

Species distribution and differentiation of Eurasian *Hypolagus* (Lagomorpha: Leporidae)

Fostowicz-Frelik, L., 2003 - Species distribution and differentiation of Eurasian *Hypolagus* (Lagomorpha: Leporidae) - in: Reumer, J.W.F. & Wessels, W. (eds.) - DISTRIBUTION AND MIGRATION OF TERTIARY MAMMALS IN EURASIA. A VOLUME IN HONOUR OF HANS DE BRUIJN - DEINSEA 10: 197-216 [ISSN 0923-9308] Published 1 December 2003

Features of p3 (width, length, AER and PER depth, and AER-factor and PER-factor), as well as of mandible (diastema length, lower tooth row length, and mandible height) of five Eurasian *Hypolagus* species were analysed. The "*beremendensis-igromovi*" morphological group is distinguished on the basis of similar dimensions and proportions of mandible and teeth. The Pleistocene Central European populations of *Hypolagus beremendensis*, characterised by larger dimensions, resemble *Hypolagus igromovi* (Don Region). The division of *Hypolagus beremendensis* into two, previously proposed, subspecies is maintained. *H. beremendensis beremendensis* existed from Late Ruscinian to Late Villányian and *H. beremendensis brachygnathus* was known from Late Villányian to Steinheimian (Q3). Similarity between *Hypolagus b. brachygnathus* resemble *Hypolagus igromovi* could be the result of either parallel evolution or closer relationships. Thus, it is possible that the significantly larger, Late Villányian and Early Pleistocene populations of *Hypolagus beremendensis* are the descendants of *Hypolagus igromovi*, which invaded Central Europe in the Villányian. *Hypolagus schreuderae*, described from the Nihewanian deposits, is characterised by a long diastema, a simple enamel pattern and forms a distinct species.

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Keywords: *Hypolagus*, Lagomorpha, Evolution, Taxonomy, Pliocene, Pleistocene, Turolian, Biharian, Nihewanian, Eurasia

INTRODUCTION

Leporids are known in Asia from the Middle Eocene (McKenna & Bell 1997). During the Late Oligocene to Late Miocene interval there has been a significant decrease of leporid abundance in some regions of Asia, especially in China, where after the Late Oligocene, and up to the latest Miocene, leporids have been missing from the fossil record (Qiu 1987). *Hypolagus* DICE, 1917 was one of the newcomers, which originated in North America in the Early Miocene (Hemingfordian) and migrated to Asia probably before the Late Miocene through Beringia

land bridge (Gureev 1964; Qiu 1987, Chaline *et al.* 2000). There are approximately 16 *Hypolagus* species known up to now, of which five (or six) were described from Eurasia. *Hypolagus* became widely distributed and abundant in the Pliocene and Early Pleistocene of Eurasia. The numerous karst sites included hundreds of *Hypolagus* bones and teeth known from Central Europe, chiefly Poland and Hungary (Sulimski 1964; Sych 1965; Jánossy 1986; Wolsan 1989). *Hypolagus* co-occurred in sediments with remains of other leporids such as *Alilepus* DICE, 1931 or *Lepus* LINNAEUS, 1758. Its dis-

tribution area bordered and sometimes overlapped the distribution area of *Trischizolagus* RADULESCO & SAMSON, 1967, *Serengetilagus* DIETRICH, 1941, and *Oryctolagus* LILLJEBORG, 1873 (Kurtén 1968; De Bruijn *et al.* 1970; Qiu 1987; Sen & Erbajeva 1995; Averianov & Tesakov 1997; Chaline *et al.* 2000).

This study tries to summarise the knowledge on *Hypolagus* species in Eurasia, basing on the analysis of dimensions and proportions (metrical characters) of mandibles and lower premolars – p3, frequently used in taxonomic investigations on American leporids, also including *Hypolagus* (White 1991; White & Morgan 1995; Voorhies & Timperley 1997).

MATERIAL AND METHODS

The material, consisting of p3 and mandibles of Eurasian *Hypolagus* species, is listed below by species, with number of specimens in brackets. The specimens come from 19 localities ranging chronologically from the very end of the Miocene to Middle Pleistocene (Fig. 1). The analysis was based on camera lucida drawings of the occlusal surface of the p3, from which the measurements were taken. Three measurements were taken from the mandibular bones: the length of the diastema, the length of the lower tooth row, and the height of the dentary between the p4 and m1. All material used belonged to the adult specimens. The teeth were selected having the parallel, not tapering, walls (in lateral view), which is typical for adult individuals. The anatomical structure of p3 and scheme of tooth measurements are shown in Figure 2. The anatomical nomenclature and indices after White (1991) and Voorhies & Timperley (1997).

In order to assess the similarity between the studied populations, average Euclidean distances were calculated on the basis of seven metrical characters (Table 1) for six *Hypolagus* populations. The phenogram by unweighted pair-group method using arithmetic averages (UPGMA) was then constructed. The method of Lubischev (after: Sneath &

Sokal 1973) was employed for testing diastema length as a possible specific discriminator. His coefficient of discrimination:

$$K = (X_{iA} - X_{iB})^2 / 2 s_i^2$$

where s_i^2 is the pooled variance for character i from taxa (here: populations) A and B. The greater K is, the better i is as a discriminator (e.g. $K = 7.68$ allows 95 % of identifications to be correct).

Material used

Hypolagus beremendensis (PETÉNYI, 1864)

Localities: Poland, Weze 1: 123 p3, 30 mandible fragments; Zamkowa Dolna Cave, fauna A: 9 p3; Rebielice Królewskie 1: 27 p3 and 7 mandible fragments, Rebielice Królewskie 2: 18 p3; Kadzielnia: 55 p3, 8 mandible fragments; Kamyk: 136 p3, 10 mandible fragments (all coll. ISEZ). Hungary, Osztramos 7: 18 mandible fragments (coll. NHMB); Villány 3: 8 p3, 4 mandible fragments (coll. HGIB). Czech Republic, Chlum: 2 p3; Holstejn: 4 p3 (Fladerer & Reiner 1996: fig. 7: 3–5, 7–9). Austria, Deutsch-Altenburg 2C1: 9 p3 and 16 mandibles, and Deutsch-Altenburg 4B: 5 (Fladerer & Reiner 1996: fig. 7: 10–18, Tab. IV).

Hypolagus igromovi GUREEV, 1964

Localities: Russia, Rasdorskaya, right bank of Don River, Rostov Region: 8 p3, measurements of 9 mandible fragments (Gureev 1964; Averianov 1996 a: fig. 1, A-F, I-J, Tab. I), Kosyakino, Northern Caucasus: 1 p3 (Averianov & Tesakov 1998: fig. 1: j).

Hypolagus multiplicatus (ERBAJEVA IN BAZAROV *et al.*, 1976)

Localities: Russia, Udunga, Western Transbaikalia: 1 p3 (Erbajeva 1996: fig 2 A); Beregovaya: 1 p3 (Erbajeva 1996: fig 3 A).

Hypolagus schreuderae TEILHARD DE CHARDIN, 1940

Localities: China, Inner Mongolia, Loc. 18

Epoch		Europe		Central Asia	
	Mammal Units	MN Zones	Faunal Sites	Mammal Units	Faunal Sites
Pleistocene		Q1	Chlum 6 Holštejn	Choukutien	
	Biharian		Betfia Deutsch-Altenburg Kamyk		Loc. 18 (near Beijing)
Pliocene	Villafranchian			Nihewanian	Nihewan Beregovaya Udunga
		17	Kadzielnia Villány 3 Osztramos 7		
	Villányian	16	Zamkova Dolna Cave Rębiełice Królewskie1	Yushean	
		15			
	Ruscinian	14	Węże1		Harr Obo
Miocene	Turolian	13	Rasdorskaya (Don River Region)	Baodean	

Figure 1 Stratigraphic record of some *Hypolagus* sites bearings from Eurasia, used to the study. The stratigraphic correlation after Qiu (1987), Kretzoi (1987), Qiu & Storch (2000).

near Beijing: 4 p3, measurements of 5 mandibles (Teilhard de Chardin 1940: fig. 22, measurements, p. 38; Cai 1989: fig. 1 d); Nihewan: 3 p3 (Cai 1989: fig. 1 a–c); Yushe: 2 p3 (Cai 1989: fig. 1 e–f).

Hypolagus sp. indet.

