

## Spumaretroviruses: Updated taxonomy and nomenclature

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1 **Spumaretroviruses: Updated taxonomy and nomenclature**

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46 **ABSTRACT**

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

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## 67 1. Introduction

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

75 The earliest reports of foamy virus isolates were of simian origin (NWM, OWM, and apes)  
76 and were originally classified serologically using neutralization assays (5, 6). The first “human”  
77 spumaretrovirus isolate was obtained from cultures of a human nasopharyngeal carcinoma in  
78 1971 and was originally designated “human foamy virus (HFV)” (7, 8), but was later found to be  
79 of chimpanzee origin based upon sequence identity to chimpanzee foamy virus and renamed as  
80 prototype foamy virus (PFV) (6, 9). Cross-species transmissions of simian foamy viruses (SFVs)  
81 to humans have occurred by exposure to fluids or tissues from infected NHPs (10-23). Although  
82 foamy viruses are exogenously transmitted viruses, endogenous foamy virus sequences have  
83 been identified and characterized in genomes of many species, including aye-aye (*Daubentonia*  
84 *madagascariensis*), sloth (*Choloepus hoffmanni*), Cape golden mole (*Chrysochloris asiatica*),  
85 coelacanth (*Latimeria chalumnae*), platyfish (*Xiphophorus maculatus*), and zebrafish (*Danio*  
86 *rerio*) (24-30). In fact, molecular evolution studies have indicated that spumaretroviruses have  
87 co-speciated with their hosts for millions of years (24, 26, 31, 32). Recently, phylogenetic  
88 analyses using amphibian and fish genomes have estimated the date of retrovirus emergence at  
89 >450 million years ago (25) with foamy viruses inferred to be the most ancient retrovirus. A

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

93 The taxonomic history of *Spumaretrovirinae* has been based only on the few early virus  
94 isolates. Although “foamy virus” was discovered in rhesus monkey kidney cultures in 1955 ([49](#)),  
95 simian foamy retroviruses, were not formally classified until the Second Report (1976) of the  
96 International Committee on Taxonomy of Viruses [ICTV], which assigned bovine syncytial virus  
97 (BSV), feline syncytial virus (FSV), hamster syncytial virus (HSV), human foamy virus (HFV),  
98 and simian foamy virus (SFV) to the “genus-less” subfamily *Spumavirinae* ([50](#)). In the Third  
99 (1979) ICTV Report, the still genus-less subfamily Spumavirinae contained only four viruses  
100 (BSV, FSV, HFV, and SFV) ([51](#)). By the Fifth (1991) ICTV Report, all three subfamilies  
101 (*Oncovirinae*, *Lentivirinae*, and *Spumavirinae*) of the *Retroviridae* were abandoned and seven  
102 genera created, including *Spumavirus*, which contained BSV, FSV, HFV, and SFV ([52](#)), with  
103 HFV designated as the type species. This taxonomy was upheld in the Sixth (1995) ICTV  
104 Report, but HFV was referred to as human spumavirus ([53](#)). The Seventh (2000) ICTV Report  
105 for the first time differentiated between species and viruses. *Chimpanzee foamy virus* was  
106 designated the type species and chimpanzee foamy virus (formerly human spumavirus) was  
107 assigned to it (according to ICTV rule, virus name is not italicized). The other species were  
108 *Bovine foamy virus* (containing bovine foamy virus; formerly bovine syncytial virus), *Feline*  
109 *foamy virus* (containing feline foamy virus, formerly feline syncytial virus), *Simian foamy virus*  
110 *1* (containing simian foamy virus type 1), and *Simian foamy virus 3* (containing simian foamy  
111 virus type 3) ([54](#)). In the Eighth (2005) ICTV Report, based upon the distinct replication  
112 pathway of foamy viruses, which contains features homologous to both retroviruses and

113 hepadnaviruses ([55](#)), the subfamily *Spumaretrovirinae* was reinstated for the genus *Spumavirus*.  
114 The species *Simian foamy virus 1* was renamed *Macaque simian foamy virus* and the virus  
115 assigned to this species, simian foamy virus 1, was renamed macaque simian foamy virus.  
116 Similarly, the species *Simian foamy virus 3* was renamed *African green monkey simian foamy*  
117 *virus* and the virus in this species, simian foamy virus 3, was renamed African green monkey  
118 simian foamy virus; the species *Chimpanzee foamy virus* was renamed *Simian foamy virus* and  
119 the virus in this species, chimpanzee foamy virus was renamed simian foamy virus. In addition,  
120 the species *Equine foamy virus* was established for equine foamy virus. No changes were made  
121 to *Bovine foamy virus* and *Feline foamy virus* ([56](#)). The most recent, Ninth (2011) ICTV Report,  
122 lists six spumavirus species for six viruses ([57](#)), and this current classification is shown in Table  
123 1.

