regulated expression systems for cloned DNA that can achieve >50% of total cellular proteins in the form of a desired product. These systems have been adapted for eucaryotic cells as well for bacteria. The T7 promoter sequence is very rare, even in mammalian cells, and with the appropriate constructs highly selective cloned gene expression can be attained. Typically, the Class III gene *10* promoter is employed, with or without gp10 translational start sequences, and T7 RNA polymerase is supplied from a resident plasmid or prophage, or by phage infection.

See also: Bacteriophage recombination; Host-controlled modification and restriction.

Further Reading

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TANAPOX VIRUS

See Yabapox and Tanapox viruses

TAXONOMY AND CLASSIFICATION–GENERAL

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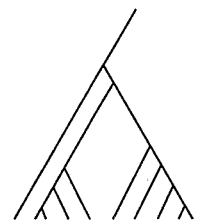

History

Humans have a tendency to classify and name everything and viruses are no exception. Classifications are extremely useful for showing similar characteristics and properties. Thus, appropriately chosen classification criteria become extremely informative in the case of newly discovered viruses. Unfortunately for virus taxonomy there are no fossils, so evolutionary relationships are very speculative. Only a virus classification would be able to provide indications of the evolution of viruses. In theory, nomenclature and classification are totally independent, but for viruses both issues are often considered at the same time. As a result, virus taxonomic names have always been the subject of passionate discussions.

Classification of viruses is a fairly new exercise considering the first evidence of the existence of a virus was made at the end of the last century. Johnson, a plant virologist, drew attention to the need for virus nomenclature and classification as early as 1927. The first efforts to classify viruses employed a range of ecological and biological properties including pathogenic properties for human and animal viruses and symptoms for plant viruses. For example, viruses that share the pathogenic property of causing hepatitis (e.g. hepatitis A virus, hepatitis B virus, yellow fever virus, Rift Valley fever virus) were grouped together as 'the hepatitis viruses'. Virology developed substantially in the 1930s and the first classifications of viruses reflected this development. Holmes published in 1939 a classification of

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plant viruses based on host reactions and differential hosts using a binomial–trinomial nomenclature based on the name of the infected plant, but only 89 viruses were classified. In the 1950s, with the development of electron microscopy and biochemical studies, the first groupings of viruses based on common virion properties emerged: the Herpesvirus group, the Myxovirus group, and the Poxvirus group. During this period, there was an explosion of newly discovered viruses. In response, several individuals and committees independently proposed virus classification systems but none was widely used. It became obvious that only an international association of virologists would be able to propose a comprehensive and universal system of virus classification.

At the International Congress for Microbiology held in Moscow in 1966, 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 unique world-wide recognized taxonomy and nomenclature system for all viruses. The name of the ICNV was changed in 1974 to a more appropriate one: the International Committee on Taxonomy of Viruses (ICTV), which is active today. The ICTV is now considered the official body for all matters related to taxonomy and nomenclature of viruses.

Since the founding of the ICTV, all virologists 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 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 for the classifying of 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. This hierarchical system has never been recognized by the ICTV; nevertheless, the rest of the proposal became the basis of the universal taxonomy system now in place and all ICTV reports reflect this scheme. Until 1990, the scheme did not utilize any hierarchical classification level higher than the family, but the system has recently begun to move in this direction. A first order, *Mononegavirales*, has been accepted in 1990, and a second one, *Caudovirales*, has been proposed for consideration in 1993. In its non-Linnean structure, the scheme is quite different from that used for the taxonomy of bacteria and other organisms. The usefulness of the scheme is being demonstrated by its wide application. It has replaced all competing classification schemes for all viruses.

At the first meeting of the ICNV in Mexico City (1970), two families with a corresponding two genera and 24 floating genera were accepted to begin the grouping of vertebrate, invertebrate and bacterial viruses. In addition, 16 plant virus groups were designated. The Fifth ICTV Report describes 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 (Table 1). While most virologists shifted to the grouping of viruses in families and genera, plant virologists have persisted in clustering plant viruses in 'groups' until very recently. It is only in 1993 that the ICTV will propose a uniform system for all viruses with two orders, 50 families, 9 subfamilies, 126 genera, 23 floating genera and 4 subgenera encompassing 2644 assigned virus species.

The descriptions of virus families can provide valuable information for new 'unknown' members. Therefore, the ICTV work is not only a taxonomic exercise for evolutionists but a valuable source of information for virologists, teachers, medical doctors and epidemiologists. Since the establishment of the ICTV, five virus taxonomic reports have been published and new reports will appear every three years.

How Does the ICTV Operate?

The ICTV is a Committee of the Virology Division of the International Union of Microbiological Societies. The ICTV operates through a number of committees, subcommittees and study groups of more than 372 eminent virologists with expertise in human, animal, insect, protozoal, bacterial, mycoplasmal, fungal, algal and plant viruses. Taxonomic proposals are initiated and formulated by the study groups. These proposals are revised and accepted by the subcommittees and presented for Executive Committee approval. All decisions are finally affirmed at a plenary session held at each virology congress where all members of ICTV and more than 50 representatives of national microbiological societies are represented. Presently, there are 45 study groups working in concert with six subcommittees, namely, the vertebrate, invertebrate, plant, bacteria, fungus and virus data subcommittees. The ICTV is a non-profit association composed of

Table 1. List of orders, families and groups of viruses[a]

