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Variability of Cranial Characters in Acclimatized Sable (*Martes zibellina*) Populations

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Abstract—Comparative analysis of metric and nonmetric variations of the sable skull in autochthonous and acclimatized populations was performed. In acclimatized sables, the skull is larger than in sables of the same origin from the Baikal region; however, they are smaller than animals of the autochthonous population. In nonmetric cranial characters, in one case, sables acclimatized in the Ob region are similar to autochthonous animals; in the other, they are similar to sables from the Baikal region. During 40 years after introduction, the population groups of acclimatized sables acquired phenotypic differences from both autochthonous sables dwelling in similar conditions and animals from the Baikal region of the same origin as acclimatizants.

Key words: sable, skull measurements, nonmetric cranial characters, acclimatization, population variability.

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INTRODUCTION

To restore exhausted resources of hunting objects in the Soviet Union, a plan of reconstruction of the fauna was adopted in 1933, which resulted in extensive reintroduction and introduction of at least 45 species (Pavlov et al., 1973), including the muskrat (*Ondatra*
1 2 3 *zibethicus*), European hare (*Lepus europaeus*), Ameri-
4 can mink (*Mustela vison*), European beaver (*Castor fiber*), sable (*Martes zibellina*), red squirrel (*Sciurus vulgaris*), racoon dog (*Nyctereutes procyonoides*), desman (*Desmana moschata*), etc. Zhitkov (1934), Manteifel (1934), and Kopylov (1958) considered theoretical and practical foundations for introduction of new species.

Kashkarov (1944) was the first to propose to regard acclimatization as an ecological process of adaptation of species to new conditions. Shaposhnikov (1958, 1963) also considered acclimatization from the point of view of population ecology and proposed the phase theory for acclimatization, which was subsequently developed by Chesnokov (1982, 1989).

Below we use the term "acclimatization" according to the definition of Shvarts (1963, p. 20), i.e., "Acclimatization is the process of establishment of a species in a new environment, process of the formation of a new population of this species, which has a number of distinctive features, including a complex set of morphological and physiological traits, which characterize the population as a whole. The major driving force of the formation of a new population is natural selection."

The sable, along with the European hare, European beaver, muskrat, and American mink were objects of the most extensive translocation works in the Soviet Union. This was caused by intense hunting, which resulted at the beginning of the 20th century in the formation of a mosaic range and in places almost complete extermination of particular species (Timofeev and Pavlov, 1973).

To restore sable population, a number of measures were taken, including five year-long prohibition and subsequent limitation of hunting, establishment of fur farms, and introduction into the regions where this species was completely exterminated. At the end of the 1950s and beginning of the 1960, the former range of sable was restored mostly due to introduction and the growth of population number in the preserved centers (Bakeev et al., 2003).

According to the data of Timofeev and Pavlov (1973), a total of 19 817 sables were translocated from 1901 to 1970 in the Soviet Union; of them 3045 animals were reintroduced in the Ob region from 1940 to 1959 and 5102 were in Yakutia from 1948 to 1961. These animals were captured in the areas where sables with dark fur prevailed, mostly from the northeastern and western Baikal region. In the majority of cases, introduction was successful, sables actively occupied new habitats.

Within most of the range, in the areas where sables were not introduced, populations were restored based on local sites where sables were preserved (Timofeev and Pavlov, 1973).

Table 1. Material studied

Designation of sample	Capturing area, status	Date of capture	Sample size, males/females	Collection, author
Dem'yanka	Ob region, autochthons	1986–1988	30/30	coll. by V.G. Monakhov
Yugan	Ob region, autochthons	1981–1985	31/37	coll. by V.G. Monakhov
Olenek	Yakutia, autochthons	1989–1990	16/16	IBPK
Barguzin	Baikal region, autochthons	1983–1989	19/16	coll. by E.M. Chernikin
Vitim	Baikal region, autochthons	1981–1983	19/20	coll. by Yu.M. Baranovskii
Vakh	Ob region, acclimatizants	1981–1985	30/30	coll. by V.G. Monakhov
Tym	Ob region, acclimatizants	1982–1989	32/26	VNIIOZ, A.A. Sinitsin
Maya	Southern Yakutia, acclimatizants	1990–1991	30/25	IBPK

Note: (IBPK) of Biological Problems of Cryolithozone, Siberian Branch, Russian Academy of Sciences; (VNIIOZ) All-Russia Research Institute of Hunting and Fur Farming.

In the Ob region, the majority of sables were moved in the stations free or almost free of autochthonous (native) animals (Timofeev and Nadeev, 1955; Monakhov, 1995). Within 30 years after introduction, the study of sable populations that appeared as a result of acclimatization showed that these animals had much darker fur than native sables and were similar in fur color to sables of the Baikal region (Poluzadov, 1974; Kryuchkov, 1975; Monakhov, 1995).

The purpose of this work is to study phenotypic differentiation of autochthonous and acclimatized sable populations based on cranial characteristics.

MATERIAL AND METHODS

The study was based on the cranial collections stored in Zhidkov All-Russia Research Institute of Hunting and Fur Farming (VNIIOZ, Kirov), Institute of Biological Problems of Cryolithozone of the Siberian Branch of the Russian Academy of Sciences (IBPK), and material collected by V.G. Monakhov. The age of animals was estimated using the combination of methods developed by Smirnov (1960) and Klevezal' and Kleinenberg (1967). To prevent damage of museum specimens, their age was determined using the method of Timofeev and Nadeev (1955), which is based on the development of cranial structures. Adults above one year old were included in analysis.

A total of eight sable geographical population groups were studied (Table 1, Fig. 1), including two samples from autochthonous populations of the Ob region, two samples of acclimatizants (descendants of animals introduced from the Baikal region) from the Ob region, a sample from autochthonous population of northwestern Yakutia, a sample of acclimatizants of southern Yakutia, and two samples of autochthonous sables of the Baikal region.

We designate particular samples after the rivers, in the basins of which animals were obtained. Sables of the Barguzin sample come from the area of the Barguzin Mountain Range.

