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A 2021 taxonomy update for the family *Smacoviridae*

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Abstract

The family *Smacoviridae* (order *Cremevirales*, class *Arfiviricetes*, phylum *Cressdnaviricota*) is comprised of viruses with small circular single-stranded DNA genomes of ~2.3–3 kb in length that have primarily been identified in fecal sample of various animals. Smacovirus genomes carry two genes in ambisense orientation encoding a capsid protein and a rolling-circle replication initiation protein, respectively. We have revised the taxonomy of the family by assigning 138 new genomic sequences deposited in GenBank to already established taxa as well as 41 new species and six new genera. Furthermore, we have adopted binomial species nomenclature, conforming to the “Genus + freeform epithet” format for all 84 species from 12 genera. The updated *Smacoviridae* taxonomy presented in this article has been ratified by the International Committee on Taxonomy of Viruses (ICTV).

Smacoviruses have small circular single-stranded DNA genomes (2.3–3.0 kb) with genes coding for a rolling-circle replication initiation protein (Rep) and a capsid protein (CP) in an ambisense orientation. To date, all smacoviruses have been identified by metagenomic analysis in diverse animal fecal samples (both feces and rectal swabs) [1–8, 11, 12, 14, 15, 18–22, 24, 25, 27–30, 32, 34, 35, 37, 41]. However, a few have also been identified in domestic animal serum and tracheal swab samples [38, 40] and in insect samples [9, 31]. Smacoviruses appear to have a broad global distribution and have so far been identified in samples collected in Botswana, Brazil, Cameroon, China, the Dominican Republic, Ethiopia, France, Germany, Hungary, New Zealand, Peru, Saint Kitts and Nevis, South Korea, Tanzania, the United Arab Emirates, the United States of America, Viet Nam, and Zambia (Supplementary Table S1). Smacoviruses have

not been cultured, and no definite host has been identified; however, a study by Díez-Villaseñor and Rodríguez-Valera [10] has suggested that gut-associated methanogenic archaea could be the actual hosts based on identification of CRISPR spacers matching regions of smacovirus genomes.

Smacoviruses are classified as members of the order *Cremevirales*, class *Arfiviricetes*, and phylum *Cressdnaviricota* [23]. The Rep proteins of smacoviruses are homologous to those of all other members of the phylum *Cressdnaviricota* and are phylogenetically most closely related to those of members of the order *Mulpavirales* [23], including the family *Nanoviridae*, with which smacovirid Reps share several unique sequence motifs, especially in the superfamily 3 helicase domain [16, 17]. During establishment of the family *Smacoviridae*, six genera (*Bovismacovirus*, *Cosmacovirus*, *Dragsmacovirus*, *Drosmacovirus*, *Huchismacovirus*, and *Porprismacovirus*) were originally created to accommodate the 83 full genome sequences available in public databases in 2017 [39]. Since then, 138 new smacovirus genome sequences have been made available in GenBank. Following the previously established demarcation criteria [39], we first used a Rep phylogeny based on amino acid sequences to determine the genus-level classification of these viral sequences (Fig. 1) and then used a genome-wide 77% pairwise sequence identity threshold to classify these into species (Fig. 2).

Based on the Rep phylogeny, we established six new genera to accommodate some of the new divergent smacoviruses and to reclassify two viruses previously included in

