

Developments in plant virus taxonomy since the publication of the 6th ICTV Report

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1. Introduction

The publication of the 6th ICTV Report [5] marked a significant shift in the way in which plant viruses were classified. Prior to this publication, most plant viruses were placed in one of 33 “Groups”, or in a few instances, into genera in families largely characterised by viruses of vertebrate or invertebrate animals [1]. In the 1995 classification, 41 new genera were recognised, of which 19 were classified into 7 new families. An unusual feature of this classification was that 22 genera were described that were not classified in families. These were unassigned genera, sometimes referred to as “floating” [3]. This shortened classification is now recognised in the International Code of Nomenclature and Taxonomy of Viruses [3] as being an intrinsic, if idiosyncratic, feature of virus classification.

There has been substantial taxonomic activity since the publication of Murphy et al. [5] that has been outlined by Pringle [6, 7] and reviewed by Martelli [2] and Mayo and Pringle [4]. There have been four types of activity. The continuation of rapid progress in the molecular characterization of viruses has led to the recognition of 32 more genera. There has been some clustering of genera so as to form families, and in a few instances, genera have been split up so as to form more genera that better represent the diversity within the previous genus. Table 1 lists the current families and genera of plant viruses, the type species for each genus and denotes the taxa created since 1995. The fourth major taxonomic activity has been attention to the delineation of species within genera and the naming of taxa. This is reviewed by Van Regenmortel et al. [8].

In this brief review, the principle changes to genera and families are outlined and the current classification of plant viruses is presented in Table 1. A key by which genera and families of plant viruses may be distinguished can be accessed at the Internet address – <http://www.scri.sari.ac.uk/vir/ictvhome.html>.

Table 1. The current classification of families and genera of plant viruses

Type of genome	Family	Genus	Type species
ss DNA	<i>Geminiviridae</i>	<i>Mastrevirus</i> ^a	<i>Maize streak virus</i>
		<i>Curtovirus</i> ^a	<i>Beet curly top virus</i>
		<i>Begomovirus</i> ^a	<i>Bean golden mosaic virus</i>
ss DNA	–	<i>Nanovirus</i> ^a	<i>Subterranean clover stunt virus</i>
Reverse transcribing	<i>Caulimoviridae</i> ^a	<i>Caulimovirus</i>	<i>Cauliflower mosaic virus</i>
		“ <i>SbCMV-like</i> ” ^a	<i>Soybean chlorotic mottle virus</i>
		“ <i>CsVMV-like</i> ” ^a	<i>Cassava vein mosaic virus</i>
		“ <i>PVCoV-like</i> ” ^a	<i>Petunia vein clearing virus</i>
		<i>Badnavirus</i>	<i>Commelina yellow mottle virus</i>
		“ <i>RTBV-like</i> ” ^a	<i>Rice tungro bacilliform virus</i>
Reverse transcribing	<i>Pseudoviridae</i> ^a	<i>Pseudovirus</i> ^a	<i>Saccharomyces cerevisiae Ty1 virus</i>
Reverse transcribing	<i>Metaviridae</i> ^a	<i>Metavirus</i> ^a	<i>Saccharomyces cerevisiae Ty3 virus</i>
ds RNA	<i>Reoviridae</i>	<i>Phytoreovirus</i>	<i>Wound tumor virus</i>
		<i>Fijivirus</i>	<i>Fiji disease virus</i>
		<i>Oryzavirus</i>	<i>Rice ragged stunt virus</i>
ds RNA	<i>Partitiviridae</i>	<i>Alphacryptovirus</i>	<i>White clover cryptic virus 1</i>
		<i>Betacryptovirus</i>	<i>White clover cryptic virus 2</i>
ds RNA	–	<i>Varicosavirus</i> ^a	<i>Lettuce big-vein virus</i>
(–)ss RNA	<i>Rhabdoviridae</i>	<i>Cytorhabdovirus</i>	<i>Lettuce necrotic yellows virus</i>
		<i>Nucleorhabdovirus</i>	<i>Potato yellow dwarf virus</i>
(–)ss RNA	<i>Bunyaviridae</i>	<i>Tospovirus</i>	<i>Tomato spotted wilt virus</i>
(–)ss RNA	–	<i>Tenuivirus</i>	<i>Rice stripe virus</i>
(–)ss RNA	–	<i>Ophiovirus</i> ^a	<i>Citrus psorosis virus</i>
(+)ssRNA	<i>Bromoviridae</i>	<i>Bromovirus</i>	<i>Brome mosaic virus</i>
		<i>Cucumovirus</i>	<i>Cucumber mosaic virus</i>
		<i>Alfamovirus</i>	<i>Alfalfa mosaic virus</i>
		<i>Ilarvirus</i>	<i>Tobacco streak virus</i>
		<i>Oleavirus</i> ^a	<i>Olive latent virus 2</i>
(+)ssRNA	<i>Closteroviridae</i> ^a	<i>Closterovirus</i>	<i>Beet yellows virus</i>
		<i>Crinivirus</i> ^a	<i>Lettuce infectious yellows virus</i>
(+)ssRNA	<i>Comoviridae</i>	<i>Comovirus</i>	<i>Cowpea mosaic virus</i>
		<i>Nepovirus</i>	<i>Tobacco ringspot virus</i>
		<i>Fabavirus</i>	<i>Broad bean wilt virus 1</i>
(+)ssRNA	<i>Luteoviridae</i> ^a	<i>Luteovirus</i>	<i>Barley yellow dwarf virus – PAV</i>
		<i>Polerovirus</i> ^a	<i>Potato leafroll virus</i>
		<i>Enamovirus</i>	<i>Pea enation mosaic virus – 1</i>
(+)ssRNA	<i>Potyviridae</i>	<i>Potyvirus</i>	<i>Potato virus Y</i>
		<i>Rymovirus</i>	<i>Ryegrass mosaic virus</i>
		<i>Bymovirus</i>	<i>Barley yellow mosaic virus</i>
		<i>Macluravirus</i> ^a	<i>Maclura mosaic virus</i>
		<i>Ipomovirus</i> ^a	<i>Sweet potato mild mottle virus</i>
		<i>Tritimovirus</i>	<i>Wheat streak mosaic virus</i>

