

**On the classification and nomenclature of baculoviruses:
A proposal for revision**

Brief Review

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Summary. Recent evidence from genome sequence analyses demands a substantial revision of the taxonomy and classification of the family *Baculoviridae*. Comparisons of 29 baculovirus genomes indicated that baculovirus phylogeny followed the classification of the hosts more closely than morphological traits that have previously been used for classification of this virus family. On this basis, dipteran- and hymenopteran-specific nucleopolyhedroviruses (NPV) should be separated from lepidopteran-specific NPVs and accommodated into different genera. We propose a new classification and nomenclature for the genera within the baculovirus family. According to this proposal the updated classification should include four genera: Alphabaculovirus (lepidopteran-specific NPV), Betabaculovirus (lepidopteran-specific Granuloviruses), Gammabaculovirus (hymenopteran-specific NPV) and Deltabaculovirus (dipteran-specific NPV).

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The taxonomy and classification of living organisms is itself a living and steadily evolving process. The same holds true for taxonomy and classification of viruses.

In recent years, the nucleotide sequences of virus genes and genomes have become one of the most important tools for virus classification, not least because other distinguishing traits are often difficult to identify. Nucleotide sequence data have rationalised taxonomy in two ways. First, nucleotide sequences and deduced amino acid sequences can be compared and analysed using molecular phylogenetics, with methods based on objective mathematical models. Second, sequence data and molecular phylogenetic analysis can be transformed into quantifiable parameters, such as genetic distances or degrees of sequence identity, which may allow for defining taxon demarcation criteria. In the light of the increased knowledge of baculovirus genomes, the classification of the family *Baculoviridae* needs to be adapted to the emerging picture of baculovirus diversity.

Present status of baculovirus classification

Baculoviruses are classified as a group of arthropod-specific viruses with rod-shaped nucleocapsids of 30–60 nm × 250–300 nm. Two virion phenotypes, occlusion-derived virions (ODV) and budded virions (BV) are commonly found in baculoviruses but there might be exceptions. ODV are occluded in a crystalline protein matrix, the occlusion body (OB), and initiate infection in the midgut epithelium of infected insects. The BV are produced after initial infection and bud through the plasma membrane of infected cells. BV typically contain a single nucleocapsid within an envelope that is derived from the host plasma membrane that is modified by one or more viral proteins. In contrast, ODV consist of single or multiple nucleocapsids that are present in an envelope that has a different origin and composition of viral proteins as compared with the BV envelope. These two morphologically different but genetically identical viral forms reflect their respective roles in cell-to-cell (BV) and insect-to-insect (ODV) transmission of baculovirus infection.

Two OB morphologies are reported, which correlate with the current classification of baculoviruses. Members of the genus *Nucleopolyhedrovirus* (NPV) have occlusion bodies of 0.15 to 3 (–15) μm in size and characteristically contain many ODV. The genus *Granulovirus* (GV) is characterized by smaller, often ovoid occlusion bodies of 0.13 × 0.50 μm in size which normally contain a single ODV [1].

Baculovirus genomes consist of a circular double-stranded DNA molecule of about 80–180 kbp. Replication of baculoviruses occurs in the nucleus (NPV) or nucleo-cytoplasmic stroma after disintegration of the nuclear membrane (GV). NPVs have been reported predominately from the insect orders Lepidoptera, Diptera and Hymenoptera. GVs have been exclusively found in Lepidoptera. Although other insect orders such as Coleoptera, Neuroptera, Thysanura and Trichoptera have been reported as hosts, a molecular identification of those putative baculoviruses is lacking. Also, occluded crustacean baculoviruses (*Baculovirus penaei*) have been reported but are not well characterized [8].

With the 6th report of the ICTV [31], the family *Baculoviridae* was classified into two genera, *Nucleopolyhedrovirus* (NPV) and *Granulovirus* (GV). Since then, the classification remained unchanged [5, 38]. Also, with the 6th ICTV report the previously assigned “non-occluded” baculoviruses (NOB), which are

a diverse collection of dsDNA viruses with circular genomes that replicate in the nuclei of infected cells but do not form OBs, were removed from the family. The NOB are not yet assigned to a virus genus or virus family [29]. Previously reported “non-occluded” baculovirus-like viruses have been isolated from shrimp (Decapoda: Crustaceae), including viruses now classified as members of the genus *Whispovirus*, family *Nimaviridae* [41].

