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Virology

Viral communities and identification of a parvovirus and two picornaviruses in geese with gout

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ABSTRACT. In recent years, an emerging infectious disease characterized by urate deposition in viscera and joints has outbreak in the goose farms of China, causing substantial economic losses. Although goose astrovirus (GoAstV) was believed to be the main causative pathogen, several studies have shown that co-infection with other viruses, such as goose parvovirus, alongside astrovirus, may exacerbate the disease condition. In our previous research, we isolated a goose astrovirus with a novel type of recombination that causes fatal gout in geese in Shanghai, China. By analyzing the viral community using viral metagenomics data of fecal, kidney and liver samples of geese with gout, we found that parvoviruses and picornaviruses occupied a substantial proportion, suggesting their potential involvement in the etiology of goose gout. To determine if there were other causative viruses present in these geese, fecal, kidney, and liver samples were deeply sequenced using viral metagenomics. The results indicated that goose parvovirus and picornavirus constituted the predominant part of all or partial viral communities. Subsequently, the genomes and genomic structures of two picornaviruses, as well as a parvovirus, were determined. Phylogenetic analysis revealed that this parvovirus, named dependoparvovirus_CH_SH01, belongs to the *Parvovirinae* subfamily within the family *Parvoviridae*, while the two picornaviruses were classified within the *Megrivirus* (megrivirus_CH_SH01) or *Ludopivirus* (ludopivirus_CH_SH01) genus within the *Kodimesavirinae* subfamily, respectively. Recombination analysis suggested that megrivirus_CH_SH01 was a potential recombinant virus between two megriviruses. Our study suggested that infections with viruses other than astrovirus may be associated with the occurrence of goose gout. Additionally, this work has enriched the virus sequence information for Megrivirus and picornaviruses.

KEYWORDS: goose gout, parvovirus, picornavirus, recombination, viral metagenomics

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INTRODUCTION

Since 2017, outbreaks of gosling gout characterized with urate deposition in the internal organs and joints have occurred in China, resulting in massive economic losses to the poultry industry [17]. While novel types of goose astrovirus (GoAstV) have been identified as a causative agent, experimental infection of goslings with GoAstV alone fails to consistently induce the full spectrum of the disease. This suggests that other infectious pathogens may be involved. Researches has shown that co-infection with astrovirus and other viruses including parvovirus and pegivirus may exacerbate the severity of gout [15, 27]. In our previous study, we identified a novel recombinant GoAstV in geese with fatal gout from Shanghai [19]. In the current study, we aimed to identify other potential infectious agents within these same gout-affected geese and characterize their genomic sequences using viral metagenomics methods.

Picornaviruses comprise a diverse family of non-enveloped, icosahedral viruses that possess small, single-stranded positive-sense RNA (ss+RNA) genomes enclosed within a protein capsid approximately 30 nm in diameter [6, 21]. The family Picornaviridae, currently comprising 159 species across 68 genera, is classified into five subfamilies and remains underexplored, with numerous

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unclassified members [25].

These viruses share conserved traits: tripartite capsid proteins, polyprotein processing via viral cysteine proteases, and RNA replication mediated by RNA-dependent polymerases. Structurally, picornavirus virions have a protein capsid enclosing a monopartite, positive-sense ssRNA genome (6.7–10.1 kb) with one open reading frame (ORF) flanked by replication-critical untranslated regions (UTRs) [4, 11]. This ORF encodes a large polyprotein (216–277 kDa) that is cleaved into capsid proteins (also called P1 region) and functional proteins (from P2 to P3 regions) by virus-encoded proteases. Picornaviruses commonly lead to infections that are asymptomatic; however, they can also produce serious diseases in humans and animals [2, 5, 7, 9].

As a ubiquitous DNA virus, the family *Parvoviridae* causes a broad spectrum of diseases, ranging from subclinical to lethal [1, 14, 20]. These non-enveloped small viruses contain a linear, single-stranded DNA molecule ranges from 3.9 to 6.3 kb in length. The genome typically encodes two primary proteins: the nonstructural replicase NS1 and the capsid protein VP [3]. Base on the host range and sequence diversity, viruses in the family *Parvoviridae* are classified into three subfamilies: *Parvovirinae*, *Densovirinae*, and *Hamaparvovirinae* [8]. As a member of the subfamily *Parvovirinae* in *Parvoviridae* family, Dependoparvovirus exhibits a primary tropism for avian species. Representative virus, including goose parvovirus, can cause fatal enteritis in waterfowl chicks, highlighting the clinical significance of this virus group [16, 24].

