Systematics, geographic variation, and evolution of snow voles (*Chionomys*) based on dental characters

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Analysis of dental characters of *Chionomys* supported by a comparison with biochemical and karyological criteria shows its isolation from *Microtus* (*sensu stricto*). Snow voles (*Chionomys*) consist of two lineages developed separately since the Lower Biharian. The first one has appeared and evolved in Europe (*Ch. nivalis* lineage) while the second is probably of the Near East or Caucasus origin (*Ch. roberti-gud* lineage). Variation in dental characters of extant *Ch. nivalis* permit to reconstruct affinities between particular populations comparable in this respect with biochemical data. Fossil species traditionally included in the *Chionomys* group (*Microtus malei*, *M. nivaloides*, *M. nivalinus*, *M. ratticepoides*) seem to belong to *Microtus sensu stricto*.

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Introduction

Teeth have long been intensively studied by palaeontologists because they have great value in the identification of species and the investigation of variability, microevolution and phyletic relationships. Abundant fossil record of voles (*Arvicolidae*) from Quaternary sediments of Eurasia and North America discovered in last decades (see Fejfar and Heinrich 1983, Zakrzewski 1985, Repenning 1987 for summary) provide the opportunity to reconstruct their variation, speciation and phylogeny more precisely. The major changes in the arvicolids that have been documented from the fossil materials involve changes in the cheek teeth (M₁ and M³). Although factors regulating the interspecific variation and evolution of arvicolid tooth complexity are relatively well recognized (Guthrie 1971, Chaline 1987), the mechanisms of intraspecific variation on a population level are still insufficiently known and poorly understood, particularly in comparison with comprehensive studies based on karyological and biochemical data. Information obtained from geographical variation of dental characters seems to be a suitable technique to reconstruct the taxonomic relationships on the subspecific level comparable in this respect with the biochemical methods.

Among arvicolids the genus *Microtus* (*sensu lato*) is the most diversified recent group of voles (Corbet and Hill 1986). Its origin is probably related with the first important coolings of the climate in the Northern Hemisphere, which took place about 2.0 ± 0.4 m.y. BP (cf. Zagwijn 1985) and was presumably manifested by the appearance of widely distributed open (? steppe) environments. There is a common agreement among palaeontologists that

Table 1. Recent materials of *Chionomys nivalis*, *Ch. gud*, *Ch. roberti*, *Microtus oeconomus* and *M. agrestis* used for the study. N - number of specimens examined.

Code	Population	N	Geographical region	No. of sites
n 1	*Ch. nivalis* ssp.	29	Sierra Nevada, Spain	6
n 2	*Ch. nivalis abulensis* (Morales Agacino, 1936)	160	Sierra de Gredos and Cordillera Cantabrica, Spain	8
n 3	*Ch. nivalis aquitanius* (Miller, 1908)	90	Pyrenees, Spain and France	12
n 4	*Ch. nivalis lebrunii* (Crespon, 1844)	49	Massif Central, France	5
n 5	*Ch. nivalis leucurus* (Gerbe, 1852)	63	Basses Alpes and Alpes Maritimes, France	4
n 6	*Ch. nivalis nivalis* (Martins, 1842)	64	Western Alps (Massif du Pelvoux), France	5
n 7	*Ch. nivalis nivalis* (Martins, 1842)	139	Western Alps, Italy and Switzerland	24
n 8	*Ch. nivalis nivalis* (Martins, 1842)	36	Southern Alps (vicinity of Garda Lake), Italy	5
n 9	*Ch. nivalis nivalis* (Martins, 1842)	93	Central Alps, BRD and Austria (Tirol)	17
n10	*Ch. nivalis nivalis* (Martins, 1842)	40	Eastern Alps (Niedere Tauern), Austria	3
n11	*Ch. nivalis nivalis* (Martins, 1842)	40	Eastern Alps (Dolomites and Kärnten), Italy and Austria	5
n12	*Ch. nivalis wagneri* (Martino, 1940)	14	Julijske Alpe, Yugoslavia	3
n13	*Ch. nivalis cf. malyi* (Bolkay, 1925)	29	Macedonia, Yugoslavia	4
n14	*Ch. nivalis aleco* (Paspalev, Martino, Peshev, 1952)	142	Vitosha, Rila, Pirin, Rhodope, Bulgaria	11
n15	*Ch. nivalis ulpius* (Miller, 1908)	48	Southern Carpathians, Romania	5
n16	*Ch. nivalis ulpius* (Miller, 1908)	76	Eastern Carpathians, Romania and USSR	12
n17	*Ch. nivalis mirhanreini* (Schäfer, 1935)	741	Tatra Mts., Czechoslovakia, Poland	19
n18	*Ch. nivalis olympius* (Neuhäuser, 1936)	14	Ulu Dag and Ilgaz Dag, Turkey	2
n19	*Ch. nivalis cedronim* (Spitzenberger, 1973)	12	Bey Dag, Turkey	1
n20	*Ch. nivalis spitzenbergerae* Nadachowski, 1990	12	Bolkar Daglari, Middle Taurus Mts., Turkey	2
n21	*Ch. nivalis hermonis* (Miller, 1908)	76	Anti-Lebanon, Lebanon Mts., Israel, Syria, Lebanon	3
n22	*Ch. nivalis pontius* (Miller, 1908)	4	Giresun and Lazistan Daglari, Turkey	1
n23	*Ch. nivalis trialeticus* (Shidlovskij, 1919)	49	Transcaucasia, USSR	10
n24	*Ch. nivalis loginovi* (Ognev, 1950)	52	Caucasus Mts., USSR	7
n25	*Ch. nivalis dementievi* (Heptner, 1939)	48	Kopet Dag, USSR	4
n26	*Ch. nivalis* ssp.	14	Elburz, Zagros Mts. (Zardeh Kuh), Iran	3
	Sub-total	2134		181
g1	*Ch. gud nenjukovi* (Formosov, 1931)	66	Western Caucasus Mts., USSR	3
g2	*Ch. gud gud* (Satunin, 1909)	64	Central Caucasus Mts., USSR	10
g3	*Ch. gud ighesicus* (Shidlovskij, 1919)	12	Eastern Caucasus Mts., Dagestan, USSR	1
g4	*Ch. gud lasistanius* (Neuhäuser, 1936)	8	Lazistan Daglari, Turkey	2
	Sub-total	150		16
r1	*Ch. roberti occidentalis* (Turov, 1928)	83	Caucasus Mts., USSR	10
r2	*Ch. roberti roberti* (Thomas, 1908)	72	Giresun, Trabzon and Lazistan Daglari, Turkey	5
	Sub-total	155		15
o1	*M. oeconomus* (Pallas, 1776)	49	Choszczewo, Poland	1
o2	*M. oeconomus* (Pallas, 1776)	59	Jazy Biele, Poland	1
	Sub-total	108		2
a1	*M. agrestis* (Linnaeus, 1761)	50	Dyrdy, Poland	1
a2	*M. agrestis* (Linnaeus, 1761)	42	Wymiarki, Poland	1
	Sub-total	92		2

the ancestral form - *Allophaiomys* Kormos, 1933 (treated in most cases as subgenus of *Microtus*) differentiated into main phyletic lineages in Eurasia already during Biharian in the uppermost Betfia and Nagyhársányhegy phases (ca. 1.0 ± 0.2 m.y. BP) (Chaline 1966, 1972, Van der Meulen 1973, Horáček 1981, Rabeder 1981). Snow voles (*Chionomys* Miller, 1908) are one of the earliest groups of this speciation event (Fejfar and Horáček 1983).

Taxonomic status of *Chionomys* is still controversial. Corbet (1978) and Krapp (1982) included snow voles in *Microtus* preserving sub-generic status for them, while Russian authors treated *Chionomys* as a separate genus (Gromov and Polyakov 1977, Pavlinov and Rossolimo 1987). The latter opinion has been confirmed by cranial (Pietsch 1980), karyological (Agadzhanian and Yatsenko 1984) and biochemical studies which show that genetical distance between *Chionomys* and *Microtus* is even larger than that between *Arvicola* and *Microtus* (Graf and Scholl 1975, Graf 1982).

Recent *Chionomys* consists of three species: *Ch. nivalis* (Martins, 1842), *Ch. gud* (Satunin, 1909) and *Ch. roberti* (Thomas, 1908). They inhabit mountain regions of Europe, Asia Minor and some other parts of Western Asia (Lebanon and Anti-Lebanon Mts., Trancaucasia, Zagros Mts., and Kopet Dag) (Figs 1, 2). Among the fossil taxa, those traditionally included in the *Chionomys* group are: *Microtus nivaloides* Forsyth Major, 1902, *Microtus nivalinus* Hinton, 1923, *Microtus malei* Hinton, 1907 and sometimes *Microtus ratticepoides* Hinton, 1923 (Chaline 1972, Fejfar and Horáček 1983).

This study reviews the fossil and recent taxa of the *Chionomys* group. Dental morphology was used as the main taxonomic criterion. The systematics, variation and evolution of snow voles is discussed, on the basis of palaeontological, morphological and biochemical data.

Material

Recent materials examined comprise skulls and teeth of: (1) *Chionomys nivalis* represented by 18 subspecies (26 populations) originated from its whole modern range (Table 1, Fig. 1); (2) *Chionomys gud* which consists of 4 subspecies (Table 1, Fig. 2); (3) *Chionomys roberti* represented by 2 subspecies (Table 1, Fig. 2); (4) *Microtus oeconomus* (Pallas, 1776) comprising 2 populations from N. Poland (Table 1); and (5) *Microtus agrestis* (Linnaeus, 1761) which includes 2 populations from Poland (Table 1).

Fossil materials (mainly isolated M_1) besides samples of the genus *Chionomys*, i.e. (1) *Ch. nivalis* (22 populations, Table 2); (2) *Ch. gud* (8 populations, Table 2); and (3) *Ch. roberti* (2 populations, Table 2) comprise the following taxa : (4) "*Microtus*" *burgondiae* (Chaline, 1972) (2 populations) (Table 2); (5) *Microtus malei* (3 populations) (Table 2) and (6) *Microtus nivaloides* (1 type population) (Table 2).

The skulls and teeth examined belong to the collections of Estacion Biologica de Doñana, Sevilla (abreviations in brackets, EBD); Museo National de Ciencias Naturales, Madrid, (MNCN); Institute Pirenaico de Ecologia, Jaca (IPE); Sociedad de Ciencias Naturales Aranzadi, San Sebastián (SCNA); Museum d' Historie Naturelle, Toulon (MHNT); Laboratoire de la Faune Sauvage, Jouy-en-Josas (LFS); Centre des Sciences de la Terre, Université de Bourgogne, Dijon (CSTD); Museum National d' Histoire Naturelle, Paris (MNHN); Museo Civico di Storia Naturale "Giacomo Doria", Genova (MSNG); Museo Zoologico de "La Specola", Firenze (MZS); Museo Civico di Storia Naturale, Verona (MCSN); Institut Royal des Sciences Naturelles de Belgique, Bruxelles (IRSN); British Museum (Natural History), London (BMNH); Harrison Zoological Museum, Sevenoaks (HZM); Bayerische Staatssammlung für Paläontologie und Historische Geologie, München (BSPG); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (MAK); Zoologisches Institut der Universität Bonn, (ZIB); Forschungsinstitut Senckenberg, Frankfurt am Main (FIS); Museum für Naturkunde der Humboldt-
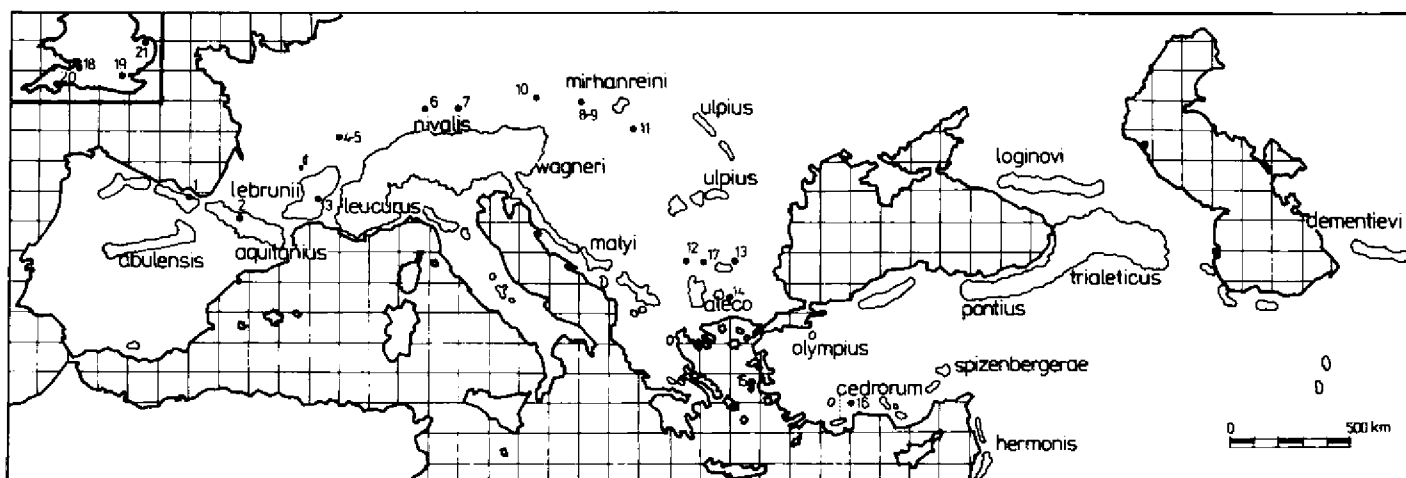
Fig. 1. Distribution of *Chionomys nivalis* [after Corbet (1978) and Krapp (1982), complemented] and location of fossil sites discussed in the text. 1 – Erralla, 2 – Cantet, 3 – Cottier, 4 – La Garenne 1, 5 – Les Valerots, 6 – Weinberghöhlen, 7 – Kemathenhöhle, 8 – Zkamĕnĕlý Zámek, 9 – Rytířská Cave, 10 – Srbsko-Nad Kačákem Cave, 11 – Maštalná Cave, 12 – Mecha Dupka Cave, 13 – Bacho Kiro Cave, 14 – Borodino, 15 – Latomi 1, 16 – Karain B, 17 – Tcherdjenitsa 2, 18 – Clevedon Cave, 19 – Crayford, 20 – Tornewton Cave, 21 – West Runton.
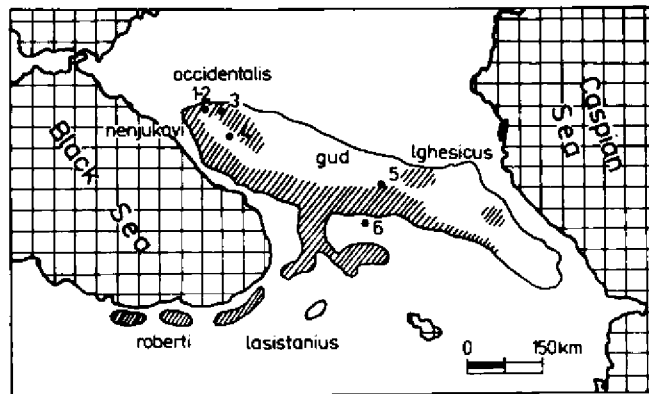
Fig. 2. Distribution of *Chionomys gud* and *Chionomys roberti* (after Shidlovskij, 1976, complemented) and location of fossil sites discussed in the text. Lined surface indicates sympatric occurrence of *Ch. gud* and *Ch. roberti*. 1 - Matuzka Cave, 2 - Mezmajskaya Cave, 3 - Monasheskaya Cave, 4 - Treugolnaya Cave, 5 - Myshtulagtylagat Cave, 6 - Kudaro Cave 1.
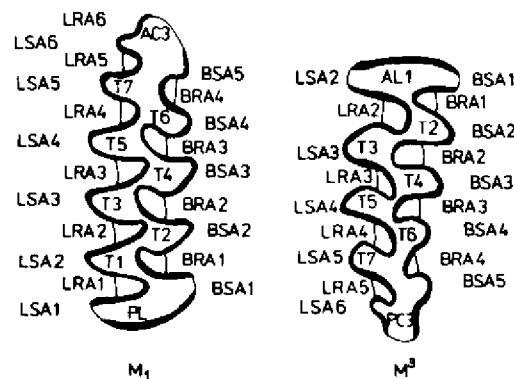

Fig. 3. Terminology of the occlusal surface elements employed for the first lower (M_1) and the third upper (M^3) molars in voles (after Van der Meulen, 1973). AC = anterior cap; AL = anterior lobe; BRA = bucal re-entrant angle; BSA = buccal salient angle; LRA = lingual re-entrant angle; LSA = lingual salient angle; PC = posterior cap; PL = posterior lobe.

Universität zu Berlin, (MNHU); National Museum of Natural History, Budapest (MNH); Naturhistorisches Museum Wien (NHMW); Institute of Geology and Geotechnics, Czechoslovak Academy of Sciences, Praha (UGG), Institute of Systematic Zoology, Charles University, Praha (KSZP); Institute of Systematic and Ecological Biology, Czechoslovak Academy of Sciences, Brno (USEB); Institut of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków (ISEZ); Mammal Research Institute, Polish Academy of Sciences, Bialowieza (ZBS); Zoological Institut, Bulgarian Academy of Sciences, Sofia (ZIS); Zoological Institute, Academy of Sciences of the Ukrainian S.S.R., Kiev (ZIUA); Zoological Museum of the Lomonosov State University, Moscow (ZMUM); Zoological Institute of Academy of Sciences of the U.S.S.R., Leningrad (ZIAS); Zoological Museum of Tel-Aviv University, Tel-Aviv (ZMTU); Regional Nature and History Museum, Ussishkin House, Dan, Israel (UH).

Table 2. Fossil materials of *Chionomys nivalis* (n), *Ch. gud* (g), *Ch. roberti* (r), (?) *Ch. burgondiae* (b), *Microtus malei* (m) and *M. nivaloides* (s). N - number of specimens examined. Absolute datings in years BP.

