

The family *Parvoviridae*

Susan F. Cotmore · Mavis Agbandje-McKenna · John A. Chiorini ·
Dmitry V. Mukha · David J. Pintel · Jianming Qiu · Maria Soderlund-Venermo ·
Peter Tattersall · Peter Tijssen · Derek Gatherer · Andrew J. Davison

Received: 11 September 2013 / Accepted: 28 October 2013 / Published online: 9 November 2013
© Springer-Verlag Wien 2013

Abstract A set of proposals to rationalize and extend the taxonomy of the family *Parvoviridae* is currently under review by the International Committee on Taxonomy of Viruses (ICTV). Viruses in this family infect a wide range of hosts, as reflected by the longstanding division into two subfamilies: the *Parvovirinae*, which contains viruses that infect vertebrate hosts, and the *Densovirinae*, encompassing viruses that infect arthropod hosts. Using a modified definition for classification into the family that no longer demands isolation as long as the biological context is strong, but does require a near-complete DNA sequence,

134 new viruses and virus variants were identified. The proposals introduce new species and genera into both subfamilies, resolve one misclassified species, and improve taxonomic clarity by employing a series of systematic changes. These include identifying a precise level of sequence similarity required for viruses to belong to the same genus and decreasing the level of sequence similarity required for viruses to belong to the same species. These steps will facilitate recognition of the major phylogenetic branches within genera and eliminate the confusion caused by the near-identity of species and viruses. Changes to taxon nomenclature will establish numbered, non-Latinized binomial names for species, indicating genus affiliation and host range rather than recapitulating virus names. Also, affixes will be included in the names of genera to clarify subfamily affiliation and reduce the ambiguity that results from the vernacular use of “parvovirus” and “densovirus” to denote multiple taxon levels.

This article is related to an ongoing taxonomic proposal, submitted to the International Committee on Taxonomy of Viruses (ICTV) and still under deliberation. The taxonomic changes discussed here may differ from any new taxonomy that is ultimately approved.

S. F. Cotmore, M. Agbandje-McKenna, J. A. Chiorini, D. V. Mukha, D. J. Pintel, J. Qiu, M. Soderlund-Venermo, P. Tattersall and P. Tijssen are the members of the ICTV *Parvoviridae* Study Group.

S. F. Cotmore (✉)
Department of Laboratory Medicine, Yale University School of
Medicine, New Haven, CT, USA
e-mail: susan.cotmore@yale.edu

M. Agbandje-McKenna
Department of Biochemistry and Molecular Biology, Center for
Structural Biology, McKnight Brain Institute, College of
Medicine, University of Florida, Gainesville, FL, USA

J. A. Chiorini
Molecular Physiology and Therapeutics Branch, National
Institute of Dental and Craniofacial Research, National Institutes
of Health, Bethesda, MD, USA

D. V. Mukha
Vavilov Institute of General Genetics, Russian Academy of
Sciences, Gubkin 3, Moscow 119991, Russia

D. J. Pintel
Department of Molecular Microbiology and Immunology, Life
Sciences Center, School of Medicine, University of Missouri-
Columbia, Columbia, MO, USA

J. Qiu
Department of Microbiology, Molecular Genetics and
Immunology, University of Kansas Medical Center, Kansas City,
KS, USA

M. Soderlund-Venermo
Department of Virology, Haartman Institute, University of
Helsinki, Helsinki, Finland

P. Tattersall
Departments of Laboratory Medicine and Genetics, Yale
University School of Medicine, New Haven, CT, USA

Introduction

A set of proposals to update the taxonomy of the family *Parvoviridae* has been submitted by a review group that includes all members of the International Committee on Taxonomy of Viruses (ICTV) *Parvoviridae* Study Group (SG), and is currently under review. Until a final ICTV decision is reached, the proposal can be downloaded at [http://talk.ictvonline.org/files/proposals/taxonomy_proposals_Vertebrate1/default.aspx](http://talk.ictvonline.org/files/proposals/taxonomy_proposals Vertebrate1/default.aspx). The taxonomy of this family was last modified in 2004, prior to publication of the 8th ICTV Report [13], and is now significantly dated. In the interim, many new candidate viruses and previously unsuspected viral hierarchies have been identified, often by the use of viral discovery approaches that rely on polymerase chain reaction DNA amplification. Unfortunately, this approach typically confounds characterization of complex secondary structures in the viral hairpin telomeres that are essential for viability [8, 10], making the recovery of viruses from DNA challenging. To accommodate these important new viruses, while avoiding inclusion of viral sequence fragments integrated into host genomes [1, 9] or metagenomic data that lack integrity or clear host attribution (for example, a full-length *Blatella germanica* densovirus-like virus sequence, GenBank JQ320376, with a probable cockroach host that was identified in bat faeces [7]), the SG developed a polythetic definition of a virus in the family *Parvoviridae*. This requires the complete DNA sequence of all viral protein-coding sequences but no longer absolutely requires isolation of a viable virus provided an infectious etiology is supported by the structure and arrangement of the genome, serology, or other biological data. The viral definition used throughout these proposals is: “In order for an agent to be classified in the family *Parvoviridae*, it must be judged to be an authentic parvovirus on the basis of having been isolated and sequenced or, failing this, on the basis of having been sequenced in tissues, secretions, or excretions of unambiguous host origin, supported by evidence of its distribution in multiple individual hosts in a pattern that is compatible with dissemination by infection. The sequence must be in one piece, contain all the non-structural (NS) and viral particle

(VP) coding regions, and meet the size constraints and motif patterns characteristic of the family”.