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

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## 137 2. Updated 2017 spumaretrovirus classification

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

- 144 • the existing genus *Spumavirus* was replaced by five genera named *Bovispumavirus*,  
145 *Equispumavirus*, *Felispumavirus*, *Prosimiispumavirus*, and *Simiispumavirus* because the  
146 spumaretrovirus phylogeny largely reflects the host phylogeny (Fig. 1), supporting the  
147 hypothesis of spumaretrovirus-host co-evolution ([18](#), [24](#), [26](#), [31](#), [32](#));
- 148 • the established species *Bovine foamy virus*, *Feline foamy virus*, and *Equine foamy virus*  
149 were included in the new genera *Bovispumavirus*, *Felispumavirus*, and *Equispumavirus*,  
150 respectively. Additionally, the species *Puma feline foamy virus* was included in genus  
151 *Felispumavirus*;
- 152 • a new species, *Brown greater galago simian foamy virus*, was included in a new genus  
153 *Prosimiispumavirus*;
- 154 • the previously established species were included in the new genera, and new species were  
155 established for previously unclassified spumaretroviruses. Species names were chosen  
156 based upon the viral host animal names. The previous species *simian foamy virus* was  
157 renamed *Eastern chimpanzee simian foamy virus*. The species *Macaque simian foamy*  
158 *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*

205 schweinfurthii, human isolate HSRV, clone 13 will be designated as SFVpsc\_huHRSV.13, and  
206 feline foamy virus Felis catus strain FUV7 will be designated as FFVfca\_FUV7 (Table 4).  
207 Similarly, in case of inter-species transmission involving nonhuman primates, SFV from western  
208 red colobus monkey (*Philiocolobus badius badius*) isolated from a wild chimpanzee subspecies  
209 *Pan troglodyes verus* (63) will be designated as SFVpba\_pveLeo. Furthermore, for recombinant  
210 viruses (including naturally-occurring and those genetically-engineered), the designation “[RF]”  
211 is included at the end (e.g., SFVmcy\_FV34[RF] (64)).

212

#### 213 **4. Conclusions**

214 The updated and expanded spumaretrovirus taxonomy presented here was initially submitted  
215 to the ICTV on June 18, 2017, and is currently provisionally approved by the ICTV Executive  
216 Committee. The proposal now awaits ratification by vote of the International Union of  
217 Microbiological Societies (IUMS) Virology Division, which will occur in the first quarter of  
218 2018. The new taxonomy format is easily expandable to accommodate new genera and species  
219 for classification of newly discovered foamy viruses. Additionally, we have established a  
220 spumaretrovirus nomenclature that considers host-virus co-speciation and cross-species  
221 transmission, and incorporates host animal species information and strain and/or animal  
222 identification codes in spumaretrovirus names and their abbreviations. This collaborative effort is  
223 aimed toward unifying classification and designations of spumaretroviruses to facilitate easy  
224 comparisons of reported foamy virus isolates.

225

#### 226 **Disclaimer**

227       The views and conclusions that are contained in this document are those of the authors and  
228       should not be interpreted as necessarily representing the official policies, either expressed or  
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238 **References**

- 239 1. **Rethwilm A, Lindemann D.** 2013. Foamy viruses, p 1613-1632. *In* Knipe DM, Howley,  
240 P. (ed), Field's Virology, 6 ed, vol 2. Lippincott, Williams & Wilkins, Philadelphia, PA.
- 241 2. **Rethwilm A, Bodem J.** 2013. Evolution of foamy viruses: the most ancient of all  
242 retroviruses. *Viruses* **5**:2349-2374.
- 243 3. **Falcone V, Leupold J, Clotten J, Urbanyi E, Herchenroder O, Spatz W, Volk B,**  
244 **Böhm N, Toniolo A, Neumann-Haefelin D, Schweizer M.** 1999. Sites of simian foamy  
245 virus persistence in naturally infected African green monkeys: latent provirus is  
246 ubiquitous, whereas viral replication is restricted to the oral mucosa. *Virology* **257**:7-14.
- 247 4. **Murray SM, Picker LJ, Axthelm MK, Hudkins K, Alpers CE, Linial ML.** 2008.  
248 Replication in a superficial epithelial cell niche explains the lack of pathogenicity of  
249 primate foamy virus infections. *J Virol* **82**:5981-5985.
- 250 5. **Hooks JJ, Gibbs CJ, Jr.** 1975. The foamy viruses. *Bacteriol Rev* **39**:169-185.
- 251 6. **Meiering CD, Linial ML.** 2001. Historical perspective of foamy virus epidemiology and  
252 infection. *Clin Microbiol Rev* **14**:165-176.
- 253 7. **Achong BG, Mansell PW, Epstein MA.** 1971. A new human virus in cultures from a  
254 nasopharyngeal carcinoma. *J Pathol* **103**:P18.
- 255 8. **Achong BG, Mansell PW, Epstein MA, Clifford P.** 1971. An unusual virus in cultures  
256 from a human nasopharyngeal carcinoma. *J Natl Cancer Inst* **46**:299-307.
- 257 9. **Herchenroder O, Renne R, Loncar D, Cobb EK, Murthy KK, Schneider J, Mergia**  
258 **A, Luciw PA.** 1994. Isolation, cloning, and sequencing of simian foamy viruses from  
259 chimpanzees (SFVcpz): high homology to human foamy virus (HFV). *Virology* **201**:187-  
260 199.

