



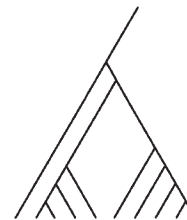
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TAXONOMY, CLASSIFICATION AND NOMENCLATURE OF VIRUSES

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History of Virus Classification and Virus Nomenclature

Humans feel the need to classify natural entities and the viruses are no exception. As in other biological systems, virus classification is an approximate and imperfect exercise. Like any other type of classification, it is a totally artificial and human-driven activity without any natural base. However, science requires workable descriptions of living systems and their constituent parts, and, when achieved properly, classifications are extremely useful for showing similar characteristics and properties across populations. Unfortunately for virus taxonomy no fossil record exists and so evolutionary relationships are very speculative, meaning that only a logical and precise virus classification can provide indications of the evolution of viruses. Appropriately chosen classification criteria are also informative in the case of newly discovered viruses. In theory, nomenclature and classification are totally independent, but for viruses both issues are often considered at the same time. As a result, taxonomic names for the viruses have always been the subject of passionate discussions and the taxonomic status of viruses is a sensitive and critical issue.

Virus classification is a relatively new exercise, as the first evidence for existence of a virus was only presented at the end of the nineteenth century by Beijerinck in 1898. It was not until 1927 that Johnson, a plant virologist, drew attention to the need for a system of virus nomenclature and classification. First efforts to classify viruses utilized a range of ecological and biological criteria, including pathogenic properties in the case of human and animal viruses, and symptoms for plant viruses. For example, viruses sharing the pathogenic properties causing hepatitis (e.g. hepatitis A virus, hepatitis B virus, yellow fever virus, and Rift Valley fever virus) were grouped together as 'the hepatitis viruses'. Virology developed substantially in the 1930s and early classifications for the viruses reflected these advances. In 1939, Holmes published a classification of plant viruses dependent on host reactions and differential host species, using a binomial-trinomial nomenclature based on the name of the infected plant; however, only 89 viruses were

described and classified in this way. With the development of electron microscopy and biochemical studies in the 1950s, the first virus groupings based on common virion properties emerged: like the Herpesvirus group described by Andrewes in 1954, the Myxovirus group by Andrewes *et al.*, in 1955, and the Poxvirus group by Fenner and Burnet in 1957. During this period there was also an explosion of newly discovered viruses; in response, several individuals and committees independently proposed virus classification systems but none was widely adopted by the scientific community. It became obvious that only an international association of virologists could propose a comprehensive and universally acceptable system of virus classification.

At the 1966 International Congress for Microbiology held in Moscow, the International Committee on Nomenclature of Viruses (ICNV) was established by an international group of 43 virologists. An international organization was set up with the aim of developing a taxonomy and nomenclature system for all viruses that would be recognized worldwide. The name of the ICNV was changed in 1974 to the more appropriate International Committee on Taxonomy of Viruses (ICTV), which remains active today. ICTV, the unique official committee of the Virology Division, is now considered the international official body for all matters related to taxonomy and nomenclature of viruses.

Since the founding of the ICTV, all virologists have agreed that the hundreds of viruses isolated from different organisms should be classified together in a unique system, but separate from other microorganisms such as fungi, bacteria and mycoplasma. However, there was much controversy on the way to do it. Lwoff, Horne and Tournier argued for the adoption of a system classifying viruses into subphyla, classes, orders, suborders and families. Descending hierarchical divisions would have been based on nucleic acid type (DNA or RNA), strandedness (single or double), presence or absence of an envelope, capsid symmetry, and so on. The hierarchy of this system has never been recognized by the ICTV; nevertheless, the types of criteria used became the basis of the universal taxonomy system now in place, and all ICTV reports have used this scheme. Until 1990, no hierarchical

classification level higher than the family was used, however, the system has recently begun to move in this direction. A first order, *Mononegavirales*, was accepted in 1990, and another two, *Caudovirales* and *Nidovirales*, were adopted in 1996. In its nonlinnean structure, the scheme is quite different from that used in the taxonomy of bacteria and other organisms. Nevertheless, the usefulness of the scheme is being demonstrated by its wide application. It has replaced all competing classification schemes for all viruses and no one would now dispute with the ICTV the international mandate to name and classify viruses.

Since its establishment, a total of seven virus taxonomic reports (also known by the names of the ICTV Presidents acting as Editors in Chief of the reports) have been published by the ICTV: Wildy in 1971; Fenner in 1976; Matthews in 1979; Matthews in 1982; Francki *et al* in 1991; Murphy *et al* in 1995; and van Regenmortel *et al* in 1999. At the first meeting in Mexico City in 1970, two families with a corresponding two genera and 24 floating genera were adopted to begin the grouping of the vertebrate, invertebrate and bacterial viruses. In addition, 16 plant virus groups were designated, as reported by Matthews in 1983. The fifth ICTV report, edited by Francki *et al* in 1991, described one order, 40 families, nine subfamilies, 102 genera, two floating genera and two subgenera for vertebrate, invertebrate, bacterial and fungal viruses, and 32 groups and seven subgroups for plant viruses. While most virologists shifted to placing viruses in families and genera, plant virologists retained the term 'groups' until 1993. It was only in 1995, as described in the sixth ICTV report, that the ICTV proposed a uniform system for all viruses, with two orders, 50 families, nine subfamilies, 126 genera, 23 floating genera and four subgenera encompassing 2644 assigned viruses. Most recently, at the 28th meeting of the ICTV in March 1998 in San Diego, California, the Universal Virus Classification was adopted; this comprises three orders, 56 families, nine subfamilies, 203 genera, 30 floating genera and a total of 3954 species, strains and/or serotypes of species and tentative species. It is a general trend that the number of described taxa and the number of species of viruses is increasing steadily, easily explained by the increasing complexity of the virus classification and by the amount of data available to demarcate viruses.

With precise and complete descriptions available for a large number of virus families, this classification now constitutes a valuable source of information for new 'unknown' viruses. Therefore, the ICTV classification is not only a taxonomic exercise for virus evolutionists but also a valuable diagnostic tool and educational system for virologists, teachers, medical doctors and epidemiologists.

How does the ICTV operate?

The ICTV is a committee of the Virology Division, which is in turn part of the International Union of Microbiological Societies. The ICTV is a nonprofit-making organization composed of prominent virologists representing countries from throughout the world who work to designate virus names and taxa through a democratic process. The ICTV operates through a number of committees, subcommittees and study groups consisting of more than 492 eminent virologists with expertise in viruses infecting humans, animals, insects, protozoa, archaea, bacteria, mycoplasma, fungi, algae, yeasts and plants. Taxonomic proposals are initiated and formulated by individuals or by the study groups. These proposals are revised and accepted by the corresponding subcommittees and presented for executive committee approval. All decisions are then ratified at a plenary session (or also now by postal vote) held at each Virology Congress where all members of ICTV and more than 50 representatives of national microbiological societies are represented. At present, there are 47 study groups working in concert with six subcommittees – namely, the vertebrate, invertebrate, plant, bacteria, fungus and virus data subcommittees. The ICTV does not impose any taxonomic terms or taxa but ensures that all propositions are compatible with ICTV rules for homogeneity and consistency. The ICTV regularly publishes reports describing all existing virus taxa with a list of classified viruses as well as descriptions of virus families and genera. An Internet web site, where the most important information relative to virus taxonomy is made available, is updated regularly. The sixth report was published by Murphy *et al* (1995) and the seventh by van Regenmortel *et al* (1999).

The increasing number of virus species and virus strains being identified, together with the explosion of data on many descriptive aspects of viruses and viral diseases, and particularly sequence data, has led the ICTV to launch an international virus database project. This project, termed ICTVdB, is scheduled to be fully operational and accessible to the scientific community around the year 2000. The ICTVdB, in addition to the taxonomic descriptions of all the taxa, will comprise all the information available about each virus species, and later each virus strain, for all the descriptors necessary to identify and recognize all viruses.

A Universal System for Virus Classification

There are currently two systems in use for classifying organisms: the linnean and the adansonian systems.

The former is the monothetic hierarchical classification applied by Linnaeus to plants and animals, while the adansonian is a polythetic hierarchical system initially proposed by Adanson in 1763. In 1984 Maurin and collaborators suggested applying the linnean classification system to the viruses. Although convenient to use, this system has shortcomings when applied to the classification of viruses. Firstly, it is difficult to appreciate the validity of a particular criteria. For example, it may not be appropriate to use the number of genomic components as a hierarchical criteria. Secondly, there are no obvious reasons for prioritizing criteria, and in consequence it is difficult to rank all the available criteria. For instance, is the nature of the genome (DNA/RNA) more important than the sense of the coding sequence of the genome or the shape of the virus particles?

The adansonian system considers all available criteria at once and makes several classifications, taking the criteria into consideration successively. The criteria leading to the same classifications are considered as correlated and are therefore not discriminatory. Subsequently, a subset of criteria are considered, and the process is repeated until all criteria can be ranked to provide the best discrimination of the species. This system has not been used frequently in the past owing to its labor-intensive nature, but this situation has changed as a result of the power and availability of today's computer technology. Furthermore, qualitative and quantitative data can be simultaneously considered when generating such a classification. In the case of viruses, it was determined by Harrison and collaborators in 1971 that at least 60 characters could be used for a complete virus description (Table 1). Thus, the limiting factor for applying the adansonian system is now not its labor-intensive nature but the lack of data for many of the viruses.

In addition, the increasing number of viral nucleic acid sequences being reported, in combination with the appropriate computer software, allows the comparison of viruses to generate different phylogenetic trees, according to the gene or set of genes used, as for example proposed by Koonin in 1991, Dolja and Koonin in 1991 and Dolja *et al* in 1991. However, to date, none of them has satisfactorily provided a clear classification of all viruses. A multidimensional classification, taking into account all the criteria necessary to describe viruses, would probably be the most appropriate way of representing a virus classification, but again the shortcomings of data for some viruses would prevent the use of this system in the foreseeable future.

For almost 25 years, the ICTV has been classifying viruses essentially at the family and genus levels using a nonsystematic polythetic approach. Viruses were

clustered first in genera and then in families. A subset of characters, including physicochemical, structural, genomic and biological criteria, is then used to compare and group viruses. This subset of characters may change from one family to another, according to the availability of the data and the importance of a particular character for a particular family. It is obvious that there is no homogeneity in this respect throughout the virus classification and that virologists weigh the criteria differently in this subjective process, leading to the generation of a nonhomogeneous classification. Nevertheless, over time we can see stability of the current ICTV classification at the genus and family level. When sequence, genomic organization and replicative cycle data are subsequently used for taxonomic purposes, they usually confirm the actual classification. It is also obvious that hierarchical classifications above the family level will encounter conflicts between phenotypic and genotypic criteria and that virologists will have to consider the entire classification process in order to progress in this direction.