Harr Obo: 2 p3 (Qiu 1987: Text fig. 32; Cai 1989: fig. 1g)

Hypolagus transbaicalicus (ERBAJEVA, in BAZAROV *et al.* 1976)
Localities: Russia, Udunga, Western Transbaikalia: 1 p3 (Erbajeva 1996: fig. 2 B); Beregovaya: 3 p3 (Bazarov *et al.* 1976: Pl II, 5, 6; Erbajeva 1996: fig. 3 B)

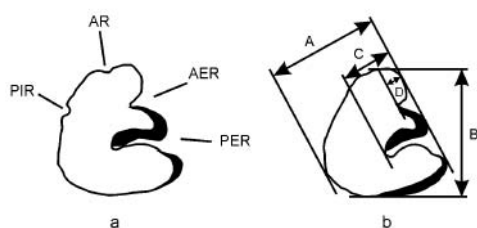


Figure 2. Diagrams of p3: (a) with labelled teeth structures, **AER** – anterior external reentrant, **AR** – anterior reentrant, **PER** – posterior external reentrant, **PIR** – posterior internal reentrant; and (b) indicating measurements of the occlusal surface, **A** – transverse width, **B** – length, **C** – PER deep, **D** – AER deep.

Abbreviations and indices

Sites: Bt – Betfia, DA – Deutsch-Altenburg, H – Chlum 6 and Holstejn, KA – Kamyk, KD1 – Kadzielnia, Os7 – Osztamos 7, RK1 – Rebielice Królewskie 1, RK2 – Rebielice Królewskie 2, V3 – Villány 3, W1 – Weze 1, ZDA – Zamkowa Dolna Cave.

ISEZ: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland

HGIB: Hungarian Geological Institute, Budapest, Hungary

NHMB: Geological and Paleontological Department of the Natural History Museum, Budapest, Hungary

PIN: Paleontological Institute, Russian Academy of Sciences, Moscow, Russia

ZIN: Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

AER: anterior external reentrant.

PER: posterior external reentrant.

AER-factor: $\text{AER deep} \times 100\% / \text{width of the p3 crown}$

PER-factor: $\text{PER deep} \times 100\% / \text{width of the p3 crown}$

Md-ratio 1: $\text{diastema length} \times 100\% / \text{lower tooth row length}$

Md-ratio 2: $\text{height of the mandible} \times 100\% / \text{diastema length}$

WHAT IS HYPOLAGUS?

Hypolagus is recognised as a genus of fossil rabbit, assigned to the problematic subfamily Archaeolaginae, including two genera intermediate in p3 morphology between Palaeolaginae and Leporinae (Dice 1929; Dawson 1958). *Hypolagus* was presumed to be derived from *Archaeolagus* in the Early Miocene and become widely distributed in North America and Eurasia (Dawson 1958; 1967; Sych 1965).

The original diagnosis given by Dice (1917) states that in *Hypolagus* "p3 has two anterior re-entrant angles, neither of which extends over half way across the tooth. The posterior angle is much deeper than the anterior. There are no grooves on the inner surface of the tooth. The upper molar has the re-entrant angle extending about half way across the crown and the enamel in the angle is coarsely folded. Cement is well developed (...)", and "p3 in *Hypolagus* differs from the corresponding tooth in *Archaeolagus* in being proportionally shorter and broader, although the enamel pattern is very similar in the two genera." This generic diagnosis holds true for the most *Hypolagus* species and specimens as a whole. It distinguishes *Hypolagus* from most of *Serengetilagus*, *Trischizolagus* or *Alilepus* species. However, in some species of *Hypolagus* there are shallow crinkles in the position of the anterior (*Hypolagus igromovi*, *Hypolagus brachygnathus* sensu Fladerer 1987) and antero-internal (*Hypolagus brachygnathus* sensu Fladerer 1987) reentrants (Fladerer 1987; Averianov 1996 a; Fladerer & Reiner 1996). The crinkles are usually very shallow and could be hardly described as reentrants, comparing with these observed in *Serengetilagus*, *Trischizolagus* or *Alilepus*. On the other hand, in *Trischizolagus*, *Serengetilagus*, and some *Lepus* species there are some of p3 teeth (respectively ca. 14.0, 3.5, and 0.07 %) showing *Hypolagus*-like crown shape (Erbajeva & Angerman 1983; Averianov & Tesakov 1997; Qiu & Storch 2000). It is also noteworthy that juvenile specimens of *Hypolagus beremendensis* (pre-

viously described as *Pliolagus* KORMOS, 1934) frequently display relatively deep antero-internal re-entrant, which vanishes during ontogeny (Sych 1965; Averianov & Tesakov 1997).

The skull and postcranial skeleton of *Hypolagus* show the conservative and uniform plan for most fossil leporids (Dawson 1967; Lopez-Martinez 1985), the significant feature is a short and robust muzzle, caused by shortening of diastema. Limb bones express cursorial and fossorial ability intermediate between *Oryctolagus* and *Lepus*, with visible tendencies toward increasing cursoriality, especially in the Pleistocene populations (Fladerer 1984; Fladerer & Reiner 1996; Fostowicz-Frelik 2001).

THE OUTLINE OF HYPOLAGUS TAXONOMY

The investigations about leporids frequently treated the structure of dentition as the general diagnostic characteristic (Dice 1929; Hibbard 1963; Radulesco & Samson 1967; White 1991; White & Morgan 1995; Voorhies & Timperley 1997). It is mainly because of the teeth and mandibular fragments abundance, while the complete skulls and postcranial bones are relatively scarce in the fossil record (Dawson 1967). Another reason is, that the first premolar teeth in rows – p3 and P2, are particularly useful in studies on the leporid evolution (Fladerer 1987), being the most exposed on forces and abrasion during chewing activity, and therefore quickly changing in response to vegetation and climatic changes. There are some differences in the postcranials of different known leporid genera, mainly in the limb bones proportions, and the cursorial ability (Sych 1965; Campbell 1969; Fladerer 1984; Fostowicz-Frelik 2001), however, they are not very helpful in the discrimination between species on intrageneric level (Averianov 1996a; Averianov and Tesakov 1997). Chinese *Hypolagus schreuderae*, as well as Transbaikalian *Hypolagus multiplicatus*, *Hypolagus transbaicalicus*, and European *Hypolagus igromovi* from Don

River sediments were described mainly based on the teeth, on mandibular and maxillar features, with minor attention given to the postcranial skeleton (Teilhard de Chardin 1940; Gureev 1964; Bazarov *et al.* 1976; Cai 1987, 1989; Qiu 1987; Averianov 1996a; Erbajeva 1996; Qiu & Storch 2000). The best known Eurasian species appears to be *Hypolagus beremendensis*, which inhabited most of Central and East Europe from Early Pliocene to Middle Pleistocene. The investigations on numerous material from Poland, published by Sych (1965), contributed much to the knowledge about the genus.

However, Sych did not specify the taxonomic features characteristic for *Hypolagus beremendensis* in comparison with other *Hypolagus* species, apart from the relative length of intermaxilla in the relation to the nasals, which cannot be regarded as diagnostic because of its high interspecific variability (observed in other leporid genus e. g. *Lepus*). He was the first author to deal with the problem of *Hypolagus* evolution, and put forward a model about gradual size increase, conforming to Bergmann's rule, presumably caused by the climatic cooling at the beginning of the Pleistocene. Sych (1965) also revised *Pliolagus* genus, recognising the specimens as juvenile *Hypolagus*.

Another progress in taxonomy of the European *Hypolagus* was the study on p3 and P2 enamel pattern, using the morphotypes concept (Fladerer 1987; Fladerer & Reiner 1996). The problem with *Hypolagus* taxonomy, as well as other leporid genera, seems to be in the high intraspecific and ontogenic variability. This, in turn, demands comparing numerous samples of specimens, and thus, most of the derived features characterise only the population as a whole, which makes it hardly useful in case of small samples.

