


Genomoviridae: a new family of widespread single-stranded DNA viruses

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Received: 2 May 2016 / Accepted: 17 June 2016 / Published online: 24 June 2016
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Abstract Here, we introduce a new family of eukaryote-infecting single-stranded (ss) DNA viruses that was created recently by the International Committee on Taxonomy of Viruses (ICTV). The family, named *Genomoviridae*, contains a single genus, *Gemycircularvirus*, which currently has one recognized virus species, *Sclerotinia gemycircularvirus 1*. *Sclerotinia sclerotiorum* hypovirulence-associated DNA virus 1 (SsHADV-1) is currently the sole representative isolate of the family; however, a great number of SsHADV-1-like ssDNA virus genomes has been sequenced from various environmental, plant- and animal-associated samples, indicating that members of family *Genomoviridae* are widespread and abundant in the environment.

Viruses with single-stranded DNA (ssDNA) genomes infect hosts in all three domains of life and include economically, medically, and environmentally important viral pathogens. Until recently, ssDNA viruses were classified into 10 different taxa—nine families and one genus not assigned to a family [14, 15]. In 2016, the International Committee on Taxonomy of Viruses (ICTV) created two new families for classification of ssDNA viruses, *Pleolipoviridae* and *Genomoviridae* [1]. The family *Pleolipoviridae* includes viruses infecting hyperhalophilic archaea, and it has recently been described elsewhere [25]. Here, we introduce the family *Genomoviridae* and provide a short overview of the properties of *Sclerotinia sclerotiorum* hypovirulence-associated DNA virus 1 (SsHADV-1), the only cultivated member of the new family, and putative SsHADV-1-like viruses.

SsHADV-1 is the first—and thus far the only—ssDNA virus known to infect fungi (all other fungal viruses have RNA genomes) [10, 33]. SsHADV-1 was isolated from a plant-pathogenic fungus, *Sclerotinia sclerotiorum* [34]. Another unique property of SsHADV-1 that has not been described for other fungal viruses is its ability to establish infection when applied extracellularly in the form of purified viral particles [35]. Virions can infect the hyphae of virus-free *S. sclerotiorum* directly when applied to hyphae or sprayed on leaves of *Arabidopsis thaliana* and *Brassica napus* infected with *S. sclerotiorum*. When applied to *S. sclerotiorum*-infected leaves, the virus can suppress the development of *S. sclerotiorum*-induced lesions. SsHADV-1 has a narrow host range and, in addition to *S. sclerotiorum*, can infect the related species *S. minor* and *S. nivalis*, but not other relatively closely related fungi, such as *Botrytis cinerea* [35]. Furthermore, SsHADV-1 has been identified in New Zealand and the USA in environmental samples and insects; however, this

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is not surprising given the near global distribution of *S. sclerotiorum* [6, 11].

SsHADV-1 virions are non-enveloped, isometric, 20–22 nm in diameter, and constructed from one capsid protein (CP) [34]. The genome is a circular ssDNA molecule of 2,166 nucleotides and contains two genes – for CP and replication initiation protein (Rep) (Fig. 1). The prediction of the *cp* gene has been validated by N-terminal sequencing of the CP purified from the virions. The large intergenic region contains a potential stem-loop structure with a nonanucleotide (TAATATTAT) motif at its apex, which is likely to be important for rolling-circle replication. The CP of SsHADV-1 is not recognizably similar to the corresponding proteins from viruses in other taxa.

Although SsHADV-1 remains the only isolated member of the group, genomes of more than 100 SsHADV-1-like putative viruses have been reported (see Table 1). These genomes have been sequenced from different environmental samples, and many were identified associated with plant material as well as various animal-associated samples, including cerebrospinal fluid and blood of humans (Table 1 and references therein). Even though the hosts of these putative viruses remain unknown, their diversity suggests that SsHADV-1-like viruses are abundant and widespread in the environment.