Recent advances in genome analyses

During the last decade, 29 baculovirus genomes have been sequenced offering a wealth of information on the genetic diversity, gene sequences, gene content, genome organisation and phylogeny of baculovirus genomes (Table 1).

Table 1. Characteristics of baculovirus genomes (January 2006)

Virus	Virus abbreviation	No. ORFs	Genome size (bp)	AT content (%)	Accession number	Ref.
<i>Autographa californica</i> MNPV	AcMNPV	155	133,894	59.3	NC_001623	[4]
<i>Choristoneura fumiferana</i> MNPV	CfMNPV	145	129,609	49.9	NC_004778	[24]
<i>Choristoneura fumiferana</i> DEF NPV	CfDEFNPV	149	131,160	54.2	NC_005137	[9]
<i>Rachiplusia ou</i> MNPV	RoMNPV	146	131,526	60.9	NC_004323	[12]
<i>Bombyx mori</i> NPV	BmNPV	143	128,413	59.6	NC_001962	[11]
<i>Epiphyas postvittana</i> NPV	EppoNPV	136	118,584	59.3	NC_003083	[18]
<i>Orgyia pseudotsugata</i> MNPV	OpMNPV	152	131,990	44.9	NC_001875	[3]
<i>Adoxophyes honmai</i> NPV	AdhoNPV	125	113,220	64.4	NC_004690	[32]
<i>Agrotis segetum</i> MNPV	AgseNPV	153	147,544	54.3	NC_007921	[20]
<i>Chrysodeixis chalcites</i>	ChChNPV	151	149,622	60.9	NC_007151	[39]
<i>Helicoverpa armigera</i> NPV (G4)	HearNPV (G4)	135	131,403	61.0	NC_002654	[6]
<i>Helicoverpa armigera</i> NPV (C1)	HearNPV (C1)	134	130,760	61.1	NC_003094	[45]
<i>Helicoverpa zea</i> SNPV	HzSNPV	139	130,869	60.9	NC_003349	[7]
<i>Mamestra configurata</i> NPV (A)	MacoNPV (A)	169	155,060	58.3	NC_003529	[26, 27]
<i>Mamestra configurata</i> NPV (B)	MacoNPV (B)	168	158,482	60.0	NC_004117	[25]
<i>Lymantria dispar</i> MNPV	LdMNPV	166	161,046	42.5	NC_001973	[21]
<i>Spodoptera exigua</i> MNPV	SeMNPV	139	135,611	56.2	NC_002169	[19]
<i>Spodoptera litura</i> NPV	SpltNPV	141	139,342	57.2	NC_003102	[34]
<i>Trichoplusia ni</i> SNPV	TnSNPV	144	134,394	61.0	NC_007383	[42]
<i>Cryptophlebia leucotreta</i> GV	CrleGV	129	110,907	67.6	NC_005068	[22]
<i>Cydia pomonella</i> GV	CpGV	143	123,500	54.8	NC_002816	[28]
<i>Phthorimea operculella</i> GV	PhopGV	130	119,217	64.3	NC_004062	–
<i>Plutella xylostella</i> GV	PlxyGV	120	100,999	59.3	NC_002593	[13]
<i>Adoxophyes orana</i> GV	AdorGV	119	99,657	65.5	NC_005038	[43]
<i>Xestia c-nigrum</i> GV	XecnGV	181	178,733	59.3	NC_002331	[14]
<i>Agrotis segetum</i> GV	AgseGV	132	131,680	62.7	NC_005839	–
<i>Neodiprion lecontei</i> NPV	NeleNPV	90	81,756	66.7	NC_005906	[23]
<i>Neodiprion sertifer</i> NPV	NeseNPV	90	86,462	66.2	NC_005905	[10]
<i>Culex nigripalpus</i> NPV	CuniNPV	109	108,252	49.1	NC_003084	[2]

Whereas the average baculovirus genome encodes 90–180 open reading frames (ORFs), more than 800 different orthologous gene groups were identified in 29 sequenced baculovirus genomes (Table 1). Thus, only a small proportion of the viral genome encodes genes that are common to all baculoviruses. As for other DNA viruses, three main mechanisms of genome formation and gene diversification are apparent in baculovirus genomes [37]. These are (i) lateral gene transfer from other virus, bacterial or eukaryotic genomes; (ii) homologous recombination with related viruses; (iii) domain and gene duplication. Baculovirus-encoded proteins can be grouped into five functional classes [33], namely, proteins involved in transcription, replication, or virion structure and proteins with auxiliary or unknown functions.

