Secoviridae

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Summary

Members of the family Secoviridae are non-enveloped viruses with mono- or bipartite (RNA-1 and RNA-2) linear positive-sense ssRNA genomes of 9 to 13.7 kilobases in total (Table 1. Secoviridae). Secoviruses are related to picornaviruses and are classified in the order Picornavirales. The majority of known members infect dicotyledonous plants and many are important plant pathogens (e.g., grapevine fanleaf virus and rice tungro spherical virus).

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

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Typical member</td>
<td>cowpea mosaic virus, (RNA-1: X00206; RNA-2: X00729), species Cowpea mosaic virus, genus Comovirus</td>
</tr>
<tr>
<td>Virion</td>
<td>Non-enveloped 25–30 nm in diameter with icosahedral symmetry</td>
</tr>
<tr>
<td>Genome</td>
<td>9 to 13.7 kb of positive-sense, mono- or bipartite RNA</td>
</tr>
<tr>
<td>Replication</td>
<td>In association with intracellular membranes derived from the endoplasmic reticulum</td>
</tr>
<tr>
<td>Translation</td>
<td>Directly from genomic RNA as large polyproteins, which are cleaved by 3C-like proteinases</td>
</tr>
<tr>
<td>Host range</td>
<td>Plants (mainly dicots), transmitted mainly by insects or nematodes. Some seed transmission demonstrated</td>
</tr>
<tr>
<td>Taxonomy</td>
<td>Realm Riboviria, order Picornavirales. The family includes 1 subfamily with 3 genera, 5 additional genera and 86 species</td>
</tr>
</tbody>
</table>

Comovirus - (subfamily Comovirinae). Bipartite genome. Comoviruses usually have a narrow host range. Mosaic and mottle symptoms are characteristic. Transmission in nature is exclusively by beetles, especially members of the family Chrysomelidae. Beetles retain their ability to transmit virus for days or weeks.

Fabavirus - (subfamily Comovirinae). Bipartite genome. Fabaviruses have a wide host range among dicotyledonous and some families of monocotyledonous plants. Symptoms are typically ringspots, mottling and wilting. In nature, they are transmitted by aphids in a non-persistent manner.

Nepovirus - (subfamily Comovirinae). Bipartite genome. The genus includes 40 species that are widely distributed in temperate regions. Ringspot symptoms are characteristic. Many nepoviruses are transmitted non-persistently by longidorid nematodes. Seed and/or pollen transmission are also common. In herbaceous plants, the symptoms induced are often transient with a so-called “recovery” phenomenon.

Cheravirus. Bipartite genome. Symptoms are usually mild or absent. Cherry rasp leaf virus is transmitted by nematodes in the field.
Sadwavirus. Includes a single bipartite species, *Satsuma dwarf virus*, members of which have a wide host range. The natural mode of transmission is unknown.

Torradovirus. Bipartite genome. The torradovirus genome contains an open reading frame (ORF) upstream and partially overlapping the large ORF2 in RNA-2. Some torradoviruses are transmitted by whiteflies in a semi-persistent manner; one torradovirus is transmitted by aphids.

Seqivirus. Monopartite genome. The natural host range of seqiviruses includes plants in several families. Transmission is by aphids in a semi-persistent manner, but is dependent on the presence of a helper virus in the genus *Waikavirus*.

Waikavirus. Monopartite genome. The natural host range of waikaviruses is usually restricted to plants within a few families. Field transmission is semi-persistent by aphids or leafhoppers. Some waikaviruses are helper viruses for the insect transmission of other viruses, for example, rice tungro spherical virus is the helper virus for rice tungro bacilliform virus (family *Caulimoviridae*).

Species unassigned to a genus. Bipartite genome. The species *Strawberry mottle virus*, *Black raspberry virus* and *Chocolate lily virus A* are unassigned in the family but members form a divergent monophyletic group with isolates of *Satsuma dwarf virus* in phylogenetic trees using the conserved Pro-Pol region (Figure 4. *Secoviridae*). The nature of their capsid protein(s) and their genomic organization are not known. The genome organization of strawberry latent ringspot virus, a member of the species *Strawberry latent ringspot virus*, is more related to that of cheraviruses (with the exception of the number of capsid proteins) and it groups more closely with cheraviruses than with sadwaviruses in the phylogenetic trees using the Pro-Pol sequence.

Virion

**Morphology**

Virions are non-enveloped 25–30 nm in diameter and exhibit icosahedral symmetry (T=1, pseudo T=3, Figure 1. *Secoviridae*). Many virus preparations contain empty particles. In the case of viruses with a bipartite genome, the two RNAs are encapsidated in separate virions.

![Virion Morphology](image)

**Figure 1. Secoviridae.** (Top left): Molecular rendering of the cowpea mosaic virus particle. (Top central): Diagrammatic representation of a T=1 lattice. A=Small capsid protein, B=C-terminal domain of the large capsid protein and C=N-terminal domain of the large capsid protein. (Top right): Molecular rendering of the red clover mottle virus particle. (Center): Diagram of the three types of comovirus particles with the B-particle containing one molecule of RNA-1, the M-particle containing one molecule of RNA-2 and the T-particle being empty. (Bottom): Negative-contrast electron micrograph of particles of cowpea mosaic virus. The bar represents 100 nm.

**Physicochemical and physical properties**

Different classes of virions are distinguished according to their buoyant densities (top, middle and bottom components, also termed T, M and B). (Figure 1. *Secoviridae*). The main virion components (M and B) contain RNA. Viruses belonging to the genera *Seqivirus* and *Waikavirus*, which have a large monopartite genome, sediment with $S_{20w}$ values of 150–190S. For viruses with a bipartite genome, virions containing RNA-1 (B component) sediment at 110–135S. Virions containing RNA-2 (M component) sediment at 84–128S and contain one or two molecules of RNA-2. In cases where the lengths of RNA-1 and RNA-2 are similar, the M and B components may be difficult to separate. Empty shells (T component) sediment with $S_{20w}$ values of 49–63S depending on the virus considered.
**Nucleic acid**

The genome consists of one or two molecules of linear positive-sense ssRNA with lengths that differ among genera (Table 2). The genomic RNA(s) contain a 3ʹ-terminal poly(A) tract of variable length. The only known exception is the genomic RNA of a sequivirus (parsnip yellow fleck virus), which is apparently not poly-adenylated. For several comoviruses and nepoviruses, and for strawberry latent ringspot virus, a protein, designated VPg (2–4 kDa) has been shown to be covalently bound at the 5ʹ-end. The presence of a 5ʹ-linked VPg has not been confirmed for other genera but has been suggested because in many cases, infectivity of the RNA(s) has been shown to be protease-sensitive.

