ISSN 1062-3590, Biology Bulletin, 2018, Vol. 45, No. 4, pp. 368–375. © Pleiades Publishing, Inc., 2018.
Original Russian Text © V.Yu. Guskov, I.N. Sheremetyeva, I.V. Seryodkin, O.Yu. Tyutenkov, 2018, published in Izvestiya Akademii Nauk, Seriya Biologicheskaya, 2018, No. 4, pp. 00000–00000.

ZOOLOGY

Cranometric Variability in Brown Bears of the Russian Far East

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Received January 26, 2016

Abstract—Morphometric analysis of 282 skulls of the brown bear *Ursus arctos* from the Far Eastern part of the range was carried out. The presence of two morphological clusters for both males and females is shown. Samples from two clusters were compared with their geographical location and subspecies. It was found that one cluster or another had no specific reference to the particular region or subspecies of a particular cluster, only the superiority of one over the other in a cluster of different subspecies and regions was changed. A comparison with the spread of brown bear genetic lines in the Far East of Russia is made. It was noted that the precise distribution of a particular cluster to a specific genetic line of haplotypes was not found.

DOI: 10.1134/S1062359018040064

INTRODUCTION

Variability is a fundamental property of living things, the diversity of attributes among representatives of one species, and the possibility of descendants to acquire differences from parental forms. Studies carried out with the help of a set of methods (morphological, genetic, and ecological) allow obtaining a more detailed picture of the general variability of the species and biological diversity in general.

The brown bear *Ursus arctos* Linnaeus, 1758 is a polymorphous species and one of the largest modern predators on the planet. Its vast continuous range covers the mountain–forest region of the Palearctic and the Nearctic. In the Asian part of its range, the brown bear inhabits areas from Chukotka in the north to Primorye Territory in the south and from the Ural Mountains in the west to Kamchatka in the east. It lives on the Shantarskie Islands (Bolshoi Shantar and Feklistova) and Kuril (Paramushir, Iturup and Kunashir) Islands, on Karaginskii Island, and also on Hokkaido Island.

In this region, attempts to study the geographic variability and intraspecific taxonomy of the brown bear are still ongoing (Chernyavsky, 1986; Yudin, 1991; Baryshnikov, 2010). A total of 16 subspecies, characterized by differences in color and size of the body, as well as in the proportions of the skull, have been described. For the Far East, eight different subspecies were substantiated at different times and by different researchers, but there is no consensus on intraspecies differentiation in this territory (Yudin, 1991; Baryshnikov, 2010).

In recent years, interest in studying the genetic diversity of the brown bear from the Asian part of the range has increased. Thus, some works show that the brown bear has seven groups of haplotypes (clade), 1
subdivided into subgroups (lodges) (Davison et al., 2011). Three such subgroups: 3a, 3b, and 4 (Tsuruga et al., 1994, Masuda et al., 1998, 2001, Matsuhashi et al., 1999, 2001) were found in Hokkaido Island. The designations of the subgroups correspond to those in the previously published work (Leonard et al., 2000). The geographical distribution of these subgroups probably reflects the successive waves of bear dispersal with the penetration of the brown bear onto Hokkaido Island. Later, in Primorye Territory, Tomsk oblast, and Krasnoyarsk krai, the presence of subgroup 3a, which was dispersed throughout the territory of the range, and rare subgroup 3b (Guskov et al., 2012, 2013, Salomashkina et al., 2012, 2014), which is described only for Hokkaido and Alaska, was found.

The craniometric variability of the species on the Asian part of the range requires additional studies (Chernyavsky, 1986; Perovsky, 1991; Yudin, 1991; Cherniavsky, Krechmar, 2001; Baryshnikov, 2010). The craniometric parameters of the island populations of the brown bear have been described more fully (Yoneda and Abe, 1976, Ohdachi et al., 1992; Baryshnikov et al., 2004; Baryshnikov and Puzachenko, 2009). So, Yoneda and Abe (Yoneda and Abe, 1976), after craniometric study of the brown bear from Hok-

2 kaido Island, revealed the presence of clinal variability in the size of animals from the southwest to the northeast. A detailed study of the craniometric parameters of the bear from Hokkaido Island on more representative material confirmed the trend of a relative increase in the height of the cerebral part of the skull and the extension of the mandibular bone in the same direction (Ohdachi et al., 1992). In later works, the relationship between geographical distribution and genetic groups was shown, as well as a clear differentiation of these groups according to craniometric criteria (Baryshnikov et al., 2004).

