

## Arctic-like lineage of rabies virus detected in Indian wild fox: a case study

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### Abstract

Rabies is a viral disease affecting both land-dwelling and flying mammals. In India, dogs have been the primary source of rabies. This study aimed to investigate the role of wild animals in the transmission and persistence of the rabies virus and analyse the viral genome to understand its characteristics. In the present study, a brain sample from a fox (*Vulpes vulpes*) found dead in the free-ranging area of Mannamangalam forest station, Thrissur, Kerala state, India, was collected for rabies screening by fluorescent antibody staining and molecular techniques. Viral proteins and nucleic acids were detected and the samples were subsequently analyzed using next-generation sequencing for characterization. The genome analysis revealed that the virus belonged to the type I genotype of the arctic-like lineage. The phylogenetic analysis indicated that the fox virus strain shared close homology with all Indian isolates irrespective of the host species and was clustered in the same arctic-like lineage, denoting the distribution of a similar lineage and genotype across all regions of India. The deduced amino acid variations of *nucleoprotein* and *glycoprotein* genes also revealed a pattern of similarity amongst isolates of Indian origin and differed from isolates of other geographical locations and lineages. This study based on genome-wide surveillance could offer novel insights into the genetic makeup of currently circulating strains in the human-wildlife conflict and their continuing spread and persistence of rabies.

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### Introduction

Rabies is an endemic disease in India and represents a significant public health and economic challenge. Rabies is more predominant in Africa and Asia, where approximately 95.00% of cases are reported. The rabies virus (RABV) is a member of the *Mononegavirales* order, *Rhabdoviridae* family, and *Lyssavirus* genus, and has a non-segmented linear negative-stranded RNA genome which is about 12.00 kb in size. The viral genome encodes five proteins: An RNA polymerase enzyme, matrix protein, glycoprotein (G), phosphoprotein, and nucleoprotein (N).<sup>1</sup> Various mammalian species serve as a specific vector or reservoir for different genotypes of RABV, thereby resulting in the co-circulation of distinct phylogenetic lineages in the mammalian hosts.<sup>2</sup> Numerous reports indicate that the arctic-like lineage of the RABV is circulating in India and other neighbouring countries.<sup>3-5</sup>

There is an existing theory suggesting that the arctic lineage of the RABV may have descended from the northern part of India to the south, possibly through transmission from foxes to dogs.<sup>6</sup>

Globally, more than 99.00% of human rabies cases are reported to be transmitted through dogs. Indeed, wild animals, such as jackals, foxes, and mongooses, have been documented as reservoirs of the RABV and play a crucial role in sustaining the sylvatic (wildlife) cycle of the disease.<sup>7</sup> Previous studies on jackals, leopards, and hyenas have primarily focused on characterizing the RABV strains without providing a detailed analysis of the virus lineage through comprehensive whole genome sequencing.<sup>8-9</sup> This highlights the need for more in-depth research to better understand the genetic diversity and evolutionary patterns of the virus in these wildlife reservoirs. The present study aimed to analyze the genetic variations of the circulating RABV in the wildlife hosts and also

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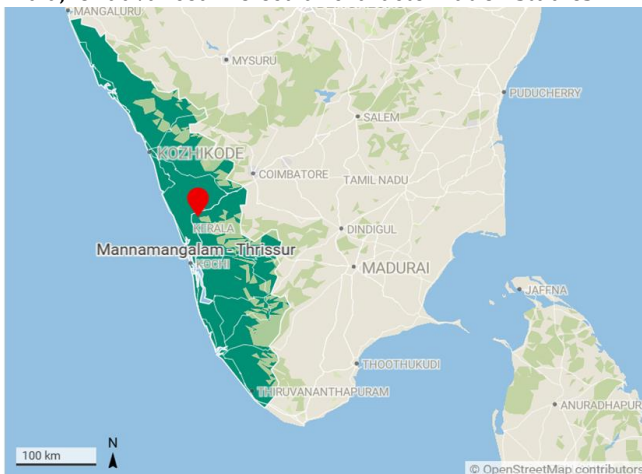


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understand the animal-human interface at the borders. In the present study, the RABV strain from the Indian wild fox was subjected to whole genome sequencing, as well as phylogenetic and amino acid variation analyses to identify the RABV lineage. These could help characterize the variations at antigenic sites and provide a comprehensive understanding of the RABV in a region. This information is crucial for effective rabies control and prevention strategies, as well as monitoring the potential spill over into human populations.

