

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

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| **Code assigned:** | **2021.005S** |  |
| **Short title:** Create 47 new taxa in the order, ranging from subfamiliesto species (*Nidovirales*) | | |
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**List the ICTV Study Group(s) that have seen this proposal**

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| *Mesoniviridae* Study Group  Also, the submitters include chair and a member of the *Roniviridae* Study Group and Chairs/members of several SGs concerned with different subsets of nidoviruses that operated during prior ICTV cycles |

**ICTV study group comments and response of proposer**

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**Authority to use the name of a living person**

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| **Is any taxon name used here derived from that of a living person (Y/N)** | **N** |

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| **Taxon name** | **Person from whom the name is derived** | **Permission attached (Y/N)** |
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**Submission dates**

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| Date first submitted to SC Chair | June 4, 2021 |
| Date of this revision (if different to above) | September 14, 2021 |

**ICTV-EC comments and response of the proposer**

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| **Peter Simmonds for the ICTV-EC on 16 July 2021 13:26**:  Many thanks for submitting proposals for new assignments within the *Nidovirales*. This was reviewed at the ICTV Executive Committee meeting yesterday and it was given a designation of Ac. This means that it is accepted pending minor changes as listed below:     1. It was appreciated that efforts had been made to assign species names using the binomial format. Although the final rules for forming species epithets are yet to be fully formulated, many of those provided in the taxonomy proposals are most likely to be compliant. One exception is *Alphamesonivirus 11*, although at this stage it may be better to follow the existing pattern of names until a later decision about renaming this  group is made. It is difficult to know whether the epithets *WA1087, BT020* *etc.*for alphacoronaviruses will be allowable and this will need to be revisited by the Study Group at a later date. For now though, the proposed names can be assigned as proposed. 2. There is a formal check done of the spreadsheet and I attach the errors detected. Most of these are very trivial abut do let me know if any help is needed in correcting these.   **Authors Response**:   1. The species names were retained; 2. The errors in the speadsheet file were corrected to the best of our knowledge; the actions taken for each error are detailed in a separate excel file; 3. The authors list of this TP was updated with three new authors, M. Brinton, R. de Groot, and P. Walker. The TP text has been slightly improved. |

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

**Name of accompanying Excel module**

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| 2021.005S.R.Nidovirales.xlsx |

**Abstract**

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| We propose to create 47 new taxa (ranging from species to subfamily) in the order *Nidovirales.* This proposal was prepared using the computational framework of DEmARC as detailed in the nidovirus proposals filed in 2017-2019 and approved by ICTV. We employed comparative genomics of 2224 sequences that included 21 recently sequenced viruses infecting either vertebrates (CoTo3 dataset of 2153) or invertebrates (Inv dataset of 71). We demarcated 8 and 7 species of vertebrate nidoviruses in the families *Coronaviridae* and *Tobaniviridae*, respectively; a single species was created in the family *Cremegaviridae*. Nine subgenera, five genera and two subfamilies were demarcated as well. Five new species were assigned to two established families of invertebrate nidoviruses, one to a new genus and subgenus of the *Roniviridae*, and four to the subfamily *Hexponivirinae* and the newly created subfamilies *Menanivirinae* and *Metotonivirinae* in the family *Mesoniviridae*. Also, two pairs of subfamilies in the families *Medioniviridae* and *Euroniviridae* were merged. |

