

This form should be used for all taxonomic proposals. Please complete all those modules that are applicable (and then delete the unwanted sections). For guidance, see the notes written in blue and the separate document "Help with completing a taxonomic proposal"

Please try to keep related proposals within a single document; you can copy the modules to create more than one genus within a new family, for example.

MODULE 1: TITLE, AUTHORS, etc

C. 1	2016 026	la acc	(to be completed by ICTV	
Code assigned:	2016.020	va-acS	officers)	
Short title: The family <i>Arteri</i> fourteen species, renaming on existing genus (e.g. 6 new species in the genus Modules attached (modules 1 and 11 are required)	e species, creat	ing five new ger	es in two new genera, moving nera, and abolishing the single $ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	
Author(s):				
N.J. Knowles S. Siddell				
Adapted from original propos	als by:			
1) M.A. Brinton, A. Gulyaeva H.J. Nauwynck, E.J. Snijder,		•	vska, K.S. Faaberg, F.CC. Leun ; and	
Lauck, D.H. O'Connor, E. Por Deriabin, B.A. Lapin, A.M. Sl Delwart, J. Le Doux Diffo, A.	stnikova, S.R. I hchetinin, Z.V. Gillis, N.O. Ko	Radoshitzky, J. F Shevtsova, T.V. ondov, M. LeBro	J.H. Kuhn, M.G. Lackemeyer, M. Rogers, S.V. Alkhovsky, P.G. Vishnevskaya, L.L. Coffey, E. eton, T.F.F. Ng, B.S. Schneider, J. L. Bollinger, A.N. Clawson, G.	
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Nick J. Knowles (<u>nick.knowles</u> Stuart Siddell (<u>stuart.siddell@</u>		<u>.uk</u>) &		
List the ICTV study group(s	that have see	en this proposal	:	
A list of study groups and contact http://www.ictvonline.org/subcom in doubt, contact the appropriate chair (fungal, invertebrate, plant, vertebrate viruses)	mittees.asp . If subcommittee	Arteriviridae	SG	
ICTV Study Group commen	ts (if any) and	response of the	e proposer:	
Date first submitted to ICTV: Date of this revision (if different	ent to above):		30/11/2016 19/12/2016	

ICTV-EC comments and response of the proposer:

MODULE 2a: NEW SPECIES

creating and naming one or more new species.

If more than one, they should be a group of related species belonging to the same genus. All new species must be placed in a higher taxon. This is usually a genus although it is also permissible for species to be "unassigned" within a subfamily or family. Wherever possible, provide sequence accession number(s) for **one** isolate of each new species proposed.

Code	<i>201</i>	6.020aS	(assigned by IC	TV office	rs)		
To crea	To create 1 new species within:						
					all that apply.		
G	enus:	Porartevirus (new	<i>v</i>)		e higher taxon has yet to be		
Subfa	mily:			created (in a later module, below) write "(new)" after its proposed name.			
Fa	mily:	y: Arteriviridae		If no genus is specified, enter			
(Order:	Nidovirales		"unassigned" in the genus box.			
Name of new species:		-	epresentative isolate: aly 1 per species please) GenBank sequence acomplex in the sequence acom				
Rat arterivirus 1		Rat arterivirus Jilin2	2014	<u>KP280006</u>			

Reasons to justify the creation and assignment of the new species:

- Explain how the proposed species differ(s) from all existing species.
 - If species demarcation criteria (see module 3) have previously been defined for the genus, **explain how the new species meet these criteria**.
 - o If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Further material in support of this proposal may be presented in the Appendix, Module 11

Currently, the taxonomy of the family *Arteriviridae* includes a single genus *Arterivirus* with fourteen species, with four of the species recognized many years ago (Faaberg et al., 2012) and the others established in 2016 (Brinton et al., 2015). All new arteriviruses were identified in the field, predominantly in different monkey species, although few have yet been characterized beyond genome sequencing (Dunowska et al., 2012; Bailey et al., 2014a,b, 2016; Lauck et al., 2011, 2013, 2015).

Data from the Arteriviridae Study Group proposal

In the proposal by Brinton et al. (2016) the development of arterivirus taxonomy is assisted by a DEmARC-mediated analysis of genomic variation to set family-wide demarcation criteria for the ranks. Some 683 full genomic sequences of arteriviruses were selected for this analysis. They were used to produce an expert-curated multiple sequence alignment of the most conserved non-structural proteins (nsps), including two domains of nsp2, the entire nsp3-nsp5, nsp7a, nsp8-9 regions, and the conserved parts of nsp10 and nsp11. To inform taxonomy, the authors employed an advanced version of the DEmARC framework (Lauber & Gorbalenya, 2012ab; Gorbalenya et al., in preparation), which provided thresholds to partition the distribution of pairwise patristic distances (PPD) into clusters (Appendix Fig. 1). These thresholds can be used as candidates for setting demarcation criteria for ranks because they satisfied two requirements: the clusters formed under these thresholds were monophyletic in the ML tree of arteriviruses and all intra- and inter-cluster PPDs were, respectively, smaller and

larger than the respective threshold (clustering cost of zero, CC=0, according to DEmARC). Eight PPD thresholds satisfying these strict conditions were identified. If all were used, the taxonomy of the family would include eight ranks, many more than the currently available 3 ranks approved by ICTV. This observation, which may be partially due to the relatively small and highly skewed arterivirus sampling available currently, indicated that the taxonomy of arteriviruses could be devised in different ways that all would be compatible with current knowledge.

The first candidate threshold that of the smallest PPD of 0.267, defines a rank that includes 17 clusters (taxa) (Appendix Figs. 1, 2 and 3). Fourteen of these clusters correspond to the established species and three include viruses that have not yet been classified. Accordingly, using this threshold for species demarcation, Brinton et al. proposed establishing three new species (see Tables in Modules 2a and 2b), which are also adopted in this proposal.

Data from the Bailey et al. (2015) proposal

For the taxonomic re-organization outlined by Bailey et al. (2015), three separate analyses were performed including all classified and all recently discovered/described potential and therefore unclassified arteriviruses (APRAV-1, DeBMV-1, FSVV (DMVV-1), KKCBV-1, KRCV-1, KRCV-2, KRTGV-1, KRTGV-2, MYBV-1, PBJV, SHEV, SWBV-1, WPDV; papers by Bailey et al.; Lauck et al.; Dunowska et al.; Giles et al.):

- 1) Appendix Fig. 5: Pairwise sequence comparison of the arterivirus proteomes using all coding regions that are shared among all analyzed arterviruses (i.e. notably without the 3-4 ORFs unique to simian arterviruses, see Appendix Fig. 4);
- 2) Appendix Fig. 6: PASC analysis (Bao et al.) using the coding-complete genomes of all analyzed arteriviruses; and
- 3) Appendix Fig. 7: Phylogenetics based on the arterivirus ORF1b as recommended by the ICTV Arteriviridae Study Group in the 9th ICTV Report (Faaberg et al.) for arterivirus classification.

