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MORPHOTYPE AND MULTIVARIATE ANALYSIS OF THE OCCLUSAL PATTERN OF THE FIRST LOWER MOLAR IN EUROPEAN AND ASIAN ARVICOLINE SPECIES (RODENTIA, *MICROTUS*, *ALEXANDROMYS*)

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Morphotype and Multivariate Analysis of the Occlusal Pattern of the First Lower Molar in European and Asian Arvicoline Species (Rodentia, *Microtus, Alexandromys*). — Synyavska, I. O., Peskov, V. N. — We studied the morphotypic variation of the occlusal pattern of m1 in 13 arvicoline species (genera *Microtus* and *Alexandromys)*. As a result, 22 m1 morphotypes were identified. In *Alexandromys*, five morphotypes of m1 were found, while in *Microtus* only seven. The morphological diversity of m1 morphotypes (H) in voles of the genus *Microtus* is significantly lower compared to *Alexandromys*. The largest number of m1 morphotypes and the highest morphological diversity of m1 were revealed in the Mongolian vole (14 morphotypes and $H = 2.134$), while the lowest values (two morphotypes and $H = 0.285$) occur in the population of *M. levis* from Orlov Island. An attempt of ecological and taxonomical interpretation of interspecific differences was made based on the m1 morphotypes.
Key words: grey voles, *Microtus*, *Alexandromys,* first lower molar, morphotype, variation, diversity, PCA.

Introduction

Voles (Arvicolinae Gray, 1821) are one of the most problematic groups of murine rodents. The taxonomy of this group was previously based on craniological and odontological features (see Miller, 1896; Méhely, 1914; Hinton, 1926; Ognev, 1950). Since the 1960s, results of karyological, biochemical, and molecular genetic methods of analysis have been actively used (Graf, 1982; Malygin, 1983; Zagorodnyuk, 1990, 1991; Mezhzherin et al., 1993; Jaarola & Tegelström, 1995; Meyer et al., 1996; Chaline et al., 1999; Conroy, Cook, 2000; Jarrola et al., 2004; Bannikova et al., 2010; Kryštufek et al., 2012). The taxonomic status of the 13 studied arvicoline species

is still a matter of debate. In the earliest works, they are considered as part of the genus *Microtus* Schrank, 1798 (Ognev, 1950; Chaline, 1970, 1980; Gromov and Polyakov, 1977; Gromov, Erbaeva, 1995, Chaline et al., 1999). In recent decades, East Asian voles have often been considered as a separate genus *Alexandromys* Ognev, 1914 (Abramson et al., 2012; Lissovsky et al., 2018). The genus *Microtus*, in the narrow sense, with two subgenera *Sumeriomys* Argyropulo, 1933 and *Microtus* s. str. is considered the most reasonable. According to results of molecular-genetic analysis (Zagorodnyuk, 1990; Jarrola et al., 2004) in addition to these subgenera, the subgenus *Agricola* Blasius, 1857 with unclear taxonomic status is also included in this group.

The aim of the work is to conduct a comparative study of the morphotypic diversity in 13 species of European and Asian gray voles based on modern taxonomic constructions.For this comparison, sets of discrete characters of the anterocinod were used, which are considered here as morphotypes, although the classic interpretation of the "morphotype" is somewhat different. The classical morphotype concept (see Maleeva, 1972, 1976 as cited in Bolshakov et al., 1980) is closely related to intrapopulation variation and is often used to clarify the specifics of microevolutionary processes in extinct and recent vole populations.

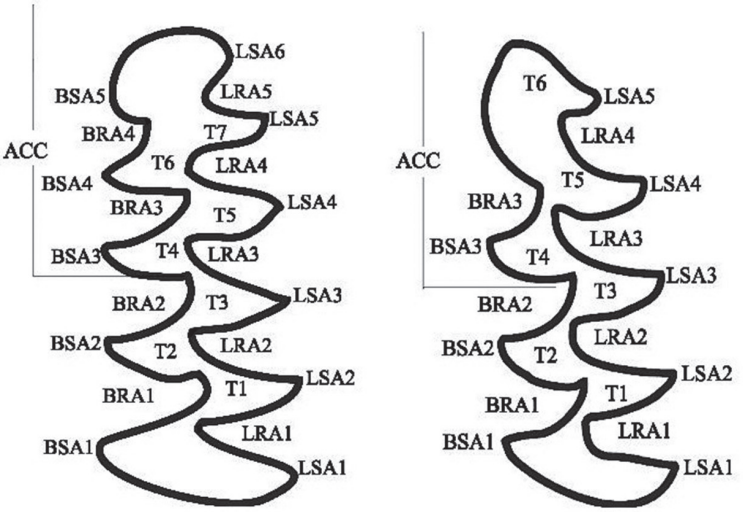
Material and methods

The study is based on data on morphotypic variation of the first lower molar (m1) in 22 European and Asian samples of 13 grey vole species (table 1). We studied rodent collections deposited in Schmalhausen Institute of Zoology NAS of Ukraine (IZAN, Kyiv), Department of Zoology of the National Museum of Natural History NAS of Ukraine (Kyiv), Zoological Museum of Taras Shevchenko National University of Kyiv, Zoological Institute of the Russian Academy of Sciences (ZIN, St. Petersburg, Russia), and the Zoological Museum of Moscow State University (ZMMU, Moscow, Russia). We also used A. A. Pozdnyakov's data (Pozdnyakov, 1993, 2003) on the occurrence frequency of m1 morphotypes in four species of Asian voles such as *Alexandromys fortis* Büchner, 1889, *A. middendorfii* Poljakov, 1881, *A. maximowiczii* (Schrank, 1859), and *A. sachalinensis* Vasin, 1955. Ukrainian samples of *M. levis* and *M. arvalis* were identified by kariological or biochemical methods (Zagorodniuk, Teslenko, 1986; Zagorodniuk, 1991). In total, 1623 first lower molars were analysed.

Table 1. Short characteristics of the studied material

Species	Sample (locality)	Abbreviation	Number of studied m1
M. socialis	Black Sea Biosphere Reserve, Ukraine	socC	94
M. socialis	Askania Nova Biosphere Reserve, Ukraine	socA	104
M. paradoxus	Kopet Dag Range, Turkmenistan	para	33
M. socialis	Republic of Azerbaijan (several localities)	socb	40
M. ilaeus	Kyrgyz Republic (several localities)	ilae	37
M. arvalis	Kyiv Region, Ukraine	arvK	226
M. arvalis	near Vinnitsa city, Vinnytsia Region, Ukraine	arvV	110
M. arvalis	near Berehove city, Zakarpattia Region, Ukraine	arvZ	106
M. arvalis	Tver Region, Russia	arvT	156
M. levis	Poltava Region, Ukraine	levP	65
M. levis	Danube Delta, Odesa Region, Ukraine	levD	77
M. levis	Orlov Island, Kherson Region, Ukraine	levO	38
M. levis	Askania Nova Biosphere Reserve, Ukraine	levA	98
M. levis	Tver Region, Russia	levT	112
M. agrestis	Carpathian Mts, Zakarpattia Region, Ukraine	agre	78
M. obscurus	Crimean Mts, Crimea, Ukraine	obs	56
A. oeconomus	Kyiv Region, Ukraine	oec	83
A. mongolicus	Mongolia (several localities)	mong	97
*A. maximowiczii**	Sokhondo Nature Reserve, Russia	max	132
*A. middendorfii**	Lake Khantayskoye, Taimyr Peninsula, Russia	midd	62
*A. fortis**	Dzhidinsky District, Republic of Buryatia, Russia	fort	315
*A. sachalinensis**	Lake Nevskoe, Sakhalin Peninsula, Russia	sach	48

Note. Literature data (Pozdnyakov, 1993, 2003).



T1–T7 — triangular loops (dentine tracks) of the occlusal surface, BRA — buccal re-entrant angles, BSA — buccal salient angles, LSA — lingual salient angles LRA — lingual re-entrant angles, ACC — anteroconide complex, PL — posterior loop of m1.

Fig. 1. Elements of the occlusal surface of m1 (the terminology follows van der Meulen, Zagwijn, 1974; Maul et al., 2007).

