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Spumaretroviruses: Updated taxonomy and nomenclature

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ABSTRACT

Spumaretroviruses, commonly referred to as foamy viruses, are complex retroviruses belonging to the subfamily *Spumaretrovirinae,* family *Retroviridae*, which naturally infect a variety of animals including nonhuman primates (NHPs). Additionally, cross-species transmissions of simian foamy viruses (SFVs) to humans have occurred following exposure to tissues of infected NHPs. Recent research has led to the identification of previously unknown exogenous foamy viruses, and to the discovery of endogenous spumaretrovirus sequences in a variety of host genomes. Here, we describe an updated spumaretrovirus taxonomy that has been recently accepted by the International Committee on Taxonomy of Viruses (ICTV) Executive Committee, and describe a virus nomenclature that is generally consistent with that used for other retroviruses, such as lentiviruses and deltaretroviruses. This taxonomy can be applied to distinguish different, but closely related, primate (e.g., human, ape, simian) foamy viruses as well as those from other hosts. This proposal accounts for host-virus co-speciation and cross-species transmission.

1. Introduction

Spumaretroviruses belong to the subfamily *Spumaretrovirinae* in the family *Retroviridae*. They are highly prevalent in animals of diverse non-primate mammalian families [Bovidae (cloven-hooved ruminants), Felidae (cats), Equidae (horses and relatives), and Rhinolophidae (horseshoe bats)], as well as nonhuman primates (NHPs), including apes, Old World monkeys (OWM), New World monkeys (NWM), and prosimians (1, 2). Members of the subfamily *Spumaretrovirinae*, commonly referred to as foamy viruses, have a broad tissue and cell tropism and virus infection is generally latent, except in some tissues of the oral cavity ((3, 4).

The earliest reports of foamy virus isolates were of simian origin (NWM, OWM, and apes) and were originally classified serologically using neutralization assays (5, 6). The first "human" spumaretrovirus isolate was obtained from cultures of a human nasopharyngeal carcinoma in 1971 and was originally designated "human foamy virus (HFV)" (7, 8), but was later found to be of chimpanzee origin based upon sequence identity to chimpanzee foamy virus and renamed as prototype foamy virus (PFV) (6, 9). Cross-species transmissions of simian foamy viruses (SFVs) to humans have occurred by exposure to fluids or tissues from infected NHPs (10-23). Although foamy viruses are exogenously transmitted viruses, endogenous foamy virus sequences have been identified and characterized in genomes of many species, including aye-aye (*Daubentonia madagascariensis*), sloth (*Choloepus hoffmanni*), Cape golden mole (*Chrysochloris asiatica*), coelacanth (*Latimeria chalumnae*), platyfish (*Xiphophorus maculatus*), and zebrafish (*Danio rerio*) (24-30). In fact, molecular evolution studies have indicated that spumaretroviruses have co-speciated with their hosts for millions of years (24, 26, 31, 32). Recently, phylogenetic analyses using amphibian and fish genomes have estimated the date of retrovirus emergence at >450 million years ago (25) with foamy viruses inferred to be the most ancient retrovirus. A

recent increase in the number of foamy virus isolates and sequences using a variety of novel molecular and genomic techniques highlights the need for updating and expanding spumaretrovirus taxonomy (15, 31, 33-48).

The taxonomic history of *Spumaretrovirinae* has been based only on the few early virus isolates. Although "foamy virus" was discovered in rhesus monkey kidney cultures in 1955 (49), simian foamy retroviruses, were not formally classified until the Second Report (1976) of the International Committee on Taxonomy of Viruses [ICTV], which assigned bovine syncytial virus (BSV), feline syncytial virus (FSV), hamster syncytial virus (HSV), human foamy virus (HFV), and simian foamy virus (SFV) to the "genus-less" subfamily *Spumavirinae* (50). In the Third (1979) ICTV Report, the still genus-less subfamily Spumavirinae contained only four viruses (BSV, FSV, HFV, and SFV) (51). By the Fifth (1991) ICTV Report, all three subfamilies (*Oncovirinae*, *Lentivirinae*, and *Spumavirinae*) of the *Retroviridae* were abandoned and seven genera created, including *Spumavirus*, which contained BSV, FSV, HFV, and SFV (52), with HFV designated as the type species. This taxonomy was upheld in the Sixth (1995) ICTV Report, but HFV was referred to as human spumavirus (53). The Seventh (2000) ICTV Report for the first time differentiated between species and viruses. *Chimpanzee foamy virus* was designated the type species and chimpanzee foamy virus (formerly human spumavirus) was assigned to it (according to ICTV rule, virus name is not italicized). The other species were *Bovine foamy virus* (containing bovine foamy virus; formerly bovine syncytial virus), *Feline foamy virus* (containing feline foamy virus, formerly feline syncytial virus), *Simian foamy virus 1* (containing simian foamy virus type 1), and *Simian foamy virus 3* (containing simian foamy virus type 3) (54). In the Eighth (2005) ICTV Report, based upon the distinct replication pathway of foamy viruses, which contains features homologous to both retroviruses and

