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Family *Genomoviridae*: 2021 taxonomy update

Arvind Varsani^{1,2} · Mart Krupovic³

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Abstract

The family *Genomoviridae* (phylum *Cressdnaviricota*, class *Repensiviricetes*, order *Geplafuvirales*) includes viruses with circular single-stranded DNA genomes encoding two proteins, the capsid protein and the rolling-circle replication initiation protein. The genomes of the vast majority of members in this family have been sequenced directly from diverse environmental or animal- and plant-associated samples, but two genomoviruses have been identified infecting fungi. Since the last taxonomic update of the *Genomoviridae*, a number of new members of this family have been sequenced. Here, we report on the most recent taxonomic update, including the creation of one new genus, *Gemytripvirus*, and classification of ~420 new genomoviruses into 164 new species. We also announce the adoption of the “Genus + freeform epithet” binomial system for the naming of all 236 officially recognized species in the family *Genomoviridae*. The updated taxonomy presented in this article has been accepted by the International Committee on Taxonomy of Viruses (ICTV).

The family *Genomoviridae* includes viruses with small circular single-stranded (ss) DNA genomes (~1.8–2.4 kb) encoding a rolling-circle replication initiation protein (Rep) and a capsid protein (CP) in an ambisense orientation [35]. Whereas the genomoviral CP is not recognizably similar at the sequence level to the CPs of other known viruses, the Rep is homologous to those of other eukaryotic ssDNA viruses and is most similar to those of plant viruses of the family *Geminiviridae*, sharing several unique sequence motifs and forming a sister group in phylogenetic analyses [21–23]. Accordingly, the families *Genomoviridae* and *Geminiviridae* were included in the order *Geplafuvirales* [36]. All eukaryotic ssDNA viruses encoding these related Reps, informally referred to as the CRESS DNA viruses [57,

82], were recently officially unified in the phylum *Cressdnaviricota* [36, 72].

The founding member of the *Genomoviridae* [35], *Sclerotinia sclerotiorum* hypovirulence-associated DNA virus 1 (SsHADV-1), infects the phytopathogenic fungus *Sclerotinia sclerotiorum* [79] but can also replicate in its transmission vector, the mycophagous insect *Lycoriella ingenua* [43]. However, the vast majority of genomoviruses have been discovered by metagenomics in diverse samples (see Supplementary Table S1), and the real extent of their host range remains unknown. In 2017, a sequence-based taxonomic framework was established for genomovirus classification [70]. In particular, 78% genome-wide pairwise identity was chosen as a species demarcation threshold, whereas Rep sequence phylogeny was used to define genera. At the time, the family consisted of 121 members, which were classified based on genome sequences into 73 species divided into nine genera: *Gemycircularvirus* (43 species and 73 members), *Gemyduguivirus* (1 species and 1 member), *Gemygorvirus* (5 species and 9 members), *Gemykibivirus* (16 species and 29 members), *Gemykolovirus* (2 species and 3 members), *Gemykrogvirus* (3 species and 3 members), *Gemykroznavirus* (1 species and 1 member), *Gemytondovirus* (1 species and 1 member), and *Gemyvongvirus* (1 species and 1 member).

In the period since the establishment of the family *Genomoviridae* [35] and the first report on the classification of then known genomoviruses (n = 122) [70], ~420 new complete genome sequences of genomoviruses had

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been deposited in the GenBank database as of May 2020, including both virus isolates and viruses discovered by metagenomics [2, 3, 6–9, 11–16, 18, 24, 26–34, 37–42, 44–46, 48, 50–56, 58, 59, 61, 62, 64–69, 71, 73–81, 83]. Furthermore, the International Committee on Taxonomy of Viruses (ICTV) has recently adopted a freeform binomial species nomenclature, whereby virus species names have to consist of two words, with the first one being the genus name and the second being a free-form species epithet, which can consist of Latin letters and/or Arabic numerals [60]. All existing species that currently do not conform to this binomial format have to be renamed before 2023. Here, we report on the classification of the new genomoviruses as well as on other taxonomic changes in the family *Genomoviridae*, which were approved by the ICTV following the annual ratification vote in March of 2021.

The first notable change implemented in the *Genomoviridae* taxonomy was adoption of the binomial species nomenclature for all 73 existing species. The correspondence between the old and new binomial species names is shown in Table 1. We note that the names of viruses that are included in the corresponding species are not affected. For instance, the virus name *Sclerotinia sclerotiorum* hypovirulence associated DNA virus 1 remains unchanged although the species name *Sclerotinia gemycirculavirus 1* has been changed to *Gemycirculavirus sclero1*.

The second taxonomic development involves the classification of ~420 new genomoviruses. We used the criteria of Rep amino-acid-based phylogeny (Fig. 1) to assign genomoviruses to genera, as outlined by Varsani and Krupovic [70]. By contrast, the recently isolated *Fusarium graminearum* gemytripvirus 1 (FgGMTV1), infecting *Fusarium graminearum*, a fungal plant pathogen with worldwide distribution that causes *Fusarium* head blight (FHB) disease in wheat and barley [39], formed a separate branch in the Rep phylogeny (Fig. 1). Notably, unlike other members of the *Genomoviridae*, which are monopartite, FgGMTV1 contains three genomic segments, each encoding a single protein [39]: DNA-A encodes a Rep protein; DNA-B encodes a genomovirus-like CP; and DNA-C encodes a protein of unknown function. DNA-A and DNA-B are mutually interdependent for their replication, whereas DNA-C relies on DNA-A and DNA-B for

replication and appears to enhance virus pathogenesis and transmission via conidia as well as accumulation of viral DNA in infected fungi [39]. Phylogenetic analysis suggests that the multipartite genome of FgGMTV1 has evolved from a monopartite genome of an ancestral genomovirus. Thus, based on the Rep phylogeny and its multipartite genome organization, FgGMTV1 has been classified as a member of a new species, *Gemytripvirus fugra1*, within a new genus, *Gemytripvirus* (**g**emini-like **my**co-infecting **t**ripartite virus) [39].

