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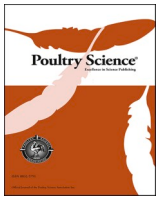

Full-Length Article

Epidemiology, genetic diversity and evolution of pigeon circovirus

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ABSTRACT

With the global prevalence of pigeon racing, pigeon infections with Pigeon circovirus (PiCV) have been reported across the world. PiCV-infected pigeons are susceptible to subsequent infections and exhibit a range of symptoms including weight loss, lethargy, anorexia, respiratory distress and diarrhea, which exerts a huge impact on the pigeon industry. However, there is currently a lack of epidemiological data on PiCV infection in pigeons. Therefore, the aim of this study was to gain a comprehensive understanding of the prevalence, genetic variations, and evolutionary dynamics of PiCV within pigeon populations. In this study, we collected 28 samples from four cities in China to assess the prevalence of PiCV. The results showed that the positive rate was 92.86%, which indicated that PiCV was widespread in Chinese pigeon flocks. Meanwhile, whole genome sequences of PiCV were obtained for partial positive samples. The results showed that there were 12 different clades of PiCV, and the samples collected in this study have been classified as types 1, 4, 6, and 11. The results of the PiCV genome analysis indicate a high incidence of recombination events. Further analysis of the encoded Cap protein at the gene and protein level revealed a high degree of variation in the Cap protein. The amino acids at positions 30-120 of the Cap protein exhibited the greatest frequency of variation. Meanwhile, we found that amino acid sequences 140-180 were relatively conserved, which was related to the immunogenicity of the circovirus Cap protein. The results of the antigenicity analysis demonstrated that amino acid sequences 140-180 exhibited strong antigenicity, indicating the potential of cap to serve as a candidate protein in the production of a PiCV vaccine. The present study provided epidemiological information on PiCV, which promises to facilitate the development of effective control measures to prevent its transmission.

Introduction

Pigeon circovirus (PiCV) belongs to the genus Circovirus of the family Circoviridae and is a non-enveloped virus with a genome consisting of single-stranded circular DNA of 1.7 to 2.5 kilobases (kb). The complete genome of PiCV was first cloned and sequenced in 2000 and consists of two open reading frames (ORF C1 and ORF V1). The ORF V1 encodes a replication-associated protein (Rep) of 318 amino acids. The ORF C1 encodes a capsid protein (Cap) of 274 amino acids (Todd et al., 2008; Zhang et al., 2015; Rosario et al., 2017; Silva et al., 2022; Wang et al., 2022). The sequence T/nA (G/t) TATTAC has been identified as a specific motif located at the top of a potential stem-loop structure between the Rep and Cap open reading frames. This structure may be related to the replication of the circovirus genome (Silva et al., 2022).

The first case of PiCV infection was reported in the United States in 1993. Subsequently, cases of infection were documented in various countries and regions, including Northern Ireland, Germany, Italy, France, Czech Republic, Belgium, Poland, Slovenia, Hungary, United Arab Emirates, Iran, China, Japan, USA, Brazil and Australia (Shabani et al., 2024; Xiaobo et al., 2024). PiCV is associated with Young Pigeon Disease Syndrome (YPDS), which includes a range of symptoms including reduced racing performance, weight loss, lethargy, anorexia, respiratory distress and diarrhea, and has had a significant impact on the pigeon industry (Woods et al., 1994).

The first documented cases of PiCV infection in China were reported in 2009. Subsequent reports indicated the emergence of PiCV in Fujian and other eastern regions between 2011 and 2017 (Yu et al., 2009). In recent years, PiCV has become increasingly prevalent among meat

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pigeons in eastern and southern China (Xiaobo et al., 2024). In addition, the prevalence of PiCV in pigeon flocks in northern China has increased significantly (Wang et al., 2022). In the present study, samples from pigeon farms in GanSu, Shanxi, Xinjiang, Hebei and other provinces were collected for detection of PiCV. The whole genome sequence of PiCV was then determined and its genomic characteristics were analyzed to elucidate the prevalence and biological features of PiCV. This study provided a comprehensive foundation for the prevention and control of PiCV.

Materials and methods

Sample collection

liver and respiratory tract samples were collected from suspected PiCV-positive pigeons from a number of pigeon farms, located in the Xinjiang, Gansu, HeBei, and Shanxi in China during 2023.

DNA extraction

Viral DNA was extracted from pigeon liver and respiratory samples using a viral DNA kit (DP304-03, TIANGEN, Beijing) according to the manufacturer's instructions (Chen et al.,2022), and the whole viral genome was amplified by PCR using primer pairs designed from the PiCV genome sequence obtained from GenBank (Table 1). All PCR products were purified using the DNA Gel Extraction Kit (TransGen Biotech, China) and ligated into the TA/Blunt Zero cloning vector (TransGen Biotech, China). At least three positive clones were randomly selected from each case and sequenced by Shanghai Sangon Biotechnology Co.