hepadnaviruses (55), the subfamily *Spumaretrovirinae* was reinstated for the genus *Spumavirus*. The species *Simian foamy virus 1* was renamed *Macaque simian foamy virus* and the virus assigned to this species, simian foamy virus 1, was renamed macaque simian foamy virus. Similarly, the species *Simian foamy virus 3* was renamed *African green monkey simian foamy virus* and the virus in this species, simian foamy virus 3, was renamed African green monkey simian foamy virus; the species *Chimpanzee foamy virus* was renamed *Simian foamy virus* and the virus in this species, chimpanzee foamy virus was renamed simian foamy virus. In addition, the species *Equine foamy virus* was established for equine foamy virus. No changes were made to *Bovine foamy virus* and *Feline foamy virus* (56). The most recent, Ninth (2011) ICTV Report, lists six spumavirus species for six viruses (57), and this current classification is shown in Table 1.

The current taxonomy for spumaretroviruses is outdated as it does not accommodate new foamy viruses discovered in NHPs of various species, including OWM and NWM (31, 36, 58). Furthermore, formal nomenclature for designating virus isolates is lacking, particularly for simian foamy viruses, which has led to some confusion in virus descriptions and references in publications and retrieval of sequences deposited in public databases. The critical need for updating spumaretrovirus taxonomy and for developing a consensus nomenclature for different foamy viruses was recognized by the scientific community and discussed at the International Foamy Virus Conference held in 2014 in Puławy, Poland (59) and in 2016 in Paris, France (60). Here, we present an updated and expanded spumaretrovirus taxonomy based upon current knowledge that accounts for host-virus co-speciation and cross-species transmission. Furthermore, the proposed virus nomenclature can be applied to all spumaretroviruses, including non-primate and primate viruses.

2. Updated 2017 spumaretrovirus classification

The recent increase in the number of primate and non-primate spumaretroviruses warranted an update of the current ICTV classification as well as establishment of a more consistent nomenclature. This updated taxonomy, which was proposed by the authors to the Executive Committee of the ICTV on June 18, 2017, is shown in Table 2. The following changes were proposed based on analyses of sequences of spumaretrovirus genomes available in public databases:

- the existing genus *Spumavirus* was replaced by five genera named *Bovispumavirus*, *Equispumavirus, Felispumavirus*, *Prosimiispumavirus*, and *Simiispumavirus* because the spumaretrovirus phylogeny largely reflects the host phylogeny (Fig. 1), supporting the hypothesis of spumaretrovirus-host co-evolution (18, 24, 26, 31, 32);
- the established species *Bovine foamy virus*, *Feline foamy virus*, and *Equine foamy virus* were included in the new genera *Bovispumavirus*, *Felispumavirus*, and *Equispumavirus*, respectively. Additionally, the species *Puma feline foamy virus* was included in genus *Felispumavirus*;
- a new species, *Brown greater galago simian foamy virus*, was included in a new genus *Prosimiispumavirus*;
- the previously established species were included in the new genera, and new species were established for previously unclassified spumaretroviruses. Species names were chosen based upon the viral host animal names. The previous species *simian foamy virus* was renamed *Eastern chimpanzee simian foamy virus*. The species *Macaque simian foamy virus* and *African green monkey simian foamy virus* were renamed *Taiwanese macaque*

159 *simian foamy virus* and *Grivet simian foamy virus*, respectively, and together with
160 *Eastern chimpanzee simian foamy virus* were included in genus *Simiispumavirus*. Eleven
161 additional NHP spumaretrovirus species were added to this genus. Each proposed species
162 is represented by at least one virus for which a complete genome sequence has been
163 deposited in public databases.

