

The International Committee on Taxonomy of Viruses

Taxonomy Proposal Form, 2024

**Part 1a: Details of taxonomy proposals**

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| **Title:** | Create a new virus family in the *Lefavirales* order named *Filamentoviridae* with two genera *Alphafilamentovirus* and *Betafilamentovirus,* and three species. | |
| **Code assigned:** | 2024.007D.N.v2.Filamentoviridae\_1nf\_2ngen\_3nsp |

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| --- | --- | --- | --- |
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**Part 1b: Taxonomy Proposal Submission**

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| **ICTV Subcommittee:** | | | |
| Animal DNA Viruses and Retroviruses | **X** | Bacterial viruses |  |
| Animal minus-strand and dsRNA viruses |  | Fungal and protist viruses |  |
| Animal positive-strand RNA viruses |  | Plant viruses |  |
| Archaeal viruses |  | General - |  |

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| **List the ICTV Study Group(s) that have seen or have been involved in creating this proposal:** |
| *Baculoviridae*/*Nudiviridae* Study Group |

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| **Optional – complete only if formally voted on by an ICTV Study Group:** | | | |
| **Study Group** | **Number of members** | | |
| **Votes in support** | **Votes against** | **No vote** |
| Baculoviridae and Nudiviridae Study Group | 8 | 0 | 2 |
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| **Submission date:** | 04/06/2024 |

**Part 1c: Feedback from ICTV Executive Committee (EC) meeting**

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| **Executive Committee Meeting Decision code:** | **X** |
| A – Accept |  |
| Ac – Accept subject to revision by relevant subcommittee chair. No further vote required | **X** |
| U – Accept without revision but with re-evaluation and email vote by the EC |  |
| Uc – Accept subject to revision and re-evaluation and email vote by the EC |  |
| Ud – Deferred to the next EC meeting, with an invitation to revise based on EC comments |  |
| J - Reject |  |
| W - Withdrawn |  |

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| **Comments from the Executive Committee:** |
| Alphafilamentovirus leheterotomae:  OR069712; OR069713; OR069714; OR069715; OR069716; OR069717; OR069718; OR069719; OR069720; OR069721  No justifications provided on why complete genome sequences in not provided and why segments of the genomes are used. Furthermore, the EC suggest that this species be removed as it is segments of the genome not the full genome.  Betafilamentovirus cocongregatae: ERZ21788700  The issue is the accession #. This a MAG accession and not a GenBank accession. Please provide an accession #. that cannot be cross referenced in RefSeq. |

**Part 1d: Revised Taxonomy Proposal Submission**

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| **Response of proposer:** |
| Revised as follows  Alphafilamentovirus leheterotomae has been removed.  Betafilamentovirus cocongregatae: GenBank OY734801 accession provided |

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| **Revision date:** | 23/10/2024 |

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

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| **Name of accompanying Excel module:** |
| 2024.007D.N.v2.Filamentoviridae\_1nf\_2ngen\_3nsp.xlsx |

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| **Taxonomic changes proposed:** | | | |
| Establish new taxon | **X** | Split taxon |  |
| Abolish taxon |  | Merge taxon |  |
| Move taxon |  | Promote taxon |  |
| Rename taxon |  | Demote taxon |  |
| Move and rename |  |