Dem'yanka. Sable sample from the Ob region, basin of the Dem'yanka River, right tributary of the Irtysh River. This area is inhabited by relatively large sables, with light fur (Poluzadov, 1975; Monakhov, 1995, 2001). By the prohibition of hunting in 1935, a small sable population had been preserved, which subsequently considerably increased in number (Timofeev and Pavlov, 1973; Bakeev et al., 2003).

Yugan. Sable sample from the Ob region, basins of the Bol'shoi and Malyi Yugan rivers, left tributaries the Ob River. This area is inhabited by relatively large sables, with light fur (Poluzadov, 1975; Monakhov, 1995, 2001). As in the Dem'yanka River Basin, by the prohibition of hunting in 1935, only small sable populations had been preserved there, which subsequently increased in number (Timofeev and Pavlov, 1973; Bakeev et al., 2003).

Vakh. Sable sample from the Ob region, basin of the Vakh River, right tributary of the Ob River. By the mid-20th century, sables had almost completely been exterminated in this area (Pavlinin and Shvarts, 1961; Poluzadov, 1974). In 1952–1957, East Siberian sables were introduced here in five series, with the total number of 535 individuals. Acclimatizants are relatively small-sized, with a dark fur color (Monakhov, 1995, 2001; Bakeev et al., 2003).

Tym. Sable sample from the Ob region, interfluve of the Tym and Ket' rivers, right tributaries of the Ob River. In the mid-20th century, this area lacked sables (Matov, 1940; Nadeev, 1947). From 1950 to 1958, East Siberian sables were 20 times brought here, with the total number of 1363 individuals. Acclimatizants are relatively small-sized, with dark fur color (Monakhov et al., 1982; Monakhov, 1995, 2001; Bakeev et al., 2003).

Olenek. Sable sample from Yakutia, Olenek River Basin. At the beginning of the 20th century, sables were infrequently recorded here (Romanov, 1941, cited after Bakeev et al., 2003). The range and population size were restored naturally; animals are relatively large-sized and their fur is darker than in autochtho-

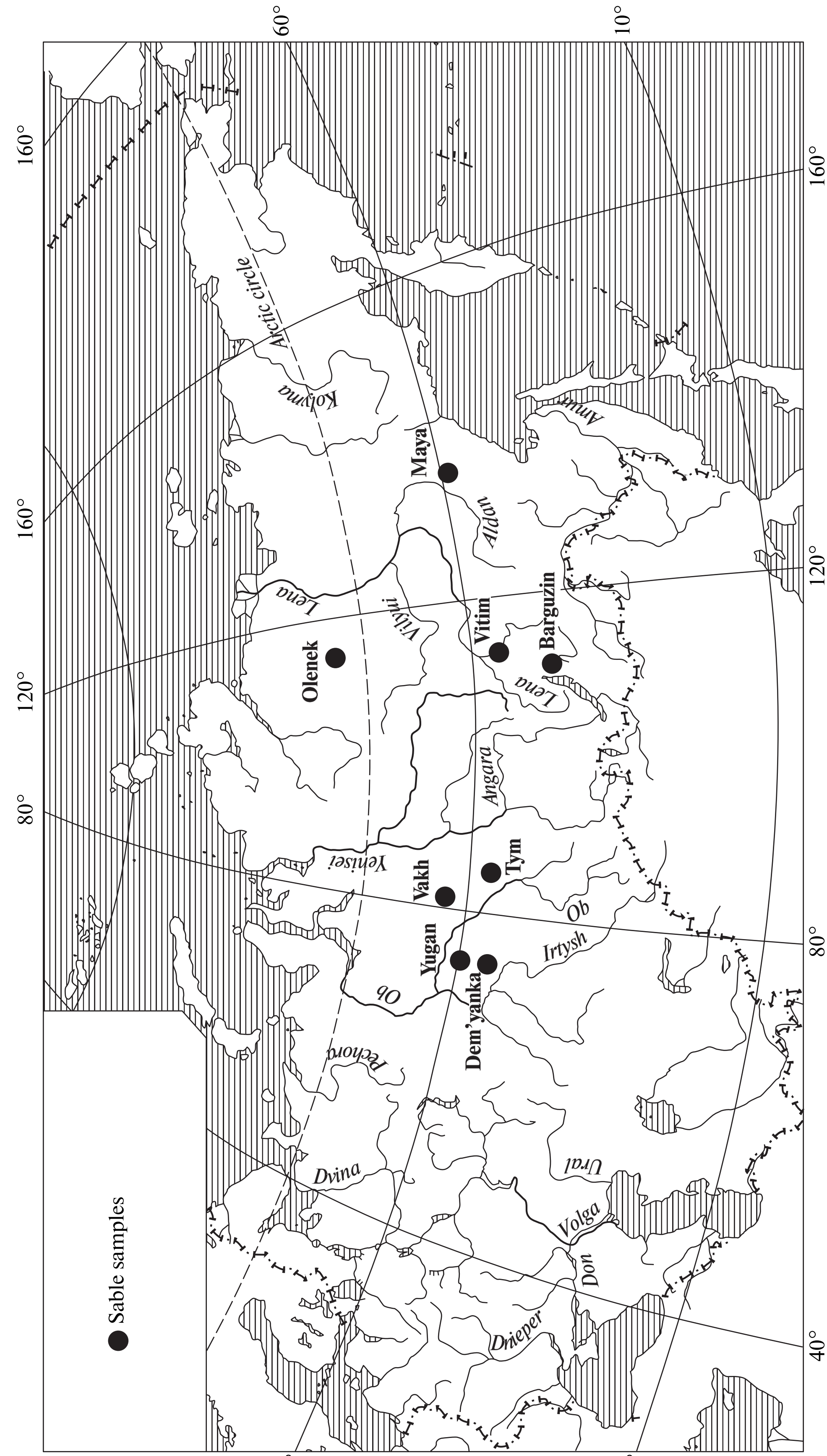

Fig. 1. Geographical location of sable samples.

