Virus Taxonomy
The ICTV Report on Virus Classification and Taxon Nomenclature
Closteroviridae Chapter

Closteroviridae


Edited by F. Murilo Zerbini and Sead Sabanadzovic

This work is dedicated to the memory of our friend and colleague Professor Giovanni Paolo Martelli, former chair of the Closteroviridae Study Group and life member of the ICTV, who passed away in January 2020.

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Summary

Plant viruses in the family Closteroviridae possess long, helically constructed filamentous particles (650–2,200 nm in length) and a large positive-sense single-stranded, mono-, bi- or tripartite RNA genome (13,000 to nearly 19,000 nucleotides) (Table 1. Closteroviridae). The presence of a cellular HSP70 homolog and a duplicated, diverged copy of the capsid protein (minor capsid protein, CPm) genes in the virus genome are hallmarks of the family. The genome expression strategy is based on proteolytic processing, a +1 ribosomal frameshift, and sub-genomic messenger RNAs. Members of the family are classified into four genera: Ampelovirus, Closterovirus, Crinivirus and Velarivirus. Their genetic diversity is primarily influenced by strong negative selection and recombination. Viruses are mostly phloem-restricted and induce specific cytoplasmic aggregates of virus particles intermingled with membranous vesicles derived from the endoplasmic reticulum and possibly mitochondria. Transmission is by aphids, whiteflies, pseudococcid mealybugs or soft scale insects in a semi-persistent manner. Experimental transmission by mechanical inoculation is very difficult or impossible, and seed transmission is not known. A few members in the family have been engineered as gene expression and RNA interference vectors.

Table 1. Closteroviridae. Characteristics of members of the family Closteroviridae

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Typical member</td>
<td>beet yellows virus (AF056575), species Beet yellows virus, genus Closterovirus</td>
</tr>
<tr>
<td>Virion</td>
<td>Non-enveloped, flexible filaments of 650–2,200 nm in length and 12 nm in diameter</td>
</tr>
<tr>
<td>Genome</td>
<td>13–19.3 kb of positive-sense, mono-, bi- or tripartite RNA</td>
</tr>
<tr>
<td>Replication</td>
<td>In association with vesicular membranes derived from the endoplasmic reticulum and mitochondria</td>
</tr>
<tr>
<td>Translation</td>
<td>Proteolytic processing, a +1 ribosomal frameshift, and sub-genomic messenger RNAs</td>
</tr>
<tr>
<td>Host range</td>
<td>Plants (mainly dicots), transmitted by aphids, whiteflies, mealybugs and soft scales. No seed transmission</td>
</tr>
<tr>
<td>Taxonomy</td>
<td>Realm Riboviria, kingdom Orthornavirae, phylum Kitrinoviricota, class Alsuviricetes, order Martellivirales, family includes four genera, and 56 species</td>
</tr>
</tbody>
</table>

Virion
Morphology

Virions are helically constructed filaments with a pitch of the primary helix in the range of 3.4–3.8 nm, containing about 10 protein subunits per turn of the helix and showing a central hole of 3–4 nm (Figure 1. Closteroviridae, top). The very flexuous and open structure of the particles is the most conspicuous trait of members of the family (Agranovskyy 2016). Virions have a diameter of about 12 nm and lengths ranging from 650 nm (viruses with a fragmented genome) to over 2,200 nm (viruses with a monopartite genome). The fragility of virions and a tendency to end-to-end aggregation contribute to the fact that many viruses are reported with a range of lengths. Two types of coat proteins (CP), the major CP and a CP analog or minor CP (CPm), are the most abundant protein components involved in the formation of (most) closterovirid particles. CPm encapsidates the 600–700 5′-terminal nucleotides of the virus RNA, at one extremity (75–100 nm) of the particle, as shown for beet yellows virus (BYV), carrot yellow leaf virus (CYLV), citrus tristeza virus (CTV), grapevine leafroll-associated virus 2 (GLRaV-2) and lettuce infectious yellows virus (LIYV), thus forming a distinct structure for which the terms “rattlesnake”, “heterodimeric” or “bipolar” have been coined (Figure 2. Closteroviridae) (Agranovsky 2016).

Figure 1. Closteroviridae. (Top) Negative-contrast electron micrograph of virions of citrus tristeza virus (CTV) (genus Closterovirus). Particles of members of the genera Ampelovirus and Crinivirus have a similar morphology. The bar represents 100 nm (Courtesy of R.G. Milne). (Bottom) Beet yellows virus (BYV) particles showing a decorated extremity (arrow heads) following exposure to an antiserum to the N-terminal peptide expressed from the CPm gene. The bar represents 100 nm (Courtsey of D.E. Lesemann).
Physicochemical and physical properties

Virions usually sediment as a single band in sucrose or Cs$_2$SO$_4$ gradients. $S_{20,w}$ is around 130–140, buoyant density is 1.33 g cm$^{-3}$ in CsCl and 1.257 g cm$^{-3}$ in Cs$_2$SO$_4$. Virions of several members are degraded by CsCl and are unstable in high salt concentration, resist moderately high temperatures (thermal inactivation is around 45–55 °C) and organic solvents, but are sensitive to RNase and chelation.

Nucleic acid

Regardless of whether the genome is monopartite or fragmented, virions contain a single molecule of linear, positive-sense, single-stranded RNA, constituting 5–6% of the particle weight. Genome size is related to particle length, ranging from 13,000 to slightly over 19,000 nucleotides. The 5′-end of the genome is likely capped. The 3′-end is not polyadenylated and does not possess a tRNA-like structure, but has several hairpin structures and a putative pseudoknot essential for replication (Agranovsky 2016).

Proteins

Structural proteins of most members of the family consist of a major CP and a diverged copy of it, denoted minor CP (CPm), with masses ranging from 22 to 46 kDa (CP) and 23 to 80 kDa (CPm), according to species. A group of ampeloviruses with a small genome (about 13,000 nt) apparently lack a true CPm. For BYV, and presumably for most other members of the family, CPm is required for the assembly of the 5′-extremity of the virion, and the ~60 kDa protein (p55-p64) is required for incorporation of both the 70 kDa heat shock protein homolog (HSP70h) and the CPm into virions, which also incorporate a 20 kDa protein (p20) that may form the tip segment of the virion head (Agranovsky 2016).

