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Pleistocene snow voles (*Chionomys* MILLER, 1908) (*Rodentia, Mammalia*) from Northern Caucasus (USSR)

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Abstract. Pleistocene remains of *Chionomys* from Paleolithic cave sites of Northern Caucasus are described. *Ch. gud* and *Ch. roberti* are present in the region at least from the beginning of Middle Pleistocene while *Ch. nivalis* seems not to appear before Early/Middle Weichselian boundary.

Key words: Pleistocene, *Chionomys*, Caucasus.

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I. INTRODUCTION

Among voles of the genus *Microtus* (*sensu lato*), snow voles (*Chionomys* MILLER, 1908) form a well defined group of taxa comprising three species: *Chionomys nivalis* (MARTINS, 1842), *Ch. gud* (SATUNIN, 1909) and *Ch. roberti* (THOMAS, 1908) (GROMOV, POLYAKOV 1977, CORBET 1978). They inhabit mountain regions of Europe (only *Ch. nivalis*) and some parts of Asia, including the Caucasus and Transcaucasia. Crucial for the reconstruction of the origin and history of *Chionomys* are studies of fossil materials from the Caucasus because only in this region do 3 recent species occur together.

Up to now, fossil remains of *Chionomys* from this region have been described mainly from southern slopes of the Greater Caucasus or Transcaucasia. *Ch. roberti* was mentioned from Acheulean and/or Mousterian levels of Sakazhya (VEKUA et al. 1980) and Tsona (VEKUA et al. 1981). LYUBIN et al. (1971) noted *Ch.* ex gr. *gud - roberti* from Kepshinskaya Cave while GROMOV and FOKANOV (1980) described this taxon from Kudaro 1. BARYSHNIKOV and CHISTYAKOV (1985) mentioned *Ch. gud* from Sary-Leget Cave. More comprehensive studies of the new material of *Ch. gud* and *Ch. roberti* from Kudaro 1 and

3 were undertaken by BARYSHNIKOV and BARANOVA (1983). Holocene materials of the genus *Chionomys* (all three species) were described from Talyng-Leget Cave (BARYSHNIKOV et al. 1986), while Pleistocene samples from Matuzka Cave (BARYSHNIKOV and GOLOVANOVA 1989). This study reviews the Pleistocene material of *Chionomys* from the north - western part of the Greater Caucasus.

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II. LOCALITIES AND MATERIAL

The material examined comprises both recent and fossil specimens from the region of the Caucasus and Transcaucasia. For comparison, the following recent taxa have been studied: *Ch. nivalis loginovi* (OGNEV, 1950) (Greater Caucasus), *Ch. nivalis trialeticus* (SHIDLOVSKIJ, 1919) (Transcaucasia), *Ch. gud gud* (SATUNIN, 1909) (Greater Caucasus, central part), *Ch. gud nenjukovi* (FORMOSOV, 1931) (Greater Caucasus, western part), *Ch. roberti roberti* (THOMAS, 1908) (Giresun, Trabzon and Lazistan Daglari, Turkey), *Ch. roberti occidentalis* (TUROV, 1928) (Greater Caucasus, western part). The materials are stored in the Zoological Museum of Lomonosov State University, Moscow (ZMUM), Zoological Institute of Academy of Sciences of the USSR, St.-Peterburg (ZIAS), British Museum (Natural History), London (BMNH) and Naturhistorisches Museum, Wien (NHMW).

The fossil material comes from 5 cave sites located in the northern slopes of the Greater Caucasus (Fig. 1) and has been collected during archaeological excavations in eighties. It consists of isolated molars only. All material is stored in the Zoological Institute, Academy of Sciences of the USSR in St.-Peterburg. Basic information concerning localities can be summarized as follows:

Matuzka Cave

L o c a t i o n : Guamka, north-western edge of Lagonaki Plateau, (Krasnodarskij Kraj, Apsheron District).

The cave occurs at an altitude of 720 m in a zone of beech forest with addition of the box and yew trees. The excavations were undertaken by L.V. GOLOVANOVA (St.-Peterburg) in 1985-1988, while rodent remains were collected by G. BARYSHNIKOV in 1986-1988. Layers 3-7 contained Mousterian implements, while ceramics of Bronze Age were found in layers 1 and 2. Trench no. 3 contained mixed material of late Pleistocene and Holocene age.