**Text of proposal**

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| |  | | --- | | We were concerned with the taxonomical classification of nidoviruses sequenced over the last two years. Genome sequences were assigned to nidovirus families using either the Haygens tool (<http://veb.lumc.nl/HAYGENS/>) or by the authors who described the respective viruses (see **Table** **1** and Reference list). For this proposal, viruses of the family *Arteriviridae* were excluded from the analysis. We also retained only 16 SARS-CoV-2 sequences, and removed identical or low quality sequences using an in-house quality control system. In total, we analyzed 2224 sequences that included 21 recently sequenced viruses infecting either vertebrates (CoTo3 dataset of 2153) or invertebrates (Inv dataset of 71) that were subject of this proposal. The total number of new sequences, considered in this proposal, exceeded the 21 listed in **Table 1**, but all others were classified into either the already established or newly recognized species. The selected genome sequences of the two datasets represented also all established and pending taxa.  Assignments to nidoviruses were verified by alignments and phylogenetic analyses of five replicative protein domains characteristic of nidoviruses (synteny of molecular markers), namely the 3CLpro, 3C-like protease; NiRAN, nidovirus RdRp-associated nucleotidyltransferase; RdRp, RNA-directed RNA polymerase; ZBD, Zn-binding domain; and HEL1 superfamily 1 helicase (**Table 2**). They are highlighted in genomic maps of nine viruses representing four new subfamilies and four genera (**Figs. 1 and 2**). The MSA of these conserved domains were generated and purged (with the total size of 1258 aa for the CoTo3 dataset and 1361 aa for the Inv dataset), and used then in phylogenetic and DEmARC analyses [6-8]. Representatives of each established and new species were then selected for ML phylogenetic analyses of vertebrate and invertebrate nidoviruses, respectively, to illustrate the relationships. Due to the large size of the tree of the vertebrate nidoviruses, it was split into two trees: one encompassing the *Coronaviridae* (**Fig. 3**) and another encompassing the *Tobaniviridae* together with the suborders *Nanidovirineae* and *Arnidovirineae,* the latterexcluding the family *Arteriviridae* (**Fig. 4**). Each of these two large groups is the sister to each other and thus serves as an outgroup. A tree for invertebrate nidoviruses along with taxa at five ranks are shown in **Fig. 5**. The DEmARC analysis of invertebrate nidoviruses also suggested a merge of two pairs of existing subfamilies (**Fig. 6**). They were demarcated in 2017 in an analysis that included the (smaller number of) invertebrate nidoviruses available at the time and was assisted by consideration of distantly related vertebrate viruses. We propose to accept this merge.  ***Demarcation criteria***. We used either a range or a particular value of patristic pairwise distances (PPD) that were calculated using FastTree 2.1.4 SSE3 ML phylogeny based on an MSA of five concatenated protein domains (3CLpro, NiRAN, RdRp, ZBD and HEL1) as demarcation criterion for taxa at each of the following five ranks: family, subfamily, genus, subgenus, and species (**Tables 3** and **4; Figs. 7-9**). Commonly, they are selected as local minima in the CC distribution (smallest CC values in a range of PPD values), corresponding to the CC=0 or close to it (see below).  Briefly, all local minima of the CC profile were considered as candidate thresholds for demarcating ranks because they satisfied two requirements, (i) the clusters formed under these thresholds were monophyletic in the ML tree of the respective nidovirus subset, and (ii) all intra- and inter-cluster PPDs were (predominantly) smaller and (predominantly) larger, respectively, than the respective threshold. If *all* intra- and inter-cluster PPDs, respectively, were smaller and larger than the respective threshold, such clustering has a cost of zero (CC=0), according to DEmARC. We have also measured persistence of a clustering as a range of PPD values over which this clustering was supported with CC=0. The respective “threshold PPD ranges” were considered best candidates for demarcation. For this particular proposal, we tried to preserve the already established taxa by favoring respective thresholds, even if they deviated slightly from minima, unless there were substantial reasons for revising prior assignments.  That was the case with the subfamily rank for invertebrate nidoviruses. This rank was demarcated in 2017 in an analysis that also involved vertebrate nidoviruses, which were included to compensate for the paucity of available invertebrate nidovirus sampling. Because the sampling at this level of divergence increased substantially over the past few years, we now revisited this assignment by analyzing exclusively invertebrate nidoviruses (Inv dataset). The demarcation at the subfamily rank was considered along with the thresholds used at the lower genus and upper family ranks. Based on the analysis of CC profile minima, a new threshold for the subfamily rank was established (**Table 4**). Under this threshold, two pairs of established sister subfamilies merged: the *Tunicanivirinae* with the *Medionivirinae* in the family *Medioniviridae*, and the *Crustonivirinae* with the *Ceronivirinae* in the family *Euroniviridae (***Fig. 6***)*. This new threshold defined also two new subfamilies in the family *Mesoniviridae*: *Metotonivirinae* and *Menanivirinae*, respectively, which were populated with new viruses classified in this proposal (**Fig. 5**). It was also important for our decision on the rank assignment of the largest taxon prototyped by the newly classified MrGV: it was at the genus rank and the respective taxon was named *Nimenivirus*.  Note that a relatively small fraction of the established and proposed species of nidoviruses include two or more sequences (**Figs. 7-9**). It indicates that the current virus sampling, especially outside the *Coronaviridae*, remains low and its increase may prompt a revision of some of the current assignments in the future.  ***Origin of names***. Names of new taxa were designated according to the practice of the respective study groups, unless mentioned otherwise, and to satisfy the recently introduced binomial species nomenclature. These taxa names, especially those of species, may be revised after the respective study groups will have decided on a more permanent framework of taxa nomenclature that will also be applicable to the already established taxa. This revision may be time consuming due to extensive consultations involved. Although we realize that some of the proposed names may be short lived, we believe that they will serve the purpose to provide an up-to-date taxonomy of nidoviruses.  ***Coronaviridae,* *Tobaniviridae* and *Cremagaviridae***: Most names allude to words used to describe prototypic viruses. For the *Coronaviridae* species, we used virus isolate labels as the second word in the species name, following the practice used for most of the previously established species. The second word of the *Tobaniviridae* species was designed to ensure an easy pronunciation.  ***Mesoniviridae***: The name of the new *Alphamesonivirus 11* satisfies the established species nomenclature of the respective genus and the ICTV rules. Names of taxa in the two new subfamilies allude to the family and order names by including “me” and “ni”, and are easy to pronounce.  ***Roniviridae****:* Names of species and subgenus taxa in the single new genus allude to the names of the prototype virus and the order by including “ma” and “ni”, and are easy to pronounce. The *Roniviridae* SG is yet to consider these designations.  **Acknowledgements**  We thank Anastasia A. Gulyaeva for scripts used to prepare this proposal, Dmitry Penzar for DEmARC software advancement, and Igor Sidorov for help with the Viralis database. | |

