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Evolutionary-Ecological Processes in *Ondatra zibethicus* L. Populations during Acclimatization to Northern Conditions

A. G. Vasil'ev, V. N. Bol'shakov, Yu. M. Malafeev, and E. A. Valyaeva

Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences, ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia

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Abstract—On the basis of the multivariate analysis of the cranial characteristics of the common muskrat *Ondatra zibethicus* L., it was shown that, at the first early stages of acclimatization between northern and southern groupings of animals originating from one unique, genetically homogeneous group of animals from Canada, there arose steady morphological differences at a population level whose rate has remained almost the same over a half-century period of isolation. This evolutionary-ecological phenomenon emerged over a very short period of time and was accompanied by a transformation of the cranial shape and size and the pattern of nonmetrical threshold characters that govern the frequency of manifestation of certain genes. The effect of "rapid response" for steady morphological structures is unexpected since the more labile morphophysiological characteristics studied at the initial stage of acclimatization by Smirnov and Shvarts (1959) have not changed.

From the standpoint of evolutionary ecology, the study of acclimatization is of utmost interest when an introduced species is transferred to biotopic conditions that are ecologically similar to those under which it dwelt initially (Schvarts, 1959). In this case, although this process cannot be considered to be reacclimatization, it is its analogue in practice. A good example of species acclimatization to analogous biotopic conditions may be the formation over nearly the whole Palearctic of the population structure of the common muskrat (*Ondatra zibethicus* L.) introduced from Canada. Note that different forms of this muskat were introduced into different regions of the country. In particular, in some southern regions in the west of the country and in some other regions, a dark-colored form was distributed, while in most other regions, a brown form was dominant. At present, despite a general decrease in population numbers and its transition to the so-called third or populational phase of acclimatization (Chesnokov, 1976), the cross-breeding of different muskat forms has been taking place for a long time. This process may significantly affect the fur quality and produce an adverse effect on other biological properties of the acclimatized races. It is difficult today to forecast the ecological, morphological, and phenogenetic consequences of a possible mass cross-breeding; therefore, it is now necessary to develop methods and start carrying out phenetic monitoring of muskrats, both of the form originating from a strictly defined race and of mixed (hybrid) populations.

In connection with this, it is important to note an interesting attempt of Finnish researchers (Pankakoski and Nurmi, 1986) to analyze phenotypic diversity of muskrats in Finland using two approaches: a multivariate morphometric method and a nonmetric method (phenetic in the narrow sense). This case is of interest because the "Finnish" muskrat was introduced to Finland from Germany, *Czechoslovakia*, and North America in the 1920s and 1930s. According to Pankakoski and Nurmi, the combined origin of the Finnish muskrat causes certain difficulties in tracing the changes occurring in time and in assessing the differentiation of modern populations since these phenomena may largely depend on genetically specific ancestral features.

