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VIROLOGY DIVISION NEWS

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	*Alphatorquevirus*
	Betatorquevirus
	Deltatorquevirus
	Epsilontorquevirus
	Etatorquevirus
	Gammatorquevirus
	Iotatorquevirus
	Kappatorquevirus
	Lambdatorquevirus
	Mutorquevirus
	Nutorquevirus
	Thetatorquevirus
	Zetatorquevirus
	Gyrovirus
Newly established	*Chitorquevirus*
	Omegatorquevirus
	Omicrontorquevirus
	Pitorquevirus
	Psitorquevirus
	Rhotorquevirus
	Sigmatorquevirus
	Upsilontorquevirus
	Xitorquevirus
	Aleptorquevirus
	Dalettorquevirus
	Gimeltorquevirus
	Hetorquevirus
	Tettorquevirus
	Wawtorquevirus
	Zayintorquevirus

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, taw.

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].

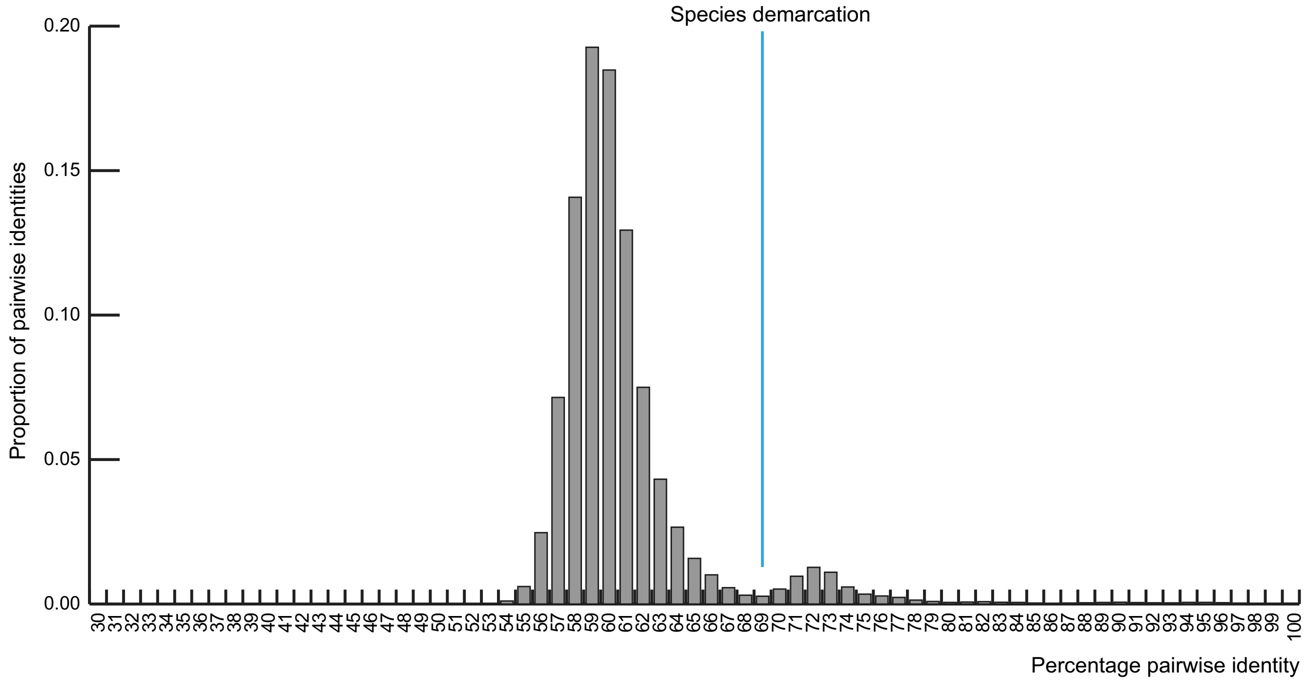

Fig. 1 Distribution of pairwise identity values of the ORF1 nucleotide sequences of anellovirus genomes available in the GenBank database (n = 749), determined using SDT v1.2 [37]

