

**Part 1:** **TITLE, AUTHORS, APPROVALS, etc**

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| **Code assigned:** | **2020.006D** |  |
| **Short title:** Create one new class (*Naldaviricetes*) including one new order (*Lefavirales*) for four families of arthropod-specific large DNA viruses | | |
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**List the ICTV Study Group(s) that have seen this proposal**

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| *Baculoviridae*/*Nudiviridae* Study Group (authors)  *Hytrosaviridae* Study Group  *Nimaviridae* Study Group |

**ICTV study group comments and response of proposer**

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| *Hytrosaviridae* Study Group:  I and two of the *Hytrosaviridae* Study Group members (Drion Boucias and Max Bergoin) enjoyed reading this proposal for a higher taxon within which are the hytrosaviruses!! No corrections or modifications from our side. However, we think that the two following references can be added to the reference list   1. [Diversity of large DNA viruses of invertebrates.](https://gcc02.safelinks.protection.outlook.com/?url=https%3A%2F%2Fwww.ncbi.nlm.nih.gov%2Fpubmed%2F27592378&data=02%7C01%7C%7Cdae1c749ccc34936983908d7cb5ff4a8%7Ced5b36e701ee4ebc867ee03cfa0d4697%7C0%7C0%7C637201485298596401&sdata=1TdswoVWyC9X7A92sKI27oRCZChowsH3iphDv%2Bp6U9E%3D&reserved=0)   Williams T, Bergoin M, van Oers MM.  J Invertebr Pathol. **2017;** 147:4-22. doi: 10.1016/j.jip.2016.08.001. Review. PMID: 27592378   1. [Hytrosaviridae: a proposal for classification and nomenclature of a new insect virus family.](https://gcc02.safelinks.protection.outlook.com/?url=https%3A%2F%2Fwww.ncbi.nlm.nih.gov%2Fpubmed%2F19458899&data=02%7C01%7C%7Cdae1c749ccc34936983908d7cb5ff4a8%7Ced5b36e701ee4ebc867ee03cfa0d4697%7C0%7C0%7C637201485298596401&sdata=27UwZ%2F2olXIUX3txR%2FBmMHSey1x0%2Fmv5UcX9YQ4rUE8%3D&reserved=0)   Abd-Alla AM, Vlak JM, Bergoin M, Maruniak JE, Parker A, Burand JP, Jehle JA, Boucias DG; Hytrosavirus Study Group of the ICTV.  Arch Virol. **2009;** 154:909-18. doi: 10.1007/s00705-009-0398-5. Review. PMID: 19458899  *Response: These references have been added to the proposal and cited in the text.*  *Nimaviridae* Study Group, comment #1:  My main comment relates to the name – Would it not be more sensible to refer to them as the Arthropod nuclear large DNA viruses (ANLDVs) – the nucleus is IN the arthropod, not the other way around!  Otherwise, this seems like a well made case, albeit it seems to leave options open for how the nimaviruses will be considered within this new class.  *Response: Rather than “arthropod” modifying “nuclear”, we regard both “nuclear” and “arthropod” to be modifying “virus” in this phrase. Also, we would prefer to stick with the name for these viruses that already exists in the literature.*  *Nimaviridae* Study Group, comment #2:  Although a previous publication (Chen et al., 2002 [DNA polymerase]) found that -- when a total of 31 viral DNA polymerase were used to construct the phylogenetic tree, the tree placed WSSV, *Adenoviridae*, *Baculoviridae* and *Poxviridae* in one clade. However, based on Fig. 2 and Table 2, I think nimaviruses still show their uniqueness compared to the similarity between *Baculoviridae*, *Nudiviridae* and *Hytrosaviridae*. It is still too early to collect *Nimaviruses* into a new class *Naldaviricetes* of NALDV. Figure 1 may not be proper to describe the current state for nimaviruses. In contrast to *Nimaviridae*, I think *Baculoviridae*, *Nudiviridae* and *Hytrosaviridae* could be included into a new order, *Lefavirales* and may be also into new order *Naldaviricetes*.  *Response: The exclusive occurrence of the* pif *signature genes in the viruses of these four families, along with other shared traits, supports their classification into a taxon of a higher rank. Nevertheless, we agree that nimaviruses stand apart from baculoviruses, nudiviruses, and hytrosaviruses, which is why we have proposed a new order in which the latter three families are to be classified, while leaving* Nimaviridae *unclassified within* Naldaviricetes. |