The purpose of this work is to reveal the regularities of the craniometric variability of the brown bear on the Asian part of the range and to compare the results of the morphological analysis with genetic groupings.

MATERIALS AND METHODS

A total of 282 skulls (108 males, 49 females, and 125 with an undetermined gender and/or region) were metrically treated from the collections of the Zoological Museum, Moscow State University (Moscow); the Zoological Institute, Russian Academy of Sciences (St. Petersburg); the Institute of Animal Systematics and Ecology, Siberian Branch, Russian Academy of Sciences (Novosibirsk); the Zoological Museum, Tomsk State University (Tomsk); the Institute of Biology and Soil Science, Far East Branch, Russian Academy of Sciences (Vladivostok); in addition, private trophies were used (Fig. 1). The measuring diagram of 27 parameters was borrowed from a work published earlier (Baryshnikov, 2007). To exclude the influence of age-related changes, skulls of adults (six years and older) were involved in the analysis (Yudin, 1991). The age was assessed with use of the diagram of age-related changes in the teeth, the degree of obliteration of the sutures, and the development of crests (Zavatsky, 1986; Klevezal, 2007; Guskov, 2014). First of all, 45 undamaged specimens were included in the analysis (29 males and 16 females). In the subsequent analysis, another 65 samples were classified (53 males and 12 females). Therefore, the final analysis included 110 samples of brown bear (82 males and 28 females) that had the parameters and data that were necessary for the study. For some samples there was no information about the field, and there was absolutely no necessary data for analysis of about 22 samples (neither gender nor geographical region). Samples of males and females were analyzed separately. The objects of the study were individuals, not preformed samples. In the work, an analysis layout was used, taken from the work of Puzachenko et al. (Boreskorov and Puzachenko, 2001; Puzachenko, 2001, 2004, 2006) and tested on other mammals (Sheremetyevo, 2007; Sheremetyeva and Sheremetyev, 2008; Sheremetyeva and Sheremetyev, 2009; Sheremetyeva et al., 2009; Sheremetyev and Sheremetyeva, 2010).

As a null hypothesis, it was assumed that the variability is random. To estimate the pairwise distance between the specimens, the Euclidean distance (ED) and the Kendall correlation coefficient were used. For statistical balancing, all parameters were standardized.

In the first stage of the analysis, undamaged skulls of bears are classified ($n = 29$ for males and $n = 16$ for females, where n is the number of samples). A decrease in the dimension is achieved by the multidimensional scaling method (MDS), which is used as a nonparametric equivalent of factor analysis, since it does not require a normal distribution (Kruskal and Wish, 1978; Kruskal, 1986; Davison, 1988; James and McCulloch, 1990). Based on the ED matrices and the Kendall correlation coefficients by the MDS method, the minimum number of hypothetical, mutually independent variables, the MDS axes, is determined. The minimum dimension (the number of MDS axes) is estimated from analysis of the measure of compliance (stress) (Cattell, 1966) and the results of the analysis of the correlation of the MDS axes with the parameters of the skull for which the Spearman correlation coefficient was calculated.

Classification of specimens is performed with use of the unweighted pair-group method (UPGMA) and the MDS axes as variables and the standard ED (Williams and Lance, 1986). The reliability of differences between groups was assessed with use of the Kruskal-Wallis test (H). Differences were found to be significant at $p < 0.01$.

Discriminant analysis was used to determine the belonging of damaged specimens to the groups (clusters) that were obtained with the use of UPGMA. The parameters most important for the separation of individuals from clusters were selected by the method of step-by-step discriminant analysis.