RESULTS

Mandibular characters

Three mandibular dimensions were analysed: the length of diastema, length of the lower

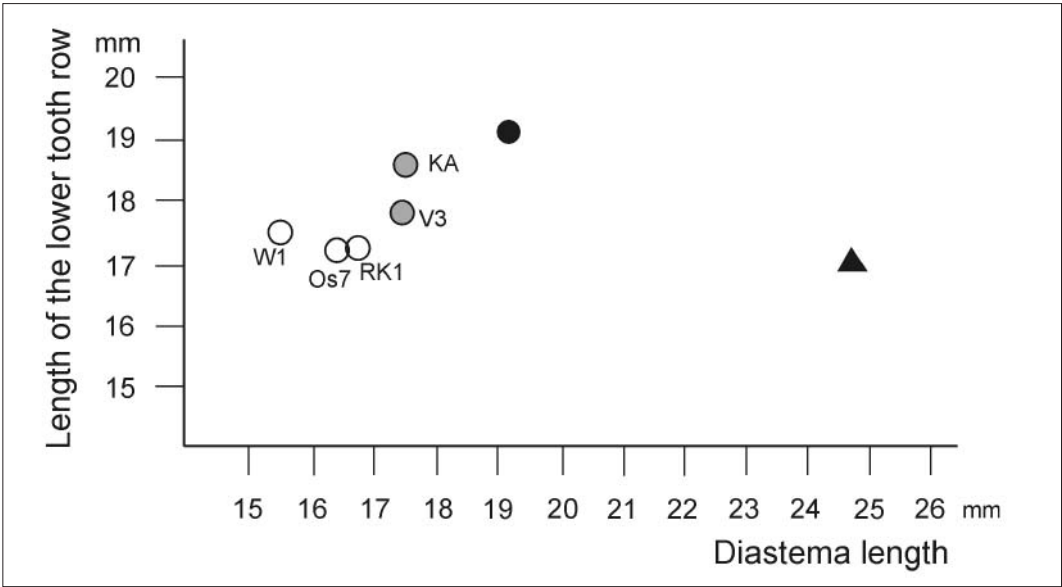


Figure 3 Relationships between diastema length and lower tooth row length (Md-ratio 1), for various Eurasian *Hypolagus* species and populations (centroids). Symbols as follows: o - *Hypolagus beremendensis-igromovi* group (white – Pliocene populations, gray – the earliest Villánian-Pleistocene populations, black – *H. igromovi*), ▲ - *H. schreuderae* (Nihewanian).

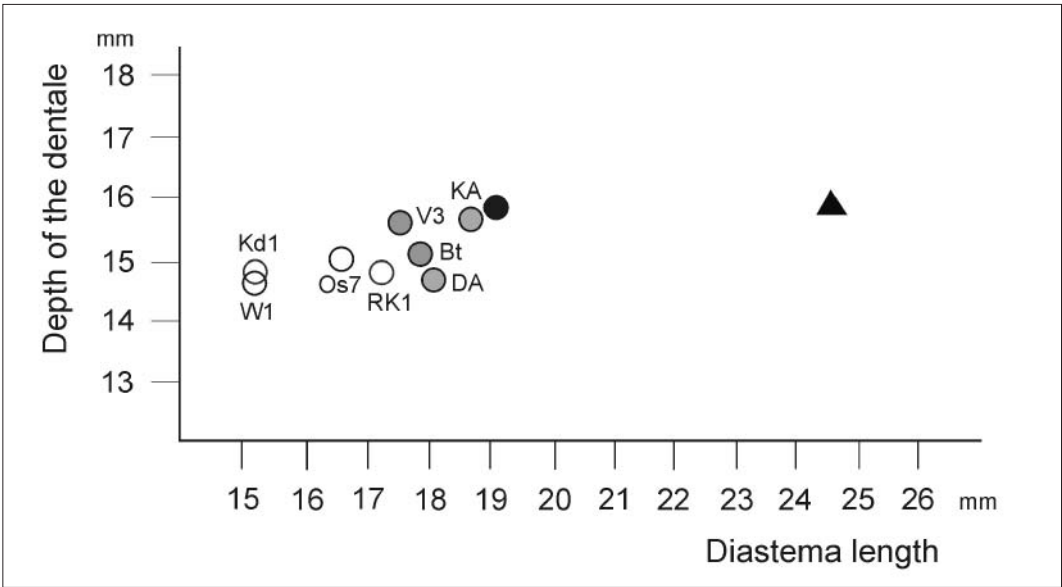


Figure 4 Relationships between diastema length and mandible height (Md-ratio 2) in different Eurasian *Hypolagus* species (centroids). Symbols as in Figure 3.

tooth row, and the height of the mandibular bone, measured between p4 and m1 (Table 1). The most discriminating dimension is the diastema length. The longest diastema is observed in *Hypolagus schreuderae* and its length seems to have the highest value among most of *Hypolagus* species, closely comparable with that of *Oryctolagus cuniculus* (Hibbard 1969; White 1991, White & Morgan 1995; Voorhies & Timperley 1997). This feature allows to distinguish two major groups: a monospecific "*schreuderae*" group and a "*beremendensis-igromovi*" group, including all Central European populations (Figs. 3, 4). The Md-ratio 1 values for this dimension for Kamyk population were taken from Sych (1965) because of the poor material preservation. The Md-ratio 1 seems to be highly statistically significant feature ($0.01 <$

$P < 0.02$, Student's t-test, for comparison between *H. schreuderae* and *H. igromovi*).

The height of the mandible is much less variable factor, and its values are very close for all species analysed. There is a tendency towards elongation of the mandible, while its height remains virtually unchanged in the Pleistocene *Hypolagus beremendensis* populations (Kamyk, Deutsch-Altenburg, Betfia; Fladerer & Reiner 1996), and in *Hypolagus igromovi*.

p3 characters

Four metrical characters of p3 (length, width, and depth of PER and AER) were measured in the studied species (Table 1). The most discriminating feature seems to be the AER depth. The largest values of each measurement are observed in *Hypolagus igromovi*

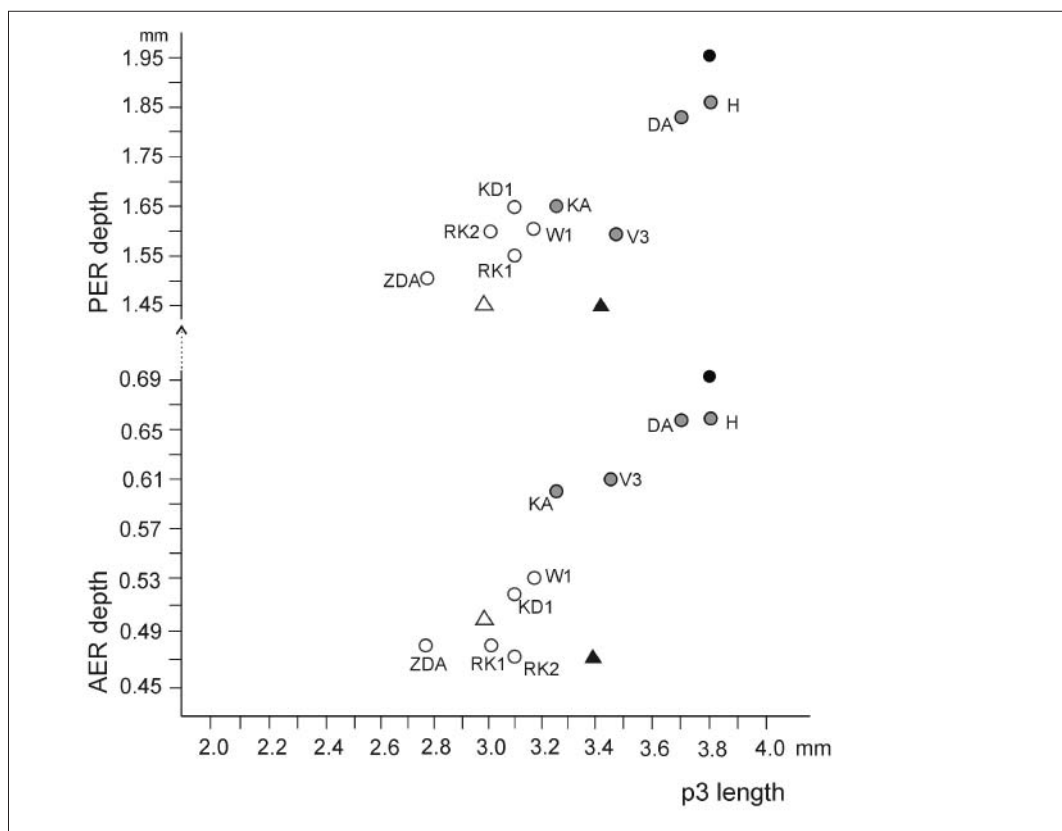


Figure 5 Relationships between AER and PER depth and the p3 length (centroids). Symbols as in Figure 3, additionally: Δ - *Hypolagus* sp. of Harr Obo (Early Pliocene).

and Pleistocene populations of *Hypolagus beremendensis*, which are grouped with the former, and are distinct from the smaller *Hypolagus schreuderae* and Pliocene populations of *Hypolagus beremendensis* (Fig. 5, 6). The middle position is occupied by Kamyk and Villány 3 populations, which display relatively small p3 width and length, but a significant increase in re-entrant depth. The width to length ratio (W/L) is similar and

generally uniform in all species. The most square-shaped p3 are observed in *Hypolagus transbaicalicus* and *Hypolagus multiplicatus*, with W/L index 97 % and 99 %, respectively. The PER and AER-factors show the relations between the re-entrant depth and the width of the p3 crown. The highest values of both factors are observed in *H. beremendensis* from Kamyk and in *Hypolagus igromovi*. The distinctively lowest values of both factors are