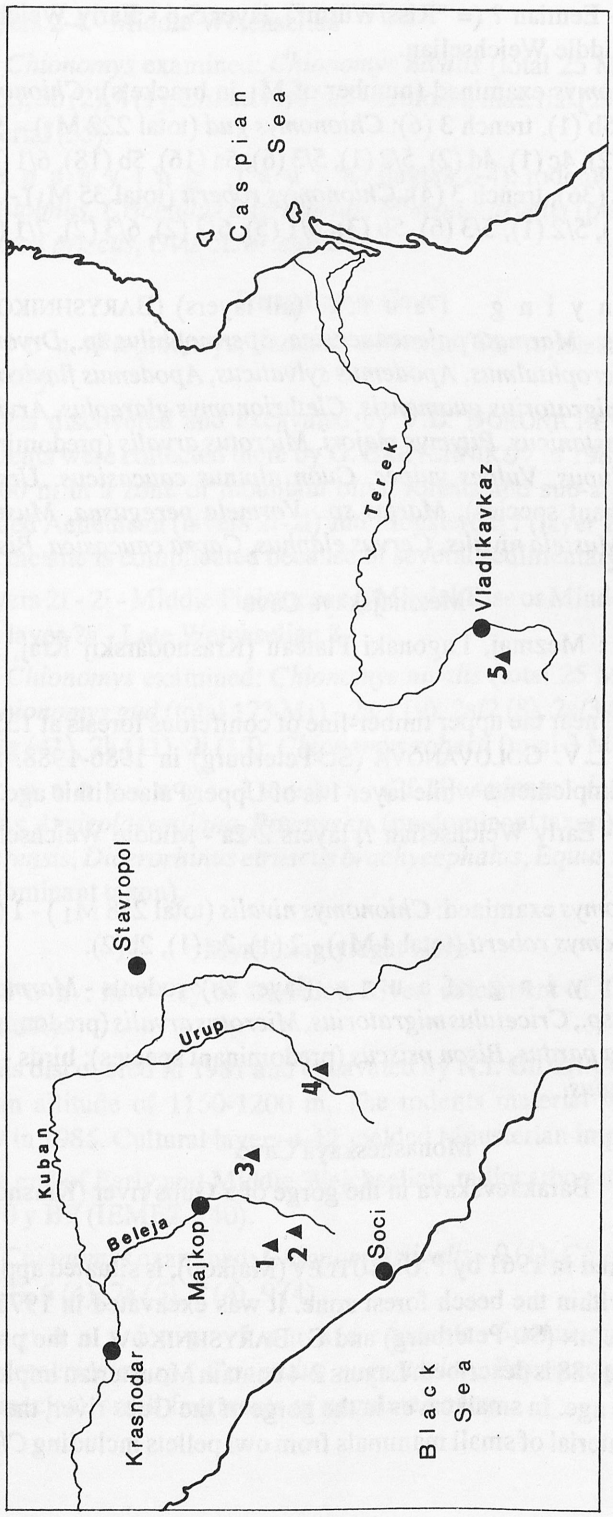

Fig. 1. Location of fossil sites in Northern Caucasus. 1 – Matuzka Cave, 2 – Mezmajskaya Cave, 3 – Monashevskaya Cave, 4 – Treugolnaya Cave, 5 – Myshtulagtylagat Cave.

A g e : layer 7 - Eemian ? (= "Riss/Würm"), layer 5-6 - Early Weichselian (early Würm), layer 3-4 - Middle Weichselian.

Material of *Chionomys* examined (number of M_1 in brackets): *Chionomys nivalis* (total 8 M_1) - 5/1 (1), 5b (1), trench 3 (6); *Chionomys gud* (total 222 M_1) - 3a (6), 3b (5), 4a/1 (3), 4a/2 (7), 4b (2), 4c (1), 4d (2), 5/2 (1), 5/3 (6), 5a (16), 5b (18), 6/1 (21), 6/2 (29), 6/3 (28), 7/1 (37), 7/2 (36), trench 3 (4); *Chionomys roberti* (total 35 M_1) - 3a(1), 3b (1), 4a/1 (1), 4b (1), 4d (1), 5/2 (1), 5/3 (6), 5b (3), 6/1 (5), 6/2 (2), 6/3 (2), 7/1 (11), trench 3 (3).

A c c o m p a n y i n g f a u n a (all layers) (BARYSHNIKOV, GOLOVANOVA 1989): rodents - *Marmota paleocaucasica*, *Spermophilus sp.*, *Dryomys nitedula*, *Sicista sp.*, *Spalax microphtalmus*, *Apodemus sylvaticus*, *Apodemus flavicollis*, *Cricetus cricetus*, *Cricetulus migratorius guamensis*, *Clethrionomys glareolus*, *Arvicola* cf. *chosarica*, *Pitymys daghestanicus*, *Pitymys majori*, *Microtus arvalis* (predominant species); megafauna - *Canis lupus*, *Vulpes vulpes*, *Cuon alpinus caucasicus*, *Ursus deningeri kudarensis* (predominant species), *Martes sp.*, *Vormela peregusna*, *Mustela erminea*, *Mustela boccamela*, *Mustela nivalis*, *Cervus elaphus*, *Capra caucasica*, *Bison sp.*

Mezmajskaya Cave

L o c a t i o n : Mezmaj, Lagonaki Plateau (Krasnodarskij Kraj, Adygejskaya AO)

The cave is located near the upper timber-line of coniferous forests at 1350 m altitude. It was excavated by L.V. GOLOVANOVA (St.-Peterburg) in 1986-1988. Lower layers supplied Mousterian implements while layer 1 is of Upper Palaeolithic age.

