Virus taxonomy – 1997

M. A. Mayo[1] and C. R. Pringle[2]

[1] Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK

[2] Biological Sciences Department, University of Warwick, Coventry CV4 7AL, UK

1. 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 (= taxa), is a relatively recent endeavour. 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 six Reports reviewing the state of virus taxonomy, the latest of which was published in 1995 (Murphy *et al.*, 1995). These Reports have reflected the huge increase in the amount of fundamental information that has accrued in the last 24 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. Thus, taxonomy must adapt to continuing advances in knowledge, but in as conservative a manner as possible.

Since publication of the Sixth Report of the ICTV (Murphy *et al.*, 1995), more taxa and changes to taxa have been ratified, both at the International Congress of Virology in Jerusalem in 1996, and subsequently by postal ballot of the full membership of the ICTV. Most of the changes have been published in Virology Division News (Pringle, 1996, 1997). The purpose of this review is (1) to re-state the overall taxonomy of viruses to include these changes, (2) to explain to virologists how ICTV operates on their behalf, and (3) to illustrate some of the current areas of taxonomic debate in answer to the criticisms 'why is taxonomy not up-to-date?' or even 'what use is taxonomy for virology?'.

2. The current scheme

The four principal taxa recognized by the ICTV are Species, Genus, Family and Order. The last two are not always used as, particularly for Orders, it is sometimes judged that the necessary relatedness or distinctiveness among the lower taxa

Author for correspondence: Mike Mayo.

Fax +1382 564246. e-mail mmayo@scri.sari.ac.uk

are not sufficiently clear. Intermediate taxa, such as sub-family, are used in some instances but only when their use solves a difficult taxonomic problem, as allowed by Rule 29 of the International Code of Nomenclature (ICN) (see Section 7). The ICTV does not classify viruses below the level of species (ICN, Rule 3), mainly because this would require detailed knowledge of the species concerned and is also often driven by particular needs, such as the discrimination of, for example, pathovars or serotypes of plant viruses, or serogroups of animal viruses.

At present, viruses are classified into 184 genera. Of these, 161 are classified in 54 families. For the remainder, there are no families as it is not yet clear how the genera can best be clustered into distinctive higher taxa. Two groups of families have been classified in Orders. The families *Paramyxoviridae*, *Rhabdoviridae*, *Filoviridae* and *Bornaviridae* constitute the Order *Mononegavirales* (Pringle, 1991*a*, 1995) and the families *Coronaviridae* and *Arteriviridae* constitute the Order *Nidovirale*s (Cavanagh, 1997; De Vries *et al.*, 1997). Both are instances in which supra-family relatedness is obvious. The policy being followed at the moment is that the taxon Order should only be recognized when it seems highly probable that the constituent families share a common phylogeny (Murphy *et al.*, 1995) (see Section 7).

The current scheme of classification for Genera, Families and Orders is shown in Fig. 1. Many of the details are as published in the Sixth Report of the ICTV (Murphy *et al.*, 1995). Taxa described or named since this publication are denoted by an asterisk in Fig. 1. As in the Sixth Report of the ICTV, the families have been grouped in Fig. 1 according to their genome types: dsDNA, ssDNA, dsRNA, negative-sense ssRNA, positive-sense ssRNA and those whose replication involves reverse transcription. These *de facto* higher taxa are obvious and useful. But they have not been described as formal taxa because such a classification would suggest parallelism, such that, for example, the cluster of all viruses with dsDNA genomes is predicted to be at a similar taxonomic level to the cluster of all viruses with dsRNA genomes. There is no such suggestion; thus the division is only one of convenience.

