

Pleistocene hares from the East Siberian Arctic (Lagomorpha: Leporidae)

Alexander O. Averianov, Tatyana V. Kuznetsova & Pavel A. Nikol'skii

ABSTRACT. Isolated fossil hare bones from seven Pleistocene localities in the east Siberian Arctic are attributed to *Lepus tanaiticus vereschagini* Averianov, 1995 (Mamontovaya Khayata) and to *L. tanaiticus* subsp. indet. (other localities).

KEY-WORDS: *Lepus*, Pleistocene, Siberia, Arctic.

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Плейстоценовые зайцы Восточно-Сибирской Арктики (Lagomorpha: Leporidae)

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РЕЗЮМЕ. Изолированные ископаемые остатки зайцев из семи плейстоценовых местонахождений Восточно-Сибирской Арктики отнесены к *Lepus tanaiticus vereschagini* Averianov, 1995 (Мамонтовая Хаята) и к *L. tanaiticus* subsp. indet. (другие местонахождения).

КЛЮЧЕВЫЕ СЛОВА: *Lepus*, плейстоцен, Сибирь, Арктика.

Introduction

White hare is one of the typical elements of the modern Arctic theriofauna and was very abundant in the Pleistocene periglacial Arctic-like steppes. In Siberia hare remains are quite common in both Paleolithic sites and natural permafrost localities (see review in Averianov, 1995). However, little taxonomic work was done on these materials. Earlier authors usually referred this hare to the modern species *Lepus timidus* Linnaeus, 1758. Later some authors referred it to the extinct *Lepus tanaiticus* Gureev, 1964, described previously from the Late Pleistocene of European Russia (Gureev, 1964). Averianov (1995) confirmed the latter referral and established a new subspecies, *L. tanaiticus vereschagini* Averianov, 1995 for the Late Pleistocene hares from continental Yakutia. He studied also materials from the Laptev Sea coast and Bol'shoi Lyakhovskii Island, but taxonomic attribution of these samples was not clarified, mostly because of lack of diagnostic remains, notably dentaries and anterior premolars (P2 and p3). Here a new material from the Laptev Sea area is described and taxonomic attribution of these hares is discussed.

Material and localities

Majority of the materials was collected during the field work (1998–2000) of the Russian-German expedition in the frame of the “Laptev Sea System 2000”

project (Kuz'mina *et al.*, 1999; Kuznetsova & Kuz'mina, 2000, 2001). Additional specimens were provided by Pavel A. Nikol'skii (Geological Institute RAS, Moscow). All of these materials are temporarily housed in the Paleontologicheskii Institute RAS in Moscow (abbreviated PIN) and published with field numbers. For comparison the Pleistocene hare bones from Siberia and European Russia, published previously by Averianov & Kuz'mina (1993) and Averianov (1995, 1999), as well as materials on the modern Arctic hares from the collec-

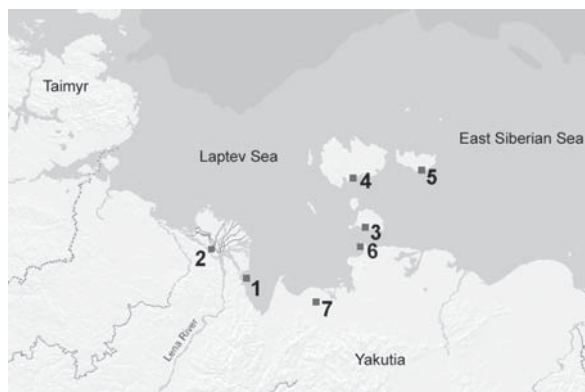


Figure 1. Map of the East Siberian Arctic with position of the Pleistocene hare localities studied in this paper: 1 — Mamontovaya Khayata; 2 — Buor-Khaya; 3 — Bol'shoi Lyakhovskii Island; 4 — Balyktakh; 5 — Tordokh; 6 — Svyatoi Nos; 7 — Yana River Paleolithic Site.

tion of Zoological Institute RAS, were used. Altogether 116 hare bones from seven localities (Fig. 1) were studied:

Locality 1. Mamontovaya Khayata.

Position. Bykovsky Peninsula, Laptev Sea coast, northern Yakutia.

Age. Late Pleistocene.

Material. Four p3, one P2, one skull fragment, five dentary fragments, 35 postcranial bones.

Collector. T.V. Kuznetsova, 1998, 2000.

Locality 2. Buor-Khaya.

