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Comparative analysis of Fowl Aviadenovirus 11 genomes from India in the global context

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Abstract

Background: Fowl aviadenovirus D (FAdV-D), particularly FAdV-11, is an important poultry pathogen associated with inclusion body hepatitis and exhibits considerable genomic diversity. Whole-genome analysis can provide greater insight into evolutionary relationships than single-gene analyses.

Methods: Three Indian FAdV-11 whole-genome sequences (OR855393, OR192509, and OR194526) were compared with 84 global FAdV-D whole-genome sequences showing more than 98% nucleotide identity and complete coverage. Additionally, the complete hexon gene sequence of OR194526 was used to identify closely related hexon sequences, including FAdV-2 and a recombinant FAdV-2/11 sequence. Multiple sequence alignment and phylogenetic analyses were performed using MAFFT, with phylogenetic tree visualization and annotation using Phylo.io and iTOL.

Results: The three Indian FAdV-11 genomes clustered closely with FAdV-D strains from Pakistan and Austria. Iranian and Brazilian strains formed a neighboring clade sharing a common ancestral node with the Indian-associated cluster, supported by a high bootstrap value. The phylogenetic pattern indicated relationships among geographically diverse strains collected between approximately 2008 and 2024.

Conclusion: Whole-genome comparative analysis revealed evolutionary relationships between Indian FAdV-11 strains and globally distributed FAdV-D isolates, highlighting genomic relatedness across geographically distant regions. These findings contribute to understanding FAdV-D evolution, dissemination, and genetic diversity and may support future molecular surveillance and epidemiological investigations.

Keywords: Fowl aviadenovirus D, FAdV-11, whole-genome sequencing, comparative genomics

1. Introduction

Fowl aviadenoviruses (FAdVs) are non-enveloped, double-stranded DNA viruses belonging to the genus *Aviadenovirus* within the family *Adenoviridae*. They are important pathogens of poultry and have been associated with a range of clinical conditions, particularly inclusion body hepatitis (IBH), hepatitis-hydropericardium syndrome (HHS), and, in some cases, respiratory and enteric diseases. Based on molecular and phylogenetic characteristics, FAdVs are currently classified into five species, FAdV-A to FAdV-E, comprising several serotypes (Islam *et al.*, 2026) [5]. Among these, Fowl aviadenovirus D (FAdV-D), corresponds to serotypes FAdV-2, 3, 9 and 11. FAdV-11 is of particular interest because of its considerable genetic variability and its association with IBH in chickens (Chavan *et al.*, 2023; Karnam *et al.*, 2026) [1, 6].

The FAdV genome is a linear, double-stranded DNA molecule of approximately 43-45 kb and contains several conserved and variable genomic regions. Although the overall genome organization is relatively conserved, substantial genetic variation occurs among FAdV-D isolates (Islam *et al.*, 2026) [5]. The hexon gene, particularly its hypervariable regions, has traditionally been used for molecular classification because the hexon protein is the major capsid protein and contains important antigenic determinants (Franzo *et al.*, 2023, Schachner *et al.*, 2019) [4, 10]. However, analyses based solely on partial hexon sequences may not fully represent the genomic relationships among isolates. Other regions, including the fiber genes, penton base, and several non-structural genes, also contribute to genetic differentiation and

may provide additional information about the evolutionary history of FAdV-D. Genomic diversity in FAdV-D can arise through the accumulation of nucleotide substitutions, insertions and deletions and recombination processes involving different genomic regions. Recombination is particularly important in adenoviruses, as it can generate genomes containing distinct evolutionary histories in different regions (Schachner *et al.*, 2019) [10]. Consequently, isolates showing close relationships based on one gene may exhibit greater divergence when their complete genomes are compared. Whole-genome sequencing and comparative genomic analyses therefore provide a more comprehensive approach for understanding FAdV-D evolution than single-gene analysis alone.

The study of FAdV-D genomic diversity is important for understanding virus evolution, epidemiology, geographic dissemination, host adaptation, pathogenicity, and vaccine effectiveness. Characterizing the genetic relationships between contemporary field isolates and previously reported strains can also help identify emerging lineages and conserved genomic regions that may be useful for diagnostic, epidemiological, and vaccine-development purposes. Therefore, comprehensive genomic characterization of the Indian FAdV-D, especially FAdV11 strains from India, is essential for elucidating their evolutionary dynamics and for improving surveillance and control strategies in poultry populations.

