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ORIGINAL ARTICLE

Effects of recombination on densovirus phylogeny

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Abstract Densoviruses are a group of arthropod-infecting viruses with a small single-stranded linear DNA genome. These viruses constitute the subfamily *Densovirinae* of the family *Parvoviridae*. While recombination in between vertebrate-infecting parvoviruses has been investigated, to date, no systematic analysis of recombination has been carried out for densoviruses. The aim of the present work was to study possible recombination events in the evolutionary history of densoviruses and to assess possible effects of recombination on phylogenies inferred using amino acid sequences of nonstructural (NS) and capsid (viral protein, VP) proteins. For this purpose, the complete or nearly complete genome nucleotide sequences of 40 densoviruses from the GenBank database were used to construct a phylogenetic cladogram. The viruses under study clustered into five distinct groups corresponding to the five currently accepted genera. Recombination within each group was studied independently. The RDP4 software revealed three statistically highly credible recombination events, two of which involved viruses of the genus *Ambidensovirus*, and the other, viruses from the genus *Iteradensovirus*. These recombination events led to mismatches between phylogenetic trees constructed using comparison of amino acid sequences of proteins encoded by genome regions of recombinant and non-recombinant origin (regulatory NS1 and NS3 proteins and capsid VP protein).

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Introduction

The densoviruses (DVs) are a group of viruses that infect invertebrates and constitute the subfamily *Densovirinae* of the family *Parvoviridae*. In addition to the subfamily *Densovirinae*, the family *Parvoviridae* contains another subfamily, *Parvovirinae*, which includes viruses that infect various vertebrate hosts, predominantly mammals. Parvoviruses are considered to be among the smallest and most simply organized animal viruses and to encapsidate one of the smallest genomes.

Both DVs and vertebrate parvoviruses are characterized by a non-enveloped capsid, 18–26 nm in size, which contains a single-stranded linear DNA genome. DV genome sizes vary from approximately 4.0 to 6.0 kb. The genome is subdivided into two portions, containing open reading frames (ORFs) encoding regulatory (NS) and capsid (VP) proteins, respectively. DVs usually contain one or two ORFs for capsid proteins in the right half of the genome. DVs also have two regulatory proteins, NS1 and NS2, of which NS2 is encoded completely within the ORF for NS1. Ambisense DVs also have an ORF upstream of NS1 and NS2, coding for NS3. The distinctive feature of the genome is the presence of noncoding inverted terminal repeats (140–550 bases in size), capable of self-annealing to form hairpins; these terminal repeats are necessary for replication initiation and encapsidation [4, 50, 64].

Differences in their genome organization and nucleotide composition show that DVs are an extremely diverse

group, encompassing viruses that are pathogenic for members of seven insect orders, namely Hemiptera, Homoptera, Lepidoptera, Diptera, Orthoptera, Dictyoptera and Odonata, and one order of crustaceans, the Decapoda. DVs cause severe diseases in their hosts, which are usually lethal, and are generally characterized by high host specificity. Some viruses, such as Galleria mellonella densovirus (GmDV) and Casphalia extranea densovirus (CeDV), are pathogenic only for members of the species from which they were originally isolated, and the majority of other DVs are able to infect a restricted number of other insects from the same genus or from closely related genera. At the same time, DVs that are pathogenic for members of the order Diptera appear to infect members of a broad range of mosquito species and replicate in different mosquito-derived cell lines, with Culex pipens densovirus (CpDV) being the only possible exception. Mythimna loreyi densovirus (MlDV) and Junonia coenia densovirus (JcDV) are also characterized by a comparatively broad host range within the order Lepidoptera [2, 15, 25, 43, 54].

Genome replication and assembly of new DV particles take place in the nuclei of infected cells. DVs are usually polytropic but demonstrate different tissue tropism. For example, DVs infecting some lepidopteran hosts (*Bombyx mori, Casphalia extranea*) and the cockroach *Periplaneta fuliginosa* are detected in the midgut epithelium; the DV from the cockroach *Blattella germanica* replicates in the digestive system and fat body [38], while DVs infecting members of the genera *Aedes* (Diptera) and *Penaeus* (Decapoda) and a number of Lepidopteran hosts (*Galleria mellonella, Pseudoplusia includens*) can be found in various tissues, but not in the midgut epithelium [5, 15, 16, 27, 58].

The taxonomy of parvoviruses is quite complicated, which is particularly the case for the DVs. The major obstacles encountered in classifying DVs are the above-mentioned extreme diversity of DVs and the small number of described representatives of this group, for a number of which only partial genome sequences are available without any further characterization. Taken together, these factors make it difficult to choose the proper virus characteristics that would serve as adequate classification criteria and render it impossible to obtain a comprehensive idea of the evolutionary history and the extant diversity of this virus subfamily. For this reason, the classification of DVs is continually revised, and modifications are regularly introduced.

Until now, the taxonomy of the subfamily *Densovirinae* was based primarily on morphological features such as genome organization, the structure of the inverted terminal repeats, and the number of open reading frames encoding capsid or regulatory proteins. At the time of the 9th ICTV report issued in 2011 [60], the subfamily included four genera: *Densovirus*, *Iteravirus* (both infecting lepidopterans), *Brevidensovirus* (infecting mosquitoes), and *Pefudensovirus* (infecting cockroaches) and a number of yet unassigned viruses infecting crustaceans, cockroaches, mosquitoes, orthopterans and hemipterans.

Recently, new proposals to improve DV taxonomy were put forward [13] and subsequently approved, including the addition of new genera and new virus species and the formulation of new criteria of classifying viruses into one of the *Densovirinae* genera. These criteria are based primarily on quantifiable parameters such as the percent sequence similarity between certain viruses and their relative position on the corresponding phylogenetic tree. The tree is proposed to be built using amino acid sequences of the viral regulatory protein NS1, which is considered the most conserved and believed to be the most reliable for reconstructing phylogeny. Applying this new criterion, a new classification was obtained which includes five genera: *Ambidensovirus* (combines the two previous genera, *Densovirus* and *Pefudensovirus*), *Brevidensovirus* (includes viruses infecting dipterans), *Iteradensovirus* (includes viruses infecting lepidopterans), *Hepandensovirus* (includes the shrimp-infecting viruses with large-sized genomes), and *Penstyldensovirus* (includes the shrimp-infecting viruses with small genomes).

An interesting observation was made when the phylogenetic tree based on NS1 amino acid sequences was compared with that based on the main capsid protein. Although the trees were nearly identical overall, an obvious discrepancy appeared in the relative positions of some of the viruses on the trees based on divergent protein sequences [60].

Modern systematics makes use of molecular phylogeny to define the taxonomic structure of different taxa. This approach appears to be quite reliable, quantitative and direct, but at the same time, it should be kept in mind that the inferred genetic distances between individual viruses do not always represent the actual evolutionary history and their relationships. This could be accounted for by two main factors – directed selection pressure (i.e., positive selection) and recombination. In the former case, two viruses somewhat distant from each other on the whole, and with differing origins may appear to be close on the phylogenetic tree if their protein sequences have undergone convergent evolution to adapt to similar conditions in their respective hosts [7, 51, 55]. In the latter case (recombination), a problem may arise, for instance, if a particular virus has acquired, as a result of a recombination event, a significant part of its genome from one ancestral virus and another part from the second ancestral virus. Then, two phylogenies based on nucleotide or amino acid sequences encoded by the two genome regions that originated from different ancestral virus species will demonstrate two

different evolutionary histories for the same virus, thus introducing ambiguity in the analysis. In some cases, even if only small genome regions have recombinant origins, inconsistencies may appear in the phylogenies inferred using different genome segments. Thus, in order to obtain clear and correct data about the relationships between certain viruses, it is important to understand the roles that different evolutionary processes have played in shaping virus genomes. However, both processes are generally not taken into account when considering the phylogeny of certain virus groups, and this is especially so in the case of recombination, a process whose role in virus evolution tends to be underestimated.

Nevertheless, it is becoming evident that recombination may play a unique role in the evolution of viruses [28]. Recombination can generate variation by creating new combinations of existing variants possessing features distinct from both parental genotypes, making possible the rapid emergence of new virus genome types, which could result in speciation. Recombination also purges unfavorable mutations and combines adaptive mutations in one genome, as well as making possible the exchange of genetic information between divergent viruses and between the virus and its host. Recombination is a key mechanism underlying the unmatched ability of viruses to quickly adapt to changing conditions and to infect new cell types and new host species, enabling rapid virus evolution.

For certain virus groups, such as the single-stranded DNA viruses and the positive-sense single-stranded RNA viruses, including retroviruses – for example HIV [24] and FIV [3] – it has been shown that recombination is one of the main evolutionary processes leading to their diversity [11, 12, 22, 23, 30, 33, 34, 36, 57, 63]. Recombination events have also been shown to be significant in the emergence of new viruses in other virus groups, including circular double-stranded DNA viruses (e.g., caulimoviruses [10] and plant pararetroviruses [49]) and linear double-stranded DNA viruses, including adenoviruses and herpesviruses [46, 56, 67].

Previously, the role of recombination in genome evolution was studied for a number of vertebrate-infecting parvoviruses, such as bocaviruses [20], Aleutian mink disease parvoviruses, and rodent parvoviruses [48], the feline panleukopenia virus group [37, 42], and porcine parvoviruses [32, 48], and it was demonstrated that recombination events took place quite often in their evolutionary history. At the same time, no systematic studies of recombination were ever performed for DVs. Only recently (during the preparation of this article), was recombination reported as the possible mechanism of genome formation of a DV, similar to the viruses of the genus *Iteradensovirus* [19]. It was shown that this novel DV may be a product of the intragenous recombination between Danaus plexippus plexippus densovirus (DpplDV) and Dendrolimus punctatus densovirus (DpDV).

Therefore, our goal was to determine whether recombination events could be detected in the genomes of viruses from the subfamily *Densovirinae* and to examine their possible effect on the inferred phylogeny of this group. In the present paper, we show that by eliminating saturated and nonhomologous positions and using improved alignment methods, it is possible to define the taxonomy of DVs, at least up to the genus level, based on DNA sequence comparisons. A thorough recombination analysis revealed three independent interspecies recombination events in this virus group. These recombinations led to exchange between viruses of extended DNA fragments corresponding to ORFs of regulatory (NS) or capsid (VP) proteins. Clustering of the analyzed DVs on the cladograms reconstructed using NS and VP protein sequences revealed a correlation with the described recombination events and unequivocally demonstrated the influence of recombination on the phylogenies inferred based on sequences derived from different parts of the genome.

Materials and methods

Dataset

For the analysis of recombination in the subfamily *Densovirinae*, 40 DVs with complete or nearly complete genome sequences were initially taken. The corresponding genome sequences and, when necessary, amino acid sequences for the regulatory (NS1 and NS3) and capsid (VP) proteins were obtained from GenBank. The corresponding accession numbers are as follows: AalDV2 (X74945), AalDV3 (AY310877), AalDV1 (AY095351), HeDV (AY605055), AgDV (EU233812), AaeDV1 (M37899), AaeDV2 (FJ360744), CppDV (EF579756), PmoHDV1 (DQ002873), PmoHDV3 (EU588991), PmoHDV2 (EU247528), PmoHDV4 (FJ410797), PmeDV (DQ458781), FchDV (JN082231), PchDV (AY008257), PmoPDV1 (GQ411199), PstDV2 (GQ475529), PstDV1 (AF273215), PmoPDV2 (AY124937), BmDV (AY033435), CeDV (AF375296), DpDV (AY665654), HaDV2 (HQ613271), PpDV (JX110122), SfDV (JX020762), DpplDV (KF963252), MlDV (AY461507), CpDV (FJ810126), DsDV (AF036333), GmDV (L32896), JcDV (S47266), HaDV1 (JQ894784), PiDV (JX645046), PfDV (AF192260), BgDV2 (JQ320376), BgDV1 (AY189948), PcDV (AY032882), AdDV (HQ827781), AdMADV (KF275669), MpDV (AY148187).

Phylogenetic analysis

DNA- and protein-based phylogenetic trees were constructed using probabilistic methods: maximum likelihood (ML) and Bayesian [17, 21]. ML was implemented in the software package MEGA v.6.0 [53]. Bayesian analysis was performed using MrBayes version 3.2.2 software [47] for DNA sequence analysis and BEAST v.1.8.2 [14] for the analysis of protein sequences.

The DNA sequences of the 40 analyzed DVs were aligned using MAFFT v.7 software [26] (http://mafft.cbrc.jp/alignment/server/). The E-INS-i algorithm (optimal for sequences with multiple conserved domains and long gaps) was used. At the next step, the Gblocks version 0.91 (http://www.phylogeny.fr/one_task.cgi?task_type=gblocks) software program [9] was used to eliminate poorly aligned and highly divergent regions; the default parameters were used, with smaller final blocks, gap positions within the final blocks, and less-strict flanking positions allowed.

MEGA v.6.0 was used to identify the best-fit model of sequence evolution for the trees estimated using ML. The evolutionary history of the analyzed DVs was inferred using the ML method based on the general time-reversible with the gamma distribution shape parameter (GTR+G) model [40]. Branch support was assessed using the bootstrap method [18] (1,000 replicates).

To analyze the genome nucleotide sequences of 40 DVs by the Bayesian method, two replicate tests of 1.3 million generations each for each dataset were performed, sampling every 500 generations. The hierarchical likelihood ratio test (hLRT) implemented in MrModeltest version 2.3 [41] was used to find the best-fitting GTR+I+G model. Trees from the first 325,000 generations were discarded as burn-in. The Bayesian tree was estimated from the majority-rule consensus of the post-burn-in trees.