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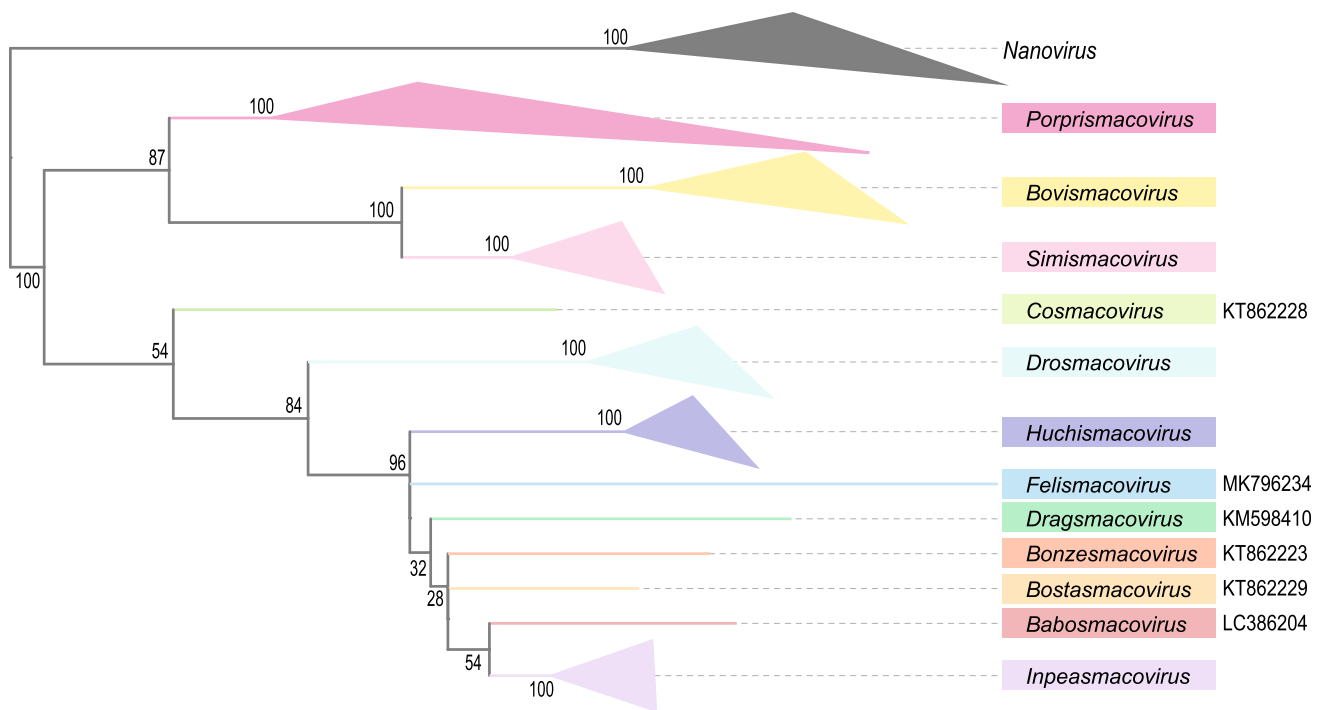


Fig. 1 Maximum-likelihood phylogenetic tree of the Rep amino acid sequences of 220 smacoviruses and a subset of nanoviruses [36], which were used as an outgroup. The Rep sequence alignment was constructed using MAFFT [15] and trimmed with TrimAL [5] using the gappyout option. The final alignment contained 202 amino acid sites and was used to construct a maximum-likelihood phylogenetic

tree in PhyML [13] with the LG+F+I+G4 substitution model. Numbers at the nodes represent bootstrap support values (%). Accession numbers are provided for the single members of the genera *Babosmacovirus*, *Bonzesmacovirus*, *Bostasmacovirus*, *Cosmacovirus*, *Dragsmacovirus*, and *Felismacovirus*

the genus *Huchismacovirus* (bovine faeces associated smacovirus 1 and bovine faeces associated smacovirus 2) into two distinct new genera.

The following names have been adopted for the six new genera

1. ***Babosmacovirus*** (name derived from **baboon** – the host/source of the virus).
2. ***Bonzesmacovirus*** (name derived from **bovine New Zealand** – the host/source of the virus).
3. ***Bostasmacovirus*** (name derived from **Bos taurus** – the host/source of the virus).
4. ***Felismacovirus*** (name derived from **feline** – the host/source of the virus).
5. ***Inpeasmacovirus*** (name derived from **Indian peaflowl** – the host/source of the virus).
6. ***Simismacovirus*** (name derived from **Simian** – the simian host/source of the virus).

