Aquaculture 579 (2024) 740247

Contents lists available at ScienceDirect

Aquaculture

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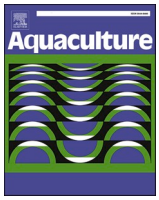

Full genome analysis of a novel genotype of *Decapod hepandensovirus 1* (DHPV) infecting Pacific whiteleg shrimp, *Penaeus vannamei*

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ARTICLE INFO

Keywords:
Decapod hepandensovirus 1
Hepatopancreatic parvovirus
Penaeus vannamei
Complete genome
Phylogenetic tree

ABSTRACT

Decapod hepandensovirus 1 (DHPV) is a viral pathogen that causes growth retardation and decreased feed conversion efficiency in penaeid shrimp. The virus exhibits high genetic variation between different hosts and geographical locations. It has been primarily reported in cultured *Penaeus monodon*, *P. chinensis*, and *P. merguiensis*, and a new type of DHPV has recently been reported in *P. vannamei* cultured in Korea and Taiwan. In this study, the genome of a recently reported new type of DHPV was fully sequenced by conventional Sanger sequencing combined with a next-generation sequencing approach. Similar to the other types of DHPVs infecting several shrimp species other than *P. vannamei*, a new type of DHPV contained a linear, single-stranded DNA genome of 6173 bp comprising three major open reading frames. However, by detailed comparative genome and phylogenetic analysis, the virus was not clustered with the pre-existing genotypes, suggesting the emergence of a possible novel genotype of DHPV in cultured shrimps. This study is the first to report the complete genomic sequence of DHPV identified in *P. vannamei*.

1. Introduction

The family *Parvoviridae* has a linear, single-stranded DNA genome that can infect both vertebrates and invertebrates. There are two subfamilies within *Parvoviridae*: *Densovirinae* and *Parvovirinae* (Pénzes et al., 2020). The subfamily *Densovirinae* consists of five genera, namely *Ambidensovirus, Brevidensovirus, Hepandensovirus, Iteradensovirus,* and *Penstyldensovirus*, with various invertebrates (insects, crustaceans, echinoderms, etc.) as hosts. Among these, the genus *Hepandesovirus* consists of a single species, *Decapod hepandensovirus 1* (DHPV), formerly known as the hepatopancreatic parvovirus.

Genetically, like any other virus in *Parvoviridae*, DHPV contains three major Open reading frames (ORFs): ORF2 (or Left ORF), ORF1 (or Mid ORF), and ORF3 (or Right ORF); encoding non-structural protein 2 (NS2), non-structural protein 1 (NS1), and viral capsid protein (VP), respectively (La Fauce et al., 2007; Sukhumsirichart et al., 2006). Three genotypes, Types I, II, and III, are currently defined based on the sequence of the ORF3 and the geographical region of the virus (Jeeva et al., 2012; Tang et al., 2008).

The first DHPV infection was reported from cultured *Penaeus merguiensis* and *P. semisulcatus* in Korea, Kuwait, and the Philippines (Lightner and Redman, 1985), and the virus has been found in various penaeid shrimps from many different parts of the world, including Australia, China, Korea, Southeast Asia, Kenya, Israel, and North and South America (Mahy and van Regenmortel, 2008). DHPV generally infects the hepatopancreas of shrimp and prawns, including several species of cultured shrimp, such as *Penaeus monodon, P. chinensis, P. merguiensis,* and *P. vannamei* (Lightner and Redman, 1985; Safeena et al., 2012). Although the virus does not cause significant mortality to the host, its chronic infection disturbs digestion and reduces the feed conversion ratio, leading to growth retardation and consequently substantial economic loss to shrimp farms. Recently, we reported the emergence

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https://doi.org/10.1016/j.aquaculture.2023.740247
Received 14 March 2023; Received in revised form 28 June 2023; Accepted 17 October 2023
Available online 19 October 2023

Table 1
PCR primers used in determining the new Korean DHPV sequence.

Primers	Sequence (5′-3′)	Reference
F1	CTCGATGAGGAGAGTTATGGACTT (24 mer)	This study
R1	CTATCATGAACTGCAGCACTTATA (24 mer)	
F2	CAAATTTGCACAGTGGTTGT (20 mer)	
R2	CTCAAACAGCGCGTCATAAA (20 mer)	
F3	GGACAGTAACAGCGGGAAGA (20 mer)	
R3	AAAACCACTTCGACCACTCG (20 mer)	
F4	TTGGCAAGCATGCAGTATGT (20 mer)	
R4	TCTTCACCAAGGGTCTGTCC (20 mer)	
F5	CCAGACCCAAAGGGTAATGA (20 mer)	
R5	TTCCCCTCATTAGCTGGTGT (20 mer)	
1414F	GTTAGGAATGGAAAGATGTGT (21 mer)	Jeeva et al., 2012
1750R	CTCCAATAAAATGTGTAAATGAGG (24 mer)	
3510F	ATTACTTTACTGGCGGCGATAG (22 mer)	Lee et al., 2022
5395R	AGTCTGTTACTCTTCATGGACC (22 mer)	
5137F	ACGACATGAACCAGACAAAAGTCACATCAG (30 mer)	
6235R	TCTGAAGGGTAAACCACGC (19 mer)	

Table 2
Detailed information of the 10 DHPV sequences used in this study.