Protein amino acid sequences were aligned using MAFFT v.7 software. The following algorithms were used: E-INS-i for the fragments of NS1 proteins and G-INS-i (optimal for sequences with global homology) for the fragments of VP proteins and NS3 proteins. For NS and VP proteins, we used partial sequences corresponding to the domains that are well conserved among members of the genera *Ambidensovirus* and *Iteradensovirus* to obtain adequate multiple alignment and reliable phylogenies based on them. To search for evolutionarily conserved fragments of the analyzed proteins, we used the PROMALS3D software [44], which is available at http://prodata.swmed.edu/promals3d/promals3d.php. PROMALS3D constructs alignments of multiple protein amino acid sequences using information obtained from sequence database searches, secondary structure predictions, the available protein homologs with known 3D structures and user-defined constraints. The final alignments are provided in the corresponding supplementary materials.

The evolutionary history was inferred based on the Le Gascuel model [31] with the gamma distribution shape parameter (LG+G) for the fragments of NS1 and the Whelan and Goldman model (WAG) [62] for fragments of NS3 and VP proteins. Branch support was assessed using the bootstrap method (1,000 replicates) for ML analysis. In addition to the ML method, the evolutionary history of the analyzed viruses revealed by comparison of virus protein sequences was estimated in a Bayesian statistical framework using a Markov Chain Monte Carlo (MCMC) approach implemented in BEAST v.1.8.2. MCMC analyses were run for 5 million generations. The consensus trees were generated by TreeAnnotator v.1.8.2, a part of the BEAST software. Statistical support for the tree nodes was assessed based on the posterior probability value.

Recombination analysis

Recombination events were investigated only in groups of viruses with >60% similarity in their nucleotide sequences. DNA sequences were aligned using MAFFT v.7 (E-INS-i algorithm) software and further trimmed with Gblocks v.0.91 (using default parameters, allowing smaller final blocks and disallowing gap positions within blocks). Pairwise distances were computed using MEGA v.6.0. All viruses in each defined group whose degree of similarity exceeded 60% were subdivided into subgroups of four according to formal combinatorics principles. All possible combinations of the four viruses in each group were examined. New alignments were constructed for each subgroup of four viruses, and recombination was analyzed within these subgroups. Recombination analysis was carried out with different algorithms implemented in the Recombination Detection Program v.4.43 (RDP4) [35], namely RDP, GENECONV, Chimaera, MaxChi, BootScan, 3Seq and SiScan, with their default settings.

Analysis of selection

In those groups of viruses where putative recombination events were revealed, tests for possible selective pressures (positive selection or purifying selection) were performed. Nucleotide sequences corresponding to the fragments of NS1, NS3 and VP proteins that were used to retrieve protein-based phylogenies for the regions with recombinant and non-recombinant origin were tested by Z-test of Selection and Fisher's Exact Test of Selection (both tests were implemented in MEGA v.6) [39, 40, 66]. The corresponding sequences were aligned using MAFFT v.7 (E-INS-i algorithm was used for the fragments of NS1 and G-INS-I - for the fragments of NS3 and VP).

Results and discussion

To date, about 50 different DVs have been reported to infect invertebrates belonging to a number of insect and crustacean families. The majority of them have had their genomes completely or nearly completely sequenced and thoroughly characterized, but some still lack full genome sequences. For a comprehensive and systematic analysis of putative recombination events in the subfamily *Densovirinae*, we selected all DVs with well-annotated genome sequences, there being 40 of them in total. The full list of viruses taken into the analysis and their GenBank reference numbers can be found in the corresponding section of Materials and methods.

Without a doubt, the DVs described so far represent only a small fraction of all the invertebrate-infecting parvoviruses that exist in nature, especially taking into account the exceptional diversity of their natural hosts. However, even the DVs that have already been described show great heterogeneity in their genome organization, size and expression strategies [1, 15, 45, 52, 59, 61, 65], which is paralleled by significant divergence in their genomic nucleotide sequences, the mean sequence similarity between them averaging 40 %. According to numerous recommendations on performing recombination studies, including the user's manual for the RDP4 recombination detection software utilized in this study, in order to obtain information about recombination events in a group of genomes with reasonable significance and accuracy, the genome similarity in the group should be at least 60 %, optimally ranging from 70 % to 95 % [35]. If sequences under study are more divergent, there is a high probability that the inferred recombination events may be artifacts caused predominantly by the poor quality of alignments that are usually obtained when using distantly related sequences. Therefore, to ensure that we could reliably detect recombination events in a diverse group of DVs, our strategy was to cluster them so that viruses in each individual subgroup shared the recommended level of genome similarity, and we investigated recombination in each subgroup separately.

Towards this end, a cladogram was constructed, based on the complete genome nucleotide sequences of the DVs in the analysis, by the maximum-likelihood and Bayesian methods. The sequences were aligned and further processed in GBlocks to eliminate nonhomologous and poorly aligned regions in order to obtain a refined alignment fit for further phylogenetic analysis. The resultant cladogram, a consensus of trees generated by the two methods, is presented in Fig. 1, and the corresponding alignment used to retrieve it is given in Supplementary Fig. 1.

On the cladogram, the DVs under study clustered with the highest reliability into two large clades, one encompassing viruses infecting decapods and mosquitoes and the other containing viruses infecting other insect orders, mainly lepidopterans. Each of the two clades subdivided into two large subclades, one of them containing two more sub-subclades. It should be noted here that each branch of the cladogram was well supported statistically.

The overall topology of the obtained cladogram was in good conformity with the topologies of the phylogenetic tree obtained on the basis of amino acid sequences of the main nonstructural NS1 protein used to define the current DV taxonomy. The subclade structure of the cladogram strictly matched the newly proposed classification, each of the five subclades corresponding to one of the DV genera. The uppermost subclade contained viruses in the genus *Ambidensovirus* that share the common feature of a large-sized ambisense genome and infect hosts in the orders Lepidoptera, Diptera, Dictyoptera and several others. The second subclade from the same clade encompassed viruses from the genus *Iteradensovirus*, which infect exclusively lepidopterans and possess smaller-sized monosense genomes. The upper subclade of the second clade contained viruses infectious for penaeid shrimps of the genera *Penaeus* and *Fenneropenaeus* with large 6.0–6.3-kb genomes comprising the genus *Hepandensovirus*. The second subclade of this clade subdivided into two sub-subclades, one of them corresponding to the genus *Penstyldensovirus*, encompassing viruses specific for *Penaeus* or *Litopenaeus stylirostris* shrimp, and the other to the genus *Brevidensovirus*, encompassing mosquito-infecting DVs. Both genera include viruses with 4.0-kb genomes, the smallest among the known DVs, characterized by the specific feature of having unique terminal sequences instead of inverted repeats. These five DV groups were included in our subsequent analysis of recombination.

When studying the phylogenetic relationships between DVs on the basis of their full genome nucleotide sequences, we did not set our task to infer their precise positions within the clades, as it appears impossible to do so given an approximately 600-bp GBlocks-trimmed alignment. The full-genome nucleotide sequences appear to be too divergent to allow a reliable determination of evolutionary relationships. However, it is quite appropriate to utilize these sequences in studies of the macroevolution of this group of viruses as judged by the overall topology obtained above.

Prior to starting the search for potential recombination events, we calculated pairwise genetic distances between the viruses in each of the five groups included in the analysis in order to make sure that they conform to the recommended 60–95 % nucleotide sequence similarity. The results depicting the corresponding distances in each group are summarized in Supplementary Fig. 2. Among the

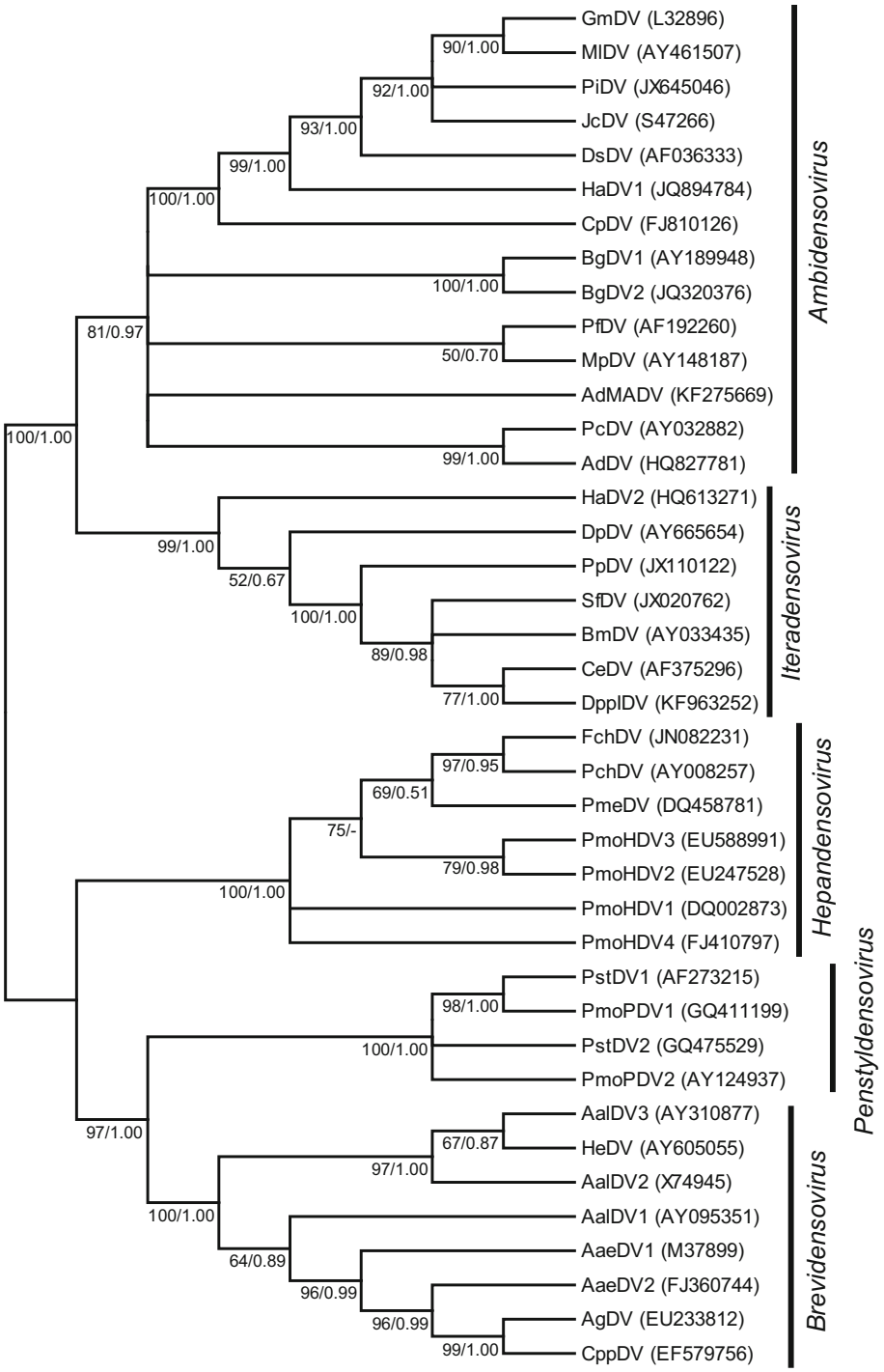

Fig. 1 Phylogenetic relationships of members of the subfamily *Densovirinae* based on virus nucleotide sequences. The consensus GBlocks-treated MAFFT tree of 40 members of the subfamily *Densovirinae* constructed using maximum likelihood (ML) and Bayesian inference. The numbers above the branches indicate bootstrap percentages and Bayesian posterior probabilities (PP). The values are listed for ML/PP. Missing or weakly supported nodes (<50 % or 0.5) are denoted by "—"

14 DVs in the genus *Ambidensovirus*, only seven, namely, GmDV, MlDV, Pseudoplusia includens densovirus (PiDV), JcDV, Diatraea saccharalis densovirus (DsDV), Helicoverpa armigera densovirus 1 (HaDV1) and CpDV, demonstrated genome similarity in the 60–93% range (Supplementary Fig. 2A), allowing the recombination study. Other virus genomes appeared to be rather distantly related to each other and to these seven more closely related viruses, with the exception of two *Blattela germanica* DVs, BgDV1 and BgDV2. The similarity between these two viruses was 63.5 %. However, these two viruses had low similarity to all other DVs, and as they could not be examined separately, they were excluded from the recombination study. In the case of the genus *Iteradensovirus*, Helicoverpa armigera densovirus 2 (HaDV2) showed a rather low level of similarity (about 50 %) to all other

viruses in this group and thus was excluded as well. The similarity between the other six virus genomes ranged from 85.5 % to 62.3 % (Supplementary Fig. 2B). In the other three groups, consisting of members of the genera *Hepandensovirus*, *Penstyldensovirus*, and *Brevidensovirus*, the viruses were more closely related to each other than in the first two groups, with the maximal similarity found within the genus *Penstyldensovirus* (about 95 %). The average similarity level in all three groups was >80 % (Supplementary Fig. 2C–E), so all viruses from these groups, namely seven hepandensoviruses, four penstyldensoviruses, and eight brevidensoviruses, were included in the subsequent recombination study.

The genetic distances we calculated were based on the complete genome sequence alignments processed with GBlocks, so hypervariable nucleotide positions were not considered. Hence, genetic distances between the viruses included in our analysis may be slightly inflated. Nevertheless, because we wanted to include in our study the largest number of viruses possible, and the distances retrieved using the unprocessed alignment did not show significant differences, we considered it acceptable to base our study on the results of GBlocks.

Besides calculating the genetic distances within each group, we also assessed the genetic similarity between virus genomes in genera that clustered together on the cladogram. In particular, we studied the genetic distances between the viruses in the *Ambidensovirus* and *Iteradensovirus* clades and the *Brevidensovirus* and *Penstyldensovirus* clades, as well as the distances between the genomes of viruses constituting three clades – *Brevidensovirus, Penstyldensovirus,* and *Brevidensovirus*. As expected, in all cases, these DV groups were too divergent from each other to be jointly analyzed for recombination.

