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GENETIC CHARACTERISTICS OF REGIONAL POPULATIONS OF NENETS REINDEER BREED (*Rangifer tarandus*)

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Abstract

Nenets breed is the most numerous indigenous breed of domestic reindeer (*Rangifer tarandus*). Due to their biological versatility, the breed's representatives easily adapt to new pastures. The breeding zone covers the territory from the Kola Peninsula in the west to Taimyr in the east. However, there is still no information on the genetic structure of the Nenets domestic reindeer breed. This paper is the first to present data on STR markers of reindeer of the Nenets breed from the Russian regional populations, the breeding zone of which almost completely covers the current range of the breed. The aim of our work was to characterize the allele pool of domestic reindeer of the Nenets breed, which originate from different regional populations. The sample included 787 specimens from 15 Nenets populations collected in Nenets (KAN, ILB, IND, TAB, HRP, PIL, IZH, SEV) and Yamalo-Nenets Autonomous Districts, the Komi Republic (INT), Murmansk (MUR) and Arkhangelsk (ARH) regions, as well as from the Taimyr municipal district (TUH, DUD). Polymorphism in 14 STR markers, including NVHRT21, NVHRT24, NVHRT76, RT1, RT6, RT7, RT9, RT27, RT30, RT25, RT13, NV03, RT5 and NV73, was studied with the genetic analyzer ABI3130xl. Data processing was performed using software GenAIEx 6.501, GENETIX 4.05 and R package "diversity". The Neighbor Net graph based on pairwise values of Nei's genetic distances was created with SplitsTree 4.14.5 software. In the studied populations, the average number of alleles per locus (N_a) ranges from 9.71 in INT to 6.07 in DUD. The effective number of alleles (N_e) is minimal in the groups DUD and KAN (N_e 3.63) and the maximum in PIL, IZN, INT, SEV, and MUR (N_e 4.55). The number of informative alleles increases from 4.42 in KAN to 5.57 in INT and TAB. Private alleles are found in the INT, MUR, TAB, and TUH groups. In 14 populations, observed heterozygosity (H_o) varies from 0.604 (DUD) to 0.693 (TAB) and 0.695 (IZM). The allelic richness (A_r) ranges from 5.727 in KAN to 7.070 in INT. A heterozygote deficiency was detected in all populations under study. The analysis of Neighbor Net graph showed that the populations of NAO (except KAN) are clustered together with the groups SEY, INT and ARH, the grazing and migratory areas of which are located in the NAO. The Taimyr groups DUD and TUH are separated from the other populations of the Nenets reindeer. The KAN differs from the other populations of the NAO territory, with F_{st} from 0.058 between KAN and IND to 0.083 between KAN and INT, which is indirectly indicated by the lowest level of genetic diversity ($H_o = 0.539$; $A_r = 5.727$). Thus, our present study provides the most complete data on the status of the allele pool and level of biodiversity of the Nenets reindeer breed.

Keywords: Nenets breed, *Rangifer tarandus*, reindeer, STR markers, genetic diversity

Nenets breed is the most numerous breed among four accredited domestic reindeer breeds of in the Russian Federation. Its herding zone covers the territory of Murmansk Region (Kola Peninsula), Nenets Autonomous District (AD), the Komi Republic, Yamalo-Nenets, Khanty-Mansiysk, and Taimyr (Dolgano-Nenets) autonomous district. Regional herding of domestic reindeers has its own characteristics deriving from the difference in the land relief, specificity of food resources, and ethno cultural component.