The results of all three analyses are in agreement with each other. In particular, these analyses indicate that DeBMV-1, FSVV (DMVV-1), KKCBV-1, KRCV-1, KRCV-2, KRTGV-1, KRTGV-2, MYBV-1, PBJV, SHEV, SWBV-1, should be grouped together with the classified SHFV because these viruses i) share the typical SHFV genomic architecture containing the SHFV-specific additional reading frames 2', 3', 4' (Appendix Fig. 4); ii) are more closely related to each other in pairwise distance analyses of genome-encoded proteins than to the proteins of the remaining arteriviruses (Appendix Fig. 5); iii) cluster more closely with SHFV in ORF1b phylogenetic analysis than with any of the other known arteriviruses (Appendix Fig. 6); and iv) infect diverse cercopithecids, whereas none of the other arteriviruses are known to infect nonhuman primates:

DeBMV-1: DeBrazza monkey (Cercopithecus neglectus), Cameroon

FSVV (DMVV-1): vervet monkeys (Chlorocebus pygerythrus), South Africa

KKCBV-1: Kinda baboons (Papio cynocephalus kindae), Zambia

KRCV-1: Ugandan red colobus (Procolobus [Piliocolobus] rufomitratus tephrosceles), Uganda

KRCV-2: Ugandan red colobus (Procolobus [Piliocolobus] rufomitratus tephrosceles), Uganda

KRTGV-1: red-tailed monkeys (Cercopithecus ascanius), Uganda

KRTGV-2: red-tailed monkeys (Cercopithecus ascanius), Uganda

MYBV-1: yellow baboons (Papio cynocephalus), Tanzania

PBJV: ?

SHEV: most likely grivets (Chlorocebus aethiops), ?

SHFV: most likely patas monkeys (Erythrocebus patas), ? SWBV-1: olive baboons (Papio anubis, Lesson 1827), ?

However, the pairwise genetic distances of most 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 PRRSV-1/2 and LDV, PRRSV-1/2 and EAV, or LDV and EAV, all of which are currently classified members of separate species. These data indicate that most of the newly discovered eleven simian arteriviruses are representatives of novel arterivirus species, rather than novel members of the current species Simian hemorrhagic fever virus. To reflect phylogeny, host range, and ORF organization, these data indicate that the monophyletic clade of simian arteriviruses needs to be classified in a new genus, separate from taxa for the remaining arteriviruses. Genetic distances (Appendix Figs. 5 and 6) and different host specificity of these remaining viruses (the classified EAV [horses], LDV-1/2 [house mice], and PRRSV-1/2 [pigs]; and the newly discovered and unclassified APRAV-1 [pouched rats] and WPDV [possums]) consequently necessitate the creation of additional genera and species for the remaining arteriviruses.

Results from PASC indicate that the most appropriate genus cut-off for all analyzed 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-1 and one for "North American" PRRSV-2), and the split of the species *Simian hemorrhagic fever virus* into ten species. However, results from PASC did not reveal the need for arterivirus subfamilies to group the 5 individual genera, although the authors were not necessarily against discussing the creation of subfamilies given the genetic distance of WPDV to all other arteriviruses.

Accordingly, they proposed the current genus *Arterivirus* to be replaced with five genera: *Dipartevirus* (for WPDV); *Equartevirus* (for EAV); *Nesartevirus* (for APRAV-1); *Rodartevirus* (for LDV-1, LDV-2, PRRSV-1, and PRRSV-2); and *Simartevirus* (for DeBMV-1, FSVV/DMVV-1, KKCBV-1, KRCV-1, KRCV-2, KRTGV-1, KRTGV-2, MYBV-1, PBJV, SHEV, SWBV-1).

Based on the presented analyses, they proposed the genus *Simartevirus* to include 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 DeBMV-1; *Chlorocebus 1 simartevirus* for DMVV-1; *Papio 1 simartevirus* for MYBV-1 and SWBV-1; *Papio 2 simartevirus* for KRCBV-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 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 APRAV-1 (*Cricetomys 1 nesartevirus*).

Current proposal

In the current proposal we have chosen to retain the already established species names and to adopt the genus names based mainly on those described by Bailey et al. (2015) (see Appendix Table 1).

MODULE 2b: **NEW SPECIES**

creating and naming one or more new species.

If more than one, they should be a group of related species belonging to the same genus. All new species must be placed in a higher taxon. This is usually a genus although it is also permissible for species to be "unassigned" within a subfamily or family. Wherever possible, provide sequence accession number(s) for **one** isolate of each new species proposed.

Code	le $2016.020bS$ (assigned by IC			CTV office	ers)	
To cre	ate 2 ne	ew species within:				
					all that apply.	
(Genus:	Simartevirus (ne	w)		ne higher taxon has yet to be	
Subf	Subfamily:				ated (in a later module, below) write ew)" after its proposed name.	
F	Family: Arteriviridae			 If no genus is specified, enter 		
	Order:	Nidovirales		"unassigned" in the genus box.		
Name of new species:		Representative iso (only 1 per species p		GenBank sequence accession number(s)		
Kafue kinda chacma baboon virus		Kafue kinda x chacma baboon virus		<u>KT447550</u>		
Free State vervet virus		Free State vervet virus		<u>KR862307</u>		

Reasons to justify the creation and assignment of the new species:

- Explain how the proposed species differ(s) from all existing species.
 - o If species demarcation criteria (see module 3) have previously been defined for the genus, **explain how the new species meet these criteria**.
 - o If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Further material in support of this proposal may be presented in the Appendix, Module 11

See text in Module 2a

MODULE 3a: NEW GENUS

creating a new genus

Ideally, a genus should be placed within a higher taxon.

Code	<i>201</i>	6.020cS	(assigned by ICTV officers)	
To create a	a new	genus within:		Fill in all that apply.
Subfan	nily:			If the higher taxon has yet to be created (in a later reached helper) write "(a see)"
Fan	nily:	Arteriviridae		(in a later module, below) write "(new)" after its proposed name.
Oı	rder:	Nidovirales		 If no family is specified, enter "unassigned" in the family box

naming a new genus

Code	2016.020dS	(assigned by ICTV officers)
To name t	he new genus: Equartevirus	

Assigning the type species and other species to a new genus

				
Code	2016.020eS	(assigned by ICTV officers)		
To designa	ate the following as the type sp	pecies of the new genus		
Equine arteritis virus		Every genus must have a type species. This should be a well characterized species although not necessarily the first to be discovered		
 ,				
_	•	species created and assigned to it (Module 2) and any that		
are being m	oved from elsewhere (Module 7b).	Please enter here the TOTAL number of species		
(including the type species) that the genus will contain:				
One				

Reasons to justify the creation of a new genus:

Additional material in support of this proposal may be presented in the Appendix, Module 11

Besides the species demarcation threshold described in Module 2a, DEmARC identified seven other candidate thresholds, from 0.376 to 2.651, for consideration. They define seven candidate ranks, from 2 to 8, that are candidates for genus and subfamily. The requirement to choose two ranks from seven is conditional and is based on the current taxonomy structure, which recognizes only these two ranks between species and family ranks. Since it is man-made, it could be revised to better accommodate the evolutionary relationships of the viruses of this family in the most biologically sensible manner. Such a revision would require a change of the ICTV Code that will be proposed separately.

