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Densovirinae: An Eco-Friendly Alternative in Biological Control

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Abstract

Entomopathogenic viruses are among the most important biological control agents due to their narrow host spectrum, low *in vivo* production costs, and environmentally friendly properties. In particular, asymptomatic viruses with the potential to cause oral infection are seen as an environmentally sustainable alternative to chemical pesticides in the control of harmful insects. The fact that these viruses do not harm non-target organisms and their ability to protect the natural balance of the ecosystem offer significant advantages in the field of biological control. In addition, their minimal environmental impact contributes to the implementation of sustainable approaches to agricultural pest management. Densoviruses are non-enveloped, single-stranded, linear DNA genome viruses of very small size in the subfamily Densovirinae of the family Parvoviridae that infect only invertebrates. These viruses have been isolated from many insect orders including Blattodea, Diptera, Hemiptera, Hymenoptera, Coleoptera, Lepidoptera and Orthoptera. They have also been reported to infect decapod crustaceans and echinoderms. Although the discovery of densoviruses dates back some sixty years, their use as biological control agents was not seriously considered until it was demonstrated that these viruses do not infect vertebrates. However, *in vivo* and *in vitro* studies in mammals have shown that densoviruses do not infect vertebrates, and this has accelerated research into their potential use in biological control over the last two decades. In this review, the general characteristics of densoviruses and their potential use in biological control are discussed in detail.

Keywords: Entomopathogenic viruses, Parvoviridae, densovirinae, biocontrol agent

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Introduction

Biological control is a control method that has been developed using the natural pressure mechanisms of nature and has a very low probability of harming the environment (1). In this type of control, predators, parasitoids or pathogens are used to reduce the numbers of harmful insects, whose populations have

increased significantly in some years, below the economic damage threshold. While predators and parasitoids in biological control are methods based on the use of beneficial insects against the target organism, pathogens are micro-organisms that cause the target organism to become sick or die. These microorganisms include viruses, fungi, bacteria, protozoa and nematodes, and are bioagents that can reduce pest populations well below the economic damage threshold in a short period of time (2). The main reasons for the widespread use of microbial agents in biological control are that, unlike chemicals, they are host-specific, do not harm non-target organisms, do not leave residues in nature, are environmentally friendly and reliable (3). Microbial insecticides are used effectively to control many harmful insects. The fact that microbial insecticides are not toxic to non-target humans and other living organisms, and that the toxins they produce are generally specific at the species or genus level, makes biological control preferable to chemical control (4). Viruses are the most commonly used of these micro-organisms, and viruses usually enter their hosts orally through the digestive system and cause infection (1). The digestive system of the virus-infected insect is disrupted, many organs are damaged and as a result the insect becomes sick and dies. The main factors limiting the use of entomopathogenic viruses are their narrow host range, the need to replicate in the host and their slow action. One of the most important viruses in the field of microbial control are the members of the family Baculoviridae, which are more resistant to natural conditions (1). Most of the known hosts of baculoviruses belong to the order Lepidoptera, while others belong to the orders Diptera and Hymenoptera (5). Another group of viruses, densoviruses, have a wider distribution and have been isolated from many insect orders, including Blattodea, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata and Orthoptera (6). In addition, recent studies have reported the presence of densoviruses in some Coleoptera species that are storage pests (7-10). Densoviruses, also known as densonucleosis viruses (DNV), are so named because infected cells characteristically develop intensely stained nuclei (11, 12). These viruses, which belong to the subfamily Densovirinae of the family Parvoviridae in the order Piccovirales, are known to be among the smallest DNA viruses with dimensions of 18-28 nm (13-15). DNVs replicate in the nuclei of invertebrate hosts and form large circular inclusions. First identified in 1964 from Galleria mellonella larvae, DNVs have a non-enveloped single-stranded DNA genome, making them more resistant to environmental conditions and distinct from other viruses (8). DNVs offer significant advantages for biological control because they are specific to invertebrates, can be spread by oral infection, are stable, and show distinct morphological symptoms in the host (16).