**Authority to use the name of a living person**

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| **Taxon name** | **Person from whom the name is derived** | **Permission attached (Y/N)** |
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**Submission dates**

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| Date first submitted to SC Chair | May 11, 2020 |
| Date of this revision (if different to above) | August 28, 2020 |

**ICTV-EC comments and response of the proposer**

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**Part 3:** **TAXONOMIC PROPOSAL**

**Name of accompanying Excel module**

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| 2020.006D.R.Naldaviricetes |

**Abstract**

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| Viruses of four families of arthropod-specific, large dsDNA viruses (the nuclear arthropod large DNA viruses, or NALDVs) possess homologs of genes encoding conserved components of a baculovirus host midgut cell infection mechanism. The presence of these homologs, along with their absence from other viruses and the occurrence of other shared characteristics, suggest a common origin for the viruses of these families. We thus propose the creation of a class, *Naldaviricetes*, for these four families. We further propose the creation of a subordinate order, *Lefavirales*, for three of these families whose members encode homologs of baculovirus transcriptional complex genes. |

**Text of proposal**

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| |  | | --- | | ***Naldaviricetes*: a new class for arthropod-specific large dsDNA viruses**  Arthropod-infecting large DNA viruses of four families – *Baculoviridae*, *Nudiviridae*, *Hytrosaviridae*, and *Nimaviridae* – have a set of features in common which separates them from other arthropod-infecting large dsDNA viruses (Table 1). These viruses were collectively referred to as nuclear arthropod large DNA viruses (NALDVs) to distinguish them from what was previously referred to as the nucleo-cytoplasmic large DNA viruses (NCLDVs; now *Nucleocytoviricota*) [24].  NALDVs contain genes that encode proteins collectively known as *per os* infectivity factors (abbreviated as PIFs; Table 2). *pif* genes were originally discovered in the genomes of baculoviruses, and were found to be required exclusively for oral infectivity of host insects [7, 21]. Sequencing and analysis of nudivirid, hytrosavirid, and nimavirid genomes identified homologs of four *pif* genes – *p74/pif-0*, *pif-1*, *pif-2*, and *pif-3* – in the genome sequences of these viruses, as well as bracoviruses of family *Polydnaviridae* [1, 20, 22]. Recent sequencing and analysis of additional nimavirid genomes identified a fifth *pif* gene, *odv-e56/pif-5*, that was conserved in NALDV genomes [13]. Homologs of *pif* genes have not been identified in other viruses, and thus are signature genes for members of the NALDV families.  The conservation of *pif* genes in NALDVs, along with other shared characteristics, indicated a common evolutionary origin for these viruses and led to the suggestion of creating a new order in which to include the NALDV families [21, 22, 24]. A phylogenetic analysis of NALDVs and nucleocytoviricots based on alignments of genes that were conserved or encode conserved functions indicated that the NALDVs formed a monophyletic group separate from them [24]. A bipartite network analysis of dsDNA virus genes and genomes showed that NALDV genomes and core genes formed a well-supported supermodule, separate from other modules [11]. However, other analyses have not grouped the NALDV families together [2, 25, 26], suggesting that a significantly high degree of genetic divergence exists among members of different NALDV families.  Members of the three families of order *Herpesvirales* also exhibit a high degree of genetic divergence [16], but these families are classified in the same order on the basis of shared virion structural features that allude to their common evolutionary origin [9]. Unlike the capsids of herpesvirals, the rod-like capsids of NALDV particles vary from family to family, with observable differences in dimensions (length and width), features (presence or absence of a tail or a terminal cap), and protein composition. Recently, sequencing of Apis mellifera filamentous virus (AmFV; currently unclassified) revealed that its genome contained homologs of the same five *pif* genes found in viruses of the other NALDV families [10], suggesting that this unclassified virus is also a NALDV. In sharp contrast with the rod-shaped capsids of the other NALDVs, the capsid of AmFV is a very long (>3 µm), flexuous filament that is coiled into an envelope [3]. These observations indicate that, in addition to genetic divergence, *pif* homolog-containing large dsDNA viruses can exhibit a considerable degree of structural divergence.  