

Classification and Nomenclature of Plant Viruses: State of the Art

Classification is the arrangement of biological entities into taxonomic categories (taxa) on the basis of similarities and/or relationships, whereas *nomenclature* is the assignment of names to taxa according to international rules. To apply these (apparently) simple concepts to viruses, the Virology Division of the International Union of Microbiological Societies established, some 30 years ago, the International Committee for the Nomenclature of Viruses (ICNV), whose name was subsequently changed to the present International Committee on Taxonomy of Viruses (ICTV).

The composition of ICTV is rather complex (7,16). The committee operates through subcommittees and their specialized study groups. Five of these subcommittees address viruses affecting specific groups of organisms, namely, vertebrates, invertebrates, fungi, bacteria, and plants. Taxonomic and nomenclatorial matters treated by study groups are referred to the appropriate host-oriented subcommittees for scrutiny and approval, and from these to the Executive Committee, which, after further examination, submits the approved proposals to ICTV for final endorsement, ratification, or both. This procedure, although lengthy and cumbersome, produces a stable taxonomic outcome, derived from the cooperative and coordinated efforts of panels of specialists rather than from the initiative of single individuals, as is common in other scientific disciplines.

By statutes, the objectives of ICTV are:

- (a) To develop an internationally agreed taxonomy for viruses;
- (b) To establish internationally agreed names for taxonomic groups of viruses; and
- (c) To communicate latest results on the classification and nomenclature of

viruses to virologists, by holding meetings and publishing results.

Whereas objectives (a) and (b) have been consistently and rather successfully pursued over time, objective (c) has been only partially fulfilled. To date, five ICTV reports have been issued, but with a 10-year gap between the fourth (16) and the fifth (7), just published last year. This delay has hindered the timely publication of new taxonomic proposals approved at the ICTV meetings in Sendai, Japan, in 1984, in Edmonton, Canada, in 1987, and in Berlin, Germany, in 1990.

History

The history of viral taxonomy was reviewed exhaustively by Matthews (17), and I refer readers to that and other sources (5,19) for further details. Here I relate only issues that have divided animal and plant virologists since the Moscow International Congress of Microbiology in 1966. The decision at that conference was not to apply the code of bacterial nomenclature to viruses. Virologists would build their own code, a "rudimentary one," according to Kingsbury (14), in which, oddly enough, suffixes used in the botanical and bacteriological codes for subclass and subtribe were chosen to denote families and subfamilies, respectively (Table 1).

Apart from these trivial differences, which were not subjects of contention, the reasons for controversy were embodied in the Rules of Nomenclature of Viruses that were promulgated by ICNV in 1966 and amended in 1981 (16). Plant virologists raised fundamental objections to:

Rule 4: An effort will be made toward a latinized nomenclature;

Rule 12: The genus name and the species epithet, together with the strain designation, must give an unambiguous identification of the virus; and

Rule 13: The species epithet must follow the genus name and be placed before the designation of strain, variant or serotype.

Application of these rules was not enforced. For plant viruses, this meant

rejection of binomial latinized nomenclature, applicability of the concept of species, and use of a taxonomy based on family-genus-species. The alternative was the adoption of the "virus group," a category that is not a recognized taxon but consists of a coherent cluster of members (individual viruses) sharing major characterizing properties. Group members were not intended to represent "species" and bore vernacular names, most of which were in English.

The alleged advantages of this approach were that the designations "virus group" and "virus" were practical and convenient, did not encompass formal taxonomic implications in terms of Linnean hierarchy, and, above all, did not require acceptance and therefore definition of "species" for viruses, especially those in which processes underlying speciation (e.g., genome recombination or reassortment) did not, or were not known to, occur.

The first 16 groups of plant viruses were approved by ICTV in 1970 and described shortly afterward (12). Notwithstanding the unusual, if not funny, sound of some of the names, the group approach caught on, winning the support of most plant virologists. Therefore, for the past 20 years or so, different taxonomic systems coexisted for plant viruses, as opposed to vertebrate, invertebrate, bacterial, and fungal viruses.