Nature of the presentation criteria		Order	Family or group	Morphology	Genome configuration	Genome size (kbp)	Virus host	Number of species		
								Members	Tentative	Total
dsDNA	Enveloped		*Baculoviridae*	Bacilliform	1 circular supercoiled	90–230	Invertebrate	14		14
			Hepadnaviridae	Isometric	1 circular	3	Vertebrate	5		5
			Herpesviridae	Isometric	1 linear	120–220	Vertebrate	19	4	23
			Lipothrixviridae	Rod	1 linear	16	Bacteria	2		2
			Plasmaviridae	Pleomorphic	1 circular	12	Bacteria	2	5	7
			Polydnaviridae	Rod, fusiform	1 circular supercoiled	2–28	Invertebrate	2		2
			Poxviridae	Ovioid	1 linear	130–375	Vertebrate, invertebrate	61	16	77
			SSV-1 group	Lemon-shape	1 circular supercoiled	15	Bacteria	3		3
dsDNA	Nonenveloped	(*Caudovirales*)	*Myoviridae*	Tailed phage	1 linear	336	Bacteria	83		83
			Podoviridae	Tailed phage	1 linear	40	Bacteria	51		51
			Siphoviridae	Tailed phage	1 linear	53	Bacteria	111		111
			Adenoviridae	Isometric	1 linear	32–48	Vertebrate	111		111
			Caulimovirus	Isometric	1 circular	8	Plant	11	6	17
			Commelina yellow mottle virus group	Bacilliform	1 circular	8	Plant	4	11	15
			Corticoviridae	Isometric	1 circular supercoiled	10	Bacteria	1	1	2
			Iridoviridae	Isometric	1 linear	160–400	Vertebrate, invertebrate	70	2	72
			Papovaviridae	Isometric	1 circular	5–8	Vertebrate	28		28
			Phycodnaviridae	Isometric	1 linear	250–350	Algae	47		47
			Rhizidiovirus	Isometric	1 linear	27	Fungus	1		1
			Tectiviridae	Isometric	1 linear	16	Bacteria	8		8
ssDNA	Nonenveloped		*Geminivirus*	Isometric	1 or 2 circular	3–6	Plant	35	13	48
			Inoviridae	Rod	1 circular	7–20	Bacteria, mycoplasmas	32		32
			Microviridae	Isometric	1 circular	6	Bacteria	28		28
			Parvoviridae	Isometric	1 – strand	6–8	Vertebrate, invertebrate	4	11	15
dsRNA	Enveloped		*Cystoviridae*	Isometric	3 segments	17	Bacteria	1		1
dsRNA	Nonenveloped		*Birnaviridae*	Isometric	2 segments	6	Vertebrate, invertebrate	5		5
			Cryptovirus	Isometric	2 segments	3–5	Plant	20	10	30
			Partitiviridae	Isometric	2 segments	4–10	Fungus	9	5	14
			Reoviridae	Isometric	10–12 segments	19–62	Vertebrate, invertebrate, plant	136	33	169
			Totiviridae	Isometric	1 segment	5–7	Fungus	4	8	12

Nature of the presentation criteria		Order	Family or group	Morphology	Genome configuration	Genome size (kb)	Virus host	Number of species		
								Members	Tentative	Total
ssRNA	Enveloped; no DNA step; positive sense genome		*Coronaviridae*	Pleomorphic	1+segment	28–33	Vertebrate	11	3	14
			Flaviviridae	Isometric	1+segment	10–22	Vertebrate, invertebrate	35	19	54
			Togaviridae	Isometric	1+segment	10–13	Vertebrate, invertebrate	29	2	31
ssRNA	Enveloped; no DNA step; negative non-segmented genome	*Mononegavirales*	*Filoviridae*	Bacilliform	1 – segment	13	Vertebrate	2		2
			Paramyxoviridae	Helical	1 – segment	15–16	Vertebrate	32	4	36
			Rhabdoviridae	Bacilliform	1 – segment	10–13	Vertebrate, invertebrate, plant	75	100	175
ssRNA	Enveloped; no DNA step;		*Arenaviridae*	Spherical	2 – segments	11	Vertebrate	15		15
			Bunyaviridae	Spherical	3 – segments	12–23	Vertebrate invertebrate, plant	253	45	298
	negative segmented genome		*Orthomyxoviridae*	Helical	8 – segments	13–14	Vertebrate	3	2	5
ssRNA	Enveloped; DNA step		*Retroviridae*	Spherical	dimer 1+segment	7–10	Vertebrate	32		32
ssRNA	Nonenveloped; monopartite genome; Isometric particles		*Caliciviridae*	Isometric	1+segment	8	Vertebrate	4	1	5
			Carmovirus	Isometric	1+segment	4	Plant	8	9	17
			Leviviridae	Isometric	1+segment	3–4	Bacteria	43		43
			Luteovirus	Isometric	1+segment	6	Plant	14	12	26
			Maize chlorotic dwarf virus group	Isometric	1+segment	9	Plant	1	2	3
			Marafivirus	Isometric	1+segment	6–7	Plant	3		3
			Necrovirus	Isometric	1+segment	4–5	Plant	2	2	4
			Parsnip yellow fleck virus group	Isometric	1+segment	10	Plant	2	1	3
			Picornaviridae	Isometric	1+segment	7–8	Vertebrate, invertebrate	215	13	228
			Sobemovirus	Isometric	1+segment	4	Plant	10	6	16
			Tetraviridae	Isometric	1+segment	5	Invertebrate	1	14	15
			Tombusvirus	Isometric	1+segment	5	Plant	12		12
			Tymovirus	Isometric	1+segment	6	Plant	18	1	19
ssRNA	Nonenveloped; monopartite genome; rod-shaped particles		*Capillovirus*	Rod	1+segment	7	Plant	2	2	4
			Carlavirus	Rod	1+segment	7–8	Plant	27	29	56
			Closterovirus	Rod	1+segment	7–18	Plant	10	12	22
			Potexvirus	Rod	1+segment	6	Plant	18	21	39
			Potyvirus	Rod	1+segment	8–10	Plant	73	84	157
			Tobamovirus	Rod	1+segment	6	Plant	12	2	14