To study recombination within the selected DV genera, we used two different approaches for grouping virus genomes. The first was a generally used approach in which all genome nucleotide sequences under study are aligned and the resulting multiple alignment is then tested for all possible recombination signals. However, in our case, the DV genomes were highly divergent even within each genus group, compromising the alignment quality and generating considerable false positive recombination signals; in turn, this resulted in a large number of artefacts, recombination events with undefined breakpoints and other anomalies. Moreover, even for recombination events identified with reasonable confidence, the *p*-values were unusually low, and their statistical significance seemed to be underestimated.

To manage the problem of poor alignment quality, we employed a second approach, a slightly modified form of a commonly exploited method of verifying the automatically detected recombination events in RDP4. Here, recombination is studied in small groups of four genomes, consisting of two potential parents, one potential recombinant and an outlier. When only four genomes are aligned, a decreasing number of subjects is bound to lead to decreasing variation (better alignment due to chance), the quality of the resulting alignment is improved, which renders the subsequent search for recombination events more accurate. For each set of genomes within each genus, all possible combinations of four were defined, and the search for recombination events in each combination was performed by seven different methods implemented in the RDP4 software. The retrieved results were examined thoroughly and compared with each other, and the most significant recombination events were noted. On the whole, this approach was more sensitive and informative and gave more reliable results with a high level of statistical support than the first approach.

Nevertheless, the possible recombination events identified by both approaches for each group appeared to be the same on the whole, adding further support to our analysis. The statistical confidence parameter values were generally higher when the recombination event was detected using the second approach. For this reason, only the results obtained using the second approach are presented here.

The search for recombination in the subfamily *Densovirinae* resulted in three potentially significant recombination events. Two of them were identified in the group corresponding to the genus *Ambidensovirus*, and one in the genus *Iteradensovirus*.

The first event, which involved JcDV, PiDV and HaDV1 ambidensoviruses, was detected by all seven recombination detection methods with an exceptionally high level of confidence (p-value $\leq 1.233 \times 10^{-3}$, Table 1). DsDV was taken as the fourth genome, the outlier. The Bootscan plot depicting the recombination event is shown in Fig. 2a. The region with the recombinant origin is located in the left part of the alignment and encompasses approximately 1.5 kb. The DV genome grouping method recognized three other groups of four viruses, which included JcDV, PiDV and HaDV1, with one of the three remaining viruses, MlDV, GmDV and CpDV serving as an outlier. In all of these groups, the same recombination event as that shown in Fig. 2a was detected with high statistical support (data not presented).

The JcDV and PiDV genomes were clearly more similar to each other in the recombinant region, while in other genome regions, JcDV showed higher similarity to HaDV1 than to PiDV (Fig. 2a). The HaDV1 and PiDV genomes showed exceptionally low similarity to each other. Based on these results, we speculate that JcDV represents the recombinant genome, while PiDV and HaDV1 represent the descendants of the parental genome.

The second recombination event identified in the genus *Ambidensovirus* involved MlDV, GmDV, and HaDV1 and

Table 1 Recombination events detected in members of the subfamily *Densovirinae*

Recombination event	No. 1	No. 2	No. 3
Genus	*Ambidensovirus*	*Ambidensovirus*	*Iteravirus*
Virus genomes involved	JcDV (S47266), PiDV (JX645046), HaDV1 (JQ894784)	MlDV (AY461507), GmDV (L32896), HaDV1 (JQ894784)	CeDV (AF375296), DpDV (AY665654), DpplDV (KF96325)
Out-group	DsDV (AF036333)	PiDV (JX645046)	BmDV (AY033435)
P-values determined by seven different programs implemented in RDP4			
RDP	8.553×10^{-17}	8.232×10^{-14}	6.659×10^{-13}
GENECONV	1.233×10^{-03}	4.375×10^{-9}	ND
BootScan	2.720×10^{-19}	4.176×10^{-14}	1.556×10^{-18}
MaxChi	3.897×10^{-15}	1.995×10^{-19}	3.968×10^{-12}
Chimaera	1.442×10^{-15}	$6{,}936 \times 10^{-22}$	1.445×10^{-08}
SiScan	4.658×10^{-20}	6.261×10^{-29}	2.697×10^{-04}
3Seq	3.909×10^{-11}	5.948×10^{-31}	ND
Probability (MC uncorrected/MC corrected)	$6.800\ E^{-20}/2.720\ E^{-19}$	$1.487\ E^{-31}/5.948\ E^{-31}$	$3.891\ E^{-17}/1.556\ E^{-16}$

ND, recombination was not detected by this program; MC, multiple comparisons

was also detected by all seven recombination detection methods with a *p*-value of 4.375×10^{-9} (Table 1). In this case PiDV was taken as the outlier genome. The Bootscan plot for this event is presented in Fig. 2b. It shows that the region with the recombinant origin occupies the central part of the alignment. As with the recombination event described above, there also exist three other combinations of four with these three viruses (MlDV, GmDV and HaDV1), with different outliers (JcDV, CpDV, or DsDV), and in all three groups, the same recombination event as that shown in Fig. 2b was detected with high statistical support (data not presented).

In Fig. 2b, it can be seen that the genomes of MlDV and GmDV have considerable similarity within the region that was identified as having a recombinant origin, whereas the genome of MlDV is more similar to the genome of HaDV1 within the non-recombinant regions. This suggests that MlDV may be a recombinant virus that originated from a recombination event between the ancestors of GmDV and HaDV1.

The viruses involved in recombination events in the second group, corresponding to the genus *Iteradensovirus*, were CeDV, DpplDV and DpDV. The recombination event was detected by five out of the seven recombination detection methods with a *p*-value $\leq 2.697 \times 10^{-4}$ (Table 1). Bombyx mori densovirus (BmDV) served as the outlier genome. The segment with an apparent recombinant origin is a ~600-bp region in the right part of the alignment, with CeDV most probably having obtained this segment from the ancestor of DpDV as a minor parent. The corresponding Bootscan plot is shown in Fig. 2c. The other two combinations of four including these three viruses (CeDV, DpplDV and DpDV) with different outliers, Sibine fusca densovirus (SfDV) and Papilio polyxenes densovirus (PpDV), also confirm this recombination event (data not presented).

It is common practice to treat alignments that are intended for use in recombination studies with GBlocks, and several investigators have indicated that such treatment may improve the results [8, 12]. All of the alignments used in our recombination studies were processed with GBlocks, and indeed, comparison with results obtained without GBlocks showed that the deletion of gaps and hypervariable nucleotide positions augmented the sensitivity and the accuracy of recombination detection and increased the significance level of the recombination events.

Notably, all of the observed recombination events in DVs led to the exchange of nucleotide sequences corresponding to nearly the entire protein-coding ORF or a significant part of the ORF. In the case of JcDV, the recombinant region corresponded to the ORF encoding the major nonstructural NS1 protein; for MlDV, the recombinant region almost perfectly coincided with the ORF encoding the small NS3 regulatory protein; and in the case of the third event, the recombinant region occupied a large part of the CeDV capsid protein ORF. It appears, therefore, that such recombination events might affect the relative positions of the recombinant viruses on the phylogenetic tree and bring incongruence to phylogenies based on the protein sequences encoded by ORFs with recombinant and non-recombinant origins [10]. To confirm this supposition for each of the three identified recombination events, we compared the phylogenetic trees constructed on the basis of two amino acid sequences: one corresponding to the

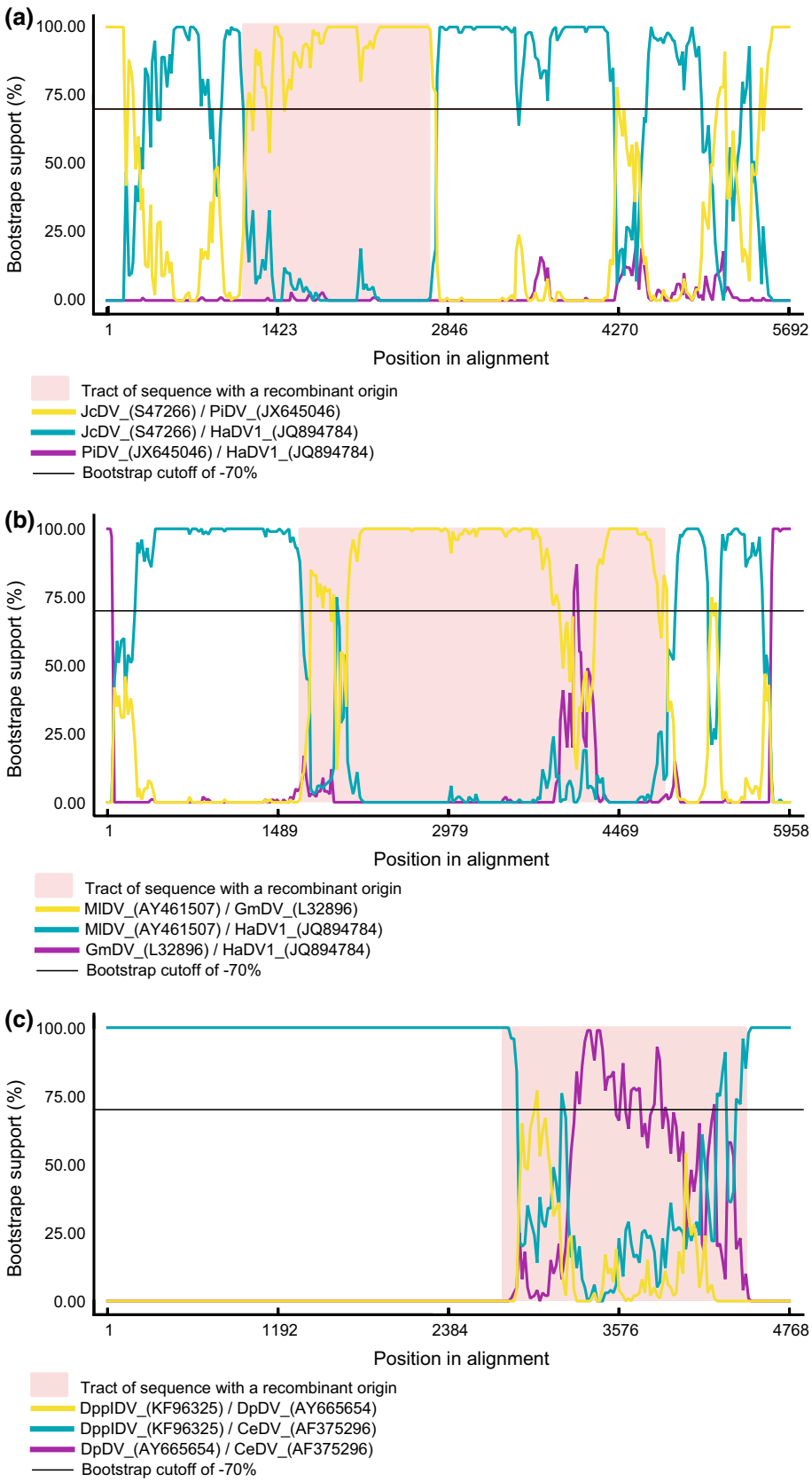

Fig. 2 BOOTSCAN plots of the three recombination events detected by the RDP4 software. Plotted on the *y*-axis is the bootstrap support of each pair of sequences, and their position in the alignment is on the *x*-axis. Recombinant regions (shown in pink) were detected within the following groups of viruses: **A** – JcDV, PiDV, HaDV1 and DsDV; **B** – MlDV, GmDV, HaDV1 and PiDV; **C** – CeDV, DpplDV, DpDV and BmDV. Symbols are listed under each of the figures

protein encoded by the ORF that had undergone recombinational exchange, and the other to the protein encoded by the ORF with non-recombinant origin. The resulting consensus trees are presented in Fig. 3. The multiple amino acid sequence alignments used for phylogenetic analysis are given in Supplementary Figs. 3–5.

For the first recombination event, involving JcDV, HaDV1 and PiDV, phylogenetic trees were constructed on the basis of the NS1 regulatory protein in which the recombinant region was detected and the VP capsid protein, corresponding to a non-recombinant ORF. As shown in Fig. 3a, on the NS1 tree, the putative recombinant JcDV clearly clusters with PiDV, from whose ancestor it might have acquired the recombinant region of its genome, encoding this protein. At the same time, on the non-recombinant VP tree (Fig. 3b), JcDV is more closely related to HaDV1, in good agreement with what was demonstrated by the recombination analysis. Thus, the recombination event that took place in the evolutionary history of these three viruses has a considerable effect on the relative phylogenetic positions of these DVs.

