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Short communication

Meta-transcriptomic sequencing reveals divergent RNA viruses in geckos

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SUMMARY

Geckos are generally small, predominantly nocturnal reptiles, with several species commonly found close to human habitations. However, little is known about viral diversity in geckos. Using meta-transcriptomic sequencing we identified four novel RNA viruses – provisionally denoted Gecko astrovirus, Gecko parechovirus, Gecko reptillovirus, and Gecko hartmanivirus – in geckos sampled in October 2019 from Hainan Province, China. The presence of these viruses was confirmed by reverse transcription (RT)-PCR. Phylogenetic analyses revealed that these viruses were most closely related to those identified in various gecko species from China and Australia, such that they represent gecko-specific lineages, yet were also genetically distinct, with amino acid sequence identities to their closest relatives ranging from 38.6 % to 74.2 %. A co-phylogeny analysis revealed a complex interplay between long-term virus-host co-divergence and more recent host jumping, which differed in frequency among groups. In sum, we demonstrate the presence of four novel gecko-associated RNA viruses, expanding our understanding of viral diversity in these common animal species.

1. Introduction

Reptiles exhibit remarkable diversity, comprising approximately 12,000 species globally (Waller et al., 2024) and residing in diverse habitats, sometimes in close proximity to human settlements. Advances in metagenomic sequencing have enabled the identification and characterization of many viruses in various reptilian species (Marschang, 2011; Harding et al., 2022), including several reptile-specific viruses as well as arthropod-borne viruses (i.e., arboviruses) that primarily infect mammals or birds. Indeed, it is notable that a number of zoonotic viruses are associated with reptilian hosts (Mendoza-Roldan et al., 2021), including West Nile Virus, Chikungunya virus, and Rift Valley Fever Virus (Mendoza-Roldan et al., 2021; Bosco-Lauth et al., 2018; Gutiérrez-Bugallo et al., 2019; Rissmann et al., 2020). However, compared to many other groups of vertebrates, particularly mammals and birds, there have been a marked lack of studies of reptile viromes, such that our knowledge of the viruses that infect this large and important group of animals is fragmentary at best (Harvey and Holmes, 2022). Herein, using a meta-transcriptomics (i.e. total RNA sequencing) approach, we identified four novel RNA viruses – provisionally denoted Gecko astrovirus, Gecko parechovirus, Gecko reptillovirus, and Gecko hartmanivirus – in geckos collected from Hainan Province, China. The evolutionary relationships of these novel viruses, as well as the extent of virus-host co-divergence relative to that of host jumping in their respective phylogenetic groups, were also explored.

2. Materials and methods

2.1. Sample collection and processing

Six individual animals belonging to two species of gecko (*Hemidactylus frenatus:* $n = 3$; *Gekko chinensis:* $n = 3$) were collected from

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Table 1
Detailed information on the novel viruses identified in this study.

Virus name	Segment	Classification	Library ID	Host	Length (bp)	Closest relative (aa identity)	Abundance (RPM)
Gecko hartmanivirus	L	*Arenavridae*	HN55	*Hemidactylus frenatus*	5851	39.8 %	2988.6
	S				2016	38.6 %	1859.3
Gecko reptillovirus	L	*Hantavridae*	HN55	*Hemidactylus frenatus*	6493	74.2 %	2.0
	M				3443	59.1 %	2.2
	S				1080	50.3 %	0.6
Gecko astrovirus	–	*Astrovridae*	HN55	*Hemidactylus frenatus*	13,700	63.6 %	51.3
	–	*Astrovridae*	HN43	*Gekko chinensis*	13,637	63.8 %	92.7
Gecko parechovirus	–	*Picornavridae*	HN43	*Gekko chinensis*	7684	43.2 %	18.3

Hainan Province, China in October 2019. Gecko species were initially identified morphologically by an experienced field biologist and subsequently validated using the mitochondrial cytochrome c oxidase subunit 1 (COI) gene sequence assembled from meta-transcriptomic sequencing. These samples were frozen in liquid nitrogen and subsequently ground into fine powder using a mortar and pestle, and thereafter divided into two groups (denoted HN43 and HN55) based on species. Each group was pooled, and two sequencing libraries were prepared (Table 1). Total RNA was extracted using TRIzol reagent (Thermo Fisher) with ~50 mg of the powder from each pool. Ribosomal RNA (rRNA) was removed using the MGIEasy rRNA Depletion Kit, with RNA sequencing libraries then constructed using the MGIEasy mRNA library Prep Kit. Paired-end (100 bp) sequencing of the two libraries on the BGISEQ-500RS sequencing platform (BGI) yielded a total of 92.94 Gb reads (Table 1).

