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VIROLOGY DIVISION NEWS



Developments in the classification and nomenclature of arthropodinfecting large DNA viruses that contain *pif* genes

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Abstract

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 involved in the baculovirus primary infection mechanism. The presence of such homologs encoding *per os* infectivity factors (*pif* genes), along with their absence from other viruses and the occurrence of other shared characteristics, suggests a common origin for the viruses of these families. Therefore, the class *Naldaviricetes* was recently established, accommodating these four families. In addition, within this class, the ICTV approved the creation of the order *Lefavirales* for three of these families, whose members carry homologs of the baculovirus genes that code for components of the viral RNA polymerase, which is responsible for late gene expression. We further established a system for the binomial naming of all virus species in the order *Lefavirales*, in accordance with a decision by the ICTV in 2019 to move towards a standardized nomenclature for all virus species. The binomial species names for members of the order *Lefavirales* consist of the name of the genus to which the species belongs (e.g., *Alphabaculovirus*), followed by a single epithet that refers to the host species from which the virus was originally isolated. The common names of viruses and the abbreviations thereof will not change, as the format of virus names lies outside the remit of the ICTV.

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Introduction

Arthropod-infecting large DNA viruses belonging to four families – *Baculoviridae*, *Nudiviridae*, *Hytrosaviridae*, and *Nimaviridae* – share a set of common features that separate them from other arthropod-infecting large dsDNA viruses (Table 1). These viruses have collectively been referred to as nuclear arthropod large DNA viruses (NALDVs) [31–33] to distinguish them from what was previously referred to as the nucleo-cytoplasmic large DNA viruses (NCLDVs; now in the phylum *Nucleocytoviricota*) [9, 35]. In this paper, we explain recent developments in the classification of the NALDVs in the class *Naldaviricetes* and the recently established binomial nomenclature for viruses in the order *Lefavirales*, accommodating three of these virus families.

The *pif* genes as a signature for the new class *Naldaviricetes*

NALDVs contain genes that encode proteins collectively known as *per os* infectivity factors (abbreviated as PIFs; Table 2). The *pif* genes were originally discovered in the genomes of baculoviruses, in which they are required exclusively for oral infectivity in host insects [7, 29]. Sequencing and analysis of nudivirid, hytrosavirid, and nimavirid genomes showed that homologs of four *pif* genes (*pif0/ p74, pif1, pif2*, and *pif3*) were conserved in the genome sequences of all of these viruses [1, 30]. More recently, a fifth *pif* gene (*pif5/odve56*) was added to this list of conserved genes [15]. Furthermore, PIF proteins are also found in the viriform particles formed in the calyx of female braconid wasps, which are classified in the genus *Bracoviriform* in the recently renamed family *Polydnaviriformidae* [5, 6, 23]. These expressed bracoviriform PIF proteins originate from the endogenization of an ancient nudivirus [5, 12, 27].

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 genomic and phenotypic characteristics, such as their rod-shaped nucleocapsids and large double-stranded circular DNA genomes that replicate in the nucleus of infected cells (Table 1), indicate a common evolutionary origin for these viruses. Consequently, it was suggested to create a higher taxon in which to classify the four NALDV families [31-33] as well as unassigned viruses that may share these features. This idea was further supported by the fact that phylogenetic analysis indicated that the NALDVs formed a monophyletic group, separate from the nucleocytoviricots [35]. Bipartite network analysis of dsDNA virus genes and genomes showed that NALDV genomes and the encoded core genes formed a well-supported supermodule, separate from other observed modules [13]. However, several other analytical methods have not grouped the NALDV families together [2, 36, 37], suggesting that a significant degree of genetic divergence exists between members of different NALDV families. Members of the three families in the order Herpesvirales also exhibit a high degree of genetic divergence [21], but these families are classified in the same order on the basis of shared virion structural features that allude to their common evolutionary origin [10]. Unlike the capsids of herpesvirals, the structure of the rod-like NALDV particles varies from family to family, with observable differences in dimensions (length and width), features (presence or absence of a tail and/or terminal nucleocapsid cap), and protein composition. Furthermore, sequencing of Apis mellifera filamentous virus (AmFV; currently unclassified) revealed that its genome

Table 1 Characteristics of arthropod-specific large dsDNA virus families and subfamilies