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| **Is any taxon name used here derived from that of a living person:** | | **N** |
| **Taxon name** | **Person from whom the name is derived** | **Attached X** |
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| **Abstract of Taxonomy Proposal:** |
| ***Taxonomic rank(s) affected*:**  Establishment of a new highly diverse viral family within the order *Lefavirales* in the class *Naldaviricetes*, the *Filamentoviridae,* comprising two genera: the *Alphafilamentovirus*, with the species *Alphafilamentovirus leboulardi*, and the *Betafilamentovirus*, with the species *Betafilamentovirus cocongregatae* and *Betafilamentovirus altercocongregatae.*  ***Description of current taxonomy*:**  The class of *Naldaviricetes* currently includes four families: *Baculoviridae*, *Nudiviridae*, *Hytrosaviridae,* and *Nimaviridae*, the first three belonging to the order of *Lefavirales*.  ***Proposed* *taxonomic change(s):***  Create *Filamentoviridae*, a new family in the order *Lefavirales* within *Naldaviricetes,* with two genera (*Alphafilamentovirus* and *Betafilamentovirus*), and three species.  ***Justification*:**  New large arthropod-specific dsDNA viruses, which have been described as filamentous particles since the 1970s, have recently been characterized at the genomic level [7]. These viruses share signatures of the *Naldaviricetes* and the *Lefavirales,* while encoding specific core genes that distinguish them from the established families of this order. Phylogenetic tree reconstruction indicates that these filamentous viruses (FVs) form a monophyletic clade distinct from that of their closest relatives, the *Hytrosaviridae,* and supports the creation of a new family, that we propose to name *Filamentoviridae.* These viruses appear to be preferentially associated with hymenopteran insects with a parasitoid lifestyle [7]. The effects of FVs on their hosts are still poorly assessed, with respect to other members of the *Naldaviricetes*. So far, only the Leptopilina boulardi filamentous virus (LbFV)has been studied for its effect and described as inducing a behavioral manipulation of wasp oviposition decisions and benefiting from vertical and horizontal transmission. |

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| * **Text of Taxonomy proposal:** |
| ***Filamentoviridae: a new family within the Lefavirales order***.  Recently characterized filamentous viruses (*i.e*., filamentoviruses) share specific features with the nuclear arthropod large DNA viruses (NALDVs) of the class *Naldaviricetes* (Table 1), suggesting a common evolutionary origin [17, 8, 9, 1, 13, 21]. The filamentoviruses share 29 core genes [7]. Fourteen are common to all the *Lefavirales,* seven of which are shared by all *Naldaviricetes.* Theseinclude in particular genes encoding the *per os* infectivity factors and the components of the viral RNA polymerase, which were originally used to define *Naldaviricetes* and *Lefavirales,* respectively (Table 2). Phylogenetic analyses based on concatenated alignments of twenty core genes indicate that filamentoviruses form a monophyletic clade distinct from the previously described families: *Baculoviridae*, *Nudiviridae,* *Hystrosaviridae,* and *Nimaviridae* (Figure 1) [7]. In addition, filamentoviruses share five specific core genes that distinguish them from their closest relatives, the *Hytrosaviridae* (Table 2). Therefore, we propose the creation of a fifth virus family within the *Naldaviricetes*, named *Filamentoviridae*, which together with *Baculoviridae*, *Nudiviridae* and *Hytrosaviridae,* belongs to the order *Lefavirales* (Figure 2).  ***Demarcation criteria for the delimitation of two genera within Filamentoviridae***.  