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Population Affinities of the Ancient Northern Okhotsk People: Cranial Evidence from a Collective Burial in a Rock Niche on Cape Bratyev, the Northern Okhotsk Coast

This study reconstructs biological affinities in a cranial sample from a collective burial on Cape Bratyev in Babushkin Bay. The burial, found in a rock niche on the Okhotsk Coast, was excavated by S.P. Efimov in 1976 and tentatively attributed to the Old Koryak culture. The sample consists of 13 adult skulls of differing preservation—five male, five female, and three undeterminable. Genome-wide analysis was carried out at the Center for Geogenetics of the University of Copenhagen. Paleogenetic data support the archaeological hypothesis attributing the burial to the Old Koryak culture. The results of the craniometric analysis suggest that the Old Koryak population was heterogeneous. Cranial data indicate population contacts between ancient Koryaks and the Epi-Jōmon people of Hokkaido. Also, they reveal common episodes in the population history of the group from Cape Bratyev and the Okhotsk culture people. Two of the three Okhotsk samples used for comparative analysis demonstrate very close affinities with individuals studied. According to the previous studies and our current analysis, the Okhotsk people resulted from the admixture of ancient groups related to Chukchi and Eskimo, on the one hand, and Tungus-Manchu groups, on the other. A significant difference between the Old Koryak population and that of Okhotsk culture is that the former includes a component related to Nivkhs.

Keywords: Northern Okhotsk Coast region, Cape Bratyev, craniometry, paleogenetics, population history, Old Koryak culture.

Introduction

This study sets out to describe and compare a cranial sample from a collective burial in a rock niche on Cape Bratyev* in Babushkin Bay. The niche is one of very few archaeological sites in the Northern Okhotsk Coast region containing human skeletal remains. The burial belongs to a group of sites located at the coast of the Sea of Okhotsk, 150 km east of Magadan (59°5′22″ N, 153°20′12″ E). The group includes a settlement, a cave with manifestations of human occupation, and several burials. The archaeological and ethnic attribution of some of these sites remains a matter of debate.

The cave at Cape Bratyev was studied by K.A. Novikova in 1946, and later by B.E. Lipovsky, G.A. Pytlyakov, and R.S. Vasilyevsky in 1954, 1955, and 1965 (Pytlyakov, Belyaeva, 1957; Vasilyevsky, 1971: 92–98). These sites, as well as the settlements in neighboring Astronomicheskaya Bay, were assigned to the Old Koryak culture. But the association of the burials with this culture is less clear. The burial ground at Cape Bratyev and the interments in Astronomicheskaya Bay were studied by Vasilyevsky in 1964 and were determined by him to be Tungusian (1971: 28). The skeletal samples from those excavations, as well as the skulls from Astronomicheskaya Bay, excavated in 1955, were lost. The latter were studied by N.N. Mamonova from the Institute of Anthropology of Moscow State University (Pytlyakov, Belyaeva, 1957: 10). N.A. Belyaeva notes: "According to the conclusions of anthropologists (G.F. Debets, N.N. Mamonova), the skulls found in the burials likely belonged to the Yukaghirs or Lamuts. For a more precise determination of the ethnic affiliation of the burial grounds, the anthropological research should be continued" (1967: 84).

The specimens employed in the present study were excavated later. In 1976, fellows of a meteorological station reported the discovery of several skulls at Cape Bratyev. An archaeological survey carried out by S.P. Efimov detected a collective burial (Efimov, 1991) in a rock niche about 25 m from the coastal line, 8–10 m above the sea level. A small stone wall 50–60 cm wide surrounded the niche from the outside. Probably some stones of this enclosure eventually fell to the sea, and some inside the niche, resulting in the emergence of a gap, which made the burial visible.

According to Efimov, the artifacts excavated at the site support the determination of the collective burial in the niche at Cape Bratyev as Old Koryak. However, according to some other researchers, those artifacts are not numerous enough to accept or reject this hypothesis

convincingly. On the other hand, any results from anthropological and paleogenetic studies of the remains can only be viewed as indirect evidence for the ethnic attribution of the deceased.

The archaeological data suggest that the Old Koryak culture was formed on the base of the Tokareva culture (Lebedintsev, 2008: 71) and is dated to the 5th–17th centuries AD. The question of the origin of the culture and its population has been a matter of debate, since the northeasternmost part of Asia at that time was an area of contact between a number of ethnocultural communities that later gave rise to the modern Koryak, Chukchi, Itelmen, and Eskimo.

In the present state of knowledge, it can be hypothesized that the bearers of the preceding Tokareva culture might have already had a complex anthropological composition. According to some archaeologists, several components have taken part in the formation of the culture, including populations from the Chukchi and Kamchatka peninsulas, Eskaleutians, continental groups from the Amur River basin, and probably the Late Neolithic population of Kolyma (Lebedintsev, 2019: 175). The formation of the Old Koryak culture per se is thought to be related to some additional influence of the Amur Basin people on the population of the Tokareva culture (Lebedintsev, 1999; Grebenyuk et al., 2019).