Lipids

None reported.

Carbohydrates

None reported.

Genome organization and replication

Members of the family have one of the largest genomes among plant viruses, reflecting duplication and the acquisition of nonviral coding sequences (e.g., protease, HSP70 protein) via RNA recombination (Figure 3. Closteroviridae). Recombination may also explain differences in genome organization between members of different genera and members of the same genus (Agranovsky 2016, Dolja et al., 2006, Karasev 2000, Rubio et al., 2013, Ruiz et al., 2018). The complex ORF1a-ORF1b invariably encodes the replication-related proteins, with methyltransferase (Mtr), helicase (Hel) and RNA-directed RNA polymerase (RdRP) conserved domains. Downstream ORFs, which encode in a 5′ to 3′ direction a 6 kDa small hydrophobic protein, HSP70h, a ~60 kDa protein, CP and CPm, form a five-gene module which is conserved, with few modifications, among most members of the family (Agranovsky 2016, Dolja et al., 2006). The HSP70h and the ~60 kDa proteins are integral virion components present in all members of the family for which the particle structure was studied. The functions postulated for HSP70h include mediation of cell-to-cell movement through plasmodesmata, involvement in the assembly of multi-subunit complexes for genome replication and/or subgenomic RNAs synthesis, and assembly of virus particles (Agranovsky 2016, Dolja et al., 2006). The ~60 kDa protein is required for incorporation of both HSP70h and CPm into virion heads. The duplication of the capsid protein gene seems to be unique among viruses with elongated particles (Agranovsky 2016, Dolja et al., 2006). In general, capsid proteins and their homologs (CPm) show a significant degree of sequence conservation, and the duplicate copies probably retain the general spatial folding and some other crucial properties of the CPs. A notable exception is a group of ampeloviruses with the smallest genomes in the family [e.g. grapevine leafroll-associated virus 4 (GLRaV-4) and related viruses, pineapple mealybug wilt-associated virus 1 (PMWaV-1) and pineapple mealybug wilt-associated virus 3 (PMWaV-3)] which do not appear to possess CPm. For lettuce infectious yellows virus (LIYV), the replication of both genomic RNAs is asynchronous as genomic RNA1 and sub-genomic RNAs (sgRNAs) accumulate before significant accumulation of genomic RNA2 can be detected, suggesting that RNA1 likely replicates in cis while RNA2 replicates in trans. Knockout mutation studies showed that the single-stranded RNA-binding protein p34 that is encoded by RNA1 is a trans enhancer of RNA2 replication (Kiss et al., 2013).
**Closterovirus**

beet yellows virus (15,468 nt)

- L-Pro, leader proteinase
- Mtr, methyltransferase
- Hel, helicase
- RdRP, RNA-directed RNA polymerase
- HSP70h, heat shock protein 70 homolog
- ~60 kDa protein
- CP, coat protein
- CPm, minor coat protein

The genome expression strategy is based on: (i) proteolytic processing of the polyprotein encoded by ORF1a; (ii) +1 ribosomal frameshift for the expression of the RdRP domain encoded by ORF1b, a mechanism not found in other positive-sense RNA plant viruses; and (iii) expression of the downstream ORFs via the formation of a nested set of 3′-co-terminal sgRNAs (Agranovsky 2016, Dolja et al., 2006, Karasev 2000, Rubio et al., 2013). The double-stranded (ds) RNA patterns are very complex and variable among species, reflecting the different numbers and sizes of the ORFs present in individual genomes and, in some cases, the existence of defective RNAs (D-RNAs). Replication occurs in the cytoplasm, possibly in association with endoplasmic reticulum-derived membranous vesicles and vesiculated mitochondria. From an evolutionary point of view, closteroviruses represent a monophyletic virus lineage that might have evolved from a smaller filamentous virus when higher plants differentiated (Agranovsky 2016, Dolja et al., 2006). This progenitor virus, thought to be composed of three genes encoding replication-associated proteins, a protein (p6) with affinity for cell membranes, and a single CP, acquired the HSP70h and a ~60 kDa protein derived from a fusion of two domains, an N-terminal domain of unknown evolutionary provenance, and a duplicated CP domain. Under the pressure of further modular evolutionary events, i.e. duplication of the CP gene, acquisition of diverse suppressors of RNA silencing and of additional genes acquired via horizontal gene transfer (e.g. papain-like cysteine proteinase and AlkB domains), this family ancestor gave rise to the progenitors of the four extant genera of the family. Viruses belonging to one of these genera (Crinivirus), differentiated further by the genome splitting into two or three components.

**Ampelovirus**

grapevine leafroll-associated 3 virus (18,498 nt)

- L-Pro, leader proteinase
- Mtr, methyltransferase
- AlkB, AlkB domain
- Hel, helicase
- RdRP, RNA-directed RNA polymerase
- HSP70h, heat shock protein 70 homolog
- CP, coat protein
- CPm, minor coat protein

**Velarivirus**

grapevine leafroll-associated 7 virus (16,496 nt)

- L-Pro, leader proteinase
- Mtr, methyltransferase
- AlkB, AlkB domain
- Hel, helicase
- RdRP, RNA-directed RNA polymerase
- HSP70h, heat shock protein 70 homolog
- CP, coat protein
- CPm, minor coat protein

**Crinivirus**

lettuce infectious yellows virus (RNA1; 8,118 nt; RNA2: 7,193 nts)

- L-Pro, leader proteinase
- Mtr, methyltransferase
- Hel, helicase
- RdRP, RNA-directed RNA polymerase
- HSP70h, heat shock protein 70 homolog
- CP, coat protein
- CPm, minor coat protein