This definition allows inclusion of 134 new viruses and virus strains in the family *Parvoviridae*, together with 47 of the 53 previously recognized isolates [14]. Six recognized viruses for which no sequence information is currently available have been withdrawn from the formal taxonomy pending further analysis but will remain listed in subsequent reports as unassigned in their current genus. To improve taxonomic clarity and to facilitate the ready assimilation of present and future candidate viruses, a root-and-branch re-evaluation of the taxonomic structure and nomenclature of the family was also instituted, leading to the development of new systematic guidelines. Proposed changes to the taxonomy are summarized in Table 1. In the subfamily *Parvovirinae*, these changes include the introduction of three new genera and the expansion of five existing genus names with the affixes “*parvo*” or “*proto*”. In the subfamily *Densovirinae*, proposed changes include the introduction of two new genera for shrimp viruses and the expansion of the existing genus names *Iteravirus* and *Densovirus* to *Iteradensovirus* and *Ambidensovirus*, respectively. In both subfamilies, species identity levels will be lowered, numbered, binomial species names adopted, and new species introduced.

Changes in taxonomic structure and nomenclature

Taxon demarcation criteria

Parvoviruses encode two gene cassettes: an NS gene essential for replication and a VP gene encoding various forms of the structural protein [reviewed in 2, 14]. The amino acid sequence of the NS1 protein is used for phylogenetic analysis in the current proposals. NS1 is a multidomain ~70–80 kDa nuclear phosphoprotein that encodes highly conserved enzymatic activities, including a site-specific DNA-binding and single-strand endonuclease function and an AAA+ helicase [reviewed in 2, 3]. These well-conserved domains facilitate amino acid sequence alignment, allowing insights from structural biology and the derivation of a reliable sequence-based phylogeny (see the summary tree in Fig. 1). However, the core capsid protein sequence (defined as the smallest VP protein that contains all residues comprising the virion shell, as determined by X-ray crystallography) was analyzed in parallel, with conspicuously similar overall results although the data appeared less reliable at the greater distances apparent between the two subfamilies. Thus, the proposed taxonomic changes are supported by protein alignments of both major viral proteins. Previously, genera were defined largely by non-quantifiable criteria, including helper-virus

P. Tijssen
INRS-Institut Armand-Frappier, Laval, QC, Canada

D. Gatherer · A. J. Davison
MRC, University of Glasgow Centre for Virus Research,
Glasgow, UK

Present Address:
D. Gatherer
Division of Biomedical and Life Sciences, Lancaster University,
Lancaster LA1 4YQ, UK

Table 1 Summary of changes between the current and proposed taxonomy

Current taxonomy			Proposed taxonomy		
Genus	# Species	# viruses or strains	Genus	# Species	# viruses or variants
Subfamily <i>Parvovirinae</i> - vertebrate hosts					
<i>Amdovirus</i>	1	1	<i>Amdoparvovirus</i>	2	2
-	-	-	<i>Aveparvovirus</i> ^a	1	2
<i>Bocavirus</i>	2	6	<i>Bocaparvovirus</i>	12	22
-	-	-	<i>Copiparvovirus</i> ^a	2	2
<i>Dependovirus</i>	12	13	<i>Dependoparvovirus</i>	7	23
<i>Erythrovirus</i>	4	9	<i>Erythroparvovirus</i>	6	12
<i>Parvovirus</i>	12	18	<i>Protoparvovirus</i>	5	25
-	-	-	<i>Tetraparvovirus</i> ^a	6	10
Subfamily <i>Densovirinae</i> - arthropod hosts					
<i>Densovirus</i>	2	2	<i>Ambidensovirus</i>	6	11
<i>Brevidensovirus</i>	2	2	<i>Brevidensovirus</i>	2	8
-	-	-	<i>Hepandensovirus</i> ^a	1	7
<i>Iteravirus</i>	1	1	<i>Iteradensovirus</i>	5	6
-	-	-	<i>Penstyldensovirus</i> ^a	1	4
<i>Pefudensovirus</i> ^b	1	1	-	-	-

Bold type in genus names denotes new affixes

^a Denotes new genera

^b Denotes a retired genus

requirements and genome characteristics, which provided little taxonomic structure [13, 14]. The current proposals add the requirement that all viruses in a genus should be monophyletic and encode NS1 proteins that are generally >30 % identical to each other at the amino acid sequence level but <30 % identical to those of other genera as determined by pairwise sequence alignments. Within the subfamily *Parvovirinae*, these criteria work well to separate all current and proposed genera, with the minor exception of the proposed genus *Erythroparvovirus*, where marginally greater divergence is evident between some virus pairs. The resulting eight genera in this subfamily are well supported by phylogenetic analysis, as illustrated in Fig. 1 and detailed in the proposals.

