKI 1964). SYCH's (1965) survey of fossil Leporidae from the Pliocene and Pleistocene of Poland is regarded as an extraordinarily detailed monographic work on *Hypolagus beremendensis*. On the basis of a critical revision of remains assigned to the genus *Pliolagus* (KORMOS 1934; KRETZOI 1941;

KOWALSKI 1958a) it is stated that they are juvenile stages of individual development of this *Hypolagus* species (SYCH 1965). It is recognized as the only leporid species besides *Lepus* and *Pliopentalagus* in the Plio-Pleistocene of Central Europe (The Middle Pliocene *Pliopentalagus dietrichi* [FEJFAR, 1961] from Ivanovce is the westernmost and northernmost evidence of a second archaeolagine species [DAXNER & FEJFAR 1967]). SYCH's monograph was followed by continuing investigations on morphologic features of *H. beremendensis* (SYCH 1966, 1967a, 1967b; CZYŻE-WSKA 1985). Overviews of the fossil Lagomorpha of Poland are given by SYCH (1980) and WOLSAN (1989). Further treatment of Central European finds of *Hypolagus* from Germany (KOENIGSWALD 1974), Czechia and Slovakia (e. g., FEJFAR 1961; MUSIL 1966; TOBIEN 1972), Hungary (JÁNOSSY 1986) and Dalmatia (KOWALSKI 1958b; MALEZ 1961) preceded the first investigations of Austrian material. A first contribution (FLADERER 1984) emphasized the forelimb morphology of *H. beremendensis* and of contemporaneous *Lepus* sp. and supplemented the results obtained by SYCH (1965).

A c k n o w l e d g m e n t s. We thank Prof. Dr. O. FEJFAR and Drs. I. HORÁČEK, D. JÁNOSSY, L. KORDOS, A. NADACHOWSKI, and L. SEITL for help in providing us with material from their institutions. We are grateful to Prof. Dr. G. RABEDER and the Fonds zur Förderung der wissenschaftlichen Forschung in Österreich (FWF project no. 9320 GEO [Pleistozäne Faunen von Österreich]) for financial support.

### II. MATERIAL

The fissure fillings and cave deposits from Deutsch-Altenburg ranging between MN 15 and Early Pleistocene (MAIS & RABEDER 1984, RABEDER 1981) have yielded rich material of *H. beremendensis* on which to define the morphotypes of the species. As a second step, it was compared with material from the Carpathian Basin (FLADERER 1987). The supplementing and corresponding results of the study of the postcranial skeleton characters of *H. beremendensis* from Poland (SYCH 1965) reinforced the results of the comparison of dental features from the same sites.

The following institutions provided us with material: Institute of Palaeontology, Universität Wien, Austria (PIUW); Geological and Paleontological Department of the Natural History Museum, Budapest (NHMB) and Hungarian Geological Institute, Budapest (HGIB), Hungary; Geological Institute, Praha (UUGP), Department of Quarternary, Czech Academy of Sciences, Institute of Geology and Geotechnics, Praha (UGAP) and Moravské muzeum, Geological and Paleontological Department, Brno (MMGB), all Czech Republic; Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland (ISEK).

The number of examined teeth and the localities from which they were obtained are listed in Table I: The taphocoenoses from which *H. beremendensis* remains were derived are fairly well studied. For comparison we use the biochronological interpretions summarized for most sites in HORÁČEK & LOŽEK (1988). Differences that exist between the interpretations of these and other authors (e. g., RABEDER 1981) result mainly from different dating concepts. The problems of the assemblage zone concept emerging from the difficulties in defining the zone boundaries are well known but not a topic of this paper.

### **III. METHODS**

Morphotype dentition analysis as introduced into arvicolid phylogenetics (see NADACHOWSKI 1991; RABEDER 1981) has been applied to *H. beremendensis* in a previous paper (FLADERER 1987). ERBAJEVA & ANGERMANN (1983) took a similar approach to *Serengetilagus praecapensis* DIETRICH,

## Table I

Hypolagus beremendensis mate	rial studied in this p	paper, $P^2$ - und P <sub>3</sub> -indices of	
some samples. Zones - biozones	after HORÁČEK &	LOŽEK 1988. For further	
information see text			

