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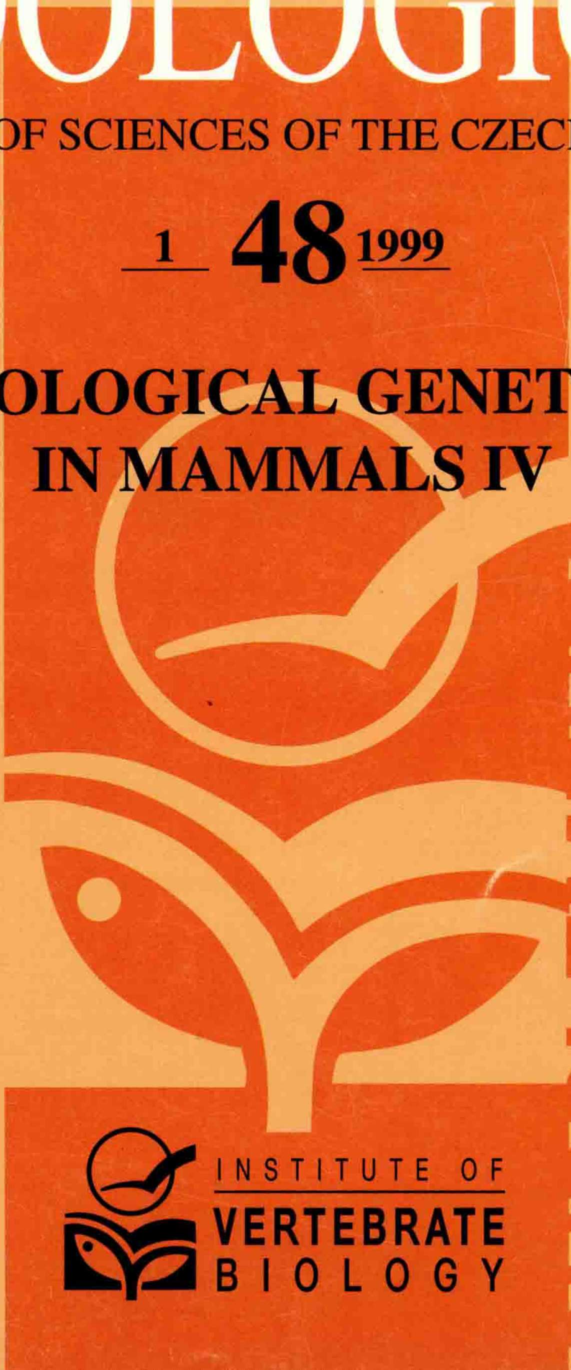

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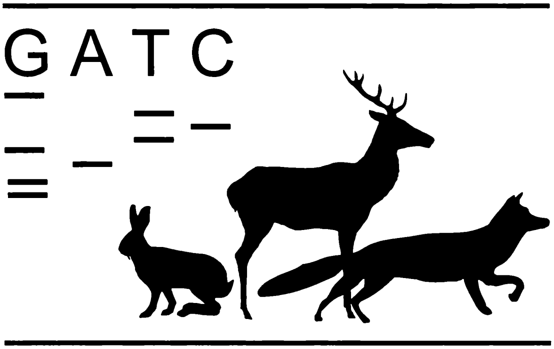

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Epigenetic divergence of Asian high-mountain voles of the subgenus *Aschizomys* from southern and north-eastern Siberia

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Abstract. To reveal the pattern of epigenetic divergence among the Asian high-mountain voles of the genus *Alticola* (subgenus *Aschizomys*), 944 skulls from 11 localities in southern and north-eastern Siberia, and from four laboratory colonies (*Alticola macrotis vinogradovi* from the Altai Mts., *A. m. macrotis* from Lake Baikal, *A. lemminus* from the Kolyma plateau and the Chukotka peninsula) were examined. The frequencies of 21 non-metric traits, and the mean measures of divergence (MMD) between populations were estimated. The cluster analyses based on the MMD matrix showed that these populations are vicariant forms at different stages of divergence. This pattern seems to be related to an incomplete process of geographic speciation.