Comparison of the results of independent classification of specimens with their distribution by subspecies and geographic samples is carried out by the method of cross-tabulations. For this, the corresponding samples were generated from the specimens studied. Nine geographic samples were formed: western Siberia (Altai and Tomsk oblast), the Republic of Sakha (Yakutia), the Magadan oblast, the Amur oblast and Khabarovsk krai, the Primorye Territory, Sakhalin Island, Kamchatka, the Northern Kuril Islands, and the Chukotka Autonomous Region. Samples are assigned to subspecies *U. arctos arctos* Linnaeus, 1758, *U. arctos jeniseensis* Ognev, 1924, *U. arctos lasiotus* Gray, 1867, and *U. arctos piscator* Pucheran, 1855 (Baryshnikov, 2007). In addition, the parameters of the clustered specimens were compared with the data given in the published literature on the subspecies of the brown bear (Ognev, 1931; Yudin, 1991; Aristov, Baryshnikov, 2001; Baryshnikov, 2007; Baryshnikov and Puzachenko, 2009). All calculations were performed with use of the program Statistica 6.0 for Windows (StatSoft, Inc., 1995).

Fig. 1. The volume of the material of brown bear skulls for craniometric studies. The size of the circle and the number correspond to the sample size.

RESULTS

Morphological Analysis of Skulls of Males

For each intact specimen, ten MDS axes were found: eight (D1–D8) as a result of scaling the matrix of distances and two (K1–K2) as a result of the scaling coefficient matrix Kendall correlations. All the parameters of the skull significantly correlate with the first axis (D1); the length of the upper row P4–M2 cheek teeth (L9) correlates with the second (D2); the front length (L6) and the largest diameter of the orbit (W19) correlate with the third (D3); the height of the mandibular bone behind m1 (H26) correlates with the fourth (D4); the zygomatic width (W10) and the height of the mandibular bone in the coronoid process (H25) correlate with the fifth (D5); the length of the upper row of the buccal tooth P4–M2 (L9) and the length of the lower row of teeth of the cheek p4-MH (L24) correlate with the sixth (D6); the mastoid width (W15) correlates with the seventh (D7); the width of the palate in the guttural bone cuttings (W16) and the largest width of the bone palate (W17) correlate with the eighth (D8). The ninth axis (K1) describes the relative volatility (associated with sizes) of a parameter such as the length of the upper row of cheek teeth P4–M2 (L9), and the tenth (K2) correlates with the total length (L1), the length of the backskull (L4), the width occipital condyles (W14), and the largest diameter of the orbit (W19).

As a result of specimens classified with the use of the MDS axes, three clusters can be selected. At the first level of clustering (two clusters), the maximum contribution was made by the axes D1, D2, D7, D6, D3, K1, D4, and D5 (in decreasing order of importance). Significant differences between the specimens of cluster 1 and the rest were found for all parameters, except for L9 and W10, the smallest width of the skull (width of the crotaphic narrowing) (W12), W15, and W17. At the second level (three clusters), the maximum contribution was made by the axes D1, D7, K1, D2, D5, D4, D3, D6, and K2. The greatest differences between clusters 2 and 3 were found from the total length (L1), the condylobasal length (L2), and the main length (L3), but the difference did not exceed $p < 0.01$. Thus, only two clusters are reliably confirmed (Fig. 2).

The efficiency of the classification of damaged specimens, taking into account all the craniometric parameters, was 61.6%, with nine parameters included in the discriminant function: the length of the facial section (L5), the length of the bone palate (L7), L24, W16, L1, W19, the length of the mandibular to the angular process (L22), W17 and W12. The effectiveness of the classification of damaged specimens, taking into account only the parameters of the axial cranium or mandibular bone, was 52.5% and 65.7%, respectively; six parameters of the axial cranium (width in the canines (W18), W16, W19, W12, W15,