**Table 2. Secoviridae.** Accession numbers and genome content (bases), of representative viruses in the family Secoviridae

<table>
<thead>
<tr>
<th>Genus/Virus</th>
<th>RNA-1</th>
<th>RNA-2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Comovirus</strong></td>
<td>5,850–6,100</td>
<td>3,300–4,000</td>
</tr>
<tr>
<td>cowpea mosaic virus</td>
<td>X00206 (5,889)</td>
<td>X00729 (3,481)</td>
</tr>
<tr>
<td><strong>Fabavirus</strong></td>
<td>5,800–6,000</td>
<td>3,300–4,000</td>
</tr>
<tr>
<td>broad bean wilt virus 2-ME</td>
<td>AF225953 (5,951)</td>
<td>AF225954 (3,607)</td>
</tr>
<tr>
<td><strong>Nepovirus</strong></td>
<td>7,200–8,400</td>
<td>3,700–7,300</td>
</tr>
<tr>
<td>grapevine fanleaf virus-F13 (Subgroup A)</td>
<td>D00915 (7,342)</td>
<td>X16907 (3,774)</td>
</tr>
<tr>
<td>beet ringspot virus-S (Subgroup B)</td>
<td>D00322 (7,356)</td>
<td>X04062 (4,662)</td>
</tr>
<tr>
<td>Tomato ringspot virus-Raspberry (Subgroup C)</td>
<td>L19655 (8,214)</td>
<td>D12477 (7,273)</td>
</tr>
<tr>
<td><strong>Cheravirus</strong></td>
<td>6,800–7,100</td>
<td>3,200–3,700</td>
</tr>
<tr>
<td>cherry rasp leaf virus-USA</td>
<td>AJ621357 (5,992)</td>
<td>AJ621358 (3,274)</td>
</tr>
<tr>
<td><strong>Sadwavivirus</strong></td>
<td>6,800–7,000</td>
<td>5,300–5,600</td>
</tr>
<tr>
<td>satsuma dwarf virus-S58</td>
<td>AB009958 (6,795)</td>
<td>AB009959 (5,345)</td>
</tr>
<tr>
<td><strong>Torradovirus</strong></td>
<td>7,000–7,800</td>
<td>4,700–5,900</td>
</tr>
<tr>
<td>tomato torrado virus-PRI-0301</td>
<td>DQ388879 (7,793)</td>
<td>DQ388880 (5,389)</td>
</tr>
<tr>
<td><strong>Sequivirus</strong></td>
<td>9,800–10,000</td>
<td></td>
</tr>
<tr>
<td>parsnip yellow fleck virus-P121</td>
<td>D14066 (6,871)</td>
<td>NA</td>
</tr>
<tr>
<td><strong>Waikavirus</strong></td>
<td>11,700–12,500</td>
<td></td>
</tr>
<tr>
<td>rice tungro spherical virus-Shen</td>
<td>M95497 (12,226)</td>
<td></td>
</tr>
<tr>
<td><strong>Unassigned species in the family</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>strawberry latent ringspot virus-MEN 454</td>
<td>AY860979 (7,496)</td>
<td>AY860979 (3,842)</td>
</tr>
<tr>
<td>strawberry mottle virus-Thompson</td>
<td>AJ311875 (7,036)</td>
<td>AJ311876 (5,619)</td>
</tr>
<tr>
<td>black raspberry necrosis virus-1</td>
<td>DQ344639 (7,581)</td>
<td>DQ344640 (6,364)</td>
</tr>
<tr>
<td>chocolate lily virus A-KP2</td>
<td>JN052073 (6,139)</td>
<td>JN052074 (4,735)</td>
</tr>
<tr>
<td>Dioscorea mosaic associated virus-goiana</td>
<td>KU215538 (5,979)</td>
<td>KU215539 (3,810)</td>
</tr>
</tbody>
</table>

NA: not applicable.

**Proteins**

Nepoviruses have a single capsid protein (CP) of 52–60 kDa. Comoviruses, fabaviruses, sadwaviruses and strawberry latent ringspot virus have two CPs of 40–45 kDa and 21–29 kDa. Cheraviruses, torradoviruses, sequiviruses and waikaviruses have three CPs of similar sizes (24–35 kDa, 20–26 kDa and 20–25 kDa). The size and number of the CP(s) of viruses from three unassigned species of the family (Strawberry mottle virus, Black raspberry necrosis virus and Chocolate lily virus A) have not been determined yet. Virions have 60 copies of each CP per particle. For three comoviruses (cowpea mosaic virus, bean pod mottle virus and red clover mottle virus) and three nepoviruses (tobacco ring spot virus, grapevine fanleaf virus and arabis mosaic virus), the atomic structure has been solved and found to be very similar (pseudo T=3) to that of viruses belonging to the family Picornaviridae (Chandrasekar and Johnson 1998, Schellenberger et al., 2011, Lai-Kee Him et al., 2013, Lin et al., 2000, Chen et al., 1989). Each capsid subunit consists of three beta-barrels (jelly roll domains) that can be present in one large CP with three jelly roll domains (Nepovirus), two CPs (one large CP including two jelly roll domains and one smaller CP with a single jelly roll domain; Comovirus, Fabavirus and Sadwavirus and strawberry latent ringspot virus) or three CPs each containing a single jelly roll domain (Cheravirus, Torradovirus, Sequivirus, Waikavirus) (Figure 2, Secoviridae).
Genome organization and replication

Unfractionated viral RNA is highly infective. In the case of viruses with a bipartite genome, neither RNA species alone can infect plants systemically. RNA-1 carries all the information required for replication and can replicate in individual cells in the absence of RNA-2 although no virus particles are produced (as demonstrated for comoviruses and nepoviruses).

Viral proteins are usually expressed as large polyproteins, which are cleaved by 3C-like proteinases. Each RNA usually encodes a single polyprotein (Figure 3. Secoviridae). A notable exception is the RNA-2 of torradoviruses, which contains two ORFs. Another exception is the RNA-2 of comoviruses. Although a single large ORF is present, internal initiation at a second AUG allows the formation of two distinct polyproteins. In some cases, extensive regions of sequence identity between RNA-1 and RNA-2 are found in the 5′- and/or 3′-untranslated regions (UTRs) (Figure 3. Secoviridae).

### Comovirinae

<table>
<thead>
<tr>
<th>Virus</th>
<th>RNA-1</th>
<th>RNA-2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Comovirus</td>
<td>NTB</td>
<td>MP CP(s)</td>
</tr>
<tr>
<td>Fabavirus</td>
<td>NPB</td>
<td>CP(s)</td>
</tr>
<tr>
<td>Nepovirus</td>
<td>MP</td>
<td>CP(s)</td>
</tr>
<tr>
<td>Sg A (arabis mosaic virus)</td>
<td>CP</td>
<td>CP(s)</td>
</tr>
<tr>
<td>Sg B (tomato black ring virus)</td>
<td>CP</td>
<td>CP(s)</td>
</tr>
<tr>
<td>Sg C (tomato ringspot virus)</td>
<td>CP</td>
<td>CP(s)</td>
</tr>
</tbody>
</table>

### Other genera

- **Cheravirus** (cherry rasp leaf virus)
- **Sadnavirus** (satsuma dwarf virus)
- **Torradovirus** (tomato torrado virus)
- **Soquivirus** (ponytail yellow flock virus)
- **Waikavirus** (rice tungro spherical virus)