The natural and experimental host ranges of individual viruses are usually restricted, except for a few members of the genus Crinivirus.
Disease symptoms are of the discoloration type (i.e. yellowing or reddening of the leaves, small and late ripening fruit), as well as stunting, rolling, pitting and/or grooving of the woody cylinder of woody hosts. Infection is systemic, but usually limited to the phloem, which may necrotize to a varying extent. Members of a few species of the genus Closterovirus are transmissible by mechanical inoculation, though with difficulty, but no members of the genera Ampelovirus, Crinivirus and Velarivirus are mechanically transmissible. In vegetatively propagated crops, long-distance virus dissemination is primarily through infected propagating material. Members of some species can be transmitted through dodder (Cuscuta spp.). Transmission through seeds has not been proven. According to the genus, natural vectors are aphids, whiteflies, pseudococcid mealybugs and soft scale insects. Transmission is semi-persistent regardless of the type of vector. Virus geographical distribution varies from restricted to widespread, depending on the species, mostly in temperate or subtropical regions. Virions are usually found in the phloem (sieve tubes, companion cells and phloem parenchyma), occasionally in the mesophyll and epidermis. Ultrastructural modifications arise by membrane proliferation, degeneration and vesiculation of mitochondria, and formation of inclusion bodies. These are made up of aggregates of virions or membranous vesicles, or a combination of the two. Virions accumulate in conspicuous cross-banded fibrous masses or, more typically, in more or less loose bundles intermingled with single or clustered membranous vesicles. Inclusions of this type are one of the hallmarks of infection by members of the family. The vesicles contain a fibrillar network and derive either from the endoplasmic reticulum, or from peripheral vesiculation of mitochondria. Virus-encoded polyproteins 1a and 1b direct membrane remodeling and formation of multi-vesicular replication factories. Polyprotein 1a of BYV contains a variable central region between the Mtr and Hel domains (aa 1,368–1,432) which induces the formation of 1 μm mobile globules originating from endoplasmic reticulum membranes. Part of the central region is conserved in all members of the genus Closterovirus and contains a predicted amphipathic helix. This region may be involved in the biogenesis of closterovirus replication factories (Gushchin et al., 2017). The LIVY-encoded p26 localizes to plasmadesmata and is involved in systemic plant infection (Qiao et al., 2018) (Qiao et al., 2018). Members of some species in the family Closteroviridae have been engineered as gene expression and RNA interference vectors (Dawson et al., 2015, Dolja and Koonin 2013, Kurth et al., 2012).

Antigenicity

Virion proteins are moderately antigenic. Members of most virus species within a particular genus are serologically unrelated or distantly related to one another. No intergeneric serological relationship has been detected.

Derivation of names

- Ampel: from Greek ampelos, meaning grapevine, the host of members of the type species of the genus Ampelovirus.
- Closto: from Greek kloster, meaning spindle or thread.
- Crini: from Latin crinis, meaning hair, from the appearance of the very long thread-like particles.
- Velar: from Latin velare, meaning cryptic or veiled, because members of the type species of the genus Velarivirus do not cause any apparent disease symptoms upon infection of their natural host

Genus demarcation criteria

Members of different genera are distinguished by multiple properties (Table 2. Closteroviridae):

- Phylogenetic relationships in the RdRP, CP, HSP70h amino acid sequence
- Vector
- Number of genomic RNAs
- Number and organization of ORFs
- Virion length

Table 2. Closteroviridae. Distinguishing properties of the viruses belonging to four genera in the family Closteroviridae

<table>
<thead>
<tr>
<th>Genus</th>
<th>Virion length (nm)</th>
<th>Number of genomic RNA species</th>
<th>Genome size (kb)</th>
<th>ORF (No.)</th>
<th>Replicase (kDa)</th>
<th>HSP70h (kDa)</th>
<th>CP (kDa)</th>
<th>CPm (kDa)</th>
<th>Vector</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ampelovirus</td>
<td>1,400–2,200</td>
<td>1</td>
<td>13.0–18.5</td>
<td>7–12</td>
<td>245–293</td>
<td>57–59</td>
<td>28–36</td>
<td>50–56</td>
<td>Mealybugs, soft scales</td>
</tr>
<tr>
<td>Velarivirus</td>
<td>1,500–1,700</td>
<td>1</td>
<td>16.2–16.9</td>
<td>9</td>
<td>260–270</td>
<td>62–69</td>
<td>34–46</td>
<td>89–76</td>
<td>None known</td>
</tr>
</tbody>
</table>

Relationships within the family

Phylogenetic relationships within the family are depicted in Figure 4. Closteroviridae. Members of the family group in four distinct genera (Martelli et al., 2012).
Figure 4. *Closteroviridae*. Phylogenetic tree showing the relationships between the species and genera of the family *Closteroviridae* based on the amino acid sequence of the HSP70h gene. The maximum-likelihood tree was produced and bootstrapped using MUSCLE and inferred using RAxML in the T-REX web server. Branch lengths are proportional to sequence distances, and the bar represents the genetic distance. This phylogenetic tree and corresponding sequence alignment are available to download from the Resources page.

Relationships with other taxa

Virions of members of some genera in the families *Alphaflexiviridae* and *Betaflexiviridae* have a similar particle morphology as those of members of the family *Closteroviridae*, although tending to be somewhat shorter. However, the CP amino acid sequences of members of these families are very different. Major differences also exist in genome length and organization, as well as in their strategy of expression. Replication-associated proteins (RdRP, Mtr and Hel) contain signature sequences homologous to those of other taxa of the "alpha-like" supergroup of positive-sense ssRNA viruses, the closest affinity being with members of the families *Bromoviridae* and *Virgaviridae*. The replication strategy, based on polyprotein processing, translational frameshifting and multiple sgRNA generation, closely resembles that of viruses in the families *Coronaviridae* and *Arteriviridae*. However, unlike closterovirids, the RdRP of coronaviruses and arteriviruses belong to the "picorna-like" supergroup of polymerases. Hence, the transcriptional strategy of members of the family *Closteroviridae* follows the mechanism of other alpha-like viruses, and is distinct from the discontinuous, leader-primed transcription of coronaviruses and arteriviruses.
**Genus: Ampelovirus**

**Distinguishing features**

The genus comprises species whose members have virions that are 1,400–2,000 nm long, a monopartite genome of 13.0–18.5 kb, and are transmitted by pseudococcid mealybugs and soft scale insects.

**Virion**

**Morphology**

See discussion under family description.

**Physicochemical and physical properties**

See discussion under family description.

