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Review

Polydnaviruses: From discovery to current insights

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ABSTRACT

The International Committee on Taxonomy of Viruses (ICTV) recognized the Polydnaviridae in 1991 as a virus family associated with insects called parasitoid wasps. Polydnaviruses (PDVs) have historically received limited attention but advances in recent years have elevated interest because their unusual biology sheds interesting light on the question of what viruses are and how they function. Here, we present a succinct history of the PDV literature. We begin with the findings that first led ICTV to recognize the Polydnaviridae. We then discuss what subsequent studies revealed and how these findings have shaped views of PDV evolution.

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Introduction

In the recent inaugural issue of The *Annual Review of Virology* (ARV), Summers (2014) examined the question of what viruses are and the ever-changing ways virologists have defined them since their discovery in the 19th century. In the same issue, we reviewed the Polydnaviridae (Strand and Burke, 2014), which was recognized as a family of insect viruses by the International Committee on Taxonomy of Viruses (ICTV) in 1991 but has largely languished in obscurity in the broader virology literature. Even among insect virologists, polydnaviruses (PDVs) have historically received limited attention because their life cycle makes them difficult to work with and their unusual biology was a disincentive for labs vested in other, primarily model, species. Yet advances in recent years have elevated interest in PDVs, precisely because their unusual biology sheds interesting light on virus evolution and what the essential qualities of viruses are. These considerations also underlie why we were asked to provide a review on PDVs for the 60th anniversary issue of *Virology.* We cannot avoid overlap here with other recent summaries including the aforementioned ARV article (Beckage and Drezen, 2012; Burke and Strand, 2012a; Strand and Burke, 2012, 2013, 2014; Gundersen-Rindal et al., 2013; Herniou et al., 2013). However in keeping with an anniversary issue, we orient this paper a bit differently by discussing the PDV literature in largely historical order. We begin with the findings that first led ICTV to recognize PDVs as viruses. We then discuss

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what later studies found and how these results have progressively shaped views of PDV evolution.

Early years: formal recognition of PDVs as a virus family

The study of PDVs began in the late 1960s and 1970s when particles resembling viruses were observed by electron microscopy (EM) in the reproductive tracts of a few insect species called parasitoid wasps (Hymenoptera) (Rotheram, 1967; Vinson and Scott, 1975; Stoltz et al., 1976). These insects are well known to entomologists because of their widespread abundance, high species diversity, and importance as biocontrol agents for many pest species in agriculture and forestry. In contrast, they are generally not familiar to other life scientists including virologists because of their small size and specialized habits. In brief then, parasitoid wasps are defined as insects that are free-living during their adult stage, which reproduce by laying eggs on or in the bodies of other arthropods referred to as hosts (Godfray, 1994; Pennacchio and Strand, 2006). Wasp progeny develop into adults by feeding parasitically on a single host and the host usually dies as a consequence of being parasitized. Most parasitoid wasps are also specialists that parasitize only one or a few host species.

The Hymenoptera is one of the largest insect orders (> 200,000 species) and is divided into several superfamilies and many families. Most of these taxa consist primarily or exclusively of parasitoids. Studies in the late 1970s and early 1980s, however, suggested that PDVs are only associated with wasps in one superfamily, the Ichneumonoidea, which is divided into two families named the Braconidae and Ichneumonidae (Krell and Stoltz, 1979, 1980; Stoltz and Vinson, 1979). Studies during this period also noted that PDV particles from braconid and ichneumonid wasps morphologically differ from one another with the former having cylindrical, often tailed nucleocapsids surrounded by a single envelope that resembled some non-occluded baculoviruses (see below), and the latter having fusiform nucleocapsids with two envelopes (Stoltz and Vinson, 1979).

Despite their dissimilar morphology, early studies also showed that PDVs from braconids and ichneumonids share several features including a common life cycle. Both persist in all cells of braconid or ichneumonid wasps as integrated proviruses (Stoltz, 1990; Fleming and Summers, 1991). Both also only replicate in pupal and adult stage female wasps in nuclei of cells located in the ovaries called calyx cells. Replication produces large numbers of virions that are released by lysis of calyx cells in the case of braconids or budding in the case of ichneumonids. Virions are then stored at high density in the lumen of the reproductive tract (Stoltz and Vinson, 1979). Nucleic acid analysis showed that virions from braconid and ichneumonid wasps contain multiple circular, double-stranded DNAs that are non-equimolar in abundance. The number and size of DNA segments was noted to vary between wasp species (Krell and Stoltz, 1979; Stoltz and Vinson, 1979; Krell et al., 1982) with subsequent studies estimating aggregate sizes for these DNAs to range from ~150 kb to more than 600 kb (see below).