A g e : layer 2b - Early Weichselian ?, layers 2-2a - Middle Weichselian, layer 1 - Late Weichselian ?

Material of *Chionomys* examined: *Chionomys nivalis* (total 258 M_1) - 1 (2), 2 (53), 2a (21), 2b (182); *Chionomys roberti* (total 4 M_1) - 2 (1), 2a (1), 2b(2).

A c c o m p a n y i n g f a u n a (layer 2b): rodents - *Marmota paleocaucasica*, *Spermophilus sp.*, *Cricetulus migratorius*, *Microtus arvalis* (predominant species); megafauna - *Panthera pardus*, *Bison priscus* (predominant species); birds - *Pyrrhocorax pyrrhocorax*, *P. graculus*.

Monasheskaya Cave

L o c a t i o n : Barakaevskaya in the gorge of a Gubs river (Krasnodarskij Kraj, Mostovskoj District).

The cave, discovered in 1961 by P.U. AUTLEV (Majkop), is situated approximately at 600-700 m altitude within the beech forest zone. It was excavated in 1975, 1976, 1987 and 1988 by V.P. LYUBIN (St.-Peterburg) and G. BARYSHNIKOV. In the present paper a collection from 1987-1988 is described. Layers 2-4 contain Mousterian implements, while layer 1 is of Holocene age. In small caves in the gorge of the Gubs river, the junior author collected subfossil material of small mammals from owl pellets including *Chionomys gud* and *Ch. roberti*.

A g e : layers 2-4 - Middle Weichselian

Material of *Chionomys* examined: *Chionomys nivalis* (total 25 M_1) - 2 (3), 3a/1 (4), 3a/2 (13, 3a/3 (2), 3b (2), 4 (1); *Chionomys gud* - subfossil material (2); *Chionomys roberti* - subfossil material (35).

A c c o m p a n y i n g f a u n a (layers 2-4): rodents - *Spermophilus sp.*, *Spalax microphtalmus*, *Cricetulus migratorius*, *Microtus arvalis* (predominant species); megafauna - *Bison priscus*, *Ovis* cf. *orientalis*.

Treugolnaya Cave

L o c a t i o n : Pregradnaya, Baranakha Plateau (Stavropolskij Kraj, Karachaevo-Cherkesskaya AO).

This cave was discovered and excavated by V.B. DORONICHEV (St.-Peterburg) in 1986-1988; rodents were collected there by G. BARYSHNIKOV in 1987. It is situated at an altitude of 1500 m in a zone of mountain birch forests and sub-alpine meadows. The sediments yielded Acheulean (layers 2f-2i) and Mousterian ? (layer 2b) implements. The stratigraphy of the site is complicated because of several sedimentary gaps.

A g e : layers 2f - 2i - Middle Pleistocene ("Mindel/Riss or Mindel"), layer 2b - Early Weichselian ?, layer 2a - Late Weichselian ?

Material of *Chionomys* examined: *Chionomys nivalis* (total 25 M_1) - 2a/1 (13), 2a/2 (4), 2a/3 (8); *Chionomys gud* (total 173 M_1) - 2a/1 (9), 2a/2 (8), 2a/3 (27), 2b (42), 2c (6), 2e (5), 2f (7), 2g (41), 2h (11), 2i (17); *Chionomys roberti* (total 3 M_1) - 2a/3 (2), 2c (1).

A c c o m p a n y i n g f a u n a (2f-2i): rodents - *Lagurus cf. transiens*, *Eolagurus luteus*, *Arvicola cantiana*, *Pitymys sp.* (predominant taxon); megafauna - *Ursus deningeri kudarensis*, *Dicerorhinus etruscus brachycephalus*, *Equus sp.*, *Cervus elaphus*, *Bison sp.* (predominant taxon).

Myshtulagtylagat Cave

L o c a t i o n : in valley of Gizeldon River, catchment of Terek river (Severo-Osetinskaya ASSR).

The cave was discovered in 1981 and excavated by N.I. GIDZHRATI (Vladikavkaz). It is situated at an altitude of 1150-1200 m. The rodents material was collected by G. BARYSHNIKOV in 1985. Cultural layers 4-12 yielded Mousterian implements.

A g e : the end of Early and Middle Weichselian, radiocarbon date (^{14}C) for layer 5 is 32980 ± 1070 y BP (IEMEZ-740).

Material of *Chionomys* examined: *Chionomys nivalis* - 9 (1); *Chionomys gud* (total 29 M_1) - 4 (5), 5 (7), 6 (4), 7a (5), 7 (4), 9 (4).

A c c o m p a n y i n g f a u n a : rodents - *Spalax microphtalmus*, *Cricetus cricetus*, *Mesocricetus sp.*, *Cricetulus migratorius*, *Pitymys sp.*, *Microtus arvalis* (predominant species), small fragments of ungulate bones.