Continued

Table 1. Continued

Nature of the presentation criteria		Order	Family or group	Morphology	Genome configuration	Genome size (kb)	Virus host	Number of species		
								Members	Tentative	Total
ssRNA	Nonenveloped; bipartite genome; isometric particles		*Comovirus*	Isometric	2+segments	9	Plant	14		14
			Dianthovirus	Isometric	2+segments	4	Plant	3		3
			Fabavirus	Isometric	2+segments	10	Plant	3		3
			Nepovirus	Isometric	2+segments	12	Plant	28	8	36
			Nodaviridae	Isometric	2+segments	5	Invertebrate	6		6
			Pea enation mosaic virus group	Isometric	2+segments	9	Plant	1		1
ssRNA	Nonenveloped; bipartite genome; rod-shaped particles		*Furovirus*	Rod	2+segments	9–11	Plant	5	6	11
			Tobravirus	Rod	2+segments	9–11	Plant	3		3
ssRNA	Nonenveloped; tripartite genome; bacilliform particles		Alfalfa mosaic virus group	Bacilliform	3+segments	8	Plant	1		1
ssRNA	Nonenveloped; tripartite genome; isometric particles		*Bromovirus*	Isometric	3+segments	8	Plant	6		6
			Cucumovirus	Isometric	3+segments	9	Plant	3	1	4
			Ilarvirus	Isometric	3+segments	8	Plant	20		20
ssRNA	Nonenveloped; tripartite genome; rod-shaped particles		*Hordeivirus*	Rod	3+segments	10	Plant	4		4
ssRNA	Nonenveloped; tetrapartite genome		*Tenuivirus*	Rod	4 – ? segments	19	Plant	3	4	7
Total no. species								1970	530	2500

[a] The taxa are listed according the Fifth ICTV Report with the following criteria: nature and strandedness of the nucleic acid, presence or absence of a lipoprotein envelope, the single-stranded (ss)RNA enveloped viruses are arranged on the basis of genome strategy and the ssRNA nonenveloped viruses are arranged on the basis of the number of segments of their genome and their particle morphology. For each family or group of viruses, also indicated are the morphology of the virions, the genome configuration, the genome size in kb, the virus host, the number of species and tentative members in the taxa, and the total number of species listed in 1990.

prominent virologists representing countries from throughout the world and names and taxa are accepted following a democratic process. ICTV does not impose any taxonomic word or taxa but ensures that the propositions are compatible with ICTV rules for homogeneity and consistency. The ICTV regularly publishes reports that describe all the virus taxa with a list of classified viruses as well as compilations of virus families and genera. A last report was published in 1991 and the next will be published in 1994. With the increasing number of viruses and virus strains and the explosion of data on many descriptive aspects of viruses and viral diseases, ICTV decided 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.

System for Virus Classification

There are two systems for classifying organisms: the Linnean and the Adansonian systems. The Linnean system is the monothetic hierarchical classification applied by Linnaeus to plants and animals while the Adansonian system is a polythetic hierarchical system proposed by Adanson in 1763. Maurin and collaborators proposed to apply the Linnean classification system to viruses in 1984. Although the system is very convenient to use, there are shortcomings when it is applied to the classification of viruses. First, it is difficult to appreciate the validity of a particular criterion. For example, it may not be appropriate to use the number of genomic components as a hierarchical criterion. Second, there are no reasons for privileging a particular criterion from another so it is difficult to rank all the available criteria. For example, is the nature of the genome (DNA/RNA) more important than the presence of an envelope or the shape of the virus particles?

The Adansonian system considers all available criteria at once and makes several classifications considering the criteria successively. The criteria leading to the same classifications are considered as correlated and are therefore not discriminatory. Subsequently, a subset of criteria are considered. The process is repeated until all criteria can be ranked to provide the best discrimination of the species. This system was not frequently used due to its labor-intensive nature, but with present-day computers it can be easily implemented. Furthermore, qualitative and quantitative data can be simultaneously considered to generate such a classification. In the case of viruses, it has been determined that at least 60 characters would be needed for a complete virus description. Thus, the limiting factor for applying the Adansonian system is the lack of data in many instances. The increasing number of viral nucleic acid sequences allows the comparison of viruses to generate different phylogenetic trees according to the gene or set of genes used. 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 the virus classification but it would not be very easy to use.

For nearly the last 20 years, ICTV has been classifying viruses essentially at the family and genus levels using a nonsystematic polythetic approach. This has clustered viruses first in genera and then in families. A subset of characters including physicochemical, structural, genomic and biological criteria has then been 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. It is obvious that there is no homogeneity in this respect throughout the virus classification and that virologists weigh differently the criteria in this subjective process. Nevertheless, we can see a rather good stability of the current ICTV classification. When sequence, genomic organization and replicative cycle data are 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 to progress in this direction.

Currently, and for practical reasons only, virus classification is structured according to the presentation indicated in Tables 1 and 2. This order of presentation of virus families and groups does not reflect any hierarchical or phylogenetic classification but only a convenient order of presentation. Since a taxonomic structure above the level of family or group (with the exception of the order *Mononegavirales* and the pending order *Caudovirales*) has not been developed extensively, any listing must be arbitrary. The order of presentation is generally the same as in the Fifth ICTV Report. The order of presentation of virus families and groups follows three criteria: (1) the nature of the viral nucleic acid, (2) the strandedness of the nucleic acid and (3) the presence or absence of a lipoprotein

Table 2. Order of presentation of virus classification in the Fifth ICTV Report

A. DNA/RNA
B. Double-stranded/single-stranded
C. Enveloped/nonenveloped
for the ssRNA enveloped viruses only:
DNA/no DNA step in the replication cycle
Positive/negative sense genome
Monopartite/multipartite genome
for the ssRNA nonenveloped viruses only:
Mono/bi/tri/tetrapartite genome
Isometric/bacilliform/rod-shaped particles

envelope. There are no known single-stranded (ss)DNA viruses with envelopes, so these three criteria give rise to seven clusters comprising the 73 families and groups of viruses (comprising one floating genus). Within two of these clusters, the ssRNA enveloped and nonenveloped viruses, the families have been arranged as follows: the ssRNA enveloped viruses are arranged on the basis of genome strategy, i.e. DNA/no DNA step in the replication cycle, positive/negative sense genome and monopartite/multipartite genome. The ssRNA nonenveloped viruses are arranged on the basis of number of segments of RNA of their genome, i.e. mono-/bi-/tri-/tetrapartite genome and their virion morphology: isometric/bacilliform/rod-shaped particles.