Position. Lena River delta, Kurungnah Island, Laptev Sea coast, northern Yakutia.

Age. Late Pleistocene.

Material. One p3, two dentary fragments, one postcranial bone.

Collector. T.V. Kuznetsova, 2000.

Locality 3. Bol'shoi Lyakhovskii Island.

Position. Laptev Sea, New Siberian Islands, northern Yakutia.

Age. Middle–Late Pleistocene.

Material. One skull fragment, 16 postcranial bones.

Collector. T.V. Kuznetsova, 1999.

Locality 4. Balyktakh.

Position. Kotel'nyi Island, Laptev Sea, northern Yakutia.

Age. Late Pleistocene.

Material. One P2, one skull fragment.

Collector. P.A. Nikol'skii.

Locality 5. Tordokh River.

Position. Novaya Sibir' Island, East Siberian Sea, northern Yakutia.

Age. Late Pleistocene.

Table 1. Anterior premolars measurements (L — length, W — width) in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	LP2	WP2	Lp3	Wp3
Mamontovaya Khayata	2.6	2.2	4.3–4.4 4.33±0.03 n=4	3.3–4.3 3.75±0.21 n=4
Buor-Khaya			4.6	4.2
Balyktakh	2.2	4.2		
Svyatoi Nos			~4.3	3.7
Yana Paleolithic Site			4.4	4.0

Table 4. Scapula measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	S3	S4	S5	S6
Mamontovaya Khayata	8.3, 8.4	14.0	13.7	11.7, 12.6
Tordokh			12.6	11.4

Measurements: S3 — minimal length of scapular neck; S4 — ventral end maximal length; S5 — glenoid anteroposterior diameter; S6 — glenoid width.

Table 2. Dentary measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	M1	M2	M3	M4	M5	M6	M7
Mamontovaya Khayata	71.0	50.2	21.3, 21.4	18.8–19.3 19.05±0.25 n=4	22.9–24.6 23.58±0.38 n=4	16.4–17.8 17.10±0.40 n=3	17.2–18.8 18.10±0.47 n=3
Buor-Khaya			21.2	19.5	27.0	18.1	20.2
Svyatoi Nos*	73.8	48.6	20.0, 21.9		21.2–25.1 23.47±1.17 n=3	15.4–17.6 16.65±0.47 n=4	19.5, 20.2
Yana Paleolithic Site			22.8		25.7	17.5	19.2

Measurements: M1 — dentary length; M2 — height of coronoid process; M3 — alveolar length of p3–m3; M4 — crown length of p3–m3; M5 — diastema length; M6 — dentary depth at p3; M7 — dentary depth at m3.

* one specimen added from Averianov (1995).

Table 3. Skull measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	C4	C5	C6	C7	C8	C10	C11	C12	C13	C14	C16	C18	C19
Mamontovaya Khayata	7.4	14.7	26.0	11.6	11.7	21.1	30.0	42.4	48.4	52.4	21.4	22.2	17.2
Bol'shoi Lyakhovskii Island	8.0	14.8	24.4	11.2	10.3	19.6	29.2					24.0	18.2
Balyktakh	9.1			9.1	11.4	21.1							

Measurements: C4 — bony palate length; C5 — bony palate width between P3; C6 — incisive foramen length; C7 — incisive foramen width; C8 — choanae width; C10 — alveolar length of P2–M3; C11 — diastema length; C12 — zygomatic arch length; C13 — skull width at anterior zygomatic roots; C14 — skull width at posterior zygomatic roots; C16 — maximal nasal length along midline; C18 — frontals width anterior to supraorbital processes; C19 — frontals width posterior to supraorbital processes.

Table 5. Humerus measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	H3	H5
Mamontovaya Khayata		13.2, 13.9
Bol'shoi Lyakhovskii Island		13.0–14.5 13.97±0.4 8n=3
Tordokh	18.9	
Svyatoi Nos		12.8–13.9 13.34±0.1 8n=5
Yana Paleolithic Site		12.3

Measurements: H3 — proximal end maximal width; H5 — distal end width.

Table 6. Radius measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	R1	R2	R3
Mamontovaya Khayata	114.8	8.7–10.3 9.56±0.27 n=5	10.3, 10.7
Bol'shoi Lyakhovskii Island			10.6
Yana Paleolithic Site		9.5	

Table 7. Ulna measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	U3
Mamontovaya Khayata	9.8
Svyatoi Nos	8.5

Measurements: U3 — humerus articulation surface width.