The left and right molars were analysed separately, because voles of both genera usually have directional asymmetry of the dental pattern (Polly et al., 2011). Age differences are noted quite often in the form of juvenile folding of the enamel, sharpness of re-entrant angles, etc. (Borodin, 2009). Therefore, we analysed the teeth of only subadult and adult animals to exclude the age factor. When describing the m1 morphotypes, we focused (see fig. 1) mainly on qualitative features corresponding to the development of additional salient and re-entrant angles on the lingual or/and buccal side of a tooth, and on the number of triangles (Bol'shakov et al., 1980). Drawings of most morphotypes were made according to our own digitized micrographs, and for morphotypes III, V, XII, XVI — according to literature data (Meyer et al., 1996; Voyta et al., 2013; Lissovskiy et al., 2018). Micrographs of the occlusal surface of the teeth were made using a LEICA M165 stereomicroscope. The technique used in this work involves the combination between the classical morphotypic approach (description of morphotypes and calculation of intrapopulation diversity indices μ, h, r, I according to Zhivotovsky, 1982) and methods of multivariate statistics (principal component analysis).

The occurrence frequency of m1 morphotypes compared to the sample volume (N) was calculated for each sample. The population similarity index (*r,* see table 7) was estimated as well in order to compare the samples. We also calculated the criterion of identity (*I,* see table 7) to estimate the statistical significance of *r* (Zhivotovsky, 1982).

$$r = \sqrt{p_1 q_1} + \sqrt{p_2 q_2} + \ldots + \sqrt{p_m q_m}, \quad I = \frac{8 N_1 N_2}{N_1 + N_2}\left(1 - r - \frac{p^0 + q^0}{4}\right),$$

where N_1 and N_2 — the volume of samples of the first and second populations, $p_1 \ldots p_m$ — frequencies of different morphotypes in the first population, and $q_1 \ldots q_m$ — frequencies in the second population.

If *I* exceeds the table value of χ^2 with a given level of significance and degrees of freedom (m–1), the difference between the samples is statistically significant. The value of the population similarity index (*r*) does not exceed 1 and $r = 1$ when the compared populations are identical by the number of morphotypes. If there is no common morphotype, then $r = 0$. If *r* differs significantly from 1 (by criterion *I*), then its sample error is calculated by the following formula:

$$S_r = \frac{1}{2}\sqrt{\frac{1 - q^0 - r^2}{N_1} + \frac{1 - p^0 - r^2}{N_2}}.$$

Morphological diversity (Shannon–Weaver index, *H*), the mean number of morphotypes (μ) and rare morphotypes (*h*) were calculated for each sample (Zhivotovsky, 1982).

$$H = \sum p_i \ln p_i$$

$$\mu = \left(\sum_{i=1}^{m} \sqrt{p_i} \right)^2 ; \quad h = 1 - \frac{\mu}{m} .$$

Phenetic similarity matrixes (*r*, see table 7) were processed by PCA to determine the similarity structure of the samples being compared. The similarity (*r*) of each sample compared to all others in the studied population was analysed. In this case, factor loadings of each sample on the corresponding PC show the sample's position in the structure of similarity relations between the samples, described by this component. All calculations were performed in PAST 3 statistical packages (Hammer et al., 2001).

Results and discussion

Morphotypic analysis

Twenty-two m1 morphotypes were identified (table 2). Among them, 10 were recorded in two genera of voles (see table 2); five were found only in *Alexandromys* and seven in *Microtus* s. str.The main differences between the distinguished variations of the occlusal pattern were revealed by the degree of simplification/complication of the buccal and/or lingual sides (Pozdnyakov, 2011; Markova et al., 2010). Some morphotypes are described according to A. G. Maleeva (Bolshakov et al., 1980), A. Nadachowski (Nadachowski, 1982), L. I. Rekovets (Rekovets, 1994), A. Lissovsky and co-authors (Lissovsky et al., 2018), and A. V. Borodin (Borodin, 2009).

The revealed morphotypes can be divided into 4 groups according to the degree of transformation of the anteroconid complex:

1) Teeth with asymmetrically complicated ACC and simplified buccal side (BSA4 is undeveloped). This type is more common in *A. oeconomus* and *A. fortis*, and among the studied *Microtus* s. str. it occurred only in a few specimens (morphotype IV 1.3–2.6 % of all m1, see table 2). This group includes four morphotypes.

Morphotypes I and IV are characterised by elongated anterior loop (type "*longyratticeps*" according to Rekovets, 1994; I, IV, fig. 2), LSA6 is developed (I, fig. 2), less often expressed (IV fig. 2). Morphotypes II and III have simplified buccal side of AC, do not fused to T4 (type "*fortis*" according to Lissovsky et al., 2018), LRA5 is undeveloped (II, fig. 2) or well defined (III, fig. 2).

2) Asymmetrically complicated ACC, BSA4 is distinctly developed.This group includes nine morphotypes.

Morphotypes V and XII. Relatively short anterior loop, the lingual side is slightly differentiated, LSA6 do not occur (type "*maximowiczii*", according to Lissovsky et al., 2018); BRA4 can be poorly developed (V, fig. 2) or clearly noticeable, because of which m1 acquires "*arvalis*" features (XII, fig. 2).

Morphotype IX. AC is elongated and straight, BRA4 is undeveloped (IX, fig. 2), LSA6 is well developed, that is, the tooth acquires the features of "*gregalis*" morphotypes. This type of pattern was noted in *A. mongolicus* and *A. middendorffii* (23.7 % and 25.8 %), occasionally in *M. levis*, and in 10 % of *M. agrestis*.

Morphotype XIV. The m1 is with well-developed BRA4 and LSA6 (XIV, in fig. 2) with features of "*gregalis*" and "*arvalis*" morphotypes (Borodin, 2009; Vojta et al., 2013). This type was found in 17 samples. It is common in *A. mongolicus* and *A. middendorffii* (23.7 % and 25.8 %), occurs occasionally in *M. levis*, and in 10 % of *M. agrestis*.

Morphotype X teeth have features of "*gregalis*" morphotypes, but with slightly more rounded anterior loop (X, fig. 2) were observed only in voles of the "*socialis*" group.

Morphotype VIII AC has the form of an "asymmetric trefoil" (VIII, fig. 2) in both fossil and modern *S. gregalis*, (morphotype VI–P fig. 24, p. 82 in Bolshakov et al., 1980), in the studied material it is common for *A. mongolicus*, *A. maximowiczii*, and *M. agrestis*.

Morphotype VII m1 with truncated anterior loop separated by T5 and T6, the lower part of the head hangs as in *Chionomys nivalis* (VII fig. 2 — type "*nivalis*" according to Nadachowski, 1991). It is observed everywhere in fossil *A. oeconomus* (Nadachowski, 1982; Borodin, 2009) and in our samples of *A. oeconomus* and *A. mongolicus* with a frequency of 10–15 %.

Morphotype XVIII. T6 is completely separated from the lingual side (XVIII, fig. 2 — "*extratriangulatus*" after Nadachowski, 1982 — common for *M. agrestis*). Teeth with such pattern are often found in *M. obscurus* and *M. arvalis*, occasionally among *M. socialis* and *M. levis*, and they are rare or absent in high mountain *M. agrestis* and *M. ilaeus* and in isolated populations of Eastern European voles (Askania Nova, Orlov Island)

3) Symmetrically complicated ACC due to well–developed BRA4, BSA5, LSA6, and LRA5.Morphotype XX m1 differentiated from both the lingual and buccal sides of the ACC has the shape of a "trefoil"; enamel triangles T6 and T7 are separated (XIX, XX, fig. 2). Thus, m1 has a typical "*arvalis*" structure ("*campestris*" according to Rekovets, 1994). This type of pattern prevails in 15 samples of voles of the genus *Microtus* s. str, and is practically not recorded in East Asian voles. When analysing the frequencies of morphotypes of sibling species, E. A. Markova et al. also established the dominance of teeth having this pattern in most of the studied samples (in Markova et al., 2010 morphotype I, see fig. 1, table 1), except for voles from the Central and Southern Urals .