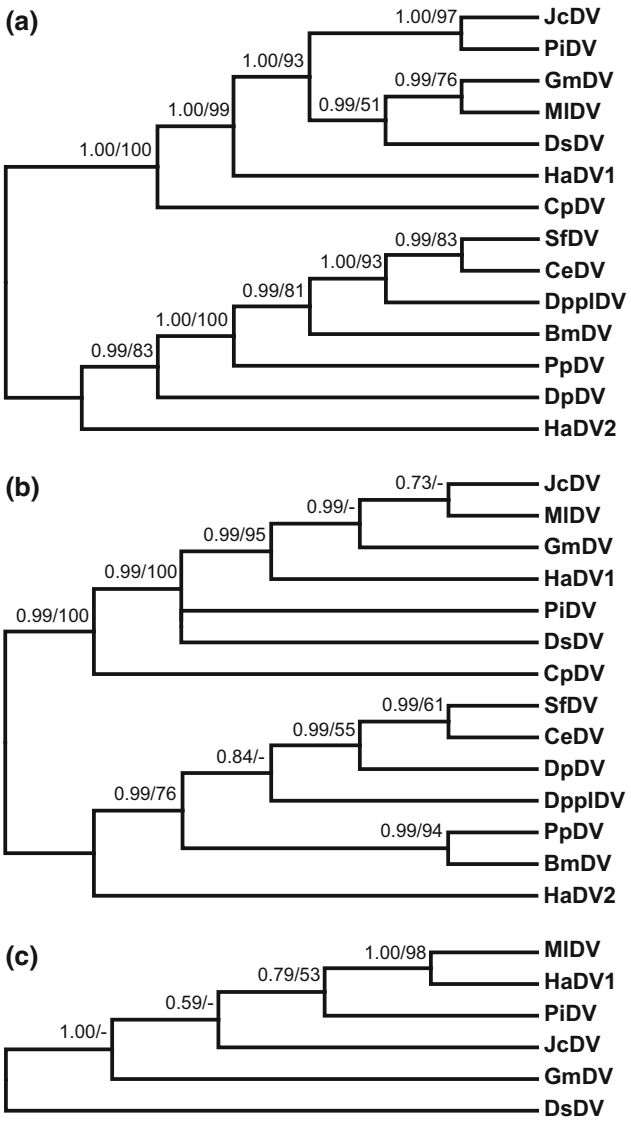

Fig. 3 Phylogenetic relationships of members of the subfamily *Densovirinae* based on virus amino acid sequences. The consensus MAFFT trees of members of the subfamily *Densovirinae* constructed using maximum likelihood (ML) and Bayesian inference based on amino acid sequences corresponding to the different virus proteins: **A** – NS1, **B** – capsid (VP), and **C** – NS3. The numbers above the branches indicate bootstrap percentages and Bayesian posterior probabilities (PP). The supporting value is shown in the order of PP/ML. Missing or weakly supported nodes (<50 % or 0.5) are denoted by "—"

For the third event, which was detected in the *Iteradensovirus* genus group, and in which CeDV, DpplDV and DpDV were involved, the same NS1 and VP trees were used, but this time with the VP amino acid sequence corresponding to the recombinant region and NS1 corresponding to the non-recombinant region. On a tree based on the VP capsid protein amino acid sequence (Fig. 3b), CeDV appeared to be more closely related to DpDV than to DpplDV, as was expected, because about half of the ORF encoding this protein is shared by CeDV and DpDV due to the recombinational exchange. On the NS1 tree (Fig. 3a), however, CeDV and DpplDV cluster together, as they do in whole-genome analysis (Fig. 1), while DpDV is much more distant from both of them. This recombination event thus also causes inconsistencies in the relative positions of iteradensoviruses on phylogenetic trees constructed using different protein sequences.

For the second event in the genus *Ambidensovirus* (MlDV, GmDV and HaDV1), we constructed an additional phylogenetic tree based on the small NS3 regulatory protein, which is encoded by an ORF within a region with a recombinant origin. The VP protein corresponded to the genome region with non-recombinant origin. In the case of this recombination event, the nucleotide sequence containing the NS3-coding region was apparently obtained by the ancestor of MlDV from an ancestor of HaDV1. On the NS3 tree (Fig. 3c), these two viruses cluster together with exceptionally high bootstrap support. On the VP tree (Fig. 3b), however, HaDV1 localizes separately from the rest of the group, which includes JcDV, MlDV and GmDV, which are apparently more closely related to each other than to HaDV1. It appears that in this case, similar to the two recombination events discussed above, the recombinational exchange of a genome segment affects the reconstructed phylogenies retrieved on the basis of two different genome segments.

Another evolutionary process that shapes virus genomes and can cause convergence of certain protein sequences, but not others, is positive selection [6, 7, 29, 51, 55]. To assess whether selection pressure on protein sequences can

affect the phylogenetic tree topology, we tested for the possible selection forces acting on the DV genomes in each group where protein phylogenetic analysis was performed.

The fragments of the ORFs corresponding to recombinant and non-recombinant genome regions (NS1, VP and NS3) were examined separately in each group of viruses used in the recombination studies; the alignments of these DNA fragments are shown in Supplementary Fig. 6. For viruses in the genus *Ambidensovirus,* which included JcDV, PiDV, MlDV, GmDV, DsDV, HaDV1 and CpDV, NS1 appeared to be subjected to purifying selection in all of the viruses, and no positive selection was detected for any virus. In the case of the VP protein, all viruses except for CpDV were subjected to purifying selection as well, with no positive selection being shown for any of the seven viruses under study. For viruses in the genus *Iteradensovirus* (SfDV, CeDV, DpplDV, BmDV, PpDV, DpDV, HaDV2), no positive selection was detected for NS1 and VP, and both proteins in all seven viruses appeared to be subjected to purifying selection. For the NS3 protein, possible selection pressure was tested in only six viruses of the genus *Ambidensovirus*, because in CpDV, the NS3 ORF is split into two parts and could not be analyzed without compromising the resulting multiple alignment. In this case, clear positive selection was demonstrated for DsDV, but none for JcDV, HaDV1, MlDV, GmDV and PiDV; however, all of the latter five viruses appeared to be subjected to purifying selection. Notably, DsDV is not involved in any detectable recombination event, and its position on the protein-based phylogenetic trees (Fig. 3) shows no bias regardless which genome region (NS or VP-coding) was used for the analysis. Therefore, we may conclude that in the genus *Ambidensovirus*, the tree topology is unaffected by positive selection of protein sequences and that the observed incongruence in the relative positions of viruses on the tree is solely caused by recombination.

These results demonstrate that recombination events in the evolutionary history of a group of viruses can shape the phylogenies inferred on the basis of different genome segments and sequences of the corresponding proteins. Such recombination may affect virus systematics at the sub-genus level. Therefore, recombination should always be considered, and putative recombination events should be tested in investigations of virus systematics. We also recommend that a set of features, including the joint topology of several phylogenetic trees based on different proteins or nucleotide sequences should be used to develop an accurate taxonomy of the group.

DVs seem to have a rather complicated evolutionary history, and the origins of these viruses remain obscure. Studying recombination may provide some hints about the evolution of at least some viruses in this subfamily. For example, the recombination detected in the genus *Iteradensovirus* suggests that at some time in the past, the ancestral DpplDV virus might have acquired through recombination a genome segment from DpDV's ancestor, and thereby a new virus, the common ancestor of CeDV and the very closely related SfDV, might have emerged. This idea is supported by the same recombination event in both the CeDV and SfDV genomes, although the latter event had lower statistical support (data not presented). At the same time, it should be noted that the hosts of CeDV and SfDV are from different continents (West Africa and South America, respectively), but both occur in oil palm plantations. It is interesting that according to Francois et al. [19], a newly-described DV, tentatively named HormaDV, is also a possible product of recombination between the DpDV and DpplDV ancestors, implying that it may represent the third DV that might have emerged in the same way.

Considering the possible origins of the DVs in the genus *Ambidensovirus*, our recombination studies suggest that JcDV, GmDV and MlDV may all be the descendants of an ancestral virus related to the present-day HaDV1. We may also speculate that the present-day JcDV might have emerged as a product of recombination between the HaDV1-related common ancestor of JcDV, GmDV and MlDV and a PiDV ancestor, with this event leading to the segregation between JcDV and the related GmDV and MlDV viruses.

In addition to the three major recombination events discussed in this paper, we also detected a number of other putative recombinations in all of the groups we analyzed (data not presented). However, statistical support for these events was low, and some could not be confirmed by tree reconstructions based separately on the recombinant and non-recombinant regions. Therefore, we could not determine whether these represented genuine events or artefacts. The presence of major, readily verified recombinations, together with other putative recombination events support our speculation that recombination might have played a significant role in shaping the genomes of DVs and that new recombination events will be described in this virus group in the future, when new virus genomes are sequenced and added to the group to fill in the existing gaps in DV diversity.

The factors that might facilitate recombination in the subfamily *Densovirinae* are still poorly understood. Recombination across two virus genomes requires coinfection of a host cell. Although a number of DVs have the ability to infect a range of other species other than their known hosts, to our knowledge, coinfection of the same host with two or more DVs has not been described. However, we cannot know whether some DVs co-infected the same organism at some time in their evolutionary history.

To conclude, we have, for the first time, performed a systematic analysis of recombination in the subfamily *Densovirinae* of the family *Parvoviridae* and have identified with a high degree of confidence three recombination events in the genomes of viruses in the genera *Ambidensovirus* and *Iteradensovirus*. By comparing phylogenetic tree topologies based on amino acid sequences of proteins encoded by genome regions with different origins, we demonstrated clear and substantial effects of recombination events, suggesting that recombination always should be taken into account in investigations of virus phylogeny.

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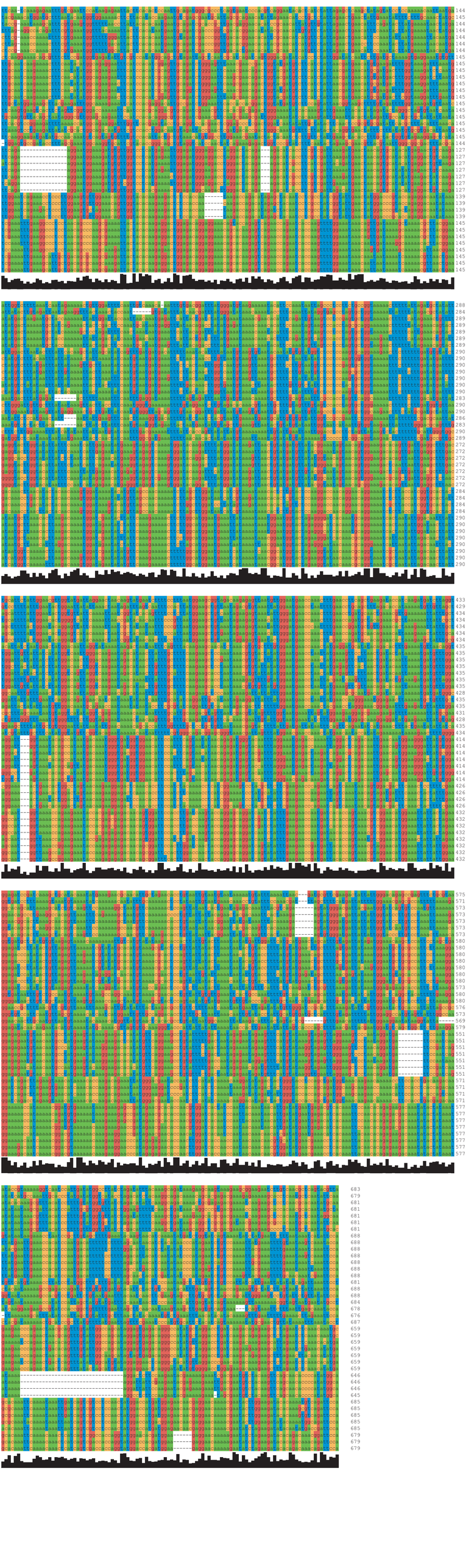

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>PmoPDV2_(AY124937)
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>AaeDV2_(FJ360744)

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Supplementary Figure 1.

DNA alignment of 40 densovirus species built in Mafft v.7 and treated by Gblocks v.0.91b.

The following parameters were used.

Mafft: E-INS-i with scoring matrix – 200PAM / k=2, gap opening penalty – 1.53 and offset value – 0.0;

Gblocks: minimum number of sequences for a conserved position – 21, minimum number of sequences for a flanking position – 35, maximum number of contiguous nonconserved positions – 8, allow gap positions within the final blocks – yes, allow smaller final block – yes.

Estimates of Evolutionary Divergence between Sequences

The number of base differences per site between sequences are shown.
Standard error estimate(s) are shown above the diagonal (blue fonts).
The values of base differences per site less than 0.4 are highlighted in yellow; species names used in the analysis of recombination highlighted in green.

A. *Ambidensovirus*

Species	PfDV	DsDV	GmDV	MlDV	JcDV	HaDV1	PiDV	CpDV	BgDV2	BgDV1	PcDV	AdDV	AdMADV	MpDV
PfDV		0.011	0.010	0.010	0.011	0.010	0.010	0.010	0.011	0.011	0.010	0.011	0.010	0.010
DsDV	0.451		0.007	0.006	0.006	0.007	0.006	0.010	0.010	0.011	0.011	0.011	0.011	0.009
GmDV	0.448	0.118		0.005	0.006	0.006	0.006	0.011	0.010	0.010	0.010	0.011	0.011	0.010
MlDV	0.450	0.118	0.071		0.006	0.006	0.006	0.010	0.011	0.010	0.011	0.011	0.011	0.009
JcDV	0.449	0.111	0.087	0.074		0.006	0.006	0.011	0.011	0.011	0.011	0.011	0.011	0.010
HaDV1	0.454	0.144	0.127	0.115	0.102		0.007	0.011	0.011	0.010	0.011	0.012	0.011	0.010
PiDV	0.452	0.131	0.123	0.115	0.099	0.146		0.010	0.011	0.011	0.010	0.011	0.011	0.010
CpDV	0.493	0.363	0.375	0.365	0.376	0.372	0.383		0.011	0.010	0.010	0.011	0.011	0.010
BgDV2	0.519	0.518	0.514	0.518	0.518	0.525	0.520	0.547		0.010	0.010	0.010	0.011	0.011
BgDV1	0.509	0.513	0.505	0.514	0.511	0.499	0.504	0.537	0.365		0.010	0.011	0.010	0.010
PcDV	0.512	0.490	0.489	0.486	0.481	0.489	0.490	0.519	0.549	0.546		0.010	0.011	0.010
AdDV	0.502	0.473	0.473	0.473	0.468	0.476	0.481	0.507	0.552	0.542	0.453		0.010	0.010
AdMADV	0.553	0.542	0.546	0.546	0.542	0.536	0.545	0.563	0.580	0.563	0.553	0.562		0.010
MpDV	0.530	0.527	0.519	0.526	0.522	0.530	0.530	0.551	0.568	0.568	0.546	0.548	0.582	

The overall average is 0.438

B. *Iteradensovirus*

Species	HaDV2	DpDV	PpDV	BmDV	SfDV	CeDV	DpplDV
HaDV2		0.007	0.008	0.007	0.007	0.007	0.007
DpDV	0.510		0.007	0.007	0.007	0.008	0.006
PpDV	0.506	0.368		0.007	0.006	0.006	0.006
BmDV	0.499	0.377	0.245		0.006	0.006	0.006
SfDV	0.494	0.354	0.220	0.204		0.005	0.006
CeDV	0.499	0.354	0.217	0.198	0.137		0.006
DpplDV	0.503	0.371	0.232	0.203	0.157	0.145	

