



















Reorganization and expansion of the nidoviral family *Arteriviridae*

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Abstract The family *Arteriviridae* presently includes a single genus *Arterivirus*. This genus includes four species as the taxonomic homes for equine arteritis virus (EAV), lactate dehydrogenase-elevating virus (LDV), porcine respiratory and reproductive syndrome virus (PRRSV), and simian hemorrhagic fever virus (SHFV), respectively. A revision of this classification is urgently needed to accommodate the recent description of eleven highly

divergent simian arteriviruses in diverse African nonhuman primates, one novel arterivirus in an African forest giant pouched rat, and a novel arterivirus in common brushtails in New Zealand. In addition, the current arterivirus nomenclature is not in accordance with the most recent version of the International Code of Virus Classification and Nomenclature. Here we outline an updated, amended, and improved arterivirus taxonomy based on current data. Taxon-specific sequence cut-offs are established relying on a newly established open reading frame 1b phylogeny and pairwise sequence comparison (PASC) of coding-complete arterivirus genomes. As a result, the current genus *Arterivirus* is replaced by five genera: *Equartevirus* (for EAV), *Rodartevirus* (LDV + PRRSV), *Simartevirus* (SHFV + simian arteriviruses), *Nesartevirus* (for the arterivirus from forest giant pouched rats), and *Dipartevirus* (common brushtail arterivirus). The current species *Porcine reproductive and respiratory syndrome virus* is divided into two species to accommodate the clear

The content of this publication does not necessarily reflect the views or policies of the US Department of the Army, the US Department of Defense, the US Department of Health and Human Services, or the institutions and companies affiliated with the authors. The taxonomic changes suggested/proposed/described here have been submitted as an official taxonomic proposal to the International Committee on Taxonomy of Viruses (ICTV) as TaxoProp #2015.001a-uS “Reorganization of the family *Arteriviridae* to accommodate 13 new species” (<http://www.ictvonline.org>). These changes (i) have not yet been endorsed by the ICTV Executive Committee, (ii) may differ from any new taxonomy that is ultimately approved by the ICTV, and (iii) are presented for discussion only but has no official standing at this point in time.

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divergence of the European and American “types” of PRRSV, both of which now receive virus status. The current species *Simian hemorrhagic fever virus* is divided into nine species to accommodate the twelve known simian arteriviruses. Non-Latinized binomial species names are introduced to replace all current species names to clearly differentiate them from virus names, which remain largely unchanged.

Introduction

In comparison to prokaryotic and eukaryotic taxonomy, viral taxonomy is still in its infancy. The most recent updates issued by the International Committee on Taxonomy of Viruses (ICTV) list <10,000 viruses that have been classified in <3,000 species [2, 3, 6, 7, 30]. The development and increasing adoption of metagenomic approaches in recent years have revealed that current measurements of global viral diversity are vast underestimates [8, 13]. For the foreseeable future, virus taxonomy will have to be revised continuously and sometimes substantially as new discoveries are made that challenge current taxonomic thinking [38]. Objective techniques, such as viral genome sequence-based alignments and comparison algorithms, and automatic tools (*in silico* taxonomy decision trees) are used increasingly for virus classification to circumvent virus culture bias (i.e., the acceptance and classification of only that minority of viruses that can be grown in the laboratory). Updating existing taxonomies is crucial for classification to become database-compliant and user-friendly, while not violating the Rules of the International

Code of Virus Classification and Nomenclature (ICVCN), which also are updated continuously [4, 5, 30].

Here, we address the taxonomy of the family *Arteriviridae* (order *Nidovirales*). Arteriviruses have monopartite, single-stranded RNA genomes of positive polarity. Large nonstructural polyproteins are directly translated from these genomes, whereas additional structural proteins are typically translated from nested sets of subgenomic mRNAs [24]. We outline an updated arterivirus classification and nomenclature to incorporate recent discoveries and to address current shortcomings and inconsistencies for ease of application, clarity, and ICVCN compliance.

History of arterivirus taxonomy

The taxonomic history of equine arteritis virus (EAV), lactate dehydrogenase-elevating virus (LDV), porcine respiratory and reproductive syndrome virus (PRRSV), and simian hemorrhagic fever virus (SHFV)—currently the only accepted members of the family *Arteriviridae*—is complex. The reason for this complexity is in part because these viruses were discovered before the advent of modern molecular biological techniques. The isolation of EAV, the causative agent of equine viral arteritis, was reported in 1957 [15]; the isolation of LDV, which can cause disease in laboratory mice, was reported in 1963 [44]; and the isolation of SHFV, which causes simian hemorrhagic fever in Asian macaques, was reported in 1968 [52]. Even the isolation of PRRSV, the etiological agent of porcine reproductive and respiratory syndrome, in 1991 [57] (European/Lelystad “strain” or “type 1”) and 1992 [12, 19] (North American “strain” or “type 2”) predates the availability of routine genome sequencing. Consequently, initial classification of these viruses relied primarily on morphological features of their virions (Fig. 1), with subsequent reclassifications based on nucleotide sequences of genome fragments or, eventually, coding-complete or complete genomes generated from viruses isolated *in vitro*.

None of these four arteriviruses were mentioned in the First Report (1971) of the International Committee on Nomenclature of Viruses (ICNV), the predecessor of the ICTV [58]. In the Second ICTV Report (1976), EAV and LDV were considered related due to their similar protein composition [59] and listed as unclassified members of the family *Togaviridae* because of the similarity of their virions to those of classified togaviruses [26]. SHFV joined this group of unclassified togaviruses in the Third (1979) and Fourth (1982) Reports [39, 40]. During subsequent years, the family *Togaviridae* was reorganized thoroughly. As a consequence, the genus *Arterivirus* was established and included in the family *Togaviridae* as a taxonomic home for EAV. LDV was considered a second member of this

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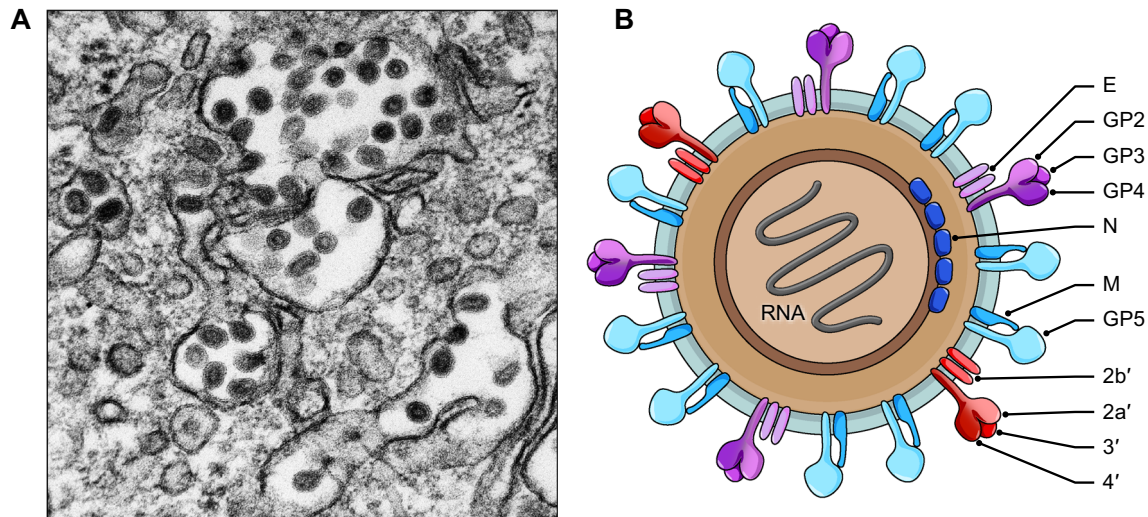