We also adopted binomial species nomenclature for all smacovirid species (40 existing species, two that have been reassigned to new genera and 42 new species). We have changed the virus species names for this family to a manageable and easy-to-navigate form using a “Genus + freeform epithet” binomial system [33]. The name changes are summarized in Table 1. A detailed summary of all of the smacoviruses and their taxonomic assignments is provided in Supplementary Table S1, and a breakdown of the sources of classified smacoviruses is provided in Fig. 3.

Since the present taxonomy assessment, 22 genomic sequences of smacoviruses have been deposited in the GenBank database (15 May 2021), and of these, 15 are tagged as circular, and nine of them can be assigned to currently established species.

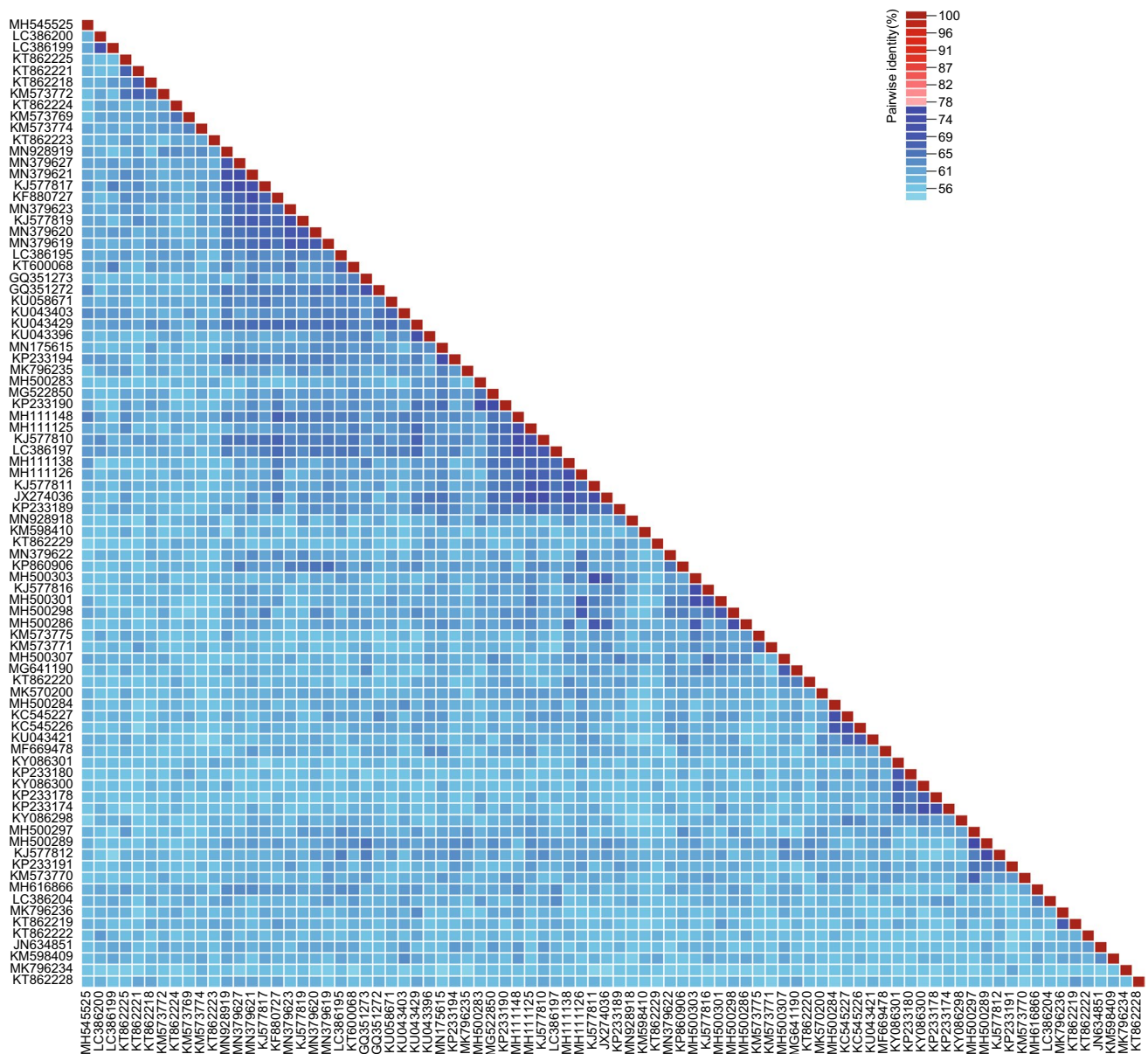


Fig. 2 Pairwise identity matrix of the genome sequences of representative members of each species of smacoviruses ($n = 84$) determined using SDT v1.2 [26], supporting the 77% nucleotide sequence identity between viruses proposed as a species demarcation criterion

Table 1 Taxonomic update of the family *Smacoviridae*, including nomenclatural changes and establishment of new species and genera

Genus	New species name	Previous species name	Virus name	Accession no.	Ref.
<i>Babosmacovirus</i>	<i>Babosmacovirus babas1</i>		Papio cynocephalus associated smacovirus	LC386204	[3]
<i>Bonzesmacovirus</i>	<i>Bonzesmacovirus bovas1</i>	<i>Bovine associated huchismacovirus 1</i>	Bovine faeces associated smacovirus 1	KT862223	[35]