The overall average is 0.323

C. *Hepandensovirus*

Species	FchDV	PchDV	PmoHDV3	PmoHDV2	PmeDV	PmoHDV1	PmoHDV4
FchDV		0.001	0.005	0.005	0.005	0.004	0.005
PchDV	0.011		0.005	0.005	0.004	0.004	0.005
PmoHDV3	0.132	0.131		0.004	0.005	0.006	0.005
PmoHDV2	0.136	0.134	0.110		0.004	0.005	0.005
PmeDV	0.145	0.145	0.160	0.152		0.005	0.005
PmoHDV1	0.171	0.170	0.172	0.170	0.178		0.004
PmoHDV4	0.158	0.157	0.165	0.167	0.173	0.115	

The overall average is 0.145

D. *Penstyldensovirus*

Species	PstDV1	PstDV2	PmoPDV2	PmoPDV1
PstDV1		0.004	0.005	0.004
PstDV2	0.048		0.004	0.004
PmoPDV2	0.079	0.063		0.005
PmoPDV1	0.046	0.057	0.083	

The overall average is 0.063

E. *Brevidensovirus*

Species	AalDV3	HeDV	AalDV2	AalDV1	AaeDV1	AaeDV2	AgDV	CppDV
AalDV3		0.002	0.003	0.007	0.007	0.007	0.007	0.007
HeDV	0.018		0.003	0.007	0.007	0.007	0.007	0.006
AalDV2	0.041	0.036		0.007	0.007	0.007	0.006	0.006
AalDV1	0.178	0.173	0.173		0.005	0.006	0.005	0.005
AaeDV1	0.181	0.179	0.183	0.097		0.004	0.004	0.004
AaeDV2	0.185	0.183	0.187	0.111	0.071		0.003	0.003
AgDV	0.186	0.185	0.186	0.110	0.073	0.039		0.001
CppDV	0.185	0.183	0.185	0.110	0.071	0.039	0.009	

The overall average is 0.127

```
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SfDV/1-559      1 FRAVERRMGI-LADQLCRAFE-NNTVNARRILHDSIELRRNQN--FREMVFGIRKVLDKRGSYAIWFHET--DKGTEDYPEDICRGYPPDYDFGVISTGFRLSGKPAIEPVGRGG---RGGRDEPDPRIKFKTYKYYPETK 132
CeDV/1-559      1 FRAVERRMGI-LADQLCRAFE-NNTSNARRILHDSIELRRNQN--FRKMVFDIRKVLDKRGSYAIWFHET--NKGTEDYPEDICRGYPPDYDFGVISTGFRLSGKPAIEPIGRGG---RGGRDPPDPRIKFKTYKYYPETK 132
DpplDV/1-558    1 FRAVERRMGI-LADQLCRASE-DNTVNARRILHDSIELRRNQN--FREMVFGIRKVLDKRGSYAIWFHET--DKGTEDYPEDICRGYPPDYDFGVISTGFRYSGKPAIEPIGRGE---R-GRDSPDPRIKFKIYKYYPETK 131
BmDV/1-558      1 FRAVERRMGI-LADQLCRAFE-NNTVNARRILHDSIEFRPGHR--FREMVYKIRRALDSRGSYAIWFHET--NKGTEDYPEDISRGYPPDYDFGVIPTRYRYCGKPAIEPI-RIR---EGGGESQEPTIEFKTYKYYSEKK 131
PpDV/1-562      1 FAAVERRMGI-LATQLCESYK-INSTNARRILHDSIEYRGNKA--FREVVFNLRKVLDKRGSYAIWFHET--DKYQEDYPEDICRGYPPDYDFGVISTGFRYTGKPVVEPLPRTRDRTEPIPHGSRDTDAFRVYKYYPETK 135
HaDV2/1-543     1 YASIQREWTLSVSERLFRYFT-EGDHGARRLLHDSVYFKNQRE--FVEFHKRILSVLQNTDGWIVAVHD---ESSTASYKLKFSGWQSEGKPWGLLP-------KPALRKE-------DTHDEAGRRHI--------IERDR 114
DsDV/1-478      1 FQYMAEELEK-MGNQFFGYVTGQSVKPSSAYISDVIILRDIQL-------------------------------------------------------------------------------------RDQC 46
JcDV/1-478      1 FQYMAEELEK-MGSEFFGYVTGQSIKPSSAYISDVIILRDIQL-------------------------------------------------------------------------------------RDQC 46
PiDV/1-478      1 FQYMAEELEK-MGSEFFGYVTGQSIKPSSAYISDVIILRDIQL-------------------------------------------------------------------------------------RDQC 46
GmDV/1-478      1 FQYMAEELEK-MGSEFFRYVTGQDIKPSSAYISDVIILRDIQL-------------------------------------------------------------------------------------RNQC 46
MlDV/1-478      1 FQHMAEELEK-MGGEFFGYVTGQSIKPSSAYISDVIILRDIQL-------------------------------------------------------------------------------------RDQC 46
HaDV1/1-478     1 FQHMAEELEK-MGGEFFGYVTGQSIKPSSAYISDVIILRDIQL-------------------------------------------------------------------------------------RDQC 46
CpDV/1-473      1 YEDLAKEIEE-MGDIFIRYVTGKNIKNTWRYLSDVFFPRGESN-------------------------------------------------------------------------------------ANFA 46

Conservation    9328378744-884386354 5-3532674474+4*67447234 1-------------------------------------------------------------------------------1624
Quality
Consensus       FQA+ARE+EK-MGDQ+FRYVTGQNIK++RRYL+D+I+LRDIQL--FREMVF+IRKVLDKRGSYAIWFHET--DKGTEDYPEDICRGYPPDYDFGVISTGFRYSGKPAIEPIGRG+---RGGRD+P+PRIKFKTYKYYRDQ+

DpDV/1-570    138 IKKVNEVGKSWPFERSDLTPFPVPVKG-HFHVLHACTWYNQECRCLSRHFDVNPRKNNALRSECISAEHIRNIL-LYNTKWPRWAIYIKVSN----EEKFRFVYRTESVREEELRPIEQNELEGSSSPLEIRRKR-DREGS 271
SfDV/1-559    133 VYHDTQR------QIYEEEAFDEPTEG-HFHILHACQWYNNECRCLGRSFDVNPRKSKAIPIDPVDTEHIRNIM-FYNTKWPRWPVYIKVAD----GPEFEYVYRTESISKESIQP------ERQSQQLEEGNNQ-NESGP 254
CeDV/1-559    133 IYHDVYR------EIYEEEAFDEPTEG-HFHILHACQWYNNECRCLGRSFDVNPRKNKAIPIDPVDTEHIRNIM-FYNTKWPRWPVYIKVAD----GPEFEYVYRTESISKESIQP------ERQSQQLEESNNQ-DESGP 254
DpplDV/1-558  132 IYHDTQR------EIYQEEDFDEPTEG-HFHILHACQWYNNECRCLGRSFDVNPRKNKAIPIDPVDTEHIRNIM-FYNTKWPRWPVYIKVAD----GPEFEYVYRTESISKESIQP------ERQSQQLEESNDQ-DESGP 253
BmDV/1-558    132 VYHNIEG------RAYEEKKFEEPTQG-HFHILHACRWYNNECRCLGRSFDVNPRKNKAIPIDPVDTEHIRNIV-FYNTKWPRWPVHIKVAD----GPEFEYVYRTESVCKESIQP------KRHSQQLEESNDQ-DESGP 253
PpDV/1-562    136 VFHDPER------SIYEEEDFEEPTEG-HFHILHACQWYNNECRCLGRSFDVNPRKNKAIPIAPLDEEHIRNIM-LYNTKWPRWPVYIKVAN----GPEYEYVYRTESISKESVQP------ERQSQQLEESNYQ-NESGP 257
HaDV2/1-543   115 IIWDVGT------LEEETEVIPIPKYG-HFHILHPCRWYNSNCRHLGKHLDVAKRYRQIRTMGALSESHVRNTL-IYLQTNGKWLLDYKSPS----GQEFGFVYRAQCLQSKRVCS------GEEERKVEDSTGE-NEVYG 236
DsDV/1-478     47 LDVLREYG-----RSRRNGLFGFSEEGDHIHVIHDCSYTNRSCR------DIWLGQVKPFGTVQKTGKPVKYIWEFKRTDWYDVFIYFFIRK----RGERAIYIRGESGKIPS---------NDECVRWAREFKE-REMVS 162
JcDV/1-478     47 LDVLREYG-----RSRRNGLFGFSEEGDHIHVIHDCSYTNRSCR------DIWISQVKPFGSVQKTGKPVKFIWEFKRTDWYDVFIYFFVRK----RGERAIYVRGESGKIPS---------NDECVRWTREFKE-REMVS 162
PiDV/1-478     47 LDVLREYG-----RSRRNGLFGFSEEGDHIHVIHDCSYTNRSCR------DIWISQVKPFGSVQKTGKPVKFIWEFKRTDWYDVFIYFFVRK----RGERAIFVRGESGKIPS---------NDECVRWTREFKE-REMVS 162
GmDV/1-478     47 LDILREYG-----RSRRNGLFGFSEEGDHIHVIHDCSYTNRSCR------DIWISQVKPFGSVQKTGKPVKYIWEFKRTDWYDVFIYFFVRK----RGERAIFVRGESGKIPS---------NDECVRWAREFKE-REVVS 162
MlDV/1-478     47 LDVLREYG-----RSRRNGLFGFSEEGDHIHVIHDCSYTNRSCR------DIWISQVKPFGSVQKTGKPVKYIWEFKRTDWYDVFIYFFVRK----RGERAIYIRGESGKIPS---------NDECVRWAREFKE-REVVS 162
HaDV1/1-478    47 LDILREYG-----RSRRNGLFGFSEEGDHIHVIHDCSYTNRSCR------DIWLSQVKPFGTVQKTGKPVKYVWEFKRTDWYDVFIYFFVRK----RGERAIFIRGESGKIPS---------NDECVRWTREFKE-REVVS 162
CpDV/1-473     47 MERLREYG-----RSRRDRMFGFINEGDHIHIIHDCAYSGGHCR------DVFRKHLEPYGSFGPARPENKPIWKFTTTDWYDVFQYFFLRKLRNGNDTGEIYIGGESWKKPS---------NDQLVRWEKKLGTWRPLVR 167

Conservation  8234332------22364318334345*-*8*9+*4*4+6743**------*95346355435253532269566-8549574664646476534----335337664787542 35---------333334643333 26-64353
Quality
Consensus     LDHLREYG-----RSRRNGLFGFPEEGDH+H++HDCS+YNR+CRCLGRSFDV+PR+VKPFGSVQKTG+HV+NIWEFY+TDWYD+FIYF+VRK----+GE++IVYRGESGK+PSIQP------NDE+VRWEREFKE-RESVS

DpDV/1-570    272 SDGE-----HDCGRPNYKNSR----------------------SSQKGDSVQKIIRFIQQKPTWPLEHVFQTKEWLDGPFGTWVSSDKTVKRAIEIFSLQTMHYTYTQFVDYYRSLECN---------PIWAAPSFNGFTDYY 378
SfDV/1-559    255 S-GR-----QPSSVPNKRDNRCT-----------DVPHGKSSRNGNPVEKFVEQFKLRPTWPLEHILDTKDWLESEWGTYIASDKQIQRTFQILMKITMNMTYSELKMLYQNEHTM---------PIWGAISSKDLMNTY 368
CeDV/1-559    255 S-GR-----QPTSLPNKRDNKCT-----------NVPHGKSSRNGNPVEKFVEQFKLRPTWPLEHILDTKDWLESEWGTYIASDKQIQRTFQILMKITMNMTYSELKMLYQNEHTM---------PIWGAISSKDLLNTY 368
DpplDV/1-558  254 S-GR-----QPPSLPTKRDNRCT-----------DVPHGKSSRNGNPVEKFVEQFKLRPTWPLEHILDTKDWLESEWGTYIASDKQIQRTFQILMKITMNMTYDELKMLYQNEHTM---------PIWGAISSKDLLNTY 367
BmDV/1-558    254 S-GQ-----QSSRLPTKRDNRCA-----------DVPHGRSSRNGNPVEKFVEQFKLRPTWPLEHILDTKDWLESEWGTYIASDKQIQRTFQILMKITMNMTYSDLKMLYQNEHTM---------PIWGAISSNDLLNTY 367
PpDV/1-562    258 S-GQ-----QPSRLPNKRDNRCS-----------DVPHGKSSRNGNTVEKFVEQFKLRPTWPLEHILDTKDWLESEWCTYIAGDKQIQRTFQILMKITMNMTFEELRMLYQNENTM---------PIWGATGSKDLLKTY 371
HaDV2/1-543   237 E-GELAD-SQGNHATCKRRKRET----------AGTSGERNISTENLLEHITSIVCYPMDHVFQTRDWYTGKYKYLISSDKLVKRCYSILQKQLMNWSYNDFLNHYRKDDTK---------LIFGAPSLDTFNDYY 351
DsDV/1-478    163 S-SDCTDYYECEQQEHKISRRSDAGSTNGRLYEKKTYSAGKFAYIRQKTKALLRKY---YVSPISAICDVPEFRDDDLLCDPKNRDYIQAACEDFGKDLNAMSLREIYNLLTEDYNFTDDKELNPYAQFIS------SMKY 293
JcDV/1-478    163 S-SDCTDYYECEQQEHKISRRSDAGSSNGRLYEKKAYSAGKFAYIRKKTKALLRKY---YVSPVSAICDVPEFRDDDLLCDPKNRDYIQAACDDFGKDLNAMSLREIYNLLTEDYNFTDEQELNPYALFIS------SMKY 293
PiDV/1-478    163 S-SDCTDYYECEQQEHKISRRSDAGSSNGRLYEKKAYSAGKFAYIRKKTKALLRKY---YVSPVSAICDVPEFRDDDLLCDPKNRDYIQAACDDFGKDLNAMSLREIYNLLTEDYNFTDEKELNPYALFIS------SMKY 293
GmDV/1-478    163 S-SDCTNYYECEQQEHKISRRSNVSSTNGRLYEKKTYSAGKFAYIRQKTKALLRKY---YVSPISAICDVPEFRDDDLLCDPKNRDYIQAACDDFGKDLNAMSLREIYDLLTEDYNFTDEKELNPYAQFIS------SMKY 293
MlDV/1-478    163 S-SDCTDYYECEQQEHKISRRSDAGSTNGRLYEKKAYSAGKFAYIRQKTKALLRKY---YVSPISAICDVPEFRDDDLLCDPKNRDYIQAACDDFGKDLNAMSLREIYDLLTEDCNFTDEKELNPYAQFIS------SMKY 293
HaDV1/1-478   163 S-SDSTDYYECEQQEHKISRRSDAGSTNGRFYEKKTYSAGKFAYIRQKTKALLRKY---YCSPIIAIRDVDEFRDDDLLCDPKNRDYVEAACEDFGKDLNDMSLRQIYNLLTEDYNFTDEKELNPYALFIS------SMKY 293
CpDV/1-473    168 Q-QDNGDHLLDQRSGLKRSNREVAGTPFDEVYGKKTKSSGKYAAIKQETKALLLKY---YPCPLSAIRDVSEFRNNNLLSDPKNREYIDAAFVDFGKDVNQMTIRQIYEILKGHTD---------PIFYA------GMEY 288

Conservation  6-66-----34333333755590 1-----------1110315824432764894 57---465*834937729947537453647765954763486646728975783557632360---------57958------544*
Quality
Consensus     S-GDCTDYY+CEQQ+HKRS+RSDAGSTNGRLYEKK+YSAGKSAYI++KTKALLRKYKLRYT+PL++I+D+KE+RDDDLL+DPKN+KYIQ+A+Q+FGKDL+NM++REIY+L+TEDY+FTDEKELNPYP IF+AISSKDLSMKY

DpDV/1-570    379 HTLDESIDIIERLLNYQCEQDEYLSEMSQNDAKKVFINDLWDILEKKRPKQNTFQIIGEPSAGKNYFIDAILSFYLNTGIILNFNRFSQFPLMEAVNRRVNVWNEPNFEPAALDTIKMLLAGDPLKVNVKYQKEQYLQKTP 519
SfDV/1-559    369 YSIDESQLIVEELLDFQLNNDQLEYFENLEEAKRKFITDLYEILEKKHQKTNTFQIVSPPSAGKNFFIETVLAFYWNTGVIQNFNRYNNFPLMEAVNRRVNYWDEPNFEPDAVETLKKLFAGTALKATVKFQKEANVQKTP 509
CeDV/1-559    369 YTLDESQEIVEELLDYQMNNDQLEYFDNIEEAKRKFITDLYEILEKKHQKTNTFQIVSPPSAGKNFFIETVLAFYWNTGVIQNFNRYNNFPLMEAVNRRVNYWDEPNFEPDATETLKKLFAGTALKATVKFQKEANVQKTP 509
DpplDV/1-558  368 YTLDEPQDIVEELLDFQMHNDQLEYFDSLEDAKRKFITDLYEILEKKHQKTNTFQIVSPPSAGKNFFIETVLAFYWNTGVIQNFNRYNNFPLMEAVNRRVNYWDEPNFEPDATETLKKLFAGTALKATVKFQKEANVQKTP 508
BmDV/1-558    368 YTIEESQQIVEELLDFQMHNDQLEYFDSIEDAKKRFITDLYEILEKKHQKTNTFQIVSPPSAGKNFFIETVLAFYWNTGVIQNFNRYNNFPLMEAVNRRVNYWDEPNFEPDATETLKKLFAGTALKATVKFQKEANVQKTP 508
PpDV/1-562    372 FSLDESETIVEELLDYQLTNDRLEYFDDLFDAKRRFITDLYEILEKKHQKTNTFQIVSPPSAGKNFFIETVLAFYWNTGVIQNFNRYHSFPLMEAVNRRVNYWDEPNFEPDATETLKKLFAGTALKASVKFQKEANVQKTP 512
HaDV2/1-543   352 MSLEDSIDAIEELLDFQLSNISEFSDLNVTDKKREFVTDLWDVLEKKVPKKNTFQIISPPSAGKNFLLDAIFAFYWNVGMIRNFNKYESFPLMEAVDKRVNCWNEPNFEPSAEDTIKMILGGDPIKAAYKYESERNIARTP 492
DsDV/1-478    294 DNLEGSLNIVNELLKYQCNDDE--------DLIVEFLTNLVNVLDRRIPKLNAFLIISPPSGGKNFFFDMIFGLLLSYGQLGQANRHNLFAFQEAPNKRVLLWNEPNYESSLTDTIKMMFGGDPYTVRVKNRMDAHVKRTP 426
JcDV/1-478    294 DNLENSLNIIIELLKFQCNDDE--------DLIVEFLTNLVNVLDRRIPKLNAFLIISPPSAGKNFFFDMIFGLLLSYGQLGQANRHNLFAFQEAPNKRVLLWNEPNYESSLTDTIKMMFGGDPYTVRVKNRMDAHVKRTP 426
PiDV/1-478    294 DNLENSLNIIVELLKYQCNDDE--------DLIVEFLTNLVNVLDRRIPKLNAFLILSPPSAGKNFFFDMIFGLLLSYGQLGQANRHNLFAFQEAPNKRVLLWNEPNYESSLTDTIKMMFGGDPYTVRVKNRMDAHVKRTP 426
GmDV/1-478    294 DNLEGSLNIIDELLKYQCNDDE--------GLIVEFLTNLVNVLDRRIPKLNAFLVMSPPSAGKNFFFDMIFGLLLSYGQLGQANRHNLFAFQEAPNKRVLLWNEPNYESSLTDTIKMMFGGDPYTVRVKNRMDAHVKRTP 426
MlDV/1-478    294 DNLEGSLNIIDELLKYQCNDDE--------GLIVEFLTNLVNVLDRRVPKLNAFLVMSPPSAGKNFFFDMIFGLLLSYGQLGQANRHNLFAFQEAPNKRVLLWNEPNYESSLTDTIKMMFGGDPYTVRVKNRMDAHVKRTP 426
HaDV1/1-478   294 DNLENSLNIVTELLTFQCNDDE--------SLIVEFLTNLVNVLDRKKPKLNTFVVYSPPTAGKNFFFDMIFGFCLSYGQLGQANKQNLFAFQEAPNKRVLLWNEPNYESSLTDTVKMMLGGDPYTVRVKNRGDQHVKRTP 426
CpDV/1-473    289 ATQEESFAILEDFLKFQFEDND--------EKITQFLVDLIDVLDKRVPKQNAFAVISPPSSGKNFFFDMIMAICLNYGQLGQANRHNLFAFQEAPNKRLLLWNEPNYESAMTDTIKMMMGGDPYTVRVKYQGDTHVTRTP 421

Conservation  2979474379478*59*73745--------44643*978*679*99937*4*7*59685*98***9889698886795*6+397*9535*788**789*966*8****9*75749*9*798+*8776846*674945949**
Quality
Consensus     DNLEESLNIVEELL++QCNDDELEYFD+LED++VEFLTDLVNVL+KKHPKLNTFQI+SPPSAGKNFFFDMIFAFYLNYGQ+G++NR+NLF+++EA+NKRV+LWNEPN+E+SATDTIKMMFGGDPY+VRVKNQK+AHV+RTP

DpDV/1-570    520 IIVMTNKPV-FPNDLAFHDRVCTYFWKRAPFLKEYHAKLHPMIWSYLVNTYV 570
SfDV/1-559    510 VIITANYDK-FTKE-VWDDRIIKYYWYPCPKLKEYNKRLHPFVWCYLVDKYV 559
CeDV/1-559    510 VIITANHDK-FTKE-VWDDRIIKYYWYQCPKLKQYNKRLHPFVWCYLVDKYV 559
DpplDV/1-558  509 VIITANYDK-FTKE-VWDDRIIKYYWYPCPKLKQYNKRLHPFVWCYLVDKYV 558
BmDV/1-558    509 VIITANYDK-FTKE-VWDDRIIKYYWYPCPKLKEYNKRLHPFAWVYLVDKYV 558
PpDV/1-562    513 VIITANRDK-FTSE-VWDDRIIKYEWYQCPMLKKYTKRLHPFVWCYLVDKYV 562
HaDV2/1-543   493 VIVMSNKNV-FKINDAFEDRIITYYWDRAEFLRKYRKKVNPLIWPYLVDNYV 543
DsDV/1-478    427 VIILTNNTVPFMYELAFSDRIIQYKWNAAPFLKDYELKPHPMTFFLLLSKYN 478
JcDV/1-478    427 VIILTNNTVPFMYETAFSDRIIQYKWNAAPFLKDYELKPHPMTFFLLLSKYN 478
PiDV/1-478    427 VIILTNNTVPFMYETAFSDRIIQYKWDAAPFLKDYELKPHPMTFFLLLSKYN 478
GmDV/1-478    427 VIILTNNTVPFMYETAFADRIIQYKWNAAPFLKEYELKPHPMTFFLLLSKYN 478
MlDV/1-478    427 VIILTNNTVPFMYETAFADRIIQYKWNAAPFLKDYELKPHPMTFFLLLSKYN 478
HaDV1/1-478   427 VIVLTNNIVPFMYEIAFNERIVQYKWNVAPFLKDYELKPHPMTFFLLLSKYN 478
CpDV/1-473    422 VLILTNNYVSFLQESAFKDRIKVYKWREAPFLKDVHVKPYPMAFFDILNKYN 473

Conservation  9+967*525-*327-8929*954*4*41956*9564496 5*8593 3+976*7
Quality
Consensus     VIILTNN+VPFMYETAFDDRIIQYKW+AAPFLKDYE+KPHPMT+FYL++KY+
```