2.2. Virus discovery and PCR confirmation

Raw sequencing reads were trimmed for quality control using Fastp v.0.19 (Chen et al., 2018) and Trimmomatic (Bolger et al., 2014), and then *de novo* assembled using Trinity version v2.5.1 (Grabherr et al., 2011). Assembled sequence contigs were compared against the non-redundant nucleotide (nt) and protein (nr) databases at NCBI using BLASTn (Camacho et al., 2009) and Diamond BLASTx (Buchfink et al., 2015), with E-value thresholds of 1×10^{-10} and 1×10^{-5}, respectively. Viral contigs were identified and merged into longer sequences using Geneious Prime (Kearse et al., 2012). To evaluate virus abundance and coverage, sequencing reads were mapped onto the predicted

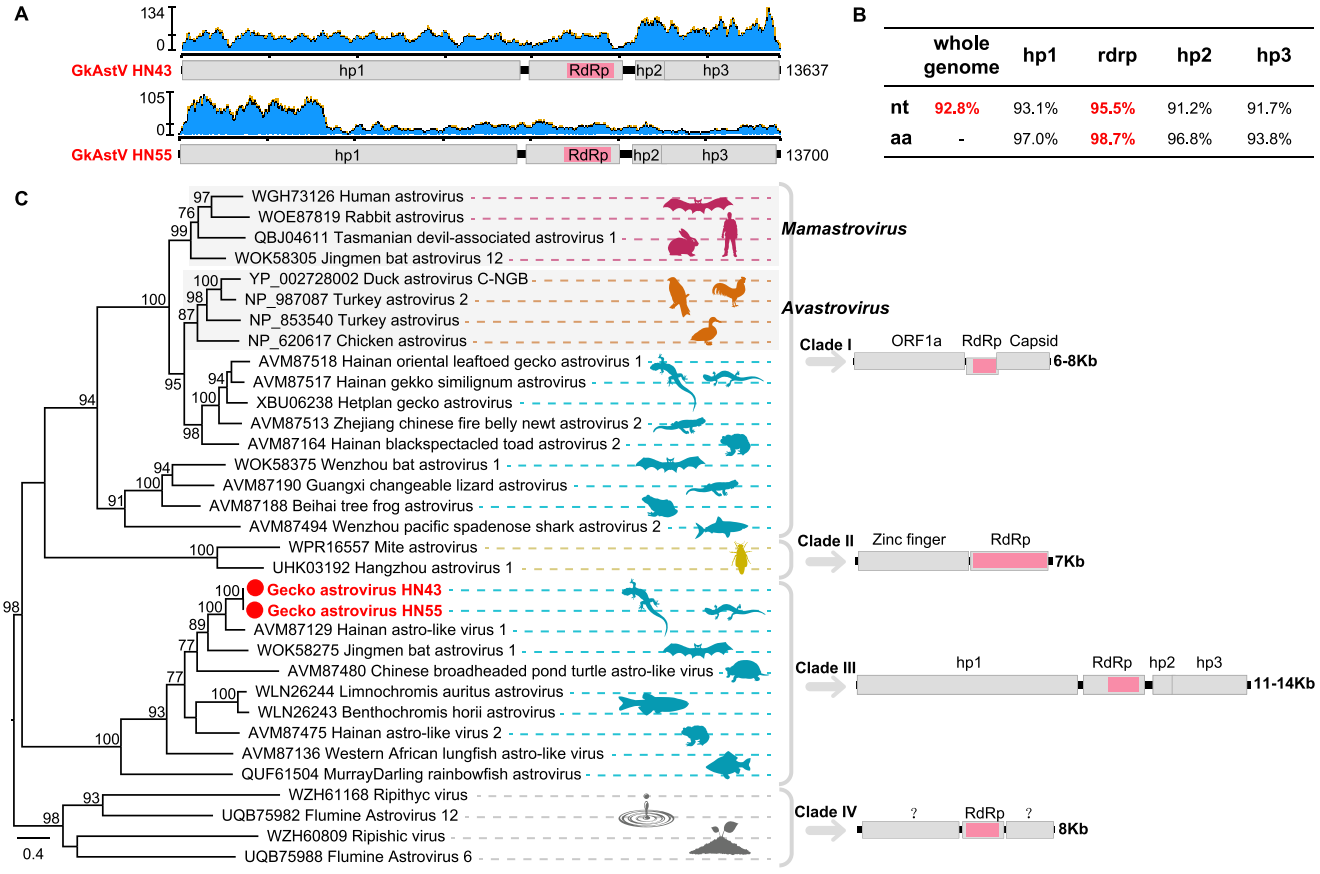

Fig. 1. Genome characterization and evolutionary relationships of GkAstV. (A) Schematic representation and read abundance of the two genomes of GkAstV. (B) Pairwise sequence identities between gecko astroviruses from this study and three closest astroviruses. (C) Maximum likelihood phylogenies of the RdRp of gecko astroviruses identified in this study and selected representative members of the family *Astroviridae*, including those from the genera *Mamastrovirus* and *Avastrovirus*. The two gecko astrovirus sequences are highlighted in red with red sold circles. The tree was midpoint rooted for clarity and branch lengths are scaled to the number of amino acid substitutions per site. Bootstrap values of >70 % are shown for key nodes. Genome structures and corresponding average genome lengths of four clades (Clade I - IV) are also provided.