Key words: non-metrical traits, vicariant populations, evolutionary relationships

Introduction

The taxonomy of the Asian high-mountain voles of the genus *Alticola* Blanford, 1881 is not yet fully understood. In particular, this concerns the subgenus *Aschizomys* Miller, 1898 that is distributed in remote mountain areas of Siberia. Originally, three separate species were recognized (*A. macrotis* Radde, 1862 from the Sayany Mts. and the Transbaikal region, *A. vinogradovi* Rasorenova, 1933 from the Altai Mts., and *A. lemminus* Miller, 1898 from north-eastern Siberia). All the known forms of this taxonomic group were later included into a single polytypic species, *A. macrotis* by various authors (Gromov & Polyakov 1977, Gromov & Baranova 1981, Gromov & Erbaeva 1995), however, some taxonomists accepted *A. lemminus* as an independent species (Pavlinov & Rossolimo 1987, Musser & Carletton 1993, Pavlinov et al. 1995). Recently, a new species, *A. fetisovi*, was described from the North Khantey Mts. in Mongolia (Galkina & Epifantseva 1988). Validity of this species has not yet been accepted generally. A number of studies appeared dealing with various skeletal, chromosomal, and molecular characters in populations of *Aschizomys*, and a remarkable extent of variation was revealed (Bykova et al. 1978, Bolshakov et al. 1980, Vasilyeva & Vasilyev 1984, Bolshakov et al. 1985, Rybnikov et al. 1986). This extensive variation pattern apparently represents the main reason for difficulties in understanding the taxonomic structure of *Aschizomys*. According to Bolshakov et al. (1985), this group of typical mountain mammals experience an active evolutionary process. *A. macrotis* from the vicinity of Lake Baikal in southern Siberia, and *A. vinogradovi* from the Altai Mts. were successfully interbred in captivity, and several generations of fertile hybrids were obtained (Bolshakov et al. 1982). The authors, therefore, suggested the conspecific character of both the forms. However, hybridisation experiments failed in *A. macrotis* and *A. lemminus* . In this study, an analysis of non-metric skull traits (Berry 1963, 1964, 1986, Sjøvold 1973, 1977, Sikorski 1982, Vasiľev 1984) is applied and used to estimate the extent of divergence between various populations of *Aschizomys* in southern and north-eastern Siberia.

Material and Methods

Skulls from zoological collections of the Institute of Plant and Animal Ecology, Ural Division of RAS (IPAE) and some other institutions were examined. The location of collecting sites of the samples from 11 free-living populations is shown in Fig.1, sample sizes and the collecting periods are given in Tables 1 and 2. The samples no. 1-5 were assigned to *A. macrotis*, no. 6-11 to *A. lemminus*. Individuals from four laboratory colonies were also examined. The colonies originated from the same localities as certain samples of free-living populations, i.e. from the Terektinski Ridge in the Altai Mts. (1+), , the Khamar-Daban Ridge in the Baikal State Reserve (5+), the Kolyma river plateau (9+), and the Chaun Inlet, Chukotka peninsula (10+).