### Unassigned species

- strawberry motto virus
- black raspberry necrosis virus
- chocolate fly virus A
- strawberry latent ringspot virus

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Figure 2. *Secoviridae*. Architecture of the capsid of members of the family *Secoviridae*. In sequiviruses, waikaviruses, cheraviruses and torradoviruses, each subunit is composed of three separate small capsid proteins (CPs) each containing a single beta-barrel domain (VP1-VP3, top). In comoviruses, fabaviruses and sadwaviruses, the three beta-barrels are present in two CPs (VPL with two barrels and VPS with a single barrel, middle). In nepoviruses, the single CP is folded in three barrels (bottom).
Within the polyproteins, protein domains are organized in a manner common to that of other members of the order Picornavirales (Figure 3. Secoviridae). The replication block contains domains characteristic of NTP-binding proteins (NTB or putative helicase), 3C-like proteinase (Pro) and RNA-directed RNA polymerase (Pol). In viruses with a monopartite genome, the structural proteins are located upstream of the replication block in the single polyprotein. In viruses with a bipartite genome, structural proteins are contained in the RNA-2-encoded polyprotein. In comoviruses, cheraviruses and nepoviruses, the movement protein is located upstream of the CP(s), and enables viral movement to adjacent cells. Both movement protein and CP(s) are required for cell-to-cell movement of the virus. The movement protein of comoviruses and nepoviruses is a structural component of tubular structures that traverse the cell wall and contain virus-like particles (Laporte et al., 2003, Pouwels et al., 2004). Putative movement proteins have been suggested to be encoded upstream of the CP(s) coding regions for many other viruses in the family but their biological function has not been confirmed.

The RNA-1-encoded 3C proteinase cleaves both RNA-1 and RNA-2-encoded polyproteins. The cleavage site specificity of the proteinase differs with the specific genera (and in the case of nepoviruses it differs with the specific subgroup, Table 3) (Wellink and van Kammen 1988, Gorbalenya et al., 1989, Margis and Pinck 1992, Thole and Hull 1998, Carrier et al., 1999, Ferriol et al., 2016). An amino acid in the substrate binding pocket of the protease interacts directly with the amino acid in the -1 position of the cleavage site and plays a key role in the specificity of the proteinase.

### Table 3. Secoviridae. Cleavage site specificity of the 3C-like proteinase of viruses in the family Secoviridae

<table>
<thead>
<tr>
<th>Genus</th>
<th>Proteinase substrate binding pocket#</th>
<th>Peptide at cleavage site†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Comovirus</td>
<td>His</td>
<td>Q/G, Q/M, Q/S, Q/T*, Q/A*</td>
</tr>
<tr>
<td>Fabavirus</td>
<td>His</td>
<td>Q/S*, Q/A*, Q/G*</td>
</tr>
<tr>
<td>Nepovirus</td>
<td>Leu</td>
<td>R/G, C/S, C/A/S, G/E*, G/V*, G/C*</td>
</tr>
<tr>
<td>Subgroup A</td>
<td>Leu</td>
<td>K/S, K/A, R/A, R/S*, R/G</td>
</tr>
<tr>
<td>Subgroup B</td>
<td>Leu</td>
<td>Q/G, Q/S, D/S</td>
</tr>
<tr>
<td>Subgroup C</td>
<td>His</td>
<td>Q/G, E/G</td>
</tr>
<tr>
<td>Cheravirus</td>
<td>?</td>
<td>R/G, T/S, T/N, A/N, A/S, A/A</td>
</tr>
<tr>
<td>Torradovirus</td>
<td>His</td>
<td>O/A, Q/S, Q/V</td>
</tr>
<tr>
<td>Sequivirus</td>
<td>Leu</td>
<td>?</td>
</tr>
<tr>
<td>Waikavirus</td>
<td>His</td>
<td>Q/S*, Q/M*, Q/V*, Q/A*</td>
</tr>
<tr>
<td>Unassigned species in the family</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strawberry latent ringspot virus</td>
<td>His</td>
<td>S/G</td>
</tr>
<tr>
<td>Strawberry mottle virus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black raspberry necrosis virus</td>
<td>His</td>
<td>E/G*, Q/G*</td>
</tr>
<tr>
<td>Dioscorea mosaic associated virus</td>
<td>His</td>
<td>Q/G*, Q/A*, Q/S*, E/G*</td>
</tr>
<tr>
<td>Chocolate lily virus A</td>
<td>His</td>
<td>Q/G*, Q/S*</td>
</tr>
</tbody>
</table>

# The indicated amino acid in the substrate-binding pocket of the proteinase interacts with the amino acid at the -1 position of the cleavage site and plays an important role in determining the cleavage site specificity of the proteinase. In the case of sadwaviruses, neither a His nor a Leu are found at the equivalent position in the deduced amino acid sequence of the proteinase.

† Cleaved dipeptides at the cleavage sites are shown with the scissile bond indicated with the slanted line. The amino acids are shown using the one-letter code. Proteolytic cleavages at dipeptides have been confirmed experimentally except for those indicated by an asterisk which are putative cleavage sites, inferred from sequence alignments.

Formation of replication complexes has been studied for comoviruses and nepoviruses. Replication occurs in association with intracellular membranes derived from the endoplasmic reticulum. Two RNA-1-encoded proteins (the NTB protein and the protein immediately upstream of NTB) interact directly with ER membranes and have been implicated in the proliferation of membrane vesicles in the cytoplasm of infected cells and in the assembly of the replication complex (Sanfacon 2012). This has not been studied for other viruses in the family.
All members of the family infect plants. Host range and symptoms vary with the genera and viruses considered (Table 4). Many viruses in the family have a known biological vector, although some (sequiviruses) require a helper virus and others do not have a known vector. Most viruses are transmissible experimentally by mechanical inoculation. However, waikaviruses are not known to be sap-transmissible. Many viruses are readily transmissible by seed or pollen.

**Table 4. Secoviridae.** Biological properties of viruses in the family Secoviridae

<table>
<thead>
<tr>
<th>Genus</th>
<th>Host range</th>
<th>Vector</th>
<th>Seed or pollen transmission</th>
</tr>
</thead>
<tbody>
<tr>
<td>Comovirus</td>
<td>Narrow (Leguminosae)</td>
<td>Beetle</td>
<td>Rare</td>
</tr>
<tr>
<td>Fabavirus</td>
<td>Wide</td>
<td>Aphid</td>
<td>Rare</td>
</tr>
<tr>
<td>Nepovirus</td>
<td>Wide</td>
<td>Nematode (most), mite (blackcurrant reversion virus) or unknown</td>
<td>Seed, pollen</td>
</tr>
<tr>
<td>Cheravirus</td>
<td>Wide or narrow</td>
<td>Nematode (cherry rasp leaf virus) or unknown</td>
<td>Seed</td>
</tr>
<tr>
<td>Sadwavirus</td>
<td>Wide</td>
<td>Unknown</td>
<td>Seed</td>
</tr>
<tr>
<td>Torradovirus</td>
<td>Narrow</td>
<td>Whitefly or aphid</td>
<td>unknown</td>
</tr>
<tr>
<td>Sequivirus</td>
<td>Relatively wide</td>
<td>Aphid (requires helper virus)</td>
<td>None</td>
</tr>
<tr>
<td>Waikavirus</td>
<td>Narrow</td>
<td>Aphid or leafhopper</td>
<td>None</td>
</tr>
<tr>
<td>Unassigned species</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strawberry latent ringspot virus</td>
<td>Wide</td>
<td>Nematode</td>
<td>Seed</td>
</tr>
<tr>
<td>Strawberry mottle virus</td>
<td>Relatively wide</td>
<td>Aphid</td>
<td>None</td>
</tr>
<tr>
<td>Black raspberry necrosis virus</td>
<td>Few host species tested</td>
<td>Aphid</td>
<td>unknown</td>
</tr>
</tbody>
</table>