In the subfamily *Densovirinae*, attributable sequences are available only for a small number of economically significant viruses, which is likely to reflect poorly the diverse nature of viruses infecting hosts from the immense phylum Arthropoda. Accordingly, the >30 % identity requirement is applied less rigorously within this subfamily, in order to allow clustering of monophyletic viruses with conspicuously similar characteristics from host orders separated by large evolutionary distances. Constituent viruses in most of these genera are closely related and infect arthropods from the same host order. However, in the proposed genus *Ambidensovirus*, certain pairs of viruses that infect different orders of hosts fall short of the proposed identity requirements. Nevertheless, all of these viruses exhibit a complex genomic rearrangement that allows them to co-ordinate bidirectional transcription, which is not seen in viruses from any other parvovirus

taxon. In the existing taxonomy, most of these “ambisense” viruses cluster in the genus *Densovirus*, with a single outlier (*Periplaneta fuliginosa densovirus*) that infects a blattodean host and is the sole member of genus *Pefudensovirus*. Recently, this organization was challenged by the identification of four new isolates with ambisense organization, which infect insects from different host orders and are closely related to, albeit not monophyletic with, viruses from both of the existing ambisense genera. To resolve this situation, it is proposed that the six groups should be combined as distinct species in a single monophyletic *Ambidensovirus* genus, which will have slightly relaxed demarcation criteria that likely reflect the host diaspora. Members of the proposed genus *Ambidensovirus* thus appear to illustrate how host divergence may mask and complicate underlying sequence-based phylogeny: using current approaches, it would prove challenging to track viral lineages with less conspicuous genomic rearrangements against this background of host-related genetic drift.

Previously, species in the family were generally required to be >95 % related in the NS1 DNA sequence, which is so high a level that many current species consist of single isolates. This has fuelled confusion between taxa and viruses in the literature, and it allows the species level to contribute little to taxonomic structure. The proposals will decrease species identity criteria significantly, requiring viruses in a species to encode NS1 proteins that show >85 % amino acid sequence identity while diverging by >15 % from viruses in other species. This adjustment permits a species to contain a greater diversity of viruses than is currently the case, so that it typically designates a

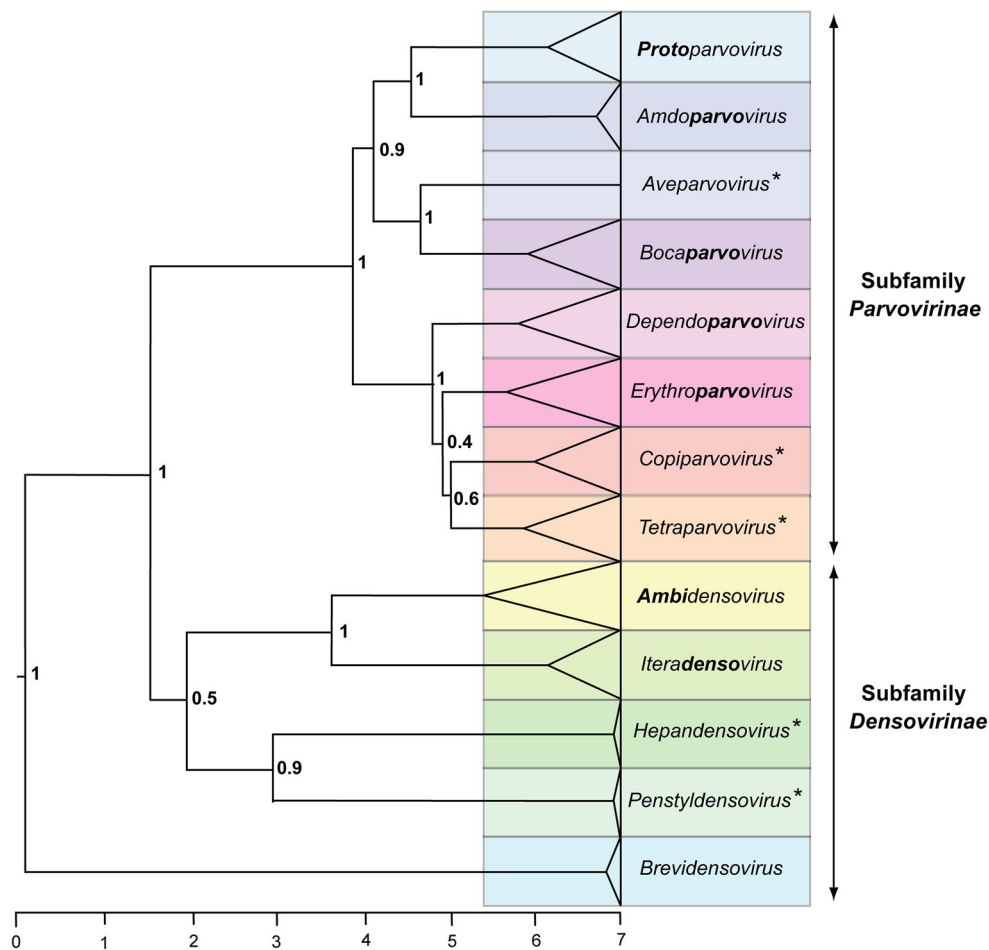


Fig. 1 Phylogenetic tree showing genera in the family *Parvoviridae*. Phylogenetic analysis based on the amino acid sequence of the viral replication initiator protein, NS1, which contains a conserved AAA+ helicase domain corresponding to the Parvo_NS1 Pfam domain: http://pfam.sanger.ac.uk/family/Parvo_NS1. This region was aligned by incorporating insights from structural biology using the ehmmalign application in EMBASSY [6], and sequences flanking the Pfam domain were aligned using the modification of the Needleman-Wunsch local alignment method [11] as implemented in MOE-Align