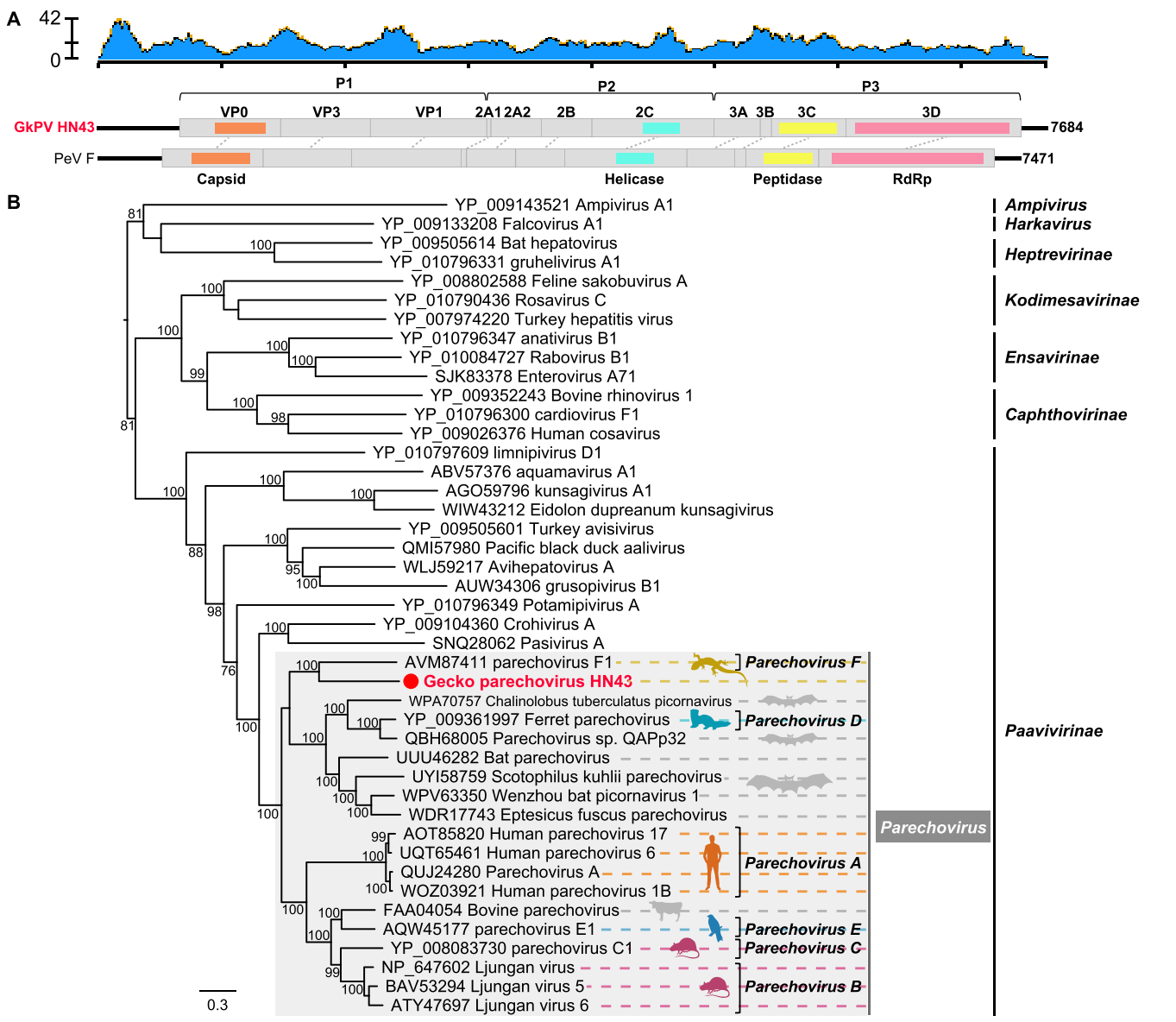

Fig. 2. Genome characterization and evolutionary relationships of GkPV. (A) Schematic representation and read abundance of the genome of GkPV. (B) Maximum likelihood phylogenies of polyprotein of GkPV and selected representative members of the family *Picornaviridae*. GkPV is highlighted in red with red sold circles. The grey-shaded region indicate sequences from the genus *Parechovirus* (Subfamily: *Paavivirinae*). The tree was midpoint rooted for clarity. Bootstrap values of >70 % are shown for key nodes.

virus-associated contigs using Bowtie2 (Langmead and Salzberg, 2012). Virus abundance was estimated as the number of Reads per Million (RPM, mapped viral reads/total library reads*one million). Overlapping primers (Supplementary material: Table S1) were designed based on the assembled sequences, and RT-PCR was performed to verify the viral sequences (Supplementary material: Figures S1-S2, Table S1).