Materials and Methods

Data set and sequence retrieval

The sequence of three Indian whole genome sequences of FAdV-11 (OR855393, OR192509 and OR194526) were used to retrieve 84 FAdV-D global whole genome sequences with more than 98% nucleotide identity from GenBank Nucleotide collection. The complete hexon gene coding sequence of OR194526 FAdV-11 strain of India was used to retrieve 59 complete hexon gene sequences with more than 98% nucleotide identity and three FAdV2 complete hexon sequences and one recombinant sequence FAdV2/11 hexon sequence from GenBank nucleotide collection.

Sequence alignment and phylogenetic analysis

Sequence alignment and phylogenetic analysis were performed with online Multiple sequence alignment based on fast Fourier transform (MAFFT) online server

(<https://mafft.cbrc.jp/alignment/server/>) (Kato *et al.*, 2019) [7]. Multiple sequence alignment were performed using Fast Fourier Transform and Neighbor-Joining with two progressive alignment steps (FFT-NS-2) strategy. The phylogenetic trees were constructed using the Jukes-Cantor substitution model with 1,000 bootstrap replicates to assess the reliability of the inferred tree topology.

Phylogenetic tree visualization

The tree was visualized using *Phylo.io* (<https://phylo.io/viewer/>) (Robinson *et al.*, 2016) [9] and the phylogenetic tree was further annotated using iTOL (iTOL: Interactive Tree of Life (<https://itol.embl.de/>) (Letunic *et al.*, 2024) [8]. The minimum spanning tree visualization was rendered using GrapeTree visualization program (https://achtman-lab.github.io/GrapeTree/MSTree_holder.html) (Zhou *et al.*, 2018) [12].

Results

Whole genome based phylogenetic analysis

Whole genome based phylogenetic analysis of the three Indian FAdV-11 near complete whole genome sequences (OR855393 - 43,832 bp, OR192509 - 43,631 bp and OR194526 - 43,443 bp) with 84 FAdV-D global whole genome sequences (ranging from 43,026 bp to 45,193 bp), with more than 98% nucleotide identity and 100% coverage with Indian whole genome sequences, revealed the clustering of the three Indian strains with one Pakistan and one Austrian strain (clade with yellow background in Fig 1). Interestingly, a clade with two strains, one each from Iran and Brazil, shared a common ancestral node with the clade containing the Indian strains revealing a potential shared ancestor with a high bootstrap value. Among these 7 whole genome sequences, the Austrian strain was the earliest to be collected from the field in 2008, followed the Pakistan and Iran strains in 2018, followed by the Indian strains in 2021 and 2022, and then the Brazil strain in 2024. A strain from UK (MK572874 - 685 CORR), in the same super clade, one node up from the clade containing the Indian and Iranian strains, is the earliest to be collected from the field approximately in the 1950s to 1960s. The same super clade also has genomes from Ivory coast and Lebanon, in West Africa and West Asia, respectively, both reported collected in 2013.