Site	Z	Cones	References	Collection	Hypolagus beremendensis n P <sup>2</sup> : n P3	P <sup>2</sup> - Index	P <sub>3</sub> - Index
Stránská skála 2 (Cave)	CZ	Q 3	Horáček & Ložek 1988	MMGB	0:1		
Mladeč 3	CZ		Horáček & Ložek 1988	UGAP	0:1		
Kövesvárad Stránská skála 1	H CZ	Q 2	Jánossy 1963, Fladerer 1987 Tobien 1972	NHMB MMGB	0:1 2:3		
Mladeč 1 Holštejn Chlum 6 Dautsch, Altonhurz	CZ CZ CZ	Q 1	Horáček & Ložek 1984, 1988 Musil 1966 Fejfar & Horácek 1983	UGAP MMGB UUGP	1:2 6:16 0:10	383	282 255
4B	Α	in an	MAIS & RABEDER 1984, FLADERER 1984, 1987	PIUW	26:43	357	272
Deutsch-Altenburg 2C1	A		Mais & Rabeder 1984, Fladerer 1984, 1987	PIUW	137:232	334	283
Deutsch-Altenb. 22	A		RABEDER 1981	PIUW	5:4		
Deutsch-Altenb. 30A	A		MAIS & RABEDER 1984, FLADERER 1984	PIUW	5:4		
Včeláre 4	SK		Horáček 1985	UGAP	2:9		
Kamyk	P		Kowalski 1960, Sych 1965	ISEK	99:197	223	217
Mokrá 1	CZ		Fejfar & Horáček 1983	UGAP	0:1		
Villány 3	Н	MN 17	Kormos 1934, Kretzoi 1956, Fladerer 1987	HGIB	0:1		
Kadzielnia 1	P		Kowalski 1958a, Sych 1965	ISEK	45:70	196	120
Včeláre 5	SK		Horáček 1985	UGAP	2:1		
Včeláre 7	SK		Horáček 1985	UGAP	1:0		
Včeláre 3	SK		Horáček 1985	UGAP	1:2		
Koliňany 1	SK		Fejfar & Horáček 1983	UGAP	0:1		
Deutsch-Altenburg 9,20,21	Α	MN 16	Fladerer 1987, Rabeder 1977	PIUW	8:7		
Rebielice 1	Р	distant of	Kowalski 1960, Sych 1965	ISEK	20:19	130	121
Hajnáčka 1	SK		Fejfar 1961, 1964	UUGP	1:2		
Zamkowa Dolna Cave C	Р	?MN 15	Sych 1980, Wolsan 1989	ISEK	0:3	Factory)	
Węże 1	Р	MN 15	SULIMSKI 1964, SYCH 1965	ISEK	37:56	105	102
Ivanovce 1	SK		Fejfar 1961	UUGP	2:1	100	102
Csarnóta 1,3	Н		Kretzoi 1956, 1962, Fladerer 1987	HGIB	2:4	0.500	

1941 from the Upper Pliocene of East Africa. The variability observed in the material is grouped into morphological classes (Figs. 1, 2). The morphotypes are arranged in a scheme which corresponds to the functional aspect of the character. To quantify the classes the steps are evaluated: the more advanced the class character the higher the multiplicatory factor. The frequencies of the classes are multiplied by the factor to obtain the morphodynamic index (Table II). Transitional forms are included in the higher class with the exception of the transition between trigonid classes I and II. The morphodynamic indices of the first upper and first lower premolar of one sample are plotted on a diagram that reflects the evolutionary change between the samples. It is very probable that the morphotype scheme has to be supplemented or even modified in the light of further research on the genus.

The drawings in the paper as well as the identifications were made using a binocular microscope. The orientation of the examined tooth must be strictly normal to the axis at the point of the



Fig. 1. Hypolagus beremendensis, Plio-Pleistocene of Central Europe, morphodynamic scheme of the P<sub>3</sub>. The morphotypes are arranged in classes according to the two characteristic features: (1) the shape of the trigonid (Trig-types I-V), (2) the major buccal reentrant angle (MBR-types A-E). The steps are marked by arrows. Arabic numerals indicate the evaluation of the evolutionary step. It is used as a multiplicatory factor to compute the morphodynamic index. The mesial and mesiolingual concavities are counted as equivalent (factor 3). The variation in the buccal talonid wall is grouped into 5 classes (Tal-types a - e) (after FLADERER 1987, modified). I (from below): DA 21/5/4, We-6, DA 20/9/6, DA 9/3/4, Kad-46; I/II: We 61, DA 30/12/9, Reb-10, DA 21/5/3, DA2C1/68/27; II: DA 2C1/68/36, DA 2C1/68/7, DA2C1/68/168; III: DA2C1/68/178, DA2C1/68/173, DA2C1/68/213, DA2C1/68/188.

