



Taxonomic update for mammalian anelloviruses (family *Anelloviridae*)

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Abstract

Anelloviruses are small negative-sense single-stranded DNA viruses with genomes ranging in size from 1.6 to 3.9 kb. The family *Anelloviridae* comprised 14 genera before the present changes. However, in the last five years, a large number of diverse anelloviruses have been identified in various organisms. Here, we undertake a global analysis of mammalian anelloviruses whose full genome sequences have been determined and have an intact open reading frame 1 (ORF1). We established new criteria for the classification of anelloviruses, and, based on our analyses, we establish new genera and species to accommodate the unclassified anelloviruses. We also note that based on the updated species demarcation criteria, some previously assigned species ($n = 10$) merge with other species. Given the rate at which virus sequence data are accumulating, and with the identification of diverse anelloviruses, we acknowledge that the taxonomy will have to be dynamic and continuously evolve to accommodate new members.

Anelloviruses are circular negative-sense DNA viruses. They have genomes ranging in size from 1.6 to 3.9 kb. Anelloviruses that infect mammals have one large and two or three smaller open reading frames (ORFs) [5, 6, 71]. Gyroviruses (genus *Gyrovirus*) were assigned to the family *Anelloviridae* in 2017 [57]. Gyroviruses that have been identified primarily in avian species have at least three large ORFs.

Mammalian anelloviruses have been identified in a broad range of animals of the families Aotidae, Callitrichidae, Canidae, Cercopithecidae, Cricetidae, Didelphidae, Equidae, Felidae, Hominidae, Indriidae, Leporidae, Molossidae,

Muridae, Mustelidae, Otariidae, Phocidae, Phyllostomidae, Procyonidae, Suidae, Tupaiidae, Ursidae, and Viverridae [1–4, 7, 8, 12–27, 29, 32–34, 39–56, 61–65, 72–76] (Supplementary Table S1). They have also been found in blood-feeding invertebrates of the families Culicidae [38] and Ixodidae [70] (likely derived from the blood meal from their host, but they do not infect these invertebrates), and in faecal samples of predators such as the South Polar skua (family Stercorariidae) [17] (Supplementary Table S1).

The family *Anelloviridae* was composed of 14 genera (Table 1). Except for viruses in the genus *Gyrovirus*, all

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Table 1 List of genera in the family *Anelloviridae*

	Genus
Previously established	<i>Alphatorquevirus</i>
	<i>Betatorquevirus</i>
	<i>Deltatorquevirus</i>
	<i>Epsilontorquevirus</i>
	<i>Etatorquevirus</i>
	<i>Gammatorquevirus</i>
	<i>Iotatorquevirus</i>
	<i>Kappatorquevirus</i>
	<i>Lambdatorquevirus</i>
	<i>Mutorquevirus</i>
	<i>Nutorquevirus</i>
	<i>Thetatorquevirus</i>
	<i>Zetatorquevirus</i>
	<i>Gyrovirus</i>
	Newly established
<i>Omegatorquevirus</i>	
<i>Omicrontorquevirus</i>	
<i>Pitorquevirus</i>	
<i>Psitorquevirus</i>	
<i>Rhotorquevirus</i>	
<i>Sigmatorquevirus</i>	
<i>Upsilon-torquevirus</i>	
<i>Xitorquevirus</i>	
<i>Aleptorquevirus</i>	
<i>Dalettorquevirus</i>	
<i>Gimeltorquevirus</i>	
<i>Hetorquevirus</i>	
<i>Tettorquevirus</i>	
<i>Wawtorquevirus</i>	
<i>Zayintorquevirus</i>	

anelloviruses had previously been classified based on pairwise identity values derived from a global alignment of nucleotide sequences of the ORF1 coding region. Previously a 65% sequence identity threshold was established for species demarcation, whereas a 44% sequence identity threshold was used for genus demarcation classification [5, 6]. The use of global alignment-derived pairwise identity values can result in the deflation of the sequence identity values due to fixed gaps. This becomes problematic, especially when diverse sequences are included in such alignments. Thus, here, we use true pairwise sequence identity values to determine their distribution in order to establish species demarcation thresholds. We analysed the annotated ORF1 coding (complete ORF1) regions of complete anellovirus genome sequences (n = 749) available in the GenBank database (downloaded 10 July 2020). We determined the pairwise identity values for all the ORF1 nucleotide sequences using

SDT v1.2 [37]. The plot of the distribution of the pairwise identity values (Fig. 1) revealed a trough at ~69%.

Using 69% as a species demarcation threshold, of the 75 currently established species, viruses in only 10 species did not fit this criterion, and thus these species were abolished and the corresponding viruses were reassigned to already established species (see Table 2 for abolished species and the reassignment of viruses). The 69% species demarcation threshold has also been used for the classification of the viruses in the genus *Gyrovirus*, which now has nine new species (see Kraberger *et al.* [30]).