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Feature	NALDV families				Other virus (sub)families			
	Baculoviridae	Nudiviridae	Hytrosaviridae	Nimaviridae	Polydnaviriformidae	Ascoviridae	Entomopox- virinae	Betairido- virinae
pif genes	+	+	+	+	+1	-	_	-
Circular genome	+	+	+	+	\pm^2	+	-	-
Enveloped, rod-shaped nucleocapsids	+	+	+	+	+	\pm^3	-	-
Nuclear site of replication	$+^{4}$	+	+	+	+	+4	-	±
Occlusion	+	±	-	-	-	-	+	

¹ Only polydnaviriforms of the genus *Bracoviriform* contain *pif* gene homologs.

² Polydnaviriform particles contain circular DNA molecules originating from the genome of the parasitoid wasp host, while virus-derived sequences remain integrated in the wasp genome.

³ Virions of this family are variably described as allantoid (sausage-shaped), reniform (kidney-shaped), or bacilliform (rod-shaped).

⁴ For ascovirids and betabaculoviruses, the host cell nuclear membrane ruptures prior to the completion of replication and virion assembly.

Core genes and their function		Naldaviricetes			
		Baculoviridae	Nudiviridae	Hytrosaviridae	Nimaviridae
Per os infectivity factors (pifs)*	pif0 /p74	+	+	+	+
	pif1	+	+	+	+
	pif2	+	+	+	+
	pif3	+	+	+	+
	pif4	+	+		+
	pif5 /odv-e56	+	+	+	+
	pif6	+	+		
	pif8 /vp91	+	+		
Viral transcription complex	lef-4	+	+	+	
	lef-8	+	+	+	
	lef-9	+	+	+	
	<i>p</i> 47	+	+		
	lef-5	+	+	+	
	vlf-1	+	+		
DNA replication	Dnapol	+	+	+	+
	Helicase	+	+	+	
Nucleocapsid proteins	38k	+	+		
	vp39	+	+		
	p6.9	+	+		
Sulfhydryl oxidase	р33	+	+	+	+
Unknown function	ac81	т	т	т	

Table 2 Core genes conserved among members of the class *Naldaviricetes*. A number of genes are found in all naldaviricete families; other genes are conserved in lefaviral families only.

*pif7 is not included here, as it is only conserved in lepidopteran-infecting baculoviruses (alphabaculoviruses and betabaculoviruses).

contained homologs of the same five *pif* genes found in viruses of the other NALDV families [11], suggesting that this unclassified virus is also an NALDV. In sharp contrast to the rod-shaped capsids of the other NALDVs, the capsid of AmFV is a very long (> 3 μ m), flexuous filament that is coiled into an envelope [3]. This observation illustrates that, in addition to genetic divergence, *pif*-homolog-containing large dsDNA viruses can exhibit a considerable degree of structural divergence. Also, Leptopilina boulardi filamentous virus (LbFV; Fig. 1) is currently unclassified but encodes homologs of the *pif* genes [20].

Recently, the ICTV approved the use of taxa above the rank of "order" for virus classification [26]. We took advantage of the newly introduced hierarchy for virus classification and in 2020 proposed a class to harbour the four NALDV families (Fig. 1) (https://ictv.global/ictv/proposal s/2020.006D.R.Naldaviricetes.zip). We felt that this higher rank would allow for classification of families of arthropodinfecting large dsDNA viruses that are distinguished by the inheritance of *pif* gene homologs but otherwise exhibit considerable genetic and structural variability and would therefore not be adequately classified within a single order. Based on the abbreviation NALDV, the approved class is named *Naldaviricetes*. The unclassified filamentous viruses (AmFV, LbFV) also appear to belong to this class but await assignment to species. Below, we describe why several other large dsDNA viruses that share some characteristics with the viruses now classified as *Naldaviricetes* members are not included in this new class.

