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Original Article

Conserved Internal PB2–PB1–PA–NP–M Genes and Divergent HA/NA in Bat Influenza A Viruses H9N2, H17N10, and H18N11

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Abstract

Background: *Bats (Chiroptera) are well-known reservoirs of zoonotic infectious diseases, such as SARS-CoV-2, EBOV, and others, that have caused pandemics and pose challenges to modern society. Bats, being a global species, could pose a threat to human life, domestic animals, agricultural livestock, and wildlife due to environmental spillovers and cross-transmission.*

Methods: *Multiple sequence alignments (MSA) on the nucleotide and protein segment sequences of bat influenza A virus (BIV), including H9N2, H17N10, and H18N11, were performed. Phylogenetic and sequence identity analysis further supported the comparative analysis in the study.*

Results: *The internal gene cassette comprising the polymerase complex (PB2, PB1, PA), nucleoprotein (NP), and matrix protein (MP) demonstrates remarkable conservation across diverse viral lineages. However, the surface glycoproteins, neuraminidase (NA) and hemagglutinin (HA), exhibit high variability.*

Conclusion: *Conserved sequences suggest potential primer designs for detection and serve as targets for long-term vaccines and antivirals, while highly mutated sequences may serve as seasonal targets. Addressing bat-borne diseases is crucial for both human health, environmental sustainability, and animal health, as it helps mitigate the risk of transmission for infectious diseases. However, experimental studies are still needed to pave the way for the clinical use of a possible vaccine target against the bat influenza virus.*

Keywords

Chiroptera, bat influenza A virus (BIV), multiple sequence alignment (MSA), bat-borne virus, H9N2, H17N10, and H18N11, zoonotic transmission, infectious diseases

INTRODUCTION

Chiroptera, or bats, are a well-known reservoir of zoonotic viruses that are and may be harmful to birds, mammals, and humans (Babu et al., 2022). As viral reservoirs, bats facilitate the exchange and mutation of viruses, contributing to the emergence of new pathogenic viruses that threaten both humans and animals (Nabi et al., 2020). Remarkably, bats remain asymptomatic carriers of viruses due to their potent titer of antibodies and effective immunomodulation response to viral infections (Weinberg & Yovel, 2022).

For instance, SARS-CoV-2, the virus responsible for the COVID-19 pandemic, showed 96% genome sequence similarity to bat coronavirus (Zhou et al., 2020). Similarly, the Ebola virus (EBOV), known to cause severe fatal disease that affected most of West Africa, showed high mutation adaptivity on human and bat

cells (Whitfield et al., 2020). Hendra (HeV) and Nipah (NiV) viruses, which are hosted by pteropid and non-pteropid fruit bats, caused an outbreak affecting horses, pigs, and humans across Australia and Southeast Asia (Clayton, 2017). In Latin America, frugivorous bats play a key role in the enzootic cycle of the Venezuelan equine encephalitis virus (VEEV) (Guzmán et al., 2018). These bat-borne viruses can lead to fatal diseases that pose significant concerns for public health, livestock agriculture, companion animals, wildlife reserves, and the global economy (Bonilla-Aldana et al., 2020; Louten, 2016; Tian et al., 2022).

Zoonotic transmission from bats to humans, either direct or indirect, holds the potential to trigger future pandemics (Rajeev et al., 2020; Van Brussel & Holmes, 2021). Routes of transmission include environmental contamination (such as bat urine and feces), direct contact (e.g., scratches or bites), or indirect transmission via other animals or vectors (Afelt et al., 2017; Nabi et al., 2020).

Influenza viruses are one of the most common viruses that threaten humans and other mammals (Wiwanitkit, 2014). These viruses are also present in *Chiroptera* species, for example, bat influenza A virus (BIV) (Maruyama et al., 2016). The transmission of influenza viruses from bats to birds and other animals, or directly to humans, increases the risk of viral exchange and mutation that may be fatal to humans and other animals(Brook & Dobson, 2015).