Accession No.	Genotype	Origin	Host species
NC_014357	I	China	*P. chinensis*
AY008257	I	Korea	*P. chinensis*
JN082231	I	Korea	*P. chinensis*
EU247528	I	Madagascar	*P. monodon*
MT980830	I	Madagascar	*P. monodon*
EU588991	I	Tanzania	*P. monodon*
NC_011545	II	India	*P. monodon*
NC_007218	II	Thailand	*P. monodon*
DQ458781	III	Australia	*P. merguiensis*
ON872187	This study	Korea	*P. vannamei*

of a new type of DHPV from cultured *P. vannamei* in Korea (Lee et al., 2023). However, its genetic characterization was conducted using only partial ORFs of the virus, and the genome of the DHPV infecting *P. vannamei* was not fully elucidated.

Therefore, the present study provides the complete genomic sequence of DHPV infecting *P. vannamei* in Korea. Detailed comparative genome analysis indicates that the virus is a unique variant inconsistent with pre-existing DHPV genotypes infecting cultured shrimp species other than *P. vannamei*.

2. Materials and methods

2.1. Shrimp sample collection

Previously, a number of *P. vannamei* samples exhibiting growth retardation were collected from shrimp farms located in Incheon (Ganghwa-gun), Korea, in 2021 and diagnosed with DHPV by PCR assay (Jeeva et al., 2014) and histopathological examination (Lee et al., 2023). Among the collected samples, a representative sample (21-044B1) was used for sequence analysis.

2.2. Primer design and sequencing analysis

To determine the complete sequence of the viral genome, we first of all performed PCR assays and sequencing analysis using the sample DNA (21-044B1) and DHPV-specific primers, designed using Primer3 (version 2.3.7) based on the whole genome sequence (WGS) of three reference DHPV strains from *P. chinensis* (Korea), *P. monodon* (Madagascar), and *P. merguiensis* (Australia) (Accession No. AY008257, EU247528, and DQ458781, respectively). The primer information is presented in Table 1. Eight amplicons were obtained by PCR and sent for sequence analysis at Bioneer (Daejeon, Korea). Additionally, the DNA of the sample (21-044B1) was sent to Macrogen (Seoul, Korea) for next-generation sequencing (NGS) analysis to proofread the eight internal amplicons retrieved from PCR assays and to determine the sequence of the 5′ and 3′ termini of the viral genome. The extracted DNA samples were sequenced on a HiSeq X™ Ten platform (Illumina) by preparing a DNA library using the TruSeq® Nano DNA Library Prep Kit (Illumina).

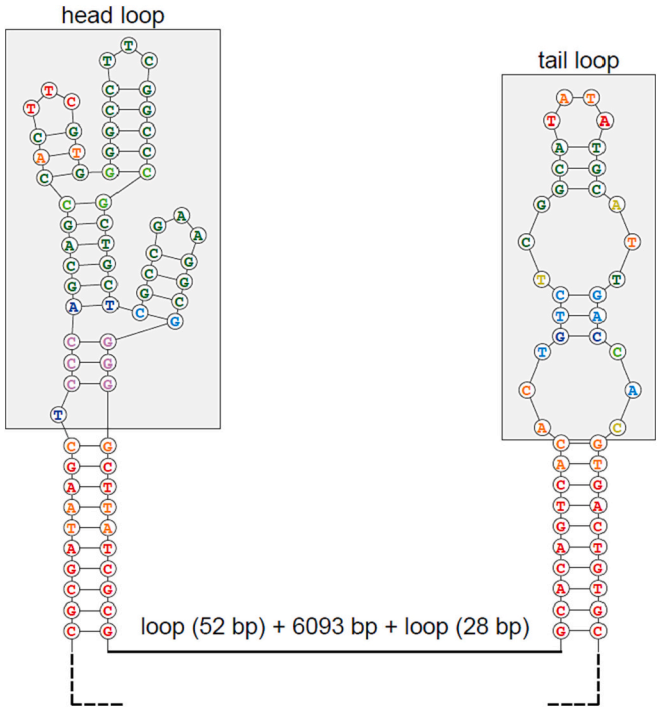

Fig. 2. The terminal structure of the 5′ and 3′ ends of the viral genome.

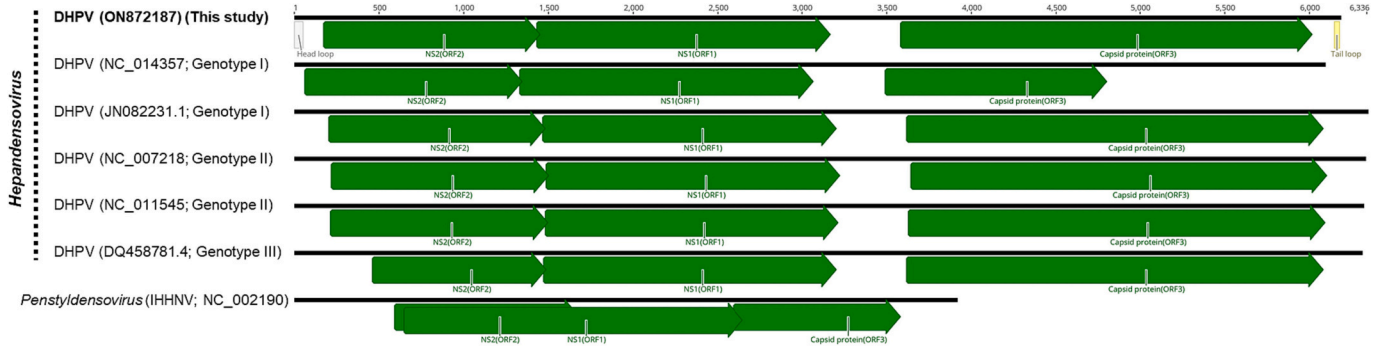

Fig. 1. Genomic organization of the representative DHPVs including the new genotype of Korean DHPV sequenced in this study.