Further comparison of baculovirus genomes revealed that all lepidopteran-specific NPVs and GVs that have been sequenced share 62 common ORFs. This finding, which was based on comparison of twelve genomes [16], still holds for 26 lepidopteran NPV and GV genomes sequenced. Early phylogenetic analyses based on the polyhedrin gene further suggested that the lepidopteran NPVs might be subdivided into two groups, the so-called group I and group II NPVs [44]. Genome sequence comparisons further corroborated this finding and suggest that group II NPVs utilize an ancient furin-cleaved envelope fusion protein (or F proteins) for cell-to-cell spread of the virus, whereas its function is replaced in group I NPV by GP64. GP64 proteins have homology to certain orthomyxovirus envelope proteins, and F proteins have homology to the ENV proteins of errantiviruses, a genus of insect retroviruses [35].

The current classification of baculoviruses was challenged by the characterization of a NPV isolated from the dipteran *Culex nigripalpus* (CuniNPV) [30, 2]. CuniNPV infects the midgut epithelial cells but no other tissues of mosquito larvae. The polyhedral OB protein of CuniNPV is about 90 kDa in size and appears to be non-homologous to the 25–33-kDa OB protein of other baculoviruses [36]. The genome of CuniNPV shares only 30 ORFs with other lepidopteran-specific NPVs and GVs. This indicates that the phylogenetic distance between CuniNPV and lepidopteran NPVs is much greater than between lepidopteran NPVs and GVs (Table 2). Our current picture of baculovirus genome diversity was further advanced by the genome characterization of two viruses infecting hymenopteran hosts, the *Neodiprion lecontei* NPV (NeleNPV) and *N. sertifer* NPV (NeseNPV) [23, 10]. These two viruses have relatively small genomes of only 82–86 kbp encoding about 90 ORFs. Their replication is restricted to the midgut. NeleNPV and NeseNPV share all the baculovirus core genes with CuniNPV and lepidopteran NPVs and GVs except for one gene: the homologues of the envelope fusion protein, either F protein or GP64. However, there are 43 putative ORFs shared between hymenopteran NPV and lepidopteran NPV and GV.

Early attempts to establish genome-wide phylogenies of baculoviruses were performed by Herniou et al. [15, 16]. In addition to using single gene trees for phylogenetic analyses they also used sets of core genes, gene content and gene order. It was found that concatenation of core genes resulted in robust trees that were congruent with gene content and gene order trees.

Table 2. Common genes identified in 29 baculovirus genomes

Function	AcMNPV ORF	Name	CuniNPV	Hymenoptera-spec. NPV	Lepidoptera-spec. NPV und GV
Transcription	28	<i>lef-6</i>	-	-	+
	36	<i>pp31/39K</i>	-	-	+
	37	<i>lef-11</i>	-	+	+
	40	<i>p47</i>	+	+	+
	50	<i>lef-8</i>	+	+	+
	62	<i>lef-9</i>	+	+	+
	77	<i>vlf-1</i>	+	+	+
	90	<i>lef-4</i>	+	+	+
	99	<i>lef-5</i>	+	+	+
	Replication	6	<i>lef-2</i>	+	+
14		<i>lef-1</i>	+	+	+
65		<i>dnapol</i>	+	+	+
67		<i>lef-3</i>	-	-	+
95		<i>helicase</i>	+	+	+
139		<i>me53</i>	-	-	+
147		<i>ie-1</i>	-	-	+
Structural proteins	25	<i>dbp1</i>	-	+	+
	8	<i>polh</i>	(+)*	+	+
	10	<i>pk1</i>	-	-	+
	22	<i>pif-2</i>	+	+	+
	23	<i>efp/ld130</i>	+	-**	+
	46	<i>odv-e66</i>	-	-	+
	54	<i>vp1054</i>	+	+	+
	61	<i>fp25K</i>	-	-	+
	80	<i>gp41</i>	+	+	+
	83	<i>vp91/p95</i>	+	+	+
	89	<i>vp39</i>	+	+	+
	94	<i>odv-e25</i>	-	-	+
	100	<i>p6.9</i>	+	+	+
	115	<i>pif-3</i>	+	+	+
	119	<i>pif-1</i>	+	+	+
138	<i>p74</i>	+	+	+	
	<i>odv-ep</i>				
143	<i>odv-e18</i>	-	+	+	
144	<i>odv-e27</i>	+	+	+	
148	<i>odv-e56</i>	+	+	+	