4) Symmetrically complicated ACC, T6 and T7 are fused. The head of the AC is differentiated with partial (XVI fig. 2) or complete separation of T8 (XXI fig. 2 — the "*maskii*" form according to the classification by Rörig, Börner, 1905,). In Morphotype XXI, triangles T6 and T7 are merged, T4 and T5 are completely separated, because of which m1 acquires "*pitymys*" features (Rekovets, 1994). This type of pattern dominates in Tien Shan voles; in other species, it is found only in single specimens. In extinct populations of *Microtus* s. str., "*pitymys*" morphotypes along with "*arvalis*" are the basic variations of the occlusal pattern (Nadachowski, 1982; Rekovets, 1994). In *M. obscurus* from the Crimea, teeth attributed to the "*maskii*" form were not observed either in fossil material (Markova, 1999) or in modern samples (our data, table 2). Also interesting was the fact that this morphotype was found in single individuals of*M. arvalis* from Ukraine, and only in the southern *M. levis* (except the sample from Orlov Island). Teeth with T6 and T7 fusion were found in fossil *M. agrestis* from Belarus (Ivanov, 2008) and south-eastern Serbia (Bogićević et al., 2012) with a frequency of 4.2 to 5.4 %. Teeth with such pattern are absent in recent *M. agrestis* from the highlands of the Ukrainian Carpathians (our data) and from Germany (Kapischke et al., 2009), as well as in fossil *M. agrestis* from Poland (Nadachowski, 1982) and northern Hungary (Luzi et al., 2019).

In the studied samples, a low frequency of teeth of the "*phayomis*" type with weakly differentiated ACC was also noted (XI, XIII, fig. 2 — type "*contigua*" according to Rekovets, 1994). Teeth without complicated anteroconid complex, that is, with archaic structural features ("*phayomis*" morphotypes, see Rekovets, 1994; Pozdnyakov, 1995) are presented as single specimens. Among East Asian voles, this pattern is noted only in *A. mongolicus* and in species of the "*socialis*" group of *Microtus* s. str. Such structure is not represented in the studied populations of *M. arvalis*, although it prevailed in the Early Pleistocene *M. arvalinus–M. arvalis* (see Rekovets, 1994). In some samples, there were single m1 with asymmetry (XV, XVII fig. 2), recesses on the head of the paraconid (VI, fig. 2), or additional incoming corners (XXII fig. 2).

We also investigated the distribution of morphotype frequencies in the studied samples.

According to their occurrence frequency in populations, all morphotypes can be divided into three groups: dominant (> 36 %), reserve (< 36 %), and rare (see Maleeva, 1976; Bolshakov et al., 1980; Markova et al., 2010). The dominant morphotypes are present in the population most of the time, and the reserve may disappear and re-appear. The number of

reserve morphotypes in different samples ranges from 1 to 10, while they have both archaic (primitive) and progressive features. In 15 samples of voles of the genus *Microtus* s. str., morphotype XX was the dominant (table 2), while in *A. oeconomus*, *A. fortis*, *A. maximowiczii*, *A. sachalinensis*, and *A. middendorfii* the dominant morphotypes are I, II, III, V, and XIV. In the Mongolian vole, all of the identified variations should be classified as reserve ones (there are no morphotypes with a frequency > 30 %).

As a result of primary analysis of the occlusal pattern of m1, it can be concluded that in the majority of populations (15 out of 22), morphotypes of the third group with a symmetric structure of ACC prevail. This mainly concerns the population samples of *Microtus* s. str., while in *M. ilaeus* "*arvalis*" and "*pitymys*" morphotypes (groups 3 and 4) are equally represented.

Teeth of *A. middendorfii* and *A. mongolicus* with asymmetrically complicated ACC (group 2) have both "*gregalis*" and "*arvalis*" features (Borodin, 2009; Voyta et al., 2013). In this case, m1 of the first species can be distinguished from the tooth of *Stenocranius gregalis* by the shape of BRA4 (Borodin, 2009). Mongolian voles sometimes have a poorly developed protrusion on the paraconide, and with age, due to abrasion of the m1 enamel, they become similar to the teeth of western narrow–headed voles (Gromov and Polyakov, 1977). The number of "*oeconomus*" morphotypes in the *A. mongolicus* population is slight-

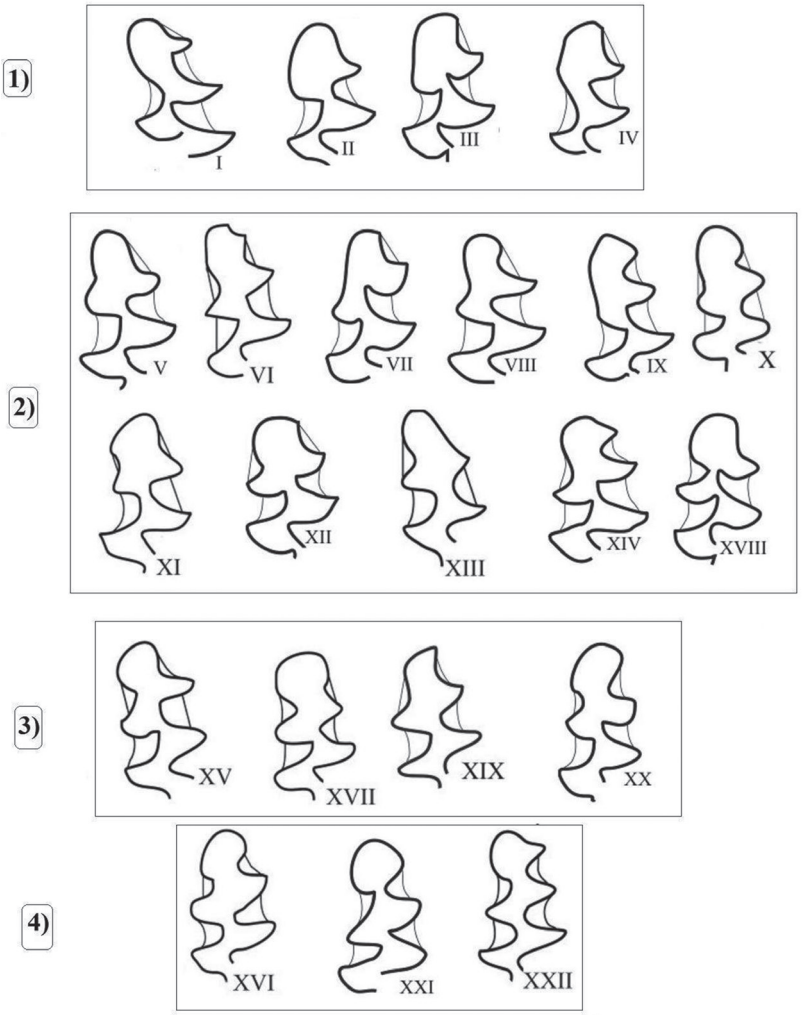


Fig 2. Tooth morphotypes in *Alexandromys* and *Microtus*.

