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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 nonprimate 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 (Rethwilm and Lindemann, 2013; Rethwilm and Bodem, 2013). 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 (Falcone et al., 1999; Murray et al., 2008).

The earliest reports of foamy virus isolates were of simian origin (NWM, OWM, and apes) and were originally classified serologically using neutralization assays (Hooks and Gibbs, 1975; Meiering and Linial, 2001). The first "human" spumaretrovirus isolate was obtained from cultures of a human nasopharyngeal carcinoma in 1971 and was originally designated "human foamy virus (HFV)" (Achong et al., 1971a, 1971b), but was later found to be of chimpanzee origin based upon sequence identity to chimpanzee foamy virus and renamed as prototype foamy virus (PFV) (Meiering and Linial, 2001; Herchenroder et al., 1994). Cross-species transmissions of simian foamy viruses (SFVs) to humans have occurred by exposure to fluids or tissues from infected NHPs (Betsem et al., 2011; Calattini et al., 2007; Engel et al., 2013; Heneine et al., 2003, 1998; Mouinga-Ondémé et al., 2012; Schweizer

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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[d]	simian foamy virus, human isolate (SFVcpz(hu))[e]

[a] Ref. Stoye et al. (2012).
[b] Synonym: simian foamy virus 3 (SFV-3).
[c] Synonym: simian foamy virus 1 (SFV-1).
[d] Type species.
[e] Synonyms: chimpanzee foamy virus (CFV), human foamy virus (HFV) and prototype foamy virus (PFV).

et al., 1995; Stenbak et al., 2014; Switzer et al., 2004, 2012; Wolfe et al., 2004; Khan, 2009; Brooks et al., 2002; Callahan et al., 1999). 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*) (Katzourakis et al., 2014, 2009; Aiewsakun and Katzourakis, 2017; Han and Worobey, 2012a, 2012b, 2014; Ruboyianes and Worobey, 2016). In fact, molecular evolution studies have indicated that spumaretroviruses have co-speciated with their hosts for millions of years (Katzourakis et al., 2014, 2009; Ghersi et al., 2015; Switzer et al., 2005a). Recently, phylogenetic analyses using amphibian and fish genomes have estimated the date of retrovirus emergence at > 450 million years ago (Aiewsakun and Katzourakis, 2017) 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 (Mouinga-Ondémé et al., 2012; Ghersi et al., 2015; Ayouba et al., 2013; Liu et al., 2008; Wu et al., 2012; Muniz et al., 2013; Troncoso et al., 2015; Blasse et al., 2013; Calattini et al., 2006, 2004; Goldberg et al., 2009; Huang et al., 2013; Jones-Engel et al., 2007; Mouinga-Ondémé et al., 2010; Richard et al., 2015; Yoshikawa et al., 2014; Kehl et al., 2013; Hechler et al., 2012).

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 (Rustigian et al., 1955), 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 (not italicized at the time) (Fenner, 1976). In the Third (1979) ICTV Report, the still genus-less subfamily Spumavirinae contained only four viruses (BSV, FSV, HFV, and SFV) (Matthews, 1979). 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 (Coffin et al., 1991), 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 (Coffin et al., 1995). 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 the ICTV rules, virus names are 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) (Hunter et al., 2000). In the Eighth (2005) ICTV Report, based upon the distinct replication pathway of foamy viruses, which contains features homologous to both retroviruses and hepadnaviruses (Linial, 1999), 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* (Linial et al., 2005). The most recent, Ninth (2011) ICTV Report, lists six spumavirus species for six viruses (Stoye et al., 2012), 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 (Ghersi et al., 2015; Muniz et al., 2013, 2015). 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 (Materniak et al., 2015) and in 2016 in Paris, France (Buseyne et al., 2016). 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 8, 2017, is shown in Table 2. The following changes were proposed based on analyses of sequences of spumaretrovirus genomes available in public databases: