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Virological surveillance of bats in Southern Kazakhstan

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Bats are known as an important natural reservoir of many viral infections, from which transmission into the human population occurs. This article aimed to examine bats in Kazakhstan for possible circulation of viruses dangerous to humans and other animals. Two hundred sixty samples, including nasal and rectal swabs and blood sera, were collected from bats in southern Kazakhstan. Studies of the bat virome applying high-throughput sequencing revealed the presence of five large families: Circoviridae, Parvoviridae, Retroviridae, Adenoviridae, and Orthoherpesviridae. All of them were found in southern Kazakhstan from Myotis blythii adult individuals of both sexes. Genomic studies of bat herpesviruses have shown that they are potentially representatives of novel species, genetically different from existing ones. Their epidemic potential for humans and other animals requires further research. Serological studies for possible circulation of antibodies to coronaviruses and influenza A viruses have shown negative results, indicating the absence of antibodies in the tested samples. The results demonstrate the need for more profound research to identify the relationship between human and bat viruses in the future.

KEYWORDS

bat, virus, metagenome, virome, Kazakhstan, next generation sequencing

Introduction

Bats belong to the order Chiroptera. The current total number of bat species worldwide is 1487 (1), which constitutes about 1/5 of all mammals. Bats play a vital role in maintaining healthy ecosystems and biodiversity across the globe. As key species, they provide essential ecosystem services that directly benefit both natural environments and human activities. Insectivorous bats contribute significantly to pest control by consuming vast quantities of insects, including agricultural pests and disease-carrying mosquitoes. Frugivorous and nectar-feeding bats are important pollinators and seed dispersers, particularly in tropical and subtropical regions, facilitating forest regeneration and the reproduction of numerous plant species. These roles highlight their importance as keystone species, sustaining ecosystem balance beyond their often-discussed virological significance and various unsubstantiated human phobias.

Worldwide studies on bat viruses identified more than 130 viral species, including more than 60 anthropozoonotic viruses that are pathogenic for humans, including Ebola, Nipah, and Hendra (2–5). The SARS outbreak that arose in China in 2002 infected more than 8000 people worldwide, and approximately 10% of them died. The role of bats as a natural reservoir of SARS-CoV has been proved then (6). MERS-associated coronavirus was also detected in bats (7).

The use of high-throughput sequencing for metagenomic analysis of viral communities, or viromes, is one of the fastest-growing methods for identifying rare, and novel viruses (8, 9). In recent years, Next Generation Sequencing (NGS) technology allowed researchers to describe a multitude of viruses from bats: hepatitis B virus (10), rotavirus (11), novel bat coronavirus (12) and other important viruses of Nairoviridae (13), Circoviridae, Retroviridae, Orthoherpesviridae, Papillomaviridae (14) and Paramyxoviridae (15) families, indicating that bat species might be associated with a wide diversity of viruses worldwide. It should be noted that the Orthoherpesviridae sequence obtained by Sanger sequencing was used in the work since its sequence was longer than that obtained by the NGS. Past research has indicated that the structure of the virome in bats varies according to both the geographic area and the species of bat.

Kazakhstan has recorded 27 species of bats (16). All of them make up more than 70 percent of the bat population in the territories of the former USSR and represent approximately half of the bat species found in the Palearctic region. This high level of diversity is due to Kazakhstan's wide range of climatic zones. Almost all types of them are inhabited by specific species for those regions, from the southern mountains and deserts to the northern landscapes (17).

In this regard, bats have become essential for virus screening studies worldwide. The Central Asian region has been little studied for various viral infections spread by bats. This study aimed to identify potential natural foci of various infections common among bats.

Materials and methods

Laboratory studies were carried out in compliance with all bioethical standards in accordance with the instructions of the local ethics commission No. 02-09–106 from 25.03.2022, Order of the Minister of Health and Social Development of the Republic of Kazakhstan dated May 27, 2015 No. 392 "On approval of good pharmaceutical practices", May 29, 2015 No. 415. "On approval of the Rules preclinical studies, requirements for preclinical bases," as well as the order of the Minister of Agriculture of the Republic of Kazakhstan dated June 29, 2015, No. 7-1/587 "Veterinary (veterinary and sanitary) rules".