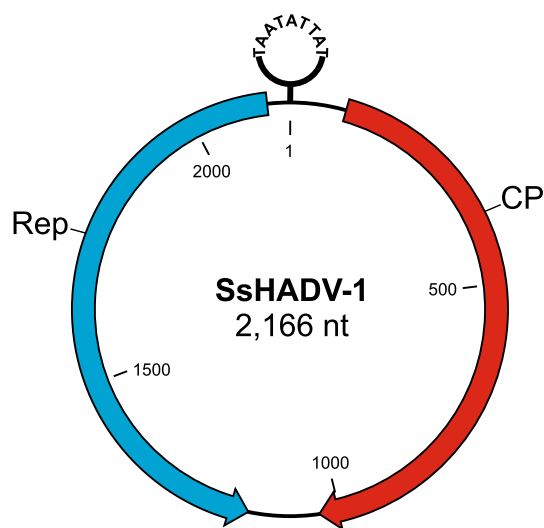


Fig. 1 Genome map of SsHADV-1. Genes encoding the replication-initiation protein (Rep) and capsid protein (CP) are shown with blue and red arrows, respectively. The position of the nonanucleotide (TAATATTAT) at the apex of a potential stem-loop structure is also indicated³

All putative SsHADV-1-like viruses encode homologous Rep and CP, and in phylogenetic analyses form monophyletic clades with SsHADV-1 (Figures 2 and 3). Their genomes are of similar size, in the range of 2,089–2,290 nucleotides. Structural and genomic features of SsHADV-1 differ considerably from those of all other currently classified viruses. The Rep of SsHADV-1 is most closely related to the corresponding proteins of members of the family *Geminiviridae*. It shares with geminiviral proteins two conserved domains, namely geminivirus Rep catalytic domain (Gemini_AL1; PF00799) and geminivirus Rep protein central domain (Gemini_AL1_M; PF08283), with conserved motifs for rolling-circle replication. Notably, similar to some geminiviruses [31], certain SsHADV-1-like viruses also contain introns within their Rep-encoding genes [6, 7, 12, 13, 18, 19, 26–28, 30]. However, Rep-based phylogenetic analysis shows that SsHADV-1 and other related putative viruses form a well-supported, monophyletic clade, which branches as a sister group to geminiviruses (Fig. 2). Unlike the Rep, the CP of SsHADV-1 (and related viruses) does not display any recognizable sequence similarity to proteins of geminiviruses or any other group of known viruses. Furthermore, all geminiviruses possess distinctive geminate virions constructed from two incomplete $T = 1$ icosahedra [2, 36], whereas the virion of SsHADV-1 is isometric [34]. Finally, the number of genes and size of the genome differ considerably between SsHADV-1-like viruses and geminiviruses. In particular, all putative SsHADV-1-like viruses lack the movement protein, which is essential for the plant geminiviruses.

In recognition of the unique features described above, SsHADV-1 has been classified into the species *Sclerotinia gemycircularvirus 1* within the new genus *Gemycircularvirus* (Gemini-like mycro-infecting circular virus) [26] within the new family *Genomoviridae* (sigl: Ge- for geminivirus-like, nomo- for no movement protein).

Although *Genomoviridae* currently includes only a single representative, new members, possibly including uncultivated viruses, are expected to be added to the family in the near future. Based on the available genetic data and phylogenetic analyses (Figures 2 and 3), it is already clear that many new genera will have to be introduced to adequately reflect the diversity of SsHADV-1-like viruses.