Table 9. Pelvis measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

	P2	P3	P4	P5
Mamontovaya Khayata	15.2–17.6 16.48±0.50 n=4		18.7–21.7 20.30±0.87 n=3	10.9–12.2 11.55±0.35 n=3
Bol'shoi Lyakhovskii Island	16.0–17.5 16.94±0.21 n=8	23.2	17.7–20.6 19.52±0.52 n=5	11.0–12.7 11.91±0.20 n=8
Svyatoi Nos	16.0–16.8 16.33±0.24 n=3			11.4–13.1 12.13±0.50 n=3

Measurements: P2 — acetabulum length; P3 — symphysis length; P4 — obturator foramen length; P5 — minimal ilium height anterior to acetabulum.

Measurements: R1 — maximal length; R2 — proximal end width; R3 — distal end width.

Table 8. Metacarpals (II–IV) measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	LII	WpII	WdII	LIII	WpIII	WdIII	LIV	WpIV	WdIV
Svyatoi Nos	31.0, 32.1	4.4, 4.5	4.7, 5.1	29.6, 29.9	4.3, 4.3	4.6, 4.8	26.7	3.8	4.9

Measurements: L — length; Wp — proximal end width; Wd — distal end width.

Table 10. Femur measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	F1	F2	F3	F4	F5	F6	F7
Mamontovaya Khayata	123.4	116.8	27.1–28.6 28.00±0.46 n=3	24.3–26.0 25.25±0.36 n=4	10.3–11.1 10.75±0.18 n=4	9.1–9.8 9.35±0.16 n=4	19.6–21.0 20.15±0.31 n=4
Svyatoi Nos							18.4

Measurements: F1 — maximal length; F2 — distance from femoral head to distal end; F3 — proximal end width from femoral head to greater trochanter; F4 — proximal end width at level of lesser and third trochanters; F5 — femoral head anteroposterior diameter; F6 — diaphysis minimal width; F7 — distal end width.

Table 11. Tibia measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	T1	T2	T3	T4	T5
Mamontovaya Khayata	144.0	20.6	7.6–8.7 8.18±0.23 n=4	13.3–15.3 14.54±0.28 n=8	9.7–10.9 10.30±0.13 n=8
Buor-Khaya				14.5	10.2
Bol'shoi Lyakhovskii Island			8.2, 8.5	14.3, 14.9	9.8, 9.9
Tordokh		20.1		15.3	10.8
Svyatoi Nos				14.4, 15.3	10.0, 10.3
Yana Paleolithic Site				14.1	10.1

Measurements: T1 — maximal length; T2 — proximal end width; T3 — diaphysis minimal width; T4 — distal end width; T5 — distal end anteroposterior diameter.

Material. Four postcranial bones.

Collector. P.A. Nikol'skii, 2002.

Locality 6. Cape Svyatoi Nos, Kondrat'eva River.

Position. Laptev Sea coast, northern Yakutia.

Age. Late Pleistocene.

Material. One p3, three dentary fragments, 31 postcranial bones.

Collector. P.A. Nikol'skii.

Locality 7. Yana River Paleolithic Site.

Position. Lower Yana River, northern Yakutia.

Age. Late Pleistocene.

Material. One p3, two dentary fragments, five postcranial bones.

Collector. P.A. Nikol'skii.

Table 12. Astragalus and calcaneus measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	A1	A2	C1	C2
Mamontovaya Khayata			32.5	20.6
Bol'shoi Lyakhovskii Island			31.6, 33.0	20.2, 20.5
Svyatoi Nos	17.2–18.0 17.70±0.19 n=4	7.2–9.0 8.01±0.25 n=6	33.2–37.2 34.38±0.95 n=4	20.7–23.3 21.55±0.60 n=4

Measurements: A1 — astragalus maximal length; A2 — astragalus trochlea width; C1 — calcaneum maximal length; C2 — distance from tuber calcanei proximal end to fibular facet distal end.

Table 13. Metatarsals (II–V) measurements in the Late Pleistocene *Lepus tanaiticus* from the East Siberian Arctic.

Samples	LII	WpII	WdII	LIII	WpIII	WdIII	LIV	WpIV	WdIV	LV	WpV	WdV
Mamontovaya Khayata		4.7										
Bol'shoi Lyakhovskii Island	49.9	4.9	6.4	53.0	5.4	6.4						
Tordokh				52.3	5.5	6.4						
Svyatoi Nos				53.5	5.7	6.7	52.2, 52.7	6.0, 6.2	5.9, 6.4	48.6	8.5	5.6
Yana				53.0	5.2	6.3				43.2	8.5	5.5

Measurements: L — length; Wp — proximal end width; Wd — distal end width.