A different situation is observed in the north of the Tyumen oblast, where, at present, almost the entire muskrat population is originated from the animals of one Canadian population. The first group of animals from Canada was released in the central part of the region in the basin of the Dem'yanka River (tributary of the Ob') in 1929. From this point on, the muskrat was artificially and naturally dispersed over the lakes of the Kurgan oblast and later, in 1936, throughout the northern part of the Tyumen oblast. A special study of southern (Kurgan) and northern (Tyumen) muskrat populations was performed in the 1950s by Smirnov and Schvarts (1959). The authors demonstrated that, according to a complex of morphophysiological characters, southern and northern muskrat populations had not assumed any population-specific features by that time. It should be stressed, however, that the most conservative characters of the phenotype, i.e., craniometric characters, were not studied. In connection with this, the purpose of this work was to perform a cranial comparison of northern and southern muskrats based on the museum materials described by Smirnov and Schvarts (1959) in the 1950s with the most modern samples using methods of multivariate morphometry and phenetics that allow an indirect genetic interpretation of morphological differences (Berry, 1964; Festing, 1973; Hartman, 1980; Yablokov,
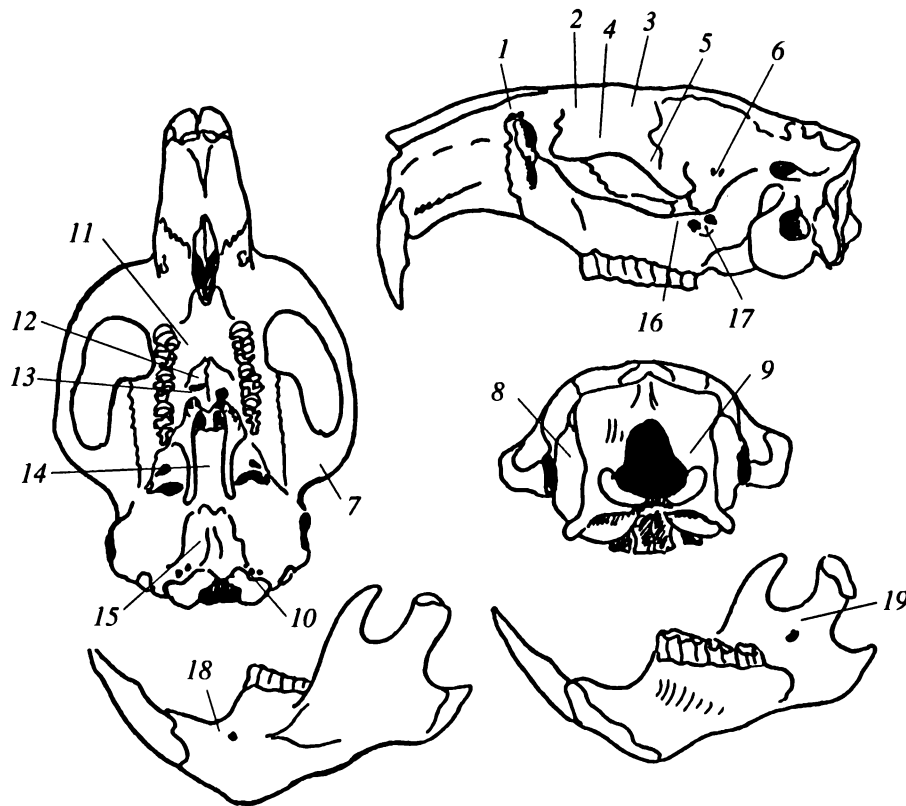
Fig. 1. Location of phenes of nonmetric traits of the muskrat skull. Phenes and their Latin codification: 1. FPodu, doubled preorbital foramen; 2. FFran, presence of the foramen frontale; 3. FFr, manifestation of the great frontal foramen; 4. Etdu, doubled ethmoidal foramen; 5. Pnlo, presence of the anterior pterygoid foramen; 6. FTmdu, doubled scaly (temporal) foramen; 7. MeTm, foramen of a temporal duct beneath the zygomatic process base; 8. FeMs, "central" foramen of the petrous temporal bone; 9. FOcsi, large foramen in the condyloid fossa; 10. FHgtr, triple subglossal foramen; 11. FMxVI, great "anterior palatine" foramen; 12. OPlbi, cleft of palatine plate; 13. MgPl1, posterior palatine margin closed; 14. FBsme, median foramen of the principal sphenoid bone; 15. FBome, great "inferior occipital" foramen in the area of the clivus; 16. FRacan, accompanying canal of the foramen ovale; 17. FOvacan, foramen at "the median plate" of the foramen ovale; 18. FMtdu, doubled mental foramen; 19. FMbdu, doubled mandibular foramen.

1980; Atchley et al., 1981; Vasil'ev et al., 1986). This study enables us to assess the magnitude and the relative rate of possible morphometric and nonmetric (phenetic) changes that have occurred in the Tyumen North since the 1950s. It was of special interest to compare our results of acclimatization of genetically homogeneous muskrats with the data obtained by Finnish authors on heterogeneous hybrid populations.

MATERIALS AND METHODS

For this research, we used series of skulls collected by V.S. Smirnov and S.S. Schvarts in 1955 in the Lebyazh'e muskrat farm in the vicinity of the district center of Lebyazh'e and from the lakes of the Zverinogolovskii raion of the Kurgan oblast (259 ind.), as well as in the Polar region in the vicinity of the Shuryshkary, Priural'e, and Yamal raions of the Yamal-Nenets National District (114 ind.). In addition, collection materials collected in 1965 in the vicinity of Lake Sukhmen' in the Kurgan oblast (161 ind.) and preserved in the Zoological Museum of the Institute of Plant and Animal Ecology (Ural Division, Russian