-						-
11	9	h		0		
1	а	υ	T	U	. 1	T

H. beremendensis, Plio-Pleistocene, Poland and Austria. Frequencies of P<sub>3</sub> morphotypes

P3 trig-type	Węże	Rębielice Królewskie 1	Kadzielnia 1	Kamyk	Deutsch- Altenburg 2C1	Deutsch- Altenburg 4B
I	96.4	68.4	68.6	0.5	_	-
I/II	3.6	21	22.6	12.2	5.2	9.3
II	1000 <u>-</u> 0000	10.6	8.6	73.6	31.9	37.2
III	_	-	-	4.1	18.1	11.6
IV	-	-	-	9.1	22	18.6
v	-	-	-	0.5	22.8	23.3

plane of observation. Measurements (length, width) have been taken on every tooth using an electronic caliper square. In isolated teeth two pairs of measurements were taken near the grinding surface as well in the root area.

Attention has been paid to nondental and postcranial distinctive characters to corroborate the results. For mandible measurements see Table IV.

Variation in the P3 pattern (after FLADERER 1987, slightly modified) Trigonid types (differentiation of the trigonid):

I – short, triangular trigonid; the mesio-distal length of the trigonid is approximately the same as its width

I/II - transitional type - same as type I, but the length of the talonid is greater than its width

II – enlargement of the mesial margin

III - same as type II, but a concavity is developed on the mesial margin

IV – same as type II, but an anterior lingual groove is developed

V - same as type III, but an anterior groove is also developed.

MBR-types (differentiation of the major buccal reentrant angle):

A – simple MBR with uncrenulated enamel

B – the distal side of the MBR is undulated or crenulated

C – the thick mesial side of the MBR slightly bent into a thin continuation

D - the thick mesial side of the MBR slightly bent into a thick continuation

E – the lingual portion of the MBR is crenulated and islets are possible.

Talonid-types (differentiation of the buccal talonid margin):

a - beremendensis-edge: the bucco-distal part of the MBR forms an edge

b – bilobate talonid: a groove is developed

c - concave talonid: the mesio-buccal margin of the talonid is concave

d – great length of the buccal margin; no concavity or groove is developed

e – same as type d, but the length of the buccal margin is smaller. Therefore the MBR shows a broad gap.

Variation in the  $P^2$  pattern

LL-types (differentiation of the mesial margin of the lingual lobe; depth of the lingual mesial reentrant angle):

I – well rounded lingual lobe

II – lingual lobe with flattened or straight margin

III – slightly concave margin

IV - shallow but distinct LMR

V – short u-shaped LMR

VI - deep LMR (this is the also the primitive stage of Lepus!).

BMR-types (differentiation of the mesial margin of the buccal rhomboid; depth of the buccal mesial reentrant angle):

0 – no BMR

A – shallow BMR

B - distinct BMR.

F. A. FLADERER , G. REINER



Fig. 2. *Hypolagus beremendensis*, Plio-Pleistocene of Central Europe, morphodynamic scheme of the P<sup>2</sup>. The morphotypes are arranged in classes according to (1) the shape of the lingual lobe (LL-types I - V) and (2) depth of the buccal mesial reentrant angle (BMR-types). Arabic numerals indicate the multiplicatory factor. LL-type VI is typical P<sup>2</sup> of Early Pleistocene *Lepus* sp. I (from below): DA20/9/1, We-19, Kad-1; II: Kad-2, Kad-3; III: DA4B/68/20, Kad-5; IV: DA2C1/67/774, DA2E//1; V: DA4B/68/39; VI: DA2C1/67/811, DA4B/68/53.

### **IV. RESULTS**

The measurements – taken from all teeth – showed no significant distinctions between the samples. The ratio of length and width is also very variable in the ontogeny of a single tooth.

The frequencies of the morphotypes of *H. beremendensis* from Węże, Rębielice Królewskie, Kadzielnia, Kamyk and Deutsch-Altenburg 2C1 and 4B are shown in Fig. 3 and Table II. The comparison with samples from different localities from MN 15, MN 16, and MN 17, and the Biharian corroborates the results (Fig. 4).

The most distinct character of *H. b. beremendensis* (PETÉNYI, 1864) is the edged margin of the talonid (*beremendensis*-edge, FLADERER 1987) associated with trigonid type I (Fig. 3-4, pie diagrams). Morphotypes III to V are not observed. Only morphotypes I and II are seen in the  $P^2$ 

Table III

*H. b. brachygnathus*, Deutsch-Altenburg 2C1. How to compute the morphodynamic index of the first lower premolar

Site	Position	Trigonid type	Multiplicatory factor	n	%	Product
DA 2C1	P3	I	1	1	0.7	0.7
	Gidlen aprovati	II	2	27	19.7	39.4
		III	3	50	36.5	109.5
		IV	4	43	31.4	125.6
		V	5	16	11.7	58.5
				137	100.0	333.7





# Evolution of premolar pattern in Hypolagus beremendensis

153



Fig. 4. For explanation, see Fig. 3.

(Fig. 8). This subspecies, whose type locality is Beremend in southern Hungary, has a significant presence from MN 14 to the lower part of MN 17.

