

The new plant virus family *Flexiviridae* and assessment of molecular criteria for species demarcation

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Summary. The new plant virus family *Flexiviridae* is described. The family is named because its members have flexuous virions and it includes the existing genera *Allexivirus*, *Capillovirus*, *Carlavirus*, *Foveavirus*, *Potexvirus*, *Trichovirus* and *Vitivirus*, plus the new genus *Mandarivirus* together with some related viruses not assigned to any genus. The family is justified from phylogenetic analyses of the polymerase and coat protein (CP) sequences. To help to define suitable molecular criteria for demarcation of species, a complete set of pairwise comparisons was made using the nucleotide (nt) and amino acid (aa) sequences of each fully-sequenced gene from every available accession in the family. Based on the distributions and on inspection of the data, it was concluded that, as a general rule, distinct species have less than *ca.* 72% identical nt or 80% identical aa between their entire CP or replication protein genes.

Introduction

The International Committee on Taxonomy of Viruses (ICTV) has recently approved a proposal to create a plant virus family *Flexiviridae*. The family is named because its members have flexuous virions and it includes the existing genera *Allexivirus*, *Capillovirus*, *Carlavirus*, *Foveavirus*, *Potexvirus*, *Trichovirus* and *Vitivirus* together with the new genus *Mandarivirus*,

and some related viruses not assigned to any genus. The chief characteristics of members of the family are:

1. Flexuous filamentous virions 12–13 nm in diameter
2. Monopartite, positive sense, ssRNA genomes with a 3'-polyA tail
3. Translation of at least some ORFs from subgenomic mRNAs (there is increasing evidence that viruses in the family employ both 5'- and 3'-coterminal subgenomic mRNAs [7, Bar-Joseph unpublished data])
4. Up to 6 open reading frames ordered from 5' to 3':
 - a) An alpha-like replication protein (150–250 kDa) containing conserved methyl transferase, helicase and RNA-dependent RNA polymerase (RdRp) motifs [9]
 - b) One or more movement proteins (MP)
 - c) A single capsid (coat) protein (CP) (22–44 kDa)
 - d) A sixth ORF in some viruses, which may partially overlap the 3'-end of the CP gene and is thought to have nucleotide-binding properties.

It contains some viruses in which there is a single MP of the '30K' superfamily [10] and others which encode a triple gene block (TGB) [11] but sequence analyses of the polymerase and the CP suggest that the viruses form a coherent taxonomic unit (see below). Some properties of the 8 genera included in the family and the 6 viruses that are not assigned to any genus are summarized in Table 1 and their genome organization is shown in Fig. 1. Biologically, the viruses are fairly diverse. They have been reported from a wide range of herbaceous and woody mono- and dicotyledonous plant species but the host range of individual members is usually limited. Natural infections by members of the genera *Mandarivirus*, *Foveavirus*, *Capillovirus*, *Vitivirus* and *Trichovirus* are mostly or exclusively of

Table 1. Genera and viruses included within the family *Flexiviridae*

Genus	Virion length (nm)	ORFs	Movement protein(s) ^a	CP (kDa)
<i>Potexvirus</i>	470–580	5	TGB	22–27
<i>Mandarivirus</i>	650	6	TGB	34
<i>Allexivirus</i>	~800	6	TGB	26–29
<i>Carlavirus</i>	610–700	6	TGB	32–36
<i>Foveavirus</i>	800+	5	TGB	28–44
<i>Capillovirus</i>	640–700	2 or 3	30K	25–27
<i>Vitivirus</i>	725–785	5	30K	18–22
<i>Trichovirus</i>	640–760	3 or 4	30K	21–24
Viruses not assigned to a genus:				
<i>Banana mild mosaic virus</i>	580	5	TGB	27
<i>Cherry green ring mottle virus</i>	1000+	5	TGB	30
<i>Cherry necrotic rusty mottle virus</i>	1000+	5	TGB	30
<i>Citrus leaf blotch virus</i>	960	3	30K	41
<i>Potato virus T</i>	640	3	30K	24
<i>Sugarcane striate mosaic-associated virus</i>	950	5	TGB	23

^aTGB, Triple Gene Block [11]; 30K, single protein of the '30K' superfamily [10]