MATERIALS AND METHODS

Sample collection and preparation

Detailed sample information has been previously reported [19]. Briefly, seven goslings exhibiting clinical gout symptoms were sampled in March 2020 from a commercial flock in Shanghai, China. Fecal specimens and paired liver/kidney tissue samples were collected following standard biosafety protocols. Fecal material was resuspended in ten volumes of Dulbecco's phosphate-buffered saline (D-PBS) and subjected to vigorous vortexing for 10 min. Clarified supernatants were obtained by centrifugation at 15,000 *g* for 15 min at 4°C. Tissue samples (~25 mg) underwent mechanical homogenization on ice, followed by three freeze-thaw cycles using liquid nitrogen. Post-processing, tissue homogenates were centrifuged at 15,000 *g* for 15 min, at 4°C to obtain supernatants. All clarified preparations were aliquoted into 1.5 mL clean tubes and stored at −80°C until use.

Viral nucleic acid extraction and library construction

The suspensions from the three types of samples were mixed together, respectively, and formed into 500 µL of suspension, which was then filtered through a 0.45 µm filter (Millipore, Billerica, MA, USA) to remove cell-sized particles, including both bacterial and eukaryotic cells. The filtrates were subsequently treated with a nuclease cocktail (contain DNase and RNase) to degrade free nucleic acids for 1.5 hr at 37°C. Both Viral RNA and DNA were extracted by using the QIAamp MinElute Virus Spin Kit (Qiagen, Germany) according to the manufacturer's protocol. The concentrations of nucleic acid were determined using the Qubit 4 (Invitrogen, Carlsbad, CA, USA).

For cDNA synthesis, the first strand was generated using the SuperScript III First-Strand Synthesis System (Invitrogen) with random hexamer primers, followed by second strand synthesis performed with Klenow fragment DNA polymerase (New England Biolabs, Ipswich, MA, USA) according to the manufacturer's protocol. Finally, three libraries were constructed using the XT DNA Sample Preparation Kit (Illumina, San Diego, CA, USA) and sequenced by the Illumina HiSeq instrument with dual barcoding for each pool, generating 250 bp paired-end reads. The original sequence data analyzed in our study have been deposited in the Genome Sequence Archive (Genomics, Proteomics, and Bioinformatics 2021) at the National Genomics Data Centre (Nucleic Acids Res 2021), China National Centre for Bioinformation, Beijing Institute of Genomics, and Chinese Academy of Sciences (GSA: PRJCA040738). It is also publicly available at https://ngdc.cncb. ac.cn/gsa. gsa.doc.faq.h4CB1.

Bioinformatics analysis

The paired-end raw reads of 250 bp generated by the HiSeq platforms were processed through customized analysis pipeline running on a 32-bit Linux operation system, following a standard procedure that included debarcoding, trimming, and assembling. Breafly, debarcoding was performed using the vendor software from Illumina, and duplicate reads with identical bases 5–55 were reduced to one copy. Tails of low-quality sequences were trimmed by Phred software with a quality score threshold of 10, and sequencing barcodes were removed by using VecScreen with default parameters. To prevent host and bacterial sequence interference, Bowtie2 software was employed to remove human, bacterial, and other eukaryotic genomic sequences from the data. Subsequently, the cleaned reads were subjected to *de novo* assembly via SOAPdenovo2, employing a Kmer size of 63 with default parameters. Contigs were compared against a customized viral proteome database by using BLASTx program build in diamond (v2.1.12) software, with an E-value cutoff of $<10^{-5}$. In order to remove the false positive hits, candidate viral contigs were further compared to an in-house nonvirus nonredundant protein database, which was extracted from virus kingdom of NR database from NCBI.