Function	AcMNPV ORF	Name	CuniNPV	Hymenoptera-spec. NPV	Lepidoptera-spec. NPV und GV
Aux.1	32	<i>fgf</i>	-	-	+
	35	<i>ubiquitin</i>	-	-	+
Unknown	133	<i>alk-exo</i>	+	+	+
	38		-	-	+
	13	<i>38.7K</i>	-	-	+
	29		-	-	+
	53		-	+	+
	66	<i>desmop</i>	-	-	+
	68		+	+	+
	75		-	+	+
	76		-	+	+
	78		-	+	+
	81		+	+	+
	82	<i>tlp20</i>	-	-	+
	92	<i>p33</i>	+	+	+
	93		-	+	+
	96	<i>19kda</i>	+	+	+
	98	<i>38K</i>	+	+	+
	101	<i>p40</i>	-	+	+
	102	<i>p12</i>	-	-	+
103	<i>p45</i>	-	+	+	
106		-	+	+	
109		+	+	+	
110		-	-	+	
142	<i>p49</i>	+	+	+	
145		-	+	+	
146		-	-	+	

¹Auxiliary proteins

*the *polh* of CuniNPV does not appear to be homologous to the *polh* of hymenopteran and lepidopteran-specific baculoviruses [2, 36]

**not found in NeleNPV and NeseNPV. The gene may have been lost or not identified due to low sequence homology[23, 10]

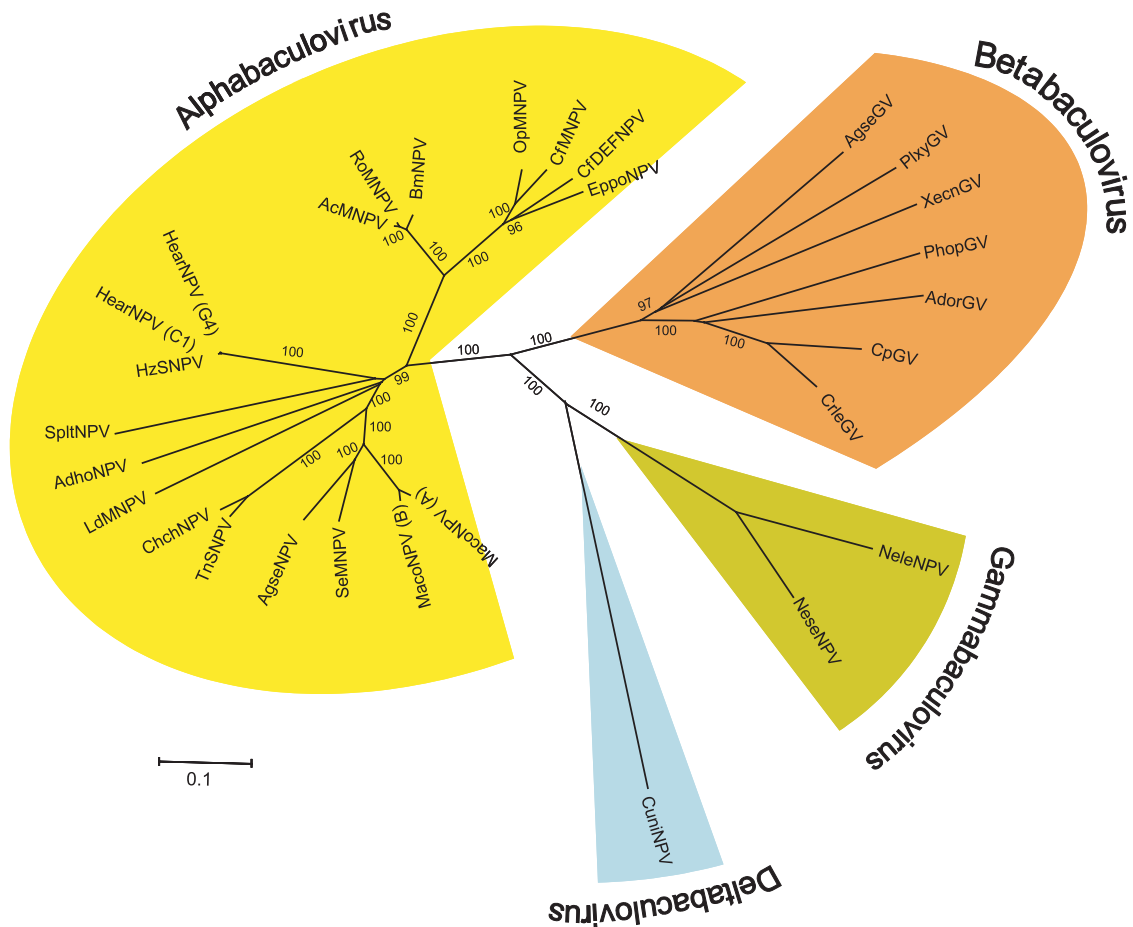


Fig. 1. Neighbour-joining tree of the amino acid alignment of 29 baculovirus core genes (Table 2) of 29 sequenced baculovirus genomes (Table 1). The alignment comprised 16349 positions. All branches have bootstrap values exceeding 50%. Bootstrap values >95% are given along the branches

Figure 1 shows an updated core gene tree. This tree is based on alignment of the amino acid positions of the 29 baculovirus core genes of 29 sequenced baculovirus genomes (Tables 1 and 2). The unrooted baculovirus tree consists of 4 major clades, which are the NPVs infecting Lepidoptera, the GVs, the Hymenoptera-specific NPVs and CuniNPV. It is anticipated that other clades will eventually need to be accommodated, e.g. the crustacean baculoviruses, when more molecular data are available. Based on phylogenetic evidence and further biological and morphological characteristics, we propose that the family *Baculoviridae* should be subdivided into four genera:

Alphabaculovirus

The proposed genus Alphabaculovirus should include all lepidoperan-specific nucleopolyhedroviruses. These can be of the single nucleocapsid (SNPV) or multiple nucleocapsid (MNPV) type, and they produce both BV and ODV. The

OB size is about 0.4–3 (–15) μm , and their genome sizes range from 100 to 180 kbp.

Proposed type species: *Autographa californica* \times *nucleopolyhedrovirus* (AcMNPV).

Betabaculovirus

The proposed genus *Betabaculovirus* would comprise the existing lepidopteran-specific genus *Granulovirus*. They produce both BV and ODV. The OB size is about 300–500 \times 130–250 nm, and their genome sizes range from 100 to 180 kbp.