To establish genus demarcation criteria, since the pairwise identity plot does not give a clear demarcation threshold, we opted for a phylogeny-based approach using the ORF1 amino acid sequences. A dataset of the ORF1 amino acid sequences of a representative member of each species was assembled, and this was then aligned using MAFFT [28]. The alignment was trimmed with TrimAL [11] using the gappyout option, and the alignment was used to infer a maximum-likelihood tree with IQTree [35] with the LG+F+G4 substitution model. The TrimAL alignment contained 361 amino acid sites in the final alignment. The resulting maximum-likelihood phylogenetic tree was rooted at the midpoint and edited in iTOL v4 [31]. Based on the phylogeny (Fig. 2), we established a total of 16 new genera (Table 1).

We used the Greek alphabet for naming new genera. In the spirit of using ancient alphabets, we adopt the Phoenician alphabet for an additional six new genera in series without using 'bet' (to avoid confusion with "beta"). In the future, the following letters of the Phoenician alphabet can be used for new genus names with minimal conflict with current names: yod, lamed, mem, samek, ayin, pe, sade, qop, res, sin, tau.

Furthermore, based on the criteria discussed above, we have established 80 new species (see Table 3). A comprehensive list of the new classification of anelloviruses is provided in Supplementary Table S1. This includes all sequences with sufficient information for their classification available in GenBank on 20 May 2021. The new species (n = 9) associated with the genus *Gyrovirus* are discussed in detail in Kraberger *et al.* [30].

We recommend that true pairwise identity determination tools be used for determining anellovirus species assignments. We also recommend the following guideline for determining new species of mammalian viruses within the family *Anelloviridae*, which aligns with previous recommendations for full-genome pairwise identity-based classification for single-stranded DNA satellite molecules in the family *Alphasatellitidae* [9] and viruses in the families *Circoviridae* [57], *Geminiviridae* [10, 36, 66, 67], *Genomoviridae* [68], and *Smacoviridae* [69].

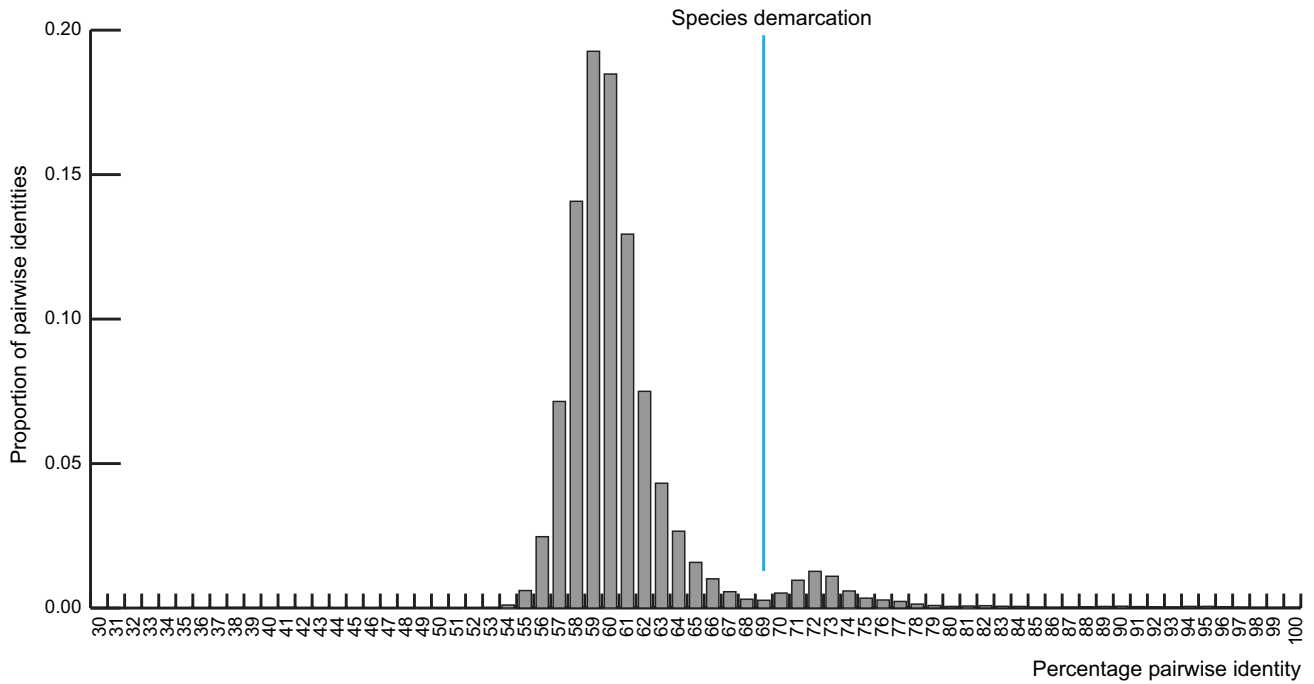


Fig. 1 Distribution of pairwise identity values of the ORF1 nucleotide sequences of anellovirus genomes available in the GenBank database (n = 749), determined using SDT v1.2 [37]