Currently, and for practical reasons only, virus classification is structured according to the presentation indicated in Tables 2 and 3. This 'Order of Presentation of the Viruses' does not reflect any hierarchical or phylogenetic classification but only a convenient order of presentation of the virus taxa. Since a taxonomic structure above the level of family (with the exception of the orders *Mononegavirales*, *Caudovirales* and *Nidovirales*) has not been developed extensively, any listing must be arbitrary. The order of presentation of virus families and genera follows four criteria: (1) the nature of the viral nucleic acid; (2) the strandedness of the nucleic acid; (3) the use of a reverse transcription process (DNA or RNA); and (4) the positive or negative sense of gene coding on the encapsidated genome. These four criteria give rise to six clusters comprising the 86 families and floating genera of viruses. In the past, two other criteria were also taken in account: the presence or absence of a lipid envelope and the segmentation of the genome as mono-, bi-, tri-, tetra- or multipartite. However, it has become clear that the presence of an envelope was entirely related to the nature of the host and that families could comprise genera having viruses with segmented or nonsegmented genomes, but sharing all other properties, including genome organization and sequence homology. These criteria have been therefore abandoned.

The Virus Species Concept and its Application

In 1991 the ICTV accepted the concept that viruses

Table 1 Virus family descriptors used in virus taxonomy*I Virion properties***A Morphology properties of virions**

- 1 Size
- 2 Shape
- 3 Presence or absence of an envelope and peplomers
- 4 Capsomeric symmetry and structure

B Physical properties of virions

- 1 Molecular mass
- 2 Buoyant density
- 3 Sedimentation coefficient
- 4 pH stability
- 5 Thermal stability
- 6 Cation (Mg^{2+} , Mn^{2+}) stability
- 7 Solvent stability
- 8 Detergent stability
- 9 Radiation stability

C Properties of genome

- 1 Type of nucleic acid DNA or RNA
- 2 Strandedness: single-stranded or double-stranded
- 3 Linear or circular
- 4 Sense: positive, negative or ambisense
- 5 Number of segments
- 6 Size of genome or genome segments
- 7 Presence or absence and type of 5' terminal cap
- 8 Presence or absence of 5' terminal covalently linked polypeptide
- 9 Presence or absence of 3' terminal poly(A) tract (or other specific tract)
- 10 Nucleotide sequence comparisons

D Properties of proteins

- 1 Number
- 2 Size
- 3 Functional activities (especially virion transcriptase, virion reverse transcriptase, virion hemagglutinin, virion neuraminidase, virion fusion protein)
- 4 Amino acid sequence comparisons

E Lipids

- 1 Presence or absence
- 2 Nature

F Carbohydrates

- 1 Presence or absence
- 2 Nature

II Genome organization and replication

- 1 Genome organization
- 2 Strategy of replication of nucleic acid
- 3 Characteristics of transcription
- 4 Characteristics of translation and post-translational processing
- 5 Site of accumulation of virion proteins, site of assembly, site of maturation and release
- 6 Cytopathology, inclusion body formation

III Antigenic properties

- 1 Serological relationships
- 2 Mapping epitopes

IV Biological properties

- 1 Host range, natural and experimental
- 2 Pathogenicity, association with disease
- 3 Tissue tropisms, pathology, histopathology

Table 1 Continued

-
- 4 Mode of transmission in nature
 - 5 Vector relationships
 - 6 Geographic distribution
-

Adapted from ICTV guidelines for family descriptions.

exist as species, in a similar manner to other organisms, and adopted a definition for a virus species proposed by van Regenmortel in 1990: 'A virus species is a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche.' This simple definition and the position taken by the ICTV has already had, and will continue to have, a profound effect on virus classification. Effectively, in the sixth ICTV report virus names were indicated in 'List of species' but they were in fact a 'List of virus names' with undefined taxonomic status. In the seventh ICTV report, according to the polythetic nature of the species definition, a 'List of species-demarcating criteria' is provided for each genus, indicating how virus species can be identified in this particular genus. Viruses are then differentiated in species and tentative species according to this list of criteria and the availability of information to demarcate the species.

First, it is intended to define for each genus the criteria demarcating a virus species, and, second, to compare these criteria from one genus to the next, searching for homogeneity throughout the virus classification. Naturally this list of criteria should follow the polythetic nature of the species definition and more than one criteria should be used to determine a new species. It is obvious that most of the criteria in the list of demarcating criteria are shared amongst the different genera, within and across families; namely, host range, serological relationships, vector transmission type, tissue tropism, genome rearrangement and sequence homology (Table 4). However, if the types of criteria are similar, the levels of demarcation clearly differ from one family to another. This may reflect differences in appreciation from one family to another but also the differential ranking of a particular criterion in different families. The huge differences (up to 30%) in sequences among nucleoproteins of species of lentiviruses does not have the same biological significance as small differences in capsid protein sequences (1–10%) of species of potyviruses, and therefore universal levels of sequence identity for similar genes may not exist for viruses! The levels of demarcation may even change from one gene to another within the same family. Homogenization of the application of the species definition concept

throughout the virus definition will be the next challenge of ICTV for the eighth report to be published by 2002. This, in turn, will contribute to homogeneity of the genus and family demarcation criteria (Table 4) and will permit creation of new families or merging of existing families. However, it is important to note that the nature of the demarcating criteria at the genus level will probably not change as these have passed the test of time. Despite the fact that they were mostly established using biochemical and structural criteria, they remained valid when correlated with genome organization and sequence data.

The Universal Virus Classification

The present universal system of virus taxonomy is set arbitrarily at hierarchical levels of order, family (in some cases subfamily), genus and species. Lower hierarchical levels, such as subspecies, strain, serotype, variant, pathotype and isolate are established by international specialty groups and/or by culture collections, but not by the ICTV. However some of them may be indicated in the ICTV report for information or because in the past these names were listed as 'viruses' in previous reports.

Virus species

The species taxon is always regarded as the most important taxonomic level in classification but it has proved to be the most difficult to apply to the viruses. ICTV definition of a virus species was long considered to be 'a concept that will normally be represented by a cluster of strains from a variety of sources, or a population of strains from a particular source, which have in common a set or pattern of correlating stable properties that separates the cluster from other clusters of strains' as stated by Matthews in 1982 and by Francki *et al* in 1991. This was a general definition, which was in fact not very useful for practically delineating species in a particular family. Furthermore, this definition directly addressed the definition of a virus strain, which had never been attempted in the history of virus taxonomy. In 1991, the ICTV Executive Committee accepted a definition proposed by van Regenmortel in 1990 (see above). This definition states: 'A virus species is a polythetic class of viruses that constitutes a replicating lineage

Table 2 Order of presentation of the viruses

Order	Family	Subfamily	Genus	Type species	Host		
The DNA viruses							
The dsDNA viruses							
Caudovirales	Myoviridae		"T4-like viruses" ^a	<i>Enterobacteria phage T4</i>	Bacteria		
			"P1-like viruses"	<i>Enterobacteria phage P1</i>	Bacteria		
			"P2-like viruses"	<i>Enterobacteria phage P2</i>	Bacteria		
			"Mu-like viruses"	<i>Enterobacteria phage Mu</i>	Bacteria		
			"SP01-like viruses"	<i>Bacillus phage SP01</i>	Bacteria		
			"φH-like viruses"	<i>Halobacterium virus φH</i>	Archaea		
		Siphoviridae		"λ-like viruses"	<i>Enterobacteria phage λ</i>	Bacteria	
				"T1-like viruses"	<i>Enterobacteria phage T1</i>	Bacteria	
				"T5-like viruses"	<i>Enterobacteria phage T5</i>	Bacteria	
				"L5-like viruses"	<i>Mycobacterium phage L5</i>	Bacteria	
	"c2-like viruses"		<i>Lactococcus phage c2</i>	Bacteria			
Podoviridae		"ψM1-like viruses"	<i>Methanobacterium virus ψM1</i>	Archaea			
		"T7-like viruses"	<i>Enterobacteria phage T7</i>	Bacteria			
		"P22-like viruses"	<i>Enterobacteria phage P22</i>	Bacteria			
Tectiviridae	Corticoviridae		"φ29-like viruses"	<i>Bacillus phage φ29</i>	Bacteria		
			<i>Tectivirus</i>	<i>Enterobacteria phage PRD1</i>	Bacteria		
			<i>Corticovirus</i>	<i>Alteromonas phage PM2</i>	Bacteria		
		Plasmaviridae		<i>Plasmavirus</i>	<i>Acholeplasma phage L2</i>	Mycoplasma	
			Lipothrixviridae		<i>Lipothrixvirus</i>	<i>Thermoproteus virus 1</i>	Archaea
		Rudiviridae			<i>Rudivirus</i>	<i>Sulfolobus virus SIRV1</i>	Archaea
			Fuselloviridae		<i>Fusellovirus</i>	<i>Sulfolobus virus SSV1</i>	Archaea
				"SNDV-like viruses"	<i>Sulfolobus virus SNDV</i>	Archaea	
		Poxviridae	Chordopoxvirinae		<i>Orthopoxvirus</i>	<i>Vaccinia virus</i>	Vertebrates
					<i>Parapoxvirus</i>	<i>Orf virus</i>	Vertebrates
	<i>Avipoxvirus</i>			<i>Fowlpox virus</i>	Vertebrates		
	<i>Capripoxvirus</i>			<i>Sheeppox virus</i>	Vertebrates		