Continued

Table 1 (continued)

Type of genome	Family	Genus	Type species
(+)ssRNA	<i>Sequiviridae</i>	<i>Sequivirus</i> <i>Waikavirus</i>	<i>Parsnip yellow fleck virus</i> <i>Rice tungro spherical virus</i>
(+)ssRNA	<i>Tombusviridae</i>	<i>Tombusvirus</i> <i>Carmovirus</i> <i>Necrovirus</i> ^a <i>Machlomovirus</i> ^a <i>Dianthovirus</i> ^a <i>Avenavirus</i> ^a <i>Aureusvirus</i> ^a <i>Panicovirus</i> ^a	<i>Tomato bushy stunt virus</i> <i>Carnation mottle virus</i> <i>Tobacco necrosis virus A</i> <i>Maize chlorotic mottle virus</i> <i>Carnation ringspot virus</i> <i>Oat chlorotic stunt virus</i> <i>Pothos latent virus</i> <i>Panicum mosaic virus</i>
(+)ssRNA	–	<i>Tobravirus</i>	<i>Tobacco rattle virus</i>
(+)ssRNA	–	<i>Tobamovirus</i>	<i>Tobacco mosaic virus</i>
(+)ssRNA	–	<i>Hordeivirus</i>	<i>Barley stripe mosaic virus</i>
(+)ssRNA	–	<i>Furovirus</i>	<i>Soil-borne wheat mosaic virus</i>
(+)ssRNA	–	<i>Pomovirus</i> ^a	<i>Potato mop-top virus</i>
(+)ssRNA	–	<i>Pecluvirus</i> ^a	<i>Peanut clump virus</i>
(+)ssRNA	–	<i>Benyvirus</i> ^a	<i>Beet necrotic yellow vein virus</i>
(+)ssRNA	–	<i>Sobemovirus</i>	<i>Southern bean mosaic virus</i>
(+)ssRNA	–	<i>Marafivirus</i>	<i>Maize rayado fino virus</i>
(+)ssRNA	–	<i>Umbravirus</i>	<i>Carrot mottle virus</i>
(+)ssRNA	–	<i>Tymovirus</i>	<i>Turnip yellow mosaic virus</i>
(+)ssRNA	–	<i>Idaeovirus</i>	<i>Raspberry bushy dwarf virus</i>
(+)ssRNA	–	<i>Ourmiavirus</i> ^a	<i>Ourmia melon virus</i>
(+)ssRNA	–	<i>Potexvirus</i>	<i>Potato virus X</i>
(+)ssRNA	–	<i>Carlavirus</i>	<i>Carnation latent virus</i>
(+)ssRNA	–	<i>Foveavirus</i> ^a	<i>Apple stem pitting virus</i>
(+)ssRNA	–	<i>Allexivirus</i> ^a	<i>Shallot virus X</i>
(+)ssRNA	–	<i>Capillovirus</i>	<i>Apple stem grooving virus</i>
(+)ssRNA	–	<i>Trichovirus</i>	<i>Apple chlorotic leaf spot virus</i>
(+)ssRNA	–	<i>Vitivirus</i> ^a	<i>Grapevine virus A</i>
Viroid	<i>Pospiviroidae</i> ^a	<i>Pospiviroid</i> ^a <i>Hostuviroid</i> ^a <i>Cocadviroid</i> ^a <i>Apscaviroid</i> ^a <i>Coleviroid</i> ^a	<i>Potato spindle tuber viroid</i> <i>Hop stunt viroid</i> <i>Coconut cadang-cadang viroid</i> <i>Apple scar skin viroid</i> <i>Coleus blumei viroid 1</i>
Viroid	<i>Avsunviroidae</i> ^a	<i>Avsunviroid</i> ^a <i>Pelamoviroid</i> ^a	<i>Avocado sunblotch viroid</i> <i>Peach latent mosaic viroid</i>