**Supporting evidence**

**Table 1.** Recently sequenced viruses that prototype 47 new nidovirus taxa, including 21 species

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **GenBank ID** | **Virus acronym** | **Species** | **Genus** | **Ref\*** |
| MH447987.1 | TSHSV-NX1 | *Sicregavirus nixi* | *Sicregavirus* | [10] |
| MN161572.1 | SerTV-25 | *Infratovirus latu* | *Infratovirus* | [2] |
| MT997160.1 | VCSTV-A | *Lyctovirus alpa* | *Lyctovirus* | [3] |
| MT997159.1 | VCSTV-B | *Vebetovirus paba* | *Vebetovirus* | [3] |
| MK182569.1 | MoVNV-BH171/14-7 | *Pregotovirus heba* | *Pregotovirus* | [1] |
| MN161566.1 | SerTV-K48 | *Septovirus foka* | *Septovirus* | [2] |
| MN161561.1 | SerTV-C18 | *Sertovirus cona* | *Sertovirus* | [2] |
| MW561977.1 | BaToV-Hrufipes2018 | *Torovirus banli* | *Torovirus* | unp |
| MK472067.1 | ACoV-WA1087 | *Alphacoronavirus WA1087* | *Alphacoronavirus* | unp |
| MG923574.2 | BtCoV/020\_16/M.dau/FIN/2016 | *Alphacoronavirus BT020* | *Alphacoronavirus* | unp |
| MN611525.1 | HipPBCoV-CHB25 | *Alphacoronavirus CHB25* | *Alphacoronavirus* | [9] |
| MK472070.1 | ACoV-WA3607 | *Alphacoronavirus WA3607* | *Alphacoronavirus* | unp |
| MK472068.1 | ACoV-WA2028 | *Alphacoronavirus WA2028* | *Alphacoronavirus* | unp |
| MK720944.1 | TyBCoV-HKU33 | *Alphacoronavirus HKU33* | *Alphacoronavirus* | [5] |
| MT663548.1 | BtCoV-AMA-L-F | *Alphacoronavirus AMALF* | *Alphacoronavirus* | unp |
| MK611985.1 | PsNV | *Alphapironavirus bona* | *Alphapironavirus* | [11] |
| KY369959.1 | YiV-HB-MLV | *Alphamesonivirus 11* | *Alphamesonivirus* | unp |
| MN714663.1 | FOaMV-1 | *Tofonivirus foami* | *Tofonivirus* | upb |
| MN961271.1 | ACMV | *Tocinivirus aphisi* | *Tocinivirus* | unp |
| MN714662.1 | InsMV-1 | *Insemevirus tami* | *Nasenivirus* | unp |
| MT907511.1 | MrGV | *Nimanivirus lahi* | *Nimanivirus* | [4] |

\*unp, unpublished

Proposed species and genera are colored in green

**Table 2.** Genomic coordinates of five conserved protein domains in the most divergent representatives of new nidoviruses

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Virus** | **Genbank ID** | **3CLpro** | **NiRAN** | **RdRp** | **ZBD** | **HEL1** |
| TSHSV-NX1 | MH447987.1 | 5141..5635 | 6973..7365 | 7654..8793 | 8899..9090 | 9448..10203 |
| PsNV | MK611985.1 | 9087..9647 | 13196..13912 | 14435..15748 | 15890..16123 | 16712..17641 |
| InsMV-1 | MN714662.1 | 4590..5153 | 8183..8797 | 9698..11077 | 11468..11680 | 12284..13261 |
| FOaMV-1 | MN714663.1 | 3555..4103 | 6860..7462 | 8387..9778 | 9959..10180 | 10820..11827 |
| ACMV | MN961271.1 | 4722..5315 | 8297..8938 | 9866..11266 | 11444..11671 | 12347..13411 |
| MrGV | MT907511.1 | 11458..12033 | 15144..15779 | 16590..17939 | 19305..19550 | 20133..21074 |