Table 2 Summary of recent taxonomic changes to previously established species

Genus	Modified / reassigned species name	Previous species name	Exemplar virus	Accession no.
<i>Alphatorquevirus</i>	<i>Torque teno virus 7</i>	◄ <i>Torque teno virus 8</i>	torque teno virus 8	AB054647
	<i>Torque teno virus 9</i>	◄ <i>Torque teno virus 11</i>	torque teno virus 11	AF345524
	<i>Torque teno virus 9</i>	◄ <i>Torque teno virus 12</i>	torque teno virus 12	AB064605
	<i>Torque teno virus 15</i>	◄ <i>Torque teno virus 16</i>	torque teno virus 16	AB017613
	<i>Torque teno virus 24</i>	◄ <i>Torque teno virus 22</i>	torque teno virus 22	AX174942
	<i>Torque teno virus 24</i>	◄ <i>Torque teno virus 23</i>	torque teno virus 23	AB049607
	<i>Torque teno virus 29</i>	◄ <i>Torque teno virus 27</i>	torque teno virus 27	AB064595
	<i>Torque teno virus 29</i>	◄ <i>Torque teno virus 28</i>	torque teno virus 28	AB064598
<i>Etatorquevirus</i>	<i>Torque teno felid virus 1</i>	■ <i>Torque teno felis virus</i>	torque teno felis virus	AB076003
	<i>Torque teno felid virus 2</i>	■ <i>Torque teno felis virus 2</i>	torque teno felis virus 2	EF538877
<i>Iotatorquevirus</i>	<i>Torque teno sus virus 1a</i>	◄ <i>Torque teno sus virus 1b</i>	torque teno sus virus 1b	AY823990
<i>Lambdatorquevirus</i>	<i>Torque teno pinniped virus 1</i>	■ <i>Torque teno seal virus 1</i>	seal anellovirus TFFN	HQ287751
	<i>Torque teno pinniped virus 2</i>	■ <i>Torque teno seal virus 2</i>	torque teno seal virus 2	KF373760
	<i>Torque teno pinniped virus 3</i>	■ <i>Torque teno seal virus 3</i>	torque teno seal virus 3	KF373758
	<i>Torque teno pinniped virus 8</i>	■ <i>Torque teno seal virus 8</i>	torque teno <i>Leptonychotes weddellii</i> virus 1	KY246582
	<i>Torque teno pinniped virus 9</i>	■ <i>Torque teno seal virus 9</i>	torque teno <i>Leptonychotes weddellii</i> virus 2	KY246547
<i>Mutorquevirus</i>	<i>Torque teno equid virus 1</i>	■ <i>Torque teno equus virus 1</i>	torque teno equus virus 1	KR902501
<i>Nutorquevirus</i>	<i>Torque teno pinniped virus 4</i>	◄ <i>Torque teno seal virus 4</i>	seal anellovirus 4	KM262783
	<i>Torque teno pinniped virus 4</i>	■ <i>Torque teno seal virus 5</i>	seal anellovirus 5	KM262782
<i>Thetatorquevirus</i>	<i>Torque teno canid virus 1</i>	■ <i>Torque teno canis virus</i>	torque teno canis virus	AB076002

Taxa that have been abolished are marked with a “◄” symbol, and taxa that have been renamed are marked with a “■” symbol

