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## An emerging shrimp pathogen: Decapod iridescent virus (DIV1)

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### Abstract

Shrimps are the most widely traded commodity among crustaceans globally. Intensification and diversification of culture practice increase the stress and susceptibility to new pathogens, affecting the sustainability of shrimp farming. Decapod Iridescent Virus (DIV1) is a nucleocytoplasmic double-stranded virus that belongs to the genus *Decapodiridovirus* and the *Iridoviridae* family that has been reported from farmed and wild captured crustaceans in China and Thailand. Clinical signs including colour fading and atrophy of the hepatopancreas and an empty gut has been observed. It is extremely likely to have a huge impact on shrimp farming since the cumulative mortality of up to 80% was recorded. Research on DIV1 is centred on viral entry, pathogenesis, epidemiology, and molecular diagnostics. Currently, DIV1 is also included as “an OIE listed pathogen” (OIE., 2021). This review will provide an overview of aetiology, genome, susceptible species, diagnostic methods, and current progress on the DIV1.

**Keywords:** DIV1, shrimp virus, SHIV, shrimp farming

### 1. Introduction

Shrimp farming represents the rapidly growing aquaculture sector because of its growing international demand and market price. Global crustacean production was 9386.5 thousand tonnes with an estimated value of USD 69.3 billion, with *Penaeus vannamei* accounting for 4966.2 thousand tonnes (FAO, 2020) [8]. The shrimp farming industry started to progress considerably in coastal regions of Southeast Asia in the 1970s. Although *P. monodon* was desired for several years, it was successively replaced by *P. vannamei* due to the latter's increased productivity and reduced susceptibility to disease (Thornber *et al.* 2020; Vaiyapuri *et al.* 2021) [32, 33]. On the other hand, Freshwater prawn farming is increasing at a slower pace and the two important species commonly farmed are *Macrobrachium rosenbergii* (giant river prawn) and *M. nipponense* (Oriental river prawn) (Thornber *et al.*, 2020; Vaiyapuri *et al.* 2021) [32, 33]. In India, shrimp production increased significantly after introducing Pacific white leg shrimp, *P. vannamei*, in 2009. Frozen shrimp is the major item exported from India, with an estimated value of US \$ 4426 million. As the second-largest aquaculture producing country, Indian shrimp production was 1.67 lakh tonnes (MPEDA,2021) [11].

Intensification of culture practices with increased stocking density and stress leads to disease incidence in shrimp. Diseases caused by bacteria, viruses, and Microsporidians remain a major menace in Asia's shrimp farming (Thitamadee *et al.*, 2016) [31]. In the past, the most catastrophic loss in shrimp farming was due to viruses like White Spot Syndrome Virus (WSSV), Infectious Hypodermal and Hemopoietic Necrosis Virus (IHHNV) and Taura Syndrome Virus (TSV) (Wang *et al.*, 2017) [34]. In India, the occurrence of infectious disease in shrimp led to a probable overall loss of 49%, with an estimate of 0.21 million metric tons of shrimp valued at US\$1.2 billion (Patil *et al.*, 2021) [19]. The shrimp diseases in Asia include several new emerging and emerged diseases, namely Acute Hepatopancreatic Necrosis Disease (AHPND), Aggregated Transformed Microvilli (ATM), Covert Mortality Disease (CMD), Hepatopancreatic Microsporidiosis (HPM), and Hepatopancreatic Haplosporidiosis (HPH) (Thitamadee *et al.*, 2016) [31]. In recent times, DIV1 reported from China is emerging as a new viral pathogen. The high fatality rate and diverse host range that DIV1 infects make it even more concerning, threatening the sustainability of shrimp farming. Currently, DIV1 is included as an “OIE listed pathogen” (OIE.,2021)

Iridoviruses are nucleocytoplasmic, icosahedral viruses with a linear, double-stranded DNA genome of 103 – 220 kbp, which mostly infect invertebrates and poikilothermic vertebrates (Chinchar *et al.*, 2017; Ince *et al.*, 2018) [5]. The virion core contains a single linear double-

