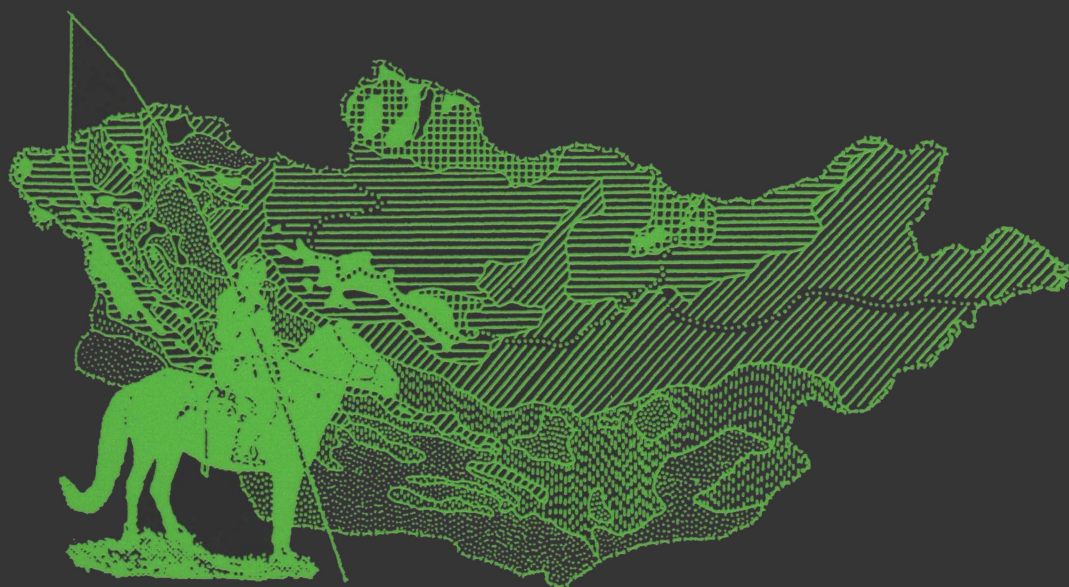


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Morphological disparity among Rock voles of the genus *Alticola* from Mongolia, Kazakhstan and Russia (Rodentia, Cricetidae)

V.N. Bolshakov, I.A. Vasilyeva & A.G. Vasilyev

Abstract

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Key words: Rock voles, dental crown patterns, disparity, geometric morphometrics

Introduction

An estimation of biological diversity within natural communities, which is considered first of all as variety of their species composition may be difficult because of insufficient readiness of systematics in many groups of organisms and ambiguity of taxonomic status of separate forms. It is obvious that in certain cases disputable situations can arise not only because of a bad level of taxonomic studies, but also because of incompleteness of the processes of divergence and speciation themselves (MAYR 1971, BOLSHAKOV et al. 1985). Therefore determining of taxonomic relations in the concrete groups of organisms besides applied value represents also theoretical biological interest in respect of studying of mechanisms and an ecological orientation of formation process.

One of examples of ambiguous situation in rodents' taxonomy is an idea about species composition of the Central Asian high-mountain, or rock voles of the genus *Alticola* Blanford, 1881. Taxonomic status of various forms included in it is not clear until now. Revision of nominative subgenus of *Alticola* s. str. was successfully conducted by ROSSOLIMO with coauthors (ROSSOLIMO & PAVLINOV 1986, ROSSOLIMO et al. 1988, 1992), but the subgenus *Aschizomys* Miller, 1898 is not yet fully revised up to now despite some preliminary attempts (BOLSHAKOV et al. 1985, VASIL'EVA 1999; VASILYEVA et al. 2008). Their taxonomic interrelations are interpreted extremely contradictory. In particular the vole from the Olchon Island, *Alticola olchonensis* Litvinov,

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One of examples of ambiguous situation in rodents' taxonomy is an idea about species composition of the Central Asian high-mountain, or rock voles of the genus *Alticola* Blanford, 1881. Taxonomic status of various forms included in it is not clear until now. Revision of nominative subgenus of *Alticola* s. str. was successfully conducted by ROSSOLIMO with coauthors (ROSSOLIMO & PAVLINOV 1986, ROSSOLIMO et al. 1988, 1992), but the subgenus *Aschizomys* Miller, 1898 is not yet fully revised up to now despite some preliminary attempts (BOLSHAKOV et al. 1985, VASIL'EVA 1999; VASLYEVA et al. 2008). Their taxonomic interrelations are interpreted extremely contradictory. In particular the vole from the Olchon Island, *Alticola olchonensis* Litvinov,