Nomenclature of Virus Taxa

The debate over virus nomenclature has generated significant controversy and discussion over the years and was the primary reason for virologists to establish the ICNV. In the earliest examples of virus taxonomy, Gibbs proposed to adopt a cryptogram to add precision to the vernacular names of the viruses. The cryptograms used a combination of letters and numbers to describe the structure, the biochemical composition of the genome, the host type and the transmission properties of the virus. This system of virus identification was set up in the first ICTV report but was never used and therefore abandoned.

When a family, genus or virus group is approved by ICTV, a type species or type member is designated. However, none of these type species has received an official name and only English vernacular names are indicated. Use of latinized binomial names for virus names was supported by animal and human virologists of ICTV for many years, but has 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 set up a different nomenclature, using the vernacular name of a virus but replacing the word 'virus' by the group (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 be found for human, animal and insect viruses (e.g. human rhinovirus, canine calicivirus, *Acheta* densovirus), it has not been adopted by the ICTV.

The ICTV has a set of rules for virus nomenclature and orthography of taxonomic names. The international genus names universally end in '-virus', the international subfamily names end in '-virinae', the international family names end in '-viridae' and the international order names end in '-virales'. In formal taxonomic usage, the virus order, family, subfamily and genus names are printed in italics (or underlined) and the first letter is capitalized. Species names, which are used in English vernacular form, are not capitalized or italicized (or underlined). 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, virus order, family, subfamily, genus and species names are written in lower case Roman script; they are not capitalized or 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 tobamovirus group'.

To avoid ambiguous identifications, it has been recommended to journal editors to follow ICTV guidelines for proper virus identification and nomenclature, and to cite viruses with their full taxonomic terminology when they are first cited in an article, as in the following examples.

- Order *Mononegavirales*, Family *Paramyxoviridae*, Subfamily *Paramyxovirinae*, genus *Paramyxovirus*, avian paramyxovirus 1.
- Order *Mononegavirales*, Family *Rhabdoviridae*, Plant rhabdovirus group, Plant rhabdovirus subgroup A, lettuce necrotic yellows virus.
- Family *Iridoviridae*, genus *Iridovirus*, *Chilo* iridescent virus.

- Family *Podoviridae*, genus T7 phage group, coliphage T7.

A Universal Classification System

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, variant, pathotype and isolate, are established by international specialty groups or/and by culture collections, but not by the ICTV.

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 for viruses. The 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'. This was a general definition which was in fact not very precise for delineating species in a particular family or in all families. Furthermore, this definition directly addressed the definition of a virus strain, which had never been attempted in the history of virus taxonomy. In 1990, Van Regenmortel proposed another species definition which has been accepted by the ICTV Executive Committee in 1991. This definition states: 'A virus species is a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche.' The major advantage in this definition is that it can accommodate the inherent variability of viruses and it does not depend 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 taxonomic level '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 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 a better usage of a virus classification. These include: (1) homogeneity of the different taxa; (2) diagnostic related matters; (3) virus collections; (4) evolution studies; (5) biotechnology; (6) sequence database projects; and (7) virus database projects.

Virus families, genera and groups

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 stable and useful; some genera have been moved from one family to another but the composition and description of these genera have remained stable over the years. The characteristics defining a genus are different 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 is very limited in current virus classification (see Table 1); only one subgenus classification exists in the entire family *Baculoviridae* and there are three other examples in plant virus groups. However, these may disappear when plant virus groups are reorganized into families and genera (see below). Since the creation of the ICTV, plant virologists have always kept the classification of plant viruses in 'groups' and strongly refused to place them in genera and families. However, due to obvious similitude, plant reoviruses and rhabdoviruses have been integrated into the families *Reoviridae* and *Rhabdoviridae* (Table 1). This position was mostly due to the refusal of plant virologists to accept binomial nomenclature. Since this form of nomenclature has been withdrawn from the ICTV rules, they have subsequently accepted classification of plant viruses into genera and families. The current classification still presents plant viruses in groups but the next report will only have families and genera for all 'virus kingdoms'. Five plant virus families and 39 genera have been proposed for the next ICTV Report.

Virus orders

As mentioned previously, the upper hierarchical levels of the virus classification are extremely difficult to establish. Despite several general propositions in the past, none of them have been accepted.

Table 3. List of descriptive characters used in virus taxonomy at the family level

I. Virion properties

A. Morphology properties of virions

1. Virion size
2. Virion shape
3. Presence or absence of an envelope and peplomers
4. Capsomeric symmetry and structure

B. Physical properties of virions

1. Molecular mass of virions
2. Buoyant density of virions
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 of proteins
2. Size of proteins
3. Functional activities of proteins (especially virion transcriptase, virion reverse transcriptase, virion hemagglutinin, virion neuraminidase, virion fusion protein)

E. Lipids

1. Presence or absence of lipids
2. Nature of lipids

F. Carbohydrates

1. Presence or absence of carbohydrates
2. Nature of carbohydrates

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

Table 3. Continued

IV. Biological properties

1. Host range, natural and experimental
2. Pathogenicity, association with disease
3. Tissue tropisms, pathology, histopathology
4. Mode of transmission in nature
5. Vector relationships
6. Geographic distribution