3. 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,

(a)

ds DNA

Myoviridae

"T4-like"
"P1-like" *
"P2-like" *
"Mu-like" *
"SPO1-like" *
"phiH-like" *

Siphoviridae

"lambda-like"
"psiM-like" *
"T5-like" *
"T1-like" *
"c2-like" *
"L5-like" *

Podoviridae

"T7-like"
"ø 29-like" *
"P22-like" *

Tectiviridae

Tectivirus

Corticoviridae

Corticovirus

Lipothrixviridae

Lipothrixvirus

Plasmaviridae

Plasmavirus

Fuselloviridae

Fusellovirus

Phycodnaviridae

Phycodnavirus

Rudiviridae *

Rudivirus *

Rhizidiovirus

Poxviridae

Orthopoxvirus
Parapoxvirus
Avipoxvirus
Suipoxvirus
Molluscipoxvirus
Capripoxvirus
Leporipoxvirus
Yatapoxvirus
Entomopoxvirus A
Entomopoxvirus B
Entomopoxvirus C

Iridoviridae

Iridovirus
Chloriridovirus
Ranavirus
Lymphocystivirus

Polydnaviridae

Ichnovirus
Bracovirus

"African swine fever-like"

Herpesviridae

Simplexvirus
Varicellovirus
Cytomegalovirus
Muromegalovirus
Roseolovirus
Lymphocryptovirus
Rhadinovirus

Papovaviridae

Polyomavirus
Papillomavirus

Adenoviridae

Mastadenovirus
Aviadenovirus

Baculoviridae

Nucleopolyhedrovirus
Granulovirus

ssDNA

Microviridae

Microvirus
Spiromicrovirus
Bdellomicrovirus
Chlamydiamicrovirus

Inoviridae

Inovirus
Plectrovirus

Circoviridae

Circovirus

Geminiviridae

Mastrevirus *
Curtovirus *
Begomovirus *

Parvoviridae

Parvovirus
Erythrovirus
Dependovirus
Iteravirus
Contravirus
Densovirus

(b)

Reverse Transcribing

Retroviridae

Lentivirus
"mammalian type B"
Spumavirus
"avian type C"
"mammalian type D"
"mammalian type C"
"BLV-HTLV"

Hepadnaviridae

Orthohepadnavirus
Avihepadnavirus

Caulimoviridae *

Caulimovirus
"SoyCMV-like" *
"CaVMV-like" *
Badnavirus
"RTBV-like" *

dsRNA

Cystoviridae

Cystovirus

Totiviridae

Totivirus
Giardiavirus
Leishmaniavirus

Partitiviridae

Partitivirus
Chrysovirus
Alphacryptovirus
Betacryptovirus

Hypoviridae

Hypovirus

Birnaviridae

Entomobirnavirus
Aquabirnavirus
Avibirnavirus

Reoviridae

Orthoreovirus
Orbivirus
Rotavirus
Aquareovirus
Coltivirus
Phytoreovirus
Fijivirus
Oryzavirus
Cypovirus

Negative Sense ssRNA

Mononegavirales

Paramyxoviridae

Paramyxovirus
Morbillivirus
Rubulavirus
Pneumovirus
"TRTV-like" *

Rhabdoviridae

Lyssavirus
Vesiculovirus
Ephemerovirus
Cytorhabdovirus
Nucleorhabdovirus

Filoviridae

Filovirus

Bornaviridae *

Bornavirus *

Orthomyxoviridae

Influenzavirus A *
Influenzavirus B *
Influenzavirus C
Thogotovirus *

Bunyaviridae

Bunyavirus
Phlebovirus
Nairovirus
Hantavirus
Tospovirus

Arenaviridae

Arenavirus

Tenuivirus
Deltavirus

Fig. 1. For legend see facing page.

