

## The order *Herpesvirales*

Andrew J. Davison · Richard Eberle · Bernhard Ehlers · Gary S. Hayward ·  
Duncan J. McGeoch · Anthony C. Minson · Philip E. Pellett · Bernard Roizman ·  
Michael J. Studdert · Etienne Thiry

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**Abstract** The taxonomy of herpesviruses has been updated by the International Committee on Taxonomy of Viruses (ICTV). The former family *Herpesviridae* has been split into three families, which have been incorporated into the new order *Herpesvirales*. The revised family *Herpesviridae* retains the mammal, bird and reptile viruses, the new family *Alloherpesviridae* incorporates the fish and frog viruses, and the new family *Malacoherpesviridae* contains a bivalve virus. Three new genera have been created in the family *Herpesviridae*, namely *Proboscivirus* in the subfamily *Betaherpesvirinae* and *Macavirus* and *Percavirus* in the subfamily *Gammaherpesvirinae*. These genera have been formed by the transfer of species from established genera and the erection of new species, and other new species have been added to some of the established genera. In addition, the names of some nonhuman primate virus species have been changed. The family *Alloherpesviridae* has been populated by transfer of the genus *Ictalurivirus*

and addition of the new species *Cyprinid herpesvirus 3*. The family *Malacoherpesviridae* incorporates the new genus *Ostreavirus* containing the new species *Ostreid herpesvirus 1*.

The classification of herpesviruses has been updated as a result of recommendations made to the International Committee on Taxonomy of Viruses (ICTV; <http://www.ictvonline.org>) by the *Herpesviridae* Study Group as it was constituted in the period 2002–2005. The purpose of this report is to convey the taxonomic changes.

Morphologically, herpesviruses are distinct from all other viruses. A linear, double-stranded DNA genome of 125–290 kbp is contained within a T = 16 icosahedral capsid, which is surrounded by a proteinaceous matrix dubbed the tegument and then by a lipid envelope

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A. J. Davison (✉) · D. J. McGeoch  
MRC Virology Unit, Institute of Virology,  
University of Glasgow, Church Street,  
Glasgow G11 5JR, UK  
e-mail: a.davison@mrcvu.gla.ac.uk