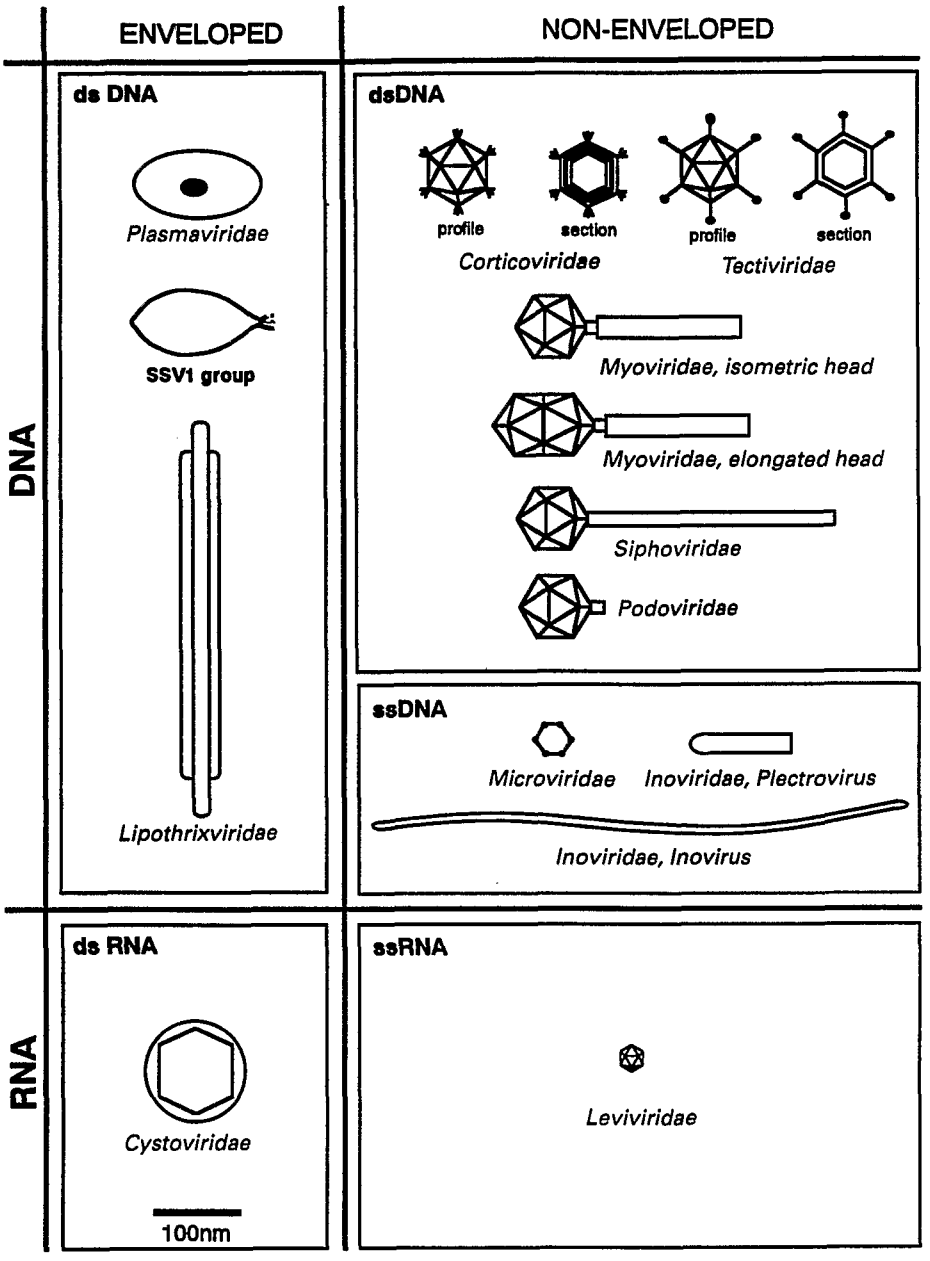

Fig. 1 Diagrammatic representation of the families of viruses infecting bacteria, grouped according to the nature and strandedness of their genome and the presence or absence of an envelope. Reproduced with permission from Springer-Verlag.