Reindeer herding on Kola Peninsula is mainly concentrated on the east with dominated plain terrain [1]. Until the middle of XIX, domestic reindeer herding was more a traditional way of life of Saami, than of coast-dwellers. Saami had domesticated forest reindeer species and maintained them in small herds. In the 1880s, first Izhma-Komi families have arrived on Kola Peninsula due to lack of pastures [2]. Colonists had brought between 2.5 and 5 thousand of Nenets reindeers, which number reached 42 thousand by 1909 [1], and had implemented large commercial reindeer husbandry in the region. Izhma reindeers had differed appreciably from the Saami in darker color. Gradually, Izhma and Saami reindeers had mixed with predominant hybrid species in herds. Recently, all population of domestic reindeers had acquired consolidated species composition [3]. Reindeer husbandry in the Komi Republic is concentrated in the Komi-Izhma Region of forest-tundra and tundra. In the XVIII century, Izhma-Komi had started borrowing economic bases of reindeer husbandry from the Nenets and, by beginning of the XIX century, had been actively breeding their own large herds for trade and food requirements [4]. Such progress was due to implementation of a set of innovative approaches, i.e. all year pasturage of large herds, night guarding of herds, increase of the share of females and fawns, new pace of changing of the seasonal pastures [5]. Recently, due to the lack of pastures Izhma-Komi actively use resources of Nenets (during summer) and Khanty-Mansiysk AD (during winter) [1]. Nenets AD remains the leading region of Nenets reindeer husbandry. By geomorphologic properties, such district refers to plain tundra bordering on the coasts of Barents and Kara Seas [1]. Modern Nenets preserve their traditional life style, which is closely related to migrations of reindeer herds during the year [6]. Main landscape of Yamalo-Nenets AD is characterized by arctic moss-and-lichen and low bush tundra merging into forest tundra on the south [1]. Camps of reindeer herds of the Northern Yamal are located in river bottoms on flat tundra plains covered by sparse vegetation [6]. Meanwhile, according to A.A. Uzhakov [7], the past 20 years had witnessed prospering of northern reindeer husbandry and intensive growth of the population, which results in exhaustion of the regional feed resource. The largest in the world tundra area is located in Taimyr Region of the Krasnoyarsk Territory, extending from the Putorana Plateau on the south and Laptev Sea on the north [1]. Noskovskaya and Tukhardskaya tundra are two dominating reindeer husbandry centers on the peninsula. Before the first half of the XX century, indigenous ethnic inhabitants of Taimyr Peninsula, Dolgans and Nganasans, were active in reindeer husbandry [5]. Explosion of wild deer population walking away domestic species was one of the reasons of the industrial crisis in the 1950s [1]. For this reason, Dolgans and Nganasans had almost completely switched over to wild reindeer [5]. Recently, domestic reindeer industry in Taimyr is slowly revived [8].

Several authors highlight several ecotypes inside the Nenets breed, division into which is based on phenotype traits (fawning term, constitutional peculiarities, live body weight, and color) [9]. Nevertheless, until present days studies of biodiversity and genetic structure of Nenets breed in all its diversity have not

been conducted.

Microsatellites, or STR markers, are successfully used in studies of reindeers and its counterparts for settlement of various issues, of which for establishment of its counter genetic structure [10] and biodiversity extent [11], as well as for studying of reindeer differentiation from mainland of the Eurasian area and arctic islands [12]. Besides, the efficacy of STR markers for identification of the genetic relations inside single specie as exemplified by the domestic cattle breeds [13] and between the regional populations inside single specie as exemplified by sheep [14] was demonstrated. However, information on genetic structure of Nenets breed of domestic reindeer is missing until present days.

Present paper introduces details of STR marker based molecular and genetic studies of Nenets reindeer breed from regional populations, breeding area of which almost completely covers contemporary area of such breed.

Our purpose was to characterize allele fund, to study biodiversity of the regional populations of domestic Nenets reindeers, and to establish phylogenetic relationship between them.

Techniques. Sample included 787 tissue specimen (ear fragments) taken from domestic reindeers (*Rangifer tarandus*) of Nenets breed in 2017 for further analysis (2018); 15 populations of different geographic origin were studied.