164 In addition to the viruses included in the updated taxonomy submitted to the ICTV in 2017,
165 there are other foamy virus isolates, that are phylogenetically distinct from the currently included
166 ones and, were not included in the proposal because of the lack of a complete coding genome
167 sequence. These are shown in Table 3 and are envisioned to be included in future taxonomic
168 updates, along with other available sequences at that time. It should be noted that the simian
169 foamy virus Macaca fascicularis (SFVmfa) is also included in this table (and in Fig. 1) since it is
170 expected to be submitted in the next update based upon a published full-genome sequence (61).
171 Additionally, based upon recent discussions related to viruses identified by metagenomics,
172 sequences that are distinct phylogenetically from the currently classified viruses and have been
173 completely sequenced in their coding regions may be classified officially by the ICTV even in
174 the absence of a virus isolate (62).

175

176 **3. Updated 2017 spumaretrovirus nomenclature**

177 Previously, different spumaretroviruses were named by adding three-letter lower-case
178 abbreviations to "SFV" (simian foamy virus) derived from the common names of the hosts from
179 which the viruses were isolated. For instance, SFVmac was used for simian spumaretroviruses
180 infecting macaques and SFVagm was used for simian spumaretroviruses infecting grivets
181 (African green monkeys, agm) (6). However, this general designation of viruses does not

182 distinguish strains infecting hosts of different species or subspecies. The genus *Macaca*
183 (macaques) includes more than 20 species the members of which are distributed throughout Asia,
184 with one also in Africa, and the genus *Chlorocebus* (African green monkeys) includes six
185 species, the members of which are distributed across sub-Saharan Africa. The most confusing
186 virus name was "simian foamy virus", which referred to foamy viruses from all NHPs except
187 macaques and African green monkeys.
188 Here we propose a spumaretrovirus nomenclature similar to that used for simian
189 immunodeficiency virus and simian T-lymphotropic virus isolates. Accordingly, all
190 spumaretrovirus names will contain the words "foamy virus" preceded by an adjectival classifier
191 indicating the host (e.g., bovine, feline, simian) followed by the name of the species, or in some
192 cases subspecies, of the particular host. The virus host name and "foamy virus" are abbreviated
193 in capital letters (e.g., feline foamy virus is abbreviated FFV, simian foamy virus is abbreviated
194 SFV) followed by lower-case three-letter abbreviations for the host species name. These
195 abbreviations are comprised of the first letter of the host genus and the first two letters of the
196 species or subspecies (e.g., simian foamy virus Macaca cyclopis is abbreviated SFVmcy) (Tables
197 2 - 3), or the first letter of the species or subspecies and the next unique letter, when the letters
198 are the same (e.g. simian foamy viruses isolated from New World primates such as
199 *Leontopithecus chrysomelas* and *Leonthopithecus chrysopygus* would be abbreviated as SFVlcm
200 and SFVlcp, respectively). In the case of an unknown host species, the first letter of the genus
201 name is followed by "*xx*" (italics letters). Virus isolate names are designated by using the virus
202 abbreviation followed by an underscore that appends additional, isolate-identifying information
203 such as the host from which it was isolated (for instance, "hu" for human), isolate designation,
204 and other identifying information. For example, simian foamy virus Pan troglodytes

schweinfurthii, human isolate HSRV, clone 13 will be designated as SFVpsc_huHRSV.13, and feline foamy virus Felis catus strain FUV7 will be designated as FFVfca_FUV7 (Table 4). Similarly, in case of inter-species transmission involving nonhuman primates, SFV from western red colobus monkey (*Philiocolobus badius badius*) isolated from a wild chimpanzee subspecies *Pan troglodyes verus* (63) will be designated as SFVpba_pveLeo. Furthermore, for recombinant viruses (including naturally-occurring and those genetically-engineered), the designation "[RF]" is included at the end (e.g., SFVmcy_FV34[RF] (64).