III. METHODS

Measurements and ratios used in the quantitative analyses and the terminology of the morphological dental elements were adopted from VAN DER MEULEN (1973) (Fig. 2). Only three parameters appear to be useful for distinguishing the *Chionomys* species (i.e. length of M_1 - L, and indices A/L and C/W). On the basis of the high polymorphism of the first lower molar pattern (ANGERMANN 1974, NADACHOWSKI 1990 a, b) the fossil material was compared with recent samples using the morphotype analysis method (Fig. 3). About 60 morphological variants of M_1 were distinguished. They were assembled in 10 following morphotypes:

Morphotype A: BSA4 absent or incipient; lack of LRA5; T5 and T6 largely confluent.

Morphotype B: BSA4 absent or incipient; LRA5 well developed; T5 and T6 largely confluent.

Morphotype C: BSA4 distinctly developed; appearance of BRA4; more or less opposite position of LSA5 and BRA4; T5 and T6 still confluent.

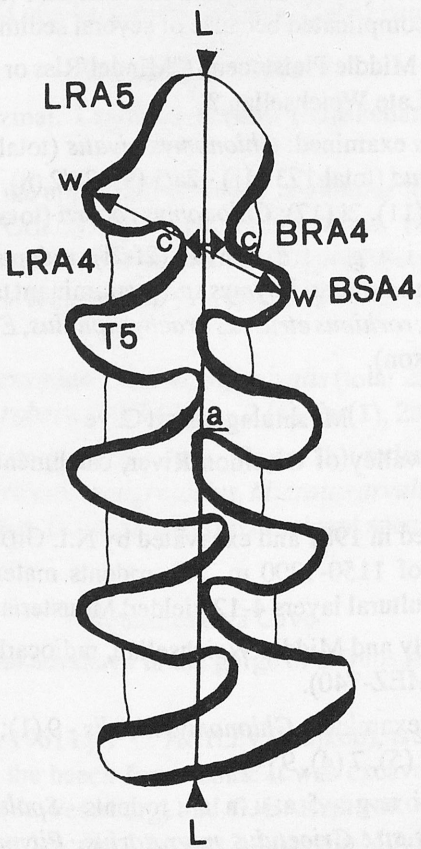

Fig. 2. Nomenclature of M_1 occlusal surface and parameters measured in voles: T - triangle, BRA - buccal reentrant angle, BSA - buccal salient angle, LRA - lingual reentrant angle; L-L = L, L-a = A, W-W = W, C-C = C (partly from VAN DER MEULEN 1973).