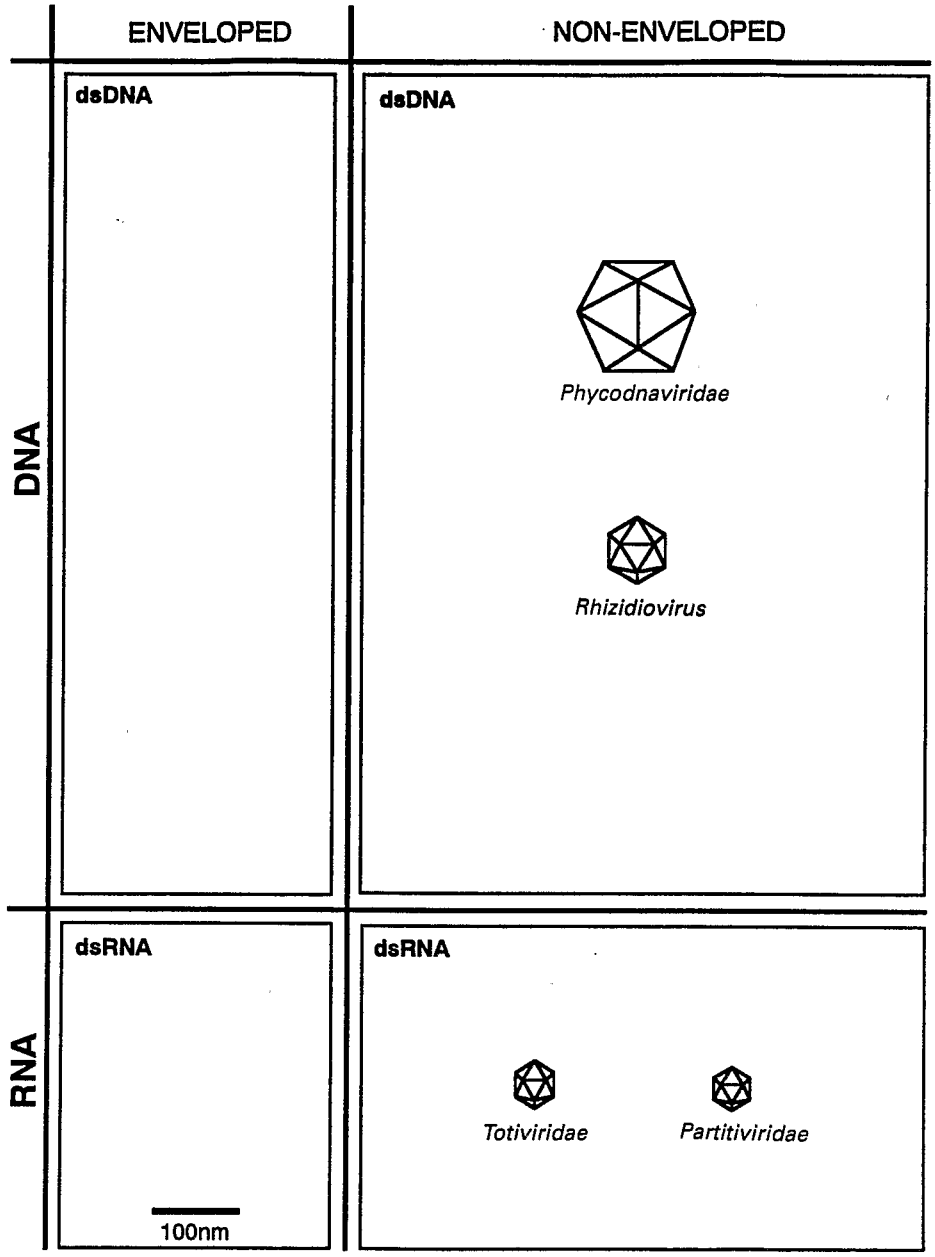

Fig. 2 Diagrammatic representation of the families of viruses infecting algae, fungi and protozoa, grouped according to the nature and strandedness of their genome and the presence or absence of an envelope. Reproduced with permission from Springer-Verlag.

Nevertheless, it has been stated several times that the creation of orders could be considered on a case-by-case basis. The first virus order *Mononegavirales* was established in 1990. This order comprises the non-segmented ssRNA negative-sense viruses, namely the families *Filoviridae*, *Paramyxoviridae* and *Rhabdoviridae*. This decision has been taken because of the great similitude between these families at many points of view including the replication strategy of these viruses. A second order is under consideration; it is named *Caudovirales*, and it includes all the families of dsDNA phages having a tail, including *Myoviridae*, *Podoviridae* and *Siphoviridae*. 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-life orders. The creation of formal taxa higher than orders, for example, kingdoms, classes and subclasses, has not been considered by ICTV.

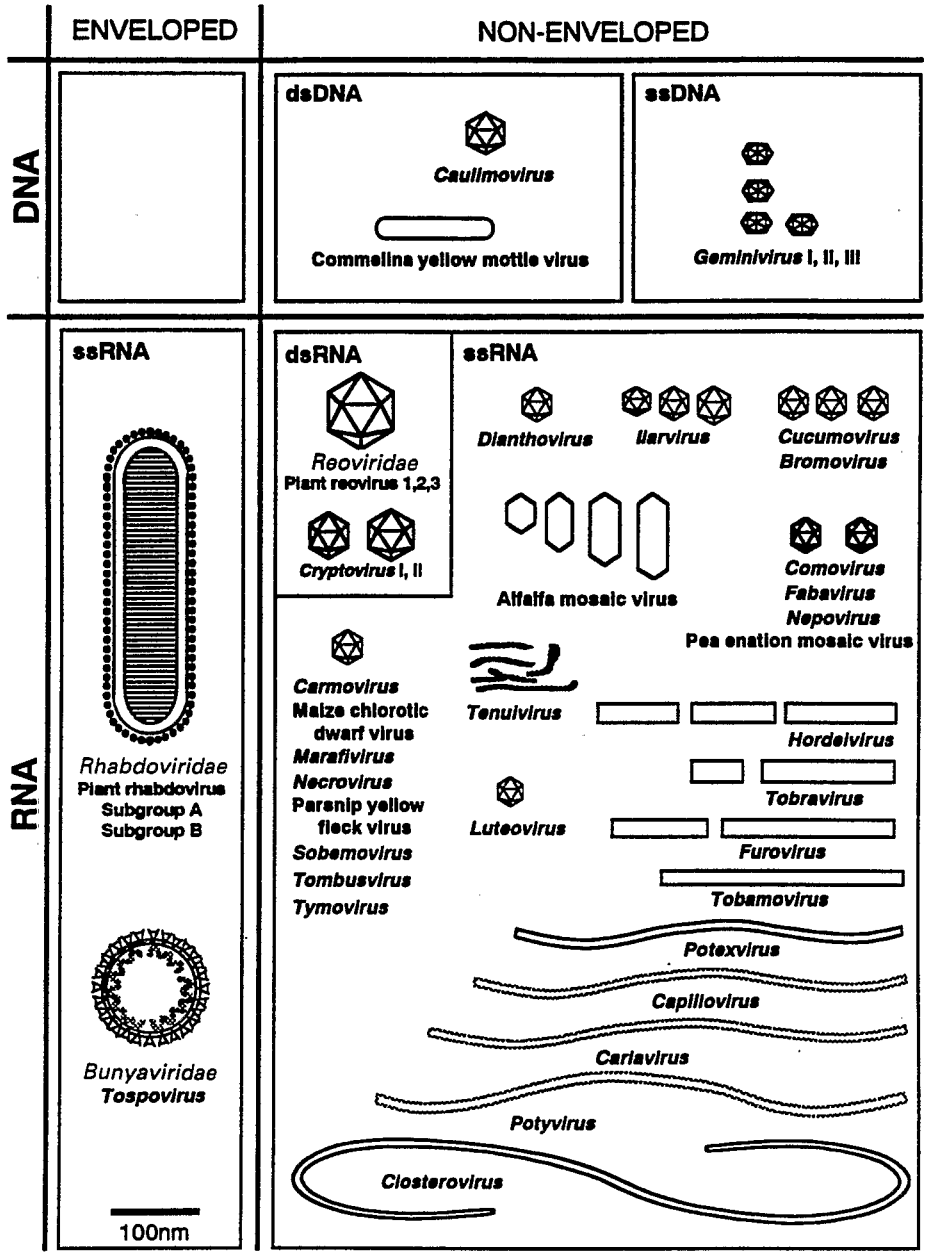

Fig. 3 Diagrammatic representation of the families of viruses infecting plants, grouped according to the nature and strandedness of their genome and the presence or absence of an envelope. Reproduced with permission from Springer-Verlag.

