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Genetic diversity of pathogenic *Leptospira* spp. in small mammals of the Northwestern Federal District of Russia

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Abstract

Introduction. Leptospirosis is a dangerous zoonotic disease maintained by small mammal reservoirs. Studying the pathogen's genetic diversity in animal populations is crucial for epidemiological surveillance.

Aim — detection and molecular genetic characterization of leptospirosis pathogens in small mammals (rodents, insectivores, bats) in the Northwestern Federal District (NWFD) of Russia to assess their species diversity and potential epidemiological significance.

Materials and methods. From 2023 to 2025, 88 bat urine samples and organ specimens from 773 rodents and insectivores trapped in the Arkhangelsk, Leningrad, and Pskov regions, the Republic of Karelia, and Saint Petersburg were collected. DNA of pathogenic leptospires was detected by real-time PCR. Genotyping of positive samples was performed by Sanger sequencing the *secY* gene fragment followed by phylogenetic analysis.

Results. Genetic markers of *Leptospira* spp. were found in 11.4% of bat urine samples and in 2.5% of organ samples from rodents and insectivores. The highest infection rates were noted in Saint Petersburg (3.2%) and the Republic of Karelia (3.0%). Phylogenetic analysis revealed the circulation of three species of pathogenic leptospires: *L. kirschneri* (the dominant species), *L. interrogans* and *L. borgpetersenii*. Genetically distinct variants were found in bats, and one isolate (PV807621) showed only 95% similarity to reference strains of *L. interrogans*, suggesting the possible discovery of a new bat-adapted genetic variant.

Conclusion. This study is the first to demonstrate that small mammal populations in the NWFD are a reservoir for a wide range of pathogenic leptospires. The detection of potentially novel genetic variants in bats underscores their important role in the maintenance and evolution of Leptospira pathogens and highlights the need to consider this factor in epidemiological risk assessment.

Keywords: *leptospirosis; pathogenic leptospires; small mammals; genotyping; Northwestern Federal District*

Ethics approval. Authors confirm compliance with institutional and national standards for the use of animals in accordance with «Consensus Author Guidelines for Animal Use» (IAVES, 23 July, 2010). The research protocol was approved by the Ethics Committee of the St. Petersburg Pasteur Institute (protocol No. 83, February 14, 2023).

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Оригинальное исследование
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Генетическое разнообразие патогенных лептоспир у мелких млекопитающих Северо-Западного федерального округа России

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Аннотация

Введение. Лептоспироз — опасная зоонозная инфекция, резервуаром которой являются мелкие млекопитающие. Изучение генетического разнообразия возбудителей в популяциях животных критически важно для эпидемиологического надзора.

Цель работы — выявление и молекулярно-генетическая характеристика возбудителей лептоспироза у мелких млекопитающих (грызунов, насекомоядных, рукокрылых) на территории Северо-Западного федерального округа (СЗФО) России для оценки их видового разнообразия и потенциальной эпидемиологической значимости.

Материалы и методы. В период с 2023 по 2025 г. было собрано 88 образцов мочи от рукокрылых и образцы органов от 773 грызунов и насекомоядных, отловленных в Архангельской, Ленинградской, Псковской областях, Республике Карелия и Санкт-Петербурге. Генетические маркеры патогенных лептоспир детектировали с помощью полимеразной цепной реакции в реальном времени. Генотипирование положительных образцов проводили путём секвенирования по Сэнгеру фрагмента гена *secY* с последующим филогенетическим анализом.

Результаты. Генетические маркеры *Leptospira* spp. были обнаружены в 11,4% образцов мочи летучих мышей и в 2,5% образцов органов грызунов и насекомоядных. Наибольший уровень инфицированности отмечен в Санкт-Петербурге (3,2%) и Республике Карелия (3,0%). Филогенетический анализ выявил циркуляцию трех видов патогенных лептоспир: *L. kirschneri* (доминирующий вид), *L. interrogans* и *L. borgpetersenii*. У рукокрылых обнаружены генетически обособленные варианты, а один изолят (PV807621) показал лишь 95% сходство с референсными штаммами *L. interrogans*, что указывает на возможное обнаружение нового, адаптированного к летучим мышам геновариант.