Geographical and temporal distribution of pigeon circovirus

The whole genome sequences of all PiCV strains available in GenBank were downloaded, and the accumulated partial sequence data were organized according to temporal and geographic variables. A geographical distribution map was then generated using ArcMap 10.8 (Esri, USA).

Phylogenetic analysis

A total of 419 genome sequences were used in this study. The whole genome sequence of PiCV obtained in this study was used for phylogenetic analysis. All PiCV sequence data from China and other regions of the world were extracted from the NCBI nucleotide database as reference sequences (N). Maximum likelihood phylogenetic trees were constructed with the GTR+G+I model by using the MEGA 7.0 software, with partial deletion to handle alignment gaps and 1,000 bootstrap iterations (Edgar 2004). The cladogram was generated and annotated using the Interactive Tree of Life (iTOL) software (https://itol.embl.de/).

The genome sequences were aligned at the nucleotide level, whereas the cap protein-coding sequences were aligned at the amino acid level, with manual adjustments.

Table 1
Primers used in this study.

Name	Sequences (5′-3′)	Fragment length
PiCV Capsid-F	TTGAAAGGTTTTCAGCCTGGC	325 bp
PiCV Capsid-R	AGGAGACGAAGGACACGCCTC	
PiCV-AV-F	TCGCGCGAGASTTCAGTGARAT	2037 bp
PiCV-AV-R	CYTCSGYCATTGCTCTTCCGGCTTTC	
Pi-GAPDH-F	AATGCTATCACCATCTTCCA	347 bp
Pi-GAPDH-R	AACTCAGAATCCATCCAACA	

Recombination analysis

Full genome sequences were analyzed separately to detect recombination events using RDP4 (Martin et al., 2015). A total of seven methods implemented in RDP4 were used including RDP (Martin & Rybicki 2000), GENECONV (Padidam et al., 1999), 3Seq (Boni et al., 2007), Chimaera (Gibbs et al., 2000), SiScan (Gibbs et al., 2000), MaxChi (Smith., 1992), and LARD. Recombination detected by at least three of the seven methods with a P-value cutoff of 0.01 was considered to be true recombination (Sabir et al., 2016). The recombinant sequences were removed, and the procedure was repeated until no more recombination events were detected. The SimPlot tool was used to detect interlineage recombination (Kolb et al., 2017). To visualize these recombination events, alignments of the whole genome were generated, and iTOL (https://itol.embl.de/) was used to infer partitioning networks.

Results

Clinical lesions and results of viral genome sequencing

A thorough examination of the diseased pigeons revealed that some exhibited a yellowish-brown liver accompanied by ascites, while others demonstrated severe fibrotic atrophy of the lungs (Fig. 1). This phenomenon may be attributed to the presence of secondary infections in the affected pigeons.

The high-throughput sequencing results revealed the presence of multiple pathogenic microorganisms in the sick pigeons, including pigeon circovirus, pigeon influenza virus and various bacteria (Fig. 2).

A total of nine whole genome sequences were obtained and deposited in GenBank, with the corresponding accession numbers listed in Table 2. These nine whole genome sequences ranged in length from 2034 nt to 2057 nt, while the cap genes ranged in length from 531 to 825 nt and the rep genes ranged in length from 948 to 954 nt.

Analysis of the geographical distribution of pigeon circovirus

Based on the geographical and temporal distribution of pigeon circovirus (PiCV), it was observed that since 2000, the frequency of PiCV detections and uploads has increased progressively year by year. PiCV was widely reported in 2014, 2018, 2020 and 2021, mainly from China in 2014 and 2018, from Poland in 2020 and from the USA in 2021. The United States and China are identified as the countries with the highest number of PiCV detections and uploads (Fig. 3). PiCV was first reported in Zhejiang province in China in 2009, followed by subsequent reports in Guangdong, Anhui, Fujian, Jiangsu, and Beijing (Fig. 3). The results show that following the first report of PiCV infection in China, the highest number of PiCV infections was reported in 2014, 2018 and 2021,

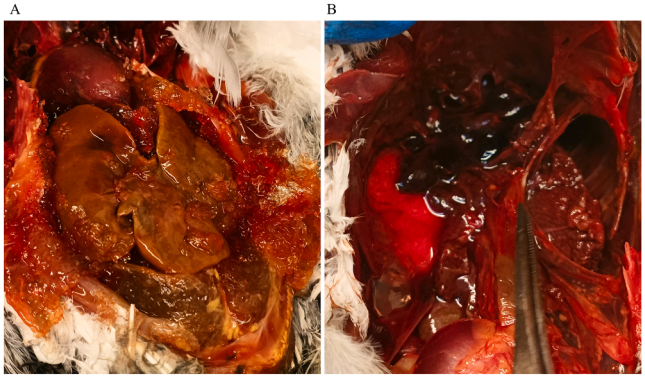

Fig. 1. Lung and liver lesions in sick pigeons (A) Liver appears yellowish brown (B) Lung atrophy.

