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# *Cheravirus* and *Sadwavirus*: two unassigned genera of plant positive-sense single-stranded RNA viruses formerly considered atypical members of the genus *Nepovirus* (family *Comoviridae*)

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## Summary

The genus *Nepovirus* (family *Comoviridae*) was known both for a good level of homogeneity and for the presence of atypical members. In particular, the atypical members of the genus differed by the number of capsid protein (CP) subunits. While typical nepoviruses have a single CP subunit with three structural domains, atypical nepoviruses have either three small CP subunits, probably corresponding to the three individual domains, or a large and a small subunit, probably containing two and one structural domains, respectively. These differences are corroborated by hierarchical clustering based on sequences derived from both genomic RNAs. Therefore, these atypical viruses are now classified in two distinct genera, *Cheravirus* (three CP subunits; type species *Cherry rasp leaf virus*) and *Sadwavirus* (two CP subunits; type species *Satsuma dwarf virus*).

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## Introduction

The taxonomy of plant viruses began with attempts to cluster entities (now referred to as species) into ''groups'' that more or less correspond to currently recognized genera. In the first such attempt [2, 27], a group of viruses with common characteristics, namely icosahedral particles and the ability to be transmitted from plant to plant by soil nematodes, was established and called ''NEPO-virus'' (accounting for NEmatode-transmitted viruses with a POlyhedral symmetry), which was later changed to ''nepovirus''. As more plant viruses were identified and characterized, especially at the molecular level, many of the original groupings proved insufficient or inadequate, resulting in the redefinition of several virus families and genera [7]. However, the nepovirus group remained relatively untouched since its members shared common biological properties, virus particle structure and genome organization. The genus *Nepovirus* was divided into three subgroups (A, B and C) based on the length of RNA-2, serological properties and the similarity of the genome sequences [39]. In spite of this division, members of the three subgroups are clearly related to each other in their biological

**Table 1.** Members and tentative members of the genera *Cheravirus* and *Sadwavirus*. The species are listed alphabetically in the left column, with commonly-used acronym. The viruses considered isolates of a given species are listed in the second column and the sequences corresponding to both genomic RNAs are given on the right (asterisks indicate partial sequences)

| Genus and species name | Isolate name | RNA-1 | RNA-2 |
|---|---|---|---|
| *Cheravirus* | | | |
| – *Apple latent spherical virus* (ALSV) | | NC_003787 | NC_003788 |
| – *Cherry rasp leaf virus* (CRLV) | potato isolate | NC_006271 | NC_006272 |
| | flat apple virus | AY764390 | AY122330 |
| Tentative cheraviruses | | | |
| – arracacha virus B (AVB) | | AJ616713* | |
| – artichoke vein banding virus (AVBV) | | | |
| – stocky prune virus (StPV) | Brugères | DQ143874* | DQ143875* |
| *Sadwavirus* | | | |
| – *Satsuma dwarf virus* (SDV) | satsuma dwarf virus | NC_003785 | NC_003786 |
| | citrus mosaic virus | | AB032751* |
| | hyuganatsu virus | AB112587* | AB112588* |
| | natsudaidai dwarf virus | | AB032750* |
| | navel orange infectious mottling virus | AB022887* | AB000282* |
| – *Strawberry mottle virus* (SMoV) | | NC_003445 | NC_003446 |
| Tentative sadwaviruses | | | |
| – lucerne Australian symptomless virus (LASV) | | | |
| – strawberry latent ringspot virus (SLRSV) | | NC_006964 | NC_006965 |
| – rubus Chinese seed-borne virus (RCSV) | | | |
| – black raspberry necrosis virus (BRNV) | black raspberry decline-associated virus | NC_00812 | NC_008183 |

properties and at the phylogenetic level, justifying their classification within a single genus. The genus *Nepovirus* is now considered to belong to the family *Comoviridae* [22]. These viruses are also related to the animal picornaviruses and to other picorna-like viruses from plants and other eukaryotes [5, 9–11].

In the light of newly published data, some viruses that were previously considered definite or tentative members of the genus *Nepovirus* [39], listed in Table 1, diverge significantly enough from typical nepoviruses to justify a revision of their taxonomical status. It must be noted that this is the case with one of the founding species of the nepovirus group, strawberry latent ringspot virus (SLRSV). The ICTV Study Group on *Comoviridae* has addressed this question and proposed that several viruses that were previously considered ''atypical nepoviruses'' should be included into two newly created genera, *Cheravirus* and *Sadwavirus*, which so far could not be assigned to a family. These taxonomy proposals were approved by ICTV in 2003 [23, 24, 29]. The rationale for the creation of these genera is given below with respect to a list of criteria, and discussed in the light of newly published data.