Table 1 Genome sequences of putative SsHADV-1-like viruses

GenBank accession no.	Virus/putative virus name	Acronym	Country	Isolation source	Common name	Sample type	Reference
GQ365709	<i>Sclerotinia sclerotiorum</i> hypovirulence associated DNA virus 1	SsHADV-1	China	<i>Sclerotinia sclerotiorum</i>	White mold	Mycelial samples	[34]
KF268025	<i>Sclerotinia sclerotiorum</i> hypovirulence associated DNA virus 1	SsHADV-1	New Zealand	River Sediments	-	River Sediments	[11]
KF268026	<i>Sclerotinia sclerotiorum</i> hypovirulence associated DNA virus 1	SsHADV-1	New Zealand	River Sediments	-	River Sediments	[11]
KF268027	<i>Sclerotinia sclerotiorum</i> hypovirulence associated DNA virus 1	SsHADV-1	New Zealand	River Sediments	-	River Sediments	[11]
KF268028	<i>Sclerotinia sclerotiorum</i> hypovirulence associated DNA virus 1	SsHADV-1	New Zealand	River Sediments	-	River Sediments	[11]
KM598382	<i>Sclerotinia sclerotiorum</i> hypovirulence associated DNA virus 1	SsHADV-1	USA	<i>Ischnura ramburii</i>	Damselfly	Abdomen	[6]
KM598383	<i>Sclerotinia sclerotiorum</i> hypovirulence associated DNA virus 1	SsHADV-1	USA	<i>Erythemis simplicicollis</i>	Dragonfly	Abdomen	[6]
KM598384	<i>Sclerotinia sclerotiorum</i> hypovirulence associated DNA virus 1	SsHADV-1	USA	<i>Pantala hymenaea</i>	Dragonfly	Abdomen	[6]
HQ335086	Mosquito VEM virus SDBVL G	MVemV	USA	<i>Culex erythrothorax</i>	Mosquito	Mosquito samples	[22]
JN704610	Meles meles fecal virus	MmFV	Netherlands	<i>Meles meles</i>	European badger	Rectal swab	[30]
JQ412057	Cassava associated circular DNA virus	CasCV	Ghana	<i>Manihot esculenta</i>	Cassava	Leaf	[5]
JX185428	Dragonfly-associated circular virus 3	DfasCV-3	Tonga	<i>Pantala flavescens</i>	Dragonfly	Abdomen	[26]
JX185429	Dragonfly-associated circular virus 2	DfasCV-2	USA	<i>Erythemis simplicicollis</i>	Dragonfly	Abdomen	[26]
JX185430	Dragonfly-associated circular virus 1	DfasCV-1	USA	<i>Miathyria marcella</i>	Dragonfly	Abdomen	[26]
KF371630	Faecal-associated gemycircularvirus-12	FaGmV-12	New Zealand	<i>Struthio camelus</i>	Ostrich	Faeces	[27]
KF371631	Faecal-associated gemycircularvirus-11	FaGmV-11	New Zealand	<i>Oryctolagus cuniculus</i>	Rabbit	Faeces	[27]
KF371632	Faecal-associated gemycircularvirus-10	FaGmV-10	New Zealand	<i>Sturnus vulgaris</i>	European starling	Faeces	[27]
KF371633	Faecal-associated gemycircularvirus-9	FaGmV-9	New Zealand	<i>Turdus merula</i>	Blackbird	Faeces	[27]
KF371634	Faecal-associated gemycircularvirus-8	FaGmV-8	New Zealand	<i>Petroica traversi</i>	Chatham Island black robin	Faeces	[27]
KF371635	Faecal-associated gemycircularvirus-7	FaGmV-7	New Zealand	<i>Anas platyrhynchos</i>	Mallard duck	Faeces	[27]
KF371636	Faecal-associated gemycircularvirus-6	FaGmV-6	New Zealand	<i>Gerygone albofrontata</i>	Chatham Island warbler	Faeces	[27]
KF371637	Faecal-associated gemycircularvirus-5	FaGmV-5	New Zealand	<i>Gerygone albofrontata</i>	Chatham Island warbler	Faeces	[27]