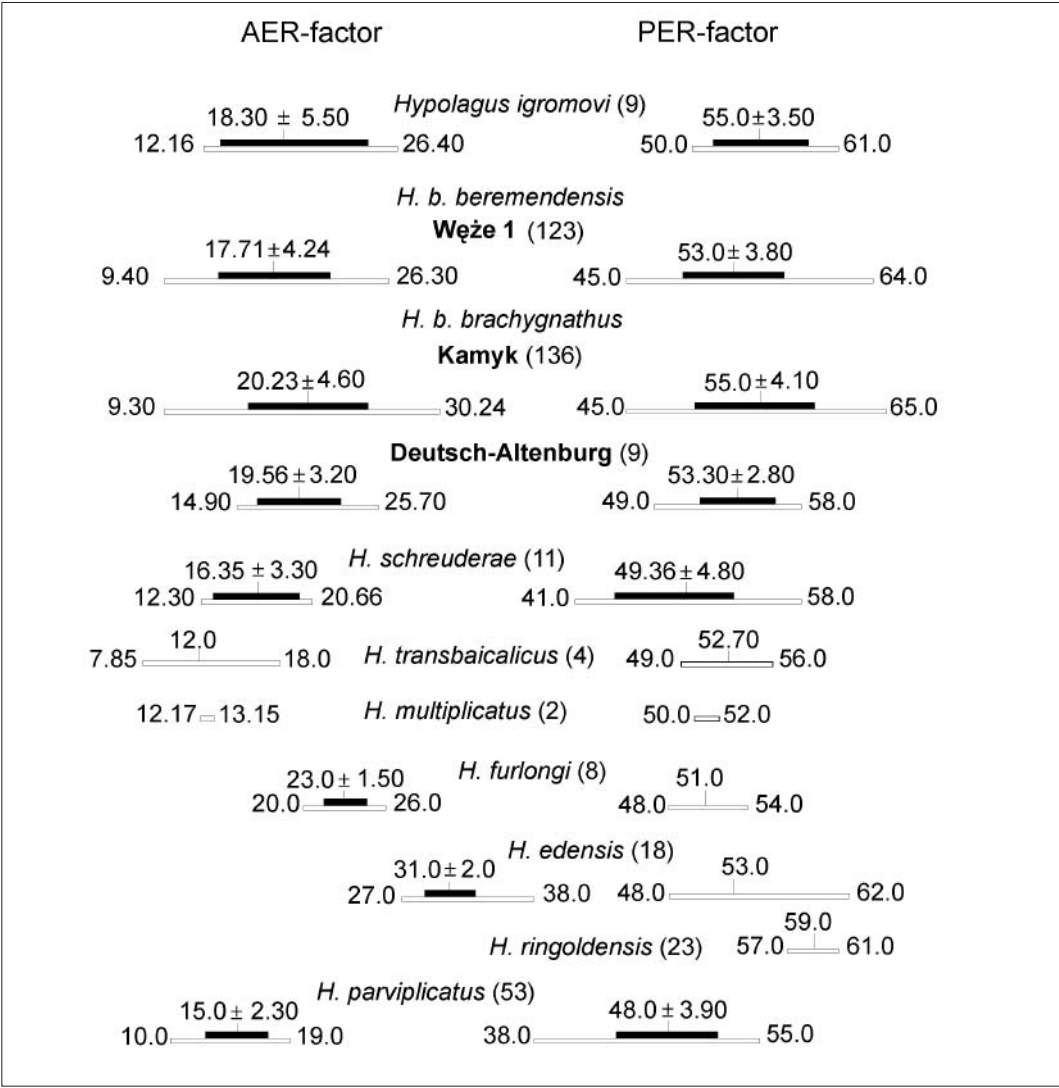


Figure 6 Comparison of the AER and PER-factors distribution among *Hypolagus* species, expressed in percentages; observed range in white, standard deviations in black (values for North American species from White 1991; White & Morgan 1995; Voorhies & Timperley 1997).

observed in the Nihewanian populations of *Hypolagus schreuderae* and of the AER-factor in the *Hypolagus transbaicalicus* and *Hypolagus multiplicatus* (Fig. 7).

Significantly, the Early Pliocene Chinese specimen from Harr Obo, presumed to belong to *Hypolagus schreuderae*, displays dimensions very similar to those of the Pliocene *Hypolagus beremendensis*, but proportions similar to the Pleistocene populations. Nihewanian *Hypolagus schreuderae* forms an obviously distinct unit (Fig. 5, 7).

The AER-factor is the most discriminating, dividing the "beremendensis - igromovi"

group into two subgroups. The first of them, characterised by a lower value of the AER-factor, includes all Pliocene populations of *Hypolagus beremendensis*. The second one, with a higher AER-factor value, groups Pleistocene *Hypolagus beremendensis* populations together with material from Villány 3, with Early Pliocene *Hypolagus* sp. from Harr Obo (China, Inner Mongolia), and with *Hypolagus igromovi* (Fig. 7). Thus, there is a visible morphological trend in *Hypolagus beremendensis* to deepening the antero-external fold, which started probably in the very Early Pleistocene. A rather unexpected

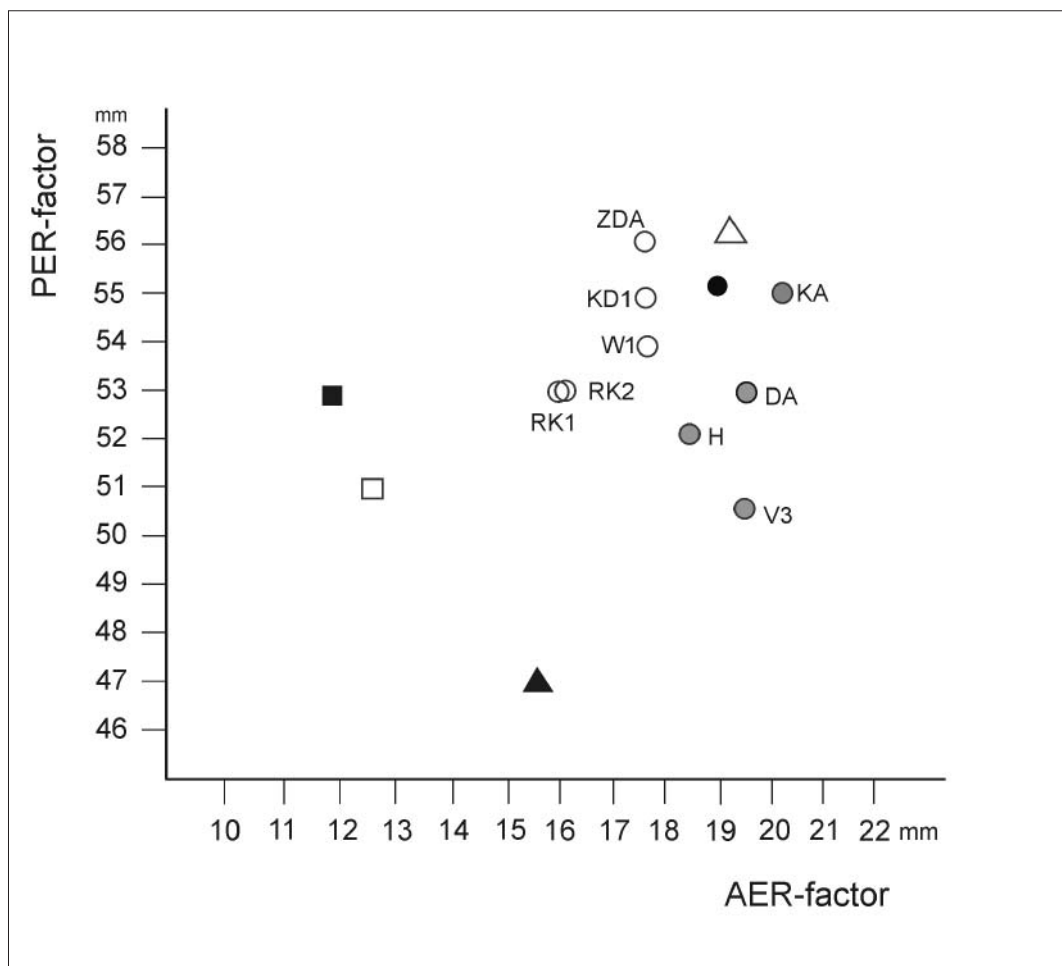


Figure 7 Relationships between PER and AER-factors for different species of Eurasian *Hypolagus* (centroids). Symbols as in Figures 3 and 5. Additionally: □ - *Hypolagus transbaicalicus*, ■ - *Hypolagus multiplicatus*.

divergent tendency is observed in Chinese populations (Cai 1989: Fig. 2).