Table 2 Summary of recent taxonomic changes to previously established species

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

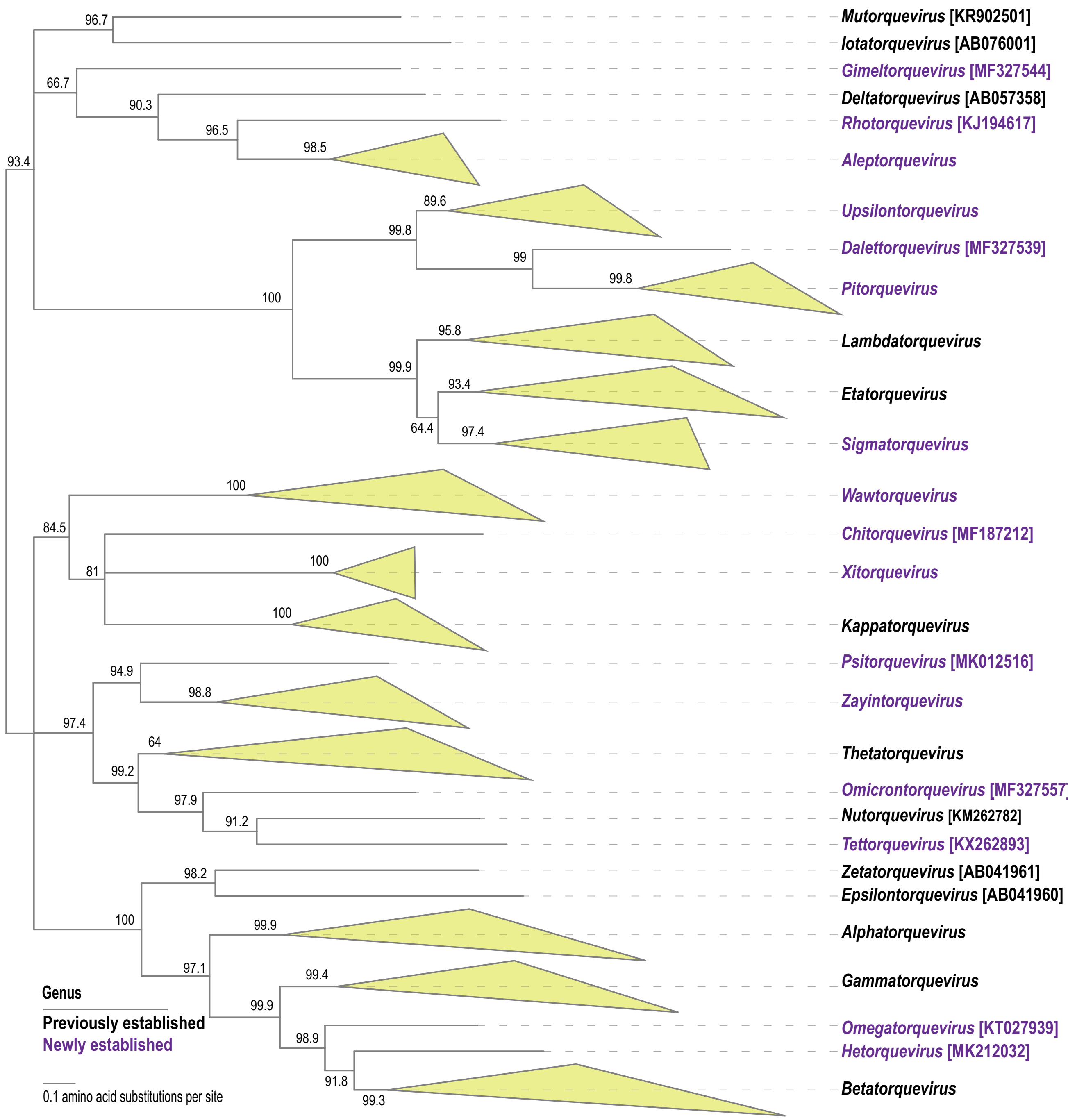

Fig. 2 Maximum-likelihood phylogenetic tree of the ORF1-encoded amino acid sequences of representative member of each species in the family *Anelloviridae*. The sequences of gyroviruses are not included, as their VP1 is not homologous to ORF1. Numbers at the nodes represent aLRT branch support values. 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
►	*Aleptorquevirus*	◊	*Torque teno leprid virus 1*	MN994854	Lepus torque teno virus 1	Lag01_EL_Anello4
		◊	*Torque teno arthrovec virus 1*	HQ335082	mosquito VEM Anellovirus SDBVL	SDBVL A
	Alphatorquevirus		*Torque teno virus 1*	AB041007	torque teno virus 1	VT416
			Torque teno virus 2	AB049608	torque teno virus 2	CH71
			Torque teno virus 3	AY666122	torque teno virus 3	HEL32
			Torque teno virus 4	AB041957	torque teno virus 4	Pt-TTV6
			Torque teno virus 5	AF345523	torque teno virus 5	TCHN-C1
			Torque teno virus 6	AF435014	torque teno virus 6	KAV
			Torque teno virus 7	AF261761	torque teno virus 7	PMV
			Torque teno virus 9	DQ187006	torque teno virus 9	BM1C
			Torque teno virus 10	AB064607	torque teno virus 10	JT34F
			Torque teno virus 13	AF345526	torque teno virus 13	TCHN-A
			Torque teno virus 14	AB037926	torque teno virus 14	s-TTV CH65-1
			Torque teno virus 15	AB028668	torque teno virus 15	TJN01
			Torque teno virus 17	AX025830	torque teno virus 17	
			Torque teno virus 18	AX025718	torque teno virus 18	
			Torque teno virus 19	AB025946	torque teno virus 19	TTV SANBAN
			Torque teno virus 20	AB060594	torque teno virus 20	SAa-10
			Torque teno virus 21	AF348409	torque teno virus 21	TCHN-B
			Torque teno virus 24	AB060597	torque teno virus 24	Saa-01
			Torque teno virus 25	AB041959	torque teno virus 25	Mf-TTV9
			Torque teno virus 26	AB041958	torque teno virus 26	Mf-TTV3
			Torque teno virus 29	AB038621	torque teno virus 29	TTVyon-KC009