In *H. b. brachygnathus* KORMOS, 1934 morphotypes I are very rarely observed in  $P^2$  and in P<sub>3</sub> (Fig. 7). The holotype is a mandible from Villány 3 with a P<sub>3</sub> of I/IIDd-morphotype (FLADERER 1987, Abb. 8a). The subspecies arose from *beremendensis*-populations in late MN 17 and is the end form of the genus in Europe.

### V. DISCUSSION

Nondental characters in the beremendensis-brachygnathus lineage

The increase in body size of the species from the middle Pliocene to the Early Pleistocene is regarded as an adaptation to climatic changes in keeping with BERGMANN's rule (SYCH 1965). In the mandible one may observe a clear difference between the uniform range of Węże, Rębielice and Kadzielnia and the range of Kamyk, which reflects a distinct difference in the shape of the muzzle. The mandibles from the Biharian sites are dorso-ventrally narrower than those of the MN



Fig. 5. The lineage *H. beremendensis beremendensis* – *H. b. brachygnathus*, Plio-Pleistocene of Austria, Czechia and Poland. The morphodynamic indices are formed by the sums of the products of the frequency of x-classes (I-V) of  $P^2$  and  $P_3$  and the multiplicatory factor (see Table III, Figs. 2-3).

15-MN 17 sites and the facial part of the skulls has undergone a lengthening during the same time period (Table IV). The similarity to the facial morphology of *Lepus* can be seen in SYCH (1965, Table 2b), but no comments are given by that author.

Study of postcranial features using the large samples from Poland (SYCH 1965) provided data that confirm the results of the morphodynamic analysis. However, this author emphasized the differences between fossil *Hypolagus* and recent species and not the differences between the fossil samples. The conclusion that *H. beremendensis* from Kamyk and the Austrian Early Pleistocene sites was better adapted to cursoriality than the Pliocene form can be reached from the measurements and ratios in SYCH (1965) and FLADERER (1984 and unpublished data). Some of these features are: (1) The coraco-glenoid distance is short relative to the length of the glenoid cavity, (2) the great height of the medial crest of the distal humerus, (3) dorso-ventrally wider olecranon, (4) short dorso-ventral diameter of the distal radius, (5) medio-laterally flattened shaft of femur, (6) medio-laterally narrow calcaneus with long tuber.



Fig. 6. H. b. beremendensis, P<sub>3</sub>, Upper Pliocene from Poland (Węże 1, Rębielice Królewskie 1, Kadzielnia) and Austria (Deutsch-Altenburg 20). Partly inverted, scale bar is 3 mm. 1: We-8 (IAa), 2: We-9 (IBa), 3: We-11 (IBa), 4: We-7 (IBb), 5: We-4 (IBb), 6: We-86 (ICb), 7: We-89 (I/II Db), 8: Re-5 (ICa), 9: Re-12 (IIAa), 10: DA20/9/7 (IIAa), 11: Kad-42 (IBa), 12: Kad-62 (IBa), 13: Kad-16 (ICa), 14: Kad-8 (ICa), 15: Kad-5 (ICa), 16: Kad-14 (I/IIDa), 17: Kad-43 (brachygnathus-morphotype IIBb). 18: H. b. brachygnathus from Koliňany, Slovakia (I/IIAd).



Fig. 7. H. b. brachygnathus, P<sub>3</sub>, Early Pleistocene from Poland (Kamyk), Czechia (Chlum 6, Stránská skála 1, Holštejn) and Austria (Deutsch-Altenburg 2C1). Morphotype VII (anterior lingual reentrant angle ALR) is not yet formally defined in Fig. 1 and the text. 1: Km-165 (IIIAc), 2: Km-175 (IVCc), 3: Chlum 6553/9 (IIBd), 4: Chlum 6553/7 (IIIAc), 5: Str 1941/2545 (IIICd), 6: Hol-12 (I/IIAd), 7:Hol-25 (I/IIDb), 8: Hol-13 (IVAd), 9: Hol-14 (VIIAd), 10: DA2C1/67/101 (I/IIBc), 11: DA2C1/67/69 (I/IICc), 12: DA2C1/67/221 (IIIBd), 13: DA2C1/67/178 (IIIDc), 14: DA2C1/67/222 (IIIDd), 15:), 15: DA2C1/67/164 (IVAd), 16: DA2C1/67/137 (IVBb), 17: DA2C1/67/217 (VCc, atavistic main lingual reentrant angle), 18: DA2C1/67/145 (VIIDc). Size see Fig. 6.



