

Evolutionary trends in Mio-Pliocene Leporinae, based on *Trischizolagus* (Mammalia, Lagomorpha)

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With 7 figures and 4 tables

Kurzfassung: Aus Moldavien und der Ukraine wird neues Material von *Trischizolagus dumitrescuae* beschrieben. In der Variationsbreite des p3 von *Trischizolagus* sind mehrere Morphotypen mit unterschiedlichen Häufigkeiten zu erkennen. Sie enthalten den 'Hypolagus-Typ' aus dem Turolium, eine Mischung von drei Typen (einschliesslich des 'Nekrolagus' Morphotypes) aus dem frühen Ruscinium und den dominierenden 'Alilepus-Typ' des späten Ruscinium. Diese Merkmalsveränderung verlief parallel zu jener in der nordamerikanischen Gattung *Nekrolagus*. Vermutlich haben *Sylvilagus*, *Brachylagus* und *Romerolagus* ihren Ursprung in Nordamerika mit *Nekrolagus*. Die eurasiatischen und afrikanischen Gattungen *Oryctolagus*, *Caprolagus*, *Nesolagus* und *Poelagus* könnten vom altweltlichen *Trischizolagus* abstammen.

Abstract: New material of *Trischizolagus dumitrescuae* from Moldova and Ukraine is described. The variation of p3 in *Trischizolagus* shows the gradual shift of morphotype frequencies from the 'Hypolagus' pattern in Turolian through the mixture of three patterns (including 'Nekrolagus' morphotype) in Early Ruscinian to the dominant 'Alilepus' pattern in the Late Ruscinian samples. These transformations took place parallel to that of the North American *Nekrolagus*. Probably North American *Sylvilagus*, *Brachylagus*, and *Romerolagus* had an North American origin from *Nekrolagus*, whereas Eurasiatic and African *Oryctolagus*, *Caprolagus*, *Nesolagus*, and *Poelagus* could have originated in the Old World from *Trischizolagus*.

Introduction

The complex and diagnostic lagomorph p3 has traditionally attracted the attention of authors and served as the basis for evolutionary speculations, as well as for a supra-generic classification and definition of the leporid genera. DICE (1929) used characters of only this tooth to divide the family Leporidae into three subfamilies:

- Palaeolaginae, having a p3 with both posterointernal and posteroexternal enamel folds,
- Archaeolaginae, characterized by a p3 lacking an internal fold and with the posteroexternal fold crossing no

more than half the occlusal surface, and
 – Leporinae, in which p3 has only one deep posteroexternal fold between the trigonid and talonid, crossing nearly to the lingual side of the tooth.

KORMOS (1934) noted that the Neogene *Hypolagus* has a palaeolagine p3 in the early stages of wear and an archaeolagine p3 in the later stages. Therefore, he concluded that these subfamilies could not be separated. The same situation was observed in *Palaeolagus* and *Megalagus*, where the original palaeolagine pattern of the p3 is replaced by an archaeolagine pattern during ontogeny (WOOD 1940; DAWSON 1958). Thus, transformations of the p3 during ontogeny were found to be important for understanding the evolution and origin of leporid genera and supra-generic groups. Concerning the origin of the peculiar leporine pattern of the p3 with one deep posteroexternal fold, which is characteristic particularly for the genus *Lepus*, the most distributed and flourishing taxon within modern leporids, two alternative hypothesis were proposed (Fig. 1).

The first hypothesis was worked out by HIBBARD (1963), who argued that the condition of the p3 in *Lepus* and other leporines ('*Lepus*' morphotype in Fig. 1a) was derived from the 'Alilepus' morphotype by a subsequent isolation of the posterointernal groove as an 'enamel lake' ('Nekrolagus' morphotype in Fig. 1a) and a fusion of this lake with the posteroexternal groove (Fig. 1a). This conclusion was supported by the actual changes of the frequencies of the p3 morphotypes in the paleopopulations of the Late Cenozoic North American leporids. These forms belong to the lineage *Alilepus* spp. – *Nekrolagus progressus* (HIBBARD 1939) – *Sylvilagus* spp. and *Lepus* spp. (HIBBARD 1963). Discoveries of the rare p3 variants with the 'Nekrolagus' pattern in Recent populations of *Sylvilagus*, *Oryctolagus*, and *Lepus* (HIBBARD 1944, 1963) further contributed to this hypothesis. HIBBARD's idea was

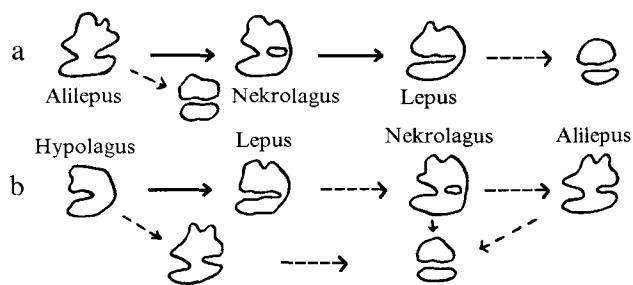


Fig. 1. Two alternative hypotheses explaining the origin of the *Lepus* p3 tooth pattern (from CORBET 1983).

confirmed by Recent paleontological investigations where this lineage appears as follows: *Hypolagus parviplicatus* DAWSON 1958 – *Alilepus hibbardi* WHITE 1991 – *Nekrolagus progressus* – *Sylvilagus* spp. and *Lepus* spp. (WHITE 1991: fig. 13).