## Biology

### *Host range and symptoms*

All nepoviruses infect vascular plants. The host range of nepoviruses is typically broad, covering various plant species in several families for a given virus species, but there are some exceptions to this general rule both among typical and atypical nepoviruses [22–24]. Similarly, while typical nepovirus symptoms are characterized by the occurrence of ring spots, this is neither constant nor restricted to these viruses. Therefore, these traits cannot be considered to have a good taxonomic value.

### *Transmission*

The type of biological vector is considered important for taxonomical purposes, especially as a demarcation criterion between genera within a family [1, 22].

Nepoviruses are, by definition, typically transmitted semi-persistently by soil nematodes. Specifically, their vectors belong to the family *Longidoridae*, a type of vector described for no other virus taxon. However some typical nepoviruses differ in either showing no evidence for biological transmission in the field, or even in being transmitted by other types of biological vectors (e.g., blackcurrant reversion virus is transmitted by mites) [18]. In addition, several nepoviruses are transmitted through pollen and/or by seed.

When information is available, the situation among atypical nepoviruses with respect to biological transmission is the following: SLRSV and cherry rasp leaf virus (CRLV) are transmitted by *Xiphinema spp.* nematodes [16, 36]. Satsuma dwarf virus (SDV) and stocky prune virus (StPV) do not have a known vector. However, the observed patterns of

spread in the field suggest soil transmission [3, 14]. Black raspberry necrosis virus (BRNV) and strawberry mottle virus (SMoV) are transmitted by aphids [12, 34]. Arracacha virus B (AVB) is pollen-borne. Apple latent spherical virus (ALSV), AVB, CRLV, lucerne Australian symptomless virus (LASV), rubus Chinese seed-borne virus (RCSV), SDV and SLRSV are seed-borne, but not SMoV [23, 24].

## Virion properties

All definite and atypical nepoviruses have icosahedral particles about 30 nm in diameter. Virus preparations contain three types of components differing in their buoyant densities: T ("Top", empty particles), M ("Middle", particles usually containing a single molecule of RNA-2) and B ("Bottom", particles containing a single molecule of RNA-1 or, in some nepoviruses, two molecules of RNA-2). Among picorna-like viruses, the genus *Nepovirus* is the only taxon in which the icosahedral pseudo-T = 3 capsids are made of a single type of capsid protein (CP) subunit containing three structural domains, each consisting of a jelly-roll [22]. In the two other genera within the family *Comoviridae*, *Comovirus* and *Fabavirus*, the capsid is made of 2 types of CP subunits: the small subunit (21–27 kDa) which contains a single jelly-roll and the large one (40–45 kDa) which contains two jelly-rolls [4]. Plant picorna-like viruses in the family *Sequiviridae* have 3 CP subunits of 22–34 kDa probably corresponding each to a single jelly-roll as in the viruses of the family *Picornaviridae* [30].

The number of CP subunits is one of the distinctive features of the "atypical nepoviruses" discussed here: LASV, RCSV, SDV, SLRSV have 2 CP subunits, a large one and a small one as in comoviruses and fabaviruses, while ALSV, AVB, CRLV and StPV have 3 CP subunits of similar sizes, like sequiviruses and picornaviruses [3, 12, 23, 24]. The number of CP subunits has not been experimentally determined for SMoV and BRNV [12, 34].

## Genome structure and expression

Picorna-like viruses have single-stranded (+)-sense RNA genomes with a 3′ poly(A) tail and are covalently bound to a VPg at their 5′ end (Fig. 1). The genome of nepoviruses and other members of the family *Comoviridae* is divided into two segments [22], whereas in the other family of plant picorna-like viruses, *Sequiviridae*, the genome consists of a