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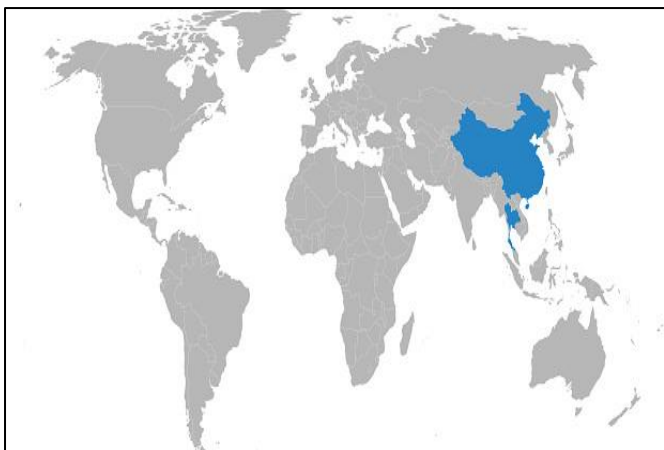
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stranded DNA (dsDNA) molecule of 140–303 kbp that includes unique and terminally redundant sequences (Jancovinch *et al.*, 2012; Qiu *et al.*, 2017) [15, 21]. It comprises an extensive host range and a huge variation in virulence over species (Eaton *et al.*, 2010) [7]. The *Iridoviridae* family has six genera: *Chloriridovirus*, *Decapodiridovirus*, *Iridovirus*, *Megalocytivirus*, *Lymphocystivirus*, and *Ranavirus* (Chinchar and Duffus, 2019) [6]. Amid them, iridescent viruses infecting the invertebrates may be transmitted via endoparasitic wasps, parasitic lines, or cannibalism (King *et al.*, 2012). *Lymphocystivirus*, *Ranavirus*, and *Megalocytivirus* were described in over 140 aquatic vertebrates like amphibians, fish, and reptiles, causing huge losses in animal conservation programs and breeding all over the world (Zhang and Gui, 2015) [38].

Montanie *et al.*, 1993 [18] reported an Irido-like virus in marine crab *Macropipus depurator* that infects crustaceans. Lightner and Redman (1993) [17] were the first to discover an iridescent virus infecting the Shrimps in Ecuador. Tang *et al.* (2007) [30] detected the iridescent virus cultured *Acetes erythraeus* in Madagascar, and they reported it as a new iridovirus (*Sergestid iridovirus*, SIV) through sequencing. Piégu *et al.* (2014) [20] detected an invertebrate iridescent virus 31 (IIV-31) in the pill bug *Armadillidium vulgare*. In China, Xia *et al.* (2016) found a new iridescent virus from the red claw crayfish *Cherax quadricarinatus*, named *Cherax quadricarinatus* iridovirus (CQIV). Following this discovery, Shrimp Hemocyte Iridescent Virus (SHIV) was reported from *P. vannamei* in China by Qiu *et al.* (2017) [21]. It was assigned to a new genus, '*Xiairidovirus*', a member of the *Iridoviridae* family. Based on the two isolates, SHIV 2014I215 and CQIV CN01 (ICTV, 2019), the International Committee on Taxonomy of Viruses (ICTV) designated it a new genus, *Decapodiridovirus*, in the *Iridoviridae* family. Despite all the crustacean species it infects, *P. vannamei* has a greater economic impact since it is a highly traded commodity among the crustaceans.

## 2. Geographical distribution

Since 2014, DIV1 occurrence has been recorded in China's coastal provinces, including Zhejiang, Guangdong and Hebei Provinces (Qiu *et al.*, 2017) [21]. Target surveillance conducted in China from 2017 to 2018 explained that DIV1 was found in 11 of 16 provinces (Qiu *et al.*, 2019b; Qiu *et al.*, 2018c) [27, 26]. DIV1 was also reported in wild *P. monodon* brooders captured from the North-eastern Indian Ocean (Srisala *et al.*, 2021) [29]. There are currently no reports of DIV1 in India.



**Fig 1:** Geographical Distribution of DIV1

## 3. Host range & Strain

Susceptible species include *C. quadricarinatus*, *Exopalaemon carinicauda*, *Macrobrachium nipponense*, *M. rosenbergii*, *Penaeus vannamei*, and *Procambarus clarkii*, *P. monodon* (Chen *et al.*, 2019a; Qiu *et al.*, 2017; Qiu *et al.*, 2019a; Xu *et al.*, 2016; Srisala *et al.*, 2021) [21, 25, 37, 29]. The experimental infection has been found in two crab species, namely *Eriocheir sinensis*, *Pachygrapsus crassipes* (Pan *et al.*, 2017). Positive PCR results have been reported for *Macrobrachium superbum*, *Penaeus chinensis*, *Penaeus japonicus*, *Nereis succinea* or some cladocerans (Qiu *et al.*, 2017; Qiu *et al.*, 2018c; Qiu *et al.*, 2019a; Qiu *et al.*, 2019b) [21, 26, 25, 27]. Complete genomic sequences alignment imparted that SHIV and CQIV could be distinct genotypes or strains of the same species of Virus (Qiu *et al.*, 2018a) [22]. Chen *et al.* (2019) [3] proposed the name *Decapod iridescent virus 1* (DIV1) concurrently when its infection in *Exopalaemon carinicauda* was reported. Later in 2019, SHIV and CQIV were considered as two virus isolates of *Decapod Iridescent Virus* (DIV1) by the International Committee on Taxonomy of Virus (ICTV).