Academy of Sciences) were used. The most modern series of muskrat skulls was collected by Yu.M. Malafeev in southern Yamal (the Khadyta-Yakha River) from 1987 to 1989 (330 ind.), the trapping being regularly carried out in adjoining settlements spaced no more than 16–20 km apart. The total number of muskrat skulls studied was 864. The comparison included only those materials that were collected in the autumn months and at the beginning of winter. The relative age of the muskrats was assessed according to the degree of tooth root development and molar crowns' grinding (Tsygankov, 1955). To correct the identification of age groups, we used the method of age determination according to osteal laminated structures (Klevezal' and Kleinenberg, 1967). The most numerous fully grown group, aged from eight to ten months, that was sufficiently homogeneous in cranial shape and size (Pankakoski and Nurmi, 1986) was used as the basis for cranial assessments. Eleven skull characteristics were measured: condylobasal length (CBL), rostral width (RW), zygomatic width (ZW), interorbital width (IOW), and the greatest (lambdoidal) width (GW), facial part

length (FPL), height in the area of the brain capsule (HBC), length of the incisive foramen (LIF), length of the diastem (LD), and alveolar length of the upper (LUTR) and lower tooth row of cheek teeth (LLTR). Measurements were performed using a caliper with an accuracy of 0.05 mm. As well as standard statistical processing of material according to particular characters, the multiple statistical methods of factor, discriminant, and cluster analysis were used. Discriminant analysis was performed with a transition to a canonical system of coordinates and the calculation of generalized Makhalanobis distances between sample centroids (Kim et al., 1989). The use of a great number of cranial traits allows us to interpret results obtained during the discriminant analysis along the same lines used in comparing mandible shape and size by M. Festing's method (Festing, 1973). Calculations were performed using the ECOSTAT original software package of statistical programs developed with our participation at the Institute of Plant and Animal Ecology in the Ural Division of the Russian Academy of Sciences.

Phenetic analysis was performed according to the frequency of occurrence of 19 phenes of nonmetric cranial traits representing small, stable aberrations in its structure: the presence or absence of certain openings for blood vessels and nerves, the absence of bone fragments, etc. (Fig. 1). During skull classification, the presence of a certain character for each individual was recorded, then, in each sample, for bilaterally manifested characters, the number of sides at which the phene (a stable state of the threshold character) manifested itself and the total number of the studied sides were counted. For the characters located along the axis of skull symmetry (medial axis), the number of individuals in which the phene was manifested and the total number of the individuals studied were calculated. When skulls were injured, the number of sides or skulls at which phene observation of the respective characters was possible was taken into consideration. A list of phenes of nonmetric cranial traits and their Latin coding are given in the explanations to Fig. 1. Due to the present lack of standard nomenclature, phene names should be considered only as working names.

To compare samples according to the phene complex of nonmetric cranial traits, we used the mean measure of divergence method suggested earlier by Berry and Smith (Berry, 1963, 1964) in the modification of Sjøvold (1973). The averaged mean standard deviation was calculated following Sjøvold (1973). For dummy variables, Bartlett's correction of 1/4 n was used, where n is the number of the individuals studied. Phenetic distances were calculated using PHEN software (Version 3.0), developed by A.G. Vasil'ev.

RESULTS AND DISCUSSION

Multivariate morphometric analysis. Before performing the comparison of the available collection material, we had to determine the magnitude of possi-

ble shifts of quantitative assessments. Theoretically, these shifts may be associated with different forms of group variability: limitations posed by sex; differences related to sex, seasonal generation, and local biotopic conditions; chronographic fluctuations related to weather or climatic, demographic, and biotic factors; etc. It is clear that the task could not be completed using the available material; however, we tried to assess the scale of the possible shift using the maximum available number of factors. Note that age and seasonal factors should not have affected the results of our studies since we specifically used materials collected in one season that were sufficiently homogenous with respect to age.