DNA was extracted by columns Nexttec™ (Nexttec Biotechnologie GmbH, Germany). PCR analysis was conducted for 14 microsatellite loci, 9 of which (NVHRT21, NVHRT24, NVHRT76, RT1, RT6, RT7, RT9, RT27 and RT30) were previously successfully tested in genetic studies of reindeer [15]. Loci RT25, RT13, NV03, RT5, and NV73 were used for *R. tarandus* for the first time. A 14 µl reaction mixture contained (per sample) 1.5 µl of 10 % PCR buffer, 1.5 µl of 2 mM dNTPs solution, 0.15 µl of 100 mM MgCl₂, 2.54 µl of 10 mM primers, 0.2 µl (1 U) Taq DNA polymerase (Dialat Ltd, Russia), 8 µl bidistilled water, and 1 µl (50-100 ng) matrix DNA. Stock solution of PCR buffer contained 16.6 mM (NH₄)₂SO₄, 67.7 mM Tris-HCl (pH 8.8) and 0.1 % Tween 20. The annealing temperature for the primers was chosen based on their melting points. PCRs were carried out by standard protocols (a thermal cycler Mastercycler, Eppendorf, Germany).

Allele sizes were determined using a genetic analyzer ABI3130xl (Applied Biosystems, USA) with Gene Mapper v. 4 software. Matrix for genotypes was created with Microsoft Excel software.

Allele diversity indicators were calculated with GenAIEx 6.501 [16], including average allele number per locus (N_a), effective allele number (N_e), informative allele number (with frequency of over 5 %) ($N_a 5 \%$), and the number of private alleles. Expected (H_e) and observed (H_o) heterozygosity, inbreeding coefficient (F_{is}) with 95 % confidence interval (CI, $t_{0.05} \times SEM$), rarified allele diversity (Ar) values were calculated in package R “diveRsity” [17] in the software environment R [18].

To establish genetic relations between the populations, pair genetic distances D_N by M. Nei [19] were calculated with GENETIX 4.05 software [20], and paired F_{st} values [21] were calculated with GenAIEx 6.501 software. Genetic relations between the reindeer groups were visualized by Neighbour Networks based on matrix of paired D_N values using SplitsTree 4.14.5 software (<http://www.splits-tree.org/>) [22]. Previously obtained data [15] of microsatellite analysis of wild Taimyr deer genome (WLD, $n = 57$) was used as outgroup for construction of genetic networks.

Samples of wild individuals were collected in three geographical regions of Taimyr AD, the Belogolovka Village (BEL, $n = 13$; 72°9'33.13"N, 91°18'92"E), Kongudoyar township (KGR, $n = 19$; 72°7'62.05"N, 91°36'09"E) and Ust-

Avam township (UAV, $n = 20$; $71^{\circ}11'40.71''N$, $92^{\circ}82'07''E$). Geographical map illustrating the sample collection points was created with package R “maps” [18] and visualized with R “ggplot2” [19] in software environment R.

Results. Characteristics of the studied domestic reindeer are provided in Table 1. Figure 1 shows location of sampling points of domestic and wild deer.

1. Characterization of the samples of domestic Nenets reindeer (*Rangifer tarandus*) used in molecular studies (2017-2018)