Table 3
Nucleotide similarity and divergence estimated using whole genome (A), ORF1 (B), ORF2 (C), and ORF3 (D) obtained from the 10 DHPV isolates used in this study. The nucleotide similarities were analyzed and calculated % identity (percentage of bases/residues which are identical) using Geneious Prime (ver. 2023), and MEGAX (ver. 10.0) (Kumar et al., 2018).

(A)

Genome	NC_014357	AY008257	JN082231	EU247528	MT980830	EU588991	NC_011545	NC_007218	DQ458781
AY008257	91.4								
JN082231	91.6	98.8							
EU247528	85.6	86.4	86.2						
MT980830	84.7	85.8	84.4	96.7					
EU588991	84.7	86.7	86.5	88.9	88.2				
NC_011545	83.1	84.1	83.5	82.9	81.7	83.1			
NC_007218	82.4	82.8	82.8	82.8	81.4	82.4	87.7		
DQ458781	84.6	85.3	84.6	84.4	82.4	83.7	81.2	81.0	
ON872187	75.4	76.1	75.5	75.4	74.4	75.6	73.5	73.9	74.2

(B)

ORF1 (NS2)	NC_014357	AY008257	JN082231	EU247528	MT980830	EU588991	NC_011545	NC_007218	DQ458781
AY008257	96.3								
JN082231	95.9	98.3							
EU247528	88.0	87.0	87.1						
MT980830	86.3	86.0	85.4	99.1					
EU588991	85.9	86.0	86.1	94.2	93.5				
NC_011545	86.7	87.7	87.4	86.9	86.0	85.9			
NC_007218	86.0	85.6	85.4	86.6	84.1	84.2	87.8		
DQ458781	86.3	86.5	87.0	85.4	84.2	84.7	84.9	83.6	
ON872187	75.4	74.6	75.7	73.6	73.7	74.3	74.0	73.9	73.6

(C)

ORF2 (NS1)	NC_014357	AY008257	JN082231	EU247528	MT980830	EU588991	NC_011545	NC_007218	DQ458781
AY008257	96.3								
JN082231	96.4	98.9							
EU247528	91.0	91.2	90.6						
MT980830	90.7	90.7	90.2	99.3					
EU588991	90.1	89.8	89.6	92.3	91.9				
NC_011545	88.9	88.8	88.7	89.2	88.9	88.9			
NC_007218	87.6	87.9	87.6	87.8	87.3	87.5	89.0		
DQ458781	91.6	91.4	91.2	89.9	89.4	88.7	88.7	87.6	
ON872187	86.1	86.1	86.2	85.2	84.9	84.4	84.6	83.3	85.0

(D)

ORF3 (VP)	NC_014357	AY008257	JN082231	EU247528	MT980830	EU588991	NC_011545	NC_007218	DQ458781
AY008257	91.6								
JN082231	91.3	98.8							
EU247528	85.5	83.1	83.1						
MT980830	84.1	82.4	82.5	93.8					
EU588991	84.9	85.3	85.2	83.4	82.8				
NC_011545	81.9	79.5	79.1	77.8	77.8	78.4			
NC_007218	82.0	78.1	78.0	78.4	78.0	78.5	87.0		
DQ458781	82.5	80.9	81.1	81.0	79.3	80.4	78.1	77.4	
ON872187	71.0	71.2	71.3	70.7	71.1	71.7	69.9	70.7	70.1

Using the obtained reads (90,431,267,668 bp; 606,911,560 reads), the adapter-trimmed and quality-filtered reads were mapped against the reference genome of *P. vannamei* (NW_020868286.1), and only unmapped reads (1,039,451 bp; 6954 reads) against the reference shrimp genome were used for de novo assembly using SPAdes for the viral genome. Assembling the amplicons from PCR and analysis of the sequence obtained from NGS identified the complete genome sequence of DHPV from *P. vannamei*. The open reading frames (ORFs) were initially determined by the NCBI ORFfinder, and three major ORFs were confirmed by manual comparison with other DHPVs in the GenBank database. To determine the length and validate the structures of 5′ and 3′ terminals in the viral genome, Illumina sequencing reads (150 bp paired-end library) were aligned using the bowtie2 program (v2.4.2; Langmead and Salzberg, 2012), and the aligned reads on the terminal structures, including their flanking inverted repeat sequences, were manually validated by Geneious Prime (ver. 2023, https://www.geneious.com). To predict secondary structures of each terminal region in the viral genome, the DNA/RNA structure program (default options for analysis of DNA sequences; Web version, v6.0.1; https://rna.urmc.rochester.edu/RNAstructureWeb/Servers/Predict1/Predict1.html) was used. The determined DHPV sequence has been deposited in the GenBank database under accession No. ON872187.

