Genetic Characteristics of Kodar Snow Sheep Using SNP Markers[1]

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Abstract—For the first time nuclear DNA polymorphisms were studied in Kodar snow sheep (*Ovis nivicola kodarensis*, KOD). KOD is a representative of a small isolated population of Asian snow sheep *(Ovis nivicola* Eschscholtz, 1829*)* inhabiting the Kodar Ridge (Irkutsk oblast, Transbaikal krai). We compared KOD with the geographically closest Yakut subspecies *(Ovis nivicola lydekkeri)*. Genome-wide study of single-nucleotide polymorphisms (SNPs) was performed using the Illumina OvineSNP50 BeadChip (Illumina, United States). The final set of markers for analysis included 1030 SNPs. We found that Kodar snow sheep had almost 10 times lower level of genetic diversity evaluated by multilocus heterozygosity—MLH (0.027 for KOD vs 0.215–0.270 for individuals of Yakut subspecies) and standardized MLH—stMLH (0.116 against 0.910–1.147). The results of multidimensional scaling (MDS), Nei distances calculations (D_N) and STRUCTURE analysis showed a clear genetic differentiation of Kodar snow sheep from Yakut subspecies. Our data is the first step to understanding the demographic history of the original Kodar population of snow sheep.

Keywords: snow sheep, Kodar, genetic analysis, SNP

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INTRODUCTION

Asian snow sheep (*Ovis nivicola* Eschscholtz, 1829) is an endemic of the mountain systems of Eastern Siberia and the Northern Far East and belongs to a priority species for the conservation of biological diversity in Russia. It inhabits the mountains of Yakutia, Okhotsk region, Kamchatka, Koryak upland, Chukotka, the Putoran plateau (Zheleznov-Chukotskii, 1994). Currently, it is recognized as a clearly defined species. It is often subdivided into 3–5 subspecies, of which the nominative *O. n. nivicola* (Kamchatka), *O. n. lydekkeri* (Yakutia) and *O. n. borealis* (the Putoran Plateau) are most distinct (Pavlinov, 2012). The taxonomic division within the species is mainly based on differences in color, position and size of patches in the rear end and body proportions. How-

ever, starting from the end of XIX century several authors have pointed out to the existence of another isolated population of snow sheep inhabiting the Kodar Ridge (Polyakov, 1873; Pavlov, 1949; Skalon, 1935, 1949, 1951; Vodop'yanov, 1971; Sopin, 1986, 1988; Revin, 1988), although it was not mentioned in the famous summaries on the geographic distribution of the genus *Ovis* (mountain and snow sheep) (Severtsev, 1873; Dorogostaiskii, 1915; Nasonov, 1923). Medvedev (1994) first described Kodar snow sheep *(Ovis nivicola kodarensis* Medvedev, 1994*)* (Fig. 1) during the field research in the Northern Transbaikal region. Later the use of photo and video records allowed to conduct monitoring studies and to capture a unique coal eating by these rare animals. Kodar snow sheep is listed in the Red Data Books of the Irkutsk region (*Kranaya Kniga Irkutskoi oblasti*, 2010) and Transbaikal area (*Krasnaya Kniga Zabaikal'skogo kraya*,

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Fig. 1. Kodar snow sheep. Note: two adult rams (after moulting, in summer "plumage") on the plateau-like area—"table" in the interfluve of Apsat and Middle Sakukan rivers (rubbly mountain tundra, altitude 2650 m above sea level). Medvedev D.G., June 28, 2016.

2012) and will possibly be listed in the Red Data Book of the Russian Federation.

Kodar snow sheep is a small population, inhabiting a limited area within the Kodar ridge, the highest in Vitim-Olekma highlands. This population is estimated to number between 270 and 400−500 individuals and remains relatively stable over years (Medvedev, 2003). Its areal ranges from the Suliban River basin (117° E) to an extreme east point of the Kodar mountainous region, which is limited by Chara River (119° E). The southern part of its habitat is located between 56°40′ and 56°30′ in the mountains surrounding the river Suliban. The northern part starts from the Nichatka lake towards the Chara River between 57°50′ N and 57°30′ N or a little to the south of it (Medvedev, 2009). It is believed that Kodar population survived due to the high altitude of the Kodar Ridge, the steepness of its slopes and the presence of so called "ice shield" − the large number of glacier sets with different sizes, forms and positions, the reason why this area is called "Glacial Kodar district" (Preobrazhenskii, 1960; Danilkin, 2005). Combination of natural conditions, specific Kodar geobiocenosis and climatic features (low snow coverage) were the key factors for the survival of snow sheep in this area. In fact, the Kodar Ridge and the relict population of snow sheep, inhabiting its slopes, are unique natural environmental model for investigation