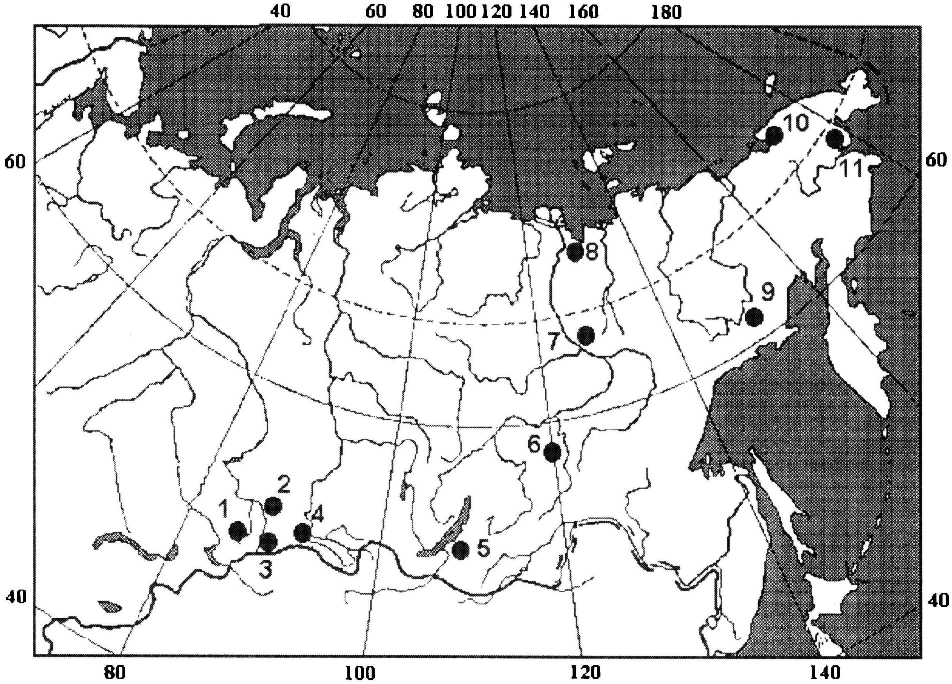

Fig. 1. Geographical location of the studied populations of *Alticola macrotis* and *Alticola lemminus* in southern and north-eastern Siberia: 1. Altai Mts., Terektinski Ridge; 2. Altai Mts., Lake Teletskoe; 3. Altai Mts., Chikhachev Ridge; 4. Tuva, Tsagan-Shybetu Ridge; 5. Baikal State reserve, Khamar-Daban Ridge; 6. southern Yakutia, Olekma River; 7. central Yakutia, Verkhoyanski Ridge; 8. northern Yakutia, Laptev Sea Coast; 9. Kolyma plateu, Kulu River; 10. Chukotka Peninsula, Chaun Inlet; 11. Chukotka Peninsula, Gulf of Anadyr.

A total of 944 skulls was used for the non-metric analysis, and following 21 traits were scored (see Fig. 2): 1 - preorbital foramen doubled; 2 - *foramen frontale anterior* present; 3 – *foramen frontale* present; 4 – *foramen ethmoidale* doubled; 5 – *foramen temporale* absent; 6 – *fenestra flocculi* present; 7 – *foramen occipitale* single; 8 – internal condylar foramen present; 9 – internal *foramen hypoglossi* single; 10 – *foramen premaxillare anterior* present; 11 – *foramen*

Table 1. Percentage frequencies of the non-metric skull traits in the samples of *Alticola macrotis* from southern Siberia. The sample numbers are the same as in Fig. 1.

trait	sample number						
	1	1+	2	3	4	5	5+
1	12.1	4.5	0	5.2	1.8	6.8	0.8
2	23.5	4.7	40.6	18.9	27.3	34.9	19.5
3	29.4	41.4	24.2	36.8	26.8	34.9	45.8
4	5.9	9.0	12.9	13.5	5.6	4.7	1.9
5	11.8	8.4	0	0	14.8	0	2.3
6	0	0	6.7	18.2	10.2	0	0
7	15.2	12.3	15.1	25.8	12.0	9.5	20.6
8	61.8	39.5	12.5	21.9	37.3	14.3	29.6
9	48.5	50.0	25.0	37.5	22.0	2.3	3.2
10	17.7	22.4	5.9	31.6	40.7	4.5	13.5
11	38.2	38.9	44.1	31.6	55.6	6.8	5.8
12	3.7	14.3	11.5	21.2	21.4	5.4	24.4
13	0	3.7	18.2	23.5	28.0	0	0.8
14	0	0.7	0	0	4.0	0	0
15	0	0	0	2.8	16.4	0	0
16	30.8	28.0	0	0	0	4.7	2.9
17	0	0	0	0	0	0	0
18	0	0.7	41.2	21.6	16.7	83.7	91.2
19	0	4.2	0	0	0	0	10.4
20	19.3	26.7	12.1	15.8	33.9	27.3	22.7
21	9.7	1.8	0	2.6	0	2.3	1.5
Sample size	17	139	17	21	28	22	131
Years of capture	74-75	74-77	66-68	72-74	79	75	75-77