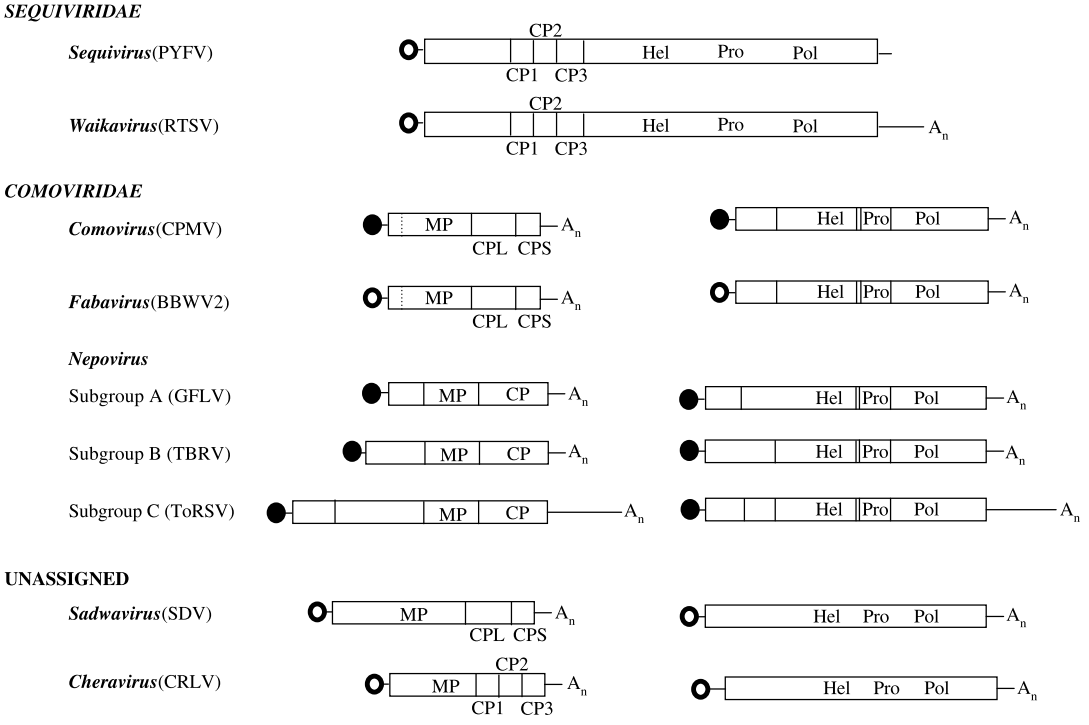


**Fig. 1.** Genome organization of plant picorna-like viruses. The abbreviations are *Hel* Helicase, *Pro* 3C-like Proteinase, *Pol* RNA-dependent RNA polymerase, *CP* capsid protein, *MP* movement protein, *An* poly(A). The VPg is shown with a circle (open circle: no experimental evidence for a VPg; a sequence homologous to the VPg of other members of the family is found in the RNA-1 of fabaviruses). The RNA-2 of members of the genera *Comovirus* and *Fabavirus* encode two polyproteins differing by their translation initiation site, which is denoted by a dotted line

single RNA molecule [25]. The ''atypical nepoviruses'' have a bipartite genome [23, 24], which historically was a strong argument to consider them nepoviruses.

In addition, some nepoviruses replicate and encapsidate satellite RNAs. Nepovirus satellite RNAs are of either two types: (i) linear, longer than 1000 nucleotides, with a VPg, a poly(A) tail and an open reading frame coding for a single protein of unknown function, or (ii) circular, shorter than 500 nucleotides and with no significant open reading frames [22]. The only information available for the ''atypical nepoviruses'' is that some SLRSV isolates are associated with a satellite RNA of the first type [20, 28].

The genomic RNAs of typical and atypical nepoviruses are expressed each as a single polyprotein which is processed by a virus-encoded proteinase, as are those of members of the family *Sequiviridae* [22–25]. In comoviruses, RNA-2 encodes two carboxy co-terminal polyproteins, due to the presence of two alternative translation initiation codons. This feature is unique to these viruses, although it has been reported for SLRSV [13] without independent confirmation to date.

## Sequence affinities

The atypical character of the ''tentative nepoviruses'' was further confirmed when sequence data became available and suggested that they were distinct from other members of the genus *Nepovirus* [21], and even of the family *Comoviridae* [6]. Instead, the recent availability of full-length or partial sequences of the genomes of several ''atypical nepoviruses'' revealed that most of them if not all were closer to members of the family *Sequiviridae* [6, 14, 16, 19, 21, 26, 34].