R. Eberle  
Center for Veterinary Health Sciences, Oklahoma State  
University, Stillwater, OK, USA

B. Ehlers  
Robert Koch Institute, Berlin, Germany

G. S. Hayward  
Johns Hopkins School of Medicine, Baltimore, MD, USA

A. C. Minson  
Department of Pathology, University of Cambridge,  
Cambridge, UK

P. E. Pellett  
Wayne State University School of Medicine, Detroit, MI, USA  
e-mail: ppellett@med.wayne.edu

B. Roizman  
Marjorie B. Kovler Viral Oncology Laboratories,  
University of Chicago, Chicago, IL, USA

M. J. Studdert  
School of Veterinary Science, University of Melbourne,  
Melbourne, VIC, Australia

E. Thiry  
Faculty of Veterinary Medicine, University of Liège,  
Liège, Belgium

**Table 1** The order *Herpesvirales*

Taxon	Name <sup>a</sup>	Acronym <sup>b</sup>	Former name <sup>c</sup>	Common name <sup>d</sup>
Order	<i>Herpesvirales</i>			
Family	<i>Herpesviridae</i>			
Subfamily	<i>Alphaherpesvirinae</i>			
Genus	<i>Simplexvirus</i>			
Species in the genus	<i>Ateline herpesvirus 1</i>	AtHV1		Spider monkey herpesvirus
	<i>Bovine herpesvirus 2</i>	BoHV2		Bovine mammillitis virus
	<i>Cercopithecine herpesvirus 2</i>	CeHV2		SA8
	<i>Human herpesvirus 1<sup>e</sup></i>	HHV1		Herpes simplex virus type 1
	<i>Human herpesvirus 2</i>	HHV2		Herpes simplex virus type 2
	<i>Macacine herpesvirus 1</i>	McHV1	<i>Cercopithecine herpesvirus 1</i>	B-virus
	<i>Macropodid herpesvirus 1</i>	MaHV1		Parma wallaby herpesvirus
	<i>Macropodid herpesvirus 2</i>	MaHV2		Dorcopsis wallaby herpesvirus
	<i>Papiine herpesvirus 2</i>	PaHV2	<i>Cercopithecine herpesvirus 16</i>	Herpesvirus papio 2
	<i>Saimiriine herpesvirus 1</i>	SaHV1		Marmoset herpesvirus
Genus	<i>Varicellovirus</i>			
Species in the genus	<i>Bovine herpesvirus 1</i>	BoHV1		Infectious bovine rhinotracheitis virus
	<i>Bovine herpesvirus 5</i>	BoHV5		Bovine encephalitis herpesvirus
	<i>Bubaline herpesvirus 1</i>	BuHV1		Water buffalo herpesvirus
	<i>Canid herpesvirus 1</i>	CaHV1		Canine herpesvirus
	<i>Caprine herpesvirus 1</i>	CpHV1		Goat herpesvirus
	<i>Cercopithecine herpesvirus 9</i>	CeHV9		Simian varicella virus
	<i>Cervid herpesvirus 1</i>	CvHV1		Red deer herpesvirus
	<i>Cervid herpesvirus 2</i>	CvHV2		Reindeer herpesvirus
	<i>Equid herpesvirus 1</i>	EHV1		Equine abortion virus
	<i>Equid herpesvirus 3</i>	EHV3		Equine coital exanthema virus
	<i>Equid herpesvirus 4</i>	EHV4		Equine rhinopneumonitis virus
	<i>Equid herpesvirus 8</i>	EHV8		Asinine herpesvirus 3
	<i>Equid herpesvirus 9</i>	EHV9		Gazelle herpesvirus
	<i>Felid herpesvirus 1</i>	FeHV1		Feline rhinotracheitis virus
	<i>Human herpesvirus 3<sup>e</sup></i>	HHV3		Varicella-zoster virus
	<i>Phocid herpesvirus 1</i>	PhoHV1		Harbour seal herpesvirus
	<i>Suid herpesvirus 1</i>	SuHV1		Pseudorabies virus
Tentative species in the genus	Equid herpesvirus 6	EHV6		Asinine herpesvirus 1
Genus	<i>Mardivirus</i>			
Species in the genus	<i>Columbid herpesvirus 1</i>	CoHV1	None	Pigeon herpesvirus
	<i>Gallid herpesvirus 2<sup>e</sup></i>	GaHV2		Marek's disease virus type 1
	<i>Gallid herpesvirus 3</i>	GaHV3		Marek's disease virus type 2
	<i>Meleagrid herpesvirus 1</i>	MeHV1		Turkey herpesvirus
Genus	<i>Iltovirus</i>			
Species in the genus	<i>Gallid herpesvirus 1<sup>e</sup></i>	GaHV1		Infectious laryngotracheitis virus
	<i>Psittacid herpesvirus 1</i>	PsHV1	None	Pacheco's disease virus
Unassigned species in the subfamily	<i>Chelonid herpesvirus 5</i>	ChHV5	None	Chelonid fibropapilloma-associated herpesvirus
	<i>Chelonid herpesvirus 6</i>	ChHV6	None	Lung-eye-trachea disease-associated virus
Subfamily	<i>Betaherpesvirinae</i>			
Genus	<i>Cytomegalovirus</i>			
Species in the genus	<i>Cercopithecine herpesvirus 5</i>	CeHV5		African green monkey cytomegalovirus
	<i>Human herpesvirus 5<sup>e</sup></i>	HHV5		Human cytomegalovirus
	<i>Macacine herpesvirus 3</i>	McHV3	<i>Cercopithecine herpesvirus 8</i>	Rhesus cytomegalovirus
	<i>Panine herpesvirus 2</i>	PnHV2	<i>Pongine herpesvirus 4</i>	Chimpanzee cytomegalovirus
Tentative species in the genus	<i>Aotine herpesvirus 1</i>	AoHV1		Herpesvirus aotus type 1
	<i>Aotine herpesvirus 3</i>	AoHV3		Herpesvirus aotus type 3