Code	Locality and geographical region	N	Layer	Stratigraphy	Absolute datings	References
1	2	3	4	5	6	7
nA	Erralla (Cestona, Guipuzcoa Prov., Spain	138	levels VI and V	Older Dryas	$16270\pm 240 - 15740\pm 240$ (3 dates)	Peman 1985
nB	Cantet (Espeche, Hautes Pyrenees, France)	12	trench 7	Allerød/Younger Dryas	10920 ± 160	Clot *et al.* 1984
nC	Cottier (Retournac, Massif Central, France)	31	levels IV and III	Cottier	$21100\pm 600 - 19880\pm 520$ (2 dates)	Chaline 1976
nD	La Garenne 1 (Cote-d'Or, France)	10	layers C and p1	Weichselian 3 ?	–	Chaline 1972
nE	Renne and Bison Caves (Yonne, France)	33	layers XI, RGS, H	Arcy Interglacial	$31700\pm 950 - 28400\pm 850$ (3 dates)	Chaline 1972, Brochet, unpubl.
nF	Weinberghöhlen(Mauern, BRD)	23	layer D	Denekamp Interstadial	28265 ± 325	Koenigswald 1974
nG	Kemathenhöhle (Kipfenberg, Bavaria, BRD)	20	layers e and d	Middle Weichselian	43920 ± 3880	Koenigswald 1978
nH	Kemathenhöhle (Kipfenberg, Bavaria, BRD)	26	layers c and b₂	Middle Weichselian	33383 ± 933	Koenigswald 1978
nI	Kemathenhöhle (Kipfenberg, Bavaria, BRD)	35	layers b₁ and b	Denekamp Interstadial	$30910\pm 660 - 30084\pm 600$ (2 dates)	Koenigswald 1978
nJ	Zkamčnelý Zámek Cave (N-Moravia, Czechoslovakia)	14	–	Weichselian 2/3 ?	–	Horáček and Sánchez Marco 1984 (1)
nK	Rytířská Cave (S-Moravia, Czechoslovakia)	27	–	Weichselian 3 ?	–	(1)
nL	Srbsko-Nad Kačákem Cave (Central Bohemia, Czechoslovakia)	63	–	Pleniglacial	–	(1)
nM	Maštalná Cave (SE-Slovakia, Czechoslovakia)	11	layers 13-15	Late Weichselian		(1)
nN	Mecha Dupka Cave (W-Balkan Mts., Bulgaria)	53	upermost layer	Pleniglacial	–	Popov 1984, 1985
nO	Bacho Kiro Cave (Gabrovo, Balkan Mts., Bulgaria)	162	layers 14-11	Early Weichselian, 47500 ± 43000 Lower Pleniglacial	Nadachowski 1984 (2 dates)	
nP	Bacho Kiro Cave (Gabrovo, Balkan Mts., Bulgaria)	96	layers 10-4b	Middle Weichselian	$32700\pm 300 - 29150\pm 950$ (2 dates)	Nadachowski 1984
nR	Bordino, Smolian Dist., Rhodope Mts., Bulgaria)	76	–	Holocene		Popov, pers. comm.
nS	Latomi 1, Chios, Greece	42	–	Middle Pleistocene ?	–	Storch 1975
nT	Karain B, Antalya, Turkey	44	layers 32-17	Pleniglacial and Late Glacial	14160 ± 210	Storch 1988
nU	Mezmajskaya Cave, North. Caucasus Mts., USSR	170	layer 2b	Early Weichselian	–	Nadachowski and Baryshnikov 1991 (2)
nV	Mezmajskaya Cave, North. Caucasus Mts., USSR	74	layers 2-2a	Middle Weichselian	–	(2)
nW	Monasheskaya Cave, North. Caucasus Mts., USSR	24	layers 2-4	Middle Weichselian	–	(2)
	Sub-total	1184				

| 1	2	3	4	5	6	7
gA	Matuzka Cave, North. Caucasus Mts., USSR	56	layer 7/2, 7/1	Eemian (Riss/Würm)	–	(2)
gB	Matuzka Cave, North. Caucasus Mts., USSR	68	layers 5-6	Early Weichselian	–	(2)
gC	Matuzka Cave, North. Caucasus Mts., USSR	23	layers 4-3	Middle Weichselian	–	(2)
gD	Treugolnaya Cave, North. Caucasus Mts., USSR	65	layers 2e-2i	Middle Pleistocene	–	(2)
gE	Treugolnaya Cave, North. Caucasus Mts., USSR	46	layers 2d-2b	Early Weichselian	–	(2)
gF	Treugolnaya Cave, North. Caucasus Mts., USSR	36	layer 2a	Late Weichselian	–	(2)
gG	Myshtulagtylagat Cave, North. Caucasus Mts., USSR	26	layers 4-9	Middle Weichselian	32980±1070	(2)
gH	Kudaro Cave 1, South. Caucasus Mts., USSR	24	layers 3-4	Early/Middle Weichselian	44150±2400	Baryshnikov and Baranova 1983
Sub-total		344				
rA	Matuzka Cave, North. Caucasus Mts., USSR	23	layers 6-7	Eemian ?-Early Weichselian	–	(2)
rB	Matuzka Cave, North. Caucasus Mts., USSR	14	layers 3-5	Early and Middle Weichselian	–	(2)
Sub-total		37				
bA	Les Valerots, Cote-d'Or, France	83	unit 2	Lower Pleistocene, Menapian	–	Chaline et al. 1985
bB	Tcherdjenitsa 2, Karlukovo Balkan Mts., Bulgaria	43	red dry clay	Lower Pleistocene Betfia phase	–	Popov pers. comm.
Sub-total		126				
mA	Clevedon Cave, Somerset, England	335	–	Ipswichian (sensu lato)	–	Sutcliffe and Kowalski 1976 (3)
mB	Crayford, Kent, England	62	–	Ipswichian (sensu lato)	–	(3)
mC	Tornewton Cave, Devon, England	93	Glutton Stratum	Ipswichian (sensu lato)	–	(3)
Sub-total		490				
sA	West Runton, Norfolk, England	82	Upper Freshwater Bed	Cromerian	–	(3)
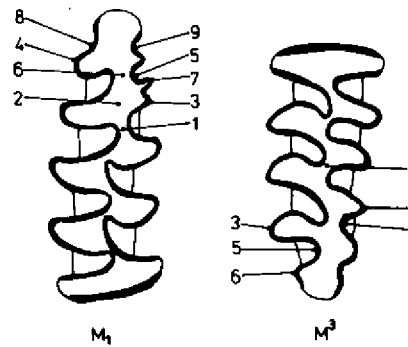
Fig. 4. Characters of M_1 and M^3 occlusal surface analyzed. For detailed explanation see Table 3.

Table 3. Characters analyzed in the occlusal surface of M_1 and M^3.

No	Characters	State of charcters		
		1	2	3
	M_1			
1	Confluence of T4 and T5	broad	narrow	separation
2	Confluence of T5 and T6	broad	narrow	separation
3	Development of BSA4	absent	incipient	developed
4	Development of LSA5	absent	incipient	developed
5	Development of BRA4	absent	incipient	developed
6	Confluence of T6 and T7	broad	narrow	separation
7	Development of Mimomys-ridge on BSA4	absent	incipient	developed
8	Development of LRA5	absent	incipient	developed
9	Development of BRA5	absent	incipient	developed
	M^3			
1	Confluence of T4 and T5	broad	narrow	separation
2	Development of BSA4	absent	incipient	developed
3	Development of LSA5	absent	incipient	developed
4	Development of BRA4	absent	incipient	developed
5	Development of LRA5	absent	incipient	developed
6	Development of LSA6	absent	incipient	developed

Methods

Morphotype analysis

Van der Meulen (1973) introduced the terminology employed for the morphology of the occlusal surface of teeth (Fig. 3). Morphological variability of dental pattern of first lower molars (M_1) and third upper molars (M^3) was studied according to the method proposed by Nadachowski (1990a). On each adult specimen of M_1 nine morphological characters were recorded. They referred to the structure and size of particular triangles and re-entrant angles as well as the manner of confluence of triangles (Fig. 4). Characters show three states marked
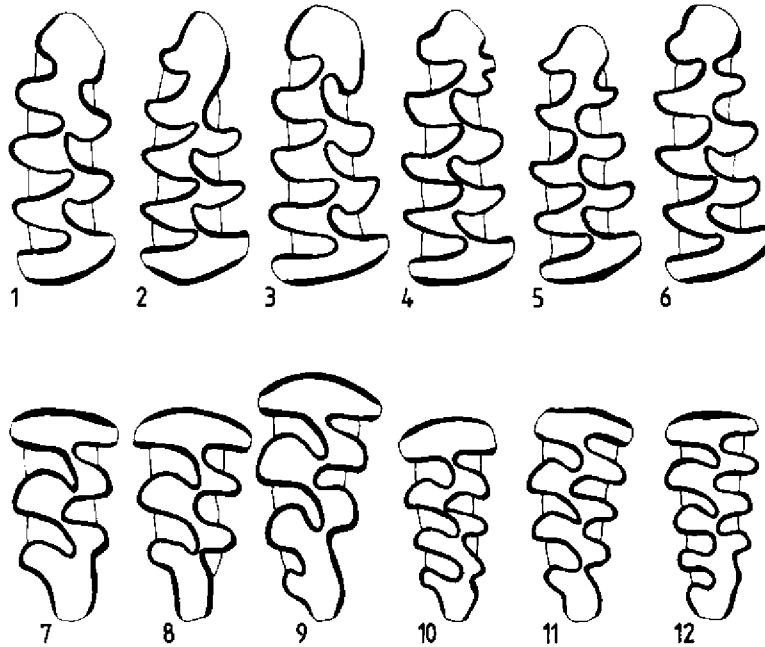
Fig. 5. Examples of the M₁ (1 – 6) and M³ (7 – 12) patterns in voles described using the numerical formula method.
1 – 112211100, 2 – 312211121, 3 – 333311111, 4 – 333322321, 5 – 323322121, 6 – 313333121, 7 – 111000, 8 – 311000,
9 – 312121, 10 – 323221, 11 – 333321, 12 – 333233.

with numeral 1, 2 or 3 according to their formation (Table 3). Lack of a given structure is indicated by "0". On the basis of such analysis the morphological variability was inscribed using numerical formulas. Each character has a stable position within the formula. Among almost 150 variants found in the material examined, 52 were figured. The same method was used in description of the variability of M³ where 6 characters were analyzed (Fig. 4, Table 3). Among almost 50 variants of M³, 20 were figured. Examples of some morphological variants and their numerical formulas are shown in Fig. 5. For particular populations (samples) studied the frequency of variants (formulas) was established. Variants described by numerical formulas were grouped into morphotypes (defined below), which were analyzed qualitatively and quantitatively on population level. In literature the morphotypes are named with letters or combinations of letters and numbers (Van der Meulen 1973, Nadachowski 1982) or with the names of subspecies and species (Angermann 1974, 1984, Chaline 1972, Rabeder 1981, Nadachowski 1985). Matrices of similarity for the samples have been calculated with the coefficient of Jaccard. Cluster analysis of the similarity matrices was performed with the unweighted pair-group method using arithmetic means (UPGMA) (Sneath and Sokal 1973).

Morphotypes of M1

Morphotype "pliocaenicus" (pl, Fig. 14*/ 1, 2): T4, T5 and T6 confluent; BSA4 and LSA5 developed or BSA4 incipient and LSA5 normally developed (= morphotype "superpliocaenicus" acc. to Rabeder (1981)). Dental pattern typical of *Microtus* (*Allophaiomys*) *pliocaenicus* Kormos, 1933.

Morphotype "prachintoni" (pr, Fig. 14 / 4): T4, T5 and T6 confluent; BSA4 incipient; appearance of LRA5. Morphotype characteristic of *Microtus* (*Allophaiomys*) *pliocaenicus prachintoni* Rabeder, 1981.

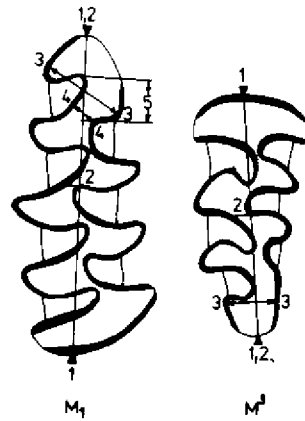*Figs 8 – 20 are placed at the end of the paper (on pp. 28 – 34).

Fig. 6. Measurement methods of M₁ and M¹ (partly after Van der Meulen 1973). For detailed explanation see the text.
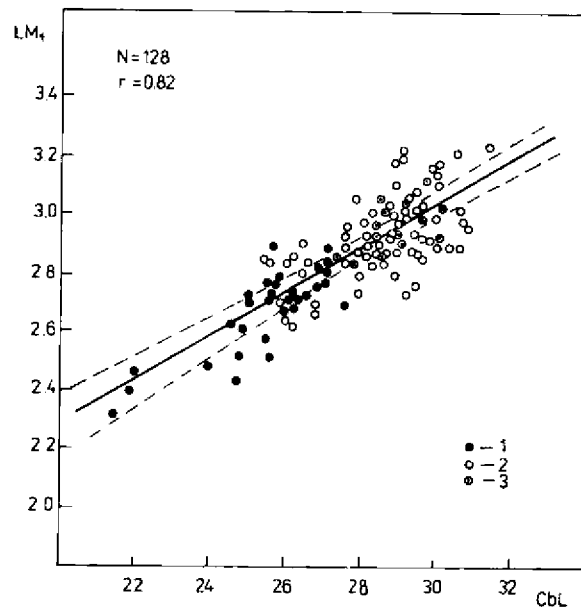

Fig. 7. Relationship between the condylobasal length of the skull (CbL) and the length of M₁ in *Chionomys nivalis mirhanrcini* from Tatra Mountains. 1 – juveniles, 2 – adults, 3 – two adult specimens.

Morphotype "nutiensis" (nu, Fig. 14 / 5): T4 and T5 confluent, T5 and T6 separated; LSA5 better developed than BSA4; appearance of incipient BRA4. Morphotype typical for *Microtus nutiensis* (Chaline 1972).

Morphotype "oeconomus" (oc, Figs 8, 10, 12, 15, 17 /3, 6, 7, 8): T4 and T5 separated; T5 and T6 largely confluent; lack of BSA4 (or incipient in variant 7); LRA5 incipient or well developed. Dental pattern characteristic of *Microtus oeconomus*.

Morphotype "lebrunii" (lc, Figs 8, 10, 12, 14, 17 / 9, 10, 11, 12, 13, 14, 15): T5 and T6 confluent; BSA4 and LSA5 developed; absence or incipient development of BRA4 and LRA5. The pattern commonly found in *Ch. nivalis lebrunii* and *Ch. n. leucurus*.

Morphotype "abulensis" (ab, Fig. 8 / 17, 18, 19, 20): T5 and T6 confluent or separated; BSA4 well developed; absence or incipient development of LSA5. The morphotype relatively common in *Ch. nivalis abulensis*.

Morphotype "aquitanius" (aq, Figs 8, 14 / 21, 22): T5 and T6 always separated; BSA4 and LSA5 well developed; absence of BRA4 and LRA5. Characteristic morphotype for *Ch. nivalis aquitanius*, also commonly found in other populations of the snow vole.

Morphotype "nivalis" (ni, Figs 8, 10, 12, 14, 15, 17, 19, 20 / 23, 26, 27, 28, 29, 30, 31, 32, 35, 36): T5 and T6 always separated; BSA4 and LSA5 well developed; BRA4 and LRA5 incipient; anterior cap short. The predominant morphotype of *Ch. nivalis*.

Morphotype "gud" (gu, Figs 8, 10, 12 / 37, 38, 39, 44, 46, 47): T5, T6 and T7 always confluent; BRA4 better developed than LRA5. A typical morphotype of *Ch. gud*.

Morphotype "mirhanreini" (mi, Figs 8, 10, 12 / 40, 41, 42, 43, 45, 52): T5 and T6 confluent; T6 and T7 separated; BRA4 better developed than LRA5. A rare morphotype, more frequently found in *Ch. nivalis mirhanreini* (cf. Nadachowski 1985).

Morphotype "malei" (ma, Figs 15, 17 / 16, 24): T5 and T6 confluent; LSA5 better developed than BSA4; anterior cap slightly bent lingually. A dental pattern typical of *Microtus malei*.

Morphotype "gregalis" (gr, Fig. 15 / 25): T5 and T6 separated; BSA4 incipient, LSA5 well developed; anterior cap slightly bent lingually. Morphotype characteristic of *Microtus gregalis* (Pallas, 1779).

Morphotype "arvalis" (ar, Figs 19, 20 / 33, 34): T5 and T6 separated; BSA4 and LSA5 as well as BRA4 and LRA5 well developed; anterior cap high. Very common morphotype of *Microtus arvalis* (Pallas, 1979) and of other species of *Microtus*.

Morphotype "agrestis" (ag, Figs 19, 20 / 48): T5 and T6 separated; BSA4 and LSA5 as well as BRA4 and LRA5 well developed; appearance of LRA6. This dental pattern relatively frequently occurs in *Microtus agrestis*.

Morphotype "coronensis" (co, Fig. 19, 20 / 49): T5 and T6 separated; occurrence of strong narrowing between T6 and T7.; BSA4 and LSA5 well developed. This pattern is characteristic of a fossil form *Microtus coronensis* Kormos, 1933 which most probably belongs to *Microtus agrestis* group (Nadachowski 1985).

Morphotype "extratriangulatus" (cx, Fig. 19, 20 / 50, 51): T5 and T6 as well as T6 and T7 separated. This pattern occurs sporadically in most of *Microtus* species, more frequently in *Microtus agrestis* (Nadachowski 1985).

Additionally in almost all morphotypes there occurred variants with so-called *Mimomys*-ridge expressed by the development of a small prismatic fold on BSA4 or rarely on BSA5 (for example: Fig. 8 / 15, 32, 36, 39, 42; Fig. 10 / 39; Fig. 12 / 32; Fig. 19 / 34, 51).

Morphotypes of M^3

Morphotype "lebrunii" (lc, Fig. 9 / 1, 2, 3): T4 and T5 confluent; lack of BSA4 and LSA5. A pattern very common in *Ch. n. lebrunii*.

Morphotype "mirhanreini" (mi, Figs 9, 16 / 4): T4 and T5 confluent; incipient development of LSA5. A rare morphotype, relatively frequent in *Ch. n. mirhanreini*.

Morphotype "nivalis" (ni, Figs 9, 16 / 5, 6): T4 and T5 separated; lack of BSA4 and LSA5. The most common morphotype for the majority of the *Ch. nivalis* populations.

Morphotype "malei" (ma, Figs 9, 16, 18 / 7): T4 and T5 separated; a distinct development of LSA5. A pattern characteristic of *M. malei*.

Morphotype "oeconomus" (oe, Figs 9, 11, 13, 16, 18 / 8, 10): T4 and T5 separated; distinct development of LSA5 and BSA4 (the latter sometimes incipient). A characteristic morphotype of *M. oeconomus*.

Morphotype "hermonis" (he, Fig 9 / 9): T4 and T5 separated; incipient development of LSA5, BSA4 and BRA4. An occasional morphotype being more frequent of *Ch. nivalis hermonis*.

Morphotype "gud" (gu, Figs 11, 13, 18 / 11, 12, 13, 14, 15); distinct development of BSA4 and LSA5; appearance of incipient BSA5 in some variants; lack of LSA6. Dental pattern typical of *Ch. gud*.

Morphotype "roberti" (ro, Figs 11, 13 / 16, 17, 18, 19, 20); distinct development of BSA4 and LSA5, in some variants appearance of incipient BSA5; distinct development of LSA6. A morphotype characteristic of *Ch. roberti*.