			Torque teno virus 31	KJ082064	torque teno virus	TTV-Hebei-1
		◊	*Torque teno chlorocebus virus 1*	KP296857	simian torque teno virus 30	VWP00522.2
		◊	*Torque teno chlorocebus virus 2*	KP296856	simian torque teno virus 34	VGA00120.1
		◊	*Torque teno chlorocebus virus 3*	KP296853	simian torque teno virus 31	VGA00123.3
		◊	*Torque teno chlorocebus virus 5*	KP296854	simian torque teno virus 32	VGA00154.2
	Betatorquevirus		*Torque teno mini virus 1*	AB026931	torque teno mini virus 1	TLMV-CBD279
			Torque teno mini virus 2	AB038629	torque teno mini virus 2	TLMV-NLC023
			Torque teno mini virus 3	AB038630	torque teno mini virus 3	TLMV-NLC026
			Torque teno mini virus 4	AB041963	torque teno mini virus 4	Pt-TTV8-II
			Torque teno mini virus 5	AB041962	torque teno mini virus 5	TGP96
			Torque teno mini virus 6	AB026929	torque teno mini virus 6	TLMV-CBD203
			Torque teno mini virus 7	AB038627	torque teno mini virus 7	TLMV-CLC156
			Torque teno mini virus 8	AF291073	torque teno mini virus 8	PB4TL
			Torque teno mini virus 9	AB038625	torque teno mini virus 9	TLMV-CLC062
			Torque teno mini virus 10	EF538880	torque teno mini virus 10	LIL-y1
			Torque teno mini virus 11	EF538881	torque teno mini virus 11	LIL-y2
			Torque teno mini virus 12	EF538882	torque teno mini virus 12	LIL-y3
		◊	*Torque teno mini virus 13*	KY856742	TTV-like mini virus	zhenjiang
		◊	*Torque teno mini virus 14*	MH017546	torque teno mini virus 10	BNI-700620-G1-CS
		◊	*Torque teno mini virus 15*	JX134044	TTV-like mini virus	TTMV_LY1
		◊	*Torque teno mini virus 16*	KM259874	torque teno mini virus ALH8	TTMV-ALH8
		◊	*Torque teno mini virus 17*	MH648907	Anelloviridae sp.	ctcf040
		◊	*Torque teno mini virus 18*	KF764701	TTV-like mini virus	D11
		◊	*Torque teno mini virus 19*	JX134046	TTV-like mini virus	TTMV_LY3
		◊	*Torque teno mini virus 20*	MH648989	Anelloviridae sp.	ctga035
		◊	*Torque teno mini virus 21*	MH648910	Anelloviridae sp.	ctcd026

Table 3 (continued)

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

Table 3 (continued)