## Materials and Methods

**Sample collection.** A fox (*Vulpes vulpes*) was found dead in the free-ranging area of Mannamangalam forest station, Thrissur, Kerala state, India (Fig. 1), and the carcass was sent to the Department of Veterinary Pathology, College of Veterinary and Animal Sciences, Kerala Veterinary and Animal Sciences University, Thrissur, India, for post-mortem examination. The Mannamangalam forest station in Kerala state experiences a consistent ambient temperature range of approximately 20.00 - 25.00 ° C throughout the year. At the time of necropsy, the carcass exhibited partial resolution of rigor mortis, suggesting that death likely occurred within the preceding 24 to 36 hr. Mild putrefactive changes were observed in internal organs, such as the liver and intestinal tissues; whereas, other vital organs, including the brain, heart, lungs and kidneys, appeared grossly unremarkable without any evident pathological alterations and further, the brain sample was collected for rabies screening. Viral protein was detected by Seller's staining, and further, the sample was transferred under the cold chain to the Rabies Diagnostic Laboratory (ISO/IEC 1702:2017 accredited laboratory) of the Department of Animal Biotechnology, Faculty of Basic Sciences, Madras Veterinary College, Tamil Nadu Veterinary and Animal Sciences University, Chennai, India, for advanced molecular characterization studies.



**Fig. 1.** Geographical location showing the place of rabies suspected fox sample collection.

The protocol and procedures employed were reviewed and approved by the Institutional Animal Ethical Committee of Madras Veterinary College, Tamil Nadu Veterinary and Animal Sciences University, Chennai, India (Approval Number: 01/LA/IAEC/2023).

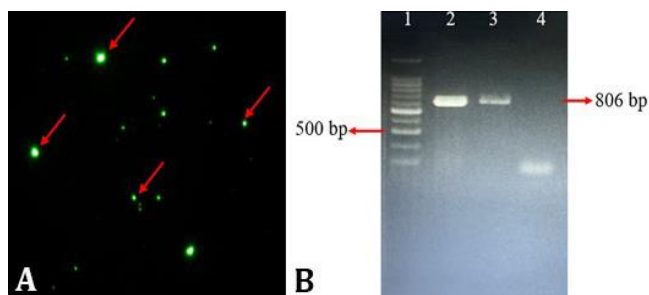
**Direct fluorescent antibody testing.** Direct fluorescent antibody testing was performed on the brain impression. The brain impression smear was fixed with acetone at 4.00 ° C for 20 min and air dried. The fluorescent antibody conjugate (Merck, Darmstadt, Germany) against the G was added and incubated at 37.00 ° C for 1 hr in a humid chamber.<sup>10</sup> The slides were then observed under a fluorescent microscope (Olympus, Tokyo, Japan).

**RNA isolation and reverse transcription-polymerase chain reaction (RT-PCR).** The RNA of RABV was isolated from the brain sample using the Trizol method, and cDNA synthesis was carried out using a PrimeScript™ RT reagent kit (Takara Bio Inc., Kusatsu, Japan). The virus was preliminarily detected by amplifying the 805 bp sequence of the *N* gene through RT-PCR using primers FP5'-CATTGCAGATAGGATAGAGC-3' and RP 5'-GCTTGATGATTGGAAGTACTG-3' as previously described.<sup>8</sup> The PCR reaction was carried out with an initial denaturation at 94.00 ° C for 2 min, 30 cycles of denaturation at 94.00 ° C for 30 sec, annealing at 58.00 ° C for 45 sec, and elongation at 72.00 ° C for 30 sec, followed by final elongation at 72.00 ° C for 5 min. A real-time PCR was also performed against the *N* gene for further confirmation with 5'-ATGTAACACCYCTACAATG-3' as forward and 5'-GCAGGGTAYTTRTACTCATA-3' as reverse primers.<sup>11</sup>

**Whole genome sequencing and phylogenetic analysis.** The RNA isolated from the brain tissue was quantified and the purity was determined using spectrophotometry. The sample with RNA concentration of 50.00 ng  $\mu$ L<sup>-1</sup> and A260/230 2.0 was sent for complete genome sequencing at M/s LifeCell International Pvt Ltd., Chennai, India, using the Illumina sequencing platform to generate 150 bp paired-end reads. The obtained reads were then analyzed using the Galaxy software (version 25.1.rc1; <https://usegalaxy.org/>). The quality of the trimmed sequence reads was assessed prior to their mapping with the reference genome using BWA-MEM alignment. Multiple sequence alignment was performed for the RABV genome from NCBI (<https://www.ncbi.nlm.nih.gov/>) with the MAFFT tool, and the phylogenetic analysis was carried out to determine the lineage and genotype of the RABV. The iTOL version 7.3 (Biobyte Solutions GmbH, Heidelberg, Germany) was used for viewing and editing the phylogenetic tree. The *N* and *G* genes amino acid sequence analyses were performed using BioEdit version 7.2 (Ibis Therapeutics, Carlsbad, USA) to analyze the variations at antigenic sites.

## Results

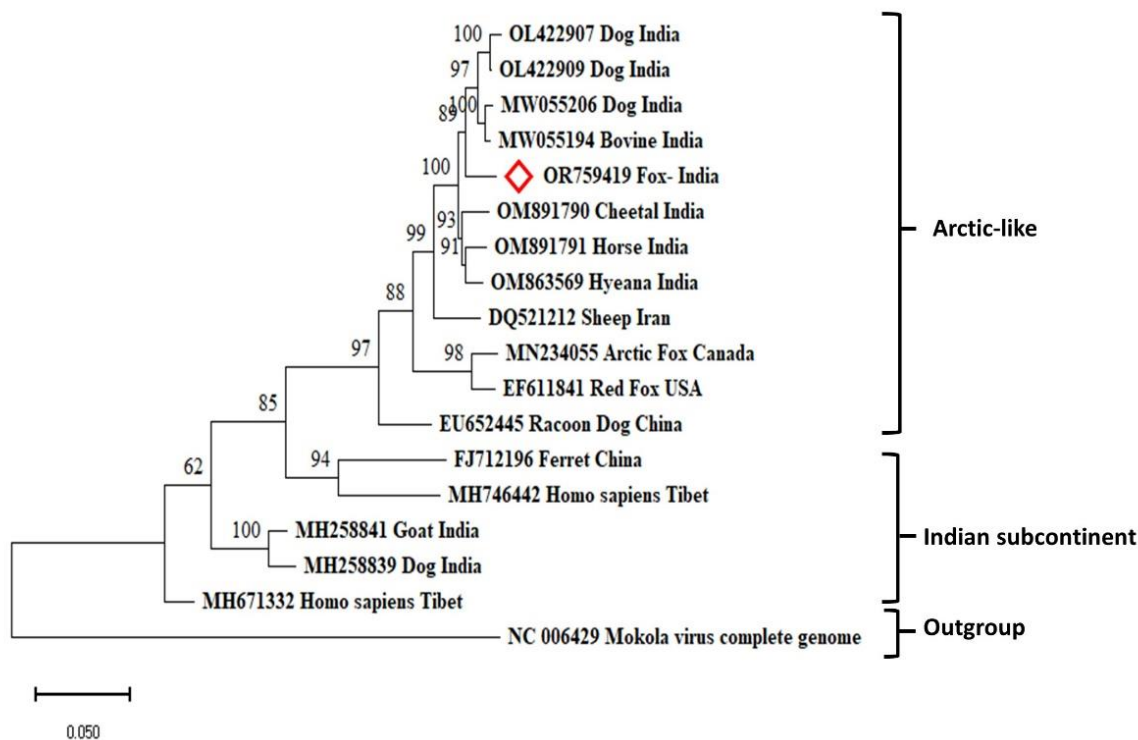
**Direct fluorescent antibody testing for G and RT-PCR.** The brain impression of the fox sample showed green fluorescence signals, indicating the sample was positive for rabies antigen by direct fluorescent antibody testing (Fig. 2A). Further, the *N* gene of the fox sample was amplified by RT-PCR and real-time PCR, further confirming the presence of RABV by molecular methods (Fig. 2B).