1960, is the least clear. Both its specific status and subgeneric relationships were discussed over a period of 50 years. Originally it was described as a subspecies of *A. argentatus*, but GROMOV & POLYAKOV (1977) suggested that *olchonensis* belonged to the subgenus *Aschizomys*. Later PAVLINOV & ROSSOLIMO (1987) had included *olchonensis* into *A. tuvnicus* as a subspecies, thereby again associated it with the nominative subgenus *Alticola*. However in 2003 PAVLINOV reconsidered, that *olchonensis* should be returned to *Aschizomys*. So its systematic position and taxonomic status need to be reassessed (MUSSER & CARLETON 2005).

We believe that taxonomic revisions demand to carry out complex and comprehensive analysis of population variations in various systems of traits by means of different methods. Combination of traditional morphological approaches with advanced molecular techniques seems to be the most promising. Among species of the genus *Alticola* the pattern of the third molar crown considered as the most significant taxonomic morphological trait both at generic and species level. Flat chewing surface of arvicoline's teeth can be described by a set of homologous landmarks and analyzed by means of multivariate statistics (PAVLINOV 1999, VASILYEVA et al. 2008).

In this paper we aim to evaluate morphological disparity among Asian rock voles of the genus *Alticola* from 8 localities in East Mongolia, East Kazakhstan and South Siberia (Russia), as revealed by geometric morphometrics of the third upper molar patterns. The special attention was paid to position of *Alticola olchonensis* among other species.

Materials and methods

We studied 258 third upper molars of 130 specimens of Asian high-mountain voles of the genus *Alticola* (further tooth sample sizes are placed in parentheses, left and right jointly). The samples examined represent four nominative species of the subgenus *Alticola*: *A. argentatus* Severtzov, 1879 (Kazakhstan: Talassian Ala-Tau; N = 32), *A. tuvnicus* Ognev, 1950 (Russia: Tuva; N = 14), *A. olchonensis* Litvinov, 1960 (Russia: Olchon Island; N = 44) and *A. semicanus* Allen, 1924 (Mongolia; N = 40) (fig. 1). The last species was represented by two samples of subspecies *A. semicanus alleni* Argiropulo, 1933: the first one from Hentij Aimak (North-East Mongolia; N = 30) and the second one from Suhbaatar Aimak (East Mongolia; N = 10). In order to decide the problem of subgeneric affinity of *A. olchonensis* we included in our study three samples from Russia of species belonging to the subgenus *Ashizomys* Miller, 1898: *A. macrotis* Radde, 1861 (Transbaikalian region: Khamar-Daban ridge; N = 42), *A. lemminus vicina* Portenko, 1963 (South Yakutia: Chara Upland; N = 42) and *A. fetisovi* Galkina et Yepifantseva, 1988 (Transbaikalian region: Sokhondo Mnt; N = 44). The last form was separated from *A. macrotis* as distinct species based on its morphological peculiarities only (GALKINA & YEPIFANTSEVA 1988). The samples of *A. argentatus* and *A. macrotis* were collected by ourselves, but the others were allowed for study by the Institute of Biology of Yakutian Science Center of Siberian Department of Russian Academy of Science (*A. lemminus vicina*), Sochondian State Reserve (*A. fetisovi*), and all the rest by the Zoological Museum of the Moscow State University.

To make results of multivariate statistics comparable, samples were selected to be of approximately equal size where possible (i.e. between 30 and 44). Juveniles and senile specimens with a higher degree of tooth-wear were excluded. Because we did not find any significant differences between males and females in crown pattern shape in *Alticola macrotis* in our previous study (VASILYEVA et al. 2008), we ignored these weak differences and pooled sexes in the subsequent analyses.

Variations of shape of dental crown patterns were examined by means of geometric morphometrics (BOOKSTEIN 1991, PAVLINOV & MIKESHINA 2002, ZELDITCH et al. 2004). Enamel contours of occlusal surface of the third upper molars were outlined with the help of sketching ocular. Tooth pictures were scanned and the images were digitized. We used both left and right molar images, but the latter were inverted horizontally on 180° and then digitized as right ones. For each molar 25 landmarks were collected using the software tpsDig (ROHLF 2010a). The shape of each

tooth pattern was represented as a configuration of the same set of two-dimensional homologous landmarks (fig. 2). Information unrelated to shape, including position, orientation, and size was removed from the shape configuration by translation, rotation, and rescaling. Centroid size (CS) was calculated for each specimen as the square root of the sum of the squared distances between every landmark and the centroid of all landmarks (BOOKSTAIN 1991). Molar Folding Index (MFI) values was calculated as ratio of empiric contour length to theoretical one by the formula:

$$MFI = C / 2(\pi S)^{0.5},$$

where C – the empiric contour length of molar crown configuration (the sum of the distances between successive landmarks along the perimeter), S – the area of the configuration of molar occlusal surface.