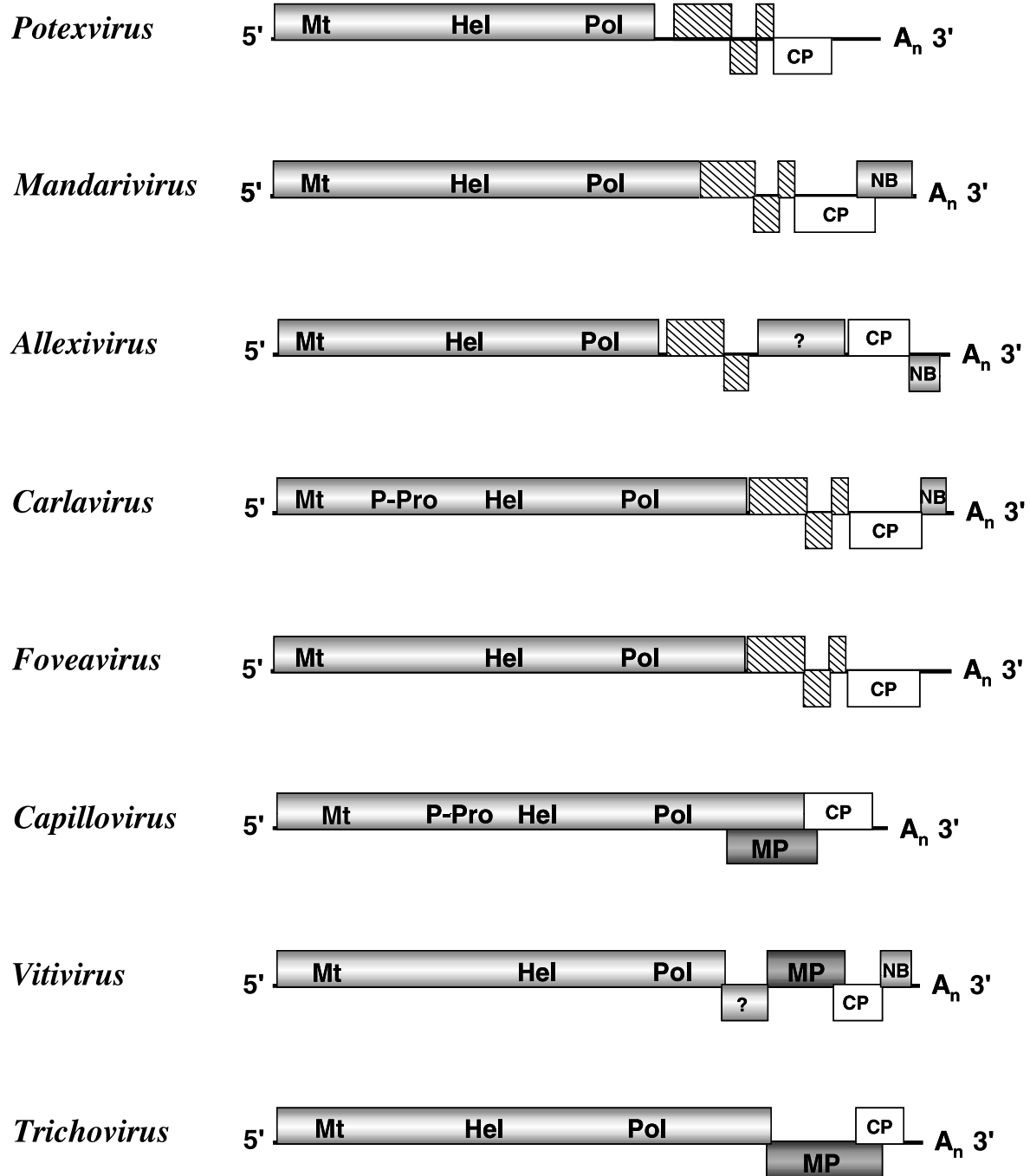


Fig. 1. Diagrams showing the typical genome organization for each of the genera in the family *Flexiviridae*. Motifs in the replication protein ORF1 are Methyltransferase (*Mt*), Helicase (*Hel*), Papain-like protease (*P-Pro*) and RNA-dependent RNA polymerase (*Pol*). Triple gene block proteins (*TGB*) are cross-hatched. CP, coat protein; *MP*, movement protein of the '30K' superfamily; *NB*, nucleic acid binding protein. In most (and perhaps all) genera there is a 5'-cap