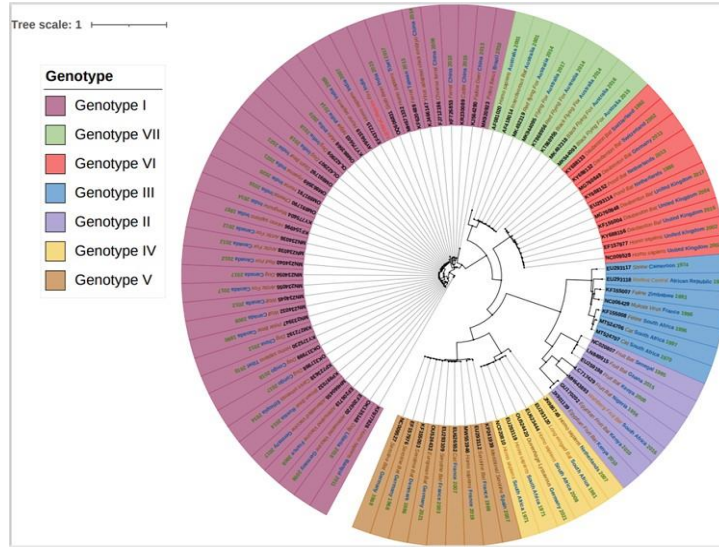
**Fig. 2. A)** Direct fluorescent antibody testing on the fox sample showing bright green fluorescence in the presence of rabies viral particles under  $400\times$  magnification (red arrows); **B)** Agarose gel electrophoresis of the *nucleoprotein* gene product of 586 bp amplified by reverse transcription-polymerase chain reaction of the rabies suspected fox sample. Lane 1: 100 bp ladder; Lane 2: Rabies suspected fox sample; Lane 3: Positive control; Lane 4: Negative control.

**Whole genome analysis.** The RABV genome was 11,909 bp long and consisted of five major regions. The position and size of the five genes of the RABV genome were *N* gene from 61 - 1,413 nucleotide (1,353 bp), *phosphoprotein* gene from 1,504 - 2,397 nucleotide (894 bp), *matrix protein* gene from 2,456 - 3,094 nucleotide (639 bp), *G* gene from 3,355 - 4,884 nucleotide (1,530 bp), and *large RNA-dependent RNA-polymerase* gene from 5,403 - 11,786 nucleotide (6,384 bp), followed by the non-coding region. The complete genome of RABV from the fox was submitted to NCBI GenBank under the Accession Number of OR759419.

**Phylogenetic analysis.** The lineage tree constructed by comparing the *N* gene sequences of RABV strains obtained from the NCBI database belonging to different lineages is given in Figure 3. The RABV strain from the present study was identified to belong to the arctic-like lineage and a close relationship was identified with the RABV strain isolated from the Cheetal (OM891790) and Bovine (MW055194) in India. The phylogenetic tree with the whole genome sequence is shown in Figure 4. It revealed that the RABV isolated from the fox sample clustered with other isolates from other parts of the world belonging to genotype I. A close relationship was determined with the RABV strain being isolated from the sloth bear (OQ606831) in Tamil Nadu, India.



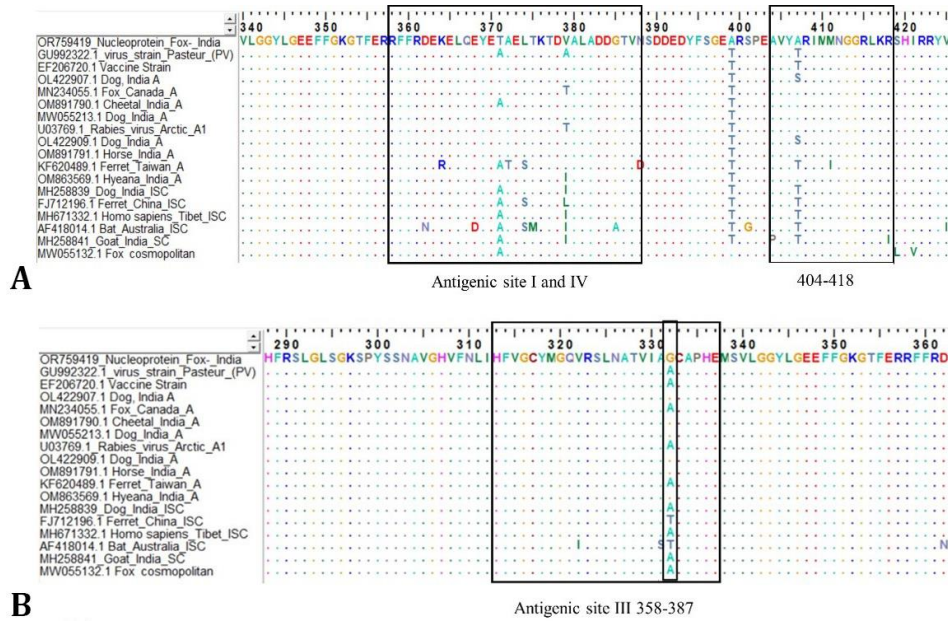
**Fig. 3.** Phylogenetic tree with *N* gene sequence constructed using maximum likelihood method and 1,000 bootstrap replications in Mega Software version 11.0 (BioDesign Institute, Tempe, USA), displaying the lineage classification of the rabies virus isolates.