Sex-related differences were considered in the most representative samples of northern and southern muskrats: in most modern Yamal samples (1987–1989) and in the Kurgan samples collected in 1965. It is seen from Table 1 that craniometric differences between the sexes in northern muskrats are not pronounced, and in southern muskrats, sexual dimorphism is obvious. The results of the discriminant analysis support our conclusions. Males in the southern Kurgan population are slightly larger than females according to some measurements and are distinguished by a combination of more developed zygomatic arches with an elongated row of upper cheek teeth and a narrowed rostrum. According to the discriminant canonical function, on the basis of the 11 measurements, males can be correctly identified in 80.7% of cases and females and in 83.3% of the southern population, and this is statistically reliable ($p < 0.01$). Nevertheless, the scale of sex-related craniometric differences is not very large in the southern population and, according to paired comparisons of particular characters, is statistically unreliable in many instances (see Table 1). Muskrats of this age category that dwell in Finland (Pankakoski and Nurmi, 1986) also have a well-pronounced sexual dimorphism: males are slightly larger than females, the differences being most strongly pronounced in the diastema length, rostrum width, and the mandibular length (we did not use this measurement).

The factors responsible for the emergence of differences in the manifestation of sexual dimorphism between southern and northern muskrat populations are not quite clear, and it is hardly possible that they are confined only to the short duration of the muskrat growth period and more rigid climatic conditions in the north that induce the animals to spend most of their energy on physical maintenance rather than on maturation. It may also be assumed that, under the milder climatic conditions of the Southern trans-Ural region and southern regions of Finland, the breeding season starts earlier, allowing the animals to reach maturity earlier, which is accompanied by the manifestation of sexual dimorphism. However, if general cranial sizes in northern and southern muskrats are compared, it turns out that females in the south are slightly smaller than in the north, and males do not, in fact, differ according to the condylobasal cranial length (Table 1). Thus, general

Table 1. Craniometric comparison of southern and northern muskrats according to sex (discriminant function coefficients are standardized)

Character	Northern population (1988–1989)			Southern population (1965)		
	males ($n = 79$)	females ($n = 66$)	discriminant function coefficient	males ($n = 25$)	females ($n = 18$)	discriminant function coefficient
CBL	57.3 ± 0.18	57.0 ± 0.18	0.564	57.6 ± 0.26	57.0 ± 0.25	−0.063
RW	7.6 ± 0.04	7.6 ± 0.05	−0.200	7.1 ± 0.07	7.2 ± 0.07	−0.601
ZW	34.6 ± 0.13	34.5 ± 0.14	−0.128	34.7 ± 0.18	34.0 ± 0.15	0.690
IOW	6.3 ± 0.04	6.3 ± 0.04	−0.286	6.2 ± 0.05	6.0 ± 0.09	0.450
GW	24.1 ± 0.09	24.0 ± 0.08	0.209	24.7 ± 0.14	24.0 ± 0.14	−0.047
FPL	37.9 ± 0.13	37.8 ± 0.11	0.367	38.5 ± 0.17	37.9 ± 0.13	0.177
HBC	19.2 ± 0.07	19.2 ± 0.07	−0.175	19.2 ± 0.09	18.8 ± 0.10	0.529
IFL	11.4 ± 0.08	11.3 ± 0.07	0.314	12.0 ± 0.14	12.3 ± 0.17	−0.487
DL	20.4 ± 0.10	20.3 ± 0.10	−0.267	20.4 ± 0.11	20.1 ± 0.17	−0.060
UTRL	14.2 ± 0.05	14.2 ± 0.05	−0.643	14.5 ± 0.08	14.2 ± 0.09	0.779
LTRL	14.7 ± 0.04	14.6 ± 0.04	0.154	14.9 ± 0.09	14.8 ± 0.11	−0.576
Eigenvalues			0.0174			1.0622
Significance level			$p = 0.99$			$p < 0.01$

sizes of the animals of this age group in the south and in the north are essentially similar in size. Therefore, it may be concluded that, whatever the actual factors governing this phenomenon, southern muskrats differ from their northern animals in the apparently higher rate of animal maturation in nature, which results in sexual dimorphism in the south.