No systematic study of the skeletal collections of the Old Koryak culture has been carried out to date. Only one of the female skulls from the burial at Cape Bratyev was measured (Zubov, Lebedinskaya, 1985: 137–138), but no ethnogenetic conclusion was made from the metric data obtained.

The main aim of the present study was an analysis of the population affinity of the individuals from the Cape Bratyev burial on the basis of their craniometric features. The findings were compared with the molecular genetic data for the same sample obtained by C. de la Fuente at the Center for Geogenetics of the University of Copenhagen (2018: 55).

Materials and methods

The excavation of the burial at Cape Bratyev carried out in 1976 revealed 14 skulls and more than 100 various bones from several individuals. This skeletal collection was sent to the Shilo North-East Interdisciplinary Scientific Research Institute (NEISRI), Far East Branch, Russian Academy of Sciences (Magadan). We were only able to study 13 of the skulls. Unfortunately, the fate of one skull that was studied by G.V. Lebedinskaya is unknown, and her measurements do not match up to any of the individuals housed at the NEISRI today. Five of the skulls are male, five female, and the sex of

^{*}Sometimes also referred to as Cape Trekh Bratyev (Vasilyevsky, 1971: 92–98).

three adult individuals was not determined owing to poor preservation. The mid-facials of all the skulls were destroyed, which made measurement of bizygomatic breadth impossible, while zygomaxillary dimensions were taken in only one individual. The mandibles were absent in all the skulls.

The sample was measured by M.S. Kishkurno following the protocol of R. Martin in the modification of V.P. Alekseev and G.F. Debets (1964) (Table 1). Craniometric data from the Far East were employed as a reference (Table 2). As individual measurements of female skulls are not available for many of the reference samples, only male skulls were analyzed.

The comparison of the individuals from the burial at Cape Bratyev and the reference samples was performed using canonical discriminant analysis in Statistica 7.0. Individual measurements of the following variables and indices were employed: 1, 8, 17, 9, 48, 51, 52, 54, 55, 77, zm, SS: SC (12 in total). Missing data were replaced via substitution of the mean of the respective sample. As was demonstrated by Kenyhercz and Passalacqua (2016: 193), if imputation of missing data is carried out using correct statistical methods, the outcome of an intergroup analysis remains qualitatively unchanged even if 50 % of the measurements are missing. Accordingly, the imputation could not bias the results of our analyses.

Results and discussion

Results of the statistical analysis. Our comparison of the cranial metrics of the individuals from the burial at Cape Bratyev and reference samples of the ancient and modern population of the Okhotsk Coast region has shown that the first canonical vector (CV1) accounts for 38 % of the total variation and differentiates two groups of populations (Fig. 1). Ancient and modern series from the Japanese archipelago (Jōmon, Epi-Jōmon, Satsumon culture, and the Ainu of Hokkaido) display positive values of CV1, while negative values are typical of the groups from the Amur River basin and northeasternmost Asia. The series of the Okhotsk culture from Hokkaido are similar to the last-named group, and the Eskimo and Nanai display the most distinctive position in respect to the Japanese samples.

The main features distinguishing the two groups of populations are facial, nasal, and orbital heights. Also, the samples from the Japanese archipelago, in contrast to those from the mainland, are characterized by smaller sizes of most cranial features and less horizontally-protruding faces (Table 3). Differences between CV1 scores of Japanese and continental groups are highly statistically significant (Student's t-test: t = 14.37, p = 0.000). Such a level of differentiation unequivocally suggests that those groups of populations originated from ancestral meta-populations differing in origin.

The sample from Cape Bratyev belongs to the "continental" block, but the individuals are widely scattered along CV1. Three of the skulls (7, 8, and 10) are clearly closer to the continental samples, while two others (6 and 2) display a similarity to the Epi-Jōmon ones (Fig. 1). This is not an occasional aberration and likely reflects the real history of the population from Cape Bratyev, because several genetic studies revealed similar results. The connections between the Epi-Jōmon population and the Koryaks were explored through the study of the genome of an individual from a burial at the Tankovoye-2 site (Iturup Island), which was archaeologically attributed to the Epi-Jōmon culture. The results of the analysis of nuclear SNPs confirmed the high degree of genetic similarity of this individual to modern Koryaks and Itelmen (Moiseyev et al., 2019: 141). The closer genetic affinity of the Ainu of Hokkaido (being the descendants of the Epi-Jōmon population) to the Koryaks, Itelmen, Chukchi, and Eskimo (rather than to other populations of East Asia) is also the evidence of the ancient genetic connections between the populations of the Northern Okhotsk Coast region with the indigenous groups of Japanese archipelago (Jeong, Nakagome, Di Rienzo, 2016: 267). The craniometric similarity between some individuals of the sample from Cape Bratyev and the skulls from Hokkaido points toward the considerable antiquity of these genetic affinities.

