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A Comparative Analysis of Craniological Variability of Eurasian (Sable and Pine Marten) and North American (American Marten) Species of the *Martes* Genus

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Abstract—This paper studies the craniological variability of closely related species—the pine marten *Martes martes*, the American marten *M. americana*, and the sable *M. zibellina*. The study included the data on 22 nonmetric characters of skulls in 2344 individuals. The studied *Martes* species were revealed to have an evident species-specific manifestation of the investigated craniological characters. Sables stand apart most of all in the interspecific comparison of populations. The degree of epigenetic variability is somewhat higher in the sable than in the pine marten. The American marten significantly differs from Eurasian species in the manifestation of the nonmetric skull characters, which is noted when analyzing even a small number of samples.

Keywords: sable, pine marten, American marten, epigenetic distances, craniological characters
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INTRODUCTION

The Mustelidae family is considered to be very ancient among predatory mammals (Romer, 1939), although the modern representatives of the *Martes* genus, or martens themselves, appeared comparatively not long ago (the middle of the Pleistocene, 100000–700000 years ago). It is assumed that the global climate changes have caused the division of the range of the common ancestor of modern martens, and the ranges of the currently existing *Martes* species have formed out of the intact habitat nidi.

Modern martens are typical representatives of forest biocenoses in the temperate zone of the northern hemisphere. The pine marten (*M. martes*) inhabits the greater part of Europe, the Caucasus, and some regions of Western Asia (Geptner et al., 1967; Grakov, 1981). In sum, eight subspecies of the pine marten are described (Wozencraft, 2005); however, Geptner et al. (1967) noted that the subspecies taxonomy of the pine marten needed revision and that the probability of the existence of some subspecies described was very doubtful. The studies into the morphological variability of the species have shown that the skull size in the pine marten increases in its range from east to west (Monakhov, 2009) and from north to south (Reig, 1992). The studies into the interspecific epigenetic features of the pine marten have shown the stability of the frequencies of phenes in individuals of different generations and sexes, which were captured in different seasons (Grakov, 1972).

The sable (*M. zibellina*) lives in the taiga zone of Siberia and northeastern Europe. Due to the high polymorphism as well as a result of numerous introductions of the sable, the research into the taxonomic structure of the species is rather complicated (Monakhov, 2011). Different authors identify 4–17 sable subspecies (Geptner et al., 1967; Monakhov, 1976; Pavlinov and Rossolimo, 1979; Aristov and Baryshnikov, 2001). In the western part of the range, in the territory of the Urals, the habitats of sable are overlapped with the eastern part of the range of the pine marten, where a hybrid of the two species is encountered, i.e., kidas.

Since the late 19th century, two American marten species have been described in the fauna of Continental North America: *M. americana* (Turton, 1806) and *M. caurina* (Merriam, 1980). In 1953, Philip Wright, relying upon the results from studying the morphological properties of North American martens, supposed that the territory of North America was inhabited by one species *M. americana*, so *M. caurina*, which had been described earlier, was suggested to be considered as a subspecies of the American marten—*M. americana caurina* (Wright, 1953). Thus, until the late 20th century, the fauna of North America was described to include one species *M. americana* (Clark et al., 1987). In 1997, according to the results from studying molecular data, Carr and Hicks showed that the divergence of these two morphological forms of martens reached the species level and suggested again describing two marten species, i.e., the American marten (*M. americana*) and the Pacific marten (*M. caurina*) (Carr and Hicks, 1997). The American marten lives in the central parts of North America up to the Atlantic Ocean, whereas the Pacific marten occurs along the western coast of North America. The ranges of these two species overlap in the territory of southeastern Alaska, Montana, and British Columbia (Carr and Hicks, 1997; Hosoda et al., 1997).

However, despite the relative geographical isolation, the martens have retained a morphological similarity to each other. Thus, the pine marten, sable, and American marten are barely distinguishable by the skull structure. This peculiarity permits us to make a comparative analysis of the variability of homological cranial structures in order to assess the phylogenetic relationships inside the genus and specify the ways of radiation of the species.

The goal of this study is to analyze the interspecific variability of the *Martes* genus on the basis of craniological characters. The tasks include the classification of the skulls of the sable, pine marten, and American marten on the basis of 22 homological nonmetric skull characters.

MATERIALS AND METHODS

In sum, this study involved the data on 856 pine marten individuals from 16 geographical regions, 1434 sable individuals from 20 geographical regions, and 44 American marten individuals, of which six were defined by collectors as the Pacific marten (*M. caurina*) (Table 1, Fig. 1).