(<http://www.chemcomp.com>). Pairwise p -distance matrices were constructed from this alignment using MEGA version 5.10 [12]. Bayesian trees were calculated over one billion iterations using BEAST [5], using a Yule model of speciation and an exponential relaxed molecular clock [4]. Trees were viewed in FigTree (part of BEAST) in ultrametric format on an arbitrary scale, midpoint-rooted, and with posterior probability scores indicated at statistically significant nodes. Bold type in genus names indicates affixes used to expand existing names. Asterisks denote the names of new genera

distinct phylogenetic branch and thus adds useful structure within the genus. Other existing criteria, such as host, antigenic properties, and genome characteristics, are still considered.

The two subfamilies, *Parvovirinae* and *Densovirinae*, are distinguished primarily by their respective ability to infect vertebrate and arthropod hosts, and this remains the case in the proposals. This separation is supported by Bayesian phylogeny, although it is not immediately apparent under the rooting procedure used in Fig. 1.

Taxon nomenclature

Systematic changes are proposed at the level of species, in part because decreasing the mandatory level of sequence

identity for this taxon effectively does away with current species divisions. The call for new names that encompass broader groups of viruses thus provides an opportunity for the field to adopt a non-Latinized, binomial system that has been discussed extensively in the literature [15, 16] and is commonly in use in other viral families. In the proposed nomenclature, species names are emphatically different from virus names and typically consist of a host taxon, a genus affiliation, and a distinguishing numerical or letter suffix, for example, *Rodent protoparvovirus 1* (type species of the genus *Protoparvovirus*, which includes both the existing type species, *Minute virus of mice*, and a group of closely related rodent viruses, as detailed in Table 2). Since these names indicate the range of viruses included and their branch within the family, they provide useful information

Table 2 Proposed taxonomy for the subfamily *Parvovirinae*

Genus	Species	Virus or virus variants	Abbreviation	Accession #	
<i>Amdoparvovirus</i>	<i>Carnivore amdoparvovirus 1</i>	Aleutian mink disease virus	AMDV	JN040434	
	<i>Carnivore amdoparvovirus 2</i>	gray fox amdovirus	GFAV	JN202450	
<i>Aveparvovirus</i>	<i>Galliform aveparvovirus 1</i>	chicken parvovirus	ChPV	GU214704	
		turkey parvovirus	TuPV	GU214706	
<i>Bocaparvovirus</i>	<i>Carnivore bocaparvovirus 1</i>	canine minute virus	CnMV	FJ214110	
	<i>Carnivore bocaparvovirus 2</i>	canine bocavirus 1	CBoV	JN648103	
	<i>Carnivore bocaparvovirus 3</i>	feline bocavirus	FBoV	JQ692585	
	<i>Pinniped bocaparvovirus 1</i>	California sea lion bocavirus 1	CsIBoV1	JN420361	
		California sea lion bocavirus 2	CsIBoV2	JN420366	
	<i>Pinniped bocaparvovirus 2</i>	California sea lion bocavirus 3	CsIBoV3	JN420365	
	<i>Primate bocaparvovirus 1</i>	human bocavirus 1	HBoV1	JQ923422	
		human bocavirus 3	HBoV3	EU918736	
	<i>Primate bocaparvovirus 2</i>	gorilla bocavirus	GBoV	HM145750	
		human bocavirus 2a	HBoV2a	FJ973558	
		human bocavirus 2b	HBoV2b	FJ973560	
	<i>Ungulate bocaparvovirus 1</i>	human bocavirus 2c	HBoV2c	FJ170278	
		human bocavirus 4	HBoV4	FJ973561	
		<i>Ungulate bocaparvovirus 1</i>	bovine parvovirus	BPV	DQ335247
		<i>Ungulate bocaparvovirus 2</i>	porcine bocavirus 1	PBoV1	HM053693
			porcine bocavirus 2	PBoV2	HM053694
			porcine bocavirus 6	PBoV6	HQ291309
		<i>Ungulate bocaparvovirus 3</i>	porcine bocavirus 5	PBoV5	HQ223038
		<i>Ungulate bocaparvovirus 4</i>	porcine bocavirus 7	PBoV7	HQ291308
		<i>Ungulate bocaparvovirus 5</i>	porcine bocavirus 3	PBoV3	JF429834
			porcine bocavirus 4-1	PBoV4-1	JF429835
	porcine bocavirus 4-2		PBoV4-2	JF429836	
	<i>Copiparvovirus</i>		<i>Ungulate copiparvovirus 1</i>	bovine parvovirus 2	BPV2
<i>Ungulate copiparvovirus 2</i>			porcine parvovirus 4	PPV4	GQ387499
<i>Dependoparvovirus</i>	<i>Adeno-associated dependoparvovirus A</i>	adeno-associated virus-1	AAV1	AF063497	
		adeno-associated virus-2	AAV2	AF043303	
		adeno-associated virus-3	AAV3	AF028705	
		adeno-associated virus-4	AAV4	U89790	
		adeno-associated virus-6	AAV6	AF028704	
		adeno-associated virus-7	AAV7	AF513851	
		adeno-associated virus-8	AAV8	AF513852	
		adeno-associated virus-9	AAV9	AX753250	
		adeno-associated virus-10	AAV10	AY631965	
		adeno-associated virus-11	AAV11	AY631966	
		adeno-associated virus-12	AAV12	DQ813647	
		adeno-associated virus-13	AAV13	EU285562	
		adeno-associated virus-S17	AAVS17	AY695376	
	<i>Adeno-associated dependoparvovirus B</i>	adeno-associated virus-5	AAV5	AF085716	
		bovine adeno-associated virus	BAAV	AY388617	
	<i>Anseriform dependoparvovirus 1</i>	caprine adeno-associated virus	CapAAV	DQ335246	
		duck parvovirus	DPV	U22967	
	goose parvovirus-PT	GPV2	JF926695		