The issue of the presence of an esco-Aleutian influence that has been traced in the Old Koryak culture on the basis of archaeological data (Lebedintsev, 2019) is rather complicated. The Ekven series of the Old Bering Sea culture does not exhibit a close similarity to the skulls from Cape Bratyev. It is morphologically distinct from all the other populations, as is evident from the position of this series on the negative pole of CV2 (17 % of the total variation). The difference between the samples from Cape Bratyev and Ekven in CV2 scores is highly statistically significant (t = -4.07, p < 0.005). The most specific morphological feature of this group is a high and long cranial vault (Table 3).

The difference between the Cape Bratyev sample and modern Chukchi and Eskimo does not reach threshold for statistical significance. This means that during the period after the formation of the Old Bering Sea culture, but before or simultaneously with the dispersal of the Old Koryak culture in the Okhotsk Coast region, a population related to the ancestors of modern Chukchi and Eskimo might have migrated to the region. Unfortunately, the question of the origin of this population remains open so far. Two possible scenarios can be suggested: the first is that the population changes are resulted from gene flow from North Asia, while the second implies a back migration of some groups from the New World. It is impossible at the moment to give a

Table 1. Cranial metrics of the skulls from the burial at Cape Bratyev

	Males					Females							
Variable	Skull No.					Skull No.							
	7	6	2	8	10	Mean	1	3	5	9	4	Mean	
1	2	3	4	5	6	7	8	9	10	11	12	13	
Cranial length	172	176	178	181	172	175.80	161	165	184	176	164	170	
8. Maximum cranial breadth	136	136	140	148	150	142.00	_	135	148	143	132	139	
17. Cranial height (from basion)	136	132	139	130	_	134.25	_	_	_	132	132	132	
20. Cranial height (from porion)	111	116	119	_	_	115.33	_	_	_	_	_	_	
5. Cranial base length	100	96	103	98.5	_	99.38	_	_	_	98	93	95.5	
9. Minimal frontal breadth	88	102	96	95	96	95.40	88	94	97	92	88	91.8	
Transverse frontal curvature subtense	16.1	22.3	19.9	18.2	13.1	17.92	13	18.6	15.8	12.8	17.9	15.62	
10. Maximal frontal breadth	110	119	120	122	125	119.20	_	113	_	115	_	114	
11. Cranial base breadth	127	122	131	_	_	126.67	_	_	_	_	119	119	
29. Nasion-bregma chord	108	114	113	112	108	111.00	103.7	108	113	108	105	107.54	
26. Sagittal frontal arch	123	135	135	133	126	130.40	119	128	130	122	120	123.8	
SubNB. Longitudinal frontal curvature subtense	28.2	30.7	27.1	26.1	28.3	28.08	22.3	17.1	21.3	22.9	24	21.52	
12. Occipital breadth	114	109	114	112	109	111.60	105	100	115	109	110	107.8	
31. Lambda-opisthion chord	96	99	87	97	_	94.75	_	_	100	96	93	96.33	
30. Bregma-lambda chord	102	_	112	107	105	106.50	105	104	110	_	103	105.5	
27. Sagittal parietal arch	115	123	125	123	119	121.00	120	118	120	117	119	118.8	
Occipital curvature height	29.5	26.5	24.6	30.2	_	27.70	_	_	25.2	25.4	26.2	25.6	
40. Basion-prosthion length	_	_	96	_	_	96.00	_	_	_	96	_	96	
48. Upper facial height	_	_	75	_	_	75.00	_	_	_	70	_	70	
43. Upper facial breadth	104	107	106	100	104	104.20	106	100	108	105	99	103.6	
51. Orbital breadth from mf.	42.3	43.3	44.8	_	40	42.60	43.2	42.8	_	43.2	42.6	42.95	
51a. Orbital breadth from d.	_	_	42.2	_	_	42.20	40.7	39.2	_	_	_	39.95	
52. Orbital height	37	33.1	36.8	_	34	35.23	34.7	34.6	_	35.2	_	34.83	
54. Nasal breadth	_	_	25.2	_	_	25.20	_	_	31.3	26.8	_	29.05	
55. Nasal height	_	_	50.1	_	_	50.10	_	_	_	55.4	_	55.4	
60. Alveolar length	_	_	58	_	_	58.00	_	_	_	_	50	50	
61. Alveolar breadth	61	_	66	_	_	63.50	_	_	_	62	67	64.5	
62. Palate length	_	_	46.5	_	_	46.50	_	_	_	_	39.5	39.5	
63. Palate breadth	38.2	_	39.9	_	_	39.05	_	_	_	34	34.8	34.4	
43 (1). Biorbital breadth (fmo-fmo)	97.4	100	99.6	94.2	91.8 (?)	96.60	99.2	92.6	97.8	96.5	93	95.82	
Subtense from nasion to fmo-fmo	12.1	17.2	14.4	10.5	8.3	12.50	12.4	15.5	13.7	10	16.9	13.7	
77. Nasomalar angle	152.1	142	147.9	155	158.7	151.14	151.9	143.1	148.7	156.7	140.2	148.12	
Zygomaxillary width	96.2 (?)	_	_	_	_	96.2 (?)	_	_	_	_	_	_	