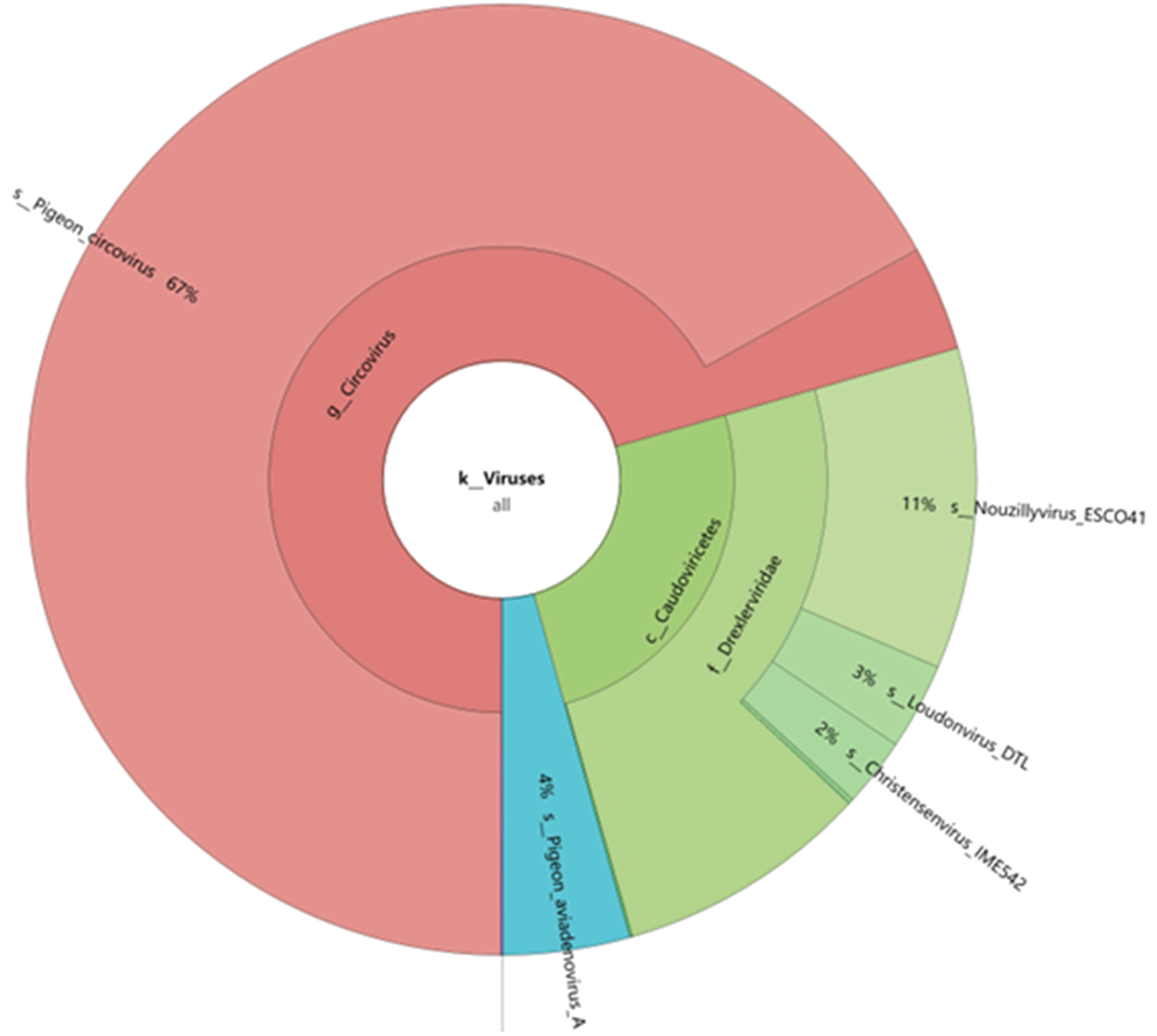

Fig. 2. The proportion of species identified in the sample. High-throughput sequencing of diseased material showed 67% pigeon circovirus and 4% pigeon adenovirus type A in diseased material.

Table 2
Information on PiCV isolates.

GenBank	Name	Isolate	Time
OR611917	GS-DN2023 (PiCV-1-1)	Gansu	2023
PP405066	GS-DN2023-1-3 (PiCV-1-3)	ShanXi	2023
PP405067	HB-DN2023-3-3 (PiCV-3-3)	HeBei	2023
PP405068	HB-DN2023-4-1 (PiCV-4-1)	HeBei	2023
PP405069	DN2023-5-2 (PiCV-5-2)	XinJiang	2023
PP405070	SX-DN2023-6-1 (PiCV-6-1)	ShanXi	2023
PP405071	SX-DN2023-6-2 (PiCV-6-2)	ShanXi	2023
PP504907	4-2 (PiCV-4-2)	HeBei	2023
PP504908	5-4 (PiCV-5-4)	XinJiang	2023

mainly in Guangdong, Shaanxi, Beijing and other places in China.