Table 2 Continued

Order	Family	Subfamily	Genus	Type species	Host
			<i>Leporipoxvirus</i>	<i>Myxoma virus</i>	Vertebrates
			<i>Suiipoxvirus</i>	<i>Swinepox virus</i>	Vertebrates
			<i>Molluscipoxvirus</i>	<i>Molluscum contagiosum virus</i>	Vertebrates
			<i>Yatapoxvirus</i>	<i>Yaba monkey tumor virus</i>	Vertebrates
		<i>Entomopoxvirinae</i>	<i>Entomopoxvirus A</i>	<i>Melolontha melolontha entomopoxvirus</i>	Invertebrates
			<i>Entomopoxvirus B</i>	<i>Amsactia moorei entomopoxvirus</i>	Invertebrates
			<i>Entomopoxvirus C</i>	<i>Chironomus luridus entomopoxvirus</i>	Invertebrates
	<i>Asfarviridae</i>		<i>Asfivirus</i>	<i>African swine fever virus</i>	Vertebrates ^b
	<i>Iridoviridae</i>		<i>Iridovirus</i>	<i>Chilo iridescent virus</i>	Invertebrates
			<i>Chloridovirus</i>	<i>Mosquito iridescent virus</i>	Invertebrates
			<i>Ranavirus</i>	<i>Frog virus 3</i>	Vertebrates
			<i>Lymphocystivirus</i>	<i>Flounder virus</i>	Vertebrates
	<i>Phycodnaviridae</i>		<i>Chlorovirus</i>	<i>Paramecium bursaria Chlorella virus 1</i>	Algae
			<i>Prasinovirus</i>	<i>Micromonas pusilla virus SP1</i>	Algae
			<i>Prymnesiovirus</i>	<i>Chrysochromulina brevifilum virus</i>	Algae
			<i>Phaeovirus</i>	<i>Ectocarpus siliculosus virus 1</i>	Algae
	<i>Baculoviridae</i>		<i>Nucleopolyhedrovirus</i>	<i>Autographa californica nucleopolyhedrovirus</i>	Invertebrates
			<i>Granulovirus</i>	<i>Cydia pomonella granulovirus</i>	Invertebrates
	<i>Herpesviridae</i>				
		<i>Alphaherpesvirinae</i>	<i>Simplexvirus</i>	<i>Human herpesvirus 1</i>	Vertebrates
			<i>Varicellovirus</i>	<i>Human herpesvirus 3</i>	Vertebrates
			"Marek's disease-like viruses"	<i>Marek's disease virus</i>	Vertebrates
			"ILTV-like viruses"	<i>Infectious laryngotracheitis virus</i>	Vertebrates
		<i>Betaherpesvirinae</i>	<i>Cytomegalovirus</i>	<i>Human herpesvirus 5</i>	Vertebrates
			<i>Muromegalovirus</i>	<i>Mouse cytomegalovirus 1</i>	Vertebrates
			<i>Roseolovirus</i>	<i>Human herpesvirus 6</i>	Vertebrates

Table 2 Continued

Order	Family	Subfamily	Genus	Type species	Host
		<i>Gammaherpesvirinae</i>			
			<i>Lymphocryptovirus</i>	<i>Human herpesvirus 4</i>	Vertebrates
			<i>Rhadinovirus</i>	<i>Ateline herpesvirus 2</i>	Vertebrates
			"Ictalurid herpes-like viruses"	<i>Ictalurid herpesvirus 1</i>	Vertebrates
	<i>Adenoviridae</i>		<i>Mastadenovirus</i>	<i>Human adenovirus 2</i>	Vertebrates
			<i>Aviadenovirus</i>	<i>Fowl adenovirus 1</i>	Vertebrates
			<i>Rhizidiovirus</i>	<i>Rhizidiomyces virus</i>	Fungi
	<i>Polyomaviridae</i>		<i>Polyomavirus</i>	<i>Murine polyomavirus</i>	Vertebrates
	<i>Papillomaviridae</i>		<i>Papillomavirus</i>	<i>Cottontail rabbit papillomavirus</i>	Vertebrates
	<i>Polydnaviridae</i>		<i>Ichnovirus</i>	<i>Campolepis sonorensis virus</i>	Invertebrates
			<i>Bracovirus</i>	<i>Cotesia melanoscela virus</i>	Invertebrates
	<i>Ascoviridae</i>		<i>Ascovirus</i>	<i>Spodoptera frugiperda ascovirus</i>	Invertebrates
The ssDNA viruses					
	<i>Inoviridae</i>		<i>Inovirus</i>	<i>Coliphage fd</i>	Bacteria
			<i>Plectrovirus</i>	<i>Acholeplasma phage L51</i>	Mycoplasma
	<i>Microviridae</i>		<i>Microvirus</i>	<i>Coliphage φX174</i>	Bacteria
			<i>Spiromicrovirus</i>	<i>Spiroplasma phage 4</i>	Spiroplasma
			<i>Bdellovirovirus</i>	<i>Bdellovibrio phage MAC1</i>	Bacteria
			<i>Chlamydia microvirus</i>	<i>Chlamydia phage 1</i>	Bacteria
	<i>Geminiviridae</i>		<i>Mastrevirus</i>	<i>Maize streak virus</i>	Plants
			<i>Curtovirus</i>	<i>Beet curly top virus</i>	Plants
			<i>Begomovirus</i>	<i>Bean golden mosaic virus</i>	Plants
	<i>Circoviridae</i>		<i>Circovirus</i>	<i>Chicken anemia virus</i>	Vertebrates
			<i>Nanovirus</i>	<i>Subterranean clover stunt virus</i>	Plants

Table 2 Continued

Order	Family	Subfamily	Genus	Type species	Host
The DNA and RNA reverse transcribing viruses <i>Hepadnaviridae</i>	<i>Parvoviridae</i>	<i>Parvovirinae</i>	<i>Parvovirus</i>	<i>Mice minute virus</i>	Vertebrates
			<i>Erythrovirus</i>	<i>B19 virus</i>	Vertebrates
			<i>Dependovirus</i>	<i>Adeno-associated virus 2</i>	Vertebrates
		<i>Densovirinae</i>	<i>Densovirus</i>	<i>Junonia coenia densovirus</i>	Invertebrates
			<i>Iteravirus</i>	<i>Bombyx mori densovirus</i>	Invertebrates
			<i>Brevidensovirus</i>	<i>Aedes aegypti densovirus</i>	Invertebrates
	<i>Orthohepadnavirus</i>	<i>Hepatitis B virus</i>	Vertebrates		
		<i>Avihepadnavirus</i>	<i>Duck hepatitis B virus</i>	Vertebrates	
	<i>Caulimoviridae</i>	<i>Caulimovirus</i>	<i>Cauliflower mosaic virus</i>	Plants	
		"PVCV-like viruses"	<i>Petunia vein-clearing virus</i>	Plants	
		"SbCMV-like viruses"	<i>Soybean chlorotic mottle virus</i>	Plants	
		"CsVMV-like viruses"	<i>Cassava vein mosaic virus</i>	Plants	
		<i>Badnavirus</i>	<i>Commelina yellow mottle virus</i>	Plants	
		"RTBV-like viruses"	<i>Rice tungro bacilliform virus</i>	Plants	
<i>Pseudoviridae</i>		<i>Pseudovirus</i>	<i>Saccharomyces cerevisiae Ty1 virus</i>	Yeast, Plants	
		<i>Hemivirus</i>	<i>Drosophila melanogaster copia virus</i>	Yeast, Invertebrates	
<i>Metaviridae</i>		<i>Metavirus</i>	<i>Saccharomyces cerevisiae Ty3 virus</i>	Yeast, Plants, Invertebrates	
		<i>Erranivirus</i>	<i>Drosophila melanogaster gypsy virus</i>	Invertebrates	
<i>Retroviridae</i>	<i>Alpharetrovirus</i>	<i>Avian leukosis virus</i>	Vertebrates		
	<i>Betaretrovirus</i>	<i>Mason-Pfizer monkey virus</i>	Vertebrates		
	<i>Gammaretrovirus</i>	<i>Mouse mammary tumor virus</i>	Vertebrates		
	<i>Deltaretrovirus</i>	<i>Bovine leukemia virus</i>	Vertebrates		
	<i>Epsilonretrovirus</i>	<i>Walleye dermal sarcoma virus</i>	Vertebrates		
	<i>Lentivirus</i>	<i>Human immunodeficiency virus 1</i>	Vertebrates		
	<i>Spumavirus</i>	<i>Human spumavirus</i>	Vertebrates		

Table 2 Continued

Order	Family	Subfamily	Genus	Type species	Host
The RNA viruses					
The dsRNA viruses					
	Cystoviridae		Cystovirus	<i>Pseudomonas phage φ6</i>	Bacteria
	Reoviridae		Orthoreovirus	Reovirus 3	Vertebrates
			Orbivirus	<i>Bluetongue virus 1</i>	Vertebrates
			Rotavirus	<i>Simian rotavirus SA11</i>	Vertebrates
			Coltivirus	<i>Colorado tick fever virus</i>	Vertebrates
			Aquareovirus	<i>Golden shiner virus</i>	Vertebrates
			Cypovirus	<i>Bombyx mori cypovirus 1</i>	Invertebrates
			Fijivirus	<i>Fiji disease virus</i>	Plants
			Phytoreovirus	<i>Wound tumor virus</i>	Plants
			Oryzavirus	<i>Rice ragged stunt virus</i>	Plants
	Birnaviridae		Aquabimavirus	<i>Infectious pancreatic necrosis virus</i>	Vertebrates
			Avibimavirus	<i>Infectious bursal disease virus</i>	Vertebrates
			Entomobimavirus	<i>Drosophila X virus</i>	Invertebrates
	Totiviridae		Totivirus	<i>Saccharomyces cerevisiae virus L-A</i>	Fungi
			Giardiavirus	<i>Giardia lamblia virus</i>	Protozoa
			Leishmanivirus	<i>Leishmania RNA virus 1-1</i>	Protozoa
	Partitiviridae		Partivirus	<i>Gaeumannomyces graminis virus 019/6-A</i>	Fungi
			Chrysovirus	<i>Penicillium chrysogenum virus</i>	Fungi
			Alphacryptovirus	<i>White clover cryptic virus 1</i>	Plants
			Betacryptovirus	<i>White clover cryptic virus 2</i>	Plants
	Hypoviridae		Hypovirus	<i>Cryphonectria hypovirus 1-EP713</i>	Fungi
			Varicosavirus	<i>Lettuce big-vein virus</i>	Plants
The negative-stranded ssRNA viruses					
Mononegavirales					
	Bornaviridae		Bornavirus	<i>Borna disease virus</i>	Vertebrates

Table 2 Continued

Order	Family	Subfamily	Genus	Type species	Host
	<i>Filoviridae</i>		"Ebola-like viruses" Zaire "Marburg-like viruses"	<i>Ebola virus</i> <i>Marburg virus</i>	Vertebrates Vertebrates
	<i>Paramyxoviridae</i>	<i>Paramyxovirinae</i>	<i>Respirovirus</i> <i>Morbillivirus</i> <i>Rubulavirus</i>	<i>Human parainfluenza virus 1</i> <i>Measles virus</i> <i>Mumps virus</i>	Vertebrates Vertebrates Vertebrates
		<i>Pneumovirinae</i>	<i>Pneumovirus</i> <i>Metapneumovirus</i>	<i>Human respiratory syncytial virus</i> <i>Turkey rhinotracheitis virus</i>	Vertebrates Vertebrates
	<i>Rhabdoviridae</i>		<i>Vesiculovirus</i> <i>Lyssavirus</i> <i>Ephemerovirus</i> <i>Novirhabdovirus</i> <i>Cytorhabdovirus</i> <i>Nucleorhabdovirus</i>	<i>Vesicular stomatitis Indiana virus</i> <i>Rabies virus</i> <i>Bovine ephemeral fever virus</i> <i>Infectious hematopoietic necrosis virus</i> <i>Lettuce necrotic yellows virus</i> <i>Potato yellow dwarf virus</i>	Vertebrates Vertebrates Vertebrates Vertebrates Plants Plants
	<i>Orthomyxoviridae</i>		<i>Influenzavirus A</i> <i>Influenzavirus B</i> <i>Influenzavirus C</i> <i>Thogotovirus</i>	<i>Influenza A virus</i> <i>Influenza B virus</i> <i>Influenza C virus</i> <i>Thogoto virus</i>	Vertebrates Vertebrates Vertebrates Vertebrates
	<i>Bunyaviridae</i>		<i>Bunyavirus</i> <i>Hantavirus</i> <i>Nairovirus</i> <i>Phlebovirus</i> <i>Tospovirus</i> <i>Tenuivirus</i> <i>Ophiovirus</i>	<i>Bunyamwera virus</i> <i>Hantaan virus</i> <i>Nairobi sheep disease virus</i> <i>Sandfly fever Sicilian virus</i> <i>Tomato spotted wilt virus</i> <i>Rice stripe virus</i> <i>Citrus psorosis virus</i>	Vertebrates Vertebrates Vertebrates Vertebrates Plants Plants Plants
	<i>Arenaviridae</i>		<i>Arenavirus</i> <i>Deltavirus</i>	<i>Lymphocytic choriomeningitis virus</i> <i>Hepatitis delta virus</i>	Vertebrates Vertebrates

