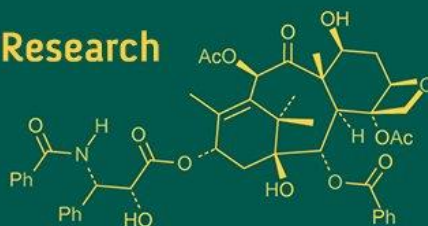
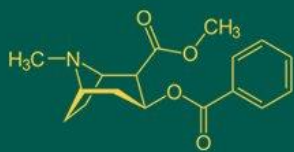


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Genomic conservation of the transforming growth factor-beta (TGF-β) gene in Fowlpox virus isolated from field outbreaks in India

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Abstract

Fowlpox virus (FWPV) is a slow-spreading viral pathogen of poultry. The genetic diversity of FWPV influences virus-host interactions, resulting in varied severity of the disease. The viral transforming growth factor-beta (TGF-β) homologue is considered a putative immunomodulatory gene; however, its genetic characterisation among Indian FWPV remains limited. In the present study, scab/tissue samples collected from FWPV-affected chickens and turkeys with varied clinical severity from different states of India during 2006-2025 were investigated. Sequence analysis revealed high conservation of the TGF-β gene among FWPV field viruses circulating in India. Phylogenetic analysis placed Indian FWPV within subclade A1, with distribution across multiple subclusters. Selection-pressure analysis revealed no significant positively or negatively selected sites on the deduced amino acid sequences of TGF-β in Indian FWPV field strains, indicating an overall conserved evolutionary pattern. These findings highlight the genetic stability and evolutionary pattern of the FWPV TGF-β gene among Indian field viruses causing varied clinical severity in backyard poultry over the past two decades.

Keywords: Fowlpox virus, backyard poultry, TGF-β gene, genetic characterization, phylogenetic analysis

Introduction

Fowlpox virus (FWPV) is one of the largest and most complex DNA viruses, belonging to the genus *Avipoxvirus*, subfamily *Chordopoxvirinae*, and family *Poxviridae*,^[1, 2] having a significant economic impact on the poultry industry. It affects a wide range of domestic and wild birds, resulting in production loss, morbidity, and mortality in the affected flocks. Clinically, FWPV manifests in two forms: cutaneous and diphtheritic. The cutaneous (dry pox) form is characterised by fibroproliferative nodular lesions on non-feathered areas of the body, including beak, face, and eyelids, leading to blindness, decreased productivity and low to moderate mortality. However, the diphtheritic/wet pox exhibits fibro-necrotic proliferative lesions that develop in the upper respiratory and gastrointestinal tracts, often resulting in high mortality due to asphyxia^[3]. The transmission of the virus primarily occurs through direct contact with contaminated wounds, infected aerosols, and mechanical arthropod vectors, including mosquitoes (*Culex* and *Aedes*) and mites (*Dermanyssus gallinae*)^[4, 5]. Structurally, the virus is covered with a lipid envelope, measuring approximately 330 × 280 × 200 nm, with a centrally located electron-dense core with two lateral bodies^[6]. Its genome comprises a single linear double-stranded DNA of approximately 288 kbp, comprising a central region encoding around 250 putative genes, flanked by two identical inverted terminal repeats (ITRs) of approximately 9.5 kb^[5, 6].

Inside the host, viral replication occurs in a discrete cytoplasmic site (viroplasm) of the affected cell. However, the virus can be propagated experimentally *in-ovo* via embryonated chicken eggs and *ex-vivo* using avian-origin cell lines and/or primary cell cultures like chicken embryo fibroblasts, producing distinct cytopathic effects (CPE) of rounding, aggregation and detachment within 4-6 days post-infection^[7].

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For prevention and control of FWPV, attenuated vaccines of cell culture or chicken embryo origin are used [5, 8]. Despite regular vaccination, several outbreaks have been reported even in vaccinated flocks, which pose a great threat to the poultry industry.

