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Farahanaz Rasool

Sher-e-Kashmir University of
Agricultural Sciences and
Technology of Kashmir Shalimar
Campus, Jammu and Kashmir,
India

Purshottam Singh

Sher-e-Kashmir University of
Agricultural Sciences and
Technology of Kashmir Shalimar
Campus, Jammu and Kashmir,
India

Ali Anwar

Sher-e-Kashmir University of
Agricultural Sciences and
Technology of Kashmir Shalimar
Campus, Jammu and Kashmir,
India

Najeeb Mughal

Sher-e-Kashmir University of
Agricultural Sciences and
Technology of Kashmir Shalimar
Campus, Jammu and Kashmir,
India

Sushil Kumar

Sher-e-Kashmir University of
Agricultural Sciences and
Technology of Kashmir Shalimar
Campus, Jammu and Kashmir,
India

Sabiya bashir

Sher-e-Kashmir University of
Agricultural Sciences and
Technology of Kashmir Shalimar
Campus, Jammu and Kashmir,
India

Corresponding Author

Farahanaz Rasool

Sher-e-Kashmir University of
Agricultural Sciences and
Technology of Kashmir Shalimar
Campus, Jammu and Kashmir,
India

Classification and nomenclature of viruses: A review

Farahanaz Rasool, Purshottam Singh, Ali Anwar, Najeeb Mughal, Sushil Kumar and Sabiya bashir

Abstract

The official nomenclature of animals and plants is under the control of international zoological and botanical nomenclature committees, which have codes laying down rules and recommendations. The Fourth International Microbiological Congress held in Copenhagen in 1947 decided that viruses came within the field of jurisdiction of the microbiological code. The botanists, however, have taken an interest in the nomenclature of plant viruses and their International Congress in 1930 appointed an International Committee on plant virus classification and nomenclature. It was in 1966 when the first internationally organized initiative was taken to set up International Committee on Nomenclature of Viruses. This became the International Committee on Taxonomy of Viruses (ICTV) in 1973 and first report on Nomenclature of viruses was published in 1971. Till now ten reports have been published time to time. The International Committee on Taxonomy of Viruses (ICTV) is responsible for the classification of viruses into taxa. Importantly, the ICTV is currently not responsible for the nomenclature of viruses or their sub classification into strains, lineages, or genotypes. ICTV virus classification into taxa and taxa nomenclature rules are laid out in a code, the International Code of Virus Classification and Nomenclature (ICVCN). The most recent version of the Code makes it difficult for the unfamiliar reader to distinguish between viruses and taxa, thereby often giving the impression that certain Rules apply to viruses.

Keywords: Nomenclature of viruses, international committee on taxonomy of viruses, microbiological

Introduction

Virus taxonomy, which can be defined as the arranging of viruses into related clusters, identification of the extent of relatedness within and among these clusters, and the giving of names to the clusters is a relatively recent endeavour (Mayo and Pringle, 1998) [14]. Earlier viruses were often classified by the name of the disease they cause. Johnson (1937) [9] stressed the need for using some criteria other than disease symptoms and host plants for identifying viruses. He suggested that a virus should be named by adding the virus and a number to the common name for the host in which it was first found for e.g. tobacco virus 1 for TMV. Johnson and Hoggan (1935) [9] compiled a descriptive key based on five characters: i). modes of transmission ii). natural or differential host iii). longevity *in vitro* iv). thermal death point v). distinctive or specific symptoms. Using the above key 50 viruses were identified and placed in groups. Smith (1937) outlined a classification in which the known viruses or virus diseases were divided into 51 groups. Viruses that were quite unrelated in their basic properties were put in the same group. Holmes (1939) [7] published a classification based primarily in host reactions and methods of transmission. He used a latin binomial trinomial systems of naming. Between 1940 and 1966, various schemes were proposed either for plant viruses only or for all viruses.

