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Coronaviruses (*Coronaviridae*) of bats in the northern Caucasus and south of western Siberia

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Abstract

Introduction. Bats are natural reservoirs of coronaviruses (*Coronaviridae*), which have caused three outbreaks of human disease SARS, MERS and COVID-19 or SARS-2 over the past decade. The purpose of the work is to study the diversity of coronaviruses among bats inhabiting the foothills and mountainous areas of the Republics of Dagestan, Altai and the Kemerovo region.

Materials and methods. Samples of bat oral swabs and feces were tested for the presence of coronavirus RNA by reverse transcription-polymerase chain reaction (RT-PCR).

Results. It has been shown that the greater horseshoe bats (*Rhinolophus ferrumequinum*), inhabiting the Republic of Dagestan, are carriers of two different coronaviruses. One of the two coronaviruses is a member of the *Sarbecovius* subgenus of the *Betacoronavirus* genus, which includes the causative agents of SARS and COVID-19. The second coronavirus is assigned to the *Decacovirus* subgenus of the *Alphacoronavirus* genus and is most similar to viruses identified among *Rhinolophus* spp. from European and Middle Eastern countries. In the Altai Republic and Kemerovo region, coronaviruses belonging to the genus *Alphacoronavirus*, subgenus *Pedacovirus*, were found in the smooth-nosed bats: Ikonnikov`s bat (*Myotis ikonnikovi*) and the eastern bat (*Myotis petax*). The virus from the Altai Republic from *M. ikonnikovi* is close to viruses from Japan and Korea, as well as viruses from *Myotis* spp. from European countries. The virus from the Kemerovo region from *M. petax* groups with coronaviruses from *Myotis* spp. from Asian countries and is significantly different from coronaviruses previously discovered in the same natural host.

Keywords: *coronavirus; bats; phylogenetic analysis*

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Ethics approval. Authors confirm compliance with institutional and national standards for the use of laboratory animals in accordance with Consensus author guidelines for animal use (IAVES 23 July 2010). Authors confirm compliance with institutional and national standards for the use of wild animals in accordance with Russian guideline 3.1.0211-20 issued on 03.09.2020. The research protocols were approved by the Ethics Committee of the Institute of Systematics and Ecology of Animals (Protocol No 2020-02 dated 14.04.2020) and Dagestan State University (Protocol No 2 dated 13.05.2021).

ОРИГИНАЛЬНОЕ ИССЛЕДОВАНИЕ

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Выявление коронавирусов (*Coronaviridae*) у рукокрылых на территории Северного Кавказа и юга Западной Сибири

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Резюме

Введение. Рукокрылые являются природным резервуаром коронавирусов (*Coronaviridae*), вызвавших за последнее десятилетие три вспышки заболевания людей: SARS, MERS и COVID-19, или SARS-2.

Цель работы – исследование многообразия коронавирусов среди рукокрылых, населяющих предгорные и горные районы республик Дагестан, Алтай и Кемеровской области.

Материалы и методы. Образцы ротовых смывов и фекалии рукокрылых исследовали на присутствие РНК коронавирусов с помощью полимеразной цепной реакции с обратной транскрипцией (ОТ-ПЦР).

Результаты. Показано, что большие подковоносы (*Rhinolophus ferrumequinum*), обитающие в Республике Дагестан, являются носителями двух разных коронавирусов. Один из двух коронавирусов входит в состав подрода *Sarbecovius* рода *Betacoronavirus*, включающего возбудителей SARS и COVID-19. Второй коронавирус отнесен к подроду *Decacovirus* рода *Alphacoronavirus* и наиболее близок вирусам, выявленным среди *Rhinolophus* spp. из европейских и ближневосточных стран. В Республике Алтай и Кемеровской области у гладконосых летучих мышей, ночницы Иконникова (*Myotis ikonnikovi*) и восточной ночницы (*Myotis petax*), обнаружены коронавирусы, входящие в род *Alphacoronavirus,* подрод *Pedacovirus*. Вирус от *M. ikonnikovi* из Республики Алтай близок вирусам из Японии и Кореи, а также вирусам от *Myotis* spp. из европейских стран. Вирус из Кемеровской области от *M. petax* группируется с коронавирусами от *Myotis* spp. из азиатских стран и значительно отличается от коронавирусов, ранее обнаруженных в том же природном носителе.

Ключевые слова: *коронавирус; рукокрылые; филогенетический анализ*

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Этическое утверждение. Авторы подтверждают соблюдение институциональных и национальных стандартов по использованию лабораторных животных в соответствии с Consensus author guidelines for animal use (IAVES 23 July 2010). Авторы подтверждают соблюдение институциональных и национальных стандартов по отлову животных в соответствии с протоколом и рекомендациями по безопасной работе МУ 3.1.0211-20 (утв. 03.09.2020). Протокол исследования одобрен Этическим комитетом Института систематики и экологии животных СО РАН (Протокол № 2020-02 от 14.05.2020) и Дагестанского государственного университета (Протокол № 2 от 13.05.2021).