Fig. 1 Structure of arterivirions. A) Electron micrograph of simian hemorrhagic fever virus particles inside of cellular vacuoles. B) Cartoon of a generalized simian arterivirus particle depicting all structural proteins. Arteriviruses from non-simian hosts, such as

African pouched rat virus 1, equine arterivirus virus, lactate dehydrogenase-elevating viruses, porcine reproductive and respiratory syndrome viruses, or wobbly possum disease virus have a similar particle organization but lack proteins 2a', 2b', 3', and 4'

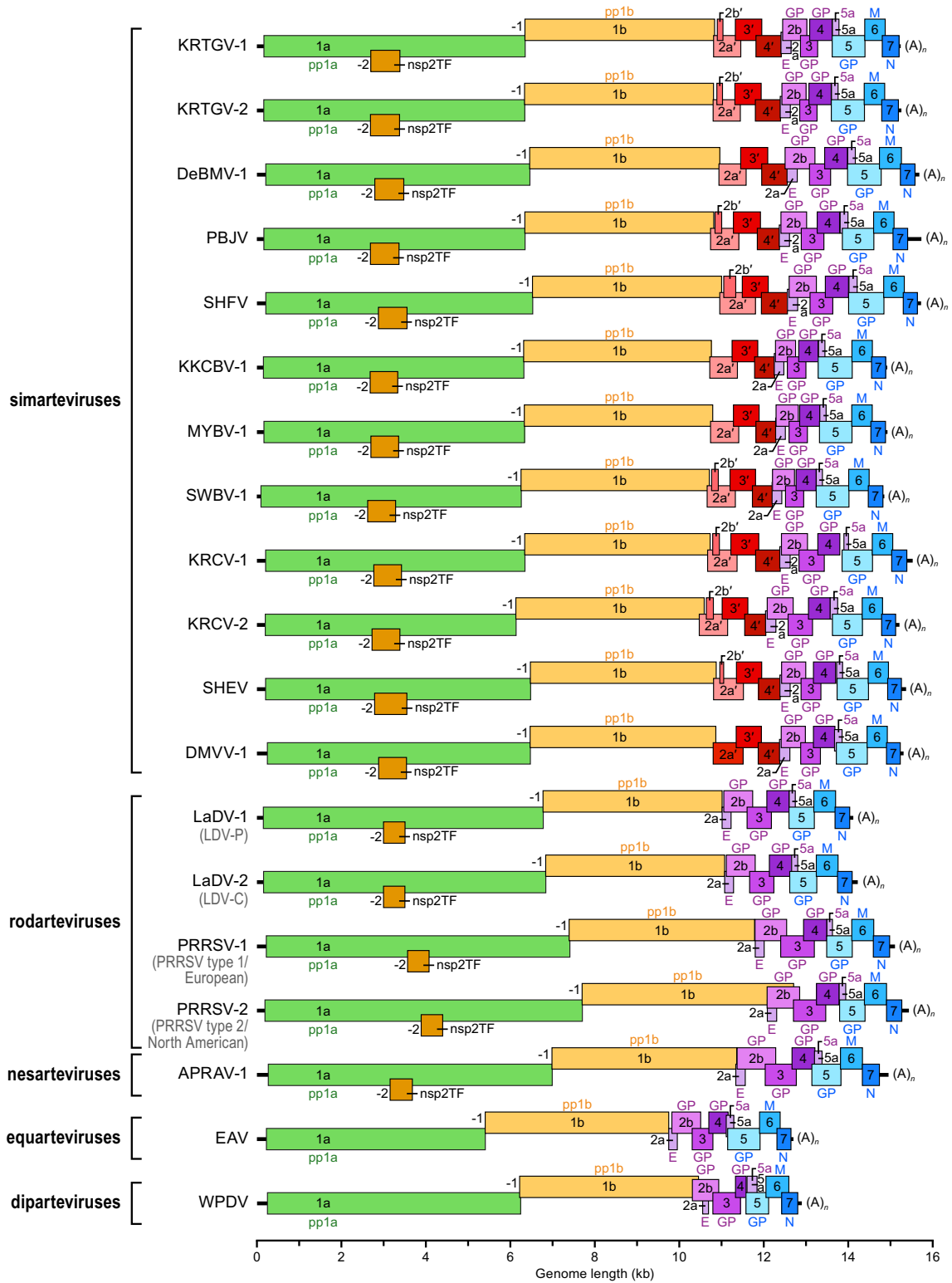
Table 1 Current ICTV-accepted arterivirus taxonomy [24]

Order (name of taxon members)	Family (name of taxon members)	Genus (name of taxon members)	Species	Virus (abbreviation)
<i>Nidovirales</i> (nidoviruses)	<i>Arteriviridae</i> (arteriviruses)	<i>Arterivirus</i> (arteriviruses)	<i>Equine arteritis virus</i> ¹	equine arteritis virus (EAV)
			<i>Lactate dehydrogenase-elevating virus</i>	lactate dehydrogenase-elevating virus (LDV)
			<i>Porcine reproductive and respiratory syndrome virus</i>	porcine reproductive and respiratory syndrome virus (PRRSV)
			<i>Simian hemorrhagic fever virus</i>	simian hemorrhagic fever virus (SHFV)

¹ Type species

genus, and SHFV was removed from the family *Togaviridae* and placed into a group with hepatitis C virus in the newly established family *Flaviviridae* [51, 56]. However, the Fifth Report failed to take into account that EAV replication occurs via a 5'-3'-coterminal set of nested subgenomic mRNAs, a strategy not used by togaviruses or flaviviruses, but is characteristic of coronaviruses [20, 21, 28, 48]. Subsequent genomic studies confirmed the relatedness of EAV, LDV, PRRSV, and SHFV. Therefore, in the ICTV's Sixth Report (1995), all four viruses were assigned to a free-floating genus *Arterivirus* [18]. The ICTV's Seventh Report (2000) formalized the relationship

of arteriviruses and coronaviruses by including the genus *Arterivirus* in a new family, *Arteriviridae*, and by including this family and the family *Coronaviridae* in a new order, *Nidovirales*. EAV, LDV, PRRSV, and SHFV were assigned as single members to the four arteriviral species *Equine arteritis virus*, *Lactate dehydrogenase-elevating virus*, *Porcine respiratory and reproductive syndrome virus*, and *Simian hemorrhagic fever virus*, respectively [14, 23]. This taxonomy was upheld in the ICTV's Eight (2005) and Ninth Reports (2011) and is still valid at the time of writing [24, 46]. A summary of this arterivirus taxonomy is given in Table 1.