Recently, a computational analysis of the whole-genome sequence of past pandemic avian influenza was reported (Gomez et al., 2019). The use of multiple sequence alignment (MSA) is a growing trend in computational biology, driven by its promising predictions and cost-effective analysis (Caucchiolo & Cicalese, 2023).

This study aimed to characterize the genetic similarities and differences among bat influenza A viruses H9N2, H17N10, and H18N11 by performing multiple-sequence alignment, constructing a phylogenetic tree, and analyzing sequence identity across all genome segments. Specifically, we sought to identify conserved gene segments across bat influenza viruses, and to determine which surface glycoproteins exhibit high sequence variability. This analysis provides insight into long-term vaccine target selection and primer design, especially for conserved regions, and offers potential strategies for seasonal vaccine updates in response to mutations.

METHODS

Sequence Retrieval

Nucleotide sequences of bat influenza viruses were systematically retrieved from the NCBI Influenza Virus Database. The selection criteria focused on specific strains and their associated host species to ensure a representative dataset for phylogenetic analysis. The included sequences were H9N2 strains isolated from Egyptian fruit bats or Egyptian rousettes (*Rousettus aegyptiacus*) in both Egypt and South Africa. Additionally, H17N10 from a little yellow-shouldered bat (*Sturnira lilium*) in Guatemala, H18N11 from a great fruit-eating bat (*Artibeus lituratus*) in Brazil, H18N11 from a dark fruit-eating bat (Artibeus obscurus) in Bolivia, and H18N11 from a flat-faced Fruit-eating Bat (*Artibeus planirostris*) in Peru were added to the dataset. All eight gene segments of the bat influenza virus, namely Polymerase Basic 2 (PB2), Polymerase Basic 1 (PB1), Polymerase Acidic (PA), Hemagglutinin (HA), Nucleoprotein (NP), Neuraminidase (NA), Matrix Protein (MP), and Non-Structural Protein (NS), were included to provide a comprehensive genetic overview. The sequences were checked for completeness and potential anomalies before processing to ensure data quality and accuracy.

Multiple Sequence Alignment (MSA)

Multiple sequence alignment (MSA) was performed using MEGA software version 11.0.13 (Tamura et al., 2021), a widely recognized tool for sequence analysis. The MUSCLE (Multiple Sequence Comparison by Log-Expectation) algorithm was employed for its accuracy and efficiency in aligning diverse sequences, particularly for large datasets. The alignment process was conducted with 1000 iterations to optimize the alignment quality and minimize alignment errors. Following the automated alignment, the resulting MSA was visually inspected for any misalignments or regions with ambiguous gaps. Gaps and missing data were handled by pairwise deletion to maximize the use of available sequence information while minimizing the introduction of artificial relationships. This step is crucial for ensuring that subsequent phylogenetic inferences are based on homologous positions across all sequences.

Phylogenetic Analysis

Phylogenetic trees were constructed using the maximum likelihood (ML) method, implemented within MEGA software version 11.0.13. The maximum likelihood approach is preferred for its statistical rigor and

ability to infer evolutionary relationships based on explicit models of sequence evolution. The Tamura-Nei (TN93) model with Gamma distribution and Invariant sites (GTR+I) was selected as the best-fit model of nucleotide substitution. The determination of this optimal model was performed using the built-in model selection utility in MEGA, which evaluates various models based on criteria such as the lowest Bayesian Information Criterion (BIC) as the best-fit substitution in this study. Tree topology robustness was assessed by performing 1000 bootstrap replicates, as bootstrap values provide a measure of confidence for each node in the phylogenetic tree, indicating the reliability of the inferred evolutionary relationships. A bootstrap cut-off of 90% was applied to identify well-supported nodes.