The comparison of Yamal muskrats in the time aspect was performed in two ways. The first, a paired morphometric comparison of certain craniometric characters in samples of successive years (1988 and 1989), showed significant differences in only two measurements: skull height in the site of the tympanic capsules and the length of the upper row of cheek teeth (Table 2). The discriminant analysis performed according to 11 cranial measurements revealed significant differences along the first canonical variable ($p < 0.001$). The animals from 1988 were characterized by a consistent combination of a higher skull height and the length of the upper row of cheek teeth with a smaller condylobasal length of the skull. It is well known that the variability of the general skull measurements is related to environmental effects to a greater degree than to other craniometric characters (Atchley *et al.*, 1981). For the

Table 2. Craniometric comparison of Yamal muskrat samples from 1988 and 1989

Character	Muskrat sample		Standardized discriminant function coefficients
	1988 ($n = 58$)	1989 ($n = 75$)	
CBL	57.24 ± 0.17	57.18 ± 0.21	−0.400
RW	7.54 ± 0.04	7.58 ± 0.04	0.069
ZW	34.57 ± 0.14	34.56 ± 0.14	−0.141
IOW	6.23 ± 0.04	6.35 ± 0.04	−0.492
GW	24.13 ± 0.09	24.04 ± 0.10	−0.094
FPL	37.94 ± 0.12	37.84 ± 0.13	0.219
HCC	19.36 ± 0.07	19.06 ± 0.07	1.115
IFL	11.39 ± 0.09	11.19 ± 0.07	0.348
DL	20.31 ± 0.10	20.39 ± 0.11	−0.601
UTRL	14.32 ± 0.06	14.13 ± 0.04	0.401
LTRL	14.65 ± 0.04	14.68 ± 0.04	−0.345

Table 3. Discriminant analysis of allochronic northern muskrat samples

Character	Standardized discriminant function coefficients	
	DCF1	DCF2
Rostrum width	−0.327	0.447
Zygomatic width	−0.485	0.746
Interorbital width	−0.093	−0.156
Facial part length	0.174	−0.851
Incisive foramen length	0.159	0.213
Diastema width	0.314	0.025
Upper tooth row length	0.918	0.585
Lower tooth row length	−0.481	0.015
Eigenvalues	0.611	0.091
Significance level	$p < 0.001$	$p < 0.21$

same reason, the measurements that correlate strongly with the general skull sizes (condylobasal length, greatest cranial width, and skull height) were excluded from further consideration.

In the second comparison, the most modern Yamal samples were compared with a sample taken at the peak of muskrat numbers in the same region in 1955 (Table 3). The discriminant analysis allows for the graphical representation of results (Fig. 2). It is seen that ellipsoids that include 95% of observations from each sample substantially overlap each other, although the differences along the first canonical variable are statistically significant (see Table 3). It is obvious that differences between samples of different years are comparable in scale to differences between the most modern sample and a sample taken in 1955. This suggests that if these differences exist, they are not very large in scale and are comparable to normal yearly variations. Therefore, it may be assumed that the most modern populations and those closest in time to the start of acclimatization are similar morphometrically.

In comparing the initial samples of 1955 from the southern and northern muskrat populations according to certain characters, significant differences were revealed in rostrum width, facial part length, incisive foramen, and length of the lower tooth row (Table 4). The multivariate comparison also revealed significant differences between these characteristics ($p < 0.001$). It is interesting to note that the transgression between the samples according to values of the first discriminant canonical function is insignificant: 93.1% of the function values for individuals of the northern population and 89.2% of the southern do not overlap. This demonstrates a high level of conservative specifity in the groups under comparison; therefore, by 1955, despite a similarity in the complex of morphophysiological characters (Smirnov and Shvarts, 1959), the groups already differed significantly in skull size and shape.

In different muskrat samples, different forms of group variability in the understanding of Yablokov (1966) may manifest themselves. In order to consider the effects of these factors of variability, we included in the general comparison of southern and northern muskrats parallel to the mentioned samples of 1955, the following samples that mark this variability. Of the modern northern samples, we took three samples from Yamal Peninsula to characterize the scale of the chronographic variability and the scale of local differences between muskrats of neighbouring habitats: (1) micropopulation-1 (1988); (2) micropopulation-1 (1989); and (3) micropopulation-2 (1989). In the south, for the characteristics of the scope of sex-related differences, collections from 1965 were represented by male and female samples. In the remaining cases, samples of both sexes were grouped together.