premaxillare posterior present; 12 – posterior margin of palate unclosed; 13 – *foramen sphenoidale medium* present; 14 – *fenestra sphenoidale medium* present; 15 – accessory transversal lamina of *foramen ovale*; 16 – joining of *foramen ovale* and *foramen lacerum medium*; 17 – joining of *foramen ovale* and *foramen lacerum laterale*; 18 – accessory bone lamina joining the infraorbital alveolar bump with alisphenoid; 19 – mental foramen doubled; 20 – supra-dentary foramen present; 21 – internal supra-dentary foramen present.

Bilateral traits were scored on the both sides of the skull, as present or absent, and the frequencies were calculated for each trait on the basis of the total number of studied skull sides (Sjøvold 1973, 1977). The correlation between the occurrence of individual traits was determined, as well as the dependence of the occurrence on sex and age, with the use of the Spearman's coefficient (R_{sp}). Multiple comparisons between all the samples for particular traits were carried out by G-tests (Sokal & Rohlf 1981).

The mean measure of divergence (MMD) between the pairs of samples and the associated mean standard deviations (MSD) were calculated using the formula of C. A. B. Smith (Sjøvold 1977). The differences were considered statistically significant at $p = 0.05$ if the MMD was twice as high as the MSD. In each sample the measure of uniqueness (MU) was calculated as the sum of MMD's from all other samples (Berry 1964).

The cluster analysis was carried out by UPGMA on the basis of the MMD distance matrix (Sneath & Sokal 1973). The relationships between populations resulting from the MMD's matrix were summarized by multidimensional nonmetric scaling, with the use of the Kruskal's minimal „stress“ method (Kruskal 1964).

Table 2. Percentage frequencies of the non-metric skull traits in the samples of *Alticola lemminus* from north-eastern Siberia. The sample numbers are the same as in Fig. 1.

trait	sample number							
	6	7	8	9	9+	10	10+	11
1	19.0	14.5	5.4	12.3	0	3.7	8.0	11.1
2	38.5	16.1	8.7	13.3	10.0	31.5	18.8	42.9
3	60.3	40.7	45.3	43.4	40.0	40.5	39.1	50.0
4	3.3	1.7	1.6	6.1	15.0	14.9	3.2	7.1
5	9.3	11.1	6.0	1.0	0	3.4	0	0
6	20.8	67.6	49.6	39.2	35.0	88.0	82.0	92.0
7	10.2	20.6	22.7	13.9	25.0	47.9	25.4	30.8
8	18.6	14.7	7.7	59.7	70.0	36.7	15.6	57.7
9	11.9	23.5	27.9	16.4	5.0	5.8	3.1	11.5
10	20.3	63.3	72.5	5.7	5.0	7.8	3.2	0
11	22.6	29.3	13.6	2.8	5.0	2.9	0	3.6
12	38.6	23.6	16.6	51.9	55.0	11.4	2.2	10.7
13	6.1	0	8.5	0	0	17.3	0	21.4
14	0	4.8	8.6	0	0	0	0	14.3
15	6.3	66.0	84.1	11.3	45.0	6.1	4.7	3.6
16	51.7	51.0	87.3	34.6	25.0	76.8	64.2	100
17	0	0	0	0	0	0	0	21.4
18	0	0	0	0	0	0	0	0
19	4.4	0	2.6	1.0	5.0	0	0	0
20	41.3	45.5	64.3	1.0	0	6.1	1.6	14.8
21	15.7	45.5	55.0	28.2	75.0	74.8	54.7	14.8
Sample size	127	33	211	53	10	74	32	14
Years of capture	61-78	87-89	63-82	82-83	82	78-80	74-80	75-7