Each skull specimen studied in this work was classified according to the set of the following nonmetric characters (Ranyuk and Monakhov, 2011):

Characters	Phenes
1. First upper premolar	1.0 The first upper premolar is absent 1.1. The first upper premolar is present
2. Foramina in the maxillary bone near P^1	2.0 No foramina 2.1 One foramen 2.2 Two foramina 2.3 More than two foramina
3. Additional foramina before the incisive foramina	3.0 No foramina 3.1 One foramen 3.2 Two foramina 3.3 More than two foramina
4. Additional incisive foramina	4.0 No foramina 4.1 One foramen 4.2 Two foramina 4.3 More than two foramina
5. Foramina medial to M^1	5.0. No foramina 5.1 One foramen 5.2 Two foramina 5.3 More than two foramina
6. Palatine process	6.0 The process is absent 6.1. The process is present
7. Additional foramina near the interatrial foramen	7.0 No foramina 7.1 One foramen 7.2 Two foramina 7.3 More than two foramina
8. Additional foremen of the facial canal	8.0. No foramina 8.1 One foramen 8.2 Two foramina
9. Ethmoidal foramen	9.0. No foramina 9.1 Single olfactory foramen 9.2 Double olfactory foramen 9.3 The septum between the foramina is not complete
10. Foramen in the lower part of the condylar fossa	10.0 The foramen is absent 10.1 The foramen is absent
11. Foramina on the horizontal surface of the temporal bone	11.0 No foramina 11.1 One foramen 11.2 Two foramina 11.3 More than two foramina
12. Foramina near the middle part of the occipital ridge	12.0 No foramina 12.1 One foramen 12.2 Two foramina 12.3 More than two foramina
13. Foramen before the occipital protuberance	13.0 No foramina 13.1 One foramen 13.2 Two foramina 13.3 More than two foramina
14. Foramina in the upper part of the condylar fossa	14.0. No foramina 14.1 One foramen 14.2 Two foramina 14.3 More than two foramina
15. Supraorbital foramina near the postorbital process	15.0 No foramina 15.1 One foramen 15.2 Two foramina 15.3 More than two foramina
16. Foramina in the frontal bone behind the malar processes	16.0 No foramina 16.1 One foramen 16.2 Two foramina 16.3 More than two foramina
17. Anterior mental foramen	17.0. No foramina 17.1 One anterior mental foramen 17.2 Two anterior mental foramina 17.3 There are additional foramina

Table 1. Studied materials

	Sample	Geographic location	Number of individuals studied (including males)	Collection (years of gathering)
American marten				
1	*M. americana*	The Alaska Peninsula, United States; Montana, the United States; Ontario, Canada; the Labrador Peninsula, Canada	38 (19)	A(1952–1962); B (1960–1961); C (1864–1907)
2	*M. caurina*	The environs of Cariboo Lake, British Columbia, Canada	6 (4)	A (1953)
Pine marten				
3	Brandenburg	The environs of the city of Brandenburg, Eastern Germany	32 (23)	F(1992–1998)
4	Upper Lusatia	The environs of the city of Gorlitz, Eastern Germany	20 (14)	E (1966–1999)
5	Arkhangelsk	Arkhangelsk oblast	57 (27)	C (1954–1971)
6	Bashkiria	Belaya River Basin, Bashkiria	47 (28)	C (1957–1967)
7	Vologda	Vologda oblast	50 (26)	C (1953–1973)
8	Caucasus	Caucasian Nature Reserve	67 (33)	C (1954–1956)
9	Karelia	Republic of Karelia	63 (35)	C (1959–1974)
10	Kirov	Kirov oblast	63 (32)	C (1961–1971)
11	Leningrad	Leningrad oblast	66 (34)	C (1960–1972)
12	Moscow	Moscow oblast	35 (21)	C (1907–1980)
13	Novgorod	Novgorod oblast	62 (39)	C (1957–1971)
14	Perm	Perm oblast	48 (26)	C (1960–1967)
15	Pechora	Pechora-Ilych Nature Reserve	62 (30)	C (1948-1962)
16	Sverdlovsk	Shalya region, Sverdlovsk oblast	105 (60)	A (1964–1970); C (1949–1974)
17	Tatarstan	Republic of Tatarstan	38 (22)	C (1949–1967)
18	Tobolsk	Tobolsk region, Tyumen oblast	41 (19)	C (1958–1962)
Sable				
19	Alatau	Kuznetskii Alatau Plateau	60 (35)	B (1942)
20	Aldan	Upper Aldan River Basin, Yakutia	117 (70)	G (1960, 2005–2006)
21	Altai	The environs of the city of Gornoaltaisk, Altai krai	40 (26)	B (1951–1952)
22	Angara	Angara River Basin, Boguchany region, Kransnoyarsk krai	55 (29)	B (1941–1947)
23	Baikal	Baikal Nature Reserve	142 (74)	H (1995–1997, 2004–2006)
24	Vakh	Vakh River Basin, Khanty-Mansiysk Autonomous District, Nizhnevartovsk region	60 (30)	A (1979–1989)
25	V. Yana	The environs of the city of Verkhoyansk, Yakutia	54 (31)	G (1962)
26	Demyanka	Demyanka River Basin, Tyumen oblast, Uvat region	60 (30)	A (1986–1987)
27	Kamchatka	Kamchatka Peninsula	76 (48)	B (1941–1946)
28	Kamchatka 19	Kamchatka Peninsula	71 (37)	B (1884–1890)

Table 1. (Contd.)