Fig. 1: The map-scheme showing the location of samples of the seven *Alticola* species used in this study: 1 – *A. argentatus*; 2 – *A. tuvunicus*; 3 – *A. olchonensis*; 4 – *A. macrotis*; 5 – *A. lemminus*; 6 – *A. fetisovi*; 7-8 – *A. semicanus* (1-2).

The information about variation of proper shape was extracted using generalized least squares (GLS) Procrustes superimposition. Procrustes distances were calculated as the square root of the summed squared distances between homologous landmarks (ROHLF & SLICE 1990, BOOKSTEIN 1991). Canonical variates analysis (CVA) of shape based on partial warp scores was carried out. Mahalanobis distances were used to assign each specimen to various groups. Jack-knife test was used to estimate the correctness of group assignments (SHEETS 2007).

For the reason that the matrices of Mahalanobis distances (D) and Procrustes distances were closely correlated with each other (Mantel $r = 0.92$; $p = 0.0002$) we preferred to use the Procrustes distances for further cluster analysis. The latter one characterizes distances between each sample mean and reference consensus more correctly. The squared Procrustes distances were used to construct a similarity tree based on UPGMA (Unweighted pair-group method, arithmetic average). Cophenetic correlation coefficient was the highest for the Chord measure of squared Procrustes distances (Coph. corr. = 0.94). The same distance was used to measure morphological

disparity (MD) following FOOTE (1993): $MD = \sum (d_i^2) / (N - 1)$, where d_i^2 is the squared Procrustes distance between the mean shape of a species and the mean shape over all species in the total sample; N is the number of species (ZELDITCH et al. 2004, CHAKRABARTY 2005). A total of 100 bootstrap sets were used for estimation of standard errors of MD (SHEETS 2007). Difference in morphological disparity between two groups (subclades) was estimated by means of permutation pairwise test under 1000 trials (SHEETS 2004).

In order to remove size-dependent shape variation we used a multivariate regression model and conducted the standardization of intraspecific variability of landmark data on LN CS as independent variable x . The residuals obtained were then added to the predicted specimen at some specified value of LN CS, where the predicted value was taken from the regression model (CHAKRABORTY 2005).

All calculations were performed in PAST 2.14 (HAMMER et al. 2001), MorphoJ 1.4 (KLINGENBERG 2011), and IMP (SHEETS 2004, 2007).

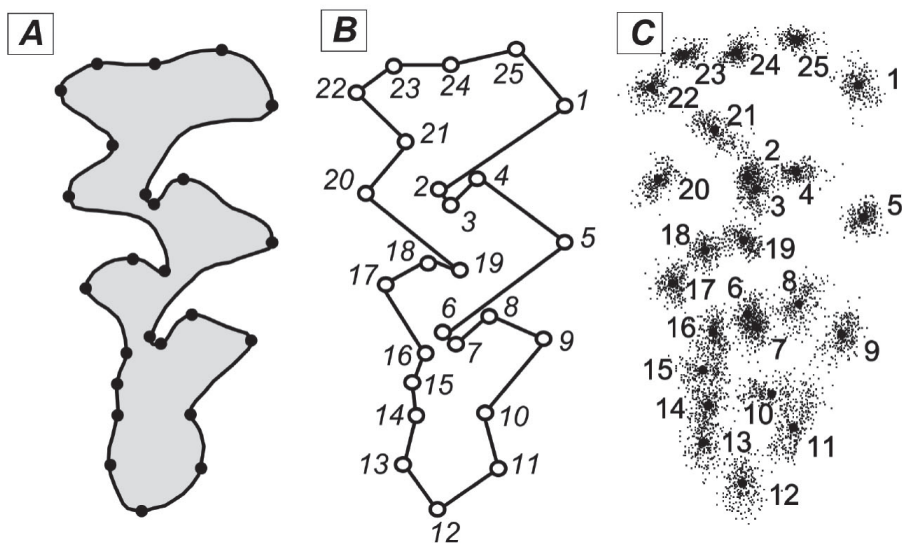


Fig. 2: Geometric landmarks (1-25) used in this study: contour of the third upper molar of *Alticola* species in ventral view (A); set of landmarks with wireframe graph (B); projection of landmark locations for all specimens, after General least-square (GLS) alignment (C).