The first internationally organized initiative was the formation of the International Committee on Nomenclature of Viruses in 1966. This became the International Committee on Taxonomy of Viruses (ICTV) in 1973 and, since then, has produced ten reports reviewing the state of virus taxonomy, the latest of which was published in 2017 (https://talk.ictvonline.org/ictv-reports/ictv_online_report/). The First Report was published in 1971 by the then International Committee on Nomenclature of Viruses (ICNV) (Wildy, 1971) [27]. This report, covering the period 1966 to 1970, established five subcommittees: Bacteriophage (now Prokaryote Virus), Invertebrate Virus, Plant Virus, Vertebrate Virus and Cryptograms. The sub committees were responsible for approving taxonomic proposals relevant to their groups of viruses and presenting these proposals for approval by the Executive Committee (EC), the ICNV, with the provision that “a sizable number of virologists working in the relevant field were to be consulted”. This report included the designations family, genus (group) and type species, thus

establishing and setting the foundations for viral taxonomy. By the Second Report (Fenner, 1976) ^[3], the name change to ICTV had been approved (in 1973), and a formal structure of ICTV officers had been established, consisting of the President, Vice-president, two Secretaries, Chairs of the subcommittees, elected members and life members. There was now a Fungal Virus Subcommittee (created from the disbanded Cryptograms Subcommittee) and a Coordination Subcommittee (disbanded 1995) charged with ensuring that the Study Groups included virologists with interests in particular virus groups in each class of host affected.

In the Third Report (Matthews, 1979) ^[11], the viruses were listed on the basis of the kind and strandedness of the nucleic acid making up the viral genome, and the presence or absence of an envelope. It was noted that although the ICTV had approved families and genera, there was no such approved "taxon equivalent to species, lying between genus and strain or variant". The problem of defining species for viruses and naming these species was presented, and an extensive discussion of the various points of view as presented by representatives of different groups of viruses was outlined for the first time. It was suggested that it might take 10–20 years to provide these taxa, and an appeal was made to Study Groups to put forward species proposals for consideration by the ICTV. This was also the first ICTV Report to include virus diagrams, grouped according to the major hosts (animal, bacteria or plant). There was also a list of some unclassified viruses and virus-like agents, including the agents of scrapie, Kuru and Creutzfeldt–Jakob diseases, viroids, and satellite viruses and satellite RNAs in plants.

The same general arrangement was followed in the Fourth (Matthews, 1982) ^[12] and Fifth (Francki *et al.*, 1991) ^[4] Reports. By the time of the Sixth Report (Murphy *et al.*, 1995) ^[16], the ICTV had finally accepted the controversial category of virus species based on a proposal made in 1990 (van Regenmortel, 1990) ^[23]. A virus species was defined as "a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche". There was also a clear description of the usage of formal taxonomic nomenclature and an attempt to explain its appropriate usage and how it differs from informal vernacular usage. More than 15 years later, this issue continues to elicit controversy.

In the Seventh Report (van Regenmortel *et al.*, 2000) ^[25], there was an extensive discussion of the species concept in virus taxonomy, and an appeal to the virology community to establish demarcation criteria which could be used to discriminate between different virus species within a genus. Some, but not all, genus descriptions in the Seventh Report included criteria by which species could be differentiated.

The Eighth Report (Fauquet *et al.*, 2005) ^[2] continued this process and provided an epic compilation of virus taxonomy illustrated with 436 electron micrographs, diagrams of virus particles, diagrams of genome organization and phylogenetic trees in a book of 1259 pages. As this approached the limit for publication in a single volume, it was becoming obvious that a different vehicle for transmission of virus taxonomy would soon be required.

Nevertheless, the Ninth Report was also published as a book of 1327 pages listing 2284 virus and viroid species distributed amongst 349 genera, 19 subfamilies, 87 families and 6 orders. There was also a chapter of unassigned viruses that provided information on several viruses that had not yet been classified but which were probably representatives of new genera or families. The final chapters described the satellites (and other

virus-dependent nucleic acids) and prions (which include the agents of spongiform encephalopathies of humans), which are not formally classified by ICTV but were simply listed for historical reasons.

These Reports have reflected the huge increase in the amount of fundamental information that has accrued in the last many years and there has been a corresponding increase in the extent of the taxonomy and the sizes of the Reports. An ideal of all classification and naming work is to form a permanent meaningful structure. But new types of virus and new arrangements of viruses or taxa are continuing to appear as research becomes more incisive and analytical techniques become more revealing.