Measurements

The initial comparison started with 10 measurements for M_1 and 6 measurements for M^3, of which only 5 (for M_1) and 3 (for M^3) were used for analysis to reduce the number of highly correlated measurements. Following measurements appear to be useful for distinguishing species and populations of the *Chionomys* group (Fig. 6): (1) the length of the occlusal surface of M_1 and M^3 (= L, acc. to Van der Meulen 1973); (2) the length of anteroconid complex (for M_1) (= a, acc. to Van der Meulen 1973) or the length of posteroconid complex (for M^3) (= p, acc. to Nadachowski 1990b); (3) the width of the posterior part of the anteroconid complex for M_1 and posteroconid complex for M^3 measured from the tip of BSA4, so that of LSA4 (= E, acc. to Van der Meulen 1973 and = W_2 acc. to Nadachowski 1982), taken from the inner sides of the enamel; (4) the shortest distance between BRA3 and LRA4 (= b, acc. to Van der Meulen 1973 and B_1 acc. to Nadachowski 1982) taken again from the inner sides of the enamel; (5) the distance taken along the line 1-1 from the projection point of the anteriormost point of BRA3 to the projection point of the anteriormost point of LRA4.

Most of the above defined parameters have been employed to calculate the following ratios: 2/1 (= A/L, acc. to Van der Meulen 1973) which expresses the relative length of the anteroconid complex (for M_1) and posteroconid complex (for M^3) in comparison to the tooth length; 4/3 (= B_1/W_2, acc. to Nadachowski 1990b) which gives the degree of separation of the anterior cap of M_1 from T5; 5/1 which expresses the mutual position of BSA4 and LSA5. Differences in mean values observed have been checked by Student's and Scheffe's tests.

Differences and changes in size were analyzed using the length of M_1 which appear to be highly correlated ($r = 0.82$) with the condylobasal length of the skull (Fig. 7).

Results

The recent snow vole (*Chionomys nivalis*) served as a model for studying variations within the group. Its widely separated geographical populations exhibit a high degree of intra- and interpopulational variability of the dental pattern (Figs 8, 9*; Tables 4, 9, 10, 14). The most common of the M_1 morphotypes is "nivalis" (total frequency 58.5%), followed by "lebrunii" (17.0%) and "aquitanius" (11.8%) and for M^3 "nivalis" (44.1%), "lebrunii" (34.8%) and "malei" (10.2%). The West-European populations from Spain and France (*Ch. n. abulensis, Ch. n. aquitanius, Ch. n. leucurus, Ch. n. lebrunii*) show simple dental pattern with high frequency of "lebrunii" morphotype, and "oeconomus" morphotype (for M_1) which is especially common in the populations from Massif Central (17.5 - 18.4%). The pattern "aquitanius" which occurs in most of the snow vole samples is predominant in the population from the Pyrenees (44.5%). Generally, West-European populations constitute one group well separated from most other subspecies as far as morphology of M^3 is concerned (Fig. 22), while their structure of M_1 is not so homogeneous and consists of two clusters (Figs 21 and 23). Additionally, Spanish populations show some peculiar features (morphotype "abulensis"). The isolated population from Sierra Nevada (n1) is more similar in its structure of M_1 to the samples from the Alps than to *Ch. n. abulensis* from Cordillera Cantabrica. West-European populations are of large (especially *Ch. n. abulensis*) or medium size with exception of *Ch. n. leucurus* (M – LM_1 = 2.83) which is the smallest sub-

species in Europe. The simple dental pattern of these populations is also manifested by low mean values of 2/1 index and very high values of 4/3 index.

The nominative subspecies *Ch. n. nivalis*, inhabitant of the Alps (samples n6 – n11), is characterized by higher frequency of "nivalis" and decrease of "lebrunii" morphotypes. Some populations which inhabit Western Alps (e. g. n6 for M_1 or n6, n7 for M^3) show an intermediate pattern and belong to the cluster related to the "lebrunii-leucurus-aquitanius" group. The series of contiguous populations from the Alps show a size cline. A gradual size increase is observed from the west to the east and the biggest populations live in the easternmost part of the Alps (Niedere Tauern) ($M - LM_1 = 3.12$). Differences between extreme samples are statistically significant ($p < 0.01$, Scheffe's test). Other parameters measured fluctuate around the mean values for the whole species. An important change in dental morphology is observed in contiguous populations from Western part of the French Alps (n6) and Switzerland (n7).

Populations of the snow vole from the Dinaric Mountains, Balkan Peninsula and Carpathians (*Ch. n. wagneri*, *Ch. n. malyi*, *Ch. n. aleco* and *Ch. n. ulpius*) are generally characterized by smaller variation with absolute predominance of the "nivalis" morphotype. Simple morphotypes of M_1 "oeconomus" and "lebrunii" are rare or absent. In the structure of M^3 a distinct increase of more complicated morphotype "malei" is observed. *Ch. n. mirhanreini* from Tatra Mountains exhibits peculiar features in M_1 manifested by the greatest variability and higher frequency of morphotypes "gud" and "mirhanreini" (9.9 and 7.4%, respectively). In the structure of M^3 the predominance of morphotypes "lebrunii", "mirhanreini" and "malei" is observed. These differences in comparison with other populations point to a distinct separation of this population from all other examined samples of *Chionomys nivalis*. (Figs 21, 22).

The snow vole populations from Asia Minor (*Ch. n. olympius*, *Ch. n. cedrorum* and *Ch. n. spitzenbergerae*) are characterized by a very simple dental pattern of M_1 with a very high frequency of "oeconomus" (up to 41.7%) and "leucurus" (up to 75.0%), morphotypes manifested also by high values of 4/3 index. The dental pattern of M^3 in *Ch. n. spitzenbergerae* shows very peculiar features with absolute predominance of the morphotype "malei" (78.6%). This subspecies is similar to the *Microtus oeconomus* group as far as the M^3 structure is concerned (Fig. 22). In the cluster analysis of M_1 all Turkish populations occupy a separate position (Figs 21, 23).

Asiatic populations of *Ch. nivalis* from Caucasus (*Ch. n. loginovi*), Trancaucasia (*Ch. n. trialeticus*) and Kopet Dag (*Ch. n. dementievi*) are very closely related with regard to tooth morphology. They exhibit small variability of M_1 with predominance of the "nivalis" morphotype. Third upper molar is more variable with a relatively complicated dental pattern (morphotypes "oeconomus" and "hermonis"). *Ch. n. hermonis* from Lebanon and Anti-Lebanon Mts., is rather similar to the Balkan populations (*Ch. n. ulpius*, *Ch. n. aleco*). Populations of the snow vole from Asia Minor and the Caucasus region are distinctly smaller in comparison with Middle and East European samples and differences are statistically significant ($p < 0.05$, Scheffe's test). Phenetically these subspecies are closely related to Central and Eastern European populations of *Ch. nivalis* (Figs 21, 22, 23).
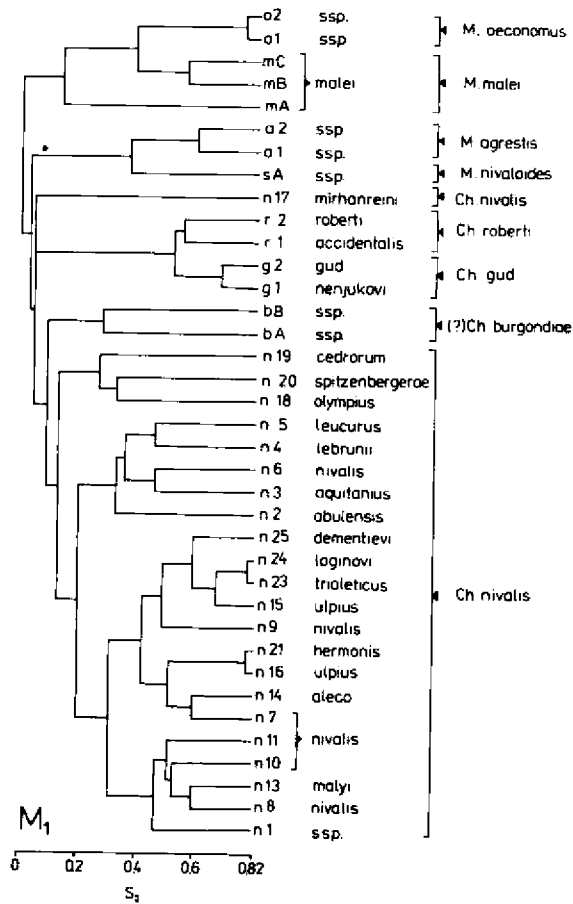
Fig. 21. Phenetic dendrogram (UPGMA) for M₁ based on Jaccard's similarity values (Sⱼ) for 37 recent and fossil populations of the *Chionomys* group and some allied taxa. The cophenetic correlation coefficient is 0.89. Explanation of abbreviations to be found in Tables 1 and 2.

The above data make it possible to distinguish the following groups of populations: (1) the "lebrunii" group (comprising subspecies *lebrunii, leucurus, aquitanius, abulensis*); (2) the "nivalis" group (*nivalis, ?wagneri, malyi, aleco, ulpius, loginovi, trialeticus, ?pontius, dementievi, hermonis*); (3) the "mirhanreini" group (*mirhanreini*); (4) the "cedrorum" group (*cedrorum, olympius*); (5) the "spitzenbergerae" group (*spitzenbergerae*).

Fossil samples of *Ch. nivalis* from Pleistocene show similar variation as extant populations, however, the frequency of simple morphotypes "lebrunii" (total 22.3%) and "aquitanius" (20.1%) is higher while more complicated patterns exhibit lower frequencies ("nivalis" – 51.2%, "mirhanreini" – 0.3%). West European fossil populations (nA – nE) show for M₁ the predominance of morphotype "lebrunii" while "aquitanius" is rather less frequent. Measured parameters have not changed significantly in relation to extant populations from this area. Fossil samples from Germany north to the present distribution of *Ch. nivalis* (nF – nl) do not differ distinctly from recent nominative subspecies (Fig. 23).
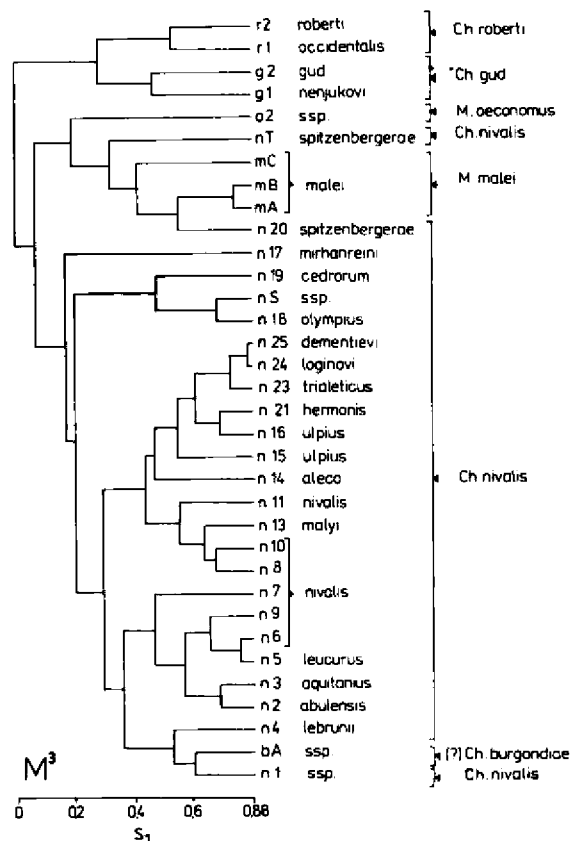
Fig. 22. Phenetic dendrogram (UPGMA) for M^3 based on Jaccard's similarity values (S_J) for 34 recent and fossil populations of the *Chionomys* group and some allied taxa. The cophenetic correlation coefficient is 0.91. Explanation of abbreviations to be found in Tables 1 and 2.

Populations from Czechoslovakia (nJ – nM) also show more simple dental pattern in comparison with the Middle and East European snow voles. Despite being most close geographically to *Ch. n. mirhanreini* from Tatra Mountains, they do not exhibit the peculiar characters of this taxon being phenetically similar to typical *Ch. n. nivalis* (Fig. 23). Fossil populations from Balkan Peninsula (nN – nR) show slightly higher frequencies of morphotypes "lebrunii" and "aquitanius" in comparison with present inhabitants of this territory (*Ch. n. aleco* and *Ch. n. ulpius*). From among the two populations from Asia Minor studied, the Middle Pleistocene M_1 sample from Latomi 1 (nS) is related morphologically to the simple populations of *Ch. n. lebrunii* and *Ch. n. leucurus*. The Karain B population (nT) is closely related to recent *Ch. n. spitzenbergerae* and is characterized by very high frequencies of "oeconomus" morphotype (41.7%) for M_1 and "malei" (63.6%) for M^3. Fossil samples from the Caucasus region (nU – nW) show a more simple dental pattern in comparison with the extant descendants, which is manifested by higher frequencies of morphotypes
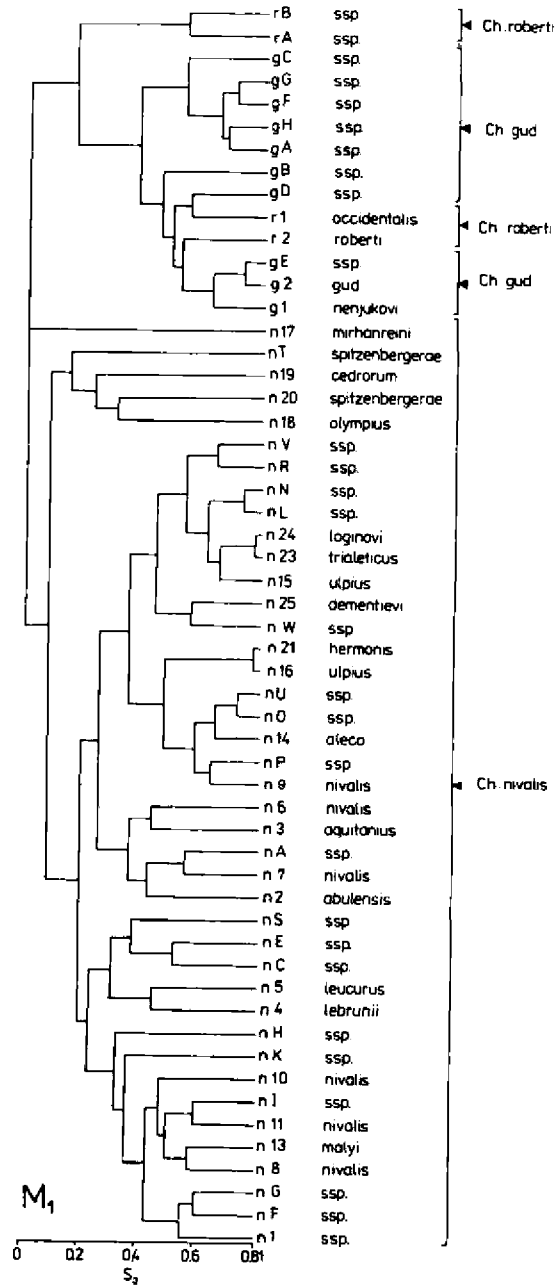
Fig. 23. Phenetic dendrogram (UPGMA) for M_1 based on Jaccard's similarity values (S_J) for 55 recent and fossil populations of the *Chionomys* group. The cophenetic correlation coefficient is 0.85. Explanation of abbreviations to be found in Tables 1 and 2.

"lebrunii" and "aquitanius". They are also characterized by distinctly longer M_1, especially in comparison with *Ch. n. loginovi*.

The dental pattern of two Caucasus species of *Chionomys* are generally very similar (Figs 10, 11, 12, 13). In the M_1 of *Ch. gud* the morphotype "gud" is clearly dominant (total frequency 54.6%) while for *Ch. roberti* it shows lower frequencies, in average 43.2%. In both species under study the simple morphotype "lebrunii" plays an important part being also generally less frequent in *Ch. gud* (total frequency 34.7%) than in *Ch. roberti* (41.9%). Other morphotypes of M_1 ("oeconomus", "nivalis" and "mirhanreini") are only accessorial. The dental pattern of M^3 of both species is distinctly different from *Ch. nivalis*. In these species, the complicated morphotypes "gud" and "roberti" prevail, with total frequency of 58.7% and 13.6% for *Ch. gud* and 16.1% and 65.8% for *Ch. roberti*, respectively. The only common morphotype with *Ch. nivalis* is "oeconomus" – relatively frequent, especially in *Ch. gud* (28.6%). Fossil populations of *Ch. gud* are very similar in the frequency distribution of M_1 morphotypes to the recent materials, with the exception of Middle Pleistocene samples from Matuzka Cave (gA) and Treugolnaya Cave (gD); these are characterized by a more simple dental pattern manifested by predominance of "lebrunii" morphotype (51.7 and 55.4%, respectively). Pleistocene populations of *Ch. roberti* from Matuzka Cave show a distinctly different percentage representation of morphotypes "lebrunii" and "gud" in comparison with recent subspecies. Generally, fossil samples of *Ch. gud* and *Ch. roberti* show smaller dimensions and lower values of 2/1 index than their recent descendants (Tables 11, 15). In phenetic dendrograms (Figs 21, 22, 23) they are well separated from *Ch. nivalis*.

The lower Biharian population from Les Valerots described under the name *Microtus malei burgondiae* Chaline, 1972 differs distinctly from the populations referred to the *M. malei* group (Fig. 14, Tables 10, 14). Its peculiar dental pattern of M_1 is characterized by mixing of different morphotypes. Among simple morphotypes "pliocaenicus", "nutiensis" and "prachintoni" which are typical for some evolved forms of *Allophaiomys*, the latter is the most frequent (26.5%). All other morphotypes ("lebrunii", "aquitanius", "malei", "nivalis") can be considered as nivaloid ones, although they all represent variants of confluent T4 and T5. Their total frequency prevails in the population (56.6%). The type population is relatively big (MLM$_1$ = 2.79), characterized by low values of 2/1 index (45.8) and very high values of 4/3 and 5/1 indices (25.1 and 11.3, respectively). The morphology of M^3 is very simple with absolute predominance of "lebrunii" morphotype (94.1%). Another population from Tcherdjenitsa 2 (bB) also referred to the same taxon represents much more primitive stage of evolution with distinct predomination of morphotypes characteristic of evolved *Allophaiomys* (74.4%), while nivaloid variants compose 25.6%. Both samples, however, form a separate cluster related to the *Chionomys* group named (?) *Chionomys burgondiae* (Fig. 21).

An analysis of dental pattern of the type population of *Microtus malei* from Clevedon Cave as well as two other samples studied show extremely high polymorphism (Figs 15, 16; Tables 12, 16). In the M_1 pattern there occur morphotypes characteristic of *Chionomys* (morphotype "nivalis" with total frequency of 45.1%), *M. oeconomus* (morphotypes "oeconomus" and "malei" with total frequency 18.9% and 29.9%, respectively) and even

accessorial pattern characteristic of *M. gregalis* (6.1%). The characters of M^3 are also peculiar with absolute predominance of "malei" morphotype (total frequency 74.4%). A very characteristic feature of *M. malei* is its great interpopulational variation. Each sample studied shows its own spectrum and frequency of M_1 morphotypes, with the predominance of "nivalis", "malei" or "oeconomus" patterns. It is a large, specialized taxon with high values of 2/1 index. Mean values of 4/3 and 5/1 indices occupy intermediate position between *Chionomys nivalis* and *Microtus oeconomus*. Generally, *M. malei* is most closely related to *M. oeconomus* (Figs 17, 18, Tables 12, 16) and has nothing in common with *Chionomys* in spite of high frequency of nivaloid variants in dentition (Figs 21, 22).