>DpDV
YQCVKRRMER-LGADLYETFR-NNSRGTRRILHDSIEYEESRHGCFNTMVEKLIERLDKG
NGCAIFFHESPDQKGEWPYPENISRGYYPDFDFCVFKNDEVWNGKLAQEPTEEDS--SDG
REFGGRRWLDLEEYTYFHDSKIKKVNEVGKSWPFERSDLTPFPVPVKG-HFHVLHACTWY
NQECRCLSRHFDVNPRKNNALRSECISAEHIRNIL-LYNTKWPRWAIYIKVSN----EEK
FRFVYRTESVREEELRPIEQNELEGSSSPLEIRRKR-DREGSSDGE-----HDCGRPNYK
NSR-------------------SSQKGDSVQKIIRFIQQKPTWPLEHVFQTKEWLDGPF
GTWVSSDKTVKRAIEIFSLQTMHYTYTQFVDYYRSLECN---------PIWAAPSFNGFT
DYYHTLDESIDIIERLLNYQCEQDEYLSEMSQNDAKKVFINDLWDILEKKRPKQNTFQII
GEPSAGKNYFIDAILSFYLNTGIILNFNRFSQFPLMEAVNRRVNVWNEPNFEPAALDTIK
MLLAGDPLKVNVKYQKEQYLQKTPIIVMTNKPV-FPNDLAFHDRVCTYFWKRAPFLKEYH
AKLHPMIWSYLVNTYV

>SfDV
FRAVERRMGI-LADQLCRAFE-NNTVNARRILHDSIELRRNQN--FREMVFGIRKVLDKR
GSYAIWFHET--DKGTEDYPEDICRGYPPDYDFGVISTGFRLSGKPAIEPVGRGG---RG
GRDEPDPRIKFKTYKYYPETKVYHDTQR------QIYEEEAFDEPTEG-HFHILHACQWY
NNECRCLGRSFDVNPRKSKAIPIDPVDTEHIRNIM-FYNTKWPRWPVYIKVAD----GPE
FEYVYRTESISKESIQP------ERQSQQLEEGNNQ-NESGPS-GR-----QPSSVPNKR
DNRCT------------DVPHGKSSRNGNPVEKFVEQFKLRPTWPLEHILDTKDWLESEW
GTYIASDKQIQRTFQILMKITMNMTYSELKMLYQNEHTM---------PIWGAISSKDLM
NTYYSIDESQLIVEELLDFQLNNDQLEYFENLEEAKRKFITDLYEILEKKHQKTNTFQIV
SPPSAGKNFFIETVLAFYWNTGVIQNFNRYNNFPLMEAVNRRVNYWDEPNFEPDAVETLK
KLFAGTALKATVKFQKEANVQKTPVIITANYDK-FTKE-VWDDRIIKYYWYPCPKLKEYN
KRLHPFVWCYLVDKYV

>CeDV
FRAVERRMGI-LADQLCRAFE-NNTSNARRILHDSIELRRNQN--FRKMVFDIRKVLDKR
GSYAIWFHET--NKGTEDYPEDICRGYPPDYDFGVISTGFRLSGKPAIEPIGRGG---RG
GRDPPDPRIKFKTYKYYPETKIYHDVYR------EIYEEEAFDEPTEG-HFHILHACQWY
NNECRCLGRSFDVNPRKNKAIPIDPVDTEHIRNIM-FYNTKWPRWPVYIKVAD----GPE
FEYVYRTESISKESIQP------ERQSQQLEESNNQ-DESGPS-GR-----QPTSLPNKR
DNKCT------------NVPHGKSSRNGNPVEKFVEQFKLRPTWPLEHILDTKDWLESEW
GTYIASDKQIQRTFQILMKITMNMTYSELKMLYQNEHTM---------PIWGAISSKDLL
NTYYTLDESQEIVEELLDYQMNNDQLEYFDNIEEAKRKFITDLYEILEKKHQKTNTFQIV
SPPSAGKNFFIETVLAFYWNTGVIQNFNRYNNFPLMEAVNRRVNYWDEPNFEPDATETLK
KLFAGTALKATVKFQKEANVQKTPVIITANHDK-FTKE-VWDDRIIKYYWYQCPKLKQYN
KRLHPFVWCYLVDKYV