	Sample	Geographic location	Number of individuals studied (including males)	Collection (years of gathering)
29	Kolyma	Lower Kolyma River Basin, Yakutia	86 (44)	G (1972–1978, 2006–2007)
30	Krasnoyarsk	The environs of the city of Krasnoyarsk	44 (24)	B (1892)
31	Maya	Lower Maya River basin, Yakutia	56 (30)	A (1991)
32	Narym	The environs of the settlement of Narym, Parabel region, Tomsk oblast	50 (23)	B (1953–1954)
33	Olekma	Olekma River Basin, Yakutia	68 (44)	G (1961–2003)
34	Olenek	Olenek River Basin, Yakutia	151 (87)	A (1989); G (2005–2006)
35	Pechora	Pechora-Ilych Nature Reserve	42 (25)	C (1961–1962)
36	Tomsk	The environs of the city of Tomsk, Tomsk oblast	76 (39)	B (1964–1965)
37	Tym	Tym River Basin, Tomsk oblast	58 (32)	I (1982–1989)
38	Yugan	Yugan River Basin, Khanty-Mansiysk Autonomous District, Surgut region	68 (31)	A (1981–1985)

A is the Institute of Plant and Animal Ecology, Ural Branch Russian Academy of Sciences, Yekaterinburg; B is the Zoological Institute, Russian Academy of Sciences, St. Petersburg, C is the Zoological Museum, Moscow State University, Moscow; D is the Natural Science Museum, Berlin; E is the Senckenberg Natural History Museum, Gorlitz, Germany; F is Dresden University, Institute of Forest Botany and Zoology, Tharandt, Germany; G is the Institute of Biological Problems of the Cryolithozone, Siberian Branch, Russian Academy of Sciences, Yakutsk; H is the Baikal Nature Reserve, the settlement of Tankhoi, Buryatia, I is the All-Russia Research Institute of Hunting and Animal Breeding, Russian Academy of Agricultural Sciences, Kirov.

18. Incisive mental foramen	18.0. No foramina 18.1 One incisive mental foramen 18.2 Two incisive mental foramina 18.3 There are additional foramina
19. Foramina in the mandibular bone near the internal edge of alveolus P_1	19.0. No foramina 19.1 One foramen 19.2 Two foramina 19.3 More than two foramina
20. Foramen in the frontal part of the masseteric fossa near M_2	20.0 No foramina 20.1 One foramen 20.2 Two foramina 20.3 More than two foramina
21. Foramina in the back part of the masseteric fossa near the articular process	21.0 No foramina 21.1 One foramen 21.2 Two foramina 21.3 More than two foramina
22. First lower premolar	22.0 The first lower premolar is absent 22.1. The first lower premolar is present

The location of the nonmetric characters studied in the skull is shown in Fig. 2.

All characters, except for the medial third, sixth, and thirteenth characters, were fixed on the left and right sides of the skull. This work was carried out using a 8 × 23 MBS 10 binocular microscope.

Thus, the study involved 22 nonmetric skull characters, which were in sum described by 79 phenes. The studied material was divided into samples according to the species, sex, and geographical location of the sample.

The statistical analysis of digital data was carried out using the Statistica 5.5 software package (StatSoft, Inc., 1995). To estimate the epigenetic similarity, the mean measure of divergence (MMD) was calculated by the formula proposed by Smith (Smith, 1972) and subsequently modified by Sjovold (Sjovold, 1977) and Hartman (Hartman, 1980).

In order to calculate the MMD, the transformed frequencies of phenes (Q) were used: $Q = 1/2\sin^{-1}[1 - 2k/(n + 1)] + 1/2\sin^{-1}[1 - 2(k + 1)/(n + 1)]$, where k is the frequency of a phene and n is the number of observations (the number of investigated sides of the skull for the bilateral characters).