Using the previously established species demarcation criteria [70], namely, genome-wide pairwise identity of 78%, 35 viruses can be assigned to eight known species, while the remaining 389 viruses are classified to 164 new species (Table 1). The new species were named using the free-form binomial system. The greatly expanded dataset of genomoviruses has reinforced the validity of the previously established species demarcation criteria. Indeed, pairwise comparison of the representative sequences from each of the species (except for *Gemytripvirus fugra1*, whose members have a tripartite genome) showed that they share less than 78% genome-wide pairwise identity (Figs. 2 and 3). A summary of the genome sequences of genomoviruses belonging to specific genera and their source are summarized in Figure 4, and additional details are provided in Supplementary Table S1. Accordingly, this threshold will continue to be used for further taxonomic classification of new genomoviruses.

Finally, we note that following the taxonomic assessment described herein, a number of new genomoviruses ($n = 201$; GenBank, download 15 May 2021) have been discovered [4, 5, 10, 25, 63]. Of these, 42 can be assigned to currently established species, and 161, once classified, are likely to represent new species and genera within the family *Genomoviridae*. However, we would like to discourage naming newly discovered viruses using official taxon names. For instance, an ssDNA virus infecting the phytopathogenic fungus *Botrytis cinerea* has been isolated recently and named *Botrytis cinerea* genomovirus 1 (BcGV1) [17]. Although BcGV1 displays a genomic organization similar to that of genomoviruses and encodes a related Rep, the CP encoded by this virus is unrelated to that of genomoviruses. Thus, placement of BcGV1 within the family *Genomoviridae* is questionable.

Table 1 Nomenclatural and taxonomic changes in the family *Genomoviridae*

Genus	New species name	Former species name	Exemplar virus	Accession no.
<i>Gemycircularvirus</i>	<i>Gemycircularvirus abati1</i>	-	Genomoviridae sp.	MK032723
	<i>Gemycircularvirus alces1</i>	-	Alces alces faeces associated genomovirus MP84	MG641204
	<i>Gemycircularvirus alces2</i>	-	Alces alces faeces associated genomovirus MP157	MG641207
	<i>Gemycircularvirus ansal1</i>	-	Genomoviridae sp.	MN928911
	<i>Gemycircularvirus aspar1</i>	-	Plant associated genomovirus 21	MH939436
	<i>Gemycircularvirus austro1</i>	-	Blackfly genomovirus 2	MK433234
	<i>Gemycircularvirus austro2</i>	-	Blackfly genomovirus 7	MK433239
	<i>Gemycircularvirus austro3</i>	-	Blackfly genomovirus 4	MK433236
	<i>Gemycircularvirus austro4</i>	-	Blackfly genomovirus 9	MK433241
	<i>Gemycircularvirus austro5</i>	-	Blackfly genomovirus 5	MK433237
	<i>Gemycircularvirus austro6</i>	-	Blackfly genomovirus 10	MK433242
	<i>Gemycircularvirus bemt1</i>	-	Bemisia-associated genomovirus AdO	KY230614
	<i>Gemycircularvirus blabi1</i>	<i>Blackbird associated gemycircularvirus 1</i>	Faecal-associated gemycircularvirus 1a	KF371643
	<i>Gemycircularvirus bovas1</i>	<i>Bovine associated gemycircularvirus 1</i>	Faeces associated gemycircularvirus 22	KT862253
	<i>Gemycircularvirus bromas1</i>	<i>Bromus associated gemycircularvirus 1</i>	Bromus-associated circular DNA virus 3	KM510192
	<i>Gemycircularvirus canlup1</i>	-	Lupine feces-associated gemycircularvirus 2	KY214442
	<i>Gemycircularvirus cassa1</i>	<i>Cassava associated gemycircularvirus 1</i>	Cassava associated circular DNA virus	JQ412056
	<i>Gemycircularvirus chिकास1</i>	<i>Chicken associated gemycircularvirus 1</i>	Faeces associated gemycircularvirus 20	KT862243
	<i>Gemycircularvirus chिकास2</i>	<i>Chicken associated gemycircularvirus 2</i>	Faeces associated gemycircularvirus 17	KT862242
	<i>Gemycircularvirus chickad1</i>	<i>Chickadee associated gemycircularvirus 1</i>	Poecile atricapillus GI tract-associated gemycircularvirus	KT309029
	<i>Gemycircularvirus citas1</i>	-	Citrus Tunisia genomovirus 2	MN708485
	<i>Gemycircularvirus cybusi1</i>	-	Spider associated circular virus 1	MH545503
	<i>Gemycircularvirus denbre1</i>	-	Bark beetle-associated genomovirus 1	MG571096
	<i>Gemycircularvirus denbre2</i>	-	Bark beetle-associated genomovirus 2	MG571098
	<i>Gemycircularvirus denbre3</i>	-	Bark beetle-associated genomovirus 3	MG571099
	<i>Gemycircularvirus denbre4</i>	-	Bark beetle-associated genomovirus 4	MG571100
	<i>Gemycircularvirus denpol</i>	-	Bark beetle-associated genomovirus 5	MG571101
	<i>Gemycircularvirus derva1</i>	-	Tick-associated genomovirus 1	MF173065
	<i>Gemycircularvirus dichism1</i>	-	Plant associated genomovirus 19	MH939446
	<i>Gemycircularvirus draga1</i>	<i>Dragonfly associated gemycircularvirus 1</i>	Dragonfly-associated circular virus 2	JX185429
	<i>Gemycircularvirus echiam1</i>	-	Thrips-associated genomovirus 1	KY308268
-	<i>Gemycircularvirus equas1</i>	<i>Equine associated gemycircularvirus 1</i>	Faeces associated gemycircularvirus 18	KT862248
	<i>Gemycircularvirus erati1</i>	-	Giant house spider associated circular virus 1	MH545509
	<i>Gemycircularvirus euhet1</i>	-	Euphorbia heterophylla associated gemycircularvirus	MH047858

Table 1 (continued)

