# VIROLOGY DIVISION NEWS

# The family Parvoviridae

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**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,

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.

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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.

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#### 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. 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, Gen-Bank 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

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(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 rootand-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

**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 Parvov	virinae - vertel	brate hosts			
Amdovirus	1	1	Amdo <b>parvo</b> virus	2	2
-	-	-	Aveparvovirus <sup>a</sup>	1	2
Bocavirus	2	6	Boca <b>parvo</b> virus	12	22
-	-	-	Copiparvovirus <sup>a</sup>	2	2
Dependovirus	12	13	Dependo <b>parvo</b> virus	7	23
Erythrovirus	4	9	Erythro <b>parvo</b> virus	6	12
Parvovirus	12	18	<b>Proto</b> parvovirus	5	25
-	-	-	$Tetraparvovirus^a$	6	10
Subfamily Densor	virinae - arthro	opod hosts			
Densovirus	2	2	<b>Ambi</b> densovirus	6	11
Brevidensovirus	2	2	Brevidensovirus	2	8
-	-	-	$He pandens ovirus^a$	1	7
Iteravirus	1	1	Itera <b>denso</b> virus	5	6
-	-	-	Penstyldensovirus <sup>a</sup>	1	4
Pefudensovirus <sup>b</sup>	1	1	-	-	-

Bold type in genus names denotes new affixes

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 phylogenic 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



a Denotes new genera

<sup>&</sup>lt;sup>b</sup> Denotes a retired genus

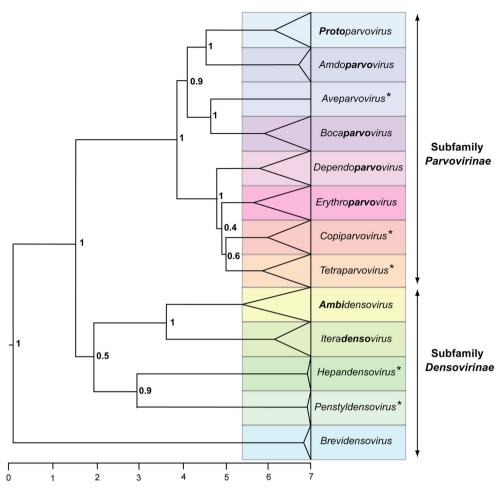


Fig. 1 Phylogenetic tree showing genera in the family *Parvoviridae*. Phylogenetic analysis based on the amino acid sequence of the viral replication initiator protein, NS1, which contains a conserved AAA+ helicase domain corresponding to the Parvo\_NS1 Pfam domain: http://pfam.sanger.ac.uk/family/Parvo\_NS1. 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 implented 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 #
Amdoparvovirus	Carnivore amdoparvovirus 1	Aleutian mink disease virus	AMDV	JN040434
	Carnivore amdoparvovirus 2	gray fox amdovirus	GFAV	JN202450
Aveparvovirus	Galliform aveparvovirus 1	chicken parvovirus	ChPV	GU214704
		turkey parvovirus	TuPV	GU214706
Bocaparvovirus	Carnivore bocaparvovirus 1	canine minute virus	CnMV	FJ214110
	Carnivore bocaparvovirus 2	canine bocavirus 1	CBoV	JN648103
	Carnivore bocaparvovirus 3	feline bocavirus	FBoV	JQ692585
	Pinniped bocaparvovirus 1	California sea lion bocavirus 1	CslBoV1	JN420361
		California sea lion bocavirus 2	CslBoV2	JN420366
	Pinniped bocaparvovirus 2	California sea lion bocavirus 3	CslBoV3	JN420365
	Primate bocaparvovirus 1	human bocavirus 1	HBoV1	JQ923422
		human bocavirus 3	HBoV3	EU918736
		gorilla bocavirus	GBoV	HM145750
	Primate bocaparvovirus 2	human bocavirus 2a	HBoV2a	FJ973558
		human bocavirus 2b	HBoV2b	FJ973560
		human bocavirus 2c	HBoV2c	FJ170278
		human bocavirus 4	HBoV4	FJ973561
	Ungulate bocaparvovirus 1	bovine parvovirus	BPV	DQ335247
	Ungulate bocaparvovirus 2	porcine bocavirus 1	PBoV1	HM053693
		porcine bocavirus 2	PBoV2	HM053694
		porcine bocavirus 6	PBoV6	HQ291309
	Ungulate bocaparvovirus 3	porcine bocavirus 5	PBoV5	HQ223038
	Ungulate bocaparvovirus 4	porcine bocavirus 7	PBoV7	HQ291308
	Ungulate bocaparvovirus 5	porcine bocavirus 3	PBoV3	JF429834
		porcine bocavirus 4-1	PBoV4-1	JF429835
		porcine bocavirus 4-2	PBoV4-2	JF429836
Copiparvovirus	Ungulate copiparvovirus 1	bovine parvovirus 2	BPV2	AF406966
	Ungulate copiparvovirus 2	porcine parvovirus 4	PPV4	GQ387499
Dependoparvovirus	Adeno-associated dependoparvovirus A	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
	Adeno-associated dependoparvovirus B	adeno-associated virus-5	AAV5	AF085716
		bovine adeno-associated virus	BAAV	AY388617
		caprine adeno-associated virus	CapAAV	DQ335246
	Anseriform dependoparvovirus 1	duck parvovirus	DPV	U22967
		goose parvovirus-PT	GPV2	JF926695