The differences intrinsic to these systems are more profound than they may appear on the surface. In fact, when the two existing virus classifications are compared critically, the plant virus "group" does not correspond to any single taxon in the parallel classification. Thus, group = family, subgroup = genus, and type (or virus) = species, as advocated by Kingsbury (13,14), does not hold except in the few cases where subgroups are identified (e.g., reoviruses, rhabdoviruses, cryptoviruses, and geminiviruses). If indeed, as maintained (14), "the same hierarchical levels are designated by different terms," shifting from one system to the other would consist of an exercise in semantics more than anything else. But this does not seem to be the case.

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The coexistence of two taxonomic systems did not cause serious conflicts because reasonable solutions were found whenever the necessity arose. For example, with viruses that cross the plant-animal kingdom boundary, there were no objections to the inclusion of those infecting plants as genera and species in the families Rhabdoviridae and Reoviridae and, more recently, in the family Bunyaviridae (Table 2).

How Plant Viruses Are Classified Today

The number of ICTV-approved taxonomic groups has doubled in the last two decades. Table 2 lists the three existing families and the 32 groups of plant viruses as they appear in the fifth ICTV report (7). The fifth report has nine additions: cryptoviruses, furoviruses, capilloviruses, tenuiviruses, carmoviruses, marafiviruses, fabaviruses, commelina yellow mottle virus, and parsnip yellow fleck virus. Two of these originated when established groups were split. Capilloviruses were separated from closteroviruses because of: 1) differences in morphology, size of particles, and coat protein subunits; 2) ultrastructural modifications induced in host cells; and 3) lack of a known vector. Furoviruses were split from tobamoviruses because they possess a fragmented genome and are transmitted by soil fungi.

Outstanding because of unusual properties are: 1) cryptoviruses = isometric viruses with two molecules of dsRNA, occurring in very low concentration in hosts, and apparently unable to induce diseases and to move from cell to cell; 2) badnaviruses = commelina yellow mottle virus group, bacilliform retroid plant viruses with a dsDNA genome, and transmitted primarily by mealybugs; and 3) tenuiviruses = characterized by an absolutely peculiar particle morphology (i.e., occasionally branched filament 3 nm thick) with a multipartite nonmesenger (negative-sense) RNA genome, and transmitted persistently by leafhoppers.

The geminivirus group was split into three subgroups designated I, II, and III

on the basis of host range, type of vector, and genome fragmentation: subgroup I = monocotyledonous hosts, leafhopper vectors, and monopartite genome; subgroup II = dicotyledonous hosts, leafhopper vectors, and monopartite genome; and subgroup III = dicotyledonous hosts, whitefly vectors, and bipartite genome. Subgroup II is somewhat intermediate between subgroups I and III

because its monopartite genome is similar to RNA-1 of the bipartite genome subgroup III.

Tomato spotted wilt virus (TSWV) has the same particle morphology, maturation sequence, type of genome (three molecules of negative-sense ssRNA), and structural organization as members of the family Bunyaviridae. This recognition has led to redefinition of the former

Table 2. The current three families and 32 groups of plant viruses according to the fifth report of the International Committee on Taxonomy of Viruses

Classification	Genome properties ^a	Number of viruses ^b
Families		
Rhabdoviridae	(-)ssRNA (1)	
Subgroup A		9
Subgroup B		4
Subgroup C (nonenveloped particles)		4
Unclassified possible species		68
Bunyaviridae	(-)ssRNA (3)	
Tospovirus		1
Reoviridae	dsRNA (10-12)	
Phytoreovirus		3
Fijivirus		3
Unnamed genus		2
Groups		
Isometric particles		
Caulimovirus	dsDNA (1)	17
Cryptovirus	dsRNA (2)	
Subgroup I		26
Subgroup II		5
Carmovirus	ssRNA (1)	17
Luteovirus	ssRNA (1)	21
Maize chlorotic dwarf virus	ssRNA (1)	3
Marafivirus	ssRNA (1)	3
Necrovirus	ssRNA (1)	4
Parsnip yellow fleck virus	ssRNA (1)	3
Sobemovirus	ssRNA (1)	16
Tombusvirus	ssRNA (1)	12
Tymovirus	ssRNA (1)	19
Comovirus	ssRNA (2)	13
Dianthovirus	ssRNA (2)	3
Fabavirus	ssRNA (2)	3
Nepovirus	ssRNA (2)	36
Pea enation mosaic virus	ssRNA (2)	1
Bromovirus	ssRNA (3)	6
Cucumovirus	ssRNA (3)	4
Quasi-isometric to bacilliform particles		
Ilarvirus	ssRNA (3)	20
Alfalfa mosaic virus	ssRNA (3)	1
Geminate particles		
Geminivirus	ssDNA (1 or 2)	
Subgroup I		10
Subgroup II		5
Subgroup III		33
Bacilliform particles		
Commelina yellow mottle virus	dsDNA (1)	14
Rod-shaped rigid particles		
Tobamovirus	ssRNA (1)	14
Tobravirus	ssRNA (2)	3
Furovirus	ssRNA (2-4)	11
Hordeivirus	ssRNA (3)	4
Filamentous particles		
Capillovirus	ssRNA (1)	4
Carlavirus	ssRNA (1)	56
Closterovirus	ssRNA (1)	22
Potexvirus	ssRNA (1)	39
Potyvirus	ssRNA (1 or 2)	153
Tenuivirus	ssRNA (4)	7