Virus Taxa Descriptions

Virus classification continues to evolve with the technologies available for describing viruses. The first wave of descriptions, before 1940, mostly took into account the visual symptoms of the diseases caused by viruses and their modes of transmission. A second wave, between 1940 and 1970, brought 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 (sequence of genes, sequence of proteins), as well as molecular relationships with virus hosts. There has been a correlative modification of the list of virus descriptors and Table 3 lists the family and genera

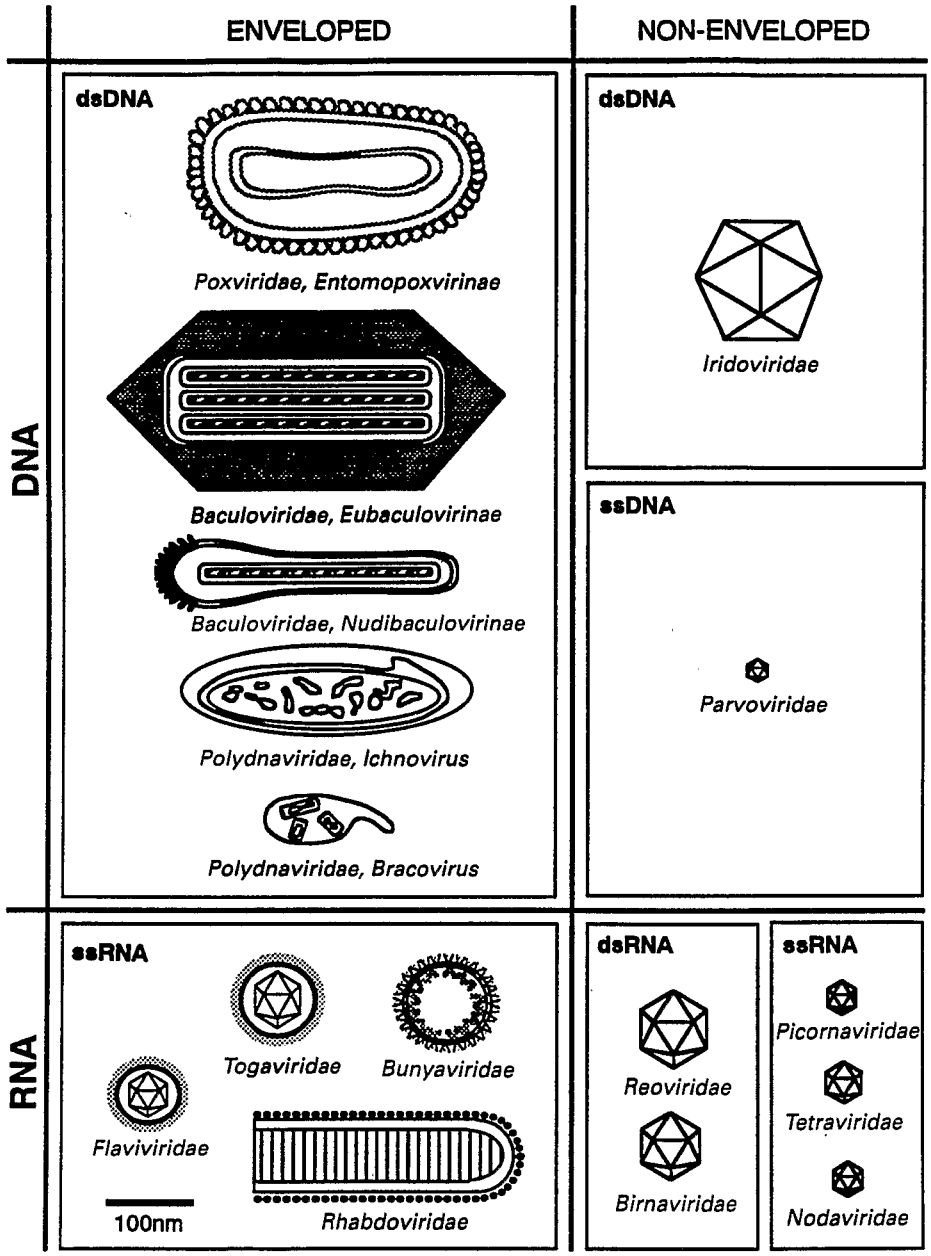

Fig. 4 Diagrammatic representation of the families of viruses infecting invertebrates, grouped according to the nature and strandedness of their genome and the presence or absence of an envelope. Reproduced with permission from Springer-Verlag.

descriptors which are used in the ICTV Fifth Report.

The impact of descriptions on virus classification has been particularly influenced by electron microscopy and the negative staining technique for virions. This technique had an immediate effect on diagnostics and classification of viruses. With negative staining, viruses could be identified from poorly purified preparations of all types of tissues and information about size, shape, structure and symmetry could quickly be 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 (Figs 1–5).