<i>Bostasmacovirus</i>	<i>Bostasmacovirus bovas1</i>	<i>Bovine associated huchismacovirus 2</i>	Bovine faeces associated smacovirus 6	KT862229	[35]
<i>Bovismacovirus</i>	<i>Bovismacovirus bovas1</i>	<i>Bovine associated bovismacovirus 1</i>	Circoviridae bovine stool/BK/KOR/2011	JN634851	[19]
	<i>Bovismacovirus bovas2</i>	<i>Bovine associated bovismacovirus 2</i>	Bovine faeces associated smacovirus 3	KT862222	[35]
	<i>Bovismacovirus draga1</i>	<i>Dragonfly associated bovismacovirus 1</i>	Odonata-associated circular virus-21	KM598409	[9]
<i>Cosmacovirus</i>	<i>Cosmacovirus bovas1</i>	<i>Bovine associated cosmacovirus 1</i>	Bovine faeces associated smacovirus 4	KT862228	[35]
<i>Dragsmacovirus</i>	<i>Dragsmacovirus draga1</i>	<i>Dragonfly associated dragsmacovirus 1</i>	Odonata-associated circular virus-5	KM598410	[9]
<i>Drosmacovirus</i>	<i>Drosmacovirus bovas1</i>	<i>Bovine associated drosmacovirus 1</i>	Bovine faeces associated smacovirus 5	KT862224	[35]
	<i>Drosmacovirus camas1</i>	<i>Camel associated drosmacovirus 1</i>	Dromedary stool-associated circular ssDNA virus	KM573769	[41]
	<i>Drosmacovirus camas2</i>	<i>Camel associated drosmacovirus2</i>	Dromedary stool-associated circular ssDNA virus	KM573774	[41]
<i>Felismacovirus</i>	<i>Felismacovirus lynas1</i>		Lynx rufus smacovirus 1	MK796234	[21]
<i>Huchismacovirus</i>	<i>Huchismacovirus chicas1</i>	<i>Chicken associated huchismacovirus 1</i>	Chicken associated smacovirus	KY086301	[24]
	<i>Huchismacovirus chicas2</i>	<i>Chicken associated huchismacovirus 2</i>	Chicken associated smacovirus	KY086300	[24]
