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Intraspecific Variability of the Shape of the Lower Third Premolar in *Ochotona hyperborea* (Pallas 1811)

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Abstract—The shape variability of the chewing surface of the third lower premolar (p_3) was analyzed in modern members of the Northern Pika (*Ochotona hyperborea*). The variability in the three main features characterizing the tooth shape was revealed: the visual position of the isthmus connecting the anteroconid and the posteroconid, and separately the shapes of both the anteroconid and the posteroconid. A combinatory matrix showing the distribution of the three morphotypes of the p_3 chewing surface was developed based on their distinguishing features. Both the northern and southern parts of the pika's distribution area are dominated by individuals differing in the p_3 morphotypes.

Keywords: teeth, morphotype, combinatory matrix, morphospace, *Ochotona hyperborea*

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INTRODUCTION

The northern pika *Ochotona hyperborea* (Pallas 1811) belongs to one of the most widespread species in northern Asia. Its habitat is mainly associated with stony placers on the open and covered with forest and shrubbery mountain slopes, the banks of rivers, and the sea coast. The wide distribution of this species naturally attracted researchers to study various aspects of its variability. The geographic variability of the skull (Lissovsky, 2003) and molecular genetic (Lissovsky, 2014), karyological (Vorontsov and Ivanitskaya, 1973; Kartavtseva et al., 2014), and bioacoustic studies (Kawamichi, 1981; Lissovsky and Lissovskaya, 2002; Lissovsky, 2005) have been conducted. Of particular interest is the study of intraspecific variability of the third lower premolar tooth p_3, which is most often used in the identification of fossil pikas, the remains of which are often represented only by individual teeth. A recent study of variability by the method of geometric morphometry of the shape of the anteroconid and anterior folds (para- and protoflexids) in four modern species of pikas showed the absence of significant differences between the studied species in the shape of these structures, which is associated with their significant intraspecific variability (Volkova and Lissovsky, 2018). At the same time, in this work, high intraspecific variability is only recorded, and the entire space of the morphological states of the shape of the third lower premolar tooth in the species under study are not considered. There are no studies on the intraspecific variability of the shape of this tooth, which significantly complicates both the diagnosis of fossil pikas and a comparative study of its morphotypic variability over time. The number of finds of the northern pika in the fossil state is increasing (Lissovskiy and Serdyuk, 2004; Panasenko and Tiunov, 2010; Kalmykov, 2015; etc.), so there is an urgent need to analyze the entire morphospace of the chewing surface of the third lower premolar tooth, primarily in modern representatives of this species.

MATERIALS AND METHODS

Examination of the third lower premolar tooth (p_3) of the northern pika was carried out on the collection materials of the theriology laboratory of the Federal Research Center of Biodiversity, Far East Branch, Russian Academy of Sciences, and the Zoological Museum, Moscow State University.

In total, 183 third lower premolars of the northern pika from ten localities were examined.

The research was carried out in several stages. At the first stage, the distribution of the dimensional characteristics of the tooth were calculated. Then the signs were identified with the help of which it is possible to characterize the morphotypic variability of the occlusal surface of the tooth studied. For various states of these signs, their frequency of occurrence was calculated. At the last stage, comparisons and analysis of the most common morphotypes were carried out.

This work used one of the methods of multivariate statistics, namely sequential discriminant analysis.

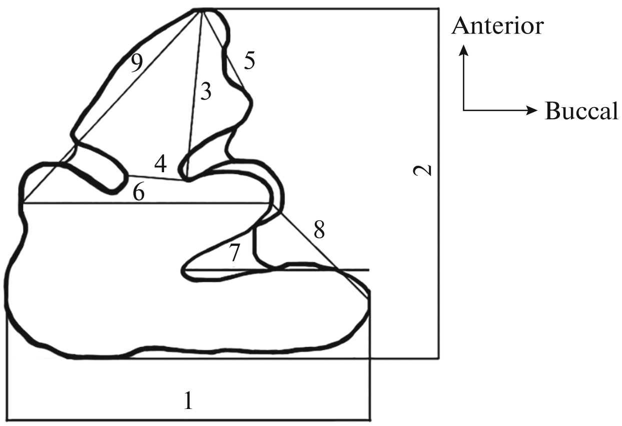

Fig. 1. Measurement scheme of p_3 of the northern pika *Ochotona hyperborea*. Explanations in the text.