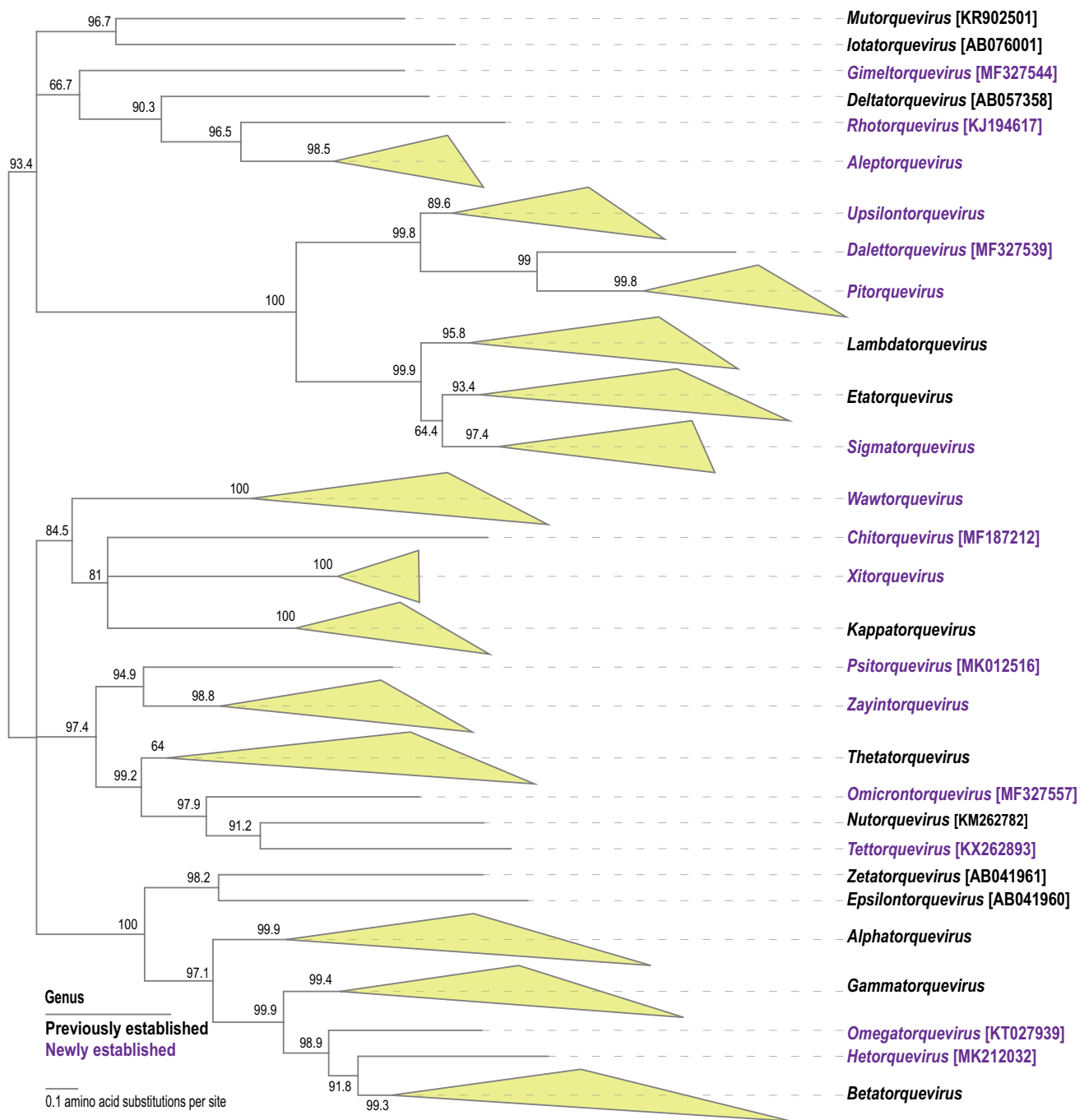


Fig. 2 Maximum-likelihood phylogenetic tree of the ORF1-encoded amino acid sequences of representative member of each species in the family *Anelloviridae*. The sequences of gyroviruses are not included,

as their VP1 is not homologous to ORF1. Numbers at the nodes represent aLRT branch support values. Branches with less than 60% support have been collapsed with TreeGraph2 [60]

1. If the complete ORF1 coding region nucleotide sequence of a new anellovirus shares >69% pairwise identity with that of any member assigned to a currently classified anellovirus species, the virus belongs to that particular species.
 - a. In the event that the complete ORF1 coding region nucleotide sequence of a new anellovirus has >69% pairwise identity to those of members of more than one anellovirus species, the virus should be considered a member of the species with whose members