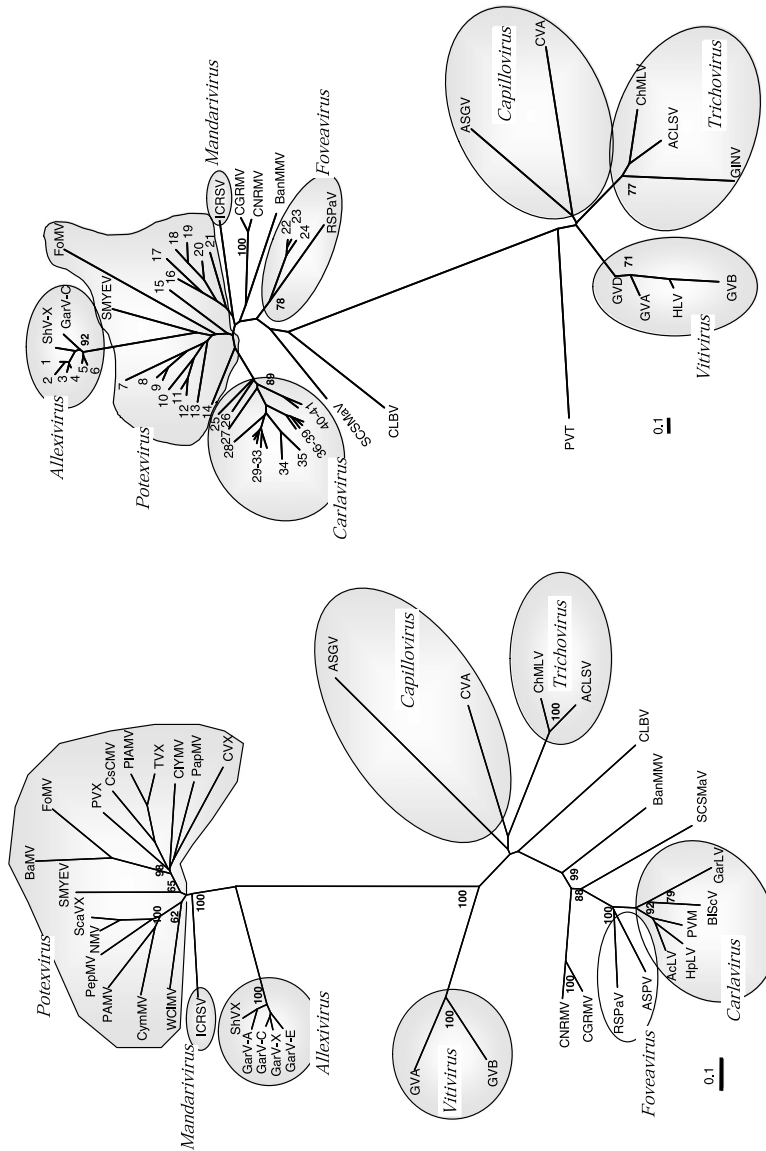


Fig. 2. Sequence analysis of viruses in the family *Flexiviridae* using the aa sequences of the RNA-dependent RNA polymerase (left) and coat protein (right). Alignments were prepared using the GCG [1] program PILEUP, with a gap creation penalty of 8 and a gap extension penalty of 2. Phylogenetic analyses were done using the programs PROTDIST (Dayhoff PAM formula) and NEIGHBOR from PHYLIP [6]. For bootstrapping, 100 data sets were generated by the program SEQBOOT from the original set and a consensus tree was obtained by the program CONSENSE. Bootstrap values are shown where >60%. Virus abbreviations are provided in the genus summaries and sequence accession numbers are: ACLSV, M58152; AcLV, AB051848; AltMV, AF080448; ApLV, AF057035; ASGV, D14995; ASPV, D21829; BaMV, D26017; BanMMV, AF314662; BiScV, L25658; CGRMV, AF017780; ChMLV, AF170028; CLB, V, AJ318061; CLV, AJ010697; CIYMV, D29630; CNRMV, AF237816; CPMMV, AF024629; CsCMV, U23414; CVA, X82547; CVB, S60150; CVX, AF308158; CymMV, U62963; FoMV, M62730; GarCLV, X81138; GarLV, AJ292226; GarMbFV, X98991; GarV-A, AB010300; GarV-B, AB010301; GarV-C, AB010302; GarV-D, AB010303; GarV-E, AJ292230; GarV-X, U89243; GINV, D88448; GVA, X75433; GVB, X75448; GVD, Y07764; HLX, X79270; HpLV, AB032469; HpMV, AB051109; HVS, D10454; ICRSV, AF406744; KLV, AJ293570; LSV, AF015286; LVX, X15342; NCLV, AJ311375; NMV, D13747; PAMV, S73580; PapMV, D13957; PepMV, AF484251; PeSRSV, AF318062; PeSV, AF354652; PIAMV, Z21647; PopMV, D13364; PVM, D14449; PVS, D00461; D10172; PVX, X05198; RSPaV, AF057136; SCSMaV, AF315308; ScaVX, AJ316085; ShVX, M97264; SMYEV, D12517; TVX, AB066288; WCIMV, X06728. Numbered positions in the right hand section of the figure are: 1, GarV-E; 2, GarV-D; 3, GarV-A; 4, GarMbFV; 5, GarV-X; 6, GarV-B; 7, CVX; 8, PapMV; 9, AltMV; 10, CsCMV; 11, PIAMV; 12, TVX; 13, CIYMV; 14, PVX; 15, LVX; 16, CymMV; 17, PAMV; 18, ScaVX; 19, NMV; 20, PepMV; 21, WCIMV; 22, PeSRSV; 23, ApLV; 24, ASPV; 25, PeSV; 26, GarLV; 27, PopMV; 28, CPMMV; 29, NCLV; 30, AcLV; 31, PVM; 32, HpLV; 33, HpmMV; 34, HVS; 35, CVB; 36, PVS; 37, BiScV; 38, KLV; 39, LSV; 40, CLV; 41, GarCLV

woody hosts. Many of the viruses have relatively mild effects upon their host. All species can be transmitted by mechanical inoculation, often readily. Many of the viruses have no known invertebrate or fungal vectors but allexiviruses and some trichoviruses are thought to be mite-borne, most carlaviruses are transmitted naturally by aphids in the non-persistent manner and a range of vectors have been reported for different vitiviruses. Aggregates of virus particles accumulate in the cytoplasm. In this paper, we summarize the evidence from sequence analysis for the creation of the family, describe studies that help to define suitable molecular criteria for demarcation of species and summarize the taxonomic structure of the family. Information on the taxonomy, viruses and sequences can be found on the ICTVdb (<http://www.ncbi.nlm.nih.gov/ICTVdb/>), DPV Web (<http://www.dpvweb.net/>) and Plant Virus Sequences (<http://www.rothamsted.bbsrc.ac.uk/ppi/links/pplinks/viruseqs/viruses.php>) web pages.

Phylogenetic considerations

The phylogenetic trees for the RdRp and CP are shown in Fig. 2. Species allocated to the same genus, group together in both analyses. If the taxonomy were to be based solely on genome organization and CP sequence analysis, the family might well contain only the genera *Potexvirus*, *Mandarivirus*, *Allexivirus*, *Carlavirus* and *Foveavirus* together with the unassigned *Cherry green ring mottle virus*, *Cherry necrotic rusty mottle virus*, *Sugarcane striate mosaic associated virus* and *Banana mild mosaic virus*. These viruses all have a TGB and analyses of these proteins show that they constitute a distinct group of TGB-containing plant viruses [15]. However, sequence analysis of the RdRp suggests that it would be unwise to exclude the three other genera (*Capillovirus*, *Vitivirus* and *Trichovirus*) and *Citrus leaf blotch virus*, because the carla- and foveaviruses associate more closely with them than with the potex- and allexiviruses. An earlier analysis gives essential similar results [8]. Our analysis forms the basis for re-classifying *Cherry green ring mottle virus* and *Cherry necrotic rusty mottle virus* (currently tentative members of the genus *Foveavirus*) and also *Potato virus T* (currently a member of the genus *Trichovirus*) as unassigned members of the newly created family. There may also be a case for re-examining the position of *Cherry virus A* in the genus *Capillovirus* but the scarcity of related sequences makes this less easy to judge.