Table 2. Morphotype frequencies (%) for the m1 in *Microtus* and *Alexandromys*

Morphotype	socC	socA	socb	para	ilae	arvK	arvV	arvZ	arvT	levP	levT	levD	levO	levA	obs	agre	oec	mong	max	midd	fort	sach
I	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	80.7	1.0	0	0	0	0
II	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.1	3.0	0	34.6	6.3
III	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41.3	0
IV	0	0	0	0	0	0	0	0	0	0	0	1.3	0	0	0	2.6	2.4	2.1	16.6	1.7	0	4.3
V	0	0	0	0	0	0	0	0	1.0	0	0	0	0	0	0	10.2	6.0	4.1	47.0	12.9	4.1	14.9
VI	0	0	0	0	0	0	0	0	1.0	0	0	0	0	0	0	3.9	0	3.1	0	0	0	0
VII	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10.8	15.5	0	0	0	0
VIII	0	0	0	0	0	0	0	0	1.9	0	0	1.3	0	0	0	9.0	0	5.2	3.0	0	0	0
IX	0	0	0	0	0	0	0	0	0	0	0	1.3	0	0	0	11.5	0	23.7	0	25.8	0	0
X	3.2	0	2.5	9.1	0	0	0	0	1.9	0	0	0	0	0	0	0	0	0	0.8	0	0	0
XI	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.1	0	0	0	0
XII	0	0	12.5	6.1	5.5	1.8	1.8	0	12.5	0	0	3.9	0	0	3.6	5.1	0	11.3	5.3	4.8	0	53.2
XIII	1.0	1.0	0	3.0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
XIV	1.1	3.9	2.5	3.0	0	2.7	3.6	0	18.3	0	2.8	3.9	13.2	0	28.6	5.1	0	24.7	16.8	54.8	19.5	21.3
XV	0	0	5.0	0	0	1.3	1.8	0	3.8	0	0	0	0	0	0	0	0	0	0	0	0	0
XVI	0	0	0	0	2.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
XVII	0	0	0	0	0	0	0	0	0	0	3.3	0	0	0	0	1.3	0	0	0	0	0	0
XVIII	7.5	1.0	0	3.0	0	12.0	17.3	5.7	20.2	3.1	31.2	1.3	0	0	16.1	1.3	0	2.1	0	0	0	0
XIX	1.1	3.9	0	3.0	0	0	0	2.8	1.0	3.1	10.0	0	0	6.1	0	0	0	0	0	0	0	0
XX	84.0	89.4	77.5	69.7	46.0	78.8	73.6	90.6	37.5	93.9	52.5	85.7	86.8	92.9	51.8	48.7	0	2.1	0	0	0	0
XXI	0	1.0	0	3.0	46.0	3.1	1.8	0.9	0	0	0	1.3	0	1.0	0	0.	0	0	0	0	0	0
XXII	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.3	0	2.1	0	0	0	0

ly higher than in the population of Middendorf vole (18.6 % in *A. mongolicus* compared to 1.7 % in *A. middendorfii*, see table 2).

The same morphotype in different populations can be both dominant, reserve and rare. For example, morphotype I prevails in *A. oeconomus* (table 2), while its frequency in other *Alexandromys* varies from 1.7 % to 16.6 %. Morphotype II predominates in *A. fortis*, however, *A. maximowiczii*, *A. sachalinensis*, and *A. mongolicus* it is marked as reserve. Morphotype V, dominant in *A. maximowiczii*, appears in other species of the genus and also in *M. agrestis* as a reserve one. Morphotype XIV was noted in 16 of 22 samples, but dominates only in *A. middendorfii*. Morphotype XXI is basic for the Tien Shan vole and rare (less than 4 % of all m1) in the samples of *M. arvalis*, *M. socialis*, and *M. levis* (see table 2).

All other morphotypes with varying frequency are found in both genera. Of all the identified morphotypes of m1, nine were extremely rare; their total frequency of occurrence is less than 6.1 %. Rare morphotypes are mainly represented in *M. socialis* and *M. levis* from the Danube Delta. The latter species is also characterized by a high level of chromosomal polymorphism (Zagorodnyuk et al., 1991).

Finally, we calculated some parameters of intrapopulation morphotypic diversity.

The value of diversity (*H*, see table 3) in the genus *Microtus* is somewhat lower than in *Alexandromys* (the differences are statistically significant, $t = 2.93–8.59$; $p < 0.01$). An exception is *M. arvalis* from the Tver Region of Russia and *M. agrestis* from the Carpathians. In these two samples, morphological diversity were significantly higher than in East Asian voles ($t = 2.23–3.92$; $p > 0.01$), except for *A. mongolicus*, in which the diversity was significantly higher ($t = 2.83–3.68$; $p > 0.01$). The level of diversity in these samples is the highest compared to other samples of the genus ($t = 5.91–10.84$, $p < 0.01$). The morphological diversity in the Kopet Dagh voles is significantly higher than in all samples of *M. socialis* ($t = 2.39–4.23$, $p < 0.01$). It is interesting to note that the level of differences between *M. arvalis* and *M. levis* ($t = 3.08–3.5$; $p > 0.01$) is higher than between *M. socialis* and *M. arvalis* ($t = 0.71–1.98$; $0.05 > p < 0.01$) and between *M. levis* and *M. socialis* ($t = 0.64–2.2$; $0.05 > p < 0.01$). A similar picture was observed in the degree of genetic divergence of these vole species (Mezhzherin et al., 1993). This fact indicates the unevenness of the rates of morphological and genetic divergence of these species, which, in our opinion, is a consequence of differences in their ecological specialization.

In the studied samples, an average of 2 to 4 moprotypes were found regardless to their species and geographic affiliation. The only exceptions were polymorphic samples of *M. agrestis* and *A. mongolicus*. Rare morphotypes of m1 in species of the genus *Microtus* are more common compared to *Alexandromys*. The largest number of m1 morphotypes and the highest indices of morphological diversity of m1 were observed in the Mongolian vole (14 morphotypes and $H = 2.134$), while the smallest values (two morphotypes and $H = 0.285$) were revealed for the population of *M. levis* from Orlov Island (table 3). Comparison of the morphological diversity of the voles from Orlov Island with other East European voles did not show significant differences ($t = 0.99–1.17$; $p > 0.05$).

The variability of morphological characters has been associated with the impact of a complex of ecological and geographical factors (Owen, 1989, Vasiliev et al., 2003). Hence, it can be assumed that the ratio of different morphotypes is influenced by climatic conditions and by the type of landscape. There are a number of works devoted to the study of correlations between occlusal pattern and climatic conditions of the habitat, trophic features, and biotopic preferences of recent species (Kretzoi, 1957, cited from Stoetzel & Montuire, 2016; Gromov, Polyakov, 1977; Pozdnyakov, 2003; Markova et al., 2017). For example, in *A. oeconomus* and *M. agrestis*, an increase in the proportion of complex morphotypes from west to east is noted (Gromov and Polyakov, 1977; Pozdnyakov, 1994). Later, A. A. Pozdnyakov (2003) showed a significant correlation between temperature conditions and complexity of the occlusal surface in East Asian voles, and the frequency of complicated morphotypes were higher in voles that exist in cooler conditions (Pozdnyakov,

Table 3. Morphological diversity, mean morphotypes and rare morphotypes share in samples of grey vole

Samples	Number of m1 variants	H	μ	Sμ	h	Sh
socC	5	0.536	2.493	0.258	0.501	0.052
socA	6	0.492	2.691	0.293	0.551	0.049
para	8	1.166	5.060	0.610	0.157	0.063
socb	5	0.792	2.610	0.435	0.565	0.078
ilae	4	0.971	3.081	0.277	0.230	0.069
arvK	7	0.798	3.140	0.232	0.551	0.033
arvV	6	0.865	3.482	0.282	0.420	0.047
arvZ	4	0.395	2.111	0.194	0.472	0.048
arvT	10	1.681	5.244	0.400	0.476	0.040
levP	3	0.275	1.745	0.184	0.418	0.061
levT	5	0.667	3.746	0.205	0.251	0.041
levD	8	0.390	3.157	0.446	0.605	0.056
levO	2	0.285	1.677	0.119	0.162	0.060
levA	3	1.137	1.718	0.150	0.427	0.050
obs	4	1.112	3.406	0.190	0.149	0.048
agre	11	1.743	7.889	0.561	0.283	0.051
oec	4	0.671	2.647	0.208	0.338	0.052
mong	14	2.134	10.822	0.595	0.227	0.043
max	7	1.389	5.581	0.245	0.203	0.035
midd	5	1.158	3.829	0.366	0.362	0.061
fort	4	1.183	3.515	0.074	0.121	0.018
sach	5	1.258	4.142	0.272	0.172	0.055

2003). According to our data, the H value is significantly lower ($t = 3.62–5.06$; $p < 0.001$) in *A. oeconomus* from Ukraine compared to *A. middendorfii*, *A. maximowiczii*, and *A. fortis* that live in colder climates.