The discriminant analysis performed according to eight skull measurements indicated that the first four canonical variables account for 96.3% of the total variability (Table 5). We think that the first two canonical
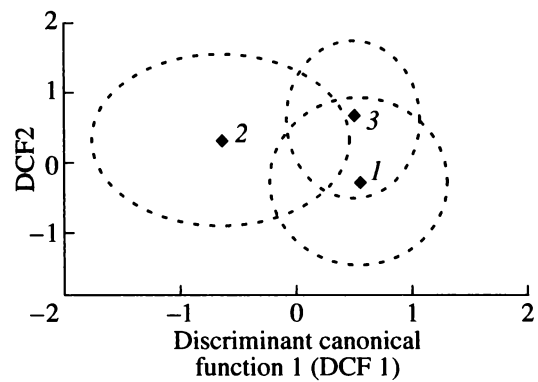

Fig. 2. Discriminant analysis of the cranial shape and size of allochronic northern muskrat samples. Samples: (1) collections of 1988; (2) of 1989; (3) of 1955. Ellipsoids include 95% of the observations for each sample.
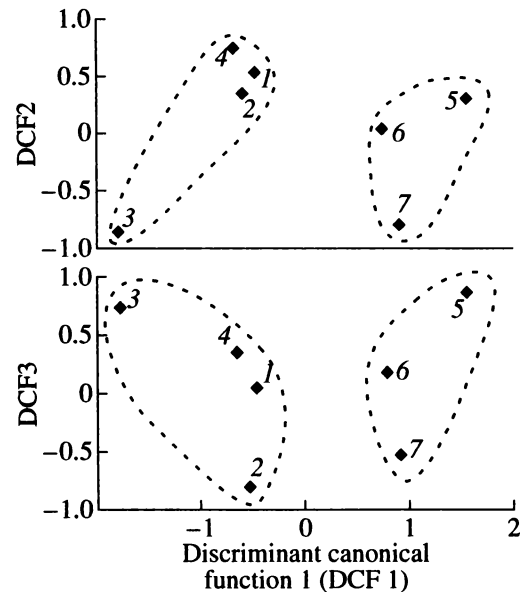

Fig. 3. Discriminant analysis of the cranial shape and size of northern and southern muskrat populations at different stages of acclimatization (projections of sample centroids on the three first discriminant functions) Northern samples: (1) micropopulation-1 (1988); (2) micropopulation-1 (1989); (3) micropopulation-2 (1989); (4) materials of Smirnov and Shvarts (1955). Southern samples: (5) materials of Smirnov and Shvarts (1955); (6) males, 1965; (7) females, 1965. The centroids of the northern and southern populations are outlined with a broken line. DCF1–DCF3 are discriminant functions.

variables, which account for 81% of the total dispersion, may be considered the most informative. A graphical representation of the results is given in Fig. 3. It is obvious that the projections of centroids of all northern samples on the first discriminant axis are compactly located in the region of negative values (on the left side of the plot), and of the southern, in the region of positive values (on the right side). Thus, differences along the first discriminant canonical axis reflect differences
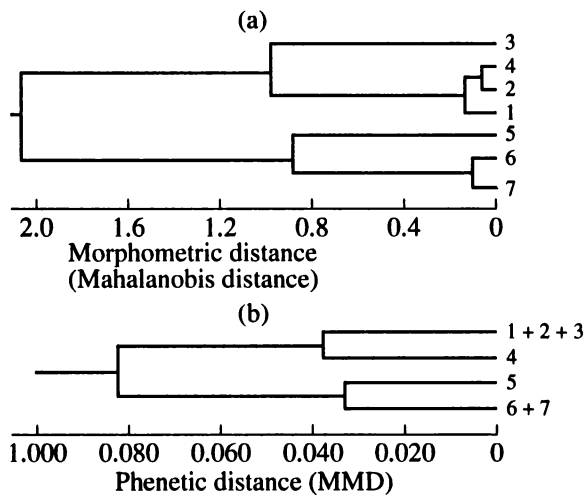
Fig. 4. Cluster analysis (UPGMA) of southern and northern allochronic muskrat populations according to morphometric (a) and nonmetric (b) distances. Sample numbers are the same as in Fig. 3. The symbol "+" denotes a unification of the respective samples.

between the southern and northern muskrats and, on the whole, characterize the geographical differences.

