This Word module should be used for all taxonomic proposals.

Please complete **Part 1** and:

either **Part 3** for proposals to create new taxa or change existing taxa

or **Part 2** for proposals of a general nature.

Submit the completed Word module, together with the accompanying Excel module named in Part 3, to the appropriate ICTV Subcommittee Chair.

The Word module explains and justifies your proposal. The Excel module is a critical document that will be used to implement the proposed taxonomic changes once they are approved and ratified. If proposals presented in the Word module are not presented accurately in the Excel module, the taxonomic changes cannot proceed.

For guidance, see the notes written in blue, below, and the Help Notes in file Taxonomic\_Proposals\_Help\_2019.

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

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| **Code assigned:** | ***2019.003G*** |  |
| **Short title:** Create a megataxonomic framework, filling all principal taxonomic ranks, for DNA viruses encoding vertical jelly roll-type major capsid proteins |
|  |
| **Author(s) and email address(es):**  |
| List authors in a single line *Archives of Virology* citation format (e.g. Smith AB, Huang C-L, Santos, F) | Provide email address for each author in a single line separated by semi-colons |
| Koonin EV, Dolja VV, Krupovic M, Varsani A, Wolf YI, Yutin N, Zerbini M, Kuhn JH | koonin@ncbi.nlm.nih.gov; doljav@science.oregonstate.edu; mart.krupovic@pasteur.fr; Arvind.Varsani@asu.edu; wolf@ncbi.nlm.nih.gov; yutin@ncbi.nlm.nih.gov; zerbini@ufv.br; kuhnjens@mail.nih.gov  |
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| **List the ICTV study group(s) that have seen this proposal:** |
| A list of study groups and contacts is provided at <http://www.ictvonline.org/subcommittees.asp> . If in doubt, contact the appropriate subcommittee chair (there are six virus subcommittees: animal DNA and retroviruses, animal ssRNA-, animal ssRNA+, fungal and protist, plant, bacterial and archaeal) | **ICTV *Adenoviridae*, *Ascoviridae*, *Asfarviridae*, *Corticoviridae*, *Iridoviridae*, *Marseilleviridae*, *Mimiviridae*, *Phycodnaviridae*, *Poxviridae*, and *Tectiviridae* Study Group Chairs; ICTV Bacterial and Archaeal Viruses Subcommittee; ICTV Animal dsRNA and ssRNA- Viruses Subcommittee Chair; ICTV Animal DNA Viruses and Retroviruses Subcommittee Chair; ICTV Plant Viruses Subcommittee Chair; ICTV Fungal and Protist Viruses Subcommittee Chair****This is a direct submission to the entire ICTV Executive Committee** |
| **ICTV Study Group/Author comments (if any) and response of the proposer:** |
| Here we propose a megataxonomic framework for a subset of DNA viruses by assigning ICTV-ratified taxa (i.e., species, genera, subfamilies, and families) to available, but presently unfilled major megataxonomic ranks (orders, classes, phyla, and kingdoms). The goal of this proposal is to provide taxonomic “buckets” or “place holders” that enable ICTV Study Groups to accommodate the close-to-exponentially increasing number of novel viruses that are related to, but distinct from, viruses that constitute the already established taxa. The awareness of these novel viruses often goes hand-in-hand with the realization that current orders might have to be promoted to classes (e.g., “megavirus group”) or that entire family structures need to be re-evaluated. We surmise that the absence of established higher taxa and the absence of ICTV Study Groups for such taxa may have had an adverse effect, leading to large groups of classifiable viruses not becoming classified. Vice versa, placing currently established taxa together into higher-rank taxa may initiate long-overdue, likely intense, discussions between currently non-interacting ICTV Study Groups to examine higher-rank evolutionary relationships of the viruses they are engaged with. The megataxonomy outlined in this proposal is to be seen only as an initial step and we fully expect this framework to change substantially over time.We:* aim to bring virus taxonomy into better accordance with other biological taxonomies, which require novel organisms to be classified into all available principle/primary ranks even if this means that certain higher-ranked taxa only include single lower-ranked taxa. For instance, in animal taxonomy, the unranked supergroup Hemimastigophora includes a single class Hemimastigidea, which includes a single order Hemimastigida, which includes a single family Spironem(atelli)idae (which includes 4 genera). Likewise, in prokaryotic taxonomy, the bacterial species *Elusimicrobium minutum* is the only included species in genus *Elusimicrobium*, which is the only genus in family *Elusimicrobiaceae*, which is the only family in order *Elusimicrobiales*—that order is the only order in class *Elusimicrobia*, which is the only class in phylum *Elusimicrobia*. Obviously, taxon demarcation criteria cannot be established for single taxon-including higher-ranked taxa and hence their definitions are identical to those of the higher-ranked taxa for the time being, i.e., until the discovery of novel organisms requires the creation of sister taxa. However, filling all principle ranks provides a sense of “scaling”, i.e. a current assessment of how distant a particular organism is from other classified taxa; this “scaling” argument was used successfully previously in TaxoProps establishing the availability of taxonomic ranks above order and the establishment realm *Riboviria*;
* deliberately propose the creation of higher-ranked taxa that currently include only single lower-ranked taxa, either because we are aware from the literature that an existing lower-rank taxon will have to be promoted to a higher rank in the near future due to overbearing virus diversity (e.g., “megavirus group”), or because we are aware from the literature of large virus groups for which higher-rank taxa will have to be established shortly; we hope that the created higher-ranked taxa will provide an impetus for the community to classify already known highly divergent virus groups;
* deliberately did not fill any secondary (sub-)ranks as the filling of such ranks is not mandatory in other biological taxonomies;
* deliberately focus this proposal only on official taxa (rather than, for instance, proposing novel species that could become the founding members of “obvious” novel higher-rank taxa we are certain will need to be established) to keep this proposal relatively simple; and
* emphasize that, although we posit that focusing on a single protein fold is initially sufficient for creation of the dsDNA virus megataxonomy outlined here (from the highest rank, realm, down to approximately class/order), such a focus must be seen as a rough guide for lower-rank taxonomy, so that other methods (e.g., sequence-based methods such as GRAViTy, pairwise genome sequence comparisons, phylogenies of individual ORFs or proteins; structural comparisons of encoded proteins or virions; phenotypic virus characteristics) will have to be used to resolve lower-rank relationships and likely to refine higher-rank relationships.
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|  |
| Date first submitted to ICTV: | June 19, 2019 |
| Date of this revision (if different to above): | October 18, 2019 |