4. Conclusions

The updated and expanded spumaretrovirus taxonomy presented here was initially submitted to the ICTV on June 18, 2017, and is currently provisionally approved by the ICTV Executive Committee. The proposal now awaits ratification by vote of the International Union of Microbiological Societies (IUMS) Virology Division, which will occur in the first quarter of 2018. The new taxonomy format is easily expandable to accommodate new genera and species for classification of newly discovered foamy viruses. Additionally, we have established a spumaretrovirus nomenclature that considers host-virus co-speciation and cross-species transmission, and incorporates host animal species information and strain and/or animal identification codes in spumaretrovirus names and their abbreviations. This collaborative effort is aimed toward unifying classification and designations of spumaretroviruses to facilitate easy comparisons of reported foamy virus isolates.

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499 **Table 1.** Current spumaretrovirus taxonomy according to ICTV[a]

Family	Subfamily	Genus	Species	Virus name
Retroviridae	*Spumaretrovirinae*	*Spumavirus*	*African green monkey simian foamy virus*	African green monkey simian foamy virus (SFVagm)[b]
			Bovine foamy virus	bovine foamy virus (BFV)
			Equine foamy virus	equine foamy virus (EFV)
			Feline foamy virus	feline foamy virus (FFV)
			Macaque simian foamy virus	macaque simian foamy virus (SFVmac)[c]
			*Simian foamy virus**	simian foamy virus, human isolate (SFVcpz(hu))[d]

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501 [a]Reference (57); [b]Synonym: simian foamy virus 3 (SFV-3); [c]Synonym: simian foamy virus 1 (SFV-1); [d]Synonyms: chimpanzee foamy virus (CFV), human

502 foamy virus (HFV) and prototype foamy virus (PFV); *Type species.

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508 **Table 2.** Updated spumaretrovirus taxonomy as proposed in June 2017[a].

Family	Subfamily	Genus	Species	Virus (name)
Retroviridae	*Spumaretrovirinae*	*Simiispumavirus*	*Eastern chimpanzee simian foamy virus*[b,*]	simian foamy virus Pan troglodytes schweinfurthii (SFVpsc)
			Western chimpanzee simian foamy virus	simian foamy virus Pan troglodytes verus (SFVpve)
			Central chimpanzee simian foamy virus	simian foamy virus Pan troglodytes troglodytes (SFVptr)
			Western lowland gorilla simian foamy virus	simian foamy virus Gorilla gorilla gorilla (SFVggo)
			Bornean orangutan simian foamy virus	simian foamy virus Pongo pygmaeus pygmaeus (SFVppy)
			Taiwanese macaque simian foamy virus[c]	simian foamy virus Macaca cyclopis (SFVmcy)
			Rhesus macaque simian foamy virus	simian foamy virus Macaca mulatta (SFVmmu)
			Japanese macaque simian foamy virus	simian foamy virus Macaca fuscata (SFVmfu)
			Grivet simian foamy virus[d]	simian foamy virus Chlorocebus aethiops (SFVcae)
			Guenon simian foamy virus	simian foamy virus Cercopithecus nictitans (SFVcni)

			Spider monkey simian foamy virus	simian foamy virus Ateles species (SFVaxx)
			White-tufted-ear marmoset simian foamy virus	simian foamy virus Callithrix jacchus (SFVcja)
			Squirrel monkey simian foamy virus	simian foamy virus Saimiri sciureus (SFVssc)
			Yellow-breasted capuchin simian foamy virus	simian foamy virus Sapajus xanthosternos (SFVsxa)
		Prosimiispumavirus	*Brown greater galago prosimian foamy virus**	simian foamy virus Otolemur crassicaudatus (SFVocr)
		Bovispumavirus	*Bovine foamy virus**	bovine foamy virus Bos taurus (BFVbta)
		Felispumavirus	*Feline foamy virus**	feline foamy virus Felis catus (FFVfca)
			Puma feline foamy virus	feline foamy virus Puma concolor (FFVpco)
		Equispumavirus	*Equine foamy virus**	equine foamy virus Equus caballus (EFVeca)

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510 [a]Based upon available complete virus genome sequences; [b]The former species *Simian spumavirus*; [c]The former species *Macaque simian foamy virus*; [d]The

511 former species *African green monkey simian foamy virus*; *Type species.

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Table 3. Projected updates for spumaretrovirus taxonomy[a].