Results

The studied species of the genus *Alticola* demonstrated extensive morphological disparity in the shape of the third molar occlusal surface. Consensus contour images of dental crown patterns for 8 samples of 7 *Alticola* species including two geographic forms of *A. semicanus* from Mongolia are shown in fig. 3. Visual estimate revealed the species of the subgenus *Aschizomys* to have more complex teeth with blunt outstanding angles (the lower row) than those of the subgenus *Alticola* (the upper row) with more sharp ones. *Alticola*'s teeth have a relatively short talon and negligible first buccal inner angle. Ranging of the samples according to the Molar Folding Index (MFI) values of the third upper molar (fig. 4) showed these peculiarities more evidently. Within the genus *Alticola* the highest MFI -value was obtained for *A. lemminus*, the lowest one – for *A. semicanus* samples. *A. olchonensis* showed up the most complex and folded teeth among all studied species of *Alticola* s. str. with intermediate MFI -value between subgenera *Alticola* and *Aschizomys*. Two populations of *A. semicanus* were rather similar with each other on the MFI -index.

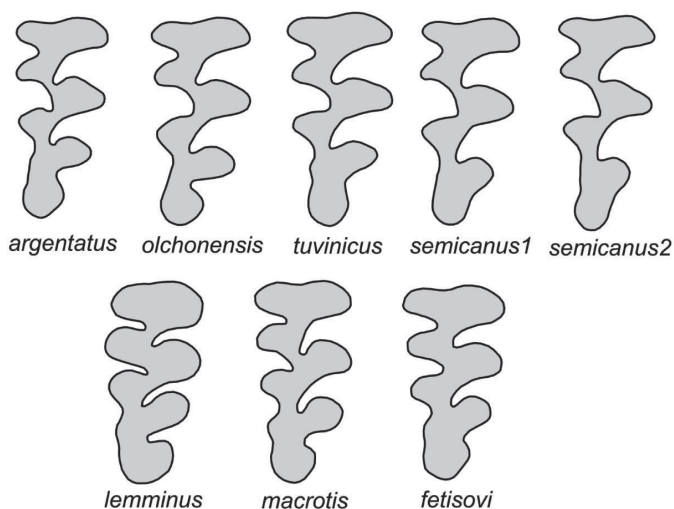


Fig. 3: Consensus contours of the third upper molars of the seven *Alticola* species including two geographic forms of *A. semicanus* (1-2) from Mongolia.

Centroid size (CS) indicated a measure of overall molar size differed significantly among the *Alticola* species (Levene's test of homogeneity of variances, based on means: $p = 0.195$; One-Way ANOVA $F_{3,126} = 30.1$; $p < 0.001$; fig. 5). Third upper molars in the subgenus *Alticola* samples were bigger than those in the subgenus *Aschizomys* with *A. semicanus* having the biggest and *A. fetisovi* – the smallest teeth among all studied species. CS in *A. argentatus* and *A. tuvinicus* were more similar to those in *Aschizomys*, but *A. olchonensis* in this respect looked like *A. semicanus*. There was no significant difference in CS between *A. lemminus* and *A. macrotis* and also between the two populations of *A. semicanus* ($p > 0.05$).