2.3. Genome comparison and phylogeny

The complete sequences of the three major ORFs and WGS of DHPV (21-044B1 sample) were further compared to those of other DHPVs available in the GenBank database. First, nine complete (or almost

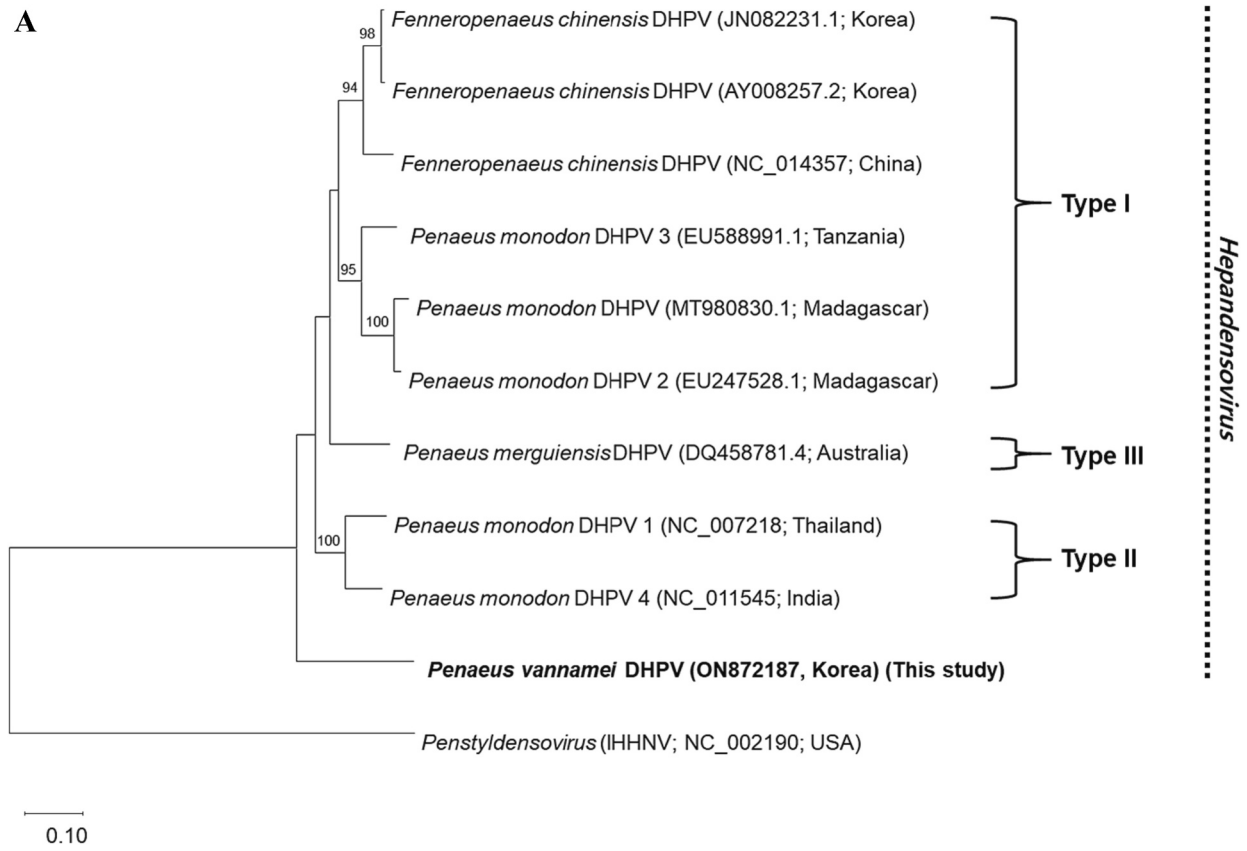

Fig. 3. Phylogenetic relationship among ten DHPV isolates based on the genomic DNA sequence (A), the deduced amino acid sequences of the 3 ORFs encoding non-structural protein 2 (NS2) (B), non-structural protein 1 (NS1) (C), and viral capsid protein (VP) (D). The numbers indicate the percentages of bootstrap support from 1000 replicates and only the values that are >70% are shown.

complete) viral genomes of DHPV identified in three penaeid shrimp from seven different countries were collected initially (Table 2). These included NC_014357 (China, *P. chinensis*), AY008257 (Korea, *P. chinensis*), JN082231 (Korea, *P. chinensis*), EU247528 (Madagascar, *P. monodon*), MT980830 (Madagascar, *P. monodon*), EU588991 (Tanzania, *P. monodon*), NC_011545 (India, *P. monodon*), NC_007218 (Thailand, *P. monodon*), and DQ458781 (Australia, *P. merguiensis*). Second, datasets of the DHPV genome and every three ORFs were constructed, obtained from the DHPV (21-044B1 sample). The nucleotide similarities were analyzed using Geneious Prime (ver. 2023), and MEGAX (ver. 10.0) (Kumar et al., 2018).