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). 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* (see Section 8), 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
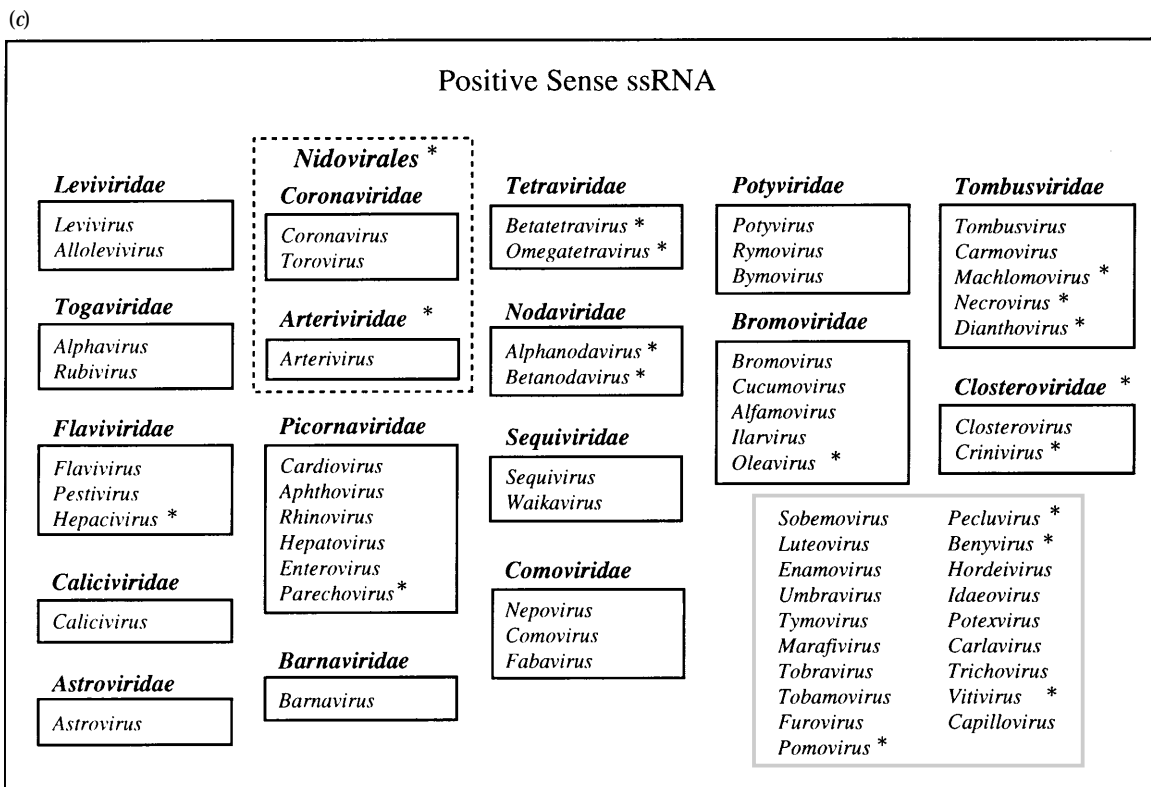
(c)

Fig. 1. Current state of virus taxonomy. The figure is a listing of virus taxa organized by genome type (outer boxes). Genera are listed in boxes below the appropriate family names. Families which make up Orders are boxed within a dashed line. Division of families into sub-families are indicated by horizontal dashed lines. Genera in untitled grey boxes are those not yet assigned to families. Where taxa, names or classifications have been decided since the publication of the Sixth Report of the ICTV (Murphy *et al.*, 1995), they are indicated by asterisks.

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 non-essential functions (Pringle, 1991*a*). The family *Paramyxoviridae* was split into two sub-families, the *Paramyxovirinae* and the *Pneumovirinae*, in recognition of the relative distinctiveness of the mammalian pneumoviruses 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).

Several recent observations have complicated this initial scheme of the taxonomy of the monopartite negative-strand RNA viruses. Firstly, an avian pneumovirus was discovered which lacks the usual inversion of the gene order of mammalian pneumoviruses, suggesting that the pneumoviruses 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 pneumoviruses (Randhawa *et al.*, 1997). 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-like virus), 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). Also, genomes can tolerate the insertion of foreign genes (Mebatsion *et al.*, 1996), and some indigenous genes (e.g. SH and G genes of mammalian pneumoviruses) appear to be dispensable (Georgiou *et al.*, 1997). 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.

4. The decision-making structure of ICTV

ICTV derives its authority from the Virology Division of the International Union of Microbiological Societies (IUMS) which represents the interests of member microbiological societies. ICTV comprises members nominated by countries with microbiological societies affiliated to IUMS, Life Members elected by ICTV, and the elected membership of the Executive Committee (EC). Decisions of ICTV are made at plenary sessions at International Congresses and by postal voting. Statutes (Murphy *et al.*, 1995) define the constitution of ICTV, how it operates and how it is constituted.