Family	Subfamily	Genus	Species	Virus names and designations
Retroviridae	*Spumaretrovirinae*	*Simiispumavirus*	*Cynomolgus macaque simian foamy virus*	simian foamy virus Macaca fascicularis (SFVmfa)[b]
			Drill simian foamy virus	simian foamy virus Mandrillus leucophaeus (SFVmle)[c]
			Mandrill simian foamy virus	simian foamy virus Mandrillus sphinx (SFVmsp)[c]
			Yellow baboon simian foamy virus	simian foamy virus Papio cynocephalus (SFVpcy)[c]
		Chispumavirus	*Intermediate horseshoe bat foamy virus**	chiropteran foamy virus Rhinolophus affinis (CFVraf)[c]

[a]Potential candidates for new species based upon phylogenetic distance from current ones; [b]To be included in next update since full-genome sequence has been published; [c]To be included in update when sequence of at least full genome open reading frames is publicly available; [*]Potential candidate for type species.

521 **Table 4.** Proposed spumaretrovirus isolate nomenclature.

Host	**Spumaretrovirus name and designation**	**Isolate description: type, strain, isolate [Previous designation(s)]**	**New isolate designation**	**GenBank accession number**	**Reference(s)** [a]
Bovine	bovine foamy virus Bos taurus (BFVbta)	BSV-11 (BSV, BFV)	BFVbta_BSV11*	U94514[b]	(65)
		BFV-Riems	BFVbta_Riems	JX307862[b]	(48)
		BFV100	BFVbta_100	JX307861[b]	(48)
Feline	feline foamy virus Felis catus (FFVfca)	type FUV7 (FSV, FFV)	FFVfca_FUV7*	Y08851[b]	(66, 67)
		type F17/951	FFVfca_F17/951	U85043[b]	(68)
	feline foamy virus Puma concolor (FFVpco)	X102	FFVpco_X102	KC292054[b]	(47)
Equine	equine foamy virus Equus caballus (EFVeca)	isolate clone 1 [EFV]	EFVeca_1*	AF201902[b]	(69)

Chiropteran	chiropteran foamy virus Rhinolophus affinis (CFVraf)	isolate 1[RaFV-1]	CFVraf_1	JQ814855[c]	(35)
Prosimian	simian foamy virus Otolemur crassicaudatus (SFVocr)	type 5, strain 1557 [SFV type 5; SFVgal]	SFVocr_1557*	KM233624[b]	(24)
Simian—New World monkeys	simian foamy virus Ateles species (SFVaxx)	serotype 8, strain S-140, Hooks40 [SFV type 8; SFVspm]	SFVa*xx*_Hooks40	EU010385[b]	(70)
	simian foamy virus Callithrix jacchus (SFVcja)	isolate FXV[SFVmar]	SFVcja_FXV	GU356395[b]	(71)
	simian foamy virus Saimiri sciureus (SFVssc)	serotype 4, strain 1224 (SFV type 4; SFVsqu]	SFVssc_1224	GU356394[b]	(71)
	simian foamy virus Sapajus xanthosternos (SFVsxa)	isolate Z17	SFVsxa_Z17	KP143760[b]	(37)

Simian—apes	simian foamy virus Pan troglodytes schweinfurthii (SFVpsc)	human isolate HSRV clone 13 [PFV; CFV; HSRV; SFVcpz(hu); HFV]	SFVpsc_huHSRV.13*	KX08159[b]	(72)
	simian foamy virus Pan troglodytes troglodytes (SFVptr)	human isolate BAD327	SFVptr_huBAD327	JQ867463[b]	(73)
		human isolate AG15	SFVptr_huAG15	JQ867462[b]	(73)
	simian foamy virus Pan troglodytes verus (SFVpve)	[SFVcpz]	SFVpve	NC_001364[b]	(9)
		serotype 6, strain CV-1, Pan-1 [SFV type 6; SFVcpz]	SFVpve_Pan1		
		serotype 7, strain CV-11, Pan-2 [SFV type 7; SFVcpz]	SFVpve_Pan2		
	simian foamy virus Gorilla gorilla gorilla (SFVggo)	[SFV-Gg; SFVgor]	SFVggo_Gg	HM245790[b]	(74)
		human isolate BAK74	SFVggo_huBAK74	JQ867464[b]	(73)
		human isolate BAD468	SFVggo_huBAD468	JQ867465[b]	(73)