Table 3 Summary of the genera, type species, species, and exemplar viruses

Genus	Species	Accession no.	Exemplar virus name	Isolate ID	
▶ <i>Aleptorquevirus</i>	◇ <i>Torque teno lepid virus 1</i>	MN994854	Lepus torque teno virus 1	Lag01_EL_Anello4	
	◇ <i>Torque teno arthrovec virus 1</i>	HQ335082	mosquito VEM Anellovirus SDBVL	SDBVL A	
<i>Alphatorquevirus</i>	<i>Torque teno virus 1</i>	AB041007	torque teno virus 1	VT416	
	<i>Torque teno virus 2</i>	AB049608	torque teno virus 2	CH71	
	<i>Torque teno virus 3</i>	AY666122	torque teno virus 3	HEL32	
	<i>Torque teno virus 4</i>	AB041957	torque teno virus 4	Pt-TTV6	
	<i>Torque teno virus 5</i>	AF345523	torque teno virus 5	TCHN-C1	
	<i>Torque teno virus 6</i>	AF435014	torque teno virus 6	KAV	
	<i>Torque teno virus 7</i>	AF261761	torque teno virus 7	PMV	
	<i>Torque teno virus 9</i>	DQ187006	torque teno virus 9	BM1C	
	<i>Torque teno virus 10</i>	AB064607	torque teno virus 10	JT34F	
	<i>Torque teno virus 13</i>	AF345526	torque teno virus 13	TCHN-A	
	<i>Torque teno virus 14</i>	AB037926	torque teno virus 14	s-TTV CH65-1	
	<i>Torque teno virus 15</i>	AB028668	torque teno virus 15	TJN01	
	<i>Torque teno virus 17</i>	AX025830	torque teno virus 17		
	<i>Torque teno virus 18</i>	AX025718	torque teno virus 18		
	<i>Torque teno virus 19</i>	AB025946	torque teno virus 19	TTV SANBAN	
	<i>Torque teno virus 20</i>	AB060594	torque teno virus 20	SAA-10	
	<i>Torque teno virus 21</i>	AF348409	torque teno virus 21	TCHN-B	
	<i>Torque teno virus 24</i>	AB060597	torque teno virus 24	Saa-01	
	<i>Torque teno virus 25</i>	AB041959	torque teno virus 25	Mf-TTV9	
	<i>Torque teno virus 26</i>	AB041958	torque teno virus 26	Mf-TTV3	
	<i>Torque teno virus 29</i>	AB038621	torque teno virus 29	TTVyon-KC009	
	<i>Torque teno virus 31</i>	KJ082064	torque teno virus	TTV-Hebei-1	
	<i>Betatorquevirus</i>	◇ <i>Torque teno chlorocebus virus 1</i>	KP296857	simian torque teno virus 30	VWP00522.2
		◇ <i>Torque teno chlorocebus virus 2</i>	KP296856	simian torque teno virus 34	VGA00120.1
		◇ <i>Torque teno chlorocebus virus 3</i>	KP296853	simian torque teno virus 31	VGA00123.3
◇ <i>Torque teno chlorocebus virus 5</i>		KP296854	simian torque teno virus 32	VGA00154.2	
<i>Torque teno mini virus 1</i>		AB026931	torque teno mini virus 1	TLMV-CBD279	
<i>Torque teno mini virus 2</i>		AB038629	torque teno mini virus 2	TLMV-NLC023	
<i>Torque teno mini virus 3</i>		AB038630	torque teno mini virus 3	TLMV-NLC026	
<i>Torque teno mini virus 4</i>		AB041963	torque teno mini virus 4	Pt-TTV8-II	
<i>Torque teno mini virus 5</i>		AB041962	torque teno mini virus 5	TGP96	
<i>Torque teno mini virus 6</i>		AB026929	torque teno mini virus 6	TLMV-CBD203	
<i>Torque teno mini virus 7</i>		AB038627	torque teno mini virus 7	TLMV-CLC156	
<i>Torque teno mini virus 8</i>		AF291073	torque teno mini virus 8	PB4TL	
<i>Torque teno mini virus 9</i>		AB038625	torque teno mini virus 9	TLMV-CLC062	
<i>Torque teno mini virus 10</i>		EF538880	torque teno mini virus 10	LIL-y1	
<i>Torque teno mini virus 11</i>		EF538881	torque teno mini virus 11	LIL-y2	
<i>Torque teno mini virus 12</i>		EF538882	torque teno mini virus 12	LIL-y3	
◇ <i>Torque teno mini virus 13</i>		KY856742	TTV-like mini virus	zhenjiang	
◇ <i>Torque teno mini virus 14</i>		MH017546	torque teno mini virus 10	BNI-700620-G1-CS	
◇ <i>Torque teno mini virus 15</i>		JX134044	TTV-like mini virus	TTMV_LY1	
◇ <i>Torque teno mini virus 16</i>		KM259874	torque teno mini virus ALH8	TTMV-ALH8	
◇ <i>Torque teno mini virus 17</i>		MH648907	Anelloviridae sp.	ctcf040	
◇ <i>Torque teno mini virus 18</i>	KF764701	TTV-like mini virus	D11		
◇ <i>Torque teno mini virus 19</i>	JX134046	TTV-like mini virus	TTMV_LY3		
◇ <i>Torque teno mini virus 20</i>	MH648989	Anelloviridae sp.	ctga035		
◇ <i>Torque teno mini virus 21</i>	MH648910	Anelloviridae sp.	ctcd026		

Table 3 (continued)