An analysis of the M_1 material of *Microtus nivaloides* from the type locality at West Runton shows the predominance of morphotype "arvalis" (56.1%) followed by "nivalis" (32.9%) (Fig. 19, Table 13). Three accessorial morphotypes "agrestis" (3.7%), "coronensis" (4.9%) and "extratriangulatus" (2.4%) are characteristic of extant *M. agrestis* (Fig. 20, Table 13) and never occur in the species of *Chionomys*. It is a rather small $(M - LM_1 = 2.62)$ and specialized taxon with relatively high values of 2/1 index (in average 50.5) and low values of 4/3 and 5/1 indices (5.1 and 6.5, respectively), again typical of *Microtus arvalis/agrestis* group. Both the mentioned species create one cluster distinctly separated from *Chionomys* and *M. oeconomus* groups (Fig. 21).

Discussion

In almost all phyletic lineages of voles one can observe a gradual and progressive increase of triangle number or at least complication of the morphological structure on the first lower and the last upper molars as well as a moderate trend of increase in size. This stable tendency, which can be considered in terms of phyletic gradualism (Chaline 1987), creates a basis for discrimination of the primitive and derived populations. It is assumed by palaeontologists that a similar dental morphology in a given lineage reflects real phylogenetic relationships between the studied taxa. This last assumption is based on the fact that complexity of dental characters is inherited and that multiple genes with additive effects rather than a single gene are responsible for a given morphological pattern (Grewal 1962, Grüneberg 1965). In the course of evolution the frequency of genes and so the frequency of the minor dental characters undergo gradual change being a morphodynamic process. As a consequence, in a given lineage primitive (= ancestral) characters are not completely lost but are preserved with smaller and smaller frequency. This phenomenon is observed in most of the *Microtus* (*sensu lato*) lineages manifested by sporadic occurrence of ancestral characters in few recent specimens. In the *Stenocranius* lineage, for example, the confluence of T4 and T5 in M_1, which is considered a primitive trait, decreases by degrees from the Biharian *Microtus* (*Stenocranius*) *gregaloides* to *M.* (*S.*) *gregalis* (Nadachowski 1985). In extant species this character "survived" with frequency 7-8% (Bolshakov et. al. 1980). It is believed that similar processes should be observed in the evolution of the *Chionomys* lineage.

Origin and evolution of Chionomys

Lower Pleistocene is the period of radiation of *Microtus* (*sensu lato*) and the fossil taxa described are direct ancestors of the extant species. The origin of *Chionomys* is enigmatic. There are two alternative possibilities of the solution of this problem. The first is based on the opinion that *Microtus* (*Allophaiomys*) *pliocaenicus*, widely distributed in Eurasia and North America in Lower Biharian, is the ancestor of all phyletic lineages of *Microtus* including *Chionomys* (Chaline 1972, Rabeder 1981, Fejfar and Horáček 1983). Literature data indicate that nivaloid patterns of M₁ (morphotypes "lebrunii", "aquitanius", "nivalis") appear, with low frequency, practically in every sample of *Allophaiomys*, independently of its geographic position. This general phenomenon seems to be a characteristic feature of the evolution of the *Allophaiomys* first lower molars and impedes identification of an ancestor population. One can also assume that *Chionomys* split from an unknown ancestor belonging to the genus *Mimomys* already in the beginning of the Lower Biharian. Although this point of view is not confirmed by the fossil evidence, it is strongly supported by biochemical and karyological data (Agadzhanian and Yatsenko 1984, Graf 1982).

Only at the end of the Belfia phase there appear populations with higher frequency of nivaloid morphotypes. Special attention should be paid to a form described from Les Valerots under the name *Microtus malei burgondiae* Chaline, 1972. The cluster analysis for M₁ shows that it is related to the *Chionomys* group and has little in common with the *Microtus oeconomus* group (including *M. malei, sensu stricto*)(Fig. 21). Its M³ pattern is very similar to the primitive populations of *Ch. nivalis* (Fig. 22). This population, however, shows some special traits i.e. a relative high frequency of primitive morphotypes "pliocaenicus", "prachintoni", "nutiensis" and confluence of T4 and T5 in nivaloid morphotypes of M₁ which never occur in extant *Chionomys*. Complete lack in recent *Chionomys nivalis* of primitive traits characteristic of "*Microtus*" *burgondiae* make the attachment of the mentioned taxon to the *Chionomys* lineage rather dubious. On the other hand, among fossil European materials it is most closely related to *Ch. nivalis*. It is proposed here to provisionally include "*Microtus*" *burgondiae* to *Chionomys*.

Haas (1966) described from the Lower Biharian site 'Ubeidiya in Israel (Tchernov 1987) a new arvicolid species with primitive dental characters and an uncertain generic assignment named *Arvicola* (?)*jordanica* Haas, 1966. Comparisons of its M₁ morphology with that of the representatives of the *Chionomys* group indicate a close similarity, especially with *Ch. roberti*. On the other hand, the structure of M³ is distinctly different. Although Tchernov (1986) still regards the taxon as a primitive member of the genus *Arvicola*, it should be treated rather as a species of derived *Allophaiomys* (Koenigswald and Van Kolfschoten, 1990) or an ancestor taxon of *Chionomys* species from the Caucasus region.

Towards the end of Biharian there appear in Europe 2 – 3 taxa which traditionally were included in *Chionomys*. Two of them described from West Runton (Major 1902, Hinton 1923, 1926) are of Cromerian age and represent relatively evolved taxa, both without features typical of the *Chionomys* group. The first one, *Microtus nivaloides*, with characters related rather to *M. agrestis* (Fig. 21), belongs to *Microtus arvalis/agrestis* group what has already been suggested by Stuart (1975). It appears to be conspecific with *Microtus*

Age My	BP	General division	Paleomagnetics	Glacial cycles	Stratigraphy	Evolution		
						Microtus	Chinomys	
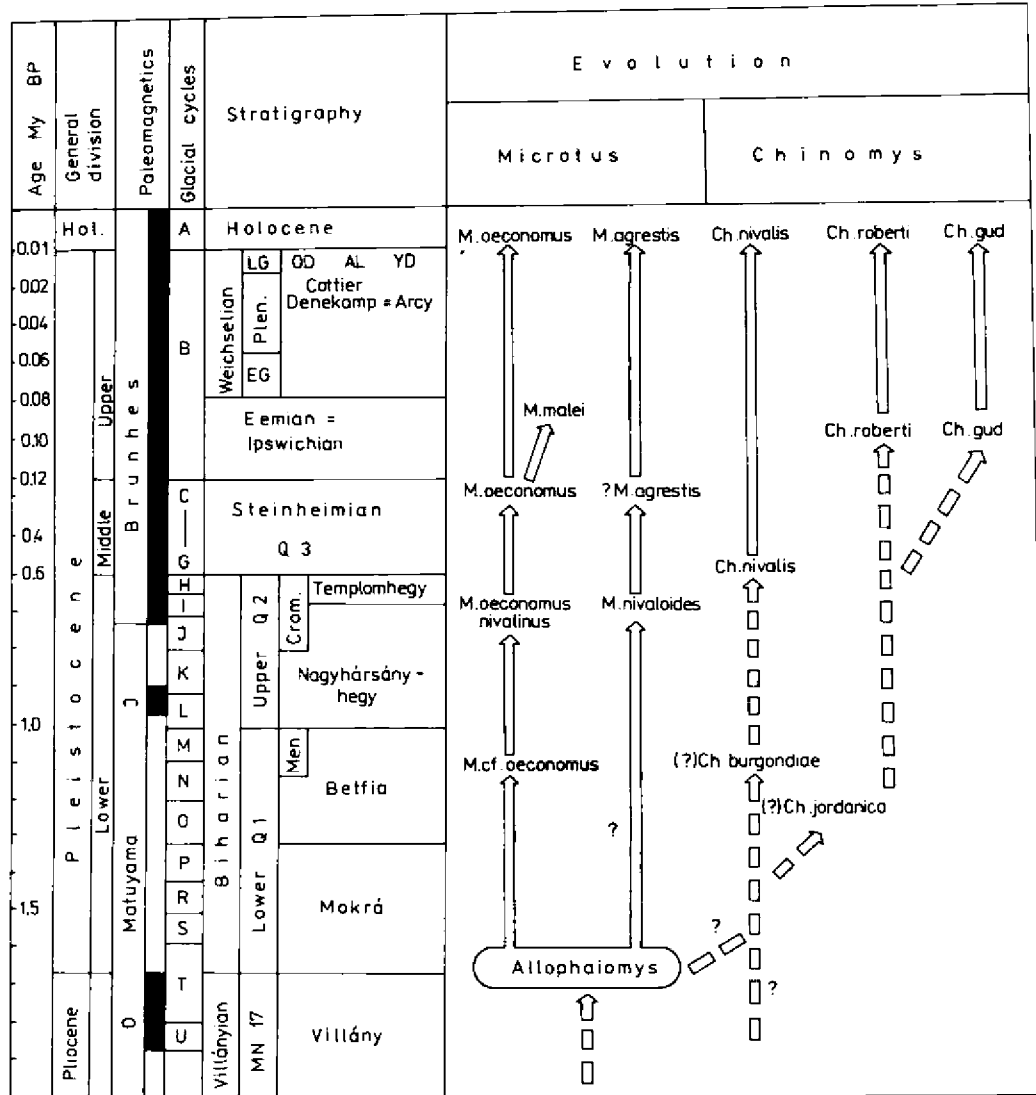
Fig. 24. Evolution of *Chionomys* and some *Microtus* lineages. Stratigraphy after Horáček (1981, supplemented and changed). AL – Allerød, Crom. – Cromerian, EG – Early Glacial, Hol. – Holocene, LG – Late Glacial, Men. – Menapian, OD – Older Dryas, Plen. – Pleniglacial, YD – Younger Dryas. Note twice change of the age scale.

arvalinus Hinton, 1923 in view of the unquestionable morphological similarity. It confirms the earlier opinion of Van der Meulen (1973) and in consequence the priority of the name *M. nivaloides* for arvaloid taxa from West Runton (Nadachowski 1990a). In continental Europe in the slightly earlier period (most probably during Nagyhársányhegy phase) there

appears a taxon also included by most students in *M. nivaloides*, however, with morphological variation distinctly different from the type West Runton population. Such materials were described for instance from Hohensülzen (Storch *et al.* 1973) and Zalesiaki 1A (Nadachowski 1990c). The mentioned taxon requires special studies and although it shows some nivaloid characters in the pattern of M_1 (especially the high frequency of morphotype "gud"), in my opinion it does not belong to the *Chionomys* group.

The second taxon from West Runton, traditionally included to *Chionomys* – named *Microtus nivalinus* belongs to *M. oeconomus* group (Nadachowski 1990a). It is identical with *Microtus ratticepoides*, also described from West Runton; they represent one taxon (Stuart 1975) ancestral to extant *Microtus oeconomus* which should be named *Microtus nivalinus* or more safely *M. oeconomus nivalinus* Hinton, 1923 (Fig. 24). The primitive ratticepoid variants appeared earlier ca. 0.8 - 1.1 My BP in the Russian Plain where well stratified sediments from the Petropavlovsk or Karai-Dubina stage (corresponding to the end of Lower Biharian) are available (e.g. Markova 1982, 1990). Thus, the root vole (*M. oeconomus*) represents a well defined lineage which split from the *Allophaiomys* general stock already towards the end of Betfia phase and/or beginning of the Nagyhársnáyhagy phase and has little in common with *Chionomys* (Fig. 24).

The phenomenon of overlapping of the dental morphological characters between *Chionomys*, *Microtus oeconomus* and to some extent of *Microtus arvalis/agrestis* group (Angermann 1974, 1984, Nadachowski 1982) led to taxonomic misunderstandings consisting in creation of new taxa (e.g. *Suranomys* of Chaline (1972)) or incorrect synonymy (e.g. Fejfar and Horáček 1983). The best example of this problem is a taxonomic status of *Microtus malei*. Hinton (1907a, b) described this species from Clevedon Cave on the basis of its peculiar dental pattern of M_1. Further studies by Chaline (1972) confirmed the specific rank of this taxon which is characterized by a very wide variation including nivaloid and ratticepoid variants. However, Sutcliffe and Kowalski (1976) suggested that *M. malei* be synonymized under *Ch. nivalis*. Crucial for the reconstruction of phylogenetic relationships are studies of M^3 preserved in Hinton's collection. Morphological analysis of 18 M^3 shows that they are relatively complicated and belong to the *M. coconomus* group (Fig. 22). Detailed studies of M_1 also confirm a close relation to *M. oeconomus* which agrees with the opinion of Stuart (1982), in spite of high frequency (49.9%) of the "nivalis" morphotype. Differences in the dental pattern of both M_1 and M^3 between *M. oeconomus* and *M. malei* are, however, sufficient to preserve the chronospecific rank of the taxon. The hypothesis of Chaline (1972) that *M. malei* is an ancestor of both *Ch. nivalis* and *M. oeconomus* is unjustified.

Variation recorded from Clevedon Cave is also commonly found in other British localities (including Tornewton Cave and Crayford, studied in the present paper) although in most cases the frequency of nivaloid variants is distinctly lower. It seems that *M. malei* is a very good biostratigraphical index fossil for early Upper Pleistocene (Ipswichian sensu lato) in the British Isles. Remains of voles from continental Europe described by Chaline (1972) under names *Microtus malei noaillensis* Chaline, 1972 from La Fage, and *Microtus malei gennii* Chaline, 1972 from Gigny distinctly differ from British materials. They belong

to typical *Microtus oeconomus* widely distributed in Europe during Middle and Upper Pleistocene.

It seems that real *Chionomys* remains appear in Europe and Asia Minor unquestionably during Middle Pleistocene in Steinheimian (Terzea 1972, Storch 1975, Popov 1989) and belong to *Ch. nivalis*. They exhibit primitive dental features related to the most primitive recent populations of *Ch. n. leucurus* and *Ch. n. lebrunii* and the population from Latomi 1 can serve as an example. Since Middle Pleistocene the snow vole shows distinct gradual changes in dental pattern in some regions, while in other areas this evolution is not observed. These changes in M_1 consist in the tendency to decrease of "lebrunii" and "aquitanius" morphotypes, increase of the typical "nivalis" pattern and relative length of the anteroconid complex. Such development is observed especially in the Balkan peninsula (Nadachowski 1984, Popov 1985, 1989).

Interpretation of variability in Chionomys

The high polymorphism of dental pattern in recent European *Ch. nivalis* is probably connected with (1) the Pleistocene history of species, (2) isolation of particular populations during postglacial period and (3) different patterns of competition occurring in the mountainous regions. Middle and Late Pleistocene climatic fluctuations played an important role in changing the geographical range of the species. Generally speaking, coolings resulted probably in widespreading of *Ch. nivalis* from mountainous regions to the lowlands. The fossil evidence indicates, however, that it does not leave far from mountains (Terzea 1972) (Fig. 1), most probably because of its specific ecology. Its distribution is determined by special adaptation to a petricolic way of life (Kratochvíl 1956, 1981; Kowalski 1957, Le Louarn and Janeau 1975, Krapp 1982). According to Kryštufek and Kovacić (1989) the snow vole is adapted to a cavernicolous habitat, with stable, mainly stenothermal conditions manifested also by its heterothermia and almost identical energy budgets for winter and summer (Bieńkowski and Marszalek 1974).

The most primitive populations survived in Spain and France (the "lebrunii" group). They are very closely related and form an isolated cluster as far as tooth morphology is concerned. The biochemical studies justify the separation of the mentioned taxa from the nominative subspecies (Graf 1982) and, on the other hand, their closeness. During stadial (cool) periods the populations of the "lebrunii" group which at present live mainly in relatively low altitudes (e.g. Massif Central, Basses-Alpes, Cordillera Cantabrica) were not forced to change their habitats, although their ranges were probably extended southward. Thus, they were able to preserve their primitive character. High mountain populations, however, e.g. *Ch. n. nivalis* from Alps were displaced to bordering areas out of glaciated territories and underwent distinct changes. During postglacial warmings, the range of West-European "lebrunii" group was fragmented into isolates where a suitable cavernicolous habitat with stenothermal conditions was preserved, while mountainous regions of Europe were reinvaded by lowland populations. The analysis of dental characters indicate that the Western Alps were colonized by members of the primitive West European "lebrunii" group, while Central and Eastern Alps as well as most of the Carpathians and the Balkan Peninsula were inhabited by already changed derived populations which survived glacial

periods in lower altitudes or/and in East-Southern Europe. This suposition is confirmed by biochemical studies (Graf 1982).

In the postglacial the mountains constituted "continental islands" which acted as speciation traps (Chaline 1987) and isolated populations of *Chionomys* started to evolve independently. In some cases these small local populations underwent dramatic changes in short time because the geographical isolation brakes the gene flow. For example, the population from the Tatra Mountains (*Ch. n. mirhanreini*) is so different from the other *Chionomys* samples that it should be treated as a separate species as far as dental morphology is concerned. However, only the biochemical studies could confirm the level of diversification processes. Peculiar features of *Ch. n. spitzenbergerae* (Nadachowski 1990b) caused its earlier wrong assignation to *Chionomys gud* (Spitzenberger 1971, Nadachowski 1990a). Generally, the "northern" high mountain populations - especially from the Alps, the Balkan Peninsula, the Carpathians but also from Caucasus and even Kopet Dag - constituting the "nivalis" and "mirhanreini" groups, are more derived. They inhabited the mentioned territories relatively late, in most cases after the retreat of glaciers. The "southern" populations belonging to the "lebrunii", "cedrorum" and "spitzenbergerae" groups occupy very often lower altitudes and inhabit areas which never had been covered by ice sheet. They preserved the primitive traits characteristic of *Ch. nivalis* from the Middle Pleistocene period. The only exception is the most southern *Chionomys* population from Lebanon and Anti-Lebanon Mountains (*Ch. n. hermonis*) which is related to the "nivalis" group.

Contrary to the high dental polymorphism and biochemical differenciation, the karyotype of *Ch. nivalis* is stable consisting of 54 chromosomes with 26 pairs of acrocentric autosomes in all studied mountainous regions (Todorović *et al.* 1971, Král 1972, Meylan and Graf 1973, Peshev and Belcheva 1979, Dias de la Gardia *et al.* 1981, Sablina *et al.* 1988).

Studies of recent *Ch. gud* and *Ch. roberti* from the Caucasus region show both a close relationship in dental morphology between them and a distinct separation from *Ch. nivalis*. This is also confirmed by karyological data (Sablina *et al.* 1988). Although karyotypes of all three species of snow voles consist of 54 chromosomes, they differ in the structure of the smallest pair of autosomes which in *Ch. gud* and *Ch. roberti* is metacentric while it is acrocentric in *Ch. nivalis*. The occurrence of fossil remains of both species exclusively in the territory of their present distribution (Nadachowski and Baryshnikov 1991) suggest the Caucasus region or its surroundings as a center of origin, as already indicated by Steiner (1972) and Gromov and Polyakov (1977).