CLASSIFICATION

Lagomorpha BRANDT, 1855

Leporidae FISCHER DE WALDHEIM, 1817

Hypolagus DICE, 1917

Type species *Lepus vetus* KELLOGG, 1910

Holotype Left mandible having incisor and p3-m2 (Collection of University California, Vertebrate Palaeontology No. 12567), from U.C. locality No. 1100, Thousand Creek beds, Humboldt County, Nevada; Middle Pliocene.

Emended diagnosis Medium to large-sized rabbit, with significant shortening of the diastema (Md-ratio, in most species, between 85 and 105 %, the only exception is *Hypolagus schreuderae* where it is ca. 140 %). Orbital process of maxilla is at the right or slightly obtuse angle according to the zygomatic process. p3 with two external folds (re-entrants): shallower AER and deeper PER, the former extending up to 38%, the latter extending up to 65% of the crown width.

Studied Asian and European species

Hypolagus beremendensis, *Hypolagus igromovi*, *Hypolagus multiplicatus*, *Hypolagus schreuderae*, *Hypolagus transbaicalicus*.

Hypolagus beremendensis (PETÉNYI, 1864)

Holotype A left mandible with teeth, No. Ob/3689 (HGIB), from Villány 3, latest Villányian.

Emended diagnosis Middle sized *Hypolagus* having short and stocky muzzle. Diastema is short, in *H. b. beremendensis* generally shorter than the lower tooth row (Md-ratio 1: 85-95%), in *H. b. brachygnathus* slightly longer (Md-ratio 1: 95-105%).

Choanae broader than in *Oryctolagus cuniculus* and narrower than observed in *Lepus*. The outline of p3 in *H. b. beremendensis* clearly triangular, with narrow pointed anterior part of the trigonid and angular internal side of the talonid, in *H. b. brachygnathus* the outline of p3 trapezoidal, with broader anterior part of the trigonid and rounded internal margin. AER of p3 of moderate depth (average 17-20 % of crown width, not exceeding 30%); PER ca. 50 % of crown width (not exceeding 65%). *H. b. brachygnathus* occupies higher values of the observed range. The buccal lobe of P2 smooth or expressing a shallow groove (external anterior re-entrant), the lingual lobe of P2 in *H. b. beremendensis* smooth and rounded or flattened at the front, in *H. b. brachygnathus* it may express a shallow groove. The postcranial skeleton expressing better cursorial ability than *Oryctolagus*, but lesser than *Lepus*. The ulnar olecranon shorter and wider than that of *Oryctolagus*, but longer than that of *Lepus*.

Stratigraphic range Most of continental Europe and Sicily. *H. b. beremendensis*: Early to Late Pliocene (Late Ruscinian, MN 15 to Late Villányian, MN 17). *H. b. brachygnathus* from Late Villányian to Middle Pleistocene (Steinheimian, Q3).

History Kormos (1934) described *Hypolagus brachygnathus* from the Hungarian site of Villány 3. Kretzoi (1962), who continued the work on Hungarian fossil localities, put both taxa into synonymy, and retained the species name *Hypolagus beremendensis* due to its priority. The author of this name was the Hungarian 19th century researcher S.J. Petényi. However, Petényi did not complete his work on fossil mammals from Beremend before he died; in the posthumous edition of his monography, completed by his co-worker F. Kubinyi, the mandible of *Hypolagus beremendensis* was illustrated (Petényi 1864: Table II: 1 a, b). The drawings were not accompanied by any diagnosis or description. Remarks on skeletal findings assigned by

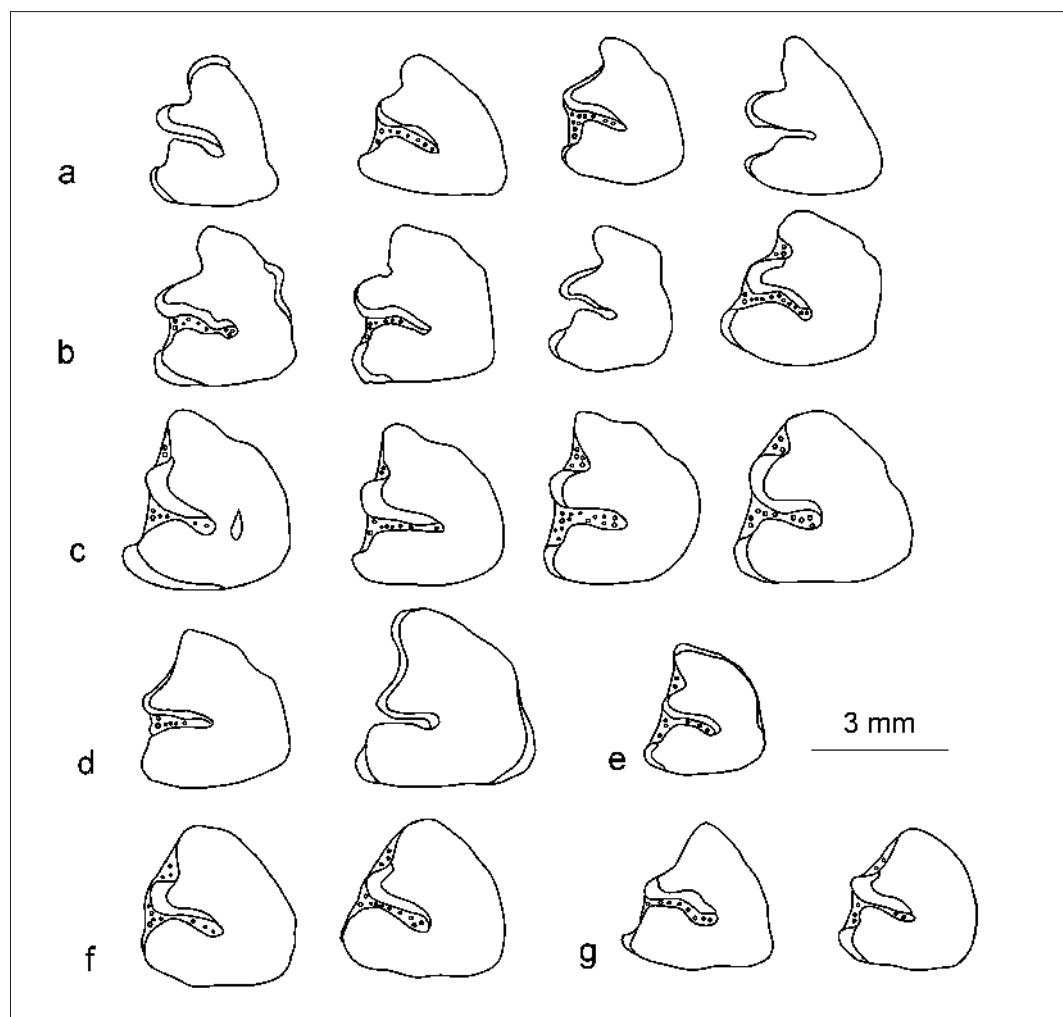


Figure 8. Enamel patterns of the occlusal surfaces of p3. **A** – *Hypolagus beremendensis beremendensis* from Weze I, Poland (from left: MF 2220/T/7, 23– reversed, 21, 54), **B** – *Hypolagus beremendensis brachygnathus* from Kamyk, Poland (from left: MF 2160/T/13, 8, 153, 166– reversed), **C** – *Hypolagus igromovi* (from Averianov 1996a: Figure 1. A, C, D– reversed, I, J), **D** – *Hypolagus schreuderae* from Loc. 18 near Beijing (from Teilhard de Chardin 1940: Figure 22: A, B), **E** – *Hypolagus* sp. from Harr Obo (V 7990, from Qiu 1987: Text fig. 32), **F** – *Hypolagus multiplicatus* (from Udunga – left and Beregovaya – right; after Erbajeva 1996: Fig. 2: A, 3: A), **G** – *Hypolagus transbaicalicus* (from Udunga – left and Beregovaya – right; after Erbajeva 1996: Fig. 2: B, 3: B). The dotted areas – cement.