Заключение. Впервые показано, что популяции мелких млекопитающих СЗФО являются резервуаром для широкого спектра патогенных лептоспир. Обнаружение потенциально новых генетических вариантов у рукокрылых подчёркивает их важную роль в поддержании и эволюции возбудителей лептоспироза и требует учёта данного фактора при оценке эпидемиологических рисков.

Ключевые слова: *лептоспироз; патогенные лептоспиры; мелкие млекопитающие; генотипирование; Северо-Западный федеральный округ*

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Источник финансирования. Авторы заявляют об отсутствии внешнего финансирования при проведении исследования.

Конфликт интересов. Авторы декларируют отсутствие явных и потенциальных конфликтов интересов, связанных с публикацией настоящей статьи.

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Introduction

Leptospirosis remains one of the most widespread naturally occurring zoonotic infections in the Russian Federation, characterized by multiple organ damage and high mortality [1, 2]. A key component of epidemiological surveillance for this infection is epizootic monitoring, aimed at detecting the circulation of the pathogen among reservoir animals [3].

Wild mammals, primarily rodents and insectivores, serve as the source and main reservoir of pathogenic leptospires in natural foci [4–7]. In recent years, there has been increasing evidence of the important role of chiroptera (in particular bats) as a potential reservoir for leptospires, capable of excreting the pathogen in their urine for long periods of time, thereby creating a risk of infection for other animals and humans [8–10]. In St. Petersburg and the Leningrad Region, at least 106 cases of human contact with bats were recorded in 2022–2023 [11].

High humidity and an abundance of water bodies in the Northwestern Federal District (NWFD) create favorable conditions for the long-term preservation of leptospires in the external environment, which exacerbates epidemiological risks. The relevance of the problem is confirmed by the continuing epizootic activity of foci and the registration of cases of human leptospirosis in Russia and the NWFD, including fatalities [1, 12].

The genetic diversity of circulating leptospira strains in small mammal populations in the NWFD has been studied only fragmentarily. Meanwhile, molecular genetics methods allow not only to accurately identify leptospira species, but also to detect new genetic variants, trace the transmission routes of the pathogen, and study its evolution, which is the basis for epidemiological forecasting and risk assessment. Currently, there are no comprehensive studies devoted to the simultaneous study of infection and genotyping of leptospires in a wide range of reservoir hosts (rodents, insectivores, bats) in the NWFD.

The aim of this study was to identify and characterize the molecular genetics of leptospirosis pathogens in small mammals (rodents, insectivores, and bats) in the Northwestern Federal District to assess their species diversity and potential epidemiological significance.

Materials and methods

The sampling and animal handling protocols used in this study were reviewed and approved by the local ethics committee of the Pasteur Institute of Epidemiology and Microbiology (protocol No. 83 dated February 14, 2023). The research methods comply with international and national ethical standards and laws relating to research involving animals.

Bats were captured in 2023–2025 in the Leningrad Region: Tanechkina Cave (60.01° N, 32.31° E) — 51 individuals, Sablinsky Caves (59.66° N, 30.79° E) — 37 individuals. Urine was collected using a non-invasive method that did not harm the animals, using sterile capillaries. The collected urine was immediately transferred to a sterile test tube for collecting biological samples. No bats died during capture, and all were released into the wild after sampling. The samples were transported to the laboratory in a portable refrigerator at a temperature of +4–8°C. A few hours after collection, the samples were frozen at –20°C for subsequent analysis. Before performing the polymerase chain reaction (PCR), the samples were thawed at room temperature and centrifuged for 5 minutes to precipitate any possible impurities; the supernatant was collected for further analysis.

The bats collected were identified as *Myotis daubentonii* (31 individuals), *Myotis dasycneme* (20), *Myotis nattereri* (16), *Myotis brandtii* (15), *Plecotus auritus* (5), and *Eptesicus nilssonii* (1).