^aNumber of functional species of nucleic acid in parentheses.

^bDefinitive and possible.

Table 1. Suffixes for taxonomic categories in three codes of nomenclature

Taxon	Suffix	
	Botanical and bacteriological codes	Viral code
Subclass	-idae	...
Order	-ales	-ales
Suborder	-ineae	...
Family	-aceae	-idae
Subfamily	-oideae	-inae
Tribe	-eae	...
Subtribe	-inae	...

TSWV group as the genus tospovirus of that family.

The current classification of viruses infecting plants is a consequence of the conservative attitude of the Plant Virus Subcommittee (PVS) of ICTV and the plant virology community, both of which have maintained and enforced the principles that led to divergence in the 1960s. As recently as 1986, an opinion poll of members of the Virology Group of the Association of Applied Biologists, largely British but with representatives from 18 different countries, overwhelmingly favored conservation of the “virus-group” classification system. In a comparable inquiry conducted by the Virology Committee of the American Phytopathological Society in 1987, opinions were evenly divided for the traditional vs. the plant virus system, but the promoting committee commented that: “The adoption of classical taxa for viruses should await clarification of genetic relationships.” Furthermore, under R. I. Hamilton’s chairmanship (1986) and mine (1988), the PVS of ICTV was asked to comment on the feasibility of extending the family-genus-species classification to plant viruses. In both instances, the vote was against, although opinions were diverse among members.

By the mid-1980s, the once compact front of plant virologists began to loosen

under mounting pressure exerted by those who strongly advocated the adoption of an unified taxonomic system, among whom were a former (R. E. F. Matthews) and an acting (the late R. I. B. Francki) president of ICTV (5,16). New perspectives opened by molecular studies and the outcome of negotiations with ICTV on the contents of the Rules of Nomenclature of Viruses made the time ripe for a reconsideration of the plant virologists’ position.

The New Trend

Changes in rules of nomenclature. A debate on “Progress and Opportunities in Plant Virus Classification” was moderated by R. I. B. Francki at the Fifth International Congress of Plant Pathology, held in Kyoto, Japan, in 1988. Later (1990, Berlin), after a formal request by the PVS, ICTV agreed to abolish rules 4 and 13 and to modify rules 5, 12, and 14 of the Rules of Nomenclature of Viruses as follows: rule 5, “Existing names shall be retained whenever feasible”; rule 12, “A virus name, together with the strain designation, must provide unambiguous identification and need not include the genus or group name”; and rule 14, “A virus name should be meaningful and consist of as few words as possible.”

In practice, the use of a latinized binomial system is no longer advocated by ICTV and will not be enforced. Rules recommending “latinization” have been abolished (rule 4) or modified (rule 5). Likewise, rules stating that virus binomials be made up of the genus name and the species epithet have been abolished (rule 13) or modified in such a way that no constraints are placed on how to formulate a virus name (rules 12 and 14). It follows that plant virologists can now “legally” continue to name viruses just as they have done in the past.

