

Ecological and Molecular Genetic Features of *Ixodes persulcatus* and *I. pavlovskyi* Ticks in Southern West Siberia

N. N. Livanova^{a, b, *}, S. G. Livanov^a, A. Yu. Tikunov^b, N. V. Fomenko^{b, c}, and N. V. Tikunova^b

^a Institute of Systematics and Ecology of Animals, Siberian Branch, Russian Academy of Sciences, Novosibirsk, 630091 Russia

^b Institute of Chemical Biology and Fundamental Medicine, Siberian Branch, Russian Academy of Sciences, Novosibirsk, 630091 Russia

^c ZAO Vector-Best, Novosibirsk, 630127 Russia

*e-mail: nata-livanova@yandex.ru

Received August 31, 2015; in final form, April 25, 2016

Abstract—Ixodidae ticks have been counted and sampled in six distant locations within the Altai-Sayan Mountain Area and northern forest steppe in 2012. In total, 1829 individuals of *I. persulcatus* and 719 of *I. pavlovskyi* ticks were collected by flagging. *I. persulcatus* is found in all six examined locations and *I. pavlovskyi* is found in Western Altai, Northeastern Altai, and Northern Altai, as well as in forest parks near Akademgorodok of Novosibirsk. In total, 16S rRNA and *COI* sequences have been determined in 144 and 164 *I. persulcatus* individuals, as well as in 60 and 55 *I. pavlovskyi*. Selectively equivalent mutant forms are present in *I. pavlovskyi* populations of Northeastern Altai and Northern Altai. The hydrothermal regime in the forest parks near Novosibirsk is optimal for the *I. pavlovskyi* ticks. These ticks have recently colonized the forest parks near Novosibirsk and therefore are genetically close to *I. pavloskyi* from the Altai–Sayan Mountain Area populations.

Keywords: 16S rRNA, *COI*, *Ixodes persulcatus*, *Ixodes pavlovskyi*, the Altai–Sayan Mountain Area, northern forest–steppe, abundance, resettlement

DOI: 10.1134/S1995425516060081

INTRODUCTION

The genus *Ixodes* (Acari: Ixodidae) consists of 220 species. It includes ticks most aggressive to men: *Ixodes persulcatus* Schulze, 1930, *I. pavlovskyi* (Pom., 1946), *I. ricinus* (Linnaeus, 1758), *I. scapularis* Say, 1821, and *I. pacificus* Cooley & Kohls, 1943. *I. persulcatus* and *I. pavlovskyi* are epidemically the most significant in the Asiatic part of Russia. They participate in the circulation of the tick-borne encephalitis virus and tick-borne borrelioses, *Borrelia burgdorferi* s.l., *Borrelia miyamotoi*, “Candidatus Rickettsia tarasevichiae,” and *Anaplasma phagocytophilum* (Chausov et al., 2010; Korenberg et al., 2010; Rar et al., 2010; Shpynov et al., 2006; Taylor et al., 2013; Tkachev et al., 2014). Due to bird migrations, these arthropods successfully cross considerable distances, thus expanding the borders of natural foci (Scott 2001; Alekseev et al., 2001). Data accumulated to the present time allowed us to consider the dispersal of *I. pavlovskyi* in the beginning of the last century, having led to the successful fixation of this blood-sucker species on new territory (Livanova et al., 2015; Romanenko and Leonovich, 2015). As a rule, the dispersal resulting from changes in environment significantly influence population dynamics (Bigon et al., 1989). At the

same time, changes in environmental conditions (amount of food, habitat availability, and abiotic factors) can influence the genetic diversity of populations (Hewitt, 2000), which either increases due to gene flow upon tick dispersal or opposite processes occur under the pressure of cleaning selection.

At the modern stage of investigation of *I. pavlovskyi* dispersal onto new territories, it was found that, in the ticks of this species, in contrast to *I. persulcatus*, genetic polymorphism is less expressed, and there is no geographic differentiation of molecular markers (Livanova et al., 2015). In addition, the analysis of available materials allowed us to reveal some new features at the level of molecular genetics between tick species having similar biological characteristics. In this context, our paper aims at not only obtaining characteristics of the modern condition of abundance and occurrence of *I. persulcatus* and *I. pavlovskyi* in the sympatric populations to the south of West Siberia, but also an estimation of the diversity level in mtDNA in the two tick species.

MATERIALS AND METHODS

Counts of the tick abundance and their sampling were conducted within the Altai–Sayan Mountain

Table 1. Abundance and distribution of the ticks *I. persulcatus* (I) and *I. pavlovskyi* (II) at the south of West Siberia in 2012

Key location	Coordinates	Total caught		Relative tick abundance per 1 flag–km (D _{lov} –D _{up})	
		I	II	I	II
Western Altai (East Kazakhstan Region, Kazakhstan)	50°11'–50°17' N, 82°51'–82°59' E	17	7	0.9 (0.6–1.3)	0.7 (0.5–1.0)
Northeastern Altai (Turochakskii district, Altai Republic)	51°47'–51°47' N, 87°18'–87°17' E	299	90	32.6 (29–36)	12.4 (10.5–14.6)
Northern Altai (Chemal'skii district, Altai Republic)	51°36'–51°39' N, 85°47'–85°43' E	662	289	52.6 (49–57)	4.5 (4.2–4.9)
Salair Ridge (Toguchinskii district, Novosibirskaya Oblast')	54°42'–54°44' N, 84°45'–84°46' E	274	0	9.3 (8.2–10.6)	0
Northern forest steppe (Toguchinskii district, Novosibirskaya Oblast')	54°53'–54°53' N, 83°21'–84°21' E	625	0	28.8 (31–36.7)	0
Belt pine forests in the valley of the River Ob (forest park zone of the Akademgorodok of Novosibirsk and its vicinity)	55°00'–55°02' N, 82°58'–83°19' E	40	666	1.5 (1.1–1.9)	35.3 (32.8–38.4)