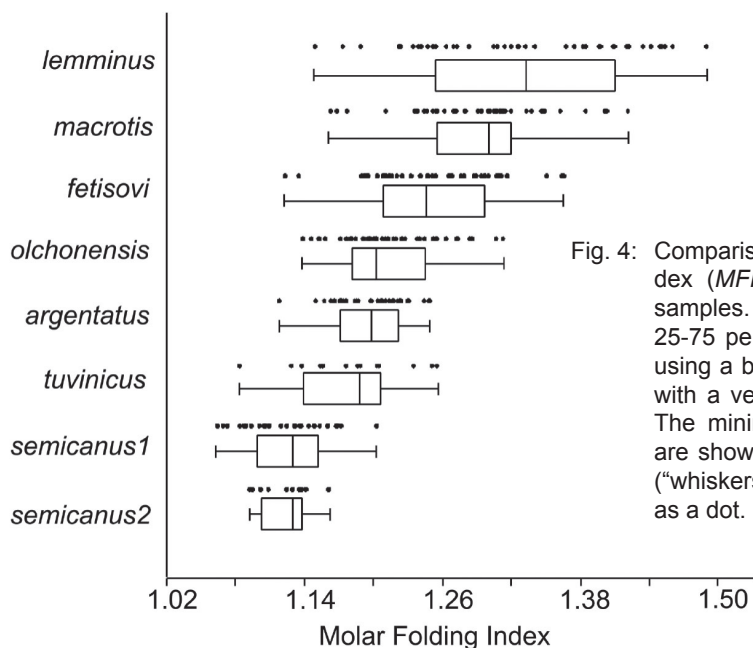


Fig. 4: Comparison of Molar Folding Index (MFI) values among *Alticola* samples. For each sample, the 25-75 percent quartiles are drawn using a box. The median is shown with a vertical line inside the box. The minimal and maximal values are shown with short vertical lines (“whiskers”). Each value is plotted as a dot.

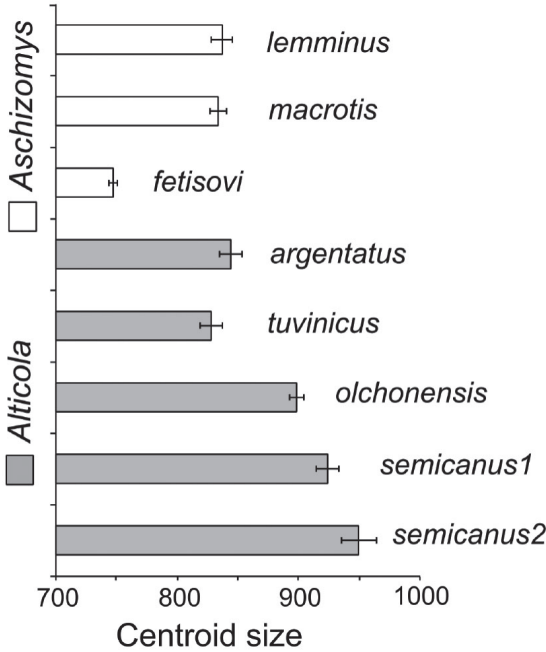


Fig. 5: Centroid size of the third upper molar (mean \pm SE) in the *Alticola* samples.

Canonical Variates Analysis was carried out using partial warps scores. Projections of specimens onto the first two canonical variate axes (75.26 % of cumulative variance in the original data set) are shown in fig 6. Along the first canonical variate (CVA1; 54.92 % of variance) the clearest distinction was revealed between species of subgenera *Aschizomys* and *Alticola*: *A. (Asch.) lemminus* on the one hand and *A. (A.) semicanus* on the other. *A. olchonensis* was clearly associated with the subgenus *Alticola* group. When analyzing the extremal configurations of molar shape along the axes we found lemming vole to have the most complex molars resembling those in the genus *Clethrionomys*, but the Mongolian silver vole - the simplest ones. Distinctions between *A. lemminus* and the rest *Aschizomys* (*A. macrotis* and *A. fetisovi*) were displayed along the second canonical variate (20.24 % of variance). In general the molars in lemming vole have the narrower anterior loop and more complex pos-terior one, named "the talon".

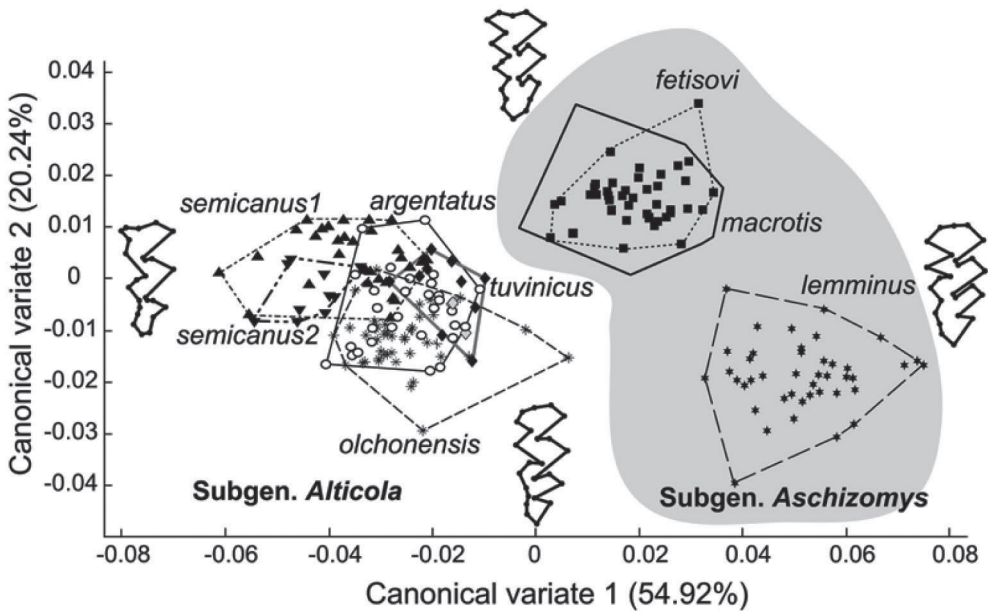


Fig. 6: Projection of specimens and convex hulls of the *Alticola* samples onto the first and second canonical variates (CVA 1, CVA 2). Shape changes associated with extremes of variation are shown as wireframe graphs.