These recurrent outbreaks and the increased severity of the FWPV infection are reported to be enhanced by the insertion of a retrovirus into its genome; however, the exact mechanism is still under investigation [9-11]. The pathogenicity and host adaptation of FWPV are influenced by multiple viral genes involved in immune modulation, host range and virus-host interactions. Comparative genomic studies have identified around 40 putative proteins associated with virulence, geographic variation and disease manifestations. Among these, ORFs 124 and 168 have been implicated in virulence, whereas several genes encode proteins that are involved in modulation of host immunity, including natural killer cell receptor homologues, CC chemokines, G-protein-coupled receptors, β -nerve growth factor, interleukin-18-binding protein, semaphorin, serine protease inhibitors (serpins), and transforming growth factor-beta (TGF- β) [12].

The FWPV TGF- β gene is the first-ever viral homologue of the eukaryotic TGF- β gene encoded by FWPV ORF080 on the reverse strand. The whole FWPV TGF- β polypeptide has 363 amino acids, of which 112 amino acids are similar to those of eukaryotic TGF- β , together with the Prosit signature PS00250 motif and conserved cysteine residues (Afonso *et al.*, 2000) [6]. The TGF- β gene facilitates growth and differentiation of connective tissue, wound healing, and suppresses proliferation of most other cell types [13]. In addition, it exhibits various immunomodulatory functions, including inhibition of both cellular and humoral immune responses, particularly cytotoxic activity of T lymphocytes, natural killer (NK) cells, and lymphokine-activated killer cells, as well as production of lymphokines (IL-1, IL-6, TNF, and IL-2), and polyclonal antibodies [13], may compromise host immune defences, thereby increasing susceptibility to infections [6].

Amongst more than 270 species of avipoxviruses reported so far, TGF- β homologues have been noted in FWPV, Pigeonpox, Penguinpox and Canarypox viruses. Only one TGF- β homologue has been reported in FWPV, Pigeonpox and Penguinpox viruses. In contrast, Canarypox viruses contain five TGF- β homologues, which are considered paralogues of FWPV based on their low amino acid sequence identity (<28%), distinct genomic locations, and phylogenetic analysis suggesting variation in the TGF- β gene among Avipoxviruses [14, 15]. Genetic variation in these viral immunomodulatory genes may influence virus-host

interactions and contribute to viral adaptation, which may affect disease severity. However, the presence and conservation of this gene among Indian FWPV and its evolutionary pattern are still less explored. Therefore, genetic characterization and phylogenetic analysis of the TGF- β gene may provide valuable insights into its evolutionary conservation and genetic diversity among Indian FWPV strains.

Materials and Methods

Sample collection and processing

A total of 40 pooled scab/tissue samples from 15 outbreaks were collected from FWPV-affected chickens and turkeys and included in the current study. The samples were collected from Odisha, West Bengal, Gujarat, Jammu and Kashmir, and Meghalaya during 2006-2025 and comprised specimens from recent outbreaks ($n = 20$) and archived samples ($n = 20$) maintained at the laboratory. The samples were processed to make 10% (w/v) tissue homogenates in sterile phosphate-buffered saline (PBS; pH 7.4). The resulting tissue suspensions were clarified by centrifugation at 6000 x g for 10 min, and the clarified supernatants were used for downstream investigations.

Extraction of genomic DNA

Genomic DNA was extracted from the tissue supernatant using the DNeasy Blood & Tissue kit (QIAGEN, Germany) as per the manufacturer's instructions. The purity and concentration of extracted DNA samples were measured using the Nanodrop microvolume spectrophotometer.

Molecular detection of FWPV P4b and TGF- β gene

Initially, the presence of FWPV in the collected samples was confirmed by polymerase chain reaction (PCR) targeting the conserved P4b gene using previously published primers. [16] Samples positive for FWPV were subsequently screened for the presence of the viral TGF- β gene homologue using primers previously reported by Kim *et al.* (2022) (Table 1).