An alternative hypothesis speculating on the phylogenetic transformations of the p3 pattern leading to the appearance of leporines was proposed by CORBET (1983). According to this viewpoint (Fig. 1b), the ‘*Lepus*’ pattern of the p3 is derived directly from the ‘*Hypolagus*’ morphotype (Fig. 1b) by the deepening of a shallow postero-external groove. This assumption requires less transformations and, therefore „seems more probably“ (CORBET 1983: 12). This cannot be considered, however, as a reference to the parsimony principle, because it implies the choice among hypotheses which are equally supported by facts (i.e. have equal probability). Moreover, CORBET’s idea is not supported by the fossil record.

HIBBARD’s idea on the origin of the leporines p3 is therefore more acceptable on the basis of paleontological evidence. This hypothesis, however, has a deficiency: all modern leporines, including endemic Asiatic *Caprolagus* and endemic Afro-European *Oryctolagus*, were derived by HIBBARD from the North American *Nekrolagus*. The reason for this conclusion was the lack of reliable data about Late Cenozoic leporids of Eurasia at that time. The purpose of this article is the description of new material of the European *Trischizolagus*. This genus is in many respects similar to *Nekrolagus*. Thus, the analysis of the dental evolution of *Trischizolagus* is indispensable in any attempt to reconstruct the late history of Eurasiatic leporids.

Abbreviations: GIN – Geological Institute, Russian Academy of Sciences, Moscow; SMNH – Swedish Museum of Natural History, Stockholm; ZIN – Zoological Institute, Russian Academy of Sciences, Saint Petersburg; ZMMU – Zoological Museum, Moscow University, Moscow; L – length; W – width. Capital and lower-case letters: P/p (premolar) and M/m (molar), refer to upper and lower teeth. – All measurements are in mm.

Material, methodology, and terminology

The cheek teeth of *Trischizolagus dumitrescuae* RADULESCO & SAMSON 1967 studied by us and figured in this article come from the following localities:

Novaya Andriashevka, right bank of the Kuchurgan River near the village of N. Andriashevka, Tiraspol district, Republic of Moldova, Early Ruscinian, lower part of the MN 14 mammal zone. 5 P2, 3 adult and 1 juvenile p3, some other cheek teeth. GIN collection N 21.

Grebeniki 2, Velikomikhailov district, Odessa Region, Ukraine. Early Ruscinian, upper part of the MN 14 mammal zone. 14 P2, 10 adult and 2 juvenile p3, some other cheek teeth. GIN collection N 1074.

Nikolskoe, Tiraspol District, Moldova, Early Ruscinian, upper part of the MN 14 mammal zone. 1 P2, 4 p3. GIN collection N 1080.

Stavnichevo, Velikomikhailov district, Odessa Region, Ukraine, Early Ruscinian, upper part of the MN 14 mammal zone. 1 p3. GIN collection N 1081.

Moskovei, Kagul district, Moldova. Late Ruscinian, MN 15 mammal zone. 2 p3 from left and right mandibles coming from one individual (AVERIANOV 1995). Collected by E.A. SHANTAR, ZIN collection N C.80457.

Lucheshty, Kagul district, Moldova. Late Ruscinian, MN 15 mammal zone. 3 P2, 6 p3, some other cheek teeth. Collected by L.I. KHOSATSKY, ZIN collection N O.34456.

Tatareshhty, Kagul district, Moldova. Late Ruscinian, MN 15 mammal zone. 7 p3. Collected by L.I. KHOSATSKY, ZIN collection N O.34457.

The age of some of the above-mentioned localities is discussed by VANGENGEIM et al. (1995).

P2 and p3 of *Trischizolagus* from the following localities were considered on the basis of data from the literature:

La Alberca, Spain, Late Turolian, MN 13 mammal zone, 1 P2 and 2 p3 (JANVIER & MONTENAT 1970: fig. 1a-c), the type material of *Hispanolagus crusafonti* JANVIER & MONTENAT 1970, referred to *Trischizolagus crusafonti* by LOPEZ MARTINEZ (1989).

Alcoy, Spain, Late Turolian, MN 13 mammal zone, 1 p3 (LOPEZ MARTINEZ 1989: fig. 55.a5), attributed to *Trischizolagus* cf. *maritsae* DE BRUIJN et al. 1970.

Salborena, Spain, Late Turolian, MN 13 mammal zone, 1 P2 (LOPEZ MARTINEZ 1989: fig. d1,2), attributed to *Trischizolagus* cf. *maritsae*.

Kholbolchi Nor C, Mongolia, near the Miocene-Pliocene boundary, MN 13-14 mammal zone, 1 p3 (FLYNN & BERNOR 1987: fig. 3), attributed to *Trischizolagus* sp.

Pul-e Charkhi, Afghanistan, Early Ruscinian, MN 13 mammal zone, 4 P2 and 2 p3 (SEN 1983: figs. 83, 84, 88; SEN & ERBAJEVA 1995: fig. 1a, b; fig. 2a-c, e), attributed to *Trischizolagus* cf. *maritsae* in the first publication. Recently the leporid material from this locality was restudied and referred to *Pliopentalagus* sp. and *Serengetilagus* sp. (SEN & ERBAJEVA 1995). Rabbits of the genus *Pliopentalagus* are known from the localities of MN 15 interval in Slovakia, Moldova and China (GUREEV 1964; DAXNER & FEJFAR 1967; CAI 1989) and differ from all other genera of the Leporidae by unique characters in the lower dentition: the anterior part of the p3 trigonid is enlarged and bears 2-3 deep anterior folds, and the anterior wall of the p4-m2 talonid is greatly folded. Unfortunately, the p3 from Pul-e Charkhi attributed to *Pliopentalagus* sp. (SEN & ERBAJEVA 1995: fig. 1a) lacks the anterior part of the trigonid. The remaining morphology is within the range of variation of *Trischizolagus*, where the anterior wall of p3’s talonid sometimes can be folded (Fig. 5 a, b, h, i). In the Afghan material no other lower molariform teeth are illustrated to prove the presence of *Pliopentalagus*. The upper cheek teeth with the folded hypostria (SEN & ERBAJEVA 1995: fig. 1c, d) are within the range of variation known for *T. dumitrescuae* (Fig. 3 v-zz). Therefore we prefer to consider the material from Pul-e Charkhi as belonging to *Trischizolagus* sp. For the discrimination of *Trischizolagus* and *Serengetilagus* see below.