**Nucleic acid**

Virions contain a single molecule of linear, positive-sense, single-stranded RNA of 13.0 to 18.5 kb. Multiple dsRNA species occur in infected tissues, the largest of which is usually the replicative form of the entire genome. Smaller dsRNAs are thought to be replicative forms of subgenomic RNAs.

**Proteins**

Structural proteins consist of a major coat protein (CP) and a minor CP (CPm), with masses ranging from 28 to 36 kDa (CP) and 50 to 56 kDa (CPm), according to virus, although subgroup II ampeloviruses apparently lack a CPm.

**Lipids**

None reported.

**Carbohydrates**

None reported.

**Genome organization and replication**

Members of the genus *Ampelovirus* show a wide variation in genome length and organization. At one extreme, there are grapevine leafroll-associated virus 1 (GLRaV-1) and grapevine leafroll-associated virus 3 (GLRaV-3), which have the largest genomes (18.5 kb). The genome of GLRaV-3 has 12 ORFs, encoding the replication related proteins (ORFs 1a and 1b), two small hydrophobic proteins (6 kDa), HSP70h, the ~60 kDa protein, coat protein (CP), minor coat protein (CPm) and the 21, 20A, 20B, 4 and 7 kDa proteins (Figure 1, *Ampelovirus*) (Maree et al., 2013). The 5´-UTR and 3´-UTR are 737 and 277 nt, respectively, in the exemplar isolate (Maree et al., 2013). The genome of GLRaV-1 differs from that of all other members of the genus in encoding two copies of CPm. At the other extreme, there is a group of viruses infecting grapevine [e.g, grapevine leafroll-associated virus 4 (GLRaV-4) and related strains] and pineapple [e.g. pineapple mealybug wilt-associated virus 1 (PMWaV-1) and pineapple mealybug wilt-associated virus 3 (PMWaV-3)] with simpler genomes made up of seven ORFs and lacking the CPm. PMWaV-1 has a genome of 13,071 nt, beginning with a 535 nt UTR at the 5´-end followed by the ORFs expressing the replication related proteins, a 6 kDa hydrophobic protein, the HSP70h, the ~60 kDa protein, the CP and a 24 kDa protein. A 3´-UTR of 132 nt terminates the genome. Replication occurs in the cytoplasm, likely in association with membranous vesicles, derived either from the endoplasmic reticulum or from peripheral vesiculation and disruption of mitochondria, as shown for GLRaV-1 and GLRaV-3. Structural and non-structural proteins are similar in type and function to those reported for the genus *Closterovirus*.
**Figure 1. Ampelovirus.** Genome organization of grapevine leafroll-associated virus 3 (GLRaV-3), a member of the type species of the genus *Ampelovirus*, showing the relative position of the open reading frames and their expression products: UTR, untranslated region; L-Pro, leader papain-like protease; Mtr, methyltransferase; AlkB, alpha-ketoglutarate-dependent hydroxylase domain; Hel, helicase; RdRP, RNA-directed RNA polymerase; HSP70h, heat shock protein 70 homolog; ~60 kDa protein; CP, coat protein; CPm, minor coat protein. The predicted sub-genomic RNAs (sgRNAs) are indicated below the genome map. Putative sgRNAs are indicated by dashed lines.

**Biology**

Members of the majority of extant ampelovirus species have been recorded from woody hosts (grapevine, plum, cherry, pistachio, blackberry and pineapple), on which, according to the host, they induce mottling, rolling yellowing and reddening of the leaves (grapevine), stem pitting (plum), wilting or symptomless infections (pineapple). Natural vectors are mealybugs and soft scale insects, which transmit in a semipersistent modality. The range of vectors varies for individual viruses from rather wide to restricted. For instance, GLRaV-1 is transmitted by species of several genera of pseudococcid mealybugs (*Heliococcus*, *Phenacoccus*, *Pseudococcus*) and soft scale insects (*Pulvinaria*, *Neopulvinaria*, *Parthenolecanium*); GLRaV-3 by pseudococcid mealybugs (*Planococcus*, *Pseudococcus*, *Heliococcus*, *Phenacoccus*) and soft scale insects (*Pulvinaria*, *Neopulvinaria*, *Parthenolecanium*, *Coccus*, *Saissetia*, *Parasaissetia*, *Ceroplastes*), whereas GLRaV-4 is transmitted by *Pseudococcus*, *Planococcus* and *Ceroplastes* spp. Vectors of pineapple ampeloviruses are two species of the genus *Dysmicoccus*, and little cherry virus 2 (LChV-2) is transmitted by *Phenacoccus aceris*. None of the viruses is transmitted through seed or mechanically. All persist in plant parts used for propagation and are disseminated with them over long distances, resulting in a very wide geographic distribution.

**Antigenicity**

Polyconal antisera and monoclonal antibodies have been raised to most of the members of the genus. A recombinant single-chain variable fragment antibody was synthesized to GLRaV-3. GLRaV-1 and GLRaV-3 are distantly serologically related based on cross-reactivity to a monoclonal antibody to GLRaV-1. Similarly, GLRaV-1 and grapevine leafroll-associated virus 13 are serologically related. GLRaV-4 and related strains, i.e., GLRaV-4 strain 5, GLRaV-4 strain 6, GLRaV-4 strain 9, GLRaV-4 strain Car, GLRaV-4 strain De, GLRaV-4 strain Pr, and GLRaV-4 strain Ob, show serological interrelations when tested with polyclonal antisera or monoclonal antibodies. The three pineapple mealybug wilt-associated viruses are serologically unrelated to one another.