The mean measure of divergence (MMD) was calculated using the formula

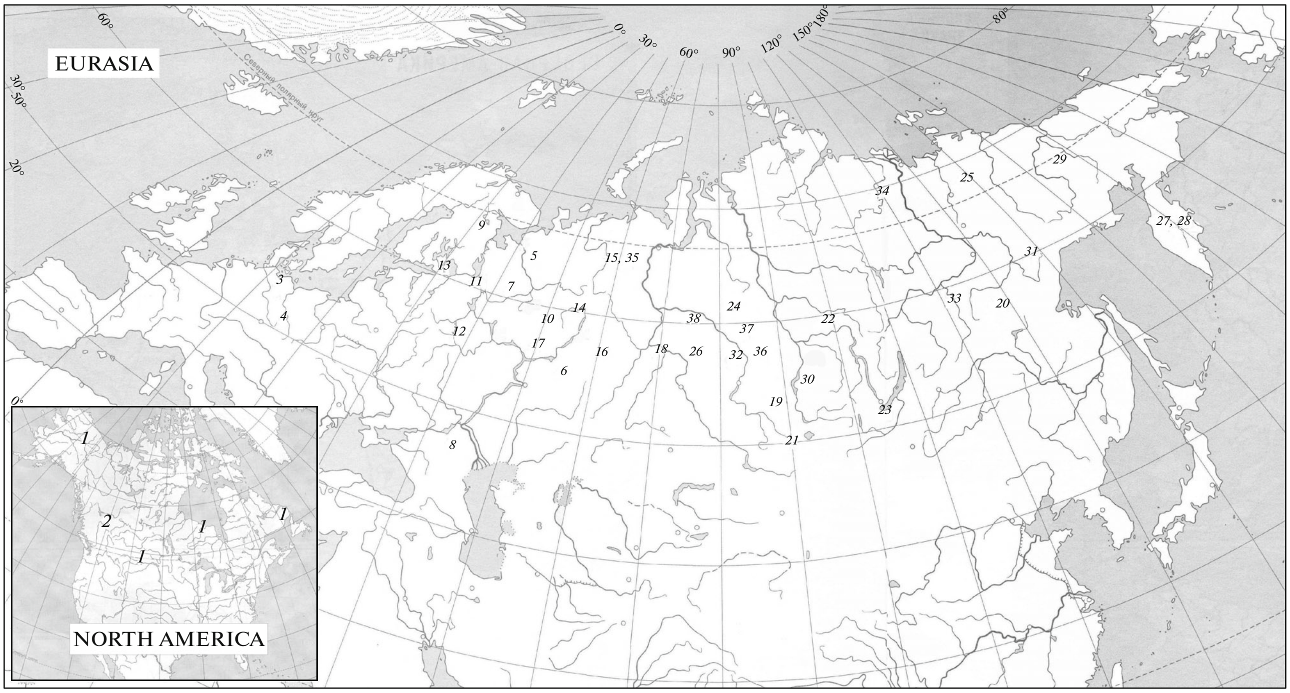

Fig. 1. Geographical localization of the investigated samples of the sable, pine marten, and American marten. The numbers in the map correspond to the numbers in Table 1.

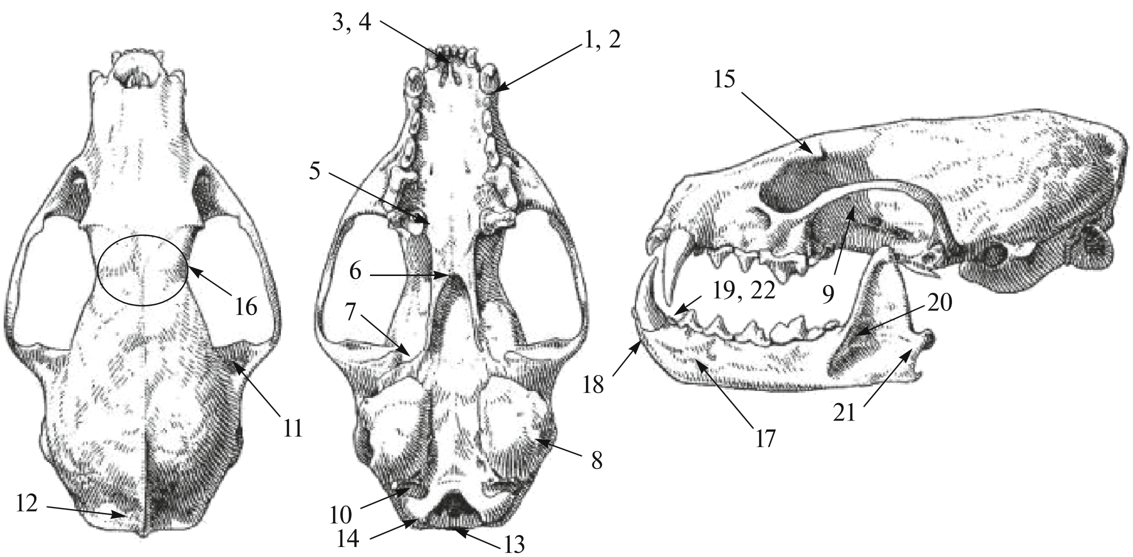

Fig. 2. Localization of the investigated nonmetric characters of martens in the skull. The characters are described in the section Materials and Methods.