ICTV is advised by its EC, which consists of elected officials among whom are the Chairs of Subcommittees representing major fields of virology: vertebrate, invertebrate, plant, fungal and bacterial. Fig. 2 summarizes the composition of the component parts of ICTV. The EC is elected every 3 years with no position being occupied for more than 6 years by one scientist and, except for the Secretaries, no scientist being a member for more than 12 consecutive years. Subcommittees usually consist of members, some or all of whom chair Study Groups concerned with particular taxa or groups of taxa. There are about 50 Study Groups currently but this number changes as needs dictate, for example by the discovery of novel types of virus or of hitherto unrecognized relationships between Study Group interests. Study Groups make proposals for changes to taxonomy within their fields of interest to accommodate new information as it emerges. Proposals approved by the Subcommittees go to the EC for consideration and, after approval, are presented to ICTV for ratification.
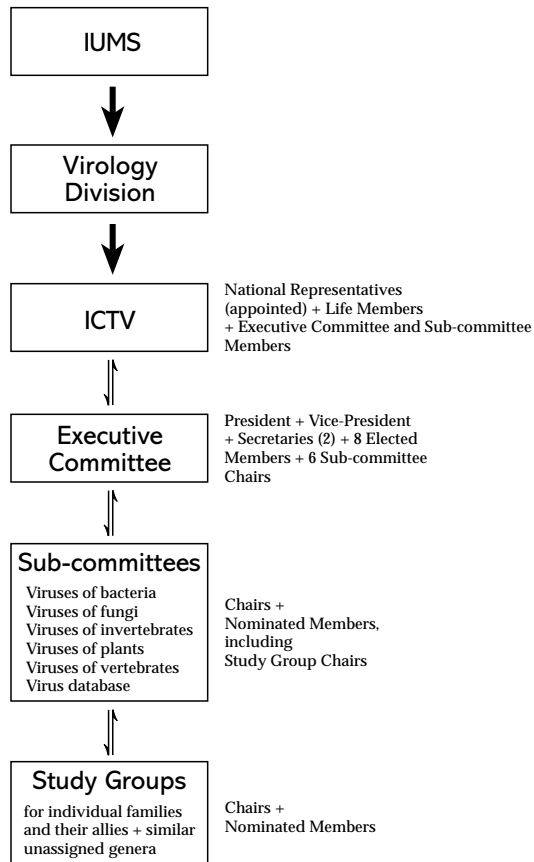
Fig. 2. Structure of the ICTV and its position in the organization of IUMS. The compositions of the ICTV Committees and Groups are indicated to the right. All members are elected unless it is indicated as otherwise.

Proposals from outside the ICTV structure are normally referred to the appropriate Study Group for discussion, or failing this, to the appropriate Subcommittee.

5. 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). 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). 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* (Fig. 1). 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*.

653

(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). 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).

The current ICTV Report (Murphy *et al.*, 1995) 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) 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. Table 1 is taken from this article and illustrates this list for the plant virus families *Potyviridae* and *Geminiviridae*. The characters considered are not the same for the two families and the quantitative values assigned to the characters (e.g. percentage sequence identity in a particular gene) also differ between the two families. Greater differences can be expected between lists for families of viruses with different genome nucleic acid or that infect different types of host. It is hoped that the Seventh ICTV Report, scheduled for publication in 1999, will contain lists of characters relevant to particular genera and thereby allow virologists to assess taxonomic relatedness in an authoritative manner. Nevertheless, there is a measure of subjectivity in this exercise. But this is intrinsic to making taxonomic decisions; 'all taxonomy is opinion' (Calisher *et al.*, 1995).