**Antigenicity**

Virus preparations are usually good immunogens and polyclonal antibodies prepared against purified virus particles recognize all CPs. Viruses of species belonging to the same genus can be serologically interrelated, but often distantly.

**Derivation of names**

*Seco:* derived from the amalgamation of the previous families Sequiviridae and Comoviridae.

*Como:* from Cowpea mosaic virus, the type species of the Comovirus genus

*Faba:* derived from the Latin *faba*, bean; also *Vicia faba*, broad bean

*Nepo:* from nematode-transmitted, polyhedral particles

*Chera:* from Cherry rasp leaf virus, the type species of the Cheravirus genus

*Sadwa:* from Satsuma dwarf virus, the type species of the Sadwavirus genus

*Torrado:* derived from Tomato torrado virus, the type species of the Torradovirus genus. In Spanish, torrado means toasted to refer to the severe necrosis (burnt-like phenotype) observed in the disease induced by ToTV.

*Sequi:* from Latin sequi, to follow, accompany (in reference to the dependent aphid transmission of parsnip yellow fleck virus)

*Waika:* from Japanese, describing the symptoms induced in rice by infection with rice tungro spherical virus alone (i.e. in the absence of rice tungro bacilliform virus)

**Subfamily demarcation criteria**

There is currently only one subfamily (*Comovirinae*) which groups together three genera (*Comovirus, Fabavirus and Nepovirus*). These three genera are closely related to each other in phylogenetic analyses (Figure 4. Secoviridae). Given the presence of only one subfamily, formal demarcation criteria have not been defined.

**Genus demarcation criteria**

The criteria demarcating genera in the family are:

- Number of genomic RNAs
Number of protein domains and/or processing sites within the polyprotein(s)
Number of CPs
Presence of additional ORFs and/or subgenomic RNAs
Clustering as a single branch in phylogenetic trees derived from amino acid sequence alignments of the conserved Pro-Pol region when compared with other genera of the family Secoviridae (Figure 4. Secoviridae). The Pro-Pol region is delineated by the “CG” motif of the 3C-like proteinase and the “GDD” motif of the polymerase. Identification of proteinase cleavage sites is not required to delineate the Pro-Pol region.

Not all criteria may need to be met simultaneously.

Species demarcation criteria

Useful criteria to demarcate species are:
- CP aa sequence with less than 75% identity (for viruses with two or three CPs, combined CP sequences are considered)
- Conserved Pro-Pol region aa sequence (as defined above) with less than 80% identity
- Differences in antigenic reactions
- Distinct host range
- Distinct vector specificity
- Absence of cross-protection
- For viruses with a bipartite genome, absence of re-assortment between RNA-1 and RNA-2

Not all criteria need to be met simultaneously. In some cases, sequence information alone can be a good indicator of a distinct species (i.e., when the percentage of sequence identity in both the Pro-Pol and CP(s) regions is well below the proposed cut-off). However, analysing only one region of the genome is generally not sufficient and both the Pro-Pol and CP(s) regions should be considered. In cases where the percentage of sequence identity in one or both sequences is near the proposed cut-off (e.g., between 75 and 85% in the Pro-Pol region or between 70 and 80% in the CP(s) region), other criteria should be considered and information on biological properties of the virus (host range, vector specificity, possibility of reassortment between RNAs) is useful. For example, beet ringspot virus (BRSV) and tomato black ring virus (TBRV) (genus Nepovirus) are closely related in the Pro-Pol sequence (89% sequence identity) but are much more divergent in the CP sequence (62% sequence identity). They differ in their antigenic reactions and also in the specificity of nematode transmission (BRSV is transmitted more efficiently by Longidorus elongatus and TBRV is transmitted more efficiently by Longidorus attenuatus).

Relationships within the family

Members of the family Secoviridae were previously classified in two different families: Comoviridae (including the genera Comovirus, Fabavirus and Nepovirus) and Sequiviridae (including the genera Sequivirus and Waikavirus) and in two unassigned genera: Cheravirus and Sadwavirus. The families and genera were amalgamated to create the new family Secoviridae, which includes all plant viruses that are members of the order Picornavirales (Sanfacon et al., 2009).

The conserved Pro-Pol region on RNA-1, delineated by the “CG” motif of the 3C-like proteinase and the “GDD” motif of the polymerase, has been used to determine the relationship among members of the order Picornavirales. Comparison of the Pro-Pol sequence among members of the family Secoviridae allows the definition of branches that generally correspond to the distinct genera. Members of the sub-family Comovirinae (genera Comovirus, Fabavirus and Nepovirus) are more closely related to each other than to other genera within the family (Figure 4. Secoviridae). Within this sub-family, fabaviruses and comoviruses are more closely related to each other than to nepoviruses. Nepovirus subgroups (see nepovirus section) are not clearly separated in the Pro-Pol tree (with the exception of subgroup B which constitutes a separate branch) but are more clearly separated in phylogenetic trees using the CP sequence (not shown).
Figure 4. Secoviridae Maximum likelihood inferred phylogenetic tree of members of the family Secoviridae based on an alignment of amino acid sequences of the conserved domains between the “CG” motif of the 3C-proteinase and the “GDD” motif of the polymerase (Pro-Pol region) using T-Coffee (Di Tommaso et al., 2011). The tree was generated with PhyML (Guindon et al., 2010) (1000 bootstrap replicates) in the TOPALi suite (Milne et al., 2009) using an RtRev (Dimmic et al., 2002) +I+G evolutionary model selected by Protest (Darriba et al., 2011). Results are presented as a midpoint rooted tree. The bar represents the genetic distance. The nepovirus subgroups A, B and C are indicated along with genus and subfamily assignments. Bootstrap values > 70% are shown. This phylogenetic tree and corresponding sequence alignment are available to download from the Resources page.