of possible reasons for reduction and fragmentation of Asian snow sheep historical habitat and can be of help to develop mechanisms for its reconstruction and recovery. If morphological characteristics of the Kodar snow sheep were described in sufficient details (Medvedev, 1994, 2003, 2009), its genetic features remain unknown.

The sequencing of complete genomes and the creating of medium- and high-density SNP arrays on their basis has opened new possibilities in understanding genetic features of different species. For non-model organisms (i.e. which genomes have not been sequenced yet) the SNP arrays developed for closely related species were applied (Seeb, 2011). Thus, BovineSNP50K BeadChip developed for domestic cattle was used to characterize the population structure of the European bison (*Bison bonasus*) (Tokarska, 2009), to differentiate the endemic North American deer species—black-tailed (*Odocoileus hemionus*) and white-tailed (*Odocoileus virginianus*) (Haynes, 2012), to evaluate the biodiversity of reindeer (*Rangifer tarandus*) (Kharzinova, 2015, 2016). OvineSNP50K BeadChip, which was developed for domestic sheep, was used to study genetic structure of Canadian bighorn sheep (*O. canadensis*), Dalla sheep (*O. Dalli*) (Miller, 2011), and Yakut snow sheep (*O. nivicola*) (Deniskova, 2016). Even though the number of polymorphic SNPs
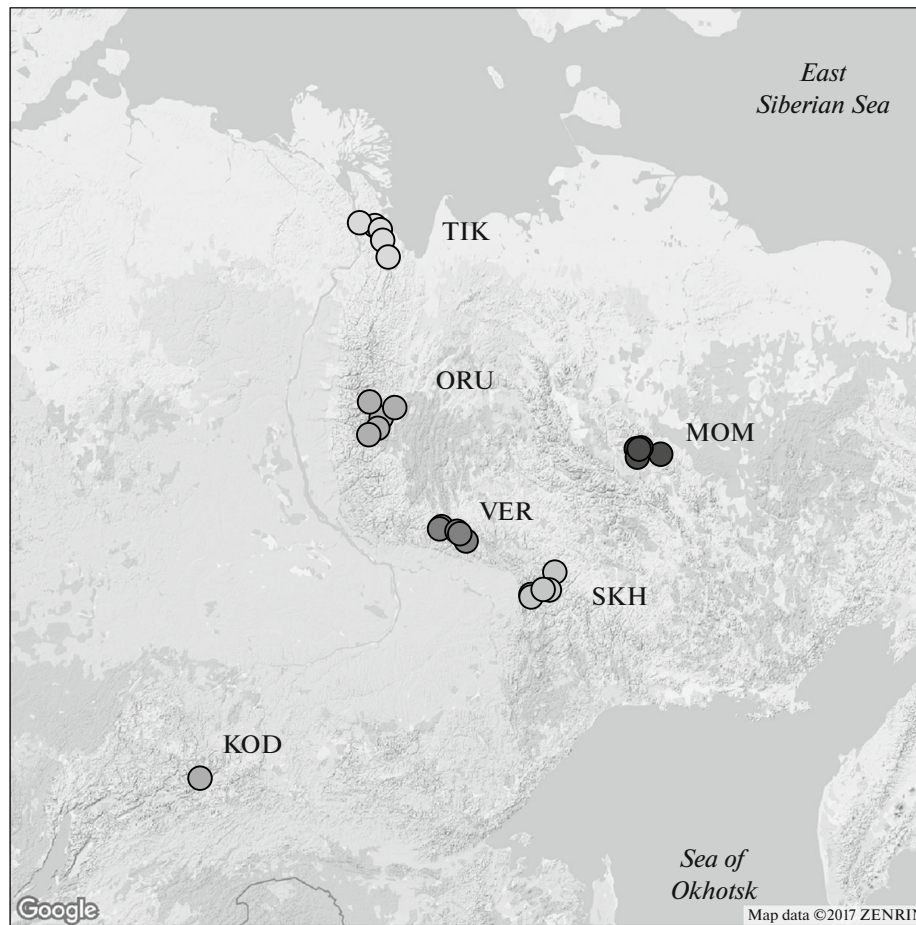
Fig. 2. Study area and location of the sampling sites. Studied populations: KOD—Kodar Ridge, TIK—Kharaulakh Ridge (Tiksi), ORU—Orulgan Ridge, VER—Central Verkhoyansk Ridge, SKH—Suntar-Khayata Ridge, MOM—Moma Ridge.