Relationships to other taxa

Polydnaviriformidae

As indicated above, members of the genus Bracoviriform of the family Polydnaviriformidae, which infect arthropods, evolved from an ancient nudivirus that integrated its genome into the genomic DNA of an ancient parasitoid wasp [5]. The integrated nudivirus sequences in the wasp genome have retained and express *pif* genes in female calyx cells [8, 34]. However, the family Polydnaviriformidae also contains the genus Ichnoviriform, whose members evolved from the genome of a different, unidentified virus that integrated into parasitoid wasps of a different family [4, 19, 28]. Ichnoviriforms do not contain *pif* homologs and thus do not meet the criteria for classification in the proposed order Naldaviricetes. A future revision of the family Polydnaviriformidae would be needed to enable movement of the bracoviriforms to a taxon within the class *Naldaviricetes*, together with the Nudiviridae.



Fig. 1 Phylogenetic analysis of members of the class *Naldaviricetes*. Concatenated alignments of five PIF amino acid sequences (*pif-0/p74*, *pif-1*, *pif-2*, *pif-3*, and *pif-5/odv-e56*), 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 of virus names are as follows: AcMNPV, Autographa californica multiple nucleopolyhedrovirus; LdMNPV, Lymantria dispar MNPV; CpGV, Cydia pomonella granulovirus; CuniNPV, Culex nigripalpus nucleopolyhedrovirus; NeleNPV, Neodiprion lecontei

Entomopoxvirinae, Betairidovirinae and Ascoviridae

Members of these three (sub)families of large dsDNA viruses infect arthropods but lack pif homologs and have other features that distinguish them from viruses in the class Naldaviricetes (Table 1) [37]. 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 they clearly share a more recent origin with viruses in the subfamily *Betairidovirinae* [24]. In 2020, the ICTV ratified a taxonomic proposal to create the order *Pimascovirales* for the families Ascoviridae, Iridoviridae, and Marseilleviridae [17]. The proposal also created a realm, Varidnaviria, in which the families of the order Pimascovirales together with the 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 jellyroll major capsid protein (VDJ-MCP). The members of the Naldaviricetes, on the other hand, do not contain homologs encoding a VDJ-MCP, but they do have other "connector"

NPV; OrNV, Oryctes rhinoceros nudivirus; GbNV, Gryllus bimaculatus NV; HzNV-2, Heliothis zea NV-2; PmNV, Penaeus monodon NV; ToNV, Tipula oleracea NV; GpSGHV, Glossina pallidipes salivary gland hypertrophy virus; MdSGHV, Musca domestica SGHV; AmFV, Apis mellifera filamentous virus; LbFV, Leptopilina boulardi FV; WSSV, white spot syndrome virus; CoBV, Chionoecetes opilio bacilliform virus. Endogenized nimaviruses from *Marsupenaeus japonicus*, *Peneaus monodon*, and *Metapeneaus ensis* were also included. This figure was reproduced and slightly modified from Kawato et al., 2019, J Virol 93:e01144-18, https://doi.org/10.1128/JVI.01144-18, with permission from the authors and the American Society for Microbiology.

genes that might link the "baculo-like" supermodule with the nucleocytoviricot-polinton supermodule in dsDNA virus gene/genome networks [13]. This observation suggests that naldoviricetes may form an ancient branch of the *Varidnaviria* that has evolved to use different proteins for capsid assembly [13, 16]. However, we are presently not proposing to place the class *Naldaviricetes* into the *Varidnaviria* hierarchy.

Establishment of the order *Lefavirales* within the class *Naldaviricetes*

Phylogenies based on various naldaviricete sequence alignments often place viruses of the families *Baculoviridae*, *Nudiviridae*, and *Hytrosaviridae* into a clade separate from the *Nimaviridae* [6, 15, 29, 31]. Baculoviruses and viruses classified as members of the *Nudiviridae* and *Hytrosaviridae* contain homologs of genes that encode components of the baculovirus late-phase transcription complex, including three of the four subunits of the baculovirus DNA-directed RNA polymerase (*lef-4*, *lef-8*, and *lef-9*) (Table 2) [14, 22]. These homologs are not found in the genomes of nimavirids.