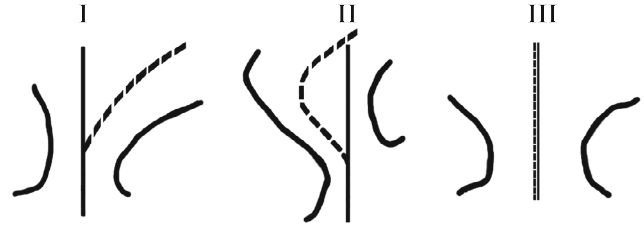

Fig. 2. Scheme of the position of the isthmus relative to the apex of the anteroconid: I, curved isthmus; II, S-shaped isthmus; III, straight isthmus. The dotted line shows the direction of the isthmus relative to the apex of the anteroconid.

The sequence of the analysis consisted in combining the samples studied using the matrix classification function and the Mahalanobis distance. To calculate the reliability of the Mahalanobis distances, it was customary to use a p-value of 0.01, since the sample size was $n > 100$ (Nasledov, 2004). To calculate the significance of differences between the samples according to the dimensional characteristics of the premolar teeth, Student's t test was calculated. Since there are no statistical differences between males and females (Lissovsky and Serdyuk, 2004; Lissovsky, 2014; Volkova and Lissovsky, 2018), the samples were analyzed without division by sex. The calculations were performed using the Statistica 13 software.

In this work, nine measurements were used (Fig. 1): 1, the width of the tooth; 2, the length of the tooth; 3, the distance between the most nasal point of the anterior segment and the deepest point of the buccal loop; 4, the width of the isthmus between the anterior and posterior segments; 5, the width of the buccal part of the anterior segment, i.e., the distance between the most nasal and buccal points of the anterior segment; 6, the distance between the most buccal point of the second segment and the most convex part from the lingual side; 7, the length of the buccal loop of the third segment, i.e., the distance between the most buccal point of the third segment and the deepest point of the posterior buccal loop; 8, the distance between the most buccal points of the second and third segments; and 9, the distance between the most nasal point of the anterior segment and the most convex part from the lingual side.

All measurements and drawings of the chewing surface of the teeth were made only in adults using a Zeiss Stemi SV 6 binocular microscope with eyepiece measurements presented in millimeters. To compile a morphological classification table, the images obtained with a microscope were scanned with subsequent processing in Photoshop CS6.

Morphological Research

Due to the lack of studies on the isolation of the phenotypes of the occlusal surface of the teeth in pikas, the search for the most important varying traits for this study was carried out by analogy with how it was carried out in other studies on mammals (Krukover, 1989; Pozdnyakov, 2005, 2011; Gimranov, 2015 ; Gimranova and Kosintsev, 2017). Below is a detailed description of the various conditions used in the work of the features of the occlusal surface of the third lower premolar tooth of the northern pika.

The shape of the isthmus connecting the anteroconid and posteroconid. The change in this feature depends on the location of the para- and protoflexid in relation to each other; the length and shape of these flexids and the apex of the anteroconid. In this work, three positions of the isthmus are used: I, curved; II, S-shaped; III, straight.

The curved isthmus is characterized by a low position of the protoflexid to the paraflexid, due to which a curved line can be drawn from the beginning of the middle of the isthmus to the apex of the anteroconid. With an S-shaped isthmus, the paraflexid is in the lower position, and, therefore, the line from the beginning of the isthmus to the apex of the anteroconid has a curved shape (Fig. 2). With a straight isthmus, the paraflexid and protoflexid are opposite each other and form a straight line; a straight line can be drawn from the beginning of the isthmus to the apex of the anteroconid.

Anteroconid shape. Since in the process of chewing in pikas, a large load falls on the anteroconid (Gureev, 1964), this structure is quite changeable. In this work, eight variants of the structure of the anteroconid are distinguished (Fig. 3).

Type a. Anteroconid in the form of a rhombus, without pronounced or with a barely noticeable incoming fold on the labial side.

Type a_2. Anteroconid in the form of a rhombus without pronounced processes and folds.

Type b. The anteroconid is rounded, with a pronounced process on the lingual or labial sides.