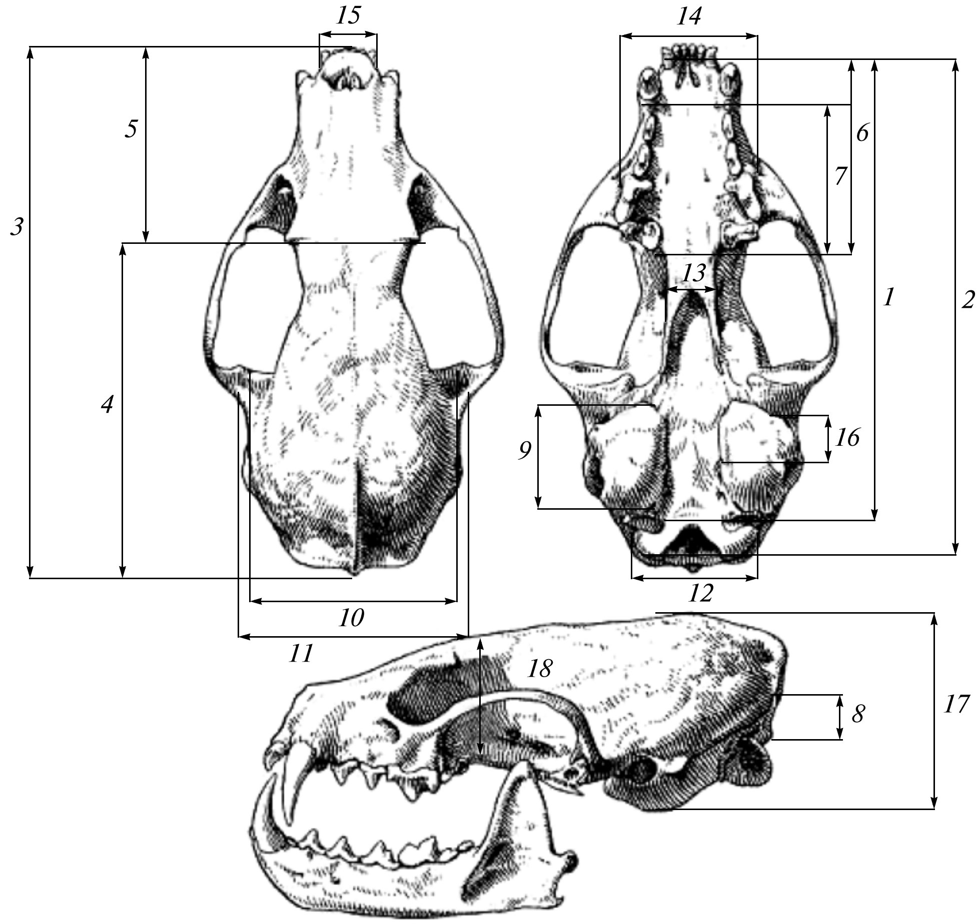

Fig. 2. Cranial measurements of sable. For designations, see the text.

nous populations of the Ob region (Eremeeva, 1952; Tavrovskii, 1971; Gryaznukhin, 1980).

Maya. Sable sample from southern Yakutia, Maya River Basin, right tributary of the Aldan River. Before the 1940s, sables were virtually absent in this area. As 248 animals were brought here in 1957 from the Baikal region, a large population was formed (Kazarinov, 1954; Timofeev and Pavlov, 1973). Acclimatizants are small-sized, with dark fur (Tavrovskii, 1971; Gryaznukhin, 1980; Monakhov, 2002).

Vitim. Sable sample from the Baikal region, lower basin of the Vitim River, inhabited by small-sized sables with dark fur (Eremeeva, 1952; Timofeev and Nadeev, 1955; Monakhov, 1976). In this area, sables were captured for translocation in other regions of Russia, including the Ob region and southern Yakutia.

Barguzin. Sable sample from the Baikal region, Barguzin Mountain Range, inhabited by small-sized sables with dark fur (Eremeeva, 1952; Timofeev and Nadeev, 1955; Monakhov, 1976). In this area, sables were captured for translocation in other regions of Russia, including the Ob region.

Thus, we studied sable samples from autochthonous populations, which, after decline in number, were restored by natural means (Dem'yanka, Yugan, and Olenek river basins); sable samples whose ancestors come from the Baikal region (Tym, Vakh, and Maya river basins); and sable samples just from the Baikal region (Barguzin Mountain Range, Vitim River Basin), where animals for translocation were captured. Comparative analysis of these samples displays differences between acclimatizants and, on the one hand, "neighboring" local sable populations dwelling in similar conditions and, on the other hand, populations of "founders," which gave rise to acclimatizants.

In 407 individuals from eight geographical sable samples, the data on 18 metric and 22 nonmetric cranial characters were obtained. In sable skulls, the following 18 cranial measurements were performed using calipers (accurate to 0.1 mm) (Fig. 2): (1) basal length (Gromov et al., 1963); (2) condylobasal length (Gromov et al., 1963); (3) profile length (Gromov et al., 1963); (4) braincase length (Timofeev and Nadeev, 1955); (5) facial length (Timofeev and Nadeev, 1955); (6) tooth row length (Ognev, 1928); (7) molar row length (Gromov et al., 1963); (8) diameter of the foramen magnum (Duerst, 1926); (9) length of tympanic bullae (Pavlinin, 1963); (10) braincase width (Duerst,