A genus threshold could be determined by starting from the candidate rank with the largest max PPD (2.651) and fewest clusters (2). Brinton et al. reasoned that if the first candidate rank in this approach is reserved for subfamily, then the next one (PPD 2.222, three taxa) could be used for genera. In this framework, two genera would be created to accommodate the most distantly related WPDV species (currently, unassigned in the family) and EAV species (part of the current *Arterivirus* genus), while all other species would remain in the current genus *Arterivirus*. Brinton et al. also explored an alternative approach where the genus rank must be the next rank above the species rank in taxonomy.. There are seven candidate ranks, from 2 to 8, and associated thresholds

above species rank. They span a very large PPD range, from 0.376 to 2.651. If the rank 8 with two clusters and the PPD 2.651 threshold is reserved for a subfamily rank, six candidate ranks remain to be considered for genus rank. Kuhn and colleagues (Kuhn et al. (2016), Bailey et al., 2016) proposed recognizing five genera, which correspond to the candidate rank 6 in the presented DEmARC analysis. Because the associated threshold of PPD 1.472 is the fifth distant from the species one, the four other thresholds that are closer to the species one must be proven false in the future for it to be the correct one for genera establishment. At this moment there are no indications to support this outcome. After considering the above options, the ASG unanimously favored the candidate rank 6 with five genera and the demarcation threshold PPD 1.472.

Kuhn et al. (2016) and Bailey et al. (2016) have also analysed the relationships of existing and newly discovered arteriviruses (Appendix Fig. 4) using three different approaches:

- 1) Pairwise sequence comparison of the arterivirus proteomes using all coding regions that are shared among all analyzed arteriviruses (i.e. notably without the 3–4 ORFs unique to simian arteriviruses, see Appendix Fig. 5);
- 2) PASC analysis (Bao *et al.*) using the coding-complete genomes of all analyzed arteriviruses (Appendix Fig. 6); and
- 3) Phylogenetics based on the arterivirus open reading frame (ORF)1b as recommended by the ICTV *Arteriviridae* Study Group in the 9th ICTV Report (Faaberg *et al.*) for arterivirus classification (Appendix Fig. 7).

The results of all three analyses indicate that DeBMV-1, FSVV-1, KKCBV-1, KRCV-1, KRCV-2, KRTGV-1, KRTGV-2, MYBV-1, PBJV, SHEV, and SWBV-1 should be grouped together with the classified SHFV because these viruses i) share the typical SHFV genomic architecture containing the SHFV-specific additional reading frames 2', 3', 4' (Appendix Fig. 4); ii) are more closely related to each other in pairwise distance analyses of genome-encoded proteins than to the proteins of the remaining arteriviruses (Appendix Fig. 5); iii) cluster more closely with SHFV in ORF1b phylogenetic analysis than with any of the other known arteriviruses (Appendix Fig. 6); and iv) infect diverse cercopithecids, whereas none of the other arteriviruses are known to infect nonhuman primates.

The analysis also showed that the pairwise genetic similarities among most of the twelve simian arteriviruses are less than 50% at the nucleotide level. Such genetic distances are similar to the distance observed between the genomes of PRRSV-1/2 and LDV, PRRSV-1/2 and EAV, or LDV and EAV, all of which are currently classified members of separate species. These data indicate that most of the newly discovered eleven simian arteriviruses are representatives of novel arterivirus species, rather than novel members of the current species *Simian hemorrhagic fever virus*. To reflect phylogeny, host range, and ORF organization, these data indicate that the monophyletic clade of simian arteriviruses needs to be classified in a new genus, separate from taxa for the remaining arteriviruses. Genetic distances and different host specificity of these remaining viruses (the classified EAV [horses], LDV-1/2 [house mice], and PRRSV-1/2 [pigs]; and the newly discovered and unclassified APRAV-1 [pouched rats] and WPDV [possums]) consequently necessitate the creation of additional genera and species for the remaining arteriviruses.

The results of the PASC analysis indicated a genus cut-off for all analyzed arteriviruses of 39–41%. The most appropriate species cut-off would be 71–77%, which is close to species cutoffs set for other viral families. Accordingly, Kuhn et al. proposed the current genus *Arterivirus* to be replaced with five genera: *Dipartevirus* (for WPDV); *Equartevirus* (for EAV); *Nesartevirus* (for

APRAV-1); *Rodartevirus* (for LDV-1, LDV-2, PRRSV-1, and PRRSV-2); and *Simartevirus* (for DeBMV-1, DMVV-1, KKCBV-1, KRCV-1, KRCV-2, KRTGV-1, KRTGV-2, MYBV-1, PBJV, SHEV, SWBV-1).

In this taxonomic proposal, the authors suggested adoption of the ranking structure proposed by both Brinton et al. and Bailey et al., namely a family comprised of five genera that include a total of 17 species, with the species demarcation criteria explained in Module 2a.

Nomenclature

For consistency with the *Coronaviridae* and *Mesoniviridae* families in the order *Nidovirales*, Brinton et al. (2016) proposed a genus naming convention that is based on the usage of a Greek alphabet letter in conjunction with the word "arterivirus". Thus the five genera were named *Alpha*, *Beta*-, *Gamma*-, *Delta*- and *Epsilonartevirus*, respectively, on the basis of virus discovery date. Also, given the considerable uncertainty about the stability of the current classification, Brinton et al. proposed to keep the species names that have been designed based on the names of the prototype viruses. However, they also indicated that this proposal would be reviewed by the ASG in consultation with SGs of the other nidovirus families at the triannual Nidovirus symposium in June 2017.

In contrast, Kuhn et al. and Bailey et al. proposed a different nomenclature for both the virus species names and the genus names. Namely, they proposed the genus *Simartevirus* to include ten species. Seven of these species were named after the host species in which the viruses were discovered: *Cercopithecus 1 simartevirus* for KRTGV-1 and KRTGV-2; *Cercopithecus 2 simartevirus* for DeBMV-1; *Chlorocebus 1 simartevirus* for DMVV-1; *Papio 1 simartevirus* for MYBV-1 and SWBV-1; *Papio 2 simartevirus* for KRCV-1; *Procolobus 1 simartevirus* for KRCV-2. The hosts of the three simarteviruses known to have caused epizootics among captive macaques are unknown. Consequently, the names of the host species to which these viruses belong to were 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 APRAV-1 (*Cricetomys 1 nesartevirus*).