One possible way to define the boundaries of viral genera is based on the host spectrum of the viral species. However, our data indicate that this method is not applicable to *Filamentoviridae*, in the sense that, several hosts from different wasp families are found mixed in the viral clades (Figure 1).  Here, we considered that filamentoviruses would belong to different genera for a patristic distance threshold greater than 2.6 (Table 3). For the moment, we also chose to define genera only for a restricted set of viruses belonging to highly supported clades, including at least one virus with a complete genome and biological data such as viral particle and/or morphogenesis description. Among the eight available filamentoviruses, a complete circularized genome and electron microscopy images have been obtained for both Cotesia congregata filamentous viruses (CcFV1 and CcFV2) and LbFV [4, 5, 7, 14, 18, 19] (Figure 1, Figure 3). Based on the criteria defined above, we therefore distinguish two genera: *Alphafilamentovirus*, which includes the filamentous virus that infect *Leptopilina* *boulardi* (LbFV), and *Betafilamentovirus*, which includes the two filamentous viruses that infect *Cotesia* wasps (CcFV1 and CcFV2).  We have classified the five remaining viruses (*i.e*., with complete or nearly complete genomes: Encarsia formosa filamentous virus (EfFV), Leptopilina heterotoma filamentous virus (LhFV), Microctonus hyperodae filamentous virus (MhFV), Psyttalia concolor filamentous virus (PcFV) and Platygaster orseoliae filamentous virus (PoFV)) at the rank family only, until the necessary data (*e.g*., complete or additional genomes and biological descriptions of the virus) are obtained to justify their inclusion in the genera defined herein or in additional genera*.*  ***Etymology of the name***.  From the Latin filamentum, meaning “filament”, referring to the filamentous-shape of virus particles observed in infected tissues and the *–viridae* suffix for family taxa.  ***Species members***.  Of the filamentoviruses identified to date, only three have been classified at the genus rank. Leptopilina boulardi filamentous virus (LbFV) belong to the genus *Alphafilamentovirus* (*Alphafilamentovirus leboulardi*)*,* whereas Cotesia congregata filamentous viruses 1 and 2 (CcFV1 and CcFV2) belong to the the genus *Betafilamentovirus* (*Betafilamentovirus cocongregatae* and *Betafilamentovirus altercocongregatae*, respectively).  ***Related, unclassified viruses***.  Five other filamentoviruses remain unclassified as *Filamentoviridae,* including Encarsia formosa filamentous virus (EfFV) and Microctonus hyperodae filamentous virus (MhFV), for which complete and circular genomes are available [7, 11], and Leptopilina heterotoma filamentous virus (LhFV), Psyttalia concolor filamentous virus (PcFV) and Platygaster orseoliae filamentous virus (PoFV), for which nearly complete genomes are available [7], although they have not been circularized likely due to the presence of repeated sequences (see supplementary xlsx file). Of note, the filamentous virus that infects *Apis mellifer*a (AmFV) [6] does not belong to the family *Filamentoviridae*.  Based on sequencing data mining and phylogenetic tree reconstruction (Figure 1) [7], additional filamentoviruses are suspected from *Cotesia vestalis*, *Cotesia flavipes*, *Dolichomitus* sp., and *Microplitis mediator* [2, 5, 7] (see supplementary xlsx file). Related sequences have also been identified in *Drosophila melanogaster* (Diptera), which, based on genomic similarity, most likely belong to the species *Alphafilamentovirus leheterotomae* likely transmitted by a *L. heterotoma* parasitoid during parasitization [7, 20]. |