Table 2 continued

Genus	Species	Virus or virus variants	Abbreviation	Accession #
		goose parvovirus	GPV	U25749
	<i>Avian dependoparvovirus 1</i>	avian adeno-associated virus	AAAV	AY186198
	<i>Chiropteran dependoparvovirus 1</i>	bat adeno-associated virus	BtAAV	GU226971
	<i>Pinniped dependoparvovirus 1</i>	California sea lion adeno-associated virus	CsIAAV	JN420372
	<i>Squamate dependoparvovirus 1</i>	snake adeno-associated virus	SAAV	AY349010
<i>Erythroparvovirus</i>	<i>Primate erythroparvovirus 1</i>	human parvovirus B19-Au	B19V-Au	M13178
		human parvovirus B19-J35	B19V-J35	AY386330
		human parvovirus B19-Wi	B19V-Wi	M24682
		human parvovirus B19-A6	B19V-A6	AY064475
		human parvovirus B19-Lali	B19V-Lali	AY044266
		human parvovirus B19-V9	B19V-V9	AJ249437
		human parvovirus B19-D91	B19-D91	AY083234
	<i>Primate erythroparvovirus 2</i>	simian parvovirus	SPV	U26342
	<i>Primate erythroparvovirus 3</i>	rhesus macaque parvovirus	RhMPV	AF221122
	<i>Primate erythroparvovirus 4</i>	pig-tailed macaque parvovirus	PtMPV	AF221123
	<i>Rodent erythroparvovirus 1</i>	chipmunk parvovirus	ChpPV	GQ200736
	<i>Ungulate erythroparvovirus 1</i>	bovine parvovirus 3	BPV3	AF406967
<i>Protoparvovirus</i>	<i>Carnivore protoparvovirus 1</i>	feline parvovirus	FPV	EU659111
		canine parvovirus	CPV	M19296
		mink enteritis virus	MEV	D00765
		raccoon parvovirus	RaPV	JN867610
	<i>Primate protoparvovirus 1</i>	bufavirus 1a	BuPV1a	JX027296
		bufavirus 1b	BuPV1b	JX027295
		bufavirus 2	BuPV2	JX027297
	<i>Rodent protoparvovirus 1</i>	H-1 parvovirus	H1	X01457
		Kilham rat virus	KRV	AF321230
		LuIII virus	LuIII	M81888
		minute virus of mice (prototype)	MVMp	J02275
		minute virus of mice (immunosuppressive)	MVMi	M12032
		minute virus of mice (Missouri)	MVMm	DQ196317
		minute virus of mice (Cutter)	MVMc	U34256
		mouse parvovirus 1	MPV1	U12469
		mouse parvovirus 2	MPV2	DQ196319
		mouse parvovirus 3	MPV3	DQ199631
		mouse parvovirus 4	MPV4	FJ440683
		mouse parvovirus 5	MPV5	FJ441297
		hamster parvovirus	HaPV	U34255
		tumor virus X	TVX	In preparation
		rat minute virus 1	RMV1	AF332882
	<i>Rodent protoparvovirus 2</i>	rat parvovirus 1	RPV1	AF036710
	<i>Ungulate protoparvovirus 1</i>	porcine parvovirus Kresse	PPV-Kr	U44978
		porcine parvovirus NADL-2	PPV-NADL2	L23427
<i>Tetraparvovirus</i>	<i>Chiropteran tetraparvovirus 1</i>	Eidolon helvum (bat) parvovirus	Ba-PARV4	JQ037753
	<i>Primate tetraparvovirus 1</i>	human parvovirus 4 G1	PARV4G1	AY622943
		human parv4 G2	PARV4G2	DQ873391
		human parv4 G3	PARV4G3	EU874248
		chimpanzee parv4	Ch-PARV4	HQ113143
	<i>Ungulate tetraparvovirus 1</i>	bovine hokovirus 1	B-PARV4-1	EU200669

Table 2 continued

Genus	Species	Virus or virus variants	Abbreviation	Accession #
		bovine hokovirus 2	B-PARV4-2	JF504697
	<i>Ungulate tetraparvovirus 2</i>	porcine hokovirus	P-PARV4	EU200677
	<i>Ungulate tetraparvovirus 3</i>	porcine Cn virus	CnP-PARV4	GU938300
	<i>Ungulate tetraparvovirus 4</i>	ovine hokovirus	O-PARV4	JF504699