Sequences and phylogenetic analysis

The putative ORFs of the target virus were predicated by using Geneious Prime (2023.0.1 version) and NCBI ORFfinder (https://www.ncbi.nlm.nih.gov/orffinder/). The amino acid sequence regions selected for constructing the phylogenetic tree were based on the guidelines of the International Committee on Taxonomy of Viruses (ICTV). After conducting multiple sequence alignments with MAFFT, phylogenetic trees were constructed via the Maximum-Likelihood (ML) method in MEGA 12 software, with 1,000 bootstrap replicates.

Recombination analysis

To investigate potential viral recombination events, complete genomes of all available picornavirus and parvovirus strains in the GenBank database were retrieved, and multiple sequence alignments were performed by using MAFFT within Geneious Prime, alongside the viral sequences identified in this study. Potential parental sequences and recombination sites of the recombinant strains were identified using multiple approaches, including BootScan, RDP, MaxChi, SiSCan, Chimaera, GENECONV, LARD, and 3Seq, integrated in Recombination Detection Program (RDP, v5.0).

RESULTS

Viral metagenomic overview

Three libraries yielded 2,415,494, 447,690, and 154,420 clean sequence reads for fecal, kidney, and liver samples, respectively. The average GC contents (GC%) of the three libraries were 50.2%, 54.0%, and 53.6%, respectively. Viral reads constituted 170,006 (7.0%), 30,755 (6.8%), and 2,097 (1.4%) of the total clean reads in each library. *Parvoviridae* reads were the most dominant across all three libraries, representing 72.2% (feces), 98.2% (kidney), and 74.4% (liver) of viral reads. Additionally, *Picornaviridae* and *Microviridae* ranked second: *Picornaviridae* accounted for 20.8% of viral reads in feces, while *Microviridae* represented 1.1% (kidney) and 7.5% (liver), respectively (Fig. 1A). As depicted in the Upset diagram, at the family level, the three libraries shared six families, with the *Parvoviridae* family being the most predominant among them (Fig. 1B).

A parvovirus belonging to the parvovirinae subfamily of the parvoviridae

Due to the absolute dominance of parvovirus in all three libraries, the genome sequence of this virus was assembled, and its complete genome sequence was obtained. The genome of this parvovirus, named dependoparvovirus_CH_SH01 (GenBase accession no. GB0006231), was 5,045 nucleotides (nt) in length, which included a 414 nt inverted terminal repeat, a 1884 nt replication protein, a 2,199 nt structural protein, and an additional 413 nt inverted terminal repeat (Fig. 2A). The GC content of this genome was 47.0%. This strain shared the highest nucleotide identity (99.7%) with a goose parvovirus strain DY16 (GenBank accession no. MH209633), which was determined from China. Phylogenetic analysis indicated that this parvovirus, along with strain DY16, belonged to the Parvovirinae subfamily within the family Parvoviridae (Fig. 2B).

Two picornaviruses classified within the Megrivirus or Ludopivirus genus within the Kodimesavirinae subfamily

In the current study, two picornaviruses were identified. The genome of the Megrivirus strain, named megrivirus_CH_SH01 (GenBase accession no. GB0006182), was found to be 9,873 nucleotides long and contained a single open reading frame (ORF) that encoded a polyprotein, as well as a 5' untranslated region (UTR) and a 3' UTR at its respective ends (see Fig. 2A). At the genomic level, megrivirus_CH_SH01 shared the highest nucleotide identity of only 73% with a goose megrivirus isolate SC02/China/2023 (GenBank accession no. PQ368551), which was identified in Sichuan Province, China. Based on the phylogenetic trees constructed