decreases significantly with increasing genetic distances between the studied non-model species and the species for which the DNA-array was developed, reaching only 5% for species that diverged several million years ago (Miller, 2011), the obtained information is invaluable for genetic characteristics of organisms for which DNA-arrays are not available.

The aim of the present study was to evaluate genetic characteristics of Kodar snow sheep and its differentiation degree from geographically closest subspecies — Yakut snow sheep using medium density Ovine SNP50 BeadChip.

MATERIALS AND METHODS

The tissue sample of Kodar snow sheep, KOD *(Ovis nivicola kodarensis* Medvedev, 1994*),* was collected from an adult male, which was killed in the avalanche in 2016. Genomic DNA was extracted using Nexttec column (Nexttec Biotechnologie, Germany) according to the guideline of the manufacturer. SNP screening was performed using Illumina OvineSNP50 BeadChip (Illumina, United States), including 54241 SNPs. The

generated SNP profile of Kodar snow sheep was included into the dataset consisting of SNP profiles of five different geographical groups of Yakut snow sheep individuals *(O. n. lydekkeri,* Kowarzik, 1913): Kharaulakh Ridge, Tiksi (TIK, $n = 5$), Orulgan Ridge (ORU, $n = 5$), Central Verkhoyansk Ridge (VER, $n = 5$), Suntar-Khayata Ridge, SKH, $n = 5$) and Moma Ridge (MOM, $n = 5$). Geographic map of the sampling sites is shown in Fig. 2.

Genotyping quality control was performed using PLINK 1.07 software. SNPs were included into the final dataset, if they were genotyped at least in 90% of individuals with GenCall Score > 0.5, had minor allele frequency (MAF) > 1% and were in Hardy-Weinberg equilibrium ($p < 1e-6$). Genetic diversity was evaluated using multilocus heterozygosity (MLH) and standardized MLH (stMLH) using R package "inbreedR" (Stoffel, 2016). MLH was calculated as the total number of heterozygous loci in an individual divided by the overall number of genotyped loci, stMLH was estimated as the total number of heterozygous loci in an individual divided by the sum of average observed heterozygosity in the studied population over the subset
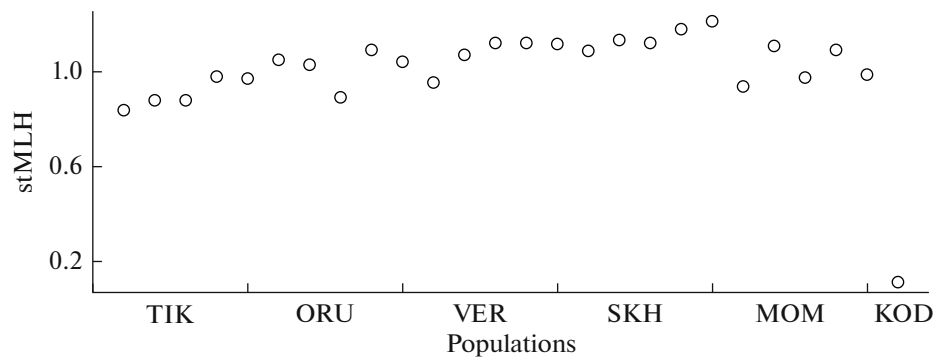
Fig. 3. Standardized individual multilocus heterozygosity in Kodar snow sheep as compared to Yakut snow sheep. Axis X—studied populations: KOD—Kodar Ridge, TIK—Kharaulakh Ridge (Tiksi), ORU—Orulgan Ridge, VER—Central Verkhoyansk Ridge, SKH—Suntar-Khayata Ridge, MOM—Moma Ridge.