This proposal has essentially adopted the nomenclature proposed by Kuhn et al. and Bailey et al. with regard to the genus rank and the nomenclature proposed by Brinton et al. with regard to the virus species names. The authors recognize that there are valid arguments to support either nomenclature (which are explained in more detail in the relevant proposals) but consider this variant as the best option available at the present time. It is recognized that the issue of nomenclature as a whole may be considered again following the triannual Nidovirus symposium in June 2017. It should be noted, however, that this proposal names the genus that includes *Lactate dehydrogenase-elevating virus*, *Rat arterivirus 1*, *Porcine respiratory and reproductive syndrome virus 1* and *Porcine respiratory and reproductive syndrome virus 2*, as *Porartevirus*. The proposed classification and nomenclature is summarized in the Appendix: Table 1.

Origin of the new genus name:

Equartevirus from the mammalian family Equidae and arterivirus

Reasons to justify the choice of type species:

Genus includes a single species

Species demarcation criteria in the new genus:

If there will be more than one species in the new genus, list the criteria being used for species demarcation and explain how the proposed members meet these criteria.

Species demarcation criteria are detailed in Module 2a and Annex.

MODULE 3b: NEW GENUS

creating a new genus

Ideally, a genus should be placed within a higher taxon.

Code	201	016.020fS (assigned by I		CTV officers)
To create	a new	genus within:		Fill in all that apply.
Subfai	mily:			If the higher taxon has yet to be created (in a later metalled halos) write "(result)"
Fai	mily:	Arteriviridae		(in a later module, below) write "(new)" after its proposed name.
0	rder:	Nidovirales		 If no family is specified, enter "unassigned" in the family box

naming a new genus

Code	2016.020gS	(assigned by ICTV officers)
To name t	he new genus: Porartevirus	

Assigning the type species and other species to a new genus

2016.020hS Code (assigned by ICTV officers) To designate the following as the type species of the new genus Every genus must have a type species. This should be a well characterized species although not Lactate dehydrogenase-elevating virus necessarily the first to be discovered The new genus will also contain any other new species created and assigned to it (Module 2) and any that are being moved from elsewhere (Module 7b). Please enter here the TOTAL number of species (including the type species) that the genus will contain: Four

Reasons to justify the creation of a new genus:

Additional material in support of this proposal may be presented in the Appendix, Module 11

See explanation in Module 3a

Origin of the new genus name:

Porartevirus from porcine & rodent and arterivirus

Reasons to justify the choice of type species:

LDV was the first virus discovered

Species demarcation criteria in the new genus:

If there will be more than one species in the new genus, list the criteria being used for species demarcation and explain how the proposed members meet these criteria.

Species demarcation criteria are detailed in Module 2a and Annex.

MODULE 3c: NEW GENUS

creating a new genus

Ideally, a genus should be placed within a higher taxon.

<i>201</i>	6.020iS	(assigned by ICTV officers)		
new	genus within:	Fill in all that apply		
		Fill in all that apply.		
nily:		If the higher taxon has yet to be created (in a later readule, helper) write "(ready)"		
nily:	Arteriviridae	(in a later module, below) write "(new)" after its proposed name.		
rder:	Nidovirales	 If no family is specified, enter 		
		"unassigned" in the family box		
)	nily:	nily: Arteriviridae		

naming a new genus

Code	2016.020jS	(assigned by ICTV officers)
To name t	he new genus: Simartevirus	

Assigning	Assigning the type species and other species to a new genus					
Code	2016.020kS	(assigned by ICTV officers)				
To designa	To designate the following as the type species of the new genus					
Simian hemorrhagic fever virus		Every genus must have a type species. This should be a well characterized species although not necessarily the first to be discovered				
The new genus will also contain any other new species created and assigned to it (Module 2) and any that are being moved from elsewhere (Module 7b). Please enter here the TOTAL number of species (including the type species) that the genus will contain: Ten						

Reasons to justify the creation of a new genus:

Additional material in support of this proposal may be presented in the Appendix, Module 11

See explanation in Module 3a

Origin of the new genus name:

Simartevirus from simian and arterivirus

Reasons to justify the choice of type species:

The priority of virus discovery

Species demarcation criteria in the new genus:

If there will be more than one species in the new genus, list the criteria being used for species demarcation and explain how the proposed members meet these criteria.

Species demarcation criteria are detailed in Module 2 and Annex.

MODULE 3d: **NEW GENUS**

creating a new genus

Ideally, a genus should be placed within a higher taxon.

Code	201	16.020lS	(assigned by ICTV officers)		
To create	a new	genus within:		Fill in all that apply.	
Subfar	mily:			• If the higher taxon has yet to be created	
Far	mily:	Arteriviridae		(in a later module, below) write "(new)" after its proposed name.	
О	rder:	Nidovirales		 If no family is specified, enter "unassigned" in the family box 	

naming a new genus

Code	2016.020mS	(assigned by ICTV officers)
To name the	he new genus: Dipartevirus	

Assigning the type species and other species to a new genus

Assigning the type species and other species to a new genus					
Code	2016.020nS	(assigned by ICTV officers)			
To designa	ate the following as the type sp	oecies of the new genus			
Wobbly po	Wobbly possum disease virus Every genus must have a type species. This should be a well characterized species although not necessarily the first to be discovered				
The new genus will also contain any other new species created and assigned to it (Module 2) and any that are being moved from elsewhere (Module 7b). Please enter here the TOTAL number of species (including the type species) that the genus will contain: One					

Reasons to justify the creation of a new genus:

Additional material in support of this proposal may be presented in the Appendix, Module 11

See explanation in Module 3a

Origin of the new genus name:

Dipartevirus from the mammalian order Diprotodontia and arterivirus

Reasons to justify the choice of type species:

Genus includes a single species

Species demarcation criteria in the new genus:

If there will be more than one species in the new genus, list the criteria being used for species demarcation and explain how the proposed members meet these criteria.

Species demarcation criteria are detailed in Module 2 and Annex.

MODULE 3e: **NEW GENUS**

creating a new genus

Ideally, a genus should be placed within a higher taxon.

Code	2016.020	OoS	(assigned by ICTV officers)			
To create a	To create a new genus within:					
				Fill in all that apply.		
Subfam	nily:			• If the higher taxon has yet to be created		
Fam	nily: Arteriv	riridae		(in a later module, below) write "(new)" after its proposed name.		
Ore	der: <i>Nidovi</i>	rales		If no family is specified, enter		
				"unassigned" in the family box		

naming a new genus

Code	2016.020pS	(assigned by ICTV officers)
To name th	he new genus: Nesartevirus	

Assigning the type species and other species to a new genus

Assigning the type species and other species to a new genus						
Code	2016.020qS	(assign	(assigned by ICTV officers)			
To designa	te the following as the type sp	ecies of	the new genus			
African poor module 9)	African pouched rat arterivirus (new name see Every genus must have a type species. This should be a well characterized species although not					
The new genus will also contain any other new species created and assigned to it (Module 2) and any that are being moved from elsewhere (Module 7b). Please enter here the TOTAL number of species (including the type species) that the genus will contain:						
One						

Reasons to justify the creation of a new genus:

Additional material in support of this proposal may be presented in the Appendix, Module 11

See explanation in Module 3a

Origin of the new genus name:

Nesartevirus from the mammalian family Nesomyidae and arterivirus

Reasons to justify the choice of type species:

Genus includes a single species

Species demarcation criteria in the new genus:

If there will be more than one species in the new genus, list the criteria being used for species demarcation and explain how the proposed members meet these criteria.