Fig. 2 Taxonomic hierarchy of families of nuclear arthropod large DNA viruses. A new class, *Naldaviricetes*, was established for classification of the viruses in the four currently established families *Baculoviridae*, *Nudiviridae*, *Hytrosaviridae*, and *Nimaviridae*. A new order, *Lefavirales*, was introduced to include three of these families. The two

We thus created an order within the class Naldaviricetes into which the families Baculoviridae, Nudiviridae, and Hytrosaviridae were placed (Fig. 2). This order is named Lefavirales, from the term "late expression factor" (abbreviated as *lef*), which was previously coined to refer to genes identified in a screen for ORFs required for (or supporting) late-phase baculovirus transcription [22]. Lefavirals are characterized by the possession of conserved baculovirus transcription gene homologs and can also be distinguished from nimavirids in phylogenetic analysis (see Fig. 1). At present, we have refrained from creating an order for the family Nimaviridae, as there is insufficient information from which to extrapolate the distinguishing features of viruses in such an order. This strategy is consistent with the International Code of Virus Classification and Nomenclature (ICVCN; March 2021) Rule 3.2, which indicates that it is not mandatory to use all levels of the taxonomic hierarchy.

Binomial naming system for virus species in the order *Lefavirales*

In 2021, the ICTV membership ratified a proposal (2018.001G.R) to adopt a binomial virus species naming system that follows the method of Linnaeus. This means that the Linnaean binomial format needs to be implemented for all virus species names, with a 2023 deadline. Accordingly, ICVCN Rule 3.21 now reads:

"A species name shall consist of only two distinct word components separated by a space.

The first word component shall begin with a capital letter and be identical in spelling to the name of the genus to which the species belongs. The second word component shall not contain any suffixes specific for viruses indicated at the top of the figure (Apis mellifera filamentous virus [3, 10] and Leptopilina boulardi filamentous virus [15]) are currently unclassified, but based on their genome content, they bear the hallmarks of members of the taxa *Naldaviricetes* and *Lefavirales*, respectively.

taxa of higher ranks. The entire species name (both word components) shall be italicized".

Since the order Lefavirales has three families, Baculoviridae, Nudiviridae, and Hytrosaviridae, it makes sense to name the species belonging to these families in a similar way. The two ICTV Study Groups concerned have therefore joined forces, designed a general method to convert all existing species names into binomial names, and submitted a formal ICTV taxonomic proposal in 2022 for con-(https://ictv.global/ictv/proposals/2022.003D. sideration Lefavirales 106rensp.zip). The same strategy is also used to assign species names to newly discovered lefavirals. Below, we present the new system and explain the reasoning behind the chosen method. As such, we aim to provide guidance for scientists in the field for naming new lefaviral species. In the following explanations, we will use baculovirids as examples. All updated lefaviral species names are provided in Table 3. Please be aware that the renaming only applies to virus species names. The names of viruses and their isolates remain unchanged. Since only names of virus species and higher taxa are regulated by the ICTV, it is expected that the way the viruses themselves are routinely named in the literature will remain unchanged. Thus, for naming old and new naldaviricete virus isolates, the historic conventions and practices should be continued as indicated in Table 3.

Issues with the previous lefaviral species naming system

In the past, the species names for lefavirals varied in format from family to family. For the family *Baculoviridae*, species names previously consisted of the binomial name of the host species, sometimes followed by a virion structural characteristic ("multiple" in *Autographa californica*

Table 3	List of currently	valid lefaviral	binomial specie	es names along wit	h common	virus names	and their	abbreviations.	Please note	that virus
names v	will remain unaffed	cted by recent	nomenclatural c	hanges.						