Petényi to *Lepus* come only from his letters to Dr. K.C. Leonhard and Dr. H.G. Bronn enclosed in this edition (Petényi 1864). The original specimen illustrated by Petényi is missing, but the type specimen of *Hypolagus brachygnathus*, the left mandible with teeth, No. Ob/3689, from Villány, described by Kormos (1934), is kept in the Geological Museum of the Hungarian Academy of

Sciences, and should be accepted as lectotype of *Hypolagus beremendensis*. Further study on these populations, based on p3 and P2 morphotypes, made a distinction into two species: *Hypolagus beremendensis* and *Hypolagus brachygnathus*, that were subsequently changed into two subspecies: *Hypolagus b. beremendensis* and *Hypolagus b. brachygnathus*. The former was thought to

be mainly a Pliocene form, characterised by a p3 of simple shape without any tracks of anterior or internal folds, with a talonid slightly concave at the buccal side, and forming a sharp edge at the margin of PER, the so-called "*beremendensis* edge" (Fladerer 1987; Fladerer & Reiner 1996). The latter subspecies was characterised by the more complicated tooth outline, with traces of AR, AIR, or PIR (see Fig. 2), and is believed to arise from a *beremendensis* population in the late MN 17. The specimen No. Ob/3689 was stated as a holotype for this form (Fladerer & Reiner 1996).

***Hypolagus igromovi* GUREEV, 1964**

Holotype A fragment of left maxilla with P3-M1, No. 48636 (ZIN) from Rasdorskaya, right bank of Don River, Rostov Region, Russia; Upper Miocene, Lower Pontian beds.

Diagnosis Dimensions of big mountain hare (*Lepus timidus*). Mandible robust with high alveolar part and broad angular process. Mandibular diastema short, nearly equal to the tooth row (Md-ratio 1 ca. 100%). Incisors robust like in modern mountain hare. Maximal breadth of upper molars 1.5–1.75 times more than length. Upper teeth (P4-M2) re-entrants strongly crenulated. Re-entrants of p3 deep (AER ca. 19% of the crown width, PER 52–61% of the crown width); the crown outline usually triangular, with narrow and pointed anterior part of the trigonid, rounded internal margin. In over 50% of the teeth a crinkle occupies the anterointernal part of the crown observed.

Stratigraphic range Late Turolian (MN 13) to ?Early Ruscinian, in Don River Region, foothills of the Caucasus (Gureev 1964; Averianov 1996a; Averianov & Tesakov 1998; Bajgusheva *et al.* 2001).

***Hypolagus multiplicatus* (ERBAJEVA in BAZAROV *et al.*, 1976)**

Holotype A fragment of maxilla with P2–M2, No. 56311 (ZIN), Beregova farm, River Czika valley, Baikal Region, Russia.

Diagnosis A leporid of intermediate dimensions. P2 (width x length—1.6 x 3.0 mm) with two anterior re-entrants; p3 rounded, with nearly equal width and length, and extended internal margin; the re-entrants shallow (AER ca. 12% and PER 50–52% of the crown width). Upper cheek teeth possessing highly crenulated internal folds. *Hypolagus multiplicatus* differs from the others *Hypolagus* species by possessing higher crenulated upper cheek teeth. It differs from *H. beremendensis* and *H. schreuderae* in being smaller, and from *Hypolagus transbaicalicus* in being larger.

Stratigraphic range Late Pliocene and the Early Pleistocene of Baikal Region, Udunga, Beregovaya, Dodogol, Zasuchino 2 (Erbajeva 1996).

***Hypolagus schreuderae* TEILHARD DE CHARDIN, 1940**

Holotype Almost complete specimen from Locality 18 near Peking, China, Late Pliocene.

Diagnosis According to Teilhard de Chardin (1940): "A large sized hare, with the lower p3 of a typical *Hypolagus* pattern (posterior outer cleft incomplete, no anterior furrow). First upper incisors relatively large. Auditory bullae relatively small and narrow. Posterior tip of the maxillary extending back of the fronto-nasal suture. Triangular extension of the frontal between the nasalia large and broad." Diastema significantly long (21,5–26,0 mm; Md-ratio 1 ca. 140%); p3 of relatively shallow re-entrants depth (AER 15–17% of the crown width, and PER ca. 47–48%).

Stratigraphic range Late Pliocene - Early Pleistocene (Villafranchian/Nihewanian) of China, typical in such sites as Yushe III or Loc. 18 near Beijing.

***Hypolagus transbaicalicus* (ERBAJEVA in BAZAROV et al., 1976)**

Holotype Left P2, No. 56310 (ZIN, collection of M.A. Erbajeva 1963); River Czika valley, Beregova farm, Russia.

Diagnosis Small leporid. P2 with single anterior reentrant of a depth equal 1/3 of tooth length. Upper cheek teeth possessing variably crenulated reentrants. Crenulation developed weaker than in *Hypolagus multiplicatus* towards the back of the tooth row. The smallest of all Eurasian *Hypolagus*. Both p3 reentrants relatively shallow (AER: 8-18%, and PER: 49-56 % of the crown width).

Stratigraphic range The same as for *Hypolagus multiplicatus*, co-occurring in sediments.

Note The coexistence of small and large *Hypolagus* (*H. multiplicatus* & *H. transbaicalicus*) which share a unique derived character (plications of the hypostria) suggests juvenile and adult specimens of the same species. The large individual variability within the lagomorph populations (see the *Alilepus annectens* study by Qui 1987) can be misleading. Thus, to keep separately these two species would need a further study on their common range of variability against that expected for intraspecific variation.

DISCUSSION

The dendrogram (Fig. 9) shows one complex cluster, with an inner group consisting of Villányian to Early Biharian populations of *Hypolagus beremendensis* with externally attached *Hypolagus igromovi* and the Early Pliocene population of *Hypolagus beremendensis* from Weze 1. The Nihewanian *Hypolagus schreuderae* is placed externally of this "*beremendensis-igromovi*" group. The Transbaikalian species *Hypolagus multiplicatus* and *H. transbaicalicus* were not included into the dendrogram because of inadequate

data and small samples.

The clustering places *Hypolagus igromovi* among "*H. beremendensis*" populations, grouping it very close with the populations from Kamyk and Villány 3 (Jánosy 1986). This suggests that the status of this species needs revision. The external position of the Weze 1 population in relation to the Villányian and Early Biharian *H. beremendensis* stresses the previously suggested sub-specific differentiation within *H. beremendensis*. The external position of *H. schreuderae* supports the distinction of this species from the European populations, marked previously by the significant longer diastema.

The "*beremendensis-igromovi*" group

The data on *H. beremendensis* included in the present study, show mosaic evolution of the dental and mandibular features. From a morphological point of view, the "*beremendensis-igromovi*" group forms a continuous group, with *H. igromovi* and Biharian populations of *H. beremendensis* at the edge of the highest dimensions. Intermediate positions are occupied by the Late Villányian and earliest Biharian populations.

A statistical search for some metrical features as discriminators between the different populations within the "*beremendensis-igromovi*" group was performed. The most useful feature proved to be the diastema length. According to the Lubischev factor K, there is a significant difference between *H. beremendensis* from Weze 1 on the one hand, and both *H. igromovi* (K=8.40) and the Kamyk *H. beremendensis* population (K=7.68) on the other hand. There are no such differences between *H. igromovi*, and Kamyk or Villány 3 populations of *H. beremendensis*, nor between *H. igromovi* and the Rebielice Królewskie 1 *H. beremendensis* population. Thus, a morphological discontinuity is observed between Weze 1 and the remaining populations of the "*beremendensis-igromovi*" group. In this study, following Fladerer & Reiner (1996), the Central European *H. beremendensis* populations are

divided into two subspecies: *H. b. beremendensis* (Ruscinian-Early Villanian), which is small and has shallower re-entrants in p3, and *H. b. brachygnathus* (Late Villányian-Steinheimian), which is larger and has a p3 with more complicated enamel pattern and deeper reentrants.

H. b. beremendensis was abundant in Northwestern and Central European Pliocene. Its distribution extended over parts of France, through the Netherlands, Germany, Austria, the Czech Republic to Slovakia, and Poland in the north, and Hungary, Serbia, Romania, and probably Greece in the south (Schreuder 1936; Sulimski 1964; Sych 1965; Koenigswald 1974; Jánossy 1986; Wolsan 1989; Chaline *et al.* 2000). It is also known from the Late Pliocene of Sicily, Monte Pellegrino site (Thaler 1972). The oldest and most numerous remains assigned to this subspecies come from Polish sites: Weze 1, 2 (Sulimski 1962, 1964; Sych 1965). Late Ruscinian *H. b. beremendensis* is known also from the karst sites of Slovakia (Ivanovce 1, Fladerer 1996), and Hungary (Csarnóta 1 and 3, Jánossy 1986).