2.3. Sequence alignment and phylogenetic analysis

Open reading frames (ORFs) were predicted from the verified virus genomes using ORFfinder (https://www.ncbi.nlm.nih.gov/orffinder/). Amino acid sequences of the viruses identified in this study were aligned with representative reference viruses using the E-INS-i algorithm in MAFFT v7 (Katoh and Standley, 2013). Phylogenetic trees of each virus group were then estimated using the maximum likelihood method in IQ-TREE v1.6.1241 (Nguyen et al., 2015), employing the best-fit amino acid substitution model and 1000 bootstrap replicates.

2.4. Data availability

All sequencing reads have been uploaded onto the NCBI Sequence Read Archive (SRA) database under BioProject PRJNA1207091. The four consensus genome sequences of the identified viruses generated in this study have been uploaded in GenBank under accession numbers PQ622675-PQ622682.

3. Results and discussion

3.1. Identification of novel RNA viruses in geckos

Two unsegmented virus sequences were identified, comprising one astrovirus in both libraries and one picornavirus in the library HN43 (Table 1), referred as Gecko astrovirus (GkAstV) and Gecko parechovirus (GkPV), respectively (Table 1). BLASTX analysis indicated that GkAstV shared the highest amino acid identity (~63 %) in the RNA-dependent RNA polymerase (RdRp) with Hainan astro-like virus 1