Classification of densoviruses: The family Parvoviridae, introduced in 1975, was split into two subfamilies in 1993 as Parvovirinae, which infects vertebrates, and Densovirinae, which infects invertebrates (14). This two-subfamily classification has long been supported by phylogenetic analyses, as both subfamilies have a very narrow host spectrum. In 2012, a genus known as Chapparvovirus was introduced, but isolates belonging to this genus have been detected in some vertebrate tissues (kidney and liver), faeces, and even blood (17-23). At the same time, the identification of endogenous chapparvovirus sequences in arthropod genomes has highlighted the need to revise the classification of both the family Parvoviridae and the subfamily Densovirinae (24, 25). Densoviruses have been divided into genera based on the sequence similarity of the NS1 protein, which has been isolated from many insect species and is highly conserved in all densoviruses. If the NS1 proteins have more than 85% amino acid sequence similarity, densoviruses can be considered members of the same

species. In addition, members of the same genus should have at least 35% similarity between their NS1 proteins (26).

As new isolates are identified, revisions are made to the classification of both the Parvoviridae family and the Densovirinae subfamily. According to the latest update of the ICTV, the family Parvoviridae is now divided into three subfamilies (Densovirinae, Parvovirinae and Hamaparvovirinae) and one unclassified genus (Metalloincertoparvovirus) (26). The subfamily Densovirinae is divided into 11 genera in 2020 (Figure 2). According to data from the ICTV taxonomy browser, the 11 genera of the subfamily Densovirinae contain 64 species, and the distribution of these species within the genera is as follows Aquambidensovirus (24 species), Leafambidensovirus(6species),Diciambidensovirus (3species) ,Hemiambidensovirus (3 species), Iteradensovirus (7 species), Miniambidensovirus (1 species), Muscodensovirus(2 species), Pefuambidensovirus(2species),Protoambidensovirus(7species), Scindoambidensovirus(6species) and Tetuambidensovirus (3 species). All genera except Aquambidensovirus have been isolated from insects of these genera. Studies to isolate insects that are harmful to households, agriculture and forestry and to evaluate the usefulness of these isolates for biological control are very valuable.