**Table 3**: Taxa increase at five ranks of the order *Nidovirales* for vertebrate viruses since 2019\*

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Rank** | **Taxa #** | | **Threshold** | | **Support** |
| **Year 2019** | **Year 2021** | **PPD1** | **PUD2** | **CC3** |
| **Family** | 7 | 7 | 2.580-3.468 | 0.606-0.681 | 0 |
| **Subfamily** | 12 | 14 | 1.472-1.757 | 0.468-0.510 | 0.005025 |
| **Genus** | 20 | 25 | 0.873-0.909 | 0.351-0.360 | 0.007678 |
| **Subgenus** | 45 | 54 | 0.200-0.221 | 0.132-0.142 | 0.005541 |
| **Species** | 70 | 86 | 0.095-0.095 | 0.075-0.075 | 0.010339 |

\*CoTo3 dataset including 2153 sequences

**1**The demarcation threshold is depicted as a range of PPD values for which the number of clusters (taxa) remained constant. PPD values account for repeated replacements of amino acid residues and may exceed 1.

**2**The demarcation threshold is depicted as a range of PUD values, deduced from PPD values for which the number of clusters (taxa) remained constant. PUD values were calculated as the % of different residues in the compared proteins.

**3**CC value of the respective PPD threshold. It was selected for each rank to preserve the already established taxa at the respective rank. For the family and subfamily ranks, the depicted CC corresponds also to local minima of the CC distribution indicating that these selections are also best possible. For the species, subgenus and genus ranks, the selected CC are in the vicinity of local minima. If those had been selected, one-two established taxa would have been revised at each of these ranks.

**Table 4**: Taxa increase at five ranks of the order *Nidovirales* for invertebrate viruses since 2019\*

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Rank** | **Taxa #** | | **Threshold** | | | **Support** |
| **Year 2019** | **Year 2021** | | **PPD** | **PUD** | **CC1** |
| **Family** | 6 | 6 | | 2.546-3.364 | 0.681-0.744 | 0 |
| **Subfamily** | 8 | 8 | | 1.697-2.151 | 0.577-0.639 | 0 |
| **Genus** | 8 | 12 | | 0.942-1.534 | 0.419-0.550 | 0 |
| **Subgenus** | 16 | 21 | | 0.103-0.160 | 0.063-0.098 | 0 |
| **Species** | 20 | 25 | | 0.050-0.072 | 0.030-0.044 | 0 |

\* Inv dataset including 71 sequences

**1**For every rank threshold, CC=0 and is associated with local minimum of the CC distribution, indicating strongest possible support.

See Table 3 for other details

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**Fig. 1**. Genome and domain organizations of five vertebrate nidoviruses that prototype two new subfamilies or three new genera in the order *Nidovirales*. See **Table 1** for information on the depicted viruses. The five conserved replicative domains (5d, 5 domains) used in the DEmARC analysis (**Tables 2 and 3, Figs. 7-8**) and phylogenetic analyses (**Figs 3-4**) are labelled. These replicative domains are depicted in relation to the genome and open reading frames (ORFs). The two largest ORFs, ORF1a and ORF1b, encode replicative proteins. Downstream ORFs encode structural proteins and, optionally, accessory proteins.

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**Fig. 2**. Genome and domain organizations of four invertebrate nidoviruses that prototype two new subfamilies and one new genus in the order *Nidovirales*. See **Table 1** for information on the depicted viruses. The subfamily *Metotonivirinae* is represented by two viruses, ACMV and FOaMV-1, each prototyping a separate new genus (**Table 4, Fig. 5**). The five conserved replicative domains (5d, 5 domains) used in the DEmARC analysis (**Table 2, Fig. 9**) and phylogenetic analyses (**Figs 5-6**) are labelled. These replicative domains are depicted in relation to the genome and open reading frames (ORFs). The two largest ORFs, ORF1a and ORF1b, encode replicative proteins. Downstream ORFs encode structural proteins and, optionally, accessory proteins.

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**Fig. 3.** Cluster partitioning of the ML phylogenetic tree of the *Coronaviridae*. Newly classified viruses and the respective taxa are indicated in green. The tree is mid-point rooted; this rooting is also supported by using the viruses shown in **Fig. 4** as outgroup. Branch support was estimated using the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT) with 1000 replicates, whose results are depicted with white/black shades of dots at the internal nodes, according to three brackets detailed within the key-box in the upper-left corner.