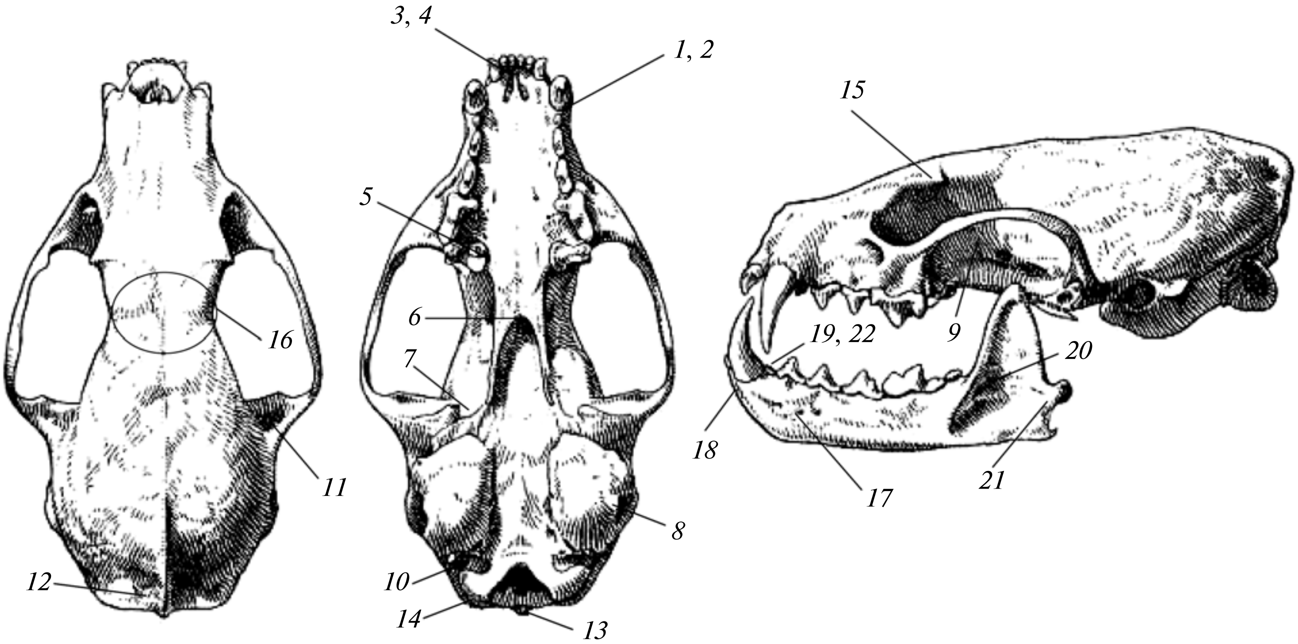

Fig. 3. Nonmetric cranial characters of sable. For designations, see the text.

1926); (11) greatest skull width (Gromov et al., 1963); (12) width of occipital condyles (Duerst, 1926); (13) choanal width (Pavlinin, 1963); (14) facial width in line with zygomatic foramina (Duerst, 1926); (15) width of upper incisor row (Duerst, 1926); (16) width of tympanic bullae (Pavlinin, 1963); (17) skull height at tympanic bullae (Ognev, 1928); and (18) skull height at interorbital narrowing (Duerst, 1926).

The classification of nonmetric cranial characters of sables was developed based on works of Glushkova
4 and Korablev (1997) on the European mink (*Mustela lutreola*) and Monakhov and Trushin (2000) on sable.

Each sable skull investigated in this work was classified based on the following set of nonmetric characters (Monakhov and Ranyuk, 2005):

Characters

1. First upper premolar
2. Foramina in the maxilla near P^1
3. Additional foramina before incisive foramina
4. Additional incisive foramina
5. Foramina medial to M^1
6. Process of palatine incisure
7. Additional foramina near foramen ovale
8. Additional foramen of the facial duct
9. Ethmoid foramen
10. Foramen in lower part of condylar fossa
11. Foramina in horizontal surface of the temporal
12. Foramen near middle part of occipital crest
13. Foramen before occipital protuberance
14. Foramen in upper part of condylar fossa
15. Supraorbital foramina near postorbital process
16. Foramina in the frontal posterior to zygomatic processes
17. Anterior mental foramen
18. Incisive mental foramen
19. Foramina in the dentary at internal margin of alveolus for P_1
20. Foramen in anterior part of fossa for masticatory muscle near M_2
21. Foramen in posterior part of fossa for masticatory muscle near articular process
22. First lower premolar

Phenes

1.0 Absence of the first upper premolar
2.0 Absence of foramina
2.1 One foramen
2.2 Two foramina
2.3 More than two foramina
3.1 One foramen
3.2 Two foramina
3.3 More than two foramina
4.0 Absence of foramina
4.1 One foramen
4.2 Two foramina
4.3 More than two foramina
5.1 One foramen
5.2 Two foramina
5.3 More than two foramina
6.0 Absence of process

7.0 Absence of foramina
7.1 One foramen
7.2 Two foramina
7.3 More than two foramina
8.1 One foramen
8.2 Two foramina
9.1 Ethmoid foramen single
9.2 Ethmoid foramen double
9.3 Incomplete septum between foramina
10.0 Absence of foramen
10.1 Presence of foramen
11.0 Absence of foramina
11.1 One foramen
11.2 Two foramina
11.3 More than two foramina
12.0 Absence of foramina
12.1 One foramen
12.2 Two foramina
12.3 More than two foramina
13.0 Absence of foramina
13.1 One foramen
13.2 Two foramina
13.3 More than two foramina
14.1 One foramen
14.2 Two foramina
14.3 More than two foramina
15.0 Absence of foramina
15.1 One foramen
15.2 Two foramina
15.3 More than two foramina
16.0 Absence of foramina
16.1 One foramen
16.2 Two foramina
16.3 More than two foramina
17.1 One anterior mental foramen
17.2 Two anterior mental foramina
17.3 Presence of additional foramina
18.1 One incisive mental foramen
18.2 Two incisive mental foramina
18.3 Presence of additional foramina
19.1 One foramen
19.2 Two foramina
19.3 More than two foramina
20.0 Absence of foramina
20.1 One foramen
20.2 Two foramina
20.3 More than two foramina
21.0 Absence of foramina
21.1 One foramen
21.2 Two foramina
21.3 More than two foramina
22.0 Absence of the first lower premolar

Figure 3 shows the positions of the above nonmetric characters in the skull.

All characters, except for characters 3, 6, and 13 with the medial position, were recorded on the left and right sides of the skull, with the aid of a MBS 10 binocular microscope, at magnification 8×23.

Thus, a total of 22 nonmetric cranial characters, described by 68 phenes were used. The material examined is divided into particular samples by sex (males and females) and geographical location. A total of 16 sable samples are analyzed.

Data processing was performed using software package STATISTICA 5.5 (StatSoft Inc. 1995).