**Fig. 4.** Phylogenetic tree of whole genome sequence of the *Lyssavirus* genus constructed using sequences derived from NCBI, showing the classification of rabies isolates and their genotype.

**Nucleoprotein gene.** The amino acid sequence analysis of the *N* gene of the RABV of the fox sample with other *Lyssavirus* isolates of different hosts and lineages is given in Figure 5. Amino acid differences were found in the location of antigenic determinants at position 379, where the fox RABV strain had valine and was different from the Pasteur strain alanine, the Indian sub-continent lineage isoleucine, and a ferret RABV strain from China (FJ712196) had leucine. The RABV isolates from foxes reported in Canada contained amino acid threonine at position 379. The amino acid position 332 in the

antigenic site III also revealed variation between glycine present at 332 for Indian strains and alanine for strains of different origins. Similarly, amino acid at position 370 of the fox RABV was threonine; whereas, alanine was determined in *Lyssavirus* of the Indian sub-continent and cosmopolitan lineages, including RABV from cheetal, India (OM891790). The amino acid position 404 of the antigenic site IV was alanine in wild animals of arctic-like lineage; however, dogs of arctic lineage had serine, while threonine was discovered at the same site for the other lineages.

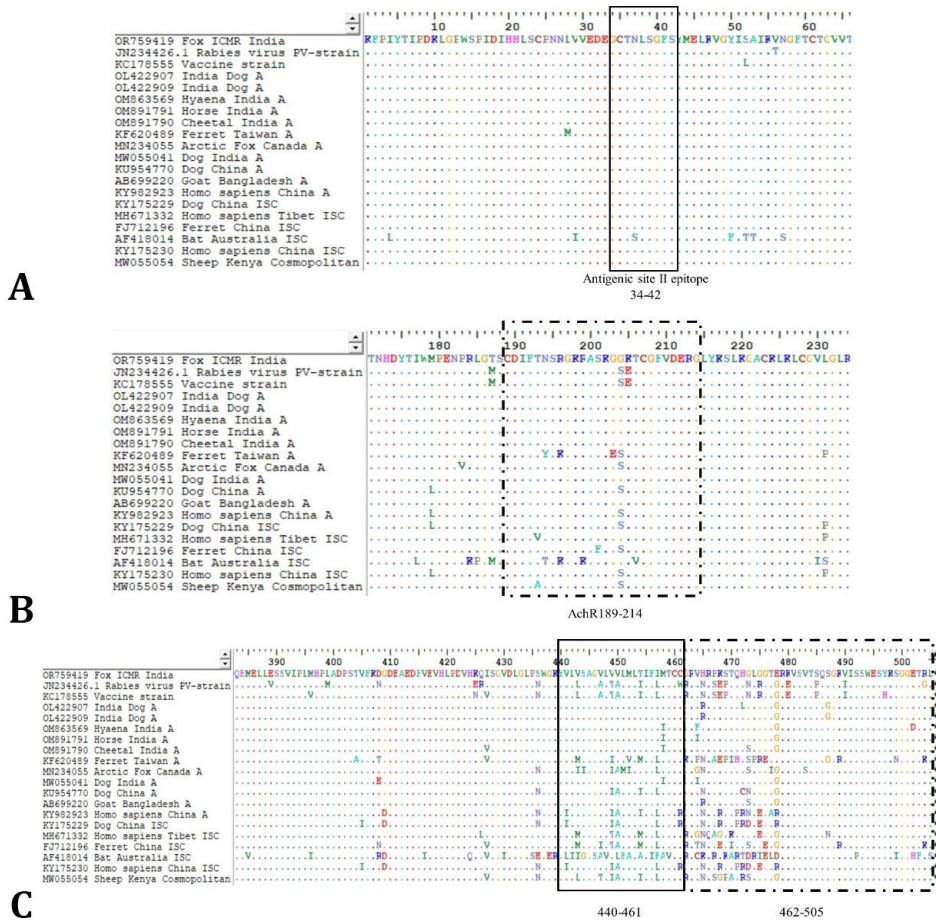


**Fig. 5.** Alignment of amino acid sequences of *nucleoprotein* gene of different street rabies isolates retrieved from NCBI of arctic-like (A), Indian sub-continent (ISC), and cosmopolitan lineages along with the rabies strain from fox sample of the present study (OR759419). **A)** Amino acid sequences of antigenic sites I and IV 358 - 387 and 404 - 418, respectively; **B)** Amino acid sequences of antigenic site III 358 - 387, revealing variations.

**Glycoprotein gene.** The *G* gene of the rabies *Lyssavirus* encoded for 524 amino acids. It contains antigenic sites I, II, and III. Similar to the *N* gene analysis, *G* gene amino acid analysis between RABV of different lineages and hosts disclosed highly conserved regions and variations in the antigenic sites. The Figure 6 shows the comparison of the amino acid sequences of the *G* gene. The predominant antigenic sites or epitopes of *G* gene include amino acids at positions 33, 132, 147, 198, 330, and 333. No variations in the amino acid sequence were detected at these positions between