For phylogenetic analyses, the deduced amino acid sequences of the three ORFs from the previously collected datasets were subjected to Maximum-likelihood estimations with the Poisson substitution model using MEGAX (ver. 10.0) (Kumar et al., 2018) with 1000 bootstrap replications. Moreover, the phylogenetic position of the DHPV (21-044B1 sample) among the DHPVs was analyzed using the WGS obtained by Maximum-likelihood estimations with the Tamura-Nei substitution model using MEGAX (ver. 10.0).

3. Results

3.1. Identification of the DHPV genome

Assembly of the sequenced amplicons and NGS results yielded a 6173 nucleotide sequence. The genome included the complete length of all three major ORFs; ORF2 (1275 bp), ORF1 (1734 bp), and ORF3 (2430 bp), and each of the nucleotide sequences were deduced to be 425, 578, and 810 amino acids, respectively. The ORF2 and ORF3 are in the same reading frame. The ORF1, on the other hand, was in a different reading frame. There was a 16-nucleotide overlap between the ORF2 and the ORF1, and a 418-nucleotide gap between the ORF1 and the ORF3. The genome map and positions of each ORF are shown in Fig. 1. The 5′ and 3′ termini of the viral genome were estimated to be 52 and 28 bp, respectively. The terminal structure of the 5′ end (i.e., the head) of the viral genome includes three short stem-loop structures, and the 3′ end (i.e., the tail) has a continuous stem-loop structure with two internal loops (Fig. 2). The complete genome sequence of a DHPV (21-044B1 sample) identified in the present study has been deposited in the GenBank database under accession number ON872187.

3.2. DHPV genome comparison and phylogenetic analysis

The obtained WGS and three ORF sequences of a potential new type of DHPV (21-044B1 sample) identified in the present study were then compared with the other nine DHPV reference strains available in the GenBank database. The results show that among the new type of Korean DHPV (ON872187) and the nine reference strains, the ORF3 exhibited the lowest percentage identity among the three ORF sequences, ranging from 69.6% (DQ458781) to 71.3% (EU588991). The percentage identity of the ORF2 and ORF1 between the new type of Korean DHPV (ON872187) and the nine reference strains ranged from 73.6% (DQ458781) to 75.7% (JN082231), and 83.2% (NC_007218) to 86.2% (JN082231), respectively. In addition, the overall similarity among the DHPV strains was also lowest for the sequence of the ORF3. The percentage identities of WGS and each of the three ORFs among the DHPV sequences are shown in Table 3.

Phylogenetic analysis based on WGS and the three ORFs (Fig. 3)