**Table 1** continued

Taxon	Name <sup>a</sup>	Acronym <sup>b</sup>	Former name <sup>c</sup>	Common name <sup>d</sup>
Genus	<i>Muromegalovirus</i>			
Species in the genus	<i>Murid herpesvirus 1</i> <sup>e</sup>	MuHV1		Mouse cytomegalovirus
	<i>Murid herpesvirus 2</i>	MuHV2		Rat cytomegalovirus
Genus	<i>Roseolovirus</i>			
Species in the genus	<i>Human herpesvirus 6</i> <sup>e</sup>	HHV6		Human herpesvirus 6
	<i>Human herpesvirus 7</i>	HHV7		Human herpesvirus 7
Genus	<i>Proboscivirus</i>			
Species in the genus	<i>Elephantid herpesvirus 1</i> <sup>e</sup>	EIHV1	None	Elephant endotheliotropic herpesvirus
Unassigned species in the subfamily	<i>Caviid herpesvirus 2</i>	CavHV2		Guinea pig cytomegalovirus
	<i>Suid herpesvirus 2</i>	SuHV2	None	Pig cytomegalovirus
	<i>Tupaïid herpesvirus 1</i>	TuHV1		Tree shrew herpesvirus
Subfamily	<i>Gammaherpesvirinae</i>			
Genus	<i>Lymphocryptovirus</i>			
Species in the genus	<i>Callitrichine herpesvirus 3</i>	CalHV3		Marmoset lymphocryptovirus
	<i>Cercopithecine herpesvirus 14</i>	CeHV14		African green monkey EBV-like virus
	<i>Gorilline herpesvirus 1</i>	GoHV1	<i>Pongine herpesvirus 3</i>	Gorilla herpesvirus
	<i>Human herpesvirus 4</i> <sup>e</sup>	HHV4		Epstein-Barr virus
	<i>Macacine herpesvirus 4</i>	McHV4	<i>Cercopithecine herpesvirus 15</i>	Rhesus lymphocryptovirus
	<i>Panine herpesvirus 1</i>	PnHV1	<i>Pongine herpesvirus 1</i>	Herpesvirus pan
	<i>Papiine herpesvirus 1</i>	PaHV1	<i>Cercopithecine herpesvirus 12</i>	Herpesvirus papio
	<i>Pongine herpesvirus 2</i>	PoHV2		Orangutan herpesvirus
Genus	<i>Rhadinovirus</i>			
Species in the genus	<i>Ateline herpesvirus 2</i>	AtHV2		Herpesvirus ateles strain 810
	<i>Ateline herpesvirus 3</i>	AtHV3		Herpesvirus ateles strain 73
	<i>Bovine herpesvirus 4</i>	BoHV4		Movar virus
	<i>Human herpesvirus 8</i>	HHV8		Kaposi's sarcoma-associated herpesvirus
	<i>Macacine herpesvirus 5</i>	McHV5	<i>Cercopithecine herpesvirus 17</i>	Rhesus rhadinovirus
	<i>Murid herpesvirus 4</i>	MuHV4		Murine gammaherpesvirus 68
	<i>Saimiriine herpesvirus 2</i> <sup>e</sup>	SaHV2		Herpesvirus saimiri
Tentative species in the genus	<i>Leporid herpesvirus 1</i>	LeHV1		Cottontail rabbit herpesvirus
	<i>Leporid herpesvirus 2</i>	LeHV2		Herpesvirus cuniculi
	<i>Leporid herpesvirus 3</i>	LeHV3		Herpesvirus sylvilagus
	<i>Marmodid herpesvirus 1</i>	MarHV1		Woodchuck herpesvirus
Genus	<i>Macavirus</i>			
Species in the genus	<i>Alcelaphine herpesvirus 1</i> <sup>e</sup>	AIHV1		Malignant catarrhal fever virus
	<i>Alcelaphine herpesvirus 2</i>	AIHV2		Hartebeest malignant catarrhal fever virus
	<i>Bovine herpesvirus 6</i>	BoHV6	None	Bovine lymphotropic herpesvirus
	<i>Caprine herpesvirus 2</i>	CpHV2	None	Caprine herpesvirus 2
	<i>Hippotragine herpesvirus 1</i>	HiHV1		Roan antelope herpesvirus
	<i>Ovine herpesvirus 2</i>	OvHV2		Sheep-associated malignant catarrhal fever virus
	<i>Suid herpesvirus 3</i>	SuHV3	None	Porcine lymphotropic herpesvirus 1
	<i>Suid herpesvirus 4</i>	SuHV4	None	Porcine lymphotropic herpesvirus 2
	<i>Suid herpesvirus 5</i>	SuHV5	None	Porcine lymphotropic herpesvirus 3
Genus	<i>Percavirus</i>			
Species in the genus	<i>Equid herpesvirus 2</i> <sup>e</sup>	EHV2		Equine herpesvirus 2
	<i>Equid herpesvirus 5</i>	EHV5		Equine herpesvirus 5
	<i>Mustelid herpesvirus 1</i>	MusHV1		Badger herpesvirus