	simian foamy virus Pongo pygmaeus pygmaeus (SFVppy)	serotype 11, strain bella [SFV type 11; SFVora]	SFVppy_bella	AJ544579[b]	(75)
Simian—Old World monkeys	simian foamy virus Chlorocebus aethiops (SFVcae)	strain LK3 [African green monkey SFV; SFVagm; SFVagm-3]	SFVcae_LK3	M74895[b]	(76)
		Serotype 3, strain FV2014 [SFV 3; SFV type 3; SFVagm]	SFVcae_FV2014	MF582544[b]	(77)
	simian foamy virus Cercopithecus nictitans (SFVcni)	human isolate AG16	SFVcni_huAG16	JQ867466[b]	(73)
	simian foamy virus Macaca cyclopis (SFVmcy)	serotype 1, strain FV21 [SFV-1; macaque SFV; SFV type 1; SFVmac; SFVmcy-1]	SFVmcy_FV21	NC_010819[b]	(78)
		serotype 2, strain FV34 [SFV type 2; SFVmac; SFVmcy-2]	SFVmcy_FV34[RF][c]	KF026286.1[b]	(64)

	simian foamy virus Macaca fascicularis (SFVmfa)	isolate Cy5061	SFVmfa_Cy5061	LC094267[b]	(61)
	simian foamy virus Macaca fuscata (SFVmfu)	Isolate WK1, clone pJM356 [Japanese macaque SFV; SFVjm]	SFVmfu_WK1.pJM356	AB923518[b]	(46)
	simian foamy virus Macaca mulatta (SFVmmu)	isolate K3T	SFVmmu_K3T	MF280817[b]	(79)
	simian foamy virus Mandrillus leucophaeus (SVFmle)	isolate Mnd205	SFVmle_Mnd205	AY583777[c]	(40)
	simian foamy virus Mandrillus sphinx (SFVmsp)	isolate Mnd301	SFVmsp_Mnd301	AY583775[c]	(40)
	simian foamy virus Papio cynocephalus (SFVpcy)	serotype 10 [SFV type 10; SFVbab]	SFVpcy	AF049083[c]	

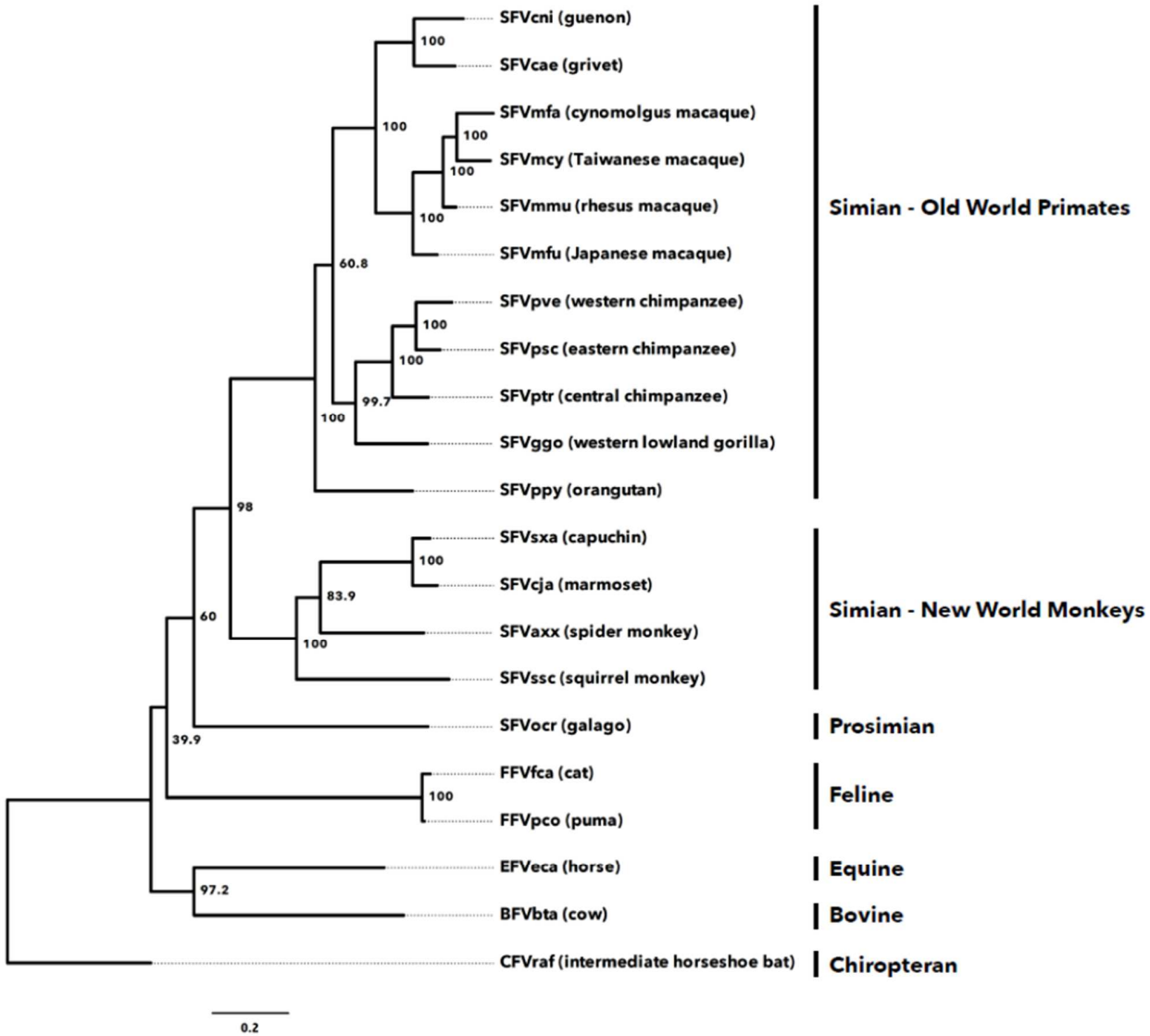
[a]reference provided for published sequences