	Genus			Species	Accession no.	Exemplar virus name	Isolate ID
			◊	*Gyrovirus homsa4*	KF294861	gyrovirus Tu243	Tu243
			◊	*Gyrovirus hydho1*	MH378452	ashy storm petrel gyrovirus	a12a1_528
			◊	*Gyrovirus myferr1*	MH638372	gyrovirus 11	GyV11
►	*Hetorquevirus*		◊	*Torque teno hominid virus 2*	MK212032	Anelloviridae sp.	vzttmv5
	Iotatorquevirus			*Torque teno sus virus 1a*	AB076001	torque teno sus virus 1a	Sd-TTV31
	Kappatorquevirus			*Torque teno sus virus k2a*	AY823991	torque teno sus virus k2a	2p
				Torque teno sus virus k2b	JQ406846	torque teno sus virus k2b	38E23
	Lambdatorquevirus			*Torque teno pinniped virus 1*	HQ287751	seal anellovirus TFFN	TGGN
				Torque teno pinniped virus 2	KF373760	seal anellovirus 2	12-410
				Torque teno pinniped virus 3	KF373758	seal anellovirus 3	12-410
				Torque teno pinniped virus 8	KY246582	torque teno Leptonychotes weddellii virus-1	gt16_wsp8
				Torque teno pinniped virus 9	KY246547	torque teno Leptonychotes weddellii virus-2	gt3_wsp24
	Mutorquevirus			*Torque teno equid virus 1*	KR902501	torque teno equus virus 1	horse 1
	Nutorquevirus			*Torque teno pinniped virus 4*	KM262782	seal anellovirus 5	SeAv5-PV13-431
►	*Omegatorquevirus*		◊	*Torque teno hominid virus 1*	KT027939	gorilla anellovirus	GorF
►	*Omicrontorquevirus*		◊	*Torque teno ursid virus 5*	MF327557	giant panda anellovirus	gpan20684
►	*Pitorquevirus*		◊	*Torque teno ursid virus 7*	MF327540	giant panda anellovirus	gpan21094
			◊	*Torque teno ursid virus 10*	MF327541	giant panda anellovirus	gpan20868
			◊	*Torque teno ursid virus 8*	MF327542	giant panda anellovirus	gpan21031
			◊	*Torque teno ursid virus 9*	MF327550	giant panda anellovirus	gpan20868
			◊	*Torque teno ursid virus 11*	MF327548	giant panda anellovirus	gpan21066
			◊	*Torque teno ursid virus 12*	MF327547	giant panda anellovirus	gpan21031
►	*Psitorquevirus*		◊	*Torque teno procyo virus 4*	MK012516	Anelloviridae sp.	ctcf003
►	*Rhotorquevirus*		◊	*Torque teno rodent virus 1*	KJ194617	rodent torque teno virus 1	AS_WM1_Sp_1
►	*Sigmatorquevirus*	●		*Torque teno pinniped virus 5*	FJ459582	torque teno zalophus virus 1	
			◊	*Torque teno pinniped virus 6*	MG837569	torque teno Arctocephalus gazella virus 1	ASV20_172
			◊	*Torque teno pinniped virus 7*	MG837571	torque teno Arctocephalus gazella virus 2	ASV35_197
►	*Tettorquevirus*		◊	*Torque teno felid virus 6*	KX262893	feline anellovirus	FelineAV621
	Thetatorquevirus			*Torque teno canid virus 1*	AB076002	torque teno canis virus	Cf-TTV10
			◊	*Torque teno arthrovec virus 3*	MF173068	tick associated torque teno virus	tick24_1
			◊	*Torque teno mustilid virus 1*	JN704611	pine marten torque teno virus 1	VS4700004
			◊	*Torque teno procyo virus 5*	MK012446	Anelloviridae sp.	ctdb009
			◊	*Torque teno procyo virus 6*	MK012439	Anelloviridae sp.	cthe000
			◊	*Torque teno ursid virus 1*	KX611132	lesser panda anellovirus	chengdu-1
			◊	*Torque teno ursid virus 2*	MF327551	giant panda anellovirus	gpan20783
			◊	*Torque teno ursid virus 3*	MF327552	giant panda anellovirus	gpan20682
			◊	*Torque teno ursid virus 4*	MF327554	giant panda anellovirus	gpan20724
			◊	*Torque teno viverrid virus 4*	LC387543	Paguma larvata torque teno virus	Pl-TTV9-2
►	*Upsilontorquevirus*		◊	*Torque teno procyo virus 1*	MK012447	Anelloviridae sp.	ctcf003
			◊	*Torque teno procyo virus 2*	MK012527	Anelloviridae sp.	ctcf007
			◊	*Torque teno procyo virus 3*	MK012497	Anelloviridae sp.	ctdc005
			◊	*Torque teno procyo virus 7*	MK012464	Anelloviridae sp.	ctbd010
			◊	*Torque teno procyo virus 8*	MK012467	Anelloviridae sp.	ctbb008
			◊	*Torque teno procyo virus 9*	MK012471	Anelloviridae sp.	ctbb005
			◊	*Torque teno viverrid virus 2*	LC387546	Paguma larvata torque teno virus	Pl-TTV9-1
►	*Wawtorquevirus*		◊	*Torque teno rodent virus 2*	MF541374	rodent torque teno virus 3	2

Table 3 (continued)

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

References

1. Agueda-Pinto A, Kraberger S, Lund MC, Gortazar C, McFadden G, Varsani A, Esteves PJ (2020) Coinfections of novel polyomavirus, anelloviruses and a recombinant strain of myxoma virus-MYXV-Tol identified in Iberian Hares. Viruses 12:340
2. Amatya R, Deem SL, Porton IJ, Wang D, Lim ES (2017) Complete genome sequence of torque teno indri virus 1, a novel anellovirus in blood from a free-living lemur. Genome Announc 5:e00698-17
3. Biagini P, Gallian P, Attoui H, Touinssi M, Cantaloube JF, de Micco P, de Lamballerie X (2001) Genetic analysis of full-length genomes and subgenomic sequences of TT virus-like mini virus human isolates. J Gen Virol 82:379–383
4. Biagini P, Uch R, Belhouchet M, Attoui H, Cantaloube JF, Brisbarre N, de Micco P (2007) Circular genomes related to anelloviruses identified in human and animal samples by using a combined rolling-circle amplification/sequence-independent single primer amplification approach. J Gen Virol 88:2696–2701