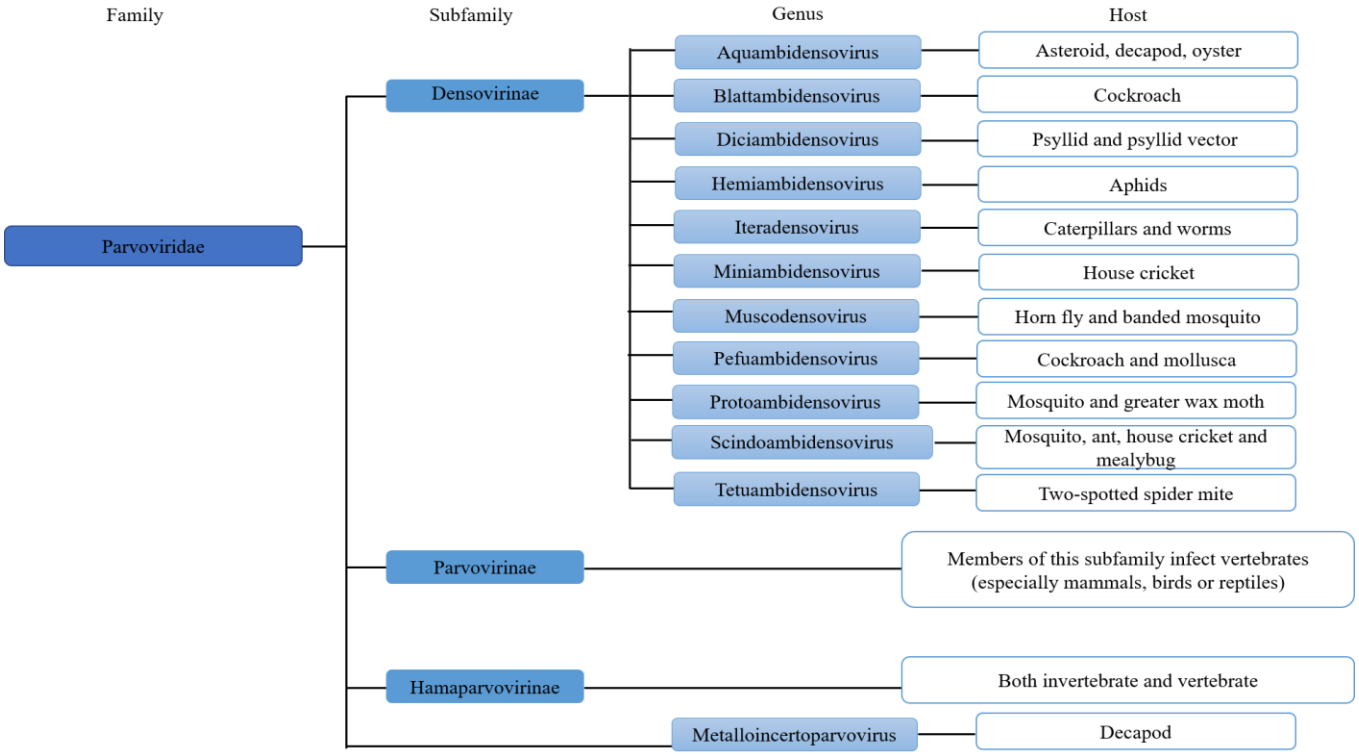

Figure 1: Classification of densoviruses (ICTV taxonomy browser)

Genome organization of densoviruses: DNVs are single-stranded, non-enveloped, single-stranded DNA viruses with icosahedral symmetry and a genome size of approximately 4000-6000 bp (27). All DNVs have a structure consisting of Y-shaped inverted terminal repeats (ITRs), which are required for replication and genome packaging (28-30) (Figure 2a). The molecular mass of DNVs is approximately 6 MDa, of which 20±30% is DNA and the remainder is mainly protein (12). Two types of proteins are encoded in the genome: structural (VP) and non-structural (NS). NS are responsible for the replication of the viral genome and

are considered an important parameter for virus classification, especially since the protein known as NS1 is highly conserved in all DNVs (14, 26) (Figure 2b). Structural proteins are responsible for the formation of the viral capsid (31). All DNV genomes have NS and VP genes equally distributed in the 5' half of each strand (12) (Figure 2c).