Sequence Identity Analysis

To quantify the genetic relatedness among the bat influenza virus sequences, pairwise percent sequence identity heatmaps were generated for each viral segment. This analysis was conducted using R with specialized bioinformatics packages. Multiple sequence alignments were performed using the msa package (Bodenhofer et al., 2015) with the ClustalW algorithm, followed by pairwise distance calculations using the ape package to compute percent identity values. The Biostrings package facilitated efficient handling of DNA sequences, while heatmap visualizations were generated using the pheatmap package with hierarchical clustering and the viridis color palette for optimal scientific presentation. This visualization approach provided a clear representation of pairwise sequence identities, highlighting clusters of highly similar sequences and divergent groups, thereby enabling systematic assessment of genetic diversity and potential evolutionary relationships within the dataset.

RESULTS

Phylogenetic Analysis

The phyloevolutionary tree of the Philippines strain of bat influenza A virus and human influenza A virus indicates that Brazil, Peru, and Bolivia form a clade of H18N11, diverging from the H17N10 clade of Guatemala. The South African and Egyptian strains of H9N2 are closer to the H3N2 and H1N2 strains of the Philippines, as seen in Figure 1.

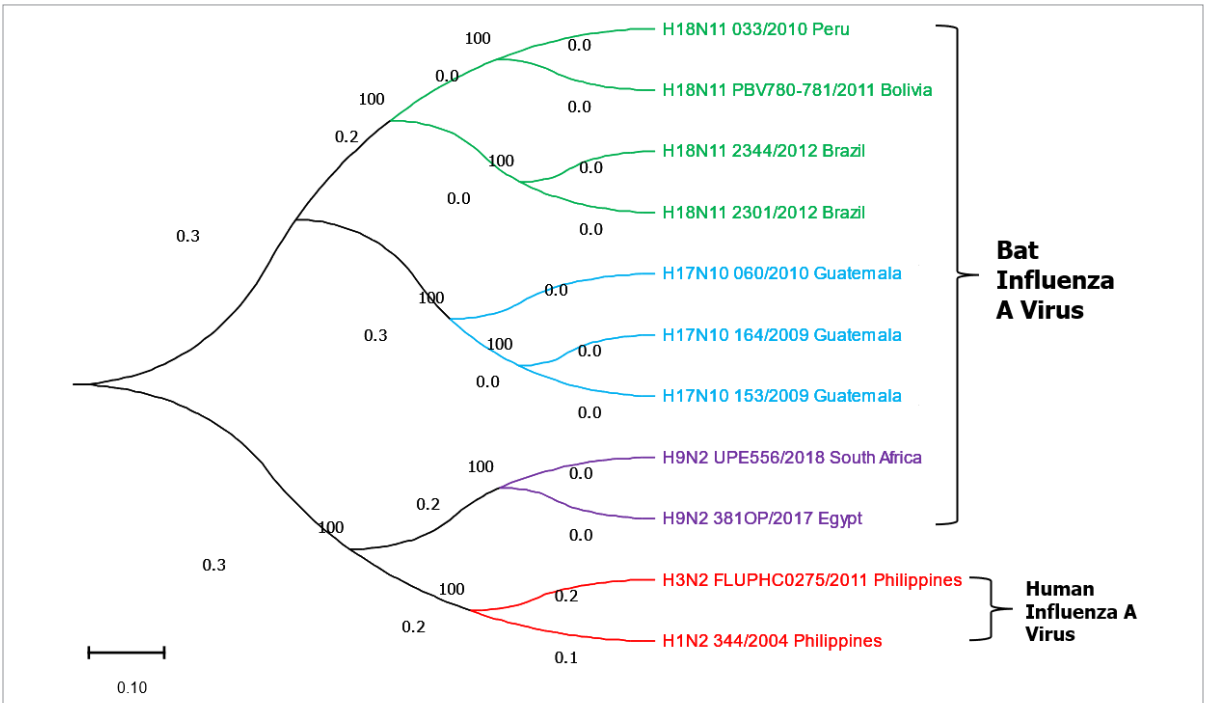

Figure 1. *Whole-genome phylogenetic tree of the bat influenza A virus and human influenza cases in the Philippines, which serve as the outgroup*