Area and in the northern forest steppe of West Siberia. Six sites locations were examined (Table 1, Fig. 1). Ticks counts were conducted using generally accepted methods (Taezhnyi..., 1985) in the period from April 24 to May 30, 2012, in main vegetation types. Within the Altai-Sayan Mountain Area we examined low- and middle-mountainous wet aspen–spruce, pine–spruce, pine–fir–spruce, and birch–aspen forests and overgrowing glades, as well as pine and secondary forests in mountain valleys. Zonal aspen–birch forests among forb–cereal steppes and fields were explored on the plain in northern forest steppe, as well as habitats in the forest park zone of Akademgorodok of Novosibirsk and its vicinity. The length of transects in each vegetation type was no less than 5 km. Results of the counts were analyzed, and the arthropods were subsequently collected where they concentrated. Then we obtained mean values of tick abundance for each sites. The species of imagoes was identified based on morphological criteria using a binocular microscope (Filippova, 1977). The ticks were stored in cameras with differentiated humidity before molecular analysis. A total of 2739 ticks were caught.

The tick DNA was extracted using Proba NK kit sets (DNA–Technology, Russia) according to user instructions. Then it was kept in 50 µL of TE buffer at –70°C. Fragments of the genes 16S rRNA and cytochrome oxydase *COI* in the samples of tick DNA were amplified with pairs of respective primers: IF3seq (5'-gggacaagaagaccctatgaa-3'); IR3seq (5'-agatagaaac-caacctggctc-3'); C1 (5'-accacaagacattggaactatata-3'), C2 (5'-aatcaggaagaataagaatata-3'). Expected sizes of fragments were as follows: 250 p.n. for the gene 16S rRNA and 650 p.n. for the gene *COI*. DNA sequences were determined using forward primer and downstream primer.

Amplified fragments were cleaned using Silica Bead DNA of the Gel Extraction Kit (Fermentas) and analyzed using BigDye Terminator v. 3.1 Cycling Sequencing Kit (Applied Biosystems). Alignment of sequences was conducted using MEGA 5.2.2 software (Tamura et al., 2011). The sequences of gene fragments from unique specimens for each territory under study were deposited in the GenBank. MEGA 5.2.2 Software was used for building dendrograms by the methods of Maximum Likelihood (ML), Neighbor Joining (NJ), and Unweighted Pair Group Method with Arithmetic Mean (UPGMA). The dendrograms built by different methods had similar topology. We provide here those built using the NJ method.

Statistical error of tick counts was calculated by the formula $D_{lov} = D(1 + 1.64 \times e(D))$ and $D_{up} = D/(1 + 1.64 \times e(D))$ (Olsson, 2005).

RESULTS AND DISCUSSION

As was shown earlier (Livanova et al., 2015), based on morphological characters of the 2548 ticks caught, they belonged to the species *I. persulcatus* (1829 individuals) and *I. pavlovskyi* (719). *I. persulcatus* was recorded on all territories under study, *I. pavlovskyi* on Western, Northwestern, and Northern Altai, as well as in valley habitats of the River Ob within the forest park zone of Akademgorodok in Novosibirsk and its vicinity. Maximum values of relative abundance of the ticks *I. persulcatus* were found in Northern Altai. In Northwestern Altai (52.6 individuals per km, χ^2 4.6) and the zonal forest steppe (28.8 individuals per km, χ^2 7.0), the values of relative abundance of *I. persulcatus* were significantly lower than those found in Northern Altai (52.6 individuals per km) (see Table 1). On the contrary, the abundance of *I. pavlovskyi* was maximum in