Introduction

Coronaviruses (Coronaviridae: *Betacoronavirus*) are among the dangerous viral pathogens that have caused three outbreaks of severe respiratory diseases SARS, MERS and COVID-19 in the last 20 years [1–3]. The pathogens have been named SARS-CoV, MERS-CoV and SARS-CoV-2, respectively. Bats were shown to be the natural reservoir of these coronaviruses, although infection of humans with SARS and MERS has occurred through an intermediate host [4–7]. Coronaviruses closest to SARS-CoV and SARS-CoV-2 have been found in Southeast Asia and Japan, and those closest to MERS-CoV have been found in Eurasia, in the regions where outbreaks have occurred [8–11].

Closely related viruses, which together with SARS-CoV and SARS-CoV-2 belong to the *Sarbecovirus* subgenus of the *Betacoronavirus* genus, have been detected in various species of horseshoe bats (*Rhinolophidae*) in Asian, African and European countries [12, 13]. The closest viruses to SARS-CoV-2 were found in China among *Rhinolopus affinis* (strain RaTG13, 96% similarity on the genome level) and in Laos among *Rh. malayanus* (strain BANAL-52, 97% similarity) [13]. Numerous SARS-CoV-2 isolates of similar coronaviruses found in European, African and Middle Eastern countries among *Rhinolopus* spp. differ from SARS-CoV-2 much more strongly; genomic sequence similarity does not exceed 79%; the receptor-binding domain of the surface glycoprotein (S) responsible for binding to target cells also differs significantly [14–17]. Coronaviruses belonging to the *Merbecovirus* subgenus of the *Betacoronavirus* genus, which includes the MERS pathogen, have been identified in Eurasia, Africa and South America among various species of bats [10, 12]. In European countries, MERS-like coronaviruses have been found in smooth-nosed bats (*Vespertilionidae* family) [18, 19]. More importantly, many recently discovered coronaviruses circulate in several bat species, and some of them are able to bind to human cell surface receptors ACE2 (SARS-CoV and SARS-CoV-2 receptors) or DPP4 (MERS-CoV receptors) [10, 13, 19, 20].

Epidemiologic studies on the detection of coronaviruses in natural reservoirs and their typing in Russia began during the COVID-19 pandemic. In 2020, SARS-like coronaviruses were discovered in two species of Horseshoe bats (RNA isolates Khosta-1 from *Rh. ferrumequinum* and Khosta-2 from *Rh. hipposideros*) in the Krasnodar region of the Russian Federation and their full-length genomes were studied [17]. The level of similarity of Russian isolates was 76–78% with SARS-CoV and SARS-CoV-2 strains from China and was highest (89%) with the European strain BM48-31/BGR/2008 from Bulgaria for Khosta-1 and with the African strain BtKY72 (80%) for Khosta-2. A MERS-like coronavirus was detected among smooth-nosed *Pipistrellus nathusii* (isolate MOW-BatCoV/15-22) in the central part of European Russia [21]. The level of similarity of the Russian isolate with MERS pathogens was 81–82%. To date, no studies of coronaviruses among bats in the North Caucasus and the Asian part of the country have been conducted. The study revealed circulation of two coronaviruses in Dagestan, belonging to the *Sarbecovirus* subgenus of the *Betacoronavirus* genus and the *Decacovirus* subgenus of the *Alphacoronavirus* genus. Coronaviruses belonging to the *Pedacovirus* subgenus of the *Alphacoronavirus* genus were detected in the south of Western Siberia.

Materials and methods

Expeditionary work aimed at collecting biomaterial was carried out in August 2020 in the Altai Republic, in June 2023 in the Kemerovo region, in December 2022 and April 2023 in the Dagestan Republic (**Fig. 1**). Catches in the Altai Republic and Kemerovo region were carried out in summer using specialized nets placed in the areas where the animals were flying. In the Dagestan Republic, the material was sampled during the period of hibernation of bats in the wintering grounds. To ensure the safety of researchers when working with potentially infected animals, the recommendations given in MG 3.1.0211-20 approved on 03.09.2020 were followed.

The authors confirm compliance with institutional and national standards for the use of laboratory animals in accordance with the Consensus author guidelines for animal use (IAVES July 23, 2010), as well as compliance with institutional and national standards for the capture of animals in accordance with the protocol and recommendations for safe work MG 3.1.0211-20 approved on 03.09.2020. The study protocol was approved by the Ethics Committee of the Institute of Systematics and Ecology of Animals, Siberian Branch of RAS (Protocol No. 2020-02 of 14.05.2020) and Dagestan State University (Protocol No. 2 of 13.05.2021).

Selected oropharyngeal washes and feces were placed in liquid nitrogen or in RNAlater stabilizing solution (QIAGEN GmbH, Germany) for subsequent RNA isolation and analysis by reverse transcription-polymerase chain reaction (RT-PCR). The taxonomic affiliation of the animals, determined on the basis of morphological features, was confirmed by analyzing a fragment of the *COI* gene encoding the first subunit of mitochondrial DNA cytochrome oxidase with primers described previously [22].