Rodents and insectivores (shrews) were caught in 2023–2024 in a number of regions of the NWFD:

Arkhangelsk region (n = 76; of which 44 *Sorex araneus*, 18 *Myodes glareolus*, 6 *Microtus oeconomus*, 4 *Microtus arvalis*, 2 *Micromys minutus*, 1 *Myodes rutilus*, 1 *Sorex minutus*);

Leningrad region (n = 155; of which 70 *Myodes glareolus*, 45 *Apodemus flavicollis*, 21 *Apodemus uralensis*, 7 *Sorex araneus*, 5 *Apodemus agrarius*, 5 *Micromys minutus*, 2 *Microtus arvalis*);

Pskov region (n = 322; of which 88 *Myodes glareolus*, 78 *Apodemus agrarius*, 60 *Apodemus flavicollis*, 22 *Apodemus uralensis*, 20 *Sorex araneus*, 19 *Mus musculus*, 16 *Microtus arvalis*, 5 *Microtus agrestis*, 5 *Sylvaemus uralensis*, 4 *Microtus oeconomus*, 2 *Micromys minutus*, 2 *Sorex minutus*, 1 *Rattus norvegicus*);

Republic of Karelia (n = 33; of which 17 *Sorex araneus*, 13 *Myodes glareolus*, 2 *Sorex minutus*, 1 *Sorex caecutiens*);

St. Petersburg (n = 187; of which 145 *Myodes glareolus*, 38 *Apodemus flavicollis*, 2 *Apodemus agrarius*, 2 *Sorex araneus*).

Snap traps were used for trapping in accordance with methodological recommendations MG 3.1.0211-20 "Trapping, recording, and forecasting the numbers of small mammals and birds in natural foci of infectious diseases." The locations where rodents and insectivores were trapped are shown in **Fig. 1**.

To extract total nucleic acid (DNA/RNA) from the samples under investigation, we used the commercial RIBO-prep kit (Central Research Institute of Epidemiology, Rospotrebnadzor). For real-time PCR, we used the AmpliSens Leptospira-FL test system (Central Research Institute of Epidemiology, Rospotrebnadzor). The analysis was performed in accordance with the manufacturer's instructions. A total of 88 bat urine samples and organs from 773 rodents and insectivores were examined: kidneys (n = 773) and spleens (n = 680). In some animals, only one type of organ (kidney or spleen) was examined, while in others, both were examined,

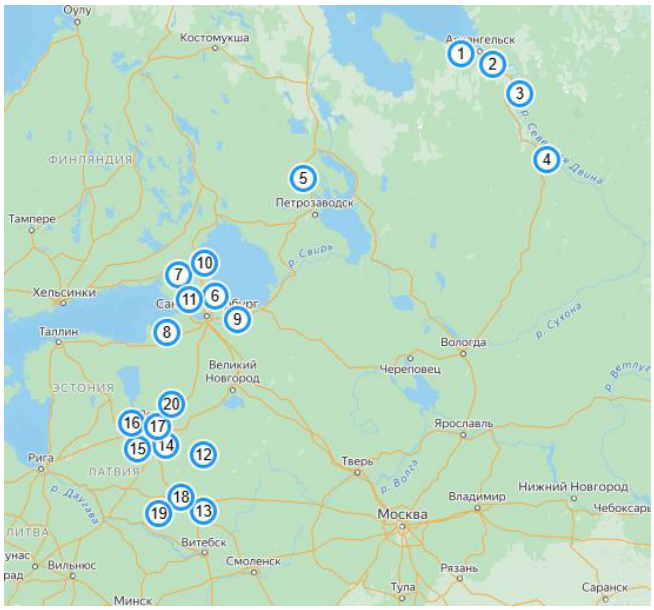

Fig. 1. Locations for catching rodents and insectivores in the Northwestern Federal District.