	<i>Huchismacovirus humas1</i>	<i>Human associated huchismacovirus 1</i>	Human smacovirus 1	KP233180	[27]
	<i>Huchismacovirus humas2</i>	<i>Human associated huchismacovirus 2</i>	Human smacovirus 1	KP233174	[27]
	<i>Huchismacovirus humas3</i>	<i>Human associated huchismacovirus 3</i>	Human smacovirus 1	KP233178	[27]
<i>Inpeasmacovirus</i>	<i>Inpeasmacovirus humas1</i>		Human associated porprismacovirus	MH500283	-
	<i>Inpeasmacovirus peafo1</i>		Smacoviridae sp.	MN928918	-
<i>Porprismacovirus</i>	<i>Porprismacovirus alecas1</i>		Alces alces faeces associated smacovirus MP78	MG641190	[20]
	<i>Porprismacovirus avias1</i>		Avian associated porprismacovirus	MN175615	[11]
	<i>Porprismacovirus babas1</i>		Papio cynocephalus associated smacovirus	LC386197	[3]
	<i>Porprismacovirus bovas1</i>	<i>Bovine associated porprismacovirus 1</i>	Bovine faeces associated smacovirus 2	KT862218	[35]
	<i>Porprismacovirus bovas2</i>		Cattle blood-associated circovirus-like virus	MF669478	[40]
	<i>Porprismacovirus camas1</i>	<i>Camel associated porprismacovirus 1</i>	Dromedary stool-associated circular ssDNA virus	KM573772	[41]
	<i>Porprismacovirus camas2</i>	<i>Camel associated porprismacovirus 2</i>	Dromedary stool-associated circular ssDNA virus	KM573770	[41]
	<i>Porprismacovirus camas3</i>	<i>Camel associated porprismacovirus 3</i>	Dromedary stool-associated circular ssDNA virus	KM573771	[41]
	<i>Porprismacovirus camas4</i>	<i>Camel associated porprismacovirus 4</i>	Dromedary stool-associated circular ssDNA virus	KM573775	[41]
	<i>Porprismacovirus capas1</i>		Capybara associated smacovirus 1_cap1_104	MK570200	[12]