Genus	New species name	Former species name	Exemplar virus	Accession no.
	<i>Gemycircularvirus furse1</i>	<i>Fur seal associated gemycircularvirus 1</i>	Faecal-associated gemycircularvirus 4	KF371638
	<i>Gemycircularvirus geras1</i>	<i>Gerygone associated gemycircularvirus 1</i>	Faecal-associated gemycircularvirus 6	KF371636
	<i>Gemycircularvirus geras2</i>	<i>Gerygone associated gemycircularvirus 2</i>	Faecal-associated gemycircularvirus 5	KF371637
	<i>Gemycircularvirus geras3</i>	<i>Gerygone associated gemycircularvirus 3</i>	Faecal-associated gemycircularvirus 3	KF371639
	<i>Gemycircularvirus giapa1</i>	-	Giant panda associated gemycircularvirus	MF327560
	<i>Gemycircularvirus giapa2</i>	-	Giant panda associated gemycircularvirus	MF327565
	<i>Gemycircularvirus giapa3</i>	-	Giant panda associated gemycircularvirus	MF327568
	<i>Gemycircularvirus giapa4</i>	-	Giant panda associated gemycircularvirus	MF327561
	<i>Gemycircularvirus giapa5</i>	-	Giant panda associated gemycircularvirus	MF327567
	<i>Gemycircularvirus giapa6</i>	-	Giant panda associated gemycircularvirus	MF327569
	<i>Gemycircularvirus giapa7</i>	-	Giant panda associated gemycircularvirus	MF327558
	<i>Gemycircularvirus giapa8</i>	-	Giant panda associated gemycircularvirus	MF327570
	<i>Gemycircularvirus gopha1</i>	-	Tortoise genomovirus 17	MK570217
	<i>Gemycircularvirus gopha2</i>	-	Tortoise genomovirus 10	MK570210
	<i>Gemycircularvirus gopha3</i>	-	Genomoviridae sp.	MK032737
	<i>Gemycircularvirus hadtis1</i>	-	Genomoviridae sp.	MK032733
	<i>Gemycircularvirus haeme1</i>	-	Finch associated genomovirus 5	MK249235
	<i>Gemycircularvirus haeme2</i>	-	Finch associated genomovirus 6	MK249242
	<i>Gemycircularvirus hydro1</i>	-	Capybara genomovirus 1	MK483072
	<i>Gemycircularvirus hypas1</i>	<i>Hypericum associated gemycircularvirus 1</i>	<i>Hypericum japonicum</i> associated circular DNA virus	KF413620
	<i>Gemycircularvirus ixode1</i>	-	Tick-associated genomovirus 3	MF173067
	<i>Gemycircularvirus lamas1</i>	<i>Lama associated gemycircularvirus 1</i>	Faeces associated gemycircularvirus 21	KT862245
	<i>Gemycircularvirus lebec1</i>	-	Plant associated genomovirus 20	MH939431
	<i>Gemycircularvirus legle1</i>	-	Plant associated genomovirus 15	MH939377
	<i>Gemycircularvirus lepa2</i>	-	<i>Lynx canadensis</i> faeces associated genomovirus CL1 46	MG641191
	<i>Gemycircularvirus lepam1</i>	-	<i>Alces alces</i> faeces associated genomovirus MP111	MG641205
	<i>Gemycircularvirus lepam2</i>	-	<i>Alces alces</i> faeces associated genomovirus MP43	MG641202
	<i>Gemycircularvirus lepam3</i>	-	<i>Lepus americanus</i> faeces associated genomovirus SHP9	MG641211
	<i>Gemycircularvirus lynca1</i>	-	<i>Lynx canadensis</i> faeces associated genomovirus CL1 48	MG641192
	<i>Gemycircularvirus lynca2</i>	-	<i>Lynx canadensis</i> faeces associated genomovirus CL1 71	MG641194
	<i>Gemycircularvirus lynca3</i>	-	<i>Lynx canadensis</i> faeces associated genomovirus CL5 48	MG641201
	<i>Gemycircularvirus lynca4</i>	-	<i>Lynx canadensis</i> faeces associated genomovirus CL1 148	MG641197

Table 1 (continued)

Genus	New species name	Former species name	Exemplar virus	Accession no.
	<i>Gemycircularvirus malas1</i>	<i>Mallard associated gemycircularvirus 1</i>	Faecal-associated gemycircularvirus 7	KF371635
	<i>Gemycircularvirus minio1</i>	<i>Miniopterus associated gemycircularvirus 1</i>	Bat circovirus	KJ641719
	<i>Gemycircularvirus miniti1</i>	-	Genomoviridae sp.	MK032736
	<i>Gemycircularvirus miniti2</i>	-	Genomoviridae sp.	MK032701
	<i>Gemycircularvirus miniti3</i>	-	Genomoviridae sp.	MK032712
	<i>Gemycircularvirus miniti4</i>	-	Genomoviridae sp.	MK032709
	<i>Gemycircularvirus minti6</i>	-	Genomoviridae sp.	MH617534
	<i>Gemycircularvirus mocha1</i>	-	Momordica charantia associated gemycircularvirus	MH047857
	<i>Gemycircularvirus monas1</i>	<i>Mongoose associated gemycircularvirus 1</i>	Mongoose feces-associated gemycircularvirus d	KP263547
	<i>Gemycircularvirus mosqi1</i>	<i>Mosquito associated gemycircularvirus 1</i>	Mosquito VEM virus SDBVL G	HQ335086
	<i>Gemycircularvirus mouti1</i>	-	Genomoviridae sp.	MK032728
	<i>Gemycircularvirus mouti10</i>	-	Genomoviridae sp.	MK032705
	<i>Gemycircularvirus mouti11</i>	-	Genomoviridae sp.	MK032718
	<i>Gemycircularvirus mouti12</i>	-	Genomoviridae sp.	MK032702
	<i>Gemycircularvirus mouti2</i>	-	Genomoviridae sp.	MK032755
	<i>Gemycircularvirus mouti3</i>	-	Genomoviridae sp.	MK032715
	<i>Gemycircularvirus mouti4</i>	-	Genomoviridae sp.	MK032719
	<i>Gemycircularvirus mouti5</i>	-	Genomoviridae sp.	MK032753
	<i>Gemycircularvirus mouti6</i>	-	Genomoviridae sp.	MK032735
	<i>Gemycircularvirus mouti7</i>	-	Genomoviridae sp.	MK032738
	<i>Gemycircularvirus mouti8</i>	-	Genomoviridae sp.	MK032752
	<i>Gemycircularvirus mouti9</i>	-	Genomoviridae sp.	MK032714
	<i>Gemycircularvirus odona1</i>	<i>Odonata associated gemycircularvirus 1</i>	Odonata associated gemycircularvirus-1	KM598385
	<i>Gemycircularvirus odona2</i>	<i>Odonata associated gemycircularvirus 2</i>	Odonata associated gemycircularvirus-2	KM598387
	<i>Gemycircularvirus oltre1</i>	-	Olive associated gemycircularvirus 1	MH444690
	<i>Gemycircularvirus opunt1</i>	-	Plant associated genomovirus 25	MK947372
	<i>Gemycircularvirus oxcor1</i>	-	Oxalis corniculata genomoviridae	MN823668
	<i>Gemycircularvirus pleca1</i>	-	Gemycircularvirus sp.	KY302866
	<i>Gemycircularvirus poass1</i>	<i>Poaceae associated gemycircularvirus 1</i>	Poaceae-associated gemycircularvirus 1	KT253577
	<i>Gemycircularvirus porci1</i>	<i>Porcine associated gemycircularvirus 1</i>	Faeces associated gemycircularvirus 19	KT862250
	<i>Gemycircularvirus porci2</i>	<i>Porcine associated gemycircularvirus 2</i>	Faecal-associated gemycircularvirus 2	KF371640
	<i>Gemycircularvirus ptero1</i>	<i>Pteropus associated gemycircularvirus 1</i>	Pacific flying fox faeces associated gemycircularvirus-10	KT732804
	<i>Gemycircularvirus ptero10</i>	<i>Pteropus associated gemycircularvirus 10</i>	Pacific flying fox faeces associated gemycircularvirus-3	KT732794
	<i>Gemycircularvirus ptero2</i>	<i>Pteropus associated gemycircularvirus 2</i>	Pacific flying fox faeces associated gemycircularvirus-2	KT732792
	<i>Gemycircularvirus ptero3</i>	<i>Pteropus associated gemycircularvirus 3</i>	Pacific flying fox faeces associated gemycircularvirus-5	KT732797
	<i>Gemycircularvirus ptero4</i>	<i>Pteropus associated gemycircularvirus 4</i>	Pacific flying fox faeces associated gemycircularvirus-13	KT732814