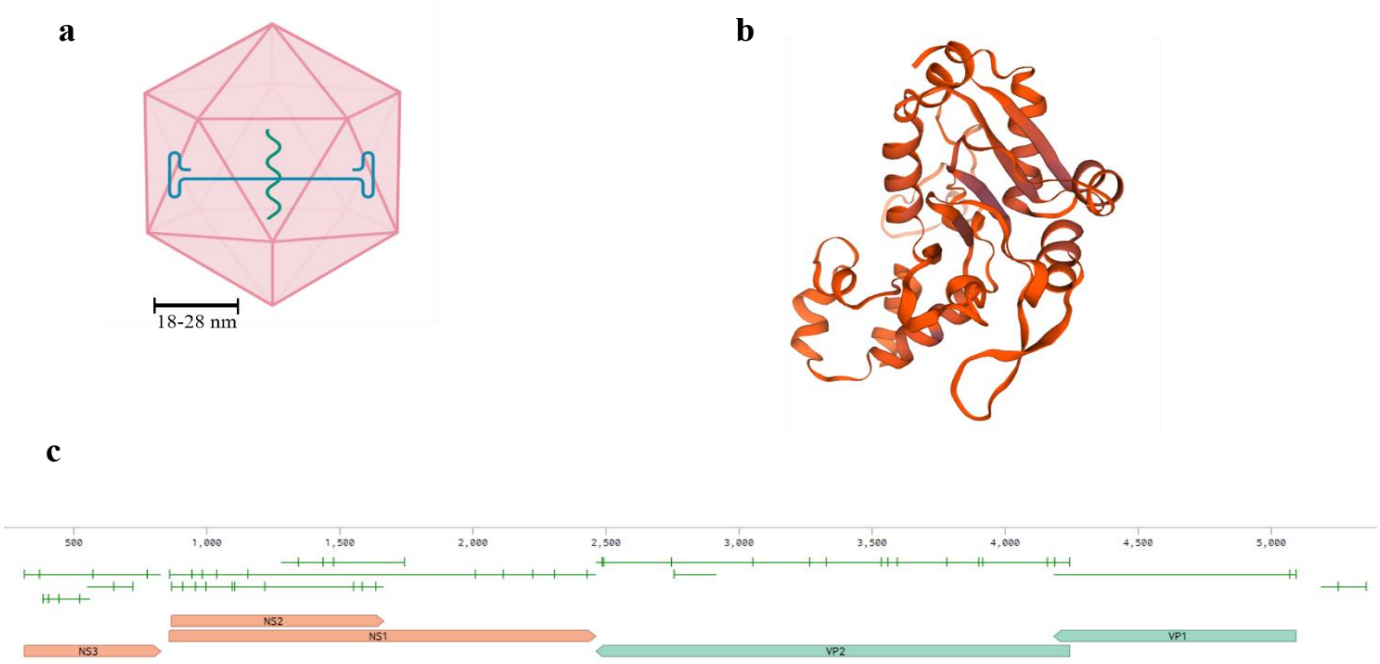

Figure 2: Structure of densoviruses **(a)** Morphological structure of the virus particle with icosahedral capsid symmetry [This figure was drawn using BioRender (https://www.biorender.com)], **(b)** Structure of the NS1 protein [This figure was drawn using SWISS-MODEL (https://swissmodel.expasy.org/)], **(c)** DNV genome map [Benchling online tool using the genome sequence of Tenebrio molitor densovirus- Türkiye (TmDNV-TR) isolate (10)].

The N-terminal extension of the minor capsid protein VP1, the largest VP in DNVs, encodes phospholipase A2 (PLA2), which is required for endosomal exit (2, 16). Other parvoviruses lacking PLA2 (notably members of the Hamaparvovirinae) use an alternative endosomal pathway (32).

Use of densoviruses as gene transfer vectors: Terminal sequences make up 8-18% of the densovirus genome. Since terminal sequences contain all the elements necessary for replication and packaging, the remaining part of the genome is suitable for foreign DNA insertion. In some cases, where viral functions are lacking, a helper plasmid (usually pUCA) containing VP and/or NS genes can be used. In this case, the transducer genome, helper plasmid and trans-producing cells must be incubated long enough to undergo at least one cell division to produce transducer particles. This is because fundamental processes such as gene expression and replication in DNVs are directly linked to host cell division (11, 33). Liu et al. (2017) developed a non-defective recombinant Aedes albopictus densovirus (AaeDV) microRNA (miRNA) expression system. Thus, it was reported that recombinant AaeDVs developed for use in mosquito control can be used to overexpress or reduce the expression of the target gene in larvae (34) (Figure 3).

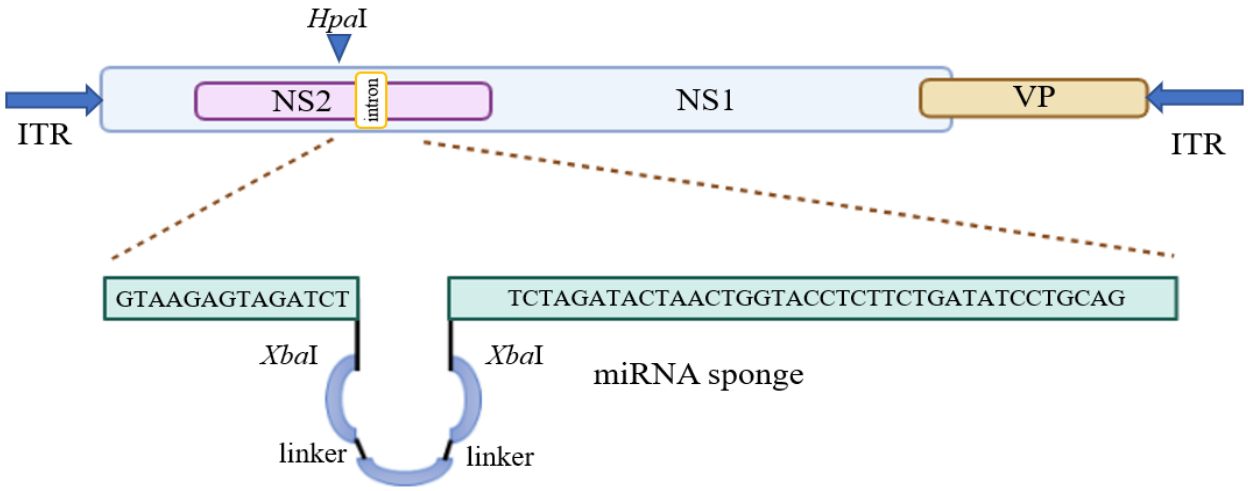

Figure 3. Schematic organization of recombinant AaeDV plasmids [This figure was drawn using BioRender (https://www.biorender.com) (modified from 34)]