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| **References:** |
| 1. Abd-Alla AM, Vlak JM, Bergoin M, et al (2009) *Hytrosaviridae*: a Proposal for Classification and Nomenclature of a New Insect Virus Family. Arch Virol 154:909-918. <https://doi.org/10.1007/s00705-009-0398-5> 2. Burke GR, Hines HM, Sharanowski BJ (2021) The Presence of Ancient Core Genes Reveals Endogenization from Diverse Viral Ancestors in Parasitoid Wasps. Genome Biol Evol 13:evab105. <https://doi.org/10.1093/gbe/evab105> 3. Chernomor O, von Haeseler A, Minh BQ (2016) Terrace Aware Data Structure for Phylogenomic Inference from Supermatrices. Syst Biol 65:997-1008. <https://doi.org/10.1093/sysbio/syw037> 4. de Buron I, and Beckage NE (1992) Characterization of a Polydnavirus (PDV) and Virus-like Filamentous Particle (VLFP) in the Braconid Wasp *Cotesia congregata* (Hymenoptera: Braconidae). J Invertebr Pathol59:315-327. https://doi.org/10.1016/0022-2011(92)90139-U 5. Gauthier J, Boulain H, van Vugt JJFA, et al (2021) Chromosomal Scale Assembly of Parasitic Wasp Genome Reveals Symbiotic Virus Colonization. Commun Biol 4:104. <https://doi.org/10.1038/s42003-020-01623-8> 6. Gauthier L, Cornman S, Hartmann U, et al (2015) The Apis mellifera Filamentous Virus Genome. Viruses 7:3798-3815. <https://doi.org/10.3390/v7072798> 7. Guinet B, Leobold M, Herniou EA, et al (2024) A Novel and Diverse Family of Filamentous DNA Viruses Associated with Parasitic Wasps. Virus Evol 10:veae022. <https://doi.org/10.1093/ve/veae022> 8. Harrison RL, Herniou EA, Jehle JA (2018) ICTV Virus Taxonomy Profile: *Baculoviridae*. J Gen Virol 99:1185-1186. <https://doi.org/10.1099/jgv.0.001107> 9. Harrison RL, Herniou EA, Bézier A, et al (2020) ICTV Virus Taxonomy Profile: *Nudiviridae*. J Gen Virol 101:3-4. <https://doi.org/10.1099/jgv.0.001381> 10. Hoang DT, Chernomor O, von Haeseler A, et al (2018) UFBoot2: Improving the Ultrafast Bootstrap Approximation. Mol Biol and Evol 35:518–522. <https://doi.org/10.1093/molbev/msx281> 11. Inwood SN, Skelly J, Guhlin JG, et al (2023) Chromosome-level Genome Assemblies of two Parasitoid Biocontrol Wasps Reveal the Parthenogenesis Mechanism and an Associated Novel Virus. BMC Genomics 24:440. <https://doi.org/>10.1186/s12864-023-09538-4 12. Kalyaanamoorthy S, Minh BQ, Wong TKF, et al (2017) ModelFinder: Fast Model Selection for Accurate Phylogenetic Estimates. Nat Methods 14:587-589. <https://doi.org/10.1038/nmeth.4285> 13. Kariithi HM, Vlak JM, Jehle JA, et al (2019) ICTV Virus Taxonomy Profile: *Hytrosaviridae*. J Gen Virol 100:1271-1272. <https://doi.org/10.1099/jgv.0.001300> 14. Lepetit D, Gillet B, Hughes S, et al (2017) Genome Sequencing of the Behavior Manipulating Virus LbFV Reveals a Possible New Virus Family. Genome Biol Evol 8:3718-3739. <https://doi.org/10.1093/gbe/evw277> 15. Minh BQ, Schmidt HA, Chernomor O, et al (2020) IQ-TREE 2: New Models and Eﬃcient Methods for Phylogenetic Inference in the Genomic Era. Mol Biol and Evol 37:1530-1534. <https://doi.org/10.1093/molbev/msaa015> 16. Sievers F, Wilm A, Dineen D, et al (2011) Fast, Scalable Generation of High-quality Protein Multiple Sequence Alignments using Clustal Omega. Mol Syst Biol 7:539. <https://doi.org/10.1038/msb.2011.75> 17. Van Oers MM, Herniou EA, Jehle JA, et al (2023) Developments in the Classification and Nomenclature of Arthropod-infecting Large DNA Viruses that Contain *pif* Genes. Arch Virol 168:182. <https://doi.org/10.1007/s00705-023-05793-8> 18. Varaldi J, Fouillet P, Ravallec M, et al (2003) Infectious Behavior in a Parasitoid. Science 302:1930-1930. https://doi.org/10.1126/science.1088798 19. Varaldi J, Ravallec M, Labrosse C, et al (2006) Artifical Transfer and Morphological Descrip-tion of Virus Particles Associated with Superparasitism Behaviour in a Parasitoid Wasp. J Insect Physiol 52:1202-1212. https://doi.org/10.1016/j.jinsphys.2006.09.002 20. Wallace MA, Coffman KA, Gilbert C, et al (2021) The Discovery, Distribution, and Diversity of DNA Viruses Associated with *Drosophila melanogaster* in Europe. Virus Evol 7:veab031. <https://doi.org/10.1093/ve/veab031> 21. Wang H\_C, Hirono I, Maningas MBB, et al (2019) ICTV Virus Taxonomy Profile: *Nimaviridae*. J Gen Virol 100:11053-1054. [<https://doi.org/10.1099/jgv.0.001248>](https://doi.org/10.1099/jgv.0.001248) |