Table 1 (continued)

Genus	New species name	Former species name	Exemplar virus	Accession no.
	<i>Gemycircularvirus ptero5</i>	<i>Pteropus associated gemycircularvirus 5</i>	Pacific flying fox faeces associated gemycircularvirus-8	KT732801
	<i>Gemycircularvirus ptero6</i>	<i>Pteropus associated gemycircularvirus 6</i>	Pacific flying fox faeces associated gemycircularvirus-9	KT732803
	<i>Gemycircularvirus ptero7</i>	<i>Pteropus associated gemycircularvirus 7</i>	Pacific flying fox faeces associated gemycircularvirus-11	KT732807
	<i>Gemycircularvirus ptero8</i>	<i>Pteropus associated gemycircularvirus 8</i>	Pacific flying fox faeces associated gemycircularvirus-14	KT732806
	<i>Gemycircularvirus ptero9</i>	<i>Pteropus associated gemycircularvirus 9</i>	Pacific flying fox faeces associated gemycircularvirus-4	KT732795
	<i>Gemycircularvirus raski1</i>	-	Genomoviridae sp.	MK032754
	<i>Gemycircularvirus ratas1</i>	<i>Rat associated gemycircularvirus 1</i>	Gemycircularvirus gemy-ch-rat1	KR912221
	<i>Gemycircularvirus rebac1</i>	-	Northern red-backed vole stool-associated gemycircularvirus 110	MK738141
	<i>Gemycircularvirus recro1</i>	-	Gemycircularvirus sp.	KY312557
	<i>Gemycircularvirus sarpe1</i>	-	Plant associated genomovirus 17	MH939397
	<i>Gemycircularvirus sclero1</i>	<i>Sclerotinia gemycircularvirus 1</i>	Sclerotinia sclerotiorum hypovirulence associated DNA virus 1	GQ365709
	<i>Gemycircularvirus sewopo1</i>	<i>Sewage derived gemycircularvirus 1</i>	Sewage-associated gemycircularvirus-8	KJ547638
	<i>Gemycircularvirus sewopo2</i>	<i>Sewage derived gemycircularvirus 2</i>	Sewage-associated gemycircularvirus-11	KJ547641
	<i>Gemycircularvirus sewopo3</i>	<i>Sewage derived gemycircularvirus 3</i>	Sewage-associated gemycircularvirus-6	KJ547636
	<i>Gemycircularvirus sewopo4</i>	<i>Sewage derived gemycircularvirus 4</i>	Sewage-associated gemycircularvirus-7b	KJ547640
	<i>Gemycircularvirus sewopo5</i>	<i>Sewage derived gemycircularvirus 5</i>	Sewage-associated gemycircularvirus-9	KJ547639
	<i>Gemycircularvirus sheas1</i>	<i>Sheep associated gemycircularvirus 1</i>	Faeces associated gemycircularvirus 16	KT862249
	<i>Gemycircularvirus siedo1</i>	-	Sierra dome spider associated circular virus 1	MH545510
	<i>Gemycircularvirus solas1</i>	-	Plant associated genomovirus 11	MH939384
	<i>Gemycircularvirus soybe1</i>	<i>Soybean associated gemycircularvirus 1</i>	Soybean leaf-associated gemycircularvirus 1	KT598248
	<i>Gemycircularvirus termi1</i>	-	Termite associated circular virus 2	MG917675
	<i>Gemycircularvirus trilo1</i>	-	Plant associated genomovirus 22	MH939442
	<i>Gemycircularvirus turti1</i>	-	Genomoviridae sp.	MK012473
	<i>Gemycircularvirus willde1</i>	-	Plant associated genomovirus 13	MH939427
<i>Gemyduguiviruses</i>	<i>Gemyduguiviruses arteca1</i>	-	Artemisia carvifolia genomoviridae	MN823676
	<i>Gemyduguiviruses austo1</i>	-	Blackfly genomovirus 8	MK433240
	<i>Gemyduguiviruses benta1</i>	-	Bemisia-associated genomovirus AdDF	KY230613
	<i>Gemyduguiviruses draga1</i>	<i>Dragonfly associated gemyduguiviruses 1</i>	Dragonfly-associated circular virus 3	JX185428
	<i>Gemyduguiviruses hydro1</i>	-	Capybara genomovirus 3	MK483075
	<i>Gemyduguiviruses hydro2</i>	-	Capybara genomovirus 8	MK483080
	<i>Gemyduguiviruses hydro3</i>	-	Capybara genomovirus 5	MK483077
	<i>Gemyduguiviruses macra1</i>	-	Plant associated genomovirus 4	MH939370
	<i>Gemyduguiviruses merre1</i>	-	Plant associated genomovirus 5	MH939417
	<i>Gemyduguiviruses minti1</i>	-	Genomoviridae sp.	MK032731
	<i>Gemyduguiviruses minti2</i>	-	Genomoviridae sp.	MK032726
	<i>Gemyduguiviruses recro1</i>	-	Gemycircularvirus sp.	KY312558