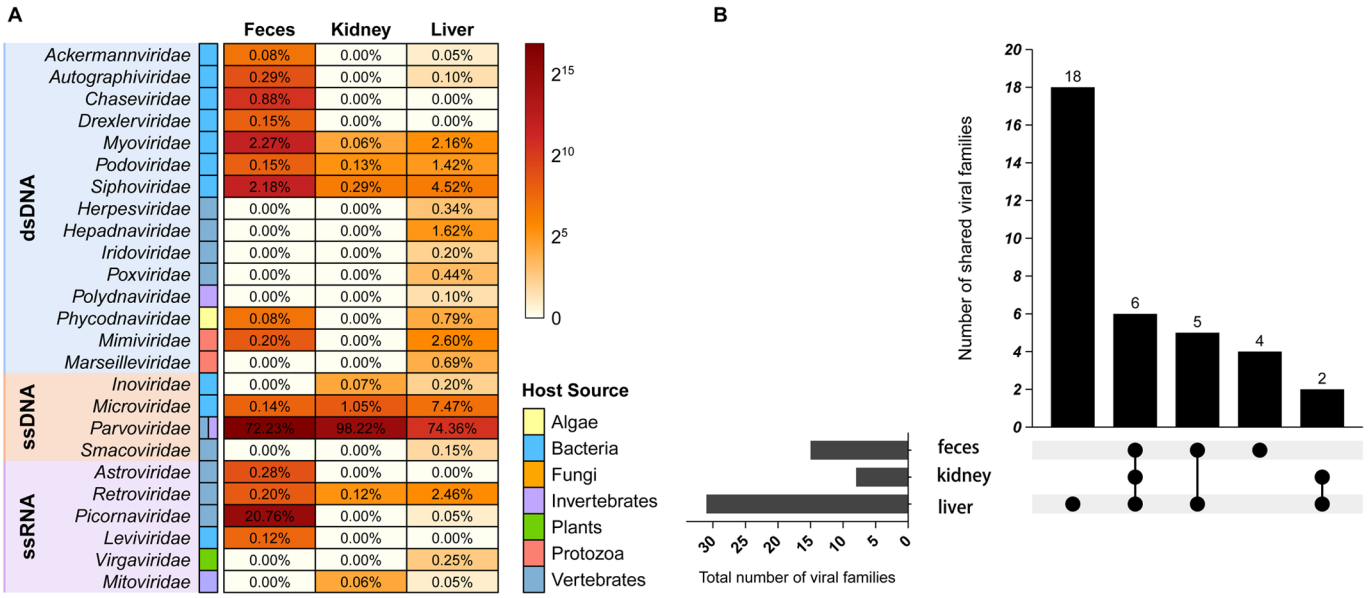

Fig. 1. Viral taxonomy and diversity analysis of the viruses in the three libraries at the family level. (A) A heatmap depicting the read counts of each viral family across libraries, presented on a $\log_2$ scale. Sample groups were color-coded according to the legend provided. (B) The UpSet plot illustrated shared and unique viruses at the family level across samples. Left-side horizontal bars depicted the number of viral libraries per farm; lines connecting dots denoted intersections between different libraries, where individual dots indicated library-specific viruses and connected nodes denote shared ones. Vertical bars indicated the count of elements in each corresponding intersection.