Household, sampling points	Symbol	n	Total population (January 1, 2018)	Geographic location, geomorphologic region
APC Indiga		48	7419	Nenets AD, Zapolyarny region, Indiga township; Malozemelskaya tundra
SRO Ilebts	ILB	58	585	Nenets AD, Nelmin-Nos township; Malozemelskaya tundra
SRO Tabseda (Sand Hill)	TAB	96	1801	Nenets AD, Nelmin-Nos township; Malozemelskaya tundra
APC Harp”	HRP	91	12266	Nenets AD, Krasnoe township, Zapolyarny region; western part of Bolshezemelskaya tundra
IAPC Kanin	KAN	31	8955	Nenets AD, Kanin Peninsula; Kanin range, Kanin tundra, White Sea-Mezen massive
APC Izhma olenevod and Co.	IZH	45	27785	Nenets AD; Bolshezemelskaya tundra (central part)
Yamal Branch of All-Russia Research Institute of Veterinary Entomology and Arachnology, deer breeding team No. 2	BRG2	49	1673	Yamalo-Nenets AD; territory, Eastern slope of Ural edge
Family Tribal Community of Indigenous People of the North Ilebts	SEY	47	11150	Yamalo- Nenets AD, Seyaha township; Yamal tundra
APC Put’ Ilyicha	PIL	37	15533	Nenets AD; Bolshezemelskaya tundra (central part)
IAPC Tundra	MUR	43	25674 (for 2010)	Murmansk Region, Lovozersky District; north and north-east of Kola Peninsula
PFE Vylko A.V.	ARH	47	607	Arkhangelsk Region, Dolgoshchelye township of Mezensky District; White Sea-Mezen massive
Complex Inta Pripolarnaya LLC	INT	96	9140	Komi Republic, Inta city; Bolshezemelskaya tundra (eastern part)
Severniy LLC	SEV	47	22507	Nenets AD; Bolshezemelskaya tundra (central and eastern parts)
Vasily Palchin’s hoshould, team No. 10	TUH	15	900 (for 2015).	Taimyr (Dolgano-Nenets) municipal district, Tukhard township; forest tundra
PFE Yarodskiy P.A., team No. 1	DUD	37	1800	Taimyr (Dolgano-Nenets) municipal district, Dudinka city; South-Taimyr low-land area

Note. n – number of heads in a group; AO – autonomous district; APC (or IAPC) – Agricultural Production Cooperative (Integrated Agricultural Production Centre), SRO – family and tribal community of indigenous small-numbered people of the north, PFE – Peasant Farm Enterprise.

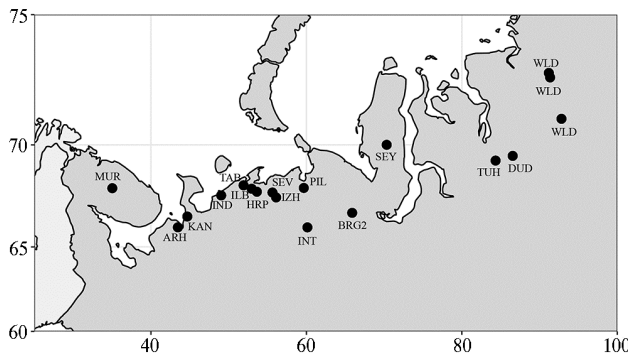


Fig. 1. Sampling of wild (WLD) and Nenets domestic reindeer (*Rangifer tarandus*) (2017). See abbreviations in Table 1.

Mean number of alleles per locus in Nenets deer was minimum for DUD (6.071 ± 0.399) and TUH (6.286 ± 0.485), and maximum for INT (9.714 ± 0.529) and HRP (9.286 ± 0.559) (Fig. 2). Mean effective number of alleles was 4.337 ± 0.108 across all populations and varied from 4.858 ± 0.491 for INT to 3.438 ± 0.341 and 3.631 ± 0.385 , respectively, for DUD and KAN.

INT and TAB groups had precedence over the remaining populations by number of informative alleles (5.571), whereas HRP, DUD and KAN had the minimum numbers (4.643, 4.643, and 4.429, respectively).

Private alleles were not identified in 11 out of 16 studied populations. Possibly, pasturage and migration ways of herds from different households and family-tribal communities have crossed in either way and, thus, gene exchange could not be excluded. Nevertheless, we found private alleles in four groups (INT, MUR, TAB, TUH) (0.286, 0.143, 0.710 and 0.710 alleles per locus), which is mainly due to selection work in these households. Thus, production cooperative Tundra is a tribal reproducer of Nenets domestic reindeer, community Vasily Palchin founded in 2001 after reformation of the Tukhard farm, possessed in use the public reindeer population, agricultural complex Inta Pripolarnaya LLC keeps up more strict tribal pedigree records and selection.