◀ **Fig. 2** Organization of arterivirus genomes. Individual arterivirus open reading frames (ORFs) drawn to scale are shown in colors. ORF1a (green) encodes polyprotein 1a (pp1a). ORF1a and ORF1b (yellow) can be joined through a “-1” programmed ribosomal frameshift to express polyprotein 1ab. pp1a and pp1ab are translated directly from genomic RNA and are subsequently proteolytically cleaved into numerous nonstructural proteins, many of which are part of the replicase complex. Nonstructural protein 2 transframe (nsp2TF) is produced through a “-2” programmed ribosomal frameshift by most, but not all, arteriviruses. The remaining ORFs are translated from subgenomic RNAs. Purple ORFs (four shades) encode minor structural proteins (envelope protein E, glycoproteins 2b, 3 and 4); blue ORFs (three shades) encode the major structural proteins GP5 (glycoprotein 5), M (matrix protein), and N (nucleocapsid protein). Red ORFs (four shades), present only in simian arterivirus (simartevirus) genomes, encode minor structural proteins of unknown function (see also Fig. 1B). Virus genomes are labeled by retained or new virus abbreviations with previous designations in grey in parentheses. Simian arteriviruses (simarteviruses) are: KRTGV-1/2, Kibale red-tailed guenon viruses 1 and 2; DeBMV-1, DeBrazza’s monkey virus 1; PBJV, Pebjah virus; SHFV, simian hemorrhagic fever virus; KKCBV-1, Kafue kinda-chacma baboon virus 1; MYBV-1, Mikumi yellow baboon virus 1; SWBV-1, Southwest baboon virus 1; KRCV-1/2, Kibale red colobus viruses 1 and 2; SHEV, simian hemorrhagic encephalitis virus; DMVV-1; Drakensberg Mountain vervet virus 1. Murine and porcine arteriviruses (rodarteviruses) are: LaDV-1/2, lactate dehydrogenase-elevating viruses 1 and 2; PRRSV-1/2, and porcine reproductive and respiratory syndrome viruses 1 and 2. Nesomyid arteriviruses (nesarteviruses) contain: APRAV-1, African pouched rat virus 1. Equine arteriviruses (equarteviruses) contain: EAV, equine arteritis virus. Possum arteriviruses (diparteviruses) include: WPDV, wobbly possum disease virus. For GenBank accession numbers used for the analyses, see Table 2 (color figure online)

Current challenges for arterivirus taxonomy

Novel arteriviruses require classification

Eleven simian arteriviruses were discovered in recent years by next-generation sequencing in apparently healthy African cercopithecoid nonhuman primates. Kibale red colobus viruses 1 and 2 (KRCV-1/2) were found in wild Ugandan red colobus (*Procolobus [Piliocolobus] rufomitratus tephrosceles* Elliot, 1907) from Uganda’s Kibale National Park [10, 35]. Kibale red-tailed guenon viruses 1 and 2 (KRTGV-1/2) were discovered in the same location in healthy red-tailed monkeys (*Cercopithecus ascanius* Audebert, 1799) [36]. Mikumi yellow baboon virus 1 (MYBV-1) was found in yellow baboons (*Papio cynocephalus* Linnaeus, 1766) in Tanzania’s Mikumi National Park, and the closely related Southwest baboon virus 1 (SWBV-1) was detected in healthy captive olive baboons (*Papio anubis*, Lesson 1827) at the Southwest National Primate Research Center in San Antonio, Texas, USA [9]. Results of a recent study identified two novel simian arteriviruses, Pebjah virus (PBJV) and simian hemorrhagic encephalitis virus (SHEV), as etiological agents of historical simian hemorrhagic fever outbreaks in Asian

macaques, but their natural hosts remain unknown [37]. During yet unpublished studies, Drakensberg Mountain vervet virus 1 (DMVV-1) and Kafue kinda-chacma baboon virus 1 (KKCBV-1) were discovered in vervet monkeys (*Chlorocebus pygerythrus* Cuvier, 1821) and Kinda baboons (*Papio kindae* Lönnberg, 1919) in South Africa and Zambia, respectively. Finally, a novel simian arterivirus was found in a DeBrazza’s monkey (*Cercopithecus neglectus* Schlegel, 1876) in Cameroon and its sequence was deposited in GenBank (Ng *et al.*, unpublished).

Analyses of the genomes of these eleven viruses clearly identify them as members of the family *Arteriviridae*. In fact, all arterivirus-defining elements (Figs. 1 and 2) can be identified unambiguously. Such elements include: open reading frame (ORF)1a and ORF1b encoding nonstructural proteins, ORFs2a–7 encoding structural proteins, and joined ORF1a and ORF1b (through a -1 programmed ribosomal frameshift site + RNA pseudoknot) encoding a polyprotein that is cleaved into main proteinase 3CL^{PRO}, RNA-dependent RNA polymerase, putative zinc-binding domain (ZBD), helicase (HEL1), and uridylate-specific endoribonuclease (NendoU) [24, 47]) (Fig. 2). More importantly, all eleven simian arteriviruses are characterized by the presence of additional ORFs that are characteristic of the SHFV genome, but which are absent from the genomes of all other currently characterized arteriviruses (Fig. 2).

A novel arterivirus was recently discovered in a forest giant pouched rat (*Cricetomys emini* Wroughton, 1910) in Cameroon (GenBank and Ng *et al.*, unpublished). In 2012, Dunowska *et al.* published the partial genome of a novel arterivirus-like pathogen, wobbly possum disease virus (WPDV), found in common brushtails (Diprodontia: Phalangeridae: *Trichosurus vulpecula* Kerr, 1972), a marsupial introduced to New Zealand [22]. The complete genomic sequences of WPDV were deposited in GenBank [unpublished data], and the virus was isolated in tissue culture in 2015 [27]. Both the virus from the forest giant pouched rat and WPDV genomes contain all arterivirus-defining elements described above, and recent electron-microscopic studies revealed that the WPDV particles assume the typical arterivirion shape (spherical to icosahedral particles) [22, 27]. However, the WPDV genome sequence is highly divergent from the genomes of classified arteriviruses [22, 47], and WPDV is the first arterivirus found in a non-eutherian host.