**Species demarcation criteria**

The criteria demarcating species in the genus are:

- Particle size.
- Size of CP, as determined by deduced amino acid sequence data.
- Serological specificity using discriminatory monoclonal or polyclonal antibodies.
- Genome structure and organization (number, relative location and size of the ORFs).
- Amino acid sequence of relevant gene products (RdRP, CP, HSP70h) differing by more than 25%.
- Vector species and specificity.
- Magnitude and specificity of natural host range.
- Cytopathological features (i.e., aspect of inclusion bodies and origin of cytoplasmic vesicles).
## Exemplar isolate of the species

<table>
<thead>
<tr>
<th>Species</th>
<th>Virus name</th>
<th>Isolate</th>
<th>Accession number</th>
<th>RefSeq number</th>
<th>Available sequence</th>
<th>Virus Abbrev.</th>
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<tbody>
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<td>★ Air potato ampelovirus 1</td>
<td>air potato ampelovirus 1</td>
<td>FL</td>
<td>MH206615</td>
<td></td>
<td>Complete genome</td>
<td>AiPoV1</td>
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<tr>
<td>★ Blackberry vein banding-associated virus</td>
<td>blackberry vein banding-associated virus</td>
<td>Mississippi</td>
<td>KC004540</td>
<td>NC_022072</td>
<td>Complete genome</td>
<td>BVBaV</td>
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<td>★ Grapevine leafroll-associated virus 1</td>
<td>grapevine leafroll-associated virus 1</td>
<td>1050</td>
<td>JQ023131</td>
<td>NC_018509</td>
<td>Complete genome</td>
<td>GLRaV1</td>
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<td>★ Grapevine leafroll-associated virus 3</td>
<td>grapevine leafroll-associated virus 3</td>
<td>NY1</td>
<td>AF037268</td>
<td>NC_004897</td>
<td>Complete genome</td>
<td>GLRaV3</td>
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<td>grapevine leafroll-associated virus 4</td>
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<td>JQ023131</td>
<td>NC_018510</td>
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<td>LC052212</td>
<td>NC_029783</td>
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<td>★ Little cherry virus 2</td>
<td>little cherry virus 2</td>
<td>USA6b</td>
<td>AF531505</td>
<td>NC_005065</td>
<td>Complete genome</td>
<td>LChV2</td>
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<td>PMWaV1</td>
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<tr>
<td>★ Pineapple mealybug wilt-associated virus 2</td>
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<td>★ Pistachio ampelovirus A</td>
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<td>W10</td>
<td>MF198462</td>
<td></td>
<td>Complete coding genome</td>
<td>PAVA</td>
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<td>NC_009992</td>
<td>Complete genome</td>
<td>PBNSPaV</td>
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</table>

Virus names, the choice of exemplar isolates, and virus abbreviations, are not official ICTV designations.

## Related, unclassified viruses

<table>
<thead>
<tr>
<th>Virus name</th>
<th>Accession number</th>
<th>Virus abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>fig leaf mottle-associated virus 2</td>
<td>FJ473383</td>
<td>FLMaV2</td>
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<td>pistachio ampelovirus A</td>
<td>MF198462</td>
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<tr>
<td>sugarcane mild mosaic virus</td>
<td></td>
<td>SCMMV</td>
</tr>
</tbody>
</table>

Virus names and virus abbreviations are not official ICTV designations.
**Genus: Closterovirus**

**Distinguishing features**

Members of the genus have particle lengths > 1,200 nm and a single-stranded monopartite RNA genome of 14.5–19.3 kb, in which the minor coat protein (CPm) gene is located upstream of the coat protein (CP) gene. Transmission is by aphids.

**Virion**

**Morphology**

Particle morphology largely conforms to that of other members of the family, with virions ranging from 1,350 to 2,000 nm in length. Citrus tristeza virus (CTV) has additional smaller than full-length particles that may encapsidate sub-genomic or multiple species of defective RNAs (D-RNAs) containing all of the cis-acting sequences required for replication. Subgenomic RNAs (sgRNAs) may be involved in the construction of recombinant D-RNAs.

**Physicochemical and physical properties**

According to the species, virus infectivity is inactivated at temperatures between 40 and 55 °C, is retained for 1 to 4 days at room temperature, up to one year in frozen sap, two years in dried leaf material, five years in lyophilized preparations stored at −20 °C, and is destroyed at a pH lower than 6. The A260/A280 ratio is around 1.20 but for some viruses [beet yellows virus (BYV), carnation necrotic fleck virus (CNFV), burdock yellows virus (BuYV)] the virions lack tryptophan, which results in a higher ratio (1.4–1.8). S20w ranges from 130 (BYV) to 140 (CTV), buoyant density is 1.33 g cm−1 in CsCl (BYV and CTV) and 1.257 g cm−1 in Cs2SO4 (CTV).

**Nucleic acid**

Virions contain a single molecule of linear, positive-sense, single-stranded RNA of 14.5 to 19.3 kb. Multiple dsRNA species occur in infected tissues, the largest of which is usually the replicative form of the entire genome. sgRNAs generate a range of smaller dsRNAs. With CTV, the presence of D-RNA makes the dsRNA pattern of virus isolates more complex than that of other members of the genus.

**Proteins**

Structural proteins consist of a CP and minor CP (CPm), with a mass ranging from 22 to 25 kDa (CP) and 23 to 27 kDa (CPm), according to virus. The CPm is required for the assembly of the 5′-extremity of the virion, and the 60 kDa protein is required for incorporation of both HSP70h and CPm into virions, which also incorporate a 20 kDa protein that may form the tip segment of the virion head.

**Lipids**

None reported.

**Carbohydrates**

None reported.