Table 2 Continued

Order	Family	Subfamily	Genus	Type species	Host
The positive-stranded ssRNA viruses					
	Leviviridae		<i>Levivirus</i>	<i>Enterobacteria phage MS2</i>	Bacteria
			<i>Altolevivirus</i>	<i>Enterobacteria phage Qβ</i>	Bacteria
	Narnaviridae		<i>Narnavirus</i>	<i>Saccharomyces cerevisiae 20S narnavirus</i>	Yeast
			<i>Mitivirus</i>	<i>Cryphonectria parasitica NB631 virus</i>	Yeast
	Picomaviridae		<i>Enterovirus</i>	<i>Poliovirus 1</i>	Vertebrates
			<i>Rhinovirus</i>	<i>Human rhinovirus 1A</i>	Vertebrates
			<i>Hepatovirus</i>	<i>Hepatitis A virus</i>	Vertebrates
			<i>Cardiovirus</i>	<i>Encephalomyocarditis virus</i>	Vertebrates
			<i>Aphthovirus</i>	<i>Foot-and-mouth disease virus O</i>	Vertebrates
			<i>Parechovirus</i>	<i>Human echovirus 22</i>	Vertebrates
			"Cricket paralysis-like viruses"	<i>Cricket paralysis virus</i>	Invertebrates
	Sequiviridae		<i>Sequivirus</i>	<i>Parsnip yellow fleck virus</i>	Plants
			<i>Waikavirus</i>	<i>Rice tungro spherical virus</i>	Plants
	Comoviridae		<i>Comovirus</i>	<i>Cowpea mosaic virus</i>	Plants
			<i>Fabavirus</i>	<i>Broad bean wilt virus 1</i>	Plants
			<i>Nepovirus</i>	<i>Tobacco ringspot virus</i>	Plants
	Potyviridae		<i>Potyvirus</i>	<i>Potato virus Y</i>	Plants
			<i>Rymovirus</i>	<i>Ryegrass mosaic virus</i>	Plants
			<i>Macluravirus</i>	<i>Maclura mosaic virus</i>	Plants
			<i>Ipomovirus</i>	<i>Sweet potato mild mottle virus</i>	Plants
			<i>Bymovirus</i>	<i>Barley yellow mosaic virus</i>	Plants
			<i>Tritimovirus</i>	<i>Wheat streak mosaic virus</i>	Plants
	Caliciviridae		<i>Vesivirus</i>	<i>Swine vesicular exanthema virus</i>	Vertebrates
			<i>Lagovirus</i>	<i>Rabbit hemorrhagic disease virus</i>	Vertebrates

Table 2 Continued

Order	Family	Subfamily	Genus	Type species	Host
			"Norwalk-like viruses"	Norwalk virus	Vertebrates
			"Sapporo-like viruses"	Sapporo virus	Vertebrates
			"Hepatitis E-like viruses"	Hepatitis E virus	Vertebrates
	<i>Astroviridae</i>		<i>Astrovirus</i>	Human astrovirus 1	Vertebrates
	<i>Nodaviridae</i>		<i>Alphanodavirus</i>	Nodamura virus	Invertebrates
			<i>Betanodavirus</i>	Striped jack nervous necrosis virus	Vertebrates
	<i>Tetraviridae</i>		<i>Betatetravirus</i>	Nudaurelia capensis β virus	Invertebrates
			<i>Omegatetravirus</i>	Nudaurelia capensis ω virus	Invertebrates
			<i>Sobemovirus</i>	Southern bean mosaic virus	Plants
			<i>Marafivirus</i>	Maize rayado fino virus	Plants
	<i>Luteoviridae</i>		<i>Luteovirus</i>	Barley yellow dwarf virus – MAV	Plants
			<i>Polerovirus</i>	Potato leafroll virus	Plants
			<i>Enamovirus</i>	Pea enation mosaic virus 1	Plants
			<i>Umbravirus</i>	Carrot mottle virus	Plants
	<i>Tombusviridae</i>		<i>Avenavirus</i>	Oat chlorotic stunt virus	Plants
			<i>Aureusvirus</i>	Poathos latent virus	Plants
			<i>Carmovirus</i>	Carnation mottle virus	Plants
			<i>Dianthovirus</i>	Carnation ringspot virus	Plants
			<i>Machlomovirus</i>	Maize chlorotic mottle virus	Plants
			<i>Necrovirus</i>	Tobacco necrosis virus	Plants
			<i>Panicovirus</i>	Panicum mosaic virus	Plants
			<i>Tombusvirus</i>	Tomato bushy stunt virus	Plants
<i>Nidovirales</i>			<i>Coronaviridae</i>		
			<i>Coronavirus</i>	Avian infectious bronchitis virus	Vertebrates
			<i>Torovirus</i>	Berne virus	Vertebrates
	<i>Arteriviridae</i>		<i>Arterivirus</i>	Equine arteritis virus	Vertebrates

Table 2 Continued

Order	Family	Subfamily	Genus	Type species	Host		
Flaviviridae	Flaviviridae		<i>Flavivirus</i>	<i>Yellow fever virus</i>	Vertebrates		
			<i>Pestivirus</i>	<i>Bovine diarrhoea virus</i>	Vertebrates		
			<i>Hepacivirus</i>	<i>Hepatitis C virus</i>	Vertebrates		
	Togaviridae	Togaviridae		<i>Alphavirus</i>	<i>Sindbis virus</i>	Vertebrates	
				<i>Rubivirus</i>	<i>Rubella virus</i>	Vertebrates	
			<i>Tobamovirus</i>	<i>Tobacco mosaic virus</i>	Plants		
			<i>Tobravirus</i>	<i>Tobacco rattle virus</i>	Plants		
			<i>Hordeivirus</i>	<i>Barley stripe mosaic virus</i>	Plants		
			<i>Furovirus</i>	<i>Soil-borne wheat mosaic virus</i>	Plants		
			<i>Pomovirus</i>	<i>Potato mop-top virus</i>	Plants		
			<i>Peclivirus</i>	<i>Peanut clump virus</i>	Plants		
			<i>Benyvirus</i>	<i>Beet necrotic yellow vein virus</i>	Plants		
		Bromoviridae	Bromoviridae		<i>Alfavirus</i>	<i>Alfalfa mosaic virus</i>	Plants
					<i>Bromovirus</i>	<i>Brome mosaic virus</i>	Plants
					<i>Cucumovirus</i>	<i>Cucumber mosaic virus</i>	Plants
	<i>Illavirus</i>			<i>Tobacco streak virus</i>	Plants		
	<i>Oleavirus</i>			<i>Olive latent virus 2</i>	Plants		
	<i>Ourniavirus</i>			<i>Ournia melon virus</i>	Plants		
	<i>Idaeovirus</i>			<i>Raspberry bushy dwarf virus</i>	Plants		
Closteroviridae	Closteroviridae				<i>Closterovirus</i>	<i>Beet yellows virus</i>	Plants
					<i>Crinivirus</i>	<i>Lettuce infectious yellows virus</i>	Plants
					<i>Capilliovirus</i>	<i>Apple stem grooving virus</i>	Plants
					<i>Trichovirus</i>	<i>Apple chlorotic leaf spot virus</i>	Plants
					<i>Vitivirus</i>	<i>Grapevine virus A</i>	Plants
					<i>Tymovirus</i>	<i>Turnip yellow mosaic virus</i>	Plants
					<i>Carlavirus</i>	<i>Carnation latent virus</i>	Plants

Table 2 Continued

Order	Family	Subfamily	Genus	Type species	Host
			<i>Potexvirus</i>	<i>Potato virus X</i>	Plants
			<i>Allexivirus</i>	<i>Shallot virus X</i>	Plants
			<i>Foveavirus</i>	<i>Apple stem pitting virus</i>	Plants
	Barnaviridae		<i>Barnavirus</i>	<i>Mushroom bacilliform virus</i>	Fungi
Unassigned viruses					
The subviral agents: viroids, satellites and agents of spongiform encephalopathies (prions)					
Subviral agent	Family	Genus	Type species	Host	
Viroids	<i>Pospiviroidae</i>	<i>Pospiviroid</i>	<i>Potato spindle tuber viroid</i>	Plants	
		<i>Hostuviroid</i>	<i>Hop stunt viroid</i>	Plants	
		<i>Cocadviroid</i>	<i>Coconut cadang-cadang viroid</i>	Plants	
		<i>Apscaviroid</i>	<i>Apple scar skin viroid</i>	Plants	
		<i>Coleviroid</i>	<i>Coleus blumei viroid 1</i>	Plants	
Satellites	<i>Avsunviroidae</i>	<i>Avsunviroid</i>	<i>Avocado sunblotch viroid</i>	Plants	
		<i>Pelamoviroid</i>	<i>Peach latent mosaic virus</i>	Plants	
Prions				Plants	
				Invertebrates	
				Fungi	
				Vertebrates	
				Fungi	

^a Quotes are used to denote taxon names that are not approved ICTV international names, and are thus temporary until formal names are approved.

^b Vertebrate arthropod-borne viruses are listed according to their vertebrate hosts.