The deduced amino-acid sequences of plant picorna-like viruses were aligned using the identity protein weight matrix implemented in ClustalX [33] and clustered hierarchically using the Neighbour-Joining procedure [31]. The confidence limit of the resulting clusterings was evaluated using the bootstrap procedure [8]. The amino-acid sequences analysed include the entire CP region (Fig. 2) or a region between proteinase-specific and polymerase-specific motifs (Pro-Pol, Fig. 3), together reflecting both genomic RNAs. The Pro-Pol-based dendrogram yielded a clearer clustering than the CP-based one because of higher levels of sequence identity.

Both dendrograms (Figs. 2 and 3) confirmed that the ''atypical nepovirus'' sequences did not cluster with definite members of the family *Comoviridae*. The region between the CG motif within the proteinase and the GDD motif within the polymerase is a good taxonomic predictor for classifying picorna-like viruses [5]. When this sequence was examined (Fig. 3), ''atypical nepoviruses'' formed two separate clusters that corresponded to ''atypical nepoviruses'' with two or three CP subunits, respectively. The only exception was SLRSV, which clustered with the viruses with three CPs although the virions contain two CP subunits. The two clusters were related to each other but did not cluster with members of the family *Sequiviridae*.

In Figs. 2 and 3, the dendrograms were derived from the CP and Pro-Pol sequences from one representative from each species only. In some species, the corresponding sequences from additional isolates are available. Including them in the analysis did not significantly change the outcome (data not shown).

## Conclusion

Based on the above observations, the creation of two new genera (*Sadwavirus* and *Cheravirus*) was proposed and approved by ICTV in 2003 [23, 24]. Sadwaviruses and cheraviruses differ from viruses in the family *Sequiviridae* in having a bipartite genome. They differ from viruses in the family *Comoviridae* in sequence clustering analysis and the number of CP subunits: two CPs in sadwaviruses as in comoviruses and fabaviruses, and three in cheraviruses unlike any member of the family *Comoviridae*. The list of tentative nepoviruses was examined for viruses with two or three CPs, and they were assigned on this basis as tentative sadwaviruses and cheraviruses, respectively. Two possible difficulties were highlighted in the taxonomy proposals and discussed at ICTV: the relationship between these two families and other taxa and the status of some species within the proposed genera.

Regarding the relationships between *Cheravirus*, *Sadwavirus* and other recognized taxa, the study group initially proposed that the two new genera should be assigned to the family *Sequiviridae*, mostly on the basis of sequence similarities, and to reflect the suggestion made by various authors [6, 14, 16, 19, 26, 34]. In this hypothesis, the segmentation of the genome could have been considered a criterion for genus demarcation within the family *Sequiviridae*. This suggestion was however not approved by ICTV, awaiting further data to become available. Therefore, the genera *Cheravirus* and *Sadwavirus* are currently unassigned, and Pro-Pol sequence clustering suggests that they might be grouped in a family yet to be created, but different from both the families *Sequiviridae* and *Comoviridae*.

Another difficulty was that the level of sequence divergence within each of these genera is higher than within other related genera of plant viruses (Figs. 2 and 3). This raises the possibility that either or both of these genera will have to be further divided with more data becoming available. The study group was hoping that these proposals would lead to further characterization of additional cheraviruses and sadwaviruses. Indeed, the knowledge regarding the genus *Cheravirus* was consolidated after the complete sequence of CRLV [17, 35] and a partial sequence of StPNV, a new candidate cheravirus [3], were determined (Figs. 2 and 3). Similarly, the recently elucidated sequence of BRNV, a new