Samples collection, their preliminary processing, and RNA extraction

Bats were sampled by taking nasal and rectal swabs with sterile cotton swabs. These swabs were then stored in vials filled with medium 199 (Gibco, ThermoFisher Scientific, USA) supplemented with antibiotics and bovine serum albumin, and kept in liquid nitrogen (–196°C). Samples were duplicated in DNA/RNA Shield reagent (Zymo, USA) for molecular biological studies and stored at room temperature. Prior to RNA extraction, the samples underwent centrifugation at 3200 rpm for 15 minutes. The supernatants were then passed through 0.45 μ m filters (Roth, Germany) and exposed to a combination of nucleases, including Turbo DNAse, DNAse I, and RNAse T1 (ThermoFisher, Lithuania). RNA was then isolated using the QIAamp Viral RNA Mini kit (Qiagen, Germany), following the protocol provided by the manufacturer.

Next generation sequencing

The libraries for high-throughput sequencing were prepared using the QIAseq FX Single Cell RNA Library Kit (Qiagen, Germany) and the NEBNext Ultra DNA Library Prep Kit for Illumina (NEB, USA) following the manufacturers' instructions. The fragmentation of cDNA to sizes ranging from approximately 450 to 600 base pairs (bp) was achieved through an enzymatic process utilizing the Fragmentase kit (NEB, USA). The libraries' concentrations were determined on a Qubit 2.0 instrument (Invitrogen, Germany). The libraries' sizes were determined by the Bioanalyzer 2100 device (Agilent, Germany). Sequencing was performed using the MiSeq Reagent v.3 kit (Illumina, USA) on a MiSeq sequencer (Illumina, USA).

Bioinformatic analyses

Bioinformatic analysis, which consists of assembling all obtained reads into longer contig sequences with subsequent annotation, was performed on a high-performance computer with the installed Geneious Prime program (Biomatters, New Zealand). Homologous sequences were searched using BLAST in the international GenBank database. The data were compared online against the GenBank non-redundant and viral reference databases with both BLASTx and BLASTn. A BLAST hit was considered significant with an E-value threshold of 10e-25. Contigs from bacteria and eukaryotes were omitted from the analysis, and sequences resembling viruses were advanced for further study.

Serology

The blood serum samples were analyzed for antibodies against coronaviruses using an enzyme-linked immunosorbent assay (ELISA) with the SARS-CoV-2 Double Antigen Multi-species ID Vet COVIDA/0520 kit. Additionally, they were tested for antibodies to the influenza A virus with the AID Screen[®] Influenza A Antibody Competition Multispecies ELISA kit, following the guidelines provided by the manufacturers. In the case of serological testing for coronavirus, a multi-species kit for the detection of antibodies to SARS-CoV-2 was used, which is capable of working with sera from a wide range of animal species sensitive to this pathogen. This study was experimental, and in case of positive results, it was planned to confirm using more specific tests. Since strictly negative results for coronavirus were obtained, serological studies were not continued.

As for serological testing for influenza A, according to information from the ELISA kit manufacturer, this kit is highly sensitive and specific to antibodies to the influenza A virus in susceptible animals. It is known that bats are susceptible to H9 influenza A subtype (18) and supposedly form a specific bat lineage (19). Commercial multi-species ELISA kits, like the validated for the bat species BioChek CK401 AI Multi ELISA kit, are commonly used to detect antibodies to the influenza A virus in bats. In our case, we also used a similar multi-species AID Screen kit from another manufacturer that detects antibodies to Influenza A nucleoprotein, regardless of the virus subtype, including H9, circulating in bats.

Results

In 2023, trips were organized to the southern region of Kazakhstan to collect samples from bats (Figure 1). At the collection sites, 260 samples were collected from 201 individuals of 3 genera: Myotis, Nyctalus (Vespertilionidae family), and Rhinolophus (Rhinolophidae family) in the Chiroptera order. The sizes of the libraries constructed ranged from 250 to 700 nucleotides (nt), fitting the length specifications for sequencing on a MiSeq device with the Reagent kit v.3 (Illumina, USA). A bioinformatics analysis was then conducted on the results from the high-throughput sequencing of bat samples. The obtained contig lengths, indicated in Table 1, were used in analyses. Unfortunately, complete viral sequences were not obtained, and this work will be carried out in the future after the viruses have been propagated on sensitive media. Illumina technology sequencing identified viruses belonging to different families.