Table 3 Orders, families and floating genera of viruses according to the seventh ICTV report (1999)

Criteria	Order	Family	Floating genus	Morphology	Genome configuration	Genome size (kb)	Virus host	Number of species			Total	
								Species	serotypes	Tentative		
dsDNA	Caudovirales	Myoviridae		Tailed phage	1 linear	336	Bacteria, archaea	15	23	117	155	
		Siphoviridae		Tailed phage	1 linear	53	Bacteria, archaea	7	0	137	144	
		Podoviridae		Tailed phage	1 linear	40	Bacteria, archaea	8	12	66	86	
		Tectiviridae		Isometric	1 linear	16	Bacteria	4	0	38	42	
		Corticoviridae		Isometric	1 circular supercoiled	10	Bacteria	1	0	2	3	
		Plasmaviridae		Pleomorphic	1 circular	12	Mycoplasma	1	0	7	8	
		Lipothrixviridae		Rod	1 linear	16	Archaea	2	0	0	2	
		Rudoviridae		Rod	1 linear	33-36	Archaea	2	0	1	3	
		Fuselloviridae		Lemon-shape	1 circular supercoiled	15	Archaea	1	0	0	1	
				"SNDV-like viruses"	Droplet-shape	1 circular	20	Archaea	1	0	0	1
		Poxviridae		Ovoid	1 linear	130-375	Vertebrate, invertebrate	62	8	23	93	
		Asfarviridae		Isometric	1 circular	170-190	Vertebrate	1	0	0	1	
		Iridoviridae		Isometric	1 linear	160-400	Vertebrate, invertebrate	17	4	3	24	
		Phycodnaviridae		Isometric	1 linear	250-350	Algae	27	0	38	65	
		Baculoviridae		Bacilliform	1 circular supercoiled	90-230	Invertebrate	17	6	7	30	
		Herpesviridae		Isometric	1 linear	120-220	Vertebrate	56	0	65	121	
		Adenoviridae		Isometric	1 linear	32-48	Vertebrate	26	102	35	163	
		Polyomaviridae		Isometric	1 linear	27	Fungus	1	0	0	1	
		Papillomaviridae		Isometric	1 circular	5	Vertebrate	12	4	0	16	
	Polydnaviridae		Isometric	1 circular	6.8-8.4	Vertebrate	7	0	88	95		
			Rhizidiovirus	Rod, fusiform	1 circular supercoiled	2-28	Invertebrate	59	0	0	59	
	Ascoviridae		Ovoid and bacilliform	1 circular	100-180	Invertebrate	3	0	1	4		
							330	159	628	117		

Table 3 Continued

Criteria	Order	Family	Floating genus	Morphology	Genome configuration	Genome size (kb)	Virus host	Number of species			
								Species	serotypes	Tentative	Total
ssDNA		<i>Inoviridae</i>		Rod	1 circular	7-20	Bacteria, mycoplasma	36	7	5	48
		<i>Microviridae</i>		Isometric	1 circular	6	Bacteria, spiroplasma	7	0	33	40
		<i>Geminivirus</i>		Isometric	1 or 2 circular	3-6	Plant	94	2	10	106
		<i>Circoviridae</i>		Isometric	1 circular	1.7-2.3	Vertebrate	3	0	1	4
		<i>Nanovirus</i>		Isometric	6-9 circular	6-9	Plant	4	0	1	5
		<i>Parvoviridae</i>		Isometric	1 - strand	6-8	Vertebrate, invertebrate	38	0	16	54
		<i>Hepadnaviridae</i>		Isometric	1 circular - strand	3	Vertebrate	182	9	66	257
RT								5	0	2	7
dsDNA		<i>Caulimoviridae</i>		Isometric, bacilliform	1 circular	8	Plant	26	0	8	34
RT											
ssRNA		<i>Pseudoviridae</i>		Ovoid	1 linear	5-8	Yeast, plant	15	0	0	15
RT											
ssRNA		<i>Metaviridae</i>		Isometric	1 linear	4-10	Yeast, fungus, invertebrate	18	0	1	19
RT											
ssRNA		<i>Retroviridae</i>		Spherical	dimer 1 + segment	7-10	Vertebrate	59	44	2	105
RT											
dsRNA		<i>Cystoviridae</i>		Isometric	3 segments	17	Bacteria	123	44	13	180
		<i>Reoviridae</i>		Isometric	10-12 segments	19-62	Vertebrate, invertebrate, plant	1	0	0	1
								62	256	39	357
		<i>Bimaviridae</i>		Isometric	2 segments	6	Vertebrate, invertebrate	4	21	1	26
		<i>Totiviridae</i>		Isometric	1 segment	5-7	Fungus, protozoa	18	0	5	23
		<i>Partitiviridae</i>		Isometric	2 segments	3-10	Fungus, plant	30	0	15	45
		<i>Hypoviridae</i>		Pleomorphic	1 segment	9-13	Fungus	3	0	2	5
		<i>Varicosavirus</i>		Rod	2 segments	14	Plant	1	0	3	4
								119	277	65	461
Negative ssRNA		<i>Mononegavirales</i>		Spherical	1 - segment	9	Vertebrate	1	0	1	2
		<i>Bornaviridae</i>									
		<i>Filoviridae</i>		Bacilliform	1 - segment	13	Vertebrate	5	19	0	24

Table 3 Continued

Criteria	Order	Family	Floating genus	Morphology	Genome configuration	Genome size (kb)	Virus host	Number of species			
								Species	Serotypes	Tentative	Total
Positive ssRNA	Paramyxoviridae Rhabdoviridae			Helical	1 - segment	15-16	Vertebrate	31	5	2	38
				Bacilliform	1 - segment	10-13	Vertebrate, plant	37	0	142	179
	Orthomyxoviridae Bunyaviridae			Helical	8 - segments	13-14	Vertebrate	5	1	0	6
				Spherical	3 - segments	12-23	Vertebrate, plant	93	236	66	395
	Arenaviridae			Filaments	4 - ? segments	15-19	Plant	6	0	5	11
				Filaments	3 - segments	12	Plant	3	0	0	3
				Spherical	2 - segments	11	Vertebrate	19	27	2	48
				Spherical	1 circular strand	1.7	Vertebrate	1	0	0	1
	Leviviridae				1 + segment	3-4	Bacteria	201	288	218	707
	Narnaviridae				1 + segment	2.5	Yeast	4	18	35	57
	Picornaviridae			Isometric	1 + segment	7-8.5	Vertebrate	16	105	137	258
				Ribonucleic complex	1 + segment	9-10	Invertebrate	5	0	0	5
	Sequiviridae Comoviridae			Isometric	1 + segment	9-12	Plant	5	0	0	5
				Isometric	2 + segments	9-16	Plant	50	0	9	59
	Potyviridae			Rod	1 or 2 + segments	8-12	Plant	106	0	92	198
	Caliciviridae			Isometric	1 + segment	8	Vertebrate	6	40	8	54
	Astroviridae Nodaviridae			Isometric	1 + segment	7	Vertebrate	1	0	0	1
				Isometric	1 + segment	7-8	Vertebrate	6	13	0	19
	Tetraviridae			Isometric	2 + segments	5	Vertebrate, invertebrate	14	0	0	14
	Luteoviridae			Isometric	1 + segment	5	Invertebrate	9	0	0	9
				Isometric	1 + segment	4	Plant	11	0	3	14
	Tombusviridae			Isometric	1 + segment	6-7	Plant	3	0	0	3
				Isometric	1 or 2 + segment	6-9	Plant	8	0	11	19
	Tombusviridae			No particles	1 + segment	4	Plant	7	0	15	22
				Isometric	1 or 2 + segment	4-5.5	Plant	38	0	11	49

Table 3 Continued

Criteria	Order	Family	Floating genus	Morphology	Genome configuration	Genome size (kb)	Virus host	Number of species				
								Species	serotypes	Tentative	Total	
ssRNA Positive sense	Nidovirales	Coronaviridae		Pleomorphic	1 + segment	28-33	Vertebrate	16	5	1	22	
		Arteriviridae		Spherical	1 + segment	13-16	Vertebrate	4	0	0	4	
		Flaviviridae		Isometric	1 + segment	10-12	Vertebrate	57	47	6	110	
		Togaviridae		Isometric	1 + segment	10-13	Vertebrate	23	6	0	29	
			<i>Tobamovirus</i>	Rod	1 + segment	6	Plant	16	0	3	19	
			<i>Tobravirus</i>	Rod	2 + segments	9-11	Plant	3	0	0	3	
			<i>Hordeivirus</i>	Rod	3 + segments	10	Plant	4	0	0	4	
			<i>Furovirus</i>	Rod	2 + segments	9-11	Plant	1	0	4	5	
			<i>Pomovirus</i>	Rod	3 + segments	12	Plant	4	0	0	4	
			<i>Pecluvirus</i>	Rod	2 + segments	10	Plant	2	0	0	2	
			<i>Benyvirus</i>	Rod	4 (or 5) + segments	14-16	Plant	2	0	0	2	
			<i>Bromoviridae</i>		Isometric, bacilliform	3 + segments	8-9	Plant	28	0	0	28
			<i>Ourmiavirus</i>		Bacilliform	3 + segments	4-5	Plant	3	0	0	3
			<i>Idaeovirus</i>		Rod	3 + segments	8	Plant	1		0	1
			<i>Closteroviridae</i>		Rod	1 or 2 + segments	15-19	Plant	18	0	16	34
		<i>Capillovirus</i>	Rod	1 + segment	7	Plant	3	0	1	4		
		<i>Trichovirus</i>	Rod	1 + segment	7.5	Plant	3	0	1	4		
		<i>Vitivirus</i>	Rod	1 + segment	7.5	Plant	4	0	1	5		
		<i>Tymovirus</i>	Isometric	1 + segment	6	Plant	20	0	1	21		
		<i>Carlavirus</i>	Rod	1 + segment	7-8	Plant	31	0	29	60		
		<i>Potexvirus</i>	Rod	1 + segment	6	Plant	26	0	18	44		
		<i>Allexivirus</i>	Rod	1 + segment	9	Plant	6	0	3	9		
		<i>Foveavirus</i>	Rod	1 + segment	8-9	Plant	2	0	1	3		
	<i>Barnaviridae</i>		Bacilliform	1 + segment	4	Fungus	1	0	1	2		
	<i>Unassigned viruses</i>						565	234	403	1202		
						All	30	0	0	30		
	<i>Viroids</i>						1550	1011	1393	3954		
	<i>Satellites</i>					Plant	27	0	8	35		
						Plant	33	0	6	39		

Table 4 List of criteria demarcating different virus taxa*I Order*

Common properties between several families including:

- Biochemical composition
- Virus replication strategy
- Particle structure (to some extent)
- General genome organization

II Family

Common properties between several genera including:

- Biochemical composition
- Virus replication strategy
- Nature of the particle structure
- Genome organization

III Genus

Common properties within a genus including:

- Virus replication strategy
- Genome size, organization and/or number of segments
- Sequence homologies (hybridization properties)
- Vector transmission

IV Species

Common properties within a species including:

- Genome rearrangement
- Sequence homologies (hybridization properties)
- Serological relationships
- Vector transmission
- Host range
- Pathogenicity
- Tissue tropism
- Geographical distribution

and occupies a particular ecological niche.' The major advantage in this definition is that it can accommodate the inherent variability of viruses and is not dependent on the existence of a unique characteristic. Members of a polythetic class are defined by more than one property and no single property is absolutely essential and necessary. Thus in each family it might be possible to determine the set of properties of the class 'species' and to check if the family members are species of this family or if they belong to a lower taxonomic level. The ICTV is currently conducting this exercise throughout all virus families. This exercise should ultimately result in an excellent evaluation of a precise definition of each virus species in the entire classification.