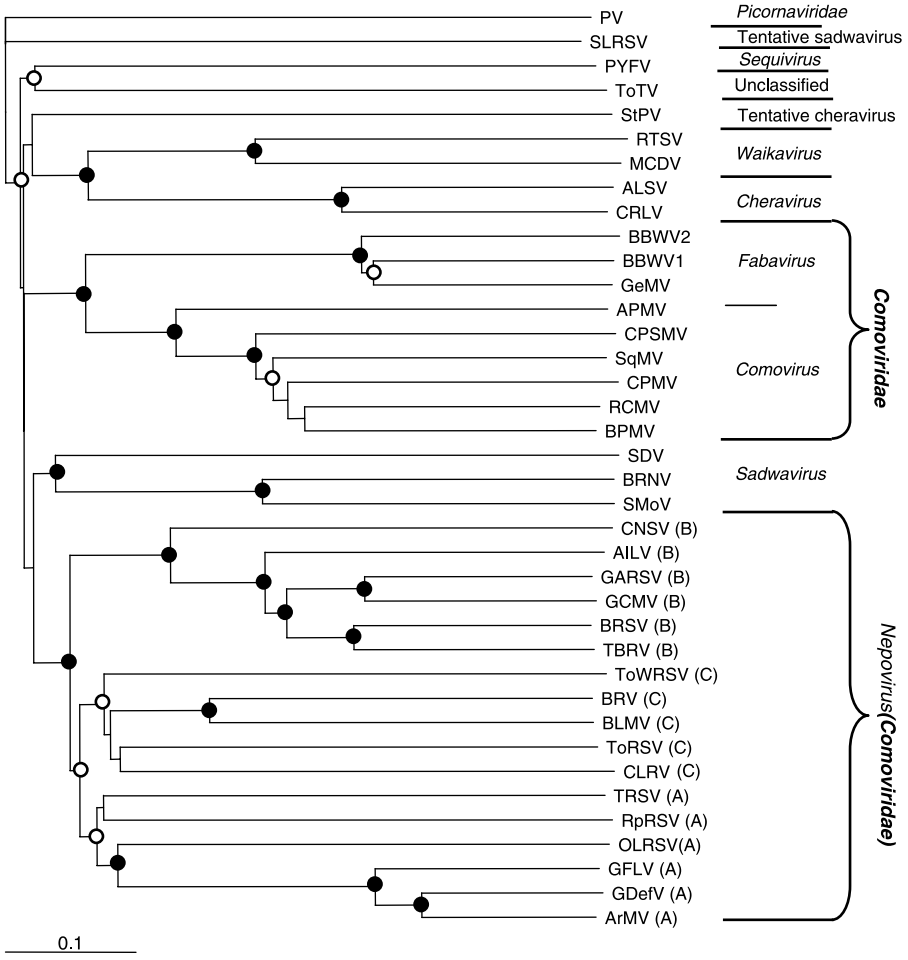


**Fig. 2.** Hierarchical clustering of plant picorna-like viruses based on the CP sequences. The families and genera are delineated on the right, with smaller bars delineating genera within each family. The letter in parenthesis after the nepovirus acronyms refer to the subgroup in which they have been classified (A, B or C). Circles indicate nodes supported by bootstrap values above 80% (closed circles) or 60% (open circles); nodes without circles are not supported to these levels. The bar represents a p-distance of 0.1. The equivalent sequence (i.e. the structural genes excluding VP4) from human poliovirus (PV, family *Picornaviridae*) was used as outgroup. (*) the StPV CP sequence is probably not complete but lacks 10–40 amino-acids at its N-terminus [3]; (**) the SMoV and BRNV CP cleavage sites are unknown [12, 34] and were therefore approximated to produce the alignment from the best homologous portion of the polyprotein (SMoV: GLPED . . . LLSRQ, 670 amino acids; BRNV: GDGMP . . . KYRKH, 684 amino acids). The GenBank accession numbers for each virus were as follows (virus acronyms are as defined in the text and in Table 1, when not defined here): PV (NP_041277), ToTV (DQ38888), maize chlorotic dwarf virus (MCDV, U67839), parsnip yellow fleck virus (PYFV, D14066), rice tungro spherical virus (RTSV, M95497), StPV (DQ143875), ALSV (AB030941), CRLV (AJ621358), SMoV (AJ311876), BRNV (DQ344640), SLRSV (AY860979), SDV (AB009959), gentian mosaic virus (GeMV, BAD99002), broad bean wilt virus 1 (BBWV1, AB084451), broad bean wilt virus 2 (BBWV2, AF225954), Andean potato mottle virus (APMV, P38485), squash mosaic virus (SqMV, AB054689), bean poddle mosaic virus (BPMV, M62738), red clover mosaic virus (RCMV, M14913), cowpea severe mosaic virus (CPSMV, M83309), cowpea mosaic virus (CPMV, X00729), artichoke Italian latent virus (AILV, X87254), tomato black ring virus (TBRV, AY157994), olive latent ringspot virus (OLRSV, CAB90217), grapevine chrome mosaic virus (GCMV, X15163), cycas necrosis stunt virus (CNSV, AB073148), beet ringspot virus (BRSV, X04062), tobacco ringspot virus (TRSV, AY363727), raspberry ringspot virus (RpRSV, AY303788), arabis mosaic virus (ArMV, AY017339), grapevine fanleaf virus (GFLV, X16907), grapevine deformation virus (GDeFV, AAQ56597), grapevine Anatolian ringspot virus (GARSV, AAQ56596), cherry leaf roll virus (CLRV, AAB27443), blueberry leaf mottle virus (BLMV, AAA64608), tomato white ringspot virus (ToWRSV which is probably an isolate of artichoke ringspot virus, ABM65096), tomato ringspot virus (ToRSV, D12477), blackcurrant reversion virus (BRV, AF020051)