Table 1 continued

GenBank accession no.	Virus/putative virus name	Acronym	Country	Isolation source	Common name	Sample type	Reference
KF371638	Faecal-associated gemycircularvirus-4	FaGmV-4	New Zealand	<i>Arctocephalus forsteri</i>	New Zealand fur seal	Faeces	[27]
KF371639	Faecal-associated gemycircularvirus-3	FaGmV-3	New Zealand	<i>Gerygone albofrontata</i>	Chatham Island warbler	Faeces	[27]
KF371640	Faecal-associated gemycircularvirus-2	FaGmV-2	New Zealand	<i>Sus scrofa</i>	Domestic pig	Faeces	[27]
KF371641	Faecal-associated gemycircularvirus-1c	FaGmV-1c	New Zealand	<i>Turdus merula</i>	Blackbird	Faeces	[27]
KF371642	Faecal-associated gemycircularvirus-1b	FaGmV-1b	New Zealand	<i>Turdus merula</i>	Blackbird	Faeces	[27]
KF371643	Faecal-associated gemycircularvirus-1a	FaGmV-1a	New Zealand	<i>Ovis aries</i>	Sheep	Faeces	[27]
KF413620	Hypericum japonicum associated circular DNA virus	HJasCV	Viet Nam	<i>Hypericum japonicum</i>	Hypericum	Leaf	[7]
KJ413144	Human genital-associated circular DNA virus-1	HuGaGmC349	South Africa	<i>Homo sapiens</i>	Human	Cervical sample	unpublished
KJ547634	Sewage-associated gemycircularvirus-4	SaGmV-4	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547635	Sewage-associated gemycircularvirus-5	SaGmV-5	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547636	Sewage-associated gemycircularvirus-6	SaGmV-6	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547637	Sewage-associated gemycircularvirus-7a	SaGmV-7a	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547638	Sewage-associated gemycircularvirus-8	SaGmV-8	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547639	Sewage-associated gemycircularvirus-9	SaGmV-9	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547640	Sewage-associated gemycircularvirus-7b	SaGmV-7b	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547641	Sewage-associated gemycircularvirus-11	SaGmV-11	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547642	Sewage-associated gemycircularvirus-2	SaGmV-2	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547643	Sewage-associated gemycircularvirus-3	SaGmV-3	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547644	Sewage-associated gemycircularvirus-10a	SaGmV-10a	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ547645	Sewage-associated gemycircularvirus-10b	SaGmV-10b	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KJ641719	Bat gemycircularvirus 23 GD2012	BtMf-CV-23 GD2012	China	<i>Miniopterus fuliginosus</i>	Bat	Pharyngeal & rectal swabs	[32]
KJ641726	Bat gemycircularvirus 8 NM2013	BtRf-CV-8 NM2013	China	<i>Rhinolophus ferrumequinum</i>	Bat	Pharyngeal & rectal swabs	[32]
KJ641737	Bat gemycircularvirus Tibet2013	BtRh-CV-6 Tibet2013	China	<i>Rhinolophus hipposideros</i>	Bat	Pharyngeal & rectal swabs	[32]
KJ938717	Caribou feces-associated gemycircularvirus	FaGmV-13	Canada	<i>Rangifer tarandus</i>	Caribou	Faeces	[21]
KM510192	Bromus-associated circular DNA virus 3	BasCV-3	New Zealand	<i>Bromus hordeaceus</i>	Soft brome/ Bull grass	Leaf	[13]
KM598385	Odonata associated gemycircularvirus-1	OdaGmV-1	USA	<i>Ischnura posita</i>	Damselfly	Abdomen	[6]