Genus	Species	Accession no.	Exemplar virus name	Isolate ID
	◇ <i>Torque teno mini virus 22</i>	MK212031	TTV-like mini virus	vzttmv4
	◇ <i>Torque teno mini virus 23</i>	KX810063	TTV-like mini virus	Emory1
	◇ <i>Torque teno mini virus 24</i>	MH649141	Anelloviridae sp.	ctbc019
	◇ <i>Torque teno mini virus 25</i>	MH648986	Anelloviridae sp.	ctcb059
	◇ <i>Torque teno mini virus 26</i>	KY462770	torque teno mini virus SHA	SHA
	◇ <i>Torque teno mini virus 27</i>	KM259873	torque teno mini virus ALA22	TTMV-ALA22
	◇ <i>Torque teno mini virus 28</i>	MH017563	torque teno mini virus 10	BNI-700835-G3-CSF
	◇ <i>Torque teno mini virus 29</i>	KX810064	TTV-like mini virus	Emory2
	◇ <i>Torque teno mini virus 30</i>	MH648912	Anelloviridae sp.	ctea38
	◇ <i>Torque teno mini virus 31</i>	MH649017	Anelloviridae sp.	ctbb016
	◇ <i>Torque teno mini virus 32</i>	KU041847	torque teno mini virus 18	222
	◇ <i>Torque teno mini virus 33</i>	MH649029	Anelloviridae sp.	ctbi042
	◇ <i>Torque teno mini virus 34</i>	MH649114	Anelloviridae sp.	ctbf050
	◇ <i>Torque teno mini virus 35</i>	MH648966	Anelloviridae sp.	ctei055
	◇ <i>Torque teno mini virus 36</i>	LC381845	torque teno virus	KS025
	◇ <i>Torque teno mini virus 37</i>	MH649209	Anelloviridae sp.	ctbg056
	◇ <i>Torque teno mini virus 38</i>	MH648982	Anelloviridae sp.	ctbf014
► <i>Chitorquevirus</i>	◇ <i>Torque teno indriid virus 1</i>	MF187212	torque teno indri virus 1	bet12.15
► <i>Dalettorquevirus</i>	◇ <i>Torque teno ursid virus 6</i>	MF327539	giant panda anellovirus	gpan20793
<i>Deltatorquevirus</i>	<i>Torque teno tupaia virus</i>	AB057358	torque teno tupaia virus	Tbc-TTV14
<i>Epsilontorquevirus</i>	<i>Torque teno tamarin virus</i>	AB041960	torque teno tamarin virus	So-TTV2
<i>Etatorquevirus</i>	<i>Torque teno felid virus 1</i>	AB076003	torque teno felis virus	Fc-TTV4
	<i>Torque teno felid virus 2</i>	EF538877	torque teno felis virus 2	PRA1
	◇ <i>Torque teno felid virus 3</i>	MK069470	torque teno ocelot virus	WF10
	◇ <i>Torque teno felid virus 4</i>	JF304938	torque teno felis virus-Fc-TTV2	VS4300008
	● ◇ <i>Torque teno felid virus 5</i>	JF304937	torque teno felis virus-Fc-TTV1	VS4300006
	◇ <i>Torque teno viverrid virus 3</i>	LC387548	Paguma larvata torque teno virus	Pl-TTV3
<i>Gammatorquevirus</i>	<i>Torque teno midi virus 1</i>	AB290917	torque teno midi virus 1	MD1-032
	<i>Torque teno midi virus 2</i>	AB290919	torque teno midi virus 2	MD2-013
	<i>Torque teno midi virus 3</i>	EF538875	torque teno midi virus 3	2PoSMA
	<i>Torque teno midi virus 4</i>	EF538876	torque teno midi virus 4	6Po-SMA
	<i>Torque teno midi virus 5</i>	AB303552	torque teno midi virus 5	MDJHem2
	<i>Torque teno midi virus 6</i>	AB303553	torque teno midi virus 6	MDJHem3-1
	<i>Torque teno midi virus 7</i>	AB303554	torque teno midi virus 7	MDJHem3-2
	<i>Torque teno midi virus 8</i>	AB303558	torque teno midi virus 8	MDJN1
	<i>Torque teno midi virus 9</i>	AB303559	torque teno midi virus 9	MDJN2
	<i>Torque teno midi virus 10</i>	AB303560	torque teno midi virus 10	MDJN14
	<i>Torque teno midi virus 11</i>	AB303561	torque teno midi virus 11	MDJN47
	<i>Torque teno midi virus 12</i>	AB303562	torque teno midi virus 12	MDJN51
	<i>Torque teno midi virus 13</i>	AB303564	torque teno midi virus 13	MDJN69
	<i>Torque teno midi virus 14</i>	AB303566	torque teno midi virus 14	MDJN97
	<i>Torque teno midi virus 15</i>	AB449062	torque teno midi virus 15	Pt-TTMDV210
► <i>Gimeltorquevirus</i>	◇ <i>Torque teno virus 30</i>	MF327544	giant panda anellovirus	gpan20806
<i>Gyrovirus</i>	<i>Chicken anemia virus</i>	M55918	Chicken anemia virus	Cuxhaven-1
	◇ <i>Gyrovirus fulgla1</i>	KR137527	gyrovirus GyV8	GyV8
	◇ <i>Gyrovirus galga1</i>	HM590588	avian gyrovirus 2	Ave 3
	◇ <i>Gyrovirus galga2</i>	KM111536	gyrovirus GyV7-SF	GyV7-SF
	◇ <i>Gyrovirus homsa1</i>	JQ308210	gyrovirus GyV3	FecGy
	◇ <i>Gyrovirus homsa2</i>	KF294862	gyrovirus Tu789	Tu789
	◇ <i>Gyrovirus homsa3</i>	JX310702	gyrovirus 4	D137