As variation of sable skull measurements were analyzed, the effect of sex and geographical location on measurements was estimated based on the two-factor model of variance analysis. The differentiation of samples of the autochthonous and acclimatized sables was estimated based on the standard model of discriminant analysis.

To estimate epigenetic similarity of populations, the mean measure of divergence (MMD) was calculated using the formula proposed by Smith (1972) and subsequently modified by Sjovold (1977) and Hartman (1980).

MMD was calculated using the transformed frequencies of phenes (Q): $Q = 1/2\sin^{-1}[1 - 2k/(n + 1)] + 1/2\sin^{-1}[1 - 2(k + 1)/(n + 1)]$, where k is frequency of a phene, n is the number of specimens (for bilateral characters, total number of skull sides).

The mean measure of divergence (MMD) was calculated as follows:

$$\mathrm{MMD} = 1/r\sum_{i=1}^{r}\{(Q_{1i} - Q_{2i})^2 - [1/(n_{1i} + 1/2) + 1/(n_{2i} + 1/2)]\},$$

where r is the number of characters examined, Q_{1i} is transformed frequency of the phene i in sample 1, n_{1i} is the number of specimens in sample 1 (for bilateral characters, the number of skull sides investigated), Q_{2i} is transformed frequency of the phene i in sample 2, n_{2i} is the number of specimens in sample 2.

Standard deviation (SD) was calculated by the formula proposed by Sjovold (1977):

$$SD = 1/r\sqrt{\sum_{i=1}^{r} 2(1/n_{i1} + 1/n_{i2})^2}$$

The distances were regarded as significant, if they were greater than twice the standard deviation (MMD $> 2SD$).

According to the previous study (Ranyuk, 2006), as phene frequencies are compared using the chi-square test (χ^2), in the majority of samples, nonmetric characters 12, 16, 21, and 22 depend on sex and age; therefore, as MMD matrix was calculated, these characters were excluded. Thus, a total of 19 characters, with 55 phenes were included in the analysis. In the sample

Table 2. Results of two-factor multivariate variance analysis of sable samples based on cranial measurements: Main effects

Independent variables	Rao test	Degrees of freedom (df1, df2)	Significance level
Geographical location	6.722	126 ... 2381	<0.0001
Sex	113.336	18 ... 361	<0.0001
Geographical location × sex	1.226	126 ... 2381	0.0479

Table 3. Values ($X \pm SD$) of some cranial measurements of sables

Sample	Condylobasal length (character 2)	Length of tooth row (character 6)	Braincase width (character 10)	Skull height at tympanic bullae (character 17)
		Males		
Dem'yanka	85.11 ± 1.91	32.10 ± 0.88	36.11 ± 1.05	31.34 ± 1.14
Yugan	84.13 ± 1.83	31.87 ± 1.08	36.21 ± 0.85	32.08 ± 1.15
Olenek	84.15 ± 1.80	32.21 ± 0.93	34.76 ± 1.07	31.64 ± 1.56
Barguzin	80.29 ± 2.24	31.23 ± 1.13	35.03 ± 1.07	30.65 ± 1.17
Vitim	81.86 ± 1.91	31.77 ± 1.00	35.34 ± 1.19	30.70 ± 1.30
Vakh	82.86 ± 1.71	31.21 ± 0.86	35.23 ± 0.80	30.99 ± 1.09
Tym	82.99 ± 2.05	31.63 ± 0.97	35.36 ± 0.84	31.65 ± 0.92
Maya	81.76 ± 1.56	31.81 ± 0.94	35.40 ± 0.93	31.28 ± 1.19
		Females		
Dem'yanka	77.26 ± 1.33	28.62 ± 0.75	33.67 ± 1.02	28.93 ± 1.03
Yugan	77.48 ± 1.91	28.94 ± 0.81	34.01 ± 0.87	29.58 ± 0.98
Olenek	76.21 ± 1.23	29.02 ± 0.42	33.14 ± 0.88	29.95 ± 1.13
Barguzin	73.62 ± 1.48	28.53 ± 0.75	33.46 ± 0.96	29.11 ± 1.14
Vitim	74.31 ± 1.65	28.65 ± 0.74	32.95 ± 0.64	28.88 ± 0.91
Vakh	75.31 ± 1.42	28.12 ± 0.80	33.31 ± 0.90	28.87 ± 0.79
Tym	75.94 ± 2.19	28.52 ± 1.13	33.10 ± 0.93	29.28 ± 1.13
Maya	75.07 ± 1.55	28.61 ± 0.68	32.90 ± 0.40	29.48 ± 0.97

from the Baikal region, lower jaws are absent; therefore, MMD was calculated based on 15 characters, with 42 phenes. The distances obtained were analyzed using the method of multidimensional scaling.

RESULTS AND DISCUSSION

The two-factor model of variance analysis has shown that sex, geographical location, and their interaction have significant effect on the measurements examined (Table 2).

Of the sable samples examined, the largest skulls are characteristic of autochthonous animals of the Ob region and the smallest skulls are in sables of the Baikal region and Yakut acclimatizants (Table 3). The intermediate position is occupied by acclimatizants of the Ob region and autochthonous Yakut sables.

Thus, acclimatized sables are larger than animals of "founders" populations, but smaller than sables from autochthonous populations. These results corroborate the hypothesis (Monakhov, 1995) of the growth of skull size of sables in the acclimatization process.

The next stage of the study was discriminant analysis of sable populations based on cranial characters. The standard model of discriminant analysis included 16 samples, independent variables were 18 skull measurements.

The analysis has shown that 14 of 18 measurements have a significant effect on discrimination of the samples ($p < 0.05$) (Table 4). Most of the distances between groups are statistically significant ($p < 0.05$), except for distances between female samples of Dem'yanka and Yugan, females and males of Barguzin and Vitim and females and males of Maya and Vitim (Table 5).

The analysis of canonical discriminant functions (CDF) has shown that the first three CDF explain 90% of the total variance (Table 4). CDF1 differentiate samples by sex; CDF2, by geographical location; and CDF3 distinguishes male and female acclimatizants of Tym from other samples (Fig. 4).