Table 1 continued

GenBank accession no.	Virus/putative virus name	Acronym	Country	Isolation source	Common name	Sample type	Reference
KM598386	Odonata associated gemycircularvirus-1	OdaGmV-1	USA	<i>Pantala hymenaea</i>	Dragonfly	Abdomen	[6]
KM598387	Odonata associated gemycircularvirus-2	OdaGmV-2	USA	<i>Aeshna multicolor</i>	Dragonfly	Abdomen	[6]
KM598388	Odonata associated gemycircularvirus-2	OdaGmV-2	USA	<i>Libellula saturata</i>	Dragonfly	Abdomen	[6]
KM821747	Sewage-associated gemycircularvirus-1	SaGmV-1	New Zealand	Sewage oxidation pond	-	Sewage	[12]
KP133075	Gemycircularvirus SL1	GemyCV-SL1	Sri Lanka	<i>Homo sapiens</i>	Human	Cerebrospinal fluid	[24]
KP133076	Gemycircularvirus SL2	GemyCV-SL2	Sri Lanka	<i>Homo sapiens</i>	Human	Cerebrospinal fluid	[24]
KP133077	Gemycircularvirus SL3	GemyCV-SL3	Sri Lanka	<i>Homo sapiens</i>	Human	Cerebrospinal fluid	[24]
KP133078	Gemycircularvirus BZ1	GemyCV-BZ1	Brazil	<i>Homo sapiens</i>	Human	Faeces	[24]
KP133079	Gemycircularvirus BZ2	GemyCV-BZ2	Brazil	<i>Homo sapiens</i>	Human	Faeces	[24]
KP133080	Gemycircularvirus NP	GemyCV-NP	Nepal	Untreated sewage	-	Sewage	[24]
KP263543	Badger faeces-associated gemycircularvirus	BafaGM588	Portugal	<i>Meles meles</i>	European badger	Faeces	[4]
KP263544	Mongoose feces-associated gemycircularvirus a	MoFaGmV181a	Portugal	<i>Herpestes ichneumon</i>	Egyptian mongoose	Faeces	[4]
KP263545	Mongoose feces-associated gemycircularvirus b	MoFaGmV160b	Portugal	<i>Herpestes ichneumon</i>	Egyptian mongoose	Faeces	[4]
KP263546	Mongoose feces-associated gemycircularvirus c	MoFaGmV541c	Portugal	<i>Herpestes ichneumon</i>	Egyptian mongoose	Faeces	[4]
KP263547	Mongoose feces-associated gemycircularvirus d	MoFaGmV478d	Portugal	<i>Herpestes ichneumon</i>	Egyptian mongoose	Faeces	[4]
KP987887	Gemycircularvirus C1c	C1c	France	<i>Homo sapiens</i>	Human	Plasma	[29]
KR912221	Gemycircularvirus gemy-ch-rat1	Gemy-ch-rat1	China	<i>Rattus norvegicus</i>	Rat	Blood	[17]
KT253577	Poaceae associated gemycircularvirus-1	PaGmV-1	Tonga	<i>Brachiaria deflexa</i>	Signalgrass	Leaf	[18]
KT253578	Poaceae associated gemycircularvirus-1	PaGmV-1	Tonga	<i>Brachiaria deflexa</i>	Signalgrass	Leaf	[18]
KT253579	Poaceae associated gemycircularvirus-1	PaGmV-1	Tonga	<i>Saccharum hybrid</i>	Sugarcane	Leaf	[18]
KT309029	Poecile atricapillus GI tract-associated gemycircularvirus	Gitract	USA	<i>Poecile atricapillus</i>	Black-capped chickadee	Buccal and cloacal swab	[9]
KT598248	Soybean leaf-associated gemycircularvirus 1	SlaGemV1	USA	<i>Glycine max</i>	Soybean	Leaf	[20]
KT732790	Pacific flying fox faeces associated gemycircularvirus-1	PfffaGmV-1	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732791	Pacific flying fox faeces associated gemycircularvirus-1	PfffaGmV-1	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732792	Pacific flying fox faeces associated gemycircularvirus-2	PfffaGmV-2	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732793	Pacific flying fox faeces associated gemycircularvirus-2	PfffaGmV-2	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]

Table 1 continued

GenBank accession no.	Virus/putative virus name	Acronym	Country	Isolation source	Common name	Sample type	Reference
KT732794	Pacific flying fox faeces associated gemycircularvirus-3	PfffaGmV-3	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732795	Pacific flying fox faeces associated gemycircularvirus-4	PfffaGmV-4	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732796	Pacific flying fox faeces associated gemycircularvirus-4	PfffaGmV-4	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732797	Pacific flying fox faeces associated gemycircularvirus-5	PfffaGmV-5	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732798	Pacific flying fox faeces associated gemycircularvirus-6	PfffaGmV-6	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732799	Pacific flying fox faeces associated gemycircularvirus-6	PfffaGmV-6	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732800	Pacific flying fox faeces associated gemycircularvirus-7	PfffaGmV-7	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732801	Pacific flying fox faeces associated gemycircularvirus-8	PfffaGmV-8	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732802	Pacific flying fox faeces associated gemycircularvirus-8	PfffaGmV-8	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732803	Pacific flying fox faeces associated gemycircularvirus-9	PfffaGmV-9	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732804	Pacific flying fox faeces associated gemycircularvirus-10	PfffaGmV-10	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732805	Pacific flying fox faeces associated gemycircularvirus-10	PfffaGmV-10	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732807	Pacific flying fox faeces associated gemycircularvirus-11	PfffaGmV-11	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732808	Pacific flying fox faeces associated gemycircularvirus-11	PfffaGmV-11	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732809	Pacific flying fox faeces associated gemycircularvirus-11	PfffaGmV-11	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732810	Pacific flying fox faeces associated gemycircularvirus-11	PfffaGmV-11	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732811	Pacific flying fox faeces associated gemycircularvirus-11	PfffaGmV-11	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732812	Pacific flying fox faeces associated gemycircularvirus-11	PfffaGmV-11	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]