Maritsa, Isle of Rhodos, Greece, Early Ruscinian, MN 14 mammal zone, 3 p3 (DE BRUIJN et al. 1970: pl.10, figs.5-8), the type material of *Trischizolagus maritsae*.

Nurnus, Armenia, Early Ruscinian, MN 14 mammal zone, 4 p3 (MELIK-ADAMYAN 1986: figs.1-3), the type material of "*Alilepus*" *gambariani* MELIK-ADAMYAN 1989, attributed here to *T. dumitrescuae*.

Trudomirovka, Odessa Region, Ukraine, Early Ruscinian, MN 14 mammal zone, 1 p3 (TOPACHEVSKY 1987: figs.1,2), the holotype of *Serengetilagus orientieuropaeus* TOPACHEVSKY 1987, attributed here to *Trischizolagus cf. maritsae*.

Novopetrovka and Kuchurgan, Odessa Region, Ukraine, Early Ruscinian, MN 14 mammal zone, 4 P2 and 23 p3 (TOPACHEVSKY 1980: figs.1-24; 1987: figs.3-5), the type material for *Pratilepus kutschurganicus* TOPACHEVSKY 1980 and *Pratilepus ucrainicus* TOPACHEVSKY 1980, and paratypes of *Serengetilagus orientieuropaeus*, all referred here to *Trischizolagus cf. dumitrescuae*.

Perpignan, France, Late Ruscinian, MN 15 mammal zone, 1 p3 of "an undescribed leporid" having an isolated lake (DAWSON 1967: 303). Referred here to *T. dumitrescuae*.

Malusteni and Beresti, Romania, Late Ruscinian, MN 15 mammal zone, 8 p3 (RADULESCO & SAMSON 1967: fig. a,b,d,f,g; DAXNER & FEJFAR 1967: fig.5a), the type material of *T. dumitrescuae*, referred previously to *Alilepus* sp. (DAXNER & FEJFAR 1967) or to *Lepus valdarnensis* WEITHOFER 1889 (SIMIONESCU 1930).

Musait, Vulkaneshty district, Moldova, Late Ruscinian, MN 15 mammal zone, 1 p3 (DAVID & SHUSHPANOV 1986: fig.2), attributed to *Pratilepus kutschurganicus* and referred here to *T. dumitrescuae*.

Tatareshty (see above), 1 p3 (DAVID et al. 1989: figs.3,4), attributed to *Trischizolagus cf. dumitrescuae*.

Megalo Emvolon, Macedonia, Greece, Late Ruscinian, MN 15 mammal zone, 2 P2 and 1 p3 (KOUFOS & KOLIADIMOU 1993: figs.2, 5), attributed to *Trischizolagus dumitrescuae*.

Obukhovka 2, Rostov Region, Russia, Early Villafranchian, MN 16 mammal zone, 7 P2 and 9 p3 (NESIN & REKOVETS 1993 and pers. comm. V.A.NESIN, 1995), attributed to *Trischizolagus* sp. 'Grotte des Rhinocéros', Marocco, Middle Pleistocene, 4 p3 (GERAADS 1994: fig.16a-d), attributed to *Serengetilagus raynali* GERAADS 1994 and referred here to *Trischizolagus* sp.

The variation of the pattern of p3 in 13 species of extant and Pleistocene hares of the Old World was studied by the first author on the basis of 2713 specimens from the col-

lection of ZIN, ZMMU and SMNH. In contrast to the data of HIBBARD on this subject (HIBBARD 1963), only the tooth from one mandible side of every specimen was considered.

For the understanding of the evolutionary changes in the cheek teeth of lagomorphs, including the p3, the hypothetical model of a constantly growing but never worn tooth, a 'synthetic PM', proposed by SYCH (1975), is useful. The ontogeny of the lagomorph p3 can be divided into ontogenetic phases of varied duration which correspond to the specific parts of this synthetic tooth height. The ontogeny of these dental structures extends far beyond sexual maturity and is not connected with this event. So, the term heterochrony (terminology after MCNAMARA 1986) means here only the morphological modifications of structures and does not consider their correlation with sexual maturation.

In the nomenclature of parts of the p3 we follow WHITE (1991: fig.1; Fig. 2 here). The morphotypes of p3 found in the samples of *Trischizolagus* and in Recent populations of *Lepus* are shown on Fig. 2.

Description

The P2 shows considerable variation both in size and morphology. Smaller P2 with 1-2 grooves may come from younger individuals, larger P2 with three grooves are probably from older individuals, or the size of P2 and number of grooves are the matter of individual and/or sexual variation. P2 increases in size from Early to Late Ruscinian localities (Tab. 3). In Late Ruscinian *Trischizolagus* from Moldova the variants with 3 grooves on the anterior side predominate (Tab. 1). In all cases the main anterior reentrant is the deepest groove.