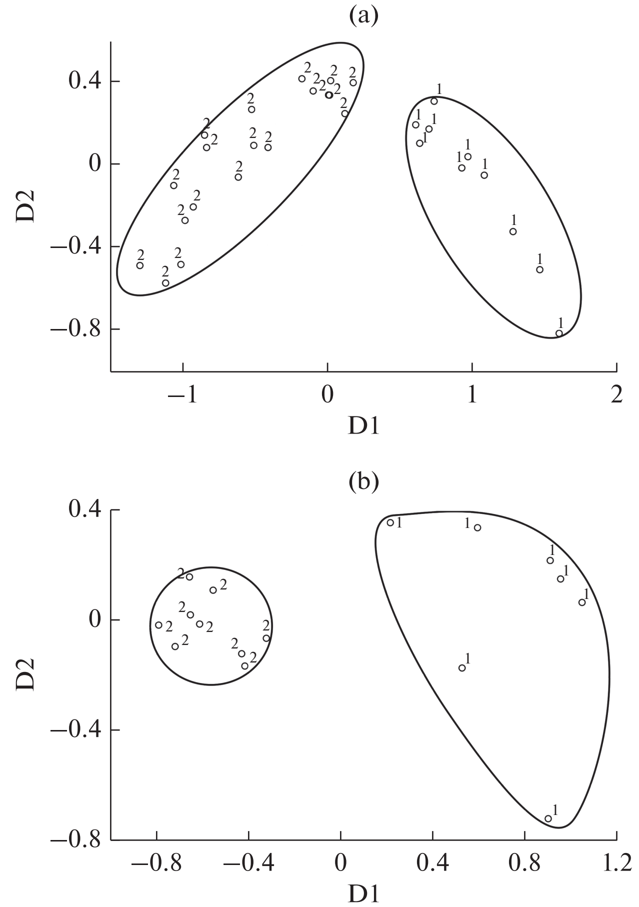

Fig. 2. Distribution of samples of male and female brown bears of two morphological clusters (1 and 2) in the plane of two axes of multidimensional scaling D1 and D2.

and L2) and three parameters of the mandibular bone (length of the lower row of teeth c1–m3 (L23), and the length of the mandibular bone (L21) and (L24) were included in the discriminant function. In this case, all three types of classification of damaged specimens coincided by 95%.

Cluster 1 includes specimens with the smallest parameters; cluster 2 includes those with the largest ones. The differences between clusters for the average values of the parameters were 5.02–16.14%. The largest differences between clusters were in H26 and the height of the mandibular bone in the region of the diastema (H27). Among the indices, the greatest differences are demonstrated by the L9 and W14 index relative to L1.

Comparison of the samples, formed by the geographical principle, shows weak significant differences in the composition and correlation of specimens of different clusters in them (χ^2 = 20.11, df = 8, p = 0.009). In the samples from western Siberia (Altai and the Tomsk oblast), the Republic of Sakha (Yakutia), and Magadan oblast, individuals of cluster 1 predominate, while in the samples of Primorye Territory, Sakhalin Island, Kamchatka, the Northern Kuril Islands, and Chukotka Autonomous Region, cluster 2 predominates. The sample of the left bank of the Amur contains an equal proportion of individuals of both cluster 1 and cluster 2 (Table 1).

Comparison of the samples formed in accordance with the representations of the subspecies ranges showed slightly significant differences in the composition and ratio of specimens of different clusters in them (χ^2 = 10.78, df = 8, p = 0.013). In the samples of *U. a. lasiotus* and *U. a. piscator*, individuals of cluster 2 predominated, whereas in samples *U. a. arctos* and *U. a. jeniseensis,* individuals of cluster 1 predominated (Table 1). The mean values of the parameters of the skulls of the specimens of cluster 2 correspond to the data for the subspecies *U. arctos ferox*, given by Baryshnikov (Baryshnikov et al., 2004).

Morphological Analysis of Skulls of Females

For each intact specimen, six MDS axes were found: three (D1–D3) as a result of the scaling of the distance matrix and three (K1–K3) as a result of scaling the Kendall correlation coefficient matrix. Most of the parameters of the skull reliably correlate with the first axis (D1), except for W12, W16, L24; (D2)–W12 and W16 correlate with the second axis, (D3)–L24 correlate with the third axis. The index of the width of the cerebral cortex (W11) correlates with the fourth (K1), L5 correlates with the fifth (K2), and W17 correlates with the sixth (K3).