**Genome organization and replication**

Members of the genus *Closterovirus* whose genomes have been sequenced show three types of genome organization exemplified by those of BYV (Figure 1. *Closterovirus*), CTV (Figure 2. *Closterovirus*) and beet yellow stunt virus (BYSV): (i) the BYV genome contains eight ORFs flanked by 5′- and 3′-UTRs of 107 and 181 nt, respectively; (ii) the genome of CTV has 12 ORFs and UTRs of 107 nt at the 5′-end and 275 nt at the 3′-end, and differs from the BYV genome in having two papain-like protease domains in the ORF1a-encoded protein, an extra 5′-proximal ORF (ORF2) encoding a 33 kDa product with no similarity to any other protein in databases, and two extra 3′-proximal ORFs (ORF9 and ORF11); and (iii) the genome of BYSV has 10 ORFs and a 3′-UTR of 241 nt, intermediate between that of the BYSV and CTV UTRs. A further difference with the BYSV genome rests in the presence of an extra ORF (ORF2) encoding a 30 kDa polypeptide with no similarity to any other protein in databases. This ORF is located downstream of ORF1b, i.e. in the same position as the unrelated ORF2 of CTV. Thus, organization of the BYSV genome is intermediate between that of BYV and CTV, suggesting that these three viruses might represent three distinct stages in closterovirus evolution. In addition to CP and CPm, all members of the genus encode proteins such as: (i) a large polypeptide (over 300 kDa) containing the conserved domains of papain-like protease (P-Pro), methyltransferase (Mtr), and helicase (Hel); (ii) an approximately 50 kDa protein with all the sequence motifs of a viral RNA-directed RNA polymerase (RdRP) of the "alpha-like" supergroup of positive-strand RNA viruses; (iii) a 6 kDa hydrophobic protein with membrane-binding properties; (iv) the homolog of the cellular HSP70; and (v) a 85–86 kDa product, referred to as the ~60 kDa protein. Some of the structural and nonstructural proteins function as suppressors of the plant RNA silencing defense machinery. For instance, the CP, p20 and p23 proteins of CTV have suppressor activity, much the same as the homologs of p21 of BYSV, CTV and grapevine leafroll-associated virus 2 (GLRaV-2). CTV p23 is a unique protein in the family and has a nucleolar localization (Flores et al., 2013, Ruiz-Ruiz et al., 2019). Silencing suppressors contribute to the accumulation of virus particles and are important determinants of pathogenesis.
**Biology**

Most viruses in the genus infect herbaceous hosts, berry crops and fruit crops. Symptoms are primarily of the discoloration type (yellowing or reddening) or rolling of the leaves. Some CTV strains induce stem pitting. Transmission is by aphids with a semipersistent modality. The range of vectors varies for individual viruses from rather wide to restricted. For instance, BYV is transmitted by 23 aphid species (*Myzus persicae* and *Aphis fabae* being the main natural vectors), CTV by seven species (*Toxoptera citricida* and *Aphis gossypii* being the most efficient vectors) and a number of other viruses [e.g. CNFV, wheat yellow leaf virus (WYLV), BuYV, mint virus 1 (MV-1)] by a single aphid.
species, or the vector is unknown (e.g. GLRaV-2). The specific interaction between CTV and its aphid vector *Toxoptera citricida* indicates the cibarium of the foregut as the virus retention site, and the critical role of a protein-carbohydrate complex for transmission, with CPm, p61 and p65 binding to sugar moieties on the surface of the foregut (Killiny et al., 2016). Members of some species can be transmitted by inoculation of sap, though with difficulty (e.g. CTV, GLRaV-2, BYV), but none are transmitted through seeds. Members of species that infect vegetatively propagated hosts (citrus, grapevine, raspberry) are transmitted by grafting and can be disseminated over long distances with infected propagating material. Geographic distribution ranges from very wide (e.g. CTV, GLRaV-2, BYV) to restricted (e.g. BuYV, MV-1, WYLV).

### Antigenicity

No serological relationships are reported among members of different virus species in the genus. Monoclonal antibodies have been produced to BYV, CTV and GLRaV-2 and polyclonal antisera have been raised to BYV, CTV and carrot yellow leaf virus (CYLV) from fusion proteins obtained in bacterial expression systems. Polyclonal antisera have been raised to purified particles of BYV, BYSV, GLRaV-2 and BuYV.

### Species demarcation criteria

The criteria demarcating species in the genus are:

- Particle size.
- Size of CP, as determined by deduced amino acid sequence data.
- Serological specificity using discriminatory monoclonal or polyclonal antibodies.
- Genome structure and organization (number and relative location of the ORFs).
- Amino acid sequence of relevant gene products (RdRP, CP, HSP70h) differing by more than 25%.
- Vector species and specificity.
- Magnitude and specificity of natural and experimental host range.
- Cytopathological features (i.e., aspect of inclusion bodies and origin of cytoplasmic vesicles).

### Member species

**Exemplar isolate of the species**

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Virus names, the choice of exemplar isolates, and virus abbreviations, are not official ICTV designations.

### Related, unclassified viruses

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Virus names and virus abbreviations are not official ICTV designations.

*partial sequence
**Genus: Crinivirus**

**Distinguishing features**

The genus comprises species whose members are transmitted by whiteflies. Virions are 650–900 nm long and have a bipartite genome, but potato yellow vein virus (PYVV) has a tripartite genome.

**Virion**

**Morphology**

See discussion under family description.

**Physicochemical and physical properties**

See discussion under family description.

**Nucleic acid**

The virions of members with a bipartite genome contain a single molecule of linear, positive-sense, single-stranded RNA of 7,801 to 9,127 nt (RNA1) and another of 7,903 to 8,530 nt (RNA2). In the case of PYVV, the tripartite genome consists of single-stranded RNAs of 8,035 nt (RNA1), 5,399 nt (RNA2) and 3,892 nt (RNA3).

**Proteins**

Structural proteins consist of a coat protein (CP) and a minor CP (CPm), with masses ranging from 22 to 29 kDa (CP) and 53 to 80 kDa (CPm), according to virus.

**Lipids**

None reported.

**Carbohydrates**

None reported.

**Genome organization and replication**

The genome of most criniviruses [e.g. lettuce infectious yellows virus (LIYV)] is divided between two linear, positive-sense, single-stranded RNAs totaling 15.6–17.9 kb (Figure 1, Crinivirus), but PYVV possesses a tripartite genome. All molecules are needed for infectivity and are separately encapsidated. RNA1 of LIYV contains three ORFs, i.e. the ORF1a–ORF1b complex plus a 3′-proximal ORF coding for a 32 kDa protein with no similarity to any protein in databases. This ORF is similar in size and location to ORF2 of citrus tristeza virus (CTV) and beet yellow stunt virus (BYSV) but the respective expression products are not related. RNA1 has 5′- and 3′-UTRs of 97 and 219 nt, respectively. A with other members of the family, the ORF1a–ORF1b complex codes for the replication-related proteins including the RdRP. RNA2 has seven ORFs flanked by a 5′-UTR of 326 nt and a 3′-UTR of 187 nt. RNA2 contains the five-gene module, which, however, differs from that of members of the genus Closterovirus by the insertion of an extra gene (ORF4) upstream of the coat protein (CP) gene. The replication of both genomic RNAs of LIYV is asynchronous, with genomic RNA1 and sgRNAs accumulating before genomic RNA2, and the single-stranded RNA-binding protein p34 encoded by RNA1 acting as a trans enhancer of RNA2 replication (Kiss et al., 2013).
**Figure 1. Crinivirus.** Genome organization of lettuce infectious yellows virus (LIYV), a member of the type species of the genus *Crinivirus*, showing the relative position of the open reading frames and their expression products: UTR, untranslated region; L-Pro, papain-like protease; Mtr, methyltransferase; Hel, helicase; RdRP, RNA-directed RNA polymerase; HSP70h, heat shock protein 70 homolog; ~60 kDa protein; CP, coat protein; CPm, minor coat protein.