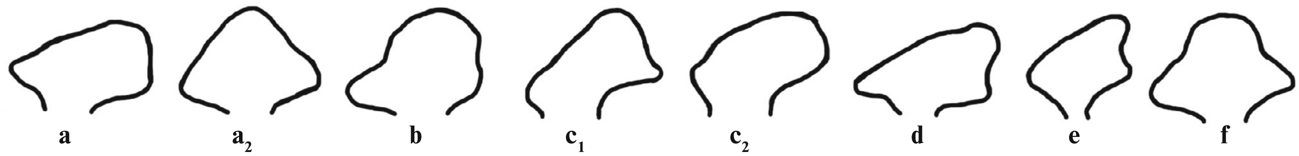

Fig. 3. Anteroconid shape. Explanations in the text.

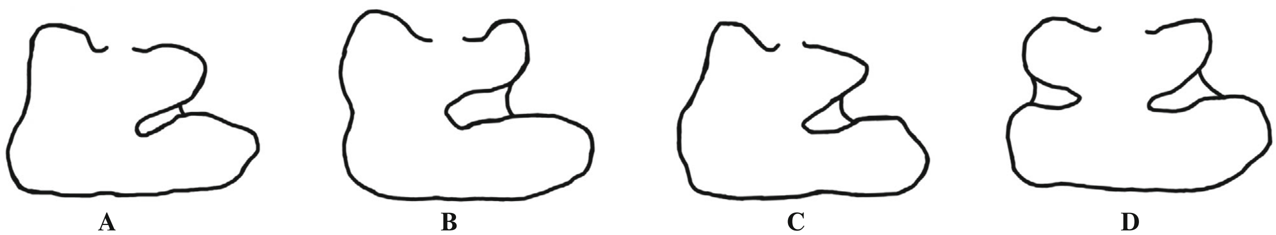

Fig. 4. Posteroconid shape. Explanations in the text.

Type c_1. Anteroconid in the form of an oval with a short process on the labial side.

Type c_2. Anteroconid in the form of an oval without pronounced processes.

Type d. Anteroconid in the form of a rhombus or trapezoid. The difference from other types is the presence of an incoming fold on the labial side, a flat upper part of the paraflexid fold, and a long lingual side.

Type e. The anteroconid is rhomboid, with an elongated apex, and has an incoming fold and a small process on the labial side.

Type f. The anteroconid is trapezoidal, with pronounced processes on the lingual and labial sides. The apex of the anteroconid is flat or conical. In rare cases, the processes on the lingual and labial sides may be barely visible.

Posteroconid shape. The most characteristic changing structures are the form of the protoconid, the presence/absence of a mesoflexid (Fig. 4).

Type A. Wide protoconid, with apex elongated in a straight direction. It is the most common in the sample under study.

Type B. Wide protoconid, rounded and extended upward with its apex.

Type C. The protoconid is very short and has a pointed, triangular shape.

Type D. The only type with a presumptive aberrant trait is the presence of a mesoflexid. It is the rarest in the entire study sample.

Expanding the features by states, we obtain a combinative lattice showing the distribution of morphotypes of the occlusal surface p_3 by their distinguishing features. Such a lattice allows one to see the limits of the variety of the shape of the chewing surface of the third lower premolar of the northern pika and clearly shows which cells remain empty and which morphotypes can still be expected.

The defining criteria for morphological classification are the shape of the isthmus connecting the anteroconid and the posteroconid and the type of structure of the anteroconid and posteroconid (Table 4). The classification table is a rectangular grid of eight vertical rows equal to the number of anteroconid types and 12 horizontal rows. For greater compactness of the table, the distribution of the characteristic by the shape of the isthmus was decided to be located on the left-hand part of the table. Due to this, the series of posteroconid types are divided into three groups, numbered in Roman numerals. Each vertical and horizontal cell contains graphical representations of the isthmus shape and the types of anteroconid and posteroconid, with the assignment of a letter designation to them.

In the cells obtained from the intersection of rows and rows, the graphical schemes of the pattern of the chewing surface of the teeth are placed. Each model corresponds to a specific pattern of the chewing surface of the teeth.

When any new state of a trait is found in modern or fossil teeth, the classification table can be changed and supplemented. It is also possible that some models of the occlusal surface of the third lower premolar do not exist in principle and the cells will remain empty.

Any morphotype can be written as the following expression:

$$X - y - Z,$$

where X is the digital designation of the isthmus shape, y is the letter designation of the anteroconid shape, and Z is the letter designation of the posteroconid shape.