Replication of densoviruses: DNVs enter the cell via clathrin-mediated endocytosis and replicate in the host nucleus (13, 35). They enter the cell using various receptors such as glycoproteins, glycans and glycolipids on the cell surface (36-38). After endocytosis, they pass through the endolysosomal system of the host cell and reach the nucleus. During this time, the viral particle is exposed to an acidic environment ranging from pH 7.4 to pH 4.0 (32, 39). Although this acidic environment is known to induce conformational changes in the viral capsid, the mechanism of viral escape from endosomes is not fully understood (35). Once the virus reaches the nucleus, mRNA is transcribed and NS1 initiates replication. It then begins to replicate using the host's S-phase replication mechanism (37). During replication, the hairpin structure is continuously opened and replicated. The rolling hairpin replication process then begins. In this process, it refolds to change the direction of replication to move along the genome. This produces a molecule containing many copies of the genome, and newly formed ssDNAs are removed from this concatemer and packaged into the capsid. Finally, mature virions exit the cell by exocytosis or lysis, terminating the replication process (Figure 4). Vendeville et al (2009) infected the Lymantria dispar 652 cell line with Junonia coenia DNV to determine the early endocytotic steps in DNV infection. According to the data obtained, DNV infection progressed with rapid clathrin-mediated uptake, slow traffic from low pH and late endosomal compartments, and integration of the cytoskeletal network (35).