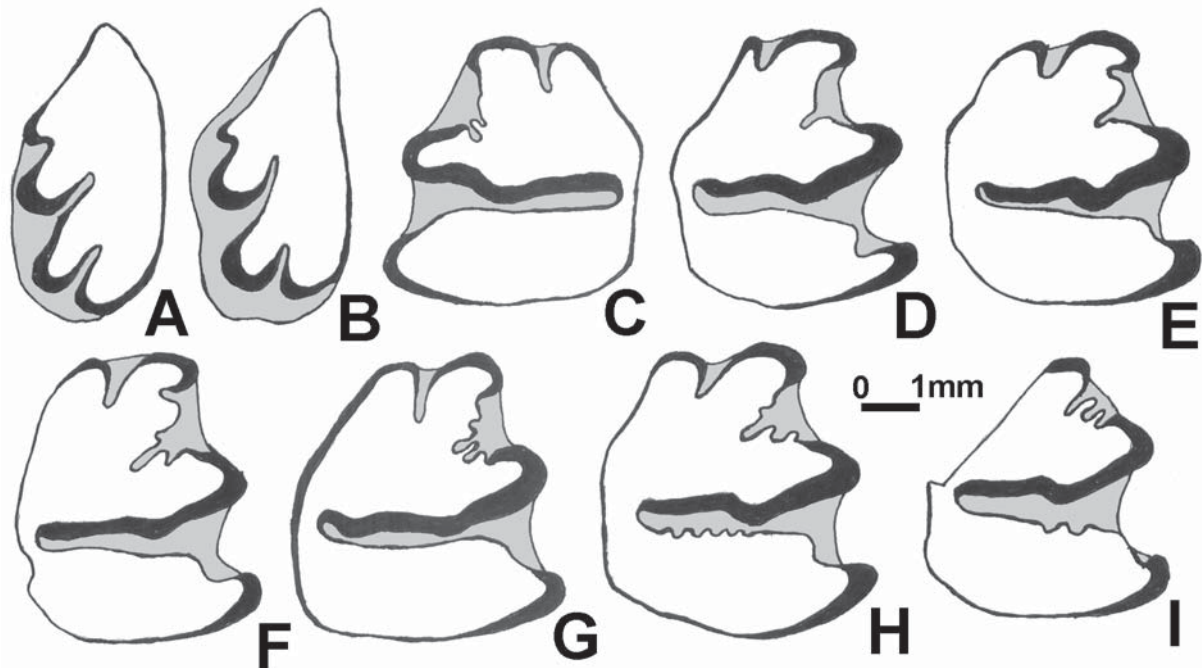


Figure 2. P2 (A, B) and p3 (C–I) of *Lepus tanaiticus* from the East Siberian Arctic in occlusal view. Dentine is white, enamel is black, and cement is gray. Scale bar is 1 mm.

A, C–F — Mamontovaya Khayata, PIN MKh-O276 (left), MKh00-O115 (left), MKh-O83 (right), MKh-O164 (right), and MKh-O82 (right); B — Balyktakh, PIN without number (left); G — Buor-Khaya, PIN BKh-O93 (right); H — Yana River Paleolithic Site, PIN without number (right); I — Svyatoi Nos, PIN without number (right incomplete).

