

Taxonomy of the *Picornaviridae*: Species Designations and Three New Genera

Glyn Stanway¹, Fred Brown², Peter D. Christian³, Tapani Hovi⁴, Timo Hyypiä⁵, Andrew M.Q. King⁶, Nick J. Knowles⁶, Stan M. Lemon⁷, Philip D. Minor⁸, Mark A. Pallansch⁹, Ann C. Palmenberg¹⁰, Tim Skern¹¹



(ICTV *Picornaviridae* Study Group)

1) Dept. of Biological Sciences, Univ. of Essex, Colchester CO4 3SQ, UK; 2) Plum Island Animal Disease Ctr., Greenport, NY 11944, USA; 3) Div. Entomology, CSIRO, Canberra, Australia; 4) Dept. Virol., Natl. Pub. Health Inst., Mannerheimintie 166, SF-00300 Helsinki, Finland; 5) Univ. Helsinki, Haartman Inst., Dept. of Virol., 00014 Helsinki, Finland; 6) Inst. Animal Health, Pirbright Lab., Woking, GU24 0NF, UK; 7) Dept Microbiol. & Immunol., UTMB Galveston, 4.104 Med Res Bldg, 301 Univ Bvd, Galveston, TX 77555-1019, USA; 8) NIBSC, Blanche Lane, South Mimms, Potters Bar, Herts, EN6 3QG, UK; 9) Div. of Viral and Rickettsial Dis., Natl. Ctr. for Infect. Dis., Centers for Dis. Ctrl. and Prev., Atlanta, GA, USA; 10) Inst. Mol. Virol., Univ Wisconsin, Madison, WI 53706, USA; 11) Inst für Biochemie, Universität Wien, Austria.

Three New Genera

Three new genera, each consisting of a single species, have been created bringing the total number of picornavirus genera to nine. The genus *Erbovirus* contains the species *Equine rhinitis B virus* (formerly equine rhinovirus 2); the genus *Kobuvirus* contains the species *Aichi virus* (a single serotype); and the genus *Teschovirus* contains the species *Porcine teschovirus* (consisting of 10 serotypes, formerly named porcine enterovirus types 1-7 and 11-13).

The nine genera now contain a total of 20 species (Table 1). Additionally a number of other candidate picornaviruses remain to be classified, however, those isolated from invertebrates have been excluded from the family based on recently published sequence data (see below). The phylogenetic basis for classifying the three new genera is shown in Figures 1 (P1 region) and 2 (combined 2C, 3C and 3D regions). Figure 3 shows the genome maps of members of each of the genera and additionally those which differ between species within a genus.

Picornavirus Species Definition

Until recently each picornavirus serotype was designated as a separate species. However, related serotypes have now been brought together to form species using the following definition: "A picornavirus species is a polythetic class of phylogenetically related serotypes or strains which would normally be expected to share (i) a limited range of hosts and cellular receptors, (ii) a significant degree of compatibility in proteolytic processing, replication, encapsidation and genetic recombination, and (iii) essentially identical genome maps". A list of species is shown in Table 1. A full list of serotypes and the species in which they are classified can be found on the Picornavirus Sequence Database at:

<http://www.iah.bbsrc.ac.uk/virus/Picornaviridae/SequenceDatabase/Index.html>

Unassigned Viruses in the Family

A list of (candidate) picornaviruses which have not yet been assigned to any genus are listed in Table 2.

Fig. 1. Neighbor-joining tree based on a comparison of amino acid similarities of P1 (capsid)

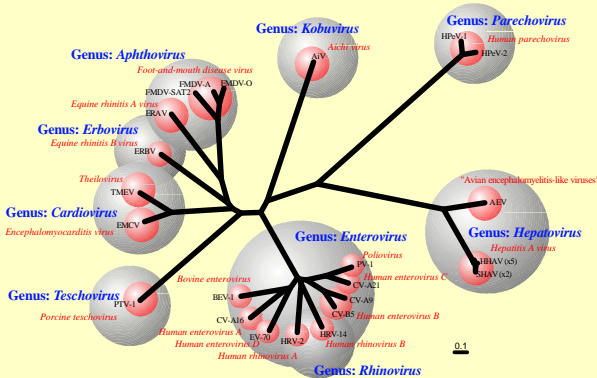


Fig. 2. Neighbor-joining tree based on a comparison of amino acid similarities of 2C+3CD