- 261 10. **Betsem E, Rua R, Tortevoye P, Froment A, Gessain A.** 2011. Frequent and recent  
262 human acquisition of simian foamy viruses through apes' bites in central Africa. *PLoS*  
263 *Pathog* **7**:e1002306.
- 264 11. **Calattini S, Betsem EBA, Froment A, Mauclère P, Tortevoye P, Schmitt C, Njouom**  
265 **R, Saib A, Gessain A.** 2007. Simian foamy virus transmission from apes to humans,  
266 rural Cameroon. *Emerg Infect Dis* **13**:1314-1320.
- 267 12. **Engel GA, Small CT, Soliven K, Feeroz MM, Wang X, Kamrul Hasan M, Oh G,**  
268 **Rabiul Alam SM, Craig KL, Jackson DL, Matsen Iv FA, Linial ML, Jones-Engel L.**  
269 2013. Zoonotic simian foamy virus in Bangladesh reflects diverse patterns of  
270 transmission and co-infection. *Emerg Microbes Infect* **2**:e58.
- 271 13. **Heneine W, Schweizer M, Sandstrom P, Folks T.** 2003. Human infection with foamy  
272 viruses. *Curr Top Microbiol Immunol* **277**:181-196.
- 273 14. **Heneine W, Switzer WM, Sandstrom P, Brown J, Vedapuri S, Schable CA, Khan**  
274 **AS, Lerche NW, Schweizer M, Neumann-Haefelin D, Chapman LE, Folks TM.**  
275 1998. Identification of a human population infected with simian foamy viruses. *Nat Med*  
276 **4**:403-407.
- 277 15. **Mouinga-Ondémé A, Caron M, Nkoghé D, Telfer P, Marx P, Saïb A, Leroy E,**  
278 **Gonzalez J-P, Gessain A, Kazanji M.** 2012. Cross-species transmission of simian  
279 foamy virus to humans in rural Gabon, Central Africa. *J Virol* **86**:1255-1260.
- 280 16. **Schweizer M, Turek R, Hahn H, Schliephake A, Netzer K-O, Eder G, Reinhardt M,**  
281 **Rethwilm A, Neumann-Haefelin D.** 1995. Markers of foamy virus infections in  
282 monkeys, apes, and accidentally infected humans: appropriate testing fails to confirm  
283 suspected foamy virus prevalence in humans. *AIDS Res Hum Retroviruses* **11**:161-170.

- 284 17. **Stenbak CR, Craig KL, Ivanov SB, Wang X, Soliven KC, Jackson DL, Gutierrez**  
285 **GA, Engel G, Jones-Engel L, Linial ML.** 2014. New World simian foamy virus  
286 infections in vivo and in vitro. *J Virol* **88**:982-991.
- 287 18. **Switzer WM, Bhullar V, Shanmugam V, Cong M-E, Parekh B, Lerche NW, Yee JL,**  
288 **Ely JJ, Boneva R, Chapman LE, Folks TM, Heneine W.** 2004. Frequent simian foamy  
289 virus infection in persons occupationally exposed to nonhuman primates. *J Virol*  
290 **78**:2780-2789.
- 291 19. **Switzer WM, Tang S, Ahuka-Mundeke S, Shankar A, Hanson DL, Zheng H,**  
292 **Ayouba A, Wolfe ND, LeBreton M, Djoko CF, Tamoufe U, Esteban A, Heneine W,**  
293 **Peeters M, Wright LL, Muyembe-Tamfum JJ, Wemakoy EO, Mulembakani P, Hoff**  
294 **NA, Rimoin AW.** 2012. Novel simian foamy virus infections from multiple monkey  
295 species in women from the Democratic Republic of Congo. *Retrovirology* **9**:100.
- 296 20. **Wolfe ND, Switzer WM, Carr JK, Bhullar VB, Shanmugam V, Tamoufe U, Prosser**  
297 **AT, Torimiro JN, Wright A, Mpoudi-Ngole E, McCutchan FE, Birx DL, Folks TM,**  
298 **Burke DS, Heneine W.** 2004. Naturally acquired simian retrovirus infections in central  
299 African hunters. *Lancet* **363**:932-937.
- 300 21. **Khan AS.** 2009. Simian foamy virus infection in humans: prevalence and management.  
301 *Expert Rev Anti Infect Ther* **7**:569-580.
- 302 22. **Brooks JI, Rud EW, Pilon RG, Smith JM, Switzer WM, Sandstrom PA.** 2002. Cross-  
303 species retroviral transmission from macaques to human beings. *Lancet* **360**:387-388.
- 304 23. **Callahan ME, Switzer WM, Matthews AL, Roberts BD, Heneine W, Folks TM,**  
305 **Sandstrom PA.** 1999. Persistent zoonotic infection of a human with simian foamy virus  
306 in the absence of an intact orf-2 accessory gene. *J Virol* **73**:9619-9624.