Standard PCR reactions were performed in a final volume of 25 μ L, containing 12.5 μ L of 2 $\times$ Sapphire Amp Fast PCR Master Mix (Takara, Japan), 1 μ L each of forward and reverse primers (10 pmol/ μ L), 3 μ L of DNA template, and 7.5 μ L of nuclease-free water. PCR amplification was carried out in a thermal cycler using the following conditions: initial denaturation at 94°C for 3 min, followed by 30 cycles of denaturation at 94°C for 40 sec, annealing at 52°C for 30 sec for the P4b gene and 57°C for 30 sec for the TGF- β gene, and extension at 72°C for 1 min. A final extension was performed at 72°C for 5 min.

Table 1: Primer pairs used for amplification of FWPV P4b and TGF- β gene

Sl.	Gene	Primer sequence (5'-3')	Amplicon (bp)
1	P4b (Core protein)	Forward: CAGCAGGTGCTAAACAACAA Reverse: CGGTAGCTTAAACGCCGAATA	578
2	TGF- β (ORF80)	Forward: TCTCACCGTCTATGAGGTT Reverse: ATGCGTCAAGCGTTAAATGGT	1274

Generation of nucleotide sequences of the FWPV TGF- β gene: Nucleotide sequence data of the TGF- β gene for 18 Indian FWPV, representing 15 outbreaks in backyard poultry over the past two decades, were generated from purified amplicons through bidirectional Sanger's dideoxy

sequencing. The resulting chromatograms were analysed for confirmation of the quality of the reads. The raw sequences obtained from forward and reverse reads were assembled using EditSeq (DNA Star) and further confirmed by BLASTN.

Phylogenetic and sequence analyses of the TGF- β gene

Phylogenetic analysis was performed to investigate the evolutionary relationships and genetic diversity of Indian FWPV based on the TGF- β gene. Published nucleotide sequences of Indian and global FWPV isolates, along with representative avipoxviruses, retrieved from the National Centre for Biotechnology Information (NCBI) database, were included for comparative analysis. Multiple sequence alignment of TGF- β gene sequences was performed using the ClustalW algorithm in MEGA version 12. The aligned sequences were used to construct a phylogenetic tree using the Maximum Likelihood method with the best-fit nucleotide substitution model (Tamura 3). The reliability of the inferred phylogenetic relationships was assessed using 1,000 bootstrap replicates. Nucleotide and deduced amino acid sequence analyses of the TGF- β gene were performed using Meg Align software.

Selection pressure analysis

Selection pressure analysis was performed using SLAC (Single-Likelihood Ancestor Counting), FEL (Fixed Effects Likelihood) and MEME (Mixed Effects Model of Evolution) methods implemented in the HyPhy framework through the Datamonkey web server to identify codon sites within the TGF- β gene showing evidence of purifying and episodic diversifying selection.

Results: Investigation of outbreaks

FWPV infection was evident in both vaccinated and unvaccinated birds in the backyard poultry. The affected birds presented cutaneous pox lesions with varied severity (Fig 1). Characteristic lesions were found on the beak, comb, eyelids and, in a few cases, on shanks. Mortality in birds was noted; however, there was no presentation of diphtheric lesions in the carcasses.



Fig 1: Birds exhibiting cutaneous nodules with varying severity (a: mild, b: severe)

Detection of FWPV P4b and TGF- β genes

Out of 40 tissue samples screened, 32 were found positive for the presence of the FWPV P4b gene in conventional PCR. An amplicon of 578 bp was visible in all the positive

cases (Fig 2). The P4b-positive samples were also positive for the TGF- β gene, as evident by the presence of 1274 bp amplicons in an agarose gel electrophoresis (Fig 3).