the RABV isolates of India and different hosts. Variations were recorded at the amino acid position 204, where glycine was found in RABV of the fox sample and serine was found in strains of different hosts and regions. This variation was detected in the region between 189 - 214, which coded for the acetylcholine receptor (AchR). Further, amino acid variations were observed at eight positions between 440 - 461 and 15 variations between 462 - 505 amino acid region. These two regions corresponded to the transmembrane domain and endodomain of the *G* protein of *Lyssavirus*.

**Discussion**

To the best of our knowledge, this was the first report of RABV detected in wild foxes in India. Previously, Madhusudana *et al.* reported a case of human rabies infection caused due to a bite from a rabid fox.<sup>12</sup> The RABV was obtained from the human brain sample and partial sequencing of the *N* gene was done; however, the lineage characterization was not performed. Various studies have reported that the arctic/arctic-like lineage of the RABV was the most predominant lineage circulating in India along with cosmopolitan and sub-continent lineages.<sup>3,8,13</sup> In the present study, the dominance and spread of the arctic lineage RABV strain in wild animals in the southern parts of India were determined. The whole genome analysis provided concrete data required for accurate strain identification, diagnosis validation, and tracking of the evolution pattern of the virus by phylogeny construction. The prevalence of the same RABV genotype (genotype I) throughout India and occurrence of a single predominant lineage suggested a constant viral gene flow between state boundaries with little diversification. It has



**Fig. 6.** Alignment of amino acid sequences of glycoprotein gene of different rabies isolates retrieved from NCBI of arctic-like (A), Indian sub-continent (ISC), and cosmopolitan lineages along with isolate from fox sample (OR759419). **A)** Sequences of antigenic sites II, highlighting the epitope 34 - 42; **B)** Sequences of acetylcholine receptor (AchR) site 189 - 214; **C)** Sequences of transmembrane domain of glycoprotein 440 - 461 and endodomain 462 - 505.

been previously reported that dogs are considered to be the reservoir of the arctic-like lineage RABV strain in India.<sup>12</sup> Further, the present study report provided additional evidence that wild animals preserved RABV strains pertaining to an arctic-like lineage.