Table 1 continued

GenBank accession no.	Virus/putative virus name	Acronym	Country	Isolation source	Common name	Sample type	Reference
KT732813	Pacific flying fox faeces associated gemycircularvirus-12	PfffaGmV-12	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732814	Pacific flying fox faeces associated gemycircularvirus-13	PfffaGmV-13	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT732806	Pacific flying fox faeces associated gemycircularvirus-14	PfffaGmV-14	Tonga	<i>Pteropus tonganus</i>	Bat	Faeces	[19]
KT862238	Faecal-associated gemycircularvirus-14	FaGmV-14	New Zealand	<i>Anas platyrhynchos</i>	Duck	Faeces	[28]
KT862239	Faecal-associated gemycircularvirus-14	FaGmV-14	New Zealand	<i>Anas platyrhynchos</i>	Duck	Faeces	[28]
KT862240	Sewage-associated gemycircularvirus-3	SaGmV-3	New Zealand	<i>Gallus gallus domesticus</i>	Chicken	Faeces	[28]
KT862241	Faecal-associated gemycircularvirus-4	FaGmV-4	New Zealand	<i>Gallus gallus domesticus</i>	Chicken	Faeces	[28]
KT862242	Faecal-associated gemycircularvirus-17	FaGmV-17	New Zealand	<i>Gallus gallus domesticus</i>	Chicken	Faeces	[28]
KT862243	Faecal-associated gemycircularvirus-20	FaGmV-20	New Zealand	<i>Gallus gallus domesticus</i>	Chicken	Faeces	[28]
KT862244	Faecal-associated gemycircularvirus-20	FaGmV-20	New Zealand	<i>Lama glama</i>	Llama	Faeces	[28]
KT862245	Faecal-associated gemycircularvirus-21	FaGmV-21	New Zealand	<i>Lama glama</i>	Llama	Faeces	[28]
KT862246	Faecal-associated gemycircularvirus-20	FaGmV-20	New Zealand	<i>Equus ferus caballus</i>	Horse	Faeces	[28]
KT862247	Faecal-associated gemycircularvirus-21	FaGmV-21	New Zealand	<i>Equus ferus caballus</i>	Horse	Faeces	[28]
KT862248	Faecal-associated gemycircularvirus-18	FaGmV-18	New Zealand	<i>Equus ferus caballus</i>	Horse	Faeces	[28]
KT862249	Faecal-associated gemycircularvirus-16	FaGmV-16	New Zealand	<i>Ovis aries</i>	Sheep	Faeces	[28]
KT862250	Faecal-associated gemycircularvirus-19	FaGmV-19	New Zealand	<i>Sus scrofa domestica</i>	Pig	Faeces	[28]
KT862251	Faecal-associated gemycircularvirus-16	FaGmV-16	New Zealand	<i>Ovis aries</i>	Sheep	Faeces	[28]
KT862252	Sewage-associated gemycircularvirus-3	SaGmV-3	New Zealand	<i>Bos taurus</i>	Cow	Faeces	[28]
KT862253	Faecal-associated gemycircularvirus-22	FaGmV-22	New Zealand	<i>Bos taurus</i>	Cow	Faeces	[28]
KT862254	Faecal-associated gemycircularvirus-15	FaGmV-15	New Zealand	<i>Canis lupus familiaris</i>	Dog	Faeces	[28]
KT862255	Sewage-associated gemycircularvirus-3	SaGmV-3	New Zealand	<i>Lepus europaeus</i>	Hare	Faeces	[28]
LK931483	HCBI8.215 virus	HCBI8_215	Germany	<i>Bos taurus</i>	Cow	Serum	[16]
LK931484	HCBI9.212 virus	HCBI9_212	Germany	<i>Bos taurus</i>	Cow	Serum	[16]
LK931485	MSSI2.225 virus	MSSI2_225	Germany	<i>Homo sapiens</i>	Human	Blood	[16]

Fig. 2 Phylogenetic analysis of the replication-initiation proteins (Reps) of ssDNA viruses. The type species of the proposed genus *Gemycircularvirus* within the family *Genomoviridae* is highlighted in boldface. For phylogenetic analysis, protein sequences were aligned using PROMALS3D [23], and columns containing gaps were removed from the alignment using trimAl (*strict* mode) [3]. Maximum-likelihood phylogenetic analysis was carried out using PhyML 3.1 [8] with the RtREV +G6 +I +F model, which was selected by PhyML as the best-fitting model. Numbers at the branch points represent aBayes local support values. Branches with lower than 60 % support were collapsed. The scale bar represents the number of substitutions per site. For clarity, the tree was mid-point rooted. All taxa are indicated with the corresponding GenBank accession numbers, followed by abbreviated virus names (full virus names are provided in Table 1)