Species demarcation criteria are detailed in Module 2 and Annex.

MODULE 7a: MOVE

Use this module whenever an existing taxon needs to be moved and re-assigned (e.g. when a species is moved from one genus to another).

moving an existing taxon

Code	201	16.020rS (assigned by		CTV officers)			
To move	To move the following taxon (or taxa) from their present position:						
Species I	Equin	e arteritis virus					
The pres	sent ta	exonomic position of the	se taxon/taxa:				
G	enus:	Arterivirus					
Subfa	mily:			Fill in all that apply			
Fa	mily:	Arteriviridae		Fill in all that apply.			
C	rder:	Nidovirales					
Code	201	6.020sS	(assigned by IC	CTV officers)			
To re-as	sign t	he taxon (or taxa) listed	in Part (a) as	follows:			
				Fill in all that apply.			
G	enus:	Equartevirus		If the higher taxon has yet to be are stad write "frame," often its			
Subfa	mily:		`	created write "(new)" after its proposed name and complete			
Fa	mily:	Arteriviridae		relevant module to create it.			
C	rder:	Nidovirales		If no genus is specified, enter "unassigned" in the genus box.			

Reasons to justify the re-assignment:

- If it is proposed to re-assign species to an existing genus, please explain how the proposed species differ(s) from all existing species.
 - If species demarcation criteria (see module 3) have previously been defined for the genus, explain how the new species meet these criteria.
 - o If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Provide accession numbers for genomic sequences
- Further material in support of this proposal may be presented in the Appendix, Module 11

MODULE 7b: MOVE

Use this module whenever an existing taxon needs to be moved and re-assigned (e.g. when a species is moved from one genus to another).

moving an existing taxon

Code	201	6.020tS	(assigned by IC	CTV officers)				
To move	Γο move the following taxon (or taxa) from their present position:							
-	Species Lactate dehydrogenase-elevating virus, Porcine reproductive and respiratory syndrome virus 1, and Porcine reproductive and respiratory syndrome virus 2							
The pre	sent ta	xonomic position of the	se taxon/taxa:					
G	enus:	Arterivirus						
Subfa	mily:			Fill in all that apply.				
Fa	mily:	Arteriviridae						
	Order:	Nidovirales						
Code	201	6.020uS	(assigned by IC	CTV officers)				
To re-as	sign t	he taxon (or taxa) listed	in Part (a) as t	follows:				
				Fill in all that apply.				
G	enus:	Porartevirus		• If the higher taxon has yet to be				
Subfa	mily:			created write "(new)" after its proposed name and complete				
Fa	mily:	Arteriviridae		relevant module to create it.				
	Order:	Nidovirales		If no genus is specified, enter				
				"unassigned" in the genus box.				

Reasons to justify the re-assignment:

- If it is proposed to re-assign species to an existing genus, please explain how the proposed species differ(s) from all existing species.
 - If species demarcation criteria (see module 3) have previously been defined for the genus, explain how the new species meet these criteria.
 - o If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Provide accession numbers for genomic sequences
- Further material in support of this proposal may be presented in the Appendix, Module 11

MODULE 7c: MOVE

Use this module whenever an existing taxon needs to be moved and re-assigned (e.g. when a species is moved from one genus to another).

moving an existing taxon

Code	<i>201</i>	6.020vS	(assigned by IC	y ICTV officers)				
To move	To move the following taxon (or taxa) from their present position:							
colobus	Species Simian hemorrhagic fever virus, Kibale red-tailed guenon virus 1, Kibale red colobus virus 1, Kibale red colobus virus 2, Mikumi yellow baboon virus 1, Pebjah virus, Simian hemorrhagic encephalitis virus, and DeBrazza's monkey arterivirus							
The pres	sent ta	exonomic position of the	se taxon/taxa:					
G	enus:	Arterivirus						
Subfa	mily:			Fill in all that apply.				
Fa	mily:	Arteriviridae						
C	rder:	Nidovirales						
Code	<i>201</i>	6.020wS	(assigned by IC	CTV officers)				
To re-as	To re-assign the taxon (or taxa) listed in Part (a) as follows:							
				Fill in all that apply.				
G	enus:	Simartevirus		If the higher taxon has yet to be areated write "(new)" ofter its				
Subfa	Subfamily:			created write "(new)" after its proposed name and complete				
Fa	mily:	y: Arteriviridae		relevant module to create it.				
C	rder:	Nidovirales		If no genus is specified, enter				

Reasons to justify the re-assignment:

- If it is proposed to re-assign species to an existing genus, please explain how the proposed species differ(s) from all existing species.
 - o If species demarcation criteria (see module 3) have previously been defined for the genus, explain how the new species meet these criteria.
 - o If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Provide accession numbers for genomic sequences
- Further material in support of this proposal may be presented in the Appendix, Module 11

MODULE 7d: MOVE

Use this module whenever an existing taxon needs to be moved and re-assigned (e.g. when a species is moved from one genus to another).

moving an existing taxon

Code	201	16.020xS (assigned by		/ ICTV officers)			
To move	To move the following taxon (or taxa) from their present position:						
Species 1	Wobbl	y possum disease virus	_				
The pres	sent ta	exonomic position of the	se taxon/taxa:				
G	enus:	Arterivirus					
Subfa	mily:			Fill in all that apply.			
Fa	mily:	Arteriviridae		гін III ан шасарріу.			
C	rder:	Nidovirales	·				
Code	201	16.020yS	(assigned by IC	CTV officers)			
To re-as	sign t	he taxon (or taxa) listed	in Part (a) as	follows:			
				Fill in all that apply.			
G	Genus: Dipartevirus			If the higher taxon has yet to be are at a divisite "fraces" often its			
Subfa	mily:			created write "(new)" after its proposed name and complete			
Fa	mily:	Arteriviridae		relevant module to create it.			
C	rder:	Nidovirales		If no genus is specified, enter			
				"unassigned" in the genus box.			