Recently, the ICTV approved the use of taxa above the rank of order for classification [19]. We propose to take advantage of the newly-available higher ranks for classification and create a class for the NALDV families, instead of an order (Figure 1). We feel that this higher rank will allow for classification of families of arthropod-infecting large dsDNA viruses that are distinguished by the inheritance of *pif* gene homologs, but otherwise exhibit considerable genetic and structural variability. Based on the now discouraged abbreviation NALDV, we propose this class to be named *Naldaviricetes*).  ***Lefavirales*: an order within *Naldaviricetes* for viruses possessing homologs of baculovirus transcription complex genes**  Phylogenies based on various naldaviricete sequence alignments often place viruses of *Baculoviridae*, *Nudiviridae*, and *Hytrosaviridae* into a clade separate from *Nimaviridae* [6, 13, 21, 22]. Viruses of *Nudiviridae* and *Hytrosaviridae* contain homologs of genes that encode parts of the baculovirus late-phase transcriptional complex, including three of the four subunits of the baculovirus core DNA-directed RNA polymerase (Table 2; [12, 17]). These homologs are not found in the genomes of nimavirids. We thus propose to create an order within *Naldaviricetes* into which *Baculoviridae*, *Nudiviridae*, and *Hytrosaviridae* will be placed (Figure 1). We propose the name of this order to be *Lefavirales*, from the term “late expression factor” (abbreviated as *lef*) which was coined to refer to genes identified in a screen for ORFs required for (or supporting) late-phase baculovirus transcription [17]. Lefavirals are characterized by the possession of conserved baculovirus transcription gene homologs, and can be distinguished from nimavirids in phylogenetic analyses (Figure 2).  We are not proposing to create an order for family *Nimaviridae* at this time, as there is insufficient information from which to extrapolate the distinguishing features of viruses in such an order. This is consistent with the comment for Rule 3.2 of the ICVCN, which indicates that it “…is not mandatory to use all levels of the taxonomic hierarchy.”  **Groups of similar viruses not classified in *Naldaviricetes***  The following large dsDNA viruses share some characteristics with viruses to be classified in proposed class *Naldaviricetes*, but are not being included in this new class.  *Polydnaviridae*  Members of the arthropod virus genus *Bracovirus* in family *Polydnaviridae* evolved from an ancient nudivirus that integrated its genome into the genomic DNA of a parasitoid wasp [5]. The integrated nudivirus sequences in the wasp genome retains and expresses *pif* genes [8, 24]. However, *Polydnaviridae* also contains a separate genus, *Ichnovirus*, whose members evolved from the genome of a different, unidentified virus which integrated into parasitoid wasps of a different wasp family [4, 20]. Members of *Ichnovirus* contain no *pif* homologs and thus aren’t suitable for classification in the proposed order *Naldaviricetes*. A future revision of polydnavirus classification might enable movement of the bracoviruses to an order or family within *Naldaviricetes*.  *Entomopoxvirinae, Betairidovirinae, Ascoviridae*  Members of these groups infect arthropods but lack *pif* homologs and have other features that distinguish them from NALDVs (Table 2) [26]. Entomopoxvirins and betairidovirins possess linear genomes which are partially or wholly synthesized in the cytoplasm of infected cells. Ascovirids have circular genomes whose replication is initiated in the nucleus, but clearly share a more recent origin with viruses of *Betairidovirinae* [18].  Recently, the ICTV ratified a taxonomic proposal (2019.003G: “Create a megataxonomic framework, filling all principal taxonomic ranks, for DNA viruses encoding vertical jelly roll-type major capsid proteins”) which creates higher taxa for NCLDV families. This proposal created an order, *Pimascovirales*, for families *Ascoviridae*, *Iridoviridae*, and *Marseilleviridae*. The proposal created a realm, *Varidnaviria*, in which the families of *Pimascovirales* and other nucleocytoviricots are classified. The distinguishing characteristic of viruses classified in the realm *Varidnaviria* is the occurrence of a virus hallmark gene encoding a vertical double jelly-roll major capsid protein (VDJ-MCP). Naldoviricetes do not contain homologs encoding a VDJ-MCP, but they do have other “connector” genes that link the “Baculo-like” supermodule with the nucleocytoviricot-polinton supermodule in dsDNA virus gene/genome networks [11]. This observation suggests that naldoviricetes may be an ancient branch of *Varidnaviria* that evolved to use different proteins for capsid assembly [11, 14]. However, we are not proposing to place *Naldaviricetes* into the *Varidnaviria* hierarchy at this time. | |