Fig. 8. *H. beremendensis*, P<sup>2</sup>, Upper Pliocene to Early Pleistocene from Poland (Węże 1, Kadzielnia), Czechia (Holštejn), Austria (Deutsch-Altenburg) and Hungary (Villány 3). Size as in Fig. 7. 1: We-44 (IA), 2: We-42 (IB), 3: We-17 (IA), 4: We-23 (IA), 5: DA20/9/4 (IB), 6: Vill-Ob3691 (IIB), 7: Kad-4 (IIIB), 8: DA21/1/1 (IB), 9: DA2C1/67/680 (IB), 10: DA2C1/67/737 (III/B), 11: DA2C1/67/679 (IIA), 12: DA2C1/67/756 (aberrant IIIB), 13: DA2C1/67/725 (13a:occlusal, 13b radical, IIIA), 14: DA2C1/67/766 (IVA), 15: DA2C1/67/787 (IVB), 16: DA2C1/67/781 (VB), 17: DA2C1/67/713 (aberrant IIIA), 18: DA4B/69/36 (IVA), 19: Hol-6 (IVA). Size see Fig. 6.

### Table IV

*H. beremendensis* from Poland and Austria. Mandible measurements, in part after SYCH (1965). Measurements and abbreviations: Length of diastema, LD – distance between the posteriormost point of the alveolus of the incisor and the anteriormost point of the alveolus of P<sub>3</sub>. Height of the mandible HM – measured between the P<sub>4</sub> and M<sub>1</sub> on the lingual side. o. r. – observed range

		Węże	Rębielice	Kadzielnia	Kamyk	Deutsch- Altenburg 2C1	Deutsch- Altenburg 4B
LD	М	16.07	16.45	16.93		18.12	18.35
	n	11	5	7		16	4
	o.r.	15.2-17.5	15.5-17.5	15.7-17.5	19.0-20.8	16.6-21.0	16.3-19.5
HM	M	14.49	15.21	14.90	15.12	14.83	14.50
	n	13	14	14	9	16	5
	o.r.	14.0-16.3	14.8-15.9	14.6-15.7	14.9-15.3	13.2-15.7	13.8-15.0

Paleoecological interpretation

In the assemblages from Csarnóta 1 and 3, Ivanovce and Węże (MN 15) dense vegetation is indicated by the presence of Petauristinae and Gliridae (SULIMSKI 1964; FEJFAR & HEINRICH 1985; JÁNOSSY 1986). These localities provide the first clear evidence of Hypolagus in the regions concerned. However, it is very probable that the rare leporid remains from Osztramos 1 (JÁNOSSY 1986) and Podlesice (KOWALSKI 1964; SYCH 1980), dated to MN 14, belong to the same species. The MN 16 localities of Deutsch-Altenburg (DA 9, DA 20), situated close to the Danube, yielded Desmana, Sciurus and Apodemus (MAIS & RABEDER 1977; RABEDER 1977). The presence of numerous amphibians and Desmana indicate that the fauna of Rebielice Królewskie also represents a humid climate. The time span between late MN 16 and early MN 17 is characterized as a relatively warm and humid period with diversified wood cover (HORÁČEK & LOŽEK 1988). Taphocoenoses from MN 17 are in general different. The faunal spectrum from Kadzielnia Hill, although it may comprise several levels from MN 17 to Early Biharian (BOCHEŃSKI 1993; NADACHOWSKI et al. 1989), indicates the presence of forests along with open areas: Lemmus and some cricetid species appear for the first time. Glis and Muscardinus are present, but tree squirrels and flying squirrels are absent (NADACHOWSKI 1989). The type locality of H. brachygnathus KORMOS, 1934, Villány 3, as well as the Včeláre complex (Vc 3/3, 5, 7) (HORÁČEK 1985) show the same greatly diversified character. The climate became similiar to but slightly dryer than the present one (KOWALSKI 1989). The dental pattern of *H. beremendensis* from these localities shows increased variability.

In the lowermost Biharian, steppelike environments seem to have expanded. In Kamyk only *Glis sackdillingensis* suggests the presence of forests (KOWALSKI 1960). By this time, *Hypolagus* has reached an advanced level of variability. The analysis of cranial as well as postcranial features of the abundant *Hypolagus* material (SYCH 1965) demonstrates a clear shift to *Lepus*-like features. In Deutsch-Altenburg 30A glirids and *Sciurus* are absent and in DA 2C1 very rare. The snails reflect a dry forest-steppe habitat (MAIS & RABEDER 1984). In the lagomorph record of Central Europe the Betfia-phase is characterized by a rapid expansion of *Lepus*. The ratio *Hypolagus:Lepus* in DA 2C1 is 70:1 (FLADERER 1987) whereas no *Lepus* is reported from Kamyk. In the slightly younger assemblages we see a distinct difference that may result from facies or environmental differences: DA 4B (1:1) and Chlum 6 (1:4) yielded taphocoenoses that indicate less dense vegetation (MAIS & RABEDER 1984; FEJFAR & HORÁČEK 1983) than the taphocoenosis from Holštejn, where *H. beremendensis* is very abundant, with 16 P3 of *H. beremendensis* are as against 4 from *Lepus*. The high percentage of woodland forms in the association (e. g., *Capreolus süssenbornensis, Sus scrofa priscus, Meles meles*; MUSIL 1966) reflects the same environmental