Principles of virus taxonomy

The main guiding principles in devising a taxonomy for viruses are stability (that is, names and relationships once decided should remain unaltered for as long as possible, thereby facilitating reference to older literature), utility (that is, the scheme of taxonomic relationships should be found useful by the wider virology community), acceptability (that is, working virologists are happy to use the names and taxonomic relationships listed), and flexibility (that is that the taxonomy is amenable to revision and reassessment in the light of new discoveries). The rationale for these principles is as follows.

(a) Stability

Nomenclatural debates among taxonomists of other disciplines have cast a shadow over taxonomy as a worthwhile activity (Hawksworth, 1997) ^[6]. The main cause is the issue of Priority, which results in familiar names being abandoned in favour of more legitimate but less familiar names. This seems to be due to the numbers of new species described being very large and the Rule of Priority being applied to arbitrate between rival claimants in the naming of any particular species. Happily for virologists, the number of viruses currently recognized is much less than the number of animal species being described annually. Thus, no Priority rule is needed for virus nomenclature, and it is formally excluded (ICN, Rule 10). Once a taxon has been recognized and named, both the taxon and its name should be altered only with great reluctance. For the sake of continuity in the literature, names should be changed only rarely and when the name change is unavoidable. This ideal clearly means that there will be a delay between proposal and acceptance of a name and taxon. In the interests of achieving a stable nomenclature, the virology community is obliged to accept some waiting period before new names and taxa are formally accepted.

(b) Utility

When a taxon is recognized and named, this is done on the basis of wide consultation among virologists to ensure that the taxon is useful. This is done through the relatively democratic operation of the Study Group and Subcommittee structure of the ICTV. This involves around 470 virologists worldwide. Sometimes ideas are submitted to wider consultation by publication in the Virology Division News of *Archives of Virology* which serves as a forum for interested virologists to communicate with ICTV committees directly. The current hierarchy of taxa has four principal ranks and intermediate taxa are rarely added. Such parsimony is useful to the virologists as this way there is no need to be much concerned

about the niceties of precise levels of relatedness and there are fewer names to memorize. The ICTV attempts only to create taxa when such constructions are useful to practising virologists.

(c) Acceptability

The corollary of the utility principle is that if a taxon is useful, it will be acceptable to the majority of virologists who will be using the taxon and its name. The acceptability principle also extends to the naming of taxa. A name which is difficult to use because it is complex or difficult to remember is likely to be less acceptable than one which is easy to use. And the International Code of Nomenclature (Rules 12, 13 and 14) seeks to control this. However, it is generally the choices of experts on Study Groups, who are supposed to be, or at least represent, the specialists who will use the taxa and names, which carry most weight in the decision-making process.

(d) Flexibility

Virology is an expanding field of knowledge and virus taxonomy has to be flexible enough to accommodate occasional revisions and reinterpretation of perceived relationships between viruses in the light of accumulating knowledge. An example is the monopartite negative-strand RNA viruses. The three families, *Filoviridae*, *Paramyxoviridae* and *Rhabdoviridae*, have been grouped together principally because they consist of viruses with monopartite negative-strand RNA genomes that contain a basic complement of five genes of homologous function in a similar linear orientation. The orientation appears to be important in the control of gene expression. The absence of homologous genetic recombination between genomes of viruses in these families, together with the conservation of gene order, suggested a phylogenetic relationship reflecting either a progression from a basic complement of five genes towards greater complexity by accretion of genes through the expansion of intergenic junctions, or the reverse process of progressive loss of nonessential functions (Pringle, 1991). The family *Paramyxoviridae* was split into two sub-families, the *Paramyxoviridae* and the *Pneumoviridae*, in recognition of the relative distinctiveness of the mammalian pneumovirus from other paramyxoviruses. Subsequently, the family *Bornaviridae* was included in the Order because bornaviruses have negative-strand RNA genomes and the conserved gene order, while being significantly distinctive in other respects from viruses in the other three families (Pringle, 1997; Pringle & Easton, 1997)^[19-20].