of successfully typed loci. We calculated the expected correlation (r^2) between heterozygosity of marker loci and the heterozygosity of functional loci in the genome to assess the accuracy of the SNP dataset in prediction of heterozygosity at the genomic level. Multidimensional scaling (MDS) based on the IBS distances (IBS, identical-by-state), was performed using PLINK 1.07 (−cluster, −mds-plot 4) and was visualized using R package "ggplot2" (Wickham, 2009). Population structure was evaluated using admix-model in STRUCTURE 2.3.4 (Pritchard, 2000). Analysis was carried out for K (the number of assumed populations) from 1 to 6 using the following settings: length of burn-in period—100000 and Markov chain model Monte-Carlo (MCMC)—100000 repeats. For each *K* value 10 iterations were performed. The STRUCTURE results were visualized with R package "pophelper" (Francis, 2016). Pairwise Nei genetic distances (D_N) (Nei, 1972) were calculated in GENETIX 4.05 (Belkhir, 2004). Calculation of pairwise Fst values (Weir, 1984) was carried out in R package "diversity" (Keenan, 2013). A rooted tree was constructed based on D_N values (Nei, 1972), using neighbor-joining method in Neighbour software of Phylip 3.695 package (Felsenstein, 1993), and was visualized using FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/). SNP data of argali (*Ovis ammon*) was included into the dataset as an outgroup. The map showing the locations for sampling points was drawn using the *R* package ggmap (Kahle, 2013). *R* package version 3.2.3 was used to generate the input files (R Development Core Team, 2012).

RESULTS AND DISCUSSION

The final set of markers after the quality control of genotyping included 1030 SNPs. We observed almost 10 times lower level of genetic diversity evaluated by MLH in Kodar snow sheep comparing to the individuals of Yakut subspecies: 0.027 in KOD against 0.215 ± 0.007, 0.241 ± 0.008, 0.254 ± 0.008, 0.270 ± 0.005 and 0.241 ± 0.008 in TIK, ORU, VER, SKH and MOM, respectively. The same tendency was observed for stMLH (Fig. 3). The value of stMLH in KOD was 0.116, whereas the minimal value in the individuals of Yakut subspecies was 0.839 (TIK). In TIK, ORU, VER, SKH and MOM groups mean stMLH values were 0.910 ± 0.028, 1.022 ± 0.034, 1.077 ± 0.032, 1.147 ± 0.022 and 1.021 ± 0.037, respectively. The calculation of expected correlation showed that the MLH and stMLH values accurately reflect genome-wide heterozygosity ($r^2 = 0.936$). Significantly lower level of genetic diversity in KOD comparing to individuals of Yakut subspecies indicates the high degree of inbreeding in Kodar population, which is probably due to their long-time isolation and the population small size.

The results of multidimensional scaling (MDS) are presented in figure 4. The first component (PC1) is responsible for 16.11% of genotypic variability and separates the geographical groups of Yakutia subspecies from each other. According to McVean G. (McVean, 2009), the first principal component can be interpreted as more distant coalescence event at phylogenetic tree. The projection of individuals on this axis shows the location of KOD individual in the region of SKH population, probably due to the fact that the SKH population inhabits the Southern part of Verkhoyansk mountain chain, geographically closest to the Kodar population. That suggests gene flow between them before geographic isolation of KOD. The second principal component (PC2) is responsible for 8.58% of the genotypes variability and clearly separates KOD from all geographical groups of Yakut subspecies, indicating genetic isolation of Kodar snow sheep.

Analysis of the cladogram structure, based on D_N (Fig. 5), shows that KOD diverges from Yakut subspecies clade already in the first node. The mean values of D_N between KOD and groups of Yakut subspecies were 0.216 ± 0.006, 0.202 ± 0.007, 0.181 ± 0.005, 0.176 ± 0.006 and 0.196 ± 0.008 for TIK, ORU, VER, SKH and MOM, respectively, that was significantly higher