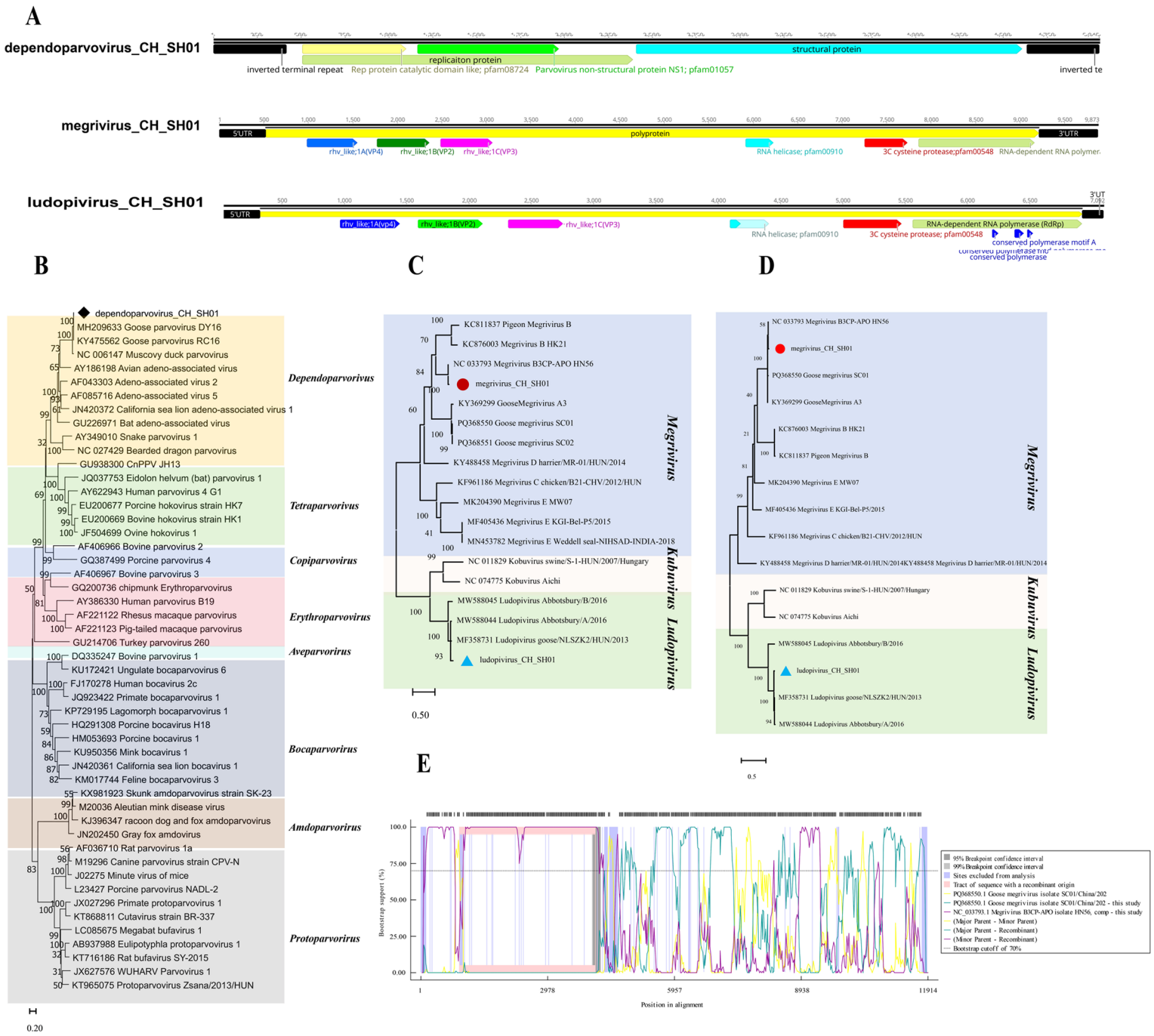

Fig. 2. Genomic structure, phylogenetic, and recombination analysis of parvovirus and picornavirus identified in the current study. (A) Genomic structure of dependoparvovirus_CH_SH01, megrivirus_CH_SH01, and ludopivirus_CH_SH01. (B) Phylogenetic tree of parvovirus based on the amino acid sequences of NS1, constructed using the maximum likelihood (ML) method with 1,000 bootstrap replicates. The strain obtained in this work was marked with a black diamond. (C) Phylogenetic tree of picornavirus based on the amino acid sequences of P1, constructed using ML method with 1,000 bootstrap replicates. The two strains identified in this work are marked with a red circle and blue triangle. (D) Phylogenetic tree of picornavirus based on the amino acid sequences of 3D, constructed by ML method with 1,000 bootstrap replicates. The two strains identified in this work are marked with a red circle and blue triangle. (E) Recombinant identification of the megrivirus_CH_SH01 strain. BOOTSCAN analysis provides evidence for the recombinant origin, based on pairwise distances, with parameters including a window size of 200, step size of 20, and 1,000 bootstrap replicates. Yellow and purple shaded boxes denote the parental strains.

from amino acid sequences of the p1 and 3D regions, this strain was classified within the *Megrivirus* genus of the *Kodimesavirinae* subfamily, closely related to a China goose megrivirus isolate HN56 (GenBank accession no. NC_033793) (see Fig. 2C and 2D). These two inconsistent clustering results suggested that megrivirus_CH_SH01 may be a recombinant strain. Subsequently, recombination analysis was performed based on the alignment of all available genomes, with the results revealing an obvious recombination event with megrivirus_CH_SH01 (GenBank accession no. PQ368550) (see Fig. 2E). The major parental strain was a goose megrivirus isolate SC01/China/2023, identified from Sichuan province of China, and the minor parent was isolate HN56, with the beginning and ending breakpoints located at 894 nt and 4113 nt, respectively.