**Supporting evidence**

**Table 1.** Characteristics of arthropod-specific large dsDNA virus families and sub-families

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Characteristics | Virus Family (NALDV family names are in bold type) | | | | | | | |
|  | ***Baculo-viridae*** | ***Nudiviridae*** | ***Hytrosa-viridae*** | ***Nimaviridae*** | *Polydna-viridae* | *Ascoviridae* | *Entomopox-virinae* | *Betairido-virinae* |
| Circular genome | + | + | + | + | ±1 | + | - | - |
| Enveloped, rod-shaped nucleocapsid | + | + | + | + | + | ±2 | - | - |
| Nuclear site of replication | +3 | + | + | + | + | +3 | - | ± |
| Occlusion bodies | + | ± | - | - | - | - | + |  |
| *Pif* genes | + | + | + | + | +4 | - | - | - |

1Polydnavirid particles contain circular DNAs originating from the parasitoid wasp host, while virally-derived sequences remain integrated in the wasp genome.

2Virions of this family are variably described as allantoid (sausage-shaped), reniform (kidney-shaped), or bacilliform (rod-shaped).

3For ascovirids and betabaculoviruses, the host cell nuclear membrane ruptures prior to the completion of replication and virion assembly.

4Only polydnavirids of genus *Bracovirus* contain *pif* gene homologs.



Figure 1. Proposed taxonomic hierarchy for families of nuclear arthropod large DNA viruses. A new class, *Naldaviricetes*, is proposed for classification of the viruses in the four currently established families *Baculoviridae*, *Nudiviridae*, *Hytrosaviridae*, and *Nimaviridae*, and a new order, *Lefavirales*, is proposed for the further inclusion of three of these families. Apis mellifera filamentous virus [3, 10] and Leptopilina boulardi filamentous virus [15] are currently unclassified but encode homologs of the *pif* genes found in naldaviricetes. The latter of these viruses also contains some *lef* homologs and exhibits similarity to members of family *Hytrosaviridae*.

**Table 2.** Core genes conserved among naldaviricetes. Core genes found in all naldaviricete families are highlighted in yellow; core genes in all families except *Nimaviridae* are highlighted in green.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Core genes** | | ***Naldaviricetes*** | | | |
| *Baculoviridae* | *Nudiviridae* | *Hytrosaviridae* | *Nimaviridae* |
| Per os infectivity factors | *pif-0 /p74* | ✓ | ✓ | ✓ | ✓ |
| *pif-1* | ✓ | ✓ | ✓ | ✓ |
| *pif-2* | ✓ | ✓ | ✓ | ✓ |
| *pif-3* | ✓ | ✓ | ✓ | ✓ |
| *pif-4* | ✓ | ✓ |  |  |
| *pif-5 /odv-e56* | ✓ | ✓ | ✓ | ✓ |
| *pif-6* | ✓ | ✓ |  |  |
| *pif-8 /vp91* | ✓ | ✓ |  |  |
| Viral transcription complex | *lef-4* | ✓ | ✓ | ✓ |  |
| *lef-8* | ✓ | ✓ | ✓ |  |
| *lef-9* | ✓ | ✓ | ✓ |  |
| *p47* | ✓ | ✓ |  |  |
| *lef-5* | ✓ | ✓ | ✓ |  |
| *vlf-1* | ✓ | ✓ |  |  |
| DNA replication | *dnapol* | ✓ | ✓ | ✓ | ✓ |
| *helicase* | ✓ | ✓ | ✓ |  |
| Nucleocapsid proteins | *38k* | ✓ | ✓ |  |  |
| *vp39* | ✓ | ✓ |  |  |
| *p6.9* | ✓ | ✓ |  |  |
| Sulfhydryl oxidase | *p33* | ✓ | ✓ | ✓ | ✓ |
| Unknown function | *ac81* | ✓ | ✓ | ✓ |  |