7. Virus evolution and virus classification: is phylogeny a receding goal?

Inherent in being a biologist, and most virologists are biologists, is the conviction that taxonomic clustering of similar individuals into a taxon reflects the evolutionary history of those individuals. Thus it is felt that, given three broadly similar organisms (A, B and C), if A is relatively similar to B, and both differ a lot from C (given careful choice of discriminatory properties), A and B arose by divergent evolution from an ancestor that itself arose at an earlier date from an ancestor shared with C. Put succinctly, there is a feeling that taxonomy should represent phylogeny.

Before nucleotide sequencing resulted in detailed analyses of the structures of virus genomes, viruses were described by using relatively few characters and there were few attempts to deduce the phylogeny of viruses and virus taxa. The ability to determine nucleotide sequences of genomes has greatly changed this. Gene arrangements, and in particular gene sequences, have allowed many authors to make comparative studies that have generated many speculations based on phylogenetic trees linking some viruses and discriminating between others. Where viruses are known to be related, for example when they are classified in the same genus, such analyses are very suggestive. But the problem for this approach is precisely in the area for which most hope was held out, that is the comparison of distantly related groups. Some genes, especially those for RNA-dependent RNA polymerase

Table 1. Characters which would demarcate virus isolates as distinct species in the families *Potyviridae* and *Geminiviridae* (Van Regenmortel *et al.*, 1997)

Character	*Potyviridae*	*Geminiviridae*
Genome features	–	Different numbers of genome components
	–	Different organization of genes in the genome
	–	No transcomplementation of gene products
	–	No pseudorecombination between components
Genome sequence	< ca. 85 % identical over whole sequence	< ca. 90 % identical in coat protein sequence
	< ca. 75 % identical in 3′ noncoding sequence	–
Protein features	Different polyprotein cleavage sites	–
	Virions react differently with key antibodies	Virions react differently with key antibodies
	< ca. 90 % identical in coat protein sequence	< ca. 90 % identical in coat protein sequence
Transmission	Different vector species	Different vector species
	Different seed transmissibility	–
Effects in infected tissue	Different inclusion body morphology	–
	No cross-protection effects	–
	–	Different tissue tropism
Host range	Different in key species	Different in key species

(RDRP), are sufficiently similar for comparisons between viruses in distinct genera, or even families, to yield values of similarity greater than that for sequences known to be unrelated. The polymerase-based phylogenetic trees thus generated suggested, for example, a putative link between the polymerases of plant and animal viruses not previously suspected (Koonin & Dolja, 1993). These trees are reasonable candidates for a representation of the relatedness among viruses and of their phylogenetic history. But the complication is that the trees are derived from the sequences of a single gene whereas the deduction of a phylogenetic relationship is made for the whole virus. The reliability of some relationships deduced from trees has recently been questioned on statistical grounds (Zanotto *et al.*, 1996). Nevertheless the most salient point is that trees deduced for one gene do not necessarily link viruses in the same way as trees deduced for a different gene.

One explanation for the above is that virus genomes, particularly RNA virus genomes, seem often to have evolved in a 'modular' fashion by acquiring genes or blocks of genes as intact pieces of nucleic acid from the genomes of other viruses (Simon & Bujarski, 1994; Lai, 1995), or from the genomes of their hosts (Meyers *et al.*, 1995). There is evidence that this process of recombination has been involved in the evolution of genomes of viruses in at least eight families of viruses, which infect all the major classes of host (Lai, 1995).

The application of polymerase-based phylogenetic trees to classification generally has in some instances been directly confounded by what has been discovered in virus genomes. A clear example is the classification of certain plant viruses with ssRNA genomes in the genus *Luteovirus*. These viruses share many biological and physico-chemical features as well as sequence characters, but the RDRP of luteoviruses are either of two types from evidently distinct lineages (Mayo & Ziegler-Graff, 1995). It seems clear that the evolution of luteovirus genomes has involved recombination which exchanged one type of RDRP for another (Gibbs & Cooper, 1995). The current view of the *Luteovirus* specialists is that it is unreasonable to separate viruses with either of the two types of RDRP by much more distance than that between genera in a single family (D'Arcy & Mayo, 1997). It is thus impossible for classification of these viruses to be based on polymerase lineages.