Relationships with other taxa

Members of the family Secoviridae are related to members of other families in the order Picornavirales (Thompson et al., 2014). They all share a common virion structure, organization of the replication block within the polyproteins and conserved properties of the replication proteins, including the 3C-like proteinase. Members of the Secoviridae are also related to members of the families Potyviridae and Caliciviridae in some aspects (common replication block, polyprotein strategy, VPg bound to the 5'-end of the genome and poly(A) tail at the 3'-end of the genome) but differ in other properties.
Subfamily: Comovirinae

Distinguishing features

The genome of members of the subfamily Comovirinae consists of two ssRNAs with a 5ʹ-bound polypeptide (VPg) and a 3ʹ-poly(A) tail. Members of the subfamily group as a single branch in phylogenetic trees using the conserved Pro-Pol region (see family section on phylogenetic relationships and Figure 4. Secoviridae). Other genera are more distantly related. Within the sub-family, genera are distinguished by their specific genomic organization, biological properties and phylogenetic relations. Each genus within the sub-family Comovirinae represents a single sub-branch in the Pro-Pol phylogenetic tree.

Member taxa

- Comovirus
- Fabavirus
- Nepovirus
Genus: Comovirus

Distinguishing features

Comoviruses have bipartite genomes encapsidated by two capsid proteins (CP); these viruses are transmitted by beetles.

Virion

The comovirus capsid is made of two types of polypeptides (large CP: 40–45 kDa and small CP: 21–27 kDa). The small CP suppresses RNA silencing and surface-exposed amino acids are required for this function.

Genome organisation and replication

The 5ʹ- and 3ʹ-UTRs of RNA-1 and RNA-2 are similar in sequence but not identical. RNA-2 is translated into two largely overlapping polypeptides that are processed into three domains. Production of the smaller polypeptide results from internal initiation at a downstream AUG, which is placed in a more favourable context than the upstream AUG (Figure 1. Comovirus). The 58K protein released from the N-terminus of the larger polypeptide (P2) is necessary for replication of RNA-2. The 48K protein released from the N-terminus of the smaller polypeptide (P2) is the movement protein (MP), with a typical “LPL” motif. The CP domains are encoded at the C-terminus of both polypeptides. The MP and the CPs are required for cell-to-cell movement of the virus (Wellink and Van Kammen 1989). The MP is a structural component of tubular structures containing virus-like particles that traverse the cell wall. The C-terminal region of the MP also interacts with the large CP (Carvalho et al., 2003). RNA-1 is translated into a single polypeptide that is processed into five domains, through alternative processing pathways (Figure 1. Comovirus). The N-terminal 32K protein limits the processing of the RNA-1-encoded polyprotein in cis and assists the processing of the RNA-2-encoded polyprotein (Peters et al., 1992). This protein is often referred to as the protease co-factor or Co-Pro. The replication block on the RNA-1-encoded polyprotein includes the 58K protein with sequence motifs characteristic of an NTP-binding helicase, the VPg, the Pro and the Pol. The 32K Co-Pro and 58K NTB proteins are involved in inducing the cytopathic structure through proliferation of ER-derived membranes (Carette et al., 2002).

Figure 1. Comovirus. Genome organization and polyprotein processing of cowpea mosaic virus. The ORFs are boxed and the function of the proteins is indicated. MP: movement protein; CPL and CPS: large and small capsid proteins; Co-Pro: proteinase co-factor; NTB: NTP-binding proteins; Pro: proteinase; Pol: RNA-dependent RNA polymerase. Proteolytic cleavage sites are indicated on the polyproteins with the vertical lines. All intermediate and final cleavage products have been detected in infected cells. The black circles at the 5ʹ-end of the RNA represents the VPg, and A(n) at the 3ʹ-end the poly-A tail.

Biology

Comoviruses have narrow host ranges, 11 of the 15 species being restricted to a few species of the family Leguminosae. Mosaic and mottle symptoms are characteristic, but usually not ringspots. Transmission in nature is exclusively by beetles, especially members of the family Chrysomelidae. Beetles retain their ability to transmit virus for days or weeks.

Species demarcation criteria

See discussion under family description.

Member species

www.ictv.global/report/secoviridae
### Exemplar isolate of the species

<table>
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<tr>
<th>Species</th>
<th>Virus name</th>
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<th>RefSeq number</th>
<th>Available sequence</th>
<th>Virus Abbrev.</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.

Turnip ringspot virus (TuRSV) is related to radish mosaic virus (RaMV). They infect similar hosts. The degree of aa sequence identity between the two viruses is close to the proposed species demarcation criteria (73% aa sequence identity in the combined CP region and 80% aa sequence identity in the Pro-Pol region) (Petrzik and Koloniuk 2010). It is not known whether re-assortment between the RNAs of TuRSV and RaMV is possible. Therefore, the taxonomic position of TuRSV as a distinct species in the genus *Comovirus* or as a distant strain of the species *Radish mosaic virus* remains unclear.
**Genus: Fabavirus**

**Distinguishing features**

Fabaviruses have bipartite genomes encapsidated by two capsid proteins (CP) and are transmitted by aphids.

**Virion**

See discussion under family description.

**Genome organisation and replication**

The genomic organization of fabaviruses is similar to that of comoviruses. Similar to comoviruses, RNA-2 encodes two overlapping polyproteins with the N-terminal protein playing a role in the replication of RNA-2 and the overlapping movement protein being synthesized through initiation at the second AUG codon (Lin et al., 2014). The movement protein was also confirmed to be a structural component of the tubular structures that traverse the cell wall (Liu et al., 2011) (Figure 3. Secoviridae). The cleavage of polyproteins is presumed to be similar to that of comoviruses but this has not been investigated in detail.

**Biology**

Fabaviruses have wide host ranges among dicotyledonous plants and some families of monocotyledonous plants. Symptoms are ringspots, mottling, mosaic, distortion, wilting and apical necrosis. In nature, fabaviruses are transmitted by aphids in a non-persistent manner.

**Species demarcation criteria**

See discussion under family description.

**Member 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>
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<td>RNA-1: NC_038760; RNA-2: NC_038759</td>
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<td>RNA-1: NC_039077; RNA-2: NC_039078</td>
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Virus names, the choice of exemplar isolates, and virus abbreviations, are not official ICTV designations.
Genus: Nepovirus

Distinguishing features

Nepoviruses are the only known members of the family that encode a single large capsid protein (CP) of 52–60 kDa (Fuchs et al., 2016). These viruses are transmitted by nematode vectors and through pollen.

Virion

See discussion under family description.

Genome organisation and replication

Genome organization and expression are similar to those of comoviruses, except that RNA-2 specifies a single polypeptide of 105–207 kDa. Nepoviruses can be divided into three subgroups based on their sequences, genome organization and cleavage sites. Subgroup A has an RNA-2 of 3,700–4,000 bases, present in both M and B components. Subgroup B has an RNA-2 of 4,400–4,700 bases, present only in the M component. Potato virus B and red clover nepovirus A are newly characterized viruses with phylogenetic relationships to nepoviruses of subgroup B (De Souza et al., 2016, Kolonicki et al., 2018). Subgroup C has an RNA-2 of 6,400–7,300 bases, present in M component particles that are sometimes barely separable from those of B component. The three subgroups also differ in the cleavage sites recognized by their protease (Table 3. Secoviridae).