Table 1. Mahalanobis distance squared

Groups	Chukotka	Kamchatka	Polar Ural	Amur region	Tuva	Yakutia	Transbaikalia	Khabarovsk krai	Primorskii krai	Sakhalin
Chukotka		1.42 (0.00)	5.75 (0.02)	12.88 (0.00)	5.27 (0.00)	7.94 (0.00)	6.05 (0.00)	7.78 (0.00)	10.74 0.00	11.37 (0.00)
Kamchatka	1.42 (0.00)		5.97 (0.02)	8.87 (0.00)	3.22 (0.00)	4.85 (0.00)	3.16 (0.00)	4.28 (0.00)	7.54 (0.00)	6.60 (0.00)
Polar Urals	5.75 (0.02)	5.97 (0.02)		22.75 (0.00)	10.21 (0.00)	14.64 (0.00)	12.26 (0.00)	11.63 (0.00)	19.12 (0.00)	16.77 (0.00)
Amur oblast	12.88 (0.00)	8.87 (0.00)	22.75 (0.00)		4.67 (0.00)	2.10 (0.27)	2.85 (0.05)	9.55 (0.00)	2.38 (0.61)	8.96 (0.00)
Tuva	5.27 (0.00)	3.22 (0.00)	10.21 (0.00)	4.67 (0.00)		1.08 (0.56)	2.33 (0.02)	7.74 (0.00)	7.03 (0.00)	8.27 (0.00)
Yakutia	7.94 (0.00)	4.85 (0.00)	14.64 (0.00)	2.10 (0.27)	1.08 (0.56)		1.26 (0.30)	6.09 (0.00)	3.73 (0.16)	6.44 (0.00)
Transbaikalia	6.05 (0.00)	3.16 (0.00)	12.26 (0.00)	2.85 (0.05)	2.33 (0.02)	1.26 (0.30)		3.94 (0.00)	2.36 (0.43)	3.44 (0.09)
Khabarovsk	7.78 (0.00)	4.28 (0.00)	11.63 (0.00)	9.55 (0.00)	7.74 (0.00)	6.09 (0.00)	3.94 (0.00)		4.72 (0.09)	3.72 (0.14)
Primorskii krai	10.74 (0.00)	7.54 (0.00)	19.12 (0.00)	2.38 (0.61)	7.03 (0.00)	3.73 (0.16)	2.36 (0.43)	4.72 (0.09)		6.86 (0.04)
Sakhalin	11.37 (0.00)	6.60 (0.00)	16.77 (0.00)	8.96 (0.00)	8.27 (0.00)	6.44 (0.00)	3.44 (0.09)	3.72 (0.14)	6.86 (0.04)	

Significance criteria are in parentheses.

RESULTS

Statistical Analysis

When conducting sequential discriminant analysis, the samples studied were classified among themselves in several stages. After the first stage, the samples from Chukotka, Kamchatka, and the Polar Urals turned out to be statistically different from the other groups, since their values of the significance level p-level <0.01 (Table 1). These samples were combined into a general group.

The next repeated stage of the discriminant analysis included the remaining unclassified groups. The end result of such successive stages was the unification of all the samples studied into three large groups: northern, southern, and eastern (Fig. 5). The northern group consists of tooth samples from pikas from Kamchatka (28), Chukotka (68), and the Polar Urals (4). The southern group consists of samples of pika teeth from the southern part of Yakutia (15), Transbaikalia (22), Amur oblast (9), and Tuva (15). The eastern group included samples of pika teeth from the Khabarovsk krai (11), Primorsky krai (5), and Sakhalin (5).

The groups formed almost completely repeat the distribution of the northern pika by acoustic races (Lissovskiy, 2005). The difference is that the samples from the Amur region are in the southern group, and in terms of acoustic races, this area belongs to the eastern group.

The teeth of the northern group are smaller than those of the southern and eastern groups (Table 2). The sizes of the teeth from the eastern and southern groups are similar to each other. At the same time, the Mahalanobis distance between the southern and eastern groups is much less. Thus, the samples from these groups are the closest to each other in terms of the dimensional characteristics of the lower premolar tooth, relative to the northern group (Table 3).

Frequency of Occurrence Of Morphotypes in the Classification Table

After isolating the most significant morphological characters, a classification morphological table of the chewing surface of the third lower premolars of the northern pika was constructed (Table 4). A total of 39 combinations were found on three grounds.