Table 1 (end)

1	2	3	4	5	6	7	8	9	10	11	12	13
Subtense from subspinale to zygomaxillary width	14.6 (?)	_	_	_	_	14.6 (?)	_	_	_	_	_	-
Zygomaxillary angle	146.4 (?)	_	_	_	_	146.4 (?)	-	_	_	_	_	_
SS. Simotic subtense	_	2.9	1.9	2.6	4.5 (?)	2.98	1.3	2.2	3.1	2.3	2.7	2.32
SC. Simotic width	_	11.4	5.5	5.8	8.5	7.80	5.5	9.6	6.8	8.2	7.8	7.58
Maxillofrontal subtense	5.7	6.3	5.6	6.6	6.8	6.20	_	5.3	7.3	_	5.2	5.93
Maxillofrontal width	19.8	19.7	17.2	17.9	20.7	19.06	_	19.5	17.7	_	18.6	18.6
FC. Canine fossa depth	_	_	5.1	_	_	5.10	2.3	-	2.8	5.7	_	3.6
32. Frontal profile angle from nasion	83	_	86	_	_	84.50	_	_	_	_	_	_
Frontal profile angle from glabella	78	_	82	_	_	80.00	_	_	_	_	_	_
72. General facial angle	84	_	89	_	_	86.50	-	_	_	_	_	-
73. Mid-facial angle	87	_	90	_	_	88.50	-	_	_	_	_	-
74. Alveolar angle	65	_	81	_	_	73.00	_	_	_	_	_	-
75. Nasal bones inclination angle	_	_	75	_	_	75.00	_	_	_	_	_	_
75 (1). Nasal protrusion angle	_	_	14	_	_	14.00	_	_	_	_	_	_

Table 2. Reference samples

Sample	No.	Collection	Publication
Ainu of Hokkaido	15	Sapporo Medical University	Unpublished data of V.G. Moiseyev
Satsumon culture	2	"	"
Epi-Jōmon culture	9	Sapporo Medical University, Kioto University	Unpublished data of V.G. Moiseyev and T.A. Chikisheva
Okhotsk culture, Omisaki	8	Sapporo Medical University, Museum of the Hokkaido University	(Moiseyev, 2008)
Ditto, Moyoro	17	Museum of the Hokkaido University	(Ibid.)
Ditto, Hamanaka	10	Museum of the Hokkaido University, Sapporo Medical University	п
Jōmon era, Hokkaido	10	Sapporo Medical University, Kioto University, Museum of the Hokkaido University	Unpublished data of V.G. Moiseyev
Old Bering Sea culture (Ekven)	13	Research Institute and Museum of Anthropology of the Moscow State University	(Debets, 1975)
Ancient Aleuts (Chaluka)	9	Smithsonian Institution, USA	(Alekseev, Laughlin, 1983)
Mohe (Troitsky)	5	Institute of Archaeology and Ethnography of the Siberian Branch of the Russian Academy of Sciences	Unpublished data of V.G. Moiseyev and E.A. Krebs
Ainu of Sakhalin	10	Museum of Anthropology and Ethnography (the Kunstkamera)	Unpublished data of A.V. Zubova and V.G. Moiseyev
Chukchi	12	"	Unpublished data of V.G. Moiseyev
Eskimo	7	"	"
Ulchi	11	"	"
Nanai	7	"	"
Nivkhs	10	"	· ·

Fig. 1. Canonical discriminant analysis of 17 samples from the Far East. X-axis: CV1, Y-axis: CV2.
a – ancient samples; b – modern populations; c – single individuals from the burial at Cape Bratyev (labels k2, k6, k7, k8, k10 correspond to the numbers of the skulls in Table 1).

preference to one of these hypotheses, because of the absence (except for the skulls from Cape Bratyev) of materials from Northeast Asia or North America which would be chronologically intermediate between the Old Bering Sea culture and modern Chukchi and Eskimo. According to CV2 loadings (Table 3), this hypothetical ancestral population differed from the sample from Ekven by a relatively short and low cranial vault and a face flatter at the upper level.

It is also worth keeping in mind that CV1 of this analysis differentiates mainly the Japanese and continental series, and any similarity between continental groups cannot be interpreted as a close affinity but rather as a consequence of their equal separation from the Japanese samples. Thus, we carried out a canonical analysis, excluding the Japanese groups, in order to explore the differentiation of the continental populations in more detail. The positive pole of CV1 of this analysis (33 % of total variation) is occupied by the two ancient samples from Chaluka (pre-Aleuts) and Ekven, while the Nivkhs and the sample from Cape Bratyev are found at the negative pole of the axis (Fig. 2). The loadings on CV1 are similar to the loadings on CV2 of the previous analysis (Table 4). The modern groups of the Chukchi and Eskimo are again much more similar to the Old Koryaks than Ekven are. This observation confirms the idea about a later change of the anthropological composition of the Chukchi and Eskimo as compared to the bearers of the Old Bering Sea culture, and a relatedness of at least a part of the Old Koryak population with this particular substrate.