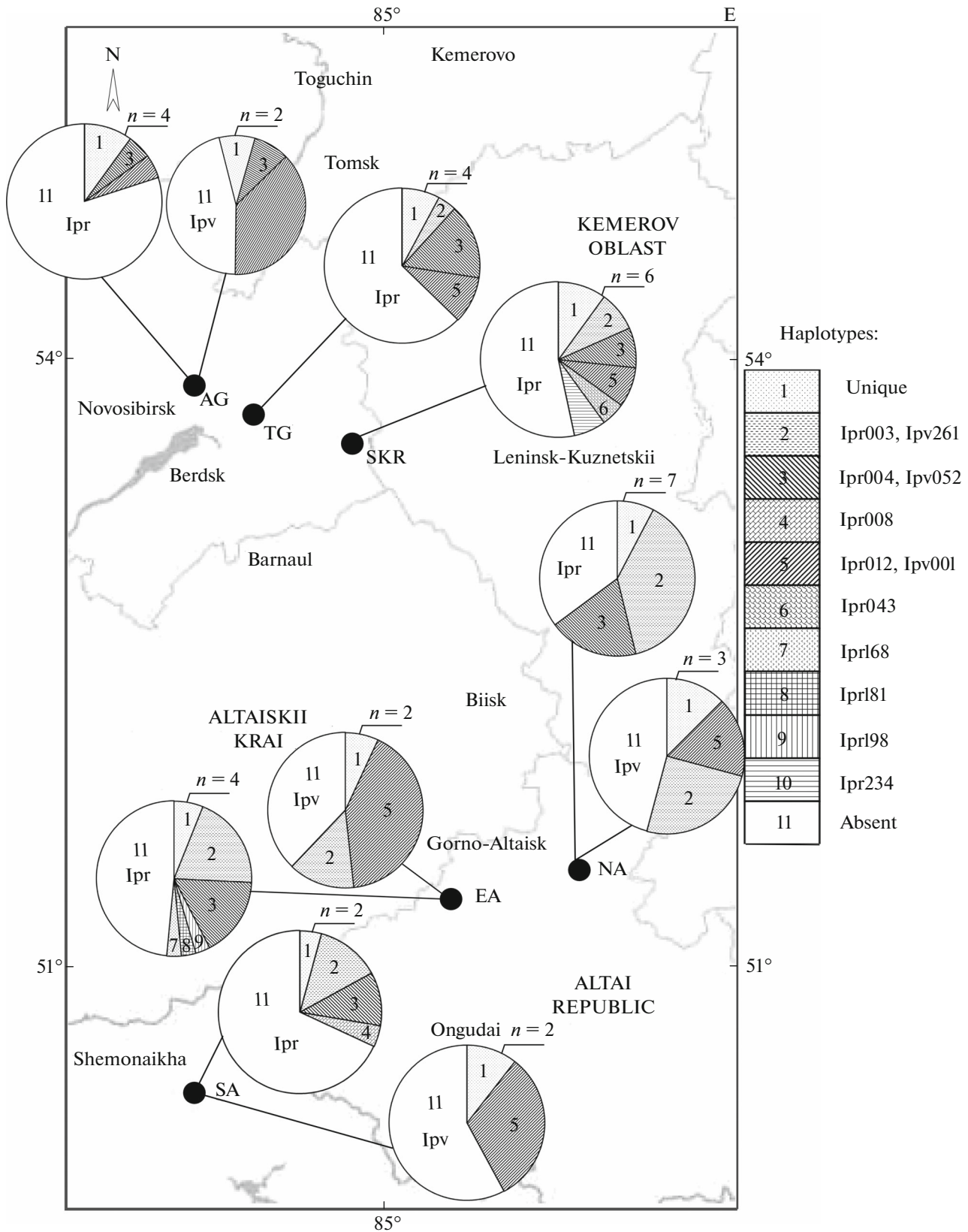


Fig. 1. Schematic map of the study sites and distributions of the *COI* haplotypes in *I. persulcatus* and *I. pavlovskyi*. Places where *I. persulcatus* and *I. pavlovskyi* were collected: SA, Western Altai (Kazakhstan); EA, Northeastern Altai (Altai Republic, Russia); NA, Northern Altai (Altai Republic, Russia); SKR, Salair Ridge (Novosibirsk oblast, Russia); TG, northern forest steppe (Novosibirsk oblast, Russia); and AG, forests in the Ob River valley (city of Novosibirsk, Russia). The number of unique haplotypes for each tick species and sites under study is designated by *n*.

the forest park of Akademgorodok (35.3 individuals per kilometer) and significantly exceeded the abundance of ticks of this species on the Western (0.9 individuals per km, χ^2 16.2), Northwestern (12.4 individuals per km, χ^2 11.1), and Northern Altai (4.5 per km, χ^2 23.8).

Within the western part of *I. pavlovskiy* range in sympatric populations of *I. pavlovskiy* and *I. persulcatus* with *I. persulcatus*, the latter occurs on wider areas and on most of the territories has higher population numbers. It is known that optimal survival of *I. persulcatus* was noted in the years with modest temperatures and high humidity (Korotkov and Kislenko, 2002). According to data from <http://www.atlas-yakutia.ru> within the study area on the Northern and Northeastern Altai in the period of activity of arthropods, the values of positive temperatures for the period with mean daily temperature above 10°C are 1200–1800°; humidity is from 800 mm and more. Such thermal and humidity characteristics were given for the study area we studied on Salair Ridge and on the plain northern forest–steppe. An opposite situation was formed on the territories under study on the Western Altai and in Akademgorodok, where the population number of *I. persulcatus* is low. The mean daily sum of temperatures above 10°C there reaches 2200° and the amount of precipitation during frostless period in some years below 200 mm. Such types of data are singular for the *I. pavlovskiy* ticks. However, having analyzed the values of relative abundance of the *I. pavlovskiy* ticks, we can assume that, in contrast to *I. persulcatus*, this species prevails on territories with high values of the sum of temperatures in spring and summer, but humidity there is low. It is interesting that, according to data from Bolotin et al. (1977) for the Western Sikhote Alin, the *I. pavlovskiy* ticks, unlike *I. persulcatus*, occur more frequently on territories with a higher sum of temperatures, but the level of precipitation does not play a decisive role for this tick species. On the lower part of the Salair Ridge explored by us in 2012, which is characterized as regions with high humidity and modest spring and summer temperatures, conditions for the survival of *I. pavlovskiy* populations are unfavorable. Despite the proximity of large *I. pavlovskiy* populations (Chigirik et al., 1974) and confirmed facts of its translocation by birds there (Bogdanov, 2006), the ticks did not form populations in the part of Salair Ridge explored by us.