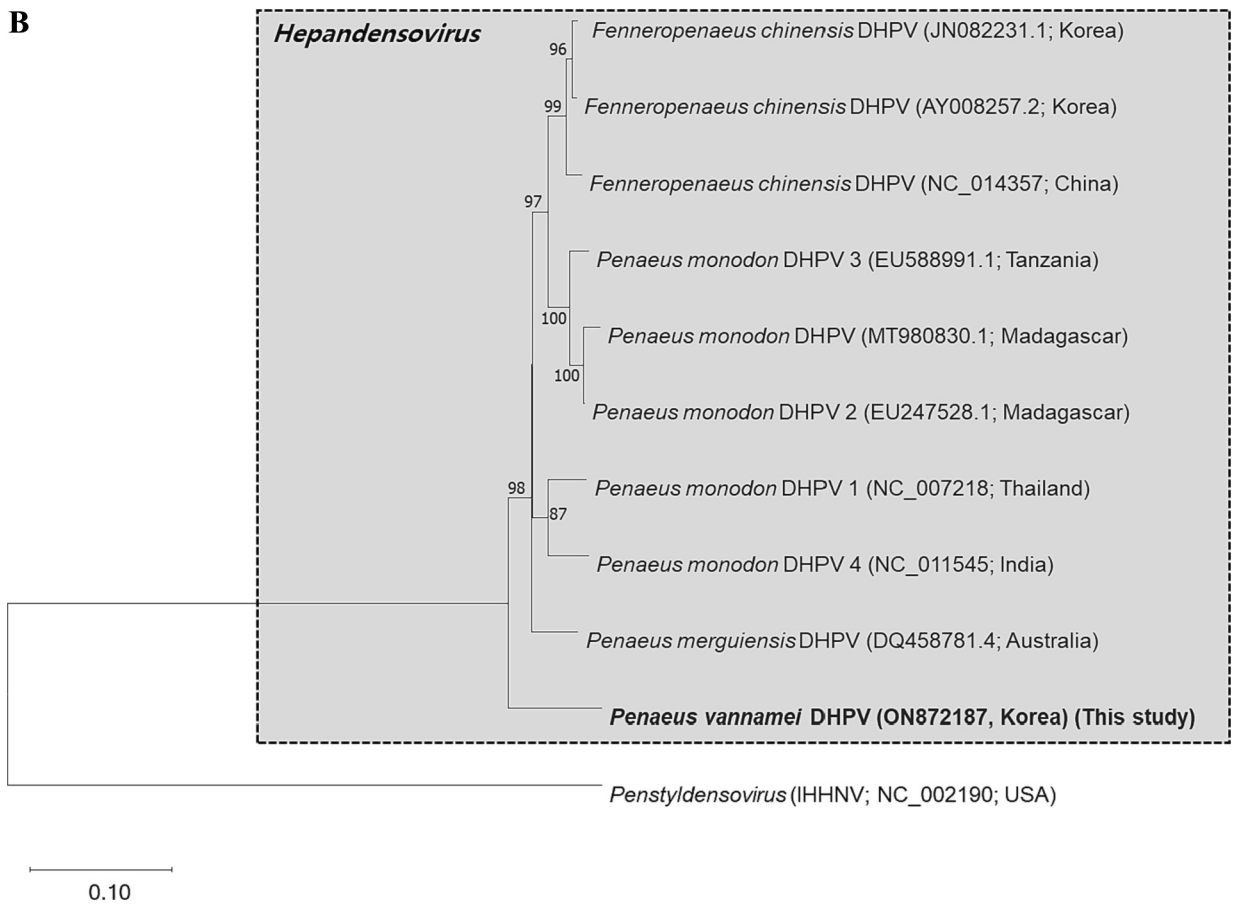

Fig. 3. (*continued*).

revealed the presence of three genotypes of DHPV. Type I: DHPV from *P. chinesis* (Korea and China) and *P. monodon* (Tanzania and Madagascar), Type II: DHPV from *P. monodon* (Thailand and India), and Type III DHPV from *P. merguiensis* (Australia), and previous reference DHPV strains were grouped within each genotype. However, the three ORFs and WGS of the Korean DHPV (21-044B1 sample) determined in this study were clearly separate from other known genotypes, thus indicating that the potential new type of Korean DHPV from *P. vannamei* could be considered a novel genotype of shrimp DHPV.

4. Discussion

To date, several DHPV strains have been isolated from many geographical locations, in various penaeid shrimp species (Mahy and van Regenmortel, 2008). However, all complete genome sequences of DHPV available in GenBank have been obtained from three penaeid shrimps: *P. monodon* (Safeena et al., 2010; Sukhumsirichart et al., 2006; Tang et al., 2008), *P. chinensis* (Bonami et al., 1995; Jeeva et al., 2012), and *P. merguiensis* (La Fauce et al., 2007). The genomic sequence of the virus exhibits high genetic diversity with respect to host and geographic location. For example, the nucleotide sequence of DHPV isolated from *P. chinensis* (JN082231) was 16% of the mean distance to DHPV isolates from *P. monodon* (DQ002873) and *P. merguiensis* (DQ458781) (Tang et al., 2008). The nucleotide sequences of Madagascar DHPV (EU247528) was 17% of the mean distance to isolates from Korea (AY008257), Thailand (DQ002873), Australia (DQ458781), and Tanzania (EU588991) (Tang et al., 2008). In contrast, Infectious hypodermal and hematopoietic necrosis virus (IHHNV), another virus belonging to the family *Parvoviridae*, showed only 4% variation in genomic sequences. (Tang et al., 2003).

Among the three major ORFs of the viral genome, the ORF3, which encodes VP, exhibits the highest variation (Tang et al., 2008), which is responsible for the high genetic variation of the virus. This is consistent with the results of the present study; sequence comparison showed that the ORF3 had the lowest shared identity among the three ORFs that were compared (Table 3). In previous studies, phylogenetic analysis was based on the ORF3 sequence, which classifies three known DHPV genotypes, and genetic variation was primarily associated with the geographical distribution of the host (Jeeva et al., 2012; Tang et al., 2008). However, the existing genotype variations grouped by geographical distribution were considered to be tentative due to the exception of genotype I (Tang et al., 2008); the distance between Korea and Madagascar or Tanzania is over 6200 miles by air, not even in the same ocean, whereas the viruses in genotypes II and III were isolated within a radius of a few hundred miles, all in the South Pacific. Thus, the establishment of a new grouping of viruses should be considered, and more studies regarding the isolates around the world are needed to accurately classify the virus.

The WGS comparison between the new type (ON872187) and previously reported types (AY008257, JN082231) of Korean DHPV also highlights the need for a new grouping of the virus. The WGSs of two previously reported types of Korean DHPVs identified from *P. chinensis* (AY008257 and JN082231) shared 98.8% nucleotide identity with each other. However, the WGS of the new type of Korean DHPV identified from *P. vannamei* (ON872187) was inconsistent with these two previous Korean DHPVs, sharing only 76.1% identity with AY008257 and 75.5% identity with JN082231. Furthermore, nucleotide sequence comparisons among the nine reference strains yielded consistent results. The nucleotide identity among the nine previous reference DHPVs ranged from 81.0% to 98.8% based on WGS, and 77.4% to 98.8% based on the