Table 1 (continued)

Genus	New species name	Former species name	Exemplar virus	Accession no.	
<i>Gemygorvirus</i>	<i>Gemygorvirus canial</i>	<i>Canine associated gemygorvirus 1</i>	Faeces associated gemycircularvirus 15	KT862254	
	<i>Gemygorvirus hydro1</i>	-	Capybara genomovirus 6	MK483078	
	<i>Gemygorvirus malas1</i>	<i>Mallard associated gemygorvirus 1</i>	Faeces associated gemycircularvirus 14	KT862238	
	<i>Gemygorvirus opunt1</i>	-	Plant associated genomovirus 26	MK947373	
	<i>Gemygorvirus poaspel</i>	-	Plant associated genomovirus 1	MH939361	
	<i>Gemygorvirus pterol</i>	<i>Pteropus associated gemygorvirus 1</i>	Pacific flying fox faeces associated gemycircularvirus-1	KT732790	
	<i>Gemygorvirus sewopol</i>	<i>Sewage derived gemygorvirus 1</i>	Sewage-associated gemycircularvirus-5	KJ547635	
	<i>Gemygorvirus stara1</i>	<i>Starling associated gemygorvirus 1</i>	Faecal-associated gemycircularvirus 10	KF371632	
	<i>Gemykibivirus</i>	<i>Gemykibivirus abati1</i>	-	Genomoviridae sp.	MK032696
		<i>Gemykibivirus abati2</i>	-	Genomoviridae sp.	MK032759
<i>Gemykibivirus anima1</i>		-	Porcine feces-associated gemycircularvirus	KY214433	
<i>Gemykibivirus badas1</i>		<i>Badger associated gemykibivirus 1</i>	Badger feces-associated gemycircularvirus	KP263543	
<i>Gemykibivirus bema1</i>		-	Bemisia-associated genomovirus NfO	KY230625	
<i>Gemykibivirus blabi1</i>		<i>Blackbird associated gemykibivirus 1</i>	Faecal-associated gemycircularvirus 9	KF371633	
<i>Gemykibivirus blarol</i>		<i>Black robin associated gemykibivirus 1</i>	Faecal-associated gemycircularvirus 8	KF371634	
<i>Gemykibivirus bovas1</i>		<i>Bovine associated gemykibivirus 1</i>	HCBI8.215 virus	LK931483	
<i>Gemykibivirus canfam1</i>		-	Canine feces-associated gemycircularvirus	KY214441	
<i>Gemykibivirus cowchi1</i>		-	Cattle blood-associated gemycircularvirus	MF669480	
<i>Gemykibivirus cybusi1</i>		-	Cybaeus spider associated circular virus 2	MH545507	
<i>Gemykibivirus cynas1</i>		-	Plant associated genomovirus 3	MH939438	
<i>Gemykibivirus draga1</i>		<i>Dragonfly associated gemykibivirus 1</i>	Dragonfly-associated circular virus 1	JX185430	
<i>Gemykibivirus echi1</i>		-	Thrips-associated genomovirus 3	KY308269	
<i>Gemykibivirus galga1</i>		-	Chicken genomovirus mg7_73	MN379612	
<i>Gemykibivirus galga2</i>		-	Chicken genomovirus mg8_401	MN379615	
<i>Gemykibivirus galga3</i>		-	Chicken genomovirus mg4_1218	MN379608	
<i>Gemykibivirus giapa1</i>		-	Giant panda associated gemycircularvirus	MF327571	
<i>Gemykibivirus hadtis1</i>		-	Genomoviridae sp.	MK032708	
<i>Gemykibivirus haeme1</i>		-	Finch associated genomovirus 3	MK249305	
<i>Gemykibivirus haeme2</i>		-	Gopherus associated genomovirus 1	MF373638	
<i>Gemykibivirus haeme3</i>		-	Finch associated genomovirus 2	MK249239	
<i>Gemykibivirus haeme4</i>		-	Finch associated genomovirus 4	MK249240	
<i>Gemykibivirus haeme5</i>		-	Finch associated genomovirus 1	MK249294	
<i>Gemykibivirus hipla1</i>		-	Bat gemycircularvirus	MK050014	
<i>Gemykibivirus humas1</i>		<i>Human associated gemykibivirus 1</i>	MSSI2.225 virus	LK931485	
<i>Gemykibivirus humas2</i>		<i>Human associated gemykibivirus 2</i>	Gemycircularvirus SL1	KP133075	
<i>Gemykibivirus humas3</i>		<i>Human associated gemykibivirus 3</i>	Gemycircularvirus C1c	KP987887	
<i>Gemykibivirus humas4</i>		<i>Human associated gemykibivirus 4</i>	Human gemycircularvirus GeTz1	KT363839	
<i>Gemykibivirus humas5</i>		<i>Human associated gemykibivirus 5</i>	Gemycircularvirus HV-GeV2	KU343137	

Table 1 (continued)