Conclusions

Studies of dental variation and evolution of the *Chionomys* group supported by a comparison with biochemical and karyological criteria show its isolation from *Microtus* (sensu stricto). Its origin can be connected with the event of *Allophaiomys pliocaenicus* speciation during Lower Biharian (what is more probable) or with splitting from an

unknown ancestor much earlier, may be as early as the Pliocene/Pleistocene boundary. Probably already at the end of Lower Biharian *Chionomys* split into two lineages. The first one appeared and evolved in Europe (*Ch. nivalis* lineage) while the second is probably of Near East or Caucasus origin (*Ch. gud-roberti* lineage). A relict character of the taxon, especially of *Ch. nivalis*, is manifested by its primitive and stable karyotype, generally primitive dental pattern and attachment to the stenothermal habitats. On the other hand, its variation in dental characters and biochemical divergence is connected with the disjunctive character of its range and different patterns of competition occurring in local communities. Detailed studies of dental characters appeared to be useful for reconstruction of affinities between particular samples comparable in this respect with biochemical data. Five groups of populations were distinguished, named: "lebrunii", "nivalis", "mirhanreini", "cedrorum" and "spitzenbergerae". Differences observed in their dental pattern are sufficient for the separation on subspecific level. In the postglacial, the high mountain regions of Europe were occupied by derived populations of *Ch. nivalis*, while Western Europe (Spain and Southern France) as well as Asia Minor were inhabited by primitive populations. Most of the fossil taxa traditionally included in the *Chionomys* group appear to belong to *Microtus sensu stricto* (e. g. *M. malei, M. nivaloides, M. nivalinus, M. ratticepoides*).

References

Agadzhanian A. K. and Yalsenko V. N. 1984. Filogeneticheskie svyazi polevok Severnoi Evrazii. Sbor. Trud. Zool. Mus. MGU 22: 135 – 189.

Angermann R. 1974. Die Zahnvarabilität bei Microtinen im Lichte von Vavilov's "Gesetz der homologen Serien". Symp. Theriol., II, 1971, Praha: 61 – 73.

Angermann R. 1984. Intraspezifische Variabilität der Molarenmuster bei der Nordischen Wühlmaus (*Microtus oeconomus* (Pallas, 1776)). Zool. Abh. 39: 115 – 136.

Baryshnikov G. and Baranova G. I. 1983. Gryzuny rannego paleolita Boshogo Kavkaza. [In: Fauna , sistematika i biologia mlekopitayushchikh. P. P. Strelkov, ed.]. Tr. Zool. Inst. AN SSSR, Leningrad: 100 – 138.

Bieńkowski P. and Marszalek U. 1974. Metabolism and energy budget in the snow vole. Acta theriol. 19: 55 – 67.

Bolshakov V. N., Vasileva I. A. and Maleeva A. G. 1980. Morpholipicheskaya izmenchivost' zubov polevok. Nauka: 1 – 139, Moskva.

Chaline J. 1966. Un exemple d'évolusion chaz les Arvicolidés (*Rodentia*): les lignées *Allophaiomys, Pitymys* et *Microtus*. C.R. Acad. Sci., Paris D 263: 1022 – 1024.

Chaline J. 1972. Les rongeurs du Pléistocène moyen et supérieur de France. Cahiers Paléont., CNRS, Paris: 1 – 410.

Chaline J. 1976. Le stade arctique de Cottier: une nouvelle climatozone würmienne. Nouv. Arch. Mus. Hist. nat. Lyon 14: 43 – 48.

Chaline J. 1987. Arvicolid data (*Arvicolidae, Rodentia*) and evolutionary concepts. [In: Evolutionary biology. M. K. Hecht, B. Wallace, G. T. Prance, eds]. Plenum Publ. Corp.: 237 – 310., New York.

Chaline J. and Graf J.-D. 1988. Phylogeny of the *Arvicolidae* (*Rodentia*): biochemical and paleontological evidence. J. Mamm. 69: 22 – 33.

Chaline J., Renault-Miskovsky J., Brochet G., Clement-Dels C., Jammot D., Mourer-Chauvire C., Bonvalot J., Lang J., Leneuf N. and Pascal A. 1985. L'aven des Valerots (Nuits-Saint-Georges, Cote-d'Or), site de reference du Pléistocène inferieur. Rev. Geol. Dynam. Geogr. Phys., 26: 109 – 118.

Clot A., Brochet G., Chaline J., Desse G., Evin J., Granier J., Mein P., Mourer-Chauvire C., Omnes J. and Rage J.C. 1984. Faune de la grotte préhistorique du bois du Cantet (Espèche, Hautes-Pyrénées, France). Munibe 36: 33 – 50.

Corbet G. B. 1978. The mammals of the Palaearctic region. A taxonomic review. Cornel University Press: 1 – 314, London and Ithaca.

Corbet G. B. and Hill J. E. 1986. A world list of mammalian species. Second edition. British Museum (Natural History) and Facts of File Publications: 1 – 254, London.

Dias de la Guardia R., Burgos M. and Jimenez R. 1981. About the karyotype of *Microtus nivalis* Martins (*Rodentia, Microtinae*). Caryologia 34: 377 – 383.

Fejfar O. and Heinrich W.-D. 1983. Arvicoliden-Sukzession und Biostratigraphie des Oberpliozäns und Quartärs in Europa. Schriftenr. geol. Wiss. 19/20: 61 – 109.

Fejfar O. and Horáček I. 1983. Zur Entwicklung der Kleinsäugerfaunen im Villanyium und Alt-Biharium auf dem Gebiet der ČSSR. Schriftenr. geol. Wiss. 19/20: 111 – 207.

Graf J.- D. 1982. Genetique, biochemique, zoogeographie et taxonomie des *Arvicolidae* (*Mammalia, Rodentia*). Rev. Suisse Zool. 89: 749 – 787.

Graf J.- D. and Scholl A. 1975. Variations enzymatiques et relations phyletiques entre neuf species de *Microtinae* (*Mammalia, Rodentia*). Rev. Suisse Zool. 82: 681 – 687.

Grenwal M. S. 1962. The development of an inherited tooth defect in the mouse. J. Embryol. exp. Morph. 10: 202 – 211.

Gromov I. M. and Polyakov I. Ya. 1977. Polevki (*Microtinae*). Fauna SSSR. Mlekopitayushchie. 3, 8: 4 – 504.

Grüneberg H. 1965. Genes and genotypes affecting the teeth of the mouse. J. Embryol. exp. Morph. 14: 137 – 159.

Guthrie R. D. 1971. Factors regulating the evolution of *Microtinae* tooth complexity. Z. Säugetierk. 36: 37 – 54.

Haas G. 1966. On the vertebrate fauna of the Lower Pleistocene site 'Ubeidiya. Israel Acad Sci. 1 – 68.

Hinton M. A. C. 1907a. On the existence of the alpine vole (*Microtus nivalis* Martins) during Pleistocene times. Proc. Geol. Ass. 20: 39 – 58.

Hinton M. A. C. 1907b. Note on the occurrence of the alpine vole (*Microtus nivalis*) in the Clevedon Cave deposit. Proc. Bristol Nat. Soc. 1: 190 – 191.

Hinton M. A. C. 1923. Diagnoses of species of *Pitymys* and *Microtus* occurring in the Upper Freshwater Bed of West Runton, Norfolk. Ann. Mag. nat. Hist. 12: 541 – 542.

Hinton M. A. C. 1926. Monograph of the voles and lemmings (*Microtinae*) living and extinct. British Museum (Natural History), London: 1 – 488.

Horáček I. 1981. Comments on the lithostratigraphic context of the Early Pleistocene mammal biozones of Central Europe. IUGS-UNESCO Internat. Geol. Corr. Progr., Project 73/1/24, Quaternary Glaciations in the Northern Hemisphere, rep. 6: 99 – 107.

Horáček I. and Sánchez Marco A. 1984. Comments on the Weichselian small mammal assemblages in Czechoslovakia and their stratigraphical interpretation. N. Jb. Geol. Paläont. Mh. 1984: 560 – 576.

Koenigswald von W. 1974. Die pleistozäne Fauna der Weinberghöhlen bei Mauern. [In: Die Archäologie und Paläontologie in den Weinberghöhlen bei Mauern (Bayern), Grabungen 1937-1967. W. von Koenigswald, II.-J. Müller-Beck, E. Pressmar, eds]. Archeologica Ventoria, Inst. für Urgeschichte, Tübingen: 53 – 106.

Koenigswald von W. 1978. Die Säugetierfauna des Mittel-Würms aus der Kemathenhöhle im Altmühltal (Bayern). Mitt. Bayer. Staatsslg. Paläont. hist. Geol. 18: 117 – 130.

Koenigswald von W. and Van Kolfschoten T. 1990. The significance of *Arvicola* in the European Pleistocene. Cromer Symp. Abstr., Norwich 1990, SEQS: 19 – 20.

Kowalski K. 1957. *Microtus nivalis* (Martins, 1842) (*Rodentia*) in the Carpathians. Acta theriol. 1: 159 – 182.

Král B. 1972. Chromosome characteristics of *Muridae* and *Microtidae* from the ČSSR. Acta Sc. Nat. Brno 6: 1 – 78

Krapp F. 1982. *Microtus nivalis* (Martins, 1842) – Schneemaus. [In: Haundbuch der Säugetiere Europas. J. Niethammer and F. Krapp, eds). Akadem. Verlagsgesellschaft, Wiesbaden: 261 – 283.

Kratochvíl J. 1956. Tatra-Schneemaus *Microtus* (*Chionomys*) *nivalis mirhanreini* (Schäfer, 1935). Pr. Brnenske Zak. Čes. Acad., Věd 28: 1 – 39.

Kratochvíl J. 1981. *Chionomys nivalis* (*Arvicolidae, Rodentia*). Acta Sc. Nat. Brno 15: 1 – 62

Kryštufek B. and Kovacić D. 1989. Vertical distribution of the Snow vole *Microtus nivalis* (Martins, 1842) in Northwestern Yugoslavia. Z. Säugetierk. 54: 153 – 156.

Le Louarn H. and Janeau G. 1975. Répartition et biologie du campagnol des neiges *Microtus nivalis* Martins dans la région de Briançon. Mammalia 39: 589 – 604.

Major C. I. F. 1902. Exhibition of, and remarks upon, some jaws and teeth of Pliocene voles (*Mimomys*, gen. nov.). Proc. zool. Soc. Lond. 1902: 102 – 107.

Markova A. K. 1982. Pleistocene rodents of the Russian Plain. Nauka, Moscow: 1 – 186. [In Russian]

Markova A. K. 1990. Pleistocene microtheriofauna of the European part of the USSR. [In: International Symposium Evolution, Phylogeny and Biostartigraphy of Arvicolids (*Rodentia, Mammalia*). O. Fejfar and W.-D. Heinrich, eds]. Geological Survey, Prague: 313 – 338.

Meylan A. and Graf J.-D. 1973. Caryotype du campagnol des neiges, *Microtus nivalis* (Martins), en Europe occidentale (*Mammalia, Rodentia*). Bull. Soc. vaud. Sc. nat. 71: 441 – 446.

Nadachowski A. 1982.: Late Quaternary rodents of Poland with special reference to morphotype dentition analysis of voles. Państw. Wyd. Nauk., Warszawa-Kraków: 1 – 108.

Nadachowski A. 1984. Morphometric variability of dentition of the Late Pleistocene voles (*Arvicolidae, Rodentia*) from Bacho Kiro Cave (Bulgaria). Acta zool. cracov. 27: 149 – 176.

Nadachowski A. 1985. Biharian voles (*Arvicolidae, Rodentia, Mammalia*) from Kozi Grzbiet (Central Poland). Acta zool. cracov. 29: 13 – 28.

Nadachowski A. 1990a. Comments on variation, evolution and phylogeny of *Chionomys* (*Arvicolidae*). [In: International Symposium Evolution, Phylogeny and Biostratigraphy of Arvicolids (*Rodentia, Mammalia*). O. Fejfar and W.-D. Heinrich, eds]. Geological Survey, Prague: 353 – 368.

Nadachowski A. 1990b. On the taxonomic status of *Chionomys* Miller, 1908 (*Rodentia: Mammalia*) from Southern Anatolia (Turkey). Acta zool. cracov. 33: 79 – 89.

Nadachowski A. 1990c. Lower Pleistocene rodents of Poland: faunal succession and biostratigraphy. Quartärpaläont. 8: 215 – 223.

Nadachowski A. and Baryshnikov G. 1991. Pleistocene snow voles (*Chionomys* Miller, 1908) (*Rodentia, Mammalia*) from Northern Caucasus (USSR). Acta zool. cracov. 34: 437 – 451.

Pavlinov I. Ya. and Rossolimo O. L. 1987. Sistematika nlekopitajuščih SSSR. Arch. Zool. Mus. Moscow State Univ. 25: 3 – 284. [In Russian]

Peman E. 1985. Aspectos climáticos y ecológicos de los Micromamíferos del yacimiento de Erralla. Munibe 37: 49 – 57.

Peshev T. and Belcheva R. 1979. Karyological studies on snow vole *Microtus nivalis* Martins (*Mammalia, Rodentia*) collected in Bulgaria. Zool. Anz. 203: 65 – 68.

Pietsch M. 1980. Biometrische Analyse an Schädeln von neun Kleinsäger-Arten aus der Familie *Arvicolidae* (*Rodentia*). Z. f. zool. Systematik u. Evolutionsforsch. 18: 196 – 211.

Popov V. V. 1984. Small mammals (*Mammalia - Insectivora, Rodentia, Lagomorpha*) from Late Pleistocene deposits in Mecha Dupka Cave (the Western Balkan Mountain). I. Taphonomy, paleoecological and zoogeographical pecularities of the fauna. Acta zool. bulg. 24: 35 – 44. [In Bulgarian]

Popov V. V. 1985. Small mammals (*Mammalia - Insectivora*, Rodentia, Lagomorpha) from Late Pleistocene deposits in Mecha Dupka Cave (the Western Balkan Mountain). II. Description of species. Acta zool. bulg. 26: 23 – 48. [In Bulgarian]

Popov V. V. 1989. Middle Pleistocene small mammals (*Insectivora, Lagomorpha, Rodentia*) from Morovitsa Cave (North Bulgaria). Acta zool. cracov. 32: 561 – 588.

Rabeder G. 1981. Die Arvicoliden (*Rodentia, Mammalia*) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. Beitr. Paläont. Österreich 8: 1 – 373.

Repenning C. A. 1987. Biochronology of the *Microtinae* rodents of the United States. [In: Cenozoic Mammals of North America. Geochronology and biostratigraphy. M. O. Woodburne, ed.]. Univ. of California Press, Berkeley, Los Angeles, London: 236 – 268.

Sablina O. V., Radzhabli S. I., Malikov V. G., Meyer M. N. and Kuliev G. N. 1988. Taxonomy of voles of the genus *Chionomys* (*Rodentia, Microtinae*) based on karyological data. Zool. Zh. 67: 472 – 475. [In Russian with English summary]

Shidlovskij M. V. 1976. Opredelitel' gryzunov Zakavkazya. Metsniereba, Tbilisi: 1 – 255.

Sneath P. H. A. and Sokal R. R. 1973. Numerical taxonomy. W. H. Freeman and Company, San Francisco: 1 – 573.

Spitzenberger F. 1971. Zur Systematik und Tiergeographie von *Microtus* (*Chionomys*) *nivalis* und *Microtus* (*Chionomys*) *gud* (*Microtinae, Mamm.*) in S-Anatolien. Z. Säugetierk. 36: 370 – 380.

Steiner H. M. 1972. Systematik und Ökologie von Wühlmäusen (*Microtinae. Mammalia*) der vorderasiatischen Gebirge Ostpontus, Talysch und Elburs. S.B. österr. Akad. Wiss., mathem. naturw. Kl. 180: 99 – 193.

Storch G. 1975. Eine mittelpleistozäne Nager-Fauna von der Insel Chios, Ägäis (*Mammalia: Rodentia*). Senckenbergiana biol. 56: 165 – 189.

Storch G. 1988. Eine jungpleistozäne / altholozäne Nager-Abfolge von Antalya, SW-Anatolien (*Mammalia, Rodentia*). Z. Säugetierk. 53: 76 – 82.

Storch G., Franzen J. L. and Malec F. 1973. Die altpleistozäne Säugerfauna (*Mammalia*) von Hohensülzen bei Worms. Senckenberg. Lethaea 54: 311 – 343.

Stuart A. J. 1975. The vertebrate fauna of the type Cromerian. Boreas 4: 63 – 76.

Stuart A. J. 1982. Pleistocene vertebrates in the British Isles. Longman: 1 – 212, London, New York.

Sutcliffe A. J. and Kowalski K. 1976. Pleistocene rodents of the British Isles. Bull. Brit. Mus. (Nat. Hist.) 27: 33 – 147.

Tchernov E. 1986. The rodents and logomorphs from 'Ubeidiya formation: systematics, paleoecology and biogeography. Mem. Trav. Centr. Res. Francais de Jerusalem, Ass. Paleorient 5: 235 – 350.

Tchernov E. 1987. The age of the 'Ubeidiya formation, early Pleistocene hominid site in the Jordan valley, Israel. Isr. J. Earth Sci. 36: 3 – 30.

Terzea E. 1972. Remarques sur la morphologie dentaire et la repartition de *Microtus nivalis* Martins dans le Pléistocène de Roumanie. Trav. Inst. Speol. "Emile Racovitza" 11: 271 – 298.

Todorović M., Soldatović B. and Savić I. 1971. The karyotype of *Microtus nivalis* Martins, 1842 (*Rodentia*) from the Šar Planina. Arh. biol. nauka 23: 7 – 8.

Van der Meulen A. 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (*Arvicolidae, Rodentia*). Quaternaria 17: 1 – 144.

Zagwijn W. H. 1985. An outline of the Quaternary stratigraphy in the Netherlands. Geol. Mijn. 64: 17 – 24.

Zakrzewski R. J. 1985. The fossil record. [In: Biology of New World *Microtus*. R. H. Tamarin, ed.]. Spec. Publ. American Soc. Mammal., Lawrence: 1 – 51.

FIGS 8 – 20. MORPHOLOGICAL VARIATION OF M^3 AND M_1.

Fig. 8. *Chionomys nivalis*, morphological variation of M_1. Two-literal abbreviations refer to morphotypes (see the text). 3 – Maden Köy, Taurus Mts., NIIMW 13292; 6 – Mirador del Asón, Cordillera Cantabrica, MNCN 46; 7 – Ramales de la Victoria, Cordillera Cantabrica, ZIB 2714; 9 – Espinosa de los Monteros, Cordillera Cantabrica, MNCN 43; 10 – Chanac, Massif Central, MNIIN 3870; 11 – Larra, Pirenees, IPE 72102401; 12 – Barcelonnette, Alps, owl pellets, MIINT; 13 – National Parc Aigues Torta, Pirenees, IPE 58; 15 – Retezat, Carpathians, KSZP 1097; 17 – Ramales de la Victoria, Cordillera Cantabrica, ZIB 2712; 18 – Espinosa de los Monteros, Cordillera Cantabrica, MNCN 9; 19 – Volayerbachtal, Alps, NIIMW 26722; 20 – Espinosa de los Monteros, Cordillera Cantabrica, MNCN 35; 21 – La Moleta, Confranc, Pirenees, IPE 68091903; 22 – Mansgunteralpe, Alps, NIIMW 33490; 23 – Säntis, Appenzell, Alps, MNHU 62018; 27 – Aussois, Alps, MNIIN 1083; 28 – Pirin, USEB 24; 30 – Tauplitzalm, Steiermark, Alps, NIIMW 24672; 31 – Furka Pass, Alps, MBNII 28447; 32 – Tatra Mts, USEB 6; 37 – Tatra Mts., USEB 175; 38 – Briancon, Alps, LFS 2252; 39 – Tatra Mts., USEB 76; 40 – Tatra Mts., USEB 2; 41 – Barcelonette, Alps, owl pellets, MIINT; 42 – Tatra Mts., USEB 158; 43 – Mt. Hermon, Anti-Lebanon Mts., ZMTU 5460.