Table 1 (continued)

Genus	New species name	Previous species name	Virus name	Accession no.	Ref.
	<i>Porprismacovirus chिकास1</i>		Chicken associated smacovirus	KY086298	[24]
	<i>Porprismacovirus chिकास2</i>		Chicken smacovirus mg4_881	MN379619	-
	<i>Porprismacovirus chिकास3</i>		Chicken smacovirus mg5_1212	MN379623	-
	<i>Porprismacovirus chिकास4</i>		Chicken smacovirus mg4_885	MN379620	-
	<i>Porprismacovirus chिकास5</i>		Chicken smacovirus mg7_67	MN379627	-
	<i>Porprismacovirus chिकास6</i>		Chicken smacovirus mg4_964	MN379621	-
	<i>Porprismacovirus chिकास7</i>		Chicken smacovirus mg5_1081	MN379622	-
	<i>Porprismacovirus chimas1</i>	<i>Chimpanzee associated porprisma-covirus 1</i>	Chimpanzee stool associated circu-lar ssDNA virus	GQ351272	[4]
	<i>Porprismacovirus chimas2</i>	<i>Chimpanzee associated porprisma-covirus 2</i>	Chimpanzee stool associated circu-lar ssDNA virus	GQ351273	[4]
	<i>Porprismacovirus flas1</i>		Fly associated circular virus 4	MH545525	[31]
	<i>Porprismacovirus goas1</i>		Goat associated porprismacovirus	MH500307	-
	<i>Porprismacovirus goras1</i>	<i>Gorilla associated porprismaco-virus 1</i>	Gorilla smacovirus	KP233191	[27]
	<i>Porprismacovirus howas1</i>	<i>Howler monkey associated porpris-macovirus 1</i>	Black howler monkey smacovirus	KP233189	[27]
	<i>Porprismacovirus humas1</i>	<i>Human associated porprismaco-virus 1</i>	Human feces smacovirus 2	KT600068	[28]
	<i>Porprismacovirus humas2</i>	<i>Human associated porprismaco-virus 2</i>	Chimpanzee smacovirus	KP233190	[27]
	<i>Porprismacovirus humas3</i>		Human feces smacovirus 3	MG522850	[2]
	<i>Porprismacovirus humas4</i>		Human associated porprismacovi-rus 3	MH111125	-
	<i>Porprismacovirus lemas1</i>	<i>Lemur associated porprismacovi-rus 1</i>	Lemur smacovirus	KP233194	[27]
	<i>Porprismacovirus leo1</i>		Panthera leo smacovirus 1	MK796236	[21]
	<i>Porprismacovirus lynas2</i>		Lynx rufus smacovirus 2	MK796235	[21]
	<i>Porprismacovirus macas1</i>		Macaca mulatta feces associated virus 7	KU043421	[14]
	<i>Porprismacovirus macas2</i>		Macaca mulatta feces associated virus 4	KU043429	[14]
	<i>Porprismacovirus macas3</i>		Macaca mulatta feces associated virus 3	KU058671	[14]
	<i>Porprismacovirus macas4</i>		Macaca mulatta feces associated virus 2	KU043403	[14]
	<i>Porprismacovirus macas5</i>		Macaque stool associated virus 11	MH616866	[37]
	<i>Porprismacovirus macas6</i>		Macaca mulatta feces associated virus 10	KU043396	[14]
	<i>Porprismacovirus malbas1</i>		Chlorocebus cynosuros associated smacovirus	LC386195	[3]
	<i>Porprismacovirus peafo1</i>		Smacoviridae sp.	MN928919	-
	<i>Porprismacovirus porci1</i>	<i>Porcine associated porprismaco-virus 1</i>	Porcine associated stool circular virus	JX274036	[34]
	<i>Porprismacovirus porci10</i>	<i>Porcine associated porprismaco-virus 10</i>	Porcine faeces associated smaco-virus 1	KT862225	[35]
	<i>Porprismacovirus porci11</i>		Porcine associated porprismaco-virus	MH111138	-
	<i>Porprismacovirus porci12</i>		Porcine associated porprismaco-virus	MH500297	-
	<i>Porprismacovirus porci13</i>		Porcine associated porprismaco-virus	MH500303	-
	<i>Porprismacovirus porci14</i>		Porcine associated porprismaco-virus	MH500301	-

Table 1 (continued)