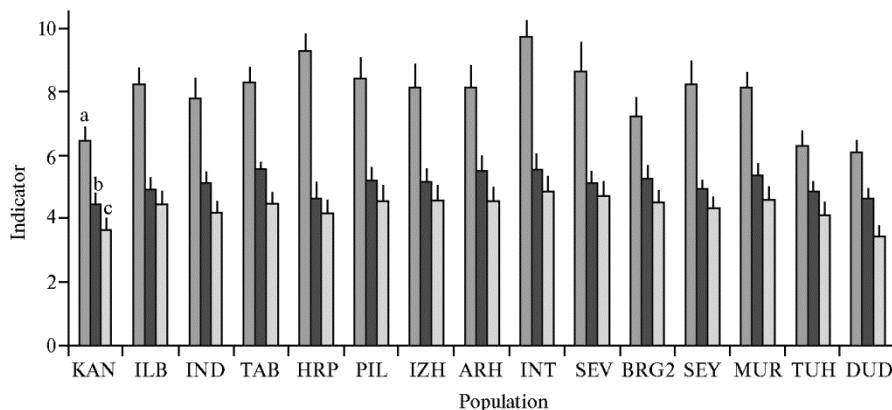


Fig. 2. Allele profiles of studied populations of Nenets reindeer (*Rangifer tarandus*) (2017): a — mean number of alleles per locus, N_a ; b — number of informative alleles, N_a 5 %; c — effective number of alleles per locus, N_e . See abbreviations in Table 1.

Observed heterozygosity exceeded 0.600 in 14 out of 15 populations with maximum values for TAB (0.693) and IZM (0.695) (Table 2). Allele diversity values varied from 5.727 for KAN to 6.921 in PIL and 7.070 for INT. Positive values of inbreeding coefficient F_{is} confirmed the heterozygote deficit occurred in all studied populations. Note, the KAN group is the least genetically diverse by several parameters ($H_o = 0.539$; $Ar = 5.727$) and shows the greatest heterozygote deficit, which could be possibly explained by geographical isolated area of this population (Kanin Peninsula).

2. Genetic diversity of Nenets reindeer (*Rangifer tarandus*) populations (2017) for 14 STR markers

Group	n	H_o	H_e	F_{is}	Ar
KAN	31	0.539±0.043	0.673±0.042	0.178 (0.063; 0.294)	5.727±0.381
ILB	58	0.612±0.040	0.735±0.033	0.166 (0.090; 0.242)	6.505±0.400
IND	48	0.617±0.031	0.729±0.028	0.147 (0.077; 0.216)	6.287±0.395
TAB	96	0.693±0.045	0.759±0.019	0.090 (-0.012; 0.191)	6.741±0.342
HRP	91	0.633±0.036	0.723±0.029	0.112 (0.008; 0.215)	6.598±0.443
PIL	37	0.651±0.040	0.744±0.029	0.116 (0.009; 0.223)	6.921±0.482
IZH	45	0.695±0.030	0.748±0.027	0.061 (-0.026; 0.147)	6.622±0.479
ARH	47	0.640±0.043	0.752±0.024	0.148 (0.052; 0.243)	6.750±0.448
INT	96	0.654±0.034	0.762±0.027	0.142 (0.081; 0.202)	7.070±0.433
SEV	47	0.673±0.049	0.760±0.024	0.112 (-0.000; 0.224)	6.791±0.577
BRG2	49	0.650±0.054	0.758±0.020	0.146 (0.014; 0.278)	6.172±0.425
SEY	47	0.637±0.049	0.739±0.026	0.143 (0.042; 0.245)	6.590±0.495
MUR	43	0.629±0.039	0.750±0.028	0.164 (0.087; 0.241)	6.741±0.348
TUH	15	0.657±0.045	0.711±0.038	0.057 (-0.064; 0.178)	6.286±0.485
DUD	37	0.604±0.050	0.670±0.034	0.086 (-0.038; 0.211)	5.317±0.346

Note. n — number of individuals per sample, year; H_o — observed heterozygosity, H_e — expected heterozygosity, F_{is} — inbreeding coefficient, Ar — rarefied allele diversity. Range variation coefficient F_{is} at confidence interval of 95 % is provided in parenthesis. See abbreviations in Table 1.