The sequences were obtained from hosts classified primarily as mammals and insects, with their closest matches in GenBank listed. Key parameters such as the contig identifier, GenBank hit, accession number, identified gene, E-value, identify percentage, contig length, and coverage are provided. Genomic analysis and identification of viral sequences through BLAST search in GenBank were summarized in Table 1. All the mammalian viral sequences obtained in this research were deposited in GenBank and their accession numbers are shown in Supplementary Table 1.

Mammalian viral families

The viral sequences identified included representatives from five distinct viral families: Orthoherpesviridae, Adenoviridae, Circoviridae, Parvoviridae, and Retroviridae. Notably, all these viral families were detected in adult individuals of both sexes from a single bat species, Myotis blythii, in the Southern Kazakhstan population. Further studies of other bat species in Kazakhstan are required to determine the presence of the detected viral families and possibly others not detected in the Myotis blythii species.

The most concerning finding was the identification of herpesvirus sequences (Orthoherpesviridae family) showing 72.86% similarity to Human alphaherpesvirus 1 isolate 0145 by the 233 nt fragment of DNA polymerase gene. This similarity level indicates a related but distinct virus rather than direct contamination, as human viral contaminants would typically show >95% similarity. Further amino acid sequence analyses have shown that the virus under study is closer (83%) to Bat simplexvirus



Contigs #	Host	GenBank hit	Accession #	Gene	E- Value	Identity	Contig length	Contig coverage
PCR * fragment	Mammals	Human alphaherpesvirus 1 isolate 0145 DNA	MF615314	Polymerase	1e-05	72.86%	233	84%
k141.1431	Mammals	Pipistrellus pipistrellus adenovirus isolate MAVG44	PP410068	hexon	8e-26	88.24%	349	58%
k141.345	Mammals	Rodent circovirus isolate RtCb-CV- 3/HeB2014	KY370032	Capsid	3e-35	85.62%	223	69%
k141.630	Mammals	Myotis capaccinii feces-associated cyclovirus 2 isolate MAVG32	PP410066	Capsid	8e-21	79.29%	201	83%
k127_30164	Mammals	Anser anser dependoparvovirus isolate wig220par02	MW046577	VP1	7e-11	72.11%	180	82%
k127_30164	Mammals	Adeno-associated virus 2 isolate JBL5	OP161118	VP1	3e-9	71.52%	180	87%
3	Mammals	Rousettus_leschenaultii_retrovirus	JQ951958	polymerase	2e-116	100%	233	100%
k141.162616	Mammals	Myotis daubentonii endogenous retrovirus isolate EuB-RV3	MN851303	NS	4e-99	93.55%	627	39%
9	Insect	Sibine_fusca_densovirus	JX020762	nonstructural	5.63e- 126	97.0%	300	94.0%
3	Insects	Casphalia_extranea_densovirus	AF375296	nonstructural	5.63e- 126	97.0%	300	94.0%
12	Insects	Danaus_plexippus_plexippus_iteravirus	KF963252	nonstructural	2.58e- 134	97.8%	300	95.7%
2	Insects	Dragonfly-associated_circular_virus	JX185429	replication- associated protein	5.02e- 27	61.2%	99	90.0%
2	Insects	Odonata-associated gemycircularvirus-1	KM598385	replication- associated protein	2.38e- 15	37.7%	144	77.9%
8	Insects	Choristoneura occidentalis granulovirus	DQ333351	hypothetical protein	1.10e- 18	33.2%	77	90.9%
5	Insects	Deformed wing virus	JX185667	polyprotein	8.36e- 25	69.8%	187	78,7%
3	Plants	Grapevine leafroll-associated virus	HQ442266	coat protein-like	5.93e- 16	32.9%	76	88.2%

TABLE 1 BLAST search in GenBank.

*The sequence was obtained by Sanger sequencing.

1 isolated from frugivorous tropical bats (Pteropodidae and Phyllostomidae bat families) than to human alphaherpesvirus (75.32%) (20, 21). This finding suggests a potentially novel bat herpesvirus with partial genetic similarity to frugivorous bat and human herpesviruses, which aligns with the known pattern of coevolution between herpesviruses and their mammalian hosts.