Differentiation between subgenera *Alticola* and *Aschizomys* is distinctly demonstrated by signs of the mean scores of species samples along the first canonical variate (table 1) with all representatives of the subgenus *Alticola* having positive mean values, but on the contrary the subgenus *Aschizomys* having negative ones. The first five canonical variates explained about 96.98 % between-group variance, though between-group differences were significant along all canonical variates. Distinctness of *A. olchonensis* in comparing with two nearest species – *A. argentatus* and *A. tuvinicus* was revealed along the fifth CVA-axis (3.62 % of variance), and the latter two species differed along the sixth axis (2.8 % of variance). The shape differences between two geographic forms of *A. semicanus* from Mongolia appeared along the last seventh axis.

Table 1: Canonical Variates Analysis of partial warps describing the shape variation of the third upper molar in *Alticola* samples (in the upper part are the sample means). All differences between groups for all CVA's are significant (** – $p < 0.01$; *** – $p < 0.001$)

Species	Canonical variates						
	CVA1	CVA2	CVA3	CVA4	CVA5	CVA6	CVA7
1 - lemminus	6.013	3.068	0.594	-0.739	-0.068	-0.009	-0.061
2 - macrotis	1.816	-2.958	-2.045	-1.452	0.118	-0.306	0.048
3 - fetisovi	2.299	-2.513	1.372	1.931	0.228	0.382	0,112
4 - argentatus	-2.939	0.996	-1.248	0.142	-1.440	1.250	0.068
5 - tuvinicus	-2.022	0.442	0.290	1.599	-2.336	-2.157	0.136
6 - olchonensis	-2.998	1.907	-1.280	1.104	1.302	-0.257	-0.059
7 - semicanus1	-4.158	-0.664	2.203	-1.517	0.126	-0.043	-0.963
8 - semicanus2	-5.102	0.392	2.666	-2.295	0.566	-0.079	2.301
Eigenvalues	13.5543	4.9960	2.4489	1.9445	0.8941	0.5129	0.3301
Variance, %	54.92	20.24	9.92	7.88	3.62	2.08	1.34
Cumulative, %	54.92	75.16	85.08	92.96	96.58	98.66	100.00
Wilk's Lambda	0.0003	0.0043	0.0258	0.0891	0.2624	0.4969	0.7518
Chi-square	1868.8	1252.8	840.9	556.1	307.8	160.8	65.6
D.f.	322	270	220	172	126	82	40
p-level	***	***	***	***	***	***	**

The high correctness of group assignments of specimens for the absolute majority of species was found (table 2). The minimal percent of correct identification appeared for *A. argentatus* (71.88 %), the seven specimens of which were wrongly assigned as *A. olchonensis*. The shape of molars in *A. argentatus* is the most typical for the subgenus *Alticola*, so some single specimen were wrong assigned as belonging to *A. tuvinicus* and even to *A. semicanus*. Using the Jackknifed Groupings based on CVA-distances weakly decreases the percent of correct assignments in many species except from *A. argentatus*, *A. semicanus*, and *A. tuvinicus*. However in the latter form it may be explained by too small sample size as well as in the sample of *A. semicanus2*.

As a result of cluster analysis (UPGMA) of squared Procrustes distances dissimilarity matrix (fig. 7) two main clusters were revealed: the first included all species of the subgenus *Alticola*, and the second one – of the subgenus *Aschizomys*. The cluster *Alticola* branched into two subclusters. The first of them included two geographic forms of *A. semicanus* and the second consisted of *A. olchonensis* differentiated from the two others *A. argentatus* and *A. tuvinicus* more similar with each other. The subcluster of *Aschizomys* divides in two branches: *A. lemminus* versus *A. macrotis* and *A. fetisovi* joined together. The most similar were two samples of *A. semicanus*. Differentiation between them can be considered as a measure of intraspecific level of differences. Distinctness of *A. olchonensis* is yet more expressed than differences between separate species *A. tuvinicus* and *A. argentatus*.