Results and Discussion

The intertrait correlations were calculated first in the large captive samples of *A. m. macrotis* and *A. m. vinogradovi*. In *A. m. macrotis* only the 8 out of 441 Spearman rank correlation coefficients between traits were significant; in *A. m. vinogradovi* the 10 out of 441, respectively. So, the number of the significant Spearman rank correlation coefficients ($R_{sp} = 0.127 - 0.237$) did not exceed the random level of 5% (1.80 % and 2.27 %, respectively).

No significant correlation with sex and age was found in *A. m. macrotis*. In *A. m. vinogradovi* only one trait (no. 10) correlated with sex ($R_{sp} = - 0.141$; $p < 0.05$), and the traits no. 1 and 4 correlated with age ($R_{sp} = 0.126$; $p < 0.01$, and $R_{sp} = -0.234$; $p < 0.01$, respectively). The proportion of the significant R_{sp} coefficients in respect of sex (2.38 %) and age (4.76 %) did not exceed the random level of 5 %. Therefore, all the traits were included in further analyses. To support this conclusion, many MMD distances were calculated between males and females, and between juvenile and adult animals. All the MMD distances found were negligible and nonsignificant. The low level of these differences allowed to pool the individuals of different sex and age in a single geographic sample.

The frequencies of the 21 non-metric traits in the samples studied are given in Tables 1 and 2. Sharp differences were occasionally found in the frequencies of individual traits. For example, the samples from captive populations originated from the Altai and Transbaikal area strongly differed in the frequency of the trait no. 9. The variant no.18 was almost absent in the Altai sample, whereas it occurred in more than 90 % of individuals of the Transbaikal sample. In the samples belonging to *A. lemminus,* this trait was not found at all.