Several practical matters are related to the definition of a virus species with the goal of improving the usefulness of virus classification. These include: (1) homogeneity of the different taxa; (2) diagnosis-related matters; (3) virus collections; (4) evolution studies; (5) biotechnology; (6) sequence database

projects; (7) virus database projects; and now (8) intellectual property rights.

Virus families and genera

There is no formal definition for a genus, but it is commonly considered as: 'a population of virus species that share common characteristics and are different from other populations of species'. Although this definition is somewhat elusive, this level of classification seems enduring and useful; some genera have been moved from one family to another over the years, but the composition and description of the genera has remained stable. The characters defining a genus differ from one family to another and there is a tendency to create genera with fewer differences between them. Upon examination, there is more and more evidence that the members of a genus have a common evolutionary origin. The use of subgenera has been abandoned in current virus classification.

Notwithstanding the creation of the ICTV, plant

virologists continued to classify plant viruses in 'groups', refusing to place them in genera and families. However, owing to obvious similarities, plant reoviruses and rhabdoviruses had been integrated into the families *Reoviridae* and *Rhabdoviridae* (Table 2). This position was mostly due to plant virologists' refusal to accept binomial nomenclature. Since this form of nomenclature was withdrawn from the ICTV classification rules in 1995, they subsequently accepted the placing of plant viruses into species, genera and families as shown in the sixth ICTV report. However, there are still 30 of so-called 'floating genera' that do not pertain to any family. This is mostly due to the fact that plant virologists prefer to accumulate data on virus species and genera before clustering appropriate genera in families. It is remarkable that this attitude has also been adopted by other virologists as a convenient way of classifying viruses, without having to move genera out of families when it becomes apparent that they are part of a distinct family. For example, the members of the floating genus 'cricket paralysis-like viruses' share enough properties with picornaviruses to be included in the family *Picornaviridae*; however, they also possess properties that would justify their classification in a separate family. Only new data or new viruses will permit a definitive position, therefore for the time being it remains a floating genus. Similarly the same strategy is used to create a floating genus 'ictalurid herpes-like viruses', within the family *Herpesviridae*, although in this case it is a floating genus within the family because of uncertainty as to whether the members of this genus should be classified in one of the existing subfamilies or to a new subfamily.

Virus orders

As mentioned above, the higher hierarchy levels for virus classification are extremely difficult to establish. Despite several propositions in the past, only three have been accepted: *Caudovirales*, *Mononegavirales* and *Nidovirales*. The first virus order, *Mononegavirales*, was established in 1990 and comprises the nonsegmented single-stranded RNA negative-sense viruses, namely the families *Bornaviridae*, *Filoviridae*, *Paramyxoviridae* and *Rhabdoviridae*. This decision was taken because of the great similarity of many criteria between these families, including their replication strategy. A second order, *Caudovirales*, contains all the families of double-stranded DNA phages possessing a tail, including the families *Myoviridae*, *Podoviridae* and *Siphoviridae*. A third order, *Nidovirales*, comprising the families *Coronaviridae* and *Arteriviridae*, was accepted in 1996 because of the

impossibility of grouping together these two taxonomic entities, which share many properties and yet are so different, as a single family. Many members of the ICTV advocate the creation of many more orders, but it has been decided to proceed cautiously to avoid creation of short-lived orders. The creation of formal taxa higher than the orders, for example, kingdoms, classes and subclasses, has not been considered by the ICTV.

Virus Taxa Descriptions

Virus classification continues to evolve with the technologies available for describing viruses. The first wave of descriptions, those before 1940, mostly took into account the visual symptoms of the diseases caused by viruses, along with their modes of transmission. A second wave, between 1940 and 1970, brought together an enormous amount of information from studies of virion morphology (electron microscopy, structural data), biology (serology and virus properties) and physicochemical properties of viruses (nature and size of genome, number and size of viral proteins). Since 1970, the third wave of virus descriptions has included genome and replicative information as well as molecular relationships with virus hosts. There is a correlative modification of the list of virus descriptors and Table 1 lists the family and genera descriptors which are used in the current ICTV report. Figures 1–5 are diagrammatic representations of families and genera of viruses infecting vertebrates, invertebrates, plants, fungi, yeasts, protozoa and bacteria. The most recent wave of information used to classify viruses is naturally nucleotide and amino acid sequences. It is becoming more and more prevalent in virus taxonomy, as exemplified by the presence of a significant number of 'phylogenetic trees' in the seventh ICTV report, and by the huge number of scientific publications on this topic. Some scientists promote the concept of 'quantitative taxonomy' aimed at demonstrating that virus sequences contain all the coding information required for all the biological properties of the viruses. This is in complete agreement with the polythetic concept of the virus species definition, as demonstrated for example by Padidam *et al* in 1995, van Regenmortel *et al* in 1997, Hyppia *et al* in 1998, and Aleman *et al* in 1999.

The impact of descriptions on virus classification has been particularly influenced by electron microscopy and of the negative staining technique for virions. This technique had an immediate influence on diagnostics and classification of viruses. With negative staining, viruses could be identified from poorly purified preparations of all tissue types, and informa-

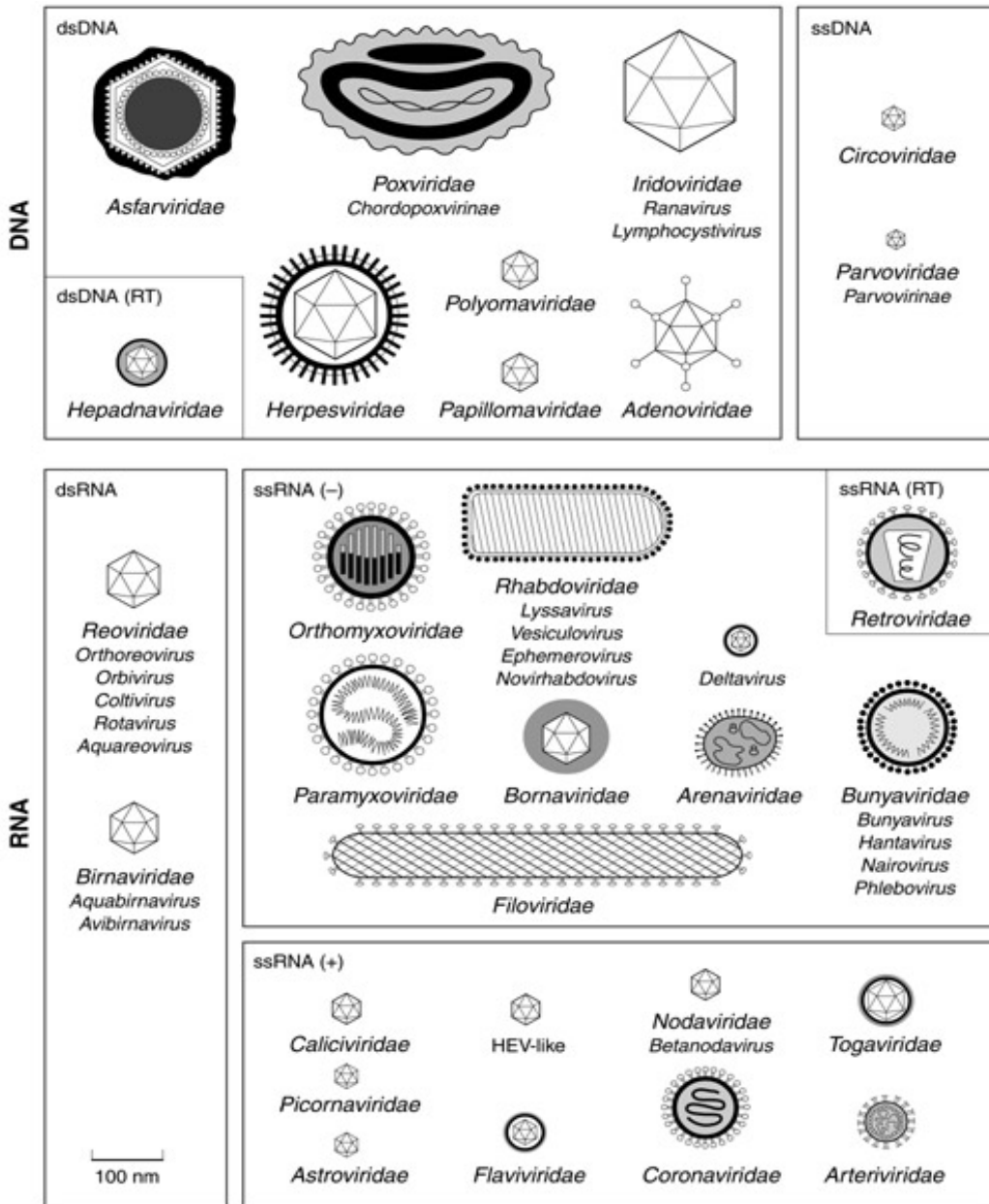


Figure 1 Families and genera of viruses infecting vertebrates.

tion about size, shape, structure and symmetry could be quickly provided. As a result, virology progressed simultaneously for all viruses infecting animals, insects, plants and bacteria. Thin sections of infected tissues brought a new dimension to virus classification by providing information about virion morphogenesis and cytopathogenic effects. These techniques, in conjunction with the determination of the nature of the genome, provided a major source of information for the system of virus classification established in the 1980s, as shown by the large number of viruses listed in the fifth ICTV report in 1989.

In many instances the properties of viruses belong-

ing to the same genus are correlated. Thus, the classification of a few of them will likely be sufficient to allow the classification of a new virus into an established genus. For example, a plant virus with filamentous particles of 700–850 nm and transmitted by aphids is likely to be a member of the genus *Potyvirus*. Establishment of new genera in the future will require more information. Most of the properties listed in **Table 3** will have to be precisely analyzed to warrant the formation of a new genus.

Table 3 lists 45 different categories of properties but each category includes many items. Lists of virus descriptors usually comprise 1000–2000 descriptors.