Table 2 continued

Genus	Species	Virus or virus variants	Abbreviation	Accession #
		goose parvovirus	GPV	U25749
	Avian dependoparvovirus I	avian adeno-associated virus	AAAV	AY186198
	Chiropteran dependoparvovirus 1	bat adeno-associated virus	BtAAV	GU226971
	Pinniped dependoparvovirus 1	California sea lion adeno-associated virus	CslAAV	JN420372
	Squamate dependoparvovirus 1	snake adeno-associated virus	SAAV	AY349010
Erythroparvovirus	Primate erythroparvovirus 1	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
	Primate erythroparvovirus 2	simian parvovirus	SPV	U26342
	Primate erythroparvovirus 3	rhesus macaque parvovirus	RhMPV	AF221122
	Primate erythroparvovirus 4	pig-tailed macaque parvovirus	PtMPV	AF221123
	Rodent erythroparvovirus 1	chipmunk parvovirus	ChpPV	GQ200736
	Ungulate erythroparvovirus 1	bovine parvovirus 3	BPV3	AF406967
Protoparvovirus	Carnivore protoparvovirus 1	feline parvovirus	FPV	EU659111
		canine parvovirus	CPV	M19296
		mink enteritis virus	MEV	D00765
		racoon parvovirus	RaPV	JN867610
	Primate protoparvovirus 1	bufavirus 1a	BuPV1a	JX027296
		bufavirus 1b	BuPV1b	JX027295
		bufavirus 2	BuPV2	JX027297
	Rodent protoparvovirus 1	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 preparatio
		rat minute virus 1	RMV1	AF332882
	Rodent protoparvovirus 2	rat parvovirus 1	RPV1	AF036710
	Ungulate protoparvovirus 1	porcine parvovirus Kresse	PPV-Kr	U44978
		porcine parvovirus NADL-2	PPV-NADL2	L23427
Tetraparvovirus	Chiropteran tetraparvovirus I	Eidolon helvum (bat) parvovirus	Ba-PARV4	JQ037753
•	Primate tetraparvovirus 1	human parvovirus 4 G1	PARV4G1	AY622943
	•	human parv4 G2	PARV4G2	DQ873391
		human parv4 G3	PARV4G3	EU874248
		chimpanzee parv4	Ch-PARV4	HQ113143
	Ungulate tetraparvovirus 1	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
	Ungulate tetraparvovirus 2	porcine hokovirus	P-PARV4 EU200677
	Ungulate tetraparvovirus 3	porcine Cn virus	CnP-PARV4 GU938300
	Ungulate tetraparvovirus 4	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 #
Ambidensovirus	Blattodean ambidensovirus 1	Periplaneta fuliginosa densovirus	PfDV	AF192260
	Blattodean ambidensovirus 2	Blattella germanica densovirus 1	BgDV1	AY189948
	Dipteran ambidensovirus 1	Culex pipens densovirus	CpDV	FJ810126
	Hemipteran ambidensovirus 1	Planococcus citri densovirus	PcDV	AY032882
	Lepidopteran ambidensovirus 1	Diatraea saccharalis densovirus	DsDV	AF036333
		Galleria mellonella densovirus	GmDV	L32896
		Helicoverpa armigera densovirus	HaDV1	JQ894784