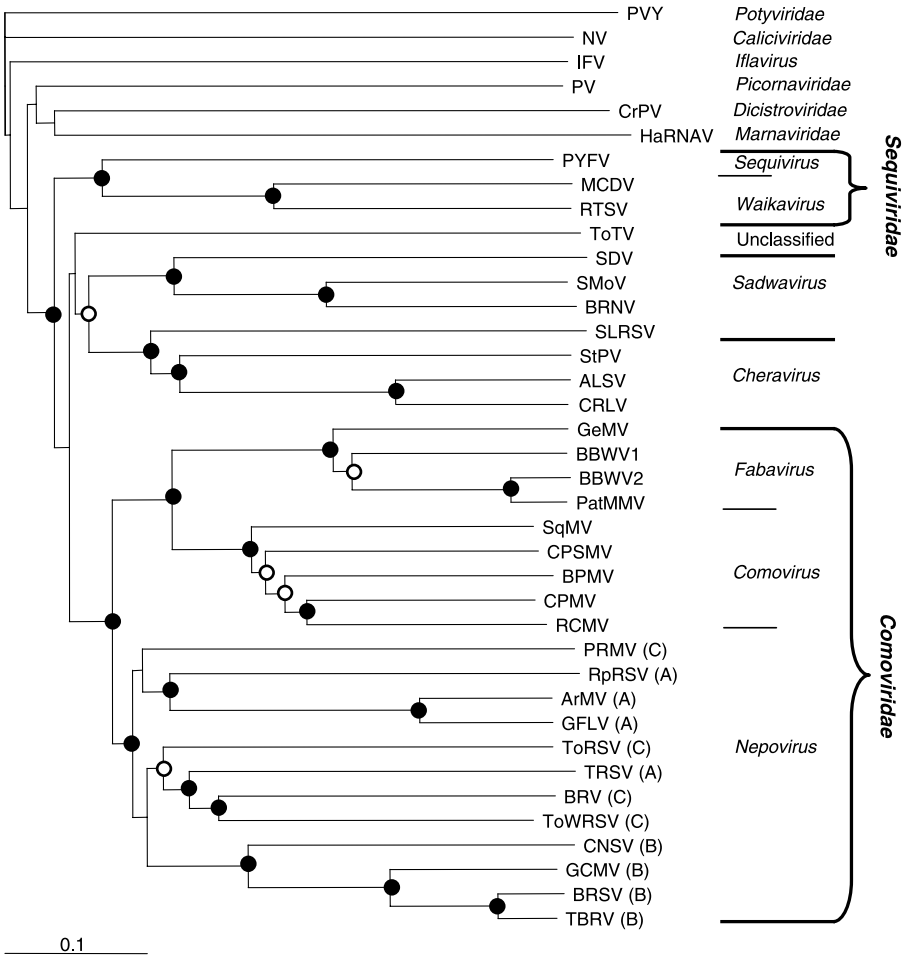


**Fig. 3.** Hierarchical clustering of plant picorna-like viruses based on the Pro-Pol sequence. The families and genera are delineated on the right, with smaller bars delineating genera within each family. The letter in parenthesis after the nepovirus acronyms refer to the subgroup in which they have been classified (A, B or C). Circles indicate nodes supported by bootstrap values above 80% (closed circles) or 60% (open circles); nodes without circles are not supported to these levels. The bar represents a p-distance of 0.1. The amino-acid sequence clustering is based on the region between the Pro (CG) and the Pol (GDD) sequence motifs. The GenBank accession numbers for each virus were as follows (virus acronyms are as defined in the text, in Table 1 or in Fig. 2, when not defined here): infectious flacherie virus (IFV, AB000906), cricket paralysis virus (CrPV, AF318039), PV (V01149), Norwalk virus (NV, M87661), Heterosigma akashiwo RNA virus (HaRNV, AY337486), potato virus Y (PVY, X12456), MCDV (U67839), PYFV (D14066), RTSV (M95497), GeMV (BAD99001), BBWV1 (AB084450), BBWV2 (AF225953), patchouli mild mosaic virus (PatMMV, AB050782), SqMV (AB054688), BPMV (U70866), RCMV (X64886), CPSMV (M83830), CPMV (X00206), ToTV (DQ388879), StPV (AAZ76594), BRNV (DQ344639), SMoV (AJ311875), SLRSV (AY860978), SDV (AB009958), ALSV (AB030940), CRLV (AJ621357), ToWRSV (ABM65096), peach rosette mosaic virus (PRMV, AAB69867), BRV (AF3682772), ToRSV (L19655), TBRV (AY157993), GCMV (X15346), CNSV (AB073147), BRSV (D00322), TRSV (U50869), RpRSV (AY303787), ArMV (AY303786), GFLV (D00915)