- 307 24. **Katzourakis A, Aiewsakun P, Jia H, Wolfe ND, LeBreton M, Yoder AD, Switzer**  
308 **WM.** 2014. Discovery of prosimian and afrotherian foamy viruses and potential cross  
309 species transmissions amidst stable and ancient mammalian co-evolution. *Retrovirology*  
310 **11:61.**
- 311 25. **Aiewsakun P, Katzourakis A.** 2017. Marine origin of retroviruses in the early  
312 Palaeozoic Era. *Nat Commun* **8:13954.**
- 313 26. **Katzourakis A, Gifford RJ, Tristem M, Gilbert MT, Pybus OG.** 2009.  
314 Macroevolution of complex retroviruses. *Science* **325:1512.**
- 315 27. **Han GZ, Worobey M.** 2012. An endogenous foamy-like viral element in the coelacanth  
316 genome. *PLoS Pathog* **8:e1002790.**
- 317 28. **Han G-Z, Worobey M.** 2012. An endogenous foamy virus in the aye-aye (*Daubentonia*  
318 *madagascariensis*). *J Virol* **86:7696-7698.**
- 319 29. **Han GZ, Worobey M.** 2014. Endogenous viral sequences from the Cape golden mole  
320 (*Chrysochloris asiatica*) reveal the presence of foamy viruses in all major placental  
321 mammal clades. *PLoS One* **9:e97931.**
- 322 30. **Ruboyanes R, Worobey M.** 2016. Foamy-like endogenous retroviruses are extensive  
323 and abundant in teleosts. *Virus Evol* **2:vew032.**
- 324 31. **Ghera BM, Jia H, Aiewsakun P, Katzourakis A, Mendoza P, Bausch DG, Kasper**  
325 **MR, Montgomery JM, Switzer WM.** 2015. Wide distribution and ancient evolutionary  
326 history of simian foamy viruses in New World primates. *Retrovirology* **12:89.**
- 327 32. **Switzer WM, Salemi M, Shanmugam V, Gao F, Cong M-E, Kuiken C, Bhullar V,**  
328 **Beer BE, Vallet D, Gautier-Hion A, Tooze Z, Villinger F, Holmes EC, Heneine W.**  
329 2005. Ancient co-speciation of simian foamy viruses and primates. *Nature* **434:376-380.**



- 330 33. **Ayouba A, Duval L, Liegeois F, Ngin S, Ahuka-Mundeke S, Switzer WM, Delaporte**  
331 **E, Ariey F, Peeters M, Nerrienet E.** 2013. Nonhuman primate retroviruses from  
332 Cambodia: high simian foamy virus prevalence, identification of divergent STLV-1  
333 strains and no evidence of SIV infection. *Infect Genet Evol* **18**:325-334.
- 334 34. **Liu W, Worobey M, Li Y, Keele BF, Bibollet-Ruche F, Guo Y, Goepfert PA,**  
335 **Santiago ML, Ndjango J-B, Neel C, Clifford SL, Sanz C, Kamenya S, Wilson ML,**  
336 **Pusey AE, Gross-Camp N, Boesch C, Smith V, Zamma K, Huffman MA, Mitani JC,**  
337 **Watts DP, Peeters M, Shaw GM, Switzer WM, Sharp PM, Hahn BH.** 2008.  
338 Molecular ecology and natural history of simian foamy virus infection in wild-living  
339 chimpanzees. *PLoS Pathog* **4**:e1000097.
- 340 35. **Wu Z, Ren X, Yang L, Hu Y, Yang J, He G, Zhang J, Dong J, Sun L, Du J, Liu L,**  
341 **Xue Y, Wang J, Yang F, Zhang S, Jin Q.** 2012. Virome analysis for identification of  
342 novel Mammalian viruses in bat species from chinese provinces. *J Virol* **86**:10999-  
343 11012.
- 344 36. **Muniz CP, Troncoso LL, Moreira MA, Soares EA, Pissinatti A, Bonvicino CR,**  
345 **Seuáñez HN, Sharma B, Jia H, Shankar A, Switzer WM, Santos AF, Soares MA.**  
346 2013. Identification and characterization of highly divergent simian foamy viruses in a  
347 wide range of New World primates from Brazil. *PLoS One* **8**:e67568.
- 348 37. **Troncoso LL, Muniz CP, Siqueira JD, Curty G, Schrago CG, Augusto A, Fedullo L,**  
349 **Soares MA, Santos AF.** 2015. Characterization and comparative analysis of a simian  
350 foamy virus complete genome isolated from Brazilian capuchin monkeys. *Virus Res*  
351 **208**:1-6.

- 352 38. **Blasse A, Calvignac-Spencer S, Merkel K, Goffe AS, Boesch C, Mundry R,**  
353 **Leendertz FH.** 2013. Mother-offspring transmission and age-dependent accumulation of  
354 simian foamy virus in wild chimpanzees. *J Virol* **87**:5193-5204.
- 355 39. **Calattini S, Nerrienet E, Maucière P, Georges-Courbot M-C, Saïb A, Gessain A.**  
356 2006. Detection and molecular characterization of foamy viruses in Central African  
357 chimpanzees of the *Pan troglodytes troglodytes* and *Pan troglodytes vellerosus*  
358 subspecies. *J Med Primatol* **35**:59-66.
- 359 40. **Calattini S, Nerrienet E, Maucière P, Georges-Courbot M-C, Saïb A, Gessain A.**  
360 2004. Natural simian foamy virus infection in wild-caught gorillas, mandrills and drills  
361 from Cameroon and Gabon. *J Gen Virol* **85**:3313-3317.
- 362 41. **Goldberg TL, Sintasath DM, Chapman CA, Cameron KM, Karesh WB, Tang S,**  
363 **Wolfe ND, Rwego IB, Ting N, Switzer WM.** 2009. Coinfection of Ugandan red colobus  
364 (*Procolobus [Piliocolobus] rufomitratus tephrosceles*) with novel, divergent delta-, lenti-,  
365 and spumaretroviruses. *J Virol* **83**:11318-11329.
- 366 42. **Huang F, Yu W, He Z.** 2013. Foamy virus in the tree shrew *Tupaia belangeri* is highly  
367 related to simian foamy virus in *Macaca mulatta*. *AIDS Res Hum Retroviruses* **29**:1177-  
368 1178.
- 369 43. **Jones-Engel L, Steinkraus KA, Murray SM, Engel GA, Grant R, Aggimarangsee N,**  
370 **Lee BPY-H, May C, Schillaci MA, Songird C, Sutthipat T, Vojtech L, Zhao J,**  
371 **Linial ML.** 2007. Sensitive assays for simian foamy viruses reveal a high prevalence of  
372 infection in commensal, free-ranging Asian monkeys. *J Virol* **81**:7330-7337.
- 373 44. **Mouinga-Ondeme A, Betsem E, Caron M, Makuwa M, Salle B, Renault N, Saib A,**  
374 **Telfer P, Marx P, Gessain A, Kazanji M.** 2010. Two distinct variants of simian foamy