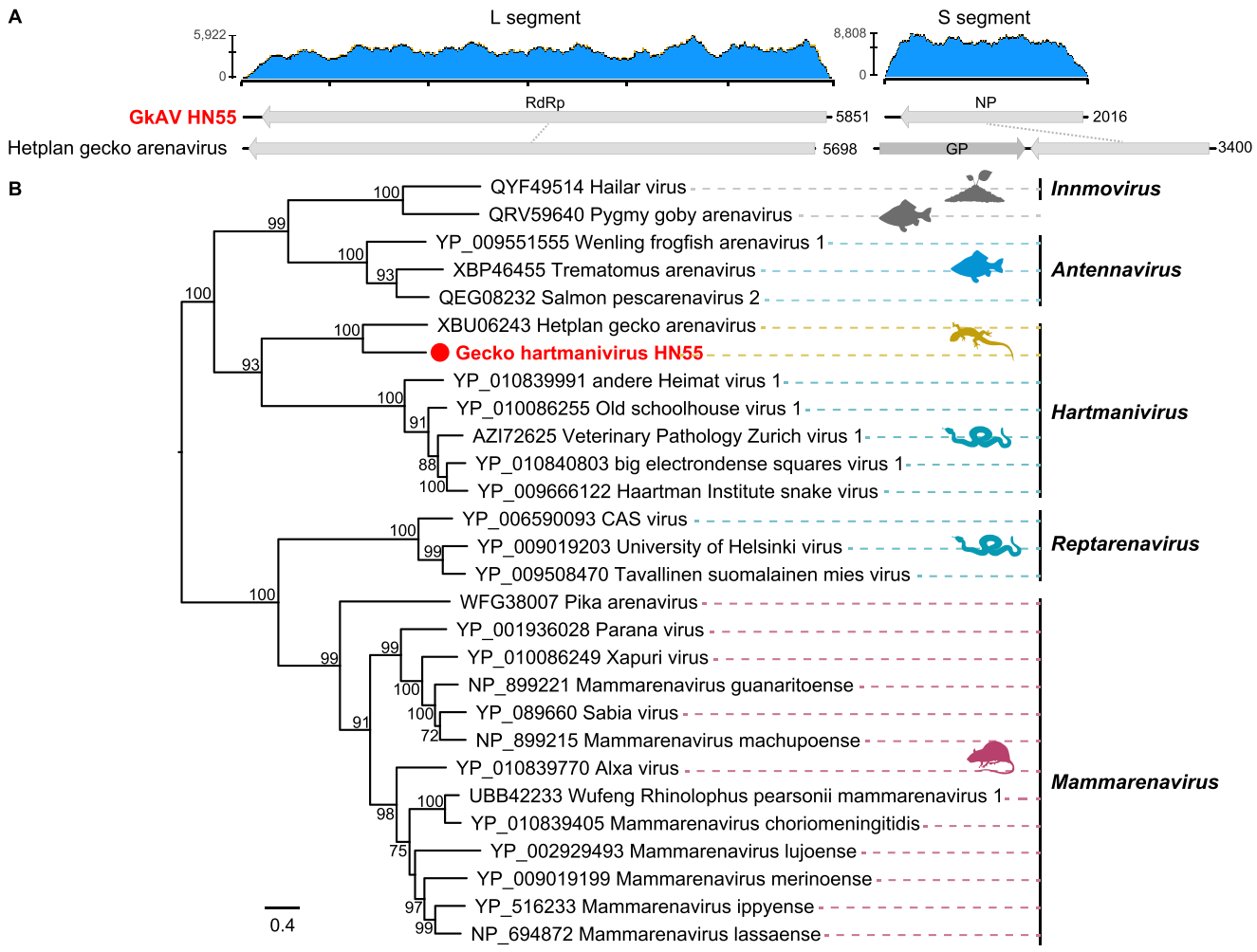

Fig. 3. Genome characterization and evolutionary relationships of GkHmV. (A) Schematic representation and read abundance of the genome of GkHmV. (B) Maximum likelihood phylogenies of RdRp protein of GkHmV and selected representative members of the family *Arenaviridae*. GkHmV is highlighted in red with red sold circles. The tree was midpoint rooted for clarity. Bootstrap values of >70 % are shown for key nodes.

(HAstV1) (GenBank accession no. AVM87129) identified in the Oriental leaf-toed gecko (*Hemidactylus bowringii*) from China (Shi et al., 2018), while GkPV shared 42.4 % amino acid identity in the polyprotein with its closest relative - parechovirus F (GenBank accession no. AVM87411) – identified in the Tibetan wonder gecko (*Teratoscincus roborowskii)*, also from China (Shi et al., 2018) (Table 1).

In addition, two arenavirus-associated contigs were identified in library HN55, with the highest amino acid identities – 39.8 % and 38.6 % in the L protein and nucleoprotein, respectively - to Hetplan gecko arenavirus (HGeAV) (GenBank accession no. XBU06243) sampled from Bynoe's prickly gecko (*Heteronotia planiceps*) in Australia (Mahar et al., 2024) (Table 1). The novel arenavirus was provisionally designated as Gecko hartmanivirus (GkHmV). Several hanta-associated contigs were also identified in the same library as GkHmV, representing the L protein, glycoprotein, and nucleoprotein, but with gaps. Overlapping primers were subsequently designed to fill the gaps and to verify the sequence obtained from the metagenomic sequencing. The final lengths of the three segments were 6493, 3443, and 1080 bp, respectively, which exhibited the highest amino acid identities (74.2 %, 59.05 %, and 50.3 %, respectively) to Hainan oriental leaf-toed gecko hantavirus (HOLGV) (GenBank accession no. YP_010085031) also identified in *Hemidactylus bowringii* from China (Shi et al., 2018) (Table 1). This novel hantavirus was provisionally named Gecko reptillovirus (GkRlV).

Finally, the abundance of each virus was estimated as the number of reads mapped per million input read (RPM). Accordingly, GkHmV exhibited the highest virus abundance (RPM), reaching to 2988.64 and 1859.32 RPM in the L and S segments, respectively (Table 1). In contrast, the three segments of GkRlV had the lowest abundance, with RPM values of only 2.02, 2.19, and 0.55, respectively (Table 1).

3.2. Phylogenetic relationships of the novel viruses

3.2.1. Gecko astrovirus

The genome lengths of the two GkAstv were 13,637 and 13,700 bp, with coverage valves of 134X and 105X, respectively (Fig. 1A), and exhibited 92.8 % genome sequence similarity (Fig. 1B). Four open reading frames (ORFs) were identified –hp1, RdRp, hp2, and hp3 (Fig. 1A) – consistent with the genome structure of its closest relative. Pairwise comparison of the four viral ORFs revealed the highest similarities of 95.5 % (nucleotide) and 98.7 % (amino acid) in the RdRp domain (Fig. 1B).

Astroviruses are currently classified into two genera – *Avastrovirus* and *Mamastrovirus* – based on their respective avian or mammalian hosts (https://ictv.global/report_9th/RNApos/Astroviridae). The advent of metagenomic sequencing has led to the discovery of many novel astroviruses in a wide range of animals, including mammals and birds, lower vertebrates, and invertebrates (Shi et al., 2018; Shi et al., 2016). Our phylogenetic analysis revealed that astroviruses cluster into four distinct clades (Clade I - IV), with varying genome lengths across clades (Fig. 1C). Of note, the astroviruses carried by reptiles fell into two clades

