

The International Committee on Taxonomy of Viruses

Taxonomy Proposal Form, 2024

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

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| **Title:** | Reorganization of the realm *Varidnaviria* | |
| **Code assigned:** | 2024.010D.N.v1.Varidnaviria\_reorg |

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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 - | **X** |

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| **List the ICTV Study Group(s) that have seen or have been involved in creating this proposal:** |
| None (there is currently no Study Group for the realm *Varidnaviria*). |

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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** |
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| **Submission date:** | 21/06/2024 |

**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| W - Withdrawn |  |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:** |
| Remove the species Livvievirus viph1044o from the excel module, because this species is renamed in a different proposal. |

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

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| **Response of proposer:** |
| Species removed. |

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| **Revision date:** | 04/10/2024 |

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

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| **Name of accompanying Excel module:** |
| 2024.010D.N.v1.Varidnaviria\_reorg.xlsx |

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

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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*: *Varidnaviria*  *Description of current taxonomy*: Realm currently including two kingdoms: *Bamfordvirae* (two phyla with a total of six classes and one unassigned family) and *Helvetiavirae* (one phylum including one class)  *Proposed* *taxonomic change(s):* Create a new realm to accommodate *Helvetiavirae*; create a new varidnavirian kingdom to accommodate five previously bamfordviraen orders; create two subphyla in bamfordviraen phylum *Preplasmiviricota*; assign *Tectiliviricetes* to one and the remaining taxa to the other, which is also expanded by three new classes to accommodate polinton-like viruses and *Adenoviridae*.  *Justification*: A thorough genomic and proteomic analysis revealed previously unrecognized evolutionary relationships among the various varidnaviraen taxa. |