- 375 virus in naturally infected mandrills (*Mandrillus sphinx*) and cross-species transmission  
376 to humans. *Retrovirology* **7**:105.
- 377 45. **Richard L, Rua R, Betsem E, Mouinga-Ondeme A, Kazanji M, Leroy E, Njouom R,**  
378 **Buseyne F, Afonso PV, Gessain A.** 2015. Cocirculation of Two env Molecular Variants,  
379 of Possible Recombinant Origin, in Gorilla and Chimpanzee Simian Foamy Virus Strains  
380 from Central Africa. *J Virol* **89**:12480-12491.
- 381 46. **Yoshikawa R, Nakagawa S, Okamoto M, Miyazawa T.** 2014. Construction of an  
382 infectious clone of simian foamy virus of Japanese macaque (SFVjm) and phylogenetic  
383 analyses of SFVjm isolates. *Gene* **548**:149-154.
- 384 47. **Kehl T, Bleiholder A, Roßmann F, Rupp S, Lei J, Lee J, Boyce W, Vickers W,**  
385 **Crooks K, VandeWoude S, Löchelt M.** 2013. Complete genome sequences of two  
386 novel *Puma concolor* foamy viruses from California. *Genome Announc* **1**:e0020112.
- 387 48. **Hechler T, Materniak M, Kehl T, Kuzmak J, Löchelt M.** 2012. Complete genome  
388 sequences of two novel European clade bovine foamy viruses from Germany and Poland.  
389 *J Virol* **86**:10905-10906.
- 390 49. **Rustigian R, Johnston P, Reihart H.** 1955. Infection of monkey kidney tissue cultures  
391 with virus-like agents. *Proc Soc Exp Biol Med* **88**:8-16.
- 392 50. **Fenner F.** 1976. Classification and nomenclature of viruses. Second report of the  
393 International Committee on Taxonomy of Viruses. *Intervirology* **7**:1-115.
- 394 51. **Matthews REF.** 1979. Classification and nomenclature of viruses. Third Report of the  
395 International Committee on Taxonomy of Viruses. *Intervirology* **12**:131-296.
- 396 52. **Coffin JM, Essex M, Gallo R, Graf TM, Hinuma Y, Hunter E, Jaenisch R, Nusse R,**  
397 **Oroszlan S, Svoboda J, Teich N, Toyoshima K, Varmus H.** 1991. Family

398 *Retroviridae*, p 193-204. In Francki RIB, Fauquet, C.M., Knudson, D.L., Brown, F. (ed),  
399 Classification and nomenclature of viruses—Fifth Report of the International Committee  
400 on Taxonomy of Viruses Archives of Virology Supplement, vol 2. Springer-Verlag,  
401 Vienna, Austria.

402 53. **Coffin JM, Essex M, Gallo R, Graf TM, Hinuma Y, Hunter E, Jaenisch R, Nusse R,**  
403 **Oroszlan S, Svoboda J, Teich N, Toyoshima K, Varmus H.** 1995. Family  
404 *Retroviridae*, p 193-204. In Murphy FA, Fauquet, C.M. Bishop, D.H.L., Ghabrial, S.A.,  
405 Jarvis, A.W., Matelli, G.P., Mayo, M.A., Summers, M.D. (ed), Virus Taxonomy - Sixth  
406 Report of the International Committee of Viruses, vol 10. Springer-Verlag, Vienna,  
407 Austria.

408 54. **Hunter E, Casey J, Hahn B, Hayami M, Korber B, Kurth R, Neil J, Rethwilm A,**  
409 **Sonigo P, Stoye J.** 2000. Family *Retroviridae*, p 369-387. In van Regenmortel MHV,  
410 Fauquet, C.M., Bishop, D.H.L, Carstens, E.B., Estes, M.K., Lemon, S.M., Maniloff, J.,  
411 Mayo, M.A., McGeoch, D.J., Pringle, C.R., Wickner, R.B. (ed), Virus taxonomy—  
412 Seventh Report of the International Committee on Taxonomy of Viruses. Academic  
413 Press, San Diego, U.S.A.

414 55. **Linial ML.** 1999. Foamy viruses are unconventional retroviruses. J Virol **73**:1747-1755.

415 56. **Linial ML, Fan H, Hahn B, Lwer R, Neil J, Quackenbush S, Rethwilm A, Sonigo P,**  
416 **Stoye J, Tristem M.** 2005. Family *Retroviridae*, p 421-440. In Fauquet CM, Mayo,  
417 M.A., Maniloff, J., Desselberger, U., Ball, L.A. (ed), Virus taxonomy—Eighth Report of  
418 the International Committee on Taxonomy of Viruses. Elsevier/Academic Press, San  
419 Diego, U.S.A.