## 4. Susceptible life stage

In experimental studies of *P. vannamei*, clinical signs of DIV1 and mortality were detected in PL to sub-adult shrimps (Qiu *et al.*, 2017) [21]. Targeted surveillance for DIV1 in China from 2017-2018 revealed that the virus was found in crayfish and shrimp in all age and length groups. 4 to 7 cm was the size range in which the maximum detection rate was reported (Qiu *et al.*, 2018c; Qiu *et al.*, 2019b) [26, 27].

## 5. Transmission

Experimental studies in *P. vannamei* and *E. carinicauda* through oral and reverse gavage have proved horizontal transmission is a major route of transmission (Qiu *et al.*, 2017; Chen *et al.*, 2019) [21, 3]. There is no proof of vertical transmission, but samples from hatcheries were found as DIV1 positive (Qiu *et al.*, 2018c; Qiu *et al.*, 2019b) [26, 27]. The biophysical attributes of the virus are not yet studied, so it is challenging to determine the relevance of indirect transmission by fomites (Qiu *et al.*, 2018c) [26].

## 6. Viral genome

DIV1 belongs to the genus *Decapodiridovirus*, a large (150 nm) icosahedral virus that infects penaeid shrimp (SHIV) and crayfish (CQIV) (Qiu *et al.*, 2019) [27]. *Decapodiridovirus* genomes have a G+C content of 34.6% and have 170 putative ORFs (Qiu *et al.*, 2017) [21]. The complete genome sequence of SHIV is a double-stranded DNA molecule 165,908 bp long, and the virion core includes both unique and terminally redundant sequences. Dot plot analysis showed that the longest repetitive region was 320 bp in length, including 11 repetitions of an 18-bp sequence and 3.1 repetitions of a 39-bp sequence (Qiu *et al.*, 2017) [21].

Phylogenetic analysis of conserved proteins based on multiple alignments proves that CQIV clusters with the *Iridoviridae* family are placed in a distinct clade from all the five known genera. It indicates that CQIV may represent a new genus in the *Iridoviridae* family. The comparison of SHIV with other members of the *Iridoviridae* family showed that the SHIV genome is quite larger than the members of the genera *Ranavirus* (103,681-140,131 bp) and *Megalocytivirus* (110,104- 112,636 bp) but smaller than the *Iridovirus* genera (197,693-220,222 bp) and the *Chloriridovirus* IIV-3 (191,100

bp). The G+C ratio of the SHIV genome is 34.6%, which is higher than the members of the *Iridovirus* genera (28.1-30.9%), except IIV-31 (35.09%) and *Lymphocystis* (27.3-33.0%), but lower than the members of the *Megalocytyivirus* genera (53.0-55.0%) and *Ranavirus* genera (48.6-57.0%) and the Chloriridovirus IIV-3. Thus, the phylogenetic trees showed that the members of the five genera of the *Iridoviridae* family formed discrete branches, and there was high bootstrap support (100%) for SHIV forming a new branch in the subfamily *Betairidovirinae*. Qiu *et al.* (2017)<sup>[21]</sup> suggested assigning SHIV to a new genus, tentatively named “*Xiairidovirus*,” which includes iridescent viruses that infect shrimp, lobster, or crayfish.

## 7. Target organs

DIV1 mainly targets hematopoietic tissue and hemocytes in the gills, hepatopancreas, pereopods, and muscle of *P. vannamei* (Qiu *et al.*, 2017; Xu *et al.*, 2016)<sup>[21, 37]</sup>. The sporadic infection has been recorded in the sub-cuticular epithelium, i.e., embryonic ectodermal origin and the lymphoid organ (Sanguanrut *et al.*, 2021)<sup>[28]</sup>.