Phylogenetic analysis

The genetic evolution tree was constructed using the whole genome sequence of PiCV downloaded from NCBI and the whole genome sequence of PiCV obtained from our isolation. The phylogenetic tree was used to classify PiCV into 12 clades (Fig. 4). Furthermore, the geographical distribution data indicated that the predominant strains in China were mainly PiCV 1,4,6,7 and 9, PiCV 10 and 12 in the USA, PiCV 5,10 and 11 in Poland, and PiCV 2,3 and 6 in New Zealand. Our samples belonged to type 1, type 4, type 6 and type 11. We found that type 1 and 2 are in the same branch, type 3, 4, 5, and 6 are in the same branch, type 7 is in a separate branch, and type 8, 9, 10, 11, and 12 are in the same branch. In addition, the genome sequence information of PiCV published in China contains almost all the major strains of each country, which may be related to the introduction of pigeons or international pigeon racing competitions (Xiaobo et al. 2024).

Recombination analysis

Recombination analysis of the whole genomes of 419 PiCV and other PiCV reference strains was performed using the RDP software. This

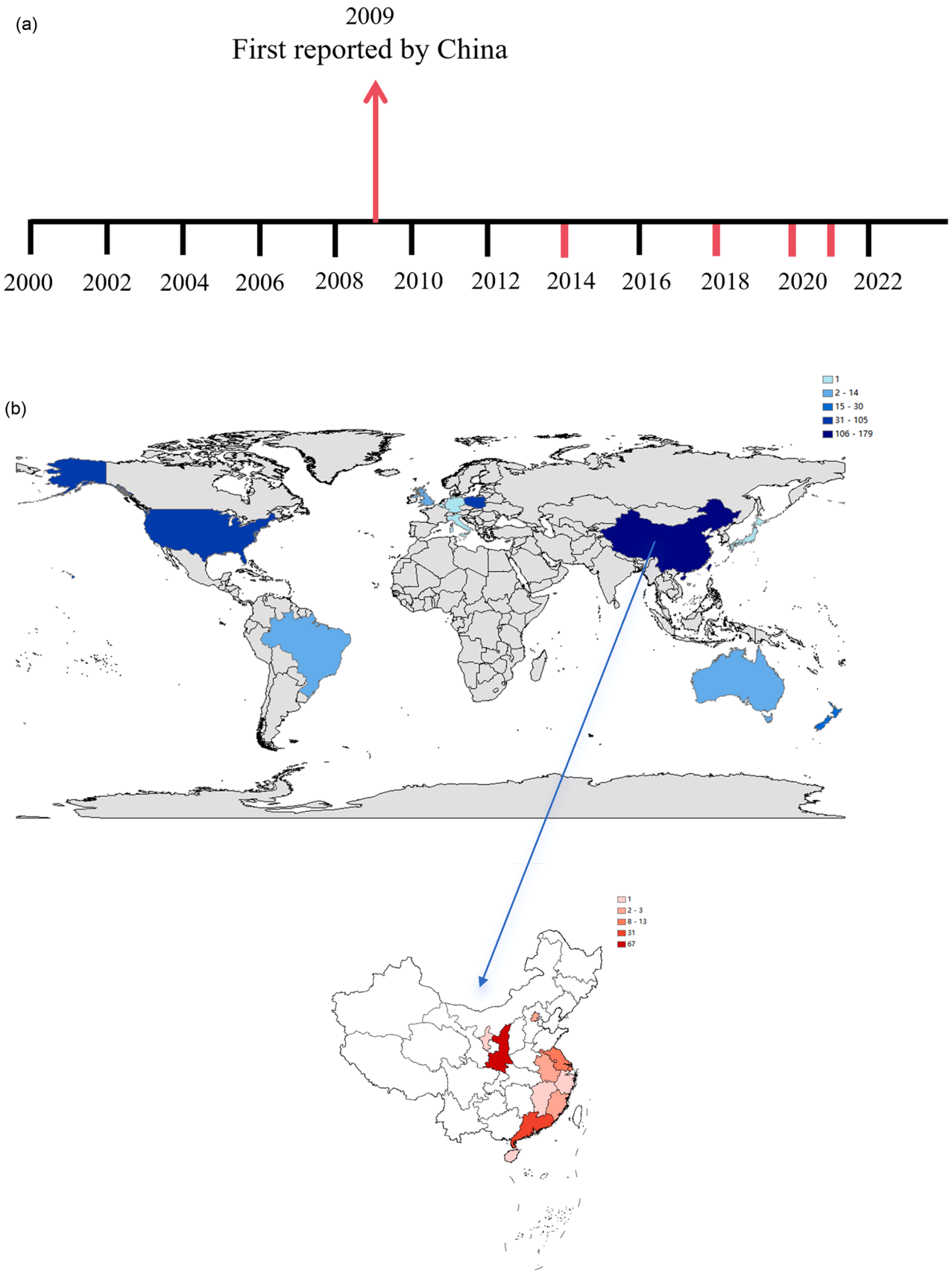

Fig. 3. Pigeon circovirus epidemic timeline and Geographical distribution (A) PiCV has been reported by NCBI since 2000. First reported in China in 2009. (B) Global distribution of pigeon circovirus and distribution of pigeon circovirus in China.