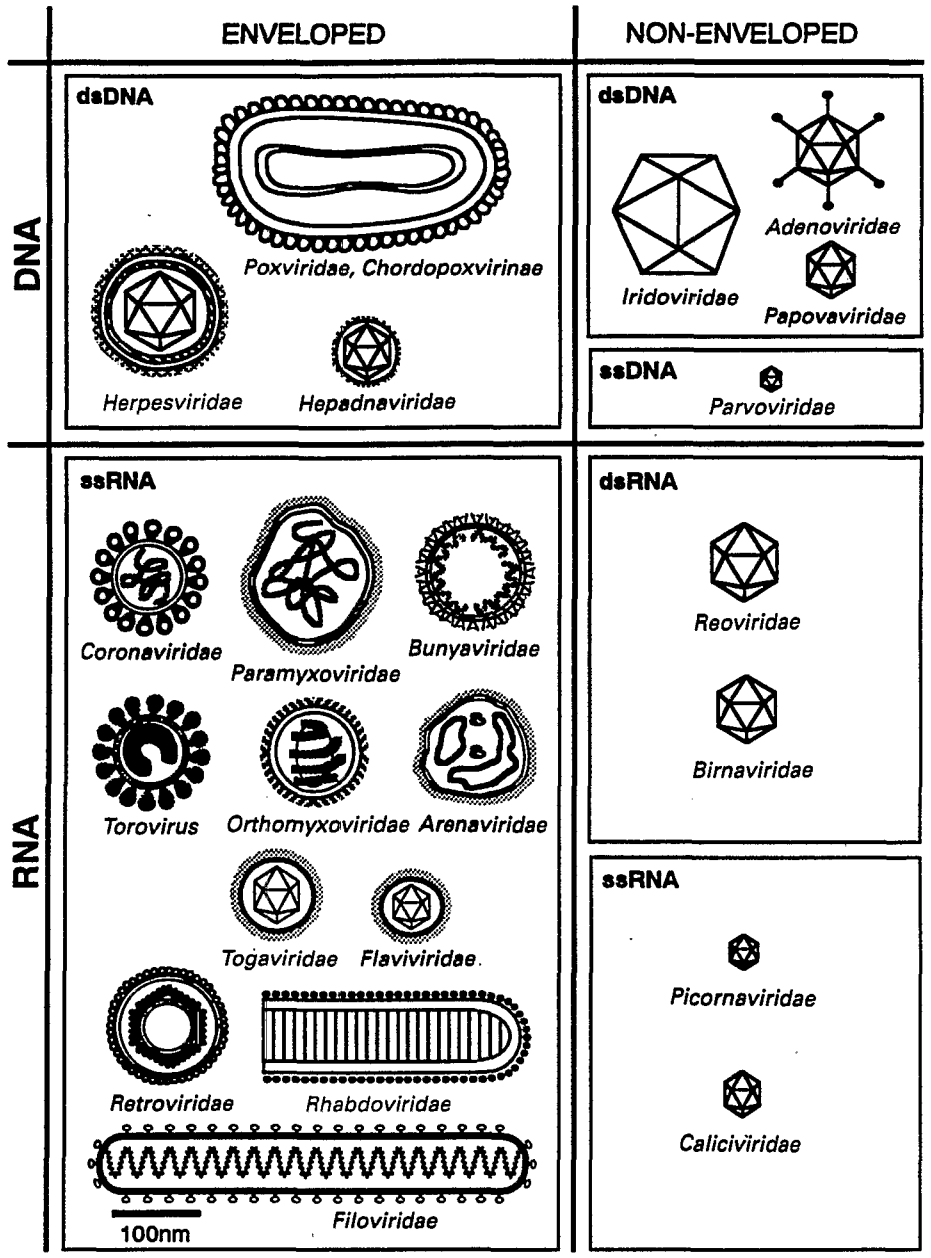

Fig. 5 Diagrammatic representation of the families of viruses infecting vertebrates, grouped according to the nature and strandedness of their genome and the presence or absence of an envelope. Reproduced wtih permission from Springer-Verlag.

In many instances the properties of viruses belonging 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 to 850 nm and transmitted by aphids is likely to be a potyvirus. Establishment of new genera in the future will require more information. Most of the properties listed in Table 3 will have to be rigorously 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 between 500 and 1000 descriptors. The establishment of a universal list of virus descriptors is under way and should be adopted by ICTV in 1993. It will contain a common set of descriptors for all viruses and discrete subsets for specific viruses in relation

to their specific hosts (human, animal, insect, plant and bacterial).

See also: Bacteriophage taxonomy and classification.

Further Reading

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TENUIVIRUSES

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Taxonomy and Classification

The tenuiviruses are a relatively newly recognized group of plant viruses, however, the diseases they cause have been known since the early 1900s. There are currently five recognized tenuiviruses including: rice stripe virus (RStV); maize stripe virus (MStV); rice hoja blanca virus (RHBV); rice grassy stunt virus (RGSV); and European wheat striate mosaic virus (EWSMV) (see also Table 1). Based upon their similar biological properties these viruses have been loosely grouped together for several years. However, only since 1981 have some of the unique and interesting molecular properties of the tenuiviruses become known.

Biological Properties

All tenuiviruses are transmitted to plants by specific delphacid planthoppers (Homoptera: Delphacidae, see Table 1). They are not mechanically transmissible even experimentally. The plant host ranges of all tenuiviruses are limited to monocotyledonous species within the family *Poaceae*. 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. The similarity of their biological properties and symptomatology led to an early artificial grouping of these viruses. Recent work on the physical, chemical and molecular properties of the tenuiviruses has confirmed their relationships to each other, and shown them to be distinctly different from most other plant viruses.

Virus Structure and Composition

The name for the tenuivirus group is derived from the slender (tenuous), filamentous ribonucleoprotein particles associated with these viruses. Such particles have been identified in cells of tenuivirus-infected plant and insect hosts. Electron microscopic analysis has shown the particles to be threadlike, very thin in diameter (8–10 nm) and often without defined lengths. These particles have often been referred to as virions or virus particles. However, recent evidence obtained by examining the filamentous particles using high-resolution electron microscopy, and by *in vitro* characterization of the particles suggests that they are likely to be ribonucleoprotein components of a yet to be identified larger, more complex virion.

Filamentous ribonucleoprotein particles (RNPs) have been purified from plants infected by MStV, RStV, RGSV and RHBV. Electron microscopic