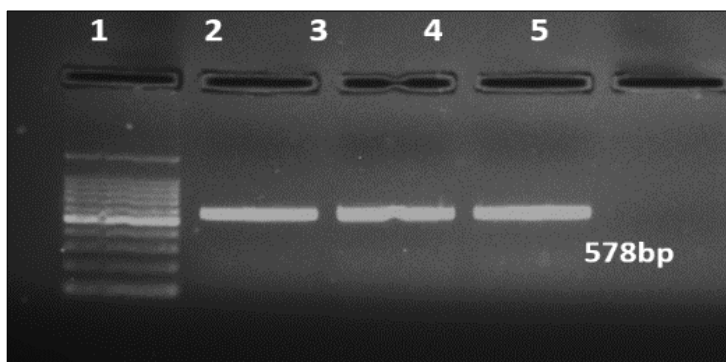


Fig 2: PCR amplification of FWPV P4b gene, L1-100 bp ladder, L2-L4- Positive sample, L5-Negative control.

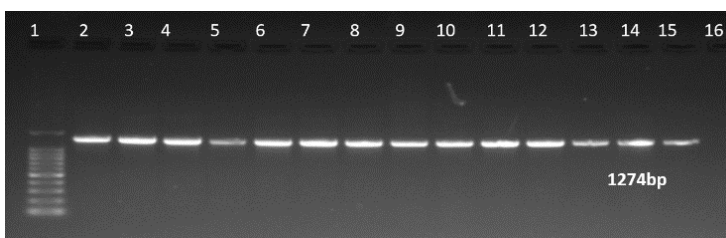


Fig 3: PCR amplification of FWPV TGF- β gene, L1:100 BP DNA ladder, L2-L15: Positive samples, L16: non-template control.

Nucleotide and amino acid sequence analysis

Nucleotide sequences of the partial TGF- β gene were generated and assembled to obtain an in-frame truncated

(upstream) form of the TGF- β polypeptide. The GenBank accession numbers of the corresponding coding sequences are presented in Table 2.

Table 2: GenBank accession numbers of the corresponding coding sequences of TGF- β gene

Sl.	Sample ID	Place of origin	Year	GenBank Accession No.
1.	FWPV96/JK/06/IND	Jammu and Kashmir	2006	PZ467411
2.	FWPV97/WB/09/IND	West Bengal	2009	PZ467410
3.	FWPV94/GUJ/09/IND	Gujarat	2009	PZ467412
4.	TKPV98/MGL/12/IND	Meghalaya	2012	PZ799011
5.	FWPV59/WB/14/IND	West Bengal	2014	PZ467415
6.	FWPV57/WB/14/IND	West Bengal	2014	PZ467416
7.	FWPV11/WB/20/IND	West Bengal	2020	PZ467418
8.	FWPV74/WB/20/IND	West Bengal	2020	PZ467413
9.	FWPV72/WB/20/IND	West Bengal	2020	PZ467414
10.	FWPV22/WB/22/IND	West Bengal	2022	PZ467417
11.	TKPV19/WB/22/IND	West Bengal	2022	PZ799012
12.	FWPV2/OD/23/IND	Odisha	2023	PZ467420
13.	FWPV3/OD/24/IND	Odisha	2024	PZ467419
14.	FWPV104/OD/24/IND	Odisha	2024	PZ467421
15.	FWPV106/OD/24/IND	Odisha	2024	PZ467422
16.	FWPV112/OD/24/IND	Odisha	2024	PZ467423
17.	FWPV118/OD/25/IND	Odisha	2025	PZ467424
18.	FWPV119/WB/25/IND	West Bengal	2025	PZ806810