It is also important in which part of the range the population lives. Since the frequencies of morphotypes may differ at the optimum of the range and at its periphery, this also applies to geographically isolated populations. At the range periphery, the morphotypic structure of the population is simplified and is reduced to two or three morphotypes (e. g., in populations of *M. levis* from Kherson Region, Ukraine, which exist at the southern edge of the species range). In samples from the optimum, e. g. *M. arvalis* and *M. levis* from Tver Region, Russia, the average number of occlusal patterns and the diversity ($t = 7.27–10.24$; $p < 0.001$) are higher compared to other samples of these species.

In geographically isolated populations, the frequency of occurrence of the main morphotypes is significantly lower, but the population's polymorphism is higher. This was noted for the sample of *M. obscurus* from the Crimea. Voles living under the same climatic conditions are characterized by a high similarity of morphotypic structure (samples of *M. arvalis* from Kyiv and Vinnitsa Regions of Ukraine). The level of differences between population samples increases with geographic distance (*M. arvalis* from Zakarpattia Region, Ukraine, and Tver Region, Russia).

In voles living in temperate latitudes, the number of pattern variations is usually reduced to one dominant and 1 to 3 reserve or rare morphotypes (*A. oeconomus*, most of *M. arvalis*, *M. socialis*, and *M. levis* populations). Populations living under extreme conditions (dry steppe, high mountains) are characterized by a complex morphotypic structure (*A. mongolicus*, *M. paradoxus*, and *M. agrestis*). This is due to the fact that animals

living in colder climates, are usually characterized by a high growth rate, while the occlusal pattern retains juvenile features leading to an increase in the percentage of complex morphotypes (Gromov, Erbaeva, 1995; Pozdnyakov, 2003).

Multivariate analysis

According to the results of principal component analysis (table 4), 96.18 % of variance of the phenetic similarity between samples (*r*) is described by the first three principal components, which suggests a highlt structured group variation of the occlusal pattern m1 in grey voles of genera *Microtus* and *Alexandromys*.

The first PC was the most informative (86.176 % of total variance) to reveal variation patterns throughout the taxonomic range. All *Microtus* s. str. samples were related with high positive loadings (0.759–0.996) according to this component (table 4). This group of samples is located on the right side of the general morphological space in fig. 3. East Asian vole samples (genus *Alexandromys*) are placed in left side of the general morphological space and are, respectively, characterized by negative loading values on PC1 from –0.575 to –0.790.

Therefore, *Microtus* and *Alexandromys* clearly differ according to the factor values of PC1, which reflects the similar relationship between grey voles in the structure of m1 morphotypic variability, as evidenced by the value of indices of population phenetic similarity (*r*) and the identity criterion (*I*) (table 7). The main differences between these groups of voles are that, according to the structure of morphotypic variation of m1, in voles of the genus *Microtus* only morphotype XX dominates (table 2), while in East Asian voles 6 other m1 morphotypes (I, II, III, V, IX, XIV).

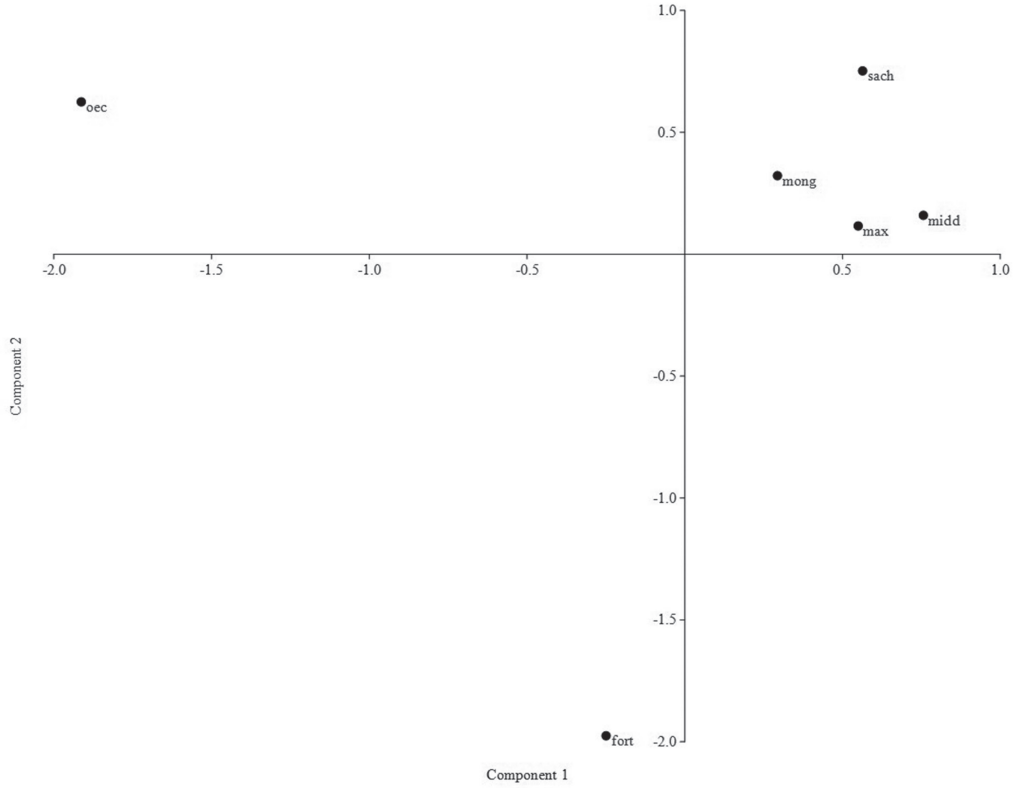


Fig. 3. Differentiation on six East Asian vole samples by the morphotypic variation of the occlusal pattern.

Table 4. Factor loadings and explained variance in principal component analysis of *Alexandromys* and *Microtus* samples

Samples	PC1	PC2	PC3
socC	**0.9962**	0.0255	0.0082
socA	**0.9952**	0.0174	–0.0155
para	**0.9826**	0.1235	0.0337
socb	**0.9691**	0.1557	0.0592
ilae	**0.9216**	–0.1059	0.0155
arvK	**0.9921**	0.0706	0.0000
arvV	**0.9873**	0.0902	–0.0042
arvZ	**0.9952**	–0.0560	–0.0025
arvT	**0.8320**	0.4894	0.0427
levP	**0.9966**	–0.0400	0.0124
levT	**0.9870**	0.0866	0.0248
levD	**0.9842**	0.1106	–0.0377
levO	**0.9887**	–0.0916	–0.0549
levA	**0.9698**	0.0698	–0.0081
obs	**0.9198**	0.3228	–0.0491
agre	**0.7592**	0.5431	0.1664
oec	–0.6047	–0.4701	0.5348
mong	–0.5752	0.6781	0.1578
max	**–0.7904**	0.5072	–0.0220
midd	–0.6884	0.6958	–0.0164
fort	–0.6434	0.1747	–0.6987
sach	–0.6566	0.6466	0.1669
% variance	86.176	7,744	2.198

Morphological differences between these two groups, according to A. A. Pozdnyakov (Pozdnyakov, 1995), consist in varying degrees of transformation of the anterior lobe and the formation of complicated morphotypes (e. g. the form "*maski*" by the classification of Rörig, Börner, 1905). In the majority of *Alexandromys*, the anteroconid complex is complicated asymmetrically (1 and 2 groups of morphotypes) and teeth with "*arvalis*" structural features prevail only in *A. sachalinensis*. The voles of *Microtus* s. str. morphotypes of groups 3 and 4 dominate with symmetric complication of ACC, morphotypes of group 1 are completely absent, and morphotypes of group 2 are reserved.

Thus, the morphological space of PC1 is formed mainly by differences in the structure of m1 morphotypic variation between East Asian voles of the genus *Alexandromys* and a group of species of the genus *Microtus*, the core of which are the social and common voles. Since most of the variance can be explained by PC1, and the part of the variance of PC2 and PC3 is insignificant (< 6 %) we analysed samples of *Alexandromys* and *Microtus* s. str. separately.

Morphotypic variation of m1 in East Asian voles (*Alexandromys*)

PC analysis of the phenetic similarity matrix of six *Alexandromys* species shows that 96.46 % of the total variance is described by the first tree PC (table 5). The first component describes 57.32 % of the total variance, while PC2 describes 25.83 % and PC3 only 12.80 %.