Additional linear or circular satellite RNAs, which sometimes modulate symptoms, are found associated with several nepoviruses of all three subgroups. They are either linear (1100–1800 bases) with a 5’-linked VPg, a 3’-poly(A) tail and encoding a 36–48 kDa polypeptide, or circular (300–460 bases) and apparently non-coding (Feldstein et al., 1997, Chay et al., 1997). They are present in some natural isolates but are not necessary for virus accumulation (Gottula et al., 2013). In aeonium plants infected with aeonium ringspot virus there is an additional species of RNA-2 (RNA-2’) in addition to the full-length RNA-2. The smaller length of this RNA-2’ is the result of a 537 nt deletion in the predicted movement protein (MP) region (Sorrentino et al., 2013).

The RNA-2-encoded polyprotein of subgroup A and B nepoviruses is processed into three domains. In grapevine fanleaf virus (GFLV), the N-terminal protein of the RNA-2-encoded polyprotein (P2A) is involved in RNA-2 replication (Gaire et al., 1999). The two other protein domains are the MP and the unique CP. Both are required for cell-to-cell movement of the virus. Similarly to comoviruses, the MP has a LPL motif, interacts with the CP and is a structural component of tubular structures containing virus-like particles and traversing the cell wall. Cell-to-cell movement depends on the secretory pathway and the cytoskeleton and requires class XI myosin motors (Laporte et al., 2003, Amari et al., 2011). In tomato ringspot virus (ToRSV) (subgroup C), the N-terminal region of the RNA-2-encoded polyprotein is cleaved at an additional site, defining two domains (X3 and X4) (Carrier et al., 2001). The X3 protein contains some sequence similarity with the P2A protein of GFLV but the X4 protein is a unique protein of unknown function. The RNA-1 of nepoviruses is translated into a single polypeptide that is processed into six domains. The C-terminal region of the polyprotein contains the replication block, and is similar to that of comoviruses (NTB-VPg-Pro-Po). In contrast, the N-terminal region of the polyprotein contains an additional cleavage site defining two protein domains (X1 and X2) instead of the single domain present upstream of NTB in the comovirus genome. Cleavage at this additional site was demonstrated for arabis mosaic virus (subgroup A) and ToRSV (subgroup C) (Wetzel et al., 2008, Wang and Sanfacon 2000). A cleavage site at this position has been proposed for other nepoviruses. The function of X1 is unknown. X2 contains a sequence motif in common with the comovirus Co-Pro protein but does not seem to modulate the activity of the proteinase. However, similarly to the comovirus Co-Pro, the X2 protein of ToRSV associates with ER-derived membranes and a role in viral replication has been proposed (Zhang and Sanfacon 2006). When comparing RNA-1 and RNA-2, the 5’- and 3’-UTRs are similar in sequence but not identical in subgroup A nepoviruses. In subgroup B nepoviruses, the 5’-UTRs also show sequence similarity between RNA-1 and RNA-2, while the 3’-UTRs are identical in both RNAs. In subgroup C nepoviruses, both UTRs are identical or nearly identical between RNA-1 and RNA-2. The region of sequence similarity extends into part of the coding region of the polyproteins in ToRSV, but not in blackcurrant reversion virus (Walker et al., 2015).

Biology

Nepoviruses are widely distributed in temperate regions. The natural host range of nepoviruses varies from wide to restricted, depending on the virus. Ringspot symptoms are characteristic, but mottling and spotting are equally frequent. Viruses of twelve species are acquired and transmitted non-persistently by longidorid nematodes (Xiphinema, Longidorus or Paralongidorus spp), three are transmitted by pollen, and viruses of one species are transmitted by mites (blackcurrant reversion virus). The others have no known biological vector (Susko 2004). Seed and/or pollen transmission is very common. In herbaceous plants, the symptoms induced by nepoviruses are often transient, with newly emerging leaves appearing symptomless a few weeks after infection (the so-called “recovery” phenomenon). Symptom recovery is associated with induction of RNA silencing, an antiviral defence, and is sometimes (but not always) accompanied with reduced concentration of viral RNAs (Ghoshal and Sanfacon 2015).

Species demarcation criteria

See discussion under family description.

Member 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>
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www.ictv.global/report/secoviridae
Related, unclassified viruses

<table>
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<tr>
<th>Virus name</th>
<th>Accession number</th>
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</table>

Virus names and virus abbreviations are not official ICTV designations.

red clover nepovirus A (Koloniuk et al., 2018)
**Genus: Cheravirus**

**Distinguishing features**

Members of the genus *Cherivirus* have bipartite genomes and encode three capsid proteins and are transmitted by nematodes and through seeds.

**Virion**

See discussion under family description.

**Genome organisation and replication**

Cheraviruses have three capsid proteins (CP) of similar sizes. In some cases, these proteins are not fully or reproducibly resolved from each other by electrophoresis. The genome of cheraviruses is bipartite and the genomic organization is similar to that of comoviruses, although RNA-2 is thought to encode a single polyprotein (*Figure 3. Secoviridae*). The RNA-2-encoded movement protein of apple latent spherical virus (ALSV) is 42 kDa, suggesting that translation initiation occurs at the second AUG, which is in a better context. Tubular structures containing virus-like particles are observed in infected cells and are likely involved in cell-to-cell movement of the virus. The movement protein and all three CPs are necessary for cell-to-cell movement of the virus (*Yoshikawa et al., 2006*). The MP binds to VP25, one of the three CPs (*Isogai et al., 2006*). VP20 of ALSV, another CP, is a suppressor of silencing that interferes with systemic movement of the silencing signal (*Yaegashi et al., 2007*).

**Biology**

The host range is broad or narrow, depending on the virus, and includes weed plants found in the vicinity of infected crops. Symptoms are usually mild or absent. Cherry rasp leaf virus is transmitted by nematodes (*Xiphinema americanum*) in the field (*Nyland et al., 1969*), and is readily seed-transmitted (*Hansen et al., 1974*). ALSV is also seed-transmitted through both embryo and pollen in apple (*Nakamura et al., 2011*). In potato, Arracacha virus B is transmitted through true seed and pollen (*Jones 1982*). Currant latent virus has been detected in oligophagous viviparous females and in nymphs of red blister aphid *Cryptomyzus ribis* and circulates in the aphid (*Petrzik et al., 2015*).

**Species demarcation criteria**

See discussion under family description.

**Member species**

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<th>Species</th>
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Virus names, the choice of exemplar isolates, and virus abbreviations, are not official ICTV designations.
Genus: Sadwavirus

Distinguishing features

The single member of the genus has a bipartite genome, two capsid proteins (CPs), is transmitted by an unknown vector; phylogenetic analysis places it as a distinct lineage of the family.

Virion

See discussion under family description.

Genome organisation and replication

Similar to comoviruses, sadwaviruses have two CPs, one large and one small. The genome of sadwaviruses is bipartite and the genomic organization is similar to that of comoviruses. The proteinase of sadwaviruses is distinct from that of other viruses in the family in that it does not have a conserved His or Leu in the active site. In addition, the cleavage sites recognized by sadwaviruses proteinases are unique with an A or a T at the -1 position (Table 3, Secoviridae). In contrast to comoviruses, there is no evidence that two overlapping polyproteins are encoded by RNA-2. Similar to some nepoviruses, extensive sequence identity between RNA-1 and RNA-2 are found in the 5' UTRs as well as in the 5'-end of the putative coding region.