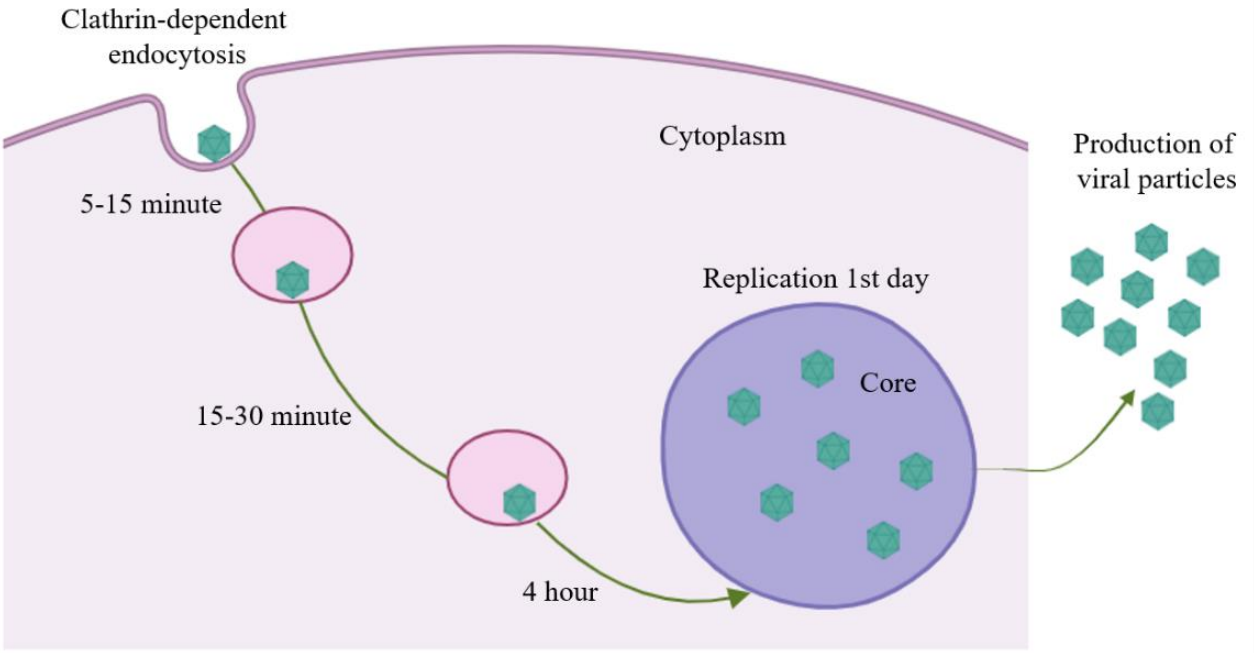

Figure 4. Densovirus replication process [This figure was drawn using BioRender (https://www.biorender.com) (modified from 31)].

Densovirus symptoms in insects: DNV infection is characterized by nuclear hypertrophy caused by the accumulation of large virion particles and cytoplasmic paracrystalline virion arrays in insect tissues (6). DNVs cause severe diseases in their host organisms and are widely used for the biological control of significant insect pests due to their high virulence and transmissibility. Additionally, densoviruses represent an advancement over classical biopesticides, offering a species-specific alternative to traditional insecticides (40). Symptoms of DNV infection typically begin with anorexia and lethargy, followed by limping and molting or inhibition of metamorphosis. Infected larvae gradually turn white and become paralyzed. In cockroaches and house crickets, common symptoms include paralysis of the hind legs and uncoordinated movements (41). DNV infect host larvae, causing a variety of symptoms such as changes in cuticle pigmentation, loss of movement, and death. The severity of parasitism and damage varies significantly depending on the type of infection. The most striking symptom observed in infected larvae is the complete blackening of the body. As a result, densovirus infections, especially in storage pests like *Zophobas morio*, are commonly referred to as "black wasting disease" (42). Prior to this blackening, dark discoloration is observed in the midgut of larvae (27). Some species of densoviruses also induce tumor-like lesions in the intestines of their hosts. Infected larvae exhibit severe deterioration of midgut epithelial cells, accompanied by thickening and opacification of the intestinal wall. These changes result in the clouding of intestinal contents. In larvae infected through feeding, the virus was found to replicate in midgut cells, leading to a pathogenic mechanism that damages the intestinal barrier (43) (Figure 5). The peritrophic membrane is a critical component in insects, serving as a protective lining in the midgut. It acts as a significant barrier, making it difficult and complex for orally ingested viruses to penetrate and initiate infection. A study to investigate how DNV capsids adhere to and cross this barrier to reach target cells used a combined

methodology including microscopy, biochemistry, proteomics and transcriptomics. The results showed that the peritrophic membrane, exposed mucins and non-mucin protein receptors serve as binding sites for DNV and other insect pathogens. This highlights the interaction between the virus and components such as chitin, glycans and proteins as key mechanisms underlying this process (16).