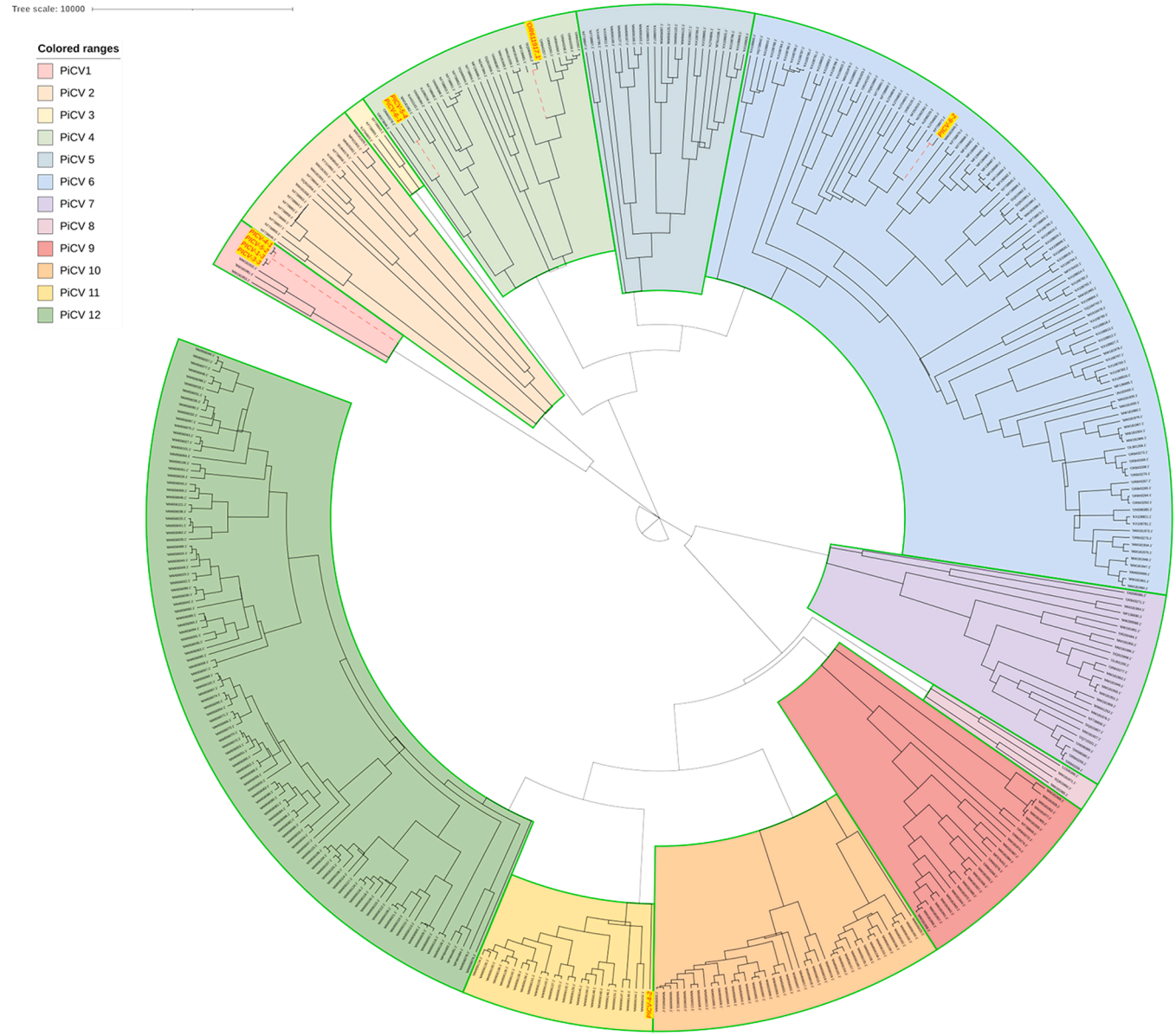

Fig. 4. Pigeon circovirus genome-wide phylogenetic tree. Phylogenetic tree based on genomic comparisons with NCBI-published PiCV in the study. Phylogenetic relationships were calculated using the model with the lowest Bayesian Information Criterion score, which was considered to best describe the substitution pattern. The hosts of the PiCV isolates analyzed in this study were pigeons.

analysis revealed that a total of 169 recombination events existed in PiCV. Five recombinant strains of PiCV isolates from our isolates fulfilled all the algorithmic criteria and were identified as PiCV-4-2 (Fig. 5A), PiCV-4-1 (Fig. 5D), PiCV-3-3 (Fig. 5B), PiCV-6-1 (Fig. 5C), and PiCV-5-2 (Fig. 5E). These strains were found to be recombinants of PiCV-5-4 and PiCV-6-2 (n=1). The results showed that PiCV-6-1 and PiCV-5-2 (n=2), MW656128 and PiCV-4-1 (n=3), PiCV-1-3 and PiCV-5-2 (n=4), and PiCV-1-3 and PiCV-3-3 (n=5) were involved in recombination events. The recombination events included recombination of Gansu and Hebei strains, recombination of Gansu and Xinjiang strains, and recombination of Xinjiang and Shaanxi strains. In addition, the recombination events included recombination within type 1, recombination between type 1 and 4, recombination between type 1 and 11, and recombination between type 4 and 6. This suggests that anthropogenic and natural factors within China promote the occurrence of different types of PiCV recombination. It was observed that PiCV had a high frequency of recombination, suggesting that recombination plays a important role in the ability of the virus to adapt to changing environmental conditions and its interaction with the host.