Results of PCA suggest that the root vole is the most separated from the five other species (fig. 3). PC1 were associated with an increase in the degree of differentiation of the occlusal pattern and also by the complication of the lingual side observed from *A. oeconomus* to *A. middendorfii*.

Table 5. Results of principal component analysis on six East Asian vole species

Species	PC_1	PC_2	PC_3
oec	–0.9007	0.4133	0.0622
mong	0.6097	0.2694	0.7179
max	0.8177	0.1299	–0.4214
midd	0.9086	0.1433	0.3353
fort	0.2505	–0.9673	0.0108
sach	0.7899	0.4749	–0.3347
% variance	57.32	25.83	12.80

Earlier it was considered that the isolation of this species into an independent line began from the end of the Late Pliocene (Agajanyan, Yatsenko, 1984), or according to the allozyme analysis (Mezhzherin et al., 1993), in the first half of the Early Pleistocene, which later was confirmed by molecular genetic methods (Conroy, Cook, 2000). This also corresponds to paleontological data, since the appearance of "*Microtus protooeconomus*" in the beginning of Early Pleistocene (Rekovets, 1994). Analysis of mitochondrial sequences of cytochrome b indicates (Bannikova et al., 2010) that the time of divergence of *A. oeconomus* from other *Alexandromys* species was approximately 1.2 Mya. The values of craniometrical characters of *A. oeconomus* and *A. middendorfii* significantly overlap (Lissovsky, Obolenskaya, 2011), but these species clearly differ by genetic (Bannikova et al., 2010) and odontological markers (Lissovsky, Kadetova & Obolenskaya, 2018; our data, fig. 3, table 2). Data from the analysis of mitochondrial *cyt b* in the group of East Asian voles (Lissovsky et al., 2018) confirm our conclusions about the high level of morphological (odontological) divergence of *A. oeconomus* from other species of the genus *Alexandromys*.

Other species are characterized by high positive factor loadings on PC1 (table 5). *A. mongolicus* and *A. middendorfii* have a similar structure of morphotypic variation of m1 (I = 42.9). Genetic differences between them are also small and about 2–3 times less than between *A. oeconomus* and other *Alexandromys* species (Lissovsky et al., 2018). *A. mongolicus* and *A. middendorfii* differ in having different frequencies of morphotypes V (12.9 %) and XIV (54.8 %) in *A. middendorfii* against 4.1 % and 24.7 % in *A. mongolicus*. Besides, morphotypes VI, VII and VIII were found in 23.8 % of individuals of the first species and they were not found at all in the other (table 2). The taxonomic proximity of *A. mongolicus* and *A. middendorfii* was substantiated earlier (Zagorodniuk, 1990; Mezhzherin et al., 1993), which is concordant with the current scheme of phylogenetic relationships between grey voles (Abramson et al., 2009; Bannikova et al., 2010; Abramson et al., 2012).

A. maximowiczii, *A. sachalinensis*, and *A. fortis* are also quite similar by craniometrical features (Lissovskii, Obolenskaya, 2011), but at the same time they differ genetically (Lissovsky et al., 2018). The differences between *A. fortis* and *A. maximowiczii* in the structure of morphotypic variation of m1 are significantly large (I = 331.2, table 7). In addition, these species differ in biotope preferences. The reed vole inhabits open areas near water, moist meadows, while Maximowicz's vole prefers closed habitats such as shrubs and humid forests (Meyer et al., 1996). The phylogenetic relationships of *A. sachalinensis* with other species are still a subject of discussion. Morphologically, this species is very similar to Maximowicz's vole (Meyer et al., 1996). However, studies on craniometrical variation of some species of the genus showed that *A. sachalinensis* is similar to the reed vole by skull measurements (Lissovsky, Obolenskaya, 2011). Our data (table 5) indicate that the level of differences by morphotypic variation of m1 between *A. sachalinensis* and *A. maximowiczii* (I = 33.24) is more than two times lower than that between *A. fortis* and *A. sachalinensis* (I = 76.97). Genetic differences between the reed and Sakhalin voles (20.4) are almost three times larger than those between the Sakhalin and Maximowicz's vole (7.0) (see Lissovsky et al., 2018). Accordingly, we can assume that the species group is taxonomically hetero-

geneous by three main criteria (genetic, morphological, and ecological differences) and it requires further in-depth and comprehensive study.

PC2 is highly negatively correlated with *A. fortis*. This sample is quite isolated from the others, primarily due to the structure of the buccal side of ACC (m1 without BSA4, in contrast to *A. middendorfii, A. maximowiczii, A. sachalinensis,* and *A. mongolicus* in which the re-entrant angle is clearly visible). The degree of development of LRA5 is not the same; in 34.6 % of m1 from the studied population, it was not noted (morphotype II, see fig. 2, table 2), and in 41.3 % it is clearly visible (morphotype III). As a result, we have a simplification of the buccal side ("*fortis*-like" simplification after Voyta et al., 2013). According to the literature (Pozdnyakov, 2003; Voyta et al., 2013; Lissovsky et al., 2018), this pattern dominates in *A. fortis*, but also occurs in other species with a frequency of 8–52 % (see Lissovsky et al., 2018). It also exists in the northern *A. oeconomus* (Lissovskiy et al., 2018), but such dental pattern was not noted in the Ukrainian sample.

PC3 describes the variability of Mongolian voles, whose teeth are extremely diverse. Among the studied m1, "*oeconomus*" (I, IV, VII — 18.6 %), "*gregalis*" (IX — 23.7 %) and "*arvalis*" (XII, XX — 19.6 %) morphotypes were noted. That is, it is difficult to clearly distinguish which type of structure is dominant in this sample. This confirms earlier data on the high polymorphism of *A. mongolicus* (Ognev, 1950; Gromov and Polyakov, 1977) and is consistent with modern data (Lissovky et al., 2018).

Summing up the results of the comparative study of morphotypic variation of m1 in six *Alexandromys* species, we can conclude that these results describe the taxonomic differences between *A. oeconomus* and *A. fortis* from other *Alexandromys* species. Samples of voles, in which morphotypes of group 1 dominate, occupy the left part of the morphological space, while the right part of the morphospace is occupied by samples the morphotypic structure of which is formed by morphotypes of group 2. The largest interspecific differences were noted between *A. oeconomus* and *A. middendorffii* (r = 0, I = 250.7), which do not have common m1 morphotypes, while the minimum interspecific differences were found between *A. maximowiczii* and *A. sachalinensis* (r = 0.750, I = 33.24).

Morphotypic variation of m1 in *Microtus* s. str.

Based on the results of factor analysis of the matrix of phenetic similarity in 16 samples of seven species of *Microtus* s. str., it was found that 96 % of the total variance was described by the first four principal components. PC1 describes the greatest part of the variance (54 %). In this case, all samples except for *M. ilaeus* have positive factor loadings by this component (table 6).

Additionally, 11 samples have highly significant factor loadings (0.71–0.97) on PC1. In all of these samples, morphotype XX dominates with a frequency of 69.7 % (*M. paradoxus*) to 93.9 % (*M. levis*, Poltava). Other variants of m1 in these samples are presented slightly. At the same time, morphotype XX is much less common among *M. arvalis* (37.5 %) and *M. levis* (52.5 %) from Tver Region of Russia, as well as among *M. ilaeus* (46.0 %), *M. agrestis* (48.7 %) and Crimean *M. obscurus* (51.8 %) (table 2). All of these samples are characterised by small positive or close to negative factor correlations with PC1.

M. arvalis from Zakarpattia Region, Ukraine, according to m1 morphotypes, is closer to *M. levis* (*I* = 7.09–12.35) than to other samples of this species (*I* = 29.57–106.43). Many researchers assume the possible co-occurrence of *M. arvalis* and *M. levis* in Hungary (Hotzi et al., 2008,), including its bordering region with Zakarpattia (Barkasi, Zagorodniuk, 2016), however this issue requires special studies.