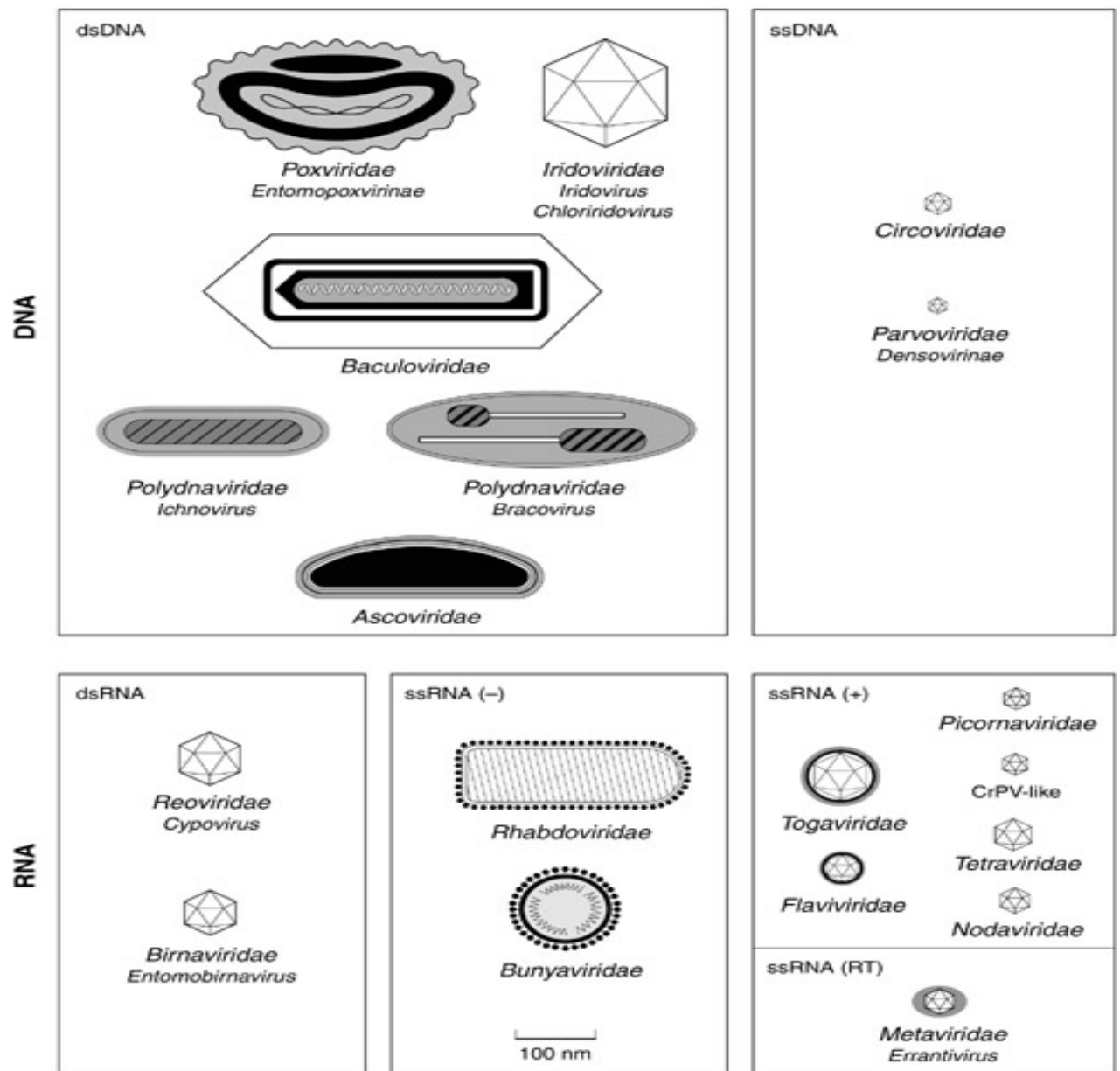


Figure 2 Families and genera of viruses infecting invertebrates.

The establishment of a universal list of virus descriptors is under way and should be adopted by ICTV around 2000 with the establishment of the ICTVdB. It will contain a common set of descriptors for *all* viruses and subsets for specific viruses in relation to their specific hosts (human, animal, insect, plant and bacterial).

A Uniform Nomenclature of Viral Taxa

When a genus is approved by ICTV, a type species is designated. However, none of these type species have received a new international name and only English

names are used. Latinized binomial names for virus names have been supported by animal and human virologists of ICTV for many years, but have never been implemented. This suggestion was in fact withdrawn from ICTV nomenclature rules in 1990 and consequently such names as *Herpesvirus varicella* or *Polyomavirus hominis* should not be used. For several years, plant virologists have adopted a different nomenclature, using the vernacular name of a virus but replacing the word 'virus' by the genus name; for example, *Cucumber mosaic cucumovirus* and *Tobacco mosaic tobamovirus*. Though this usage is favored by many scientists, and examples of such practice can

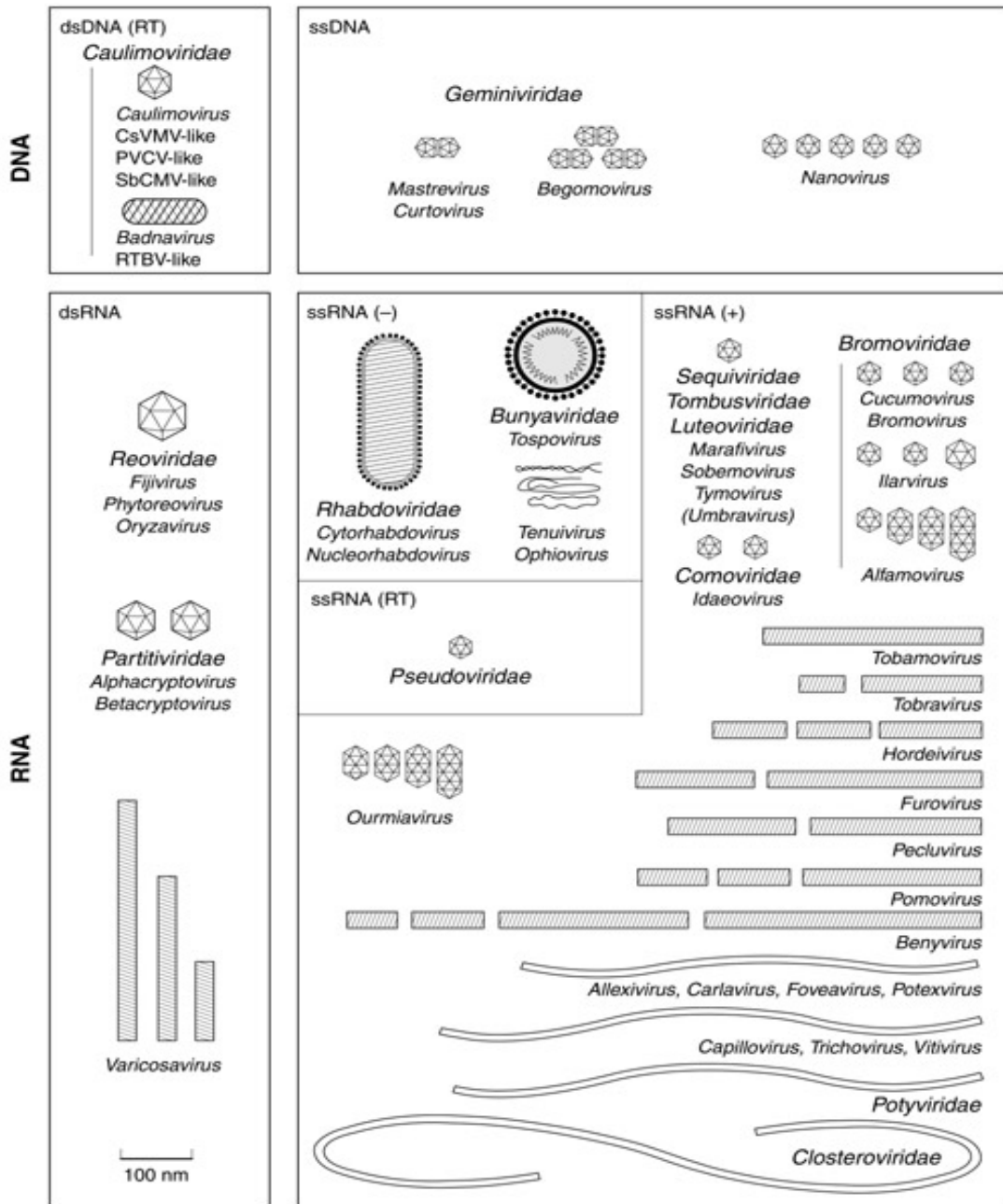


Figure 3 Families and genera of viruses infecting plants.

be found for human, animal and insect viruses (e.g. *Human rhinovirus*, *Canine calicivirus*, *Acheta densovirus*...), it has not been universally adopted by the ICTV.

The ICTV has set rules for virus nomenclature and orthography of taxonomic names that are regularly revisited and improved. The last word of international virus species names is ‘virus’, the international genus names universally end in ‘...virus’, the international subfamily names end in ‘...virinae’, the international family names end with ‘...viridae’, and

the international order names are ending in ‘...virales’. In formal taxonomic usage, the virus order, family, subfamily, genus and species names are all printed in italics (or underlined) and the first letter is capitalized. For all taxa except the species names, new names are created *de novo* following ICTV guidelines, but in the case of virus names English vernacular form is used. In formal usage, the name of the taxon precedes the name of the taxonomic unit; for example, ‘the family *Picornaviridae*’ or ‘the genus *Rhinovirus*’. In informal vernacular usage, order,