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

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

RESULTS

The Frequency of Phenes

In all the studied nonmetric skull characters, the manifestation of phenes significantly ($p < 0.05$) depends on the species (Table 2). Among the characters, the highest value of the Pearson χ^2 criterion proves to be possessed by character 21 (the foramina in the back part of the masseteric fossa near the articular process): in the pine and American martens, the foramina are absent in almost half of the individuals (45 and 43%, respectively), whereas such animals account for 12 and 17% in the sable and Pacific marten, respectively (Table 2). In a prevalent part of pine marten individuals (82%), character 9 (the ethmoidal foramen) appears as one foramen, whereas among sables animals with one foramen account for 43%, among American martens they account for 10.5%, and all the studied Pacific marten individuals have a double ethmoidal foramen. In most of the martens studied, additional incisive foramina (character 4) are absent, whereas among sables there are only 54% with this phene. In addition, among the three marten species, most individuals have one additional foremen of the facial canal (character 8); among sables, such animals account for somewhat more than half (Table 2). The characters that characterize oligodontia (1 and 22) have the lowest value of the Pearson χ^2 criterion, and the share of individuals that do not have the first upper and lower premolars varies insignificantly between the species (Table 2).

Epigenetic Distances

The results from analyzing the mean measure of divergence between the studied marten populations showed that the values of least distance were reached between the female and male samples from the same geographical point (the epigenetic distances between males and females are maximal in the Verkhoyansk sables (MMD = 0.068) and Karelian pine martens (MMD = 0.057)). In addition, relatively low distance values were obtained when comparing populations inside a species. The values of MMD between the geographical samples for American martens do not surpass 0.104 (between females of the American and Pacific martens). Among pine martens, the populations from East Germany proved to be the most distant according to the results from analyzing the values of MMD (for males, $MMD_{max} = 0.197$ between the samples from the Upper Lusatia (Saxony) and martens from Vologda oblast; for females, $MMD_{max} = 0.171$ between the samples from the environs of the city of Brandenburg (East Germany) and martens from Moscow oblast). The values of epigenetic distances between the sable populations turned out to be somewhat larger. For females, MMD_{max} reaches the value of 0.318 between the samples from the Olekma River Basin and Kuznetskii Alatau Plateau; for males, MMD_{max} is 0.270 for the samples from Kamchatka Peninsula and the Upper Yana River Basin.

The highest values of epigenetic distances were obtained in the interspecific comparison, where the upper boundary of the mean measure of divergence reached the value of 0.514 (between the populations of the pine marten and sable, Table 3).

The results of the multidimensional scaling of the epigenetic distance matrix are presented in Fig. 3. The location of the studied samples in the space of the first two axes is fairly species-specific: along the first axis, we can note the division of the sable and martens; along the second axis, the samples of the pine and American martens are divided. The cluster analysis of the epigenetic distance matrix by the method of the unpaired weighted mean results in marking out three large clusters in which the studied samples are also have a species-specific location (Fig. 4). American martens inside the cluster are divided by age into young-of-the-year individuals, to which the studied individuals of the *M. caurina* species also belong, and adult individuals. In comparing the distances between the samples of the pine marten, it is interesting to point out that two studied marten samples from Eastern Germany were put into the opposite branches of the cluster. The values of MMD between the samples from the Upper Lusatia and Brandenburg came to 0.115 for males and 0.133 for females, which may indicate a rather high degree of isolation of individual pine marten populations in the territory of Eastern Germany. The obtained data agree with the results of other researchers (Ansorge, 1992), who also noted the high degree of craniological divergence between the pine marten populations in Saxony. This may be due to the fragmentariness of forest massifs on the territory of Central Europe as well as to the high development of the network of settlements and urban motorways, which leads to a certain isolation of individual pine marten populations.

The studied sable samples were divided into two clusters, one of which proved to include samples from the central part of Western Siberia and Yakutia, and another turned out to contain populations from the Kamchatka Peninsula, the Baikal Region, the Northern Urals, and southeastern Western Siberia (Fig. 4). It is noteworthy that the Kamchatka samples of the 19th century and 1940s have very low epigenetic distances between each other (MMD is 0.015 for males and 0.001 for females), which may indicate that there is no chronographic variability in the manifestation of the nonmetric skull characters in the sable.

The values of epigenetic distances between the sable and pine marten samples from the Pechora-Ilych Nature Reserve were 0.099 for females and 0.124 for males; i.e., despite the similar habitat conditions and possible interspecific hybridization, the species retain the specificity in the manifestation of craniological characters in the transgression zone.