Toward acceptance of the species concept. Even a passing look at recent literature on the species issue in virology would prompt wholehearted assent with the statement by Matthews (19) that “although the species is widely regarded as the most important category in a taxonomy, it has proved to be the most difficult to apply to viruses.” The uncertainty that had dominated the virology community is reflected in rule 10 of the ICTV Rules of Nomenclature of Viruses: “A virus species is 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.”

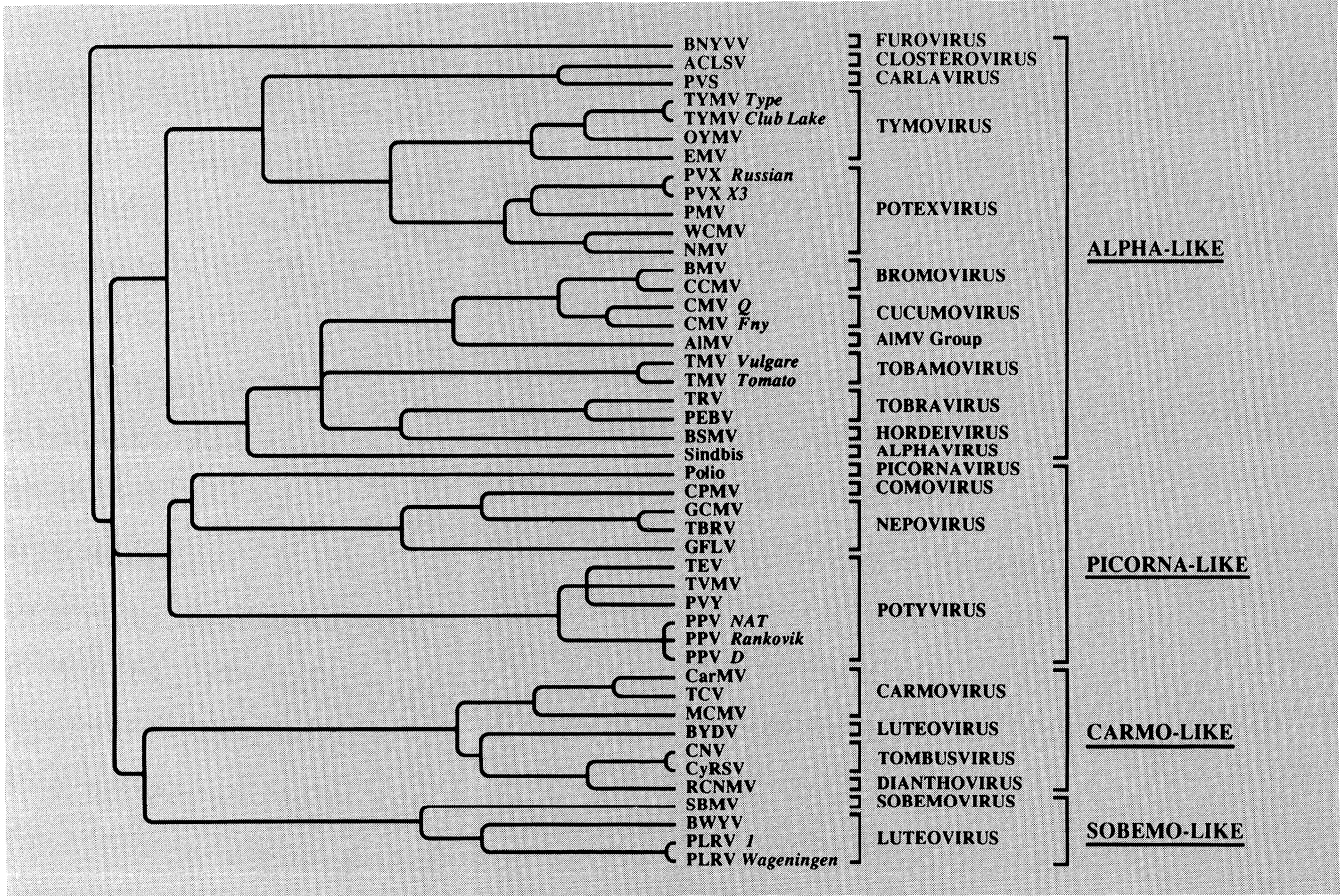


Fig. 1. Identification of ssRNA plant virus clusters using conserved polymerase motifs. The length of the branches is inversely proportional to the degree of sequence homology. (After Goldbach et al [9], by permission)

This masterpiece of noncommitment eludes basic questions: Do species exist in the virus world? How do they form? How can they be recognized as well-defined taxonomic entities stable and separated from other comparable entities? In other words, which are the parameters whereby a virus is a species?