The type species for each genus is indicated in bold type. Viruses in the current species *Canine adeno-associated virus*, *Equine adeno-associated virus*, *Ovine adeno-associated virus*, *HB parvovirus*, *Lapine parvovirus* and *RT parvovirus* do not meet the new criteria for inclusion in the family. Viruses in the current species *Chicken parvovirus* are transferred from genus *Protoparvovirus* to the new genus *Aveparvovirus* in the new species *Galliform aveparvovirus 1*

about the likely properties of the virus, and allow for facile addition of new species by simply advancing the numerical suffix, as in *Rodent protoparvovirus 2*, which currently contains a single virus, rat parvovirus 1. In addition, because the proposed species distinguish major branches within each genus, they will provide taxonomic names for groups of viruses that are now commonly discussed together in the literature. The only exceptions to this standard naming pattern involve two species from the genus *Dependoparvovirus*, which contain viruses that show excellent potential for clinical use as gene therapy delivery vectors. Viruses in one species are named “adeno-associated virus” plus a hyphenated numeral between 1-4 or 6-13, with individual isolates showing important differences in receptor-binding and tissue-specific transduction efficiency. Because these virus names are so well recognized both inside and outside the field, and because their specific numerals have such important implications, the SG considered it unwise to introduce host taxa or additional numerals into the species name. Accordingly, the proposed name for this species is *Adeno-associated dependoparvovirus A* (instead of the more systematic *Primate dependoparvovirus 1*). A second species in this genus is named *Adeno-associated dependoparvovirus B* and includes one virus, adeno-associated virus-5, which is also of current interest for gene therapy applications.

In general, host taxon descriptors at the level of order, rather than family, are selected for species names to accommodate potential host-range disparity among viruses. However, where such host names were considered confusing or awkward to pronounce, less rigid terms were preferred, as in the use of “pinniped” (fin-footed mammals, including walrus, seals, and sea lions) instead of “carnivore” for viruses of the Californian sea lion, and “ungulate” (hoofed animals) instead of “artiodactyl” for viruses of cows, pigs, and sheep.

The proposals also expand the names of most existing genera by introducing an affix into each name. Two distinct problems are addressed in this way. First, it requires specialist knowledge to recognize that *Amdovirus*, *Bocavirus*,

Dependovirus, and *Erythrovirus* are genera within one subfamily of the family *Parvoviridae*, and that *Iteravirus* is a genus in the subfamily *Densovirinae*. This dislocation will be addressed by adding the infixes “parvo” or “denso” to indicate subfamily affiliation, as in the genera *Amdoparvovirus*, *Bocaparvovirus*, *Dependoparvovirus*, *Erythroparvovirus*, and *Iteradensovirus*. One remaining genus in the subfamily *Densovirinae*, *Brevidensovirus*, already contains the infix, and proposed names for all new genera will include the appropriate notation. It is hoped that this modification will improve family recognition, thus providing information about the general properties of a virus in any given genus to people outside the field, and will obviate the need to explain the taxonomy whenever viruses in different parvovirus genera are compared. Practically, it was becoming challenging to invent names for new genera, since these commonly appeared to suggest affiliation to a different virus family. For example, a previously proposed genus name *Partetravirus*, which is widely in use in the field to encompass viruses related to human parvovirus 4 (PARV4, GenBank AY622943), was not welcomed by the ICTV because it arguably suggested that these viruses were members of the family *Alphatetraviridae*. In the current proposals, we again seek recognition for this group of viruses, but under the genus name *Tetraparvovirus*, since the infix should substantially limit ambiguity.

Although subfamily affiliations of viruses in the existing genera *Parvovirus* and *Densovirus* are explicit, vernacular use of “parvovirus” and “densovirus” is ambiguous because the terms indicate multiple taxa. Thus, “parvovirus” can refer to members of the genus *Parvovirus*, the subfamily *Parvovirinae*, or the family *Parvoviridae*, while “densovirus” can indicate genus or subfamily affiliation. To provide greater taxonomic precision, the proposals also insert the prefix “Proto” before *Parvovirus*, creating the genus name *Protoparvovirus* (from Greek, “proto” meaning “first”, in this case the first viruses identified), and “Ambi” before *Densovirus*, creating the genus name *Ambidensovirus* (from Latin or Celtic, meaning “both”, referring to ambisense transcription). Overall, these

changes should provide the field with a more self-explanatory framework and greater precision when using taxonomically derived terms.

Taxon and virus lists for the proposed classification are shown in Tables 2 and 3. In the subfamily *Parvovirinae*, there are three new genera, to be called *Aveparvovirus*, to indicate the bird (*Aves*) hosts of the founding members,

Copiparvovirus, a siglum for cow and pig, which were the hosts of the first two species identified, and *Tetraparvovirus*, from the name of the founder virus, human parvovirus 4 (PARV4), using Latin “tetra” in place of the numeral 4. In the subfamily *Densovirinae*, two new genera are proposed, in order to accommodate shrimp viruses. These will be called *Hepandensovirus*, to reflect the original name of