Abundance of hosts of ticks as a factor influencing the level of population numbers in the tick species under study comes in second place in relevance (Korotkov and Okulova, 1999). It is known that the mortality of imagoes in *I. persulcatus* in the spring and summer period, conditioned by the deficiency of large and medium-sized mammals, may be 98% (Korotkov and Kislenko, 2002). Such a dependence of the number of tick imagoes from vertebrates seems to reasonably explain the flourishing of the *I. pavlovskiy* popu-

lation in the forest park of Akademgorodok and that of *I. persulcatus* on the Northeastern and Northern Altai. In all probability, the reproduction of *I. persulcatus* in Akademgorodok is hindered by the low number of hosts of ticks of the mature phase and the annual existence of this species is ensured by the translocation of its nymphs by birds. It is also evident that the high population number in *I. pavlovskiy* within the forest park zone in Akademgorodok and its vicinity is maintained by a high number of birds foraging on land (Livanova et al., 2011). Our conclusions correspond to results of studies conducted in Tomsk and its suburbs, where a clear numeric prevalence of *I. pavlovskiy* above *I. persulcatus* ticks was noted on the areas inside the city (Romanenko and Leonovich, 2015). The earlier assumption about the positive influence of the proximity of large river valleys on the successful existence of *I. pavlovskiy* on new territories (Romanenko and Pankova, 2013), in all probability, is baseless.

The data on the genetic diversity of closely related *I. persulcatus* and *I. pavlovskiy* are shown in Table 2. The high content of A and T nucleotide bases was determined for mtDNA sequences in all specimens. Eight variable and two Pi-informative sites were determined for the 16S sequence in the rRNA of *I. persulcatus*. Only three variable sites were found in *I. pavlovskiy*. For a nucleotide sequence of the gene *COI* fragment from specimens of the *I. persulcatus* ticks, 33 variable and 7 Pi sites were found for specimens of *I. pavlovskiy* 13 and 5, respectively. The primary structure of the *COI* protein site was determined in the course of studies of the *COI* gene in *I. persulcatus* and *I. pavlovskiy* ticks (Table 3). In the amino acid sequence of the studied fragment of the *COI* protein in *I. persulcatus* ticks, the main haplotype IPr003 differs from that in the main haplotype of *I. pavlovskiy* (IPv001) by one amino acid residue in the 178 position: *I. persulcatus* (IPr003), serine (Ser); *I. pavlovskiy* (IPv001), leucine (Leu). In the sequences of 13 specimens of *I. persulcatus* ticks obtained from all explored territories, singular replacements of nucleotides have led to modifications of the protein amino acid sequence. The number of mutations leading to the change of class of the amino acid residue in sequences of gene *COI* in *I. pavlovskiy* ticks is 4. In the haplotypes IPv261(EA), IPv264(EA), IPv274(NA), and IPv284(NA), changes of nonpolar amino acids to polar ones charged positively occurred. It is important to note that the sites of replacements of amino acids of the polypeptide, found in the haplotypes IPv264(EA) and IPv284(NA), are positioned closely (sites 37 and 38).

Based on an analysis of the sequence of the 16S rRNA gene in *I. persulcatus*, nine haplotypes were determined. Among them, IPr003 is widespread (Fig. 2). The IPr003 sequence is homologous to that in *I. persulcatus* ticks (ABO73725) from Japan. Four haplotypes were determined in *I. pavlovskiy* ticks, and the sequence of the widespread IPv001 is close to that of *I. pavlovskiy* ticks (AF549835) from Japan. Based on

Table 2. Analyzed genes of the mtDNA (16S rRNA, COI) of *I. persulcatus* (I) and *I. pavlovskyi* (II) caught in the south of West Siberia in 2012

Nucleotide sequences	Species	Number of genetic variants (sequences analyzed)	Number of variable sites, %	Number of Pi-sites, %	Nucleotide composition, %				Pairwise genetic distances
					A(%)	T(%)	C(%)	G(%)	
16S rRNA	I	9 (144)	8 (2.9%)	2 (0.7%)	37.4	34.4	18.7	9.6	0.00130
	II	4 (60)	3 (1.1%)	0	38.5	35.6	16.7	9.1	0.00048
COI	I	32 (164)	33 (5.1%)	7 (1.1%)	29.0	38.4	18.2	14.4	0.00225
	II	11 (55)	13 (2%)	5 (0.8%)	28.6	40.3	16.8	14.4	0.00165

the analysis of the *COI* gene fragment in the *I. persulcatus* ticks, 32 haplotypes were determined (Fig. 3). Among them, Ipr003 and Ipr004 sequences were found in ticks caught in all key locations (see Fig. 1). Their proportions from the number of determined ones were 37.8 and 29.3%, respectively. The ticks with homologous sequences of the fragment of the *COI* gene were caught earlier in China (HM193868) and Japan (AB073725). Eleven haplotypes were determined in *I. pavlovskyi* ticks; IPv001 was found almost everywhere (see Fig. 1). The proportion of ticks with a sequence identical to IPv001 in samples under study was 59.6%. The IPv001 sequence is homologous to JX288763 of the *I. pavlovskyi* ticks caught in the parks and suburbs of Tomsk.

A shifting of the nucleotide composition towards A and T bases in the mitochondrial sequence in *I. persulcatus* and *I. pavlovskyi* ticks was found. Despite the lack of a singular universal mechanism explaining the shift of nucleotide content, these results evidenced a high degree of kinship between *I. persulcatus* and *I. pavlovskyi* ticks. A similar shift of the nucleotide content was found in mtDNA sequences in *I. ricinus* (Casati et al., 2008). Xu et al. (2003) explain this peculiarity by the fact that, among numerous members of the genus *Ixodes*, ticks of the ricinus–persulcatus complex are a relatively modern evolutionary group.