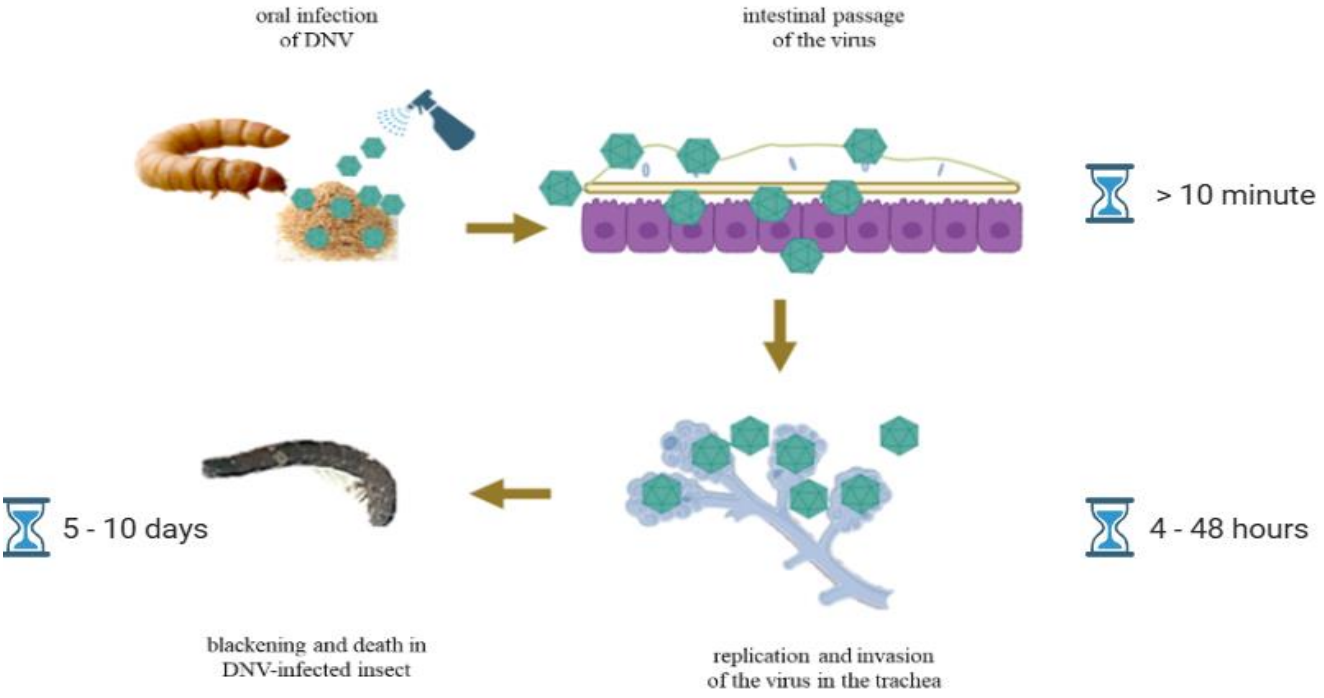

Figure 5: Schematic of densovirus pathogenesis in Tenebrio molitor. The virus is transferred to the larval food and the larva is able to ingest the virus orally. The virus quickly reaches the midgut and crosses the intestinal epithelium. It then targets the tissues, particularly the trachea, where it replicates and causes the larva to blacken and then die. [This figure was drawn using BioRender (https://www.biorender.com) (modified from 31)]

Usability of densoviruses in biological control and host range: The use of insect viruses in biological control has been known since 1911 (44). Isolates of the baculovirus group, particularly DNA viruses, have been commercially available since 1975 (45). To date, 60 baculovirus isolates have been registered and are used as an alternative to chemical pesticides in the control of insect pests (46, 47). Although densoviruses (DNV) were first discovered 60 years ago, they were not considered as candidates for biological control until it was shown that they do not infect vertebrates (12). However, since *in vivo* and *in vitro* studies over the last 20 years have shown that they cannot replicate in vertebrates at all, they are now emerging as an important biological control agent as an alternative to baculoviruses (27, 48, 49). Some characteristics of DNVs, such as high virulence and host specificity, inability to infect vertebrates, and high resistance to extreme environmental conditions, make them potentially effective biological control agents against populations of agriculturally and medically important pests (16, 42). In addition, because densoviruses are DNA viruses and therefore have a

DNA repair mechanism, they do not allow mutations to alter their host specificity (50, 51).

The first study to use densovirus as an insecticide for biological control purposes involved the use of *Galleria mellonella* cadavers infected with GmDNV to control beehives heavily infested with this pest. In this study, the formulation was applied in three doses and after 15 days of infection, 95% mortality was observed at the highest dose and 73% at the lowest dose. One month later, 100% mortality was observed for all three doses. In addition, pest parasites were not affected and contributed to the further spread of the virus (52). In another study, during the survey of arboviruses in China, a new densovirus (DNV) was isolated from adult female *Culex pipiens pallens* (CppDNV), and found to cause cytopathic effects in C6/36 cells (53). The first mosquito-specific densovirus (MDV) was found in *Aedes aegypti* larvae in a Russian laboratory colony in 1972, and to date MDVs have been isolated from many mosquito species, including important disease vectors such as *A. aegypti*, *Aedes albopictus*, *Anopheles gambiae*, *Anopheles sinensis*, *Culex pipiens* and *Culex pipiens* pallans (54). The reason for the large number of studies on densoviruses in the mosquito group is that they act as vectors and can transmit diseases from animal to animal. Another group of insects in which there has been a considerable amount of work on densoviruses are cockroaches (55). Many studies of densoviruses isolated from cockroaches have resulted in new densoviruses being isolated and entered into databases (56, 57). In addition, densoviruses isolated from species of the family Noctuidae (*Spodoptera littoralis*, *Spodoptera frugiperda*, *Pseudoplusia includens*, *Mythimna loreyi* and *Helicoverpa armigera*), an important family of agricultural pests, are also important for the biocontrol of these insects (58-61). In recent years, it has been reported that densovirus isolates have been obtained from these insects of the family Tenebrionidae, known as storage pests, which are reared in culture and sold commercially, but no biotest data are available (7-10). In future studies, biotest studies with these insects have potential importance for the biocontrol of storage pests. To date, there is only one commercial densovirus-based product (Biokiller, China). This product contains a densovirus (PfDNV) isolated from *Periplaneta fuliginosa* and has been developed and sold in gel form for cockroach control for twenty years (62).