Table 3 (continued)

Genus	Species	Accession no.	Exemplar virus name	Isolate ID
	◇ <i>Gyrovirus homsa4</i>	KF294861	gyrovirus Tu243	Tu243
	◇ <i>Gyrovirus hydho1</i>	MH378452	ashy storm petrel gyrovirus	a12a1_528
	◇ <i>Gyrovirus myferr1</i>	MH638372	gyrovirus 11	GyV11
▶ <i>Hetorquevirus</i>	◇ <i>Torque teno hominid virus 2</i>	MK212032	Anelloviridae sp.	vztm5
<i>Iotorquevirus</i>	<i>Torque teno sus virus 1a</i>	AB076001	torque teno sus virus 1a	Sd-TTV31
<i>Kappatorquevirus</i>	<i>Torque teno sus virus k2a</i>	AY823991	torque teno sus virus k2a	2p
	<i>Torque teno sus virus k2b</i>	JQ406846	torque teno sus virus k2b	38E23
<i>Lambdatorquevirus</i>	<i>Torque teno pinniped virus 1</i>	HQ287751	seal anellovirus TFFN	TGGN
	<i>Torque teno pinniped virus 2</i>	KF373760	seal anellovirus 2	12-410
	<i>Torque teno pinniped virus 3</i>	KF373758	seal anellovirus 3	12-410
	<i>Torque teno pinniped virus 8</i>	KY246582	torque teno <i>Leptonychotes weddellii</i> virus-1	gt16_wsp8
	<i>Torque teno pinniped virus 9</i>	KY246547	torque teno <i>Leptonychotes weddellii</i> virus-2	gt3_wsp24
<i>Mutorquevirus</i>	<i>Torque teno equid virus 1</i>	KR902501	torque teno equus virus 1	horse 1
<i>Nutorquevirus</i>	<i>Torque teno pinniped virus 4</i>	KM262782	seal anellovirus 5	SeAv5-PV13-431
▶ <i>Omegatorquevirus</i>	◇ <i>Torque teno hominid virus 1</i>	KT027939	gorilla anellovirus	GorF
▶ <i>Omicrontorquevirus</i>	◇ <i>Torque teno ursid virus 5</i>	MF327557	giant panda anellovirus	gpan20684
▶ <i>Pitorquevirus</i>	◇ <i>Torque teno ursid virus 7</i>	MF327540	giant panda anellovirus	gpan21094
	◇ <i>Torque teno ursid virus 10</i>	MF327541	giant panda anellovirus	gpan20868
	◇ <i>Torque teno ursid virus 8</i>	MF327542	giant panda anellovirus	gpan21031
	◇ <i>Torque teno ursid virus 9</i>	MF327550	giant panda anellovirus	gpan20868
	◇ <i>Torque teno ursid virus 11</i>	MF327548	giant panda anellovirus	gpan21066
	◇ <i>Torque teno ursid virus 12</i>	MF327547	giant panda anellovirus	gpan21031
▶ <i>Psitorquevirus</i>	◇ <i>Torque teno procyo virus 4</i>	MK012516	Anelloviridae sp.	ctcf003
▶ <i>Rhotorquevirus</i>	◇ <i>Torque teno rodent virus 1</i>	KJ194617	rodent torque teno virus 1	AS_WM1_Sp_1
▶ <i>Sigmatorquevirus</i>	● <i>Torque teno pinniped virus 5</i>	FJ459582	torque teno <i>zalophus</i> virus 1	
	◇ <i>Torque teno pinniped virus 6</i>	MG837569	torque teno <i>Arctocephalus gazella</i> virus 1	ASV20_172
	◇ <i>Torque teno pinniped virus 7</i>	MG837571	torque teno <i>Arctocephalus gazella</i> virus 2	ASV35_197
▶ <i>Tettorquevirus</i>	◇ <i>Torque teno felid virus 6</i>	KX262893	feline anellovirus	FelineAV621
<i>Thetatorquevirus</i>	<i>Torque teno canid virus 1</i>	AB076002	torque teno canis virus	Cf-TTV10
	◇ <i>Torque teno arthrovec virus 3</i>	MF173068	tick associated torque teno virus	tick24_1
	◇ <i>Torque teno mustilid virus 1</i>	JN704611	pine marten torque teno virus 1	VS4700004
	◇ <i>Torque teno procyo virus 5</i>	MK012446	Anelloviridae sp.	ctdb009
	◇ <i>Torque teno procyo virus 6</i>	MK012439	Anelloviridae sp.	cthe000
	◇ <i>Torque teno ursid virus 1</i>	KX611132	lesser panda anellovirus	chengdu-1
	◇ <i>Torque teno ursid virus 2</i>	MF327551	giant panda anellovirus	gpan20783
	◇ <i>Torque teno ursid virus 3</i>	MF327552	giant panda anellovirus	gpan20682
	◇ <i>Torque teno ursid virus 4</i>	MF327554	giant panda anellovirus	gpan20724
	◇ <i>Torque teno viverrid virus 4</i>	LC387543	<i>Paguma larvata</i> torque teno virus	PI-TTV9-2
▶ <i>Upsilontorquevirus</i>	◇ <i>Torque teno procyo virus 1</i>	MK012447	Anelloviridae sp.	ctcf003
	◇ <i>Torque teno procyo virus 2</i>	MK012527	Anelloviridae sp.	ctcf007
	◇ <i>Torque teno procyo virus 3</i>	MK012497	Anelloviridae sp.	ctdc005
	◇ <i>Torque teno procyo virus 7</i>	MK012464	Anelloviridae sp.	ctbd010
	◇ <i>Torque teno procyo virus 8</i>	MK012467	Anelloviridae sp.	ctbb008
	◇ <i>Torque teno procyo virus 9</i>	MK012471	Anelloviridae sp.	ctbb005
	◇ <i>Torque teno viverrid virus 2</i>	LC387546	<i>Paguma larvata</i> torque teno virus	PI-TTV9-1
▶ <i>Wawtorquevirus</i>	◇ <i>Torque teno rodent virus 2</i>	MF541374	rodent torque teno virus 3	2