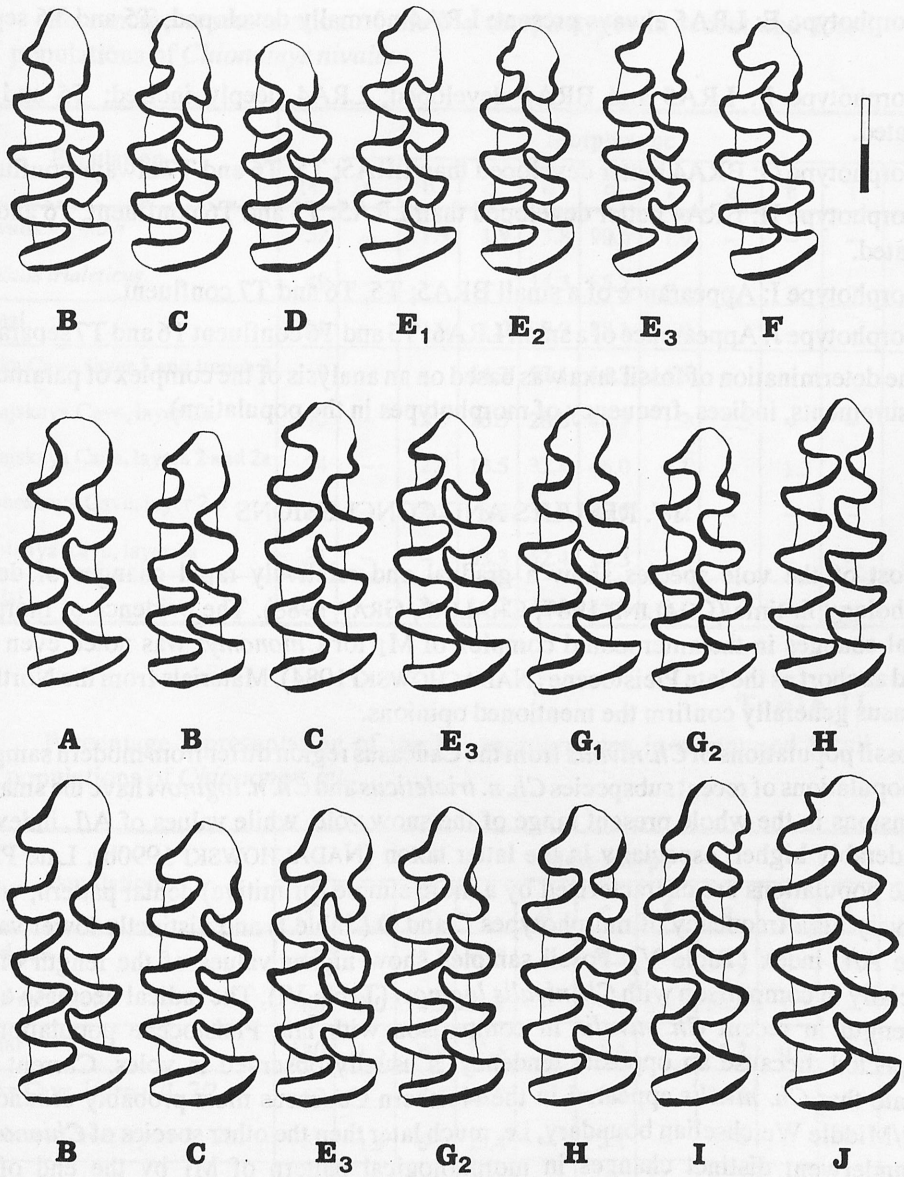

Fig. 3. Morphological variability of M_1 in the recent *Chionomys* species from Caucasus and Transcaucasia. *Ch. nivalis* - upper row: B - Mamisonskij Per., Severo-Osetinskaya Doroga ZMUM 78388, C - Kavkazkij Zapovednik ZMUM 20722, D - Kavkazkij Zap. ZMUM 20663, E_1 - Teberda ZMUM 115085, E_2 - Bambak, Kavkazkij Zap. ZIAS 31542, E_3 - Teberda ZMUM 115084, F - Teberda ZMUM 101497; *Ch. gud* - middle row: A - Kavkazkij Zap. ZMUM 78957, B - Severnyj Kavkaz ZIAS 65162, C - Teberda ZMUM 136068, E_3 - Khulem ZMUM 17796, G_1 - Kavkazkij Zap. ZMUM 20677, G_2 - Kavkazkij Zap. ZMUM 20754, H - Kavkazkij Zap. ZMUM 20697; *Ch. roberti* - lower row: B - Kambushevka ZMUM 178832, C - Kavkazkij Zap. ZMUM 7924, E_3 - Zakatelskij Zap. ZIAS 37535, G_2 - Teberda ZIAS 28685, H - Sumela, Turkey BMNH 636129, I - Sumela BMNH 636125, J - Sumela BMNH 636113. Scale represents one milimeter.

Morphotype D: LRA5 and BRA4 absent; T5 and T6 well separated.

Morphotype E: LRA5 always present; LRA4 normally developed; T5 and T6 separated.

Morphotype F: LRA5 and BRA4 developed; LRA4 deeply incised; T5 and T6 separated.

Morphotype G: BRA4 better developed than LRA5; T5, T6 and T7 always confluent.

Morphotype H: BRA4 better developed than LRA5; T5 and T6 confluent, T6 and T7 separated.

Morphotype I: Appearance of a small BRA5; T5, T6 and T7 confluent.

Morphotype J: Appearance of a small LRA6; T5 and T6 confluent T6 and T7 separated.

The determination of fossil taxa was based on an analysis of the complex of parameters (measurements, indices, frequency of morphotypes in the population).

IV. RESULTS AND CONCLUSIONS

Most of the vole species show a gradual and relatively rapid changes of dental morphology in time (CHALINE 1987, CHALINE, GRAF 1988). The evidence of morphological changes in the anteroconid complex of M_1 for *Chionomys* was noted even in a period as short as the late Pleistocene (NADACHOWSKI 1984). Materials from the Northern Caucasus generally confirm the mentioned opinions.

Fossil populations of *Ch. nivalis* from the Caucasus region differ from modern samples. The populations of recent subspecies *Ch. n. trialeticus* and *Ch. n. loginovi* have the smallest dimensions in the whole present range of the snow vole, while values of A/L index are considerably higher, especially in the latter taxon (NADACHOWSKI 1990b). Late Pleistocene populations are characterized by a more simple (primitive) dental pattern, with a relatively high frequency of morphotypes C and D (Table I) and distinctly lower values of the A/L index (Table V). Fossil samples show higher values of the length of M_1 especially in comparison with *Ch. nivalis loginovi* (Table VI). The radical decrease of the M_1 length in recent *Ch. nivalis* in comparison with late Pleistocene populations is unexpected, because an opposite tendency is usually observed in voles. Current data indicate that *Ch. nivalis* appeared in the Northern Caucasus most probably around the Early/Middle Weichselian boundary, i.e. much later then the other species of *Chionomys*, and underwent distinct changes in morphological pattern of M_1 by the end of the Pleistocene and the beginning of the Holocene.