Analysis of cap protein gene and antigenicity

The cap protein, which serves as the capsid protein of the circovirus and is a key immune antigen, exhibits high mutability, which facilitates the ability of the circovirus to adapt to its external environment. This property may also be associated with its ability to evade immune responses. Analysis of the dataset and whole genome sequences revealed frequent mutations in the genes encoding Cap proteins (Feng et al., 2023). To gain further insight, we downloaded and compared all published PiCV Cap protein amino acid sequences from NCBI. The results showed that the interval between positions 30-120 had the highest frequency of amino acid mutations or deletions in Cap proteins (Fig. 6A). However, at positions 140-180, we observed relative conservation in the amino acid sequence, which correlates with the immunogenicity of the circovirus Cap protein. We therefore selected this region for antigenicity analysis. The results showed that this specific segment is highly

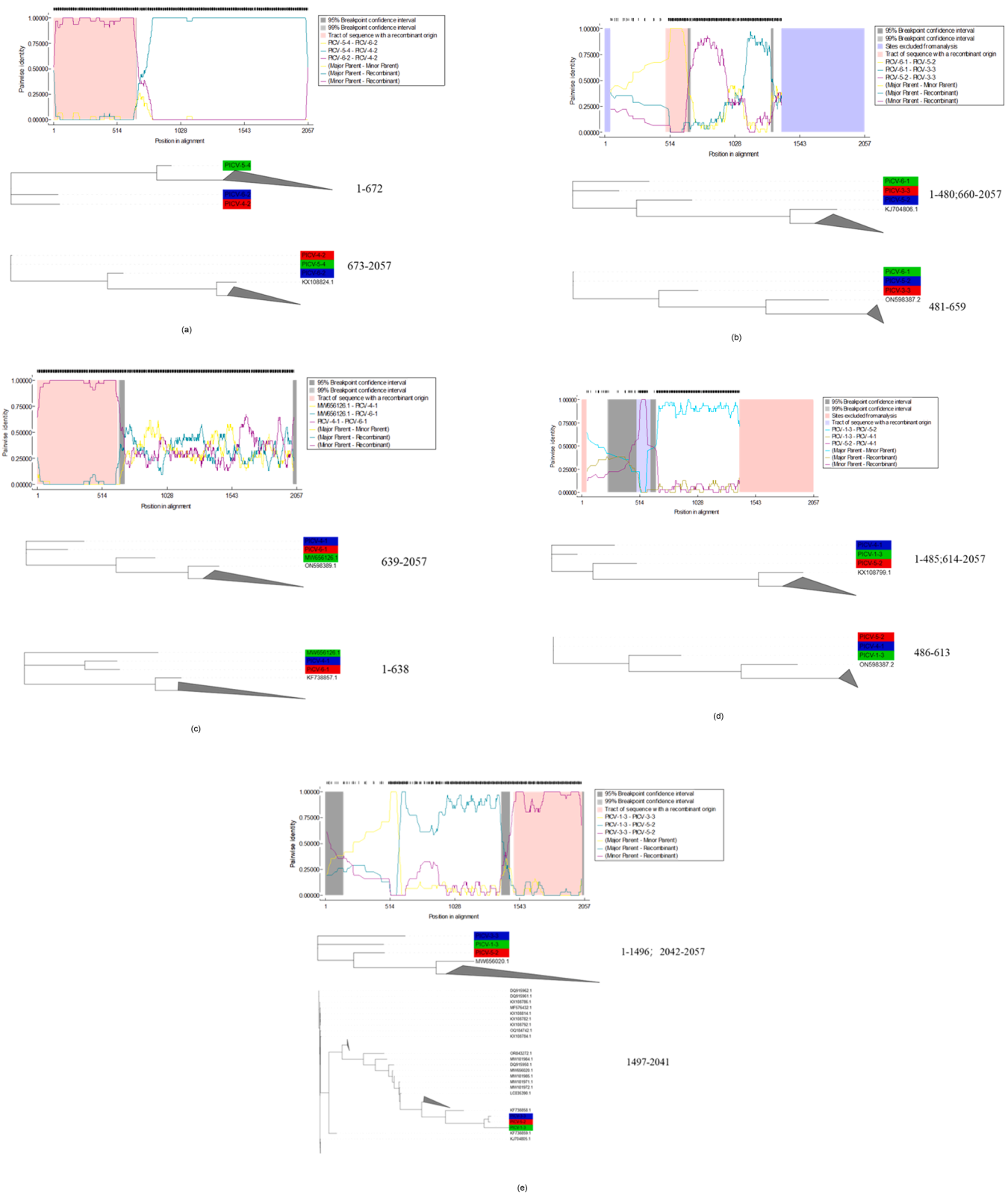