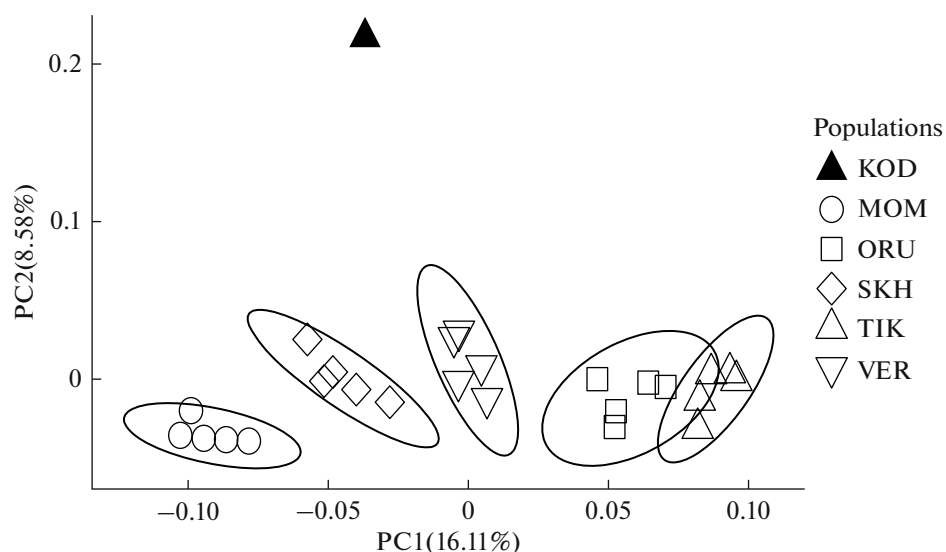**Fig. 4.** Multidimensional scaling (MDS) analysis of Kodar snow sheep genotypic variability in comparison with the individuals of Yakut subspecies based on 1030 SNPs. Axis X—principal component 1 (PC1), axis Y—principal component 2 (PC2); studied populations: KOD—Kodar Ridge, TIK—Kharaulakh Ridge (Tiksi), ORU—Orulgan Ridge, VER—Central Verkhoyansk Ridge, SKH—Suntar-Khayata Ridge, MOM—Moma Ridge.