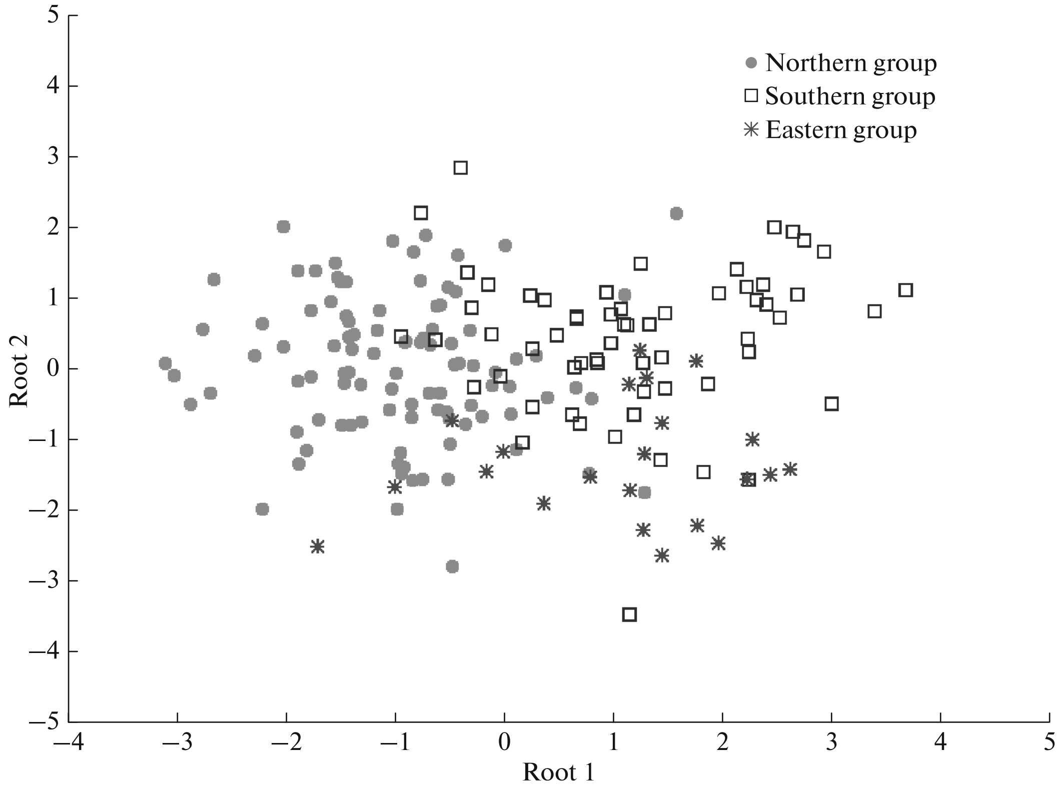

Fig. 5. Distribution of specimens of pikas by size characteristics of p_3.

Since the identified morphotypes combine a different number of specimens, the frequency of occurrence was calculated, which is displayed in Table 5. Most of the models belong to the first group with a curved isthmus (49.18%). This group contains combinations **a-A**, **d-A**, and **f-A**, with frequencies above 6%. This group also contains the largest number of morphotypes with a **C**-shaped posteroconid. In the second group, com-

Table 2. Teeth dimensions of p_3 (mm) of the northern pika *Ochotona hyperborea*

Sign	Northern group		Southern group		Eastern group	
	mean ± *SD*	min–max	mean ± *SD*	min–max	mean ± *SD*	min–max
1	1.16 ± 0.09	0.94–1.44	1.31 ± 0.12	1.00–1.52	1.33 ± 0.10	1.00–1.52
2	1.05 ± 0.09	0.84–1.30	1.23 ± 0.10	1.00–1.36	1.24 ± 0.11	1.00–1.36
3	0.44 ± 0.07	0.12–0.60	0.54 ± 0.07	0.32–0.62	0.53 ± 0.08	0.32–0.62
4	0.14 ± 0.03	0.06–0.20	0.13 ± 0.03	0.10–0.24	0.16 ± 0.04	0.10–0.24
5	0.28 ± 0.06	0.16–0.46	0.40 ± 0.08	0.22–0.56	0.40 ± 0.09	0.22–0.56
6	0.77 ± 0.09	0.56–0.96	0.92 ± 0.09	0.70–1.08	0.91 ± 0.10	0.70–1.08
7	0.55 ± 0.07	0.42–0.74	0.65 ± 0.09	0.54–0.74	0.66 ± 0.06	0.54–0.74
8	0.47 ± 0.06	0.32–0.78	0.54 ± 0.06	0.40–0.60	0.52 ± 0.06	0.40–0.60
9	0.74 ± 0.06	0.58–0.98	0.85 ± 0.08	0.60–0.90	0.80 ± 0.08	0.60–0.90

Mean is the average value, *SD* is standard deviation, min is the minimum value, and max is the maximum value.