## 8. Disease diagnosis

### 8.1. Clinical Signs

Pale and atrophied hepatopancreas, softshell, empty gut, and a reddish discoloration in the body were observed in the diseased *P. vannamei* (Qiu *et al.*, 2017)<sup>[21]</sup>. In addition to this, “Whitehead” and “yellow gills” were observed in the infected *M. rosenbergii*. The white head condition may be due to the white area under the carapace of the rostrum base, hence the name “Whitehead” disease. This condition was not observed in other species in which DIV1 was reported and can be used in field diagnosis of DIV1 in infected *M. rosenbergii* (Qiu *et al.*, 2019a)<sup>[25]</sup>. The cumulative death might reach up to 80%, and the moribund shrimp tend to sink to the pond bottom where the dead shrimp aggregates. In addition to the above signs, black body and black edge of the abdominal shell of dead individuals of experimentally infected *P. monodon* (He *et al.*, 2021)

### 8.2. Histology

The presence of distinct, lightly basophilic viral inclusions in the cytoplasm of hematopoietic tissue cells (HPT) is considered pathognomic for DIV1 (Qiu *et al.*, 2017; Qiu *et al.*, 2020)<sup>[21, 24]</sup>. Dark eosinophilic cytoplasmic inclusions consisting of tiny basophilic staining and pyknosis of hemocytes in the cuticular epithelium, hematopoietic cells, and hepatopancreatic sinus were seen in the histological sections of *Exopalaemon carinicauda* (Chen *et al.*, 2019)<sup>[3]</sup>. Sanguanrut *et al.* (2020) reported infection in the lymphoid organ (LO) characterized by loss of tubule structure and the presence of basophilic cytoplasmic inclusions comprising pyknotic and karyorrhectic nuclei. The LO abnormalities include LO-tubular matrix disarrangement, atypical nuclear morphology, karyorrhectic and pyknotic nuclei that cannot be distinguished from basophilic, cytoplasmic viral inclusions, which is similar to that of yellow head virus (YHV) LO pathology (Chantanachookin *et al.*, 1993)<sup>[2]</sup> and hence not adequate for a specific diagnosis of DIV1 infection.

### 8.3. Molecular diagnosis

A nested PCR assay for detection of SHIV was developed by Qiu *et al.* (2017)<sup>[21]</sup>, targeting the ATPase gene. Recently, Srisala *et al.* (2021)<sup>[29]</sup> developed nested PCR designed from

different target regions, ATPase and MCP genes. The LAMP assay was first developed by Chen *et al.* (2019)<sup>[3]</sup> for the detection of DIV1. Gong *et al.* (2021) developed qLAMP with a detection limit of  $1.9 \times 10^2$  copies/ $\mu$ l with diagnostic Specificity (DSp), and diagnostic sensitivity (DSe) of qLAMP were 100% and 85.71%, respectively. TaqMan probe-based real-time PCR was developed to detect DIV1 (Qiu *et al.*, 2018a; Qiu *et al.*, 2020)<sup>[22, 24]</sup> which may provide the advantage of real-time monitoring. Real-time PCR developed by Qiu *et al.* (2020)<sup>[24]</sup> was more sensitive than Qiu *et al.* (2017)<sup>[21]</sup>, Qiu *et al.* (2018a)<sup>[22]</sup> and Chen *et al.* (2019b). Recently, Gong *et al.* (2021) developed qPCR targeting ATPase gene, which has the minimum detection limit of  $1.9 \times 10^1$  copies/ $\mu$ l. Another LAMP assay was designed by Sanguanrut *et al.* (2021)<sup>[28]</sup>, targeting ATPase and MCP genes.

In situ Hybridization (ISH) developed by Qiu *et al.* (2017)<sup>[21]</sup>, targeting the MCP gene detected positive in the hemocytes in gills, hepatopancreas, and pereopods hematopoietic tissue. Sanguanrut *et al.* (2021)<sup>[28]</sup> observed strong positive ISH reactions in hepatopancreas and lymphoid organs. In situ digoxigenin-labelled loop-mediated isothermal amplification (ISDL) showed blue signals in hematopoietic tissue, haemocytes in the hepatopancreatic sinus and gills, some R- cells, myoepithelial fibres of hepatopancreas, coelomosac epithelium of the antennal gland and ovaries epithelium in *M. rosenbergii*. Besides, a similar distribution of positive signals were observed in the hepatopancreas of *M. nipponense* and *P. clarkii* and no signals were detected in cladocerans and uninfected prawn and crayfish sections (Qiu *et al.*, 2019). Similar observations were seen in *E. carinicauda*, but no positive reaction was observed in the cuticular epithelium of *P. vannamei* (Chen *et al.*, 2019)<sup>[3]</sup>. These results prove that there is a difference in tissue tropism between *E. carinicauda* and *P. vannamei* to DIV1 infection. Other than the above observations, a positive signal was reported in the Lymphoid organ section of *P. vannamei* (Sanguanrut *et al.*, 2021)<sup>[28]</sup>

Recombinase polymerase amplification (RPA) facilitates PCR-like DNA amplification via binding of three core proteins, isothermal recombinase, single-strand DNA binding protein, and strand-displacing polymerase compared with qPCR, RPA does not need sophisticated equipment for thermal cycling with comparable sensitivity and specificity (Xia *et al.*, 2014; Xia *et al.*, 2015)<sup>[36, 35]</sup>. But, RPA needs a lengthier primer (approximately 30–35 nucleotides) than that of PCR. Hence, multiple factors should be considered while designing primers, including amplification efficiency, hairpin structure, mismatch, and primer dimer. In the RPA-based study by Chen *et al.* (2021)<sup>[10]</sup>, the sensitivity was 11copies (0.05 fg) per reaction, which was better than the nested PCR developed by Qiu *et al.* (2017)<sup>[21]</sup>.