candidate sadwavirus, revealed its similarity to SMoV and confirmed the two clusters presented in Fig. 3 [12]. However, further analysis will be required to determine the number of CP subunits encoded by SMoV and BRNV.

SLRSV is currently assigned to the genus *Sadwavirus* based on the number of CP subunits [24]. However, elucidation of the complete sequence of SLRSV suggests that this classification may need to be revised [36]. Phylogenetic analysis does not strongly support clustering of SLRSV with SDV but, instead, suggests a closer relationship of SLRSV with the genus *Cheravirus* (Fig. 3). Therefore, and also considering an early report of two polyproteins being encoded by its RNA-2, SLRSV should not be considered as more than a tentative member of the genus *Sadwavirus* (Table 1), and the possibility that it belongs to another genus yet to be created should be evaluated further.

Similarly, although a newly identified bipartite plant picorna-like virus (tomato torrado virus, ToTV) possesses

some characteristic in common with cheraviruses, in particular the presence of 3 CP subunits, phylogenetic studies did not support clustering with other members of the genus *Cheravirus* [38] (Fig. 3). The taxonomic position of this virus will require further assessment.

A clearer perspective on the taxonomical relationships between plant picorna-like viruses, and particularly consolidation or reconsideration of the currently recognized taxa, will be reached when more virus species are characterised at the biological and molecular levels.

## Distinguishing features, species, type species and etymology

The species and isolates currently characterized, considered to belong to each of the two genera are listed in Table 1. The general characteristics of the genera *Cheravirus* and *Sadwavirus* are the following:

*Cheravirus:*
- Soil-borne; transmitted by longidorid nematode vectors
- Icosahedral, non-enveloped virions about 30 nm in diameter with a pseudo-T = 3 symmetry
- 3 distinct CP subunits of about 20–25 kDa
- Genome consisting of two single-stranded, positive-sense RNA segments each having a 3′ poly(A) tail and encoding a polyprotein
- A "replication block", composed of the coding regions for the NTP-binding protein (putative helicase), 3C-like proteinase and RNA-dependent RNA-polymerase, typical of picorna-like viruses

The type species of the genus *Cheravirus* is *Cherry rasp leaf virus*, without doubt the best known member from a biological point of view [32, 35], including the identification of various strains (Table 1). The genus name derives from that of the type species.

*Sadwavirus:*
- Transmitted by aphids (SMoV and BRNV) or by longidorid nematodes (SLRSV), or apparently soil-borne (SDV)
- Icosahedral, non-enveloped virions about 30 nm in diameter with a pseudo-T = 3 symmetry
- 2 distinct CP subunits of about 40 kDa (large subunit, CP-L) and 25 kDa (small subunit, CP-S), respectively
- Genome consisting of two single-stranded, positive-sense RNA segments each having a 3′ poly(A) tail and encoding a polyprotein
- A "replication block" typical of picorna-like viruses

The type species of the genus *Sadwavirus* is *Satsuma dwarf virus* (Satsuma mandarin, *Citrus reticulata*, is a typical citrus grown in Japan), of which several strains have been identified (Table 1) [15, 19, 37]. The genus name is a sigla from the name of the type species.

*Species demarcation criteria:*
Species in the genera *Cheravirus* and *Sadwavirus* (Table 1) are differentiated according to the following criteria:
- Type of biological vector
- Host range
- Absence of serological cross-reaction
- Absence of cross-protection
- Less than 80% amino-acid sequence identity in the CP subunits (cheraviruses) or in the CP-L subunit (sadwaviruses)
- Less than 80% amino-acid sequence identity in the proteinase-polymerase region

It should be noted that the threshold identity levels have been defined by analogy to the family *Comoviridae* and may require revision when more sequences become available.

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