Table 3. Squared Mahalanobis distances between groups and level of significance

Group	Northern	Southern	Eastern	Significance level
Northern	0.00	4.94	5.97	<0.01
Southern	4.94	0.00	3.24	<0.01
Eastern	5.97	3.24	0.00	<0.01

Table 4. Morphological classification table

Form of the isthmus	Form of the posteroconid	Form of the anteroconid							
		a	a_2	b	c_1	c_2	d	e	f
I	A			–					
	B					–			
	C		–				–	–	
	D	–	–	–	–	–	–	–	–
II	A								
	B		–	–					
	C	–	–	–	–	–	–	–	
	D	–	–	–	–	–		–	–
III	A	–	–	–	–	–	–	–	
	B	–	–		–	–	–	–	
	C		–	–	–	–	–	–	–
	D	–	–	–	–	–	–	–	–

For explanations, see text.

Table 5. Frequency of occurrence of morphotypes, %

Form of the isthmus	Form of the posteroconid	Form of the anteroconid							
		a	a_2	b	c_1	c_2	d	e	f
I **49.18**	A	**6.01** (11)	**1.09** (2)	–	1.09 (2)	4.92 (9)	**6.56** (12)	2.73 (5)	**6.01** (11)
	B	2.19 (4)	0.55 (1)	3.83 (7)	2.19 (4)	–	3.28 (6)	0.55 (1)	3.28 (6)
	C	2.19 (4)	–	0.55 (1)	1.09 (2)	0.55 (1)	–	–	0.55 (1)
	D	–	–	–	–	–	–	–	–
II **46.99**	A	3.83 (7)	3.28 (6)	1.09 (2)	3.83 (7)	3.83 (7)	4.37 (8)	1.09 (2)	**7.10** (13)
	B	0.55 (1)	–	–	**6.01** (11)	0.55 (1)	4.92 (9)	3.83 (7)	1.64 (3)
	C	–	–	–	–	–	–	–	0.55 (1)
	D	–	–	–	–	–	0.55 (1)	–	–
III 3.83	A	–	–	–	–	–	–	–	1.64 (3)
	B	–	–	0.55 (1)	–	–	–	–	1.09 (2)
	C	0.55 (1)	–	–	–	–	–	–	–
	D	–	–	–	–	–	–	–	–

In brackets is the number of morphotypes. The highest frequency of occurrence is highlighted in bold.

Table 6. The number and frequency of occurrence of forms of the isthmus connecting the anteroconid and posteroconid

Group		Isthmus position			N_{total}
		curved	S-shaped	straight	
Northern	*N*	56	39	5	100
	%	**56.00**	39.00	5.00	
Southern	*N*	25	36	0	61
	%	40.98	**59.02**	0	
Eastern	*N*	9	11	2	22
	%	40.91	**50.00**	9.09	

N is the number of isthmus forms, % is the frequency of occurrence of isthmus forms, N_{total} is the total number of forms. The highest frequency of occurrence is highlighted in bold.

binations of morphotypes prevail **c1-B** and **f-A**. The smallest number of morphotypes is in the third group. There are no dominant morphotypes in this group.

Occurrence of Various Forms of Isthmus

The geographic variability of the structure of the masticatory surface of the third lower premolar of the northern pika can be characterized by the frequency of occurrence of morphotypes in the sample studied (Table 6).

The prevalence of the curved isthmus is typical only for the northern group and amounts to 56%. The southern and eastern groups are dominated by the S-shaped isthmus, 59.02 and 50%, respectively.

The Occurrence of Various Forms of the Anteroconid

A complete set of anteroconid forms is found only in the northern and southern groups (Table 7). The prevailing forms for the northern group are **a** (25%) and $\mathbf{c_1}$ (23%). The southern group with form **d** occurs in 31% of cases, and the form **f** occurs in almost 33% of cases. Forms **a** and **c** have a low frequency of occurrence. Pikas from the eastern group have no forms **a**, $\mathbf{a_2}$, or **b**, but at the same time the same forms prevail as **d** (32%) and **f** (40%) in the southern group.