Sequence Identity Analysis

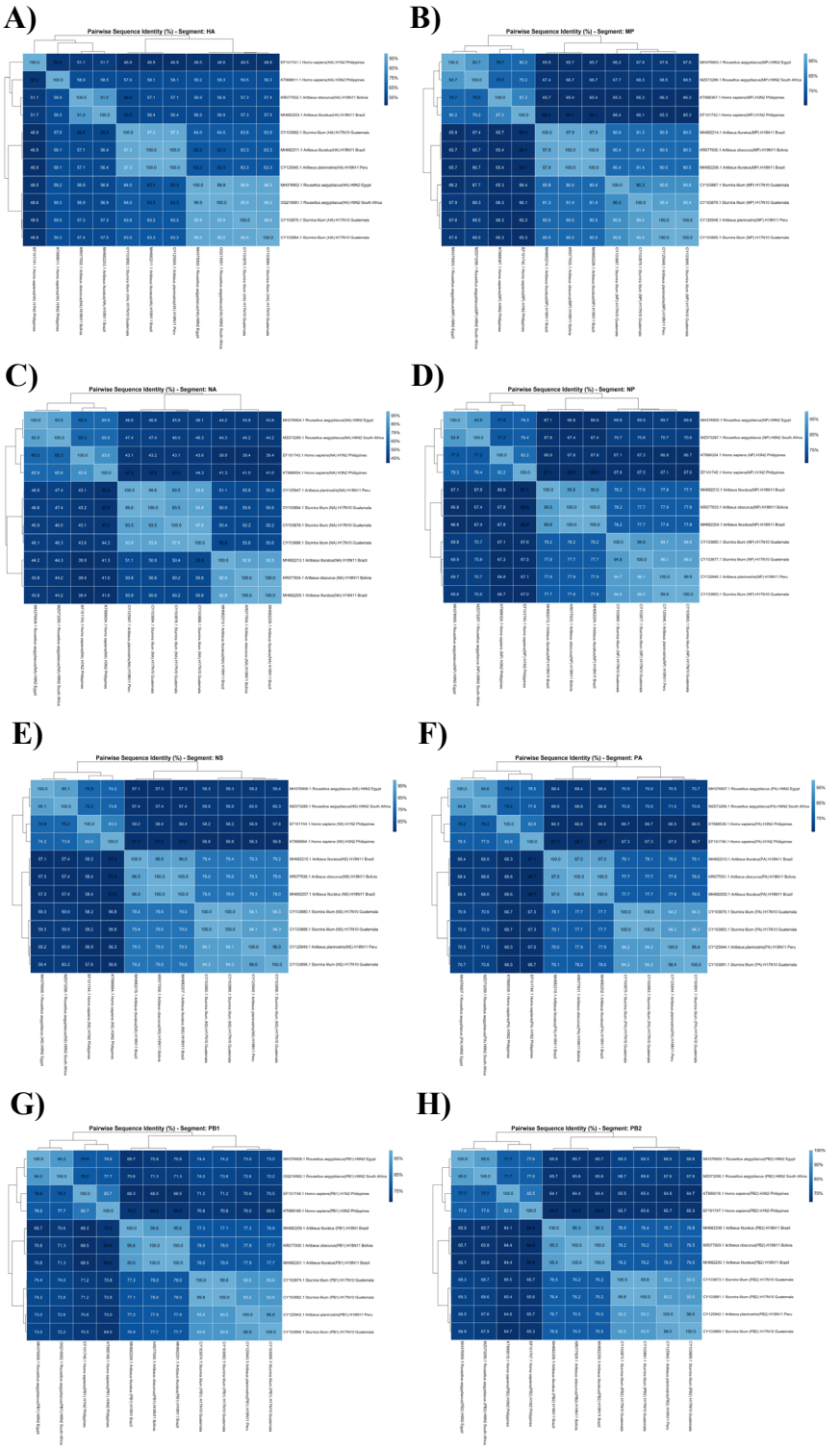

Figure 2. *Heat maps of the bat influenza A viruses and human influenza A virus of the Philippines strain A) HA segment, B) MP segment, C) NA segment, D) NP segment, E) NS segment, F) PA segment, G) PB1 segment, and H) PB2 segment*