RNA isolation was performed using the RIBO-prep kit (Central Research Institute of Epidemiology, Russia). Samples were screened by RT-PCR using reverse transcriptase M-MuLV-RH (Dia-M, Russia), Taq DNA polymerase Hot Start (Dia-M, Russia) according to the protocol and with primers for the conserved region of the coronavirus RNA-dependent RNA polymerase (RdRp) gene (397 bp fragment) described previously [23]. The newly designed primer set was used to obtain the full-length gene of spike surface glycoprotein (S) as well as fragments of the *nsp16* gene. The nucleotide sequences of each amplicon were determined on an ABI Prism 310 automated analyzer using the BigDye Terminator Cycle Sequencing kit (Applied Biosystems, USA).

Nucleotide sequence alignment was performed using the MUSCLE algorithm in the MEGA X program. The Neighbor-joining method with the Kimura 2 evolution model was used to construct phylogenetic trees. Calculations were performed for 1000 iterations.

Results

In the period 2020–2023, 101 specimens of 11 species of bats belonging to the families of horseshoe (*Rhinolophidae*) and smooth-nosed (*Vespertilionidae*) were captured in the northeastern part of the Altai Republic near Lake Teletskoye, foothill areas of the western macro-slope of the Kuznetsk Alatau, and caves and adits of the northeastern part of the Greater Caucasus. All samples were tested by RT-PCR using primers to the RdRp gene of the coronavirus genome. Viral RNA was detected in samples from 11 greater horseshoe bats (*Rh. ferrumequinum* (Schreber, 1774)) from the Dagestan Republic and 2 samples from smooth-nosed bats, Oriental

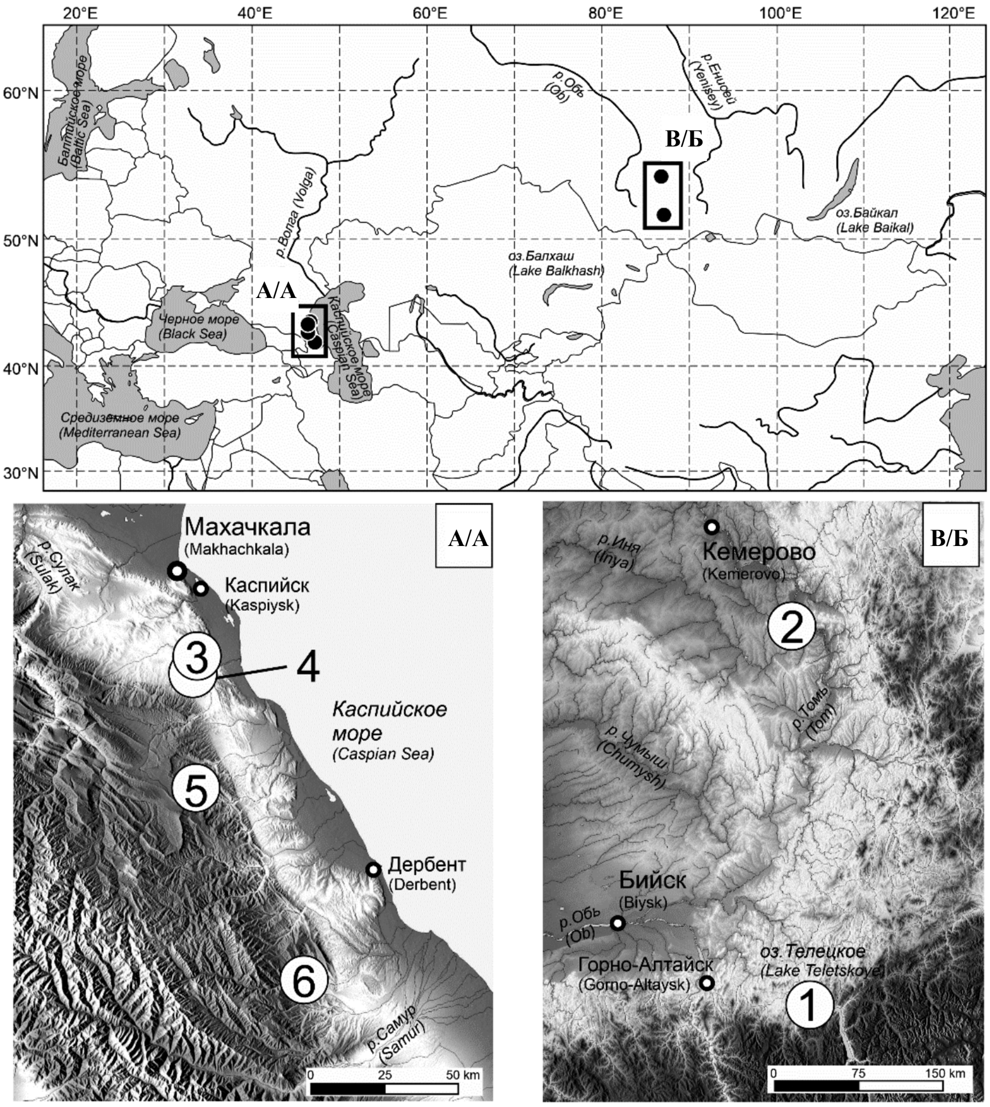

Fig. 1. Map showing the locations of bat trapping sites in Russia.