- 420 57. **Stoye JP, Blomberg J, Coffin JM, Fan H, Hahn BH, Neil J, Quackenbush S,**  
421 **Rethwilm A, Tristem M.** 2012. Family *Retroviridae*, p 477-494. In King AMQ, Adams,  
422 M.J., Carstens, E.B., Lefkowitz, E.J. (ed), Virus taxonomy—Ninth Report of the  
423 International Committee on Taxonomy of Viruses. Elsevier/Academic Press, London,  
424 U.K.
- 425 58. **Muniz CP, Jia H, Shankar A, Troncoso LL, Augusto AM, Farias E, Pissinatti A,**  
426 **Fedullo LP, Santos AF, Soares MA, Switzer WM.** 2015. An expanded search for  
427 simian foamy viruses (SFV) in Brazilian New World primates identifies novel SFV  
428 lineages and host age-related infections. *Retrovirology* **12**:94.
- 429 59. **Materniak M, Kubiś P, Rola-Luszczka M, Khan AS, Buseyne F, Lindemann D,**  
430 **Löchelt M, Kuźmak J.** 2015. Tenth International Foamy Virus Conference 2014--  
431 achievements and perspectives. *Viruses* **7**:1651-1666.
- 432 60. **Buseyne F, Gessain A, Soares MA, Santos AF, Materniak-Kornas M, Lesage P,**  
433 **Zamborlini A, Löchelt M, Qiao W, Lindemann D, Wöhrl BM, Stoye JP, Taylor IA,**  
434 **Khan AS.** 2016. Eleventh International Foamy Virus Conference-Meeting Report.  
435 *Viruses* **8**:318.
- 436 61. **Sakai K, Ami Y, Suzaki Y, Matano T.** 2016. First complete genome sequence of a  
437 simian foamy virus isolate from a cynomolgus macaque. *Genome Announc* **4**.
- 438 62. **Simmonds P, Adams MJ, Benko M, Breitbart M, Brister JR, Carstens EB, Davison**  
439 **AJ, Delwart E, Gorbalenya AE, Harrach B, Hull R, King AM, Koonin EV,**  
440 **Krupovic M, Kuhn JH, Lefkowitz EJ, Nibert ML, Orton R, Roossinck MJ,**  
441 **Sabanadzovic S, Sullivan MB, Suttle CA, Tesh RB, van der Vlugt RA, Varsani A,**

- 442 **Zerbini FM.** 2017. Consensus statement: Virus taxonomy in the age of metagenomics.  
443 Nat Rev Microbiol **15**:161-168.
- 444 63. **Leendertz FH, Zirkel F, Couacy-Hymann E, Ellerbrok H, Morozov VA, Pauli G,**  
445 **Hedemann C, Formenty P, Jensen SA, Boesch C, Junglen S.** 2008. Interspecies  
446 transmission of simian foamy virus in a natural predator-prey system. J Virol **82**:7741-  
447 7744.
- 448 64. **Galvin TA, Ahmed IA, Shahabuddin M, Bryan T, Khan AS.** 2013. Identification of  
449 recombination in the envelope gene of simian foamy virus serotype 2 isolated from  
450 Macaca cyclopis. J Virol **87**:8792-8797.
- 451 65. **Renshaw RW, Casey JW.** 1994. Transcriptional mapping of the 3' end of the bovine  
452 syncytial virus genome. J Virol **68**:1021-1028.
- 453 66. **Bodem J, Lochelt M, Winkler I, Flower RP, Delius H, Flugel RM.** 1996.  
454 Characterization of the spliced pol transcript of feline foamy virus: the splice acceptor  
455 site of the pol transcript is located in gag of foamy viruses. J Virol **70**:9024-9027.
- 456 67. **Winkler I, Bodem J, Haas L, Zemba M, Delius H, Flower R, Flügel RM, Löchelt M.**  
457 1997. Characterization of the genome of feline foamy virus and its proteins shows  
458 distinct features different from those of primate spumaviruses. J Virol **71**:6727-6741.
- 459 68. **Helps CR, Harbour DA.** 1997. Comparison of the complete sequence of feline  
460 spumavirus with those of the primate spumaviruses reveals a shorter gag gene. J Gen  
461 Virol **78 ( Pt 10)**:2549-2564.
- 462 69. **Tobaly-Tapiero J, Bittoun P, Neves M, Guillemin M-C, Lecellier C-H, Puvion-**  
463 **Dutilleul F, Gicquel B, Zientara S, Giron M-L, de Thé H, Saïb A.** 2000. Isolation and  
464 characterization of an equine foamy virus. J Virol **74**:4064-4073.