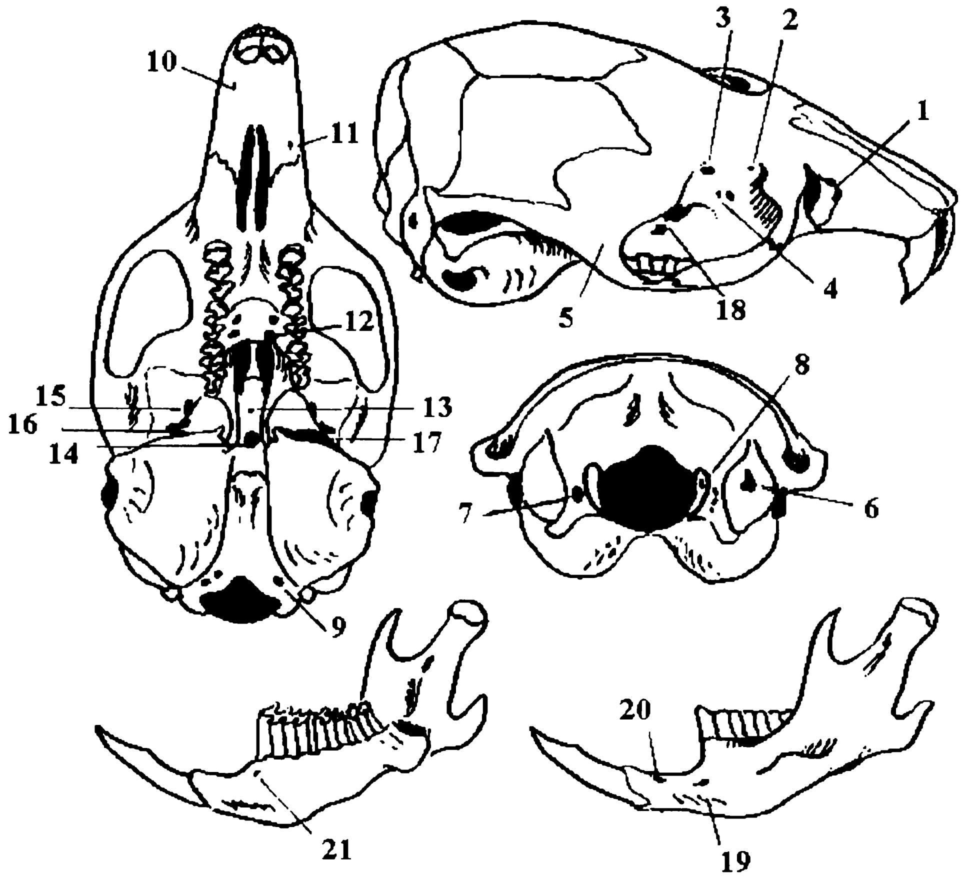

Fig. 2. Non-metric traits studied in skulls. 1-21 - trait numbers. See text for details.

The MMD distances between the studied samples are given in Table 3. The comparison of the MMD's between the samples from captive colonies and free-living populations originated in the same area permitted to evaluate environmental effects on the non-metric traits. Each of the four captive samples was most similar to the respective native population. Laboratory keeping apparently did not strongly affect the frequencies of non-metric traits.

Among the samples from free-living populations, the most similar were those from Altai and Tuva (nos. 2, 3, and 4 in Table 4), what corresponds to the smallest geographic distance between them. Despite the relatively small geographic distance between the Tuva sample and that from the Terektinski Ridge, the former was shown to be intermediate between *A. m. vinogradovi* and *A. m. macrotis*.

Prevailingly, the geographic distance seemed to be positively correlated with the MMD distance in comparisons between the samples from southern and north-eastern Siberia. However, the largest MMD distance and the highest value of MU were found between the samples no. 5 and 8, in spite of their geographic distance being smaller than between the samples no. 1 and 10. On the other hand, the Kolyma sample (no. 9) showed features which can be considered intermediate between the samples from southern and northern Siberia, respectively. The correlation between the geographic and MMD distances could be evaluated

Table 3. The MMD distances between captive and free-living populations. The MSD is given in italics. The distances between captive and free-living populations from the same area are in bold. The sample numbers are the same as in Fig 1.

free-living populations	captive populations			
	1+	5+	9+	10+
1	**0.018**^{NS}	0.456	0.398	0.473
	0.012	*0.012*	*0.028*	*0.016*
2	0.215	0.194	0.546	0.597
	0.012	*0.012*	*0.028*	*0.017*
3	0.140	0.264	0.407	0.509
	0.011	*0.011*	*0.027*	*0.016*
4	0.182	0.354	0.499	0.715
	0.008	*0.008*	*0.024*	*0.012*
5	0.405	**0.036**	0.659	0.644
	0.009	*0.009*	*0.026*	*0.014*
6	0.189	0.491	0.311	0.315
	0.006	*0.006*	*0.021*	*0.010*
7	0.489	0.882	0.325	0.363
	0.008	*0.009*	*0.025*	*0.013*
8	0.678	1.139	0.511	0.538
	0.002	*0.002*	*0.018*	*0.007*
9	0.303	0.550	**0.047**	0.191
	0.005	*0.005*	*0.021*	*0.010*
10	0.679	0.959	0.226	**0.063**
	0.004	*0.004*	*0.021*	*0.009*
11	0.699	1.039	0.473	0.209
	0.014	*0.014*	*0.030*	*0.018*

Table 4. The MMD distances between the samples from 11 free-living populations. The values of the MSD varied from 0,005 to 0,024. The sample numbers are the same as in Fig 1.

sample	2	3	4	5	6	7
1	0.205	0.154	0.176	0.377	0.167	0.428
2		0.012^{NS}	0.085	0.105	0.311	0.643
3			0.034	0.225	0.220	0.419
4				0.316	0.250	0.404
5					0.414	0.795
6						0.213

population	8	9	10	11	MU
1	0.652	0.238	0.542	0.563	2.853
2	0.939	0.413	0.705	0.772	3.269
3	0.688	0.283	0.565	0.669	3.502
4	0.667	0.416	0.743	0.810	3.567
5	1.054	0.521	0.849	0.897	3.901
6	0.378	0.177	0.353	0.370	4.184
7	0.064	0.343	0.363	0.512	4.190
8		0.581	0.500	0.628	5.032
9			0.251	0.344	5.553
10				0.161	5.726
11					6.151