		Junonia coenia densovirus	JcDV	S47266
		Mythimna loreyi densovirus	MlDV	AY461507
		Pseudoplusia includens densovirus	PiDV	JX645046
	Orthopteran ambidensovirus I	Acheta domesticus densovirus	AdDV	HQ827781
Brevidensovirus	Dipteran brevidensovirus 1	Aedes aegypti densovirus 1	AaeDV1	M37899
		Aedes albopictus densovirus 1	AalDV1	AY095351
		Culex pipiens pallens densovirus	CppDV	EF579756
		Anopheles gambiae densovirus	AgDV	EU233812
		Aedes aegypti densovirus 2	AaeDV2	FJ360744
	Dipteran brevidensovirus 2	Aedes albopictus densovirus 2	AalDV2	X74945
		Aedes albopictus densovirus 3	AalDV3	AY310877
		Haemagogus equinus densovirus	HeDV	AY605055
Hepandensovirus <sup>a</sup>	Decapod hepandensovirus 1	Penaeus monodon hepandensovirus 1	PmoHDV1	DQ002873
		Penaeus chinensis hepandensovirus	PchDV	AY008257
		Penaeus monodon hepandensovirus 2	PmoHDV2	EU247528
		Penaeus monodon hepandensovirus 3	PmoHDV3	EU588991
		Penaeus merguiensis hepandensovirus	PmeDV	DQ458781
		Penaeus monodon hepandensovirus 4	PmoHDV4	FJ410797
		Fenneropenaeus chinensis hepandensovirus	FchDV	JN082231
Iteradensovirus	Lepidopteran iteradensovirus 1	Bombyx mori densovirus	BmDV	AY033435
	Lepidopteran iteradensovirus 2	Casphalia extranea densovirus	CeDV	AF375296
		Sibine fusca densovirus	SfDV	JX020762
	Lepidopteran iteradensovirus 3	Dendrolimus punctatus densovirus	DpDV	AY665654
	Lepidopteran iteradensovirus 4	Papilio polyxenes densovirus	PpDV	JX110122
	Lepidopteran iteradensovirus 5	Helicoverpa armigera densovirus	HaDV2	HQ613271
Penstyldensovirus b	Decapod penstyldensovirus 1	Penaeus stylirostris penstyldensovirus 1	PstDV1	AF273215
		Penaeus monodon penstyldensovirus 1	PmoPDV1	GQ411199
		Penaeus monodon penstyldensovirus 2	PmoPDV2	AY124937
		Penaeus stylirostris penstyldensovirus 2	PstDV2	GQ475529

The type species for each genus is indicated in bold type

<sup>&</sup>lt;sup>b</sup> Indicates genus of viruses formerly known as infectious hypodermal and hematopoietic necrosis virus (IHHNV) of shrimp



<sup>&</sup>lt;sup>a</sup> Indicates genus of viruses formerly known as hepatopancreatic parvovirus [HPV] 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 "densonucleosis 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 preexisting 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 (IHHNV), 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.

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

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