Upper cheek teeth (P3-M2) have deep hypostria. The hypostria cross more than half of the tooth width and are usually strongly folded (Fig. 3 v-zz). They are noticeably more folded than in *T. crusafonti* (JANVIER & MONTENAT 1970: fig. 2) and *Trischizolagus cf. maritsae* (SEN 1983:

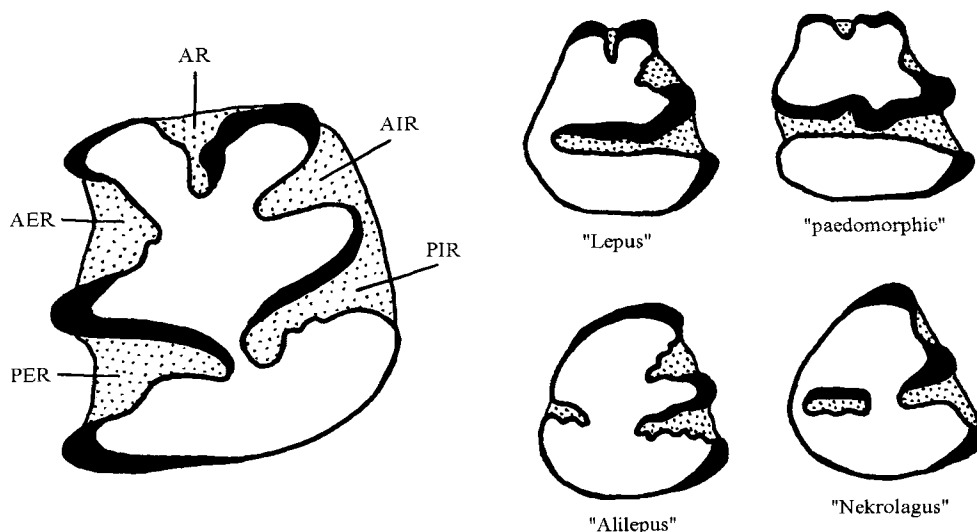


Fig. 2. Occlusal surfaces of the p3 explaining the tooth terminology (on left, after WHITE 1991) and p3 morphotypes (on right). The abbreviations are as follows: AER-anteroexternal reentrant, AIR-anterointernal reentrant, AR-anterior reentrant, PER-posteroexternal reentrant, PIR-posterointernal reentrant.

MN zone	Locality	1 fold	2 folds	3 folds	Reference
16	Obukhovka 2		3*	4*	NESIN pers. com. 1995
15	Megalo Emvolon			2*	KOUFOS & KOLIADIMOU 1993
15	Lucheshty		1	2	this paper
14	Grebeniki	3	4	7	this paper
14	Novaya Andriashevka		3	1	this paper
14	Nikolskoe		1		this paper
14	Novopetrovka & Kuchurgan		2*	2*	TOPACHEVSKY 1980
14	Pul-e Charkhi		3*	1*	SEN 1983; SEN & ERBAJEVA 1995
13	La Alberca		1*		JANVIER & MONTENAT 1970
13	Salobrena	1*			LOPEZ MARTINEZ 1989
Total					
16		—	3 (43%)	4 (57%)	
15		—	1 (20%)	4 (80%)	
14		3 (11%)	13 (48%)	11 (41%)	
13		1 (50%)	1 (50%)	—	

Tab. 1. Distribution of P2 of *Trischizolagus* with different number of folds. Asterisks refer to data taken from the literature.

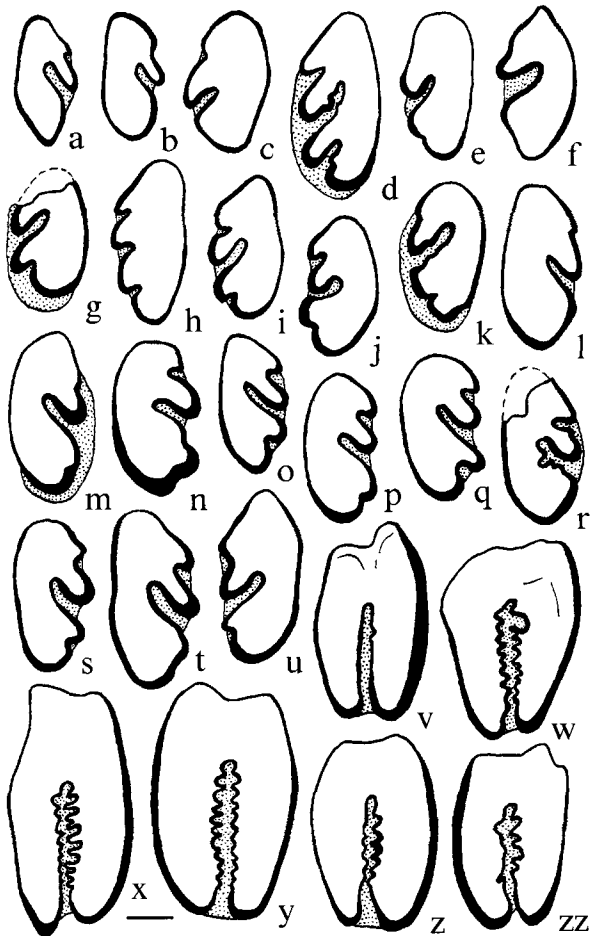


Fig. 3. Occlusal surfaces of P2 (a-u) and upper molariform teeth (v-zz) of *Trischizolagus dumitrescuae*. – a-c, v, w, zz: Novaya Andriashevka; e-r, x: Grebeniki 2; s-u: Lucheshty; y, z: Tatareshty. – Scale bar: 1 mm.