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| **Tables, Figures:** |

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**Supporting evidences**

**Table 1:** Features shared between filamentoviruses and viruses belonging to the *Naldaviricetes* class*.*

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|  | ***Naldaviricetes* class** | | | | |
|  | ***Lefavirales* order** | | | |  |
| **FEATURES** | ***Baculoviridae*** | ***Nudiviridae*** | ***Hytrosaviridae*** | ***Filamentoviridae*** | ***Nimaviridae*** |
| Replication site | Nucleus | Nucleus | Nucleus | Nucleus | Nucleus |
| ***Genome*** | | | | | |
| Molecule type | Circular dsDNA | Circular dsDNA | Circular dsDNA | Circular dsDNA | Circular dsDNA |
| Size (kbp) | 80-180 | 96-232 | 124-190 | 101-164 | 280–307 |
| Predicted ORFs | 100-200 | 89-155 | 108-174 | 104-156 | >40 |
| Core genes (in common\*) | 38 (13) | 28 (13) | 38 (13) | 29 (13) | 28 (7) |
| *pif* genes | + | + | + | + | + |
| *lef* genes | + | + | + | + | - |
| Repeat sequences | + | + | + | + | + |
| ***Virion*** | | | | | |
| Nucleocapsid shape | Enveloped, rod-shaped | Enveloped, rod-shaped or ellipsoidal, compact or elongated | Enveloped, rod to filamentous shaped | Enveloped, filamentous-shaped | Enveloped, rod-shaped |
| Size (nm) | 30-60 x 250-300 | 80-100 x 200-415 | 50–100 × 500–1000 | 40-60 x 800-1000 | 70–170 × 210–420 |

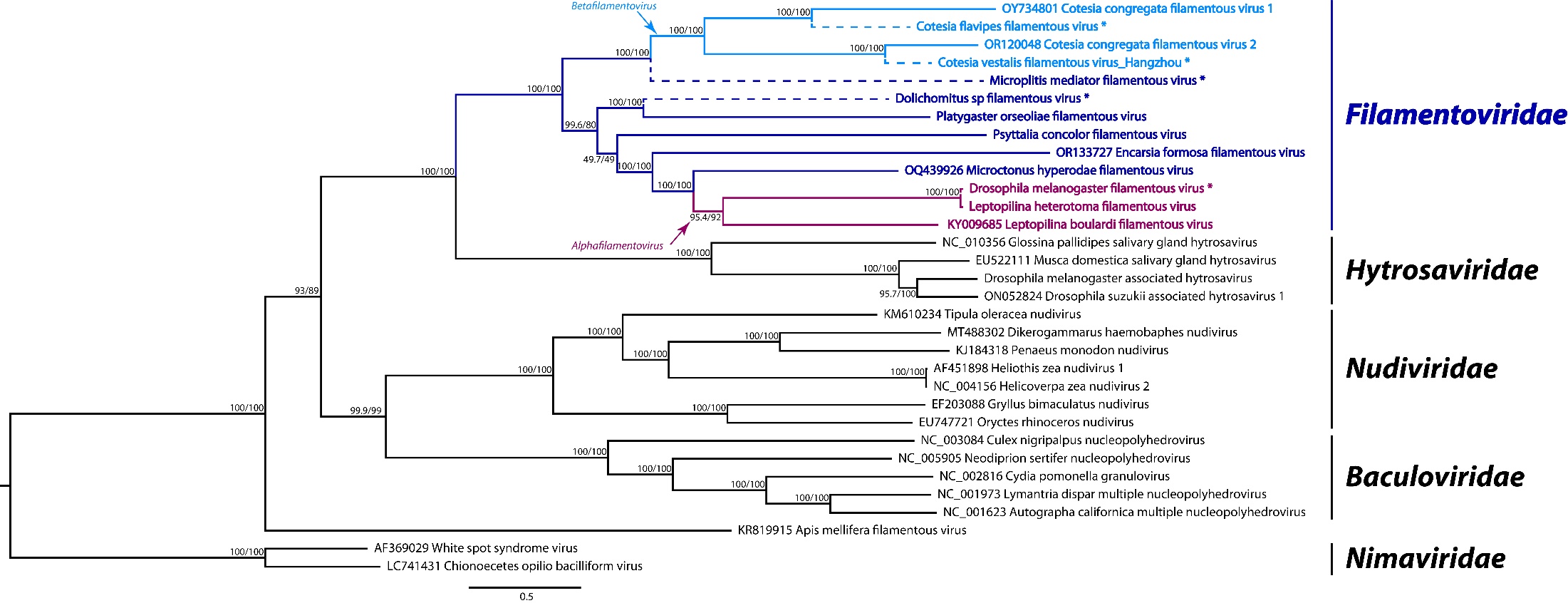
*pif* genes for *per os* infectivity factors. *lef* genes for late expressed factors. \* This number corresponds to the number of considered core genes to be conserved with other members of the higher taxon (see also Table 2).