Genus	New species name	Previous species name	Virus name	Accession no.	Ref.
	<i>Porprismacovirus porci15</i>		Porcine associated porprismacovirus	MH500286	-
	<i>Porprismacovirus porci16</i>		Porcine associated porprismacovirus	MH500298	-
	<i>Porprismacovirus porci17</i>		Porcine associated porprismacovirus	MH500284	-
	<i>Porprismacovirus porci18</i>		Porcine associated porprismacovirus	MH111148	-
	<i>Porprismacovirus porci19</i>		Porcine associated porprismacovirus	MH111126	-
	<i>Porprismacovirus porci2</i>	<i>Porcine associated porprismacovirus 2</i>	Porcine stool-associated circular virus 2	KC545226	[6]
	<i>Porprismacovirus porci20</i>		Porcine associated porprismacovirus	MH500289	-
	<i>Porprismacovirus porci3</i>	<i>Porcine associated porprismacovirus 3</i>	Porcine stool-associated circular virus 3	KC545227	[6]
	<i>Porprismacovirus porci4</i>	<i>Porcine associated porprismacovirus 4</i>	Porcine stool-associated circular virus 1	KJ577810	[7]
	<i>Porprismacovirus porci5</i>	<i>Porcine associated porprismacovirus 5</i>	Porcine stool-associated circular virus 1	KJ577811	[7]
	<i>Porprismacovirus porci6</i>	<i>Porcine associated porprismacovirus 6</i>	Porcine stool-associated circular virus 6	KJ577819	[7]
	<i>Porprismacovirus porci7</i>	<i>Porcine associated porprismacovirus 7</i>	Porcine stool-associated circular virus 7	KJ577812	[7]
	<i>Porprismacovirus porci8</i>	<i>Porcine associated porprismacovirus 8</i>	Porcine stool-associated circular virus 8	KJ577817	[7]
	<i>Porprismacovirus porci9</i>	<i>Porcine associated porprismacovirus 9</i>	Porcine stool-associated circular virus 9	KJ577816	[7]
	<i>Porprismacovirus ratas1</i>	<i>Rat associated porprismacovirus 1</i>	Rat stool-associated circular ssDNA virus	KP860906	[32]
	<i>Porprismacovirus sheas1</i>	<i>Sheep associated porprismacovirus 1</i>	Sheep faeces associated smacovirus 1	KT862220	[35]
	<i>Porprismacovirus sheas2</i>	<i>Sheep associated porprismacovirus 2</i>	Sheep faeces associated smacovirus 2	KT862221	[35]
	<i>Porprismacovirus sheas3</i>	<i>Sheep associated porprismacovirus 3</i>	Sheep faeces associated smacovirus 3	KT862219	[35]
	<i>Porprismacovirus turas1</i>	<i>Turkey associated porprismacovirus 1</i>	Turkey stool associated circular ssDNA virus	KF880727	[30]
<i>Simismacovirus</i>	<i>Simismacovirus malbas1</i>		Chlorocebus cynosuros associated smacovirus	LC386199	[3]
	<i>Simismacovirus malbas2</i>		Chlorocebus cynosuros associated smacovirus	LC386200	[3]

Fig. 3 Genus-based list of sources from which the smacovirus genome sequences were determined

		Babosmacovirus	Bonzesmacovirus	Bostasmacovirus	Bovismacovirus	Cosmacovirus	Dragsmacovirus	Drosmacovirus	Fellismacovirus	Huchismacovirus	Inpeasmacovirus	Poprismacovirus	Simismacovirus	Total
Neognathae	Neognathae											1		1
Artiodactyla	<i>Alces alces</i>											1		1
	<i>Bos taurus</i>		1	1	2	1		1				2		8
	<i>Camelus dromedarius</i>							2				4		6
	<i>Capra hircus</i>											1		1
	<i>Ovis aries</i>											3		3
	<i>Sus scrofa</i>											103		103
Carnivora	<i>Lynx rufus</i>								1			1		2
	<i>Panthera leo</i>											1		1
Diprotodontia	<i>Trichosurus vulpecula</i>											1		1
Diptera	<i>Lucilia retroversa</i>											1		1
	<i>Lucilia sp.</i>											1		1
Galliformes	<i>Gallus gallus</i>									6		13		19
	<i>Meleagris gallopavo</i>											1		1
	<i>Pavo cristatus</i>										1	1		2
Lagomorpha	<i>Lepus europaeus</i>											1		1
Odonata	<i>Erythrodiplax fusca</i>				1									1
	<i>Libellula quadrimaculata</i>						1							1
Primates	<i>Alouatta caraya</i>											1		1
	<i>Chlorocebus cynosuros</i>											2	3	5
	<i>Gorilla gorilla</i>											2		2
	<i>Homo sapiens</i>								22	1		8		31
	<i>Lemur catta</i>											1		1
	<i>Macaca sp.</i>											10		10
	<i>Pan troglodytes</i>											7		7
	<i>Papio cynocephalus</i>	1										3	1	5
Rodentia	<i>Hydrochoerus hydrochaeris</i>											1		1
	<i>Rodentia sp.</i>											3		3
Total		1	1	1	3	1	1	3	1	28	2	174	4	220

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Declarations

Conflict of interest The authors declare no conflicts of interest.

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