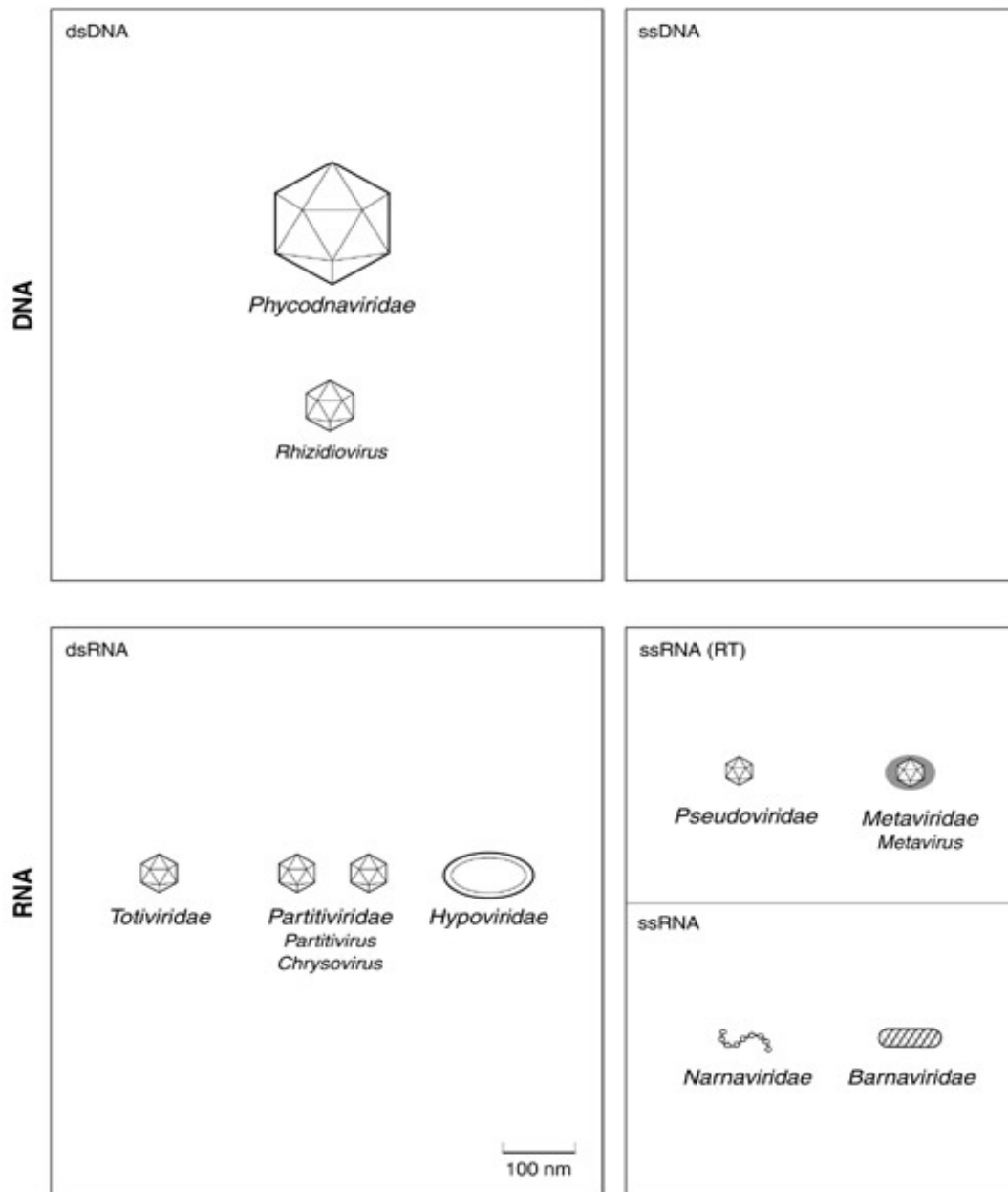


Figure 4 Families of viruses infecting algae, fungi, yeasts and protozoa.

family, subfamily, genus and species names are written in lower case Roman script; they are not capitalized nor italicized (or underlined). Additionally, in informal usage, the name of the taxon should not include the formal suffix, and it should follow the term for the taxonomic unit; for example, 'the mononegavirales order', 'the adenovirus family', 'the avihepadnavirus genus' or 'the tobacco mosaic virus' species. Virus names are often abbreviated for convenient reasons, but ICTV has not set up guidelines to generate such abbreviations. The ICTV reports list abbreviations most commonly used by

specialists and the ICTV reports help virologists to identify duplicates of abbreviations in order to decrease the number of such duplicates. In 1988 plant virologists initiated the publication of such lists and have indicated guidelines for the creation of new virus names and new abbreviations. These guidelines were last published in 1991 by Fauquet and Martelli and will be updated again in 1999.

To avoid ambiguous virus identifications, it has been recommended to journal editors that published papers follow ICTV guidelines for proper virus identification and nomenclature, and that viruses should be cited

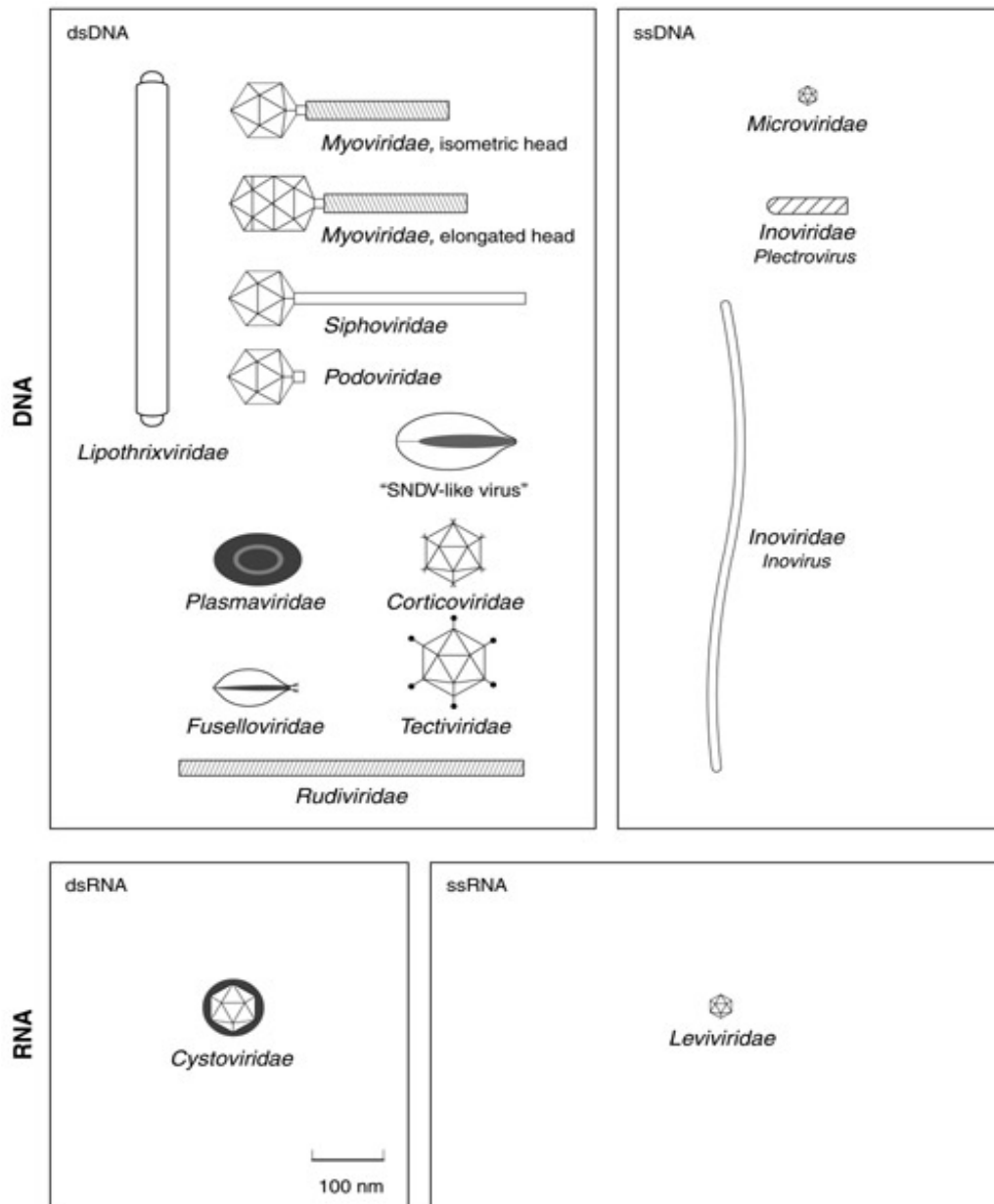


Figure 5 Families and genera of viruses infecting bacteria.

with their full taxonomic terminology when they are first mentioned in an article. For example:

- Order *Caudovirales*, family *Podoviridae*, genus 'T7-like viruses', species *Enterobacteria phage T7*.
- Order *Mononegavirales*, family *Paramyxoviridae*, subfamily *Paramyxovirinae*, genus *Rubulavirus*, species *Mumps virus*.
- Order *Nidovirales*, family *Coronaviridae*, genus *Coronavirus*, species *Avian infectious bronchitis virus*.
- Family *Iridoviridae*, genus *Iridovirus*, species *Chilo iridescent virus*.
- Family *Picornaviridae*, genus *Enterovirus*, species *Poliovirus*, serotype Human poliovirus 1.
- Genus *Tobamovirus*, species *Tobacco mosaic virus*.

See also: Phage taxonomy and classification; Virus structure: Atomic structure, Principles of virus structure.

Further Reading

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TENUVIRUSES



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History

The viruses in the genus *Tenuivirus* (tenuiviruses) have been recognized as important plant pathogens since the early 1900s. However, in 1977 it was first recognized that rice stripe virus (RSV)-infected rice (*Oryza sativa* L.) plants contained unusual fine-stranded particles. These appeared as circular or branched filaments and were distinctly different from particles associated with other plant viruses. Subsequent work showed that plants infected by several other viruses contained similar particles. This and the somewhat unique biological properties shared by these viruses led to the early grouping together of RSV and other plant viruses, including maize stripe virus (MSPV) and rice hoja blanca virus (RHBV). Since 1995, RSV and related viruses have been grouped together by the International Committee on Taxonomy of Viruses (ICTV) as members of the genus *Tenuivirus* (tenuiviruses).

Taxonomy and Classification

There are currently six species within the genus *Tenuivirus*, and at least five tentative species (Table 1). The definitive tenuiviruses are: rice stripe virus (RSV; the type species of the genus); MSPV; RHBV; rice grassy stunt virus (RGSV); *Echinochloa* hoja blanca virus (EHBV) and *Urochloa* hoja blanca virus (UHBV). All tenuiviruses exhibit similar properties, and in recent years molecular biological analyses have shown that they are quite distinct from other

currently recognized plant viruses. The genus *Tenuivirus* is not placed within a formally recognized virus family; however, tenuiviruses appear in some ways to be more closely related to viruses in the genus *Phlebovirus* of the family *Bunyaviridae*, than they are to other plant viruses.

Biology, Host Range and Vector Transmission

The plant host ranges of all tenuiviruses are limited to monocotyledonous plant species within the family Poaceae, including many plants which are important food crops (i.e. rice (*Oryza sativa* L.) and maize (*Zea mays* L.)). The symptoms induced in infected plants are generally similar for the different tenuiviruses and includes general leaf striping, a distinct white coloring of the leaf stripes and stunting (Fig. 1).

Tenuiviruses generally are not mechanically transmissible to their plant hosts; however, mechanical transmission has been reported in limited instances but only under specific conditions. All tenuiviruses are transmitted to plants by specific planthoppers (Homoptera: Delphacidae, see Table 1 and Fig. 2). Transmission of a given tenuivirus is specific and may be limited to planthoppers of a single species. Compared to other vectors of plant viruses (i.e. aphids or whiteflies), delphacid planthoppers are not generally thought of as common vectors; however, they are perfectly adapted to be vectors of tenuiviruses. Delphacid planthoppers which vector tenuiviruses