Fossil teeth of *Ch. gud* can be divided into two distinct groups (Tables II, V, VI). Special attention should be paid to older (Middle Pleistocene) materials from Matuzka Cave (layers 7/2 and 7/1) and Treugolnaya Cave (layers 2e-2i) which show a "primitive" morphological pattern with a marked predomination of morphotype C (Fig. 3). These populations are characterized by an incipient development of BRA4 (in a typical *Ch. gud* it is deeply incised) and a more or less opposite position of LSA5 and BSA4. (Fig. 4). These differences can be also expressed by a special measurement (Fig. 4), which shows

Table I

Percentage representation of the M_1 morphotypes in recent and fossil populations of *Chionomys nivalis*

Population	Morphotype										
	N	a	b	c	d	e	f	g	h	i	j
Ch. nivalis loginovi	52	–	1.9	1.9	3.8	90.5	1.9	–	–	–	–
Ch. nivalis trialeticus	49	–	–	–	14.3	85.7	–	–	–	–	–
Sub-total	101	–	1.0	1.0	8.9	88.1	1.0	–	–	–	–
Matuzka Cave, layer 5 and trench 3	7	–	–	14.3	57.1	14.3	14.3	–	–	–	–
Mezmajskaya Cave, layer 2b	170	–	2.3	16.5	28.8	48.9	1.2	2.3	–	–	–
Mezmajskaya Cave, layers 2 and 2a	74	–	2.7	13.5	32.4	46.0	4.1	–	1.3	–	–
Monasheskaya Cave, layer 2-4	24	–	4.2	8.3	33.3	50.0	4.2	–	–	–	–
Treugolnaya Cave, layer 2a	21	–	–	33.3	52.4	14.3	–	–	–	–	–
Sub-total	296	–	2.4	16.2	32.4	45.0	2.4	1.3	0.3	–	–

Table II

Percentage representation of the M_1 morphotypes in recent and fossil populations of *Chionomys gud*

Population	Morphotype										
	N	a	b	c	d	e	f	g	h	i	j
Ch. gud gud	64	–	3.1	32.9	–	6.2	–	57.8	–	–	–
Ch. gud nenjukovi	66	3.0	4.5	31.9	–	4.5	–	54.6	1.5	–	–
Sub-total	130	1.5	3.8	32.3	–	5.4	–	56.2	0.8	–	–
Matuzka Cave, layers 7/1, 7/2	67	–	1.5	56.7	–	3.0	–	38.8	–	–	–
Treugolnaya Cave, layers 2e-2i	65	1.5	6.1	55.4	–	3.1	–	33.9	–	–	–
Sub-total	132	0.8	3.8	56.0	–	3.0	–	36.4	–	–	–
Matuzka Cave, layers 5-6	90	–	5.5	28.9	–	5.5	–	56.8	2.2	1.1	–
Matuzka Cave, layers 3-4	23	–	4.3	13.0	–	–	–	78.4	4.3	–	–
Treugolnaya Cave, layers 2b-2d	46	–	2.2	34.8	–	8.7	–	54.3	–	–	–
Treugolnaya Cave, layer 2a	36	–	2.9	31.4	–	5.7	–	60.0	–	–	–
Myshtulagtylagat Cave, layers 4-9	26	–	7.7	34.6	–	3.8	–	53.9	–	–	–
Sub-total	221	–	4.5	29.4	–	5.4	–	58.9	1.4	0.4	–

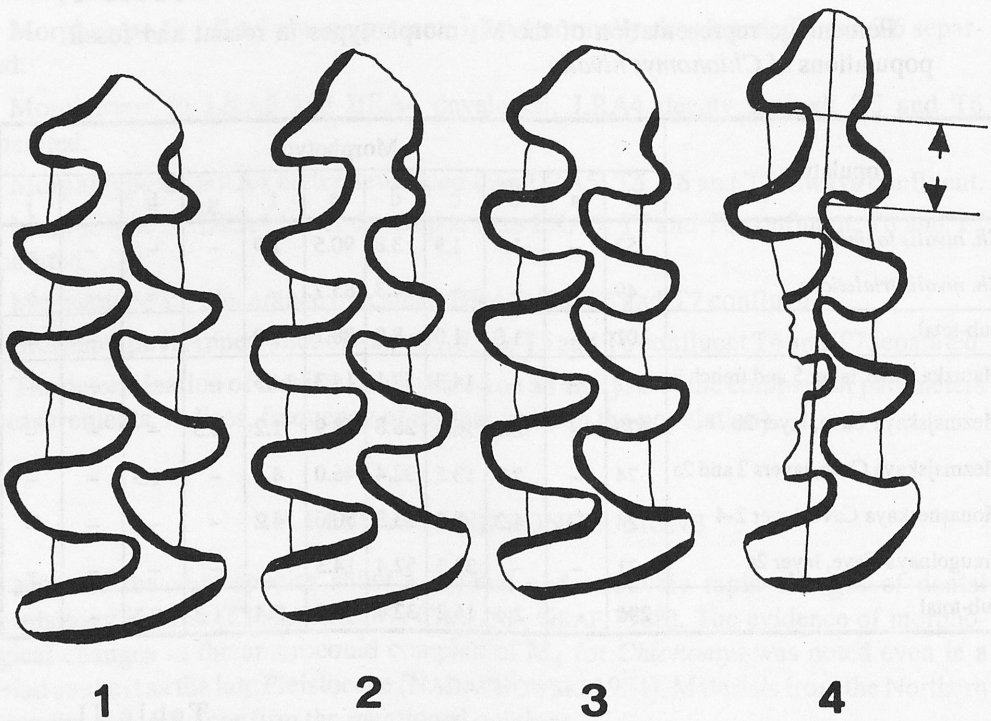

Fig. 4. Variation of M_1 of *Chionomys* cf. *gud* from Matuzka Cave, layer 7. 1, 2 - morphotype C, 3 - morphotype E, 4 - morphotype G. Measurement showing the relative position of LSA5 and BSA4 is indicated by arrows.