On the applicability of the concept of species to viruses, virologists of diverse extractions have crossed swords for a couple of decades, some in favor (2,6,13,14, 18,19,27-29), others against (11,20-22, 25), both groups presenting seemingly well-founded arguments in support of their views.

I will not attempt to review the developments of a debate that generated wide philosophical interest, as well as a few definitions of species more or less tailored to fit certain points of view. M. H. V. Van Regenmortel was one of the most persuasive contenders. His definition of species (28), i.e., "A virus species is a polythetic class of viruses consisting of a replicating lineage and occupying a particular ecological niche", met with the approval of the Executive Committee of ICTV (1991, Atlanta), which accepted it with large majority and decided that it should replace rule 10 in the Rules of Nomenclature of Viruses.

The meaning of the above definition may not be immediately perceived by all, especially the practicing virologist who may not have read Van Regenmortel's papers. An ad hoc committee was therefore appointed to define the terms "polythetic class," "replicative lineage," and "ecological niche." This definition encompasses the fact that viruses are biological entities that possess genes, replicate, interact with hosts, and are exposed to selection pressure, thus specialize and evolve.

One of the strongest objections to universal application of the species concept in viral taxonomy was that some plant viruses, especially those with monopartite ssRNA genomes, constitute a continuum of variants that replicate clonally, i.e., without the exchange of genetic information among isolates (11,20,21,25). Recent biochemical and molecular investigations on structural and nonstructural viral proteins indicate that this assumption is no longer tenable.

Comparative studies by Shukla et al (reviewed by Ward and Shukla [31]) demonstrated that tryptic polypeptide profiles of the coat protein (a structural protein) of potyviruses, separated by high-performance liquid chromatography, are consistent for individual viruses. This technique can be used to determine whether any given virus isolate is an entity in its own right (i.e., a "species") or a strain of another virus. By comparing coat protein sequences, Shukla et al showed that different potyviruses were 50-60% homologous, whereas strains of the same virus were often more than 95%

homologous. By these new analytical approaches, supported by improved serological information, the previously chaotic world of potyviruses breaks down to well-defined elements, each representing a different virus. It remains to be seen whether and to what extent present concepts will stand the test of future analyses.

Nucleotide sequences of gene coding for nonstructural proteins of many viruses with a messenger (i.e., positive-sense) ssRNA genome infecting animals and plants have been compared. Conserved sequences have been found, especially in replication-associated proteins such as those endowed with polymerase and helicase (nucleotide binding) activity (3,4,9,10,24). These conserved genes, whose presence suggests common ancestry, occur in different viral genomes with other genes unique to that particular genome. If, as postulated (3,24), these conserved genes are phylogenetically independent and can be exchanged as modules, then genomic recombination is likely to account for their dissemination in RNA virus populations. Cases of RNA recombination in plant viruses have been substantiated for single viruses (tobacco rattle tobavirus), between members of the same taxonomic group (tobaviruses and bromoviruses), and between viruses belonging to different taxonomic groups (luteoviruses, sobemoviruses, and carmoviruses) (reviewed by Goldbach [8]).

Thus, two major mechanisms for genetic diversification operate in RNA plant viruses: true genomic recombination (intragenic rearrangements) and reassortment (replacement of complete genes by others, as with pseudorecombinants of multipartite genome viruses). Therefore, should not most, if not all, reservations against the acceptance of the concept of "virus species" be abandoned?

Higher taxa. The problem of taxa above the family level was addressed as early as 1983 by Francki (6), who approached the issue essentially from a pragmatic viewpoint, i.e., the constitution of clusters of virus groups (or families) to facilitate teaching and learning. Francki was thinking of "orders" to be constructed on a few differential key characters such as genome type and strandedness, particle symmetry, and presence or absence of an envelope. There was no follow-through of Francki's proposal, and none was expected, considering the determined opposition at that time of plant virologists to the traditional taxonomic system.