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| **ICTV-EC comments and response of the proposer:** |
| Per the minutes of the last ICTV Executive Committee meeting (EC51, July 15–17, 2019, Berlin, Germany), the EC voted for minor revisions of this proposal (Uc) with 12/19 votes in favor. The EC asked for the following steps to be taken prior to submission of this revision:1. Consult all affected Study Group once again for feedback

Response: all relevant Study Group Chairs were contacted for a second time and asked to provide input and criticisms. None of the Study Groups disagreed with the overall taxonomic proposal, i.e., the proposed relationship between officially established taxa. Concerns were voiced about certain proposed taxon names and the Study Groups’ suggestion were mostly followed and names were changed accordingly for this revision.1. Provide any feedback from Study Groups to the ICTV President

Response: all relevant Study Group responses (and all TaxoProp author rebuttals or explanations) were forwarded to the ICTV President and the ICTV Executive Committee per email.1. Regarding proposed taxon names using people’s names, provide permissions from these people (if alive) to use their names to the ICTV President and the ICTV Proposals Secretary

Response: all relevant permissions were forwarded to the ICTV President, the ICTV Proposal Secretary, and the ICTV Executive Committee per email. |

**Part 3:** **PROPOSED TAXONOMY**

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| **Name of accompanying Excel module:** 2019.003G.A.v1.Varidnaviria.xlsx |

**INTRODUCTION**

Recent advances of comparative genomics and metagenomics uncover a close-to-exponentially increasing number of diverse viruses. These discoveries not only vastly improve our understanding of the evolutionary relationships within the virosphere, but also emphasize that the existing taxonomic framework is inadequate to depict the relationships within the virosphere. The currently available dataset of virus genome sequences and increasingly sophisticated methods for analysis beyond “simple” phylogenies (e.g., gene network analysis, iterative and self-optimizing sequence alignments) enable us now to roughly outline the global organization of the virus world in its entirety, including key evolutionary events that resulted in the emergence of major virus clades.