A – capture points in the North Caucasus: 4 – Bolshaya Glinyanaya cave, 3 – Karabudakhkentskaya cave, 5 – adits near the village Khantskarkamahi, 6 – cave near the village of Kug; B – capture points in the south of Western Siberia: 1 – Artybash, 2 – Azhendarovo tract.

Рис. 1. Расположение мест отлова рукокрылых на территории России.

А – точки отлова на территории Северного Кавказа: 4 – пещера «Большая глиняная», 3 – пещера «Карабудахкентская», 5 – штольни у села Ханцкаркамахи, 6 – пещера у села Куг; Б – точки отлова на территории юга Западной Сибири: 1 – Артыбаш, 2 – урочище Ажендарово.

noctuid (*Myotis petax* (Hollister, 1912)) from the foothills of the Kuznetsk Alatau and Ikonnikov's noctuid (*Myotis ikonnikovi* (Ognev, 1912)) from the Altai Republic (**Table**). Three RNA-positive samples from the Dagestan Republic were additionally analyzed using primers to the *nsp16* gene fragment, and a full-length gene of the envelope S protein was obtained for one of the samples. The new nucleotide sequences of the viruses were deposited in GenBank under the numbers PP265313–PP265325.

Phylogenetic analysis based on RdRp gene fragments revealed 3 coronavirus species among the new RNA isolates (**Fig. 2** *a*). Two coronavirus species were detected in greater horseshoe bats (*Rh. ferrumequinum*). The first coronavirus, detected in three specimens from one abandoned adit, is a member of the *Sarbecovirus* subgenus of the *Betacoronavirus* genus and is closest (99.5% similarity) to sequences available from GenBank of a virus recently discovered in smooth-nosed bats, the sharp-eared noctuid (*M. blythii*), from Georgia bordering Dagestan (GE_CoV146_Myo_bly). Other coronaviruses forming a common cluster on the phylogenetic tree have been previously identified from different species of horseshoe bats (*Rhinolophus* spp.) from neighboring regions: Georgia (GE_CoV93_Rhi_eur), Bulgaria (BB99-04/BGR/2009, BM48-31/BGR/2008), Lebanon (LBN/LB20-CO-BAT-19A), Krasnodar Krai of the Russian Federation (BtCoV/Khosta-1/Rh/Russia/2020),

Table. Detection of coronavirus infection in bats by RT-PCR and viruses identified in bats in Republics of Dagestan, Altai and Kemerovo region

Таблица. Выявление инфицированных коронавирусами рукокрылых методом ОТ-ПЦР и идентифицированные вирусы в республиках Дагестан, Алтай и Кемеровской области

Region Регион	Collection Site Место отлова	Species Вид	Year Год	Coronavirus RNA Positive/Tested Коронавирус РНК+/исследованы	Coronavirus Genus/Subgenus Род/подрод коронавируса
Dagestan Republic Республика Дагестан	Cave Big Clay Пещера «Большая глиняная»	*Myotis blythii*	2022	0/9	
	Cave near the village Kug Пещера у с. Куг	*Myotis blythii*	2022	0/4	
	Adits near the village of Khants-karkamahi Штольни у села Ханцкаркамахи	*Rhinolophus ferrumequinum*	2022	3/11	*Beta*/*Sarbecovirus*
		Rhinolophus ferrumequinum	2023	2/4	*Alpha/Decacovirus*
		Rhinolophus hipposideros	2023	0/1	
	Cave Karabudakhkent Пещера «Карабудахкентская»	*Rhinolophus mehelyi*	2023	0/9	
	Cave Big Clay Пещера «Большая глиняная»	*Rhinolophus ferrumequinum*	2023	8/25	*Alpha/Decacovirus*
Altai Republic Республика Алтай	Artybash Поселок Артыбаш	*Myotis ikonnikovi*	2020	1/4	*Alpha/Pedacovirus*
		Myotis dasycneme	2020	0/2	
		Plecotus ognevi	2020	0/4	
		Eptesicus nilssonii	2020	0/4	
		Myotis petax	2020	0/2	
		Myotis sibiricus	2020	0/5	
Kemerovo region Кемеровская область	Azhendarovo tract Урочище Ажендарово	*Myotis petax*	2023	1/3	*Alpha/Pedacovirus*
		Myotis dasycneme	2023	0/2	
		Vespertilio murinus	2023	0/3	
		Myotis ikonnikovi	2023	0/1	
		Eptesicus nilssonii	2023	0/1	