We analyzed an amino acid sequence of a fragment of the *COI* protein in *I. persulcatus* and *I. pavlovskyi*. In contrast to the *I. persulcatus* ticks living in Northeastern and Northern Altai, there are selectively equivalent

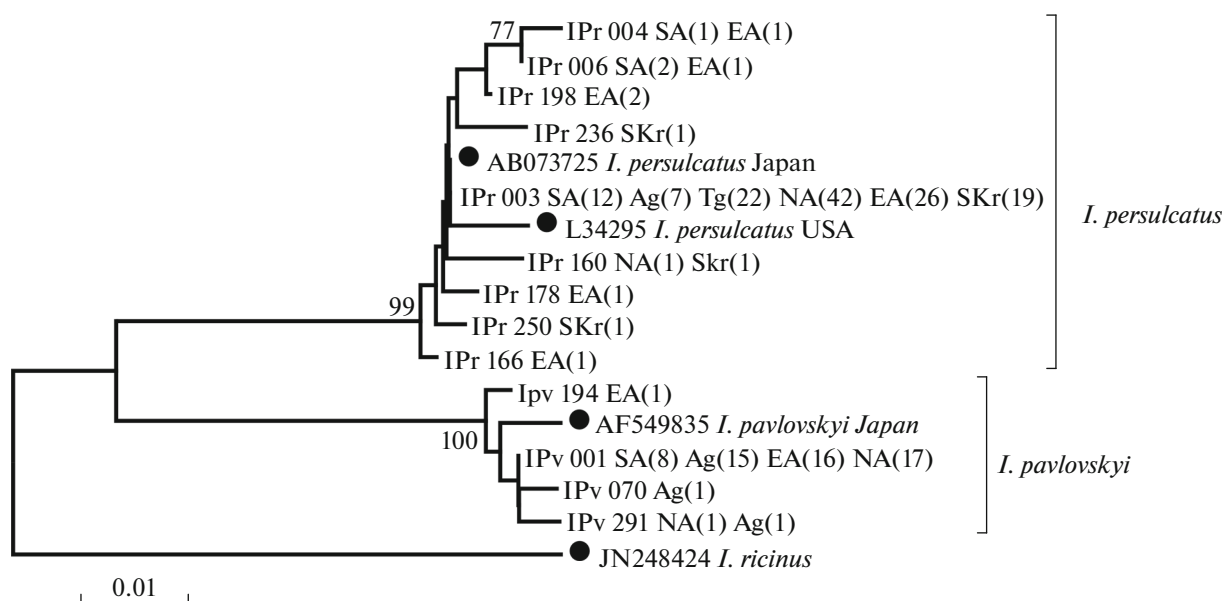


Fig. 2. NJ, dendrogram built based on analysis of sequential fragment of the gene 16S r RNA (276 p.n.). Numerals (>70% /> 0.7) in the nodes of branching designate the value of bootstrap support. The number of sequences of each haplotype is given in brackets. Places where *I. persulcatus* and *I. pavlovskyi* were collected: SA, Western Altai (Kazakhstan); EA, Northeastern Altai (Altai Republic, Russia); NA, Northern Altai (Altai Republic, Russia); SKR, Salair Ridge (Novosibirskaya oblast, Russia); TG, northern forest steppe (Novosibirsk oblast, Russia); and AG, forests in the Ob River valley (Novosibirsk, Russia). Punson is sequence in the GenBank.

Table 3. Analysis of positions of the multiple alignment of the area coding the gene *COI* in *I. persulcatus* and *I. pavelovskyi*

Haplotype	Location of collecting** (n)	no in GenBank	Totally	Position of variable site*																
				25	32	37	38	55	59	83	99	117	121	138	145	168	170	178	207	216
<i>I. persulcatus</i>				Ser	Met	Arg	Thr	Val	Ala	Ala	Leu	Val	Ala	Ser	Ala	Ile	Met	Ser	Met	Thr
IPr003***	Japan SA (12), EA (36), NA (56), SKR (24), TG (18), AG (6)	AB073725 KC688364	166	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IPr008	SA (2)	KC688366	2	-	-	-	-	-	-	-	-	-	Ser	-	-	-	-	-	-	-
IPr058	AG	JQ670070	1	-	-	-	-	-	-	-	-	-	-	-	Val	-	-	-	-	-
IPr072	AG	JQ867069	1	-	-	-	-	Ile	-	-	-	-	-	-	-	-	-	-	-	-
IPr088	TG	JQ867068	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ser
IPr113	NA	KC688378	1	-	-	-	-	-	-	Met	-	-	-	-	-	-	-	-	-	-
IPr121	NA	KC688380	1	-	-	-	-	-	-	-	-	Val	-	-	-	-	-	-	-	-
IPr128	NA	KC688381	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IPr224	SKR	KC688393	1	-	-	-	-	-	-	-	Met	-	-	-	-	-	-	-	-	-
IPr225	SKR	KC688394	1	-	Val	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IPr238	SKR	KC688398	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ile	-
IPr243	SKR	KC688399	1	-	-	-	-	-	-	-	-	-	-	-	-	-	Ile	-	-	-
IPr269	EA	KC688404	1	-	-	-	-	-	Thr	-	-	-	-	-	-	-	-	-	-	-
<i>I. pavelovskyi</i>				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IPv001***	Japan SA(8), EA (13), NA (5), AG (13)	AB231669 KC688356	39	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IPv261	EA	KC688410	10	Phe	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IPv264	EA	KC688412	1	Phe	-	Trp	-	-	-	-	-	-	-	-	-	-	-	-	-	-
IPv274	NA	KC688361	1	-	-	-	Asn	-	-	-	-	-	-	-	-	-	-	-	-	-
IPv284	NA	KC688417	1	Phe	-	-	Asn	Ser	-	-	-	-	-	-	-	-	-	-	-	-

*Variable sites were numbered from the beginning of the protein-coding gene *COI* **SA, western Altai; EA, northeastern Altai; NA, northern Altai; SKR, Salair Ridge; TG, northern forest steppe; and AG, Akademgorodok of Novosibirsk and its vicinity. ***Haplotype registered on all explored territories, for which the color gray outlines differences in the sequences in *I. persulcatus* and *I. pavelovskyi*.