5. Biagini P (2009) Classification of TTV and related viruses (anelloviruses). In: Villiers E-M, Hausen H (eds) TT Viruses. Springer, Berlin Heidelberg, pp 21–33
6. Biagini P, Bendinelli M, Hino S, Kakkola L, Mankertz A, Niel C, Okamoto H, Raidal S, Teo CG, Todd D (2012) Family anelloviridae. In: King AMQ, Adams EB, Carstens EB, EJ L (eds) Virus taxonomy: ninth report of the international committee on taxonomy of viruses. Academic press, London, pp 331–341
7. Bodewes R, Rubio Garcia A, Wiersma LC, Getu S, Beukers M, Schapendonk CM, van Run PR, van de Bildt MW, Poen MJ, Osinga N, Sanchez Contreras GJ, Kuiken T, Smits SL, Osterhaus AD (2013) Novel B19-like parvovirus in the brain of a harbor seal. PLoS ONE 8:e79259
8. Bodewes R, Contreras GJS, Garcia AR, Hapsari R, van de Bildt MWG, Kuiken T, Osterhaus A (2015) Identification of DNA sequences that imply a novel gammaherpesvirus in seals. J Gen Virol 96:1109–1114
9. Briddon RW, Martin DP, Roumagnac P, Navas-Castillo J, Fiallo-Olive E, Moriones E, Lett JM, Zerbini FM, Varsani A (2018) Alphasatellitidae: a new family with two subfamilies for the classification of geminivirus- and nanovirus-associated alphasatellites. Arch Virol 163:2587–2600
10. Brown JK, Zerbini FM, Navas-Castillo J, Moriones E, Ramos-Sobrinho R, Silva JC, Fiallo-Olive E, Briddon RW, Hernandez-Zepeda C, Idris A, Malathi VG, Martin DP, Rivera-Bustamante R, Ueda S, Varsani A (2015) Revision of Begomovirus taxonomy based on pairwise sequence comparisons. Arch Virol 160:1593–1619
11. Capella-Gutierrez S, Silla-Martinez JM, Gabaldon T (2009) trimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25:1972–1973
12. Cibulski SP, Teixeira TF, de Sales Lima FE, do Santos HF, Franco AC, Roehe PM (2014) A Novel anelloviridae species detected in tadarida brasiliensis bats: first sequence of a chiropteran anellovirus. Genome Announc 2:e01028-14
13. Cornelissen-Keijsers V, Jimenez-Melsio A, Sonnemans D, Cortey M, Segales J, van den Born E, Kekarainen T (2012) Discovery of a novel Torque teno sus virus species: genetic characterization, epidemiological assessment and disease association. J Gen Virol 93:2682–2691
14. Crane A, Goebel ME, Kraberger S, Stone AC, Varsani A (2018) Novel anelloviruses identified in buccal swabs of Antarctic fur seals. Virus Genes 54:719–723
15. de Souza WM, Fumagalli MJ, de Araujo J, Sabino-Santos G Jr, Maia FGM, Romeiro MF, Modha S, Nardi MS, Queiroz LH, Durigon EL, Nunes MRT, Murcia PR, Figueiredo LTM (2018) Discovery of novel anelloviruses in small mammals expands the host range and diversity of the Anelloviridae. Virology 514:9–17
16. Eibach D, Hogan B, Sarpong N, Winter D, Struck NS, Adu-Sarkodie Y, Owusu-Dabo E, Schmidt-Chanasit J, May J, Cadar D (2019) Viral metagenomics revealed novel betatorquevirus species in pediatric inpatients with encephalitis/meningoencephalitis from Ghana. Sci Rep 9:2360
17. Fahsbender E, Burns JM, Kim S, Kraberger S, Frankfurter G, Eilers AA, Shero MR, Beltran R, Kirkham A, McCorkell R, Berngartt RK, Male MF, Ballard G, Ainley DG, Breitbart M, Varsani A (2017) Diverse and highly recombinant anelloviruses associated with Weddell seals in Antarctica. Virus Evol 3:vex017
18. Galmes J, Li Y, Rajoharison A, Ren L, Dollet S, Richard N, Vernet G, Javouhey E, Wang J, Telles JN, Paranhos-Baccala G (2013) Potential implication of new torque teno mini viruses in parapneumonic empyema in children. Eur Respir J 42:470–479
19. Hallett RL, Clewley JP, Bobet F, McKiernan PJ, Teo CG (2000) Characterization of a highly divergent TT virus genome. J Gen Virol 81:2273–2279
20. Heller F, Zachoval R, Koelzer A, Nitschko H, Froesner GG (2001) Isolate KAV: a new genotype of the TT-virus family. Biochem Biophys Res Commun 289:937–941
21. Hijikata M, Takahashi K, Mishiro S (1999) Complete circular DNA genome of a TT virus variant (isolate name SANBAN) and 44 partial ORF2 sequences implicating a great degree of diversity beyond genotypes. Virology 260:17–22
22. Hrazdilova K, Slaninkova E, Brozova K, Modry D, Vodicka R, Celer V (2016) New species of Torque Teno miniviruses infecting gorillas and chimpanzees. Virology 487:207–214
23. Inami T, Obara T, Moriyama M, Arakawa Y, Abe K (2000) Full-length nucleotide sequence of a simian TT virus isolate obtained from a chimpanzee: evidence for a new TT virus-like species. Virology 277:330–335
24. Jazaeri Farsani SM, Jebbink MF, Deijs M, Canuti M, van Dort KA, Bakker M, Grady BP, Prins M, van Hemert FJ, Kootstra NA, van der Hoek L (2013) Identification of a new genotype of Torque Teno Mini virus. Virol J 10:323
25. Kamahora T, Hino S, Miyata H (2000) Three spliced mRNAs of TT virus transcribed from a plasmid containing the entire genome in COS1 cells. J Virol 74:9980–9986
26. Kang YJ, Zhou MF, Huang W, Deng C, Yan G, Lu ZH (2017) Identification of a novel torque teno mini virus in cerebrospinal fluid from a child with encephalitis. Virol Sin 32:541–544
27. Kapusinszky B, Mulvaney U, Jasinska AJ, Deng X, Freimer N, Delwart E (2015) Local virus extinctions following a host population bottleneck. J Virol 89:8152–8161
28. Katoh K, Standley DM (2016) A simple method to control over-alignment in the MAFFT multiple sequence alignment program. Bioinformatics 32:1933–1942
29. Khalifeh A, Blumstein DT, Fontenele RS, Schmidlin K, Richet C, Kraberger S, Varsani A (2021) Diverse cressdnaviruses and an anellovirus identified in the fecal samples of yellow-bellied marmots. Virology 554:89–96
30. Kraberger S, Opriessnig T, Celer V, Maggi F, Okamoto H, Blomström A-L, Cadar D, Harrach B, Biagini P, Varsani A (2021) Taxonomic updates for the genus Gyrovirus (family *Anelloviridae*): recognition of several new members and establishment of species demarcation criteria. Arch Virol. https://doi.org/10.1007/s00705-021-05194-9
31. Letunic I, Bork P (2019) Interactive tree of life (iTOL) v4: recent updates and new developments. Nucleic Acids Res 47:W256–W259
32. Li L, Giannitti F, Low J, Keyes C, Ullmann LS, Deng X, Aleman M, Pesavento PA, Pusterla N, Delwart E (2015) Exploring the virome of diseased horses. J Gen Virol 96:2721–2733
33. Lu L, Robertson G, Ashworth J, Pham Hong A, Shi T, Ivens A, Thwaites G, Baker S, Woolhouse M (2020) Epidemiology and phylogenetic analysis of viral respiratory infections in Vietnam. Front Microbiol 11:833
34. Luo K, He H, Liu Z, Liu D, Xiao H, Jiang X, Liang W, Zhang L (2002) Novel variants related to TT virus distributed widely in China. J Med Virol 67:118–126
35. Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R (2020) IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. Mol Biol Evol 37:1530–1534
36. Muhire B, Martin DP, Brown JK, Navas-Castillo J, Moriones E, Zerbini FM, Rivera-Bustamante R, Malathi VG, Briddon RW, Varsani A (2013) A genome-wide pairwise-identity-based proposal for the classification of viruses in the genus Mastrevirus (family Geminiviridae). Arch Virol 158:1411–1424
37. Muhire BM, Varsani A, Martin DP (2014) SDT: a virus classification tool based on pairwise sequence alignment and identity calculation. PLoS ONE 9:e108277