Italy (Rfer4675_IT_2016) with a similarity level of 95.2–97.3% for nucleotide and 99.2–100% for amino acid sequences. The second coronavirus, detected in 2 out of 4 *Rh. ferrumequinum* specimens in a nearby adit, as well as in 6 out of 25 specimens from a cave 45 km away, was assigned to the *Alphacoronavirus* genus, *Decacovirus* subgenus, according to the results of phylogenetic analysis. The closest viruses (similarity of 98.3–99.0% of nucleotide and 100% of amino acid sequences) were found among *Rh. euryale* from neighboring Georgia (GE_CoV153_Rhi_eur). Other close variants of coronaviruses were previously identified from *Rhinolophus* spp. from European and African countries: Italy (Bat Rfer4015_IT_16), France (FRA_EPI6_Rhfer999_5C_P23), Rwanda (PREDICT_CoV-42). Their level of similarity with the new isolates was 86.7–88.4% for nucleotide and 96.9–99.2% for amino acid sequences. *Alphacoronavirus* sequences from the same host from China were less similar to the new isolates (< 77.3% nucleotide and < 93.2% amino acid). The nucleotide sequence difference between the new RNA sequences of *Alphacoronavirus* isolates from the two caves was 1.0%.

Sequence analysis of a viral genome fragment from specimens captured in the same adit or cave showed them to be identical to each other at each of the three capture sites where infected *Rh. ferrumequinum* were found. Since the analysis was performed using the conserved RdRp gene, a fragment of the more variable *nsp16* gene was analyzed for RNA from SARS-like *Betacoronavirus* isolates (BtCoV/Rf-6/RUS/2022, BtCoV/Rf-14/RUS/2022, BtCoV/Rf-15/RUS/2022) to confirm the findings. The sequences of the analyzed coronavirus genome fragment from three infected specimens from the same adit were also shown to be identical. These data, as well as a relatively low level of difference (<4.0%) between geographically distant *Betacoronavirus* isolates from Dagestan, Bulgaria, Lebanon, Italy, and Krasnodar Krai, indicate high genome stability in natural carriers.

Since one of the identified virus variants from the Dagestan Republic is a member of the *Sarbecovirus* subgenus of the *Betacoronavirus* genus, which includes both SARS epidemic and COVID-19 pandemic pathogens, a phylogenetic analysis of the full-length spike surface glycoprotein (S) gene for the BtCoV/Rf-6/RUS/2022 isolate