Reasons to justify the re-assignment:

- If it is proposed to re-assign species to an existing genus, please explain how the proposed species differ(s) from all existing species.
 - If species demarcation criteria (see module 3) have previously been defined for the genus, explain how the new species meet these criteria.
 - o If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Provide accession numbers for genomic sequences
- Further material in support of this proposal may be presented in the Appendix, Module 11

MODULE 7e: MOVE

Use this module whenever an existing taxon needs to be moved and re-assigned (e.g. when a species is moved from one genus to another).

moving an existing taxon

Code	201	16.020zS	(assigned by IC	TV officers)			
To move	To move the following taxon (or taxa) from their present position:						
Species 2	Africa	n pouched rat arterivirus	(new name, se	e module 9)			
The pre	sent ta	axonomic position of the	se taxon/taxa:				
G	enus:	Arterivirus					
Subfa	mily:			Fill in all that apply.			
Fa	mily:	Arteriviridae		гііі іп ан шасарріу.			
C	order:	Nidovirales					
Code	201	16.020aaS	(assigned by IC	TV officers)			
To re-as	sign t	he taxon (or taxa) listed	in Part (a) as f	follows:			
				Fill in all that apply.			
Genus: Nesartevirus			If the higher taxon has yet to be areated write "frame" ofter its				
Subfa	Subfamily:			created write "(new)" after its proposed name and complete			
Family: Arteriviridae			relevant module to create it.				
C	Order: Nidovirales		If no genus is specified, enter "unassigned" in the genus box.				

Reasons to justify the re-assignment:

- If it is proposed to re-assign species to an existing genus, please explain how the proposed species differ(s) from all existing species.
 - o If species demarcation criteria (see module 3) have previously been defined for the genus, explain how the new species meet these criteria.
 - o If criteria for demarcating species need to be defined (because there will now be more than one species in the genus), please state the proposed criteria.
- Provide accession numbers for genomic sequences
- Further material in support of this proposal may be presented in the Appendix, Module 11

MODULE 8: **REMOVE (ABOLISH)**

Use this module if an existing taxon needs to be completely removed (abolished). Use module 9 if there is simply a change of name.

removing (abolishing a taxon)

Code	201	16.020abS	(assigned by IC	CTV officers)		
To remo	To remove the following taxon (or taxa) from their present position:					
Arterivir	us					
The pres	The present taxonomic position of these taxon/taxa:					
G	enus:					
Subfa	mily:		Fill in all that apply			
Fa	mily:	Arteriviridae		Fill in all that apply.		
C	Order:	Nidovirales				

Reasons to justify the removal:

Explain why the taxon (or taxa) should be removed

Further material in support of this proposal may be presented in the Appendix, Module 11

To comply with the reorganization of genus structure of the family as explained in the module 3a. The genus is empty after all its species were assigned to four new genera.

MODULE 9: **RENAME**

Use this module to change the name of one or more existing taxa (but note that stability of nomenclature is encouraged wherever possible). Insert extra lines in the table if needed.

.

Renaming one or more taxa

Code	2016.020acS	(ass	igned by ICTV officers)			
To rename the following taxon (or taxa): Species Forest pouched giant rat arterivirus						
Current name			Proposed name			
Forest pouched giant rat arterivirus			African pouched rat arterivirus			
	-					

Reasons to justify the renaming: Explain why the taxon (or taxa) should be renamed	
To correct a mistake in the prior proposal and match the species and virus names	

MODULE 11: APPENDIX: supporting material

additional material in support of this proposal

References:

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Bailey AL, Lauck M, Weiler A, Sibley SD, Dinis JM, Bergman Z, Nelson CW, Correll M, Gleicher M, Hyeroba D, Tumukunde A, Weny G, Chapman C, Kuhn JH, Hughes AL, Friedrich TC, Goldberg TL, O'Connor DH (2014b) High genetic diversity and adaptive potential of two simian hemorrhagic fever viruses in a wild primate population. *PloS One* 9:e90714

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Brinton MA, Gulyaeva A, Balasuriya UBR, Dunowska M, Faaberg KS, Leung FC, Nauwynck HJ, Snijder EJ, Stadejek T, Gorbalenya AE (2016) ICTV taxonomic proposal 2016.016a-acS.N.v1. In the family *Arteriviridae* replace the single existing genus, *Arterivirus*, by 5 new genera: *Alphaarterivirus*, *Betaarterivirus*, *Gammaarterivirus*, *Deltaarterivirus*, *Epsilonarterivirus*.

https://talk.ictvonline.org/files/proposals/animal_ssrna_viruses/m/animal_rna_plus_newly_submitted/6167

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Faaberg KS, Balasuriya UB, Brinton MA, Gorbalenya AE, Leung FC-C, Nauwynck H, Snijder EJ, Stadejek T, Yang H, Yoo D (2012) Family Arteriviridae. In: Virus Taxonomy, the 9th Report of the International Committee on Taxonomy of Viruses, King, A., Adams, M., Carstens, E. & E.J Lefkowitz, Eds. Academic Press, pp 796-805.

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Lauck M, Sibley SD, Hyeroba D, Tumukunde A, Weny G, Chapman CA, Ting N, Switzer WM, Kuhn JH, Friedrich TC, O'Connor DH, Goldberg TL (2013) Exceptional simian hemorrhagic fever virus diversity in a wild African primate community. *J. Virol.* 87:688-691

Lauck M, Alkhovsky SV, Bao Y, Bailey AL, Shevtsova ZV, Shchetinin AM, Vishnevskaya TV, Lackemeyer MG, Postnikova E, Mazur S, Wada J, Radoshitzky SR, Friedrich TC, Lapin BA, Deriabin PG, Jahrling PB, Goldberg TL, O'Connor DH, Kuhn JH (2015) Historical Outbreaks of Simian Hemorrhagic Fever in Captive Macaques Were Caused by Distinct Arteriviruses. *J Virol*: **89**: 8082-8087

Annex:

Include as much information as necessary to support the proposal, including diagrams comparing the old and new taxonomic orders. The use of Figures and Tables is strongly recommended but direct pasting of content from publications will require permission from the copyright holder together with appropriate acknowledgement as this proposal will be placed on a public web site. For phylogenetic analysis, try to provide a tree where branch length is related to genetic distance.

Table 1. Proposed classification and nomenclature of the family *Arteriviridae*.

Genus	Species name	Genbank Accession number
Equartevirus	Equine arteritis virus*	X53459
Porartevirus	Lactate dehydrogenase-elevating virus*	U15146
	Rat arterivirus 1 (new)	KP280006
	Porcine respiratory and reproductive syndrome virus 1	AF046869
	Porcine respiratory and reproductive syndrome virus 2	U87392
Dipartevirus	Wobbly possum disease virus*	JN116253
Simartevirus	DeBrazza's monkey arterivirus	KP126831
	Free State vervet virus (new)	KR862307
	Kibale red colobus virus 1	KC787630
	Kibale red colobus virus 2	KC787658
	Kibale red-tailed guenon virus 1	JX473849
	Mikumi yellow baboon virus 1	KM110938
	Kafue kinda chacma baboon virus (new)	KT447550
	Pebjah virus	KR133839
	Simian hemorrhagic encephalitis virus	KM677927
	Simian hemorrhagic fever virus*	AF180391
Nesartevirus	African pouched rat arterivirus*	KP026921