Depicting the evolutionary relationships among viruses necessarily depends on the identification of hallmark genes/proteins that connect them. In contrast to cellular organisms, such hallmark genes are not universally shared among all viruses [[9](#_ENREF_9)] and it is therefore currently presumed that viruses have several distinct points of origin, i.e., that they cannot be united under a single highest taxon rank on evolutionary grounds. Nevertheless, extensive analyses of the evolution of large groups of viruses, rather than all of them, have proved productive. The primary approach taken in such studies is the phylogenetic analysis of genes that are conserved across those groups, known as Virus Hallmark Genes (VHGs), which are responsible for the key functions in virus replication and virion morphogenesis [[9](#_ENREF_9)]. The most widely spread VHGs are:

* RNA-directed RNA polymerases (RdRps);
* RNA-directed DNA polymerases/reverse transcriptases (RTs) that are homologous to RdRps;
* superfamily 3 helicases (S3Hs);
* single jelly-roll major capsid proteins (SJR-MCPs);
* double jelly-roll major capsid proteins (DJR-MCPs); and
* rolling-circle replication initiation endonucleases (RCREs) [[9](#_ENREF_9), [11](#_ENREF_11), [12](#_ENREF_12)].

Using these VHGs, megataxonomic scaffolds can be established that are further informed, if necessary, by dissection of bipartite gene-genome networks of viruses into distinct modules [[4-6](#_ENREF_4), [10](#_ENREF_10), [21](#_ENREF_21)]. These analyses indicate that a substantial majority of currently classified viruses can be assigned to one of four, likely, evolutionarily independent virus realms. Because the International Committee on Taxonomy of Viruses (ICTV) has recently formally approved creation of taxa above the rank of order, the door is now open to formalize the megataxonomic scaffolds that resulted from VHG analyses within the official ICTV-supported taxonomy.

Here we propose a megataxonomic structure for one of these groups: DNA viruses that encode vertical jelly roll major capsid proteins.

**MEGATAXONOMY OF VERTICAL JELLY ROLL MAJOR CAPSID PROTEIN DNA VIRUSES**

The double jelly roll (DJR) major capsid protein (MCP) supermodule of DNA viruses includes numerous groups of viruses that produce mostly tailless icosahedral virions infecting prokaryotes and eukaryotes [[2](#_ENREF_2)]. Most of these viruses have a single gene encoding a DJR-MCP [[1](#_ENREF_1)] but one family has two genes encoding two types of MCPs [[22](#_ENREF_22)]. In both cases, the icosahedral capsid lattice is made of vertical jelly rolls (unrelated to HK97-MCPs) that typically form pseudo-hexameric or hexameric capsomers. In addition to the signature DJR-MCPs, the majority of these viruses also encode additional single jelly roll minor capsid proteins (e.g., penton proteins) and genome packaging ATPases of the FtsK-HerA superfamily [[23](#_ENREF_23)]. Apart from this morphogenetic gene triad, most of the viruses in this supermodule encode DNA polymerases and often additional components of the replication apparatus, such as superfamily 3 helicases (S3Hs) [[9](#_ENREF_9), [12](#_ENREF_12)], or replication initiation proteins (*Corticoviridae*) [[18](#_ENREF_18)]. Viruses in the family *Sphaerolipoviridae* lack recognizable genes encoding DNA polymerase or replication machinery components. These viruses encode two vertical single jelly roll MCPs and a penton protein, with the capsid lattice made of vertical single jelly roll MCPs structurally resembling the DJR-MCP-based capsid lattice of, for instance, phage PRD1, suggesting that a gene fusion event gave rise to vertical DJR-MCPs [[7](#_ENREF_7)]).

The evolutionary conservation of the three genes of the morphogenetic module in the DJR-MCP supermodule, to the exclusion of all other viruses, justifies the establishment of a realm (proposed *Varidnaviria*). This realm includes the currently established family *Sphaerolipoviridae* (proposed kingdom *Helvetiavirae*), and families *Corticoviridae*, *Tectiviridae*, and *Turriviridae* (prokaryotic viruses), *Lavidaviridae* (virophages), *Adenoviridae* (vertebrate viruses that, in addition to the DJR-MCPs, minor capsid proteins and packaging ATPases, also acquired another gene encoding a protein involved in morphogenesis, a distinct protease most likely derived from a deubiquitinylating enzyme [[12](#_ENREF_12)]), and nucleocytoplasmic large DNA viruses (NCLDVs), a vast assemblage of several families of eukaryotic viruses with large or “giant” genomes (up to 2.5 Mb) that share a larger suit of conserved genes involved in morphogenesis as well as genome replication and expression [[11-13](#_ENREF_11)]. All these virus families are proposed to compose the kingdom *Bamfordvirae*.