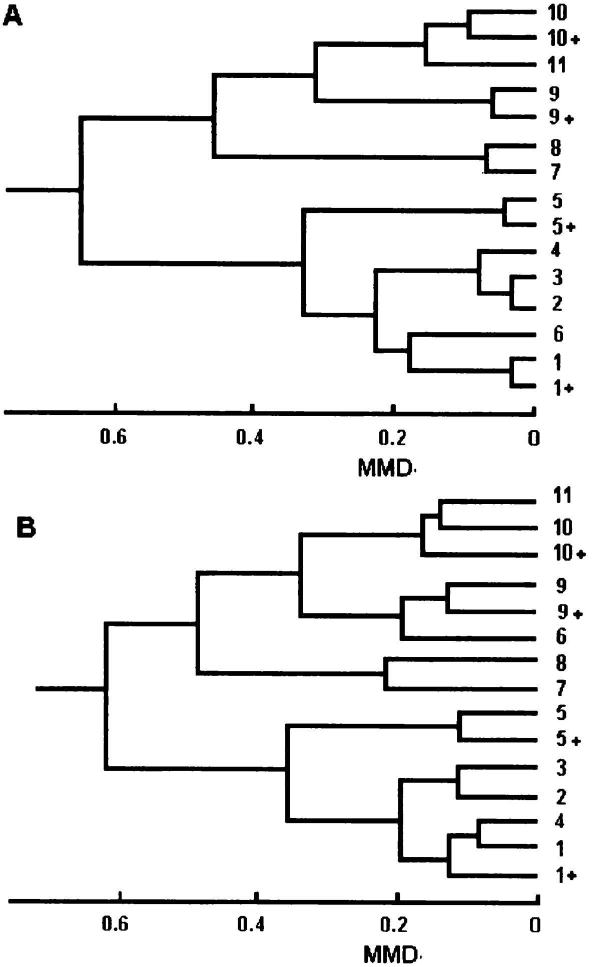

Fig. 3. Cluster analysis (UPGMA) of the MMD distances between the samples studied. A – based on the initial MMD distance matrix; B – after multidimensional nonmetric scaling of the MMD distance matrix. The sample numbers are the same as in Fig. 1.

only in respect of carefully predicted migration and dispersal routes within a continuous range (Vasiľev 1984). According to the zoogeographic data by Kischinski (1972), the Kolyma plateau could actually be a crossing area during the colonization of the *Aschizomys* ancestors in the mountain tundra of north-eastern Siberia in the upper Pleistocene. Our data support the idea of the origin of the subgenus *Aschizomys* in southern Siberia. The least unique populations were found in the Altai Mts., Tuva and southern Yakutia. These areas may be quite close to the hypothetical center of the origin and dispersal of the modern subgenus *Aschizomys*.

Our findings showed that the samples from Chukotka were more similar to those from the Altai Mts. than to those from the Transbaikal region, what is in accordance with their current distribution pattern. Rasorenova (1933), in her description of *A. vinogradovi,* noted its considerable similarity in teeth structure to the typical *A. lemminus* from Chukotka, and