lower mean values in relation to the length of M_1. This index, for recent *Ch. gud gud* and *Ch. g. nenjukovi* reaches, an average of 11.4 (N = 57, OR = 7.6-15.9) and 11.3 (N = 63, OR = 8.9-15.9), respectively, while its mean value for the population from layer 7/2 of Matuzka Cave is 10.5 (N = 32, OR = 5.8-15.2). However, these differences are statistically non-significant. The mentioned populations, especially those from Treugolnaya Cave, are also characterized by higher values of C/W index in comparison with the younger populations (Table VI). Comprehensive studies of other materials of the same age help decide whether these differences are sufficient to separate a new ancestrial taxon.

Late Pleistocene populations of *Ch. gud* are generally similar to recent samples that is manifest in the preponderance of morphotype G. *Ch. gud* did not change distinctly in size (length of M_1) (Table IV), while mean values of A/L index are lower in comparison with recent populations. It seems that *Ch. gud* is the best biostratigraphical marker among voles from the Caucasus region, because it underwent relatively distinct changes in dental morphology since middle Pleistocene.

Ch. roberti is relatively easily distinguishable from the other representatives of *Chionomys* on the basis of measurements. The length of M_1 shows values distinctly higher

Table III

Percentage representation of the M_1 morphotypes in the recent and fossil populations of *Chionomys roberti*

Population	Morphotype										
	N	a	b	c	d	e	f	g	h	i	j
Ch. roberti roberti	72	–	1.4	34.7	–	5.5	–	43.1	6.9	2.8	5.6
Ch. roberti occidentalis	83	–	3.6	48.2	–	7.2	–	41.0	–	–	–
Sub-total	155	–	2.6	41.9	–	6.5	–	41.9	3.2	1.3	2.6
Matuzka Cave, layers 6-7	23	–	4.3	78.4	–	4.3	–	13.0	–	–	–
Matuzka Cave, layers 3-5	14	–	7.1	85.8	–	–	–	7.1	–	–	–
Gubs River	35	–	5.7	65.7	–	20.0	–	8.6	–	–	–
Sub-total	72	–	5.5	73.6	–	11.1	–	9.8	–	–	–

than those of both *Ch. nivalis* and *Ch. gud* (Table IV), while its A/L index is slightly higher (Table V). The C/W index is, however, considerably lower (Table V). *Ch. roberti* is poorly represented in fossil state. Pleistocene populations from Matuzka Cave show a distinctly different percentage representation of morphotypes in comparison with recent subspecies (Table III).

The above evidence can be summarized as follows:

(1)data from the Caucasus region confirm earlier general observations of a gradual complication of anteroconid complex of M_1 towards the recent times in all species examined;

(2) materials of *Chionomys* cf. *gud* from Matuzka Cave (layers 7/2-7/1) and Treugolnaya Cave (layers 2e-2i) show a peculiar morphological pattern and can be probably treated as a separate ancestrial taxon for the late Pleistocene and recent populations;

(3) *Ch. gud* and *Ch. roberti* are present in the Caucasus region at least from the beginning of the Middle Pleistocene;

(4) *Ch. nivalis* seems not to appear in the Greater Caucasus before the Early/Middle Weichselian boundary.

Table IV

Values of the length of M_1 (L) in the recent and fossil *Chionomys* populations

Population	N	OR	M	SD
Chionomys nivalis				
Chionomys nivalis loginovi	46	2.36-2.84	2.61	0.13
Chionomys nivalis trialeticus	39	2.44-2.96	2.74	0.15
Matuzka Cave, layer 5 trench 3	7	2.65-2.85	2.74	0.06
Mezmajskaya Cave, layer 2b	163	2.45-3.07	2.78	0.13
Mezmajskaya Cave, layers 2-2a	66	2.55-3.12	2.85	0.15
Monasheskaya Cave, layers 2-4	18	2.55-2.92	2.78	0.11
Treugolnaya Cave, layer 2a	17	2.35-3.17	2.79	0.17
Chionomys gud				
Chionomys gud gud	62	2.52-3.16	2.73	0.16
Chionomys gud nenjukovi	64	2.68-3.19	2.97	0.14
Matuzka Cave, layer 7/2	32	2.52-3.00	2.82	0.13
Matuzka Cave, layer 7/1	24	2.70-3.00	2.85	0.09
Matuzka Cave, layer 6	45	2.62-3.02	2.86	0.10
Matuzka Cave, layer 5	23	2.62-3.02	2.84	0.09
Matuzka Cave, layers 3-4	16	2.52-2.97	2.74	0.12
Treugolnaya Cave, layers 2e-2i	57	2.50-2.95	2.73	0.09
Treugolnaya Cave, layers 2b-2d	30	2.60-3.02	2.77	0.11
Treugolnaya Cave, layer 2a	23	2.52-3.00	2.76	0.12
Myshtulagtylagat Cave, layers 4-9	21	2.55-2.92	2.72	0.10
Chionomys roberti				
Chionomys roberti roberti	72	2.93-3.43	3.22	0.15
Chionomys roberti occidentalis	81	2.72-3.40	3.03	0.18
Matuzka Cave, layers 6-7	21	2.87-3.25	3.06	0.09
Matuzka Cave, layers 3-5	10	2.90-3.25	3.06	0.11
Gubs River	33	2.92-3.55	3.20	0.14