Molecular criteria for species demarcation

A number of different properties are usually used to distinguish virus species within the same genus. The properties available and appropriate to use are not identical for all genera and families of viruses and in the 7th ICTV report [14], the relevant study groups provided criteria for each of the genera described. Sequence differences now form an important element of these criteria in most genera but an inspection of the molecular criteria provided for the different genera that are now included in the family *Flexiviridae* (Table 2) shows a lack of clarity in terminology and different thresholds. In particular, ‘sequence homology’ is ambiguous because it could refer to either nucleotides (nt) or amino acids (aa) and similarity or identity; it is also incorrect as ‘homology’ should mean similarity of function. Now that these viruses are recognized as members of the same family, it seemed appropriate to investigate the differences within and between species and genera and to determine if a consistent set of criteria could be established for the entire family.

Table 2. Molecular criteria for demarcation of species as provided in the 7th ICTV report [14]

Genus	Criteria
<i>Potexvirus</i>	The core region (i.e. excluding the variable N and C termini) of the CP of distinct species has <65% sequence homology with that of unrelated species (strains of individual viruses have 72–90% homology)
<i>Mandarivirus</i>	(Not listed)
<i>Allexivirus</i>	Less than 90% amino acid sequence identity in the CPs; less than 90% nucleotide identity in the 3' non-coding region
<i>Carlavirus</i>	The core region (i.e. excluding the N and C termini) of the CPs of distinct species have <68% sequence homology with other species; strains of individual viruses have 75–90% homology
<i>Foveavirus</i>	Amino acid sequences of any of the genes differing by more than 10%
<i>Capillovirus</i>	Amino acid sequences of CP and putative MP differing by more than 10%
<i>Vitivirus</i>	Amino acid sequences of any gene product differing by more than 10%
<i>Trichovirus</i>	Amino acid sequences of CPs differing by more than 15%

The distribution of values obtained by pairwise comparisons between sets of sequences have been used previously to determine the appropriate criteria for discriminating between strains of the same virus, different species within a genus and different genera within both the potyviruses and the geminiviruses [4, 5, 12, 13]. A complete set of pairwise comparisons was therefore made using the nt and aa sequences of each fully-sequenced gene from every available accession in the family *Flexiviridae* contained in the international databases. Comparisons used the GCG [1] program GAP (with a gap creation penalty of 50 and a gap extension penalty of 3 for nt comparisons and values of 8 and 2 respectively for aa). This program aligns the two sequences selected and calculates the percentage identity and similarity between them. To assist with the large numbers of comparisons, software was written (Antoniw, unpublished) to generate batch files that were run in GCG and also to extract and summarize data from the output files.

The frequency distributions of the percentage nt and aa identity values for some of the genes are shown in Fig. 3. The clearest patterns are shown for the CP genes, for which the largest numbers of comparisons were available. The largest peak, corresponding to nt identities of 30–60% and aa identities <60% clearly represents comparisons between different virus species and its lowest values (maximum peak height) are for comparisons between viruses belonging to different genera. The shoulder on the right of the peak (S in Fig. 3) probably represents comparisons of different species within the same genus but there is no discontinuity from the “genus peak”. There are then three further peaks (labeled A–C in Fig. 3); inspection of the data shows that peak A represents comparisons between closely related species while peaks B and C, which tend to fuse in the aa comparisons, are respectively for strains and isolates of the same species. Although based on fewer comparisons, the distribution patterns for the replication protein gene are similar but with a better separation of the shoulder from the main peak. The TGBp1 gene is smaller than the CP and is only present in some of the viruses in the family, but there is evidence of a similar distribution pattern. The data were also summarized by examining the range of variation within and between species using the names currently allocated to the sequence accessions. The results for the replication protein and CP (Table 3) show that, across all genera, boundaries between species are usually in the range 70–75% nt and 75–80% aa identity. This approximately corresponds to the troughs between