In contrast, some of the large dsDNA genome viruses such as the herpesviruses (McGeoch *et al.*, 1995) and the baculoviruses (cited in Carstens, 1997) exhibit clear evidence of co-evolution with their host organisms. For example, the application of molecular phylogeny analysis to the herpesviruses has both confirmed the ancient origin of these viruses and provided a timescale for their evolution. The branching pattern linking the three sub-families of the mammalian herpesviruses is congruent with that of their corresponding

host lineages, strongly suggesting an independent confirmation of the current virus taxonomy. Assuming a constant molecular clock, the sub-families *Alphaherpesvirinae*, *Betaherpesvirinae* and *Gammaherpesvirinae* appear to have diverged $1\cdot8$ to $2\cdot2 \times 10^8$ years ago, that is about the time of emergence of mammals from mammal-like reptiles. The major sub-lineages within these sub-families probably arose before the radiation of placental mammals some 6 to 8×10^7 years ago. Palaeontological dating of host lineages has suggested that the contemporary virus lineages within the *Alphaherpesvirinae* have evolved by a process of co-speciation of viruses with their mammalian hosts (McGeoch & Cook, 1994).

In summary, if major recombination has never occurred in the ancestry of groups of viruses, then classification based on sequence comparisons, usually of polymerase genes, is possible. But this cannot be applied universally to all viruses.

8. Outputs

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 the sixth (Murphy *et al.*, 1995). The next is due to be published in 1999. When there is some debate about particular taxonomic issues, or when taxa are approved at times other than just before publication of a Report, these proposals and decisions are published in the Virology Division News Section of *Archives of Virology*.

The ICTV is also in the process of organizing a database for viruses (Pringle, 1991*b*; Büchen-Osmond, 1997). This will be prepared using DELTA format (Buechen-Osmond & Dallwitz, 1996). A less detailed and less interactive source of taxonomic information is the Internet. The address to consult is http://www.ncbi.nlm.nih.gov/ICTV/

9. Murphy's Law

Many of the considerable developments in virus taxonomy and in the organization of ICTV that have happened over the last few years have been in substantial measure the result of the drive and enthusiasm of the past-President, Fred Murphy. His inputs have been the catalyst, and in many cases the energy source, for the achievements and the progress made. In particular, there has been a significant increase in the extent of democracy in the organization of the ICTV, there have been important developments in the constitutional arrangements for balancing quick decision-making with adequate consultation, and the ICTV Report has been made an authoritative source of data concerning all virology. The authors were part of the Executive Committee that Fred led, and it is a pleasure to be able to acknowledge these major contributions to virology formally.

References

Ball, L. A., Pringle, C. R., Perepelitsa, V., Brown, F. & Wertz. G. W. (1997). Phenotypic consequences of rearranging the genes of vesicular stomatitis virus. *Proceedings of the National Academy of Sciences, USA* (submitted for publication).

Büchen-Osmond, C. (1997). Further progress in ICTVdB, a universal virus database. *Archives of Virology* **142**, 1735–1739.

Buechen-Osmond, C. & Dallwitz, M. (1996). Towards a universal virus database – progress in the ICTVdB. *Archives of Virology* **141**, 392–399.

Carstens, E. B. (1997). Out of chaos order emerges. A report of a workshop held during the Society for Invertebrate Pathology 30th Annual Meeting. *Archives of Virology* **142** (in press).

Calisher, C. H., Horzinek, M. C., Mayo, M. A., Ackermann, H. W. & Maniloff, J. (1995). Sequence analyses and a unifying system of virus taxonomy: consensus via consent. *Archives of Virology* **140**, 2093–2099.

Cavanagh, D. (1997). Nidovirales: a new order comprising *Coronaviridae* and *Arteriviridae*. *Archives of Virology* **142**, 629–633.

D'Arcy, C. J. & Mayo, M. A. (1997). Proposals for changes in luteovirus taxonomy and nomenclature. *Archives of Virology* **142**, 1285–1287.

De Vries, A. A. F., Horzinek, M. C., Rottier, P. J. M. & De Groot, R. J. (1997). The genome organization of the Nidovirales: similarities and differences between arteri-, toro- and coronaviruses. *Seminars in Virology* **8**, 25–47.