Family/genus	Binominal species name	Exemplar/common virus name	Abbreviation
Family <i>Baculovirid</i>	lae		
Alphabaculovirus	Alphabaculovirus adhonmai	Adoxophyes honmai nucleopolyhedrovirus	AdhoNPV
	Alphabaculovirus agipsilonis	Agrotis ipsilon multiple nucleopolyhedrovirus	AgipNPV
	Alphabaculovirus agsegetum	Agrotis segetum nucleopolyhedrovirus A	AgseNPV-A
	Alphabaculovirus alteragsegetum	Agrotis segetum nucleopolyhedrovirus B	AgseNPV-B
	Alphabaculovirus anpernyi	Antheraea pernyi nucleopolyhedrovirus	AnpeNPV
	Alphabaculovirus angemmatalis	Anticarsia gemmatalis multiple nucleopolyhedrovirus	AgMNPV
	Alphabaculovirus ardigrammae	Artaxa digramma nucleopolyhedrovirus	ArdiNPV
	Alphabaculovirus aucalifornicae	Autographa californica multiple nucleopolyhedrovirus	AcMNPV
	Alphabaculovirus bomori	Bombyx mori nucleopolyhedrovirus	BmNPV
	Alphabaculovirus busuppressariae	Buzura suppressaria nucleopolyhedrovirus	BuzuNPV
	Alphabaculovirus capomonae	Catopsilia pomona nucleopolyhedrovirus	CapoNPV
	Alphabaculovirus chofumiferanae	Choristoneura fumiferana multiple nucleopolyhedrovirus	CfMNPV
	Alphabaculovirus alterchofumiferanae	Choristoneura fumiferana DEF multiple nucleopolyhedrovirus	CfMNPV-DEF
	Alphabaculovirus chomurinanae	Choristoneura murinana nucleopolyhedrovirus	ChmuNPV
	Alphabaculovirus chorosaceanae	Choristoneura rosaceana nucleopolyhedrovirus	ChroNPV
	Alphabaculovirus chrychalcites	Chrysodeixis chalcites nucleopolyhedrovirus	ChchNPV
	Alphabaculovirus chrincludentis	Chrysodeixis includens nucleopolyhedrovirus	ChinNPV
	Alphabaculovirus clabilineatae	Clanis bilineata nucleopolyhedrovirus	ClbiNPV
	Alphabaculovirus covestigialis	Condylorrhiza vestigialis nucleopolyhedrovirus	CovoNPV
	Alphabaculovirus crypeltasticae	Cryptophlebia peltastica nucleopolyhedrovirus	CrpeNPV
	Alphabaculovirus cycundantis	Cyclophragma undans nucleopolyhedrovirus	CyunNPV
	Alphabaculovirus dijunonis	Dione juno nucleopolyhedrovirus	DijuNPV
	Alphabaculovirus ecobliquae	Ectropis obliqua nucleopolyhedrovirus	EcobNPV
	Alphabaculovirus eppostvittanae	Epiphyas postvittana nucleopolyhedrovirus	EppoNPV
	Alphabaculovirus eupseudoconspersae	Euproctis pseudoconspersa nucleopolyhedrovirus	EupsNPV
	Alphabaculovirus helarmigerae	Helicoverpa armigera nucleopolyhedrovirus	HearNPV
	Alphabaculovirus heleucae	Hemileuca species nucleopolyhedrovirus	HespNPV
	Alphabaculovirus hycuneae	Hyphantria cunea nucleopolyhedrovirus	HycuNPV
	Alphabaculovirus hytalacae	Hyposidra talaca nucleopolyhedrovirus	HytaNPV
	Alphabaculovirus lafiscellariae	Lambdina fiscellaria nucleopolyhedrovirus	LafiNPV
	Alphabaculovirus leseparatae	Leucania separata nucleopolyhedrovirus	LeseNPV
	Alphabaculovirus lonobliquae	Lonomia obliqua nucleopolyhedrovirus	LoobNPV
	Alphabaculovirus lydisparis	Lymantria dispar multiple nucleopolyhedrovirus	LdMNPV
	Alphabaculovirus lyxylinae	Lymantria xylina nucleopolyhedrovirus	LyxyNPV
	Alphabaculovirus mabrassicae	Mamestra brassicae multiple nucleopolyhedrovirus	MbMNPV
	Alphabaculovirus maconfiguratae	Mamestra configurata nucleopolyhedrovirus A	MacoNPV-A
	Alphabaculovirus altermaconfiguratae	Mamestra configurata nucleopolyhedrovirus B	MacoNPV-B
	Alphabaculovirus mavitratae	Maruca vitrata nucleopolyhedrovirus	MaviNPV
	Alphabaculovirus myunipunctae	Mythimna unipuncta nucleopolyhedrovirus A	MyunNPV-A
	Alphabaculovirus altermyunipunctae	Mythimna unipuncta nucleopolyhedrovirus B	MyunNPV-B
	Alphabaculovirus opbrumatae	Operophtera brumata nucleopolyhedrovirus	OpbrNPV
	Alphabaculovirus orleucostigmae	Orgyia leucostigma nucleopolyhedrovirus	OrleNPV
	Alphabaculovirus orpseudotsugatae	Orgyia pseudotsugata multiple nucleopolyhedrovirus	OPMNPV
	Alphabaculovirus oxochraceae	Oxyplax ochracea nucleopolyhedrovirus	OxocNPV
	Alphabaculovirus pesauciae	Peridroma saucia nucleopolyhedrovirus	PesaNPV
	Alphabaculovirus peluscae	Perigonia lusca nucleopolyhedrovirus	PeluNPV
	Alphabaculovirus ranus	Rachiplusia nu nucleopolyhedrovirus	RanuNPV
	Alphabaculovirus speridaniae	Spodoptera eridania nucleopolyhedrovirus 251	SperNPV-251
	Alphabaculovirus altersperidaniae	Spodoptera eridania nucleopolyhedrovirus -CNPSo-165	SperNPV-CNPSo-165
	Alphabaculovirus spexemptae	Spodoptera exempta nucleopolyhedrovirus	SpexNPV
	Alphabaculovirus spexiguae	Spodoptera exigua multiple nucleopolyhedrovirus A	SeMNPV-A