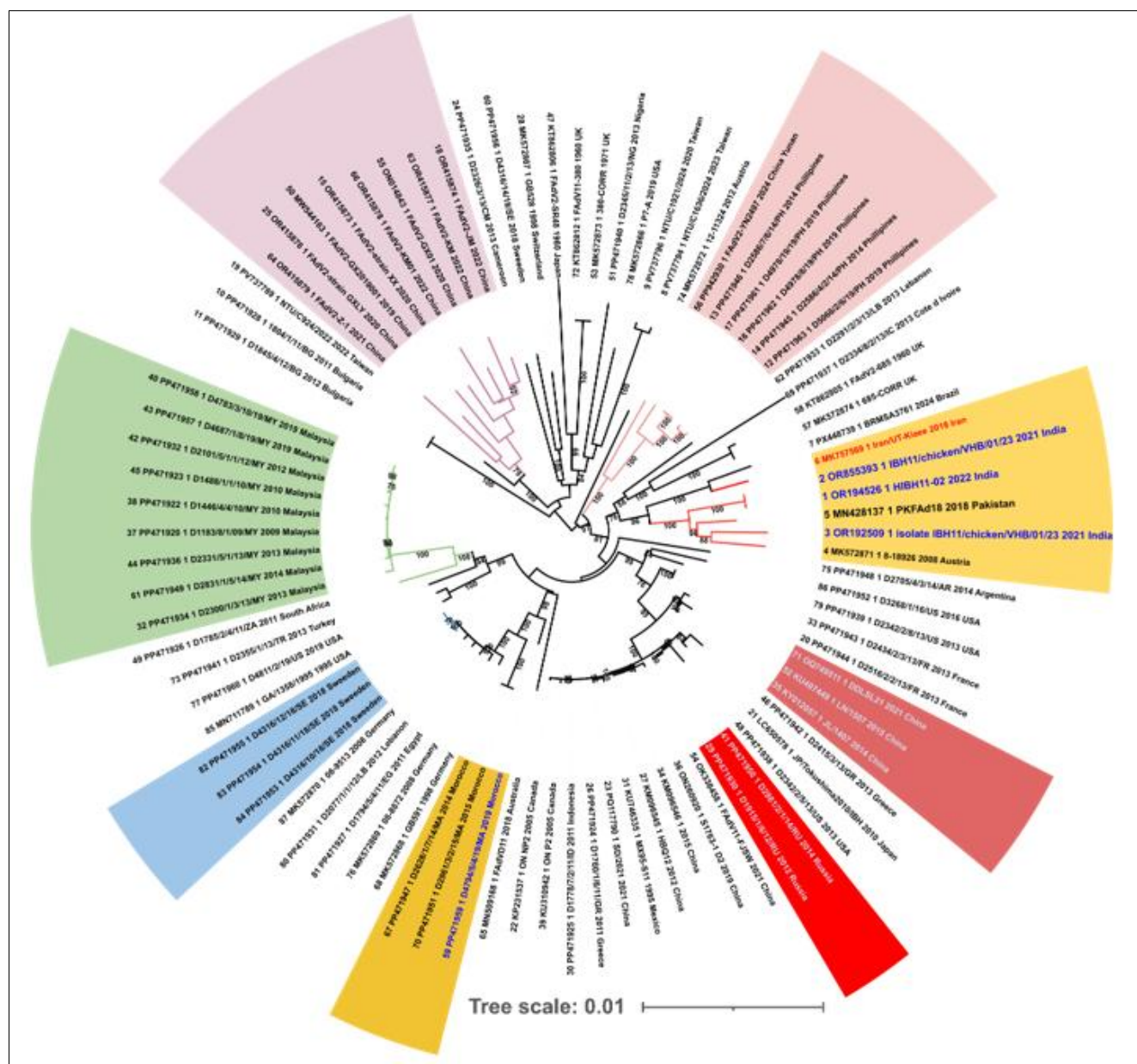


Fig 1: Phylogenetic analysis of 87 global whole genome sequences of FAdV-D with more than 98% nucleotide identity, including three Indian FAdV11 whole genome sequences; OR855393, OR192509 and OR194526. GenBank accession number, strain id, year of collection and location are mentioned for each sequence at the tips of the tree. Bootstrap values of the nodes are indicated.

In general the whole genomes were separated into two major clades, one approximately ranging from 10 o' clock to 1 o' clock in the circular phylogenetic tree in Fig.1. The other sequences were separated at four nodes, ranging from approximately 1 o' clock to 10 o' clock in the circular phylogenetic tree in Fig.1. The first node separated out only the MK572872 (Austria, 2012) from the other genomes. The second node separated out six genomes from Phillipines one from Yunan, China. The third node separated out the clade

with strains from the Indian subcontinent and Iran. The fourth node, with the most number of sequences, split into two more sub clades. On a general note, sequences from the same or contiguous geographical region were often found to cluster together in all clades (indicated with same colour backgrounds in the tree in Fig 1), even if collected at different time from the field.