^a Shows taxa and/or names changed since 1995

2. Changed taxa: new families

2.1. Retroid viruses

Family *Caulimoviridae*

Plant viruses that replicate by using reverse transcription were previously classified in either genus *Caulimovirus* or genus *Badnavirus* [5]. Recent sequence data have shown that the genomes of viruses in these genera differ appreciably and the present classification is into six genera that are clustered in a new family, *Caulimoviridae*. Viruses with isometric particles are in one of four genera, *Caulimovirus* (type species, *Cauliflower mosaic virus*), “SbCMV-like viruses” (type species, *Soybean chlorotic mottle virus*), “CsVMV-like viruses” (type species, *Cassava vein mosaic virus*) and “PVCV-like viruses” (type species, *Petunia vein clearing virus*). Viruses with bacilliform particles, previously badnaviruses, are separated into the genera *Badnavirus* (type species, *Commelina yellow mottle virus*) and “RTBV-like viruses” (type species, *Rice tungro bacilliform virus*). The genera can be distinguished mainly by the number and arrangements of the ORFs in the different genomes. Sequence similarities and differences reinforce this division into genera.

Retrotransposons

Recent taxonomic changes have brought retrotransposons into the Universal Taxonomic scheme. Two families have been recognized that differ in the possession or not of an *env* gene and in the organization of the *pol* gene. One genus in each family contains plant-“infecting” retrotransposons. For example, genus *Pseudovirus* (type species *Saccharomyces cerevisiae Ty1 virus*; family *Pseudoviridae*) contains *Arabidopsis thaliana Ta1 virus* and genus *Metavirus* (type species *Saccharomyces cerevisiae Ty3 virus*; family *Metaviridae*) contains *Lilium henryi de11 virus*.

2.2 RNA genome viruses

Family *Luteoviridae*

Sixteen definitive species were previously classified in genus *Luteovirus* [5]. However, the diverse genome structures of these viruses have made this classification untenable. In contrast, the biological properties (transmission; tissue localization; symptom type), and some molecular properties (e.g. coat protein sequences) of these viruses suggest that they should be classified together. To resolve this inconsistency, the family *Luteoviridae* was created so that the different molecular features of replication-related genes could be recognized by separation at the genus level, whilst shared structural protein features and biological properties could be recognized by membership of one family. Thus, genus *Luteovirus* now contains viruses with genomes like that of the type species, *Barley yellow dwarf virus – PAV*, that is they lack a P0 gene, have little overlap between P1 and P2 genes and lack a VPg. Genus *Polerovirus*, on the other hand, contains viruses with genomes like that of *Potato leafroll virus* (the type species), that is they contain a P0 gene, have an extensive overlap between P1 and P2, and have a 5'-linked VPg.

Pea enation mosaic virus (PEMV) was previously classified as the sole member of a genus as it was unlike other viruses [5]. However, detailed analysis of its apparently bipartite genome has shown that the disease of enation formation in peas is induced by

infection with a complex of two viruses. One component resembles viruses of genus *Polerovirus* in gene complement, except that P4 is absent, and the capsids formed in cells infected by it cannot move from cell to cell. The other component resembles viruses of genus *Umbravirus* in that it can move systemically but cells infected with it do not form particles. Thus PEMV is a complex of two viruses. The current classification re-defines genus *Enamovirus* (type species, *Pea enation mosaic virus-1*) to contain only the larger RNA species and to place it in the family *Luteoviridae*. The RNA component that resembles umbraviruses is classified as the species *Pea enation mosaic virus-2* in the genus *Umbravirus*.