Mononegavirales, the first virus order in history, was recently approved by ICTV (1990, Berlin) and described by Pringle (26). The order embraces three families of enveloped viruses with negative-sense monopartite ssRNA genome, namely, Filoviridae, Paramyxoviridae, and Rhabdoviridae.

Notwithstanding this precedent, the Executive Committee of ICTV has adopted a cautious attitude toward the approval of new orders at least until the criteria for their establishment can be defined. One question is whether higher taxa should or should not reflect evolutionary relationships and, if so, at which taxon level should phylogeny become the characterizing feature (27). Depending on the decisions to be made, different sets of characters might be used for forming a higher taxon, with unavoidable consequences on its composition.

Lately, molecular information, which is accumulating at an amazing rate, has made possible the construction of seemingly coherent aggregations of families and groups that comprise both animal and plant viruses. These clusters have been called either "supergroups" (10,24) or "superfamilies" (23,27). Although as yet these higher groupings do not have a precise taxonomic connotation, they may assume one soon, and the question of name may become relevant. The non-committal name "supergroup" seems preferable to "superfamily," which in the future may be identified as a specific taxon with connotations different from those underlying Milne's (23) examples of present viral aggregates.

Molecular data are bound to produce new and exciting developments in viral taxonomy. Such data may lead, for example, to a systematics based on phylogeny. The premises were laid down by the elaborations of various authors (3,4,9,24) who, by comparing published sequences, discovered high degrees of homology in the nonstructural proteins of the viral replicating machinery. On the basis of conserved polymerase motifs, dendograms were constructed (3,4,9), the latest of which (Fig. 1) indicates that four "supergroups" can clearly be recognized in positive-sense ssRNA viruses. Interestingly, two of these supergroups are made up exclusively of plant viruses with no animal virus counterpart and can reasonably be equated each to a family rather than to a higher taxon.

How Plant Viruses May Be Classified Tomorrow

The modifications to the Rules of Nomenclature approved by ICTV, and the realization that viruses undergo genetic processes whereby species may arise, have: 1) removed the major stumbling blocks toward agreement for the extension of the traditional taxonomic system (family-genus-species) to all viruses and 2) made the PVS of ICTV more pliable and amenable to adaptation of the current plant virus classification to the classical scheme. The latter is an undertaking not without difficulties because, as mentioned, current plant virus groups may correspond either to families or to genera, according to their

properties. Therefore, Kingsbury's (14) and Van Regenmortel's (29) suggestions that equalize groups to families and genera, respectively, do not apply. For instance, Van Regenmortel's (29) genus potyvirus deserves a family status (Poty-

viridae), according to the Potyvirus Study Group of ICTV chaired by O. W. Barnett, which in 1990 held a workshop in Braunschweig, Germany, to discuss potyvirus taxonomy. One outcome was the publication of a proposal for the

establishment of the family Potyviridae (1). Van Regenmortel's (29) family Caulimoviridae is likely to remain a genus (caulimovirus) at least until its relationships with badnaviruses of plants and hepadnaviruses of vertebrates are clarified. Hepadnaviruses, badnaviruses, and caulimoviruses are retroviruslike viruses that, like true retroviruses, replicate via reverse transcription but, unlike true retroviruses, encapsidate the DNA phase of the replicating cycle and do not involve integration into the host genome. These three virus groups may form a cluster (possibly a family) that would represent the fourth example of a taxon comprising viruses that infect members of the plant and animal kingdom.