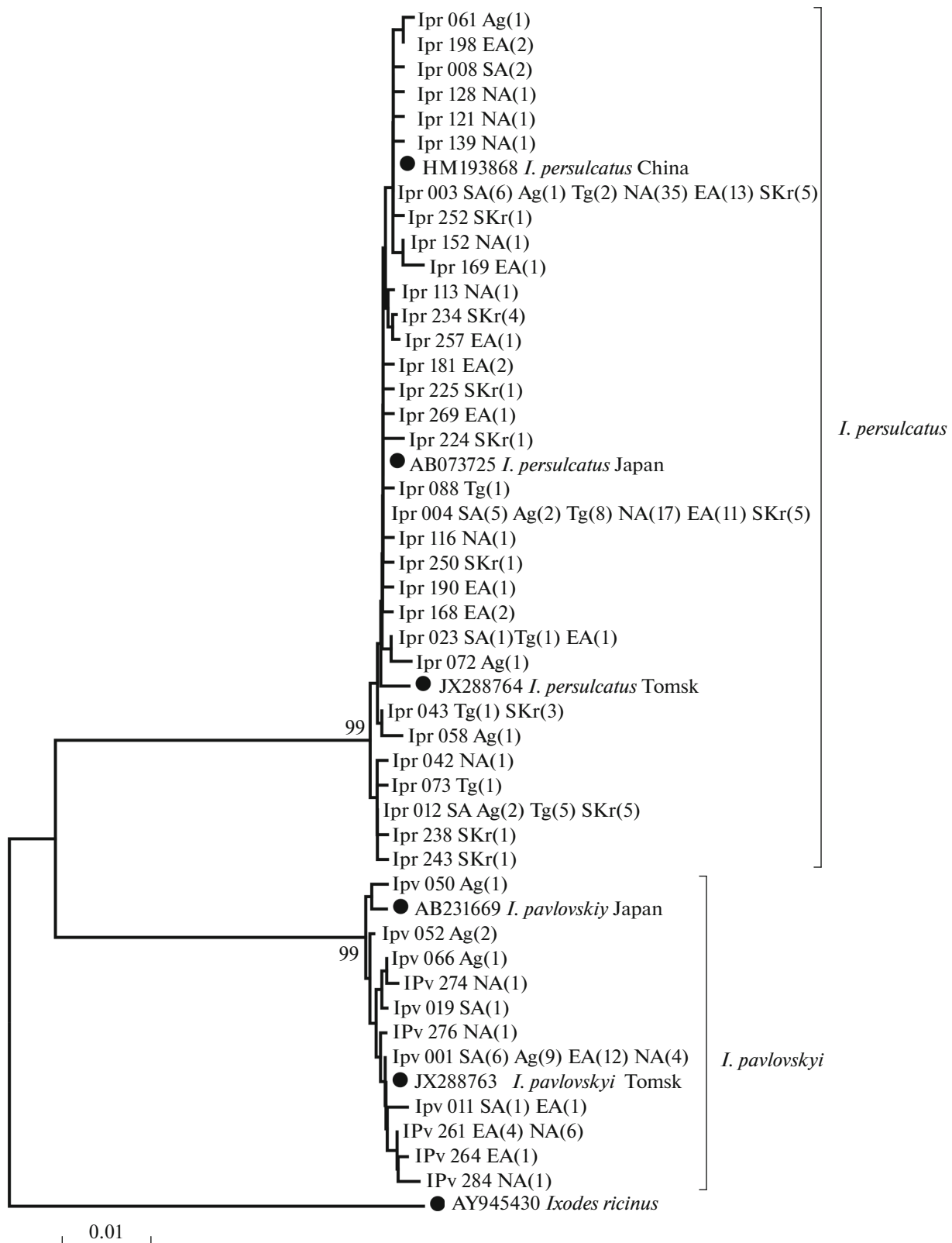


Fig. 3. NJ, dendrogram built based on an analysis of sequential fragment of the *COI* gene (647 p.n.). Numerals (>70% /> 0.7) in the nodes of branching designate the value of bootstrap support. The number of sequences of each haplotype is given in brackets. Places where *I. persulcatus* and *I. pavlovskiy* were collected: SA, Western Altai (Kazakhstan); EA, Northeastern Altai (Altai Republic, Russia); NA, Northern Altai (Altai Republic, Russia); SKR, Salair Ridge (Novosibirsk oblast, Russia); TG, northern forest steppe (Novosibirsk oblast, Russia); and AG, forests in the Ob River valley (Novosibirsk, Russia). Punson is a sequence in the GenBank.

mutant forms (haplotypes 261I_{pv}, 264P_{pv}, 274I_{pv}, and 284I_{pv}) among *I. pavlovskyi* ticks caught in the same. Despite the fact that both species of ticks on each site have undergone identical influences with a high probability, their genetic apparatus reacted to the event in different ways, which led to the appearance and fixation of different forms. Against the background of low occurrence of the Pi-informative sites in the sequences of mitochondrial markers in both tick species, this parameter is twice as low on average in *I. pavlovskyi* ticks.

Pi-informative sites are rare in the studied sequences in both tick species. This indicates that differences between haplotypes appear as a result of point mutations which, as a rule, do not play a selective role. Groups of *I. persulcatus* and *I. pavlovskyi* ticks from all explored locations have common haplotypes, most of which differ, as a rule, by the replacement of one nucleotide base.