Fig. 5. Rooted phylogenetic tree based on unbiased Nei genetic distances (Nei, 1972) using Neighbor-Joining method. Studied populations: KOD—Kodar Ridge, TIK—Kharaulakh Ridge (Tiksi), ORU—Orulgan Ridge, VER—Central Verkhoyansk Ridge, SKH—Suntar-Khayata Ridge, MOM—Moma Ridge; OAM—*Ovis ammon* (outgroup).
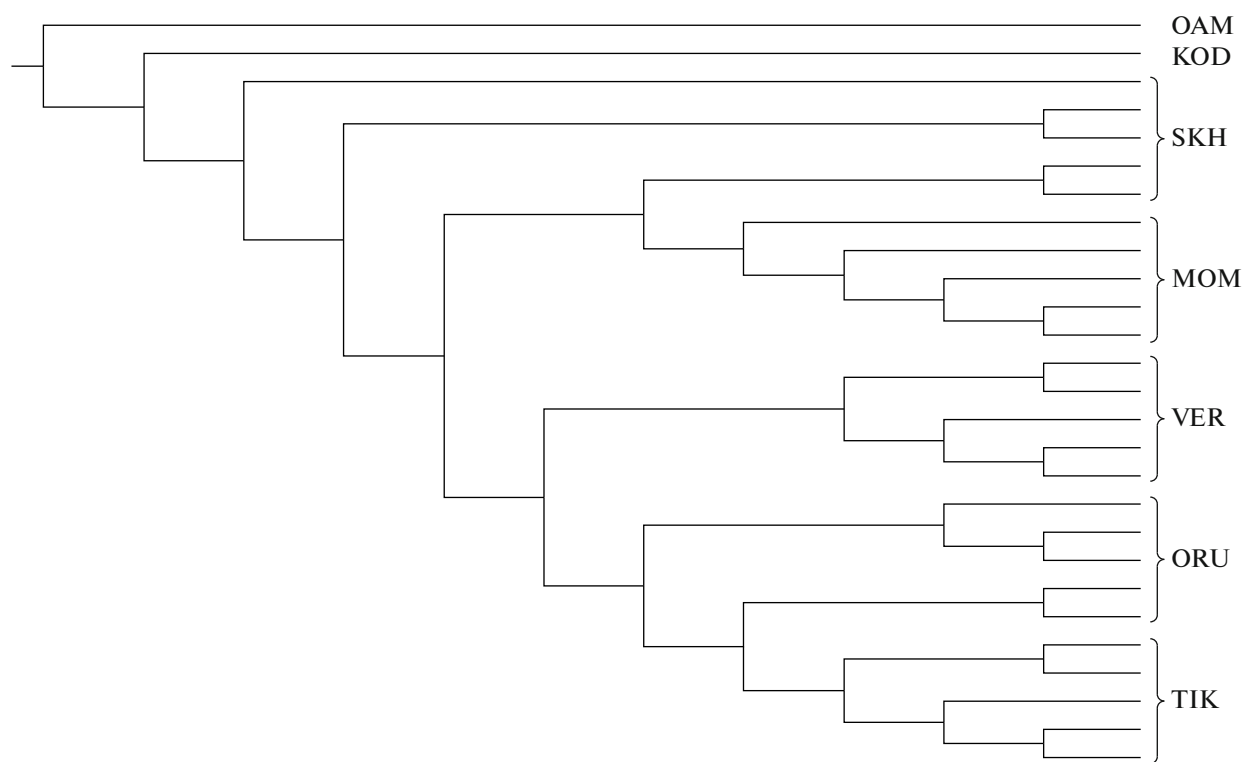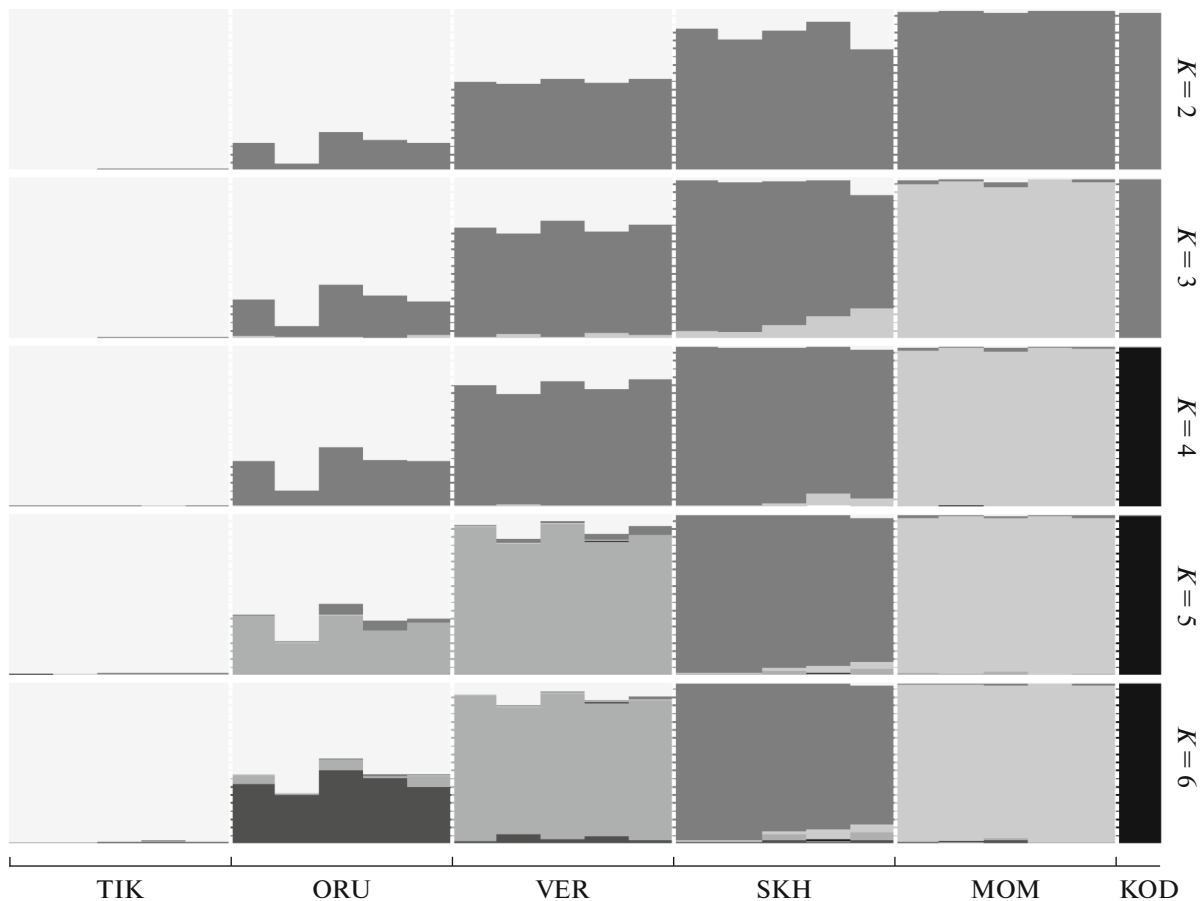
Fig. 6. Population assignment of 26 individuals based on 1030 markers using STRUCTURE analysis (Pritchard, 2000). Studied populations: KOD—Kodar Ridge, TIK—Kharaulakh Ridge (Tiksi), ORU—Orulgan Ridge, VER—Central Verkhoyansk Ridge, SKH—Suntar-Khayata Ridge, MOM—Moma Ridge; individuals are represented as vertical bands with different shades of grey, corresponding to their assumed population origin. Abbreviation of the populations is indicated at the bottom of the figure.