3 oe 6 oe 7 oe 9 le 10 le 11 le 12 le 13 le

15 le 17 ab 18 ab 19 ab 20 ab 21 aq 22 aq

23 ni 27 ni 28 ni 30 ni 31 ni 32 ni 35 ni 36 ni

37 gu 38 gu 39 gu 40 mi 41 mi 42 mi 43 mi
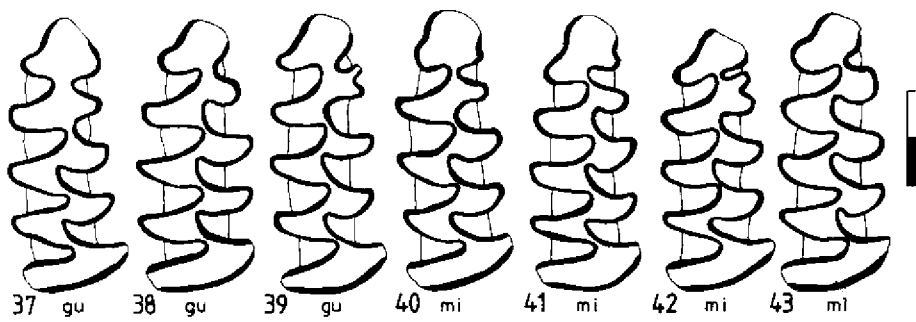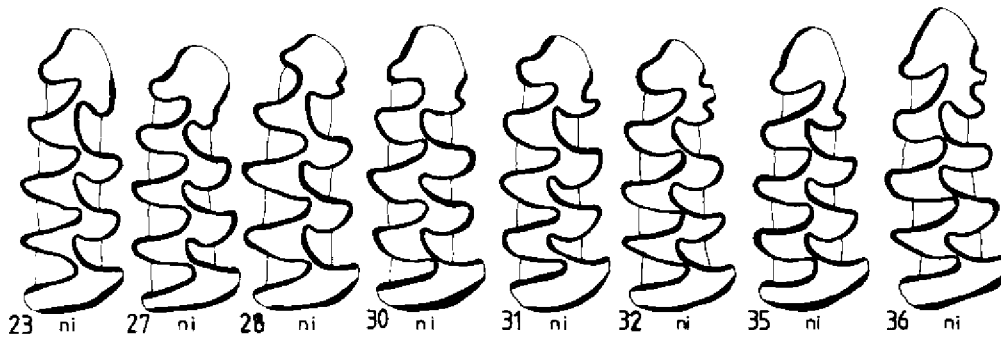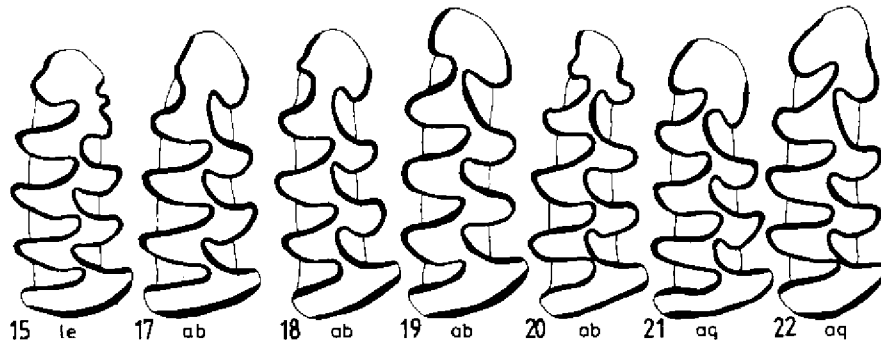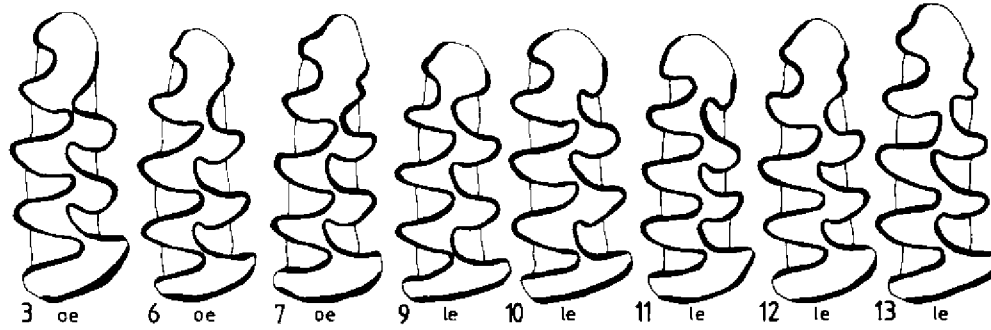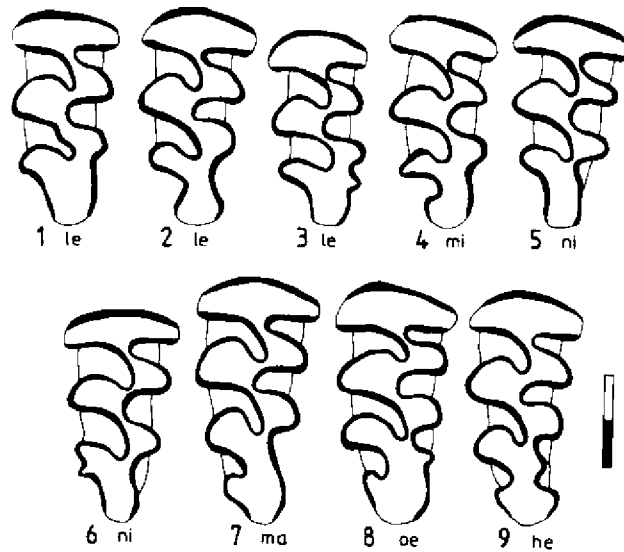
Fig. 9. *Chionomys nivalis*, morphological variation of M³. 1 - Nimes, Massif Central, MNHN 2009; 2 - Espinosa de los Monteros, Cordillera Cantabrica, MNCN 12; 3 - Barcelonnette, Alps, owl pellets, MHNT; 4 - Morskie Oko, Tatra Mts., ZBS 57121; 5 - St. Gothard, Alps, BMNH 466267; 6 - Val Piora, Ticino, Alps, BMNH 50140; 7 - Tauplizalm, Steiermark, Alps, NHMW 24685; 8 - Gössenkölle See, Kühtai, Alps, NHMW 31523; 9 - Mt. Hermon, Anti-Lebanon Mts, HUJ 150.
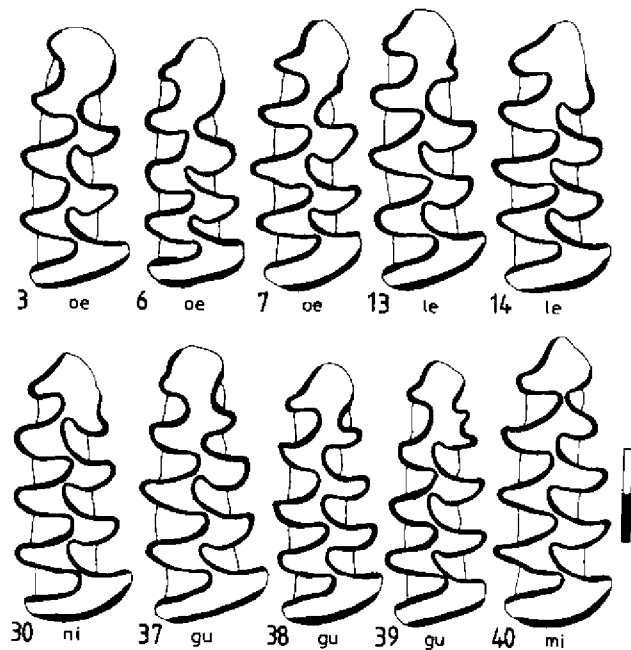
Fig. 10. *Chionomys gud*, morphological variation of M₁. 3 - Kavkaskiy Zapovednik, Caucasus, ZMUM 78957; 6 - Northern Caucasus ZIAS 65162; 7 - Teberda, Caucasus ZMUM 101440; 13 - Teberda, Caucasus ZMUM 136068; 14 - Kavkaskiy Zap., Caucasus, ZMUM 20786; 30 - Khulem, Caucasus ZMUM 17796; 37 - Kavkaskiy Zap., Caucasus, ZMUM 20677; 38 - Kavkaskiy Zap., Caucasus ZMUM 20754; 39 - Osetia, Caucasus, ZIAS 32722; 4 - Kavkaskiy Zap., Caucasus, ZMUM 20697.

Fig. 11. *Chionomys gud*, morphological variation of M³. 10 – Kobi, Caucasus. ZMUM 58130; 11 – Kavkaskiy Zapo vednik, Caucasus, ZMUM 7933; 12 – Vojenno-Gruzinskaya Doroga, Caucas us, ZMUM 5398; 13 – Osetia, Caucasus. ZMUM 15554; 14 – Teberda, Caucasus. ZMUM 101512; 15 – Kavkaskiy Zap. Caucasus, ZMUM 20697; 16 – Teberda. Caucasus, ZMUM 101499; 17 – Kavkas kiy Zap., Caucasus, ZMUM 17806; 18 – Kavkaskiy Zap., Caucasus, ZMUM 7943; 19 – Kavkaskiy Zap., Caucasus ZMUM 20750.
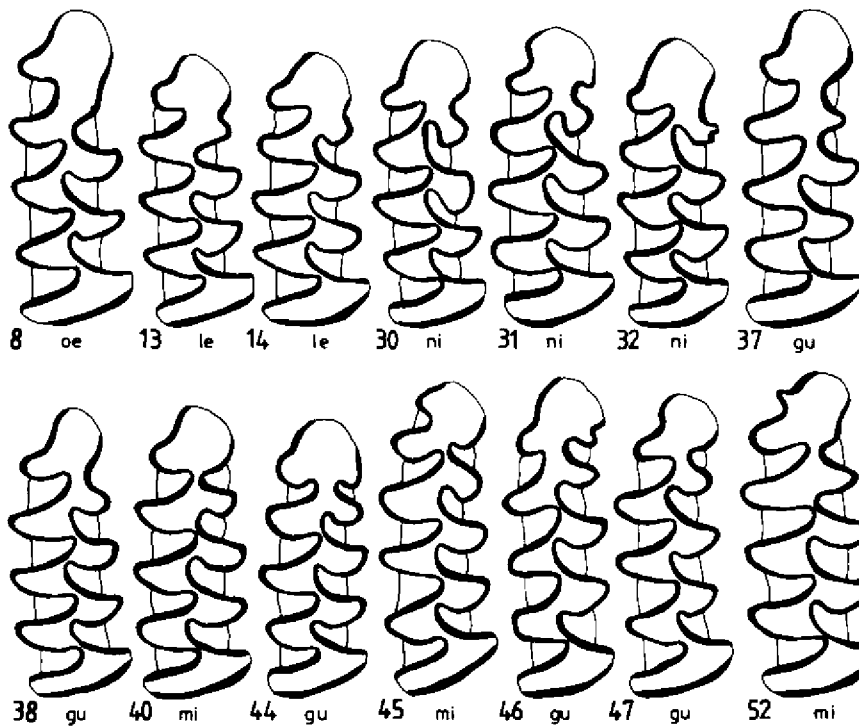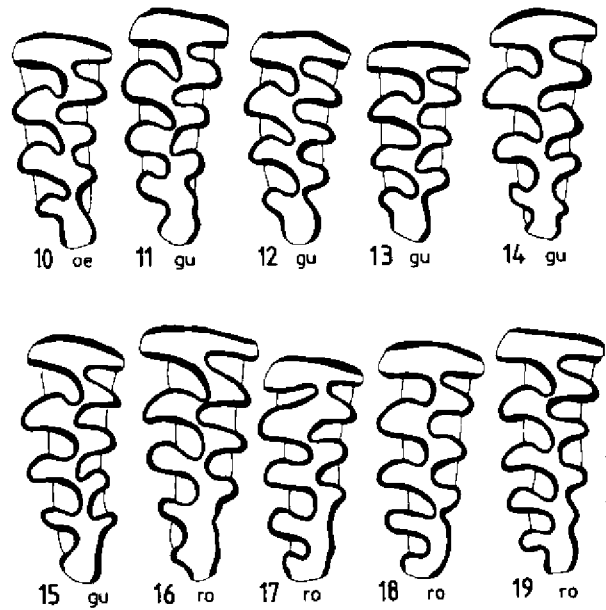
Fig. 12. *Chionomys roberti*, morphological variation of M₁. 8 – Kambushevka, Caucasus, ZMUM 17823; 13 – Kavkaskiy Zapovednik, Caucasus, ZMUM 20781; 14 – Kavkaskiy Zap., Caucasus, ZMUM 7924; 30 – Zakatelskiy Zap., Caucasus, ZIAS 37535; 31 – Dzhava, Caucasus, ZMUM 18332; 32 – Sumela, Lazistan Daglari, BMNH 636118; 37 – Biçik, Giresun Daglari, NHMW 19852; 38 – Teberda, Caucasus, ZIAS 28685; 40 – Sumela, Lazistan Daglari, BMNH 636129; 44 – Shovi, Caucasus, ZMUM 115072; 45 – Scalita, Lazistan Daglari, BMNH 636139; 46 – Sumela, Lazistan Daglari, BMNH 636125; 47 – Osetia, Caucasus, ZMUM 18234; 52 – Sumela, Lazistan Daglari, BMNH 636113.
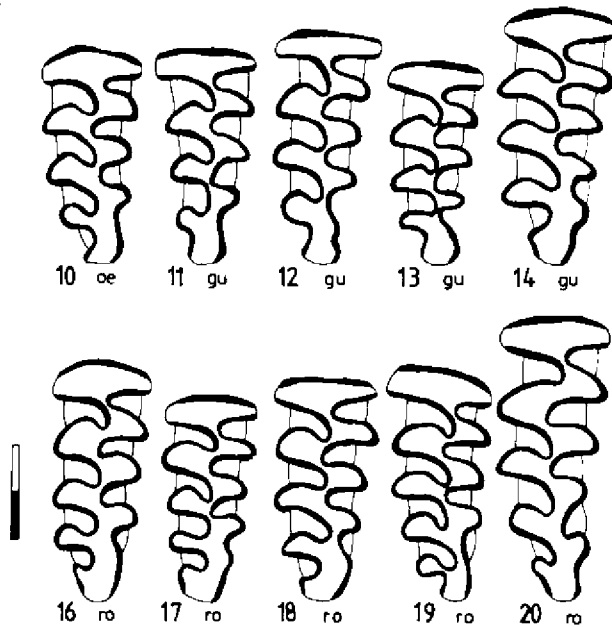
Fig. 13. *Chionomys roberti*, morphological variation of M³. 10 – Kavkaskiy Zapoviednik, Caucasus, ZMUM 90508; 11 – Kavkas Kavkaskiy Zap., Caucasus, ZMUM 20780; 12 – Kavkaskiy Zap., Caucasus, ZMUM 7537; 13 – Sumela, Lazistan Daglari, ZMUM 18715; 14 – Azhava, Caucasus, ZMUM 18332; 16 – Teberda, Caucasus, ZMUM 115074; 17 – Kavkaskiy Zap., Caucasus, ZMUM 18322; 18 – Kavkaskiy Zap., Caucasus, ZMUM 90509; 19 – Zakatelskiy Zapoviednik, Caucasus, ZIAS 37535; Biçik, Giresun Daglari, NHMW 19850.
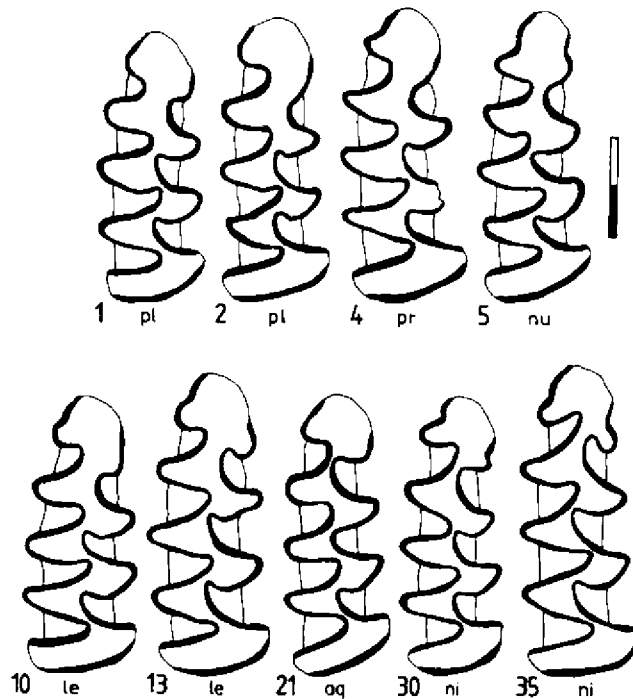
Fig. 14. (?) *Chionomys burgondiae*, morphological variation of M₁; all specimens from Les Valerots, France. 1 – CSTD 8178 (left M₁ inverted); 2 – CSTD 8427; 4 – CSTD 8345; 5 – CSTD 8316 (left M₁ inverted); 10 – CSTD 8214; 13 – CSTD 8076; 21 – CSTD 8424; 30 – CSTD 8379; 35 – CSTD 8407.
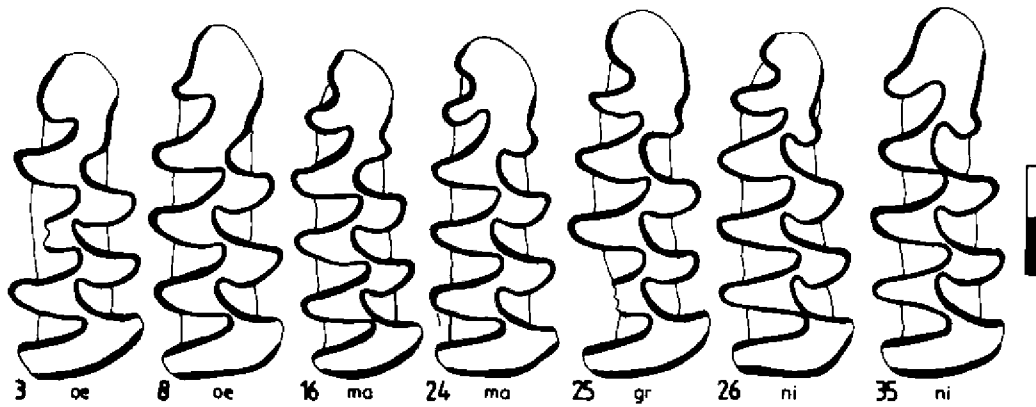
Fig. 15. *Microtus malei*, morphological variation of M_1; all specimens from Clevedon Cave. 3 – BMNH 26422 (left M_1 inverted), 8 – BMNH 26447, 16 – BMNH 26465, 24 – BMNH 26472, 25 – BMNH 26479, 26 – BMNH 26481 (holotype), 35 – BMNH 50676.
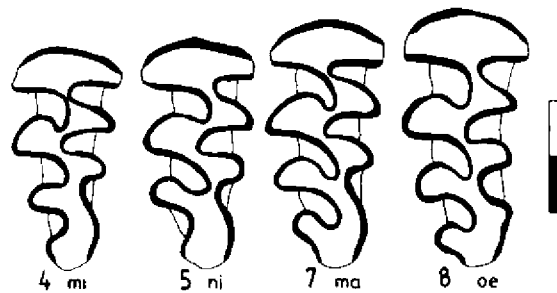
Fig 16. *Microtus malei*, morphological variation of M^3. 4 – Clevedon Cave BMNH 50680, 5 – Tornewton Cave, "Glutton Stratum" BMNH unnumbered, 7 – Clevedon Cave BMNH 50687, 8 – Crayford BMNH 3759.
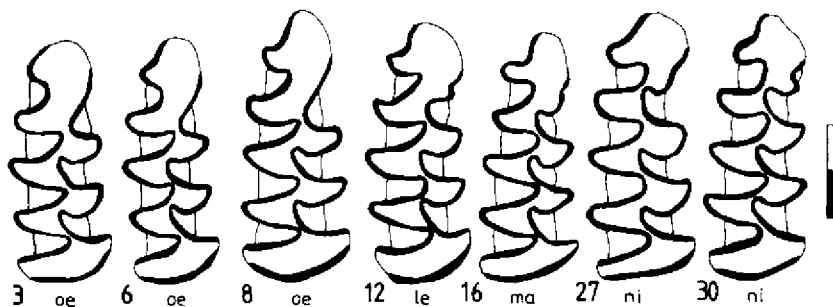
Fig 17. *Microtus oeconomus*, morphological variation of M_1. 3 – Jazy Biele, NE Poland ZBS 84864; 6 – Jazy Biele ZBS 86404; 8 – Jazy Biele ZBS 84344; 12 – Jazy Biele ZBS 84849; 16 – Jazy Biele 86403; 27 – Choszczewo, N Poland ZBS 123173; 30 – Choszczewo ZBS 123635.
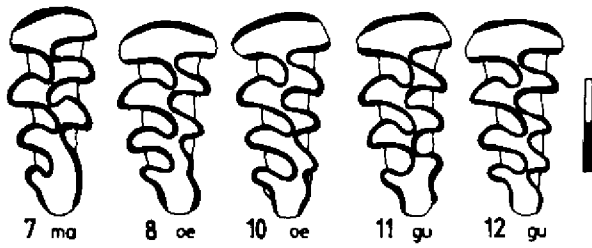
Fig. 18. *Microtus oeconomus*, morphological variation of M^3. All specimens from Jazy Biele, NE Poland. 7 – ZBS 84678; 8 – ZBS 84344; 10 – ZBS 84725; 11 – ZBS 86421; 12 – ZBS 68231.
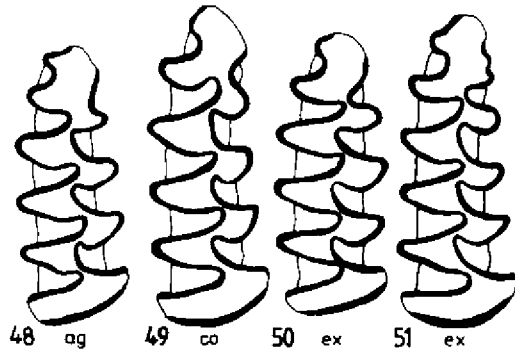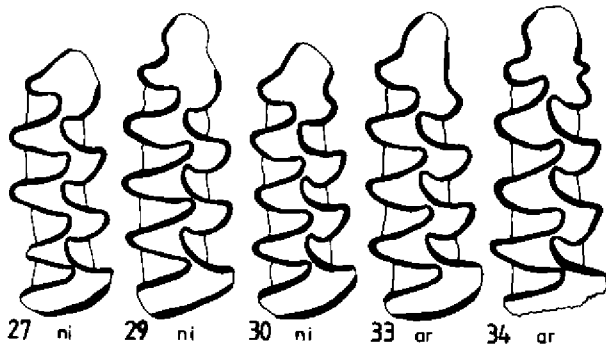
Fig. 19. *Microtus nivaloides*, morphological variation of M_1. BMNH unnumbered.
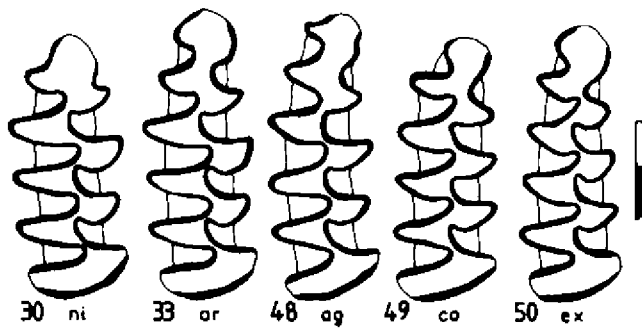
Fig. 20. *Microtus agrestis*, morphological variation of M_1. 30 – Wymiarki, ZBS 79729; 33 – Wymiarki, ZBS 79830, 48 – Dyrdy, ZBS 88277; 49 – Dyrdy, ZBS 88119; 50 – Wymiarki, ZBS 79732.