The Adenoviridae family was represented by sequences showing the highest similarity (E-value: 8e-26, 88.24% identity by the 349 nt fragment of the hexon gene) to Pipistrellus adenovirus (Vespertilionidae bat family). This virus was previously detected in the common pipistrelle insectivorous bat (22) in Europe, suggesting evolutionary conservation of genomic regions between different bat species from distant parts of the world. Unfortunately, because of their short length, analysis of the available genome fragments of newly discovered bat adenoviruses and herpesviruses in Kazakhstan did not allow the possibility of finding genetic markers associated with the pathogenicity level. The Circoviridae family was represented by sequences that were 85.62% by the 223 nt fragment of the capsid gene similar to rodent circoviruses, identified in China (23). The presence of circovirus-like sequences in bats has been reported previously in global studies (4, 24, 25), but more similarity to rodent-associated viruses rather than to Myotis capaccinii feces-associated cyclovirus 2 (79.29% by the 201 nt fragment of the capsid gene) (Vespertilionidae bat family) (22), raises interesting questions about the evolution of this viral family in distant species.

Parvoviridae sequences were also identified in the samples, though specific details on the closest matches were limited in the initial analysis. Parvoviruses are commonly found in bat populations worldwide (Myotis, Pipistrellus, Eptesicus, Vespertilio and Nyctalus bat genera), with varying levels of host specificity and potential pathogenicity (5, 25). In this research, contigs (180 nt fragments of the VP1 gene) from the Kazakhstan bats by the were closer to avian Anser anser dependoparvovirus isolate wig220par02 (72.11%) and human Adeno-associated virus 2 isolate JBL5 (71.52%) respectively than to known bat parvoviruses.

Retroviridae was identified through sequences most closely matching Myotis daubentonii endogenous retrovirus (93.55% by the 627 nt fragment of the nonstructural protein gene) (Vespertilionidae bat family) from Germany (5) and Rousettus leschenaultii retrovirus (100% by the 233 nt fragment of the polymerase gene) described in bats of the Pteropodidae family (26) in China. This finding is particularly interesting as Rousettus is a genus of fruit bats not native to Kazakhstan, suggesting either evolutionary conservation of retroviral sequences across different bat genera or potential ancestral relationships between viral strains from geographically distant bat populations.

Insect-associated viral sequences

The second category of viral sequences identified in bat samples showed the highest similarity to insect-associated viruses, likely reflecting the insectivorous diet of the sampled bat species. Densoviruses, which belong to the Parvoviridae family but specifically infect arthropods, were prominently represented. The highest similarity (97.0% by the 300 nt fragment of the NS gene) was to Sibine fusca densovirus and Casphalia extranea densovirus, suggesting recent ingestion of infected prey rather than adaptation of these viruses to bat hosts. A densovirus belonging to the Iteravirus genus, with remarkably high similarity (97.8% identity, also by the 300 nt fragment of the NS gene) to Danaus plexippus iteravirus, was also detected. This high percentage identity suggests recent consumption of infected lepidopteran prey, as Danaus plexippus (monarch butterfly) is not native to Kazakhstan, but related lepidopteran species carrying similar viruses may be present in the region. Densoviruses have previously been found in bats, and it has also been suggested that insect viruses in bats are of alimentary origin (27).

Circular virus of the Circoviridae family sequences were 61.2% and 37.7% similar to Dragonfly-associated circular virus and Odonata associated gemycircularvirus respectively (99–144 nt fragments of the Rep gene), further supporting the dietary origin hypothesis for insect-associated viral sequences. These small, circular DNA viruses are increasingly recognized as abundant and diverse in insect populations worldwide (28) including those found in bats during metagenomic assays (24).

Choristoneura occidentalis granulovirus of the Baculoviridae family is generally considered an insect-specific pathogen, primarily infecting lepidopteran larvae. These viruses are exclusively pathogenic for arthropods, particularly insects, and have not been registered in bats previously (29). Low similarity (33.2%) and very small size (77 nt) of the obtained fragment of the hypothetical protein limit our analyses.

In this study, a contig (187 nt fragment of the polyprotein gene) 69.8% similar to Deformed wing virus was found. Deformed wing virus is a pathogen of insects belonging to the family Iflaviridae within the order Picornavirales. It was detected in bats in the USA (30) and Switzerland (31). It was supposed that this virus was introduced to bats and other mammals through the consumption of infected insects (32).

Interestingly, plant virus sequences were also identified, including those with moderate similarity (32.9%) by76 nt fragment of the coat protein-like protein gene to Grapevine leafroll-associated virus. This lower similarity percentage suggests either distant evolutionary relationships or potential dietary acquisition through insects that had previously fed on infected plant material, representing a multi-trophic chain of viral genetic material transfer.