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Family/genus	Binominal species name	Exemplar/common virus name	Abbreviation
	Alphabaculovirus alterspexiguae	Spodoptera exigua multiple nucleopolyhedrovirus B	SeMNPV-B
	Alphabaculovirus spofrugiperdae	Spodoptera frugiperda multiple nucleopolyhedrovirus	SfMNPV
	Alphabaculovirus splittoralis	Spodoptera littoralis nucleopolyhedrovirus	SpliNPV
	Alphabaculovirus spliturae	Spodoptera litura nucleopolyhedrovirus	SpltNPV
	Alphabaculovirus suiuiubae	Sucra jujuba nucleopolyhedrovirus	SuiuNPV
	Alphabaculovirus thorichlaceae	Thysanoplusia orichalcea nucleopolyhedrovirus	ThohNPV
	Alphabaculovirus trini	Trichonlusia ni single nucleonolyhedrovirus	TnSNPV
	Alphabaculovirus urnrotei	Urbanus proteus nucleopolyhedrovirus	UrprNPV
	Alphabaculovirus wisignatas	Wiscone signate pueleonelyhedrovirus	WigiNDV
Retabaculovirus	Retabaculovirus adoranae	A doxonbyes orang granulovirus	AdorGV
Delubuculovirus	Betabaculovirus agsogatum	A grotis sogetum granulovirus	AgeoGV
	Betabaculovirus agsegeium	Agrous segetum granulovirus	Agsedv
	Detabaculovirus arrupae	Charisten cure functionene granulauirus	AllaGV
	Betabaculovirus chofumiferanae	Choristoneura fumiferana granulovirus	
	Betabaculovirus clanachoretae	Clostera anachoreta granulovirus	ClanGV
	Betabaculovirus clanastomosis	Clostera anastomosis granulovirus A	ClasGV-A
	Betabaculovirus alterclanastomosis	Clostera anastomosis granulovirus B	ClasGV-B
	Betabaculovirus cnamedinalis	Cnaphalocrocis medinalis granulovirus	CnmeGV
	Betabaculovirus cryleucotretae	Cryptophlebia leucotreta granulovirus	CrleGV
	Betabaculovirus cypomonellae	Cydia pomonella granulovirus	CpGV
	Betabaculovirus disaccharalis	Diatraea saccharalis granulovirus	DisaGV
	Betabaculovirus epaporemae	Epinotia aporema granulovirus	EpapGV
	Betabaculovirus erellonis	Erinnyis ello granulovirus	ErelGV
	Betabaculovirus habrilliantis	Harrisina brillians granulovirus	HabrGV
	Betabaculovirus helarmigerae	Helicoverpa armigera granulovirus	HearGV
	Betabaculovirus hycuneae	Hyphantria cunea granulovirus	HycuNPV
	Betabaculovirus lacoleraceae	Lacanobia oleracea granulovirus	LaolGV
	Betabaculovirus molatipedis	Mocis latipes granulovirus	MolaGV
	Betabaculovirus myunipunctae	Mythimna unipuncta granulovirus A	MyunGV-A
	Betabaculovirus altermyunipunctae	Mythimna unipuncta granulovirus B	MyunGV-B
	Betabaculovirus maphaseoli	Matsumuraeses phaseoli granulovirus	MaphGV
	Betabaculovirus phoperculellae	Phthorimaea operculella granulovirus	PhopGV
	Betabaculovirus plinterpunctellae	Plodia interpunctella granulovirus	PlinGV
	Betabaculovirus pluxylostellae	Plutella xylostella granulovirus	PlxyGV
	Betabaculovirus spofrugiperdae	Spodoptera frugiperda granulovirus	SfGV
	Betabaculovirus spliturae	Spodoptera litura granulovirus	SpltGV
	Betabaculovirus trini	Trichoplusia ni granulovirus	TnGV
	Betabaculovirus xecnigri	Xestia c-nigrum granulovirus	XecnGV
Gammabaculovirus	Gammabaculovirus nelecontei	Neodiprion lecontei nucleopolyhedrovirus	NeleNPV
	Gammabaculovirus nesertiferis	Neodiprion sertifer nucleopolyhedrovirus	NeseNPV
Deltabaculovirus	Deltabaculovirus cunigripalpi	Culex nigripalpus nucleopolyhedrovirus	CuniNPV
Family <i>Nudiviridae</i>			
Alphanudivirus	Alphanudivirus droinnubilae	Drosophila innubila nudivirus	DiNV
1	Alphanudivirus dromelanogasteris	Kallithea virus	KV
	Alphanudivirus alterdromelanogasteris	Tomelloso virus	TNV
	Alphanudivirus tertidromelanogasteris	Esparto virus	ENV
	Alphanudivirus	Mauternbach virus	MNV
	quartudromelanogasteris		
	Alphanudivirus grybimaculati	Gryllus bimaculatus nudivirus	GbNV
	Alphanudivirus oryrhinocerotis	Oryctes rhinoceros nudivirus	OrNV
Betanudivirus	Betanudivirus hezeae	Heliothis zea nudivirus	HzNV
Gammanudivirus	Gammanudivirus hogammari	Homarus gammarus nudivirus	HgNV
	Gammanudivirus pemonodonis	Penaeus monodon nudivirus	PmNV
	Gammanudivirus cracrangonis	Crangon crangon nudivirus	CcNV
	Gammanudivirus cameanadis	Carcinas meneas nudivirus	CmPV
Deltanudivirus	Deltanudivirus tipoleraceae	Tipula oleracea nudivirus	ToGV
	=	r	