Several recent observations have complicated these initial RNA viruses. Firstly, an avian pneumovirus was discovered which lacks the usual inversion of the gene order of mammalian pneumovirus, suggesting that the pneumovirus may be closer to the mainstream of paramyxovirus evolution than supposed previously, and that, despite the apparent lack of genetic recombination, gene rearrangement may have occurred as a rare event in the evolution of this group of viruses. Also, the avian pneumovirus resembles other paramyxoviruses in lacking the two 3-terminal genes, NS1 and NS2, which are characteristic of mammalian pneumovirus (Randhawa *et al.*, 1997)^[21]. The small number of negative-strand RNA viruses characterized in any detail in the context of the continuing discovery of new viruses (e.g. the Australian equine morbilli-likevirus), the increasing evidence of diversity within existing members of the families *Paramyxoviridae* and *Rhabdoviridae*, and the limited

knowledge of the replication cycle of bornaviruses, are additional factors which may lead to a revision of the taxonomy of the order *Mononegavirales*. Secondly, the recently acquired ability to re-engineer the genomes of negative-strand RNA viruses by reverse genetics has revealed that viruses with gross rearrangements of gene order may retain partial or complete viability (Ball *et al.*, 1997; Wertz *et al.*, 1997)^[1, 26]. Also, genomes can tolerate the insertion of foreign genes (Mebatsion *et al.*, 1996)^[15], and some indigenous genes (e.g. SH and G genes of mammalian pneumovirus) appear to be dispensable (Georgiou *et al.*, 1997)^[5]. Consequently, the conserved gene order defining the Order *Mononegavirales* may be a reflection of an overriding selection pressure rather than an indication of an evolutionary progression from simplicity to complexity or vice versa.

The international code of nomenclature

The Executive Committee of the ICTV has developed an International Code of Nomenclature based on *ad hoc* rules (Murphy *et al.*, 1995; Mayo, 1996)^[13, 16]. These lay out the *modus operandi* of the ICTV and are the justification for the decisions of its Subcommittees. The Code has the formal approval of the Virology Division of the IUMS. Many of the Rules contained in the Code are self-evident. But others have been devised in response to pressures from the virology community for guidance, or even pleas for consistency in decision-making. Some of the issues regulated are the following.

(a) Names

The proposals that always involve the most protracted and heated debates in EC meetings are those concerned with the naming of taxa. The EC has in the past made decisions about names at different times and in good faith, but which on later consideration appear to have been based on diametrically opposite principles. In order to avoid this, and to explain to virologists who devise names what is considered acceptable, or even desirable, the EC has recently refined the Rules of Nomenclature in the International Code of Virus Classification and Nomenclature, so as to give clear guidance as to how acceptable names should be devised (Mayo, 1996)^[13]. However, the ICTV is powerless to arbitrate for personal, or collective, taste. The main principles of the Rules are that a new name should be distinctive (Rule 14), easy to remember (Rule 12), be free of association with any individual's name (Rule 11) and avoid absurdity or offence in any language (Rule 19). The most difficult principle concerns possible meanings imparted by names. Inevitably, names seem to convey meanings. But when a name is devised which has a meaning, there is a risk that new discoveries will make this meaning inappropriate for that particular taxon. Rule 18 of the current Code was devised to avoid this problem. This excludes names that seem to convey meaning which might exclude legitimate members of the taxon or which would seem to include viruses that are classified in different taxa. Nevertheless, in practice, the meaning in taxon names soon diminishes so that names like '*Picornaviridae*' are workable even though of the 61 genera of 'small (plus-sense) RNA-containing viruses' (the meaning implicit in the name) only 6 are in the family *Picornaviridae*. Issues related to the naming of taxa are regulated by Rules 8 to 20 of the Code. However, the Rules of Nomenclature have needed refining in the past and may do so in the future. Changes are dealt with as taxonomic proposals. Because taxa have been named in the

past under less well-developed rules, the current list of taxon names contains a number which are in contravention of current practice. But in the interests of stability of nomenclature, few have been altered.