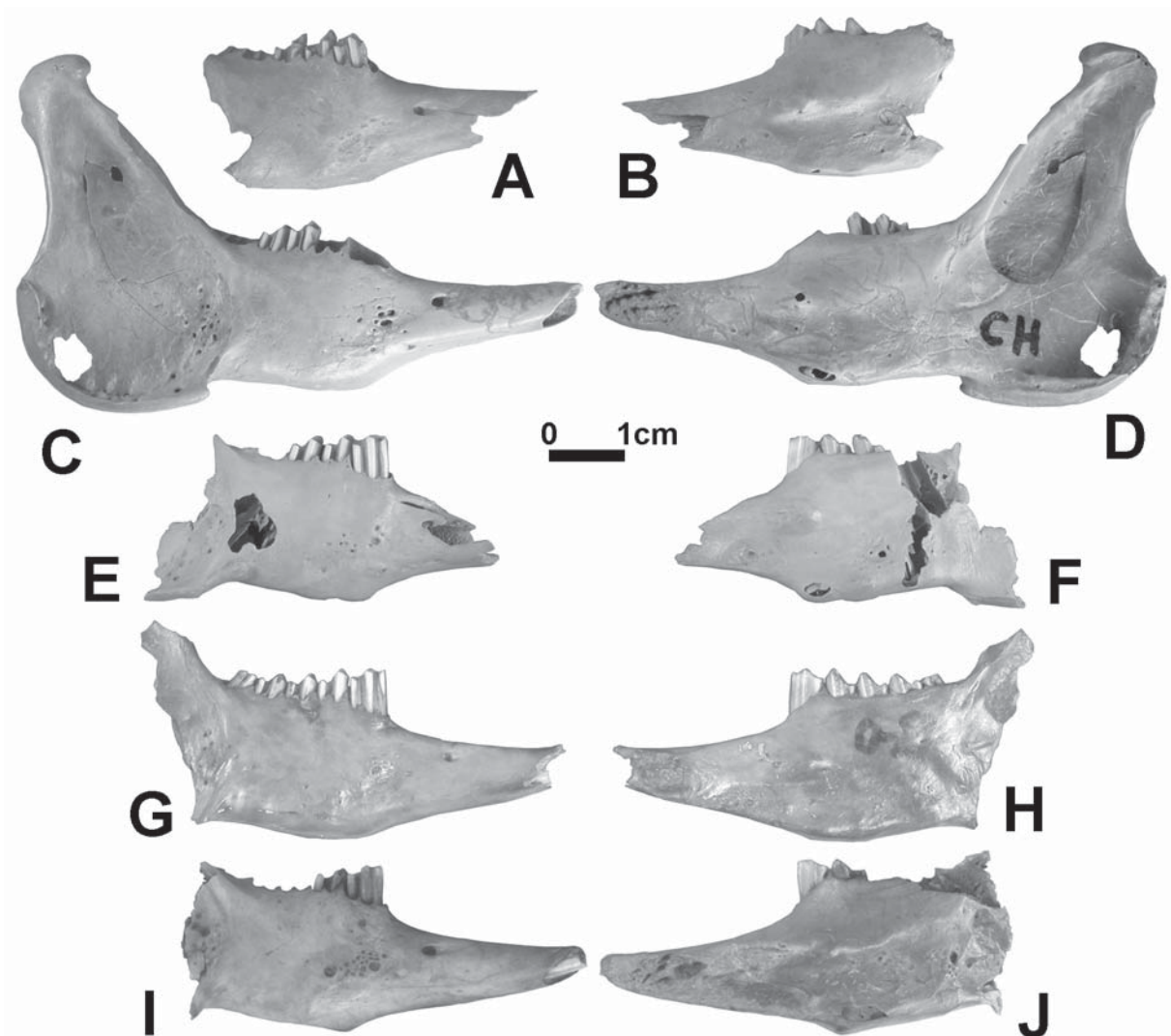


Figure 3. Right dentaries of *Lepus tanaiticus* from the East Siberian Arctic in labial (A, C, E, G, I) and lingual (B, D, F, H, J) views. Scale bar is 1 cm.

A, B — Svyatoi Nos, PIN Sv-Nos 1; C, D — Svyatoi Nos, PIN Sv-Nos 2; E, F — Mamontovaya Khayata, PIN MKh-O164; G, H — Mamontovaya Khayata, PIN MKh-O83; I, J — Yana River Paleolithic Site, PIN without number.

Description and discussion

New Pleistocene hare materials from the East Siberian Arctic agrees well with the description of *L. tanaiticus* (Gureev, 1964; Averianov & Kuz'mina, 1993; Averianov, 1999): they similarly large in size (Tabs. 1–13), have complicated p3 morphology with larger number of minute folds in the anteroexternal reentrant (Fig. 2; 1–5 folds, $M=3.0\pm 0.53$, $n=7$); in *L. tanaiticus* this mean number exceeds 2.0 in contrast with the Recent and Pleistocene *L. timidus* populations, where it varies from 0.50 to 1.79, see Averianov, 1999: tab.7), and have very deep horizontal ramus of the dentary (Fig. 3). Two p3 specimens (Fig. 2H, I) have folded anterior talonid margin, which is usually not characteristic for the white hares lineage.