Thus, discriminant analysis of sable populations based on cranial measurements has shown well-pronounced sexual differences in the samples. Geographical variation of cranial characters is less pronounced

Table 4. Results of standard discriminant analysis of sable samples based on cranial measurements

Cranial characters of sable	*F* exclusion test (15, 361)	Significance level	Standardized coefficients		
			CDF 1	CDF 2	CDF 3
1	1.77	0.037	0.39	0.02	–0.47
2	1.17	0.296	0.02	0.04	–0.90
3	1.99	0.015	0.32	–0.06	–0.27
4	2.02	0.013	0.15	0.17	0.59
5	2.91	<0.001	–0.02	0.62	0.64
6	3.22	<0.001	0.16	–0.48	0.86
7	4.98	<0.001	–0.23	–0.76	–0.44
8	3.71	<0.001	–0.02	–0.40	0.17
9	1.54	0.088	–0.15	0.22	0.13
10	3.59	<0.001	0.12	0.10	0.07
11	4.27	<0.001	0.12	0.08	0.74
12	1.63	0.065	0.09	0.12	–0.39
13	3.38	<0.001	–0.14	–0.24	–0.19
14	2.01	0.014	0.09	0.15	0.37
15	1.86	0.026	–0.02	–0.10	0.08
16	1.67	0.054	–0.10	–0.04	0.07
17	2.02	0.013	0.08	–0.15	–0.20
18	3.20	<0.001	0.27	0.05	–0.46
Proper number			6.76	1.21	0.41
Total variance			0.72	0.85	0.90

Note: (CDF) canonical discriminant function.

than sexual variation; however, sables of the Ob region differ from Baikal and Yakut populations.

As for the estimation of results of acclimatization, acclimatizants differ in cranial characters from both neighboring autochthonous population groups and sables of the Baikal region.

Cranial measurements distinguish acclimatizants of the Ob region from autochthonous populations the Ob and Baikal regions. Yakut acclimatizants (Maya) are more similar in cranial characters to sables of the Baikal region.

Based on the frequencies of phenes of nonmetric skull characters, the mean measure of divergence was calculated (MMD and *SD*); see Table 6.

In general, the epigenetic distances ranged from 0.001 to 0.210. The majority of high values of MMD are obtained in comparisons between autochthonous populations of the Baikal and Ob regions; this possibly corresponds to divergence of subspecies level. Small distances are usually observed between males and females from the same geographical sample and neighboring geographical samples. A similar variation range of MMD was shown by Ansorge (1992) for the pine marten (*Martes martes*), in which large distances between samples may result from disjunctive species range in eastern Germany. In the study of the population structure of the Kamchatka sable (Dubinin and Valentsev, 2003), epigenetic distances between sable samples from different regions were smaller by an order of magnitude (from 0.0064 to 0.0251); this suggests population homogeneity of Kamchatka sables.

The matrix of MMD was analyzed using the method of multidimensional scaling (4 axes, stress = 0.0636). It shows that autochthonous populations of the Ob region and Yakutia are separated along axis 1 from sables of the Baikal region. Acclimatizants from Maya, Vakh, and Tym occupy intermediate positions, and Vakh approaches sables from the Ob region, whereas Tym is distinguished from both Ob and Baikal samples by axis 2 (Fig. 5).

The study of a number of acclimatized species has shown that the formation of a new population results in changes in morphological, physiological, ecological, and other population characteristics. For example, acclimatized European beavers are considerably larger than their ancestors (Saveliev, 2003; Monakhov and Chernykh, 2004); this is also true of ermines (*Mustela erminea*) from New Zealand, which are 4
larger than British animals (King and Moody, 1982). Racoon dogs introduced in the European Soviet Union are smaller in skull measurements and have a denser fur than Far East individuals (Sorokin, 1953). Variation in nonmetric cranial characters at early stages of acclimatization was recorded in the muskrat (*Oryctolagus cuniculus*); cranial characters turned out to be more changeable than morphophysiological characteristics (Vasil'ev et al., 1999).

The study of variation in cranial measurements of sables has shown that the skull of acclimatizants increases in size and occupies an intermediate position between "aborigines" and "founders" (Monakhov et al., 1976; Monakhov, 1995). In addition, acclimatizants show a lower fecundity of females than autochthonous sable populations (Monakhov, Bakeev, 1981; Monakhov, 1998, 2000) and a decrease in frequency of foramen in the fossa condyloidei inferior of the skull compared with the "founders" from the Baikal region (Monakhov, 1999, 2000, 2001, 2003). As the set of nonmetric cranial traits of acclimatizants is analyzed, they tend to approach autochthonous sables (Ranyuk and Monakhov, 2004; Ranyuk, 2004, 2005).

Geographical variation in skull size reflects the spatial structure of the sable range; however, the newly formed populations of acclimatizants sometimes disturb it. The skull measurements, along with fur color and body size, were used for the recognition of sable subspecies (Tavrovskii, 1959; Geptner et al., 1967; Monakhov, 1976; Pavlinov and Rossolimo, 1979). The sable population groups considered in this study from the Baikal and Ob regions and northwestern Yakutia confirm the previously shown geographical variation in skull size (Timofeev and Nadeev, 1955; Monakhov G.I., 1976; Monakhov V.G., 2002). Sables of the Ob

Table 5. Results of standard discriminant analysis of sable samples based on cranial measurements