particularity. The presence of open ground vegetation in the vicinity is indicated by the presence of *Ochotona* sp. The first appearence of *Lepus* in Poland is documented, together with the last of *Hypolagus*, in the uppermost Lower Biharian site Zalesiaki (WOLSAN 1989).

Setting in relation the varying ratios of occurrence of *Hypolagus* and *Lepus* to the ecological character of the assemblages, one has to conclude that they reflect the species different habitat requirements. In the lower part of the Upper Biharian (Middle Biharian sensu RABEDER 1981) *Lepus* becomes the dominant genus. An even ratio between *Hypolagus* and *Lepus* can be observed at Stránská skála 1, but this highly diversified community may be the result of a mixing of layers of slightly different ages (TOBIEN 1972). In many taphocoenoses from the Upper Biharian the frequency of steppe and forest-steppe species increased. In the Slovakian site Žirany, *Lepus* is very common and the only leporid. The predominance of *Lagurus pannonicus* in the arvicolid assemblage may be regarded as an indication of a steppe environment (BARTOLOMEI et al. 1975). On the other hand, the presence of *Hypolagus* and the absence of *Lepus* in Kövesvárad (JÁNOSSY 1963) can be explained by the pronounced wet- and woodland aspect of the taphocoenosis. The occurrence of *Triturus* and the abundance of Gliridae and *Clethrionomys* here coincides with a scarcity of steppe elements. The early Upper Biharian site Podumci in Dalmatia yielded rare leporids (KOWALSKI 1958b, MALEZ & RABEDER 1984). This forest-steppe taphocoenosis includes a VAc-type *H. b. brachygnathus* P<sub>3</sub> and a *Lepus* sp.

Data on the question of the extinction of *H. beremendensis* in Europe can be supplemented by the evidence from Stránská skála 2 (Cave) (one P<sub>3</sub> of IIIAd-type) and Mladeč 3 (one P<sub>3</sub> of IVAc-type). The fossil fauna of the former has not yet been published, but according to information in the literature, a lowermost Middle Pleistocene age is very probable (HORÁČEK & LOŽEK 1988). Layers 2 and 3 in Mladeč cave with *Sciurus* sp. and *Rhinolophus hipposideros* are interpreted as belonging to an interglacial of the early Middle Pleistocene (HORÁČEK & LOŽEK 1984).

### VI. CONCLUSIONS

The significant changes in tooth pattern, with its phyletic change from *H. b. beremendensis* to *H. b. brachygnathus* between Kadzielnia and Kamyk, seems to be correlated with a change from a fairly mild climate with forest vegetation to a temperate climate with less moisture (KOWALSKI 1964).

In the *H. beremendensis beremendensis* - H. *b. brachygnathus* lineage we observe (1) an increasing complexity of the premolar pattern, (2) a lengthening of the mandible and the forehead, and (3) some postcranial characters that show a tendency towards greater efficiency of sagittal limb movement.

The tendencies are interpreted to be adaptations peculiar to the *beremendensis-brachygnathus* lineage, evolved as a response to the changing environmental conditions from Pliocene woodland to increasing open-ground vegetation towards the Lower Biharian. The fluctuating range restrictions of the woodland in the Early Pleistocene enabled the spread or immigration of open habitat species like *Lepus*.

*H. beremendensis* reached its greatest areal extent in the earliest Pleistocene as indicated by reports from England (MAYHEW 1975). From the Lower Biharian (Q 1) the frequency of the species decreases as the evidence of the sympatric *Lepus* species increases. Forest-steppe habitats in the Moravian karst upland seem to have been the early Middle Pleistocene refugia of the last *H. b. brachgnathus* populations in Europe.

With regard to the general trends in the genus, the presence of advanced *brachygnathus*-types in the Upper Pliocene of the eastern Holarctic documents either geographic range shifts or heterochronic changes in the characters (see, e. g., the P<sub>3</sub> of IIDd-type in *H. regalis* HIBBARD, 1939 in FEJFAR 1961: Abb.6).