Table V

Values of A/L ratio of M_1 in the recent and fossil *Chionomys* populations

Population	N	OR	M	SD
Chionomys nivalis				
Chionomys nivalis loginovi	46	48.4-54.5	51.1	1.5
Chionomys nivalis trialeticus	39	46.5-53.6	49.6	1.9
Matuzka Cave, layer 5 trench 3	7	45.6-50.9	47.9	1.6
Mezmajskaya Cave, layer 2b	163	42.7-52.7	48.1	1.6
Mezmajskaya Cave, layers 2-2a	66	40.0-50.0	47.7	1.7
Monasheskaya Cave, layers 2-4	18	45.6-51.4	48.5	1.6
Treugolnaya Cave, layer 2a	17	45.4-50.0	47.9	1.3
Chionomys gud				
Chionomys gud gud	62	43.1-52.3	49.1	1.7
Chionomys gud nenjukovi	64	45.6-53.3	49.1	1.7
Matuzka Cave, layer 7/2	32	44.0-50.4	47.2	1.7
Matuzka Cave, layer 7/1	24	45.0-50.0	47.7	1.2
Matuzka Cave, layer 6	45	43.2-51.7	47.6	2.0
Matuzka Cave, layer 5	23	45.8-50.9	47.9	1.6
Matuzka cave, layers 3-4	16	43.0-50.5	47.7	2.1
Treugolnaya Cave, layers 2e-2i	57	42.2-51.9	47.9	1.9
Treugolnaya Cave, layers 2b-2d	30	44.8-51.4	48.2	2.0
Treugolnaya Cave, layer 2a	23	44.3-52.2	48.6	2.2
Myshtulagtylagat Cave, layers 4-9	21	45.0-49.6	47.8	1.1
Chionomys roberti				
Chionomys roberti roberti	72	46.7-54.6	50.9	1.6
Chinomys roberti occidentalis	81	46.4-53.2	50.6	1.5
Matuzka Cave, layers 6-7	21	44.3-53.7	49.5	2.4
Matuzka Cave, layers 3-5	10	45.8-53.4	50.2	1.9
Gubs River	33	47.0-53.2	50.2	1.5

Table VI

Values of C/W ratio of M_1 in the recent and fossil *Chionomys* populations

Population	N	OR	M	SD
Chionomys nivalis				
Chionomys nivalis loginovi	46	10.5-60.8	39.3	10.5
Chionomys nivalis trialeticus	39	12.8-61.2	40.6	8.9
Matuzka Cave, layer 5 trench 3	7	13.9-58.3	36.8	12.7
Mezmajskaya Cave, layer 2b	163	11.8-61.5	39.5	9.8
Mezmajskaya Cave, layers 2-2a	69	6.1-60.0	39.0	8.9
Monasheskaya Cave, layers 2-4	18	25.0-48.3	40.0	5.7
Treugolnaya Cave, layer 2a	17	31.0-50.0	40.4	5.5
Chionomys gud				
Chionomys gud gud	62	10.2-50.9	36.8	7.2
Chionomys gud nenjukovi	64	8.8-48.9	35.5	6.5
Matuzka Cave, layer 7/2	36	22.8-52.6	37.3	7.2
Matuzka Cave, layer 7/1	24	19.3-48.5	35.0	6.9
Matuzka Cave, layer 6	45	22.5-53.8	35.1	7.3
Matuzka Cave, layer 5	23	23.5-52.0	36.1	5.9
Matuzka Cave, layer 3-4	16	27.0-51.4	38.8	6.1
Treugolnaya Cave, layers 2e-2i	57	14.7-67.9	42.9	9.8
Treugolnaya Cave, layers 2b-2d	30	21.0-60.6	37.2	9.1
Treugolnaya Cave, layer 2a	23	26.5-39.4	32.6	3.6
Myshtulagtylagat Cave, layers 4-9	21	27.6-50.0	37.0	6.4
Chionomys roberti				
Chionomys roberti roberti	72	8.2-43.9	30.7	7.5
Chionomys roberti occidentalis	81	6.1-41.3	28.8	6.8
Matuzka Cave, layers 6-7	21	20.0-44.4	31.5	6.9
Matuzka Cave, layers 3-5	11	17.1-38.5	30.5	5.5
Gubs River	33	18.9-44.1	29.2	6.5

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