38. Ng TF, Willner DL, Lim YW, Schmieder R, Chau B, Nilsson C, Anthony S, Ruan Y, Rohwer F, Breitbart M (2011) Broad surveys of DNA viral diversity obtained through viral metagenomics of mosquitoes. PLoS ONE 6:e20579
39. Ng TFF, Suedmeyer WK, Wheeler E, Gulland F, Breitbart M (2009) Novel anellovirus discovered from a mortality event of captive California sea lions. J Gen Virol 90:1256–1261
40. Ng TFF, Wheeler E, Greig D, Waltzek TB, Gulland F, Breitbart M (2011) Metagenomic identification of a novel anellovirus in Pacific harbor seal (Phoca vitulina richardsii) lung samples and its detection in samples from multiple years. J Gen Virol 92:1318–1323
41. Ng TFF, Dill JA, Camus AC, Delwart E, Van Meir EG (2017) Two new species of betatorqueviruses identified in a human melanoma that metastasized to the brain. Oncotarget 8:105800–105808
42. Niel C, Diniz-Mendes L, Devalle S (2005) Rolling-circle amplification of Torque teno virus (TTV) complete genomes from human and swine sera and identification of a novel swine TTV genogroup. J Gen Virol 86:1343–1347
43. Ninomiya M, Nishizawa T, Takahashi M, Lorenzo FR, Shimosegawa T, Okamoto H (2007) Identification and genomic characterization of a novel human torque teno virus of 3.2 kb. J Gen Virol 88:1939–1944
44. Ninomiya M, Takahashi M, Shimosegawa T, Okamoto H (2007) Analysis of the entire genomes of fifteen torque teno midi virus variants classifiable into a third group of genus Anellovirus. Arch Virol 152:1961–1975
45. Ninomiya M, Takahashi M, Hoshino Y, Ichiyama K, Simmonds P, Okamoto H (2009) Analysis of the entire genomes of torque teno midi virus variants in chimpanzees: infrequent cross-species infection between humans and chimpanzees. J Gen Virol 90:347–358
46. Nishiyama S, Dutia BM, Stewart JP, Meredith AL, Shaw DJ, Simmonds P, Sharp CP (2014) Identification of novel anelloviruses with broad diversity in UK rodents. J Gen Virol 95:1544–1553
47. Nishiyama S, Dutia BM, Sharp CP (2015) Complete genome sequences of novel anelloviruses from laboratory rats. Genome Announc 3:e01262-14
48. Nishizawa T, Sugimoto Y, Takeda T, Kodera Y, Hatano Y, Takahashi M, Okamoto H (2018) Identification and whole genome characterization of novel anelloviruses in masked palm civets (*Paguma larvata*): segregation into four distinct clades. Virus Res 256:183–191
49. Okamoto H, Nishizawa T, Tawara A, Peng Y, Takahashi M, Kishimoto J, Tanaka T, Miyakawa Y, Mayumi M (2000) Species-specific TT viruses in humans and nonhuman primates and their phylogenetic relatedness. Virology 277:368–378
50. Okamoto H, Nishizawa T, Takahashi M, Asabe S, Tsuda F, Yoshikawa A (2001) Heterogeneous distribution of TT virus of distinct genotypes in multiple tissues from infected humans. Virology 288:358–368
51. Okamoto H, Nishizawa T, Takahashi M, Tawara A, Peng Y, Kishimoto J, Wang Y (2001) Genomic and evolutionary characterization of TT virus (TTV) in tupaias and comparison with species-specific TTVs in humans and non-human primates. J Gen Virol 82:2041–2050
52. Okamoto H, Takahashi M, Nishizawa T, Tawara A, Fukai K, Muramatsu U, Naito Y, Yoshikawa A (2002) Genomic characterization of TT viruses (TTVs) in pigs, cats and dogs and their relatedness with species-specific TTVs in primates and tupaias. J Gen Virol 83:1291–1297
53. Pan S, Yu T, Wang Y, Lu R, Wang H, Xie Y, Feng X (2018) Identification of a Torque Teno Mini Virus (TTMV) in Hodgkin's Lymphoma Patients. Front Microbiol 9:1680