Pairwise sequence identity analysis revealed two distinct evolutionary patterns across the viral gene segments (Figure 2). A high degree of genetic conservation was observed for the internal protein-coding genes. The Matrix Protein (MP), Nucleoprotein (NP), and Polymerase Acidic (PA) segments consistently showed high identity scores, often exceeding 75% even between viruses from different hosts and continents. For example, the NP segment of the human H3N2 isolate from the Philippines shared 77.2% identity with the bat H9N2 isolate from Egypt. This conservation was most pronounced within defined clades, such as the Guatemalan H17N10 isolates, which displayed >99.8% sequence identity in their PB2 segments. In contrast, the surface glycoprotein segments, Hemagglutinin (HA) and Neuraminidase (NA), displayed extensive sequence divergence. Inter-group identities for these segments frequently fell below 60%, with NA being the most variable. A notable exception to the general conservation of the polymerase complex was observed in the PB1 segment of the South African H9N2 isolate. While it shared high identity with its Egyptian H9N2 counterpart, its similarity to other New World bat virus PB1 segments was low.

Multiple Sequence Alignment (MSA)

Analysis of the multiple sequence alignments revealed that the presence of insertions or deletions (indels) varied significantly across the gene segments. The alignment for the highly conserved PB2 segment was contiguous, showing a notable absence of indels across all analyzed sequences. In contrast, a significant terminal deletion of approximately 1,150 nucleotides was identified in the PB1 segment of the South African H9N2 strain, consistent with its low identity score. A shared internal indel was observed in the PA segment for all New World bat viruses (isolates from Brazil, Bolivia, Peru, and Guatemala), distinguishing them from the human and Old World bat viruses. Finally, consistent with its high sequence divergence, the NA segment alignment was the most fragmented, containing numerous and extensive indels distributed throughout its length.

DISCUSSION

Our comparative genomic analysis of bat influenza A viruses (BIVs) reveals patterns of sequence conservation and divergence across the eight genomic segments, providing critical insights into viral evolution and potential therapeutic targets. The pairwise sequence identity analysis reveals segment-specific evolutionary pressures with profound implications for pandemic preparedness and the development of antiviral therapeutics.

The internal housekeeping cassette, including the polymerase complex (PB2, PB1, PA), nucleoprotein (NP), and matrix protein (MP), exhibits remarkably high conservation levels. This functional constraint is evident in the MP and NP genes, which often show a higher degree of sequence identity across divergent viral lineages in our dataset. This conservation pattern is consistent with the essential role of the viral RNA-dependent RNA polymerase in transcription and replication, where even minor mutations can significantly impact viral fitness (Pflug et al., 2017). The high sequence identity observed in PB2 suggests functional constraints that limit mutational tolerance, making this segment an attractive target for broad-spectrum antivirals. Previous studies have demonstrated that targeting the PB2-PB1 interface can effectively disrupt polymerase function (Reuther et al., 2011); our data support the feasibility of developing pan-BIV therapeutics that target these conserved regions.

In contrast, the surface glycoproteins HA and NA display sequence divergence. This variability reflects the immune selection pressure on these antigenic determinants. The clustering patterns in our analysis reveal distinct phylogenetic relationships: H17N10 strains from Guatemala cluster separately from H18N11 strains from Peru and Bolivia, while the H9N2 strain from Egypt appears as an outlier, suggesting independent evolutionary trajectories and potential geographical isolation effects.

The genomic diversity patterns observed in BIVs have implications for assessing pandemic risk. The high conservation in internal genes coupled with surface protein variability creates conditions conducive to reassortment events, which have historically driven influenza pandemics. The presence of compatible internal gene constellations across geographically dispersed BIV strains suggests that a reassortant could emerge with altered host range or transmission properties while maintaining essential replication machinery.