Table 3 Proposed taxonomy for the subfamily *Densovirinae*

Genus	Species	Virus or virus variants	Abbreviation	Accession #		
<i>Ambidensovirus</i>	<i>Blattodean ambidensovirus 1</i>	<i>Periplaneta fuliginosa</i> densovirus	PfDV	AF192260		
	<i>Blattodean ambidensovirus 2</i>	<i>Blattella germanica</i> densovirus 1	BgDV1	AY189948		
	<i>Dipteran ambidensovirus 1</i>	<i>Culex pipens</i> densovirus	CpDV	FJ810126		
	<i>Hemipteran ambidensovirus 1</i>	<i>Planococcus citri</i> densovirus	PcDV	AY032882		
	<i>Lepidopteran ambidensovirus 1</i>	<i>Diatraea saccharalis</i> densovirus	DsDV	AF036333		
		<i>Galleria mellonella</i> densovirus	GmDV	L32896		
		<i>Helicoverpa armigera</i> densovirus	HaDV1	JQ894784		
		<i>Junonia coenia</i> densovirus	JcDV	S47266		
		<i>Mythimna loreyi</i> densovirus	MIDV	AY461507		
		<i>Pseudoplusia includens</i> densovirus	PiDV	JX645046		
		<i>Acheta domesticus</i> densovirus	AdDV	HQ827781		
		<i>Orthopteran ambidensovirus 1</i>	<i>Dipteran brevidensovirus 1</i>	<i>Aedes aegypti</i> densovirus 1	AaeDV1	M37899
			<i>Aedes albopictus</i> densovirus 1	AalDV1	AY095351	
			<i>Culex pipiens pallens</i> densovirus	CppDV	EF579756	
<i>Brevidensovirus</i>	<i>Anopheles gambiae</i> densovirus	AgDV	EU233812			
	<i>Aedes aegypti</i> densovirus 2	AaeDV2	FJ360744			
	<i>Dipteran brevidensovirus 2</i>	<i>Aedes albopictus</i> densovirus 2	AalDV2	X74945		
	<i>Aedes albopictus</i> densovirus 3	AalDV3	AY310877			
	<i>Haemagogus equinus</i> densovirus	HeDV	AY605055			
	<i>Hepandensovirus</i> ^a	<i>Decapod hepandensovirus 1</i>	<i>Penaeus monodon</i> hepandensovirus 1	PmoHDV1	DQ002873	
		<i>Penaeus chinensis</i> hepandensovirus	PchDV	AY008257		
<i>Penaeus monodon</i> hepandensovirus 2		PmoHDV2	EU247528			
<i>Penaeus monodon</i> hepandensovirus 3		PmoHDV3	EU588991			
<i>Penaeus merguensis</i> hepandensovirus		PmeDV	DQ458781			
<i>Penaeus monodon</i> hepandensovirus 4		PmoHDV4	FJ410797			
<i>Fenneropenaeus chinensis</i> hepandensovirus		FchDV	JN082231			
<i>Iteradensovirus</i>		<i>Lepidopteran iteradensovirus 1</i>	<i>Bombyx mori</i> densovirus	BmDV	AY033435	
	<i>Lepidopteran iteradensovirus 2</i>	<i>Casphalia extranea</i> densovirus	CeDV	AF375296		
		<i>Sibine fusca</i> densovirus	SfDV	JX020762		
	<i>Lepidopteran iteradensovirus 3</i>	<i>Dendrolimus punctatus</i> densovirus	DpDV	AY665654		
	<i>Lepidopteran iteradensovirus 4</i>	<i>Papilio polyxenes</i> densovirus	PpDV	JX110122		
<i>Penstyldensovirus</i> ^b	<i>Lepidopteran iteradensovirus 5</i>	<i>Helicoverpa armigera</i> densovirus	HaDV2	HQ613271		
	<i>Decapod penstyldensovirus 1</i>	<i>Penaeus stylirostris</i> penstyldensovirus 1	PstDV1	AF273215		
	<i>Penaeus monodon</i> penstyldensovirus 1	PmoPDV1	GQ411199			
	<i>Penaeus monodon</i> penstyldensovirus 2	PmoPDV2	AY124937			
	<i>Penaeus stylirostris</i> penstyldensovirus 2	PstDV2	GQ475529			

The type species for each genus is indicated in bold type

^a Indicates genus of viruses formerly known as hepatopancreatic parvovirus [HPV] of shrimp

^b Indicates genus of viruses formerly known as infectious hypodermal and hematopoietic necrosis virus (IHHNV) of shrimp

these viruses, “hepatopancreatic parvovirus”, and *Penstyldensovirus*, a siglum for *Penaeus stylirostris*, the host, and name, of the founding member of this species.

As a general rule, the proposals do not tamper with existing viral names, which remain written in Roman script, for example, canine minute virus and *Galleria mellonella* densovirus (in this case capitalized because “*Galleria*” is derived from a formal name), whereas all formal taxonomic names, for family, subfamily, genus, and species, are capitalized and written in italics. Although abbreviations of viral names also have no formal standing, those listed in Tables 2 and 3 are recommended by the SG, in order to encourage uniformity. For viruses from the subfamily *Densovirinae*, viral names have typically been assembled from binomial host names plus the word “densovirus”, for example, *Jujonia coenia* densovirus, originally abbreviated to JcDNV (where the capitalized “N” harks back to a time when these viruses were called “denso-nucleosis viruses”). However, many host species share the same initials, and viruses from multiple densovirus genera can infect a single host species. Therefore, as new viruses were identified, their abbreviations were distinguished from pre-existing isolates by the insertion of additional letters, causing them to become progressively longer. In part to offset this continued expansion, the SG suggest eliminating the vestigial N from all abbreviations, as implemented in Table 3. Finally, the proposed establishment of two new genera for shrimp viruses, each encompassing viruses that are responsible for an economically significant disease but which all infect an overlapping group of host species, was deemed to require an unusual approach. As discussed above, one of these viral clusters, formerly known as “hepatopancreatic parvovirus” of shrimp (HPV), now constitutes the genus *Hepandensovirus*, whereas the other, formerly known as “infectious hypodermal and hematopoietic virus” of shrimp (IHNV), is classified in the genus *Penstyldensovirus*. Because these names and abbreviations do not meet standard densovirus conventions, in this particular instance the SG voted to rename the viruses. However, rather than use “densovirus”, the new genus name was included, in order to improve clarity. Accordingly, in Table 3 these viruses are called, for example, *Penaeus monodon* hepandensovirus 1-4, or *Penaeus monodon* penstyldensovirus 1-2, and are abbreviated to PmoHDV (1-4) and PmoPDV (1-2), respectively.