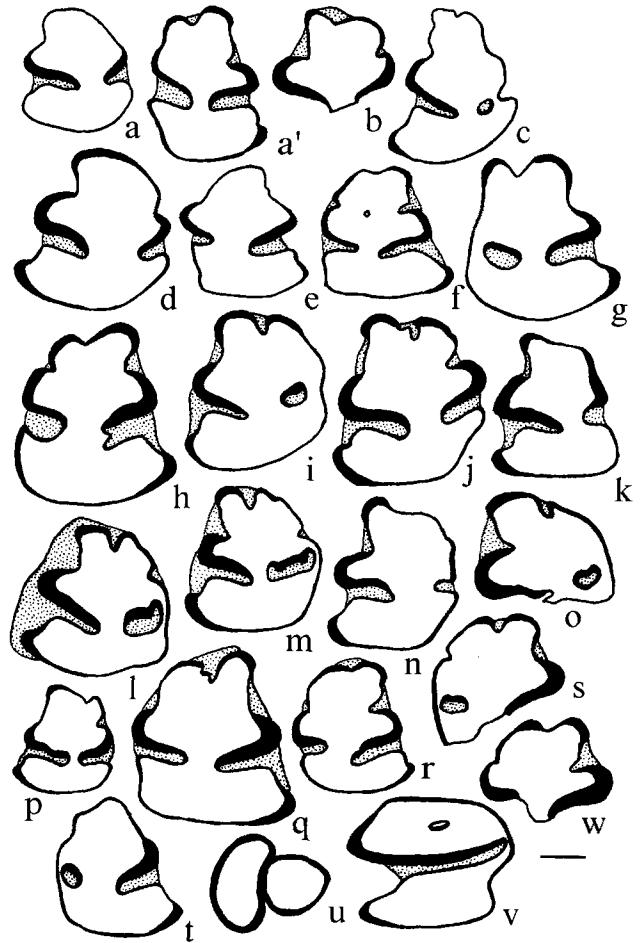


Fig. 4. Occlusal surfaces of p3 (a-t), m3 (u) and m2 (v) of *Trischizolagus dumitrescuae*. – a-d: Novaya Andriashevka (a' - 'root view' of the same tooth as in a); e: Stavnichevo; f-i: Nikolskoe; j-v: Grebeniki 2. – Scale bar: 1 mm.

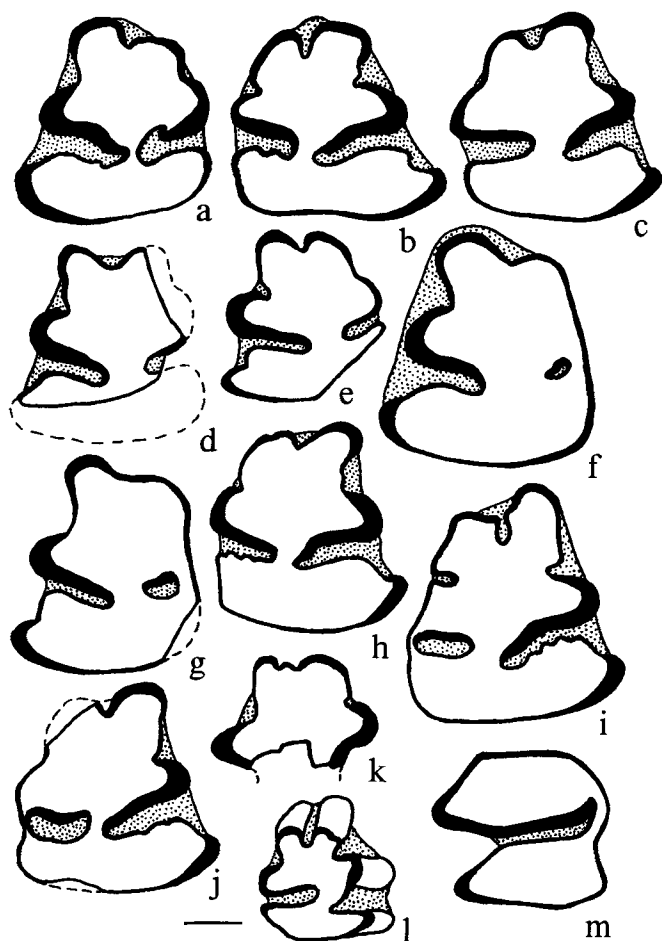


Fig. 5. Occlusal surfaces of p3 (a-k) and m1 (m) of *Trischizolagus dumitrescuae* and juvenile p3 of Recent *Lepus europaeus* (l). – a, b: ZIN 80457, Moskovei, both specimens from one individual; c-e: Lucheshty; f-k: Tatareshty; l: ZIN 28442, Iran; m: Novaya Andriashhevka. – Scale bar: 1 mm.

fig.89), and approach the condition which is seen in *Trischizolagus* from the Late Ruscinian of Greece (KOUFOS & KOLIADIMOU 1993: figs. 2-4).

The p3 show a gradual increase in size from the Early to the Late Ruscinian (Tab. 3, Figs. 4-5). This broad overlap of samples of different age allows us to ascribe all the material to the single species, *T. dumitrescuae* (Fig. 6). Only the tooth from Stavnichevo (Fig. 6 s) is close in size to the type sample of *T. maritsae*, but it comes apparently from a subadult animal. Moreover, all known p3 of *T. maritsae* from Maritsa also come from immature individuals (DE BRUIJN et al. 1970; ERBAEVA & ANGERMANN 1983), so both Ruscinian species of *Trischizolagus* may be synonymous. They differ in the frequencies of p3 morphotypes (Tab. 2), but this may be not enough for species distinction. In morphology the p3 from Moldova and Ukraine show morphotypic variation of the postero-internal re-entrant ('Alilepus' and 'Nekrolagus' morphotypes).