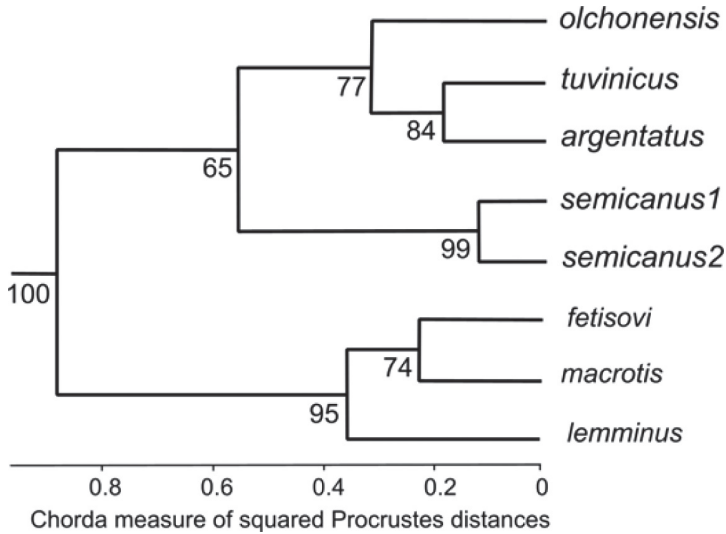


Fig. 7: Cluster tree (UPGMA) based on the matrix of squared Procrustes distances among the *Alticola* samples as derived from Canonical Variates Analysis of partial warps describing shape variations of the third upper molar (Coph. corr. R = 0.94; bootstrap values obtained from 100 replications).

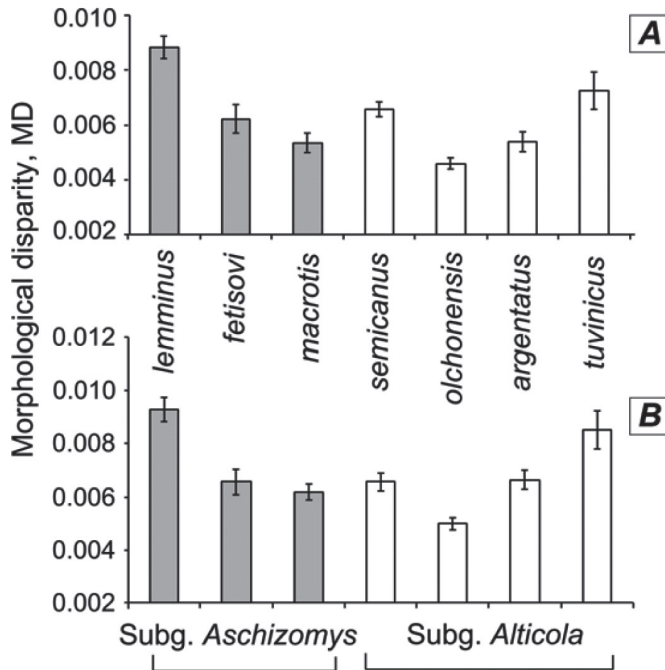


Fig. 8: Morphological Disparity ($MD \pm SE$) values among the seven *Alticola* species derived from Procrustes distances (A) and after standardization by means of multivariate regression of full set of shape variables on log-transformed centroid size to remove shape variation related in size (B).

Using FOOTE's formula (1993) we have valued morphological disparity (*MD*) of the third upper molars among the seven species of the genus *Alticola* (fig. 8 A). Two samples of *A. semicanus* from Mongolia were combined. In parallel we have estimated the standardized morphological disparity (*MDst*) in the same samples, for that shape variation connected with size (its allometric component) was removed by means of multivariate regression (fig. 8 B). Similar estimations of morphological disparity of the third upper molars among studied forms *Alticola* were received in both variants of calculation. The ratio of *MD*-values among groups in the two variants are similar. So, allometric dependencies in variability of the molar shape did not render the essential influence upon estimation of the morphological disparity of species compared. *A. lemminus* (the subgenus *Aschizomys*), as well as *A. tuvunicus* and *A. semicanus* (the subgenus *Alticola*) were found to have significantly greater shape disparity than other species. Morphological disparity of *A. olchonensis* sample was the smallest. This points out to its rather intermediate position between subgenera. The molars of *A. olchonensis* species combine some features of *Aschizomys* (complex talon) with *Alticola*'s traits (the short talon and negligible first buccal inner angle).