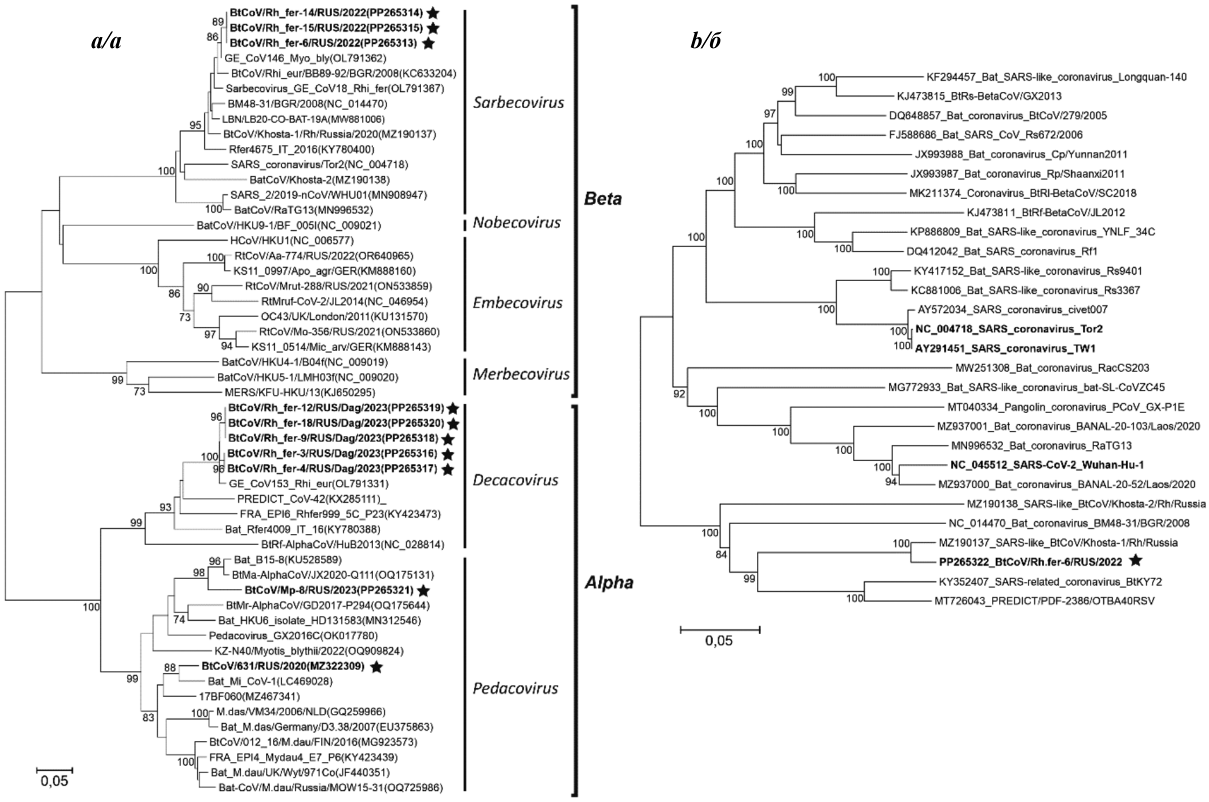

Fig. 2. Phylogenetic tree showing relationships of new coronavirus strains, associated with bats in North Caucasus and Altai-Sayan regions, with strains from other regions.

The trees were generated based on the partial RdRp gene (*a*), S gene (*b*), using a neighbor-joining method (NJ) with 1000 bootstrap replicates; bootstrap values (> 70%) are shown at relevant nodes. The scale bar depicts the number of nucleotide substitutions per site. Detected coronaviruses are labeled in bold font and by asterisk, coronaviruses which caused SARS and COVID-19 are also labeled in bold font (*b*). Two or three identical sequences of strains from the Republic of Dagestan were used for analysis (*a*).

Рис. 2. Филогенетические деревья, отображающее взаимосвязи новых РНК-изолятов коронавирусов, ассоциированных с рукокрылыми на Северном Кавказе и юге Западной Сибири, и изолятов коронавирусов из других регионов мира.

Деревья построены на основе фрагмента гена RdRp (*а*), гена белка S (*б*) с использованием метода ближайших соседей (NJ). Индексы поддержки рассчитаны для 1000 повторов, индексы поддержки (> 70%) отображены в соответствующих узлах. Масштабная линейка указывает количество нуклеотидных замен на сайт. Новые изоляты выделены жирным шрифтом и звездочкой, жирным шрифтом выделены также возбудители SARS и COVID-19 (*б*). В анализ включены по две/три идентичных последовательности РНК-изолятов из Республики Дагестан (*а*).

was obtained and performed (Fig. 2 *b*). The closest of the nucleotide sequences published in GenBank, with a similarity level of 96.9%, was found in the Khosta-1 isolate from the Krasnodar region, identified in the same natural host. The similarity of the encoded amino acid sequences of S proteins amounted to 99.1%. Other virus isolates from Georgia, European countries, and Libya, which were closer in RdRp RNA gene analysis, had only short fragments of the RdRp gene and no S protein genes available in GenBank. The exception was the full-length genome of an isolate from Bulgaria (BM48-31/BGR/2008). While the level of difference in the RdRp gene fragment of isolates from the Republic of Dagestan, Bulgaria, and Krasnodar Krai was comparable (3.3–3.5%), the level of difference in the more variable S protein genes was comparable for the Dagestan-Krasnodar Krai pair (3.1%) and significantly higher (22.7%) for isolates from Dagestan and Bulgaria, indicating the formation of a distinct *Sarbecovirus* variant on the territory of the southern part of the Russian Federation (Dagestan Republic and Krasnodar Krai) and possibly Georgia. Analysis of the coding sequence of the surface S protein showed (**Fig. 3**) that the new RNA isolate BtCoV/Rf-6/RUS/2022 lacks 4 amino acid insertion (PRRA) in the N-terminal region of the receptor site, located at the junction of the S1 and S2 subunits of the spike and forming the site of furin protease hydrolysis, which is characteristic of pathogens of the pandemic variant SARS-CoV-2 [3, 5]. Of the six positions 442(L), 472(F), 479(Q), 480(S), 487(N), 491(Y) in the receptor-binding domain that significantly affect binding to the ACE2 receptor, three positions (442, 480, 491) matched the corresponding S positions of the COVID-19 pathogen protein [24] (Fig. 3 *a*). The overall similarity of the nucleotide and amino acid sequences of the surface S proteins was 78.6 and 71.8%, respectively.

In the Altai Republic and Kemerovo region, coronaviruses belonging to the *Pedacovirus* subgenus of the *Alphacoronavirus* genus were detected in smooth-nosed bats, the eastern noctuid (*M. petax*) from the foothills of the Kuznetsk Alatau and the Ikonnikov's noctuid (*M.*