The trigonid of the p3 of young individuals usually lacks grooves filled by cement. However, in later ontogenetic stages, which are visible from the 'root view' of such

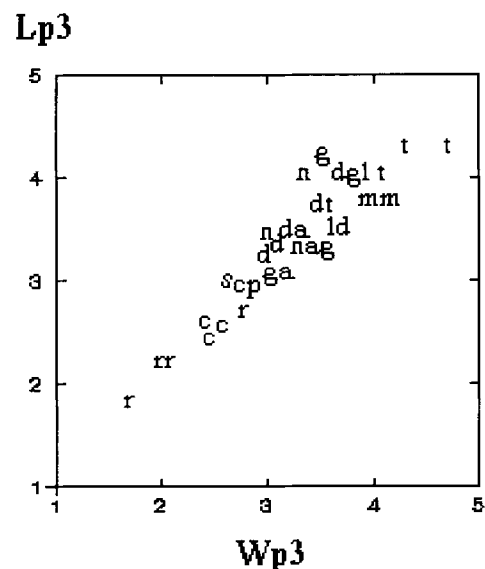


Fig. 6. Bivariate diagram showing allometric relationship of p3 of *Trischizolagus* samples. – a: Novaya Andriashhevka; c: 'Grotte des Rhinocéros', after GERAADS (1994), type material for *Serengetilagus raynali*; d: Malusteni and Beresti, after RADULESCO & SAMSON (1967), type material for *T. dumitrescuae*; g: Grebeniki; l: Lucheshty; m: Moskovei; n: Nikolskoe; p: Pul-e Charkhi, after SEN & ERBAJEVA (1995); r: Maritsa, after DE BRUIJN et al. (1970), type material for *T. maritsae*; s: Stavnichevo; t: Tatareshty.

specimens (Fig. 4a and a'), the short anterior, antero-external and antero-internal re-entrants are usually filled by cement.

The lower molariform teeth, represented in the collection (Fig. 4v, Fig. 5m), are in accordance with that of *Trischizolagus* and do not differ from the teeth of the majority species of leporids. They lack folding of the anterior wall of the talonid.

Discussion

The variation of the *Trischizolagus* p3 shows the gradual shift of morphotype frequencies from the 'Hypolagus' pattern in the Turolian *T. crusafonti* through the mixture of all three patterns in Early Ruscinian to the dominant 'Alilepus' pattern in the Late Ruscinian samples. Early Villafranchian (MN 16 mammal zone) *Trischizolagus* are known only from the locality Obukhovka-2 in the lower flow of the Don River, Russia (NESIN & REKOVETS 1993). The sample of *Trischizolagus* p3 from this locality fits into this trend (Tab. 2). If one extrapolates the observed process, one may expect the predominance of the 'Nekrolagus' morphotype in the Early - Middle Villafranchian and the appearance of the first teeth with the *Lepus* structure. A similar process is observed in the Late Pliocene populations of *Nekrolagus* in North America (HIBBARD 1963). The fossil record of the Early and Middle Villafranchian shows, however, the predominance of *Hypolagus*. The evolutionary lineage leading from *Trischizolagus* to the modern leporines seems to be greatly suppressed in

Tab. 2. Distribution of morphotypes of the p3 in samples of *Trischizolagus*. Asterisks refer to data taken from the literature.

Mn zone	Locality	'Alilepus'	'Nekrolagus'	'Hypolagus'	Reference
Middle Pleistocene	'Grotte des Rhinocéros'		4*		GERAADS 1994
16	Obukhovka 2	7*	2*		NESIN pers. com. 1995
15	Megalo Emvolon		1*		KOUFOS & KOLIADIMOU 1993
15	Moskovei	2			AVERIANOV 1995
15	Lucheshty	5	1		this paper
15	Tatareshty	2	4 + 1*		this paper; DAVID et al. 1989
15	Musait	1*			DAVID & SHUSHPANOV 1986
15	Malusteni	5*	1*		RADULESCO & SAMSON 1967; DAXNER & FEJFAR 1967
15	Beresti	2*			RADULESCO & SAMSON 1967
15	Perpignan		1*		DAWSON 1967
14	Grebeniki	7	5		this paper
14	Nikolskoe	2	2		this paper
14	Stavnichevo	1			this paper
14	Novaya Andriashevka	3	1		this paper
14	Novopetrovka & Kuchurgan	15*	5*	3*	TOPACHEVSKY 1980, 1987
14	Trudomirovka			1*	TOPACHEVSKY 1987
14	Nurnus	1*	3*		MELIK-ADAMYAN 1986
14	Pul-e Charkhi	1*		1*	SEN 1983; SEN & ERBAJEVA 1995
14	Maritsa	3*		5*	DE BRUJN et al. 1970
13-14	Kholbolchi Nor C			1*	FLYNN & BERNOR 1987
13	La Alberca			2*	JANVIER & MONTENAT 1970
13	Alcoy			1*	LOPEZ MARTINEZ 1989
Total					
Middle Pleistocene		—	4 (100%)	—	
16		7 (78%)	2 (22%)	—	
15		17 (65%)	9 (35%)	—	
14		32 (55%)	16 (28%)	10 (17%)	
13		—	—	4 (100%)	