Genetic distance - Minimum spanning tree

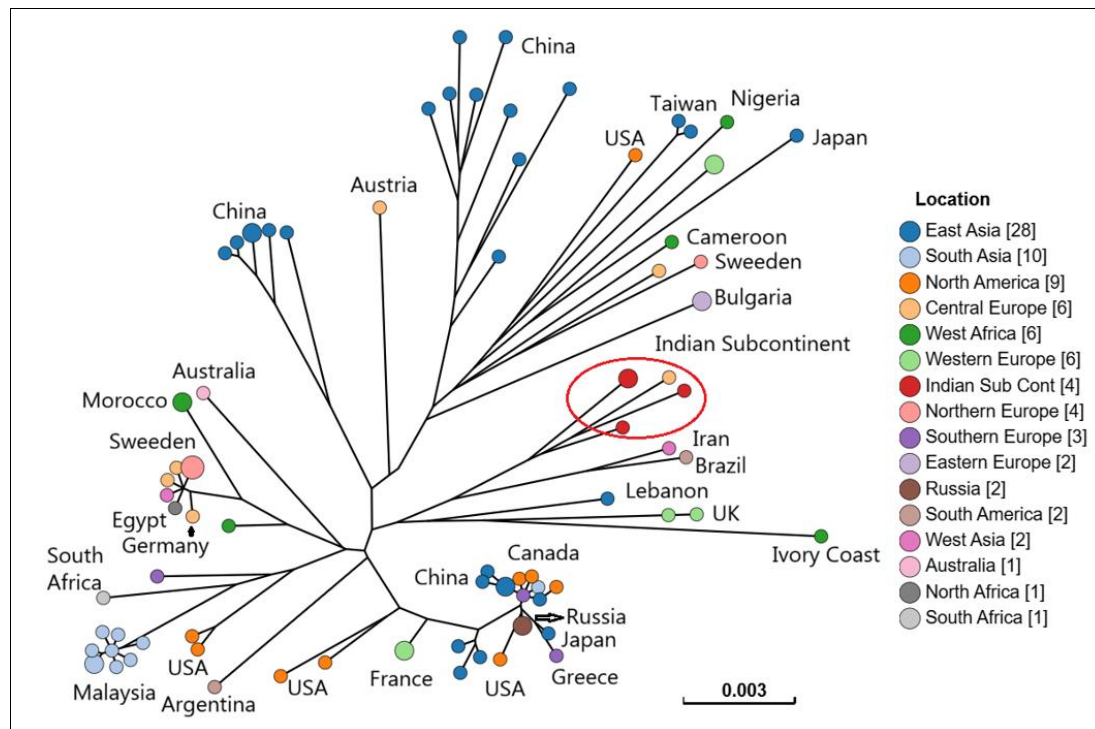


Fig 2: Minimum spanning tree indicating the genetic distance between 86 global whole genome sequences of FAdV-D with more than 98% nucleotide identity, including the cluster with three Indian FAdV11 whole genome sequences and one sequence from Pakistan (circled in red).

The unrooted minimum spanning tree reveals that multiple strains from Indian subcontinent, China and Malaysia cluster together and are genetically distant from other strains. Especially, the three Indian and one Pakistan whole genome sequences, grouped together, are genetically distant from other sequences in their clade. However, sequences from North American countries of Canada and the USA and from European countries of UK, France, Germany and Austria are

found across different clades. Interestingly, the sequences in the clade in the bottom right of the minimum spanning tree (Fig 2) are genetically close and are reported from geographically contiguous countries in the northern hemisphere, viz., Russia, Japan, China, Canada and the USA.