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| * **Text of Taxonomy proposal:** |
| *Taxonomic rank(s) affected*: *Varidnaviria*  *Description of current taxonomy*:  The realm *Varidnaviria*, proposed in 2019 and ratified in 2020, includes two kingdoms, *Helvetiavirae* and *Bamfordvirae*, for viruses with vertical single jelly-roll (SJR) and double jelly-roll (DJR) major capsid proteins (MCP), respectively. *Bamfordvirae* includes two phyla, *Nucleocytoviricota* and *Preplasmiviricota*, and one “floating” family, *Yaraviridae*, currently unassigned to any of the intermediate taxa. Phylum *Nucleocytoviricota* consists of eukaryotic viruses with large and giant double-stranded DNA (dsDNA) genomes, whereas *Preplasmiviricota* includes bacterial, archaeal, and eukaryotic viruses with small and moderately sized single-stranded DNA (ssDNA) and dsDNA genomes.  *Proposed* *taxonomic change(s)*:  During the five years that elapsed since *Varidnaviria* was proposed, major advances in structural bioinformatics and comparative genomics as well as expansion of the virus databases, have transformed our understanding of the evolution of these viruses. To reconcile the reconstructed evolution of varidnaviruses with their taxonomy, refinement of the *Varidnaviria* taxonomy is needed. The major proposed changes include:   1. Split the realm *Varidnaviria*, moving kingdom *Helvetiavirae* into a separate realm. 2. Create a new kingdom, ‘*Abadenavirae*’ and move most of the prokaryotic viruses with DJR MCPs into this kingdom. 3. Refine the taxonomy of *Preplasmiviricota*, including creation of new taxa and renaming of the existing ones. 4. Move family *Yaraviridae* into a new class within the phylum *Nucleocytoviricota.*   *Justification*:  **Creation of a new realm ‘*Singelaviria*’**  At the time when then realm *Varidnaviria* was proposed, the prevailing hypothesis was that DJR MCPs characteristic of members of the kingdom *Bamfordvirae* have evolved from fusion of the two SJR MCPs encoded by viruses within the kingdom *Helvetiaviriae*. However, recent evidence suggests that fusion of the SJR domains to produce a DJR protein has occurred in cellular organisms and that viruses exapted cellular SJR (*Helvetiaviriae*) or DJR (*Bamfordvirae*) proteins for capsid formation on independent occasions (Krupovic et al 2022). This scenario is supported by structural comparisons of the cellular and viral SJR and DJR proteins (Fig. 1A,B), which showed that viral DJR MCPs cluster with cellular glucoside hydrolases of the GH172 family (DUF2961). Importantly, similar to viral DJR MCPs, cellular DJR proteins form trimers (Fig. 1B), which is a key property of the DJR MCPs. Given the apparent independent origin of the MCPs encoded by viruses in *Helvetiairiae* and *Bamfordvirae*, it is proposed to move *Helvetiaviriae* from *Varidnaviria* into a separate realm to be named ‘*Singelaviria*’ (Koonin et al., 2024), from Latin singulus, meaning single, and gelata, meaning jelly (a reference to single jelly-roll capsid protein).  **Creation of a new kingdom “*Abadenavirae”***  Currently, prokaryotic viruses with DJR-MCPs, including tectivirids, and eukaryotic DJR-MCP viruses with shorter genomes, including the currently classified, adenovirids, and maveriviricetes (virophages) are classified within the bamfordviraen phylum *Preplasmiviricota*, whereas eukaryotic ‘giant viruses’ are unified within the bamfordviraen phylum *Nucleocytoviricota*, the sister group to preplasmiviricots. Within *Preplasmiviricota*, polintoviricetes (*Adintoviridae*) and ‘maveriviricetes constitute distinct classes. Tectivirids and adenovirids are assigned to two orders (*Kalamavirales* and *Rowavirales*, respectively) within class *Tectiliviricetes*, which also includes four other orders and one unassigned family of bacterial and archaeal DJR-MCP viruses. The fourth preplasmiviricot class, *Ainoaviricetes*, includes bacterial ssDNA viruses encoding DJR-MCPs.  Recent detailed analysis of the DNA replication proteins encoded by preplasmiviricots provided evidence of the monophyly of tectivirids, adenovirids, adintovirids, maveriviricetes and currently unclassified ‘polinton-like’ viruses, to the exclusion of other bacterial and archaeal preplasmiviricots (Krupovic et al., 2024). In particular, all these viral groups encode a protein-primed family B DNA polymerase (pPolB) or its derivatives (Fig. 2A). In most eukaryotic viruses in this assemblage, the pPolB is fused to a terminal protein (TP) (Fig. 2A, 2B), which is responsible for priming the initiation of DNA replication by pPolBs. Importantly, the TP encoded by eukaryotic preplasmiviricots is specifically related to the terminal protein of PRD1-like tectivirids, but distinct from the TPs of Bam35-like tectivirids and phi29-like phages (Fig. 2C; Krupovic et al., 2024). Previous phylogenetic analyses based on the pPolB sequences placed tectivirids at the base of eukaryotic preplasmiviricots, suggesting that the latter have evolved from within the diversity of bacterial tectivirids (Krupovic et al., 2015; Redrejo-Rodríguez et al., 2017). To reflect this evolutionary relationship, we propose moving all prokaryotic DJR-MCP viruses with dsDNA genomes, except for *Kalamavirales*, to a new phylum, ‘*Produgelaviricota*’, with a new class ‘*Belvinaviricetes*’, of a new kingdom, ‘*Abadenavirae*’, sister to *Bamfordvirae*. Within this new kingdom, *Ainoaviricetes* should be included as a sister to ‘*Belvinaviricetes’*. The closer similarity between the eukaryotic members of *Preplasmiviricota* and *Nucleocytoviricota* is supported by the conservation of the capsid maturation vUlp1 protease and structural similarities between the DJR-MCPs (Koonin et al., 2024), further justifying the unification of *Preplasmiviricota* and *Nucleocytoviricota* within *Bamfordvirae*.  **Refinement of the *Preplasmiviricota* taxonomy**  Within the remaining *Preplasmiviricota*, the ancestral form of the pPolB is found in members of the family *Adintoviridae*. Adintovirids are nearly exclusively referred to in the literature as polintons or mavericks. Thus, to maintain the continuity with the literature, we propose to rename this virus family ‘*Eupolintoviridae*’within a renamed order ‘*Amphintovirales*’. In the multidomain pPolBs of ‘eupolintovirids’, the TP domain is followed by a cysteine protease domain of the viral ovarian tumor (vOTU) deubiquilase superfamily (Fig. 2A,D), which is predicted to cleave off the TP domain from the rest of the pPolB following the initiation of DNA replication (Krupovic et al., 2024). Other eukaryotic preplasmiviricots display variations of this arrangement, which help to reconstruct the evolution of this virus assemblage (Fig. 3). In particular, in adenovirids, the TP is encoded by a separate gene, whereas the vOTU protease domain is present but inactivated. In mavirus-like maveriviricetes, the replication enzyme carries the palm domain of the pPolB as well as the TP and vOTU domains, but lacks the exonuclease domain, unequivocally indicating that this polymerase is a derived form. Many polinton-like viruses encode a replication protein containing the TP, vOTU and the polymerization Palm domain of pPolB, but the exonuclease domain is replaced by a Pif1-like superfamily 1 helicase domain, again indicating that this domain arrangement evolved from the ancestral state found in ‘eupolintovirids’ (Fig. 3).  ‘Polinton-like viruses’ represent a vast, environmentally widespread group of viruses, most of which have been described through metagenomics (Yutin et al., 2015; Bellas and Sommaruga, 2021; Bellas et al., 2023). However, none of these viruses have been classified thus far. Here we propose creating a family ‘*Phypoliviridae*’ for classification of Tetraselmis viridis virus S1 (TvV-S1), one of the few viruses in this group which have been cultivated. Given the vast diversity of these viruses, it is expected that multiple families will have to be created for their classification in the future. Thus, we propose placing ‘*Phypoliviridae*’ into a separate new order, ‘*Archintovirales*’ (Koonin et al., 2024).  As mentioned above, tectivirids and adenovirids are currently assigned to two orders (*Kalamavirales* and *Rowavirales*, respectively) within the same class, *Tectiliviricetes*. Given that adenovirids do not represent a sister group to tectivirids in any of the reported analyses, and indeed, appear to have evolved from within the diversity of ‘amphintovirals’, we propose to move family *Adenoviridae* into a separate new class, ‘*Pharingeaviricetes*’ (Koonin et al., 2024).  The fact that pPolBs of all eukaryotic preplasmiviricots, namely, *Polintoviricetes/*‘*Aquintoviricetes*’/*Maveriviricetes* /‘*Pharingeaviricetes*’, are fused to the TP and/or vOTU domains testifies to their monophyly, with the fusion taking place following their divergence from a tectivirid ancestor (Fig. 3). Thus, we propose splitting *Preplasmiviricota* into two subphyla, ‘*Polisuviricotina*’ and ‘*Prepoliviricotina*’, to include viruses of eukaryotes and prokaryotes, respectively.  To retain the connection to the widely-spread use of the term “virophage”, we propose to rename *Maverivircietes* as ‘*Virophaviricetes’.*  **Creation of a new class within *Nucleocytoviricota* for inclusion of *Yaraviridae***  Family *Yaraviridae* was created for classification of a yaravirus isolate infecting *Acanthamoeba castellanii* (de Miranda Boratto et al., 2022; Borrato et al., 2020). At the time, the placement of this family within higher-rank taxonomy was not obvious due to high divergence of the corresponding virus and lack of information on other related viruses. Recently, a large number of viruses related to yaraviruses were discovered though mining of metagenomics datasets (Yutin et al., 2024). The discovered diversity could be split into at least two monophyletic sister groups, *Yaraviridae* and an assemblage referred to as ‘*Gamadviridae*’ (Fig. 4). In the absence of coding-complete genomes in GenBank for ’*Gamadviridae*’, this family will not be officially proposed at this time. However, dramatic expansion of the yaravirus-like viruses enabled a more comprehensive comparative genomics and phylogenetic analysis of these viruses. In particular, it was found that members of the extended *Yaraviridae* encompass some of the signature genes of nucleocytoviricots, namely, virus late transcription factors 2 and 3 (VLTF2 and VLTF3, respectively). In phylogenetic trees of the conserved DJR MCPs and DNA packaging ATPases, yaravirids and ‘gamadvirids’ consistently did not show affinity to any particular branch of the *Nucleocytoviricota* (Fig. 4) and accordingly would comprise a new class. Comparison of the DJR MCP structures placed yaravirids and gamadvirids basal to the nucleocytoviricots, between the latter and preplasmiviricots(Yutin et al., 2024). Thus, we propose creating a new class, ‘*Mriyaviricetes*’, to accommodate the currently “floating” family *Yaraviridae*.  Such reorganization of virus megataxonomy would resolve all outstanding incongruences with the current scenarios of the evolution of varidnavirians. The proposed taxonomy is summarized in Figure 5.  Etymologies of all proposed taxon names are provided in the excel module. |