The alternate in-frame coding sequence of the truncated TGF- β gene was found to be 993 nucleotides long, coding for a 331-amino-acid polypeptide. Sequence analysis reported a high degree of conservation of the TGF- β gene among the investigated FWPV. Nucleotide sequence identity among the FWPV isolates from the present study ranged from 99.6-100%, while the corresponding deduced amino acid identity ranged from 98.5-99.7%. Comparison of the Indian FWPV sequences with global FWPV sequences revealed nucleotide identities of 98.9 to 100% and amino acid identities of 97.6-99.7%. In contrast, comparison with other avipoxviruses showed broader sequence divergence, with nucleotide identity ranging from 82.1-99.8% and deduced amino acid identity ranging from 73.1-99.1%. Despite high conservation, the deduced amino acid sequence analysis revealed multiple amino acid substitutions among the FWPV characterised in the present study. An isoleucine-to-methionine substitution (I213M) was observed in three viruses (FWPV 2/OD/23/IND, FWPV96/JK/05/IND, FWPV97/WB/09/IND). In contrast, six Indian FWPV (FWPV3/OD/24/IND, FWPV57/WB/ 14/IND, FWPV59/WB/14/IND, FWPV72/WB/ 20/IND, FWPV94/GUJ/09/IND, FWPV118/OD/25/IND) exhibited an isoleucine-to-threonine (I213T) substitution, a non-conservative amino acid change. Furthermore, five viruses (FWPV 2/OD/23/IND, FWPV3/ OD/24/IND, FWPV96/JK/05/IND, FWPV94/GUJ/09/IND, and FWPV112/OD/24/IND) showed a tyrosine-to-histidine (Y116H) substitution. Additionally, threonine (T) to asparagine (N) substitution at T134N and T152N, replacing a small, polar amino acid with a larger, amide-containing polar amino acid, was observed in four viruses (FWPV57/WB/14/IND, FWPV59/WB/ 14/IND, FWPV72/WB/20/IND and FWPV97/WB/09/IND).

Phylogenetic analysis

The TGF- β gene-based phylogenetic analysis showed that all FWPV and TKPV clustered within subclade A1. The FWPV were further resolved into six subclusters (A1.1-A1.6), with viruses from the present study grouping within subclusters A1.1, A1.2, A1.4, and A1.6. The global viruses that clustered with Indian FWPV strains were mostly of Asian origin. In contrast, other avipoxvirus species,

including Pigeonpox virus, Flamingo pox virus, and Penguin pox virus, clustered within subclade A2 (Fig 4).

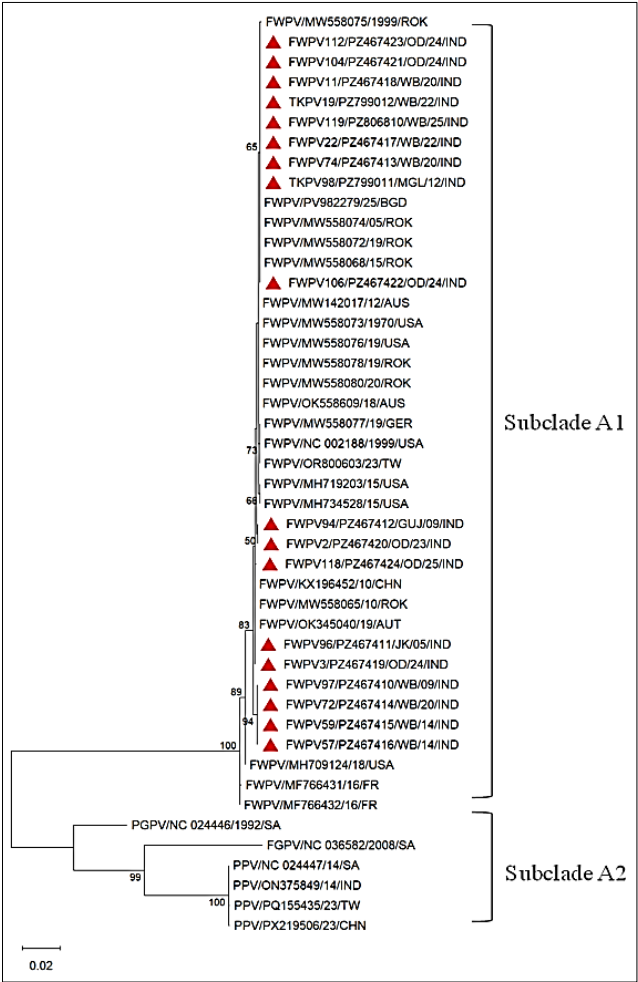


Fig 4: Phylogenetic tree of the TGF- β gene constructed using the Tamura 3-parameter model with invariant sites.