(b) Name stems

Two approaches have been taken to the selection of family names. In one, the front part, or stem, of the name of the genus held to be the unofficial type genus is added to the ending *-viridae*. Thus the family *Iridoviridae* contains the genus *Iridovirus*. The other approach is to invent a wholly new name for the family which avoids the confusion as to what is meant by the vernacular phrase 'an iridovirus'. The first approach has the advantage that the family is tied to a particular genus and its properties can be predicted from this. At present, 34 of the existing 54 families have names with a stem derived from a 'typical' genus. Other advantages are that fewer names are needed and fewer have to be remembered. A disadvantage is the potential confusion as to whether reference to an iridovirus concerns a virus in the genus *Iridovirus* or a virus in one of the other three genera in the family *Iridoviridae*.

(c) Derivation of species names

The naming of viruses, now virus species, has followed different traditions in different branches of virology. Many bacterial viruses have names consisting largely of combinations of letter and number codes. Presumably this developed because there is little or no phenetic difference between viruses, and many infect the same host species. Number series are also used in some fields of vertebrate virology (e.g. picornaviruses). Plant virus names are usually of the form 'host name' plus 'symptom name' plus 'virus'. However, many hosts are shared by several plant viruses, and many viruses have wide host-ranges. In other fields, the location at which the type isolate of a virus was isolated is used in the name (e.g. Bunyamwera virus). The current rules forbid the form 'host name' plus 'virus' (Rule 23). It is self-evidently a fruitless exercise to attempt to harmonize these different approaches.

(d) Typography

Virus taxonomy is somewhat idiosyncratic in its typography, but rules for this have evolved from the needs of publishing virologists rather than by obscure tradition. Taxon names when used formally (e.g. family *Myoviridae*) are capitalized and italicized. In their adjectival form no distinction is needed (e.g. the filovirus Ebola). At present, names of species are exceptions to these rules. In some instances, capitals are used when the virus name contains the Latin name, but not italicized, of the principal host (e.g. *Autographa californica* nucleopolyhedrovirus). However, proposals being debated currently by the EC seek to change this to obtain more uniformity.

(e) Virus names and the BioCode

An initiative from the IUMS and the International Union of Biological Societies (IUBS) has led to the development of a unified Code of Nomenclature for all living things (Greuter *et al.*, 1996). Viruses fall within this field, but as virus nomenclature does not involve the use of latin binomial forms, and there is no law of priority in naming viruses or taxa (ICN, Rule 10), names used in virus taxonomy are treated as exceptions. However, the conventional endings of

these names, *-virales* for orders, *-viridae* for families, *-virinae* for subfamilies and *-virus* for genera, are reserved for use in virus taxonomy.

6. Virus species

What is meant by the term 'virus species' has been debated at length in the last few years. The ICTV has accepted a definition that encapsulates much of what had been done, at least in some disciplines, intuitively by virologists previously (Van Regenmortel, 1989) [22]. The definition accepted by ICTV is 'A virus species is a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche' (Van Regenmortel, 1990) [23]. The current ICTV Report lists some names of species following the descriptions of the genera, and sometimes families, to which they belong. The need now is to illustrate to virologists how it is that certain viruses are considered as species whereas others are considered as strains of the one species. The criteria are discussed in some detail by Van Regenmortel *et al.* (1997) [24] and it is unnecessary to repeat the discussions here. The article gives examples of lists of characters from which a score of relatedness between two virus isolates can be calculated and a decision made as to the degree of relatedness.

The international union of microbiological societies

The International Union of Microbiological Societies (IUMS) tasks the International Committee on Taxonomy of Viruses (ICTV) to make decisions on matters of virus classification and taxa nomenclature (Khan *et al.*, 2011). According to those, virus classification into taxa and taxa nomenclature are subject to rules (the Rules) set out in an international code (the Code). The most recent version of this International Code of Virus Classification and Nomenclature (ICVCN) is available in the latest, 9th, ICTV Report, which was published in 2011 [8].