Genus	New species name	Former species name	Exemplar virus	Accession no.
	<i>Gemykibivirus hydro1</i>	-	Capybara genomovirus 4	MK483076
	<i>Gemykibivirus hydro2</i>	-	Capybara genomovirus 2	MK483073
	<i>Gemykibivirus hydro3</i>	-	Capybara genomovirus 12	MK483084
	<i>Gemykibivirus minti1</i>	-	Genomoviridae sp.	MK032742
	<i>Gemykibivirus monas1</i>	<i>Mongoose associated gemykibivirus 1</i>	Mongoose feces-associated gemycircularvirus b	KP263545
	<i>Gemykibivirus mouti1</i>	-	Genomoviridae sp.	MK032703
	<i>Gemykibivirus mouti2</i>	-	Genomoviridae sp.	MK032748
	<i>Gemykibivirus pitis1</i>	-	Genomoviridae sp.	MK032749
	<i>Gemykibivirus pitis2</i>	-	Genomoviridae sp.	MK032721
	<i>Gemykibivirus planta1</i>	-	Plant associated genomovirus 2	MH939363
	<i>Gemykibivirus planta2</i>	-	Plant associated genomovirus 29	MK947376
	<i>Gemykibivirus ptero1</i>	<i>Pteropus associated gemykibivirus 1</i>	Pacific flying fox faeces associated gemycircularvirus-12	KT732813
	<i>Gemykibivirus raski1</i>	-	Genomoviridae sp.	MK032704
	<i>Gemykibivirus rhina1</i>	<i>Rhinolophus associated gemykibivirus 1</i>	Bat circovirus	KJ641737
	<i>Gemykibivirus rhina2</i>	<i>Rhinolophus associated gemykibivirus 2</i>	Bat circovirus	KJ641726
	<i>Gemykibivirus sewopo1</i>	<i>Sewage derived gemykibivirus 1</i>	Sewage-associated gemycircularvirus-3	KJ547643
	<i>Gemykibivirus sewopo2</i>	<i>Sewage derived gemykibivirus 2</i>	Sewage-associated gemycircularvirus-2	KJ547642
	<i>Gemykibivirus turti1</i>	-	Genomoviridae sp.	MK012443
	<i>Gemykibivirus waste1</i>	-	Genomoviridae sp.	MT309857
	<i>Gemykibivirus womot1</i>	-	Genomoviridae sp.	MK032756
<i>Gemykolovirus</i>	<i>Gemykolovirus abati1</i>	-	Genomoviridae sp.	MK032717
	<i>Gemykolovirus citas1</i>	-	Citrus Tunisia genomovirus 1b	MN708482
	<i>Gemykolovirus derva1</i>	-	Tick-associated genomovirus 2	MF173066
	<i>Gemykolovirus easlul</i>	-	Grasshopper associated circular virus 1	MH545499
	<i>Gemykolovirus echia1</i>	-	Thrips-associated genomovirus 4	KY308270
	<i>Gemykolovirus gopha1</i>	-	Tortoise genomovirus 9	MK570209
	<i>Gemykolovirus gopha2</i>	-	Tortoise genomovirus 13	MK570213
	<i>Gemykolovirus hadtis1</i>	-	Genomoviridae sp.	MK032747
	<i>Gemykolovirus heris1</i>	-	Plant associated genomovirus 7	MH939374
	<i>Gemykolovirus lepam1</i>	-	Alces alces faeces associated genomovirus MP68	MG641203
	<i>Gemykolovirus poaspe1</i>	-	Plant associated genomovirus 9	MH939382
	<i>Gemykolovirus prupe1</i>	-	Amygdalus persica genomoviridae	MN823669
	<i>Gemykolovirus ptero1</i>	<i>Pteropus associated gemykolovirus 1</i>	Pacific flying fox faeces associated gemycircularvirus-6	KT732798
	<i>Gemykolovirus ptero2</i>	<i>Pteropus associated gemykolovirus 2</i>	Pacific flying fox faeces associated gemycircularvirus-7	KT732800
	<i>Gemykolovirus segpa1</i>	-	Tubeweb spider associated circular virus 1	MH545501
	<i>Gemykolovirus troti1</i>	-	Genomoviridae sp.	MK032739
<i>Gemykrogvirus</i>	<i>Gemykrogvirus abati1</i>	-	Genomoviridae sp.	MK032716
	<i>Gemykrogvirus apime1</i>	-	Apis mellifera genomovirus 2	MH973741
	<i>Gemykrogvirus bovas1</i>	<i>Bovine associated gemykrogvirus 1</i>	HCB19.212 virus	LK931484
	<i>Gemykrogvirus carib1</i>	<i>Caribou associated gemykrogvirus 1</i>	Caribou feces-associated gemycircularvirus	KJ938717

Table 1 (continued)

Genus	New species name	Former species name	Exemplar virus	Accession no.
	<i>Gemykrogvirus galga1</i>	-	Chicken genomovirus mg4_1247	MN379609
	<i>Gemykrogvirus galga2</i>	-	Chicken stool-associated gemycircularvirus	KY056250
	<i>Gemykrogvirus galga3</i>	-	Chicken genomovirus mg4_1173	MN379605
	<i>Gemykrogvirus galga4</i>	-	Chicken genomovirus mg7_78	MN379614
	<i>Gemykrogvirus galga5</i>	-	Chicken genomovirus mg4_1165	MN379604
	<i>Gemykrogvirus giapa1</i>	-	Giant panda associated gemycircularvirus	MF327559
	<i>Gemykrogvirus hadtis1</i>	-	Genomoviridae sp.	MK032724
	<i>Gemykrogvirus humas1</i>	-	Gemycircularvirus sp.	MT649486
	<i>Gemykrogvirus sewopo1</i>	<i>Sewage derived gemykrogvirus 1</i>	Sewage-associated gemycircularvirus-4	KJ547634
<i>Gemykronzavirus</i>	<i>Gemykronzavirus animal</i>	-	Genomoviridae sp.	MK032727
	<i>Gemykronzavirus haemel</i>	-	Finch associated genomovirus 8	MK249245
	<i>Gemykronzavirus hydro1</i>	-	Capybara genomovirus 10	MK483082
	<i>Gemykronzavirus poaspe1</i>	-	Plant associated genomovirus 24	MH939435
	<i>Gemykronzavirus rabas1</i>	<i>Rabbit associated gemykronzavirus 1</i>	Faecal-associated gemycircularvirus 11	KF371631
	<i>Gemykronzavirus solas1</i>	-	Plant associated genomovirus 23	MH939385
	<i>Gemykronzavirus zizan1</i>	-	<i>Zizania latifolia</i> genomoviridae	MN823671
<i>Gemytondavirus</i>	<i>Gemytondavirus ostril</i>	<i>Ostrich associated gemytondavirus 1</i>	Faecal-associated gemycircularvirus 12	KF371630
<i>Gemytripvirus</i>	<i>Gemytripvirus fugra1</i>	-	<i>Fusarium graminearum</i> gemytripvirus 1	MK430076, MK430077, MK430078
<i>Gemyvongvirus</i>	<i>Gemyvongvirus humas1</i>	<i>Human associated gemyvongvirus 1</i>	Human plasma-associated gemycircularvirus	KP974693
<i>Gemyvongvirus</i>	<i>Gemyvongvirus minit1</i>	-	Genomoviridae sp.	MK032710
	<i>Gemyvongvirus minit2</i>	-	Genomoviridae sp.	MK032740