It is more difficult to interpret differences along the second canonical axis. It is seen that, strictly in the direction of this axis, the greatest range of differences between the sexes is observed in the southern samples of 1965, as well as in the north and in the south between muskrats of different local habitats (micropopulations). Note that, in the south, samples of 1955 and 1965 were taken from neighboring lakes 30 km apart. The variability along the third axis characterizes sexual and chronographic differences (Fig. 3), and its unambiguous interpretation is also difficult. Thus, along the second and third axes, manifestations of those forms of group variability that account for the shift of quantitative interpopulation differences are represented to a greater degree. If the scale of distance between samples

specially included into the analysis as representing a certain form of variability is compared, it is obvious that it is small in comparison with the range of geographic differences. Thus, in a space formed by the first and second, as well as the first and third canonical variables, the scope of sexual differences compares well with chronographic fluctuations. The level of differences between local micropopulations does not significantly exceed the latter. Therefore, it should be acknowledged that only the first canonical variable characterizes consistent differences between the northern and southern populations, which are accounted for by environmental factors to the least extent. It is seen in Fig. 3 that, since 1955, the level of interpopulation differences had not changed. A specially performed cluster analysis of average-sample values of the first discriminant function indicated two sharply pronounced principal clusters characterizing southern and northern muskrats (Fig. 4a). It is seen from the cluster structure that the level of differences accounted for by sex and conditions of different years is significantly lower than the magnitude of random differences between micropopulations, but these are essentially lower than interpopulational differences.

Phenetic analysis. Phenetic (nonmetric) analysis of the muskrat groupings was of utmost interest to us (Table 6). Earlier, we analyzed the relation of phenes of nonmetric characters to sex in the sample from the Kurgan oblast collected in 1965, since sexual dimorphism was only observed in these animals. The calculations showed that no phene showed statistically significant differences between the sexes. The total phenetic distance (MMD) between the sexes was -0.0040 ± 0.0081 and was not statistically significant. Phenetic differences between the sexes in the north were also negligible: 0.0004 ± 0.0042 and not statistically significant ($p \gg 0.05$). Comparison of samples collected in different years in the north demonstrated that the most modern samples (1988 and 1989) slightly differed from each other and that an earlier sample (1955) was similar to them, although it differed from them slightly more

Table 4. Comparison of southern and northern muskrat samples from 1955 according to a complex of craniometric characters

Character	Northern sample ($n = 39$)	Southern sample ($n = 37$)	Standardized discriminant function coefficients
RW	7.60 ± 0.06	7.17 ± 0.06	-0.406
ZW	34.98 ± 0.20	34.66 ± 0.19	0.179
IOW	6.20 ± 0.07	6.10 ± 0.05	0.008
FPL	38.27 ± 0.18	38.86 ± 0.18	0.840
IFL	11.51 ± 0.09	12.64 ± 0.14	0.682
DW	20.59 ± 0.13	20.26 ± 0.16	-1.296
UTRL	14.53 ± 0.06	14.86 ± 0.06	-0.370
LTRL	14.75 ± 0.07	15.15 ± 0.06	0.382
Eigenvalue			1.6559
Significance level			$p < 0.001$

Table 5. Discriminant analysis of the cranial shape and size of southern and northern muskrat populations at different stages of acclimatization

Character	Standardized discriminant functions coefficients		
	DCF1	DCF2	DCF3
Rostrum width	−0.504	0.022	0.247
Zygomatic width	−0.053	−0.274	0.701
Interorbital width	0.050	0.000	0.596
Facial part length	0.361	−0.214	−0.180
Incisive foramen length	0.688	−0.440	0.178
Diastema length	−0.612	0.663	−0.497
Upper tooth row length	0.142	1.250	0.273
Lower tooth row length	0.080	−0.525	0.241
Eigenvalues	1.270	0.360	0.205
Significance level	$p < 0.001$	$p < 0.001$	$p < 0.001$

than they differed from each other (Table 7). Southern allochronic samples were also found to be similar phenetically (Table 7). Differences between two neighboring muskrat micropopulations in the Yamal Peninsula are of the same order of magnitude: 0.029 ± 0.006. The scale of all these differences agrees fairly well with the analogous data for other species, obviously not exceeding the interpopulation level (Berry, 1963; Hartman, 1980; Vasil'ev, 1984; and Vasil'ev et al., 1986).

The matrix of phenetic distances (MMD) between northern and southern samples that characterize different stages of muskrat acclimatization was processed using cluster analysis (Fig. 4b). It is obvious that differences between samples of different years collected in the same regions are almost equal in the south and in the north and do not exceed the level of specific interpopulation differences (Vasil'ev, 1984). It is also obvious that southern and northern samples form two independent clusters. The level of their isolation is 0.083 and is comparable to the magnitude of MMD-distances between separate populations of other species (Vasil'ev, 1984).