Intraspecific genetic homogeneity of *I. pavlovskyi* in the south of West Siberia is determined, most likely, by a long and uninterrupted trophic relationship with feeders, especially with mobile birds. This promotes intensive dispersal and exchange by genetic information between ticks separated by long distances.

Results from some works (Delaye et al., 1997; De Meeus et al., 2002; Casati et al., 2008) on the ticks *I. ricinus* from Western Europe also demonstrated a lack of geographic heterogeneity. In contrast, genetic differences were recorded between North African and European insular and mainland populations of *I. ricinus* (Noureddine et al., 2011; Dinnis et al., 2014). According to the authors, impassable natural barriers such as the Mediterranean Sea and the English Channel influenced the genetic heterogeneity of *I. ricinus* populations.

CONCLUSIONS

Our studies allowed the characterization of peculiarities of the modern distribution and abundance levels of *I. persulcatus* and *I. pavlovskyi* in their sympatry zone in the south of West Siberia. We obtained confirmations for our earlier assumption of *I. pavlovskyi* higher tolerance to a decrease in environmental humidity and increase in the sum of positive temperatures. In the conditions of anthropogenically transformed landscapes of cities in the south of West Siberia, Tomsk, Kemerovo, and Novosibirsk, *I. pavlovskyi* is capable of replacing *I. persulcatus*, having successfully adapted to recreational digression. A study of genetic variability of *I. persulcatus* and *I. pavlovskyi* by a set of mitochondrial markers allowed approaching the solution of problems of the genetic structure in epidemically valuable species of arthropods. A genetic relation between relatively modern populations of *I. pavlovskyi* evidences to existence of an effective genetic flow to long distances due to mobile tick hosts.

ACKNOWLEDGMENTS

This work was supported by the Russian Foundation for Basic Research, project no. 15-29-02479, and the Russian Scientific Foundation, project no. 15-14-20020.

REFERENCES

- Alekseev, A.N., Dubinina, H.V., Semenov, A.V., and Bolshakov, C.V., Evidence of ehrlichiosis agents found in ticks (Acari: Ixodidae) collected from migratory birds, *J. Med. Entomol.*, 2001, vol. 38, no. 4, pp. 471–474.
- Begon, M., Harper, J.L. and Townsend, C.R., *Ecology: Individuals, Populations, and Communities*, Oxford: Blackwell, 1990.
- Bogdanov, I.I., Ixoidic ticks of Western Siberia. Message VII. Types of populations, *Vestn. Omsk. Gos. Pedagog. Univ.*, 2006. <http://www.omsk.edu>.
- Bolotin, E.I., Kolonin, G.V., Kiselev, A.N., and Matyushkina, O.A., Distribution and ecology of *Ixodes pavlovskyi* (Ixodidae) in Sikhote-Alin, *Parazitologiya*, 1977, vol. 11, no. 3, pp. 225–229.
- Casati, S., Bernasconi, M.V., Gern, L., and Piffaretti, J.C., Assessment of intraspecific mtDNA variability of European *Ixodes ricinus* sensu stricto (Acari: Ixodidae), *Infect. Genet. Evol.*, 2008, vol. 8, no. 2, pp. 152–158.
- Chausov, E.V., Ternovoi, V.A., Protopopova, E.V., Kononova, J.V., Konovalova, S.N., Pershikova, N.L., Romanenko, V.N., Ivanova, N.V., Bolshakova, N.P., Moskvitina, N.S., and Loktev, V.B., Variability of the tick-borne encephalitis virus genome in the 5' noncoding region derived from ticks *Ixodes persulcatus* and *Ixodes pavlovskyi* in Western Siberia, *Vector Borne Zoonotic Dis.*, 2010, vol. 10, no. 4, pp. 365–375.
- Chigirik, E.D., Selyutina, I.A., Biryukova, M.P., and Istratkina, S.V., Find of the high density tick focus, *Ixodes pavlovskyi* Pom. (Parasitiformes, Ixodidae) and their spontaneous infection by tick born encephalitis virus, *Parazitologiya*, 1974, vol. 8, no. 2, pp. 181–183.
- De Meeus, T., Beati, L., Delaye, C., Aeschlimann, A., and Renaud, F., Sex biased dispersal in the vector of Lyme disease *Ixodes ricinus*, *Evolution*, 2002, vol. 59, no. 9, pp. 1802–1807.
- Delaye, C., Beati, L., Aeschlimann, A., Renaud, F., and De Meeus, T., Population genetic structure of *Ixodes ricinus* in Switzerland from allozymic data: no evidence of divergence between nearby sites, *Int. J. Parasitol.*, 1997, vol. 27, no. 7, pp. 769–773.
- Dinnis, R. E., Seelig, F., Bormane, A., Donaghy, M., Volmer, S.A., Feil, E.J., Kurtenbach, K., and Margos, G., Multilocus sequence typing using mitochondrial genes (mtMLST) reveals geographic population structure of *Ixodes ricinus* ticks, *Ticks Tick Borne Dis.*, 2014, vol. 5, pp. 152–160.
- Filippova, N.A., The ticks of subfamily Ixodinae, in *Fauna SSSR. Paukoobraznye* (Fauna of Soviet Union: Arachnida), Leningrad: Nauka, 1977, vol. 4, no. 114 (4).
- Hewitt, G., The genetic legacy of the Quaternary ice ages, *Nature*, 2000, vol. 405, no. 6789, pp. 907–913.
- Korenberg, E.I., Nefedova, V.V., Romanenko, V.N., and Gorelova, N.B., The tick *Ixodes pavlovskyi* as a host of