Sable sample	Vakh, *F*	Vakh, *M*	Dem'yanka, *F*	Dem'yanka, *M*	Yugan, *F*	Yugan, *M*	Barguzin, *F*	Vitim, *M*	Vitim, *F*	Vitim, *M*	Tym, *F*	Tym, *M*	Maya, *F*	Maya, *M*	Olenek, *F*	Olenek, *M*
Vakh, *F*		19.4	3.4	35.5	2.9	30.7	4.1	10.2	3.4	14.4	3.9	24.3	5.9	19.5	3.9	20.1
Vakh, *M*	26.1		14.3	4.7	12.4	3.2	20.2	5.0	19.9	3.4	18.3	2.7	22.3	4.3	13.0	2.8
Dem'yanka, *F*	4.5	18.9		24.9	**1.3**	22.9	7.8	9.9	7.5	13.0	5.1	18.5	9.4	17.0	4.9	15.9
Dem'yanka, *M*	47.7	6.3	32.9		25.4	3.5	34.1	12.3	34.7	8.9	33.9	8.8	41.1	12.0	23.3	4.8
Yugan, *F*	3.5	15.0	**1.6**	30.7		21.1	6.3	6.8	6.2	9.9	4.3	16.0	8.0	13.7	3.8	13.7
Yugan, *M*	40.6	4.2	29.8	4.6	25.1		28.6	9.3	29.4	5.8	30.2	5.2	33.9	7.7	19.8	3.7
Barguzin, *F*	8.3	40.9	15.5	68.9	11.9	57.1		8.4	**0.9**	12.6	3.8	20.6	2.1	14.9	3.1	19.5
Barguzin, *M*	18.2	9.0	17.5	21.9	11.2	16.4	20.5		7.9	**1.0**	9.8	5.6	10.4	2.3	6.4	5.2
Vitim, *F*	6.2	36.8	13.7	64.3	10.7	53.7	**2.4**	18.0		11.9	3.3	20.4	**1.5**	14.7	3.0	19.2
Vitim, *M*	25.7	6.0	22.8	15.8	16.3	10.2	30.9	**2.2**	27.1		13.2	3.5	14.5	**1.5**	9.4	3.7
Tym, *F*	5.6	26.2	7.2	48.3	5.6	42.4	7.9	18.2	6.4	24.6		18.5	2.8	15.9	2.7	18.3
Tym, *M*	31.2	3.5	23.3	11.2	18.4	6.6	40.2	9.7	36.4	6.1	25.1		21.9	2.9	13.9	4.5
Maya, *F*	8.8	33.2	13.9	61.4	10.8	49.8	4.5	20.1	**3.1**	28.0	4.5	31.2		16.5	2.7	20.4
Maya, *M*	25.8	5.7	22.1	15.9	16.2	10.0	29.8	4.1	26.8	**2.6**	22.4	3.6	24.2		10.5	5.1
Olenek, *F*	7.9	26.2	9.7	47.0	7.2	39.5	8.3	15.8	7.6	23.1	5.6	27.1	5.8	21.0		11.8
Olenek, *M*	38.8	5.4	30.2	9.3	24.6	7.1	50.7	12.4	46.8	8.6	36.7	8.4	42.3	9.7	30.7	

Note: (*F*) females, (*M*) males; bold type designates statistically nonsignificant values ($p > 0.05$). Distances between groups are squared Mahalanobis distances (below diagonal) and *F* test, df1 = 18, df2 = 361 (above diagonal).

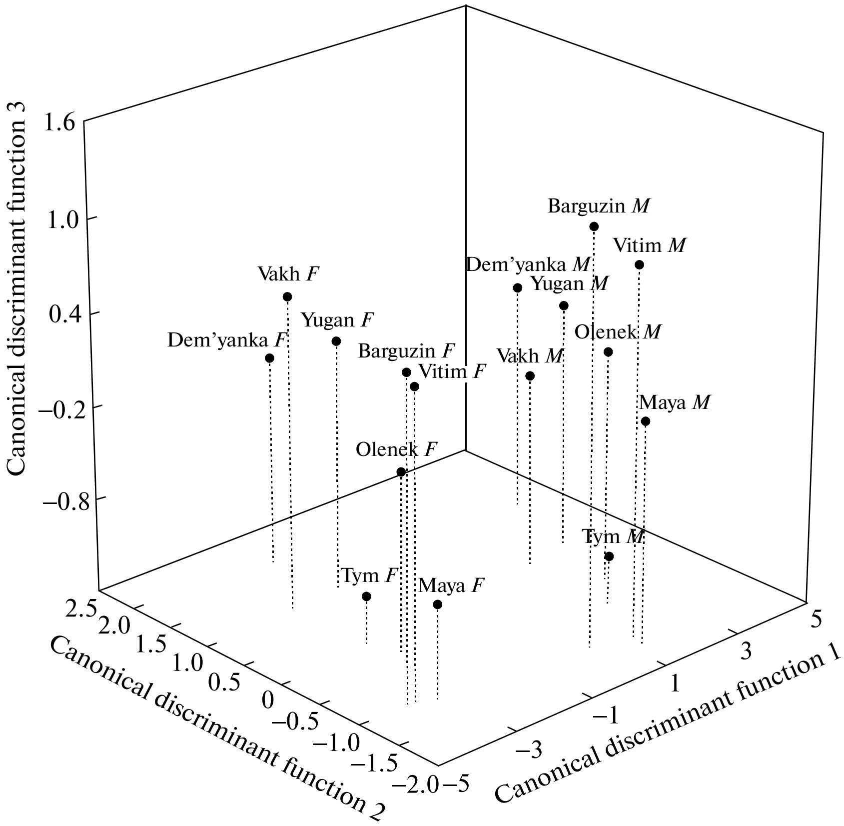

Fig. 4. Positions of samples in the space of first three canonical discriminant functions based on the results of discriminant analysis of cranial measurements of sables; (*F*) females and (*M*) males.