Occurrence of Various Forms of the Posteroconid

All three groups have a posteroconid shape. **A** is predominant and includes more than half of the specimens in each group (Table 8). Morphotype **C** is mainly characteristic of the northern group, and the only specimen with the presence of a mesoflexid was found in the eastern group (4.55%).

Based on the foregoing, the distribution of the prevailing morphotypes for the selected groups can be written in the following form: for the northern group [**I-a-A**] and [**I-**$\mathbf{c_1}$**-A**]; for the southern and eastern groups [**II-d-A**] and [**II-f-A**].

CONCLUSIONS

The northern part of the northern range of the pika is characterized by individuals with a smaller size of the third lower premolar tooth, which was also noted by other authors (Erbaeva, 1988; Lissovsky, 2003). Individuals living in the southern and eastern parts of the range are close to each other in the size and structure of the chewing surface of the third lower premolar tooth. As shown earlier, it makes sense to consider the issues of the dominance of only individual traits, and not combinations of attribute states (Kovalenko, 2003).

Thus, in the northern part of the range, individuals of the northern pika with a curved isthmus dominate, with an **f**-anteroconid shape and an **A**-posteroconid shape of the third lower premolar tooth. To the south

Table 7. The number (*N*) and the frequency of occurrence (%) of various forms of anteroconid

Group		**a**	$\mathbf{a_2}$	**b**	$\mathbf{c_1}$	$\mathbf{c_2}$	**d**	**e**	**f**	N_{total}
Northern	*N*	25	2	10	23	15	10	4	11	100
	%	**25.00**	2.00	10.00	**23.00**	15.00	10.00	4.00	11.00	
Southern	*N*	3	7	1	2	1	19	8	20	61
	%	4.92	11.48	1.64	3.28	1.64	**31.15**	13.11	**32.79**	
Eastern	*N*	0	0	0	1	2	7	3	9	22
	%	0	0	0	4.55	9.09	**31.82**	13.64	**40.91**	

N is the number of isthmus forms, % is the frequency of occurrence of isthmus forms, N_{total} is the total number of forms. The highest frequency of occurrence is highlighted in bold.

Table 8. The number (N) and the frequency of occurrence (%) of posteroconid morphotypes

Group		**A**	**B**	**C**	**D**	N_{total}
North	N	56	34	10	0	100
	%	**56.00**	34.00	10.00	0.00	
South	N	38	22	1	0	61
	%	**62.30**	36.07	1.64	0	
Eastern	N	12	9	0	1	22
	%	**54.55**	40.91	0	4.55	

N is the number of isthmus forms, % is the frequency of occurrence of isthmus forms, and N_{total} is the total number of forms. The highest frequency of occurrence is highlighted in bold.

and east, there are individuals with an S-shaped isthmus, **f**-anteroconid shape, and **A**-posteroconid form.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interests. This article does not contain any studies involving animals or human participants performed by any of the authors.

REFERENCES

Čermák, S., Obuch, J., and Benda, P., Notes on the genus *Ochotona* in the Middle East (Lagomorpha: Ochotonidae), *Lynx* (Praha), 2006, vol. 37, pp. 51–66.

Erbaeva, M.A., *Pishchukhi Kainozoya* (Cainozoic Pikas), Moscow: Nauka, 1988.

Gimranov, D.O., Morphotypic variability of teeth of *Mates martes* and *Martes zibellina, Zool. Zh.*, 2015, vol. 94, no. 5, pp. 579–587.

Gimranov, D.O. and Kosintsev, P.A., Morphotypic variability of incisors of brown (*Ursus arctros*) and white (*Ursus maritimus*) bears (Carnivora, Ursidae), *Zool. Zh.*, 2017, vol. 96, no. 5, pp. 547–562.

Gureev, A.A., *Fauna SSSR (Zaitseobraznye)* Fauna of the USSR (Lagomorpha), Moscow: Nauka, 1964.

Kalmykov, N.P., Mammals of Lake Baikal in the Paleontological Chronicle. Lagomorphs and rodents (Lagomorpha and Rodentia, Mammalia), *Baikal. Zool. Zh.* (Irkutsk), 2015, vol. 2, no. 17, pp. 7–16.