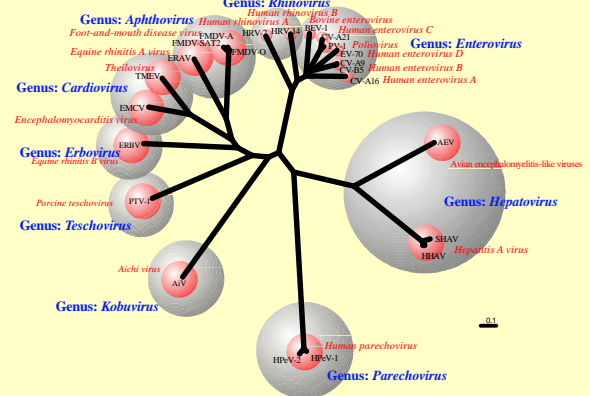


Table 1. Current Classification of the *Picornaviridae*

Genus	Species	No. of serotypes
Enterovirus	<i>Poliovirus</i>	3
	<i>Human enterovirus A</i>	12
	<i>Human enterovirus B</i>	36
	<i>Human enterovirus C</i>	11
	<i>Human enterovirus D</i>	2
	<i>Bovine enterovirus</i>	2
	<i>Porcine enterovirus A</i>	1
	<i>Porcine enterovirus B</i>	2
Rhinovirus	Unassigned serotypes (simian)	20
	<i>Human rhinovirus A</i>	18
	<i>Human rhinovirus B</i>	3
Cardiovirus	Unassigned serotypes (human & bovine)	82
	<i>Encephalomyocarditis virus</i>	1
Aphthovirus	<i>Theilovirus</i>	2 or 3
	<i>Foot-and-mouth disease virus</i>	7
Hepatovirus	<i>Equine rhinitis A virus</i>	1
	<i>Hepatitis A virus</i>	1
Parachovirus	"Avian encephalomyelitis-like viruses"	1
	<i>Hepatitis A virus</i>	1
Erbovirus	<i>Human parechovirus</i>	2
	<i>Equine rhinitis B virus</i>	1
Kobuvirus	<i>Aichi virus</i>	1
	<i>Porcine teschovirus</i>	10

Exclusion of Invertebrate Picorna-like Viruses from the Family

The complete genome sequences of *Drosophila C virus* (DCV), *Plautia stali* intestine virus (PSIV), *Rhopalosiphum padi virus* (RHPV), *Himantoni P virus* (HiPV), *Triatoma virus* (TrV), *Acyrtosiphon pisum virus* (APV), *infectious flacherie virus* (IFV) and *sacbrood virus* (SBV) have either been published or deposited with the EMBL/GenBank/DBJ databases. Additionally partial genome sequences of a number of other invertebrate picorna-like viruses, including *cricket paralysis virus* (CrPV), have been determined. A full list along with references can be found on the World Wide Web at:

<http://www.iah.bbsrc.ac.uk/virus/Picorna-like/Database.htm>

Analysis of the CrPV, DCV, PSIV, RHPV, HiPV and TrV genomes shows them to belong to a novel family having their capsid genes in the 3' end half of the genome and their non-structural genes in the 5' half. The capsid ORF is translated by means of an IRES which initiates at a codon other than AUG.

Although APV appears to have a genome layout similar to the CrPV-like viruses, ORF2 (encoding the capsid proteins) may be expressed either by a -1 translational frameshift or via a subgenomic RNA. Additionally, APV appears to be phylogenetically distinct from the CrPV-like viruses.

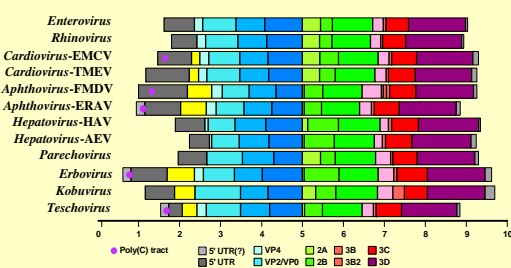
The complete genome sequences of IFV and SBV show them to be more like those of picornaviruses with the four capsid polypeptides encoded in the 5' half of the RNA, however, like the CrPV-related viruses, VP4 (picornavirus nomenclature) appears to be an N-terminal extension of VP3 rather than VP2. Like the cardio- and aphthoviruses the capsid is preceded by a leader polypeptide. The 3' half of the genome contains the usual 2C (NTP-binding), 3C (protease) and 3D (polymerase) in the correct order. Phylogenetically it appears slightly more closely related to members of the *Sequiviridae* than to the picornaviruses.

Thus these viruses probably fall into at least three new families. However, despite these major differences they have all been placed in a "floating genus" named "Cricket paralysis-like viruses".

Table 2. Unassigned viruses in the family

Mammalian
Acid-stable equine picornaviruses (EqPV)
Harbour seal picorna-like virus (SPLV)
Ljungan virus (LV) [AF020541]
Sikhote-Alyn virus (SAV)
Syr-Daria Valley fever virus (SDFV)
Avian
Avian entero-like virus 2 to 4 (AELV-2 to 4)
Avian nephritis virus 2 to 3 (ANV-2 to 3)
Cockatoo entero-like virus (CELV)
Duck hepatitis virus 1 (DHV-1)
Duck hepatitis virus 3 (DHV-3)
Guineafowl transmissible enteritis virus (GTEV)
Turkey entero-like virus (TELV)
Turkey hepatitis virus (THV)
Turkey pseudo enterovirus 1 to 2 (TPEV-1 to 2)
Fish
Barramundi virus-1 (BaV)
Sea-bass virus-1 (SBV)
Smelt virus-1 (SmV-1)
Smelt virus-2 (SmV-2)
Turbot virus-1 (TuV-1)
Invertebrate
Taura syndrome virus of marine penaeid shrimp (TSV)

Fig. 3. Genome organization of picornaviruses



Exclusion of Avian Nephritis Virus 1 (ANV-1) from the Family

The complete genome sequence of avian nephritis virus 1 strain G-4260 (accession no. AB033998; Imada *et al.*, unpub.) has been deposited with the EMBL/GenBank/DBJ databases. Analysis of the genome layout reveals that the capsid genes are at the 3' end of the genome downstream of the non-structural genes. Phylogenetic analysis shows ANV-1 to be a member of the *Astroviridae*. Therefore we are in the process of moving ANV-1 to that family. The classification of other avian picorna-like viruses (including ANV-2 and ANV-3) must await the analysis of sequence data.

References

Imada, T., Yamaguchi, S., Mase, M., Tsukamoto, K., Kubo, M., Morooka, A. Complete nucleotide sequence and construction of infectious cDNA of avian nephritis virus (ANV), a distinct member of the *Astroviridae* associated with acute nephritis in chicks. Unpublished.