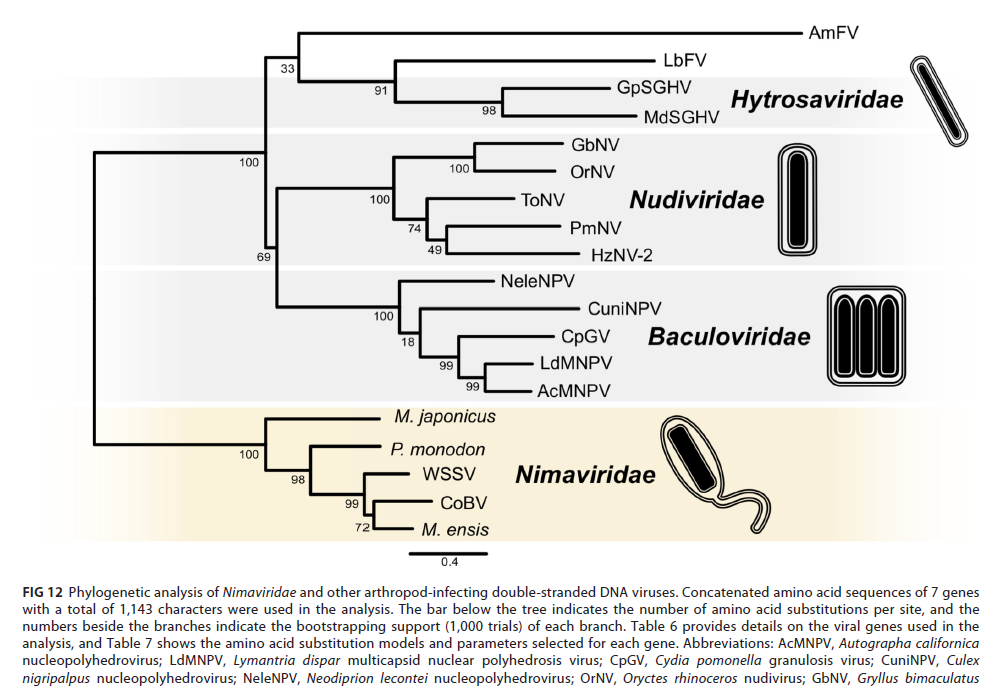
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Figure 2. Phylogenetic analysis of naldaviricetes. Concatenated amino acid alignments of five PIF sequences (*p74/pif-0*, *pif-1*, *pif-2*, *pif-3*, and *odv-e56/pif-5*), DNA polymerase (*dnapol*), and sulfhydryl oxidase (*p33*) were used to infer relationships by maximum likelihood as implemented in RAxML version 8.2.9 with substitution models and parameters selected for each alignment. Family-level classification is indicated for different clades in the midpoint-rooted tree. Abbreviations: AcMNPV, Autographa californica nucleopolyhedrovirus; LdMNPV, Lymantria dispar multiple nucleopolyhedrovirus; CpGV, Cydia pomonella granulovirus; CuniNPV, Culex nigripalpus nucleopolyhedrovirus; NeleNPV, Neodiprion lecontei nucleopolyhedrovirus; OrNV, Oryctes rhinoceros nudivirus; GbNV, Gryllus bimaculatus nudivirus; HzNV-2, Heliothis zea nudivirus-2; PmNV, Penaeus monodon nudivirus; ToNV, Tipula oleracea nudivirus; GpSGHV, Glossina pallidipes salivary gland hypertrophy virus; MdSGHV, Musca domestica salivary gland hypertrophy virus; AmFV, Apis mellifera filamentous virus; LbFV, Leptopilina boulardi filamentous virus; WSSV, white spot syndrome virus; M. japonicus, Marsupenaeus japonicus endogenous nimavirus; P. monodon, Penaeus monodon endogenous nimavirus; CoBV, Chionoecetes opilio bacilliform virus; M. ensis, Metapenaeus ensis nimavirus. Reproduced from Kawato et al., 2019, Crustacean genome exploration reveals the evolutionary origin of white spot syndrome virus, J Virol 93:e01144-18, <https://doi.org/10.1128/JVI.01144-18>, with permission from the American Society for Microbiology.

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