**Table 2:** *Filamentoviridae* core genes conservation with other *Naldaviricetes* families*.* Core genes required to belong to the class *Naldaviricetes* are highlighted in yellow, those required to additionally belong to the order *Lefavirales,* are highlighted in green, and those that are specific to the *Filamentoviridae* (*i.e*., found only in species belonging to that family) are highlighted in red.

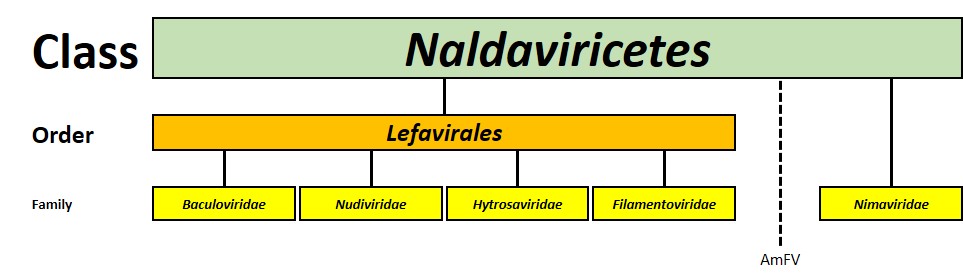
|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  |  | ***Naldaviricetes*** | | | | |
|  |  | ***Baculoviridae*** | ***Nudiviridae*** | ***Hytrosaviridae*** | ***Filamentoviridae*** | ***Nimaviridae*** |
| ***Per os* infectivity factors** | ***p74*** | **X** | **X** | **X** | **X** | **X** |
| ***pif-1*** | **X** | **X** | **X** | **X** | **X** |
| ***pif-2*** | **X** | **X** | **X** | **X** | **X** |
| ***pif-3*** | **X** | **X** | **X** | **X** | **X** |
| ***pif-5*** | **X** | **X** | **X** | **X** | **X** |
| **Viral transcription complex** | ***lef-4*** | **X** | **X** | **X** | **X** |  |
| ***lef-8*** | **X** | **X** | **X** | **X** |  |
| ***lef-9*** | **X** | **X** | **X** | **X** |  |
| ***lef-5*** | **X** | **X** | **X** | **X** |  |
| **DNA replication**  **and processing** | ***DNApol*** | **X** | **X** | **X** | **X** | **X** |
| ***helicase*** | **X** | **X** | **X** | **X** |  |
| ***integrase*** |  | **X** | **X** | **X** |  |
| ***pd-(d/e)xk*** |  |  | **X** | **X** |  |
| ***LbFVorf92*** |  |  | **X** | **X** |  |
| **Packaging, assembly, morphogenesis** | ***p33*** | **X** | **X** | **X** | **X** | **X** |
| ***Ac81*** | **X** | **X** | **X** | **X** |  |
| ***38K\*\**** | **X** | **X** | **X** | **X** |  |
| ***p6.9*** | **X** | **X** |  | **X** |  |
|  | ***lcat*** |  |  | **X** | **X** |  |
|  | ***ATPase*** |  |  | **X** | **X** |  |
|  | ***Ac38*** # |  |  |  | **X** |  |
| **Unknown** | ***LbFVorf5*** |  |  | **X** | **X** |  |
|  | ***LbFVorf20*** |  |  | **X** | **X** |  |
|  | ***LbFVorf102*** |  |  | **X** | **X** |  |
|  | ***LbFVorf23*** |  |  |  | **X** |  |
|  | ***LbFVorf54*** |  |  |  | **X** |  |
|  | ***LbFVorf87*** |  |  |  | **X** |  |
|  | ***LbFVorf94*** |  |  |  | **X** |  |
|  | ***LbFVorf99*** |  |  |  | **X** |  |

\*\* Newly identified *Lefavirales* conserved core gene [7]. # An *Ac38* homolog can be found in some baculoviruses and one hytrosavirus, this gene is therefore not specific of the *Filamentoviridae* lineage.