Our findings provide a roadmap for next-generation influenza vaccine strategies. The remarkable

conservation observed in the nucleocapsid protein (NP) segment identifies this as a prime target for universal vaccine approaches. Recent advances in T-cell-based vaccines targeting conserved internal proteins suggest that NP-based immunogens could provide broad protection against diverse BIV strains (Chenavier et al., 2025). For variant-specific vaccine development, the highly variable HA and NA segments necessitate a seasonal update strategy similar to those used for human influenza vaccines. However, the distinct clustering patterns observed suggest that geographically targeted vaccine formulations may be more effective than universal approaches for surface proteins. The identification of conserved epitopes within variable regions could enable the development of broadly neutralizing antibody responses, as demonstrated in recent studies with avian influenza viruses (Jiao et al., 2023).

The differential conservation patterns across BIV segments enable the development of sophisticated molecular surveillance systems. By leveraging conserved regions in PB1 and PB2 as stable anchoring sequences and monitoring variability in HA, NA, and NS segments, we can establish comprehensive viral fingerprinting protocols. This multi-segment approach would enable real-time tracking of viral evolution and rapid identification of potentially pandemic variants.

Our findings align with One Health principles by demonstrating the interconnected nature of human, animal, and environmental health in the context of emerging infectious diseases. The conservation patterns we observed suggest that BIV surveillance should be integrated into broader influenza monitoring networks, as these viruses represent a potentially significant reservoir for pandemics.

The geographical clustering patterns observed in our analysis underscore the importance of region-specific surveillance strategies. The distinct evolutionary trajectories of Central American, South American, and African BIV strains suggest that pandemic preparedness efforts must account for regional genomic diversity. This finding supports the establishment of distributed surveillance networks that can capture local viral evolution while contributing to global threat assessment.

Our study has some limitations. The relatively small sample size and limited geographical representation may not capture the full spectrum of BIV diversity. Future studies should prioritize expanded sampling across diverse bat species and geographical regions to provide a more comprehensive picture of global BIV evolution. The computational analysis presented here requires experimental validation to confirm the functional significance of identified conservation patterns. Cell culture studies examining the replication efficiency of chimeric viruses containing conserved and variable segments would provide critical insights into the biological relevance of our genomic observations. Additionally, structural modeling of conserved regions could identify specific amino acid residues critical for function and suitable for therapeutic targeting.

CONCLUSION

Our comparative genomic analysis reveals an evolutionary dichotomy within the genome of bat-borne influenza A viruses. The internal gene cassette, comprising the polymerase complex (PB2, PB1, PA), nucleoprotein (NP), and matrix protein (MP), demonstrates remarkable conservation across diverse viral lineages. In contrast, the surface glycoproteins, neuraminidase (NA) and hemagglutinin (HA), are highly variable and cluster according to viral subtype and geography. This genetic landscape provides a clear roadmap for pandemic preparedness. The highly conserved internal genes offer stable and robust targets for broad-spectrum diagnostics (such as primer design for PCR) and the rational design of universal antiviral drugs or T-cell-based vaccines. On the other hand, variable surface proteins necessitate adaptive, strain-specific surveillance and vaccine strategies, analogous to those for seasonal human influenza. Although these computational findings await experimental validation, they provide a fundamental basis for our risk assessment of bat-borne influenza viruses and offer a strategic framework for mitigating their pandemic potential.

Author Contributions

B. H. A. Villanueva: Conceptualization, Methodology, Writing-Original draft preparation, Writing-Reviewing and Editing, Validation, Visualization, Data curation, Software, Project Administration; **M. C. Gomez:** Writing-Reviewing and Editing, Supervision, Validation, Data curation, Writing-Original draft preparation; **Q. Hussain:**

Visualization, Investigation, Writing-Reviewing and Editing, Software; **Q. D. Hong:** Visualization, Investigation, Writing-Reviewing and Editing, Software; **K. P. Chuang:** Supervision, Validation, Data curation, Writing-Reviewing and Editing.

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Not applicable.

Competing interest
The authors declare that they have no conflicts of interest.

Data Availability
All data generated in this study are included in the manuscript.

Declaration of Artificial Intelligence Use
In this work, the authors did not utilize artificial intelligence (AI) tools and methodologies in writing the manuscript.

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