The E-values for these matches ranged from highly significant for some sequences (particularly the insect virus matches) to moderately significant for others, providing varying levels of confidence in the taxonomic assignments. This variation underscores the importance of careful interpretation of metagenomic data, particularly when viruses cross taxonomic boundaries. Serological analyses for coronaviruses and influenza A virus in ELISA have shown negative results.

Discussion

More in-depth studies of the bat virome worldwide have begun in recent years, particularly after the pandemic, in which bats were suspected as a natural reservoir (32). This study is one of the few studies in Kazakhstan that has provided initial information on the bat virome in the Central Asian region. The virus families found in bats are important to studying possible natural anthropozoonotic foci. Finding contigs from viruses of Orthoherpesviridae, Adenoviridae, Circoviridae, Parvoviridae, and Retroviridae families in bats highlights their significance as major reservoirs of viral diversity. Bats are known to harbor many viruses because of their distinct ecological, physiological, and evolutionary characteristics, such as their capability to fly, their extended lifespans, and their tendency to roost in groups, which aids in the spread and persistence of viruses within their communities (33).

Orthoherpesviridae is a large family of DNA viruses that cause infections and some diseases in animals, including humans (34). Most bat herpesviruses are isolated from apparently healthy animals collected during captures as part of random surveillance programs. Orthoherpesviruses, typically latent in their hosts, underscore the complex interactions between bats and their viruses (35). Herpesviruses have evolved alongside their hosts, allowing for longterm persistence through latent infections and occasional shedding, which can facilitate cross-species transmission in specific circumstances (36). As noted earlier, the herpesvirus found in bats in Kazakhstan is a potentially novel species. Despite its similarity to Simplexvirus, the potential for bat herpesviruses to infect humans appears limited based on current evidence, though rare cases of cross-species transmission of herpesviruses have been documented in other mammalian systems (37). More complete genomic characterization of the bat herpesviruses identified in this study would help clarify their evolutionary relationships and assess their zoonotic potential. Perhaps in the future, dozens of new herpesviruses will be discovered in bats worldwide and in Kazakhstan, since their viral diversity is only beginning to be intensively studied.

The Adenoviridae family of viruses causes a wide range of diseases, mostly respiratory and gastrointestinal, in animals and

humans (38). Adenovirus infections can be asymptomatic in hosts (39). Bat adenoviruses have been previously identified in multiple species across Europe, Asia, and the Americas, often showing hostspecificity at the bat genus level (40). Adenoviruses are known to exhibit high host specificity but may also provide insight into hostvirus co-evolution. In this research, the virus was detected in animals without any signs of disease, and its impact on the health of bats and other mammals needs to be elucidated in the future. The identification of sequences similar to Pipistrellus pipistrellus adenovirus in Myotis blythii is interesting as it suggests potential cross-genera transmission or the existence of conserved genomic regions across bat adenoviruses. The potential for zoonotic transmission of bat adenoviruses remains largely unexplored, though their usually strict host specificity makes cross-species jumps less likely than other viral families. Notably, a novel species of adenovirus from bats in Kazakhstan has been identified and genetically characterized before (41). The discovery of a new bat adenovirus in a local population is not unusual, as it is believed that there are hundreds of unknown and undiscovered adenovirus species in bats worldwide (40).

Circoviridae viruses, which have been identified in bat species, are generally small DNA viruses with circular genomes (24). Although subclinical infections are common with circoviruses, they are thought to be associated with infectious anemia in chickens, pigeon circovirus disease, and multisystem post-weaning wasting syndrome in pigs (42). Contigs of this virus have previously been detected in bats and appear to be common there (43, 44). The circovirus identified in this study was 72% similar to Myotis capaccinii feces-associated cyclovirus 2, indicating its significant genetic distance from the described species of this family. Its discovery so far has only scientific significance in the study of the diversity of bat circoviruses. A role in pathogenicity remains to be determined.