Thus, both multivariate morphometric and nonmetrical analyses of cranial muskrat traits showed the same result. At the first stages of acclimatization between northern and southern muskrats originating from one genetically homogeneous group of animals from Canada, consistent morphological differences emerged at the population level, and their level evidently had almost not changed during the subsequent half-century period of isolation. These differences emerged over a very short period of time and were accompanied by the transformation of the cranial shape and size and the pattern of nonmetric threshold characters that govern the frequency of manifestation of certain discrete phene variations. This "rapid response" is somewhat unexpected for consistent morphological structures since more labile morphophysiological characteristics studied at the initial stage of acclimatization (Smirnov and Shvarts, 1959) had not changed by the time cranial parameters had already reflected the differentiation

associated with dwelling in different natural zones. It should be stressed that the differences between northern and southern populations revealed by multivariate morphometric and nonmetric methods allow a genetic interpretation (Grüneberg, 1963; Berry, 1964; Atchley et al., 1981), indirectly pointing to a genetic specificity of the groups under comparison. Note that different maturation rates in the south and in the north and the manifestation of sexual dimorphism in southern ani-

Table 6. Frequencies of occurrence of phenes of nonmetric cranial characters in the muskrat populations under comparison

Character	Northern population		Southern population	
	1955 $(n = 94)$	1988–1989 $(n = 312)$	1955 $(n = 218)$	1965 $(n = 220)$
1	25.6	17.7	10.9	19.1
2	36.2	45.2	44.5	61.4
3	51.1	50.3	46.3	49.6
4	28.7	49.4	36.9	41.4
5	6.4	9.6	5.1	11.4
6	14.5	10.3	25.3	22.3
7	88.4	86.8	77.1	80.0
8	30.2	24.3	62.3	50.9
9	79.0	92.1	96.2	89.5
10	79.0	70.1	58.5	71.1
11	47.9	64.4	57.3	65.0
12	36.2	41.3	19.3	21.8
13	1.1	4.8	2.8	1.4
14	24.4	16.7	17.9	20.9
15	84.9	81.5	49.4	76.8
16	26.6	15.9	22.2	20.5
17	78.0	77.5	85.3	78.2
18	61.9	73.7	35.3	49.4
19	9.5	19.6	18.5	24.7

Table 7. Comparison of samples of northern and southern populations in time

Sample pairs under comparison	Phenetic distances (MMD ± MSD)
Northern samples	
1988–1989	0.013 ± 0.006
1988–1955	0.035 ± 0.008
1989–1955	0.019 ± 0.008
Southern samples	
1955–1965	0.036 ± 0.007

Note: All differences are statistically significant.

mals, which have at slightly smaller general cranial sizes in comparison with northern animals, also testify to certain epigenetic transformations that are likely to be associated with significant genetic changes (Vasil'ev *et al.*, 1986). Pankakoski and Nurmi (Pankakoski and Nurmi, (1992) also came to this conclusion when considering the differentiation of geographically distant muskrat populations in Finland and the formation of the muskrat population structure in northern Europe. They also pointed out the consistency of manifestation of epigenetic characters of the muskrat skull. However, we consider that, due to the small number of structures studied, they failed to see a parallel between the results of the multivariate morphometric and nonmetric (phenetic) approaches.

Thus, it may be concluded that muskrat acclimatization in Western Siberia was accompanied by an intensive geographical morphogenesis and population differentiation. In a comparatively short period of time (only several dozen generations), significant transformations of the epigenetic system of the newly formed northern and southern muskrat populations occurred. The phase of rapid transformation was followed by a prolonged stasis, and during a great number of subsequent generations, the changes were smaller than during the first phase of rapid transformation. The morpho-physiological characters considered to be labile turned out to be more conservative than cranial characters, which are commonly considered to be stable. The results obtained testify to a high potential of the species with respect to rapid genetic transformations. This is likely to be responsible for the successful muskrat acclimatization to most natural areas of our country. The rates of the phenotypical change of the Ural muskrat populations that are homogeneous genetically agrees with the rate of changes in the heterogeneous Finnish populations that have a mixed origin.

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