The current arterivirus nomenclature is discouraged by the International Code of Virus Classification and Nomenclature

The ICVCN has several Rules to discourage naming of taxa in ambiguous ways to avoid confusion, such as:

Table 2 Updated and amended arterivirus taxonomy

Order (name of taxon members)	Family (name of taxon members)	Genus (name of taxon members)	Species	Virus name (virus abbreviation)	GenBank accession number	
<i>Nidovirales</i> (nidoviruses)	<i>Arteriviridae</i> (arteriviruses)	<i>Dipartevirus</i> (diparteviruses)	<i>Trichosurus 1 dipartevirus</i> ¹	wobbly possum disease virus (WPDV)	JN116253	
			<i>Equartevirus</i> (equarteviruses)	<i>Equid equartevirus</i> ¹	equine arteritis virus (EAV)	X53459
		<i>Nesartevirus</i> (nesarteviruses)		<i>Cricetomys 1 nesartevirus</i> ¹	African pouched rat virus 1 (APRAV-1)	KP026921
			<i>Rodartevirus</i> (rodarteviruses)	<i>Muroid rodartevirus</i>		lactate dehydrogenase-elevating virus (LaDV-1)
					lactate dehydrogenase-elevating virus (LaDV-2)	L13298
		<i>Suid 1 rodartevirus</i> ¹		porcine reproductive and respiratory syndrome virus 1 (PRRSV-1)	M96262	
		<i>Suid 2 rodartevirus</i>		porcine reproductive and respiratory syndrome virus 2 (PRRSV-2)	AF046869	
		<i>Simartevirus</i> (simarteviruses)		<i>Alamogordo simartevirus</i>	Pebjah virus (PBJV)	KR139839
				<i>Bethesda simartevirus</i> ¹	simian hemorrhagic fever virus (SHFV)	AF180391
			<i>Cercopithecus 1 simartevirus</i>		Kibale red-tailed guenon virus 1 (KRTGV-1)	JX473847
					Kibale red-tailed guenon virus 2 (KRTGV-2)	JX473849
			<i>Cercopithecus 2 simartevirus</i>	DeBrazza's monkey virus 1 (DeBMV-1)	KP126831	
			<i>Chlorocebus 1 simartevirus</i>	Drakensberg Mountain vervet virus 1 (DMVV-1)	KR862306	
			<i>Papio 1 simartevirus</i>		Mikumi yellow baboon virus 1 (MYBV-1)	KM110938
					Southwest baboon virus 1 (SWBV-1)	KM110946
			<i>Papio 2 simartevirus</i>	Kafue kinda-chacma baboon virus 1 (KKCBV-1)	KT447550	
			<i>Procolobus 1 simartevirus</i>	Kibale red colobus virus 1 (KRCV-1)	HQ845737	
		<i>Procolobus 2 simartevirus</i>	Kibale red colobus virus 2 (KRCV-2)	KC787631		
		<i>Sukhumi simartevirus</i>	simian hemorrhagic encephalitis virus (SHEV)	KM677927		

¹ Type species

	KRTGV-1	KRTGV-2	DeBMV-1	PBJV	SHFV	KKCBV-1	MYBV-1	SWBV-1	KRCV-2	KRCV-1	SHEV	DMVV-1	LaDV-1	LaDV-2	PRRSV-1	PRRSV-2	APRAV-1	EAV	WPDV
KRTGV-1		77.2	55.3	50.0	50.4	49.2	48.6	48.8	46.0	46.7	45.7	45.2	36.6	36.5	36.7	36.1	35.7	34.4	32.5
KRTGV-2	77.2		54.6	49.6	50.3	49.2	49.1	49.3	45.5	46.3	45.6	45.4	37.1	36.8	37.1	36.0	36.4	34.9	32.2
DeBMV-1	55.3	54.6		51.1	52.4	48.7	49.1	48.6	47.0	46.5	47.1	46.5	36.7	36.6	37.2	36.6	37.3	33.8	31.7
PBJV	50.0	49.6	51.1		50.1	48.5	48.6	48.6	46.6	47.1	46.2	46.3	37.1	36.9	36.8	36.6	36.8	34.3	31.6
SHFV	50.4	50.3	52.4	50.1		48.4	49.1	49.0	46.4	46.3	45.9	45.2	36.7	36.5	37.2	36.6	37.2	33.2	31.8
KKCBV-1	49.2	49.2	48.7	48.5	48.4		57.1	57.2	45.0	46.2	45.9	45.8	37.3	36.9	36.9	35.9	36.0	34.5	32.5
MYBV-1	48.6	49.1	49.1	48.6	49.1	57.1		79.9	45.8	45.7	45.8	45.8	37.0	36.7	37.2	36.1	36.4	34.8	32.6
SWBV-1	48.8	49.3	48.6	48.6	49.0	57.2	79.9		45.2	45.5	45.6	45.4	36.9	36.7	37.0	35.9	36.2	34.6	32.5
KRCV-2	46.0	45.5	47.0	46.6	46.4	45.0	45.8	45.2		46.2	45.6	45.7	35.8	36.2	36.5	35.9	36.2	32.9	31.0
KRCV-1	46.7	46.3	46.5	47.1	46.3	46.2	45.7	45.5	46.2		46.0	46.1	36.7	35.9	37.1	35.6	36.6	33.7	31.3
SHEV	45.7	45.6	47.1	46.2	45.9	45.9	45.8	45.6	45.6	46.0		67.2	37.3	37.2	37.9	37.2	37.8	33.9	31.4
DMVV-1	45.2	45.4	46.5	46.3	45.2	45.8	45.8	45.4	45.7	46.1	67.2		37.5	37.3	37.5	36.1	36.9	33.6	31.5
LaDV-1	36.6	37.1	36.7	37.1	36.7	37.3	37.0	36.9	35.8	36.7	37.3	37.5		76.0	43.2	42.4	37.2	32.4	28.9
LaDV-2	36.5	36.8	36.6	36.9	36.5	36.9	36.7	36.7	36.2	35.9	37.2	37.3	76.0		42.6	42.2	37.3	32.4	29.1
PRRSV-1	36.7	37.1	37.2	36.8	37.2	36.9	37.2	37.0	36.5	37.1	37.9	37.5	43.2	42.6		50.8	37.9	31.3	28.5
PRRSV-2	36.1	36.0	36.6	36.6	36.6	35.9	36.1	35.9	35.9	35.6	37.2	36.1	42.4	42.2	50.8		37.2	30.9	27.5
APRAV-1	35.7	36.4	37.3	36.8	37.2	36.0	36.4	36.2	36.2	36.6	37.8	36.9	37.2	37.3	37.9	37.2		32.0	29.1
EAV	34.4	34.9	33.8	34.3	33.2	34.5	34.8	34.6	32.9	33.7	33.9	33.6	32.4	32.4	31.3	30.9	32.0		29.4
WPDV	32.5	32.2	31.7	31.6	31.8	32.5	32.6	32.5	31.0	31.3	31.4	31.5	28.9	29.1	28.5	27.5	29.1	29.4	

Nucleotide identity (%)

30	40	50	60	70	80
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Fig. 3 Pairwise sequence comparison of the arterivirus proteomes. Coding regions from each arterivirus genome (Fig. 2) were aligned in CLC Genomics Workbench version 6, and a pairwise comparison matrix was constructed. Only orthologous genes common to all known arteriviruses were used (i.e., simian arterivirus-/simartevirus-specific ORFs were ignored). Numbers represent the percent

nucleotide identity between two viruses, with red highlighting virus pairs with relatively high degrees of similarity and white showing virus pairs with lower similarity. Virus abbreviations and sequences sources for the analyses are identical to those outlined in Fig. 2 and Table 2

- “The essential principles of virus nomenclature are ... to avoid or reject the use of names which might cause error or confusion” (Rule 2.1(ii)) [4, 30]
- “New names shall not duplicate approved names. New names shall be chosen such that they are not closely similar to names that are in use currently or have been in use in the recent past” (Rule 3.14) [4, 30]
- “A species name shall consist of as few words as practicable but be distinct from names of other taxa” (Rule 3.21) [4, 30]
- “A species name must provide an appropriately unambiguous identification of the species” (Rule 3.22) [4, 30]

The current arterivirus nomenclature has species and virus names that are identical in spelling and are only differentiated by the presence or absence of italics and first word capitalization (e.g., the single member of the species *Equine arteritis virus* is called equine arteritis virus). Consequently, species names and virus names are often confused in writing, and virus abbreviations are often wrongly assigned to species rather than viruses. This practice obfuscates the distinction between species, which

are conceptual entities, and viruses, which are physical entities [16, 31, 53].