Genetic relations of the studied reindeer populations were established based on analysis of genetic network structure (Fig. 3) and F_{st} values. Two con-

ventional clusters were noted oppositely in the network.

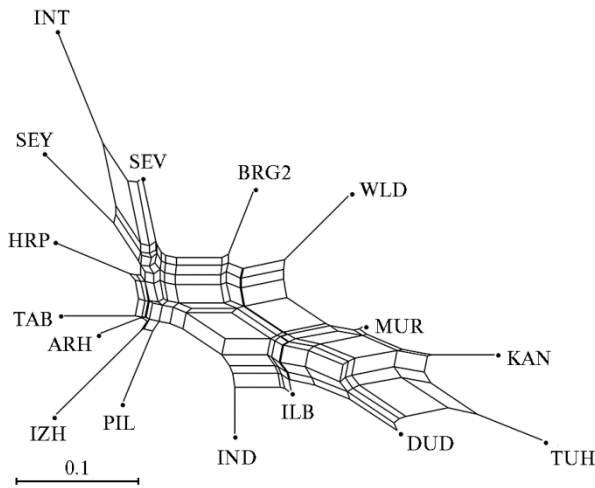


Fig. 3. Genetic relations between 15 populations of Nenets domestic reindeers (*Rangifer tarandus*) (2017) and a group of wild deer (WLD) as Neighbor Net graphs based on Nei's genetic distance matrix [19]. See abbreviations in Table 1.

The first cluster grouped populations of Nenets AD (except for KAN), and SEY, INT, and ARH, and joining branches IND, ILB and BRG2. Such distribution, probably, reflects the history of certain herds. For instance, Seyakhin herds are isolated from the main massive of the breed since they are located in tundra all year round and do not migrate for wintering to forest tundra as animals from other households of Yamal District. Nevertheless, this group originates from reindeer herds from Nenets AD, which the observed clustering possibly reflects. Besides, herd pasturage and migration territories are often located close to each other (for instance, for ARH from Mezensk Region and for INT from Komi Republic, they are close to such in Nenets AD). Deer from ARH group demonstrate some genetic relationship with populations of Nenets AD, reflected in insignificant F_{st} values (from 0.019 with TAB to 0.030 with ILB). In its turn, INT group forms one of the longest network branches and, according to F_{st} values (0.038 for TAB and 0.055 for ILB), is more clearly differentiated that evidences of the intended selection in this breeding farm. The least F_{st} value for INT was found with deer SEV ($F_{st} = 0.020$), which also initially originate from the Komi Republic. We should note genetic relationship between IND and ILB groups ($F_{st} = 0.014$), which, possibly, points out to presence of common originators of herds or close breeder exchange.

The second conventional cluster included groups KAN, DUD, and TUH. DUD and TUH groups ($F_{st} = 0.027$) are representatives of Taimyr domestic deer, separated from other populations of Nenets reindeers. Herewith, TUH is the most genetically separated group, with F_{st} from 0.053 for IND and BGR2 to 0.087 for INT. Other well differentiated group is KAN (F_{st} from 0.058 for IND to 0.083 for INT), which is bred in Kanin Peninsula. Possibly, KAN consolidation with Taimyr deer is due to their distance from other populations, but not to close relationship between each other.

MUR group formes separate branch close to network centre which is possibly due to its closeness to common ancestor form of breed. Group of wild Taimyr deer (WLD) occupies interim position, as per insignificant difference in F_{st} values (from 0.031 to 0.053).