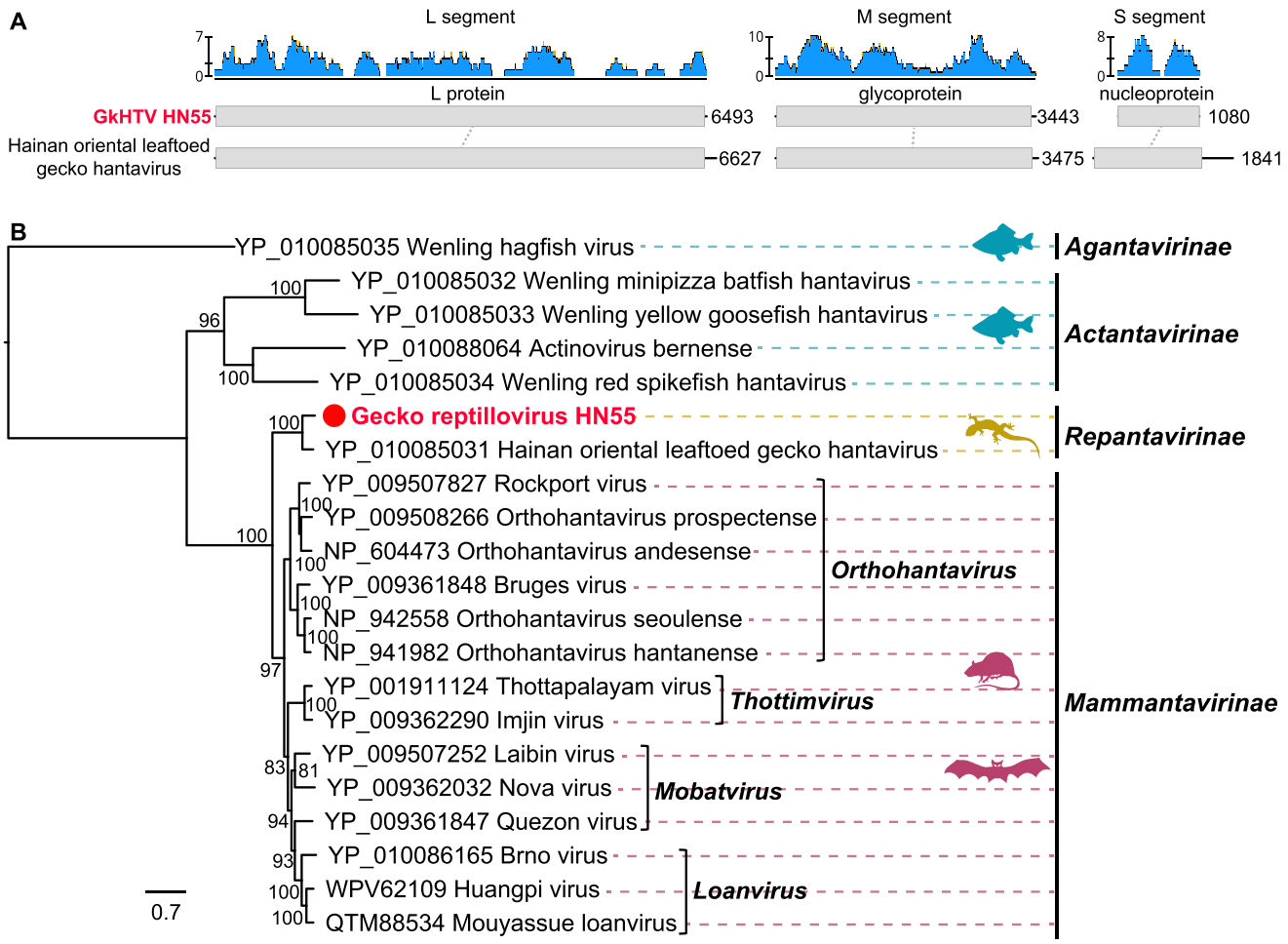

Fig. 4. Genome characterization and evolutionary relationships of GkRlV. (A) Schematic representation and read abundance of the genome of GkRlV. (B) Maximum likelihood phylogenies of L protein of GkRlV and selected representative members of the family *Hantaviridae*. GkRlV is highlighted in red with red sold circles. The tree is midpoint rooted for clarity. Bootstrap values of >70 % are shown for key nodes.

(Fig. 1C). Viruses of Clade I have genome lengths of 6–8 kb and contain three ORFs, consistent with those of classic astroviruses. However, the novel astrovirus (GkAstV) identified here belonged to clade III, and was most closely related to HAstV1. Clade III astroviruses have been found in turtles, bats, toads, and fish, and are characterized by longer genome sequences of >10k bp and four ORFs (Fig. 1C). Accordingly, the discovery of these novel astroviruses highlights the need for the classification system of astroviruses to be updated.

3.2.2. *Gecko parechovirus*

The near-complete genome of GkPV was 7684 bp in length and was predicted to encode a single polyprotein of 2270 amino acids (aa). The genes identified were typical of most picornaviruses, comprising: 5′-VP0, VP3, VP1, 2A1, 2A2, 2B, 2C, 3A, 3B, 3C, and 3D-3′ (Fig. 2A). The sequence similarity of the full-length polyprotein between GkPV and the members of the *Parechovirus* genus was relatively low, ranging from ~36 % to 43 % (Fig. 2B). The highest amino acid identity was 42.4 % to parechovirus F (GenBank accession no. AVM87411) identified in the gecko *Teratoscincus roborowskii* from China (Fig. 2B) (Shi et al., 2018). As expected from the sequence similarities, phylogenetic analyses based on the full-length polyprotein of representative species of the *Picornaviridae* indicated that GkPV was closely related to parechovirus F (Fig. 2B). The next closest group were members of parechovirus D, although there was only weak bootstrap support for a clustering of parechoviruses D and F. Hence, these data demonstrate that GkPV might likely represent a novel species within the genus *Parechovirus*, most closely related to parechovirus F.