CV2 (23 % of total variation) differentiates mainly the Amur River groups (positive values) from the Eskimo, Chukchi, and Cape Bratyev sample (negative values). The specific of the Amur population, i.e. a flattening of the nasal bridge and a widening of the nose (Table 4), is most clearly pronounced in the sample of Mohe from the Troitsky burial ground. The samples of the Okhotsk culture occupy an intermediate position between the Chukchi and Eskimo on the one hand, and both ancient and modern Tungus-Manchu groups on the other hand. These results match the conclusions of earlier studies that

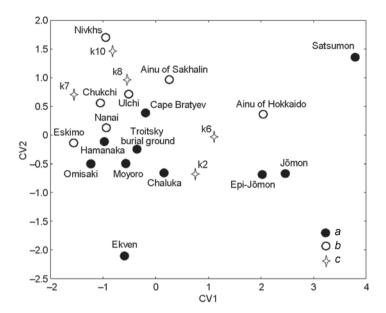


Table 3. Correlation coefficients (loadings) between the raw craniometric variables and values of the first three canonical vectors of the analysis of 17 samples from the Far East

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Variable	CV1	CV2	CV3					
1. Cranial length	0.121	-0.441	0.352					
8. Maximum cranial breadth	-0.214	0.178	-0.627					
17. Cranial height (from basion)	-0.069	-0.524	-0.068					
9. Minimal frontal breadth	0.185	-0.348	-0.046					
48. Upper facial height	-0.836	-0.044	-0.084					
55. Nasal height	-0.816	-0.002	-0.221					
54. Nasal breadth	0.082	0.374	-0.236					
51. Orbital width	-0.040	-0.141	-0.362					
52. Orbital height	-0.502	-0.234	-0.024					
77. Nasomalar angle	-0.446	-0.136	-0.275					
Zm. Zygomaxillary angle	-0.333	0.344	0.269					
SS : SC. Simotic index	0.237	0.281	0.399					
% of total variance	0.379	0.551	0.687					

Note. Bold means correlations significant at p-level < 0.05.

repeatedly pointed out the similarity of the morphological (Ishida, 1996; Komesu et al., 2008) and genetic (Sato et al., 2007; Gakuhari et al., 2020) features of the Ulchi and Okhotsk people, though the latter display a presence of an arctic component as well (Moiseyev, 2007, 2008).

The Nivkhs and Okhotsk people from Hamanaka are the closest series to Cape Bratyev in the morphospace of CV1 and CV2 (Fig. 2). Other samples of the Okhotsk culture display larger distances: Omisaki exhibits a slight shift towards Ekven, while Moyoro is the closest to the samples from the Amur region.

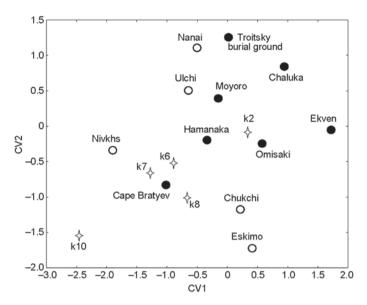


Fig. 2. Canonical discriminant analysis of 12 samples from the Far East. X-axis: CV1, Y-axis: CV2. (Legend same as on Fig. 1).

Table 4. Correlation coefficients (loadings) between the raw craniometric variables and values of the first three canonical vectors of the analysis of 17 samples from the Far East*

Variable	CV1	CV2	CV3
1. Cranial length	0.623	0.278	-0.084
8. Maximum cranial breadth	-0.534	-0.074	0.362
17. Cranial height (from basion)	0.411	0.216	-0.164
9. Minimal frontal breadth	0.224	-0.418	-0.417
48. Upper facial height	-0.095	-0.449	-0.028
55. Nasal height	-0.121	-0.054	-0.244
54. Nasal breadth	-0.598	0.439	-0.169
51. Orbital width	0.063	-0.135	0.010
52. Orbital height	0.360	-0.171	0.246
77. Nasomalar angle	0.022	-0.018	0.191
Zm. Zygomaxillary angle	-0.368	-0.304	-0.238
SS : SC. Simotic index	-0.052	-0.487	0.364
% of total variance	33.1	23.1	17.1

^{*}See note to Table 3.

On the basis of the results of both versions of canonical analysis we have arrived at the following conclusions. The outcomes of the first analysis were affected by high level of cranial specificity of series from Japanese archipelago. Thus, the distribution of the continental groups in the morphospace of CV1 and CV2 (see Fig. 1) reflects the degree of their dissimilarity to the autochthonous population of Japan, rather than their real biological affinities. Consequently, the apparent

similarity of the scores between the series from Cape Bratyev and the Amur groups does not mean relatedness. The second version of the analysis, which differentiates the continental samples much more precisely, has clearly confirmed the closer affinity between the Old Koryak people and arctic populations but not with Tungus-Manchu.