Selection pressure analysis

Selection-pressure analysis revealed an overall conserved evolutionary pattern in the FWPV TGF- β gene. When Indian FWPV sequences were analysed alone, SLAC, FEL and MEME did not identify any statistically significant selection sites. Nevertheless, analysis incorporating global

reference FWPV sequences revealed limited site-specific selection. FEL identified codon 32 ($p = 0.0836$) as a candidate site under purifying selection and codon 213 ($p = 0.0748$) as a candidate site under diversifying selection ($p \leq 0.1$). MEME independently identified codon 213 as a candidate site for episodic diversifying selection ($p = 0.098$). In contrast, SLAC did not detect any significant selection sites.

Discussion

Fowlpox is an economically important viral disease of poultry, widely distributed in tropical and subtropical countries, including India. The disease can occur in cutaneous, diphtheritic, or mixed forms, with the cutaneous form being the most commonly recognised clinical presentation. In the present study, the majority of affected birds exhibited characteristic cutaneous pox lesions. The pathogenicity and disease outcome of FWPV are influenced by multiple factors, including viral genetic determinants, virus–host interactions, and host immune responses. Among the viral genes potentially involved in immune modulation, the TGF- β homologue has been proposed to cause modulation of host immune responses and may play a role in viral persistence and immune evasion [6, 13]. Therefore, the present study was undertaken to characterise the genetic variation of the TGF- β gene among FWPV field samples, with particular emphasis on nucleotide and deduced amino acid variation, phylogenetic relationships, and evolutionary dynamics. In the present study, all 32 FWPV-positive tissue samples yielded the TGF- β gene amplicon, consistent with the other finding [12]. To the best of our knowledge, it is the first-ever study on the TGF- β -coding gene in FWPV reported from India. The gene was analysed by sequencing to assess its genetic stability and diversity, as it encodes a viral immunomodulatory factor involved in evasion of host immune responses. Nucleotide substitution analysis revealed a higher frequency of transitions than transversions, a pattern commonly exhibited by DNA viruses. The TGF- β protein exhibited both conservative (I213M) and non-conservative (I213T, Y116H) amino acid substitutions, which may reflect natural genetic variation without compromising protein function. Nevertheless, functional studies are required to determine whether these amino acid changes can influence viral replication and antigenicity. Kim *et al.* (2022) [12]. Reported a deletion of a valine residue at position 51 of the TGF- β protein of FWPV isolates associated with the diphtheritic form of FWPV. In contrast, no such deletion was observed in the present study, which may suggest the predominance of the cutaneous form of the disease among the observed cases.

Phylogenetic analysis based on the TGF- β gene placed the FWPV isolates within subclade A1, consistent with their close evolutionary relationship. The distribution of the Indian isolates among different subclusters within A1 indicates the presence of limited genetic diversification despite the overall high conservation of the gene. Such variation may reflect the accumulation of minor nucleotide and amino acid substitutions during the evolutionary process. The clustering of our Indian FWPV with viruses reported from other Asian countries may reflect their close genetic relatedness and suggest the circulation of related viral lineages across Asia.

The absence of detectable selection signals in the Indian-FWPV dataset is consistent with the high sequence

conservation observed among the Indian FWPV TGF- β sequences. In contrast, incorporation of genetically diverse global FWPV sequences increased the evolutionary variation and detected of selection sites. The identification of codon 213 by both FEL and MEME is of particular interest and can be interpreted as evidence of the site for episodic diversification across the global FWPV rather than only Indian FWPV.

Conclusion

In conclusion, the present study reported a high degree of conservation in the FWPV TGF- β gene among Indian FWPV, with limited nucleotide and amino acid variation. Phylogenetic analysis placed the Indian viruses within subclade A1, with distribution across multiple subclusters. Selection-pressure analysis of the Indian isolates did not identify any significant positively or negatively selected sites, indicating an overall conserved evolutionary pattern. Overall, these findings provide baseline information on the genetic and evolutionary stability of the TGF- β gene in Indian Fowlpox virus, which may indicate the conservation of its immunomodulatory potential across the FWPV circulating in India.

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