Table 3 (continued)						
Family/genus	Binominal species name	Exemplar/common virus name	Abbreviation			
Family <i>Hytrosaviridae</i>						
Glossinavirus	Glossinavirus glopallidipedis	Glossina pallipides salivery gland hypertrophy virus	GpSGHV			
Muscavirus	Muscavirus musdomesticae	Musca domestica salivery gland hypertrophy virus	MdSGHV			

multiple nucleopolyhedrovirus) and/or by a now obsolete genus name (nucleopolyhedrovirus, granulovirus). In most cases the virus species name did not differ from the virus name, except that the virus species name was fully written in italic letters, which made it often complicated to distinguish between the virus species and the virus itself. Nudivirid species names also started with the host species name, followed by the common name for viruses of this family (nudivirus). Species names in the family Hytrosaviridae consisted of the genus name of the host (e.g., Glossina) followed by the virus genus name (hytrosavirus). Species names for all three families featured part or all of the species names of the viral hosts. In developing specific epithets for lefaviral species names, we have retained this familiar feature in order to ease the transition to a new binomial format that is consistent among all lefaviral families.

The remaining family in the class *Naldaviricetes*, the *Nimaviridae*, was not included in this proposed binomial naming system, as the naming of the only classified species in this family is historically based on symptoms and not on host species, in contrast to lefaviral species, but it would be logical to follow the same principle for nimavirid species.

Binomial naming method for virus species in the order *Lefavirales*

The binomial species names for lefavirals are composed as follows:

- As for Linnaean binomial species names in general, the first word of the species name is the name of the genus to which the virus species belongs, starting with a capital (e.g., *Alphabaculovirus* or *Betanudivirus*).
- The second word (the epithet) reflects the Latin species name of the arthropod host from which the virus was originally isolated. It is composed of the first 2–4 letters of the host genus directly coupled to the genitive form of the epithet of the host species name. For example, <u>Autographa californica multiple nucleopolyhedrovirus</u> is now Alphabaculovirus aucalifornicae, and Cydia pomonella granulovirus is now Betabaculovirus cypomonellae. The specific epithet should be readable and pronounceable.
- Latin ordinal prefixes are added to the specific epithet to distinguish between species with isolates originating from the same host. When a second species from the

same host is identified, the prefix "alter-" is placed at the start of the epithet. For example, Mamestra configurata nucleopolyhedrovirus A, the first species identified from the bertha armyworm, Mamestra configurata, is now Alphabaculovirus maconfiguratae, while Mamestra configurata nucleopolyhedrovirus B, the second species with isolates identified from M. configurata, became Alphabaculovirus altermaconfiguratae. For subsequent species to classify viruses isolated from the same host, the appropriate Latin ordinal prefixes will be added to the specific epithet. For example, "tert(i)" and "quart(u)" will be placed in front of "-maconfiguratae" if alphabaculoviruses representing a third and fourth distinct species from M. configurata would be identified.

Explanations and examples of the epithet strategy

It might seem simpler to adapt the host-specific epithet alone as the specific epithet for lefaviral species, as was done for the microsporidium *Nosema ceranae*, a pathogen of the Asiatic honey bee, *Apis cerana*. However, this approach does not account for situations in which two distinct viruses from the same genus are isolated from different hosts that share the same specific epithet. There is already an example of this situation: in addition to Autographa californica multiple nucleopolyhedrovirus (already classified as *Alphabaculovirus aucalifornicae*), there is another alphabaculovirus identified from the California oakworm, *Phryganidia californica* [18]. Adding the 2–4 first letters of the host's genus name as the start of the epithet resolves this problem.

The genus name, per definition, ends in "-virus", and as a consequence, the genus names are all of neuter gender in Latin. We can therefore not simply use the original epithet of the host, which may have been of female, male, or neuter gender. Therefore, we proposed to use the genitive form of the epithet of the insect species in the binomial name of the virus species. Genitive forms have the meaning: "owned by, derived from, belonging to". (The singular genitive form of most Latin words ends in *-ae*, *-i*, or *-is*, depending on the declension. All plural genitive forms end in *-um*). For explanations of less obvious epithets, see Supplementary Table S1.

In the situation where the host epithet already appears to be neuter, there would not be a strict linguistic need to change it. However, for overall consistency, we decided to use the genitive form there as well. Example: *Betabaculovirus xecnigri* (from the host *Xestia c-nigrum*). But what to do if the host's epithet is already in the genitive form or looks the same as a genitive form? Then we will leave it as it is, as the use of double genitives is not useful. This is exemplified by *Alphabaculovirus anpernyi* (from the host *Antheraea pernyi*), *Betabaculovirus cnamedinalis* (from *Cnaphalocrocis medinalis*), *Betabaculovirus agsegetum* (already genitive plural in *Agrotis segetum*; from "seges", meaning from the grain fields/crops).

In the past, a capital letter was appended to the end of baculovirus species names to distinguish species with isolates originating from the same host, as described above for alphabaculoviruses from *M. configurata*. One simple approach to reproducing this solution in the context of a binomial system might have been to attach the letter to the specific epithet of a binomial name with a hyphen. However, the use of hyphens to attach numbers or letters to the end of a series of species names is specifically excluded by ICVCN Rule 3.13. Thus, ordinal prefixes are used to distinguish different species isolated from the same host, as described above. The exact form of the ordinal prefixes will depend on the ease of pronunciation of the resulting epithet.

The background for the adopted strategy and some more general rules for composing epithets can be found in: "Advice and guidelines to Study Groups on the implementation of binomial species names", to be found at https:// ictv.global/filebrowser/download/435 or in the recently published paper by Postler and collaborators [25].

Conclusions

In this paper, we report recent major changes in the taxonomy of NALVDs, which are now part of the official ICTV taxonomy. The class *Naldaviricetes* and the order *Lefavirales* were established in 2021. The binomial species naming system for lefavirals was ratified in April 2023. In case of questions on how to name new virus species, please contact the respective ICTV Study Group. It is further proposed to continue using conventional naming and abbreviations for virus isolates, which will facilitate distinguishing between viruses and virus species.

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authors, except David Theilmann. Monique van Oers drafted the first version of this manuscript based on the two proposals mentioned here. All authors commented on previous versions of the manuscript and approved the final manuscript.

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