PC2 describes the morphotypic variation of *M. ilaeus* and *M. arvalis* from Tver Region and of *M. obscurus*. Moreover, the first sample is characterised by a highly reliable positive correlation with PC2, and the other two are negative (see table 6). *M. ilaeus* (fig. 4) phenotypically is the most differentiated from the other studied species of *Microtus* s. str. This is evidenced by the sufficiently high degree of its difference from the six other species

Table 6. Results of principal component analysis on 16 *Microtus* samples

Samples	PC_1	PC_2	PC_3	PC 4
socC	**0.9794**	0.0671	–0.1112	0.0034
socA	**0.9077**	0.3082	0.1134	–0.1810
para	**0.7325**	0.1951	0.0747	0.5098
socb	0.6576	0.2696	0.5319	0.3051
ilae	–0.2322	**0.8610**	0.0545	0.3584
arvK	**0.9509**	–0.2164	0.0120	0.1266
arvV	**0.8920**	–0.3790	–0.0698	0.1558
arvZ	**0.9390**	0.2718	–0.1580	–0.1271
arvT	0.2514	**–0.9159**	0.1273	0.2483
levP	**0.9207**	0.3419	–0.1127	–0.1449
levD	**0.7848**	0.2672	0.5059	0.0353
levO	**0.8635**	0.1586	0.3527	0.0109
levA	**0.7691**	0.6230	–0.0337	–0.1234
levT	**0.7329**	–0.4372	–0.4932	–0.1104
obs	0.5380	**–0.7627**	0.1151	0.2523
agre	0.0940	–0.3475	0.7590	–0.4841
% variance	53.312	27.368	9.298	5.751

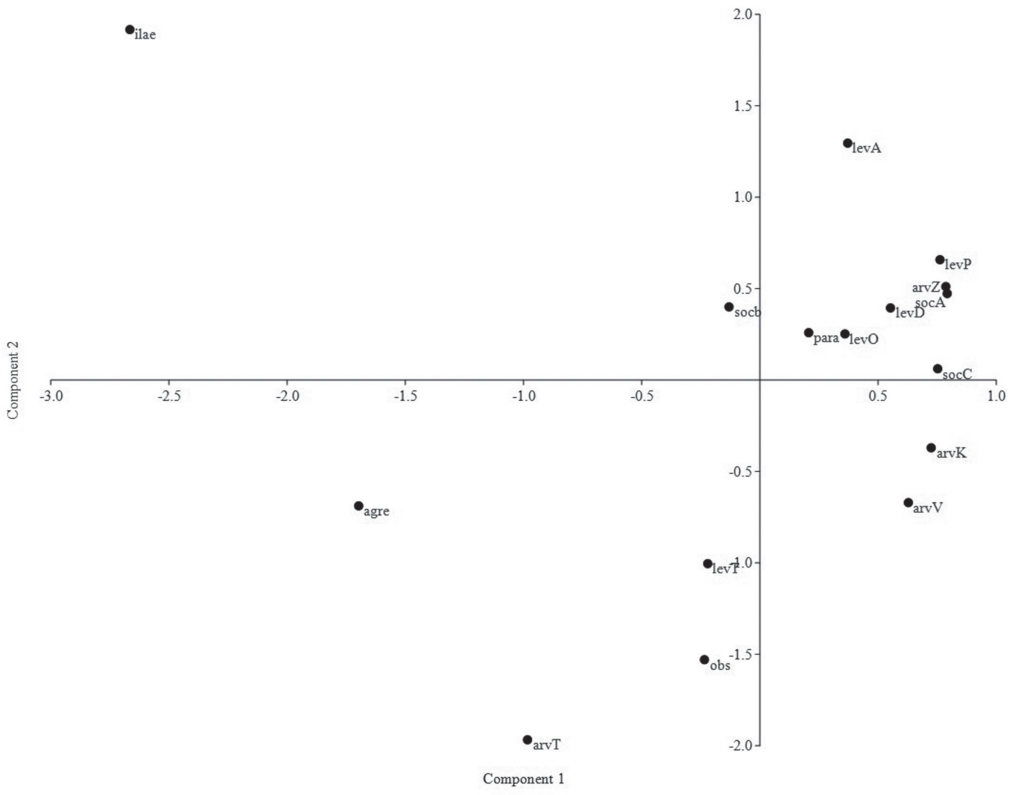


Fig. 4. Differentiation on 16 *Microtus* samples by the morphotypic variation of the occlusal pattern.

(*I* = 56.4–79.95). Analysis of the mitochondrial sequences of cytochrome b indicates that *M. ilaeus* separated from other species of *Microtus* s. str. presumably 0.315 Mya (Mahmoudi et al., 2017). *M. ilaeus* is phenotypically close to *M. paradoxus* and *M. socialis binominatus* (I = 26.6–27.6). The morphotypic structure of the Tien Shan vole sample is formed by an equal percentage of morphotypes of groups 3 and 4 (XX — 46.0 % and XXI — 46.0 %, see table 2).

The difference in morphotypic structure between the Crimean *M. obscurus*, *M. levis*, and *M. arvalis* is quite large (I = 62.8–84.93), which may be a consequence of their long geographical isolation (Malygin, 1983; Peskov and Tsudikova, 1997). Based on molecular genetic data, the divergence of *M. arvalis* and *M. obscurus* from a common ancestor took place ca. 0.478 Mya (Altai vole, 2013). According to paleontological data, *M. obscurus* appeared in the Crimean Mountains in the first half of the Late Pleistocene (Markova, 2000), and later dispersed to Eastern Eurasia (Altai vole, 2013). According to the ratio of m1 morphotypes, *M. obscurus* from the Crimea is much closer to *M. arvalis* from near Tver, Russia and Vinnitsa, Ukraine (I = 25.61–27.84), as well as to *M. levis* from the Danube Delta (I = 23.19). In all these samples, m1 with morphotype XVIII was noted with a frequency of occurrence of 12.0 to 17.9 %.

One of the most unexpected results was the isolation of *M. levis* and, especially, *M. arvalis* from Tver Region, Russia (fig. 4, table 5). In this population of *M. arvalis*, 10 morphotypes were identified, of which the most common are five (XII, XIV, XVIII, and XX) and the others were found only in single individuals (table 2). In Russian *M. levis*, five morphotypes were recorded (XIV, XVII, XVIII, XIX, and XX), among which XX (52.5 %), XVIII (30.8 %) and XIX (10.0 %) dominated. The differences between these two samples are rather large (*I* = 75.34), but much less than the differences between geographic populations of *M. levis* (*I* = 136.09, see table 7).

PC3 were associated with samples of *M. agrestis*. The field vole turned out to be extremely polymorphic in its morphotypic structure. Among the studied teeth, 48.7 % of m1 was typical "*arvalis*", 12.8 % was similar to *A. oeconomus* (IV and VIII), and 24 % similar to "*gregalis*" morphotype. The frequency of occurrence of teeth with asymmetrically complicated ACC structure is much higher in *M. agrestis* than in *M. arvalis*. This is confirmed for fossil and recent samples (Nadachowski, 1982; Bogićević et al., 2017; Luzi et al., 2019). This criterion, along with morphometric parameters, is the most reliable in the diagnosis of this pair of species (Nadachowski, 1982). For example, for *M. agrestis,A. middendorffii*, and *M. arvalis* that occur sympatrically in the Urals and Western Siberia, discriminant functions have been developed for species identification (Borodin, 2009).

Interpopulation and interspecific differences in voles of the genus *Microtus* s. str. vary in a wide range from minimum differences between populations of *M. arvalis* from near Kyiv and Vinnitsa (r = 0.970, I = 3.71) to maximum distinctness between samples of *M. arvalis* from Zakarpattia Region, Ukraine and Tver Region, Russia (r = 0.707, I = 94.6). Interspecific differences in *Microtus* s. str. are significantly lower compared to *Alexandromys*, while the similarity of the morphotypic structure, respectively, is greater (table 7). For example, insignificant interspecific differences were noted between *M. paradoxus* and *M. levis* from the Danube Delta (r = 0.895, I = 6.40). The greatest differences were noted between *M. levis* from Kherson Region, Ukraine and *M. arvalis* from Tver Region, Russia (r = 0.614, I = 136.09).