Table 2. Phenes percentage of the studied craniological characters in the sable, pine marten, American marten, and Pacific marten

Phenes	Pearson χ^2 (*df*)	*M. martes*	*M. zibellina*	*M. americana*	*M. caurina*
21.0	970 (9)	45.4	12.2	43.4	16.7
21.3		2.6	25	3.9	3.9
9.1	826.1 (9)	82.8	43.5	10.5	0
9.2		15.2	46.2	77.6	100
11.0	816.5 (9)	18.9	3.9	11.8	33.3
11.3		12.3	45.6	25	0
4.0	741 (9)	90.9	53.8	86.8	83.3
4.1		8.2	32.6	13.2	16.7
8.1	622.1 (9)	87.4	53.8	97.4	100
8.2		12.3	45.7	2.6	0
15.0	549 (9)	12.2	21.2	55.3	41.7
15.2		24.6	9.7	2.6	8.3
17.1	421 (9)	12.5	2.7	1.3	0
17.2		55.9	82	76.3	75
14.1	399.3 (9)	55.2	31.3	43.4	91.7
14.3		10.1	31.5	17.1	0
2.0	222.9 (9)	48.2	31.5	78.9	100
2.1		42.6	51.2	17.1	0
10.0	142.6 (6)	80.1	64.4	71.1	50
10.1		19.7	35.5	28.9	50
3.1	135.5 (9)	5.7	4.5	28.9	66.7
3.3		74.7	82.1	36.8	16.7
12.0	133.6 (9)	31.7	26.5	32.9	83.3
12.1		11.1	18.8	13.2	0
18.1	130.9 (9)	40.3	27.3	21.1	16.7
18.3		9.3	18.3	19.7	41.7
16.0	45.2 (9)	52.6	49.2	80.3	58.3
16.1		36.8	39	14.5	41.7
5.1	43.7 (9)	12	10	6.6	0
5.3		58	64.6	85.5	75
6.0	42.6 (3)	3.4	6.7	26.3	16.7
6.1		96.6	93.3	73.7	83.3
7.0	41.4 (9)	22	24.5	35.5	16.7
7.1		73.3	67.6	64.5	83.3
13.1	27.4 (9)	12.1	9.6	13.2	16.7
13.2		31.2	24.5	13.2	33.3
22.0	20.9 (3)	11	15.3	7.9	0
22.1		89	84.7	92.1	100
1.0	19.2 (3)	2.7	5.2	1.3	0
1.1		97.3	94.8	98.7	100

* The description of the phenes is given in the section Materials and Methods.

Table 3. Epigenetic distances (mean, minimum, maximum) in the intra- and interspecies comparison of the studied marten species

Species	Number of population samples	*M. americana*	*M. martes*	*M. zibellina*
M. americana	2	0.031 (0.001, 0.104)		
M. martes	16	0.188 (0.091, 0.394)	0.07 (0.001, 0.197)	
M. zibellina	20	0.222 (0.044, 0.469)	0.197 (0.046, 0.514)	0.092 (0.001, 0.318)

* The values obtained by the intrapopulation comparison inside the species are given in the diagonal.

Consequently, the studied *Martes* species have an evident species-specific variability of the investigated craniological characters. In the sable, the degree of epigenetic variability is higher than in the pine marten. This may be due to the peculiarity of the material studied: in this work, the range of the pine marten is represented mainly by the eastern part, whereas the range of the sable is covered completely enough. According to