54. Parras-Molto M, Suarez-Rodriguez P, Eguia A, Aguirre-Urizar JM, Lopez-Bueno A (2014) Genome sequence of two novel species of torque teno minivirus from the human oral cavity. Genome Announc 2:e00868-14
55. Peng YH, Nishizawa T, Takahashi M, Ishikawa T, Yoshikawa A, Okamoto H (2002) Analysis of the entire genomes of thirteen TT virus variants classifiable into the fourth and fifth genetic groups, isolated from viremic infants. Arch Virol 147:21–41
56. Qiu J, Kakkola L, Cheng F, Ye C, Soderlund-Venermo M, Hedman K, Pintel DJ (2005) Human circovirus TT virus genotype 6 expresses six proteins following transfection of a full-length clone. J Virol 79:6505–6510
57. Rosario K, Breitbart M, Harrach B, Segales J, Delwart E, Biagini P, Varsani A (2017) Revisiting the taxonomy of the family Circoviridae: establishment of the genus Cyclovirus and removal of the genus Gyrovirus. Arch Virol 162:1447–1463
58. Siddell SG, Walker PJ, Lefkowitz EJ, Mushegian AR, Dutilh BE, Harrach B, Harrison RL, Junglen S, Knowles NJ, Kropinski AM, Krupovic M, Kuhn JH, Nibert ML, Rubino L, Sabanadzovic S, Simmonds P, Varsani A, Zerbini FM, Davison AJ (2020) Binomial nomenclature for virus species: a consultation. Arch Virol 165:519–525
59. Simmonds P, Adams MJ, Benko M, Breitbart M, Brister JR, Carstens EB, Davison AJ, Delwart E, Gorbalenya AE, Harrach B, Hull R, King AM, Koonin EV, Krupovic M, Kuhn JH, Lefkowitz EJ, Nibert ML, Orton R, Roossinck MJ, Sabanadzovic S, Sullivan MB, Suttle CA, Tesh RB, van der Vlugt RA, Varsani A, Zerbini FM (2017) Consensus statement: virus taxonomy in the age of metagenomics. Nat Rev Microbiol 15:161–168
60. Stover BC, Muller KF (2010) TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. BMC Bioinformatics 11:7
61. Takahashi K, Hijikata M, Samokhvalov EI, Mishiro S (2000) Full or near full length nucleotide sequences of TT virus variants (Types SANBAN and YONBAN) and the TT virus-like mini virus. Intervirology 43:119–123
62. Takahashi K, Iwasa Y, Hijikata M, Mishiro S (2000) Identification of a new human DNA virus (TTV-like mini virus, TLMV) intermediately related to TT virus and chicken anemia virus. Arch Virol 145:979–993
63. Tisza MJ, Pastrana DV, Welch NL, Stewart B, Peretti A, Starrett GJ, Pang YS, Krishnamurthy SR, Pesavento PA, McDermott DH, Murphy PM, Whited JL, Miller B, Brenchley J, Rosshart SP, Rehermann B, Doorbar J, Ta'ala BA, Pletnikova O, Troncoso JC, Resnick SM, Bolduc B, Sullivan MB, Varsani A, Segall AM, Buck CB (2020) Discovery of several thousand highly diverse circular DNA viruses. eLife 9: e51971
64. Ukita M, Okamoto H, Nishizawa T, Tawara A, Takahashi M, Iizuka H, Miyakawa Y, Mayumi M (2000) The entire nucleotide sequences of two distinct TT virus (TTV) isolates (TJN01 and TJN02) remotely related to the original TTV isolates. Arch Virol 145:1543–1559
65. van den Brand JM, van Leeuwen M, Schapendonk CM, Simon JH, Haagmans BL, Osterhaus AD, Smits SL (2012) Metagenomic analysis of the viral flora of pine marten and European badger feces. J Virol 86:2360–2365
66. Varsani A, Martin DP, Navas-Castillo J, Moriones E, Hernandez-Zepeda C, Idris A, Murilo Zerbini F, Brown JK (2014) Revisiting the classification of curtoviruses based on genome-wide pairwise identity. Arch Virol 159:1873–1882
67. Varsani A, Navas-Castillo J, Moriones E, Hernandez-Zepeda C, Idris A, Brown JK, Murilo Zerbini F, Martin DP (2014) Establishment of three new genera in the family Geminiviridae: Becurtovirus, Eragrovirus and Turncurtovirus. Arch Virol 159:2193–2203