Notably, vector statistical techniques, including CVA, are aimed at exploring the most significant patterns of morphological variation in the array of groups under analysis. However, the history of any population and, accordingly, the history of the formation of its morphological specificity is often fairly complex and cannot be reduced to the dynamic of just two or three complexes of variables, which are typically analyzed when employing a vector approach. Another problem is the built-in algorithm of orthogonality of vectors common to multidimensional statistical techniques; therefore, the morphological combinations described by the vectors are mathematically independent. This can obstruct a complete description of complex population relationships, whereas the episodic emergence of similar morphological features can be due to contacts with various neighboring groups, but also can be a result of admixture from a single but very heterogeneous population. Local population contacts, while important for a particular group, can be only described by minor vectors highly susceptible to statistical noise.

In order to obtain the most complete picture of the population relationships between the studied groups, we calculated a Mahalanobis distance matrix for a cumulative assessment of similarity between the groups by the full set of craniometric variables. This analysis has shown that the series from Cape Bratyev displays the closest similarity (in descending order) to two samples of the Okhotsk culture—Hamanaka and Moyoro, followed by the Eskimo and Chukchi (Fig. 3). Despite the morphological affinity to the Nivkhs demonstrated by the canonical analysis, according to the cumulative statistic, this group is only the fifth most similar to Cape Bratyev.

This result does not contradict the presence of a component common between the Nivkhs and Cape Bratyev population detected via the canonical analysis, but just emphasizes that this component is minor. The Ekven series, unlike the modern Chukchi and Eskimo, again displays a clear dissimilarity with Cape Bratyev.

The analysis of Mahalanobis distances between single individuals of the Cape Bratyev burial and the 16 series from the Far East (Fig. 4) generally confirms the heterogeneity of the Old Koryak sample and its similarity to the people of the Okhotsk culture. Almost all the Old Koryak skulls display some affinity to the Moyoro and Hamanaka samples. The only exception is individual 6, which is more similar to the Hokkaido Ainu. The EpiJōmon series is one of the closest to individuals 2 and 6, but not to others. Three skulls (6, 8, and 10) display an affinity to the Nivkhs. The similarity of the Cape Bratyev skulls to the Chukchi at the individual level is not pronounced, while some affinity to the Ulchi and Eskimo is sporadic and minor as compared to the similarity to the Okhotsk culture samples. Thus, it seems possible that the arctic component has influenced the people of the Old Koryak culture indirectly, through the population of the Okhotsk culture.

Population status of the Cape Bratvev sample from the point of view of paleogenetics. Wholegenome analysis of the skeletal sample from the burial at Cape Bratyev in the context of variation of the modern and recent population of Northeast Asia has demonstrated a similarity between the individuals of the sample and the population of the Tokareva culture, as well as the modern Koryak and Itelmen (Fuente, 2018: 55). All these samples belong to the same genetic cluster that goes back to the ancient individual from Duvanny Yar (9.8 cal ka BP). According to the result of a principal components analysis (PCA), this cluster occupies an intermediate position between two others. The first includes people of the Old Bering Sea culture. as well as the modern and historic Eskimo and Chukchi; the second comprises continental Tungus-Manchu and some Turkic groups.

An analysis of the mitochondrial genomes of the individuals from Cape Bratyev revealed the following haplogroups: G1b, C4b2, and Z1a2a (Ibid.: Fig. A, tab. S1). All of these are present in the genepool of the modern Koryak and Itelmen (Derenko, Malyarchuk, 2010: 120–122; Gubina et al., 2013: 865–869). Haplogroup G1b is the key for the ancient Paleosiberian population known from the genome of the individual from Duvanny Yar. This population gave rise to the Tokareva culture (Sikora et al., 2019), which, in turn, is thought to be the base for the formation of the Old Koryak culture. Thus, the results of the paleogenetic analysis have demonstrated that the individuals from the collective burial in the rock niche at Cape Bratyev could be the ancestors of the modern Koryak.

Conclusions

The paleogenetic data have demonstrated a high affinity between the individuals from the burial at Cape Bratyev and the modern Koryaks on the one hand, and the population of the Tokareva culture on the other hand. Thus,

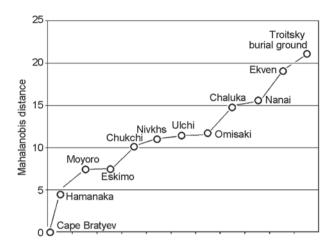


Fig. 3. Mahalanobis distances between the Cape Bratyev sample and 11 ancient and modern groups.

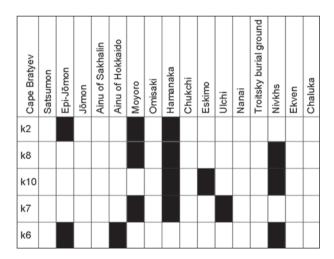


Fig. 4. Distribution of squared Mahalanobis distances between single individuals from the burial at Cape Bratyev and the ancient and modern populations.