As a result of the classification of specimens with use of the MDS axes, two clusters are identified (Fig. 2). The maximum contribution was made by the axes of D1, D3, and D2. The specimens of cluster 1 differed from cluster 2 in L1, L2, L3, L4, L5; the width of the cerebral cortex (W11), in W15, W18; the length of the mandibular bone (L21), in L22; and the length of the lower dentition series c1–m3 (L23), in H25, H26, H27.

The effectiveness of the classification of damaged specimens was 71.7%. The discriminant functions include eight parameters: H26, W12, H27, L5, L6, L23, W16, and W19. The effectiveness of the classification of damaged specimens, taking into account only the parameters of the axial skull or lower jaw, was 63.1%; the six parameters of the axial cranium (L2, W14, W12, W16, L5 and the length of the upper dentition C1–M2 (L8)) and three parameters of the lower jaw (H26, L21, and L22) were included in the discriminant function. At the same time, all three types of classification of damaged samples coincided by 99%.

Cluster 1 includes the instances with the smallest parameters; cluster 2 includes those with the largest parameters. The differences between clusters by the average values of parameters were 3.59–13.52%. The biggest differences between clusters were according to

Table 1. Portion of male and female brown bears, *Ursus arctos*, belonging to morphological clusters 1 and 2, in geographical samples and subspecies

Area	Males			Females		
	n	1*	2**	*n*	1*	2**
Western Siberia (Altai+ Tomsk oblast)	19	58	42	3	100	–
The Republic of Sakha (Yakutia)	2	100	–	–	–	–
Magadan oblast	3	100	–	–	–	–
Shantar Islands	–	–	–	3	67	33
The left bank of the Amur River (Amur oblast and Khabarovsk krai)	12	50	50	3	–	100
Primorye Territory	35	17	83	13	31	69
Sakhalin Island	5	40	60	2	50	50
Kamchatka + Northern Kurils	5	–	100	4	–	100
Chukotka Autonomous District	1	–	100	–	–	–
Total	82	31	51	28	10	18
Subspecies						
Ursus arctos arctos	7	57.1	42.9	2	100	0
U. a. jeniseensis	18	66.7	33.3	1	100	0
U. a. lasiotus	52	26.9	73.1	21	33.3	66.7
U. a. piscator	5	20	80	4	0	100
Total	82	31	51	28	10	18

* *n*, number of specimens; ** cluster 1; *** cluster 2.

H26. Among indices, the W11 and W17 indices show the greatest differences with respect to L1.

Comparison of the samples formed on a geographical basis did not reveal highly significant differences in the composition and correlation of specimens of different clusters in them (χ^2 = 10.86, df = 6, p = 0.093). However, it can be seen that in the sample from western Siberia and the Shantar Islands, cluster 1 predominates. In the Far East part of the range, the samples of the left bank of the Amur, Primorye Territory, and Kamchatka specimens of cluster 2 dominated, whereas the portion of individuals of cluster 1 does not exceed 31% (Table 1).

Comparison of the samples formed in accordance with the representations of the ranges of subspecies showed significant differences in the composition and correlation of specimens of different clusters in them ($\chi^2 = 79.91, p = 0$). In the samples of *U. a. lasiotus* and *U. a. piscator,* individuals of cluster 2 predominate, whereas in samples of *U. a. arctos* and *U. a. jeniseensis,* all samples belong to cluster 1 (Table 1).

DISCUSSION

During the study of the brown bear on the Asian part of the range, two morphological clusters were identified. The first cluster included individuals with smaller parameters of the skull, and the second cluster included individuals with larger ones. This pattern is the same for males and females, but the differences between groups of females are less pronounced than between males. The division into a larger number of clusters is not statistically reliable.

From the comparison of samples from two morphological clusters with their geographical distribution and subspecies of the brown bear, we found that a particular skull is very difficult to attribute to a specific geographical area, whereas it is quite possible to refer to a particular large region. Thus, the skulls of cluster 2 with a high degree of probability can be attributed to the regions of the Primorye Territory, Kamchatka, Sakhalin Island, and the Chukotka Autonomous Region. Skulls in cluster 1 mainly refer to the regions of western Siberia, Magadan oblast, and the Republic of Sakha (Yakutia). Sampling from the left bank of the Amur contains copies of clusters 1 and 2 equally. With some probability it is possible to assert that there are areas with overlapping populations belonging to both morphological clusters in this region.