**Table 1** continued

Taxon	Name <sup>a</sup>	Acronym <sup>b</sup>	Former name <sup>c</sup>	Common name <sup>d</sup>
Unassigned species in the subfamily	<i>Equid herpesvirus 7</i>	EHV7		Asinine herpesvirus 2
	<i>Phocid herpesvirus 2</i>	PhoHV2	None	Phocid herpesvirus 2
	<i>Saguinine herpesvirus 1</i>	SgHV1	<i>Callitrichine herpesvirus 1</i>	Herpesvirus saguinus
Unassigned species in the family	<i>Iguanid herpesvirus 2</i>	IgHV2	None	Iguana herpesvirus
Unassigned viruses in the family	Acciptrid herpesvirus 1	AcHV1		Bald eagle herpesvirus
	Anatid herpesvirus 1	AnHV1		Duck plague herpesvirus
	Boid herpesvirus 1	BoiHV1		Boa herpesvirus
	Callitrichine herpesvirus 2	CalHV2		Marmoset cytomegalovirus
	Caviid herpesvirus 1	CavHV1		Guinea pig herpesvirus
	Caviid herpesvirus 3	CavHV3		Guinea pig herpesvirus 3
	Cebine herpesvirus 1	CbHV1		Capuchin herpesvirus AL-5
	Cebine herpesvirus 2	CbHV2		Capuchin herpesvirus AP-18
	Cercopithecine herpesvirus 3	CeHV3		SA6
	Cercopithecine herpesvirus 4	CeHV4		SA15
	Chelonid herpesvirus 1	ChHV1		Grey patch disease-associated virus
	Chelonid herpesvirus 2	ChHV2		Pacific pond turtle herpesvirus
	Chelonid herpesvirus 3	ChHV3		Painted turtle herpesvirus
	Chelonid herpesvirus 4	ChHV4		Argentine turtle herpesvirus
	Ciconiid herpesvirus 1	CiHV1		Black stork herpesvirus
	Cricetid herpesvirus	CrHV1		Hamster herpesvirus
	Elapid herpesvirus 1	EpHV1		Indian cobra herpesvirus
	Erinaceid herpesvirus 1	ErHV1		European hedgehog herpesvirus
	Falconid herpesvirus 1	FaHV1		Falcon inclusion body disease virus
	Gruid herpesvirus 1	GrHV1		Crane herpesvirus
	Iguanid herpesvirus 1	IgHV1		Green iguana herpesvirus
	Lacertid herpesvirus	LaHV1		Green lizard herpesvirus
	Macacine herpesvirus 6	McHV6	Cercopithecine herpesvirus 10	Rhesus leukocyte-associated herpesvirus strain 1
	Macacine herpesvirus 7	McHV7	Cercopithecine herpesvirus 13	Herpesvirus cyclopis
	Murid herpesvirus 3	MuHV3		Mouse thymic herpesvirus
	Murid herpesvirus 5	MuHV5		Field mouse herpesvirus
	Murid herpesvirus 6	MuHV6		Sand rat nuclear inclusion agent
	Ovine herpesvirus 1	OvHV1		Sheep pulmonary adenomatosis-associated herpesvirus
	Perdicid herpesvirus 1	PdHV1		Bobwhite quail herpesvirus
	Phalacrocoracid herpesvirus 1	PhHV1		Cormorant herpesvirus
	Procyonid herpesvirus 1	PrHV1	Lorisine herpesvirus 1	Kinkajou herpesvirus
	Sciurid herpesvirus 1	ScHV1		Ground squirrel cytomegalovirus
	Sciurid herpesvirus 2	ScHV2		Ground squirrel herpesvirus
	Sphenicid herpesvirus 1	SpHV1		Black footed penguin herpesvirus
	Strigid herpesvirus 1	StHV1		Owl hepatitis virus
	Family	<i>Alloherpesviridae</i>		
Genus	<i>Ictalurivirus</i>			
Species in the genus	<i>Ictalurid herpesvirus 1<sup>c</sup></i>	IcHV1		Channel catfish virus
Unassigned species in the family	<i>Cyprinid herpesvirus 3</i>	CyHV3	None	Koi herpesvirus