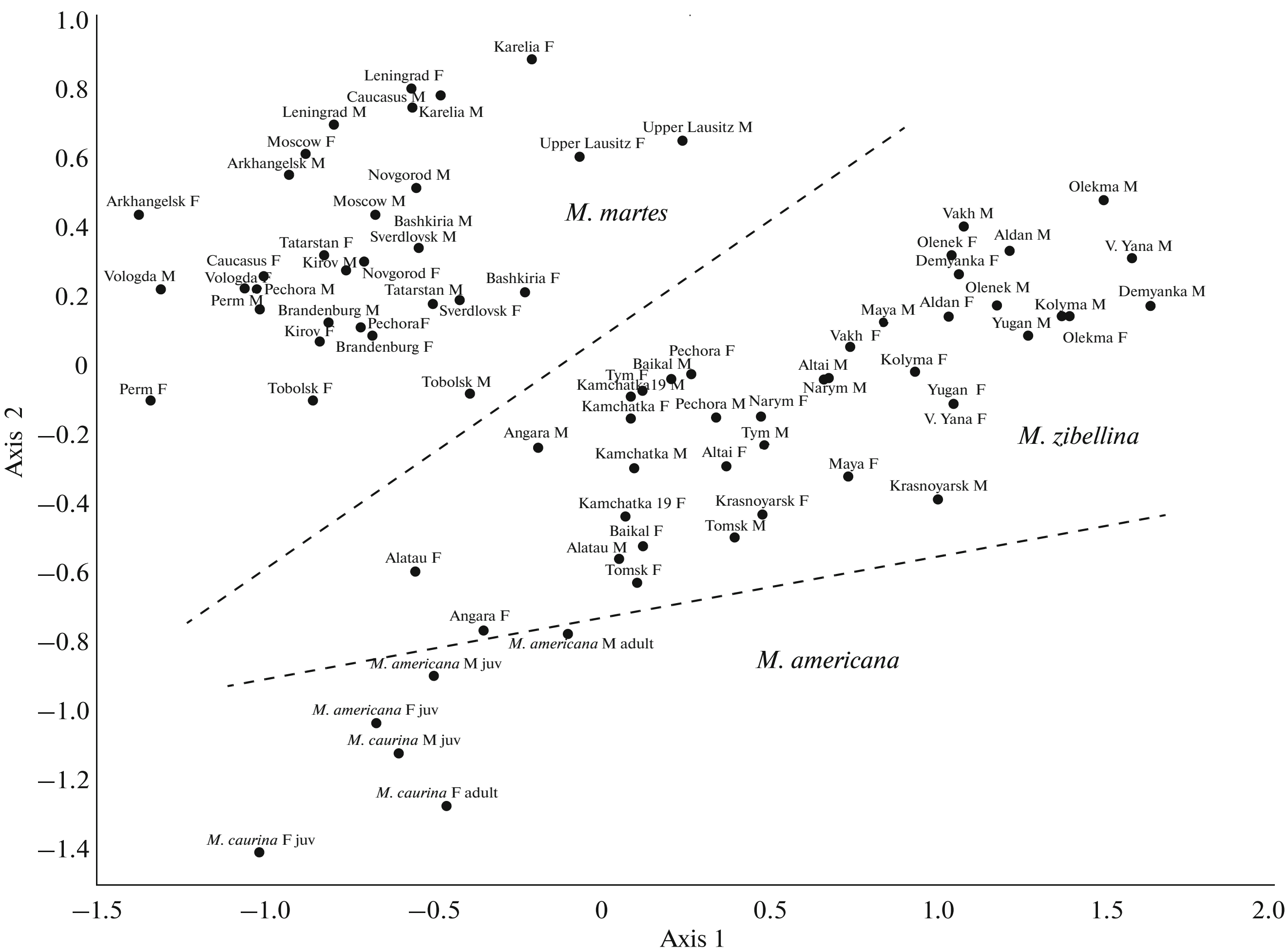

Fig. 3. Results of the multidimensional scaling of the matrix of epigenetic distances (MMD) between the investigated samples of the sable and marten. Three axes, stress 0.10. F is females, M is males, juv is young-of-the-year individuals, adult is adult individuals.