Locality	Length					Width				
	n	min	max	M	m	n	min	max	M	m
P2										
Novaya Andriashevka	4	1.4	1.9	1.68	0.13	4	2.9	4.1	3.30	0.28
Grebeniki 2	14	1.6	1.9	1.78	0.03	12	3.2	3.9	3.50	0.08
Lucheshty	3	2.0	2.0	2.00	—	3	3.5	3.8	3.70	0.10
p3										
Novaya Andriashevka	2	3.1	3.4	3.25	0.15	2	3.1	3.3	3.20	0.10
Grebeniki 2	4	3.2	4.1	3.60	0.21	4	3.0	3.5	3.23	0.11
Nikolskoe	3	3.3	4.0	3.57	0.22	3	3.1	3.3	3.23	0.07
Stavnichevo	1	3.0		—	—	1	2.7		—	—
Moskovei	2	3.7	3.7	3.70	—	2	3.9	3.9	3.90	—
Lucheshty	3	3.4	3.8	3.63	0.12	2	3.5	3.6	3.55	0.05
Tatareshty	5	3.7	4.3	4.02	0.12	5	3.5	4.7	3.96	0.23

Tab. 3. Measurements of P2 and p3 in *Trischizolagus* samples.

this time. The rare indication of the actual persistence of this group is probably the Early Villafranchian *Oryctolagus laynensis* LOPEZ MARTINEZ 1977 from Layna, Spain, that shows both 'Lepus' and 'Nekrolagus' variants of p3 (LOPEZ MARTINEZ 1989: fig. 56.3, 6). The first *Lepus* species with the dominance of 'Lepus' morphotype of p3, *L. valdarnensis*, appeared in the Middle Villafranchian (MN 17 mammal zone, Perrier, Saint-Vallier) and became abundant in the Late Villafranchian (MN 18 mammal zone, Etouaires, Pardines, Upper Val d' Amo) of France and Italy (WEITHOFER 1889; FORSYTH-MAJOR 1899; BOSCO 1900; VIRET 1954; FORTELEONI 1974). Hence, it seems probable that the Early Villafranchian was the time when the speciation events in *Trischizolagus* populations leading to the origin of *Lepus* and *Oryctolagus* species have taken place. These events were accompanied by the described sequence of a shifting in the p3 morphotype frequencies, which fit the scheme of HIBBARD (Fig. 1) proposed for the origin of North American leporines. Moreover, this sequence of phylogenetic events may be indirectly confirmed by the data on variability of the p3 pattern in the Late Pleistocene and Recent hares of the Old World. The 'Nekrolagus' morphotype is relatively more abundant in Recent hares, than the 'Hypolagus' morphotype (Tab. 4). This indicates that the former had higher frequency than the latter in the direct ancestor of modern leporines.

To explain the transformation of the p3 morphology, which could have taken place during the transition be-

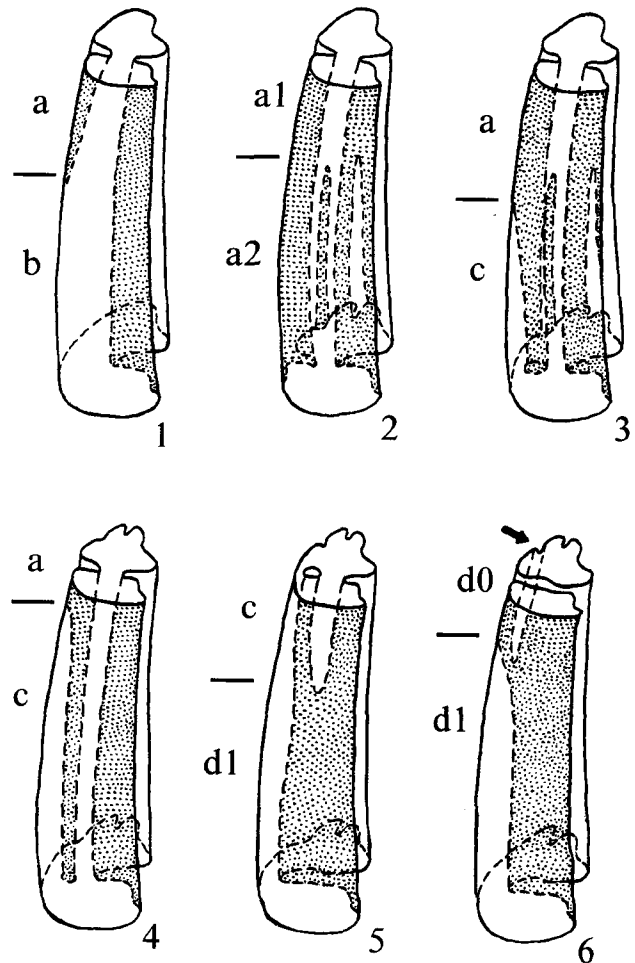


Fig. 7. Ontogenetic transformations of the p3 tooth pattern in the evolution of Leporinae shown on the 'synthetic p3'. - 1-6: tooth ontogenesis; a, a1, a2, b, c, d0, d1: dental stages. Arrow indicates 'juvenile fold'. For further explanations see text.

Tab. 4. Distribution of some rare morphotypes of the p3 (1: with 'juvenile' fold, 2: 'Nekrolagus', 3: 'Hypolagus', 4: 'paedomorphic') in Pleistocene *Lepus tanaïticus* and 12 Recent species of hares of the Old World.