Despite the territorial isolation of *Sumeriomys*, the analysis of the morphotypic structure did not show significant differences between *M. s. binominatus* Ellermann, 1941 and *M. s. nikolajevi* Ognev, 1950 (r = 0.852–0.903, I = 17.3–23.4). In addition, the differences between the Transcaucasian *M. s. binominatus* and *M. paradoxus* (r = 0.897, I = 8.7) are almost times less than the difference between the two samples of *M. s. nikolajevi* (r = 0.937, I = 24.9).

Based on the results of multivariate analysis it can be concluded that the teeth of *Microtus* s. str are characterised by a simpler morphotypic structure. In the right part of the

Table 7. Population similarity index (r) and criterion of identity (*I*)

I \r	socC	socA	socb	para	oec	mong	ilae	arvK	arvV	arvZ	arvT	levP	levD	levO	levA	levT	obs	agre	max	midd	fort	sach
socC		0.937	0.852	0.903	0.142	0.254	0.225	0.926	0.920	0.955	0.764	0.955	0.900	0.892	0.909	0.866	0.826	0.755	0.059	0.078	0.046	0.048
socA	24.95		0.864	0.893	0.146	0.250	0.641	0.906	0.890	0.966	0.728	0.969	0.926	0.953	0.960	0.834	0.826	0.716	0.081	0.146	0.087	0.115
socb	23.41	17.33		0.897	0.136	0.347	0.680	0.880	0.863	0.838	0.797	0.853	0.916	0.878	0.849	0.663	0.785	0.784	0.079	0.117	0.070	0.073
para	17.47	16.4	8.71		0.129	0.315	0.742	0.894	0.878	0.882	0.810	0.870	0.895	0.841	0.865	0.784	0.810	0.800	0.098	0.129	0.077	0.080
oec	297.94	310.99	121.79	104.18		0.162	0.105	0.138	0.133	0.147	0.183	0.150	0.143	0.144	0.149	0.112	0.111	0.395	0.591	0.205	0.243	0.363
mong	284.84	296.68	107.96	92.44	273.09		0.177	0.317	0.173	0.614	0.542	0.371	0.316	0.140	0.492	0.264	0.173	0.438	0.447	0.701	0.457	0.372
ilae	77.01	61.94	26.64	27.66	178.00	168.06		0.634	0.613	0.646	0.498	0.657	0.752	0.632	0.722	0.491	0.533	0.527	0	0	0	0
arvK	27.71	43.07	22.09	14.71	414.38	369.08	61.02		0.970	0.928	0.839	0.921	0.940	0.887	0.873	0.861	0.891	0.727	0.067	0.122	0.073	0.076
arvV	21.68	40.44	19.48	16.17	323.24	269.41	63.3	3.71		0.916	0.858	0.905	0.921	0.868	0.840	0.882	0.911	0.719	0.078	0.140	0.084	0.088
arvZ	16.99	13.8	19.11	13.08	313.69	329.8	62.01	30.91	29.57		0.707	0.994	0.919	0.887	0.968	0.875	0.781	0.691	0	0	0.173	0
arvT	87.05	105.69	38.85	33.91	202.06	158.87	61.65	99.99	57.63	94.62		0.690	0.772	0.726	0.614	0.792	0.917	0.734	0.272	0.431	0.209	0.235
levP	13.08	9.43	13.69	9.44	243.92	253.03	62.43	30.13	29.63	2	75.85		0.917	0.903	0.977	0.856	0.768	0.696	0	0	0.166	0
levD	21.53	9.36	11.69	6.4	174.08	142.67	52.43	27.11	27.41	23.65	81.09	17.37		0.934	0.904	0.765	0.855	0.767	0.081	0.204	0.087	0.115
levO	31.65	20.91	10.17	13.9	238.14	200.64	48.03	26.98	27.61	27.21	41.71	21.35	11.47		0.898	0.733	0.865	0.733	0.149	0.269	0.160	0.168
levA	33.33	11.44	22.38	14.69	302.29	329.18	58.82	66.92	63.81	12.35	136.09	6.73	21.1	31.21		0.776	0.694	0.673	0.000	0.000	0.140	0.000
levT	48.14	65.9	41.68	30.1	210.8	221.23	60.24	73.09	44.73	49.88	75.34	42.61	65.34	35.58	61.15		0.829	0.605	0.065	0.117	0.070	0.073
obs	47.97	49.85	30.29	24.01	232.36	139.48	79.95	38.7	25.61	62.8	27.84	54.28	23.19	36.67	84.93	38.45		0.712	0.219	0.396	0.236	0.247
agre	47.39	69.79	25.43	21.72	113.74	140.45	56.37	75.34	61.41	65.35	100.31	48.59	48.37	30.99	73.54	96.05	49.21		0.441	0.303	0.100	0.261
max	319.87	315.65	116.77	100.15	296.3	156.1	231.2	333.25	236.27	470.32	287.87	338.43	389.05	200.9	449.95	235.33	245.6	149.33		0.653	0.672	0.793
midd	317.56	287.76	106.1	90.68	400.39	21.43	264.16	543.46	327.69	624.31	167.69	429.14	221.19	108.49	594.29	185.49	118.35	128.3	235.14		0.540	0.601
fort	339.87	328.98	146.94	114.85	375.54	180.81	264.71	506.78	308.79	633.47	459.98	430.58	231.84	114.7	597.06	322.89	145.86	283.07	248.20	273.41		0.898
sach	135.77	123.84	90.37	73.23	164.39	33.97	167.15	153.27	126.97	264.31	163.33	220.88	107.56	71.02	257.75	131.38	78.09	106.01	33.24	84.54	76.97	

morphospace (fig. 4) are the samples with symmetrically complicated ACC according to the "*arvali"* type (group 3). The left part is occupied by samples with a polymorphic structure, i. e. a combination of "*arvalis"*, "*gregalis"*, "*pitymys"* and "*oeconomus"* morphotypes (*M. arvalis* from Tver Region, *M. levis*, *M. agrestis*, *M. obscurus*, *M. ilaeus*, *M. socialis binominatus*). In the case of *Microtus* s.str., the key role in the formation of morphological diversity is played by interpopulation rather than interspecific differences.

Conclusions

1) As a result of morphotypic analysis of 22 population samples of 13 species of *Alexandromys* and *Microtus* s. str., we identified 22 types of occlusal pattern. The selected variations of the occlusal pattern according to the degree of complexity of the anteroconid complex can be attributed to 4 groups.

2) In most samples, 3 to 5 morphotypes were identified (μ = 1.718–4.142). The largest number of m1 morphotypes was noted in the Mongolian vole (14 morphotypes), while the smallest was found *M. levis* from Orlov Island (2 morphotypes). The value of morphological diversity of m1 in these populations is, respectively, the highest (H = 2.13) and the lowest (H = 0.28).

3) In populations of *Alexandromys*, teeth with simplified buccal side prevail (group 1 of morphotypes, dominant for *A. oeconomus* and *A. fortis*), while in other species, m1 with complicated lingual and buccal sides are noted (groups 1 and 2 morphotypes). The maximum interspecific differences were noted between *A. oeconomus* and *A. middendorffii* (r = 0, I = 250.7), which have no similar morphotypes, while minimum differences were found between *A. maximowiczii* and *A. sachalinensis* (r = 0.750, I = 33.24).

4) In *Microtus* s. str., teeth of the "*arvalis*" type with symmetrically complicated anteroconid complex (group 3) prevail. *M. ilaeus* has equal portions (46 % of the total) of m1 of "*arvalis*" and "*pitymys*" types (groups 3 and 4), while in *M. arvalis*, *M. levis*, *M. agrestis*, and *M. obscurus* from Tver Region, Russia, teeth with asymmetrically complicated anteroconid complex of "*oeconomus*" and/or "*gregalis*" type occur along with the main type of structure. In species of *Microtus* s. str., compared to *Alexandromys*, interspecific differences are significantly smaller and the similarity of the morphotypic structure is, respectively, greater (r = 0.72–0.94).

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