>DpplDV
FRAVERRMGI-LADQLCRASE-DNTVNARRILHDSIELRRNQN--FREMVFGIRKVLDKR
GSYAIWFHET--DKGTEDYPEDICRGYPPDYDFGVISTGFRYSGKPAIEPIGRGE---R-
GRDSPDPRIKFKIYKYYPETKIYHDTQR------EIYQEEDFDEPTEG-HFHILHACQWY
NNECRCLGRSFDVNPRKNKAIPIDPVDTEHIRNIM-FYNTKWPRWPVYIKVAD----GPE
FEYVYRTESISKESIQP------ERQSQQLEESNDQ-DESGPS-GR-----QPPSLPTKR
DNRCT------------DVPHGKSSRNGNPVEKFVEQFKLRPTWPLEHILDTKDWLESEW
GTYIASDKQIQRTFQILMKITMNMTYDELKMLYQNEHTM---------PIWGAISSKDLL
NTYYTLDEPQDIVEELLDFQMHNDQLEYFDSLEDAKRKFITDLYEILEKKHQKTNTFQIV
SPPSAGKNFFIETVLAFYWNTGVIQNFNRYNNFPLMEAVNRRVNYWDEPNFEPDATETLK
KLFAGTALKATVKFQKEANVQKTPVIITANYDK-FTKE-VWDDRIIKYYWYPCPKLKQYN
KRLHPFVWCYLVDKYV

>BmDV

FRAVERRMGI-LADQLCRAFE-NNTVNARRILHDSIEFRPGHR--FREMVYKIRRALDSR
GSYAIWFHET--NKGTEDYPEDISRGYPPDYDFGVIPTRYRYCGKPAIEPI-RIR---EG
GGESQEPTIEFKTYKYYSEKKVYHNIEG------RAYEEKKFEEPTQG-HFHILHACRWY
NNECRCLGRSFDVNPRKNKAIPIDPVDTEHIRNIV-FYNTKWPRWPVHIKVAD----GPE
FEYVYRTESVCKESIQP------KRHSQQLEESNDQ-DESGPS-GQ-----QSSRLPTKR
DNRCA------------DVPHGRSSRNGNPVEKFVEQFKLRPTWPLEHILDTKDWLESEW
GTYIASDKQIQRTFQILMKITMNMTYSDLKMLYQNEHTM---------PIWGAISSNDLL
NTYYTIEESQQIVEELLDFQMHNDQLEYFDSIEDAKKRFITDLYEILEKKHQKTNTFQIV
SPPSAGKNFFIETVLAFYWNTGVIQNFNRYNNFPLMEAVNRRVNYWDEPNFEPDATETLK
KLFAGTALKATVKFQKEANVQKTPVIITANYDK-FTKE-VWDDRIIKYYWYPCPKLKEYN
KRLHPFAWVYLVDKYV

>PpDV

FAAVERRMGI-LATQLCESYK-INSTNARRILHDSIEYRGNKA--FREVVFNLRKVLDKR
GSYAIWFHET--DKYQEDYPEDICRGYPPDYDFGVISTGFRYTGKPVVEPLPRTRDRTEP
IPHGSRDTDAFRVYKYYPETKVFHDPER------SIYEEEDFEEPTEG-HFHILHACQWY
NNECRCLGRSFDVNPRKNKAIPIAPLDEEHIRNIM-LYNTKWPRWPVYIKVAN----GPE
YEYVYRTESISKESVQP------ERQSQQLEESNYQ-NESGPS-GQ-----QPSRLPNKR
DNRCS------------DVPHGKSSRNGNTVEKFVEQFKLRPTWPLEHILDTKDWLESEW
CTYIAGDKQIQRTFQILMKITMNMTFEELRMLYQNENTM---------PIWGATGSKDLL
KTYFSLDESETIVEELLDYQLTNDRLEYFDDLFDAKRRFITDLYEILEKKHQKTNTFQIV
SPPSAGKNFFIETVLAFYWNTGVIQNFNRYHSFPLMEAVNRRVNYWDEPNFEPDATETLK
KLFAGTALKASVKFQKEANVQKTPVIITANRDK-FTSE-VWDDRIIKYEWYQCPMLKKYT
KRLHPFVWCYLVDKYV

>HaDV2

YASIQREWTLSVSERLFRYFT-EGDHGARRLLHDSVYFKNQRE--FVEFHKRILSVLQNT
DGWIVAVHD---ESSTASYKLKFSGWQSEGKPWGLLP-------KPALRKE-------DT
HDEAGRRHI-------IERDRIIWDVGT------LEEETEVIPIPKYG-HFHILHPCRWY
NSNCRHLGKHLDVAKRYRQIRTMGALSESHVRNTL-IYLQTNGKWLLDYKSPS----GQE
FGFVYRAQCLQSKRVCS------GEEERKVEDSTGE-NEVYGE-GELAD-SQGNHATCKR
RKRET---------------AGTSGERNISTENLLEHITSIVCYPMDHVFQTRDWYTGKY
KYLISSDKLVKRCYSILQKQLMNWSYNDFLNHYRKDDTK---------LIFGAPSLDTFN
DYYMSLEDSIDAIEELLDFQLSNISEFSDLNVTDKKREFVTDLWDVLEKKVPKKNTFQII
SPPSAGKNFLLDAIFAFYWNVGMIRNFNKYESFPLMEAVDKRVNCWNEPNFEPSAEDTIK
MILGGDPIKAAYKYESERNIARTPVIVMSNKNV-FKINDAFEDRIITYYWDRAEFLRKYR
KKVNPLIWPYLVDNYV

>DsDV

FQYMAEELEK-MGNQFFGYVTGQSVKPSSAYISDVIILRDIQL----------------

----------------RDQCLDVLREYG-----RSRRNGLFGFSEEGDHIHVIHDCSYT
NRSCR------DIWLGQVKPFGTVQKTGKPVKYIWEFKRTDWYDVFIYFFIRK----RGE
RAIYIRGESGKIPS---------NDECVRWAREFKE-REMVSS-SDCTDYYECEQQEHKI
SRRSDAGSTNGRLYEKKTYSAGKFAYIRQKTKALLRKY---YVSPISAICDVPEFRDDDL
LCDPKNRDYIQAACEDFGKDLNAMSLREIYNLLTEDYNFTDDKELNPYAQFIS------S
MKYDNLEGSLNIVNELLKYQCNDDE--------DLIVEFLTNLVNVLDRRIPKLNAFLII
SPPSGGKNFFFDMIFGLLLSYGQLGQANRHNLFAFQEAPNKRVLLWNEPNYESSLTDTIK
MMFGGDPYTVRVKNRMDAHVKRTPVIILTNNTVPFMYELAFSDRIIQYKWNAAPFLKDYE
LKPHPMTFFLLLSKYN

>JcDV
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NRSCR------DIWISQVKPFGSVQKTGKPVKFIWEFKRTDWYDVFIYFFVRK----RGE
RAIYVRGESGKIPS---------NDECVRWTREFKE-REMVSS-SDCTDYYECEQQEHKI
SRRSDAGSSNGRLYEKKAYSAGKFAYIRKKTKALLRKY---YVSPVSAICDVPEFRDDDL
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MKYDNLENSLNIIIELLKFQCNDDE--------DLIVEFLTNLVNVLDRRIPKLNAFLII
SPPSAGKNFFFDMIFGLLLSYGQLGQANRHNLFAFQEAPNKRVLLWNEPNYESSLTDTIK
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>PiDV
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SRRSDAGSSNGRLYEKKAYSAGKFAYIRKKTKALLRKY---YVSPVSAICDVPEFRDDDL
LCDPKNRDYIQAACDDFGKDLNAMSLREIYNLLTEDYNFTDEKELNPYALFIS------S
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NRSCR------DIWISQVKPFGSVQKTGKPVKYIWEFKRTDWYDVFIYFFVRK----RGE
RAIFVRGESGKIPS---------NDECVRWAREFKE-REVVSS-SDCTNYYECEQQEHKI
SRRSNVSSTNGRLYEKKTYSAGKFAYIRQKTKALLRKY---YVSPISAICDVPEFRDDDL
LCDPKNRDYIQAACDDFGKDLNAMSLREIYDLLTEDYNFTDEKELNPYAQFIS------S
MKYDNLEGSLNIIDELLKYQCNDDE--------GLIVEFLTNLVNVLDRRIPKLNAFLVM
SPPSAGKNFFFDMIFGLLLSYGQLGQANRHNLFAFQEAPNKRVLLWNEPNYESSLTDTIK
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RAIYIRGESGKIPS---------NDECVRWAREFKE-REVVSS-SDCTDYYECEQQEHKI
SRRSDAGSTNGRLYEKKAYSAGKFAYIRQKTKALLRKY---YVSPISAICDVPEFRDDDL
LCDPKNRDYIQAACDDFGKDLNAMSLREIYDLLTEDCNFTDEKELNPYAQFIS------S
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SPPSAGKNFFFDMIFGLLLSYGQLGQANRHNLFAFQEAPNKRVLLWNEPNYESSLTDTIK
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>HaDV1

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NRSCR------DIWLSQVKPFGTVQKTGKPVKYVWEFKRTDWYDVFIYFFVRK----RGE
RAIFIRGESGKIPS---------NDECVRWTREFKE-REVVSS-SDSTDYYECEQQEHKI
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>CpDV

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SNREVAGTPFDEVYGKKTKSSGKYAAIKQETKALLLKY---YPCPLSAIRDVSEFRNNNL
LSDPKNREYIDAAFVDFGKDVNQMTIRQIYEILKGHTD----------PIFYA------G
MEYATQEESFAILEDFLKFQFEDND--------EKITQFLVDLIDVLDKRVPKQNAFAVI
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```

Supplementary Figure 3.

Alignments of the fragments of NS1 proteins of 14 densovirus species built in Mafft v.7.