In size the Pleistocene *L. tanaiticus* exceeds most of the modern white hares populations, except the largest Arctic subspecies *L. timidus tschuktschorum* Nordquist, 1883, which approximates the smallest samples of *L. tanaiticus* (Fig. 4). Hares from Mamontovaya Khayata are almost identical in p3 and dentary measurements with the sample from Berelekh, and could be confidently attributed to *L. tanaiticus vereschagini* described from that site (Averianov, 1995). Materials from other East Siberian Arctic localities are still insufficient for the subspecies determination. Larger specimens from Buor-Khaya and Yana Paleolithic Site may indicate existence of a distinct subspecies.

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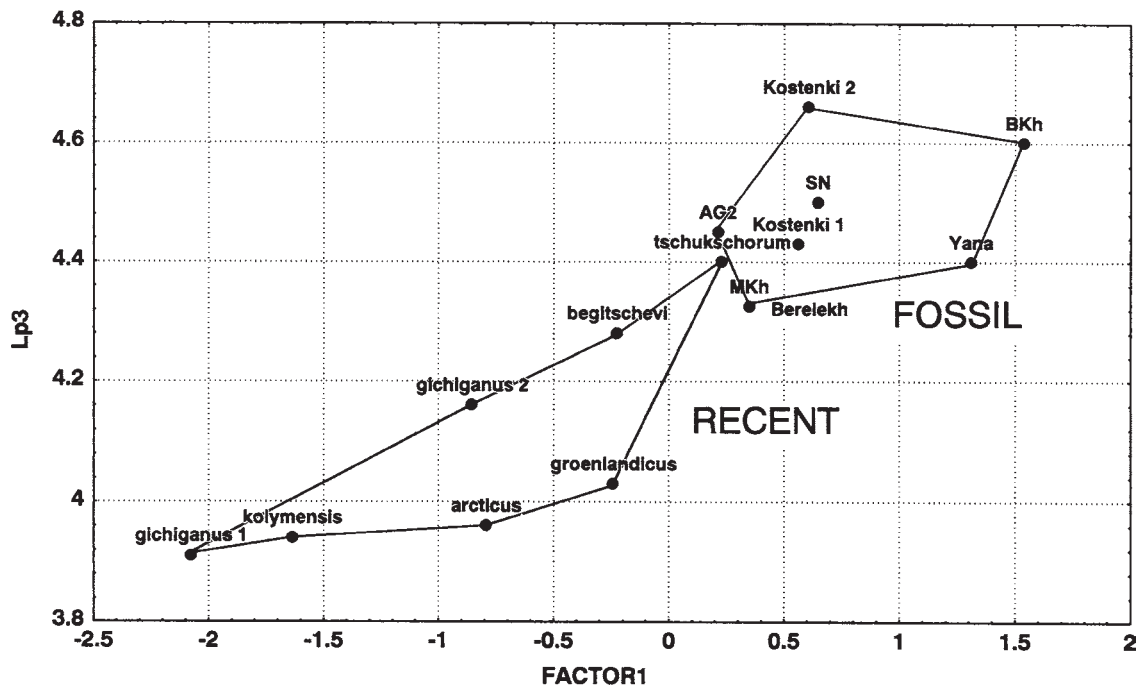


Figure 4. Scatterplot diagram of the p3 length (Lp3) relation to the dentary measurements exemplified by FACTOR 1 from the principal component analysis in the recent and Pleistocene *Lepus* samples (delineated separately). Measurements are from Averianov (1995) and this paper.

Recent samples: *L. timidus gichiganus* J.A.Allen, 1903 (1 — Yakutia, 2 — Chukotka); *L. timidus kolymensis* Ognev, 1922 (eastern Yakutia); *L. timidus begitschevi* Koljushev, 1936 (Taimyr); *L. timidus tschukschorum* Nordquist, 1883 (eastern Chukotka); *L. arcticus* Ross, 1819 (Alaska and Canada).

Fossil samples: Mamontovaya Khayata (MKh, Yakutia); Berelekh (Yakutia, type locality for *L. tanaiticus vereschagini* Averianov, 1995); Afontova Gora 2 (AG2, Krasnoyarsk Territory); Kostenki (Voronezh Province, 1 — humus deposits, type locality for *L. tanaiticus gmelini* Averianov & Kuz'mina, 1993; 2 — loess deposits, type locality for *L. tanaiticus tanaiticus* Gureev, 1964); Svyatoi Nos (SN, Yakutia); Yana River Paleolithic Site (Yakutia); Buor-Khaya (BKh).

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