Species	n	Morphotypes (%)			
		1	2	3	4
<i>Lepus tanaïticus</i>	273	4.03			0.73
<i>Lepus timidus</i>	1012	5.73	0.10		1.58
<i>Lepus capensis</i>	423	4.49	0.47		0.24
<i>Lepus europaeus</i>	709	19.75	0.42	0.14	0.56
hybr. <i>L. timidus</i> × <i>L. europaeus</i>	111	20.72	0.90	0.90	6.31
<i>Lepus saxatilis</i>	12				
<i>Lepus victoriae</i>	4	25.00			
<i>Lepus nigricollis</i>	4				
<i>Lepus peguensis</i>	6	16.67			
<i>Lepus sinensis</i>	5				
<i>Lepus yarkandensis</i>	7				
<i>Lepus oiostolus</i>	23				
<i>Lepus mandschuricus</i>	115	0.87	0.87		0.87
<i>Lepus brachyurus</i>	9				
Total	2713	9.36	0.25	0.07	1.14

tween *Trischizolagus* and the modern leporines, we propose the following scheme (Fig. 7):

1. In the normal ontogeny of the p3 in 'archaeolagines' the postero-internal re-entrant sometimes occur in the very early stages (Fig. 7, 1, stage 'a'). This was found in such a typical archaeolagine, as *Hypolagus* (KORMOS 1934: fig.1p-s; SULIMSKY 1964: fig.3a; FLADERER 1987: fig.3a, b). This fold disappears with wear in more adult animals (stage 'b' on Fig. 7, 1).
2. In 'palaeolagines', such as *Alilepus* or *Trischizolagus*, the 'archaeolagine' portion of tooth (= ontogenetic stage 'b' in Fig. 7, 1) was lost (post-displacement event in terms of heterochrony), and subsequently, the 'palaeolagine' stage (stage 'a') was prolonged (Fig. 7, 2). Thus, the p3 of *Alilepus* or *Trischizolagus* was formed by a combined post-displacement of the stage 'b' and paedomorphosis ('neoteny') of stage 'a'. In *Trischizolagus* two additional folds, anterior and antero-internal re-entrants are formed during the later ontogenetic stage (stage 'a2' on Fig. 7, 2). Juvenile p3 of *Trischizolagus* (the ontogenetic stage 'a1') lack

these folds (Fig. 4a, e, t). In early populations of *Trischizolagus* (*T. crusafonti*) the first p3 variant of ontogeny (1 on Fig. 7) was still predominant, but two additional folds had been already developed (mosaic evolution). In the Ruscinian *Trischizolagus* the ontogenies 2 and 3 of p3 (Fig. 7) dominated. The Late Turolian stage of development of the Eurasian *Trischizolagus* was preserved during more than 3 Ma up to the Early Villafranchian in the African *Serengetilagus praecapensis* DIETRICH 1941. In this form among 143 p3 only 1 % have a 'Nekrolagus' pattern, 4 % have 'Alilepus' pattern, whereas the remaining teeth have a 'Hypolagus' pattern (ERBAEVA & ANGERMANN 1983). This autochthonous development of the African lineage supports the validity of the genus *Serengetilagus* and its distinction from *Trischizolagus* (contra FLYNN & BERNOR 1987).

3. The acceleration of stage 'a' and the insertion of a new stage 'c' lead to the formation of a p3 ontogeny with an 'Alilepus' pattern in early wear stages and a 'Nekrolagus' pattern in later stages (Fig. 7, 3). Stage 'a' is still preserved (as individual variation) in some Recent leporids, for example, in juvenile specimens of *Lepus europaeus* (Fig. 5, 1).
4. The subsequent acceleration of stage 'a' and prolongation ('neoteny') of stage 'c' lead to the p3 ontogeny with the constantly present 'Nekrolagus' pattern, except for a very short juvenile period (Fig. 7, 4).
5. The enamel pocket, forming the isle of the postero-internal fold in p3 of the 'Nekrolagus' type can be fused with the postero-external fold at a certain ontogenetic stage (stage 'd1' on Fig. 7, 5). This results in the appearance of a 'Lepus' p3 structure in older wear stages. In terms of heterochrony this means pre-displacement of stage 'a', acceleration of stage 'c', and insertion of a new stage 'd1'.
6. The pre-displacement of the stage 'c' and prolongation of the stage 'd1' can account for the development of the p3 pattern characteristic for modern leporines (Fig. 7, 6). In the early stages of this ontogeny the postero-external fold often interrupts the lingual wall of the tooth and separates the talonid and trigonid of the p3. This 'paedomorphic' morphotype was described many times from juvenile teeth of leporines (e.g. LOPEZ MARTINEZ 1989: fig. 56.4). This structure (Fig. 2) can be retained by paedomorphosis throughout the tooth morphogeny (by post-displacement of 'd1' stage; Fig. 7, 6). The relative abundance of this morphotype in populations of extant hares (Tab. 4), as well as its dominance in some leporine taxa (e.g. *Nesolagus*, see HIBBARD 1963) may reflect the continuation of the paedomorphic processes in their dental morphogeny. Frequently a so-called 'juvenile' fold occurs on the lingual side of p3 (Tab. 4; arrow on Fig. 7, 6; REKOVETS 1985: fig. 6). It may be interpreted as a trace of the postero-internal re-entrant in the direct ancestors of leporines. The fold subsequently shifted anteriorly by the deep postero-external re-entrant. If this is true, it may serve as another evi-

dence in support of the HIBBARD's hypotheses versus the one of CORBET (Fig. 1).

The data presented above show that transformations of p3 pattern in Eurasian *Trischizolagus* took place independently but mainly parallel to that of the North American *Nekrolagus*. Thus, at least the diphyletic origin of the modern leporines can be considered. It seems probable that North American *Sylvilagus*, *Brachylagus*, and *Romeolagus* had a North American origin from *Nekrolagus*, whereas Eurasian and African *Oryctolagus*, *Caprolagus*, *Nesolagus*, and *Poelagus* could have originated in the Old World from *Trischizolagus*.

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