**Figure 1:** Phylogenetic interrelationships of the *Filamentoviridae* family with the *Naldaviricetes*. The five complete and tree nearly complete filamentovirus genomes were considered, as well as the sequences of five potentially related viruses. Concatenated amino acid alignments of 20 FV core genes including the 14 *Lefavirales* (see Table 2) and 6 additional (*integrase, Ac38, LbFVorf5, LbFVorf20, LbFVorf92, LbFVorf102*) core genes were used to infer relationships between *Filamentoviridae* and other *Naldaviricetes* (*Baculoviridae*, *Nudiviridae*, *Hytrosaviridae* and *Nimaviridae*). Alignments were performed using Clustal-Omega v1.2.4 [16] with 10 combined iterations (--full --iterations 10 --max-guidetree-iterations 1 --max-hmm-iterations 10) within each cluster. Evolutionary models for each cluster were determined using ModelFinder [3, 12] implemented in IQ-TREE software v2.1.2 [15]. Relationships were then inferred using ML analysis in IQ-TREE v2 from thirty-two virus species with 22,263 distinct patterns at the amino acid level. Ultra-fast bootstrap [10] and SH-aLRT (-bb 1,000 and -alrt 1,000) were computed to examine node supports. Support values are shown at each node (ultrafast bootstrap (%)/SH-aLRT support (%)). Visualization and rooting were finally performed using FigTree v1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/). The scale bar indicates the average number of amino acid substitutions per site. Labels within the *Filamentoviridae* clade are colored according to the proposed genera (purple: *Alphafilamentovirus*, light blue: *Betafilamentovirus*, and dark blue: FVs still not classified at genus rank). \* Additional filamentous-related sequences identified after data-mining the corresponding parasitoid wasp genome assembly (dashed lines). Corresponding sequence alignment and accession numbers are available in the Supplementary files.



**Figure 2:** Proposed inclusion of a new family, the *Filamentoviridae*, within the class *Naldaviricetes*, order *Lefavirales*, bringing the total number of *Naldaviricetes* families to five. Apis mellifera filamentous virus (AmFV) [6] remains currently unclassified within *Naldaviricetes*.

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**Table 3:** Matrix based on protein patristic distances measured from the phylogeny. Color gradient (green closest to red farthest) indicates patristic distances between two viruses. Here, a cut-off of 2.6 was used to infer tentative genera. The strict delimitation of genera according to the proposal groups the *Alphafilamentovirus* with LbFV on the one hand and the *Betafilamentovirus* with CcFV1 and CcFV2 on the other hand. The black boxes then represent genera with at least one complete viral genome and available biological data in the group, and the blue boxes represent groups lacking one or both of these elements. Virus names in bold indicate species for which taxonomic rank is proposed at the genus level; others are proposed at the family level only (see supplementary xlsx file for abbreviations).



**Figure 3** : Electron microscope images showing viral particles of three different filamentoviruses infecting adult parasitoid wasps. Calyx cells from (A) *C. congregata* laboratory strain (MsT wasps, reared on *Manduca sexta*)andfrom(B) *C. congregata* wild strain (CcC wasps, specific host *Ceratomia catalpae*) producing CcFV1 and CcFV2 particles, respectively. (C) Oviduct cell from *L. boulardi* females (S strain, reared on *Drosophila melanogaster*). The insets at the bottom right of each image are magnified sections of the nucleus showing filamentous particles. Ovarian sections from *L. boulardi* and *C. congregata* females were observed with an EM 10CR TEM (Zeiss) at 80 kV and a JEM-1011 TEM (Jeol) at 100 kV, respectively (see [7] for details). N: nucleus and C: cytoplasm.