^{*} denotes the type species

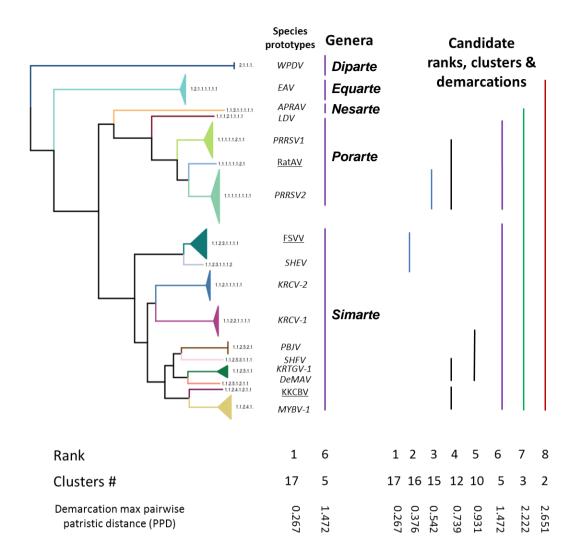


Fig. 1. Cluster partitioning of the phylogenetic tree of arteriviruses by DEmARC. Shown is the ML tree by FastTree of 683 arteriviruses colored according to 17 clusters (species) at Rank 1 which were identified by DEmARC (names of new species are underscored). Height and width of triangles at the tip of branches reflect the number and diversity, respectively, of respective species using a log scale. Arterivirus species were labelled with acronyms: EAV, Equine arteritis virus; APRAV, African pouched rat arterivirus; DeMAV, DeBrazza's monkey arterivirus; FSVV, Free State vervet virus; KKCBV, Kafue kinda chacma baboon virus; KRCV-1, Kibale red colobus virus 1; KRCV-2, Kibale red colobus virus 2; KRTGV-1, Kibale red-tailed guenon virus 1; LDV, Lactate dehydrogenase-elevating virus; MYBV-1, Mikumi yellow baboon virus 1; PBJV, Pebjah virus; PRRSV-1, Porcine reproductive and respiratory syndrome virus 1; PRRSV-2, Porcine reproductive and respiratory syndrome virus 2; RatAV, Rat arterivirus 1; SHFV, Simian hemorrhagic fever virus; SHEV, Simian hemorrhagic encephalitis virus; WPDV, Wobbly possum disease virus (for sequence accession numbers see Table 1). The proposed genera structure is detailed at the right of the virus names. Further to the right are shown eight candidate ranks with clusters and thresholds used to select species and genus ranks of arterivirus taxonomy. Colored vertical bars at each candidate rank highlight clusters that were combined at the respective rank compared to the next left rank depicted. (Gulyaeva et al & Gorbalenya, unpublished).

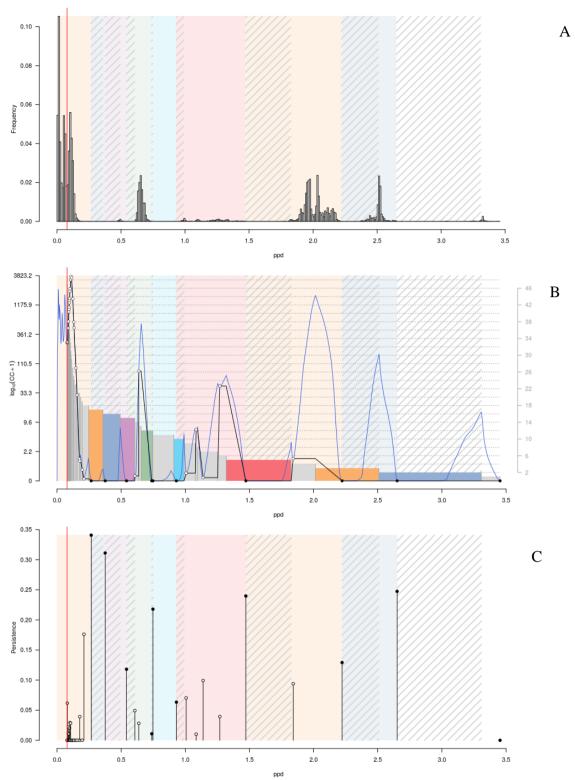


Fig. 2. Arterivirus-wide pairwise evolutionary distance distribution and distance thresholds for partitioning. The three panels starting from the top depict, respectively, frequency distribution of PPDs, change of clustering of viruses (right Y axis) and clustering cost (left Y axis) associated with partitioning at each PPD, and threshold persistence of particular clustering over the PPD range. Threshold persistence for the eight most supported thresholds (CC=0), detailed in Fig. 1, is depicted with black capped vertical bars. The pairwise distance scale reflects the estimated number of amino acid substitutions per site on average. (Gulyaeva et al & Gorbalenya, unpublished).

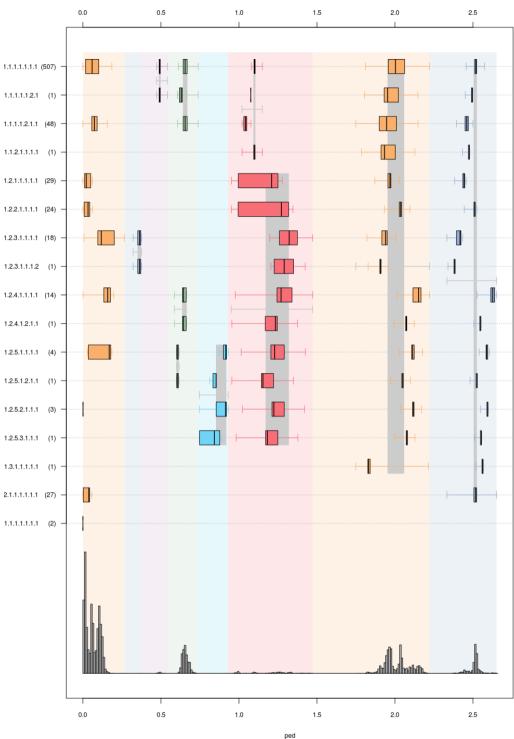


Fig. 3. Intra-group genetic divergence in eight-level hierarchical clustering of arteriviruses by DEmARC. Levels are defined by the eight strongest PPD thresholds defined in the bottom panel of Fig. 2. For simplicity, species identities are indicated via a numerical system with numbers corresponding to candidate ranks (left axis); the number of viruses in the identified clusters are shown in brackets. All identified clusters correspond to monophyletic groups in the tree of Fig. 1. Box-and-whisker graphs were used to plot distributions of distances between viruses from the same taxon (e.g. species, orange), and between viruses from different taxa of the next candidate rank. The boxes span from the first to the third quartile and include the median (bold line), and the whiskers (dashed lines) extend to the extreme values. The corresponding part of the PPD distribution (see panel A of Fig. 2) is depicted below. (Gulyaeva et al. & Gorbalenya, unpublished).