- spirochetes pathogenic for humans and its possible role in the epizootiology and epidemiology of borrelioses, *Vector Borne Zoonotic Dis.*, 2010, vol. 10, pp. 453–458.
- Korotkov, Yu.S. and Kislenko, G.S., The reasons of fluctuations of demographic structure of taiga ticks (Ixodidae) in the dark coniferous larch forests of Kemchug foothills, *Parazitologiya*, 2002, vol. 36, no. 5, pp. 345–355.
- Korotkov, Yu.S. and Okulova, N.M., Chronological structure of population of taiga ticks in Primorskii krai, *Parazitologiya*, 1999, vol. 33, no. 3, pp. 257–266.
- Livanova, N.N., Livanov, S.G., and Panov, V.V., Specific distribution of ticks *Ixodes persulcatus* and *Ixodes pavlovskyi* at the edge of forest and forest-steppe zones of Ob' region, *Parazitologiya*, 2011, vol. 45, no. 3, pp. 94–103.
- Livanova, N.N., Tikunov, A.Y., Kurilshikov, A.M., Livanov, S.G., Fomenko, N.V., Taranenko, D.E., Kvashnina, A.E., and Tikunova, N.V., Genetic diversity of *Ixodes pavlovskyi* and *I. persulcatus* (Acari: Ixodidae) from the sympatric zone in the south of Western Siberia and Kazakhstan, *Exp. Appl. Acarol.*, 2015, vol. 67, no. 3, pp. 441–456.
- Noureddine, R., Chauvin, A., and Plantard, O., Lack of genetic structure among Eurasian populations of the tick *Ixodes ricinus* contrasts with marked divergence from north-African populations, *Int J. Parasitol.*, 2011, vol. 41, no. 2, pp. 183–192.
- Olsson, U., Confidence intervals for the mean of a log-normal distribution, *J. Stat. Educ.*, 2005, vol. 13. <http://www.amstat.org/publications/jse/v13n1/olsson.html>.
- Rar, V.A., Livanova, N.N., Panov, V.V., Doroschenko, E.K., Pukhovskaya, N.M., Vysochina, N.P., and Ivanov, L.I., Genetic diversity of *Anaplasma* and *Ehrlichia* in the Asian part of Russia, *Ticks Tick Borne Dis.*, 2010, vol. 1, pp. 57–65. doi 10.1016/j.ttbdis.2010.01.002
- Romanenko, V. and Leonovich, S., Long-term monitoring and population dynamics of ixodid ticks in Tomsk city (Western Siberia), *Exp. Appl. Acarol.*, 2015, vol. 66, no. 1, pp. 103–118. doi 10.1007/s10493-015-9879-2
- Romanenko, V.N. and Pankova, T.F., Fauna of pasture ticks (Prasitiformes, Ixodidea) in vicinities of Tomsk city, *Mater. V mezhd. nauch. konf. "Chteniya pamyati prof. I.I. Barabash-Nikiforova"* (Proc. V Int. Sci. Conf. in Memoriam of Prof. I.I. Barabash-Nikiforov), Voronezh, 2013, pp. 143–147.
- Scott, J.D., Fernando, K., Banerjee, S.N., Durden, L.A., Byrne, S.K., Banerjee, M., Mann, R.B., and Morshed, M.G., Birds disperse ixodid (Acari: Ixodidae) and *Borrelia burgdorferi*-infected ticks in Canada, *J. Med. Entomol.*, 2001, vol. 38, no. 4, pp. 493–500.
- Shpynov, S., Fournier, P.E., Rudakov, N., Tarasevich, I., and Raoult, D., Detection of members of the genera *Rickettsia*, *Anaplasma*, and *Ehrlichia* in ticks collected in the Asiatic part of Russia, *Ann. N.Y. Acad. Sci.*, 2006, no. 1078, pp. 378–383.
- Taezhnyi kleshch *Ixodes persulcatus* Schulze (Acarina, Ixodidae). *Morfologiya, sistematika, ekologiya, meditsinskoe znachenie* (Taiga Tick *Ixodes persulcatus* Schulze (Acarina, Ixodidae): Morphology, Systematics, Ecology, and Role in Medicine), Leningrad: Nauka, 1985.
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., and Nei, M., SMEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods, *Mol. Biol. Evol.*, 2011, no. 28, pp. 2731–2739. doi 10.1093/molbev/msr121
- Taylor, K.R., Takano, A., Konnai, S., Shimozuru, M., Kawabata, H., and Tsubota, T., *Borrelia miyamotoi* infections among wild rodents show age and month independence and correlation with *Ixodes persulcatus* larval attachment in Hokkaido, Japan, *Vector Borne Zoonotic Dis.*, 2013, vol. 13, pp. 92–97. doi 10.1089/vbz.2012.1027
- Tkachev, S., Panov, V., Dobler, G., and Tikunova, N., First detection of Kemerovo virus in *Ixodes pavlovskyi* and *Ixodes persulcatus* ticks collected in Novosibirsk region, Russia, *Ticks Tick Borne Dis.*, 2014, vol. 5, no. 5, pp. 494–496. doi 10.1016/j.ttbdis
- Xu, G., Fang, Q.Q., Keirans, J.E., and Durden, L.A., Molecular phylogenetic analyses indicate that the *Ixodes ricinus* complex is a paraphyletic group, *J. Parasitol.*, 2003, vol. 89, pp. 452–457.

Translated by S. Kuzmin