than those between groups of Yakut subspecies (from 0.016 ± 0.002 to 0.078 ± 0.002).

STRUCTURE analysis (Fig. 6) shows that at $K = 2$, TIK and KOD + MOM distributed between two different clusters with the high membership degree in their own clusters, whereas individuals of ORU, VER and SKH revealed a different degree of admixture. At $K = 3$, KOD and MOM formed their own clusters, whereas the ORU, VER and SKH had traces of some admixture with KOD. At $K = 4$, Kodar snow sheep was clustered separately up to $K = 6$. There were no traces of KOD admixture from K 4 to 6 in the individuals of Yakut subspecies.

DISCUSSION

Recent developments in molecular genetics have opened new possibilities to study evolution processes, assess biodiversity and revise taxonomic classification. Moreover, it is believed that only molecular markers provide an opportunity to trace the genealogy of families, populations, etc. (Abramson, 2009). However,

the character of identified phylogenetic relationships is significantly affected by the type of molecular markers. The wrong choice of markers can lead to an unwarranted phylogenetic and taxonomic scheme (Abramson, 2007; Patwardhan, 2007). Until recently mtDNA polymorphisms analysis has been the most common type of DNA markers used in the study of wild *Ovis*. Markers based on mtDNA were used to clarify the taxonomy of the wild *Ovis*, comparing the data of molecular phylogeny with biogeographic, morphological, and karyotypic criteria and formation of the modern outlook on the history of the evolution of the genus *Ovis* (Hiendleder, 2002; Bunch, 2006; Rezaei, 2010; Sanna, 2015). On the other hand, the study of intraspecific structures of the genus *Ovis* using mtDNA did not reveal a clear relationship between phylogenetic and biogeographic data (Boyce, 1999; Kuznetsova, 2005). In the last decade, the development and improvement of high-throughput methods of SNP genotyping has led to a revolution in their use as molecular markers, including the studies of wild *Ovis* (Bagirov, 2016). We have conducted

genome-wide SNP analysis of a single individual of Kodar snow sheep. It is the first step toward understanding the demographic history of the ancestral form of snow sheep, which was formerly widespread in the Baikal and Transbaikal regions, but now is absent in most parts of the area which it probably inhabited since the mammoth fauna era. The genetic studies of Kodar sheep are very important for biodiversity conservation in the Russian Federation.

CONCLUSIONS

The first genome-wide study of the SNP profile of an individual of the Kodar snow sheep (*Ovis nivicola kodarensis*), a representative of an isolated small local population of the Asian show sheep with a "spot" habitat on the Kodar ridge (Irkutsk region, Trans-Baikal region), revealed the presence of a highly conserved unique genotype, which is significantly different from genotypes of the geographically closest Yakut snow sheep subspecies (*O. n. lydekkeri*). Almost 10 times lower level of genetic diversity was found. That makes the population vulnerable to changes in environmental factors and can lead to the loss of genotypes because of gene drift. It is crucial to conduct additional studies on an extended sample for an understanding the demographic history of the original Kodar population of snow sheep.

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