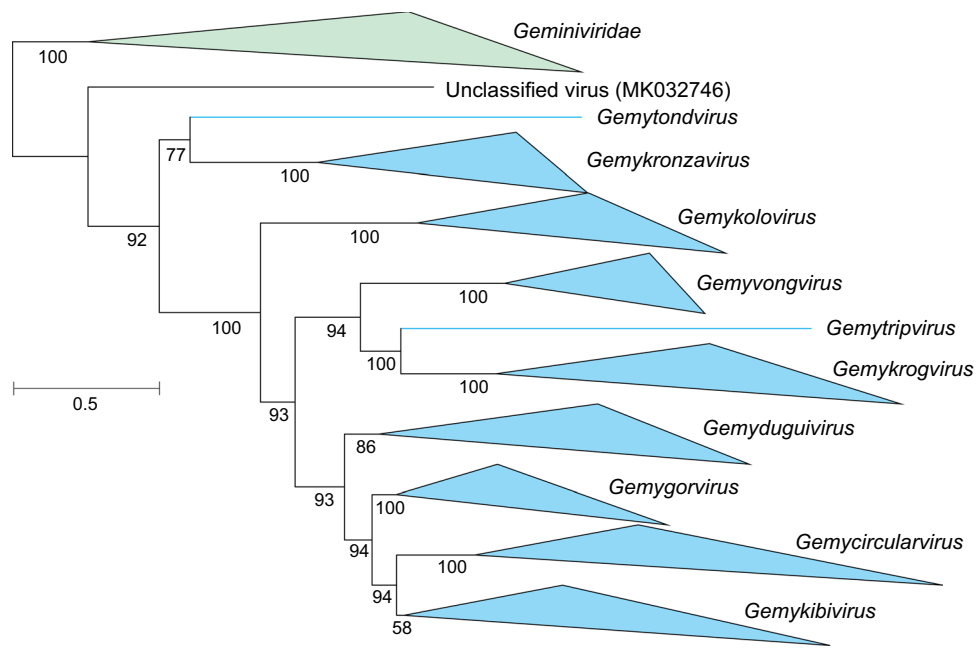


Fig. 1 Maximum-likelihood phylogenetic tree of Rep amino acid sequences of 545 genomoviruses together with a subset of geminiviruses and an unclassified virus (MK032746) that are distantly related. The tree is rooted with geminivirus sequences (green) and that of MK032746, which is most closely related to classified members of the family *Genomoviridae*. Clades corresponding to different genomovirus genera are colored blue. The Rep sequence alignment was con-

structed with MAFFT [20] and trimmed with TrimAL [1] using the gappout option. The final alignment contained 435 amino acid sites and was used to construct a maximum-likelihood phylogenetic tree using IQ-Tree [47]. The best-fitting model was determined by ModelFinder [19] and was LG+F+R9. Numbers at the nodes represent bootstrap support values (%).