### REFERENCES

- BARTOLOMEI G., CHALINE J., FEJFAR O., JÁNOSSY D., JEANNET M., KOENIGSWALD W. V., KOWALSKI K. 1975. *Pliomys lenki* (Heller 1930) (Rodentia, Mammalia) en Europe. Acta zoologica cracoviensia, **20**: 393-467.
- BOCHEŃSKI Z. 1993. Catalogue of fossil and subfossil birds in Poland. Acta zoologica cracoviensia, 36: 329-460.
- CZYŻEWSKA T. 1985. Natural endocranial casts of *Hypolagus brachygnathus* KORMOS, 1934 (Leporidae, Lagomorpha) from Węże I near Działoszyn (Poland). Acta zoologica cracoviensia, **29**: 3-12.
- DAXNER G., FEJFAR O. 1967. Über die Gattungen Alilepus DICE, 1931 und Pliopentalagus GUREEV, 1964 (Lagomorpha, Mammalia). Annalen des Naturhistorisches Museums in Wien, **71**: 37-55.
- ERBAJEVA M., ANGERMANN R. 1983. Das Originalmaterial von *Serengetilagus praecapensis* DIETRICH, 1941 ergänzende Beschreibung und vergleichende Diskussion. Schriftenreihe für geologische Wissenschaften, **19/20**: 39-60.
- FEJFAR O. 1961. Die plio-pleistozänen Wirbeltierfaunen von Hajnáčka und Ivanovce (Slowakei). ČSSR. III. Lagomorpha. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **5**: 267-282.
- FEJFAR O. 1964. The Lower Villafranchian Vertebrates from Hajnáčka near Filákovo in Southern Slovakia. Rozpravy ústredniko ustavu geologickeho, **30**: 1-115.
- FEJFAR O., HEINRICH W.-D. 1985. Zur Bedeutung der Wirbeltierfundstätten von Ivanovce und Hajnáčka für die Säugetierpaläontologie im Pliozän und frühen Pleistozän in Europa: Kenntnisstand und Probleme. Věstník ústredniko ustavu geologickeho, 60(4): 213-224.
- FEJFAR O., HORÁČEK I. 1983. Zur Entwicklung der Kleinsäugerfaunen im Villányium und Alt-Biharium auf dem Gebiet der ČSSR. Schriftenreihe für geologische Wissenschaften, 19/20: 111-207.
- FLADERER F. 1984. Das Vordergliedmaßenskelett von Hypolagus beremendensis (PETÉNYI, 1864) und von Lepus sp.(Lagomorpha, Mammalia) aus dem Altpleistozän von Deutsch-Altenburg (Niederösterreich). Beiträge zur Paläontologie von Österreich, 11: 71-148.
- FLADERER F. A. 1987. Beitrag zur Entwicklung von Hypolagus und Lepus (Lagomorpha, Mammalia) im Pliopleistozän von Mitteleuropa. Sitzungsberichte der Österreichischen Akademie der Wissenschaften, matematisch-naturwissenschaftliche Klasse, Abteilung I, 196: 123-138.
- HORÁČEK I. 1985. Survey of the fossil vertebrate localities Včeláre 1-7. Časopis mineralogii a geologii, **30**: 353-366.
- HORÁČEK I., LOŽEK V. 1984. Z vyzkumu vyplně Mladečské jeskyně u Litovle. Česky kras, **35**: 98-100. (In Czech with English summary).
- HORÁČEK I., LOŽEK V. 1988. Palaezoology and the Mid-European Quaternary past: scope of the approach and selected results. Rozpravy československe Akademie věd, ada matematickych přírodnich věd, 98: 1-4.
- JÁNOSSY D. 1963. Die altpleistozäne Wirbeltierfauna von Kövesvárad bei Répáshuta (Bükk-Gebirge). Annales Historico-naturales, Musei Nationalis Hungarici, pars mineralogica et paleontologica, **55**: 109-141.
- JÁNOSSY D. 1986. Pleistocene vertebrate faunas of Hungary. Developments in paleontology and stratigraphy, 8. 288 pp. Amsterdam: Elsevier.
- KOENIGSWALD W. v. 1974. Solnhofen 5, eine villafranchische Spaltenfüllung aus Bayern. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie, **14**: 39-48.
- KORMOS Th. 1934. Zur Frage der Abstammung eurasiatischer Hasen. Allatani Közlemenyék, 31: 5-78.
- KOWALSKI K. 1958a. An Early Pleistocene fauna of small mammals from Kadzielnia Hill in Kielce (Poland). Acta palaeontologia polonica 3: 1-47.
- KOWALSKI K. 1958b. Altpleistozäne Kleinsägerfauna von Podumci in Norddalmatien. Palaeontologia jugoslavica, **2**: 1-30.
- KOWALSKI K. 1960. An Early Pleistocene fauna of small mammals from Kamyk (Poland). Folia quaternaria, 1: 1-24.
- KOWALSKI K. 1964. Paleoekologia ssaków pliocenu i wczesnego plejstocenu Polski. Acta theriologica, 8: 73-88. (In Polish).
- KOWALSKI K. (ed.) 1989. Historia i ewolucja lądowej fauny Polski (History and evolution of the terrestrial fauna of Poland). Folia quaternaria, **59-60**: 1-278.
- KRETZOI M. 1941. Die unterpleistozäne Säugetierfauna von Betfia bei Nagyvárad. Földtani Közlöny, **71**: 7-12, 235-261, 308-335.
- KRETZOI M. 1956. Die altpleistozänen Wirbeltierfaunen des Villányer Gebirges. Geologia Hungarica, Series Paleontologia, 27: 1-264.
- KRETZOI M. 1962. Fauna und Faunenhorizont von Csarnóta. Jahresbericht der Ungarische Geologische Anstalt, 1959: 267-395.
- MAIS K., RABEDER G. 1977. Eine pliozäne Höhlenfüllung in Pfaffenberg bei Bad Deutsch-Altenburg (Niederösterreich). Die Höhle, **28**(1): 1-7.