In the Arkhangelsk Region: 1 — Severodvinsk; 2, 3 — Kholmogorsky; 4 — Vinogradovsky districts; in the Republic of Karelia: 5 — Kondopoga district; in the Leningrad Region: 6 — Vsevolozhsky, 7 — Vyborgsky, 8 — Kingiseppsky, 9 — Kirovsky, 10 — Priozersky districts; in St. Petersburg: 11 — Kurortny district; in the Pskov region: 12 — Bezhanitsky, 13 — Nevelsky, 14 — Ostrovsky, 15 — Palkinsky, 16 — Pechorsky, 17 — Pskovsky, 18 — Pustoshkinsky, 19 — Sebezhsky, 20 — Strugo-Krasnensky districts.

which explains the different number of organ samples examined for the total number of animals.

Genotyping of samples was performed using primers for the *secY* gene fragment, as it has been successfully used for this purpose in various studies and has shown high discriminatory power [13–15]. The amplification protocol and primer sequences have been described in detail by us previously [16].

The amplification products were visualized in a 1.5% agarose gel stained with ethidium bromide, in comparison with the Step50 plus molecular weight marker (Biolabmix). Electrophoresis was performed at 120 V for 20 min and visualized under ultraviolet light.

Sanger sequencing was performed on an ABI 3500 genetic analyzer (Applied Biosystems). The obtained sequences were identified and confirmed using the BLAST algorithm on the NCBI platform. MEGA 12 software was used to construct phylogenetic trees. Nucleotide sequences of various species of leptospires obtained from the international GenBank database were used as references. The phylogenetic tree was reconstructed using the maximum likelihood method (Tamura–Nei model, bootstrap analysis with 1000 repetitions).

Statistical data processing was performed using descriptive statistics methods: the proportion of positive findings and standard deviation were calculated. The analysis was conducted using the Microsoft Excel 2016 software package.

Results

Genetic markers of *Leptospira* spp. were detected in 10 samples (11.4 ± 3.4%) of bat urine. Positive results were obtained in samples collected from *M. daubentonii* individuals — 6/28 (21.4 ± 7.8%) and *M. dasycneme* — 2/20 (10.0 ± 6.7%) caught in Tanechkina Cave; *M. nattereri* — 1/16 (6.3 ± 6.1%) and *M. daubentonii* — 1/3 (33.3% ± 27.2) — in the Sablin caves.

Of the 773 rodents and insectivores studied, pathogenic leptospira DNA was detected in the organs of 19 individuals (in 13 kidneys and 6 spleens). Thus, the overall infection rate was 2.5 ± 0.6%. It is important to note that no individuals were found to have *Leptospira* spp. genetic markers present in both the kidneys and spleen.

The highest infection rates were observed in St. Petersburg (3.2 ± 1.3%) and the Republic of Karelia (3.0 ± 2.9%). In the Pskov region, the proportion of positive samples was 2.8 ± 0.9%, and in the Leningrad region, it was 1.9 ± 1.1%. At the same time, no genetic material of pathogenic leptospires was detected in the organs of rodents and insectivores from the Arkhangelsk region (**Table**).

Based on the results obtained, the overall infection rate among animals by species was as follows: *Mus musculus* — 2/19 (10.5 ± 7.0%); *Apodemus agrarius* — 4/85 (4.7 ± 2.3%); *Apodemus flavicollis* — 5/143 (3.5 ± 1.5%); *Myodes glareolus* — 7/334 (2.1 ± 0.8%); *Sorex araneus* — 1/90 (1.1 ± 1.0%).

All samples obtained from rodents and insectivores and 7 of 10 samples obtained from bat urine were genotyped using the Sanger sequencing method. The obtained nucleotide sequences (n = 26) were deposited in the international GenBank database under numbers PV550444–PV550446, PV550448–PV550452, PV590897–PV590905, PV807616–PV807622, and PX214120–PX214122.

The length of the *secY* gene fragment sequences obtained ranged from 285 to 400 nucleotide pairs. According to clustering on the phylogenetic tree, the studied individuals were infected with pathogenic leptospires of various species (**Fig. 2**).