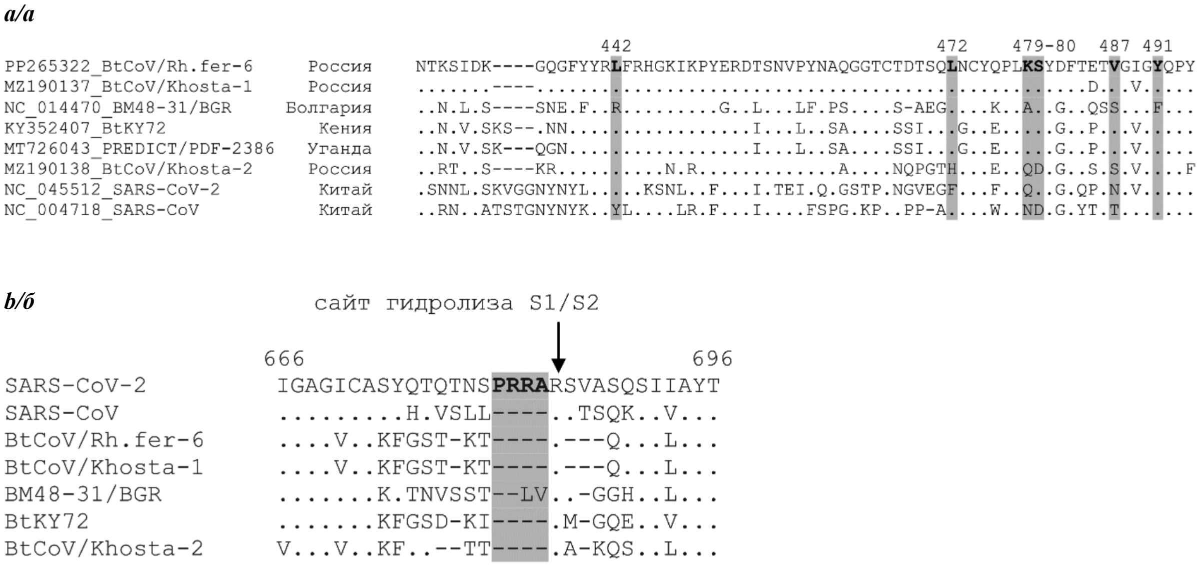

Fig. 3. Amino acid sequence alignment of the receptor-binding motif of the receptor-binding domain (RBD) of the S protein of BtCoV/Rh.fer-6 from the North Caucasus and certain coronaviruses of subgenus *Sarbecovirus*.

Six positions (442, 472, 479, 480, 487, and 491; SARS-CoV #AY278741 numbering) that are thought to be important for adaptation of SARS-CoV-like viruses to the human ACE2 receptor [24] are shown in bold (*a*). Amino acid sequence alignment of the region around the S1/S2 cleavage site in SARS-CoV-2, SARS-CoV, BtCoV/Rh.fer-6 and certain bat SARS-CoV-like viruses. Four amino acid insertion (PRRA) that forms polybasic furin cleavage site in SARS-CoV-2 is highlighted in bold (*b*).

Рис. 3. Сравнение аминокислотных последовательностей рецептор-связывающего участка рецептор-связывающего домена (RBD) коронавируса BtCoV/Rh.fer-6 из Республики Дагестан и других коронавирусов подрода *Sarbecovirus*.

Шесть позиций (442, 472, 479, 480, 487, 491; нумерация по штамму AY278741), важных для адаптации SARS-CoV-подобных вирусов к рецептору человека ACE2 [24], выделены жирным шрифтом (*а*). Сравнение аминокислотных последовательностей, окружающих сайт гидролиза SARS-CoV-2, SARS-CoV, BtCoV/Rh.fer-6, и других SARS-CoV-подобных вирусов (*б*).

ikonnikovi) from the Altai Republic. The level of similarity between geographically close isolates from two species of noctuids belonging to the same subgenus is relatively low and amounted to 80.6% for nucleotide and 96.9% for amino acid sequences. On the phylogenetic tree (Fig. 2), the virus from the Altai Republic (BtCoV/631/RUS/2020) is grouped with an isolate from Japan (Mi_CoV-1), also detected in Ikonnikov's noctuid, an isolate from South Korea (17BF060) from an unidentified species of bats, and with isolates from *Myotis spp.* (BtCoV/012_16/M.dau/FIN/2016, M.das/VM34/2006/NLD, M.daubentonii/UK/Wyt/971Co, M.das/Germany/D3.38/2007, FRA_EPI4_Mydau4_E7_P6, Bat-CoV/M.daubentonii/Russia/MOW15-31/1) from Europe and European Russia. The closest virus from Japan had 93.9% similarity for nucleotide and 99.0% similarity for amino acid sequences. In contrast to isolates from the Dagestan Republic, the new Siberian isolate from the Altai Republic had a relatively low level of similarity with all other sequences from other host species published in GenBank, which did not exceed 89.7% for nucleotide and 97.0% for amino acid sequences.

The virus from the Kemerovo region from *M. petax* (BtCoV/Mp-8/RUS/2023) on the phylogenetic tree (Fig. 2) belongs to the group of isolates from *Myotis spp.* from Asian countries: Korea, China and Kazakhstan (Bat-Cov/KZ-N40/Myotis_blythii/26-07-2022). The Siberian RNA isolate from *M. petax* has a higher level of similarity than the virus from *M. ikonnikovi* with coronaviruses detected among *Myotis* spp. in South Korea (B15-8) and China (Bt-AlfaCoV/JX2020-Q111, HD131583B, BtMr-AlfaCoV/GD2017-P294); it is 86.4–92.6% for nucleotide and 97.7–100% for amino acid sequences. At the same time, its similarity with isolates from a similar host, *M. petax*, found in South Korea (73.3–79.3 and 81.8–87.5%, respectively) is much lower.