Another picornavirus, named ludopivirus_CH_SH01 (GenBase accession no. GB0006239), measured 9,873 nucleotides in length and had a genomic structure similar to the previous one (Fig. 2A). This strain exhibited the highest nucleotide identity of 85.1% with a greater white-fronted goose (Anser albifrons) picornavirus 1 strain Abbotsbury/A/2016 from the United Kingdom. Based on the phylogenetic trees constructed from amino acid sequences of p1 or 3D regions, ludopivirus_CH_SH01 belonged to the *Ludopivirus* genus within the *Kodimesavirinae* subfamily.

DISCUSSION

Recent years, a novel form of goose gout disease, characterized by visceral urate deposition and accompanied by urate deposition in muscles, joints, or subcutaneous tissues, has caused substantial economic losses to the poultry industry in China. Numerous studies showed that gout in commercial farms arises from multiple factors, including nutritional imbalances, vitamin deficiencies, mycotoxin exposure, and pathogenic infections [12, 22]. It is believed that a series of novel GoAstV infection were the main causal pathogen for this disease [10, 23]. Studies have indicated that inoculating goslings with GoAstV isolates can induce gout; however, the mortality rate is significantly lower than that of natural infections. Additionally, the urate deposition lesions are less severe compared to those from natural infections [23, 26]. Moreover, studies have demonstrated that co-infection with other viruses, such as goose parvovirus, or different genotypes of GoAstV, can exacerbate the disease condition [15].

In our previous study, we isolated a recombinant novel type of GoAstV, which causes fatal gout in geese from China [19]. To determine if other causative viruses were present in these geese, fecal, kidney, and liver samples were deeply sequenced using viral metagenomics. Generally, bacteriophages dominate in fecal samples; however, this study found that parvovirus dominated in all three samples, ranging from 72.2% to 98.2%. Although the healthy goose virus community has not been reported, our researches on the virus community of healthy birds shows that the proportion of Parvoviridae generally does not exceed 35% [13, 18]. This suggested that parvovirus may play a partial role in the development of goose gout. Subsequently, The genome of this parvovirus was determined in this study, which shared a similar genomic structure and nucleotide identity with the DY16 strain determine in China. Due to the lack of research data, further research is needed to isolate the parvovirus, and conduct co-infection experiments with astronovirus to determine whether and how parvovirus exacerbates gout when co-infected with GoAstV.

Additionally, picornaviruses were found to account for the second largest proportion in fecal samples, indicating the necessity to consider whether this virus is related to the occurrence of gout. In this study, two picornaviruses classified within the Megrivirus or Ludopivirus genus of the Picornaviridae family were obtained. Phylogenetic analysis indicated that megrivirus_CH_SH01 was a recombinant strain. On the other hand, the genome sequence and genomic structure of ludopivirus_CH_SH01 were also elucidated. Currently, the sequence information of Ludovirus in databases such as GenBank is extremely limited (only 4 genome sequences), and to our knowledge, this strain is also the second strain identified in China.

To date, the association between parvoviruses and picornaviruses with goose gout remains unclear, and further investigations are warranted to address this research gap. To experimentally assess their role in coinfection with astrovirus in the context of goose gout, attempts were made to isolate these viruses via goose embryos but proved unsuccessful. Future studies will employ alternative approaches,including specific cell lines, for their isolation.

In summary, viral communities in fecal, kidney, and liver samples from geese with gout were described. Two viruses that predominated in these communities and were associated with gout formation were discovered using viral metagenomics. Subsequently, the genome sequences of two picornaviruses classified within the Megrivirus or Ludopivirus genera of the *Picornaviridae* family, one of which was a recombinant virus, as well as a parvovirus belonging to the *Parvovirinae* subfamily of *Parvoviridae*, were determined. On one hand, this study suggested that infections with viruses other than astrovirus may be associated with the occurrence of goose gout. On the other hand, this research enriched the genome database of Megrivirus and picornaviruses.

CONFLICT OF INTEREST. The authors declare no conflicts of interest associated with this manuscript.

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