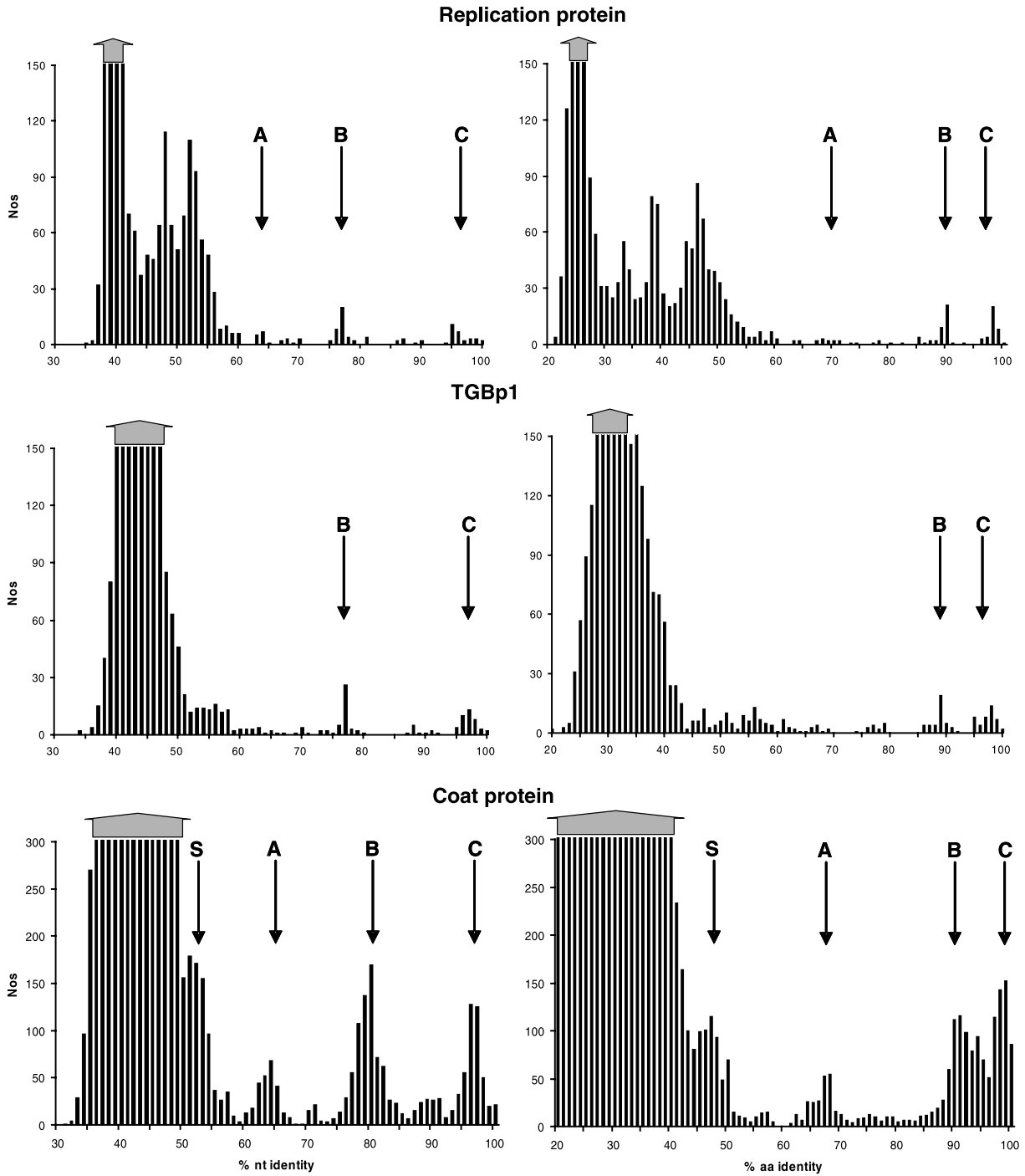


Fig. 3. Frequency distribution of the percentage nucleotide (left) or amino acid (right) identity from pairwise comparisons made using the sequences of each fully-sequenced replication protein (n = 62), TGBp1 (n = 77) and coat protein (n = 210) gene from every available accession in the family *Flexiviridae*

Table 3. Variation between and within species for each genus in the family *Flexiviridae*. Pairwise comparisons were made using the nucleotide and amino acid sequences of each fully-sequenced replication protein and coat protein gene from every available accession

	% aa identity			% nt identity		
	Between species		Within species	Between species		Within species
	min	max	min	min	max	min
Replication protein						
<i>Allexivirus</i>	66.9	81.7	93.4	63.0	69.5	89.9
<i>Capillovirus</i>	30.3	31.2	87.3	44.2	45.1	81.4
<i>Carlavirus</i>	40.3	56.4	85.6	49.4	57.4	75.5
<i>Foveavirus</i>	36.4	71.2	87.8	45.6	66.8	75.6
<i>Mandarivirus</i>	n/a ^a	n/a	n/a	n/a	n/a	n/a
<i>Potexvirus</i>	40.4	73.3	88.8	45.2	70.1	76.3
<i>Trichovirus</i>	62.7	63.8	84.7	63.4	63.9	75.4
<i>Vitivirus</i>	49.3	49.4	85.5	54.1	54.2	75.2
Coat protein						
<i>Allexivirus</i>	61.3	91.3	93.0	60.7	81.1	90.4
<i>Capillovirus</i>	34.2	36.4	94.0	41.1	45.6	89.4
<i>Carlavirus</i>	29.7	79.0	84.0	42.4	71.2	74.5
<i>Foveavirus</i>	36.0	76.7	77.8	44.4	71.2	74.4
<i>Mandarivirus</i>	n/a	n/a	82.1	n/a	n/a	73.6
<i>Potexvirus</i>	20.5	79.8	74.4	37.3	75.0	77.3
<i>Trichovirus</i>	35.1	55.2	87.1	45.2	58.2	80.8
<i>Vitivirus</i>	55.1	78.4	81.9	54.7	71.6	76.0

^aNot applicable, because there is currently only one species in this genus and only a single sequence of the replication protein

peaks A and B in Fig. 3 and the values are also very similar to those used in the potyviruses, the largest group of ssRNA viruses [2, 13].

There are a few exceptions that will need consideration for the future. For example, in the genus *Allexivirus*, the comparisons of the CPs of *Garlic mite-borne filamentous virus* with *Garlic virus A* (81.1% nt identity; 91.3% aa identity) and of *Garlic virus B* with *Garlic virus X* (75.7–77.0% nt identity; 84.8–87.7% aa identity) suggest that some amalgamation of the species may be needed. Within the genus *Potexvirus*, the unusually low value for “within species” CP aa identity is caused by some comparisons within *Cymbidium mosaic virus* that are not reflected in the nt comparisons. This suggests that the values are distorted by an apparent frameshift, possibly caused by a sequencing error.

Based on the distributions and on inspection of the data, it was concluded that, as a general rule, distinct species have less than *ca.* 72% identical nt or 80% identical aa between their entire CP or replication protein genes. Species from different genera usually have less than *ca.* 45% nt or 40% aa identity in these genes. Similar values are usually appropriate for other portions of the genome [3] but become less reliable for shorter lengths of sequence. These values will be included within the list of species demarcation criteria in the genus descriptions for the 8th ICTV report.