The genome of PYVV consists of: (i) RNA1 (8,035 nt) with three ORFs, i.e., the ORF1a-ORF1b complex and a 7 kDa hydrophobic protein containing a potential transmembrane helix; (ii) RNA2 (5,339 nt) with five predicted ORFs encoding the HSP70h; a 7 kDa protein similar to a comparable protein of cucurbit yellow stunting disorder virus (CYSDV); the ~60 kDa protein; a 9.8 kDa product with no significant similarity to any other sequence in database; and the 28.2 kDa putative CP; (iii) RNA3 (3,892 nt) with three potential ORFs encoding a 4 kDa protein with no counterpart with other proteins in the family and no significant sequence homology in databases; the 77.5 kDa minor coat protein (CPm), and a 26.4 kDa protein present in other members of the genus. In all criniviruses, the order of the CP and CPm ORFs is similar to that in members of the genera *Ampelovirus* and *Velarivirus* but reversed compared to that of members of the genus *Closterovirus*. Sweet potato chlorotic stunt virus (SPCSV) and tomato chlorosis virus (ToCV) have a particularly large CPm (75–80 kDa) compared to LIYV (53 kDa).

**Biology**

Criniviruses infect primarily herbaceous hosts, in which they induce extensive chlorosis to yellow discoloration of the leaves, often accompanied by stunting. They are transmitted semi-persistently by whiteflies of the genera *Trialeurodes* and *Bemisia* (Tzanetakis et al., 2013). Persistence and specificity of transmission by their respective vectors have been used as characters for species differentiation. Thus, the viruses of “group 1” [PYVV, blackberry yellow vein-associated virus (BYVaV), beet pseudoyellows virus (BPYYV) and strawberry pallidosis-associated virus (SpaV)] are transmitted by *T. vaporariorum*, viruses of “group 2” [ToCV, SPCSV, CYSDV and bean yellow disorder virus (BYDV)] by *B. tabaci*, whereas one of the viruses of “group 3” is transmitted by *B. tabaci* (LIYV) and the other by *T. vaporariorum* (TICV). These three groups were identified by comparative phylogenetic analyses of RdRP amino acid sequences. None of the viruses is transmitted through seed or mechanically. Geographical distribution varies from restricted (e.g. BYVaV) to very wide. The membranous vesicles with a fibrillar content derive from the endoplasmic reticulum or from vesiculated mitochondria. Structural and non-structural proteins are similar in type and function to those reported for members of the genus *Closterovirus*. Both genomic RNAs of ToCV encode RNA silencing suppressors, e.g. the p22 protein in RNA1, and the CP and CPm in RNA2. Suppressor activity is also displayed by the p25 protein of CYSDV, and by the viral RNAse III and the p22 gene present in a few isolates of SPCSV. The LIYV-encoded p26 is involved in systemic plant infection and localizes to plasmodesmata (Qiao et al., 2018).

**Antigenicity**

Monoclonal antibodies have been produced to proteins of SPCSV. Antisera have been raised from structural and nonstructural proteins produced as fusion proteins in bacterial expression systems (SPCSV and LIYV) or from CPs [tomato infectious chlorosis virus (TICV), LIYV, lettuce chlorosis virus (LCV) and ToCV]. Generally, there are no detectable serological relationships between members of different species. TICV and ToCV, however, are distantly serologically related.

**Species demarcation criteria**

The criteria demarcating species in the genus are:

- Particle size.
- Size of CP, as determined by deduced amino acid sequence data.
- Serological specificity using discriminatory monoclonal or polyclonal antibodies.
- Genome structure and organization (number and relative location of the ORFs).
- Amino acid sequence of relevant gene products (RdRP, CP, HSP70h) differing by more than 25%.
- Vector species and specificity.
- Magnitude and specificity of natural host range.
• Cytopathological features (i.e., aspect of inclusion bodies and origin of cytoplasmic vesicles).

Member species

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<th>Species</th>
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<th>Isolate</th>
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<th>RefSeq number</th>
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Virus names, the choice of exemplar isolates, and virus abbreviations are not official ICTV designations.

Related, unclassified viruses

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Virus names and virus abbreviations are not official ICTV designations.
Genus: Velarivirus

Distinguishing features

The genus comprises species whose members have virion particles of 1,500 to 1,700 nm in length, a positive-sense, single-stranded RNA genome of 16–16.9 kb, and no known insect vector.

Virion

Morphology

See discussion under family description.

Physicochemical and physical properties

See discussion under family description.

Nucleic acid

Virions contain a single molecule of linear, positive-sense, single-stranded RNA of 16,080 to 16,934 nt.

Proteins

Structural proteins consist of a coat protein (CP) and a minor CP (CPm), with masses ranging from 34 to 46 kDa (CP) and 69 to 76 kDa (CPm), according to species.

Lipids

None reported.

Carbohydrates

None reported.