Reindeer (*Rangifer tarandus*) widely spread in arctic and subarctic zones of Asia, Europe, and North America is an important element of tundra, forest-tundra, and forest ecosystems. In this regard, studying of the genetic diversity and differentiation of groups of such type of hoofed mammals is of interest for many researchers [25-30]. The mean values of the expected heterozygosity found in six caribou populations inhabiting Canadian Alberta and British Columbia provinces varied from 0.740 to 0.790 [25]. For populations inhabiting different

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Quebec ecosystems, the expected and observed heterozygosity values were 0.630-0.778 and 0.620-0.770, respectively [26]. Variability for H_e was within 0.620-0.860, and for H_o within 0.740-0.860 in four deer herds inhabiting Alaska [27, 28]. H_e (0.649-0.761) and H_o (0.374-0.530) were calculated for groups of deer selected at eight points of the Great Khingan Mountains of Inner Mongolia [29]. M.A. Cronin et al. [30] had studied genetic diversity of domestic reindeer populations using samples from Alaska ($H_e = 0.352-0.472$; $H_o = 0.325-0.456$), Northway ($H_e = 0.432$; $H_o = 0.364$), and from three points of Magadan Region ($H_e = 0.415-0.477$; $H_o = 0.375-0.402$). In our research we have obtained commensurable values of expected and observed heterozygosity, the $H_e = 0.670-0.762$; $H_o = 0.539-0.695$. A Russian deer group in research of M.A. Cronin et al. [30] possibly belongs to domestic population inhabiting small common area or represented by genetic relatives, which, possibly, resulted in lower genetic diversity parameters as compared to those we found out. Heterozygote deficit was also recorded for deer groups from China, which significantly exceeded F_{is} values established in our research paper, i.e. 0.320-0.532 [29] against 0.057-0.178. Allele diversity values calculated in our research is quite close to those obtained by K.H. Mager et al. [28]: $Ar = 5.32-7.07$ and $Ar = 5.70-7.21$, respectively.

Possibility to differentiate territorial populations inside *R. tarandus* species based on microsatellites was also studied in sufficient details; however the findings significantly varied. Thus, F_{st} between the caribou populations varied from 0.025 (maximum value between the groups inhabiting one side of Peace river) to 0.044 (minimum value between the groups inhabiting different sides of Peace river) [25]. Values F_{st} among eight reindeer groups inhabiting one and the same archipelago ranged from 0.006 to 0.075 [29]. Three caribou ecotypes (forest, plain, and mountain types) inhabit Quebec province, with F_{st} values among them from 0.087 to 0.172, and F_{st} inside forest ecotype from 0.016 to 0.097 [26]. F_{st} values between Nenets reindeer populations in our study vary from 0.014 to 0.087, which, possibly, evidences on the lack of clearly manifested ecotypes unlike data obtained by M.A. Courtois et al. [26].

Comparison of geographic location of the breeding points of certain Nenets deer herds with genetic network structure had shown that Taimyr deer are differentiated from deer inhabiting Nenets and Yamalo-Nenets Autonomous Districts, whereas clatirezation was not manifested within the districts. K.H. Mager et al. [28] had shown that several herds of domestic reindeer in Alaska were clearly differentiated from each other ($F_{st} = 0.23$), whilst the others were not (F_{st} is near zero 0). We have observed the same in populations of Nenets breed (maximum value $F_{st} = 0.087$).

Interesting, the private alleles, as we have already noted, are identified only in groups INT, MUR, TAB, and TUH. We may assume that it was mainly the result of selection work in the households (similar studies have not previously been conducted).

Thus, polymorphism analysis for 14 STR markers had shown that genetic diversity in the studied Nenets reindeer populations within the Russian Federation insignificantly differs from the similar values in its North American and European conspecifics. Probably, it reflects certain genetic stability in these deer groups. Nevertheless, these findings do not allow us to draw conclusion on existence of several ecotypes inside the Nenets reindeer breed. This is also evidenced by some conditionality of population intrabreed clustering. Possible reasons could be specific biology properties, lack of strict pedigree records, and uncontrolled forced redistribution of deer. Besides, escaping of domestic individuals to tundra and living with wild deer may provide gene transfer which shall be accounted in

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