The following parameters were used: Iterative refinement method E-INS-i with BLOSUM62 scoring matrix, gap opening penalty – 1.53 and offset value – 0.0.

```
DsDV/1-401      1 IYEIPRPFTNFGKKLSTYTKSHKFMIFGLANNVIAE--TGT-TGNLHRLLTTCLAEIPWQKIPLYMNQSEFDLL---PPGSRIVECNVKVIFRSNRIAFETSSTATKQATLNQISNLQTAVGLNKLGWGIDRSF-TAFQSDQPM----IPT 140
GmDV/1-402      1 VYIIPRPFSNFGKKLSTYTKSHKFMIFGLANNVIGP--TGTGTTAVNRLLTTCLAEIPWQKLPLYMNQSEFDLL---PPGSRVVECNVKVIFRTNRIAFETSSTVTKQATLNQISNVQTAIGLNKLGWGINRAF-TAFQSDQPM----IPT 141
JcDV/1-402      1 VYVIPRPFSNFGKKLSTYTKSHKFMIFGLANNVIGP--TGTGTTAVNRLITTCLAEIPWQKLPLYMNQSEFDLL---PPGSRVVECNVKVIFRTNRIAFETSSTATKQATLNQISNLQTAVGLNKLGWGIDRSF-TAFQSDQPM----IPT 141
MlDV/1-402      1 VYVIPRPFSNFGKKISTYTKSHKFMIFGLANNVIGP--AGTGTTAVNRLITTCLAEIPWQKLPLYMNQSEFDLL---PAGSRVVECNVKVIFRSNRIAFETSSTATKQATLNQISNLQTAVGLNKLGWGIDRSF-TAFQSDQPM----IPT 141
HaDV1/1-403     1 VYVIPRPFSNFGKKLSTYTKSHKFMIFGLANNVIGP--AGTGTTAVNRLITTCLAEIPWQKLPLYMNQSEFNLL---PPGSRVVECNVKVIFRTNRIAFETNATTTKQATLNQISNLQTAVGLNKLGWGIDRSF-TAFQSDQPM----IPT 141
PiDV/1-399      1 VYAIPRPFSNFGKKFSTYSKSHKFMIFGLANNVIAQ--TGT-TDNLNRLLTTCLAEVPWQKVPFYMNQSEFDLL---PNGSVMVECNVKVIFRSNRIAFETSATATKQATLNQISNVQTAIGLNKLGWGLDRSF-TAFQTDQPM----IPT 140
CpDV/1-429      1 EYHIERPISLFGSKISTYRKVHKFMTFGFAPKII----TSD-SNSNSRWLTTYLAEVPWHLPCFYLTPSEFNLM---PIGSRVKDVSIQVIYRGSTIQFETASSATSLATLNQINDIAVATALNKTGYGSNVSF-TEFTAGKPM----IPS 138
DpDV/1-405      1 DIFAGAPQPNQNHEL-IYGKSYHFTLTNGLPDFRHAI--TN-NAYSAQLRFKHIHGIPWERLLMYVSEGELLRLMRDYTALKVEEVVCEVYSLGVRLPFVTSATTSSVANANA----QYPIGC----FHFDNAYEIQYDATQ---VNDVIN 136
SfDV/1-407      1 DIFAGAPQPNQHHKL-VYGKSYHFTVSNGLPDFRHFLNTIS-NNYSAQLRFKHIHGIPWERLLMYLSEGELLRLRRDYTAVKAEEVVCEVYSLGVRLPFVTSATTSSVANANA----QYPIGC----FHFDQAYETIYDSNN---VADVIN 138
CeDV/1-410      1 DIYAGAPQPNQHHEF-VYGKSYHFTLTNGLPDFRHFINTIS-NNYSAQLRFKHIHGIPWERLLMYLSEGEYLRLMRDYTAVKVEEVVCEVYSLGVRLPFVTSATTSSVANANA----QYPIGC----FHFDKAYETQYDVNNINDINDIIN 141
DpplDV/1-407    1 DIYAGAPQPNQHHEL-VYGKSYHFTLTNGLPDFRHAL-VQT-NHYVAEQRFKHIHGIPWERLLMYISEGELVRLFRDYTAVKVEEVVCEVYSLGVRLPFVTSATTSSVANANA----QYPIGC----FHFDKAYQTQYDSTN---VQDIIN 137
PpDV/1-406      1 DIFSGAPQPNQHHQL-IYGKSYHFTLTNGLPDYRHFV-ASG-NNYIAQQRFKHIHGIPWERLLMYVSEGELARLFRDYTALKVEEVVCEIYSLGVRLPFVTSATTSSVANANA----QYPIGC----FHFDEAYETNYSPTN---VSDIIN 137
BmDV/1-406      1 DIFSGAPQPNQHHTL-VYGKSYHFTITNGLPEFRHLA-TTN-SGYYAQQRFKHIHGIPWERLLMYVSEGELLRMFRDYTSLKVEEVVCEVYSLGVRLPFVTSATTSSVANANA----QYPIGC----FHFDEAYETNYGINN---VADIIN 137
HaDV2/1-404     1 DVYAGSCQNPNKHIK-TFKKSYHFTISNKLPEWKRNVENGH-VEYLA--RYNSIHGIPWELVGMYLSEGEIGQLFENYSLVRVEEVNCKVYSLGVRLPFVTGQSVTTVANANA----QYPIAK----FNFDNDFFTSYEPEN---VYNVLE 136

Conservation    461534867563435-694*689*765737856500--152-625431056634449**55658*8958*7359---5455473996869755767+5*4*7696956*+7*6----6576+5----9348359-6394446------966

Quality

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JcDV/1-402    142 ATSAPKYEPIT---------GTTGYRGMIADYYGADSTNDAAFGNAGNYPH-----HQVGSFTFIQNYYCMYQQ--------TNQGTGGWPCLAEHLQQFDSKTVNNQCLIDVTYKPKMGLIKPPLNY--KIIGQPTAKGTISV--GDNLV 266
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HaDV1/1-403   142 ATAPPKYQPLT---------GTNGYRGMIADYYGADSTNDVAFGKCLVIIHI----IKLVPFTFIQNYFCMYQQ--------TNLGTGGWPCLAEHVQQFDSKTVNNQCLIDVTYKPKMGLIKPPLNY--KVIGAPTVKGTISV--GDNLV 267
PiDV/1-399    141 ATAAPKYGAVT---------GTNGYRGMIADYYGADSTNDAAFGAAGNYPH-----HQVGSFTFLQNYHCMYVQ--------TNRGTGGWPCLAEHIQQYDSKTVNNECLIDVSYKPLMGHLKLPLNY--KVVGWPTAKGVISV--GSNLP 265
CpDV/1-429    139 KIAKPRYKPIP---------GK--YRGMVADFYGTNNNHP---SFASYIPK-----HHVGRQCNIYNYHALSDEAATDTDGATTNSWGGWVCLAKHIQQMDGKTCVNQVVLSSTYSPRMGMIKNPLKSFGRGLPQPNAGGTMTIVTQGNLV 270
DpDV/1-405    137 KALGAEWKNSTRPDTPVSTQWSETFPNISASSTSRDISNPVIVNYPLPFGV-----TNVPKDVGIYDYVEIKNG--------TTAYGKCW--------------------EKRFKPKNGIL--------------YAESTLLTSGTNVSI 239
SfDV/1-407    139 KALGAEWKNTTRPAQPVTTAWSETFPNISSSTTSRDINNPVIVQYPLPYGI-----NNAPKDVGIYDYVDIKNG--------TTAHGKCW--------------------EKRFKPANGIL--------------YAESSLLTSSNNTGV 241
CeDV/1-410    142 KALGSEWKNTTRPAQPVTTSWSETFPNITASATSRDINNPVIVQYPLPYGI-----NNAPKDVGIYDYVDIKNG--------TTAYGKCW--------------------EKRFKPKNGIL--------------YAESSLLTNGNTTAV 244
DpplDV/1-407  138 KALGSEWKNFNRPSQPVTTEWSENFPNISASTTSRDINNPVIVVYPIPYGQ-----TNVPKDVGVYDYVDIKNG--------TTAYGKCW--------------------EKRFKPKNGII--------------YAESTLLGASGTSSP 240
PpDV/1-406    138 KALGAEWKNENRPAQIVTTNWSETFPNITASATSRDISNPVIVDYPLPFLY-----NNTPKDVGIYDYVDIKNG--------TTAYGKCW--------------------EKRFKPSNGIL--------------YAESTLKGNVATSEA 240
BmDV/1-406    138 KALGTEWKNATRPTAAVTTAWSEQFPNISASSTSRDINNPVIVDYSLPYFE-----NNVPKDVGIYDYVDIKNG--------TTAYGKCW--------------------EKRFKPTNGLL--------------YAESTLKGNVVTPLA 240
HaDV2/1-404   137 KCWGSEWKNMD----TTNTNWSTQFPNLTASTTSRDMNNPILVHYPRYSWITSGTREQFPKDVGIYDYCSIKNG--------STVFGLAW--------------------EMTHRPKQGIL--------------NAFTTPVITGQQFVL 240

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Quality

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JcDV/1-402    267 NMRGAVVINPPEATQ---------SVTESTHNLTRNFPANL-----FNIYSDIEKSQILHKGP--WGHEN--PQIQPSVHIGIQAVPALTTGALL----------VNSSPLNSWTDSMGYIDVMSSCTVMESQPTHFPFSTDANTNPG-- 386
MlDV/1-402    267 NMRGAVVTNPPEAVQ---------NITETTHNLTRNFPANL-----FNIYSDIEKSQILHKGP--WGHEN--PQIQPSVHIGIQAVPALTTGALL----------VNSSALNSWTDSMGYIDVMSSCTVMESQPTHFPFSTDANTNPG-- 386
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PiDV/1-399    266 NMRGAAITGP-EASQ---------NVVESLNTSDRNF-GTI-----FDIYSDIEKSQVLHKGP--WGAEQ--PQIQPSVHIGIQAVPALTTGALL----------VNSSPLNSWTDSMGYIDVVATCTVMEQQPSAFPFATEATTNPG-- 383
CpDV/1-429    271 AARSAHIMKDTAGSETTPGINGDRLQTSEVLINLSNDNDGTFPVVDDYDIYTPIEKSQIARSGF--WGAQD--PHIMPSMHIGVQPVPALSSGALI----------LEEGVFDNWTDTRAYWEVIATMNVVEHTPTEFPYANVPNVPPGEV 407
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SfDV/1-407    242 E-GPTNFMTPIPGLENGYFIGT--NQISERNDAQIRVPPKSYTATKYNATQAIVNESTVDYMGYNYFGEQKCAPQAMPKLMIGFVNIRNEDNSLLSAKWDILIKTRIHLSGLQSTREWVARTETIPP-QWFTSQYSQFRYENILTIP---L 385
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Conservation  4-44513336027 37----------352932253333212 57-----42517132353435 4*4--7*284--7558*5769*7669574777 7*3----------943568775775365394465-767537552946342134 6----

Quality

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JcDV/1-402    387 ------NTIYRINLTPNSLTSA 402
MlDV/1-402    387 ------NTIYRINLTPNSLTSA 402
HaDV1/1-403   388 ------NTIYRINLVPNSLTSA 403
PiDV/1-399    384 ------NTVYRIPLTPNTNNSA 399
CpDV/1-429    408 VISLPSNEIPQNYIDPENDHAP 429
DpDV/1-405    384 LNTSNIVKVPTNRPGMFSPNTP 405
SfDV/1-407    386 VRANDLSKLPTKRPGFISSNNP 407
CeDV/1-410    389 VRANGMQTNPTHRPGMISNYNP 410
DpplDV/1-407  386 ERSGGLTTVPSHRPLFALTYNP 407
PpDV/1-406    385 LRTGNTAKLPTKRPQMQSNVGI 406
BmDV/1-406    385 LRSLGTFKLPTKRPGMDSRIAA 406
HaDV2/1-404   383 HPNINMKNVTYNKRSMTRRLNV 404

Conservation  ------2565433335231375

Quality

Consensus     +RS+++NT+PRIRP+PNSLTSA
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LTAMRSANVSGPEIATQ----------QVSETSNNRIHNFPATF-----FDIYADIEKSQ
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IGLNKLGWGINRAF-TAFQSDQPM----IPTATTAPKYEPVT---------GDTGYRGMI
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WPCLAEHLQQFDSKTVNNQCLIDVTYKPKMGLIKSPLNY--KIIGQPTVKGTISV--GDN
LVNMRGAVVTNPPEATQ----------NVAESTHNLTRNFPADL-----FNIYSDIEKSQ
VLHKGP--WGHEN--PQIQPSVHIGIQAVPALTTGALL----------INSSPLNSWTDS
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WPCLAEHIQQFDSKTVNNQCLIDVTYKPKMGLIKPPLNY--KIIGQPTNKGTVSV--GDN
LVNMRGAVVTNPPEAVQ----------NITETTHNLTRNFPANL-----FNIYSDIEKSQ
ILHKGP--WGHEN--PQIQPSVHIGIQAVPALTTGALL----------VNSSALNSWTDS
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>HaDV1
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VGLNKLGWGIDRSF-TAFQSDQPM----IPTATAPPKYQPLT---------GTNGYRGMI
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WPCLAEHVQQFDSKTVNNQCLIDVTYKPKMGLIKPPLNY--KVIGAPTVKGTISV--GDN
LVNMRGAVVVNPPETQQ----------TVTESTHTLTRNFPTDL-----FGIYSDIEKSQ
ILHKGP--WGHEN--PQIQPSVHVGIQAVPALTTGALL----------VNSSPLNSWTDS
MGYIDVMASCTVMESQPTHFPFSADANTNPG--------NTIYRINLVPNSLTSA

>PiDV
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KVPFYMNQSEFDLL---PNGSVMVECNVKVIFRSNRIAFETSATATKQATLNQISNVQTA

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>BmDV

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>HaDV2

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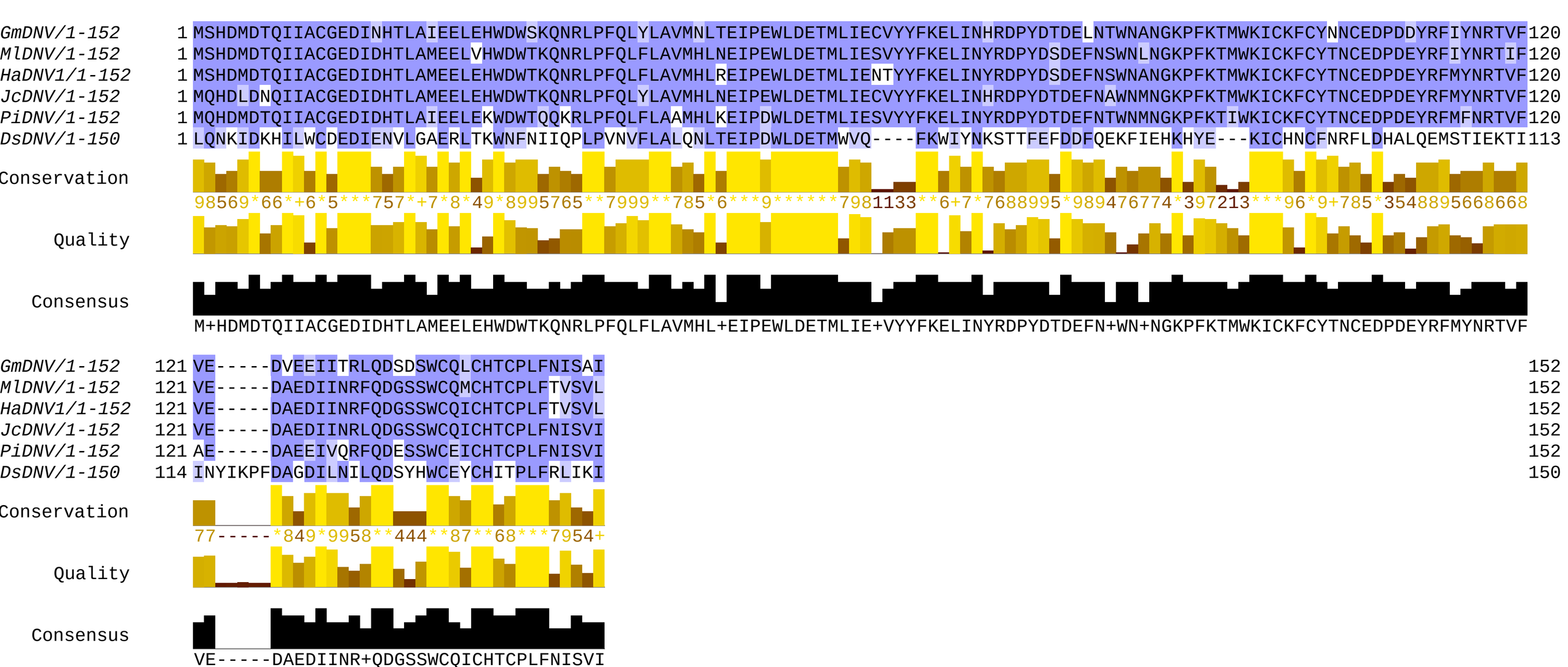
```

Supplementary Figure 4.

Alignments of fragments of capsid proteins of 14 densovirus species built in Mafft v.7.

The following parameters were used: Iterative refinement method G-INS-i with BLOSUM62 scoring matrix, gap opening penalty – 1.53 and offset value – 0.0.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Supplementary Figure 5.

Alignments of fragments of NS3 proteins of 6 densovirus species built in Mafft v.7.

The following parameters were used: Iterative refinement method G-INS-i with BLOSUM62 scoring matrix, gap opening penalty – 1.53 and offset value – 0.0.

Supplementary Figure 6.

Alignments of DNA fragments corresponding to protein sequences used for phylogenetic analysis.
A – NS1, VP, and NS3 of *Ambidensovirus*; **B** – NS1 and VP of *Iteradensovirus*.

A

NS1

>JcDV_(S47266)
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