Genome organization and replication

Little cherry virus 1 (LChV-1) has the largest genome reported for the genus at 16,934 nt (isolate UW2) and contains nine ORFs coding for the replication associated proteins [ORF 1a with a L-Pro, a methyltransferase (Mtr) and a helicase (Hel); and ORF1b with an RNA-directed RNA polymerase (RdRP)], a small hydrophobic protein (4–8 kDa) with a transmembrane domain, the HSP70h, the ~60 kDa protein, coat protein (CP), minor coat protein (CPm), and two additional proteins of 25 and 27 kDa. The genome of grapevine leafroll-associated virus 7 (GLRaV-7), a member of the type species of the genus, is of 16,496 nt (isolate Swi) and has nine ORFs encoding structural and non-structural proteins (Figure 1. Velarivirus) similar in type and function to those of LChV-1 (Al Rwahnih et al., 2012).
**Velarivirus**

*grapevine leafroll-associated virus 7, GLRaV-7 (16,496 nt)*

![Diagram of genome organization of grapevine leafroll-associated virus 7 (GLRaV-7), a member of the type species of the genus *Velarivirus*, showing the relative position of the open reading frames and their expression products: UTR, untranslated region; L-Pro, papain-like protease; Mtr, methyltransferase; Hel, helicase; RdRP, RNA-directed RNA polymerase; HSP70h, heat shock protein 70 homolog; ~60 kDa protein; CP, coat protein; CPm, minor coat protein.]

**Biology**

Velariviruses infect primarily woody hosts, in which they induce no apparent symptoms. No insect vector is known for any of the members of the genus. None of the viruses is transmitted through seed or mechanically. Geographical distribution varies from restricted (e.g. areca palm velarivirus 1, ArPV1) to wide (LChV-1).

**Antigenicity**

Antisera have been raised from purified virions of a few velariviruses. There are no detectable serological relationships between members of different species.

**Species demarcation criteria**

The criteria demarcating species in the genus are:

- Particle size.
- Size of CP, as determined by deduced amino acid sequence data.
- Serological specificity using discriminatory monoclonal or polyclonal antibodies.
- Genome structure and organization (number and relative location of the ORFs).
- Amino acid sequence of relevant gene products (RdRP, CP, HSP70h) differing by more than 25%.
- Magnitude and specificity of natural host range.
- Cytopathological features (i.e., aspect of inclusion bodies and origin of cytoplasmic vesicles).

**Member species**

<table>
<thead>
<tr>
<th>★ Exemplar isolate of the species</th>
<th>Virus name</th>
<th>Isolate</th>
<th>Accession number/RefSeq number</th>
<th>Available sequence/Virus Abbrev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Areca palm velarivirus 1</td>
<td>areca palm velarivirus 1</td>
<td>RN</td>
<td>KP859494/NC_007121</td>
<td>Complete genome/ArPV1</td>
</tr>
<tr>
<td>Cordyline virus 1</td>
<td>cordyline virus 1</td>
<td>Kahaluu1</td>
<td>HM988723/NC_038421</td>
<td>Complete genome/CV1</td>
</tr>
<tr>
<td>Cordyline virus 2</td>
<td>cordyline virus 2</td>
<td>SJ1</td>
<td>JQ599282/NC_043453</td>
<td>Partial genome/CV2</td>
</tr>
<tr>
<td>Cordyline virus 3</td>
<td>cordyline virus 3</td>
<td>SJ1</td>
<td>JQ599283/NC_043107</td>
<td>Partial genome/CV3</td>
</tr>
<tr>
<td>Cordyline virus 4</td>
<td>cordyline virus 4</td>
<td>SJ1</td>
<td>JQ599284/NC_043108</td>
<td>Partial genome/CV4</td>
</tr>
<tr>
<td>★ Grapevine leafroll-associated virus 7</td>
<td>grapevine leafroll-associated virus 7</td>
<td>AA42</td>
<td>HE588185/NC_016436</td>
<td>Complete genome/GLRaV7</td>
</tr>
<tr>
<td>★ Little cherry virus 1</td>
<td>little cherry virus 1</td>
<td>UW2</td>
<td>Y10237/NC_001836</td>
<td>Complete genome/LCV1</td>
</tr>
</tbody>
</table>

Virus names, the choice of exemplar isolates, and virus abbreviations, are not official ICTV designations.
Unassigned species

Summary

Strawberry mottle virus, black raspberry virus and chocolate lily virus A are related to satsuma dwarf virus (SDV) in phylogenetic trees using the conserved Pro-Pol region (Figure 4. Secoviridae). Dioscorea mosaic associated virus, recently isolated from yam, is most closely related to chocolate lily virus A (Hayashi et al., 2016). These viruses also have a bipartite genome. However, the nature of their capsid protein(s) and their genomic organization are not known. For this reason, they are unassigned species in the family Secoviridae. Strawberry latent ringspot virus was formerly considered a sadwavirus because it has two capsid proteins (CP) and some distant relation with SDV in phylogenetic trees using the Pro-Pol sequence (Figure 4. Secoviridae). However, its genomic organization is more related to that of cheraviruses (with the exception of the number of CPs, Figure 3. Secoviridae) and it branches more closely with cheraviruses than with sadwaviruses in the phylogenetic trees using the Pro-Pol sequence (Figure 4. Secoviridae). For these reasons, it is not considered a sadwavirus anymore, and is now an unassigned species in the family Secoviridae.

Unassigned species in family Secoviridae

<table>
<thead>
<tr>
<th>Species</th>
<th>Virus name</th>
<th>Isolate</th>
<th>Accession number</th>
<th>RefSeq number</th>
<th>Available sequence</th>
<th>Virus Abbrev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>★ strawberry latent ringspot virus</td>
<td>strawberry latent ringspot virus</td>
<td>NCGR MEN 454.001</td>
<td>RNA-1: AY860978; RNA-2: AY860979</td>
<td>RNA-1: NC_009894; RNA-2: NC_009895</td>
<td>Complete genome</td>
<td>SLRSV</td>
</tr>
</tbody>
</table>

Virus names, the choice of exemplar isolates, and virus abbreviations, are not official ICTV designations.
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Resources: Closteroviridae

The full-length genome sequence of members of 56 species in the family *Closteroviridae* is available at https://www.ncbi.nlm.nih.gov/genomes/GenomesGroup.cgi?taxid=69973

Sequence alignments and tree files:

**Figure 4. Closteroviridae**

- Tree file (newick format)
- Alignment file (FASTA format)
Further reading: Closteroviridae

References: Closteroviridae


Citation: Closteroviridae

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