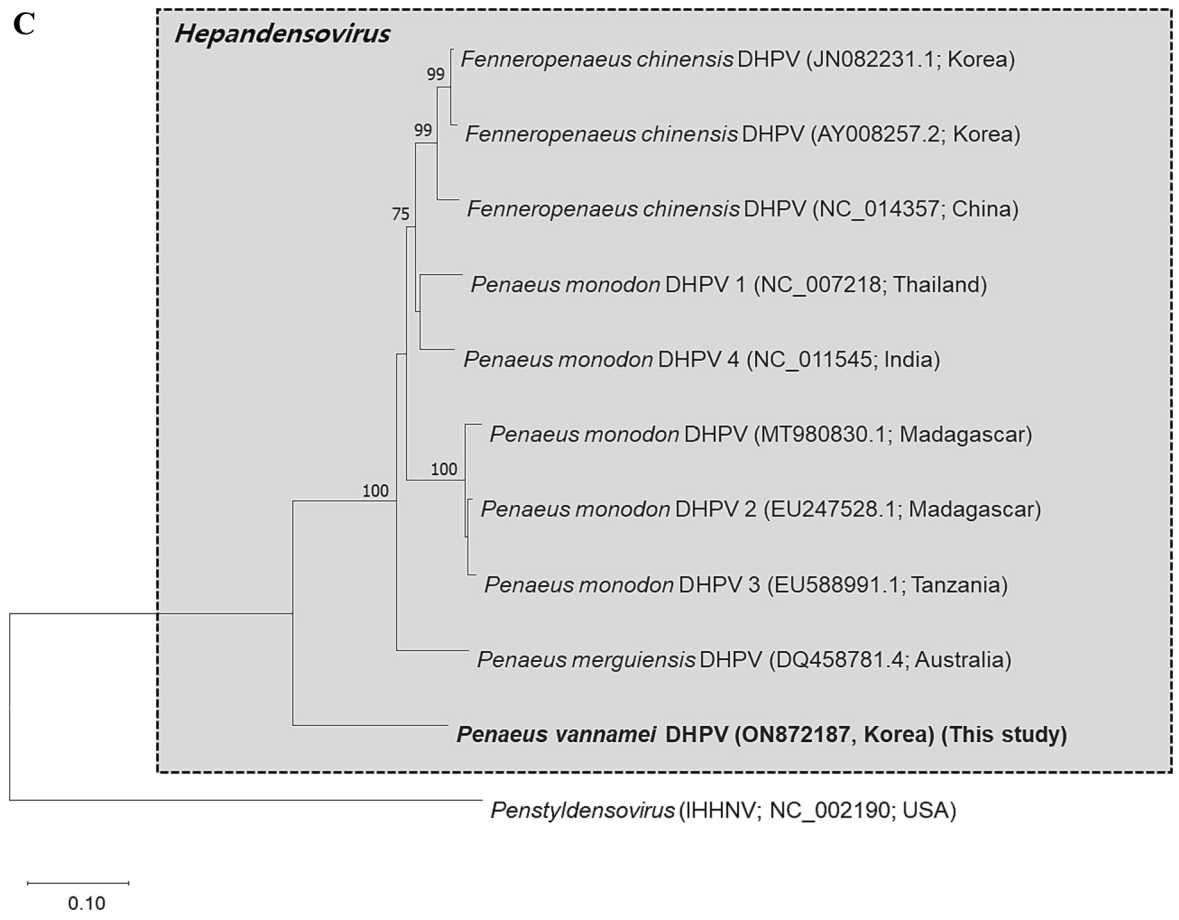

Fig. 3. (*continued*).

ORF3 sequence. However, DHPV from the present study shares a lower identity, 73.5% to 76.1% based on WGS, and 69.9% to 71.7% based on the ORF3 sequence, with all known DHPVs. Moreover, phylogenetic analysis showed that the new type of Korean DHPV was separated from the known genotypes (I, II, and III) into a distinct clade. These results indicate that the new type of Korean DHPV is distinguishable from the historic reference strains; thus, DHPV identified from *P. vannamei* in Korea in 2021 should be considered a novel genotype. In addition, a comparison of VP sequences between the new type of Korean DHPV and the recently discovered possible novel genotype of DHPV from Taiwan, also isolated from *P. vannamei* (Lee et al., 2022), showed that both sequences shared 99.3% identity, thus supporting the possibility of an emerging new genotype of DHPV.

Several previous studies have shown the prevalence of DHPV in both wild and cultured shrimps and various marine organisms. Wild stocks exhibit an exceedingly high prevalence of DHPV; *P. merguiensis* from New Caledonia (over 95%) and *P. monodon* from Madagascar (over 90%, by histology) are suspected to be infected with DHPV (Groumellec et al., 2011; Tang et al., 2008). Our previous study showed that the new type of DHPV is already widespread among Korean shrimp farms, and it is detected not only in cultured shrimp but also in pond water, shrimp feces, feed, and other marine organisms such as crabs and barnacles (Lee et al., 2023). These results suggest the spreading of DHPV within wild and farmed shrimp stocks and that various factors could facilitate viral infection. The impact on farmed shrimp is debatable, however, since previous studies showed varying results; no negative effects on shrimp growth were observed in Madagascar (Groumellec et al., 2011) whereas farmed *P. monodon* in Thailand exhibited growth reduction related to DHPV infection (Flegel et al., 1999) or even mass mortalities have been observed (Manivannan et al., 2002). In addition, DHPV is often found concurrently infected with other pathogens, such as *Enterocytozoon hepatopenaei* (Lee et al., 2022; Singaravel et al., 2021) or yellow-head disease (Chantanachookin et al., 1993), which significantly increases mortality rates (Singaravel et al., 2021).