Recently, a new method that works on the basis of Nuclei acid Isothermal Amplification technology (LAMP with Mn-quenched calcein) was developed by Cao *et al.* (2020)<sup>[11]</sup> to detect DIV1 and seven other pathogens, including WSSV, EHP, IHNV, AHPND, YHV-8 TSV, and CMNV known as Micro-detection Slide system. It can detect up to four groups of samples for eight different shrimp pathogens at a minimum cost. It possesses the advantages like high throughput nucleic acid detection technology and high portability. The method's detection limit is  $10^2$  copies/ $\mu$ l with a varying diagnostic sensitivity of 75% to 100% and diagnostic specificity of 100%.

#### 8.4. Electron Microscopy

Most DIV1 particles were observed with a mean diameter of about 157.9 nm (Qiu *et al.*, 2019) [27]. The icosahedral morphology and intracytoplasmic location of virions were similar in the reports of DIV1 infections in *P. vannamei* or *C. quadricarinatus*, *Pr. clarkii*, *P. vannamei* and *M. rosenbergii* (Qiu *et al.*, 2017; Li *et al.*, 2017; Qiu *et al.*, 2019) [21, 16]. The viral particles with typical iridescent icosahedral viral structures were observed both inside and outside hematopoietic cells in the tissue. In the cytoplasmic margins, budding virions from the plasma membrane and budded virions with an outer viral envelope obtained from the plasma membrane were seen. The formation of virion formation occurs in the cytoplasmic structurally distinct regions known as virogenic stromata. They were electron-lucent areas comprising multiple immature and empty capsids; very few mature virions lacked cellular organelles, with budding virions and a paracrystalline array of viral particles in the same cell. The assembly of the nucleocapsid was described in three progressive stages by Qiu *et al.* (2019) [27]. In stage 1, crescent-shaped structures of capsid complexes eventually assembled into spherical intermediates. Following this, in stage 2, the formation of icosahedral capsids with a small opening at one vertex occurs. Recruitment of electron-dense nucleic acid happens in stage 3. Matured nucleocapsid formation takes place later.

#### 8.5. SDS-PAGE

Twenty-four proteins were isolated from semi-purified virions from the hemolymph of *C. quadricarinatus*, including a 50 kDa major capsid protein (MCP) in the SDS – PAGE analysis by Xu *et al.* (2016) [37]. Summation of the DNA restriction endonuclease fragments revealed the viral genome to be ~150 kb in length. BLASTp analysis of the 34 aa MCP fragment encoded in the amplified product exhibited that CQIV could be related to SIV (55% identity), an unclassified iridovirus identified in Sergestid shrimp (Tang *et al.*, 2007) [30]

#### 9. Disease control and prevention

There is no treatment for DIV1 reported so far (Qiu *et al.*, 2018b) [23]. Biosecurity can be the main factor in controlling infection with DIV1, including surveillance of farms, quarantine facilities, and screening for DIV1 in bloodstock and postlarvae. Generic biosecurity measures to reduce fomite spread via equipment, vehicles or staff (i.e., cleaning and disinfection) should also be carried out (Qiu *et al.*, 2018c) [26]. Limiting the movement of live crustaceans and moribund or dead individuals' removal from infected farms will restrict the transmission of the disease. Polyculture practices in crustacean farms should be avoided. Broodstock should not be fed with live or frozen raw decapods or polychaetes (Qiu *et al.*, 2018c; Qiu *et al.*, 2019b) [26, 27].

#### 10. Conclusion

Shrimp is the most exported commodity among the crustaceans. DIV1 may cause significant risk and loss to international shrimp export. Even though it is reported only in China, Thailand; Care must be taken during the transboundary movement of Shrimps, and strict screening for DIV1 must be carried out in quarantine facilities. Strict biosecurity measures in shrimp farms are essential in preventing the transmission of DIV1. Awareness among the shrimp farmers should be created since they are the main stakeholders in Shrimp farming. New diagnostic methods and kits can be developed

to detect the presence of viruses with increased specificity and sensitivity.

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