Taxonomic structure of the family

Genus	<i>Potexvirus</i>	Type species: <i>Potato virus X</i> (PVX)
Genus	<i>Mandarivirus</i>	Type species: <i>Indian citrus ringspot virus</i> (ICRSV)
Genus	<i>Allexivirus</i>	Type species: <i>Shallot virus X</i> (ShVX)
Genus	<i>Carlavirus</i>	Type species: <i>Carnation latent virus</i> (CLV)
Genus	<i>Foveavirus</i>	Type species: <i>Apple stem pitting virus</i> (ASPV)
Genus	<i>Capillovirus</i>	Type species: <i>Apple stem grooving virus</i> (ASGV)
Genus	<i>Vitivirus</i>	Type species: <i>Grapevine virus A</i> (GVA)
Genus	<i>Trichovirus</i>	Type species: <i>Apple chlorotic leafspot virus</i> (ACLSV)

Genus Potexvirus

Virions are flexuous filaments 470–580 nm in length and 13 nm in diameter, with helical symmetry and a pitch of 3.3–3.7 nm. The genome is a ssRNA 5.9–7.0 kb in size and comprises five ORFs, encoding, in order, the replication-related proteins, the putative MPs (TGB), and the CP. Coat protein subunits are of one type, 18–27 kDa in size. The natural host range of individual species is limited. No vector is known for any of the viruses, all of which are transmitted by mechanical contact. All species have a wide geographical distribution.

Species in the genus

<i>Alternanthera mosaic virus</i>	[AF080448]	(AltMV)
<i>Asparagus virus 3</i>		(AV-3)
<i>Bamboo mosaic virus</i>	[D26017, L77962, AF018156]	(BaMV)
<i>Cactus virus X</i>	[AF308158, AY241392]	(CVX)
<i>Cassava common mosaic virus</i>	[U23414]	(CsCMV)
<i>Cassava virus X</i>		(CsVX)
<i>Clover yellow mosaic virus</i>	[D29630]	(CIYMV)
<i>Commelina virus X</i>		(ComVX)
<i>Cymbidium mosaic virus</i>	[U62963, AF016914]	(CymMV)
<i>Daphne virus X</i>		(DVX)
<i>Foxtail mosaic virus</i>	[AY121833, M62730]	(FoMV)
<i>Hosta virus X</i>	[AY181252]	(HVX)
<i>Hydrangea ringspot virus</i>	[AJ270987, AJ550524]	(HdRSV)
<i>Lily virus X</i>	[X15342]	(LVX)
<i>Narcissus mosaic virus</i>	[D13747]	(NMV)
<i>Nerine virus X</i>		(NVX)
<i>Papaya mosaic virus</i>	[D13957]	(PapMV)
<i>Pepino mosaic virus</i>	[AF484251, AJ438767]	(PepMV)
<i>Plantago asiatica mosaic virus</i>	[Z21647]	(PIAMV)
<i>Plantago severe mottle virus</i>		(PlSMoV)
<i>Plantain virus X</i>		(PIVX)
<i>Potato aucuba mosaic virus</i>	[S73580]	(PAMV)
<i>Potato virus X</i>	[D00344, M38480, X05198, X55802, M95516, Z23256,	(PVX)

	X72214, AF111193, AF172259, AF373782, AB056718]	
<i>Scallion virus X</i>	[AJ316085]	(ScaVX)
<i>Strawberry mild yellow edge virus</i>	[D12517]	(SMYEV)
<i>Tamus red mosaic virus</i>		(TRMV)
<i>Tulip virus X</i>	[AB066288]	(TVX)
<i>White clover mosaic virus</i>	[X06728, X16636]	(WCIMV)

Tentative species in the genus

Artichoke curly dwarf virus		(ACDV)
Barley virus B1		(BarV-B1)
Boletus virus X		(BoIVX)
Centrosema mosaic virus		(CenMV)
Dioscorea latent virus		(DLV)
Lychnis symptomless virus		(LycSLV)
Malva veinal necrosis virus		(MVNV)
Nandina mosaic virus		(NaMV)
Negro coffee mosaic virus		(NeCMV)
Parsley virus 5		(PaV-5)
Parsnip virus 3		(ParV-3)
Parsnip virus 5		(ParV-5)
Patchouli virus X		(PatVX)
Rhododendron necrotic ringspot virus		(RoNRSV)
Rhubarb virus 1		(RV-1)
Smithiantha latent virus		(SmiLV)
Viola mottle virus		(VmoV)
Zygocactus symptomless virus		(ZSLV)

Genus Mandarivirus

Virions are flexuous filaments about 650 nm in length and 13 nm in diameter, have helical symmetry and a surface pattern of cross-banding. The genome is a ssRNA 7.6 kb in size and comprises six ORFs, encoding, in order, the replication-related proteins, the putative MPs (TGB), the CP and a putative nucleic acid-binding regulatory protein. Coat protein subunits are of one type, 34 kDa in size. The natural host range of the single species is restricted to citrus. There is no known vector; the virus is transmitted by grafting and persists in the host propagative material. It is mechanically transmissible to some legumes and *Chenopodium* spp.

Species in the genus

<i>Indian citrus ringspot virus</i>	AF406744	(ICRSV)
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Tentative species in the genus

None reported.

Genus Allxivirus

Virions are very flexuous filaments about 800 nm in length and 12 nm in diameter, have helical symmetry and a surface pattern of cross-banding. The genome is a ssRNA about 9.0 kb in size and comprises six ORFs, encoding, in order, the replication-related proteins, the first two proteins of a TGB, a serine-rich protein of unknown function, the CP and a putative nucleic acid-binding regulatory protein. Coat protein subunits are of one type, and 28 kDa in size. The natural host range of individual species is restricted to *Allium* spp. The viruses are transmitted by mites and also persist in the host propagative material. They are mechanically transmissible to *Allium* spp., and in some cases to *Chenopodium murale*. The viruses have a wide geographical distribution.