H. b. brachygnathus is thought to exist in Europe from Early to Middle Pleistocene (Fladerer 1987; Fladerer & Reiner 1996). Its remains are known from Poland (Kamyk), Czech Republic (Chlum, Holstěj, Stránská Skála), and Austria (Deutsch-Altenburg). The abundance of this species decreased quickly in Biharian, due to the arrival and spreading of *Lepus* (Kormos 1934; Sych 1965; Wolsan 1989). The presumably last Eurasian *Hypolagus* survived in Moravian refuges (Stránská Skála 2 and Mladec 3) until the earliest Middle Pleistocene (Fladerer & Reiner 1996).

Hypolagus igromovi occurs in the Latest Miocene or, more plausibly, the Earliest Pliocene (Averianov 1996 a; Averianov & Tesakov 1998). The original material of this species is referred to be of Sarmatian or Meotian (Late Miocene) origin (Gureev 1964; Averianov 1996 a). The mandible of a subadult *Hypolagus* (corresponding "well in the morphology of p3 and the state of preservation with the type material") was found in situ in the beds of Early Pontian age, overlain

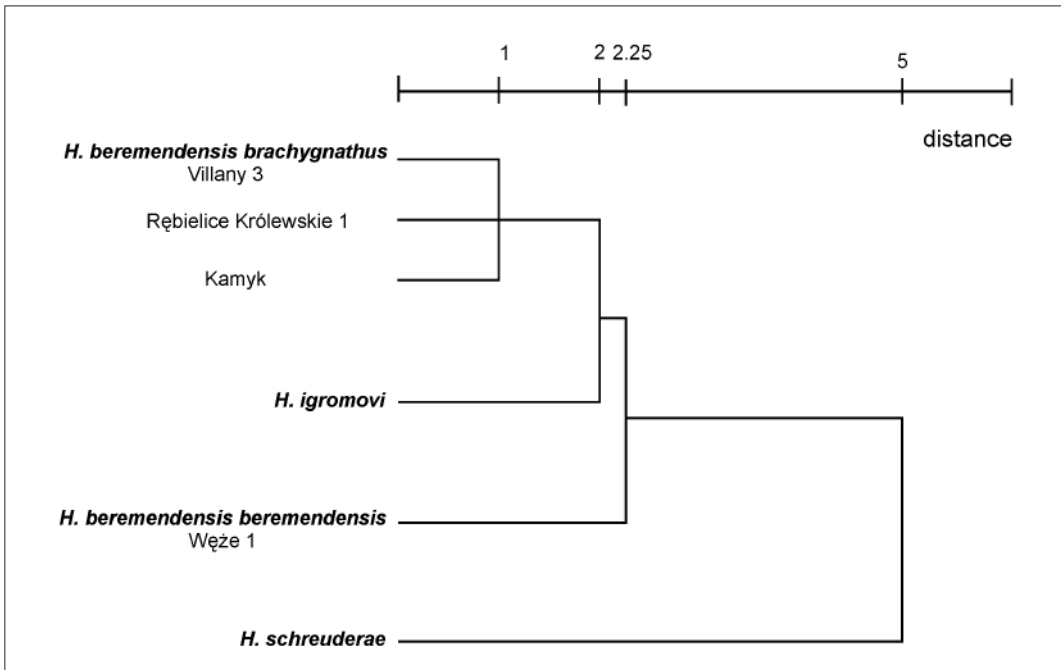


Figure 9 Phenogram of six populations of *Hypolagus* from Eurasia, based on UPGMA clustering.

by clays of Villafranchian age, at the type locality (Averianov 1996 a, following personal communication V.V. Titov & A.S. Tesakov). In the original work by Gureev (1964) this species is described as being larger than *H. beremendensis* and having a more complicated enamel pattern. However, Gureev (1964) did not know the Kamyk or Deutsch-Altenburg populations of *H. beremendensis*, because they were not yet described. On the other hand, Averianov (1996a), emending the diagnosis, stated that *H. igromovi* differs from the European Pliocene *H. beremendensis* and Pleistocene *H. brachygnathus* in being larger (mandible and postcranial skeleton), comparing with material from Weze, Rebielice Królewskie, Kadzielnia, and Kamyk. In fact, *H. igromovi* is not significantly larger than *Hypolagus* from Kamyk and most of its dimensions are well within the observed range for *Hypolagus* from Deutsch-Altenburg (Fladerer 1984) and some specimens from Pleistocene Hungarian sites. According to the enamel pattern, the p3 presented by Averianov (1996 a, Fig. 1) closely resembles those of *H. beremendensis*, except for the teeth G and H, which may either be aberrant or belong to *Serengetilagus* or *Trischizolagus*. Moreover, the teeth of *H. igromovi* show an intermediate shape between those of Weze 1 (presumed to be *H. b. beremendensis* with a clearly triangular outline), and those of Kamyk and Villány 3 (supposed to be *H. b. brachygnathus* with a more trapezoidal outline and with distinct antero- and postero-internal re-entrants; see Figure 8).

Thus, the problem of the relationship of *H. igromovi* and *H. beremendensis* arises. First, a hypothesis that *H. b. brachygnathus* originated from *H. b. beremendensis* in the latest Pliocene (Fladerer 1987; Fladerer & Reiner 1996) is one of the possibilities; these subspecies form one evolutionary lineage. On the other hand, *H. igromovi* and *H. b. brachygnathus* share close similarities e.g. in measurements of p3, which could be the result of either parallel evolution or of their close rela-

tionships.

Parallel evolution may be explained by the environmental similarity. The longer muzzle observed in the Pleistocene populations of *H. b. brachygnathus* and in the Late Miocene *H. igromovi* (Fig. 4), could be explained by the need of longer nasal ducts to moisturize and warm inhaled air. Actually, at the Miocene/Pliocene transition, a global vegetation change was observed (Cerling *et al.* 1997). It resulted in the rapid expansion of open habitats, with domination of C4 grasses, indicating drier climate. Also, the development of steppe-tundra areas in the Early Biharian (Fladerer & Reiner 1996) was related to increasing aridity and the arrival of tougher vegetation. This triggered selection towards a more complicated and thus more resistant p3 enamel pattern, with deep re-entrant folds, as observed in both species. A tentative relationship could be explained by supposing that *H. b. brachygnathus* is derived from *H. igromovi*, which was invading Europe since the Early Villányian (MN 16) and which gradually forced out *H. beremendensis*. This "relationship hypothesis" seems to be more acceptable on the basis of the close morphological similarities observed, and because it is conceivable that *H. beremendensis* and *H. igromovi* originated from a single stock. However, the taxonomic position of *H. igromovi* and *H. beremendensis* needs additional study.

Chinese *Hypolagus* and Transbaikalian species

The first problem to be dealt with is the status of *Hypolagus brachypus* (YOUNG, 1927). Young (1927) described *Caprolagus brachypus* from the Late Villafranchian of Loc. 60 (Sanchiatien near Beijing, China). It was characterised by "small dimensions and postero-internal reentrant". Later, more remains were assigned to this species (Teilhard de Chardin & Young 1931; Young 1935). Schreuder (1936) considered this taxon to be *Hypolagus*. Bohlin (1942) examined the collection, including the type specimen of "*Caprolagus*" *brachypus*, kept in the

Paleontological Museum in Uppsala, noting the great similarity of these specimens to *Alilepus*, without however ascribing these remains to *Alilepus*. Averianov (1996b) revised the collection, which resulted in ascribing the studied material of "*Caprolagus*" *brachypus* to a new genus: *Sericolagus* AVERIANOV, 1996.

Three *Hypolagus* species of Asian origin are known, but their relationships remain obscure. These are: Chinese *H. schreuderae* and two species from Transbaikalian sites, *H. transbaicalicus* and *H. multiplicatus*, all known from deposits of Villafranchian (or its Chinese equivalent, Nihewanian) age (Teilhard de Chardin 1940; Bazarov *et al.* 1976; Kretzoi 1987; Qiu 1987; Erbajeva 1996; Erbajeva & Alexeeva 2000). The best known taxon is *H. schreuderae* (Teilhard de Chardin 1940; Qiu 1987; Cai 1989). This species is characterised mainly by a relatively long diastema and simple enamel pattern, with shallow re-entrants (Fig. 3-8, Table 1). The long diastema of *H. schreuderae* seems to be a derived feature, characteristic also for evolutionary younger Leporinae, such as *Oryctolagus* or *Lepus*. In comparison, most North American *Hypolagus* species, as well as some *Alilepus* and *Pratilepus*, have shorter diastemata and an Md-ratio 1 oscillating to c. 100.0% (Hibbard 1969; White 1991; White & Morgan 1995; Voorhies & Timperley 1997). However, the mandibles of both Transbaikalian species are unknown up to now, making a detailed comparison difficult. The analysis of the p3 reveals some resemblance between *H. schreuderae* and the Transbaikalian species *H. multiplicatus* and *H. transbaicalicus* (Fig. 8): but the dental features of *H. schreuderae* seem to be highly primitive.