These examples illustrate the problems currently under discussion in the PVS of ICTV for developing a new classification scheme for plant viruses, a provisional outline of which is shown in Table 3. Nine families have been identified so far, three of which (Rhabdoviridae, Bunyaviridae, and Reoviridae) already existed. The additional six families result from either converting single groups into families (i.e., Cryptoviridae, Geminiviridae, and Potyviridae) or combining two or more previous groups, each of which was given a genus status (i.e., Tombusviridae, Comoviridae, and Bromoviridae). No new names were

Table 3. Provisional classification of plant viruses in families and genera

Families	Genera
Rhabdoviridae	Two genera (subgroups A and B) and a possible genus (subgroup C)
Bunyaviridae	Tospovirus
Reoviridae	Phytoreovirus, fijivirus, oryzavirus
Cryptoviridae	Two genera (subgroups I and II)
Geminiviridae	Three genera (subgroups I, II, and III)
Tombusviridae	Tombusvirus, carmovirus
Comoviridae	Comovirus, nepovirus, fabavirus
Potyviridae	Potyvirus, bymovirus, rymovirus, ipomovirus
Bromoviridae	Bromovirus, cucumovirus, ilarvirus, alfamovirus
	Ungrouped possible genera
	DNA viruses
	Caulimovirus, badnavirus
	RNA viruses
	Isometric particles: necrovirus, dianthovirus, tymovirus, luteovirus, sobemovirus, marafivirus, maize chlorotic dwarf virus, pea enation mosaic virus, parsnip yellow fleck virus
	Rod-shaped particles: tobamovirus, furovirus, hordeivirus, tobnavirus
	Filamentous particles: closterovirus, capillovirus, carlavirus, potexvirus, tenuivirus

coined for any of the "new" families, all of which were named after their best-characterized genus. This principle, adopted by the PVS to avoid unnecessary proliferation of names, was applied to Bromoviridae, a name chosen to denote a family that is the same as Tricornaviridae, a family described some 10 years ago (30) without previous examination and approval by ICTV.

All other existing groups are provisionally classified as possible genera until more information, especially molecular, becomes available to confirm relationships useful for establishing families. Each genus, regardless of whether or not it is a member of a family, will have its own name, an issue that is now being examined by the PVS. Because not all names of genera have been defined, Table 3 lists only those with enough support to qualify as candidates for submission for approval by ICTV.

Two possible new genera are halfway through the formalization process, as they have the approval of the PVS but not yet that of the Executive Committee of ICTV. One is umbravirus, proposed by A. F. Murrant: type species, carrot yellow mottle virus; an infectious agent with no defined particles whose ssRNA is encapsidated in the coat protein of a helper virus (usually a luteovirus) for transmission by aphids. The other is idaeovirus, proposed by A. F. Murrant and M. A. Mayo: type species, raspberry bushy dwarf virus; a virus with bipartite ssRNA genome and quasi-isometric particles that is transmitted through pollen.

In addition, the following recently described viruses may qualify, when better known, as type species of possible genera (23): 1) small bacilliform particles, fragmented ssRNA genome, Ourmia melon virus (cassava virus C, Epirus cherry virus) and olive latent virus 2; 2) rod-shaped particles, dsRNA genome, lettuce big vein virus (tobacco stunt virus); 3) small isometric particles, ssDNA genome, transmitted by aphids, coconut foliar decay virus and subterranean clover stunt virus; and 4) isometric particles, monopartite ssRNA genome, transmitted by beetles, maize chlorotic mottle virus.

Infectious Agents Other than Viruses

ICTV has recently turned attention also to agents that, like viroids, differ from and are totally unrelated to viruses or, like satellite RNAs, depend on viruses for their replication.

The fifth ICTV Report (7) contains sections devoted to viroids (by J. W. Randles and M. A. Rezaian) and to satellite RNAs (by A. M. Mayo). Whereas the classification of satellite RNAs into four types (designated A, B,

C, and D) is founded on their physical and messenger properties, that of viroids relies on comparative sequence analysis. On this basis, the 26 or so viroids known to date are separated into three groups whose type members are potato spindle tuber, avocado sunblotch, and apple scar skin viroids. This classification is tentative and has not yet been submitted for formal examination by ICTV, although a similar scheme has already been published (15).

Events and Expectations

Two major events are having a remarkable impact on plant virus taxonomy: 1) the acceptance by the PVS of ICTV and, I hope, the whole virology community, of the family-genus-species classification system and 2) the advent of the "molecular era." The former event reconciles the views of animal and plant virologists, thus enabling the development of a unified taxonomy for all viruses, regardless of the hosts they infect. The latter, by unraveling previously unsuspected similarities among plant viruses and between them and animal viruses, is expected to provide the background for a systematics increasingly aware of evolutionary relationships and their usefulness.

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