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| **References:** |
| Bellas CM, Sommaruga R. Polinton-like viruses are abundant in aquatic ecosystems. Microbiome. 2021; 9(1):13. doi: 10.1186/s40168-020-00956-0. PMID: 33436089  Bellas C, Hackl T, Plakolb MS, Koslová A, Fischer MG, Sommaruga R. Large-scale invasion of unicellular eukaryotic genomes by integrating DNA viruses. Proc Natl Acad Sci U S A. 2023; 120(16):e2300465120. doi: 10.1073/pnas.2300465120. PMID: 37036967  Boratto PVM, Oliveira GP, Machado TB, Andrade ACSP, Baudoin JP, Klose T, Schulz F, Azza S, Decloquement P, Chabrière E, Colson P, Levasseur A, La Scola B, Abrahão JS. Yaravirus: A novel 80-nm virus infecting Acanthamoeba castellanii. Proc Natl Acad Sci U S A. 2020; 117(28):16579-16586. doi: 10.1073/pnas.2001637117. PMID: 32601223  Koonin EV, Fischer MG, Kuhn JH, Krupovic M. The ‘polinton supergroup’ of viruses: evolution, molecular biology, and taxonomy. Microbiol Mol Biol Rev. 2024; In press.  Krupovic M, Koonin EV. Polintons: a hotbed of eukaryotic virus, transposon and plasmid evolution. Nat Rev Microbiol. 2015; 13(2):105-15. doi: 10.1038/nrmicro3389. PMID: 25534808  Krupovic M, Makarova KS, Koonin EV. Cellular homologs of the double jelly-roll major capsid proteins clarify the origins of an ancient virus kingdom. Proc Natl Acad Sci U S A. 2022; 119(5):e2120620119. doi: 10.1073/pnas.2120620119. PMID: 35078938  Krupovic M, Kuhn JH, Fischer MG, Koonin EV. Natural history of eukaryotic DNA viruses with double jelly-roll major capsid proteins. Proc Natl Acad Sci U S A. 2024; 121(23):e2405771121. doi: 10.1073/pnas.2405771121. PMID: 38805295  de Miranda Boratto PV, Oliveira GP, Abrahão JS. "Yaraviridae": a proposed new family of viruses infecting Acanthamoeba castellanii. Arch Virol. 2022; 167(2):711-715. doi: 10.1007/s00705-021-05326-1. PMID: 35000005  Redrejo-Rodríguez M, Ordóñez CD, Berjón-Otero M, Moreno-González J, Aparicio-Maldonado C, Forterre P, Salas M, Krupovic M. Primer-Independent DNA Synthesis by a Family B DNA Polymerase from Self-Replicating Mobile Genetic Elements. Cell Rep. 2017; 21(6):1574-1587. doi: 10.1016/j.celrep.2017.10.039. PMID: 29117562  Yutin N, Shevchenko S, Kapitonov V, Krupovic M, Koonin EV. A novel group of diverse Polinton-like viruses discovered by metagenome analysis. BMC Biol. 2015; 13:95. doi: 10.1186/s12915-015-0207-4. PMID: 26560305  Yutin N, Mutz P, Krupovic M, Koonin EV. Mriyaviruses: small relatives of giant viruses. mBio. 2024 Jun 4:e0103524. doi: 10.1128/mbio.01035-24. PMID: 38832788 |