Fig. 5. Recombination characterization of the PiCV phylogeny. (A-E) Recombination scale structure of the PiCV genome and guided scan recombination analysis based on variable genomic sites. (A) Recombinants of PiCV-5-4 and PiCV-6-2, breakpoint at nucleotide 672. (B) Recombinants of PiCV-6-1 and PiCV-5-2 (n=2), breakpoints at nucleotides 480 and 659. (C) Recombinants of MW656128 and PiCV-4-1 (n=3), breakpoint at nucleotide 638. (D) Recombinants of PiCV-1-3 and PiCV-5-2 (n=4), breakpoints at nucleotides 485, 613. (E) Recombinants of PiCV-1-3 and PiCV-3-3 (n=5), breakpoints at nucleotides 1496,2041. ML phylogenetic tree inferred for different recombination regions, which using a general time reversible model that accounts for rate heterogeneity between sites. A total of 1,000 bootstraps were evaluated to assess support values.

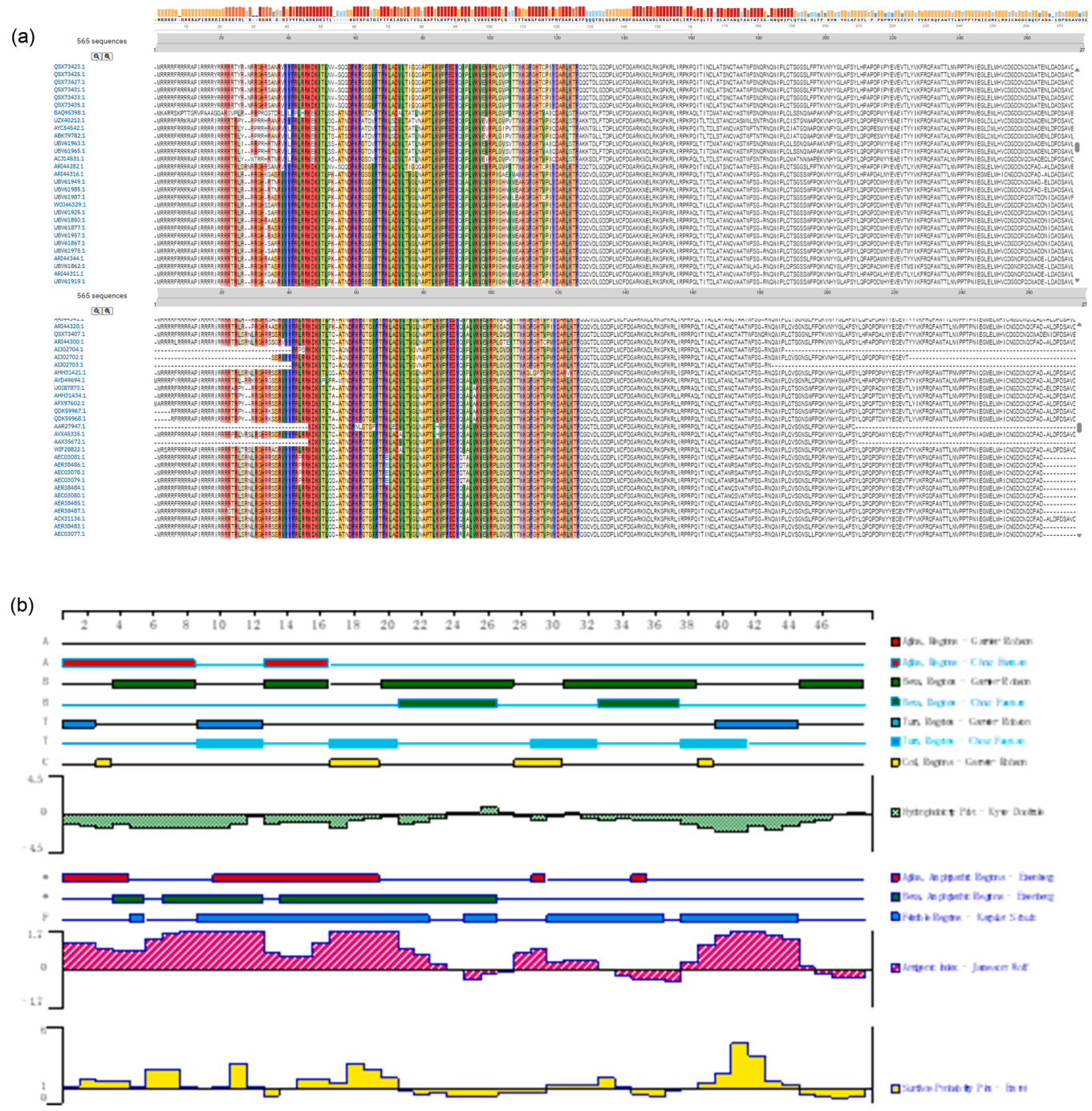

Fig. 6. Bioinformatic analysis of cap proteins (A) Amino acid differences in pigeon circovirus cap proteins (B) Antigenicity analysis of conserved sites in cap proteins.

antigenic and can serve as a potential candidate protein for PiCV vaccine development (Fig. 6B).