Sequences obtained from rodents and insectivores were grouped with three species of leptospires (*L. interrogans, L. kirschneri, L. borgpetersenii*) and did not differ significantly from sequences isolated in other countries. The similarity of the sequences in blast analysis was 99.65–100%. Two sequences had single synonymous substitutions: PV590898 fr.34C>T and PV590905 fr.160A>G.

The sequence PV807621 identified by us, as well as the sequences obtained from the database PP818623.1 and OQ793712.1, were not assigned to a specific species, but formed a sister clade within the *L. interrogans* cluster. A similar situation was observed for samples typed as *L. borgpetersenii*. In both cases,

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Positive findings of *Leptospira* spp. based on PCR testing of rodents and insectivores caught in certain areas of the Northwestern Federal District

Catch territory		Species	Number of infected individuals/ total number of individuals of this species caught in the area	Percentage of infected animals, % (*M* ± *m*)
Leningrad Region	Vyborgsky District	*Apodemus flavicollis*	1/13	7.7 ± 7.4
		Myodes glareolus	1/5	20.0 ± 17.9
	Kirovsky District	*Myodes glareolus*	1/31	3.2 ± 3.1
Pskov Region	Bezhanitsky District	*Apodemus agrarius*	3/33	9.1 ± 5.0
	Ostrovsky District	*Apodemus agrarius*	1/20	5.0 ± 4.9
		Apodemus flavicollis	1/6	16.7 ± 15.2
	Pechorsky District	*Apodemus flavicollis*	2/10	20.0 ± 12.6
	Pustoshkinsky District	*Mus musculus*	2/19	10.5 ± 7.0
The Republic of Karelia	Kondopozhsky District	*Sorex araneus*	1/17	5.9 ± 5.7
Saint Petersburg	Kurortny District	*Apodemus flavicollis*	1/38	2.6 ± 2.5
		Myodes glareolus	5/145	3.4 ± 1.5

samples from different geographical locations but with a common source (bats) formed common clusters.

The similarity of sequences obtained from bat urine was 95–100%. Single synonymous substitutions were observed in sequences PV807618 fr.396T>C, PV807622 fr.399T>C, PV807619 fr.15T>C, and fr.197T>C. The PV807620 sequence had five single synonymous substitutions: fr.12C>T, fr.15C>T, fr.159G>A, fr.195T>C, and fr.198C>T. The PV807621 sequence was only 95% similar to the reference sequences of *L. interrogans* and had a large number of non-synonymous substitutions, which affected its position in the phylogenetic tree.

The urine of *M. daubentonii* bats contained DNA from leptospires belonging to *L. kirschneri* and an unidentified species of *Leptospira* spp. close to the *L. interrogans* branch. Samples from *M. dasycneme* were genotyped as *L. kirschneri* and *L. borgpetersenii*.

Discussion

A comprehensive study conducted by us in the NWFD allowed us to identify and characterize communities of pathogenic leptospires in a wide range of small mammals, including rodents, insectivores, and bats. Identifying the species of animals that act as reservoir hosts is key to studying the epidemiology of leptospirosis, since each species has specific ecological niches and distribution patterns that determine the potential risks to humans.

The results obtained showed the presence of leptospirosis foci in the NWFD. The highest proportion of infected individuals was observed in St. Petersburg and the Republic of Karelia, indicating the importance of both natural and anthropogenic landscapes in maintaining the circulation of the pathogen. It is important to note the fact of *Leptospira* spp. carriage in bats in the Leningrad Region. Although direct transmission of leptospires from bats to humans has not been conclusively proven, the growing popularity of caving increases the frequency of contact with these animals and the potential risk of infection [8, 9]. Our data emphasize the need to assess this risk, especially given that at least three species of leptospires circulate in bat populations, including potentially new genetic variants.