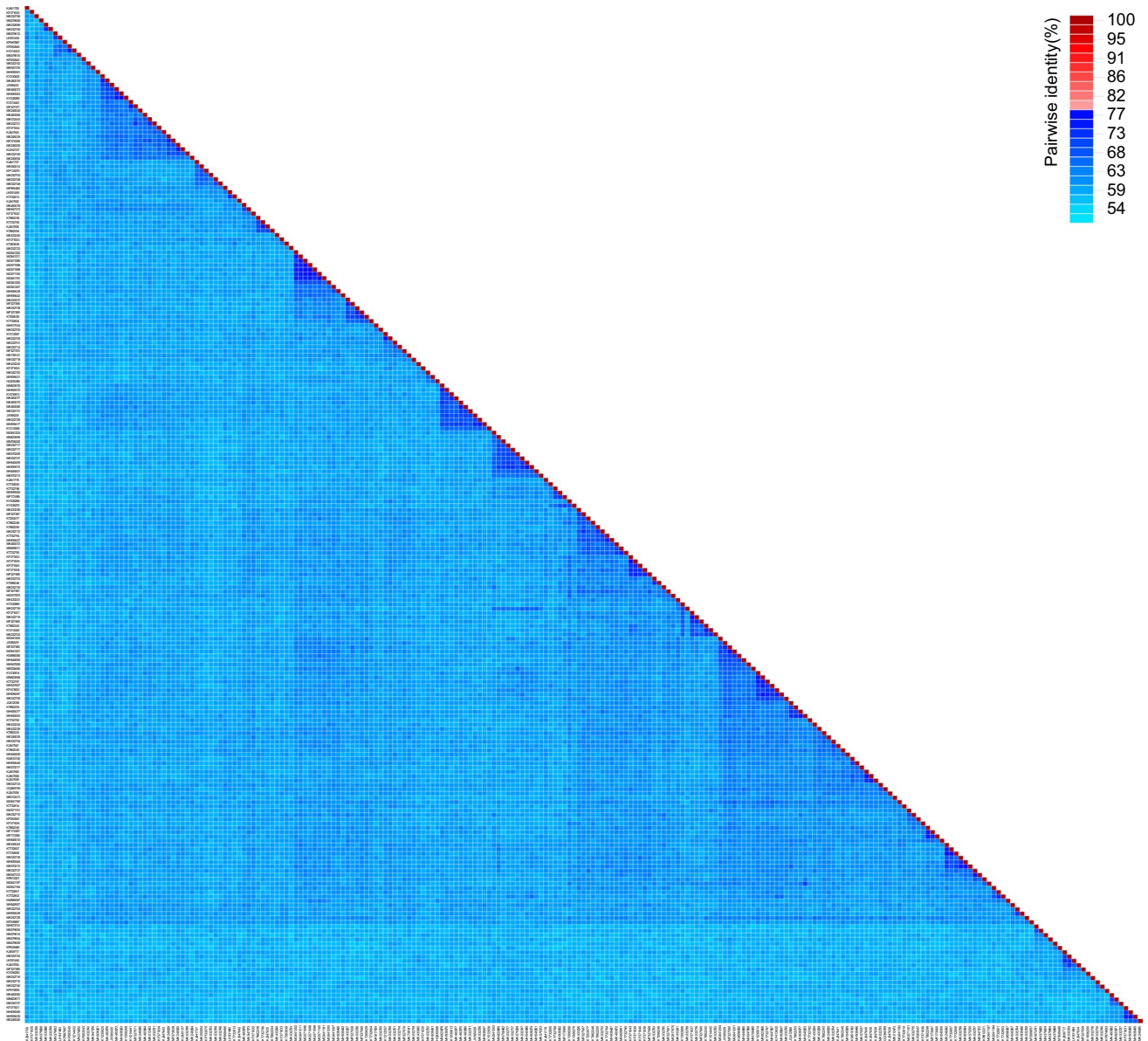


Fig. 2 Pairwise identity matrix of the genome sequence of a representative member of each species of genomovirus (n = 236) except *Gemytripvirus fugra1*, whose representative, *Fusarium graminearum*

gemytripvirus 1, has a multicomponent genome. The analysis was performed using SDT v1.2 [49].

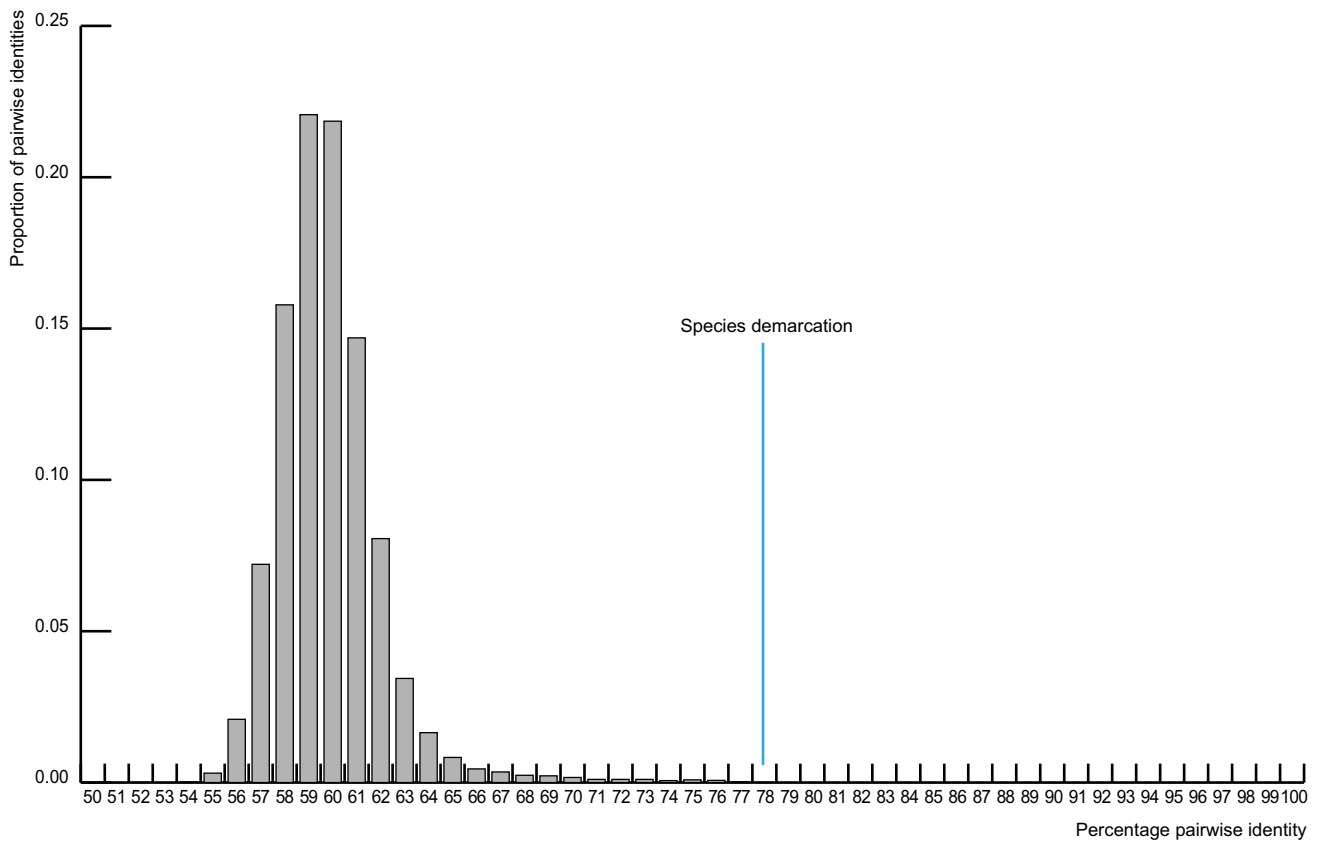


Fig. 3 Pairwise distribution plot of the 236 representative sequences of genomoviruses (except *Fusarium graminearum gemytripvirus 1* [species *Gemytripvirus fugra1*], which has a multicomponent genome), showing that no sequences from different species share >78% identity.

Fig. 4 Summary of the number of genomovirids assigned to each genus and source from which the genomes was obtained

	Actinopterygii	Arachnida	Aves	Embryophyte	Environmental	Gastropoda	Insecta	Leotiomyces	Mammalia	Reptilia	Total
<i>Gemycircularvirus</i>	8	10	49	35	13	2	28	3	94	9	251
<i>Gemyduguvirus</i>	2		1	12			3		4		22
<i>Gemygorvirus</i>			3	8	1				6		18
<i>Gemykibivirus</i>	3	1	54	17	6	2	10		46	15	154
<i>Gemykolovirus</i>	2	2		46		1	2		5	2	60
<i>Gemykrogvirus</i>	1		12		1	1	1		5	1	22
<i>Gemykronzavirus</i>			3	7					3		13
<i>Gemytondovirus</i>			1								1
<i>Gemytripvirus</i>								1			1
<i>Gemyvongvirus</i>	2								1		3
Total	18	13	123	125	21	6	44	4	164	27	545

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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