3.2.3. *Gecko hartmanivirus*

Both the L and S segments of GkHmV were detected, with lengths of 5851 and 2,016 bp, and 5,922X and 8,808X sequence coverage, respectively (Fig. 3A). The L segment contained a complete coding region, encoding only the RdRp (Fig. 3A), but not the gene region that encodes the zinc-binding matrix protein. This finding was consistent with the previously identified Hetplan gecko arenavirus and those from the genus *Hartmanivirus*. The S segment was incomplete, with only the nucleoprotein detected (Fig. 3A). Phylogenetic analyses of the RdRp sequences revealed that GkHmV clustered with Hetplan gecko arenavirus and that this pair formed a sister lineage to other members of the genus *Hartmanivirus* (Fig. 3B). Based on the genus and species demarcation criteria for *Arenaviridae* (https://ictv.global/report/chapter/arenaviridae/arenaviridae), GkHmV and HGeAV were proposed as novel species within the genus *Hartmanivirus* (Mahar et al., 2024). Notably, viruses of the genus *Hartmanivirus* have been primarily detected in snakes (Radoshitzky et al., 2015), but are now known to infect a wider range of hosts.

3.2.4. *Gecko reptillovirus*

Sequencing library HN55 also contained several contigs of the three segments for GkRlV, with coverage depths of 7X, 10X, and 8X, respectively (Fig. 4A). The three segments encoded the L protein, glycoprotein, and nucleoprotein, consistent with other members of the *Hantaviridae*.