Biology

See discussion under family description.

Species demarcation criteria

This is only a single species genus.

Member 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>
</tr>
</thead>
<tbody>
<tr>
<td>★ Chocolate lily virus A</td>
<td>chocolate lily virus A</td>
<td>CLVA-KP2</td>
<td>JN052073; JN052074</td>
<td>RNA-1: NC_016443; RNA-2: NC_016444</td>
<td>?</td>
<td>CLVA</td>
</tr>
<tr>
<td>★ Dioscorea mosaic associated virus</td>
<td>Dioscorea mosaic associated virus</td>
<td>DMaV-goiana</td>
<td>KU215538; KU215539</td>
<td>RNA-1: NC_031766; RNA-2: NC_031763</td>
<td>?</td>
<td>DmaV</td>
</tr>
<tr>
<td>★ Satsuma dwarf virus</td>
<td>satsuma dwarf virus</td>
<td>SDV-S58</td>
<td>AB009958; AB009959</td>
<td>RNA-1: NC_003785; RNA-2: NC_003786</td>
<td>?</td>
<td>SDV</td>
</tr>
<tr>
<td>★ Black raspberry necrosis virus</td>
<td>black raspberry necrosis virus</td>
<td>BRNV-Alyth</td>
<td>DQ344463; DQ344464</td>
<td>RNA-1: NC_008182; RNA-2: NC_008183</td>
<td>?</td>
<td>BRNV</td>
</tr>
<tr>
<td>★ Strawberry mottle virus</td>
<td>strawberry mottle virus</td>
<td>SMoV-NsPer3</td>
<td>AJ311876; AJ311876</td>
<td>RNA-1: NC_003445; RNA-2: NC_003446</td>
<td>?</td>
<td>SMoV</td>
</tr>
</tbody>
</table>

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

**Distinguishing features**

Sequiviruses have a monopartite genome and three capsid proteins (CP) in their virions; sequiviruses are transmitted by aphids in a presence of a helper virus.

**Virion**

Virions contain three CPs of about 32–34, 22–26 and 22–24 kDa.

**Genome organisation and replication**

The genome consists of a single molecule of ssRNA that encodes a single large polyprotein. The replication block (NTB-Pro-Pol) is contained in the C-terminal region of the polyprotein. The structural protein domains are present in the N-terminal region of the polyprotein but are separated from the N-terminus by a protein domain of about 40–60 kDa. Infectivity of the genome is susceptible to proteinase treatment suggesting the presence of a 5′-linked VPG (Murant et al., 1987). The parsnip yellow fleck virus (PYFV) RNA is not polyadenylated (Turnbull-Ross et al., 1992). This is a unique property within this family. In contrast, the RNA of carrot necrotic dieback virus is polyadenylated (Menzel and Vetten 2008). Tubular structures containing virus-like particles have been observed traversing the cell wall of PYFV-infected cells (Murant et al., 1975). However, their role in cell-to-cell movement has not been investigated and the presence of a movement protein in the polyprotein (possibly upstream of the CPs) needs to be confirmed.

**Biology**

The natural host range of sequiviruses includes species in several plant families. Transmission is by aphids in a semi-persistent manner. However, it is dependent on the presence of a helper virus in the genus *Waikavirus* (Murant and Gould 1968).

**Species demarcation criteria**

See discussion under *family description*.

**Member species**

<table>
<thead>
<tr>
<th>Species</th>
<th>Virus name</th>
<th>Isolate</th>
<th>Accession number/RefSeq number</th>
<th>Available sequence</th>
<th>Virus Abbrev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>★ Carrot necrotic dieback virus</td>
<td>carrot necrotic dieback virus</td>
<td>Anthriscus</td>
<td>EU980442/NC_038320</td>
<td>Complete genome</td>
<td>CNDV</td>
</tr>
<tr>
<td>★ Dandelion yellow mosaic virus</td>
<td>dandelion yellow mosaic virus</td>
<td>DSM2</td>
<td>JQ675189/NC_043078</td>
<td>Partial genome</td>
<td>DaYMV</td>
</tr>
<tr>
<td>★ Parsnip yellow fleck virus</td>
<td>parsnip yellow fleck virus</td>
<td>P121</td>
<td>J140466/NC_003628</td>
<td>Complete coding genome</td>
<td>PYFV</td>
</tr>
</tbody>
</table>

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

**Distinguishing features**

Similar to cheraviruses, torradoviruses have a bipartite genome with two open reading frames in RNA-2 and three capsid proteins.

**Virion**

See discussion under family description.

**Genome organisation and replication**

The genome RNAs are polyadenylated. Presence of a VPg at the 5'-end of the RNAs has not been tested experimentally. The genomic organization is similar to that of other members of the family with a bipartite genome. The replication block is found in the polyprotein encoded by RNA-1 while the structural proteins are present in the C-terminal region of the polyprotein encoded by RNA-2. A putative movement protein upstream of the capsid protein (CP) domains shares little sequence similarity with that of other bipartite members of the family with the exception of the small LPL motif (van der Vlugt et al., 2015). A distinguishing feature of the torradovirus genome is the presence of a second open reading frame upstream and partially overlapping with the large ORF2 in RNA-2 (Figure 3. Secoviridae). This reading frame encodes a putative protein of unknown function, with no apparent homology to known proteins, which exhibits a large degree of sequence diversity (61–74% identity) among tomato-infecting torradoviruses and non-tomato infecting torradoviruses but a significantly higher level of diversity (21–31% identity) between these two groups. 3'-UTRs sequences differ substantially between members of species but for most torradoviruses the 3'-UTRs of RNA-1 and RNA-2 are nearly identical (>99%) with only a relatively short 5'-terminal variable region showing clear differences in length as well as in sequence. 3'-UTRs of a given torradovirus also show extensive sequence duplications while significant stretches of homologous conserved regions in the 3'-UTRs occur between members of distinct virus species. RNA secondary structure analyses has identified several conserved stem loop structures in both 5'- UTRs and 3'-UTRs of RNA-1 and RNA-2 (van der Vlugt et al., 2015).

**Biology**

Tomato torrado virus, tomato marchitez virus and squash chlorotic leaf spot virus are transmitted by whiteflies in a semi-persistent manner (Lecoq et al., 2016). Carrot torrado virus 1 is transmitted by at least three different species of aphids (Rozado-Aguirre et al., 2016). Vector an specificity remains to be determined for the other torradoviruses.

**Species demarcation criteria**

See discussion under family description.