In addition, new families of DJR-MCP viruses are being discovered by culture-dependent approaches, metagenomics and single-cell genomics, revealing an enormous diversity: “*Autolykiviridae*” [[8](#_ENREF_8), [24](#_ENREF_24)], proposed *Finnlakeviridae* (the only single-stranded DNA viruses in this proposed realm thus far) [[14](#_ENREF_14)], polintons (“polintoviruses”), which are virus-like self-synthesizing transposons, and diverse polinton-like viruses and virophages [[10](#_ENREF_10), [12](#_ENREF_12)]. Notably, tectivirid-like and polinton-like viruses also gave rise to two groups of capsid-less elements, mitochondrial and cytoplasmic linear plasmids found in fungi, plants, and some protists [[12](#_ENREF_12)]. All these viruses will soon have to be accommodated in the megataxonomy. This proposal is to be considered as an operational move to formalize an obvious relationship between the mentioned DNA viruses based on common VHGs.

**Taxon demarcation criteria:**

The International Code of Virus Classification and Nomenclature (ICVCN) is currently ambiguous regarding the need for taxon demarcation criteria at higher ranks. Three Rules appear to be applicable (emphasis in italics is ours):

“3.5 Taxa will be established only when representative member viruses are sufficiently well characterized and described in the published literature so as to allow them to be identified unambiguously *and the taxon to be distinguished from other similar taxa*”;

“3.22 Every individual virus is a physical entity and treated as belonging to a number of taxa of hierarchical ranks, *some of which may remain undefined*”;

and

“3.24 The classification of a virus at the species and genus ranks is mandatory. *Classification may also encompass any further number of taxa at higher hierarchical ranks*”

Because our proposal only encompasses already established taxa, all viruses affected by our proposal have been “sufficiently well characterized” as otherwise they would not have been classified into these established taxa in the first place. Furthermore, Rule 3.22 permits establishing ranks that for the moment remain undefined; and Rule 3.24 indicates no restriction of ranks to be established.

Nevertheless, for the time being, we suggest the following provisional taxon demarcation criteria while being aware that these may have to be revisited whenever new members of the realm are being proposed:

1. *Varidnaviria*: a virus is a member of this realm if it has a DNA genome encoding a major capsid protein containing the vertical jelly-roll fold and forming pseudohexameric capsomers. Note that viruses that can be convincingly demonstrated to have evolved from members of *Varidnaviria*, even though they lack (apparently have lost) the major capsid protein are also included in this taxon
2. *Bamfordvirae*: a *Varidnaviria* member is a member of the included kingdom *Bamfordvirae* if it encodes a double jelly-roll major capsid protein (DJR-MCP)
3. *Helvetiavirae*: a *Varidnaviria* member is a member of the included kingdom *Helvetiavirae* if it encodes a vertical single jelly-roll fold major capsid protein.

If a principle rank taxon includes only a single lower-ranked taxon, then the definition of the lower-ranked taxon is, for now, identical to the definition of the higher-ranked taxon.

Truly useful taxon demarcation criteria will have to be established in the future, likely by incorporating yet-unclassified virus groups into the realm.