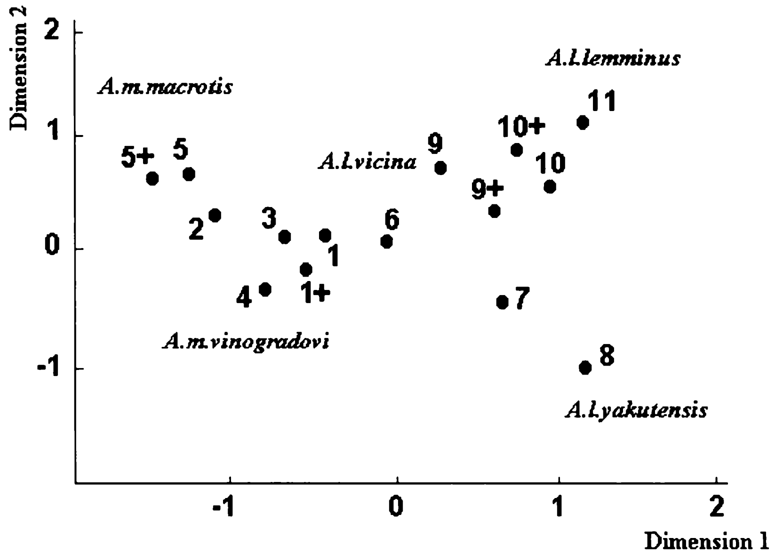

Fig. 4. Allocation of samples on a plot after multidimensional nonmetric scaling of the MMD matrix by of the Kruskal's minimal stress method. The sample numbers are the same as in Fig. 1.

included therefore both taxa in the same subgenus *Aschizomys*. The two forms appeared similar also in respect of certain molecular markers (Rybnikov et al. 1986). Obviously, all these data indicate a relatively recent divergence of these forms and support the view that the *Aschizomys* ancestors colonized the marginal areas of north-eastern Siberia as late as in the Holocene, after the Beringian land bridge disappeared. This may also explain the absence of *Aschizomys* in the American continent (Kischinski 1972). On the other hand, relatively high uniqueness of the samples from northern Yakutia and the Transbaikal region indicates their long-term isolation or, possibly, an earlier origin during the previous phases of colonization. This is in accordance with view that the extent of the MMD distances is dependent on the time of isolation (Grewal 1962) rather than on the geographic distance (Vasil'ev 1984).

Two major lineages were revealed in our analyses, corresponding largely to the traditional taxonomic treatment, i.e., the southern Siberian cluster, and the north-eastern cluster (Fig. 3A). The only exception was the sample from southern Yakutia which appeared in the former cluster. The results of multidimensional non-metric scaling of the MMD distance matrix are shown in Fig. 4. The stress level for the scaling was 6.9 % that indicates a good agreement between the original and scaled matrices according to Kruskal's ranking (Kruskal 1964). The sample no. 6 from southern Yakutia occupied then an intermediate position between the samples from southern and north-eastern Siberia, respectively, as expected from its intermediate geographic position. After repeated clustering of the non-metrically scaled MMD-matrix, the sample from southern Yakutia appeared close to the Kolyma sample (Fig. 3B). Obviously, these facts stress the objective absence of the morphological hiatus between the major clusters. It seems probable that the samples studied represent a group of vicariant populations at different stages of the divergence process.

Furthermore, there was a distinct divergence pattern within the two major clusters. The divergence between the samples ascribed to *A. lemminus* seemed to be approximately the same as between those of *A. m. vinogradovi* and *Alticola m. macrotis*. *A. lemminus* probably includes a complex of distinct forms. The populations from northern Yakutia should be considered as a separate subspecies, distinct from the nominate *A. l. lemminus* from Chukotka, and from *Alticola l. vicina* (Portenko et al. 1963) from southern Yakutia. The sample from Kolyma plateau was rather similar to those from southern Yakutia. However, it is difficult to include the Kolyma population into *A. l. vicina* because of the relatively unstable position of that subspecies in the cluster analysis. The samples from southern Yakutia thus appeared intermediate between *A. macrotis* and *A. lemminus*. The real number of the subspecies and their distribution are not yet clear, as well as the status of *A. fetisovi*. Thus, the results of this study as well as the available cytogenetic (Bolshakov et al. 1985) and molecular data (Rybnikov et al. 1986) suggest that the taxa and populations under consideration are currently subjected to the process of speciation *in statu nascendi*.

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