A possible route for the exchange of pathogens between different animal species may be direct contact, for example, traces of rodents in caves or cases described in the literature of mice attacking hibernating bats [17]. However, phylogenetic analysis data indicate complex evolutionary pathways for leptospires in different host populations.

The relatively low percentage of successful genotyping of samples obtained from urine may be associated with low bacterial load, DNA degradation, or a large number of inhibitors in urine.

Phylogenetic analysis revealed clear species clustering of pathogenic leptospires, with *L. kirschneri* dominating in both rodents and bats, confirming its ecological plasticity and ability to adapt to different hosts. This conclusion is based on the study of sequences obtained from bat urine: 5 out of 7 belonged to the species *L. kirschneri* and showed a high degree of similarity to strains circulating among terrestrial mammals in Russia and other countries, indicating its wide geographical distribution. At the same time, leptospires isolated from bats (including *L. borgpetersenii* and *L. kirschneri*) often formed isolated clusters, sister to strains from terrestrial mammals, which is a strong argument in favor of the hypothesis of the formation of specific host-associated genetic lineages in bats. The data from this study, in which *L. kirschneri* is prevalent, partially disagree with the results of other authors who found leptospires in the same geographical locations where leptospires close to *L. borgpetersenii* were more frequently found [9].

Of particular interest is sequence PV807621, isolated from *M. daubentonii*. It shows only 95% similar-