Phylogenetic analysis of Indian and global complete hexon gene sequences

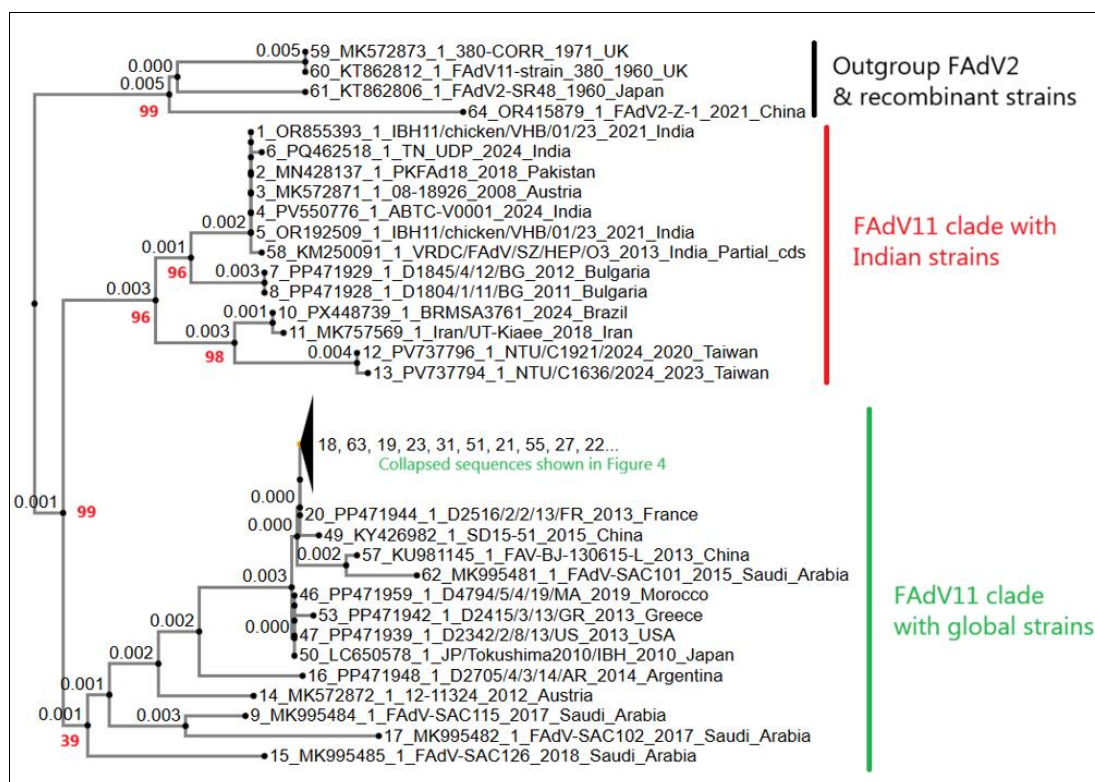


Fig 3: Phylogenetic analysis of 60 complete hexon gene sequences of FAdV11, 3 FAdV2 and one recombinant FAdV2/11 sequence. GenBank accession number, strain id, year of collection and location are mentioned for each sequence at the tips of the tree. Bootstrap values are indicated in red near the nodes and the branch length (genetic distance) is given along the edges.

The phylogenetic analysis of complete hexon sequences of five Indian strains, one Pakistan strain with 54 other global complete hexon sequences of FAdV-11 and 4 FAdV-2 related out group sequences revealed two major clades among the FAdV-11 (Fig 3) with a bootstrap value of 99. All the five Indian sequences and one Pakistan sequence are clustered together within one clade, along with an Austrian sequence. In addition, one strain each from Iran, Brazil, two each from Bulgaria and Taiwan, totaling thirteen sequences along with the above mentioned clade clustered within one super clade node higher-up to the clade containing the Indian strains. The Austrian strain was the earliest to be collected from the field in 2008 within the Indian sub clade, while all other sequences were collected ranging from 2011 to 2024.

The other FAdV-11 strains were further separated into many sub clades in the analysis but with poor bootstrap support of 39 (Fig 3). Three Saudi Arabian sequences with the exception of one sequence MK995481, also from Saudi Arabia, clustered together within this major clade. 34 sequences from diverse geographical regions around the world were almost identical and the tree was collapsed for ease of depiction (Fig 3).