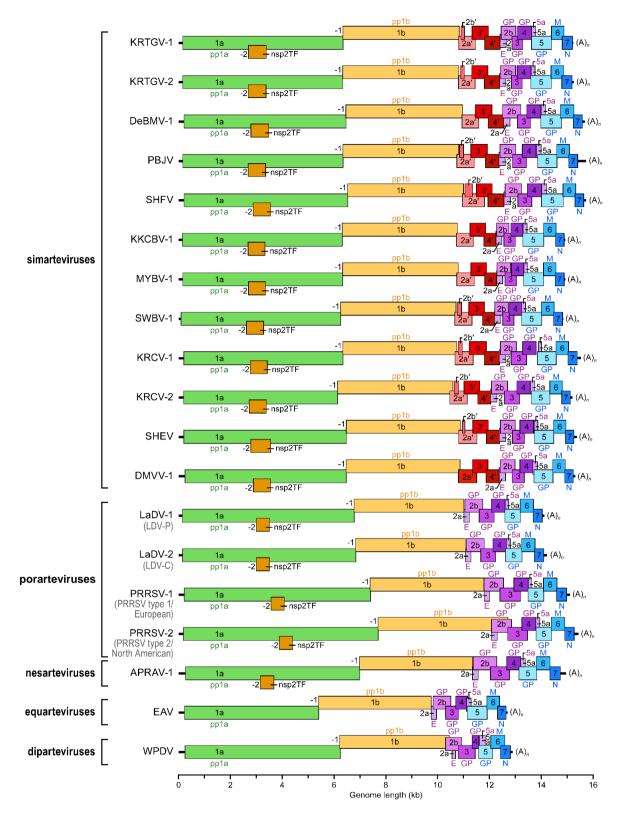


Fig. 4. Organization of arterivirus genomes. Individual arterivirus open reading frames (ORFs) drawn to scale are shown in colors. ORF1a (green) encodes polyprotein 1a (pp1a). ORF1a and ORF1b (yellow) can be joined through a "-1" programmed ribosomal frameshift to express polyprotein 1ab. pp1a and pp1ab 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 (proposed new genus *Simartevirus*) genomes, encode minor structural proteins of unknown function. 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 virus 1 (JX473849) and 2 (JX473850); 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 vellow baboon virus 1; SWBV-1, Southwest baboon virus 1; KRCV-1/2, Kibale red colobus viruses 1 and 2; SHEV, simian hemorrhagic encephalitis virus; and DMVV-1, Drakensberg Mountain vervet virus 1 (isolate of Free State vervet virus). Murine and porcine arteriviruses (porarteviruses) are: LaDV-1/2, lactate dehydrogenase-elevating viruses 1 (U15146) and 2 (L13298); PRRSV-1/2, porcine reproductive and respiratory syndrome viruses 1 and 2. Nesomyid arteriviruses (nesarteviruses) include: APRAV-1, African pouched rat virus 1. Equine arteriviruses (equarteviruses) include: EAV, equine arteritis virus. Diparteviruses include: WPDV, wobbly possum disease virus (Kuhn et al., 2016). Other accession numbers are shown in Table 1.

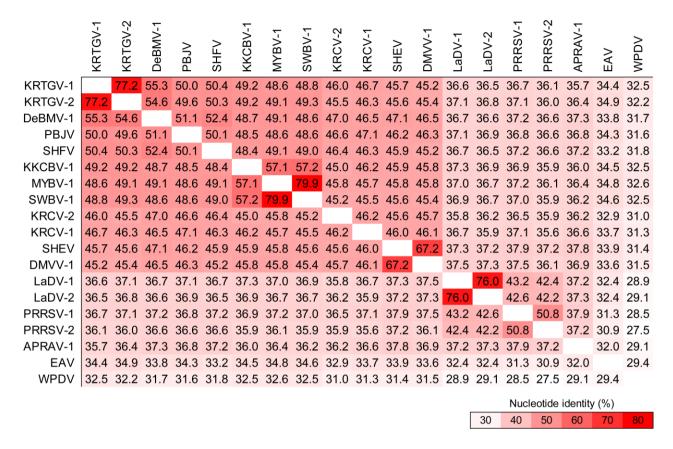


Fig. 5. Pairwise sequence comparison of the arterivirus proteomes. Coding regions from each arterivirus genome (Fig. 4) were aligned in CLC Genomics Workbench version 6, and a pairwise comparison matrix was constructed. Only orthologous genes common to all known arteriviruses were used (i.e., simartevirus-specific 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 in Fig. 4.

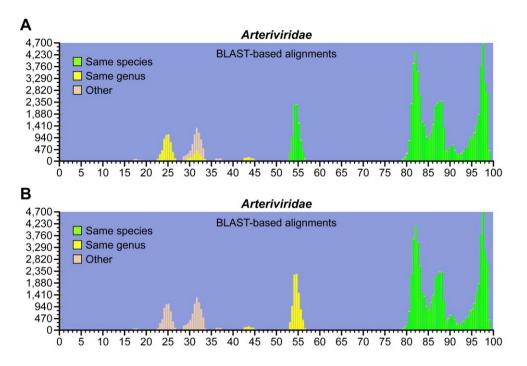


Fig. 6. PAirwise Sequence Comparison (PASC) analysis using a modified basic local alignment search tool (BLAST) algorithm (Bao *et al.*, 2014). The resulting histograms, visualizing the distribution of the number of arterivirus pairs at each identity percentage, confirm results shown in Fig. 5. The x-axis 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.

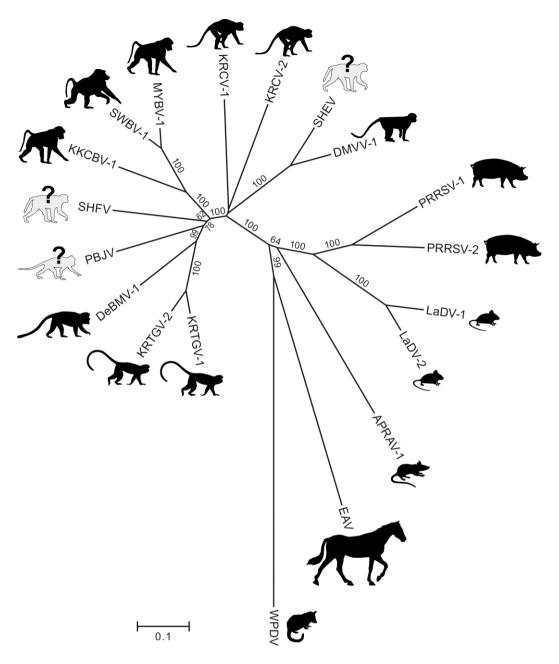


Fig. 7. Phylogenetic relationships among classified and unclassified arteriviruses based on ORF1b amino acid sequences (see Fig. 4 for genomes and virus abbreviations). Silhouettes represent mammals in which each virus was found, with question marks indicating uncertain natural hosts (viruses discovered in captive macaques). ORF1b nucleotide sequences were aligned using a codon-guided version of the multiple alignment using fast fourier transform (MAFFT) method (Katoh *et al.*) implemented in the computer program TranslatorX (Abascal et al.). Poorly aligned sites were removed using the Gblocks alignment cleaning method 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 with the Poisson distance correction method. Robustness of phylogenetic groupings was assessed using 1,000 bootstrap replicates of the data; 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).