- 465 70. **Thumer L, Rethwilm A, Holmes EC, Bodem J.** 2007. The complete nucleotide  
466 sequence of a New World simian foamy virus. *Virology* **369**:191-197.
- 467 71. **Pacheco B, Finzi A, McGee-Estrada K, Sodroski J.** 2010. Species-specific inhibition  
468 of foamy viruses from South American monkeys by New World Monkey TRIM5 $\alpha$   
469 proteins. *J Virol* **84**:4095-4099.
- 470 72. **Wagner TC, Bodem J.** 2016. Sequence errors in foamy virus sequences in the GenBank  
471 database: resequencing of the prototypic foamy virus proviral plasmids. *Arch Virol*  
472 doi:10.1007/s00705-016-3206-z.
- 473 73. **Rua R, Betsem E, Calattini S, Saïb A, Gessain A.** 2012. Genetic characterization of  
474 simian foamy viruses infecting humans. *J Virol* **86**:13350-13359.
- 475 74. **Schulze A, Lemey P, Schubert J, McClure MO, Rethwilm A, Bodem J.** 2011.  
476 Complete nucleotide sequence and evolutionary analysis of a gorilla foamy virus. *J Gen*  
477 *Virol* **92**:582-586.
- 478 75. **Verschoor EJ, Langenhuijzen S, van den Engel S, Niphuis H, Warren KS, Heeney**  
479 **JL.** 2003. Structural and evolutionary analysis of an orangutan foamy virus. *J Virol*  
480 **77**:8584-8587.
- 481 76. **Renne R, Friedl E, Schweizer M, Fleps U, Turek R, Neumann-Haefelin D.** 1992.  
482 Genomic organization and expression of simian foamy virus type 3 (SFV-3). *Virology*  
483 **186**:597-608.
- 484 77. **Nandakumar S, Bae EH, Khan AS.** 2017. Complete genome sequence of the African  
485 green monkey simian foamy virus serotype 3 strain FV2014.
- 486 78. **Kupiec J-J, Kay A, Hayat M, Ravier R, Périés J, Galibert F.** 1991. Sequence analysis  
487 of the simian foamy virus type 1 genome. *Gene* **101**:185-194.

- 488 79. **Nandakumar S, Bae EH, Khan AS.** 2017. Complete genome sequence of a naturally  
489 occurring simian foamy virus isolate from rhesus macaque (SFVmmu\_K3T). *Genome*  
490 *Announc* **5**.
- 491 80. **Switzer WM, Salemi M, Shanmugam V, Gao F, Cong ME, Kuiken C, Bhullar V,**  
492 **Beer BE, Vallet D, Gautier-Hion A, Tooze Z, Villinger F, Holmes EC, Heneine W.**  
493 2005. Ancient co-speciation of simian foamy viruses and primates. *Nature* **434**:376-380.
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499 **Table 1.** Current spumaretrovirus taxonomy according to ICTV<sup>a</sup>

<b>Family</b>	<b>Subfamily</b>	<b>Genus</b>	<b>Species</b>	<b>Virus name</b>
<i>Retroviridae</i>	<i>Spumaretrovirinae</i>	<i>Spumavirus</i>	<i>African green monkey simian foamy virus</i>	African green monkey simian foamy virus (SFV <sub>agm</sub> ) <sup>b</sup>
			<i>Bovine foamy virus</i>	bovine foamy virus (BFV)
			<i>Equine foamy virus</i>	equine foamy virus (EFV)
			<i>Feline foamy virus</i>	feline foamy virus (FFV)
			<i>Macaque simian foamy virus</i>	macaque simian foamy virus (SFV <sub>mac</sub> ) <sup>c</sup>
			<i>Simian foamy virus</i> <sup>*</sup>	simian foamy virus, human isolate (SFV <sub>cpz(hu)</sub> ) <sup>d</sup>

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501 <sup>a</sup>Reference [\(57\)](#); <sup>b</sup>Synonym: simian foamy virus 3 (SFV-3); <sup>c</sup>Synonym: simian foamy virus 1 (SFV-1); <sup>d</sup>Synonyms: chimpanzee foamy virus (CFV), human  
 502 foamy virus (HFV) and prototype foamy virus (PFV); <sup>\*</sup>Type species.

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508 **Table 2.** Updated spumaretrovirus taxonomy as proposed in June 2017<sup>a</sup>.

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

		<i>Spider monkey simian foamy virus</i>	simian foamy virus <i>Ateles</i> species (SFV <sub>axx</sub> )
		<i>White-tufted-ear marmoset simian foamy virus</i>	simian foamy virus <i>Callithrix jacchus</i> (SFV <sub>cja</sub> )
		<i>Squirrel monkey simian foamy virus</i>	simian foamy virus <i>Saimiri sciureus</i> (SFV <sub>ssc</sub> )
		<i>Yellow-breasted capuchin simian foamy virus</i>	simian foamy virus <i>Sapajus xanthosternos</i> (SFV <sub>sxa</sub> )
	<i>Prosimiispumavirus</i>	<i>Brown greater galago prosimian foamy virus</i> *	simian foamy virus <i>Otolemur crassicaudatus</i> (SFV <sub>ocr</sub> )
	<i>Bovispumavirus</i>	<i>Bovine foamy virus</i> *	bovine foamy virus <i>Bos taurus</i> (BFV <sub>bta</sub> )
	<i>Felispumavirus</i>	<i>Feline foamy virus</i> *	feline foamy virus <i>Felis catus</i> (FFV <sub>fca</sub> )
		<i>Puma feline foamy virus</i>	feline foamy virus <i>Puma concolor</i> (FFV <sub>pco</sub> )
	<i>Equispumavirus</i>	<i>Equine foamy virus</i> *	equine foamy virus <i>Equus caballus</i> (EFV <sub>eca</sub> )

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510 <sup>a</sup>Based upon available complete virus genome sequences; <sup>b</sup>The former species *Simian spumavirus*; <sup>c</sup>The former species *Macaque simian foamy virus*; <sup>d</sup>The  
511 former species *African green monkey simian foamy virus*; \*Type species.

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515 **Table 3.** Projected updates for spumaretrovirus taxonomy<sup>a</sup>.