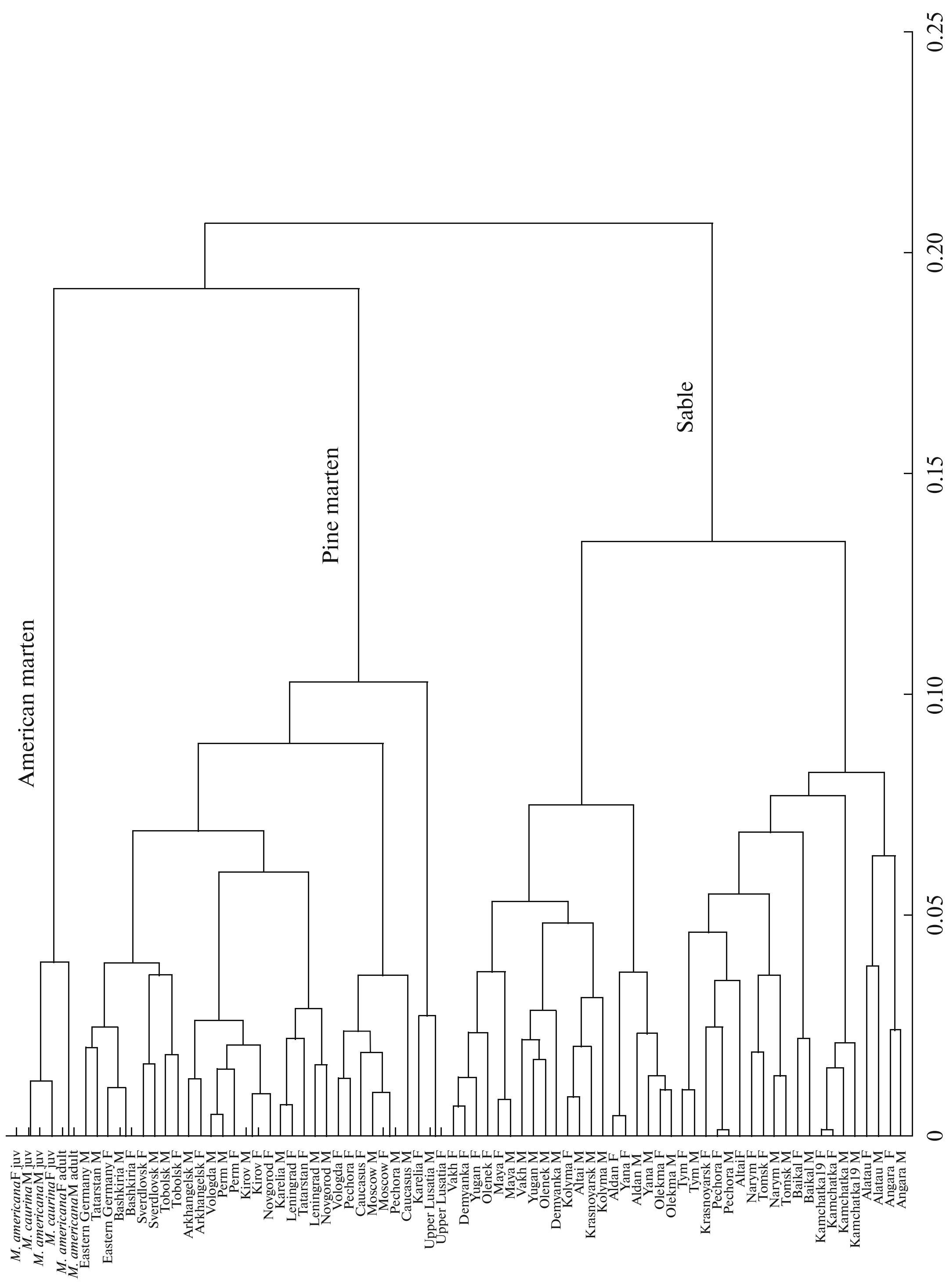

Fig. 4. Results of the cluster analysis of the matrix of epigenetic distances (MMD) between the studied samples of the sable and martens. The method of the unpaired weighted mean is used.

the data of other authors who studied the genetic properties (Pishchulina, 2013) and odontoglyphic variability (Gimranov, 2012) of the *Martes* genus, the sable is also observed to have a higher degree of variability of the properties studied than the pine marten.

DISCUSSION

The sable, pine marten, and American marten together with the Japanese sable (*M. melampus*) are allopatric marten species, which occupy analogous ecological niches within their range and have a very high morphological similarity among each other. It is assumed that these contemporary marten species came from a common ancestor approximately in the middle of the Pleistocene; moreover, relying upon the data on fossil materials and the morphology of contemporary species, H. Anderson supposed that the pine marten was a more ancient form, from which the sable, Japanese sable, and American marten descended (Anderson, 1970). Based on the similarity of cranial characters, allopatrie of the range, and similarity of ecological characteristics, Hagmeier suggested that the sable, American marten, pine marten, and, possibly, the Japanese marten should be joined into one circumboreal species (Hagmeier, 1961). Based on the phylogenetic study of the *Martes* species, Anderson suggested considering these marten species as a super-species according to Mair, that is, “a phylogenetic group of completely or almost completely allopatric species, which are too morphologically different to be joined into one species” (Mair, 1963).

Pavlinin (1962), who made a comparative study of the morphology of the American marten, sable, and pine marten, notes that the American marten has the characters of both the sable (the color of fur and fluffy feet) and marten (a long tail). Different craniological characters and the structure of the baculum vary widely enough in all three species, and so they cannot be a clear diagnostic criterion. The author assumes that the “contemporary sable and American marten came from the sablelike marten form, which was formerly common in Asia and America (moreover, the western hemisphere could also have been the motherland of the progenitor form)” (Pavlinin, 1962).

The use of the modern molecular methods in studying the species of the *Martes* genus is somewhat complicated due to the high interspecific genomic similarity; however, most researchers assume that the sable is one of the “youngest” species among true martens (Hosoda et al., 2000; Koepfli et al., 2008; Sato et al., 2009). According to the data of some authors (Hosoda et al., 2000; Koepfli et al., 2008), the divergence of the sable and pine marten was the last to take place, and the American marten and Japanese sable had formed as species somewhat earlier. However, the research by Sato et al. (2009) confirm the hypothesis of Anderson about the origin of the contemporary true martens, whereas the American marten, sable, and Japanese sable formed as species somewhat later.

According to the results of this study of the craniological variability in the *Martes* species, we can conclude that the manifestation of nonmetric skull characters is species-specific in the studied species of true martens. In the sable, the craniological variability inside the species is somewhat higher than in the pine marten. Due to the scarcity of materials for North American martens, it is difficult to make convincing conclusions about the craniological variability of these species. However, according to the preliminary results obtained, the American marten differs from the Eurasian marten species in the manifestation of the nonmetric skull characters, which is fixed even on the basis of scanty materials. The sable stands apart most of all in the interspecific comparison. It is hard to judge whether this result confirms the fact that the sable formed as a species later than other *Martes* species. The obtained level of epigenetic distinctions between the Eurasian and North American species does not surpass the level of distinctions between the species that live on the same continent. Perhaps more complete data on the range of the pine, American, and Pacific martens as well as the inclusion of the Japanese sable (*Martes melampus*) in the study will allow specifying the phylogenetic geography of the *Martes* species.

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