Worldwide cultured shrimp production is steadily rising, exceeding 50 million metric tons in 2019, and *P. vannamei* accounted for over 76% of the total production (Anderson et al., 2017). Although DHPV is known to infect all penaeid shrimp species, DHPV in *P. vannamei* has been overlooked. Despite the conflicting impact of the virus, the emergence of a possible novel genotype of DHPV emphasizes the need for detailed investigations regarding the geographical expansion of the virus, given that the changes in genomic sequence, even by a small percentage, potentially lead to a virus with different properties and characteristics, such as changes in gene expression or protein structure and function, thereby potentially affecting the virulence and transmission of the virus. Further epidemiological investigations, such as relationships between the genetic variation of the virus and the host species or geographical distribution, are needed for a better understanding of the virus and to prepare sufficient preventive measures in the future. Detailed analysis of the viral genome would provide valuable information for understanding the evolution of the virus and developing effective strategies for the prevention and treatment of the recently emerging novel genotype DHPV infecting *P. vannamei* and associated diseases.

CRediT authorship contribution statement

Bumkeun Kim: Writing – original draft. **Chorong Lee:** Formal analysis. **Hye Jin Jeon:** Formal analysis. **JunMo Lee:** Formal analysis. **Patharapol Piamsomboon:** Writing – review & editing. **Ji Hyung Kim:**

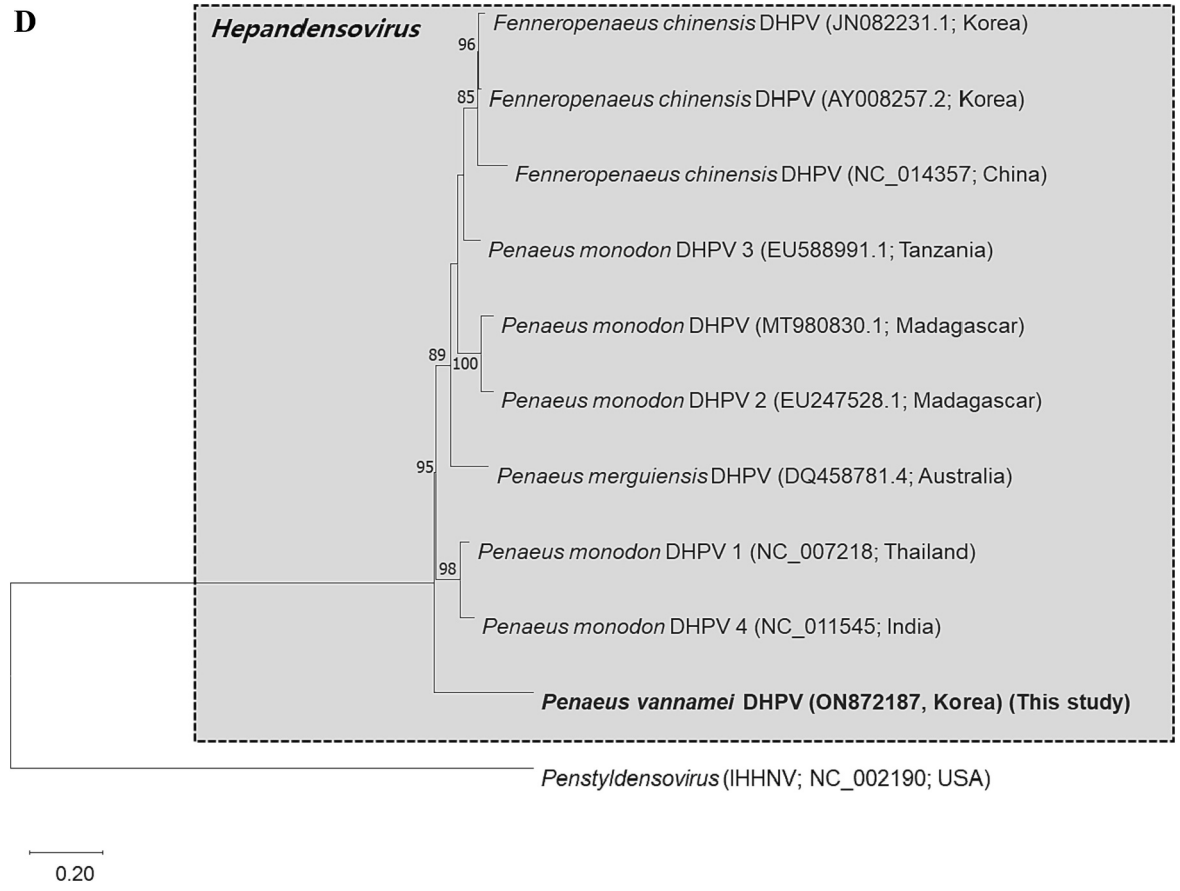

Fig. 3. (*continued*).

Supervision. **Jee Eun Han:** Supervision.

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.

Data availability

Data will be made available on request.

Acknowledgements

This research was supported by the 2022 grant from the Korean Society of Ginseng, and Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (NRF2019R1C1C1006212, NRF2021R1I1A1A01040303 and NRF-2022R1I1A3066435). The work was also supported by Development of technology for biomaterialization of marine fisheries by-products of Korea institute of Marine Science & Technology Promotion (KIMST) funded by the Ministry of Oceans and Fisheries (KIMST-20220128). Also, this work was supported by College of Veterinary Medicine & Institute for Veterinary Biomedical Science, Kyungpook National University.

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