Another problem associated with the current arterivirus nomenclature is that the current family and genus names are only differentiated by their suffixes (“-viridae” vs. “-virus”) but have an identical word stem (“Arteri-“). Since species-specific suffixes for the members of individual taxon hierarchies [55] are not yet accepted in the virology community, the members of both the family *Arteriviridae* and the genus *Arterivirus* are currently called simply “arteriviruses.” The word “arterivirus” will therefore become ambiguous as soon as a second genus is established in the family, as it will not be clear then whether “arterivirus” refers to the members of the one genus or to the members of the entire family.

Finally, the current species names *Lactate dehydrogenase-elevating virus*, *Porcine respiratory and reproductive syndrome virus*, and *Simian hemorrhagic fever virus* contradict Rule 3.21 (“...shall consist of as few words as practicable”).

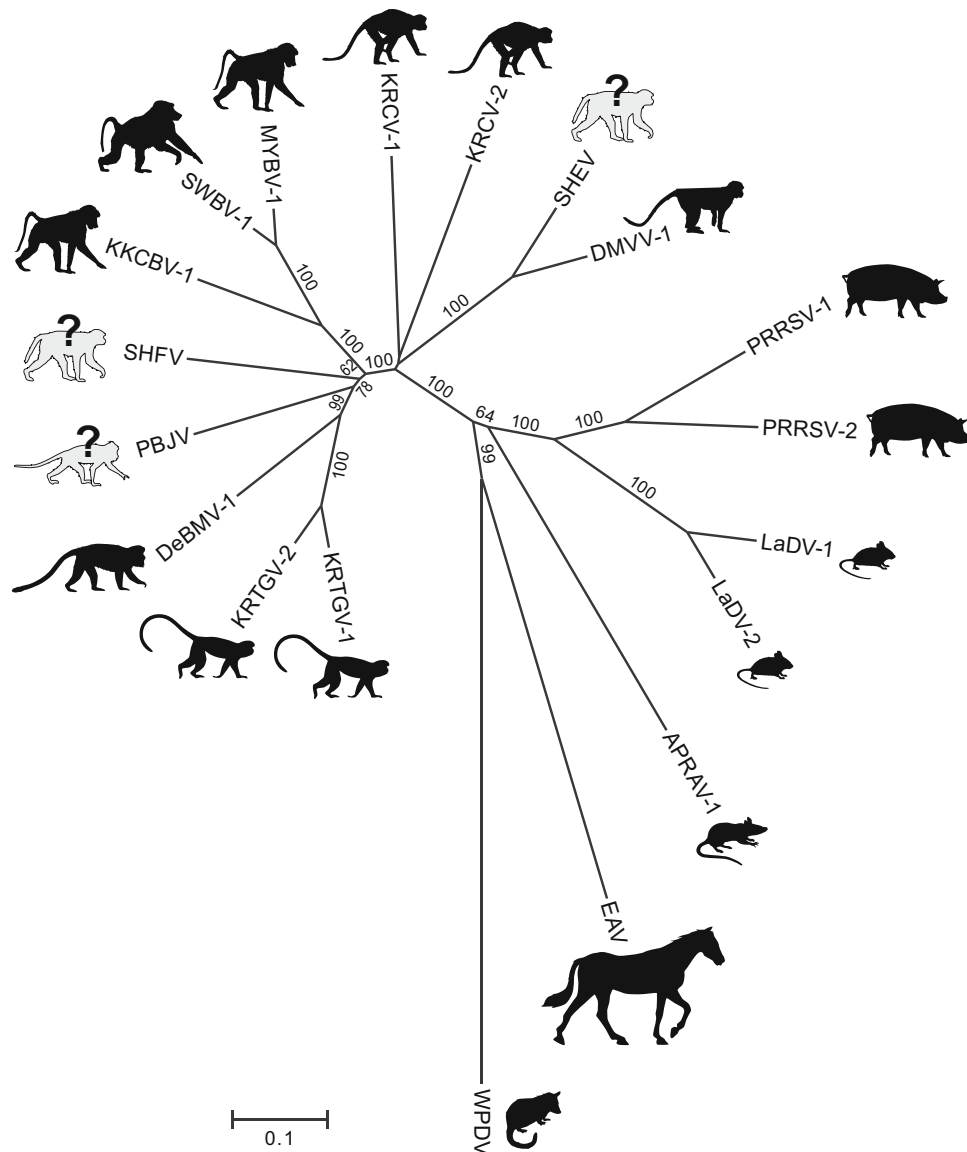


Fig. 4 Phylogenetic relationships among classified and unclassified arteriviruses based on ORF1b amino acid sequences (see Fig. 2 for genomes and virus abbreviations). Silhouettes represent mammals in which each virus was found, with question marks indicating uncertain natural hosts (viruses discovered in captive macaques). Sequences were compiled from Table 2. ORF1b nucleotide sequences were aligned using a codon-guided version of the multiple alignment using fast fourier transform (MAFFT) method [29] implemented in the computer program TranslatorX [1]. Poorly aligned sites were removed using the Gblocks alignment cleaning method [17] and the

resulting sequence was translated into amino acid sequences. Phylogenetic analyses were then conducted on aligned sequences (final alignment length of 1,055 positions) using the Neighbor-Joining method [45] with the Poisson distance correction method [60]. Robustness of phylogenetic groupings was assessed using 1,000 bootstrap replicates of the data [25]; only bootstrap values >50 % are shown. The scale bar represents amino acid substitutions per site. Analyses were conducted in MEGA7. The topology of the tree shown is identical to that of trees constructed using maximum likelihood analyses of nucleic acid sequences (not shown)