Species in the genus

<i>Garlic mite-borne filamentous virus</i>	[X98991]	(GarMbFV)
<i>Garlic virus A</i>	[AB010300, AF478197]	(GarV-A)
<i>Garlic virus B</i>	[AB010301, AF543829]	(GarV-B)
<i>Garlic virus C</i>	[AB010302, D49443]	(GarV-C)
<i>Garlic virus D</i>	[AB010303, AF519572, L38892]	(GarV-D)
<i>Garlic virus E</i>	[AJ292230]	(GarV-E)
<i>Garlic virus X</i>	[AJ292229, U89243]	(GarV-X)
<i>Shallot virus X</i>	[M97264, L76292]	(ShVX)

Tentative species in the genus

Garlic mite-borne latent virus	(GarMbLV)
Onion mite-borne latent virus	(OMbLV)
Shallot mite-borne latent virus	(ShMbLV)

Genus Carlavirus

Virions are flexuous filaments about 610–700 nm in length and 12–15 nm in diameter with helical symmetry. The genome is a ssRNA 7.4–7.9 kb in size and comprises six ORFs, encoding, in order, the replication-related proteins, the putative MPs (TGB), the CP and a putative nucleic acid-binding regulatory protein. Coat protein subunits are of one type, and 31–36 kDa in size. The natural host range of individual species is restricted to one or a few species. Most species are transmitted by aphids in the non-persistent manner but *Cowpea mild mottle virus* (CPMMV) is transmitted by whiteflies (*Bemisia tabaci*). Those viruses that infect vegetatively-propagated hosts persist in the host propagative material. Three of the legume-infecting viruses (*Pea streak virus*, *Red clover vein mosaic virus*, and CPMMV) are seedborne. Most species are mechanically transmissible to a wide range of hosts. Many of the viruses have a restricted geographical distribution but those that infect vegetatively-propagated hosts are more widely-distributed.

*Species in the genus***Aphid-borne carlaviruses:**

<i>American hop latent virus</i>	(AHLV)
<i>Blueberry scorch virus</i>	[L25658] (BlScV)

<i>Cactus virus 2</i>		(CV-2)
<i>Caper latent virus</i>		(CapLV)
<i>Carnation latent virus</i>	[AJ010697, X55897]	(CLV)
<i>Chrysanthemum virus B</i>	[S60150, AJ564854]	(CVB)
<i>Cole latent virus</i>	[AY340584]	(CoLV)
<i>Dandelion latent virus</i>		(DaLV)
<i>Elderberry symptomless virus</i> (Elderberry virus A)		(ESLV)
<i>Garlic common latent virus</i>	[AB004566, AB004804-05, AF228416, X81138-39]	(GarCLV)
<i>Helenium virus S</i>	[D10454]	(HVS)
<i>Honeysuckle latent virus</i>		(HnLV)
<i>Hop latent virus</i>	[AB032469]	(HpLV)
<i>Hop mosaic virus</i>	[AB051109]	(HpMV)
<i>Hydrangea latent virus</i>		(HdLV)
<i>Kalanchoe latent virus</i>	[AJ293570-71, AY238136-43]	(KLV)
<i>Lilac mottle virus</i>		(LiMoV)
<i>Lily symptomless virus</i> (Alstroemeria carlavirus)	[AJ564638, AJ516059]	(LSV)
<i>Mulberry latent virus</i>		(MLV)
<i>Muskmelon vein necrosis virus</i>		(MuVNV)
<i>Nerine latent virus</i> (Hippeastrum latent virus)		(NeLV)
<i>Passiflora latent virus</i>		(PLV)
<i>Pea streak virus</i>	[AF354652]	(PeSV)
(Alfalfa latent virus)	[AY037925]	
<i>Potato latent virus</i>	[AY007728]	(PotLV)
<i>Potato virus M</i>	[D14449, AY311394-95]	(PVM)
<i>Potato virus S</i> (Pepino latent virus)	[D00461, Y15625]	(PVS)
<i>Red clover vein mosaic virus</i>		(RCVMV)
<i>Shallot latent virus</i> (Garlic latent virus)	[Z68502, AJ292226]	(StLV)
<i>Sint-Jan's onion latent virus</i>		(SJOLV)
<i>Strawberry pseudo mild yellow edge virus</i>		(SPMYEV)

Whitefly-transmitted carlavirus:

<i>Cowpea mild mottle virus</i>	[AF024628-29]	(CPMMV)
(Bean angular mosaic virus)		
(Groundnut crinkle virus)		
(Psophocarpus necrotic mosaic virus)		
(Tomato pale chlorosis virus)		
(Voandzeia mosaic virus)		

Unknown vector carlaviruses:

<i>Aconitum latent virus</i>	[AB051848]	(AcLV)
<i>Narcissus common latent virus</i>	[AJ311375-76]	(NCLV)
<i>Poplar mosaic virus</i>	[D13364]	(PopMV)
<i>Verbena latent virus</i>	[AF271218]	(VeLV)

Tentative species in the genus

Anthriscus latent virus		(AntLV)
Arracacha latent virus		(ALV)
Artichoke latent virus M		(ArLVM)
Artichoke latent virus S		(ArLVS)
Butterbur mosaic virus		(ButMV)
Caraway latent virus		(CawLV)
Cardamine latent virus		(CaLV)
Cassia mild mosaic virus		(CasMMV)
Chicory yellow blotch virus		(ChYBV)
Cynodon mosaic virus		(CynMV)
Daphne virus S	[AJ535084]	(DVS)
Dulcamara virus A		(DuVA)
Dulcamara virus B		(DuVB)
Eggplant mild mottle virus (Eggplant virus)		(EMMV)
Euonymus mosaic virus		(EuoMV)
Fig virus S		(FVS)
Fuchsia latent virus		(FLV)
Garlic mosaic virus		(GarMV)
Gentiana latent virus		(GenLV)
Gynura latent virus (Chrysanthemum virus B?)		(GyLV)
Helleborus mosaic virus		(HeMV)
Impatiens latent virus		(ILV)
Lilac ringspot virus		(LiRSV)
Plantain virus 8		(PIV-8)
Potato rough dwarf virus	[AJ250314]	(PRDV)
Potato virus P		(PVP)
Prunus virus S		(PruVS)
Southern potato latent virus		(SoPLV)
White bryony mosaic virus		(WBMV)

Genus Foveavirus

Virions are flexuous filaments 800 to over 1000 nm in length and 12–15 nm in diameter, have helical symmetry and exhibit a surface pattern with cross-banding and longitudinal lines. The genome is a ssRNA 8.7–9.3 kb in size and comprises five ORFs, encoding, in order, the replication-related proteins, the putative MPs (TGB), and the CP. Coat protein subunits are of one type, and 28–44 kDa in size. The natural host range of individual species is restricted

to a single (RSPaV) or a few hosts (ASPV, ApLV). No vector is known for any of the viruses, all of which are transmitted by grafting and persist in the host propagative material. ASPV is mechanically transmissible, with some difficulty, to *Nicotiana occidentalis* and its subspecies *obliqua*. All species have a rather wide geographical distribution.