Family *Closteroviridae*

Viruses typified by *Beet yellows virus* were previously classified in a single genus, *Closterovirus* [5]. However, the discovery that some viruses of this type have bipartite genomes, and thus two size classes of particles, has led to changes. The cluster has been raised to the level of a family and has been named *Closteroviridae*. Viruses with bipartite genomes have been removed from the genus *Closterovirus* and placed in a new genus, *Crinivirus* (type species, *Lettuce infectious yellows virus*). However, within the current genus *Closterovirus*, there remain viruses in species or tentative species that have aphids, mealybugs or whiteflies as vectors, which is an unusual amount of biological diversity to have among species within one genus.

Viroids

Recently, on the basis of nucleotide sequence features, it has been possible to devise a family/genus classification of viroids. There are two families of viroids. Those in family *Pospiviroidae* contain a central conserved region (CCR), whereas those in family *Avsunviroidae* do not contain a CCR but do undergo self-cleavage. Family *Pospiviroidae* contains the genera *Pospiviroid* (type species, *Potato spindle tuber viroid*), *Hostuviroid* (type species, *Hop stunt viroid*), *Cocadviroid* (type species, *Coconut cadang cadang viroid*), *Apscaviroid* (type species, *Apple scar skin viroid*) and *Coleviroid* (type species, *Coleus blumei viroid 1*), each characterised by the CCR. Family *Avsunviroidae* contains the genera *Avsunviroid* (type species, *Avocado sunblotch viroid*) and *Pelamoviroid* (type species, *Peach latent mosaic viroid*) that are distinguishable on the basis of RNA size and secondary structure. Within the genera, the level of sequence identity that determines that two viroids are distinct species rather than strains of one species is <90%.

3. Changed taxa: new genera

3.1 DNA viruses

Genus *Nanovirus*

Viruses in the new genus *Nanovirus* (type species, *Subterranean clover stunt virus*) have 20 nm diameter, icosahedral particles that encapsidate circular ssDNA approximately 1 kb in size. Nanoviruses resemble the animal-infecting circoviruses in genome size and genome organisation, but differ from them in virion size and morphology. The species in the genus all have either 6 or 7 circular single-stranded DNAs, each of which has a single open reading

frame (ORF) and each is transcribed unilaterally. Definitive nanoviruses are transmitted by aphids. The tentative species, Coconut foliar decay virus (CFDV), has only one circular 1.3 kb ssDNA, and it is transmitted by planthoppers.

3.2 dsRNA genome viruses

Genus *Varicosavirus*

This genus was created to contain viruses typified by *Lettuce big-vein virus* (LBVV). Tobacco stunt virus resembles LBVV in a number of respects and has been added to the genus but as a Tentative Species to allow the possibility of its proving on further analysis to be very closely related to LBVV. These viruses have been known for some time to have dsRNA genomes, probably of two components, that are encapsidated in rod-shaped particles. The viruses are probably transmitted by *Olpidium* sp. In these characters, the viruses are distinct from any others.

3.3 Viruses with negative-sense RNA genomes

Genus *Ophiovirus*

Citrus psorosis virus (the type species) and related viruses were recently classified in the new genus *Ophiovirus*. These viruses resemble tenuiviruses in particle morphology but differ in having only 3 size classes (7.5 to 9 kb, 1.6 to 1.8 kb and 1.5 kb) of ssRNA. Also, particle preparations of ophioviruses are infective, possibly linked to the fact that they are not phloem-limited. And, unlike tenuiviruses, ophioviruses do not infect graminaceous plants.

3.4 Viruses with positive-sense ssRNA genomes

Family *Potyviridae*

Recent molecular characterisation has shown that some viruses previously classified as “unassigned in the family *Potyviridae*” are distinct from viruses in recognized genera. These viruses are now classified in the genera *Macluravirus* (type species, *Maclura mosaic virus*) and *Ipomovirus* (type species, *Sweet potato mild mottle virus*). Macluraviruses are aphid-transmitted and ipomoviruses are transmitted by whiteflies. Although classified previously in genus *Rymovirus*, *Wheat streak mosaic virus* (WSMV) differs markedly from *Ryegrass mosaic virus*, the type species of genus *Rymovirus*, in gene sequences and in the species of mite that transmits it. WSMV has now been made the type species of the new genus *Tritimovirus*.