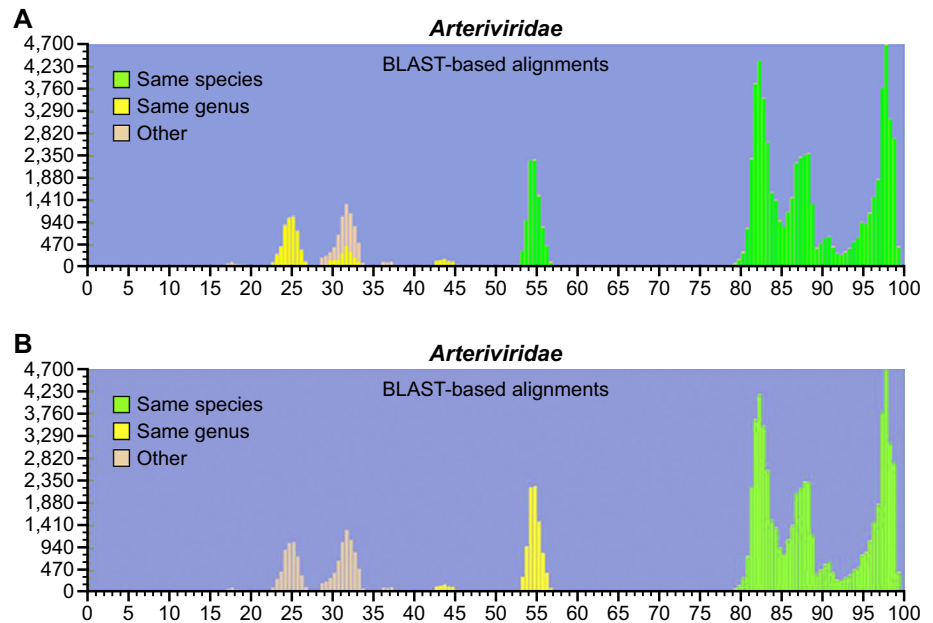
New classification and nomenclature

The currently approved arterivirus classification relies on three key characteristics [24]:

- **genomic organization and size.** The genomic organization considered typical of arteriviruses is based on the genome organization of EAV (Fig. 2). EAV, LDV, and

PRRSV genomes are 12.7 to 15.4 kb in length. The replicase ORFs 1a and 1b encoding replicase precursor polyproteins pp1a/pp1ab are followed by genes encoding envelope (E) protein, glycoproteins (GP2b-GP5), membrane (M) protein, and nucleocapsid protein (N) (5'-1a/1b-2a-2b-3-4-5a-5-6-7-3'), which justifies their grouping (Fig. 2). The SHFV genome contains

Fig. 5 PAirwise Sequence Comparison (PASC) analysis using a modified basic local alignment search tool (BLAST) algorithm [11]. The resulting histograms, visualizing the distribution of the number of arterivirus pairs at each identity percentage, confirm results shown in Figure 3. The x-axis shows percent identity (0–100 %) and the y-axis shows the number of compared arterivirus sequence pairs. A) original color coding assigned by the NCBI PASC tool, showing disarray. B) reassigned color coding after implementation of the arterivirus taxonomy proposed herein (color figure online)



the same genomic architecture but also possesses 4 additional ORFs immediately downstream of ORF1b (2a', 2b', 3', 4'). The SHFV genome is ≈ 15.7 kb in length;

- **monophyly.** Phylogenetic analyses clearly separate EAV, LDV, PSSRV, and SHFV into four clades. These analyses are based on the similarity of the ORF1b nucleotide sequences or the encoded pp1b amino acid sequences and/or on homologous and alignable portions of coding-complete viral genomes (thus excluding the additional 4 SHFV ORFs) [36, 47]; and
- **host range.** EAV, LDV, PRRSV, and SHFV are known to infect equids, rodents, suids, and nonhuman primates, respectively.

The criteria listed above indicate that DMVV-1, KKCBV-1, KRCV-1, KRCV-2, KRTGV-1, KRTGV-2, MYBV-1, PBJV, SHEV, SWBV-1, and the viruses from DeBrazza's and vervet monkeys should be grouped together with SHFV because these viruses 1) share the typical SHFV genomic architecture containing the SHFV-specific additional reading frames 2a', 2b', 3', and 4' (Fig. 2); 2) are more closely related to each other in pairwise distance analyses of genome-encoded proteins than to the proteins of the remaining arteriviruses (Fig. 3); 3) cluster more closely with SHFV in ORF1b phylogenetic analysis than with any of the other known arteriviruses (Fig. 4); and 4) infect cercopithecids (Old World monkeys), whereas none of the other arteriviruses are known to infect nonhuman primates. However, the pairwise genetic distances of the twelve simian arteriviruses are less than 50 % identical to each other on the nucleotide level. Such genetic distances

are similar to the distance observed between the genomes of PRRSVs and LDV, PRSSVs and EAV, or LDV and EAV, all of which are currently classified members of separate species. These data indicate that eleven of the newly discovered simian arteriviruses might be representatives of novel arterivirus species, rather than novel members of the current species *Simian hemorrhagic fever virus* (Fig. 3).

To confirm these results and to achieve an objective resolution of arterivirus relationships, we used the PAirwise Sequence Comparison (PASC) methodology [11] and tools available from the National Center for Biotechnology Information (NCBI). The PASC analysis aligns nucleotides in conserved protein or nucleotide regions of each virus pair. The resulting histograms visualize the distribution of the number of virus pairs at each identity percentage. A typical histogram has peaks that represent different taxon levels. The percentages of the lowest points of the valleys between the peaks can be used as taxon demarcation criteria. The results of the arterivirus PASC analysis are shown in Figure 5 (updates can be accessed at the NCBI website at <http://www.ncbi.nlm.nih.gov/sutils/pasc/viridty.cgi?textpage=overview>). Results from PASC indicate that the most appropriate genus cut-off for arteriviruses is 39–41 %. The most appropriate species cut-off would be 71–77 %, which is close to species cutoffs set for other viral families. These cut-offs result in a split of the current genus *Arterivirus* into 5 genera, a split of the current species *Porcine respiratory and reproductive syndrome virus* into two species (one for “European/Lelystad” PRRSV type 1 and one for “North American” PRRSV type 2), and the