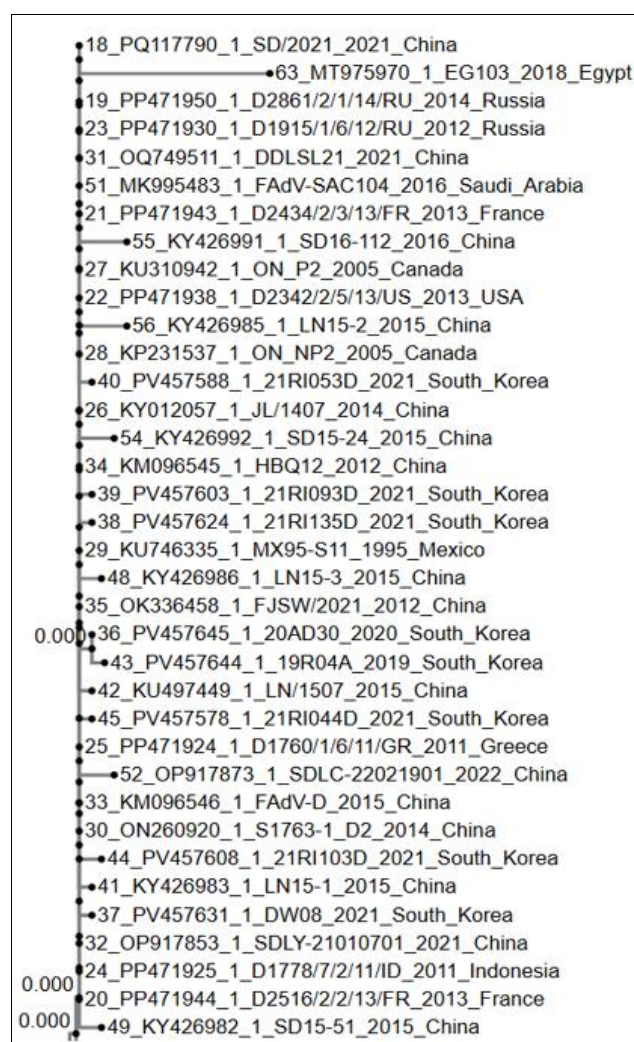


Fig 4: Collapsed sequences (n=34) from the clade with global FAdV11 strains indicated in Fig 3.

The collapsed sequences are depicted in Fig 4 revealing almost identical sequences, indicated by the branch length (genetic distance) (Fig 4), except for a few sequences and notably one Egyptian sequence (M_T 975970; 2018) with additional base changes. Twenty four of the sequences were

from the contiguous area of China, South Korea and Japan

Discussion

The presence and diversity of the FAdV-D in India and its association with IBH has been characterized in India and neighboring Pakistan based on the partial hexon gene sequences (Chavan *et al.*, 2024, Chitradevi *et al.*, 2021, Wang *et al.*, 2020) [2, 3, 11]. In this study the whole genome sequences and complete hexon gene sequences of FAdV-D from India were compared with global FAdV-D sequences. The phylogenetic tree depicting 87 whole genome sequences of FAdV (Fig 1) revealed clear clustering of the strains from the Indian subcontinent and one strain from neighboring Iran being closely related. Interestingly, the whole genome sequence of one strain from Austria (MK572871; 2008) clustered within the sub clade with the three Indian and Pakistani sequences. The same trend was also observed with the phylogenetic analysis based only on the complete hexon genes (Fig 3), which also revealed the clustering of all the five Indian sequences and one Pakistani sequence in one sub clade with the same Austrian strain. Owing to the high genetic similarity at the whole genome sequence level, this could probably indicate a significant transmission event from Europe, directly or indirectly linked to the Austrian strain, and warrants further investigation. Phylogenetic analysis at both the whole genome level and the complete hexon gene sequence level (which has more sequences in the databases), indicates that the FAdV-11 strains in Indian subcontinent are genetically distinct in comparison with most of the global FAdV-11 strains and also relatively homogenous in comparison to other global strains. Franzo *et al.*, 2023 [4], estimated the mutation rate of the FAdV-Ds in general at 1.55×10^{-3} substitutions/site/year based on the comparison of the complete hexon gene sequences available from around the world. However, the estimate is bound to be on the higher side since the hexon gene encodes the protein which is a major neutralizing immune response eliciting target and is under higher selection pressure compared to other segments of the genome of FAdV-D. The study also suggests the clustering of sequences from the Indian subcontinent and a potential spread from Europe to India in the 2000's (Franzo *et al.*, 2023) [4], corroborating the trend observed in this study with the whole genome sequences. The current study indicates that vaccine strain selection for use in India should be ideally from an Indian isolate due to the variations in the hexon gene. Further, regular surveillance of FAdV-D in India is also warranted to understand the molecular epidemiology of the FAdV-D strains implicated in the pathogenesis of IBH in chickens.

Conflict of Interest

The authors declare no conflict of interest commercial or otherwise.

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