Kartavtseva, I.V., Sheremet'eva, I.N., Gus'kov, V.Yu., Vakurin, A.A., Kumaksheva, E.V., and Frisman, L.V., To clarification of the taxonomic position of the northern pika *Ochotona hyperborea* of Sikhote-Alin, *Vestn. DVO RAN*, 2014, no. 2, pp. 79–85.

Kawamichi, T., Vocalisation of *Ochotona* as a taxonomic character, in *Proceedings of the World Lagomorph Conference*, Ontario, 1981, pp. 324–339.

Kovalenko, E.E., The effect of the norm of a trait and its theoretical significance, in *Evolyutsionnaya biologiya: istoriya i teoriya* (Evolutionary Biology: History and Theory), St. Petersburg, 2003, vol. 2, pp. 66–87.

Krukover, A.A., The structure and morphotypic variability of the chewing surface of the teeth of non-root-toothed voles, *Inst. Geol. Geofiz. Sib. Oid. Akad. Nauk SSSR*, 1989, vol. 12, p. 38.

Lissovsky, A.A., Geographical variation of skull characters in pikas (*Ochotona*, Lagomorpha) of the alpina–hyperborea group, *Acta Theriol.*, 2003, vol. 48, no. 1, pp. 11–24.

Lissovsky, A.A., Comparative analysis of the acoustic repertoire and variability of acoustic signals of pikas (Ochotona, Mammalia) of the Alpina–Hyperborea group, *Byull. Mosk. O-va Ispyt. Prir., Otd. Biol.*, 2005, vol. 110, no. 6, pp. 12–26.

Lissovsky, A.A., Taxonomic revision of pikas *Ochotona* (Lagomorpha, Mammalia) at the species level, *Mammalia*, 2014, vol. 78, no. 2, pp. 199–216.

Lissovsky, A.A. and Lissovskaya, E.V., Diagnostic of picas (Lagomorpha, Ochotonidae, Ochotona) from the Putorana Plateau, Eastern Siberia, *Russ. J. Theriol.*, 2002, vol. 1, no. 1, pp. 37–42.

Lissovsky, A.A. and Serdyuk, N.V., Identification of Late Pleistocene pikas (Ochotona, Lagomorpha, Mammalia) of the *alpina–hyperborea* group from Denisovskaya Cave (Altai) by the anterior lower premolar tooth (P_3), *Paleontol. Zh.*, 2004, vol. 38, no. 6, pp. 89–95.

Nasledov A.D., *Matematicheskie metody psikhologicheskogo issledovaniya* (Mathematical Methods of Psychological Research), St. Petersburg: Rech', 2004.

Panasenko, V.E. and Tiunov, M.P., Population of small mammals (Mammalia: Eulipotyphla, Rodentia, Lagomorpha) in the southern Sikhote-Alin in the late Pleistocene and Holocene, *Vestn. DVO RAN*, 2010, no. 6, pp. 60–67.

Pozdnyakov, A.A., The structure of morphotypic variability of M^3 of the common vole (*Microtus* Schrank, 1798), in *Sistematika, Paleontologiya Filogeniya Gryzunov*, St. Petersburg, 2005, vol. 306, pp. 102–114.

Pozdnyakov, A.A., The structure of morphological variability (on the example of morphotypes of the masticatory surface of the first lower molar of gray voles), *Zh. Obshch. Biol.*, 2011, vol. 72, no. 2, pp. 127–139.

Pozdnyakov A.A., Litvinov Yu.N., Lopatina N.V., Ecological and morphological variability of the Altai populations of the flat-headed vole *Articola strelzowi* Kastschenko (Rodentia, Cricetidae, Arvicolinae), *Sib. Ekol. Z*h., 2004, no. 4, pp. 579–587.

Volkova, V.R. and Lissovsky, A.A., The structure of morphological variation in the shape of occlusal surface of permanent teeth in pikas *Ochotona* (Lagomorpha: Ochotonidae), *Russ. J. Theriol.*, 2018, vol. 17, no. 2, pp. 91–99.

Vorontsov, N.N. and Ivanitskaya, E.Yu., Comparative karyology of pikas (Lagomorpha, Ochotonidae) of the Northern Palaearctic, *Zool. Zh.*, 1973, vol. 52, no. 4, pp. 584–588.