Table 3 Arterivirus and arterivirus taxa pronunciation guidelines

Taxa/viruses	International phonetic alphabet (IPA)	English phonetic notation
African pouched rat virus	[ˈæfrɪkən paʊtʃt ræt ˈvaɪrəs]	af-ri-kuhn poucht rat vahy-ruhs
<i>Alamogordo simartevirus</i>	[ˌæləmɑˈɡɔrdoo sɪm ˌɑrtəˈvaɪrəs]	al-uh-muh- gawr -doh sim-ahr-tuh- vahy-ruhs
<i>Arteriviridae</i>	[ˈɑrtəriˌvɪrɪdi]	ahr-tuh -ree-vee-ri-dee
arterivirus	[ˈɑrtəriˌvaɪrəs]	ahr-tuh -ree-vahy-ruhs
<i>Bethesda simartevirus</i>	[bɛθˈɛzdə sɪm ˌɑrtəˈvaɪrəs]	buh- thez -duh sim-ahr-tuh- vahy-ruhs
<i>Cercopithecine 1 simartevirus</i>	[ˌsɜrkooˈpɪθəsəm wʌn sɪm ˌɑrtəˈvaɪrəs]	sur-koh- pee -thuh-sahyn wuhn sim-ahr-tuh- vahy-ruhs
<i>Cercopithecine 2 simartevirus</i>	[ˌsɜrkooˈpɪθəsəm tu sɪm ˌɑrtəˈvaɪrəs]	sur-koh- pee -thuh-sahyn too sim-ahr-tuh- vahy-ruhs
<i>Chlorocebus 1 simartevirus</i>	[ˌklɔrəˈsɪbəs wʌn sɪm ˌɑrtəˈvaɪrəs]	klawr-uh- see -buhs wuhn sim-ahr-tuh- vahy-ruhs
<i>Cricetomys 1 nesartevirus</i>	[kraɪˈsɪtoʊmɪs sɪm ˌɑrtəˈvaɪrəs]	krahy- see -toh-mis sim-ahr-tuh- vahy-ruhs
DeBrazza's monkey virus	[dəˈbræzəz ˈmʌŋki ˈvaɪrəs]	duh-brah-zuhz muhng -kee vahy-ruhs
dipartevirus	[dɪˌpɑrtəˈvaɪrəs]	dip-ahr-tuh- vahy-ruhs
Drakensberg Mountain vervet virus	[ˈdreɪkənzbɜrg ˈmaʊntn ˈvɜrvɪt ˈvaɪrəs]	drey -kuhnz-burg moun -tn vur -vit vahy-ruhs
equartevirus	[ɛˌkwɑrtəˈvaɪrəs] or [ɪˌkwɑrtəˈvaɪrəs]	ek-wahr-tuh- vahy-ruhs or eek-wahr-tuh- vahy-ruhs
<i>Equid equartevirus</i>	[ˈɛˌkwɪd hɪpˈɑrtəˈvaɪrəs] or [ˈɪˌkwɪd]	ek -wid ek-wahr-tuh- vahy-ruhs or eek -wid
equine arteritis virus	[ˈɛˌkwɑɪn ˈvaɪrəs] or [ˈɪˌkwɑɪn]	ek -wahyn vahy-ruhs or eek -wahyn
Kibale red colobus virus	[kɪˈbali rɛd ˈkɔləbəs ˈvaɪrəs]; [kəˈloʊbəs]	kee -bah-lee red kol -uh-buhs vahy-ruhs or kuh- loh -buhs
Kibale red-tailed guenon virus	[kɪˈbali ˈrɛdˌteɪld ɡəˈnɔː ˈvaɪrəs] or [ɡəˈnɔːn]	kee -bah-lee red -teyld guh -nawn vahy-ruhs or guh-non
Kafue kinda-chacma baboon virus	[kəˈfoeɪ ˈkində ˈtʃækmə bæˈbun ˈvaɪrəs]	kuh- foo -ey keen -duh chak -muh ba- boon vahy-ruhs
lactate dehydrogenase- elevating virus	[ˈlæktet diˈhaɪdrədʒəˌneɪs ˈeləˌveɪtɪŋ ˈvaɪrəs] or [diˈhaɪdrədʒəˌneɪz]	lak -teyt dee- hahy -druh-juh-neys el -uh-vey-ting vahy-ruhs or dee- hahy -druh-juh-neyz
Mikumi yellow baboon virus	[miˈkumi ˈyelou bæˈbun ˈvaɪrəs]	mee- koo -mee yel -oh ba- boon vahy-ruhs
<i>Muroid rodartevirus</i>	[ˈmyʊər ˌɔɪd ˌroʊdɑrtəˈvaɪrəs]	mjoo -roid roh-dahr-tuh- vahy-ruhs
nesartevirus	[ˌnezɑrtəˈvaɪrəs]	nez-ahr-tuh- vahy-ruhs
<i>Nidovirales</i>	[ˈnɪdoʊ ˌviˈrɑːləs] or [ˈnɪdoʊ ˌviˈrɑːlɪz]	nid -oh-vi-rah-luhs or nid -oh-vi-rah-leez
nidovirus	[ˈnɪdoʊ ˌvaɪrəs]	nid -oh-vahy-ruhs
<i>Papio 1 simartevirus</i>	[ˈpɑpiʊ wʌn sɪm ˌɑrtəˈvaɪrəs]	pah -pee-oh wuhn sim-ahr-tuh- vahy-ruhs
<i>Papio 2 simartevirus</i>	[ˈpɑpiʊ tu sɪm ˌɑrtəˈvaɪrəs]	pah -pee-oh too sim-ahr-tuh- vahy-ruhs
Pebjah virus	[ˈpiɪbdʒɑ ˈvaɪrəs]	peeb -jah vahy-ruhs
porcine reproductive and respiratory syndrome virus	[ˈpɔrsəm ˌrɪprəˈdʌktɪv ənd ˈrespərəˌtoəri ˈvaɪrəs] or [ˈpɔrsɪn]; [ˈrespərəˌtoəri], [rɪˈspɑɪərətoəri]	pawr -sahyn ree-pruh- duhk -tiv uhnd res -per-uh-tawr-ee vahy-ruhs or pawr -sɪn; res -per-uh-tohr-ee, ri- spahyuh -uh-tohr-ee
<i>Procolobus 1 simartevirus</i>	[ˈproʊ ˌkɔləbəs wʌn sɪm ˌɑrtəˈvaɪrəs]	proh -kol-uh-buhs wuhn sim-ahr-tuh- vahy-ruhs
<i>Procolobus 2 simartevirus</i>	[ˈproʊ ˌkɔləbəs tu sɪm ˌɑrtəˈvaɪrəs]	proh -kol-uh-buhs too sim-ahr-tuh- vahy-ruhs
rodartevirus	[ˌroʊdɑrtəˈvaɪrəs]	roh-dahr-tuh- vahy-ruhs
simartevirus	[sɪm ˌɑrtəˈvaɪrəs]	sim-ahr-tuh- vahy-ruhs
simian hemorrhagic encephalitis virus	[ˈsɪmɪən ˌhɛməˈrædʒɪk ɛnˌsɛfəˈlɑɪtɪs ˈvaɪrəs]	sim -ee-uhn hem-uh- raj -ik en-sef-uh- lahy -tis vahy-ruhs
simian hemorrhagic fever virus	[ˈsɪmɪən ˌhɛməˈrædʒɪk ˈfɪvər ˈvaɪrəs]	sim -ee-uhn hem-uh- raj -ik fee -ver vahy-ruhs
Southwest baboon virus	[ˌsaʊθˈwest bæˈbun ˈvaɪrəs]	south- west ba- boon vahy-ruhs
<i>Suid 1 rodartevirus</i>	[ˈsɪd wʌn ˌroʊdɑrtəˈvaɪrəs]	soo -eed wuhn roh-dahr-tuh- vahy-ruhs
<i>Suid 2 rodartevirus</i>	[ˈsɪd tu ˌroʊdɑrtəˈvaɪrəs]	soo -eed too roh-dahr-tuh- vahy-ruhs
<i>Sukhumi simartevirus</i>	[sʊˈkumi sɪm ˌɑrtəˈvaɪrəs] or [sʊˈxumi]	soo - koo -mee sim-ahr-tuh- vahy-ruhs or soo - khoo -mee
<i>Trichosurus 1 dipartevirus</i>	[triˈkoʊsərəs dɪpˈɑrtəˈvaɪrəs]	tri- koh -suh-ruhs dip- ahr -tuh-vahy-ruhs
wobbly possum disease virus	[ˈwɒbli ˈpɔsəm dɪˈzɪz ˈvaɪrəs]	wob -lee pos -uhm dih- zeez vahy-ruhs

split of the species *Simian hemorrhagic fever virus* into ten species.