The ICVCN is organized in three major parts: Section 1 outlines the "Statutory basis for the International Committee on Taxonomy of Viruses (ICTV)". Section 2 describes the "Principles of nomenclature". Finally, section 3 outlines the "Rules of Classification and Nomenclature" [capitalization or lack thereof is identical to the headlines in the code] [8]. In contrast to the International Code of Zoological Nomenclature Code (ICZN Code; <http://iczn.org>), the International Code of Nomenclature of Bacteria (ICNB; <http://www.ncbi.nlm.nih.gov/books/NBK8817/>), and the International Code of Nomenclature for Algae, Fungi, and Plants (ICNAFP), the ICVCN is still short and much less elaborate. This article is the second of a series of manuscripts (Kuhn *et al.*, 6) that outlines proposals and suggestions that could make the ICVCN a more precise instrument for virus taxonomy, while at the same time decreasing currently existing confusion among laboratory virologists regarding the use of the Rules put forth in the Code. In particular, this article addresses the ongoing confusion among laboratory virologists regarding the difference of taxa (concepts of the mind) and viruses (physical entities), an important difference that the ICTV and the Code maintains. The current Code addresses only the classification of viruses into taxa and the nomenclature of taxa, but not the nomenclature of viruses or their sub classification.

Recently, an updated version of the Code was proposed and accepted by the ICTV Executive Committee (TaxoProp 2011.002a-uG.A.v8;

http://talk.ictvonline.org/files/proposals/taxonomy_proposals_general1/m/gen04/4418.aspx). This new Code does not address the specific problem of differentiating viruses from taxa systematically, but addresses other important issues. Since the ICTV Executive Committee-accepted new version of the Code has yet to be ratified (and because ratification is not guaranteed), proposals made here are in regard to both the valid current Code and the forthcoming new version that might supersede it.

Recent developments

Experience in producing the 8th [18] and 9th [19] Reports (published in 2005 and 2012, respectively) convinced the EC that it was no longer desirable to produce these as physical volumes through a commercial publisher. Although the printed Reports have served the community well for nearly 50 years, this approach now has significant disadvantages, including the work involved in producing a large book (the 9th Report has nearly 1500 pages), the price of the volume and the inevitable delays between writing and publication, especially at a time when both science and virus taxonomy are advancing rapidly. Historically, the costs of running the ICTV (largely for holding the annual EC meeting) have been met by grants from IUMS, the American Society of Virology and the Microbiology Society (UK), together with royalties from sales of the published Reports. There have been minimal funds to use for technological and other developments, and the EC Members were therefore delighted when, in 2015, three of their number were awarded a five-year Bioresource Grant by the Wellcome Trust (UK). This support commenced at the beginning of 2016 and is now being used to drive substantial changes to the operations and public contributions of the ICTV, as described below.

Open access resources

The ICTV Taxonomy Report is being made freely available at <http://www.ictvonline.org/Report> in a greatly enhanced format, starting in January 2017. Over a three-year cycle, the Study Groups will update the information in the chapters of the 9th Report and produce chapters for newly created taxa. In addition to internal links to the latest ICTV taxonomic database, bi-directional links will also be provided to external databases. Following an agreement with the Microbiology Society (UK), summaries of the online Report chapters (usually corresponding to individual families), also prepared by the Study Groups, are being published as citable, freely available articles in the Journal of General Virology and indexed in literature search engines such as PubMed. These summaries will include links to the full online Report, and thus will provide definitive citations to the more comprehensive information available therein.

Bio-informatics resources

To facilitate the development of taxonomy and the involvement of the virology community in this process, the ICTV web site will provide bioinformatics and database resources designed to simplify the processes involved in generating and approving taxonomic proposals. To enhance the rigor with which virus taxonomy is advanced, the web site will also provide information and tools aimed at ensuring data consistency and integrity, including standardized alignments for representative sequences from virus groups (typically, families) produced in collaboration with the Study Groups. Collectively, these resources are expected to greatly simplify

the submission and ratification of taxonomic proposals, and also significantly enhance the ability of the ICTV to keep taxonomy abreast of virus discovery.

Conclusion

The ICTV publishes at intervals a Report which describes the current taxonomy with details of properties of the taxa, the discriminatory features and a listing of viruses which belong to the particular taxa. The current report is Tenth and next is due to be published in 2021.

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