The RABV strain from the fox sample was found to be closely associated with the rabies strains of humans, ferrets, and cattle belonging to different countries, like Tibet, Taiwan, and China. This indicated that the same strain of rabies was circulating in India and the neighboring countries. The phylogenetic tree also revealed that the arctic-like lineage and genotype I were the predominant type of rabies lineage circulating in India. There are a few earlier reports on the prevalence of the sub-continent and cosmopolitan lineages of RABV in India.<sup>3,14</sup> The reports of the previous studies on the spread of the RABV across domestic and wild animals underline the significance of genomic monitoring across multiple hosts and geographical regions.

*Nucleoprotein* gene has been confirmed to contain variable regions that differentiate the RABV into lineages.<sup>15</sup> The phylogenetic tree with *N* gene sequences formed two separate clusters; namely RABV strains of dogs from India formed a separate cluster and the RABV of wild animals formed a separate cluster, denoting the presence of variations between domestic and wild strains. Hence, further research into rabies cases is necessary due to the unrestricted mobility of domestic animals and a shortage of a physical barrier separating wild animals and household animal interaction points, particularly in the context of the rise in rabies transmission by wild animals in wild-domestic interface areas.

The *N* is an integral component of the viral genome that is significantly produced in the host upon RABV infection. The amino acid variations in the *N* gene sequence would cause a direct effect on the pathogenicity of the RABV. Upon analysis, few variations were identified in the *N* gene, but predominantly remained conserved between the isolates. The region between 298 - 352 is regarded as a transcription initiation site and considered to be highly conserved.<sup>16</sup> In this study, a conserved pattern of variation was observed between the RABV, where the isolates of Indian origin were found to possess glycine at amino acid position 332; whereas, isolates of different geographical locations showed alanine at the same position irrespective of the lineage. This variation might denote the evolution of the *Lyssavirus* strains to adapt to the conditions in various geographical regions.<sup>17</sup> The change in the amino acid at the antigenic sites I and IV, and immunodominant site (amino acid 404 - 418) might point out a slight variation in the antigenic properties.<sup>18</sup> Most of the studies on the sequence analysis of the *N* region of the RABV disclosed a maximum of conserved amino acid sequences between the isolated RABV with no variations or variation at a minimum number of sites.<sup>17,19</sup>

*Glycoprotein* gene of the RABV coding for the *G* is also determined to be a major part of the RABV genome being involved in functions, like glycosylation and AchR region, and also infers pathogenicity.<sup>20</sup> *Glycoprotein* gene has been regarded as a region of interest to study the evolutionary changes of *Lyssavirus* owing to its high variability. It has been reported that this region tends to encounter a high probability of mutations even with no specific pressure, making it the least conserved region of the RABV genome.<sup>21,22</sup> The first 19 amino acids of the *G* gene are hydrophobic in nature; therefore, during translation, these amino acids are removed and a protein with 505 amino acids is formed. The amino acids at positions 333, 336, and 339 are considered to be crucial among which amino acid at 339 (arginine) is related to the virulence of the virus, which was found to be conserved amongst all the isolates.

The AchR of *G* gene (amino acid 189 - 214) is actively involved in the ability of the virus to interact and sustain in the nerve cells.<sup>23</sup> In this study, only a single variation was observed at the AchR site, denoting no hindrance to the virus functionality in the nerve cells. Carnieli *et al.*<sup>22</sup> also compared *G* gene amino acid sequences between different RABV isolates and reported variations in the trans-membrane domain and endodomain similar to our study. Similarly, Lang *et al.*<sup>20</sup> emphasized the variations in the specific epitopes at the antigenic sites of *G* and reported similar variation at the AchR site as the present study.

In conclusion, this study reflected the predominance of arctic lineages over continental RABV across canine reservoir species throughout India. The analysis of amino acid sequences of *N* and *G* genes revealed variations between RABV strains of different lineages and showed conservation within the isolates of the same geographical locations, too. This study also stressed the need to address the human-wildlife conflict by educating wildlife officials on the benefits of rabies vaccination and the drawbacks of using hunting dogs to capture wildlife animals. These methods would subsequently reduce the spread of the virus from and to a wildlife source. Variations at the antigenic sites may affect the virulence and diagnosis in identifying the strain of RABV, requiring continuous surveillance of RABV genome of different hosts and lineages.

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## Conflict of interest

The authors declare no conflict of interest.

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