The earliest Asian *Hypolagus* fossil (a single p3) comes from the Chinese site of Harr Obo (Inner Mongolia, Early Jinglian, MN 14), and was assigned to *Hypolagus* sp. (Qiu 1987; Cai 1989). However, Qiu & Storch (2000) suggested that it could be the tooth of *Trischizolagus maritsae*. This seems

less probable, although the shape of p3 from Harr Obo (a narrow anterior border, absence of a furrow or extended flattening), which is typical for *Hypolagus*, is also known to occur in some specimens of *Trischizolagus* (Averianov & Tesakov 1997; Qiu 1987; Qiu & Storch 2000). The tooth from Harr Obo shows close similarity in measurements and proportions to the "*beremendensis-igromovi*" group (Figs. 5, 7). However, until the mandible of the species is known, its status is not certain. The Asian record is completed by a number of *Hypolagus* sp. remains from Kazakhstan, Altai Region, and Bashkiria, that may either belong to *H. igromovi* or to *H. beremendensis* (Averianov 1996a; Erbajeva & Tutkova 1997).

CONCLUDING REMARKS

Comparison of the Eurasian species of *Hypolagus* with the North American record of the genus shows the uniformity of the tooth morphology in the Eurasian populations. The North American species seem to be more differentiated in the depth of the reentrants (Fig. 6). It is not definitely known which American taxa could be considered ancestral to Eurasian ones. *Hypolagus parvuplicatus*, treated as one of the more primitive and ancestral North American species (Dawson 1958; White 1991; Voorhies & Timperley 1997), displays the closest similarity in p3 with Eurasian species, especially with *H. b. beremendensis*, according to AER and PER - factors and general crown outline. The trend of deepening the reentrants in more advanced North American species (Voorhies & Timperley 1997) is also pronounced in Eur-asian *Hypolagus*, especially in *H. beremendensis*. It seems, however, that the oldest known Eurasian species (*H. igromovi* and *H. sp.* from Harr Obo) show an advanced stage of this feature. *H. schreuderae*, with rather primitive features of p3 and a significantly longer diastema, is distinct, so far being known only from the Chinese Early Pleistocene.

The tentative routes of dispersal of *Hypolagus* in Eurasia could be as follows: the genus

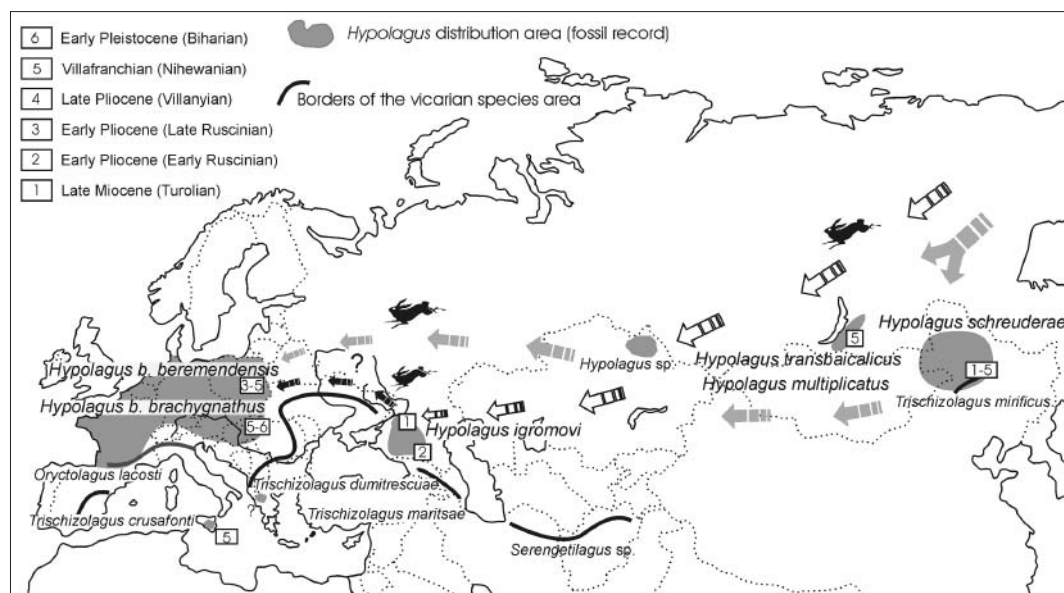


Figure 10 Distribution of the *Hypolagus* species in Eurasia during the Late Miocene to Early Pleistocene, and the probable migration tracks.

entered Asia probably no later than the Early Turolian, and then migrated to Europe (Fig. 10). Regional species evolved in the Baikal Region and in Inner Mongolia. The European record is partly the result of this first Neogene migration event. A second migration from the Don Region into Central Europe could have taken place in the Late Villányian.

ACKNOWLEDGEMENTS

I would like to thank M. Dawson and N. Lopez-Martinez for critically reading the manuscript. Special thanks are extended to L. Kordos (Geological Institute of Hungary) and M. Gasparik (Paleontological Department of the Natural History Museum, Budapest) for access to specimens and assistance. I am indebted to M. Wolsan for reading the draft of this paper and encouragement. Ms A. Holda-Michalska made the map and some drawings.

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Received 19 May 2001

Revision received 17 June 2002

Accepted 08 September 2003

Table 1. Measurements (in mm) of p3 and mandibles for *Hypolagus* species (approximated values italicized).

<i>H. beremendensis</i>					<i>H. igromovi</i>	<i>H. schreuderae</i> (Nihewanian sites)
Węże I		Rębiełice Królewskie	Villány 3	Kamyk		
p3						
width	(123) M=3.0±0.30 OR 2.16-3.48	(27) M=2.98±0.28 OR 2.33-3.40	(8) M=3.14±0.15 OR 2.95-3.41	(136) M=3.10±0.24 OR 2.50-3.54	(9) M=3.60±0.22 OR 3.13-3.97	(11) M=2.96±0.55 OR 2.22-3.77
length	(123) M=3.19±0.24 OR 2.42-3.63	(27) M=3.12±0.22 OR 2.30-3.48	(8) M=3.46±0.20 OR 3.20-3.78	(136) M=3.26±0.30 OR 2.42-3.86	(9) M=3.80±0.48 OR 3.34-5.10	(11) M=3.26±0.50 OR 2.75-4.0
AER depth	(123) M=0.53±0.12 OR 0.28-0.80	(27) M=0.48±0.13 OR 0.28-0.72	(8) M=0.61±0.12 OR 0.34-0.73	(136) M=0.60±0.15 OR 0.30-0.95	(9) M=0.67±0.18 OR 0.45-0.91	(11) M=0.48±0.10 OR 0.33-0.66
PER depth	(123) M=1.61±0.17 OR 1.20-1.96	(27) M=1.60±0.15 OR 1.33-1.84	(8) M=1.59±0.09 OR 1.50-1.75	(136) M=1.65±0.19 OR 1.20-2.12	(9) M=1.96±0.22 OR 1.77-2.11	(11) M=1.45±0.20 OR 1.11-1.83
diastema length	(39) M=15.25±0.85 OR 13.0-16.80	(6) M=16.66±1.60 OR 14.55-19.25	(3) M=18.40 OR 17.11-20.07	(10) M=17.48±1.23 OR 14.80-19.30	(4) M=19.50 OR 17.5-21.3	(5) M=24.5±1.84 OR 21.5-26.0
lower tooth row length	(18) M=17.63±0.61 OR 16.60-18.60	(5) M=17.30±0.43 OR 16.90-18.0	(3) M=17.90 OR 17.56-18.07	(2) 18.40	(4) M=19.20 OR 18.90-19.60	(5) M=17.30±0.44 OR 17.0-18.0
height of the mandible	(16) M=14.60±0.90 OR 13.0 - 15.90	(14) M=14.82±0.74 OR 14.0-16.20	(3) M=15.24 OR 14.55-15.61	(2) OR 15.0-15.90	<i>15.91</i>	(5) M=15.90±0.42 OR 15.50-16.50
Md-ratio1	(6) M=91.63±5.66 OR 83.0 -89.0	(3) 96.0 94.0-98.0	(2) 94.0-102.0	—	(4) M=101.03 OR 92.60-111.0	(5) M=141.54±8.63 OR 126.47-148.57
Md-ratio 2	(13) M=97.15±5.20 OR 89-108	(5) M=89.0±7.90 OR 82.0-104.0	(2) OR 81.0-91.0	—	—	(5) M=65.0±4.71 OR 59.0-72.0