Species in the genus

<i>Apple stem pitting virus</i>	[D21829, AB045731]	(ASPV)
(Pear vein yellows virus)	[D21828]	
<i>Apricot latent virus</i>	[AF057035]	(ApLV)
<i>Rupestris stem pitting-associated virus</i>	[AF026278, AF057136]	(RSPaV)

Tentative species in the genus

None reported.

Genus Capillovirus

Virions are flexuous filaments, 640–700 × 12 nm, constructed from helically arranged protein subunits. The genome is a ssRNA 6.5–7.4 kb in size, made up of two ORFs. ORF1 encodes the replication-related proteins and the CP at its 3' end. The putative MP belongs to the '30K' superfamily and is expressed by ORF 2 which is nested in ORF 1. Coat protein subunits are of one type, and 24–27 kDa in size. The natural host range of individual species is restricted to a few hosts. No vector is known for any of the viruses, all of which are transmitted by grafting and persist in the host propagative material. ASGV is mechanically transmissible to herbaceous hosts and is seed-borne in *Chenopodium quinoa* and lily. Geographic distribution ranges from wide to restricted, according to the virus.

Species in the genus

<i>Apple stem grooving virus</i>	[D14995, AB004063]	(ASGV)
(Citrus tatter leaf virus)	[D16681]	
<i>Cherry virus A</i>	[X82547]	(CVA)
<i>Lilac chlorotic leafspot virus</i>		(LiCLV)

Tentative species in the genus

Nandina stem pitting virus (NSPV)

Genus Vitivirus

Virions are helically constructed flexuous filaments 725–825 × 12 nm, showing distinct cross banding. The genome is a ssRNA c. 7.6 kb containing five slightly overlapping ORFs which encode, in order, the replication-related proteins, a 19–20 K protein with unknown functions, a MP of the '30K' superfamily type, the CP, and a small protein (10–14 K) with nucleotide binding properties. Coat protein subunits are of one type, and 18–21.5 kDa in size. The natural host range of individual species is restricted to a single host. All viruses are transmitted by mechanical inoculation, some with difficulty. Grapevine-infecting species persist in the propagating material and are transmitted by grafting. GVA and GVB are transmitted in a semi-persistent manner by different species of mealybugs of the genera *Pseudococcus*,

Planococcus, and *Neopulvinaria*. HLV is transmitted semi-persistently by aphids, in association with a helper virus. Geographical distribution varies from very wide to restricted, according to the virus species.

Species in the genus

<i>Grapevine virus A</i>	[X75433, AF007415, AY244516]	(GVA)
<i>Grapevine virus B</i>	[X75448]	(GVB)
<i>Grapevine virus D</i>	[Y07764]	(GVD)
<i>Heracleum latent virus</i>	[X79270]	(HLV)

Tentative species in the genus

Grapevine virus C		(GVC)
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Genus Trichovirus

Virions are helically constructed very flexuous filaments, 640–760 × 10–12 nm, that may show cross banding, criss-cross or rope-like features according to the negative contrast stain used. The genome is a ssRNA 7.6–8 kb in size containing three slightly overlapping ORFs which encode, in order, the replication-related proteins, a putative MP of the ‘30K’ superfamily type, and the CP. An additional ORF is present at the 3′ end of the CMLV genome. Coat protein subunits are of one type, and 20.5–27 kDa in size. The natural host range of individual species is relatively narrow or restricted to a single host. The viruses are transmitted by mechanical inoculation, by grafting and through propagation material. PVT is seed-transmitted. GINV, CMLV, and PcMV are transmitted by eriophyid mites of the genera *Colomerus* and *Eriophyes*. Geographical distribution ranges from very wide to restricted, according to the virus species.

Species in the genus

<i>Apple chlorotic leaf spot virus</i>	[M58152, D14996, X99752, AJ243438]	(ACLSV)
<i>Cherry mottle leaf virus</i>	[AF170028]	(CMLV)
<i>Grapevine berry inner necrosis virus</i>	[D88448]	(GINV)
<i>Peach mosaic virus</i>		(PcMV)

Tentative species in the genus

None reported.

Unassigned species in the family

The following species have not been allocated in any of the existing genera because of the equivocal definition of their phylogenetic relationships (see Fig. 2). *Cherry green ring mottle virus* and *Cherry necrotic rusty mottle virus* were previously tentative members of the genus *Foveavirus* and *Potato virus T* was a member of the genus *Trichovirus*.

<i>Banana mild mosaic virus</i>	[AF314662]	(BanMMV)
<i>Cherry green ring mottle virus</i>	[AF017780, AJ291761]	(CGRMV)
<i>Cherry necrotic rusty mottle virus</i>	[AF237816]	(CNRMV)

<i>Citrus leaf blotch virus</i>	[AJ318061]	(CLBV)
<i>Potato virus T</i>	[D10172]	(PVT)
<i>Sugarcane striate mosaic-associated virus</i>	[AF315308]	(SCSMaV)

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