Labels k2, k6, k7, k8, k10 correspond to the numbers of the skulls in Table 1. Three groups with the smallest distances are marked for each individual.

the hypothesis that the burial belonged to the Old Koryaks, formulated on the basis of archaeological evidence, can be considered confirmed. The craniometric features of the studied sample suggest some genetic contacts between the Old Koryak and Hokkaido populations (which was not represented in the genetic analysis). These contacts resulted in the presence of well-pronounced Epi-Jōmon specificity in two individuals from Cape Bratyev.

Also, the findings reveal some common episodes in the population history of the group from Cape Bratyev and the Okhotsk culture people. Two of the three series of this culture demonstrate the closest cumulative similarity to the Cape Bratyev individuals. However, the affinity to populations from the Amur River basin is only typical

for the Okhotsk people but not for the Old Koryaks. The group from Cape Bratvev is also distinct from the Okhotsk culture in terms of the much higher degree of similarity with the Nivkhs and Epi-Jomon population. The craniometric differences between the Cape Bartyev and Ekven samples exclude direct continuity between these populations. But these differences do not preclude some influence of the component related to the recent Eskaleuts, since the Cape Bratyev series exhibits a similarity to the modern Chukchi and Eskimo. It can be suggested that this morphological similarity emerged, not as a result of a direct Old Bering Sea culture influence, but owing to later contact with the population that gave rise to present Chukchi and Eskimo craniofacial morphology. That population was likely associated with the bearers of the Okhotsk culture.

Taken together, the results of our analysis have demonstrated the complexity of the anthropological composition of the Old Koryak population, which might have resulted in the extreme heterogeneity of the modern Koryak as compared to other Paleoasian groups, described by G.F. Debets basing on somatological data (1951: 114).

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References

Alekseev V.P., Debets G.F. 1964

Kraniometriya: Metodika antropologicheskikh issledovaniy. Moscow: Nauka.

Alekseev V.P., Laflin U. 1983

Materialy k antropologii drevnego naseleniya Alyaski i Aleutskikh ostrovov. II. Cherepa iz prealeutskikh pogrebeniy na stoyanke Chaluka (o. Umnak). *Sovetskaya etnographiya*, No. 1: 114–127.

Belyaeva N.A. 1967

Drevneishiye pogrebeniya na Okhotskom poberezhye. In *Istoriya i kultura narodov Severa Dalnego Vostoka*. Moscow: Nauka, pp. 80–84.

Debets G.F. 1951

Antropologicheskiye issledovaniya v Kamchatskoy oblasti. Moscow: Izd. AN SSSR. (TIE. Nov. ser.; vol. 17). (Trudy Severo-Vostochnoy ekspeditsii; vol. 1).

Debets G.F. 1975

Paleoantropologicheskiye materialy iz drevneberingomorskikh mogilnikov Uelen i Ekven. In *Problemy etnicheskoy istorii Beringomorya*. Moscow: Nauka, pp. 198–237.

Derenko M.V., Malyarchuk B.A. 2010

Molekulyarnaya filogeografiya naseleniya Severnoy Yevrazii po dannym ob izmenchivosti mitokhondrialnoy DNK, I.A. Zakharov-Gezekhus (ed.). Magadan: SVNC DVO RAN.

Efimov S.P. 1991

Ostatki kollektivnogo pogrebeniya na myse Trekh Bratyev – Noviy pamyatnik drevnekoryakskoy kultury. In *Drevniye pamyatniki Severa Dalnego Vostoka*. Magadan: SVKNII DVO AN SSSR, pp. 136–141.

Fuente C., de la. 2018

Recent population history of Siberia: PhD Dissertation. Copenhagen: Univ. of Copenhagen.

Gakuhari T., Nakagome S., Rasmussen S., Morten E., Allentoft M.E., Sato T., Korneliussen T., Chuinneagáin B.N., Matsumae H., Koganebuchi K., Schmidt R., Mizushima S., Kondo O., Shigehara N., Yoneda M., Kimura R., Ishida H., Masuyama T., Yamada Y., Tajima A., Shibata H., Toyoda A., Tsurumoto T., Wakebe T., Shitara H., Willerslev E., Sikora M., Oota H. 2020

Ancient Jomon genome sequence analysis sheds light on migration patterns of early East Asian populations. *Communications Biology*, vol. 3 (437). doi:10.1038/s42003-020-01162-2.

Grebenyuk P.S., Fedorchenko A.Y., Lebedintsev A.I., Malyarchuk B.A. 2019

Drevniye kultury krainego Severo-Vostoka Azii i etnogeneticheskiye rekonstruktsii. *Tomskiy zhurnal lingvisticheskikh i antropologicheskikh issledovaniy*, No. 2: 110–136.

Gubina M.A., Gyrgolkau L.A., Babenko V.N., Damba L.D., Maksimov V.N., Voyevoda M.I. 2013

Polimorfizm mitokhondrialnoy DNK v populyatsiyakh korennykh zhiteley Dalnego Vostoka. *Genetika*, vol. 49 (7): 862–876.