Correlation of the processed data with brown bears subspecies, distributed on the territory of the Asian part of the range, shows that attributing a particular skull to a specific subspecies is also difficult. The ratio of clusters to subspecies appears as follows. Samples formed from subspecies *U. a. lasiotus* and *U. a. piscator* contain more specimens of cluster 2. At the same time, in samples of *U. a. arctos* and *U. a. jeniseensis*, the portion of individuals in this cluster is lower than the portion of individuals in cluster 1. Accordingly, the brown bear from Primorye Territory, Kamchatka, Sakhalin Island, and the Chukotka Autonomous Region (subspecies of *U. a. lasiotus* and *U. a. piscator*) is larger than bears from Western Siberia, the Republic of Sakha (Yakutia), and Magadan oblast (subspecies of *U. a. arctos* and *U. a. jeniseensis*).

Most likely, in order to establish a more accurate accessory of the skull to a certain subspecies, it is necessary to investigate a greater number of individuals of known subspecies with a specific territorial reference, and also to use all possible morphological, and not just craniometric parameters, and features of the ecology of groupings from different territories.

At the same time, for the Far East, the presence of two genetic groups previously described for the territories of Hokkaido and Alaska islands was recorded (Tsuruga et al., 1994, Masuda et al., 1998, 2001, Matsuhashi et al., 1999, 2001, Leonard et al., 2000). Previously, native authors conducted craniometric analysis for the territory of Hokkaido Island, where the division of the brown bear population into groups was confirmed both by craniometric and by genetic parameters (Baryshnikov and Puzachenko, 2009). Based on the assumption of a clear division of brown bear populations into groups, one can assume the presence of a similar division for the mainland part of the bear's range. So, according to different authors, there are genetic groups on the mainland range of the brown bear, similar to those on Hokkaido. Based on the analysis of the cytochrome b gene and the locus of the mtDNA control region, the presence of such groups on the territory of the southern part of the Russian Far East was shown (Guskov et al., 2012, 2013), as well as in Tomsk oblast and Krasnoyarsk krai (Salomashkina et al., 2012, 2014). In this connection, we can make an assumption about the possible correlation of data on genetic groups with the results of craniometric analysis. But a similar distribution of groups obtained with the help of different analyses is not observed. The mainland population is divided into two groups, but they do not correspond to data on the distribution of genetic lines, as was shown for Hokkaido Island. The territorial coverage of our studies is greater than one island and one subspecies. Therefore, the division into groups may have a different nature.

At the moment, it is not possible to make more concrete conclusions. It is necessary to increase the sample of brown bear skulls to continue this kind of research. It is necessary to conduct an end-to-end analysis of the genetic and craniometric diversity on the same material to obtain reliable data. The latter requirement causes considerable difficulties. At this stage of the work, we have a small sample with complete material, but it is not enough to obtain reliable information.

Our results expand and supplement the available literature (Ognev, 1931; Stroganov, 1962; Pazhetnov, 1990; Yudin, 1991; Baryshnikov et al., 2004) and give new insights into the subspecies of the brown bear of the Russian Far East. The task was not to revise the subspecies of brown bear of the Asian part of the range. However, the craniometric data obtained support a less fractional subspecies structure and the possibility of reducing some subspecies to synonyms.

ACKNOWLEDGMENTS

The authors are grateful to G.F. Baryshnikov (Zoological Institute, Russian Academy of Sciences); E.V. Syromyatnikova and V.G. Yudin (Federal Research Center of Biodiversity, Far East Branch, Russian Academy of Sciences) for help in working with skull collections in museums of the country; and employees of the following institutions: the Zoological Museum, Moscow State University (Moscow); the Institute of Animal Systematics and Ecology, Siberian Branch, Russian Academy of Sciences (Novosibirsk); and the Zoological Museum, Tomsk State University (Tomsk).

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Translated by Z. Litvinenko

SPELL: 1. clade, 2. clinal