Discussion

Infection of pigeons with PiCV is usually asymptomatic, but it leads to different damage in various organs of the body, including the liver, spleen, lungs, trachea and bursa. In addition, PiCV has been shown to cause immunosuppression. It has been shown that PiCV is present in the immune organs of pigeons, leading to a decrease in immunity among young pigeons. As a result, young pigeons are susceptible to secondary infections (Stenzel et al., 2020). PiCV, combined with other pathogens, often causes huge economic losses for pigeon farms.

The regional aggregation of PiCV reports may be attributable to the distinct geographic characteristics of pigeon husbandry. Despite many studies demonstrating a strong association between PiCV and young pigeon syndrome, as well as its detrimental effects on pigeons' immune system resulting in immunosuppression, insufficient emphasis has been placed on proper detection and systematic control of PiCV epidemics. The results of several epidemiologic studies have shown that PiCV is widespread in pigeon flocks in a large number of provinces and cities in China (Woods et al., 1994; Todd et al., 2008). However, there is a lack of systematic reports on PiCV infections and prevalent strains in China and abroad. In this study, samples from pigeon farms in selected areas of China were collected and nine strains of PiCV were detected. The epidemiological survey and statistical data reveal the widespread

distribution of PiCV in China and the United States on a global scale. In China, the prevalence rate is particularly high in the southeastern region. In addition, the virus has been frequently found in Xinjiang, Hebei and other places. With the increase in the number of racing pigeons and broiler pigeons, the number of reported PiCV strains has increased in recent years, indicating that the importance of PiCV has gradually increased. Nonetheless, the presence of PiCV in pigeons has been reported for over three decades. The complexity of culturing PiCV in a laboratory setting poses significant challenges to scientific researchers, thus limiting in-depth study of PiCV and hindering the development of effective prevention and control measures.

Next, we compared the nine PiCV strains isolated in this study with the 419 PiCV sequences published by NCBI. Initially, the sequences of domestic and foreign strains were categorized into 12 clades based on their genetic evolutionary distance. Four genotypes were identified, and a subsequent analysis was conducted to investigate recombination events within these sequences. The analysis revealed a total of 163 recombination events among the 419 sequences, indicating that recombination plays a significant role in influencing the genetic evolution of PiCV (Shabani et al., 2024; Stenzel et al., 2024). Amongst them, five strains (PiCV-4-2, PiCV-4-1, PiCV-5-2, PiCV-3-3, and PiCV-6-1) met all algorithm criteria and exhibited recombination within their respective groups. It is observed that the frequency of recombination events exhibited variation between the strains isolated in this study and other NCBI-published strains.

The most effective means of preventing viral diseases remains vaccination. The Cap protein, which serves as the primary antigenic component of PiCV, can be used as an effective strategy to prevent and control PiCV infections. The major challenge in vaccine development lies in the considerable variability and inherent difficulty associated with prokaryotic expression of the PiCV Cap protein. The N-terminal segment of the PiCV Cap protein has been shown to have a high content of basic amino acids, with sequence characteristics similar to PCV2, GoCV, and PiCV-6-1. The study shows that the 41 amino acids at the N-terminal end of PCV2 ORF2 as a nuclear localization signal (NLS) sequence. Following the excision of this sequence, successful expression of the capsid protein was achieved in Escherichia coli was achieved, with antigenicity comparable to that of the PCV2 virus (Duchatel et al., 2005; Mahzounieh et al., 2014; Stenzel et al., 2020). Johne also reported that when expressing the Cap protein of BFDV in E. coli, the target protein was undetectable. However, efficient expression of the Cap protein was achieved by deleting the N-terminal arginine-rich region and fusing it with a His-Tag (Haddadmarandi et al., 2020), providing novel insights for the development of vaccines targeting the Cap protein of PiCV. In addition, through bioinformatic analysis, we identified amino acids 140-180 within the Cap protein as highly conserved and with strong antigenicity. In summary, these findings suggest that amino acids 140-180 within the Cap protein are promising as potential candidates for PiCV vaccine development.

In conclusion, the Chinese meat pigeon industry is extensive, and with the continuous increase in the number of pigeon farms, there is a corresponding rise in the prevalence of PiCV. This further emphasizes the necessity for veterinarians and pigeon farmers to priorities the implementation of measures to prevent and control PiCV, with a view to effectively mitigating secondary infections caused by PiCV invasion and reducing pigeon mortality rates.

Declaration of competing interest

The authors declare that there are no conflict of interest regarding the publication of this paper.

Acknowledgments

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.psj.2025.104928.

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