68. Varsani A, Krupovic M (2017) Sequence-based taxonomic framework for the classification of uncultured single-stranded DNA viruses of the family Genomoviridae. Virus Evol 3:vew037
69. Varsani A, Krupovic M (2018) Smacoviridae: a new family of animal-associated single-stranded DNA viruses. Arch Virol 163:2005–2015
70. Waits K, Edwards MJ, Cobb IN, Fontenele RS, Varsani A (2018) Identification of an anellovirus and genomoviruses in ixodid ticks. Virus Genes 54:155–159
71. Webb B, Rakibuzzaman A, Ramamoorthy S (2020) Torque teno viruses in health and disease. Virus Res 285:198013
72. Zhang W, Li L, Deng X, Kapusinszky B, Pesavento PA, Delwart E (2014) Faecal virome of cats in an animal shelter. J Gen Virol 95:2553–2564
73. Zhang W, Wang H, Wang Y, Liu Z, Li J, Guo L, Yang S, Shen Q, Zhao X, Cui L, Hua X (2016) Identification and genomic characterization of a novel species of feline anellovirus. Virol J 13:146
74. Zhang W, Yang S, Shan T, Hou R, Liu Z, Li W, Guo L, Wang Y, Chen P, Wang X, Feng F, Wang H, Chen C, Shen Q, Zhou C, Hua X, Cui L, Deng X, Zhang Z, Qi D, Delwart E (2017) Virome comparisons in wild-diseased and healthy captive giant pandas. Microbiome 5:90
75. Zhang Y, Li F, Shan TL, Deng X, Delwart E, Feng XP (2016) A novel species of torque teno mini virus (TTMV) in gingival tissue from chronic periodontitis patients. Sci Rep 6:26739
76. Zhu CX, Shan TL, Cui L, Luo XN, Liu ZJ, Tang SD, Liu ZW, Yuan CL, Lan DL, Zhao W, Hua XG (2011) Molecular detection and sequence analysis of feline Torque teno virus (TTV) in China. Virus Res 156:13–16