- MAIS K., RABEDER G. 1984. Das große Höhlensystem im Pfaffenberg bei Bad Deutsch-Altenburg (Niederösterreich) und seine fossilen Faunen. Die Höhle, **35**: 213-230.
- MALEZ M. 1961. Staropleistocenska fauna koštane breče poluotoka Marjana kod Splita (Die altpleistozäne Brekzienfauna der Halbinsel Marjan bei Split). Palaeontologia Jugoslavica, **4**:1-43.
- MALEZ M., RABEDER G. 1984. Neues Fundmaterial von Kleinsäugern aus der altpleistozänen Spaltenfüllung Podumci 1 in Norddalmatien (Kroatien, Jugoslawien). Beiträge zur Paläontologie von Österreich, **11**: 439-510.
- MAYHEW D. F. 1975. The Quaternary history of some British rodents and lagomorphs. Unpubl. thesis (Ph. Dr.), University of Cambridge, 306 pp.
- MUSIL E. 1966. Holštejn, eine neue altpleistozäne Lokalität in Mähren. Acta Musei Moraviensis, **61**: 133-168. NADACHOWSKI A. 1989. Gryzonie Rodentia. Folia quaternaria, **59-60**: 151-176. (In Polish).
- NADACHOWSKI A. 1991. Systematics, geographic variation, and evolution of snow voles (*Chionomys*) based on dental characters. Acta theriologica, **36**: 1-45.
- NADACHOWSKI A., PAWŁOWSKI J., STWORZEWICZ E. 1989. Charakterystyka stanowisk i ich korelacja stratygraficzna. Folia quaternaria, **59-60**: 5-19. (In Polish).
- RABEDER G. 1977. Eine weitere pliozäne Höhlenfauna aus dem Steinbruch Hollitzer bei Bad Deutsch-Altenburg (Niederösterreich). Die Höhle, 28: 84-86.
- RABEDER G. 1981. Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. Beiträge zur Paläontologie von Österreich, 8: 1-334.
- SCHREUDER A. 1937. *Hypolagus* from the Tegelen clay; with a note on recent *Nesolagus*. Archives Néerlandais de Zoologie, **2**: 225-239.
- SULIMSKI A. 1964. Pliocene Lagomorpha and Rodentia from Weże 1 (Poland). Acta palaeontologica polonica, 9: 149-244.
- SYCH L. 1965. Fossil Leporidae from the Pliocene and Pleistocene of Poland. Acta zoologica cracoviensia, **10**: 1-88.
- SYCH L. 1966. Correlation of tooth measurements in leporids. On the significance of the coefficient of correlation in the studies of microevolution. Acta theriologica, **11**: 41-54.
- SYCH L. 1967a. Unworn teeth of *Hypolagus brachygnathus* KORMOS (Leporidae, Mammalia). Acta zoologica cracoviensia, **12**: 19-25.
- SYCH L. 1967b. Fossil endocranial cast of *Hypolagus brachygnathus* KORMOS (Leporidae, Mammalia). Acta zoologica cracoviensia, 12: 27-30.
- SYCH L. 1980. Lagomorpha (Mammalia) from the Pliocene and Early Pleistocene of Poland. Folia quaternaria, **51**: 57-64.
- TOBIEN H. 1972. *Citellus* (Rodentia) und Lagomorpha aus den älteren Aufsammlungen an der pleistozänen Lokalität Stránská skála bei Brno (ČSSR). Studia musei moraviensis, Anthropos (Brno), **20** (N.S. 12): 137-146.
- WOLSAN M. 1989. 7.4. Zajęczaki Lagomorpha. Folia quaternaria, 59-60: 145-150. (In Polish).

160