**Etymology of proposed taxa:**

* *Varidnaviria*; a portmanteau of various DNA viruses; and the suffix -*viria* for realm taxa
* *Helvetiavirae*; from Latin helvetia meaning Swiss, a reference to the Swiss roles (an alternative name for jelly roll and hence a reference to the jelly roll fold of the capsid proteins of viruses in this taxon); and the suffix -*virae* for kingdom taxa
* *Dividoviricota*; from Esperanto divido, meaning division—a reference to the “split” double jelly roll (two vertical single jelly roll) major capsid protein encoded by viruses in this taxon; and the suffix -*viricota* for phylum taxa
* *Laserviricetes*; a portmanteau of Serpentine Lake, Rottnest Island, Western Australia, Australia, where the first virus of this taxon, “archaeal virus SH1” was discovered [[20](#_ENREF_20)]; and the suffix -*viricetes* for class taxa
* *Halopanivirales*; a portmanteau of *Haloarcula hispanica*, the host of founding member “archaeal virus SH1” of this clade [[20](#_ENREF_20)]; and the suffix -*virales* for order taxa
* *Bamfordvirae*; after Dennis Bamford who first promoted the evolutionary unity of all DJR-MCP viruses [[3](#_ENREF_3), [4](#_ENREF_4)]; and the suffix -*virae* for kingdom taxa
* *Preplasmiviricota*; a portmanteau of precursor of certain plasmids; and the suffix -*viricota* for phylum taxa
* *Tectiliviricetes*; from tectivirid-like; and the suffix -*viricetes* for class taxa
* *Kalamavirales*; after Kalamazoo, USA, where Pseudomonas phage PRD1 (*Tectiviridae*: *Alphatectivirus*) was first isolated [[19](#_ENREF_19)]; and the suffix -*virales* for order taxa
* *Rowavirales*; after Wallace P. Rowe†, one of the co-discoverers of adenovirids in 1953 [[21](#_ENREF_21)]; and the suffix -*virales* for order taxa
* *Vinavirales*; named after Viña del Mar, Chile, where “phage PM2” was first isolated [[6](#_ENREF_6)]; and the suffix -*virales* for order taxa
* *Belfryvirales*; from belfry, a tower (turret) that contains something (a bell); and the suffix -*virales* for order taxa
* *Maveriviricetes*; from Maverick, a reference to maviruses that shares many features with the large, virus-like transposons of the Maverick/Polinton superfamily; and the suffix -*viricetes* for class taxa
* *Priklausovirales*; from Lithuanian priklausomas, meaning dependent, a tongue-in-cheek reference to the included family *Lavidaviridae* (large virus dependent associated); and the suffix -*virales* for order taxa
* *Nucleocytoviricota*; a portmanteau of nucleocytoplasmic large DNA viruses (NCLDVs), the current unofficial name for this group of viruses; and the suffix -*viricota* for phylum taxa
* *Megaviricetes*; from Greek μέγας [mégas], meaning large, a reference to the extremely long genomes of viruses in this taxon, “*Megavirales*” [[5](#_ENREF_5)], a previously suggested name for this group of viruses; and the suffix -*viricetes* for class taxa
* *Imitervirales*; from French imiter, meaning to mimic, a reference to mimiviruses (microbe-imitating); and the suffix -*virales* for order taxa
* *Algavirales*; after alga; and the suffix -*virales* for order taxa
* *Pimascovirales*; a portmanteau of pitho-, irido-, marseille-, and ascoviruses; and the suffix -*virales* for order taxa
* *Pokkesviricetes*; from Middle English pokkes, meaning pox; and the suffix -*viricetes* for class taxa
* *Asfuvirales*; a portmanteau of *Asfarviridae* and “faustovirus” (a likely member of the order together with “pacmanviruses” and “kaumoebaviruses”); and the suffix -*virales* for order taxa
* *Chitovirales*; to honor the proposed name for a higher-rank taxon for poxviruses proposed by Lwoff and Tournier in 1966 (“Chitovirales”; from Greek χιτών, [khitōn], a specific garment and a reference to the morphological structure of poxviruses) for the “LHT system” [[15-17](#_ENREF_15)] ; and the suffix -*virales* for order taxa

One of the proposed taxon names, *Bamfordvirae,* is derived from the name of a living person. The permission of this person to use his name has been forwarded to the ICTV Executive Committee.

**List of official (ss and ds) DNA virus taxa that we propose remain unassigned to any realm, including the one proposed here, until further data become available:**

* *Anelloviridae*
* *Ampullaviridae*
* *Baculoviridae*
* *Bicaudaviridae*
* *Clavaviridae*
* *Dinodnavirus*
* *Finnlakeviridae* [proposed]
* *Fuselloviridae*
* *Globuloviridae*
* *Guttaviridae*
* *Halspiviridae* [proposed] including *Salterprovirus*
* *Hytrosaviridae*
* *Ligamenvirales*
* *Nimaviridae*
* *Nudiviridae*
* *Ovaliviridae*
* *Plasmaviridae*
* *Polydnaviridae*
* *Portogloboviridae*
* *Rhizidiovirus*
* *Spiraviridae*
* *Thaspiviridae* [proposed]
* *Tristromaviridae*

| **References:** |
| --- |
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