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

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

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

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

Chiropteran	chiropteran foamy virus Rhinolophus affinis (CFVraf)	isolate 1[RaFV-1]	CFVraf_1	JQ814855 <sup>c</sup>	<a href="#">(35)</a>
Prosimian	simian foamy virus Otolemur crassicaudatus (SFVocr)	type 5, strain 1557 [SFV type 5; SFVgal]	SFVocr_1557*	KM233624 <sup>b</sup>	<a href="#">(24)</a>
Simian—New World monkeys	simian foamy virus Ateles species (SFVaxx)	serotype 8, strain S-140, Hooks40 [SFV type 8; SFVspm]	SFVaxx_Hooks40	EU010385 <sup>b</sup>	<a href="#">(70)</a>
	simian foamy virus Callithrix jacchus (SFVcja)	isolate FXV[SFVmar]	SFVcja_FXV	GU356395 <sup>b</sup>	<a href="#">(71)</a>
	simian foamy virus Saimiri sciureus (SFVssc)	serotype 4, strain 1224 (SFV type 4; SFVsqu]	SFVssc_1224	GU356394 <sup>b</sup>	<a href="#">(71)</a>
	simian foamy virus Sapajus xanthosternos (SFVsx)	isolate Z17	SFVsx_Z17	KP143760 <sup>b</sup>	<a href="#">(37)</a>

Simian—apes	simian foamy virus Pan troglodytes schweinfurthii (SFVpsc)	human isolate HSRV clone 13 [PFV; CFV; HSRV; SFVcpz(hu); HFV]	SFVpsc_huHSRV.13*	KX08159 <sup>b</sup>	(72)
	simian foamy virus Pan troglodytes troglodytes (SFVptr)	human isolate BAD327	SFVptr_huBAD327	JQ867463 <sup>b</sup>	(73)
		human isolate AG15	SFVptr_huAG15	JQ867462 <sup>b</sup>	(73)
	simian foamy virus Pan troglodytes verus (SFVpve)	[SFVcpz]	SFVpve	NC_001364 <sup>b</sup>	(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 <sup>b</sup>	(74)
		human isolate BAK74	SFVggo_huBAK74	JQ867464 <sup>b</sup>	(73)
		human isolate BAD468	SFVggo_huBAD468	JQ867465 <sup>b</sup>	(73)

	simian foamy virus Pongo pygmaeus pygmaeus (SFVppy)	serotype 11, strain bella [SFV type 11; SFVora]	SFVppy_bella	AJ544579 <sup>b</sup>	(75)
Simian—Old World monkeys	simian foamy virus Chlorocebus aethiops (SFVcae)	strain LK3 [African green monkey SFV; SFVagm; SFVagm-3]	SFVcae_LK3	M74895 <sup>b</sup>	(76)
		Serotype 3, strain FV2014 [SFV 3; SFV type 3; SFVagm]	SFVcae_FV2014	MF582544 <sup>b</sup>	(77)
	simian foamy virus Cercopithecus nictitans (SFVcni)	human isolate AG16	SFVcni_huAG16	JQ867466 <sup>b</sup>	(73)
	simian foamy virus Macaca cyclopis (SFVmcy)	serotype 1, strain FV21 [SFV-1; macaque SFV; SFV type 1; SFVmac; SFVmcy-1]	SFMmcy_FV21	NC_010819 <sup>b</sup>	(78)
		serotype 2, strain FV34 [SFV type 2; SFVmac; SFVmcy-2]	SFMmcy_FV34[RF] <sup>c</sup>	KF026286.1 <sup>b</sup>	(64)



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

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523 <sup>a</sup>reference provided for published sequences

524 <sup>b</sup>full-length genome

525 <sup>c</sup>partial sequence

526 \*Type species

527 **Figure 1. Foamy virus phylogeny reflects long-term virus–host co-speciation.** Evolutionary relationships were inferred using  
528 maximum likelihood analysis of an alignment comprising the polymerase gene (*pol*) and envelope gene (*env*) nucleotide sequences of  
529 21 foamy viruses from diverse mammalian hosts. Branch tips are labeled with viral species names and the host common names;  
530 brackets indicate common names for subfamily/group within the class Mammalia. Nodes are labeled with bootstrap support values  
531 (based on 1000 replicates). An alignment (including insertions and deletions) beginning approximately in the middle of the *pol* gene  
532 and extending to approximately the middle of the *env* gene was generated using the MUSCLE algorithm as implemented in Geneious  
533 10.1.3. For reference, alignment corresponded to nucleotide position 5,089 - 7,927 of SFVpsc (NCBI accession number KX08159).  
534 Alignment of all of the sequences are submitted in the Supplement. Unrooted tree was generated using PhyML with the HKY85  
535 substitution model and the NNI search option. Tree was visualized using FigTree 1.4.2 (note that unrooted tree is shown as rooted for  
536 ease of visualization). Topology is similar to those published by others ([2](#), [24](#), [80](#)). Input taxa and accession numbers were: SFVcni  
537 (JQ867466); SFVcae (NC\_010820); SFVmfa (LC094267); SFVmcy (NC\_010819); SFVmmu (MF280817); SFVmfu (AB923518);  
538 SFVpve (NC\_001364); SFVpsc (KX08159); SFVptr (JQ867463); SFVggo (HM245790); SFVppy (AJ544579); SFVsxax (KP143760);  
539 SFVcja (GU356395); SFVaxx (EU010385); SFVssc (GU356394); SFVocr (KM233624); FFVfca (Y08851); FFVpco (KC292054);  
540 EFVeca (AF201902); BFVbta (NC\_001831); CFVraf (JQ814855).

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