**Table 1** continued

Taxon	Name <sup>a</sup>	Acronym <sup>b</sup>	Former name <sup>c</sup>	Common name <sup>d</sup>	
Unassigned viruses in the family	Acipenserid herpesvirus 1	AciHV1		White sturgeon herpesvirus 1	
	Acipenserid herpesvirus 2	AciHV2		White sturgeon herpesvirus 2	
	Anguillid herpesvirus 1	AngHV1		Japanese eel herpesvirus	
	Cyprinid herpesvirus 1	CyHV1		Carp pox herpesvirus	
	Cyprinid herpesvirus 2	CyHV2		Haematopoietic necrosis virus	
	Esocid herpesvirus 1	EsHV1		Northern pike herpesvirus	
	Percid herpesvirus 1	PeHV1		Walleye epidermal hyperplasia herpesvirus	
	Pleuronectid herpesvirus 1	PIHV1		Turbot herpesvirus	
	Ranid herpesvirus 1	RaHV1		Lucké tumor herpesvirus	
	Ranid herpesvirus 2	RaHV2		Frog virus 4	
	Salmonid herpesvirus 1	SalHV1		Herpesvirus salmonis	
	Salmonid herpesvirus 2	SalHV2		Oncorhynchus masou herpesvirus	
	Family	<i>Malacoherpesviridae</i>			
	Genus	<i>Ostreavirus</i>			
Species in the genus	<i>Ostreid herpesvirus 1</i> <sup>e</sup>	OshV1	None	Oyster herpesvirus	

<sup>a</sup> Formal taxonomic names are in italicized font. The names of tentative species and unassigned viruses are in non-italicized font, since these ranks have no taxonomic standing

<sup>b</sup> Acronyms apply to viruses, not species, and have no taxonomic standing. A hyphen may be included prior to the number

<sup>c</sup> Where the name has changed, the former name is given. Where the name is new, the word “None” is given. Where the name has not changed, no information is given

<sup>d</sup> Common names apply to viruses, not species, and have no taxonomic standing. They may correspond to the formal name (e.g. human herpesvirus 7 for *Human herpesvirus 7*), or they may not (e.g. Epstein-Barr virus for *Human herpesvirus 4*), or they may take multiple forms (e.g. human herpesvirus 8 and Kaposi’s sarcoma-associated herpesvirus for *Human herpesvirus 8*; pseudorabies virus and Aujeszky’s disease virus for *Suid herpesvirus 1*) and variants thereof. This list is limited to a single, common, English name for each virus