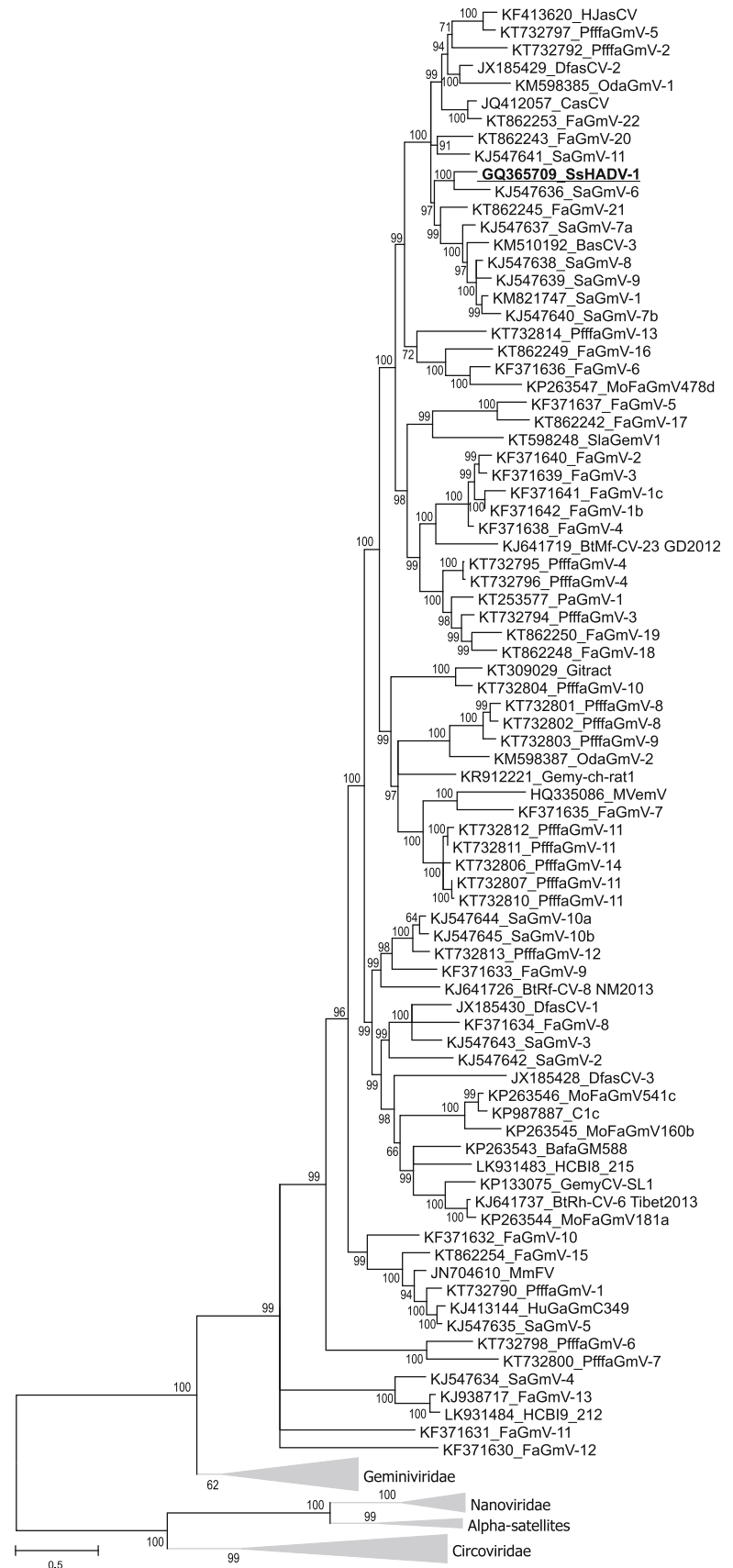
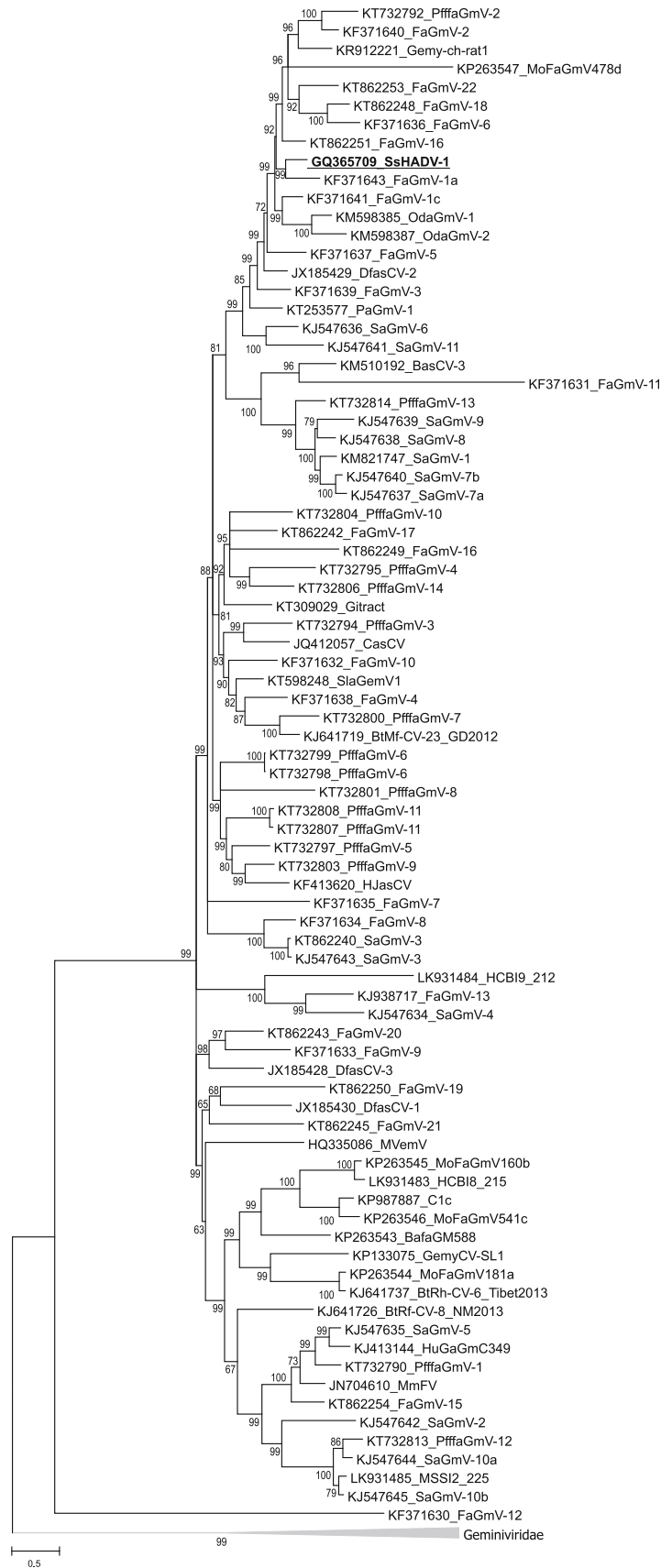


Fig. 3 Phylogenetic analysis of the SsHADV-1-like capsid proteins. The type species of the proposed genus *Gemycircularvirus* within the family *Genomoviridae* is highlighted in boldface.

For phylogenetic analysis, protein sequences were aligned using PROMALS3D [23], and columns containing gaps were removed from the alignment using trimAl (*strictplus* mode) [3]. Maximum-likelihood phylogenetic analysis was carried out using PhyML 3.1 [8] with the LG +G6 +F model, which was selected by PhyML as the best-fitting model. Numbers at the branch points represent aBayes local support values. Branches with lower than 60 % support were collapsed. The scale bar represents the number of substitutions per site. The tree was rooted with the capsid proteins of geminiviruses. All taxa are indicated with the corresponding GenBank accession numbers, followed by abbreviated virus names (full virus names are provided in Table 1)



Compliance with ethical standards

The authors declare that no competing interests exist. This article does not contain any studies with human participants or animals performed by any of the authors.

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