Table 3 (continued)

Genus	Species	Accession no.	Exemplar virus name	Isolate ID
	◇ <i>Torque teno arthrovec virus 2</i>	HQ335084	mosquito VEM Anellovirus SDRB A	SDRB
	◇ <i>Torque teno rodent virus 3</i>	MF541388	rodent torque teno virus 7	15
	◇ <i>Torque teno rodent virus 4</i>	KJ194604	rodent torque teno virus 2	AS_WM1_Se_4
	◇ <i>Torque teno rodent virus 5</i>	KM609325	rodent torque teno virus 2	RN_8_Se11
	◇ <i>Torque teno rodent virus 6</i>	MF541389	rodent torque teno virus 8	2252
► <i>Xitorquevirus</i>	◇ <i>Torque teno chiroptera virus 1</i>	KM434181	torque teno Tadarida brasiliensis virus	
	◇ <i>Torque teno didelphi virus 1</i>	MF541378	torque teno Didelphis albiventris virus	3470
► <i>Zayintorquevirus</i>	◇ <i>Torque teno viverrid virus 1</i>	LC387540	Paguma larvata torque teno virus	PI-TTV5-2
	◇ <i>Torque teno viverrid virus 5</i>	LC387536	Paguma larvata torque teno virus	PI-TTV1-1
► <i>Zetatorquevirus</i>	◇ <i>Torque teno douroucouli virus</i>	AB041961	torque teno douroucouli virus	At-TTV3

The symbol “►” indicates a new genus, and the symbol “◇” indicates a new species. The symbol “●” denotes a pending species assignment to the genus with a 2021 taxonomy proposal submitted to the ICTV. The taxonomy of the new gyroviruses is discussed in detail by Kraberger et al. [30]

it shares the highest percentage ORF1 coding region nucleotide sequence pairwise identity.

- b. In the event that the complete ORF1 coding region nucleotide sequence of a new anellovirus has >69% pairwise identity to that of one or more members assigned to a particular anellovirus species, even if it shares <69% identity with those of the majority of the members assigned to that particular anellovirus species, the virus should nevertheless be considered a member of that particular species.
2. If the complete ORF1 coding region nucleotide sequence of a new anellovirus has <69% pairwise identity to those of all members of currently classified anellovirus species, the virus should be considered a member of a new species.

We anticipate a few more changes to the taxonomy of the family *Anelloviridae*, especially in the light of diverse new sequences being deposited from various studies and large viral metagenomic projects using high-throughput sequencing approaches. We also would like to highlight that metagenomic sequence-derived genomes can be classified [59].

We would also like to inform the anellovirus research community that the International Committee on Taxonomy of Viruses (ICTV) has ratified the adoption of standardized binomial virus species names, which can be either in Latinized or free-form format [58]. In establishing the nine new species in the genus *Gyrovirus*, we adopted a binomial “Genus + freeform epithet” species nomenclature (see Kraberger et al. [30]). We plan to adopt the binomial species nomenclature for all species in the family *Anelloviridae* by

the year 2023. Thus, we encourage the community to engage with the ICTV *Anelloviridae* Study Group to determine the binomial names for current and new species in the family *Anelloviridae*.

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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