As a result of studies on the host specificity of DNVs, it has been shown that GmDNV, CeDNV and AdDNV have a host range limited to their original hosts, whereas other DNVs isolated from Lepidoptera have a wider host range (63-65). This situation is a disadvantage, albeit a minor one, for certain species and limits studies. The host range of DNVs infecting other groups of mosquitoes extends to different species. *A. albopictus*, *Aedes cantans*, *Aedes caspius*, *Aedes geniculatus*, *Aedes vexans*, *Culex pipiens*, etc. among the mosquitoes with a very wide range of species, there are many studies on densoviruses (54). In terms of sensitivity, which is an interesting aspect of the host spectrum issue, *Bombyx mori* is at the top of the list of hosts with the highest sensitivity to densoviruses. Among the economically important silkworm species, a few are susceptible to BmDNV-2 and almost all strains susceptible to BmDNV-1 are resistant to BmDNV-2. Therefore, the mode of inheritance of resistance to BmDNV infection has been investigated and it has been found that insensitivity to each virus is genetically controlled by a recessive gene that is not sex-linked (66). As a result, the host range and specificity of densoviruses vary between insect species.

Mammalian cell toxixity: The Parvoviridae family is a large group of viruses that can infect both vertebrates and invertebrates (26). However, there are uncertainties regarding the host spectrum of the Densovirinae subfamily that infects invertebrates. Although it was reported in the 1960s that densoviruses

(DNV) could infect mouse L cells (67-69), it was later understood that these observations did not indicate viral replication. DNV infection was studied in terms of viral transcription, replication, integration, and production by El Far et al (2004). The findings showed that L cells and other vertebrate cells did not support densovirus replication or transcription, whereas viral DNA replication and transcription occurred in *L. dispar* cells (LD652). It has been reported that the viral genome was removed from the plasmid in LD652 cells and both NS and VP mRNAs were detected, but not in L cells. It has been stated that the viral genome was integrated into the host chromosome in L cells, but transcription did not occur after integration. As a result, it has been shown that densoviruses can perform efficient replication and transcription in insect cells, but cannot initiate infection in mammalian cells. This increases the potential of densoviruses as gene therapy vectors (27).

Result

In today's world, where crop pressure and inadvertent use of pesticides threaten the sustainability of ecosystems, the discovery of innovative biological alternatives has become an urgent necessity. Densoviruses, viruses of the Parvoviridae family, stand out as a promising solution due to their unique mechanisms of action and positive environmental profile in pest management. The use of these viruses in biological control not only allows selective targeting of pest populations, but also contributes to the protection of biodiversity by offering a less chemical-dependent and more sustainable control method. The fact that densoviruses are DNA viruses and have a DNA repair mechanism prevents the viruses from undergoing mutations that would change their host specificity (50, 51). This feature ensures ease of use and avoids any negative impact on the ecosystem. In addition, all densoviruses have a very narrow host spectrum, making them safe to use in biological control. Densoviruses have many advantages, such as being specific to invertebrates, being able to multiply by oral infection, being stable and showing clear morphological symptoms in the host (16). For all these reasons, the use of densoviruses as biological control agents is included in many studies in the current literature, and their use as an effective biological agent can be envisaged in the future.

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