Retroviridae. Although retroviruses such as human immunodeficiency virus (HIV) are among the most important families of viruses that have been transmitted from animals to humans, it remains to be seen whether bat retroviruses are capable of infecting and causing disease in humans (45). Although primarily associated with avian and porcine hosts, their detection in bats may indicate a broader host range and ecological niche than previously thought. Similarly, the discovery of retroviral sequences such as the Myotis daubentonii endogenous retrovirus, highlights the potential for viral integration into host genomes, a phenomenon that has likely played a role in the evolutionary dynamics of bat immunity (5). Retroviridae detected in Myotis blythii from Kazakhstan adds to the growing evidence that retroviruses are widespread in bat populations globally. While retroviruses such as HIV have demonstrated significant zoonotic potential, the risk posed by bat retroviruses remains largely theoretical at present. Continued surveillance and characterization of bat retroviruses, particularly focusing on receptor usage and potential barriers to cross-species transmission, will be important for risk assessment.

Bat parvoviruses are represented by avian Anser anser dependoparvovirus and human Adeno-associated virus 2. The identification of parvoviruses in bat contigs aligns with earlier research, which indicates that these virus families often infect mammals, including bats, typically without leading to apparent disease. Parvoviruses are often associated with gastrointestinal or systemic infections in mammals but remain understudied in their bat hosts (45). The discovery of a bat parvovirus similar to avian and human parvoviruses in this research is an interesting case, but perhaps this family has not yet been studied enough in local bats. In addition to the above-mentioned Orthoherpesviridae and Adenoviridae viral families, representatives of the Circoviridae and Parvoviridae families may also be potentially novel species of mammalian viruses. Their similarity to known viruses varied from 71.52% to 100%, but further studies are needed to obtain their complete genomes. This also applies to the discovered insect viruses.

Our study has some limitations. Short viral sequences (180–627 nt) were identified in the metagenomic sequencing, and further investigations, including virus propagation, are necessary to obtain complete genomes.

A significant presence of insect viruses or their close relatives of supposedly dietary origin is revealed in bats. These include a diverse range of viral types, such as densoviruses, circular viruses, baculoviruses, and iflaviruses. The prevalence of these viruses in bats varies, with some viral groups showing notable presence in certain bat populations. The evolutionary links observed between certain insect and bat viruses highlight the interconnectedness of viromes across different taxa.

The novelty of the data obtained on the presence of insect viruses in bats is relative, expanding our understanding of the diversity of their virome, the components of which, as it turns out, are representatives of viruses from different kingdoms.

Further research is essential to fully elucidate the nature of these interactions, including determining the full host range of these viruses, their ability to replicate in bat cells, and their potential impact on bat health and the broader ecosystem. Comprehensive studies utilizing metagenomics, targeted viral detection assays, and investigations into viral replication and persistence in bats are needed to gain a deeper understanding of this complex and evolving field. Bats, as predators of insects, might also play a role in the ecology and dissemination of insect viruses within insect populations through predation and fecal shedding of viral particles (27).

It may seem that the various virus families discovered in this study are more similar to human, insect, and plant viruses than to related bat viruses that were previously collected from neighboring regions such as China, Russia, and others. We think that bats have been very little studied virologically to date and that several novel species can be found even within a single population, which is often the case. Therefore, we believe that with the accumulation of large amounts of information from different countries, conclusions can be made about the global distribution of viral families.

The findings highlight bats' critical role as reservoirs for various viral families. This discovery holds significant implications for comprehending viral ecology, the risk of zoonotic transmission, and the co-evolutionary dynamics between hosts and viruses. Future studies should focus on characterizing these viruses' functions, assessing their capability to infect other species, and examining the ecological influences on viral diversity in bats. Moreover, conducting genomic surveillance of bats in various geographic areas and habitats will enhance our understanding of their contribution to global viral evolution and emergence.

Data availability statement

The original contributions presented in the study are publicly available. This data can be found here: NCBI GenBank, accession ERS24838366–ERS24838369, PP410068, OP161118, PP410066, KY370032, MW046577, MN851303, MF615314, JQ951958, JX020762, HQ442266, JX185662, DQ333351, JX185667, AF375296, JX185429, KF963252, KM598385.

Ethics statement

The animal study was approved by Research and Production Center for Microbiology and Virology Local Ethics Commission. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

KK: Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. TS: Formal analysis, Methodology, Writing – original draft, Writing – review & editing. AK: Investigation, Writing – original draft, Writing – review & editing. YKa: Resources, Writing – original draft, Writing – review & editing. YKh: Resources, Writing – original draft, Writing – review & editing. SN: Resources, Writing – original draft, Writing – review & editing. SN: Resources, Writing – original draft, Writing – review & editing. SM: Resources, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fviro.2025.1582410/ full#supplementary-material

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