Family *Tombusviridae*

In the 6th ICTV Report, family *Tombusviridae* contains the genera *Tombusvirus* and *Carmovirus* [5]. In recognition of a number of similarities in genome organization, the previously unassigned genera, *Necrovirus* (type species, *Tobacco necrosis virus A*), *Machlomovirus* (type species, *Maize chlorotic mottle virus*) and *Dianthovirus* (type species, *Carnation ringspot virus*) were added to the family. The family has recently been further expanded by genera typified by some newly characterised viruses. A range of

molecular characteristics is used to discriminate among these genera. The genera are *Avenavirus* (type species, *Oat chlorotic stunt virus*), *Aureusvirus* (type species, *Pothos latent virus*) and *Panicovirus* (type species, *Panicum mosaic virus*).

The former genus *Furovirus*

Viruses previously grouped together on the basis of having rod-shaped particles and being transmitted by soil-inhabiting fungi, have proved to be increasingly diverse as more and more molecular characters have become apparent. The viruses are markedly diverse in the numbers of genome parts, in possession or not of a triple gene block (TGB), in the expression mechanisms used during genome translation, and in gene sequences. The present classification of these viruses is into four genera. Genus *Furovirus* is, as before [5], typified by *Soil-borne wheat mosaic virus* and thus contains viruses that lack a TGB in their bipartite genomes. Viruses with other characteristics have been re-classified in new genera. Viruses that have a tripartite genome that contains a TGB are classified in genus *Pomovirus* (type species, *Potato mop-top virus*). Viruses with a bipartite genome and a TGB, and that are transmitted by *Polymyxa graminis*, are classified in genus *Pecluvirus* (type species, *Peanut clump virus*). Viruses with a genome of two essential RNA components and two or three supplementary RNA components, and that are transmitted by *Polymyxa betae* are classified in genus *Benyvirus* (type species, *Beet necrotic yellow vein virus*).

Genus *Oleavirus*

A new genus (*Oleavirus*, type species *Olive latent virus 2*) has been added to family *Bromoviridae*. Oleaviruses are characteristic of this family in having tripartite genomes of RNAs between 2 kb and 3 kb, a subgenomic mRNA of c.1kb that encodes the coat protein and quasi-spherical to bacilliform particles. However, the genus differs from others in the family in that the subgenomic coat protein mRNA is not encapsidated and the particles contain a fourth RNA of unknown function.

Genus *Ourmiavirus*

A new genus (type species *Ourmia melon virus*) has been created for viruses that resemble those in family *Bromoviridae* in having tripartite genomes but that differ in particle properties. The particles are bacilliform but have conical ends and they are markedly resistant to the disruptive effects of a variety of chemicals that would destroy bromovirus particles. No vector is known; the virus is relatively efficiently transmitted through seed.

Genera of monopartite genome viruses with filamentous particles

Several genera have been created in order to classify the diverse viruses that have a monopartite genome and flexuous filamentous particles. The new genera are *Allxivirus* (type species, *Shallot virus X*), *Foveavirus* (type species, *Apple stem pitting virus*) and *Vitivirus* (type species, *Grapevine virus A*). They can be distinguished from genera of similar viruses described in the 6th ICTV Report largely by features of their genomes. Of the viruses in these genera that have a TGB, allxiviruses have 6 ORFs, are mite-transmitted and have particles longer than 700 nm, and foveaviruses have 5 ORFs and no known vector.

This distinguishes them from viruses in genera *Potexvirus* and *Carlavirus*. Of viruses that lack a TGB, those that are insect-transmitted and have 5 ORFs in their genomes are classified in genus *Vitivirus*, which contrasts with trichoviruses that have no known vector and fewer than 5 ORFs.

4. Future prospects

This brief review outlines new taxa of plant viruses. A full description of these and all other virus taxa can be found in the 7th ICTV Report [9]. Subsequent taxonomic changes will be published in *Archives of Virology* as soon as they are ratified, and will be drawn together in the 8th ICTV Report some time in the future.

All taxonomic structures are over-simplifications based on incomplete information. Thus, as more information becomes available, it is inevitable that virus taxonomy will change. But change for its own sake is resisted by ICTV; the guiding principles of virus taxonomy are stability, utility, acceptability and flexibility [4]. Thus, such limited changes as are made, are towards improving a fit to the needs and perceptions of virologists. ICTV aims to obtain this “fit” by having many specialist Study Groups that report to a few broad category Subcommittees (e.g. the Plant Virus Subcommittee) that report to an Executive Committee. This Committee then establishes a consensus view and makes formal proposals to the ICTV membership [4]. Comments, criticisms or complaints about the taxonomic scheme outlined here, and detailed in the 7th ICTV Report, are very much welcomed and should be channelled to ICTV via this network of representatives.

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