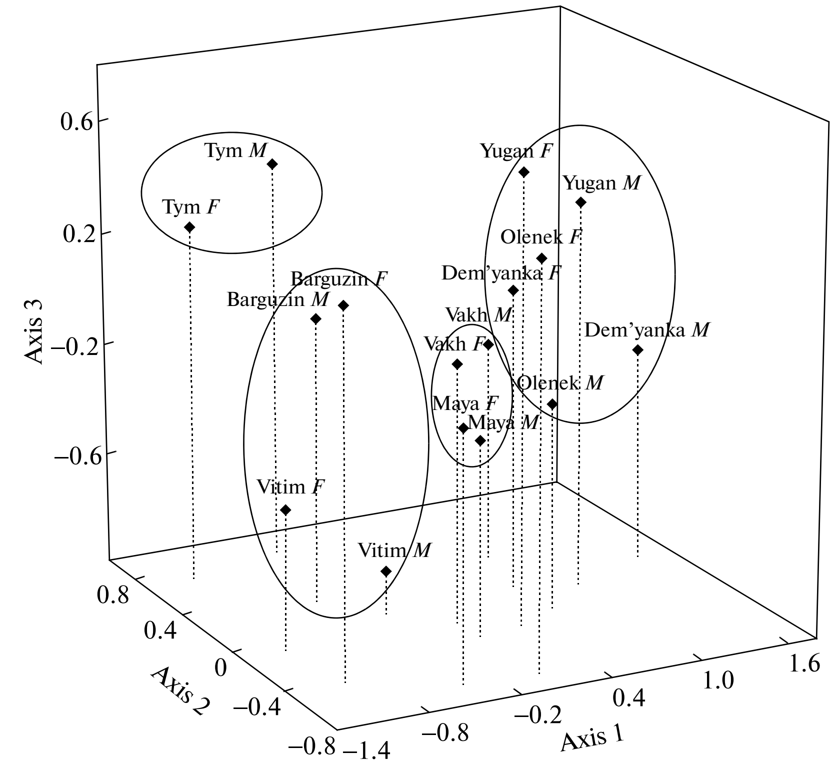

Fig. 5. Results of multidimensional scaling of the matrix of mean measure of divergence for sable populations. For designations, see Fig. 4.

Table 6. Values ($X \pm SD$) of the mean measure of divergence (MMD) in the sable population groups based on a set of nonmetric cranial characters

Sample	Dem'yanka	Yugan	Olenek	Barguzin
Dem'yanka		0.02 ± 0.007	0.034 ± 0.010	0.153 ± 0.012
Yugan	**0.013 ± 0.007**		0.023 ± 0.010	0.210 ± 0.013
Olenek	0.033 ± 0.010	**0.001 ± 0.01**		0.086 ± 0.017
Barguzin	0.108 ± 0.013	0.102 ± 0.012	0.067 ± 0.017	
Vitim	0.114 ± 0.011	0.137 ± 0.011	0.116 ± 0.015	0.035 ± 0.015
Vakh	0.017 ± 0.007	**0.012 ± 0.007**	0.021 ± 0.010	0.059 ± 0.013
Tym	0.126 ± 0.008	0.134 ± 0.007	0.148 ± 0.011	0.070 ± 0.014
Maya	0.09 ± 0.008	0.082 ± 0.007	**0.003 ± 0.011**	0.046 ± 0.014
Sample	**Vitim**	**Vakh**	**Tym**	**Maya**
Dem'yanka	0.142 ± 0.012	0.038 ± 0.007	0.178 ± 0.007	0.101 ± 0.007
Yugan	0.155 ± 0.012	0.025 ± 0.007	0.108 ± 0.007	0.076 ± 0.007
Olenek	0.033 ± 0.016	0.047 ± 0.010	0.076 ± 0.010	0.012 ± 0.010
Barguzin	0.029 ± 0.014	0.061 ± 0.012	0.028 ± 0.011	**0.023 ± 0.012**
Vitim		0.068 ± 0.012	0.062 ± 0.011	**0.021 ± 0.012**
Vakh	0.05 ± 0.011		0.084 ± 0.007	0.050 ± 0.007
Tym	0.059 ± 0.012	0.089 ± 0.008		0.079 ± 0.007
Maya	0.057 ± 0.012	0.044 ± 0.008	0.132 ± 0.009	

Note: Values for males and females are above and below diagonal, respectively. Bold type designates statistically nonsignificant values ($p > 0.05$).

region have the largest skull size among the samples considered. A relatively large size is characteristic of Yakut autochthonous population. Animals from the Baikal region have the smallest skull.

The study of descendants of introduced sables shows an increase in size in the acclimatization process (Monakhov, 1995, 2000). Acclimatizants are larger than sables inhabiting the Baikal region, where introduced animals come from. However, they do not reach the skull size of autochthonous sables inhabiting the same parts of the range.

An increase in skull size during acclimatization may be caused by adaptive mechanisms. Animals were captured in the Baikal region and translocated in certain areas of Middle Siberia with a less continental climate, higher mean temperatures, greater humidity, etc. (Pavlinov and Rossolimo, 1979), that is, areas substantially differing from natural conditions in their native land. During acclimatization, morphological changes are directed towards the phenotype of populations initially inhabiting similar environments.

It should be noted that the growth of size in animals of different species during acclimatization was marked previously. Among mammals, such data are known in the American mink in the Soviet Union (Popov, 1940); rabbit (*Felis silvestris catus*) and domestic cat (*Felis silvestris catus*) in the Kerguelen and Crozet archipelagoes in the Indian Ocean (Derenne, 1972; Derenne and Mougin, 1976); rabbit in Australia (McCluskey et al., 1974); muskrat in the Ob region (Vasil'ev et al., 1999); European beaver (Stavrovskii, 1986; Saveliev, 2003; Monakhov and Chernykh, 2004); ermine in New Zealand (King and Moody, 1982), and other species.

The population groups of acclimatized sables occupy an intermediate position between autochthonous animals of the Ob Basin and Baikal region populations of "founders," and some acclimatizants are more similar in phenotype to the founders, while others, to autochthonous animals occupying adjacent areas of the species range. The similarity between acclimatizants and sables of the Baikal region probably results from the genetic nature of the small cranial aberrations (Gruneberg, 1952; Berry and Searle, 1963; Berry and Jakobson, 1975). On the other hand, changes towards autochthonous populations in some acclimatizants of the Ob region (Vakh) could have resulted from nongenetic factors, showing the trend of natural selection towards the phenotype of populations initially dwelling in similar environments. Thus, the results obtained here and previous studies of phenotypic traits, such as fur color and fecundity of females (Monakhov, 2000, 2001), show that, in 30–40 years after introduction, acclimatizants acquired morphological features of the subspecies level.

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SPELL: 1. zibethicus, 2. Lepus, 3. europaeus, 4. Mustela