Proposed type species: *Cydia pomonella granulovirus* (CpGV).

Gammabaculovirus

This proposed genus should comprise the hymenopteran-specific NeleNPV and NeseNPV and possibly other Hymenoptera-specific NPVs isolated from *Gilpinia hercyniae* NPV [17]. They have polyhedral OBs of about 0.4–1.1 μm in size with singly enveloped nucleocapsids (SNPV) in their virions. The genomes of NeleNPV and NeseNPV are about 82–86 kbp and appear to be smaller on average than those of lepidopteran-specific NPVs. Neither budded virions nor F or GP64 genes have been identified in current members of this group, suggesting that a BV phenotype may be absent.

Proposed type species: *Neodiprion lecontei nucleopolyhedrovirus* (NeleNPV).

Deltabaculovirus

The proposed genus should include the *Culex nigripalpus* nucleopolyhedrovirus (CuniNPV) and possibly other Diptera-specific baculoviruses. Two virus phenotypes may be characteristic of a virus species: budded virions and occluded virions. CuniNPV has globular OBs of about 400 nm in diameter. The occlusion body protein of CuniNPV is not homologous to the polyhedrin or granulins genes of the baculoviruses infecting Lepidoptera and Hymenoptera.

Proposed type species: *Culex nigripalpus nucleopolyhedrovirus* (CuniNPV).

The proposed re-classification and re-naming of the baculovirus genera takes phylogenetic evidence and genome composition into consideration in alignment with morphological and pathological traits. It follows the suggestion of Lauzon et al. [23] and has the advantage that only the classification and nomenclature of genera are revised. The virus names at the species level remain unchanged. In addition, the genus name remains neutral relative to the host animal. This is essential because future genomic studies may determine that baculoviruses from different insect orders should be phylogenetically grouped. The genus name therefore remains viable compared to naming genera based on virus morphology and insect hosts alone. Finally, future genera can be added in a logical progression.

This proposal will be submitted to the ICTV for consideration through the baculovirus study group of the ICTV. The scientific community is invited to respond to this proposal to further shape baculovirus taxonomy and classification.

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