Acknowledgments This work was supported in part by Public Health Service grants from the National Institutes of Health (CA029303 and AI026109), SFC and PTa; (AI046458 and AI091588), DJP; (AI070723), JQ; (GM082946), MAM; the National Science Foundation (MCB 0718948), MAM; the UK Medical Research Council, AD and DG; the Helsinki University Research Funds and Jusélius Foundation, Finland, MSV; and the Natural Sciences and Engineering Research Council of Canada, PTi.

Conflict of interest The authors declare that they have no conflicts of interest.

References

- Belyi VA, Levine AJ, Skalka AM (2010) Sequences from ancestral single-stranded DNA viruses in vertebrate genomes: the parvoviridae and circoviridae are more than 40 to 50 million years old. *J Virol* 2010(84):12458–12462
- Cotmore SF and Tattersall P. 2013 Parvovirus diversity and DNA damage responses. *Cold Spring Harb Perspect Biol*. 2013 5(2). doi:10.1101/cshperspect.a012989
- Cotmore SF, Tattersall P (2005) A rolling-hairpin strategy: basic mechanisms of DNA replication in the parvoviruses. In: Kerr J, Cotmore SF, Bloom ME, Linden RM, Parrish CR (eds) *Parvoviruses*. Hodder Arnold, London, pp 171–181
- Drummond AJ, Ho SYW, Phillips MJ, Rambaut A (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biol* 4:e88
- Drummond AJ, Rambaut A (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol Biol* 7:214
- Eddy SR (2011) Accelerated profile HMM searches. *PLoS Comput Biol* 7:e1002195
- Ge X, Li Y, Yang X, Zhang H, Zhou P, Zhang Y, Shi Z (2012) Metagenomic analysis of viruses from bat fecal samples reveals many novel viruses in insectivorous bats in China. *J Virol* 86:4620–4630
- Huang Q, Deng X, Yan Z, Cheng F, Luo Y, Shen W, Lei-Butters DC, Chen AY, Li Y, Tang L, Söderlund-Venermo M, Engelhardt JF, Qiu J (2012) Establishment of a reverse genetics system for studying human bocavirus in human airway epithelia. *PLoS Pathog* 8:e1002899
- Kapoor A, Simmonds P, Lipkin WI (2010) Discovery and characterization of mammalian endogenous parvoviruses. *J Virol* 84:12628–12635
- Li L, Cotmore SF, Tattersall P (2013) Parvoviral left-end hairpin ears are essential during infection for establishing a functional intranuclear transcription template and for efficient progeny genome encapsidation. *J Virol* 87:10501–10514
- Needleman SB, Wunsch CD (1970) A general method applicable to the search for similarities in the amino acid sequences of two proteins. *J Mol Biol* 48:443–453
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2012) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony method. *Mol Biol Evol* 28:2731–2739
- Tattersall P, Bergoin M, Bloom ME, Brown KE, Linden RM, Muzyczka N, Parrish CR, Tijssen P (2005) *Family Parvoviridae*. In: Fauquet CM, Mayo MA, Maniloff J, Desselberger U, Ball LA (eds) *Virus taxonomy—eighth report of the International Committee on Taxonomy of viruses*. Elsevier/Academic Press, San Diego, pp 353–369
- Tijssen P, Agbandje-McKenna M, Almendral JM, Bergoin M, Flegel TW, Hedman K, Kleinschmidt J, Li Y, Pintel DJ, Tattersall P (2011) *The family Parvoviridae*. In: King AMQ, Adams MJ, Carstens EB, Lefkowitz EJ (eds) *Virus taxonomy—Ninth Report of the International Committee on Taxonomy of Viruses*. Elsevier/ Academic Press, London, pp 405–425
- van Regenmortel MHV, Mahy BWJ (2004) Emerging issues in virus taxonomy. *Emerg Infect Dis* 10:8–13
- van Regenmortel MH, Burke DS, Calisher CH, Dietzgen RG, Fauquet CM, Ghabrial SA, Jahrling PB, Johnson KM, Holbrook MR, Horzinek MC, Keil GM, Kuhn JH, Mahy BW, Martelli GP, Pringle C, Rybicki EP, Skern T, Tesh RB, Wahl-Jensen V, Walker PJ, Weaver SC (2010) A proposal to change existing virus species names to non-Latinized binomials. *Arch Virol* 155:1909–1919