Braconid and ichneumonid wasps use their ovipositors to inject eggs containing the proviral genome, PDV particles, and other secretions into the body cavity of the hosts they parasitize, which are primarily larval stage Lepidoptera (moths and butterflies). Experiments in the late 1970s and 1980s showed that PDVs rapidly infect host cells and discharge their DNAs into nuclei, which is followed by expression of viral genes (Stoltz and Vinson, 1979; Fleming et al., 1983; Blissard et al. 1986). Experiments further demonstrated that survival of wasp offspring depends on infection of the host by PDVs and associated viral gene expression because wasp offspring die in the absence of infection by its associated PDV. This is because most PDVs disable immune defenses, which prevent hosts from killing wasp offspring (Edson et al. 1981; Guzo and Stoltz, 1987; Davies et al., 1987). PDVs were noted to also alter the growth of hosts (Stoltz and Vinson, 1979; Beckage and Riddiford, 1982). Yet, parallel studies showed that PDVs do not replicate in the hosts of wasps (Theilmann and Summers, 1986). The molecular basis for altering host physiology in the absence of replication was not understood in these early studies. The biological significance of these traits, however, was interpreted to mean that PDVs are only transmitted vertically through the germline of wasps, and wasp survival depends on the genes replication-defective PDV virions deliver to hosts. The reliance of PDVs and wasps on one another for survival further suggested they form a mutualistic association (Stoltz and Vinson, 1979; Edson et al., 1981; Fleming, 1992).

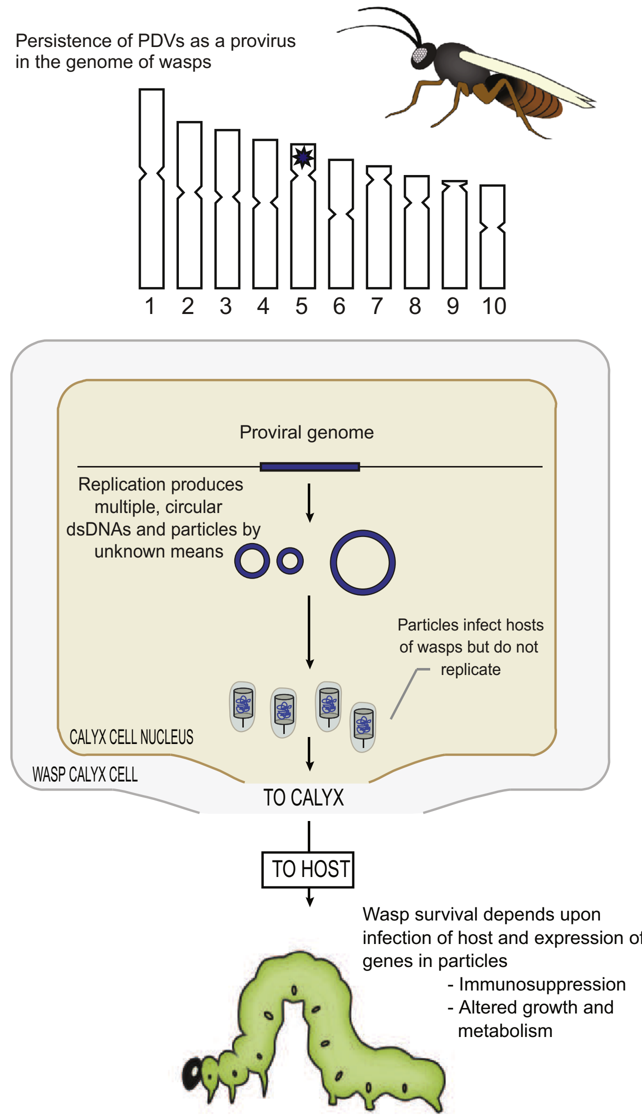

Fig. 1. Key characteristics of PDVs in 1991 when the family Polydnaviridae was formally recognized by ICTV. The upper part of the figure shows an adult female wasp whose hypothetical genome consists of 10 chromosomes. Data at this time indicated that each PDV associated with a given wasp species was genetically distinct and persisted as a provirus. Based on other known dsDNA viruses with a proviral phase, PDV proviral genomes were implicitly assumed to persist as a large, linear dsDNA that was integrated in the wasp genome (*). The middle part of the figure shows the nucleus of a calyx cell. Data showed that particles packaging multiple circular dsDNAs were produced in calyx cells by unknown means followed by storage of particles in a domain referred to as the calyx. The lower part of the figure shows a larval stage lepidopteran host. Data generated prior to 1991 showed that wasps inject PDV particles into hosts, which infect different types of cells and express genes that cause physiological alterations wasp offspring depend upon for survival. Data generated prior to 1991 also showed that no replication of PDVs occurs in the hosts of wasps.