Table 2: Groups' assignment based on Mahalanobis distances derived from the Canonical Variate Analysis (CVA) of *Alticola* samples (1-8) and the results of Jack-knife test (rows are actual groups and columns are predicted groups)

Species	1	2	3	4	5	6	7	8	N	Percent correct
1 - <i>macrotis</i>	42	0	0	0	0	0	0	0	42	100.00
2 - <i>argentatus</i>	0	23	0	0	7	1	0	1	32	71.88
3 - <i>lemminus</i>	0	0	42	0	0	0	0	0	42	100.00
4 - <i>fetisovi</i>	1	0	0	43	0	0	0	0	44	97.73
5 - <i>olchonensis</i>	0	0	0	0	44	0	0	0	44	100.00
6 - <i>semicanus1</i>	0	0	0	0	0	29	1	0	30	96.67
7 - <i>semicanus2</i>	0	0	0	0	0	0	10	0	10	100.00
8 - <i>tuvunicus</i>	0	0	0	0	0	0	0	14	14	100.00
total	43	23	42	43	51	30	25	15	258	95.74

Jackknifed groupings from CVA-distance based										
Species	1	2	3	4	5	6	7	8	N	Percent correct
1 - <i>macrotis</i>	40	1	0	1	0	0	0	0	42	95.24
2 - <i>argentatus</i>	0	18	0	0	10	0	2	2	32	56.25
3 - <i>lemminus</i>	1	0	41	0	0	0	0	0	42	97.62
4 - <i>fetisovi</i>	2	0	0	41	1	0	0	0	44	93.18
5 - <i>olchonensis</i>	0	5	0	0	39	0	0	0	44	88.64
6 - <i>semicanus1</i>	0	2	0	0	1	22	4	1	30	73.33
7 - <i>semicanus2</i>	0	1	0	0	1	3	5	0	10	50.00
8 - <i>tuvunicus</i>	0	2	0	0	1	1	0	10	14	64.29
total	43	29	42	42	52	36	13	13	258	83.72

In the whole the subgenus *Aschizomys* showed disparity value ($MD1 = 0.00335$) more than the subgenus *Alticola* ($MD2 = 0.00246$). This difference was statistically significant ($p = 0.013$: in 1000 permutation trials there were 13 negative $MD1-MD2$ values). Special including of *A. olchonensis* into *Aschizomys* subclade following to PAVLINOV' point of view (2003, 2006), caused a significant increase of disparity value in this subclade ($MD = 0.00424$; $p = 0.017$) in comparison with the original one. Therefore the position of *A. olchonensis* within the subgenus *Alticola* seems to be more correct than within the *Aschizomys*.

Discussion

Morphological disparity among the seven *Alticola* species as derived from the third molar crown shape corresponds to their traditional assignment to two subgenera: *Alticola* and *Aschizomys* (MUSSEY & CARLETON 2005; PAVLINOV 2006). Among *Alticola* s. str. species, *A. semicanus* was found to be the most distinct, that is again in agreement with results obtained from other data sets: cytogenetic (HIELSCHER et al. 1992), biochemical (HILLE & STUBBE 1996), and molecular (LEBEDEV et al. 2007). *A. olchonensis* in accordance with its molar crown shape should not be included into the subgenus *Aschizomys* as it is considered recently (MUSSEY & CARLETON 2005; PAVLINOV 2006). In spite of relatively complex shape of this molar, partly resembling that in *Aschizomys*, its specific geometric configuration is much more similar to typical *Alticola*. However our findings do not coincide with molecular results of maximal affinity of Olchon vole to *A. tuvinicus* (BODROV & ABRAMSON, 2011). According to our results *A. olchonensis* should be considered as a distinct species rather than the taxon of subspecies rank only. Our findings argue in favor of species independence of *A. fetisovi*. Distinctness of *A. lemminus* may be treated for possible restoring its subgenus rank following the original describing.

Two studied Mongolian populations of *A. semicanus alleni* had some peculiarities in their molar crown shape. Perhaps this is manifestation of geographic variation in teeth morphology between northern (Hentij Aimak) and eastern (Suhbaatar Aimak) Mongolia. Specimens from the Suhbaatar population differ by more elongated talon than the voles from Hentij. Earlier OGNEV (1950) already informed about body size geographic variation in *A. semicanus* from Tuva and Mongolia. In order to solve the problems of intraspecific structure, and understand ecological factors influencing on geographic variation and morphologic disparity in Mongolian silver voles it is necessary to study new additional materials from various localities of Mongolia.

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