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**Fig. 4.** Cluster partitioning of the ML phylogenetic tree of the family *Tobaniviridae,* and the suborders *Arnidovirineae* (except for the family *Arteriviridae*) and *Nanidovirineae*. Newly classified viruses and the respective taxa are indicated in green. The tree is mid-point rooted; this rooting is also supported by using the *Coronaviridae* as outgroup (**Fig. 3**). Branch support was estimated using the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT) with 1000 replicates, whose results are depicted with white/black shades of dots at the internal nodes, according to three brackets detailed within the key-box in the upper-left corner.

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**Fig. 5.** Cluster partitioning of the ML phylogenetic tree of the invertebrate nidoviruses. Newly classified viruses and the respective taxa are indicated in green. Merged subfamilies are indicated in red (see also Fig. 6 for the current subfamilies that were merged). The tree is mid-point rooted. Branch support was estimated using the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT) with 1000 replicates, whose results are depicted with white/black shades of dots at the internal nodes, according to three brackets detailed within the key-box in the upper-left corner.

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**Fig. 6.** Current and proposed subfamilies of the invertebrate nidoviruses. Newly classified viruses and the respective taxa are indicated in green. Merged subfamilies are indicated in red (see also **Fig. 5** for an overview of taxa at other ranks). The ML phylogenetic tree is mid-point rooted. Branch support was estimated using the Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT) with 1000 replicates, whose results are depicted with white/black shades of dots at the internal nodes, according to three brackets detailed within the key-box in the upper-left corner.

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**Fig. 7.** Intra-group genetic divergence in taxa at the five hierarchical ranks of the *Coronaviridae* by DEmARC. PPD ranges of the five ranks (from species at the extreme left to family at the extreme right) that are demarcated according to four PPD thresholds (**Table 3**) are highlighted with distinct colors at the X axis. For simplicity, identities of clusters at the lowest species rank are indicated by virus acronyms (left axis); the number of available unique virus sequences of the respective species are shown in brackets. Newly classified viruses are indicated in green. All identified clusters correspond to monophyletic groups on the phylogenetic tree (**Fig. 3**). Box-and-whisker graphs were used to plot distributions of distances between viruses belonging to the same taxon on the candidate classification level under consideration, but belonging to different taxa on the previous level. The boxes span from the first to the third quartile and include the median (bold line); and the whiskers (dashed lines) extend to the extreme values. No box-and whisker graphs are provided for singleton taxa that include a single virus. For other details of this plot, see [7].

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**Fig. 8.** Intra-group genetic divergence in taxa at the five hierarchical ranks of vertebrate nidoviruses (except for the families *Coronaviridae* and *Arteriviridae*) as determined by DEmARC. PPD ranges of the five ranks (from species at the extreme left to family at the extreme right) that are demarcated according to four PPD thresholds highlighted with distinct colors at the X axis (**Table 3**). For simplicity, the identities of clusters at the lowest species rank are indicated via virus acronyms (left axis); the number of available unique virus sequences of the respective species are shown in brackets. Newly classified viruses are indicated in green. All identified clusters correspond to monophyletic groups on the phylogenetic tree (**Fig. 4**). Box-and-whisker graphs were used to plot distributions of distances between viruses belonging to the same taxon on the candidate classification level under consideration, but belonging to different taxa on the previous level. The boxes span from the first to the third quartile and include the median (bold line); and the whiskers (dashed lines) extend to the extreme values. No box-and whisker graphs are provided for singleton taxa that include a single virus. For other details of this plot, see [7].

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**Fig. 9.** Intra-group genetic divergence in taxa at the five hierarchical ranks of invertebrate nidoviruses as determined by DEmARC. PPD ranges of the five ranks (from species at the extreme left to family at the extreme right) that are demarcated according to four PPD thresholds are highlighted with distinct colors at the X axis (**Table 4**). For simplicity, identities of clusters at the lowest species rank are indicated by virus acronyms (left axis); the number of available unique virus sequences of the respective species are shown in brackets. Newly classified viruses are indicated in green. All identified clusters correspond to monophyletic groups on the phylogenetic tree (**Fig. 5**). Box-and-whisker graphs were used to plot distributions of distances between viruses belonging to the same taxon on the candidate classification level under consideration, but belonging to different taxa on the previous level. The boxes span from the first to the third quartile and include the median (bold line); and the whiskers (dashed lines) extend to the extreme values. No box-and whisker graphs are provided for singleton taxa that include a single virus. For other details of this plot, see [7].

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