To accommodate these results, the taxonomy outlined in Table 2 is proposed. Accordingly, the current genus *Arterivirus* is replaced with five genera: *Dipartevirus* (sigil of the mammalian order *Diprotodontia* + *arterivirus*) for WPDV; *Equartevirus* (sigil of the mammalian family *Equidae* + *arterivirus*) for EAV; *Nesartevirus* (sigil of the mammalian family *Nesomyidae* + *arterivirus*) for the forest giant pouched rat virus; *Rodartevirus* (sigil of the mammalian families *Rodentia* and *Artiodactyla* + *arterivirus*) for LDV and PRRSV; and *Simartevirus* (sigil of the mammalian infraorder *Simiiformes* + *arterivirus*) for all simian arteriviruses. These genus names were consciously selected to

- not contain numbers or references to Greek letters or Arabic numbers (e.g., “*Alphaarterivirus*, *Betaarterivirus*” or “*Arterivirus 1*,” *Arterivirus 2*”) for ease of memorization and use in vernacular writing and oral communication. Future establishment of new genera in the family will not be hampered by the length of the Greek alphabet or by the addition of large numbers. In addition, by not choosing such names, the visually unpleasing double vowels *aa* (*Alphaarterivirus*, *Betaarterivirus* etc.), which formally would require diacritics, are avoided;
- not contain the complete word stems of hosts or geographic locations. This way, the genus names should remain uncontroversial even if members of the genus are discovered in areas or hosts divergent from the founding members;
- contain mnemonics for easier memorization. For instance, the genus name *Equartevirus* will be easier to remember for equine arteritis virus than, for instance, *Alphaarterivirus* or *Arterivirus 1*. But as the three letters “*Equ*” do not convey the same meaning as “equine” to the casual reader, additional genus members, not stemming from equids, can be included without making the genus name misleading;
- not contain complete word stems of higher taxa (e.g., “*arteri*” or “*nido*”) but to again use contractions (“*arte*”). This choice will allow adherence to the ICVCN “stability rule”: i.e., the chosen genus names could be retained even if future taxonomic reorganizations would require the dissolution of the family *Arteriviridae* or the order *Nidovirales*, or if individual genera would have to be moved to separate families.

To differentiate species and virus names clearly, the ICTV-supported proposal to employ non-Latinized binomial species names was followed [54]. In the proposed classification, the virus name “equine arteritis virus” and its abbreviation “EAV” are retained, therefore avoiding any significant impact of this taxonomic proposal on the arterivirus research community. However, the name of the

species for EAV, which rarely has to be used in daily proceedings by virologists, is changed to *Equid equartevirus*. Similar changes are introduced for species of the remaining genera.

The virus name “lactate dehydrogenase-elevating virus” is retained, but its current abbreviation (LDV) is changed to LaDV to differentiate it from lymphocystis disease virus (LDV, an iridovirus of teleost fishes). To reflect the relatively large distance between the two “strains” LDV-P and LDV-C, both strains are elevated to virus status (LaDV-1 and LaDV-2). The species name harboring these viruses is changed to *Muroid rodartevirus*. The current species *Porcine respiratory and reproductive syndrome virus* is split into *Suid 1 rodartevirus* and *Suid 2 rodartevirus* for “European/Lelystad” porcine respiratory and reproductive syndrome virus type 1 (now renamed PRRSV-1), and “North American” PRRSV type 2 (now renamed PRRSV-2), respectively.

The genus *Simartevirus* includes ten species. Seven of these species are named after the species for the hosts the viruses were discovered in: *Cercopithecus 1 simartevirus* for KRTGV-1 and KRTGV-2; *Cercopithecus 2 simartevirus* for the arterivirus from the DeBrazza’s monkey; *Chlorocebus 1 simartevirus* for DMVV-1; *Papio 1 simartevirus* for MYBV-1 and SWBV-1; *Papio 2 simartevirus* for KKCBV-1; *Procolobus 1 simartevirus* for KRCV-1; *Procolobus 2 simartevirus* for KRCV-2. The hosts of the three simarteviruses known to have caused epizootics among captive macaques (PBJV, SHEV, SHFV) are unknown. Consequently, the names of the species these viruses belong to were chosen based on the cities in which the outbreaks occurred: *Alamogordo simartevirus* for PBJV; *Bethesda simartevirus* for SHFV; and *Sukhumi simartevirus* for SHEV. Host names were once again used for the species established for WPDV (*Trichosurus 1 dipartevirus*) and the arterivirus from the forest giant pouched rat (*Cricetomys 1 nesartevirus*). The virus found in DeBrazza vervet monkeys was named DeBrazza’s monkey virus 1 (DeBMV-1), and the virus found in forest giant pouched rats was named African pouched rat virus 1 (APRAV-1). Pronunciation guidelines for all arterivirus names are listed in Table 3.

Together, this new taxonomy resolves all previous disagreements with the ICVCN while at the same time accommodating all newly discovered arteriviruses and providing relative consistency with previously established virus names and abbreviations.

Proposal for nomenclature below the species level

To improve retrieval of arterivirus genomic or protein data from electronic databases, we propose that arterivirus strains/variants/isolates be named according to the NCBI-

supported naming scheme recently proposed for filoviruses [32–34] and rotaviruses [41]: <virus name>/<strain>/<isolation host-suffix>/<country of sampling>/<year of sampling>/<genetic variant designation>/<isolate designation>. References [32–34] contain detailed instructions on how to fill in the individual fields of this naming template in a standardized manner. We also strongly suggest not using the word “strain” indiscriminately [32–34]. A consortium of arterivirus experts should be established under the auspices of the ICTV *Arteriviridae* Study Group to decide on the precise strain/variant/isolate names for the several thousand arteriviruses currently indexed in databases such as GenBank.

Proposal for adjustment of gene and protein designations

NCBI is currently developing gene and protein naming standards for viruses to improve electronic database management. Generally, we propose not to change gene and protein names at this point.

Future prospects

The taxonomy of the family *Arteriviridae* will most likely have to be amended and expanded repeatedly in the future. Evidence is accumulating that the diversity of arteriviruses is higher than currently appreciated [43, 49, 50]. Furthermore, the paraphyly of horses, nonhuman primates, pigs, possums, and rodents within the class Mammalia [42] suggests that many other mammalian orders may host as yet undiscovered arteriviruses. The establishment of methods-of-choice for arterivirus taxon demarcation and the implementation of unambiguous taxon and virus names in line with ICVCN will prove to be a solid foundation for the taxonomic accommodation of arteriviruses that will undoubtedly be discovered in the future.

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