TABLES 4 – 9.
FREQUENCY DISTRIBUTIONS OF THE M_1 AND M^3 MORPHOTYPES.

TABLES 10 – 16.
MEASUREMENTS AND RATIOS OF M_1 AND M^3.

Table 4. Percentage frequency distributions of the M_1 morphotypes in recent and fossil *Ch. nivalis* populations.

Popu-lation	oc	le	ab	aq	ni	gu	mi	N
n 1	–	27.6	13.8	27.6	31.0	–	–	29
n 2	5.6	38.2	19.4	14.4	18.7	2.5	1.2	160
n 3	2.2	36.7	3.3	44.5	8.9	2.2	2.2	90
n 4	18.4	36.7	2.0	24.5	14.3	4.1	–	49
n 5	17.5	60.2	3.2	3.2	12.7	1.6	1.6	63
n 6	1.6	31.2	9.4	31.2	20.4	6.2	–	64
n 7	1.4	17.4	3.4	15.1	60.5	2.2	–	139
n 8	–	11.1	2.8	19.4	63.9	–	2.8	36
n 9	–	17.2	–	28.0	52.6	1.1	1.1	93
n10	2.5	32.6	2.5	15.0	47.4	–	–	40
n11	–	15.0	5.0	32.5	45.0	2.5	–	40
n12	–	–	–	21.4	78.6	–	–	14
n13	–	13.8	3.4	17.2	65.6	–	–	29
n14	0.7	1.4	1.4	11.3	83.1	0.7	1.4	142
n15	–	6.2	–	6.2	85.5	2.1	–	48
n16	–	–	1.3	7.9	90.8	–	–	76
n17	0.5	10.9	0.3	2.8	68.2	9.9	7.4	741
n18	14.3	35.7	–	–	50.0	–	–	14
n19	–	75.0	8.3	–	16.7	–	–	12
n20	41.7	33.3	–	8.3	16.7	–	–	12
n21	–	2.6	–	2.6	92.2	1.3	1.3	76
n23	–	–	–	14.3	85.7	–	–	49
n24	1.9	1.9	3.8	–	92.4	–	–	52
n25	–	18.7	–	10.4	70.9	–	–	48
n26	–	7.1	–	28.6	64.3	–	–	14
Sub-total	2.2	17.0	3.0	11.8	58.5	4.5	3.0	2130
nA	0.7	39.2	5.8	22.5	30.4	0.7	0.7	138
nB	–	66.7	8.3	–	25.0	–	–	12
nC	3.2	67.7	9.7	9.7	9.7	–	–	31
nD	–	70.0	–	10.0	20.0	–	–	10
nE	–	42.4	6.1	18.2	21.2	12.1	–	33
nF	–	13.0	4.3	30.4	52.3	–	–	23
nG	–	20.0	–	40.0	40.0	–	–	20
nH	3.8	19.2	3.9	53.9	19.2	–	–	26
nI	2.9	25.7	2.9	14.3	54.2	–	–	35
nJ	–	35.7	–	21.5	35.7	7.1	–	14
nK	3.7	25.9	3.7	11.1	51.9	–	3.7	27
nL	–	12.7	3.2	14.3	68.3	–	1.6	63
nM	–	–	–	9.1	90.9	–	–	11
nN	–	7.5	3.8	15.1	71.7	1.9	–	53
nO	1.8	13.6	1.8	12.3	69.3	1.2	–	162
nP	2.1	7.3	–	18.7	71.9	–	–	96
nR	1.3	13.2	–	13.2	72.3	–	–	76
nS	19.1	38.0	–	11.9	28.6	2.4	–	42
nT	26.1	65.3	–	4.3	–	4.3	–	23
nU	2.3	16.5	–	28.8	50.0	2.4	–	170
nV	2.7	13.5	–	32.4	50.1	–	1.3	74
nW	4.2	8.3	–	33.3	54.2	–	–	24
Sub-total	2.7	22.3	2.1	20.1	51.2	1.3	0.3	1163

Table 5. Percentage frequency distributions of the M_1 morphotypes in the recent and fossil populations of *Ch. gud* and *Ch. roberti*.

Popu-	Morphotype					
lation	oc	lc	ni	gu	mi	N
g1	7.5	31.9	4.5	54.6	1.5	66
g2	3.1	32.9	6.2	57.5	–	64
g3	–	58.4	8.3	33.3	–	12
g4	–	37.5	–	62.5	–	8
Sub-total	4.7	34.7	5.3	54.6	0.7	150
gA	3.2	51.7	3.2	41.9	–	31
gB	5.5	28.9	5.5	57.9	2.2	90
gC	4.3	13.0	–	78.4	4.3	23
gD	7.6	55.4	3.1	33.9	–	65
gE	2.2	34.8	8.7	54.3	–	46
gF	2.9	31.4	5.7	60.0	–	36
gG	7.7	34.6	3.8	53.9	–	26
gH	–	50.0	–	50.0	–	24
Sub-total	4.7	37.8	4.4	52.2	–	341
r1	3.6	48.2	7.2	41.0	–	83
r2	1.4	34.7	5.5	45.9	12.5	72

Table 6. Percentage frequency distributions of the M_1 morphotypes in (?) *Chionomys burgondiae*.

Popu-	Morphotype							
lation	pl	pr	nu	lc	aq	ma	ni	N
bA	9.7	26.5	7.2	33.7	2.4	7.2	13.3	83
bB	46.5	23.3	4.6	23.3	2.3	–	–	43
Total	22.2	25.4	6.4	30.2	1.6	5.5	8.7	126

Table 7. Percentage frequency distributions of M_1 morphotypes in *Microtus oeconomus* and *M. malei*.

Popu-	Morphotype					
lation	oc	lc	ma	gr	ni	N
o1	59.2	6.1	28.6	–	6.1	49
o2	69.5	1.7	25.4	–	3.4	59
Sub-total	64.9	3.7	26.8	–	4.6	108
mA	14.8	–	29.3	6.0	49.9	317
mB	30.8	–	46.1	2.6	20.5	39
mC	34.6	–	21.2	9.6	34.6	52
Sub-total	18.9	–	29.9	6.1	45.1	408

Table 8. Percentage frequency distributions of M_1 morphotypes in *Microtus agrestis* and *M. nivaloides*.

Popu-	Morphotype					
lation	ni	ar	ag	co	cx	N
a1	16.0	46.0	18.0	12.0	8.0	50
a2	14.3	35.6	28.6	4.8	16.7	42
Sub-total	15.2	41.3	22.8	8.7	12.0	92
sA	32.9	56.1	3.7	4.9	2.4	82

Table 9. Percentage frequency distributions of the M^3 morphotypes in *Chionomys nivalis, Ch. gud, Ch. roberti,* (?) *Ch. burgondiae, Microtus oeconomus* and *M. malei.*

Popu-	Morphotype								
lation	lc	mi	ni	ma	hc	oc	gu	ro	N
n 1	88.5	–	11.5	–	–	–	–	–	26
n 2	57.9	–	41.2	–	–	0.9	–	–	114
n 3	57.8	–	42.2	–	–	–	–	–	83
n 4	80.8	3.8	15.4	–	–	–	–	–	52
n 5	51.9	–	46.3	1.8	–	–	–	–	54
n 6	47.0	–	50.0	3.0	–	–	–	–	66
n 7	37.7	–	61.6	–	0.7	–	–	–	138
n 8	28.6	–	45.6	22.9	2.9	–	–	–	35
n 9	40.2	3.4	46.1	2.3	1.1	6.9	–	–	87
n10	28.6	5.7	51.4	11.4	–	2.9	–	–	35
n11	17.5	15.0	60.0	5.0	–	2.5	–	–	40
n12	14.3	–	64.3	21.4	–	–	–	–	14
n13	25.0	–	70.8	4.2	–	–	–	–	24
n14	11.0	4.4	61.5	20.9	2.2	–	–	–	91
n15	6.5	4.3	60.9	19.7	4.3	4.3	–	–	46
n16	8.9	7.5	55.3	10.4	13.4	4.5	–	–	67
n17	33.9	27.0	12.8	24.8	0.4	1.1	–	–	274
n18	35.7	–	64.3	–	–	–	–	–	14
n19	66.7	–	25.0	8.3	–	–	–	–	12
n20	7.1	–	7.1	78.7	–	7.1	–	–	14
n21	17.8	–	52.1	6.8	20.6	2.7	–	–	73
n23	12.0	6.0	68.0	8.0	2.0	4.0	–	–	50
n24	22.0	4.0	62.0	2.0	4.0	6.0	–	–	50
n25	23.4	–	72.4	2.1	2.1	–	–	–	47
n26	20.0	–	53.4	13.3	13.3	–	–	–	15
nS	50.0	–	50.0	–	–	–	–	–	10
nT	9.1	–	9.1	63.6	18.2	–	–	–	11
Sub-total	34.8	6.7	44.1	10.2	2.6	1.6	–	–	1542
bA	94.1	–	5.9	–	–	–	–	–	34
o2	–	–	–	20.3	–	66.1	13.6	–	59
mA	–	5.5	–	83.4	–	11.1	–	–	18
mB	–	4.3	4.3	82.7	–	8.7	–	–	23
mC	–	7.3	4.9	65.9	–	21.9	–	–	41
Sub-total	–	6.1	3.7	74.4	–	15.8	–	–	82
g1	–	–	–	–	–	20.6	55.6	23.8	63
g2	–	–	–	–	–	33.8	60.1	6.1	65
g3	–	–	–	–	–	41.7	58.3	–	12
Sub-total	–	–	–	–	–	28.6	57.8	13.6	140
r1	–	–	–	–	–	22.9	16.9	60.2	83
r2	–	–	–	–	–	12.5	15.3	72.2	72
Sub-total	–	–	–	–	–	18.1	16.1	65.8	155

Table 10. *Chionomys nivalis* and (?) *Ch. burgondiae*. Measurements and ratios of M_1. See text for explanation of the calculated ratios 2/1, 4/3 and 5/1 .

Code		1			2/1			4/3			5/1		
	N	OR	M	SD	OR	M	SD	OR	M	SD	OR	M	SD
1	2	3	4	5	6	7	8	9	10	11	12	13	14
n1	28	2.78 – 3.29	2.98	0.15	45.2 – 51.1	48.5	2.0	2.3 – 25.6	11.1	6.4	2.6 – 10.0	5.2	2.0
n2	112	2.72 – 3.56	3.06	0.16	42.9 – 52.7	47.6	1.8	1.4 – 54.1	18.7	10.0	2.7 – 17.7	6.1	2.8
n3	63	2.67 – 3.39	2.97	0.16	45.3 – 53.6	48.8	1.4	1.1 – 43.8	15.0	7.5	3.5 – 11.5	7.0	2.6
n4	49	2.70 – 3.26	2.93	0.14	43.6 – 50.5	46.9	1.6	5.1 – 41.9	20.4	8.9	4.7 – 12.3	7.7	2.6
n5	60	2.56 – 3.15	2.83	0.13	43.3 – 56.2	48.5	2.4	6.2 – 41.9	23.7	8.6	2.2 – 14.7	7.0	2.9
n6	66	2.63 – 3.09	2.89	0.12	44.6 – 52.9	49.3	2.0	1.2 – 49.1	16.4	10.0	2.1 – 12.8	6.8	3.2
n7	130	2.44 – 3.43	2.99	0.15	44.8 – 53.7	49.6	1.8	1.1 – 40.2	11.1	6.4	2.2 – 13.8	8.5	2.7
n8	36	2.44 – 3.12	2.89	0.12	45.9 – 53.2	49.4	1.7	2.2 – 27.9	11.3	7.3	3.3 – 12.1	7.9	2.4
n9	86	2.32 – 3.39	2.95	0.19	43.5 – 53.5	49.6	1.6	1.1 – 30.3	10.2	7.4	1.4 – 13.3	7.9	2.5
n10	36	2.60 – 3.40	3.12	0.13	46.9 – 55.5	50.0	1.8	2.3 – 30.1	15.2	7.8	3.3 – 12.4	8.9	2.0
n11	38	2.71 – 3.24	3.01	0.13	45.0 – 51.5	49.3	1.5	1.1 – 31.8	11.4	7.1	4.1 – 10.7	7.7	1.8
n12	14	2.66 – 3.16	2.90	0.16	47.2 – 50.9	49.6	1.2	1.4 – 14.3	5.5	4.0	3.4 – 10.5	6.8	2.3
n13	26	2.60 – 3.20	2.95	0.15	46.0 – 51.9	48.8	1.6	1.3 – 23.7	9.8	7.6	2.0 – 13.2	7.1	2.7
n14	123	2.44 – 3.40	3.01	0.14	43.5 – 54.7	49.5	1.8	1.2 – 25.0	6.6	4.5	1.3 – 12.6	7.2	2.6
n15	46	2.70 – 3.32	3.00	0.18	45.4 – 53.1	49.5	1.9	1.2 – 26.6	7.8	5.9	3.2 – 10.2	7.3	1.6
n16	70	2.67 – 3.55	3.07	0.15	45.2 – 55.7	49.3	1.8	1.0 – 16.7	6.0	3.5	3.4 – 10.6	7.0	1.5
n17	353	2.32 – 3.28	2.92	0.13	44.2 – 54.5	50.0	1.6	1.2 – 38.6	11.8	7.8	3.7 – 16.9	10.0	2.4
n18	10	2.64 – 2.96	2.83	0.12	46.3 – 52.0	49.2	1.7	2.7 – 31.3	14.4	7.7	5.9 – 11.1	9.0	1.7
n19	8	2.68 – 2.75	2.71	0.03	46.9 – 52.2	49.1	1.7	18.9 – 26.3	22.2	2.2	5.2 – 10.9	6.8	1.8
n20	14	2.78 – 3.07	2.90	0.10	42.5 – 49.8	45.8	2.5	5.3 – 43.7	24.0	12.5	4.8 – 13.5	9.6	2.8
n21	76	2.52 – 3.32	3.00	0.15	44.3 – 52.9	49.1	1.8	1.1 – 14.3	6.8	3.5	1.8 – 12.0	7.3	2.0
n22	4	2.89 – 3.13	3.00	0.11	46.0 – 51.1	48.8	2.2	3.6 – 8.9	7.2	2.1	8.6 – 9.7	9.2	0.5
n23	39	2.44 – 2.96	2.74	0.15	46.5 – 53.6	49.6	1.9	1.2 – 13.9	7.3	3.4	2.3 – 12.7	7.5	2.0
n24	46	2.36 – 2.84	2.61	0.13	47.5 – 54.5	51.0	1.5	2.6 – 25.7	9.5	4.8	3.7 – 11.9	7.5	2.2
n25	45	2.56 – 3.22	2.85	0.18	46.9 – 52.1	49.8	1.3	2.6 – 27.8	11.0	5.7	4.5 – 14.1	10.0	2.1
n26	18	2.75 – 3.30	3.01	0.17	45.2 – 50.3	47.6	1.4	2.2 – 19.2	9.9	5.8	4.5 – 9.8	7.3	1.3
Sub-total	1596	2.32 – 3.56	2.94	0.13	42.5 – 56.2	49.3	1.3	1.0 – 54.1	11.5	6.4	1.3 – 17.7	7.6	2.3

