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A taxonomic review of viruses infecting crustaceans with an emphasis on wild hosts

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ABSTRACT

Numerous infections by viral pathogens have been described from wild and cultured crustacean hosts, yet relatively few of these pathogens have been formally characterised and classified. To date viruses have generally been tentatively assigned to families based upon morphological and developmental characteristics and their location of infection within the host cell. Often nucleotide sequence information is unavailable. Some of these viral infections have caused well-documented devastating consequences on the global crustacean farming industry whilst their effects on wild populations remain largely unstudied. This paper provides an up to date review of all known viruses described infecting crustacean hosts. Full characterisation and harmonisation of these descriptions utilising specifications proposed by the International Committee on Taxonomy of Viruses (ICTV) is required to synonymise numerous examples of differential naming or abbreviation of naming, of the same virus in some cases. Development and application of techniques such as viral purification and high throughput sequencing of viral genomes will assist with these full descriptions and, provide appropriate diagnostic targets for surveillance of known and novel relatives. This review also highlights the importance of comparative study with viruses infecting insects and other arthropods to assist this process.

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1. Introduction

Vago described the first invertebrate virus from the marine environment in 1966, infecting Macropipus depurator caught on the French Mediterranean coast (Vago, 1966). Prior to this discovery viral infections in invertebrate hosts had only been described in terrestrial insects and mites. Diseased M. depurator crabs showed slow development of paralysis, with haemolymph collected from diseased crabs provoking the same clinical signs when injected into healthy individuals. Negative staining revealed numerous paraspherical bodies, 50-60 µm in diameter. Bonami later rediscovered this virus infecting *M. depurator* sampled from the same area and the virus was then classified on morphological grounds as a reovirus (Bonami, 1973). Since this early discovery, numerous crustacean viruses have been described over a relatively short space of time (Fig. 1), some associated with devastating consequences on the global crustacean farming industry (Stentiford et al., 2012). In contrast, the effects of disease caused by viruses in wild crustacean populations remain almost completely unstudied.

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Few viruses from marine invertebrates have been taxonomically assigned (to a particular virus family) since biochemical, biophysical and immunological data are incomplete or completely lacking for many viruses. This deficit has been due largely to the lack of crustacean cell cultures for culturing viral infections, to the difficulties in producing viruses in vivo using wild host animals and the lack of sequence information. However, with increasingly availability of high throughput sequencing technologies, both comprehensive descriptions (Yang et al., 2014), and a revolution in our understanding of viral diversity (Shi et al., 2016; Simmonds et al., 2017) are occurring. The problem of multiple virus infections, which can occur in crustaceans (Johnson, 1983, 1984; Mari and Bonami, 1986), is another complicating factor and has been proposed as one of the most restricting factors for pathological and virological studies in this group of invertebrate (Mari and Bonami, 1988a). Thus, crustacean viruses have so far been tentatively assigned to families based upon morphological and developmental characteristics and their location of infection within the host cell. Several reviews of the subject have been presented, though the rate of viral pathogen discovery outpaces the production of these synopses (Bonami and Zhang, 2011; Brock et al., 1983; Couch, 1981; Edgerton, 1999; Johnson, 1984, 1988b; Johnson and Lightner, 1988; Sweet and Bateman, 2015).







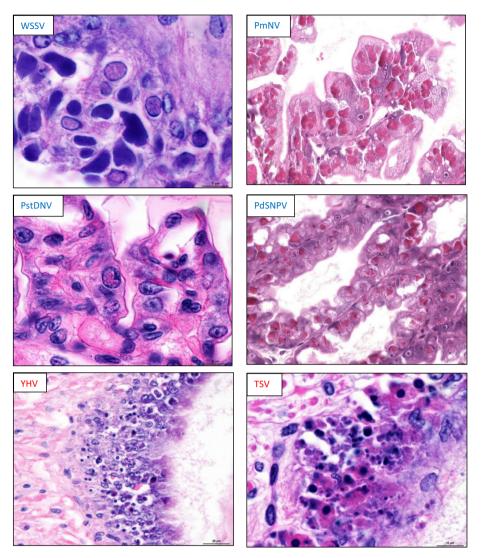


Fig. 1. Histological images of various viral infections of crustacean tissues. Names of the viral infections are shown in text boxes within each image, DNA viruses are highlighted in blue text, RNA viruses highlighted in red text. All images H&E Stain. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Viruses appear to be the most abundant biological entities on the planet, substantially outnumbering cells in most well-studied habitats (Koonin and Dolja, 2013). The growth in penaeid shrimp aquaculture has been mirrored by the emergence of numerous diseases, the majority viral in origin (Peeler, 2012). Key examples, including White Spot Syndrome Virus (WSSV), have spread rapidly across the globe through trading, mainly via live animals and potentially also commodity products (Bateman et al., 2012a; Durand et al., 2000; Jones, 2012; Nunan et al., 1998; Peeler, 2012). With the expected increase in crustacean aquaculture worldwide and the propensity for farms to share habitats with wild populations of susceptible hosts, emergent diseases are likely to be caused by opportunistic pathogens arising from these natural habitats (Stentiford, 2012). This review presents a taxonomic overview of viral pathogens of crustacean hosts with an emphasis on those infecting wild (non-farmed) populations. The review, divided into discrete sections covering the DNA and RNA viruses, lists most if not all known examples from the literature and proposes tentative allocation of these viruses to existing viral families per the available information inherent in their descriptions (see Tables 1 and 2). Unless stated otherwise viruses have been placed within the families suggested by the authors in the initial descriptions,

it is important to note that these classifications need confirmation through sequencing data, morphology alone is not adequate to classify and characterise these infections.

2. DNA viruses

2.1. Nimaviridae

The Nimaviridae family currently contains a single genus, Whispovirus, accommodating a single species, White Spot Syndrome Virus (WSSV) (Lo et al., 2012), a situation acknowledged as unusual in earlier publications of the International Committee on Taxonomy of Viruses (ICTV) (Vlak et al., 2005). Other viruses, including B virus and Rod Shaped virus of Carcinus maenas (RVCM) infecting the common shore crab, *Carcinus maenas*, B2 virus and Tau virus (τ) infecting shore crab *Carcinus maenas*, B2 virus and Tau virus (τ) infecting the blue crab, *Callinectes sapidus* have been described as 'similar' to WSSV, at least based upon morphology of the virion. The taxonomic position was tentatively defined as within the *Nimaviridae* by the ICTV (Vlak et al., 2005) though this has now been suspended due to a lack of evidence pending additional study (Lo et al., 2012). Here, we maintain the tentative

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