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| **Tables, Figures:** |

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**Figure 1.** Relationships between cellular and viral SJR proteins. (A) The matrix and cluster dendrogram are based on the pairwise Z score comparisons calculated using DALI. Different protein families are highlighted with different background colors on the dendrogram. The color scale indicates the corresponding Z scores. The DJR proteins have been manually split and the individual N-terminal and C-terminal SJR domains were labeled as SJR1 and SJR2, respectively. (B) Correspondence analysis of the cellular and viral SJR domains calculated using DALI. The data points corresponding to the SJR domains are positioned with respect to each other according to the similarity of their structural neighborhoods. The color code is the same as in A. (C) Structural comparison of the DUF2961 trimer with the trimeric capsomers of the DJR-MCPs. Individual subunits in each trimer are colored differently. The first and second columns show ribbon representations, whereas in the third column the structures are depicted using surface rendering. PDB accession numbers are provided in the figure. The C-terminal α-helix of DUF2961 is omitted for the purpose of visualization.

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**Figure 2.** Domain architectures of the pPolB domain-containing proteins of ‘polisuviricotines’. A. Schematic domain organization of pPolBs and Tlr1-like helicases with homologous domains shown with matching colors. The locations of conserved motifs of the exonuclease and polymerization domains are indicated within the corresponding circles. The locations of the TPR1 and TPR2 subdomains are also shown. B. Structural models of representative pPolBs and Tlr1-like helicase encoded by different groups of viruses, with distinct domains colored using the same scheme as in panel A. C. Structural comparison of the terminal proteins (TPs) of Enterobacteria phage PRD1 and frog adenovirus 1 (FrAdV-1) with the N-terminal domains of pPolBs encoded by eukaryotic viruses and plasmids. Models are colored using the rainbow scheme from N-terminus (blue) to C-terminus (red). Non-conserved regions of the Enterobacteria phage PRD1 and FrAdV-1 TPs are shown in grey. D. Structural comparison of structures of OTU from humans (PDB: 4BOZ) and vOTU from an RNA virus, maize rayado fino virus (PDB: 7MIC), with the vOTU domains present in pPolBs. Models are colored using the rainbow scheme from N-terminus (blue) to C-terminus (red).

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**Figure 3.** Evolutionary scenario for ‘polisuviricotines’ and derived mobile genetic elements. A scenario for the evolution of eukaryotic preplasmiviricots and related elements from a bacterial tectivirid ancestor is shown. Hexagons represent icosahedral capsids built from double jelly-roll fold major capsid proteins (DJR-MCPs). The grey hexagon indicates replacement of the DJR-MCP with an unrelated capsid protein in bidnavirids. Black and grey arrows indicate evolution and horizontal gene transfer (HGT), respectively. Asterisks indicate inactivation of vOTU domains. AEP, archaeo-eukaryotic primase-polymerase; Exo, exonuclease; PLV, polinton-like virus; PolA, family A DNA polymerase; pPolB, protein-primed B-family DNA polymerase; RVE-INT, retrovirid-like integrase; S1H, superfamily 1 helicase; S3H, superfamily 3 helicase; TP, terminal protein; TvV-S1, Tetraselmis viridis virus S1; (v)Ulp1, (viral) Ulp1-like cysteine protease; Y-Int, tyrosine superfamily integrase.

A diagram of a tree

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**Figure 4.** Phylogenetic trees of proteins conserved in mriyaviruses and the rest of the members of *Nucleocytoviricota*. (A) Major capsid protein (MCP); (B) DNA packaging ATPase; and (C) virus late transcription factor 3 (VLTF3). A phylogenetic tree was constructed from this alignment using Fasttree with a WAG evolutionary model and Gamma-distributed site rates. Phylogenetic trees of MCP, packaging ATPase (ATPase), and viral late transcription factor 3 (VLTF3) were built using IQ-TREE, with the following models chosen according to BIC by the built-in model finder: Q.pfam + F + R4 for MCP, Q.pfam + F + R6 for ATPase, and VT + F + R5 for VLTF3. The IQ-Tree bootstrap values are indicated for the key branches.

A screen shot of a computer

Description automatically generated

**Figure 5.** Proposed realm reorganization.