1	2	3	4	5	6	7	8	9	10	11	12	13	14
nA	136	2.64 – 3.25	2.91	0.14	44.3 – 53.3	48.6	1.7	1.3 – 41.3	14.8	8.0	0.7 – 14.7	7.9	2.5
nB	8	2.71 – 3.05	2.89	0.12	45.4 – 52.3	47.8	2.3	4.1 – 10.9	6.5	3.2	4.7 – 12.6	9.2	2.5
nC	31	2.67 – 3.18	2.92	0.12	44.0 – 50.9	47.7	1.7	7.5 – 44.9	17.2	9.7	6.6 – 16.0	10.4	2.1
nD	9	2.67 – 3.26	2.87	0.17	46.5 – 52.2	48.2	1.7	3.2 – 28.3	11.9	5.5	2.4 – 9.8	5.8	2.2
nE	34	2.65 – 3.18	2.87	0.12	44.8 – 52.8	48.0	1.8	2.4 – 28.3	8.4	7.2	2.2 – 19.5	7.8	3.4
nF	21	2.52 – 3.04	2.82	0.13	44.3 – 50.0	47.5	1.5	1.1 – 18.9	8.0	6.1	3.0 – 9.2	6.2	1.8
nG	20	2.48 – 2.88	2.72	0.12	43.5 – 51.5	47.7	2.0	4.7 – 25.0	11.6	6.3	3.4 – 11.8	8.2	2.0
nH	26	2.60 – 2.90	2.76	0.09	42.9 – 51.4	47.8	2.0	2.6 – 25.0	13.7	5.9	4.3 – 11.1	7.0	1.5
nI	32	2.40 – 2.96	2.77	0.13	45.5 – 51.5	48.1	1.6	1.4 – 28.6	11.0	6.6	3.5 – 12.7	8.3	2.2
nJ	14	2.68 – 2.98	2.79	0.12	46.3 – 50.7	48.7	1.1	2.4 – 32.0	12.7	8.1	3.0 – 12.7	7.9	3.0
nK	26	2.52 – 3.20	2.87	0.16	40.5 – 51.3	48.2	2.3	2.5 – 34.4	13.3	8.3	4.2 – 19.2	9.2	3.2
nL	60	2.54 – 3.12	2.84	0.14	43.7 – 53.1	48.6	1.9	1.4 – 47.5	11.1	8.2	3.4 – 15.7	7.8	3.1
nM	11	2.44 – 2.88	2.72	0.12	46.2 – 51.4	48.4	1.4	2.3 – 16.7	7.8	4.2	7.0 – 10.1	8.8	0.9
nN	50	2.56 – 3.18	2.78	0.13	43.1 – 51.4	47.2	1.6	1.3 – 22.5	7.9	5.5	0.7 – 12.2	5.4	2.8
nO	88	2.64 – 3.32	2.95	0.15	42.9 – 50.7	47.3	1.9	1.1 – 47.0	11.7	7.7	2.5 – 12.7	7.3	2.2
nP	60	2.52 – 3.26	2.87	0.17	42.7 – 52.4	46.8	1.8	1.3 – 25.0	7.4	5.1	3.1 – 10.6	7.2	1.9
nR	76	2.56 – 3.22	2.85	0.15	42.7 – 51.2	47.3	2.0	2.3 – 29.7	12.0	6.8	4.3 – 13.6	9.2	2.0
nS	33	2.70 – 3.28	2.95	0.19	44.6 – 50.6	47.6	1.7	5.4 – 36.1	16.7	9.9	4.2 – 11.8	7.8	1.9
nT	22	2.34 – 3.06	2.74	0.18	40.6 – 48.6	45.5	2.2	10.0 – 46.9	33.2	9.8	7.2 – 20.3	11.9	3.2
nU	163	2.45 – 3.07	2.78	0.13	42.5 – 52.7	48.1	1.6	–	–	–	–	–	–
nV	66	2.55 – 3.12	2.85	0.15	40.0 – 50.0	47.7	1.7	–	–	–	–	–	–
nW	18	2.55 – 2.92	2.78	0.11	45.6 – 51.4	48.5	1.6	–	–	–	–	–	–
Sub-total	1004	2.34 – 3.28	2.85	0.13	40.0 – 53.3	48.1	1.8	1.1 – 48.6	12.4	6.8	0.7 – 20.3	8.2	2.3
bA	84	2.56 – 3.15	2.79	0.11	42.3 – 49.3	45.8	1.6	3.1 – 49.3	25.1	9.6	2.2 – 31.4	11.3	8.7

Table 11. *Chinomys gud* and *Ch. roberti*. Measurements and ratios of M_1.

		Parameters											
Code		1			2/1			4/3			5/1		
	N	OR	M	SD	OR	M	SD	OR	M	SD	OR	M	SD
g1	64	2.68 – 3.24	3.00	0.14	45.6 – 53.3	49.1	1.7	9.3 – 41.9	20.4	7.1	7.4 – 15.9	11.4	1.6
g2	62	2.46 – 3.16	2.74	0.15	43.1 – 52.3	49.1	1.7	6.8 – 42.4	22.1	6.4	7.6 – 15.3	11.4	2.0
g3	12	2.44 – 2.84	2.61	0.13	44.8 – 50.8	48.2	2.0	12.5 – 32.5	22.0	5.9	8.9 – 14.3	10.6	1.4
g4	6	2.76 – 3.07	2.89	0.12	48.1 – 51.0	49.3	1.2	22.8 – 30.1	25.9	2.1	9.8 – 14.1	12.2	1.7
Sub-total	144	2.44 – 3.24	2.85	0.14	43.1 – 53.3	49.0	1.7	6.8 – 42.4	21.8	5.6	7.4 – 15.9	11.4	1.8
gA	56	2.52 – 3.00	2.83	0.10	44.0 – 50.4	47.4	1.5	–	–	–	–	–	–
gB	68	2.62 – 3.02	2.86	0.10	43.2 – 51.7	47.7	1.7	–	–	–	–	–	–
gC	16	2.52 – 2.97	2.74	0.12	43.0 – 50.5	47.7	2.1	–	–	–	–	–	–
gD	57	2.50 – 2.95	2.73	0.09	42.2 – 51.9	47.9	1.9	–	–	–	–	–	–
gE	30	2.60 – 3.02	2.77	0.11	44.8 – 51.4	48.2	2.0	–	–	–	–	–	–
gF	23	2.52 – 3.00	2.76	0.12	44.3 – 52.2	48.6	2.2	–	–	–	–	–	–
gG	21	2.55 – 2.92	2.72	0.10	45.0 – 49.6	47.8	1.1	–	–	–	–	–	–
gH	22	2.48 – 2.96	2.70	0.13	47.1 – 51.6	49.0	1.5	–	–	–	–	–	–
Sub-total	293	2.48 – 3.02	2.78	0.10	42.2 – 52.2	47.8	1.8	–	–	–	–	–	–
r1	81	2.72 – 3.40	3.03	0.18	46.4 – 53.8	50.6	1.5	4.9 – 38.5	23.1	7.1	6.0 – 15.3	11.1	1.9
r2	72	2.93 – 3.45	3.22	0.15	46.7 – 54.6	50.9	1.6	9.5 – 38.2	21.6	6.3	5.8 – 14.5	10.3	1.9
Sub-total	153	2.72 – 3.45	3.11	0.16	46.4 – 54.6	50.7	1.5	4.9 – 38.5	22.2	6.8	5.8 – 15.3	10.8	1.9
rA	21	2.87 – 3.25	3.06	0.09	44.3 – 53.7	49.5	2.4	–	–	–	–	–	–
rB	10	2.90 – 3.25	3.06	0.11	45.8 – 53.4	50.2	1.9	–	–	–	–	–	–
Sub-total	31	2.87 – 3.25	3.06	0.10	44.3 – 53.7	49.7	2.0	–	–	–	–	–	–

Table 12. *Microtus oeconomus* and *Microtus malei*. Measurements and ratios of M_1.

Code	N	Parameters 1			2/1			4/3			5/1		
		OR	M	SD	OR	M	SD	OR	M	SD	OR	M	SD
o1	49	2.72 – 3.29	2.95	0.12	43.5 – 51.7	47.9	1.8	15.8 – 43.7	30.5	5.9	5.6 – 27.3	21.0	4.5
o2	59	2.61 – 3.17	2.84	0.12	44.7 – 50.5	47.8	1.3	17.3 – 50.0	33.0	6.1	5.4 – 30.4	19.9	5.9
Sub-total	108	2.61 – 3.29	2.89	0.11	43.5 – 51.7	47.8	1.5	15.8 – 50.0	32.0	6.0	5.4 – 30.4	20.2	5.1
mA	58	2.75 – 3.39	3.07	0.15	48.8 – 56.7	52.1	1.6	2.3 – 44.8	17.8	10.6	6.2 – 23.6	10.7	4.1
mB	29	2.73 – 3.26	2.89	0.13	46.4 – 52.4	49.9	1.6	3.0 – 39.0	19.3	9.1	5.2 – 24.1	11.8	4.7
mC	52	2.63 – 3.26	2.87	0.14	48.4 – 54.6	50.9	1.6	1.3 – 42.2	11.6	11.6	3.9 – 25.9	12.4	6.7
Sub-total	139	2.63 – 3.39	2.93	0.14	46.4 – 56.7	51.0	1.6	1.3 – 44.8	15.3	10.3	3.9 – 25.9	11.7	5.2

Table 13. *Microtus agrestis* and *Microtus nivaloides*. Measurements and ratios of M_1.

Code	N	Parameters 1			2/1			4/3			5/1		
		OR	M	SD	OR	M	SD	OR	M	SD	OR	M	SD
a1	30	2.84 – 3.24	2.98	0.16	49.2 – 58.7	53.2	1.9	1.4 – 6.2	3.1	1.1	2.8 – 9.2	6.4	1.6
a2	34	2.68 – 3.37	2.95	0.14	49.6 – 57.2	53.0	1.6	1.6 – 6.9	3.5	1.4	3.7 – 9.3	6.4	1.6
Sub-total	64	2.68 – 3.37	2.96	0.15	49.2 – 58.7	53.0	1.7	1.4 – 6.9	3.4	1.2	2.8 – 9.3	6.4	1.6
sA	74	2.30 – 2.97	2.62	0.13	47.1 – 55.1	50.5	1.7	2.7 – 18.2	5.1	8.9	2.9 – 10.9	6.5	1.9

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Table 14. *Chionomys nivalis* and (?) *Ch. burgondiae*. Measurements and ratios of M^3.

Code	N	1			2/1			3		
		OR	M	SD	OR	M	SD	OR	M	SD
n 1	24	1.96 – 2.50	2.14	0.15	38.7 – 48.2	43.1	2.3	0.26 – 0.40	0.32	0.04
n 2	112	1.72 – 2.44	2.18	0.13	34.9 – 50.9	44.5	3.1	0.25 – 0.50	0.34	0.05
n 3	80	1.78 – 2.48	2.09	0.15	41.4 – 50.9	46.2	2.3	0.29 – 0.52	0.38	0.05
n 4	52	1.85 – 2.30	2.07	0.11	41.3 – 50.7	45.1	2.2	0.26 – 0.48	0.37	0.05
n 5	53	1.85 – 2.30	2.04	0.16	35.7 – 50.0	45.5	2.6	0.30 – 0.50	0.36	0.04
n 6	61	1.70 – 2.33	2.07	0.14	33.3 – 51.1	45.2	3.0	0.30 – 0.50	0.36	0.05
n 7	130	1.70 – 2.45	2.12	0.15	42.6 – 51.6	45.6	2.8	0.28 – 0.48	0.35	0.05
n 8	35	1.96 – 2.50	2.16	0.14	42.0 – 60.8	47.5	2.8	0.20 – 0.52	0.37	0.06
n 9	85	1.78 – 2.44	2.11	0.17	35.3 – 52.8	46.4	3.2	0.24 – 0.58	0.37	0.06
n10	35	1.87 – 2.41	2.20	0.12	40.2 – 51.5	47.1	2.8	0.26 – 0.51	0.37	0.06
n11	38	1.98 – 2.44	2.20	0.12	39.1 – 50.9	47.1	2.7	0.32 – 0.50	0.40	0.06
n12	14	1.96 – 2.27	2.14	0.10	44.9 – 50.9	48.5	1.9	0.28 – 0.47	0.40	0.05
n13	22	1.84 – 2.48	2.09	0.21	39.1 – 49.0	44.3	2.9	0.26 – 0.46	0.35	0.06
n14	84	1.72 – 2.54	2.11	0.16	40.2 – 52.2	46.7	2.7	0.22 – 0.54	0.36	0.07
n15	46	1.82 – 2.52	2.14	0.18	43.0 – 54.7	47.8	2.4	0.30 – 0.58	0.40	0.07
n16	58	1.80 – 2.62	2.20	0.18	39.7 – 51.7	47.3	2.3	0.29 – 0.60	0.39	0.07
n17	261	1.76 – 2.40	2.13	0.15	38.9 – 53.9	48.0	2.6	0.28 – 0.54	0.39	0.05
n18	10	1.90 – 2.28	2.13	0.10	41.7 – 47.1	44.9	1.7	0.30 – 0.36	0.33	0.02
n19	8	1.70 – 2.04	1.93	0.12	44.7 – 51.0	47.6	2.1	0.28 – 0.36	0.34	0.03
n20	14	1.84 – 2.30	2.02	0.17	47.3 – 55.3	51.3	1.9	0.29 – 0.50	0.42	0.06
n21	74	1.81 – 2.40	2.14	0.13	43.9 – 52.5	47.9	2.1	0.30 – 0.60	0.39	0.06
n22	4	1.87 – 2.20	1.96	0.08	48.1 – 52.3	50.3	2.1	0.32 – 0.36	0.34	0.02
n23	46	1.68 – 2.20	1.95	0.14	41.7 – 51.0	46.1	2.2	0.22 – 0.44	0.33	0.05
n24	46	1.52 – 2.12	1.85	0.15	42.7 – 53.3	48.2	2.7	0.24 – 0.46	0.32	0.05
n25	41	1.61 – 2.24	1.94	0.16	39.8 – 52.0	46.6	2.4	0.26 – 0.40	0.31	0.03
n26	18	1.90 – 2.53	2.17	0.24	45.2 – 54.6	49.0	2.6	0.36 – 0.51	0.43	0.04
Sub-total	1451	1.51 – 2.62	2.11	0.16	33.3 – 60.8	47.0	2.5	0.22 – 0.60	0.37	0.05
nS	10	1.84 – 2.20	2.03	0.13	40.4 – 50.0	44.9	3.1	0.30 – 0.38	0.34	0.03
nT	11	1.84 – 2.22	2.08	0.13	42.3 – 52.7	48.0	3.5	0.28 – 0.60	0.46	0.12
bA	34	1.48 – 2.07	1.76	0.12	36.5 – 44.9	41.2	2.3	0.26 – 0.42	0.35	0.04

Table 15. *Chionomys gud* and *Ch. roberti*. Measurements and ratios of M^3.

Code		Parameters								
		1			2/1			3		
	N	OR	M	SD	OR	M	SD	OR	M	SD
g1	62	2.20 – 2.88	2.49	0.17	53.2 – 63.6	58.3	2.4	0.62 – 0.92	0.76	0.07
g2	59	2.00 – 2.76	2.35	0.15	54.2 – 60.3	57.7	1.7	0.58 – 0.80	0.71	0.04
g3	12	2.08 – 2.40	2.24	0.12	56.6 – 60.3	58.4	1.3	0.60 – 0.76	0.67	0.05
g4	6	2.16 – 2.66	2.32	0.20	55.1 – 61.5	58.8	2.8	0.61 – 0.86	0.75	0.10
Sub-total	139	2.00 – 2.88	2.39	0.16	53.2 – 63.6	58.2	2.0	0.58 – 0.92	0.72	0.06
r1	82	2.12 – 2.84	2.51	0.16	50.7 – 63.9	58.4	2.5	0.65 – 0.88	0.78	0.06
r2	72	2.20 – 2.92	2.63	0.16	52.3 – 64.8	59.0	2.9	0.68 – 0.98	0.83	0.06
Sub-total	154	2.12 – 2.92	2.55	0.15	50.7 – 64.8	58.6	2.7	0.65 – 0.98	0.79	0.06

Table 16. *Microtus oeconomus* and *M. malei*. Measurements and ratios of M^3.

Code		Parameters								
		1			2/1			3		
	N	OR	M	SD	OR	M	SD	OR	M	SD
o2	59	1.81 – 2.31	2.09	0.11	44.4 – 56.8	52.0	2.2	0.51 – 0.72	0.61	0.05
mA	18	1.81 – 2.34	2.01	0.17	46.6 – 55.7	51.2	2.5	0.41 – 0.59	0.51	0.06
mB	23	1.84 – 2.30	2.01	0.10	44.8 – 54.6	48.8	2.3	0.36 – 0.63	0.50	0.07
mC	39	1.88 – 2.53	2.12	0.16	46.3 – 60.2	51.3	3.0	0.41 – 0.66	0.53	0.06
Sub-total	80	1.81 – 2.52	2.05	0.14	44.8 – 60.2	50.8	2.4	0.36 – 0.66	0.52	0.06