Ishida H. 1996

Metric and nonmetric cranial variation of the Prehistoric Okhotsk people. *Anthropological Science*, vol. 104: 233–258.

Jeong C., Nakagome S., Di Rienzo A. 2016

Deep history of East Asian populations revealed through genetic analysis of the Ainu. *Genetics*, vol. 202 (1): 261–272.

Kenyhercz M.W., Passalacqua N.V. 2016

Chapter 9 – Missing data imputation methods and their performance with biodistance analysis. In *Biological Distance Analysis: Forensic and Bioarchaeological Perspectives*, M.A. Pilloud, J.T. Hefner (eds.). London: Academic Press, pp. 181–194.

Komesu A., Hanihara T., Amano T., Ono H., Yoneda M., Dodo Y., Fukumine T., Ishida H. 2008

Nonmetric cranial variation in human skeletal remains associated with Okhotsk culture. *Anthropological Science*, vol. 116: 33–47.

Lebedintsev A.I. 1999

Stanovleniye i razvitiye primorskogo khozyaistva v Severnom Priokhotye i na Kamchatke. In *Istoriya, arkheologiya i etnografiya Severo-Vostoka Rossii*. Magadan: SVKNII DVO RAN, pp. 42–69.

Lebedintsev A.I. 2008

Problema proiskhozhdeniya severo-vostochnykh paleoaziatov. *Vestnik SVNC DVO RAN*, No. 3: 67–80.

Lebedintsev A.I. 2019

Primorskiye kultury Okhotomorya: Eskimosskoaleutskoye vliyaniye. In *Severniy arkheologicheskiy congress*, N.M. Chairkina (ed.). Yekaterinburg: Alfa-Print, pp. 175–177.

Moiseyev V.G. 2007

K voprosu o proiskhozhdenii naseleniya okhotskoy kultury Severnogo i Vostochnogo Khokkaido. In *Radlovskiy sbornik: Nauchniye issledovaniya i muzeyniye proyekty MAE RAN v* 2006 g. St. Petersburg: MAE RAN, pp. 194–197.

Moiseyev V.G. 2008

On the origin of Okhotsk populations of Northern and Eastern Hokkaido: Cranial evidence. *Archaeology, Ethnology and Anthropology of Eurasia*, vol. 33 (1): 134–141.

Moiseyev V.G., Zubova A.V., Fuente K., de la, Yanshina O.V., Kishkurno M.S., Chikisheva T.A. 2019

Noviye kraniologicheskiye i paleogeneticheskiye danniye k probleme proiskhozhdeniya korennogo naseleniya Khokkaido i Sakhalina. *Camera praehistorica*, No. 2: 137–146.

Pytlyakov G.A., Belyaeva A.V. 1957

Arkheologicheskiye raboty na Okhotskom poberezhye. In *Krayevedcheskiye zapiski*, iss. I. Magadan: Kn. izd., pp. 5–11.

Sato T., Amano T., Ono H., Ishida H., Kodera H., Matsumura H., Yoneda M., Masuda R. 2007

Origins and genetic features of the Okhotsk people, revealed by ancient mitochondrial DNA analysis. *Journal of Human Genetics*, vol. 52: 618–627.

Sikora M., Pitulko V.V., Sousa V.C., Allentoft M.E., Vinner L., Rasmussen S., Margaryan A., Barros Damgaard P., de, Fuente C., de la, Renaud G., Yang M.A., Fu Q., Dupanloup I., Giampoudakis K., Nogués-Bravo D., Rahbek C., Kroonen G., Peyro M., McColl H., Vasilyev S.V., Veselovskaya E., Gerasimova M., Pavlova E.Y., Chasnyk V.G., Nikolskiy P.A., Gromov A.V., Khartanovich V.I., Moiseyev V., Grebenyuk P.S., Fedorchenko A.Y., Lebedintsev A.I., Slobodin S.B., Malyarchuk B.A., Martiniano R., Meldgaard M., Arppe L., Palo J.U., Sundell T., Mannermaa K., Putkonen M., Alexandersen V., Primeau C., Baimukhanov N., Malhi R.S., Sjögren K.-G., Kristiansen K., Wessman A., Sajantila A., Lahr M.M., Durbin R., Nielsen R., Meltzer D.J., Laurent Excoffier L., Willerslev E. 2019 The population history of northeastern Siberia since the Pleistocene. *Nature*, vol. 570: 182–188.

Vasilyevsky R.S. 1971

Proiskhozhdeniye i drevnyaya kultura koryakov. Novosibirsk: Nauka.

Zubov A.A., Lebedinskava G.V. 1985

Rekonstruktsiya vneshnego oblika lyudey po cherepam, naidennym vo vremya arkheologicheskikh rabot na Kamchatke i Chukotke. In *Novoye v arkheologii severa Dalnego Vostoka*. Magadan: SVKNII DVNC AN SSSR, pp. 126–142.

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