Discussion

In the course of this study, the circulation of 3 coronavirus species among bats was established in three administrative regions of the Russian Federation. Coronaviruses and their natural reservoirs have not been previously studied in the regions selected for the study; however, they differ significantly in the degree of study of the surrounding areas. In Georgia, the European part of Russia bordering the Dagestan Republic, as well as in European and Middle Eastern countries, a great diversity of coronaviruses associated with bats has been identified [12, 14–17]. The area surrounding the south of Western Siberia is practically unexplored, with the exception of a few sequences available in GenBank from bats from Kazakhstan (NNo. OQ909823, OQ909824).

The detection of closely related viruses from different species of natural hosts, as well as the circulation of significantly different coronaviruses in a single host species, has been described previously [10, 20] and was detected by us among RNA isolates from the Dagestan Republic. Close variants of the SARS-like virus (<0.5% differences) were found in representatives of two families, *Rh. ferrumequinum* in Dagestan and *M. blythii* in bordering Georgia. At the same time, coronaviruses belonging to different genera and differing by 41.1–41.5% in nucleotide and 58.3% in amino acid sequences were detected among *Rh. ferrumequinum* caught in two neighboring galleries located at a distance of no more than 300 m from each other.

During breeding and hibernation, bats form large aggregations in shelters such as caves and adits. The same shelters are used by different species that do not interact with each other outside them. Sharing shelters facilitates circulation and maintenance of viruses in different species of bats and facilitates virus host switching, and infection can occur through direct contact between specimens, such as by biting or mating. The data show that a single genetic variant of the coronavirus circulates in each local group of *Rh. ferrumequinum*, with virtually identical genome sequences in different specimens.

It is known from tagging results that bats are capable of migrating considerable distances [25, 26]. Such long-distance flights may facilitate the transmission of viruses or their variants between local populations of bats [27], and infection of large horseshoe bats with different viruses could occur when specimens from different local groups jointly inhabit shelters.

The association of new coronavirus isolates from Dagestan on the phylogenetic tree into common clusters with RNA isolates from European countries indicates their common evolutionary origin. It can be assumed that the evolutionary history of *Alphacoronavirus* isolates in Dagestan-Georgia is much longer than that of *Betacoronavirus* isolates, since the levels of difference between nucleotide sequences from Dagestan-Georgia and the closest southern European variants are 11.4–14.2 and 2.3–3.3%, respectively.

The infection rate of animals (> 24%) living in each of the capture sites in the Dagestan Republic is comparable to published data on the infection rate of greater horseshoe crabs in Krasnodar Krai [17]. It is not possible to directly compare the infection rate of bats in Dagestan and Siberian regions, since the number of animals studied, the timing and methods of material collection differ significantly. In the Dagestan Republic, sampling was conducted in winter in caves and adits, in places where large colonies of bats live together and where they have intensive contacts. In the Altai Republic and the foothill areas of the Kuznetsk Alatau, animals were captured in summer by nets in hunting grounds in low-mountainous areas. No large caves were observed in these areas, and bats do not form large colonies, using tree hollows or small-sized other shelters such as small rock crevices as shelter. Outside mass aggregations, the intensity of contacts between animals is sharply reduced, limiting their interactions to brief contacts during the mating period and contacts between mother and cubs during the nesting period. It is probably the absence of large colonies in these areas that has caused not only relatively low numbers of bats in general, but also their overall low infection rates.

This study is the first work on the detection of coronaviruses among bats in the Asian part of Russia, and one of the new *Alphacoronavirus* RNA isolates was detected in a poorly studied natural host, the Ikonnikov's noctuid. RNA isolates from Western Siberia were found to differ more significantly from previously known European and Asian coronaviruses, which is most likely due to the greater remoteness of their habitats. The territories of southeastern China, South Korea, Japan and European countries, which are significantly more studied with respect to coronaviruses associated with bats, are separated from the capture sites by more than 2800 km.

The fauna of bats in the south of Western Siberia includes species with both exclusively Asian distribution (Oriental noctuid, Ikonnikov's noctuid, Ognev's ear (*Plecotus ognevi*)) and species with a significant part of their range in the European part of the continent (pond noctuid (*Myotis dasycneme*), northern leatherback (*Eptesicus nilssonii*)) [28]. The consequence of this may be the association of viral sequences found on the territory of both European and East Asian countries into common clusters. Only data on new coronavirus isolates, which will undoubtedly be discovered in the course of further studies in Siberia and the Russian Far East, can provide a clearer picture of the origin of Siberian coronavirus isolates.

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