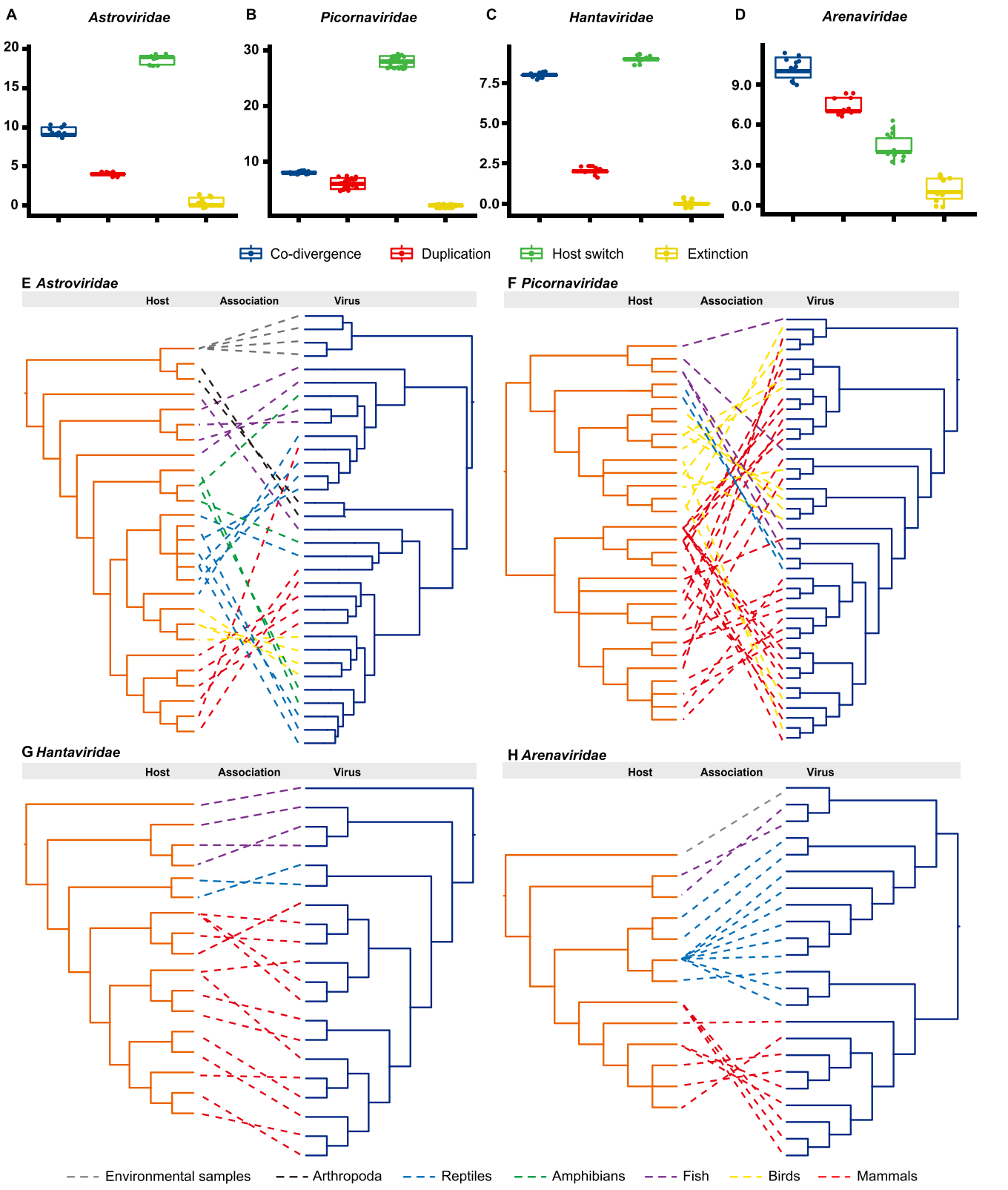

Fig. 5. Co-phylogenetic analysis of astroviruses, picornaviruses, hantaviruses and arenaviruses. (A-D) Relative frequency of co-phylogenetic events across the history of astroviruses (A), picornaviruses (B), hantaviruses (C) and arenaviruses (D). Each boxplot illustrates the estimated median (centre line), upper and lower quartiles (box limits), 1.5 × interquartile range (whiskers), and outlier (points) of the co-divergence (blue), duplication (red), host-switching (green) and extinction (yellow) events. (E-H) Comparisons of astrovirus (E), picornavirus (F), hantavirus (G) and arenavirus (H) phylogenies and those of their corresponding host taxa.

In the L protein phylogenetic tree, GkRlV clustered with HOLGV (Fig. 4B). Both viruses share the same gecko host *Hemidactylus* genus: GkRlV was hosted by *Hemidactylus frenatus,* while HOLGV was hosted by *Hemidactylus bowringii*. This cluster formed a sister lineage and fell basal to the subfamily *Mammantavirinae* (Fig. 4B). HOLGV is currently the only classified reptillovirus within the subfamily *Repantavirinae* (Laenen et al., 2019). Based on the sequence similarity between GkRlV and HOLGV, as well as their positions within the phylogenetic tree, we propose that GkRlV constitutes a novel species within the subfamily *Repantavirinae*.

3.3. Analysis of virus–host co-phylogeny

To investigate the co-phylogenetic relationships between these viruses and their hosts, particular whether there was evidence for virus-host co-divergence, we performed a phylogenetic reconciliation analysis to estimate the relative frequency of four macroevolutionary events: co-divergence, duplications, host-switching, and extinction (Fig. 5). The analysis revealed that host-switching (i.e. cross-species virus transmission) was prevalent among astroviruses ($p = 0.0099$) and picornaviruses ($p = 0.0396$) (Fig. 5A and B). For hantaviruses (Fig. 5C), both host-switching and virus-host co-divergence were relatively common ($p = 0.0099$). Strikingly, however, there was clear evidence for virus-host co-divergence in arenaviruses ($p = 0.0198$) (Fig. 5D). Similar patterns were evident from the tanglegrams connecting the virus and host phylogenies (Fig. 5E - H). Collectively, these results reflect a complex interplay among different macroevolutionary processes, the frequences of which differ among viral groups. More broadly, these data support the growing view that, in most RNA viruses, cross-species transmission occurs frequently on an evolutionary "backbone" of long-term virus-host co-divergence, the signal for which is stronger in some groups than others (Shi et al., 2018; Zhang et al., 2018).

4. Conclusions

In summary, we report the discovery of four divergent RNA viruses in geckos, highlighting the potential extensive diversity of RNA viruses in reptiles. That the viruses identified here were related to other gecko viruses, albeit relatively distantly, reveals the presence of gecko-specific lineages. Given that reptiles may serve as important reservoirs of arboviruses and other viruses, further investigation is warranted to determine whether these novel viruses cause disease in geckos and whether they have the potential to jump to other host species.

Animal and human rights statement

This study was approved of the Shandong First Medical University & Shandong Academy of Medical Sciences. All institutional and national guidelines for the care and use of animals were followed.

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CRediT authorship contribution statement

Shuqi Liu: Writing – original draft, Software, Investigation, Formal analysis, Data curation. **Ruiling Niu:** Software, Methodology, Investigation, Formal analysis. **Xinrui Wang:** Software, Methodology, Formal analysis, Data curation. **Jingxuan Cui:** Methodology, Formal analysis. **Mingxue Cui:** Resources, Methodology. **Hong Zhou:** Resources, Investigation. **Juan Li:** Resources, Investigation. **Edward C Holmes:** Writing – review & editing, Supervision. **Weifeng Shi:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Data curation, Conceptualization. **Cixiu Li:** Writing – review & editing, Writing – original draft, Software, Resources, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.virusres.2025.199551.

Data availability

I have included the source of my data in the main manuscript.

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