524 [b]full-length genome

525 [c]partial sequence

526 *Type species

Figure 1. Foamy virus phylogeny reflects long-term virus–host co-speciation. Evolutionary relationships were inferred using maximum likelihood analysis of an alignment comprising the polymerase gene (*pol*) and envelope gene (*env*) nucleotide sequences of 21 foamy viruses from diverse mammalian hosts. Branch tips are labeled with viral species names and the host common names; brackets indicate common names for subfamily/group within the class Mammalia. Nodes are labeled with bootstrap support values (based on 1000 replicates). An alignment (including insertions and deletions) beginning approximately in the middle of the *pol* gene and extending to approximately the middle of the *env* gene was generated using the MUSCLE algorithm as implemented in Geneious 10.1.3. For reference, alignment corresponded to nucleotide position 5,089 - 7,927 of SFVpsc (NCBI accession number KX08159). Alignment of all of the sequences are submitted in the Supplement. Unrooted tree was generated using PhyML with the HKY85 substitution model and the NNI search option. Tree was visualized using FigTree 1.4.2 (note that unrooted tree is shown as rooted for ease of visualization). Topology is similar to those published by others (2, 24, 80). Input taxa and accession numbers were: SFVcni (JQ867466); SFVcae (NC_010820); SFVmfa (LC094267); SFVmcy (NC_010819); SFVmmu (MF280817); SFVmfu (AB923518); SFVpve (NC_001364); SFVpsc (KX08159); SFVptr (JQ867463); SFVggo (HM245790); SFVppy (AJ544579); SFVsxa (KP143760); SFVcja (GU356395); SFVaxx (EU010385); SFVssc (GU356394); SFVocr (KM233624); FFVfca (Y08851); FFVpco (KC292054); EFVeca (AF201902); BFVbta (NC_001831); CFVraf (JQ814855).


SFVcni (guenon)
SFVcae (grivet)
SFVmfa (cynomolgus macaque)
SFVmcy (Taiwanese macaque)
SFVmmu (rhesus macaque)
SFVmfu (Japanese macaque)
SFVpve (western chimpanzee)
SFVpsc (eastern chimpanzee)
SFVptr (central chimpanzee)
SFVggo (western lowland gorilla)
SFVppy (orangutan)
SFVsxa (capuchin)
SFVcja (marmoset)
SFVaxx (spider monkey)
SFVssc (squirrel monkey)
SFVocr (galago)
FFVfca (cat)
FFVpco (puma)
EFVeca (horse)
BFVbta (cow)
CFVraf (intermediate horseshoe bat)
100
100
100
100
100
60.8
100
100
99.7
100
98
83.9
100
60
39.9
100
97.2
0.2
Simian - Old World Primates
Simian - New World Monkeys
Prosimian
Feline
Equine
Bovine
Chiropteran

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