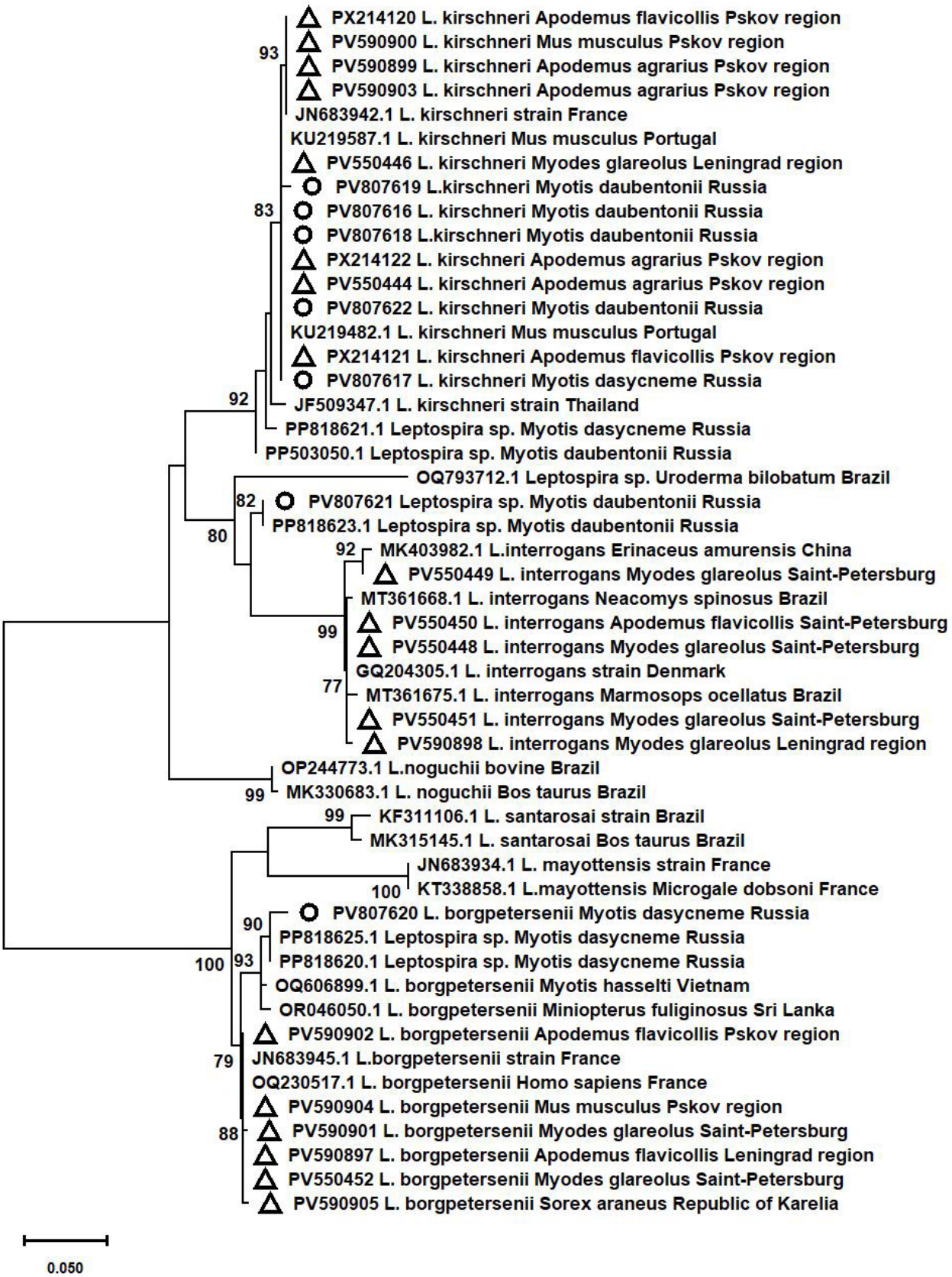

Fig. 2. Phylogenetic tree constructed based on *secY* gene fragment sequences, compared with reference sequences obtained from the international GenBank database.

Reference sequences are designated by GenBank accession numbers together with the species affiliation of the strain, source, and region of isolation. The nucleotide sequences of the *secY* gene fragment obtained from organs are marked with a sign (Δ), from urine (O), and the source and region of isolation are also indicated.

ity to the reference strains of *L. interrogans* and contains many non-synonymous substitutions, suggesting the discovery of a new, previously undescribed allele variant or species adapted to bats. These data are consistent with the results of studies conducted in other regions of the world, where *L. kirschneri* also dominates in bats and potentially new species of leptospires are found [3, 8, 9], which emphasizes the commonality of evolutionary processes in the adaptation of this pathogen to new hosts.

The presence of various species of leptospires (*L. interrogans, L. kirschneri, L. borgpetersenii*) in rodents and insectivores indicates their role as key reservoirs of the pathogen in natural foci. As is known, leptospires usually cause asymptomatic infection in their natural hosts, characterized by prolonged excretion of the pathogen into the environment [18]. Another result of our study was the discovery of phylogenetic similarity between *L. borgpetersenii* strains isolated from rodents in the Pskov region (PV590902, PV590904), and a strain isolated from a human in France (OQ230517.1). This fact indicates the widespread distribution of leptospires with similar phylogenetic properties that are capable of causing disease in humans in different countries.

Based on the analysis of *secY* gene fragment sequences, all three species of leptospires were identified in *M. glareolus* and *A. flavicollis*, which may indicate their role as an important reservoir of pathogens and testify to a broad ecological niche, making them a potential source of infection for other animals and humans. In our previous study, only *L. borgpetersenii* was detected in *M. glareolus* and *A. flavicollis* [19].

Conclusion

For the first time in the Northwestern Federal District, a comprehensive assessment of leptospira infection in various small mammals (rodents, insectivores and bats) was conducted, followed by phylogenetic analysis of the isolated strains. It was established that these animal species are potential sources of leptospirosis infection. Using Sanger sequencing of the *secY* gene fragment, it was shown that, along with known species of pathogenic leptospires (*L. interrogans, L. kirschneri, L. borgpetersenii*), genetically isolated variants potentially representing new taxa circulate in bat populations.

Thus, the results of the study emphasize the importance of monitoring the circulation and genetic diversity of leptospirosis pathogens in wild and synanthropic animal populations. When assessing the risks associated with the spread of leptospirosis, it is necessary to consider not only the species composition of leptospires, but also their evolutionary characteristics related to adaptation to specific hosts. This approach will help in the development of more effective strategies for the prevention and control of leptospirosis infection.

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