**Member 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>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Carrot torrado virus 1</strong></td>
<td>carrot torrado virus 1</td>
<td>H6</td>
<td>RNA-1: KC999058; RNA-2: NC_009032</td>
<td></td>
<td>Complete genome</td>
<td>CaTv1</td>
</tr>
<tr>
<td><strong>Lettuce necrotic leaf curl virus</strong></td>
<td>lettuce necrotic leaf curl virus</td>
<td>5317015</td>
<td>RNA-1: KC999059; RNA-2: NC_010986</td>
<td></td>
<td>Complete genome</td>
<td>LNLcV</td>
</tr>
<tr>
<td><strong>Motherswort yellow mottle virus</strong></td>
<td>motherswort yellow mottle virus</td>
<td>AD01</td>
<td>RNA-1: EF681764; RNA-2: EF681765</td>
<td></td>
<td>Complete genome</td>
<td>MYMlV</td>
</tr>
<tr>
<td><strong>Squash chlorotic leaf spot virus</strong></td>
<td>squash chlorotic leaf spot virus</td>
<td>Su12-10</td>
<td>RNA-1: EF681761; RNA-2: EF681760</td>
<td></td>
<td>Complete genome</td>
<td>SClsV</td>
</tr>
<tr>
<td><strong>Tomato marchitez virus</strong></td>
<td>tomato marchitez virus</td>
<td>PRI-1051</td>
<td>RNA-1: EF681761; RNA-2: EF681760</td>
<td></td>
<td>Complete genome</td>
<td>ToMarV</td>
</tr>
<tr>
<td><strong>Tomato torrado virus</strong></td>
<td>tomato torrado virus</td>
<td>PRI-1051</td>
<td>RNA-1: EF681761; RNA-2: EF681760</td>
<td></td>
<td>Complete genome</td>
<td>ToTV</td>
</tr>
</tbody>
</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>tomato chocolate virus</td>
<td>RNA-1: FJ60489; RNA-2: FJ60490</td>
<td>ToChV</td>
</tr>
<tr>
<td>tomato chocolate spot virus</td>
<td>RNA-1: GQ305131; RNA-2: GQ305132</td>
<td>ToChSV</td>
</tr>
<tr>
<td>tomato necrotic dwarf virus</td>
<td>RNA-1: KC999058; RNA-2: KC999059</td>
<td>ToTV</td>
</tr>
</tbody>
</table>

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

Tomato chocolate virus (ToChV), tomato chocolate spot virus (ToChSV) and tomato necrotic dwarf virus (ToNDV) are related to tomato marchitez virus (ToMarV) and to a lesser degree to tomato torrado virus (ToTV). All viruses infect tomato and cause similar symptoms (Batuman et al., 2010, Larsen et al., 1984, Verbeek et al., 2010). Comparison of the aa sequence of the Pro-Pol and combined CP regions would suggest that ToChV, ToChSV and ToNDV are distant strains of ToMarV (82–92% aa sequence identity for the Pro-Pol region and 79–
89% aa sequence identity in the combined CP region among the three viruses). However, other regions of the genome (RNA-2-encoded ORF1 and the 3'-UTR) show significant sequence variation. In addition the length of the 3'-UTR varies significantly among these viruses. It is not known whether reassortment between the RNAs of ToMarV, ToChV, ToChSV and/or ToNDV is possible. Therefore, the taxonomic position of ToChV, ToChSV, ToNDV as either three distinct species in the genus *Torradovirus*, three strains of a single new species in the genus *Torradovirus* or three distant strains of the species *Tomato marchitez virus* remains unclear.
**Genus: Waikavirus**

**Distinguishing features**

Waikaviruses have a monopartite genome encapsidated by three capsid proteins; these viruses are transmitted by aphids or leafhoppers.

**Virion**

See discussion under family description.

**Genome organisation and replication**

The genomic organization of waikaviruses is similar to that of sequiviruses. However, small ORFs have been identified near the 3’-end of the RNA or overlapping with the main polyprotein but in a different reading frame (Figure 3. Secoviridae) (Chaouch et al., 2004, Thole and Hull 1996, Firth and Atkins 2008). Some experimental evidence has been presented suggesting that subgenomic RNAs are produced from the 3’-region of the RNA (Reddick et al., 1997). The biological significance of the small open reading frames or of the putative subgenomic RNAs is not known. The genomic RNAs are polyadenylated at their 3’-end. The presence of a 5’-linked VPg has not been confirmed experimentally.

**Biology**

The natural host range of waikaviruses is usually restricted to species within a few plant families (Bockelman et al., 1982). Waikaviruses are not sap-transmitted. Field transmission is in the semi-persistent manner by aphids or leafhoppers. A virus-encoded helper protein is probably needed. Some waikaviruses are helper viruses for the insect transmission of other viruses: anthriscus yellows virus in the case of parsnip yellow fleck virus (PYFV, genus *Sequivirus* (Murant and Gould 1968)) and rice tungro spherical virus in the case of rice tungro bacilliform virus (family *Caulimoviridae*) (this association being responsible for the very damaging rice tungro disease) (Hibino 1983).

**Species demarcation criteria**

See discussion under family description.

**Member species**

<table>
<thead>
<tr>
<th>Species</th>
<th>Virus name</th>
<th>Isolate</th>
<th>Accession number (RefSeq number)</th>
<th>Available sequence</th>
<th>Virus Abbrev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>★ Anthriscus yellows virus</td>
<td>Anthriscus yellows virus</td>
<td>CT1</td>
<td>KX123881 (NC_027915)</td>
<td>Complete genome</td>
<td>AVV</td>
</tr>
<tr>
<td>★ Bellflower vein chlorosis virus</td>
<td>bellflower vein chlorosis virus</td>
<td>TN</td>
<td>JN73389 (NC_003626)</td>
<td>Complete genome</td>
<td>BVCV</td>
</tr>
<tr>
<td>★ Maize chlorotic dwarf virus</td>
<td>maize chlorotic dwarf virus</td>
<td>Shen</td>
<td>AB40407 (NC_001632)</td>
<td>Complete genome</td>
<td>MCDV</td>
</tr>
<tr>
<td>★ Rice tungro spherical virus</td>
<td>rice tungro spherical virus</td>
<td>Shen</td>
<td>AB40407 (NC_001632)</td>
<td>Complete genome</td>
<td>RTSV</td>
</tr>
</tbody>
</table>

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**Related viruses**

<table>
<thead>
<tr>
<th>Virus name</th>
<th>Accession number</th>
<th>Virus abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>blackcurrant waikavirus A</td>
<td>KJ572568*, KJ572572*</td>
<td>BCWVA</td>
</tr>
<tr>
<td>red clover associated virus 1</td>
<td>MH325329</td>
<td>RCaV1</td>
</tr>
</tbody>
</table>

* = partial sequences

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

blackcurrant waikavirus A (Ho and Tzanetakis 2014)

red clover associated virus 1 (Koloniuk and Fránová 2018)
**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_006964; RNA-2: NC_006965</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: Secoviridae**

Sequence alignments and tree files:

**Figure 4.Secoviridae:**

- Tree file (.tre format)
- Alignment file (FASTA format)
Further reading: Secoviridae


References: Secoviridae


viruses in apples. J Gen Plant Pathol 77, 48-53


Citation: Secoviridae

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