<sup>e</sup> Type species in the genus

containing membrane-associated proteins [18]. Genetically, herpesviruses fall into three distinct groupings that are related only tenuously to each other [4, 5, 7]. These groupings consist of viruses of mammals, birds and reptiles, viruses of fish and frogs, and a single virus of bivalves. Of the few proteins that are detectably conserved in sequence among the three groupings, none has homologues that are found only in herpesviruses. The protein that comes nearest to being herpesvirus-specific is the putative ATPase subunit of the terminase (a complex that is responsible for packaging virus DNA into nascent capsids), which is conserved in all herpesviruses and, to a lesser degree, T4-like bacteriophages in the family *Myoviridae*. The taxonomic outcome of the apparently large genetic distances among the groupings is that the former family *Herpesviridae* [6], which contained all herpesviruses, has now been divided into three families that comprise the new order *Herpesvirales*. The revised family *Herpesviridae* retains the viruses of mammals, birds and reptiles, the new family *Alloherpesviridae* (from ἄλλος—other, different) incorporates the fish and frog viruses, and the new family *Malacoherpesviridae* (from μαλακός—soft; μαλάκιον—mollusc) contains the bivalve virus. The revised classification is shown in Table 1.

Three new genera have been created in the family *Herpesviridae*. One is the genus *Proboscivirus* (from προβοσκίς or proboscis: elephant’s trunk), which recognizes a distinct lineage of the subfamily *Betaherpesvirinae* containing the new species *Elephantid herpesvirus 1* [9, 16, 19]. The others are the genera *Macavirus* (sigla from malignant catarrhal fever) and *Percavirus* (sigla from perissodactyl and carnivore), which form two lineages in the subfamily *Gammaherpesvirinae* that are separable from the established genera [14, 15]. The genus *Macavirus* contains the established species *Alcelaphine herpesvirus 1*, *Alcelaphine herpesvirus 2*, *Hippotragine herpesvirus 1* and *Ovine herpesvirus 2*, which were transferred from the genus *Rhadinovirus*, plus the new species *Bovine herpesvirus 6*, *Caprine herpesvirus 2*, *Suid herpesvirus 3*, *Suid herpesvirus 4* and *Suid herpesvirus 5* [1, 2, 23]. The genus *Percavirus* contains the established species *Equid herpesvirus 2*, *Equid herpesvirus 5* and *Mustelid herpesvirus 1*, which were also transferred from the genus *Rhadinovirus*. Other new species include *Columbid herpesvirus 1* and *Psittacid herpesvirus 1* in the genera *Mardivirus* and *Iltoivirus*, respectively, of the subfamily *Alphaherpesvirinae* [8, 22]. In addition, several new species were classified at the level of subfamily or family, with assignment to genera

awaiting further data. These include the reptilian species *Chelonid herpesvirus 5* and *Chelonid herpesvirus 6* in the subfamily *Alphaherpesvirinae* [3, 11, 13, 17, 26], *Phocid herpesvirus 2* in the subfamily *Gammaherpesvirinae* [10, 12], and *Iguanid herpesvirus 2* in the family *Herpesviridae* [13, 25].

Herpesvirus species are named after a taxon of the host that in its natural setting harbours the virus [20, 21]. The default host taxon employed is that of family, and, except for the species of humans, the name ends in ‘-id’. Owing to their larger numbers, species from nonhuman primates and the family Bovidae have been designated by host subfamily, with the name ending in ‘-ine’. In the revised taxonomy, species from nonhuman primates have been renamed by host genus, with the name again ending in ‘-ine’. This has resulted in name changes for several Old World and one New World nonhuman primate herpesvirus species, and has reduced the very large number of species that previously incorporated the *Cercopithecine* prefix. The new names are correlated to the former names in Table 1.

The established genus *Ictalurivirus* has been transferred to the family *Alloherpesviridae*, and the new species *Cyprinid herpesvirus 3* been added to the family [24]. The new genus *Ostreavirus* (from ὄστρεον or ostrea—oyster) has been created in the family *Malacoherpesviridae*, containing the single known species of an invertebrate host, *Ostreid herpesvirus 1* [7].

The need to balance logic and utility makes taxonomy a challenging process, and matters are often not straightforward. In addition to keeping abreast of new viruses as they are discovered, current discussions in the *Herpesviridae* (now *Herpesvirales*) Study Group (chaired by P.E. Pellett) include updating the herpesvirus species definition and the methods used for taxonomic assignment, in order to accommodate the well-established value of sequence-based phylogenetic relationships, and defining a pathway to species status for the large and increasing number of herpesviruses that have been detected only by PCR.

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