Georgiou, A. F., Buonagurio, A., Adamus, J. E., Randolph, V. B., Whitehead, S. S., Murphy, B. R., Udem, A. & Sidhu, M. S. (1997). Human respiratory syncytial virus (RSV) SH and G proteins are not essential for virus infectivity. Molecular characterisation of a cold-passaged, attenuated RSV subgroup B mutant. Abstract 261, *Proceedings of the Negative Strand Virus Conference*, Trinity College, Dublin, Ireland, September 1997.

Gibbs, M. J. & Cooper, J. I. (1995). A recombinational event in the history of luteoviruses, probably induced by base-pairing between the genomes of two distinct viruses. *Virology* **206**, 1129–1132.

Greuter, W., Hawksworth, D. L., McNeill, J., Mayo, M. A., Minelli, A., Sneath, P. H. A., Tindall, B. J., Trehane, P. & Tubbs, P. (the IUBS/IUMS International Committee for Bionomenclature) (editors) (1996). Draft BioCode: the prospective international rules for the scientific names of organisms. *Taxon* **45**, 349–372.

Hawksworth, D. L. (1997). The need for a new Bionomenclature. In *The New Bionomenclature: The BioCode Debate*. Biology International, Special Issue no. 34, pp. 12–13. Edited by D. L. Hawksworth.

Koonin, E. V. & Dolja, V. V. (1993). Evolution and taxonomy of positive strand RNA viruses: implications of comparative analysis of amino acid sequences. *Critical Reviews in Biochemistry and Molecular Biology* **28**, 375–430.

Lai, M. M. (1995). Recombination and its evolutionary effect on viruses with RNA genomes. In *Molecular Basis of Virus Evolution*, pp. 110–132. Edited by A. Gibbs, C. H. Calisher & F. Garcia-Arenal. Cambridge: Cambridge University Press.

McGeoch, D. J. & Cook, S. (1994). Molecular phylogeny of the *Alphaherpesvirinae* subfamily and a proposed evolutionary timescale. *Journal of Molecular Biology* **238**, 9–22.

McGeoch, D. J., Cook, S., Dolan, A., Jamieson, F. E. & Telford, E. A. (1995). Molecular phylogeny and evolutionary timescale for the family of mammalian herpesviruses. *Journal of Molecular Biology* **247**, 443–458.

Mayo, M. A. (1996). Recent revisions of the rules of virus classification and nomenclature. *Archives of Virology* **141**, 2479–2484.

Mayo, M. A. & Ziegler-Graff, V. (1996). Molecular biology of luteoviruses. *Advances in Virus Research* **46**, 416–468.

Mebatsion, T., Schnell, M. J., Cox, J. H., Finke, S. & Conzelmann, K. K. (1996). Highly stable expression of a foreign gene from rabies virus vectors. *Proceedings of the National Academy of Sciences, USA* **93**, 7310–7314.

Meyers, G., Tautz, N. & Thiel, H.-J. (1995). Cellular sequences in viral genomes. In *Molecular Basis of Virus Evolution*, pp. 91–102. Edited by A. Gibbs, C. H. Calisher & F. Garcia-Arenal. Cambridge: Cambridge University Press.

Murphy, F. A. , Fauquet, C. M., Bishop, D. H. L., Ghabrial, S. A., Jarvis, A. W., Martelli, G. P., Mayo, M. A. & Summers, M. D. (editors) (1995). *Virus Taxonomy*. *Sixth Report of the International Committee on Taxonomy of Viruses*. Vienna & New York: Springer-Verlag.

Pringle, C. R. (1991 *a*). The Order *Mononegavirales*. *Archives of Virology* **117**, 137–140.

Pringle, C. R. (1991 *b*). The 20th Meeting of the Executive Committee of ICTV. Virus species, higher taxa, a universal database and other matters. *Archives of Virology* **119**, 303–304.

Pringle, C. R. (1995). The order *Mononegavirales*: evolutionary relationships and mechanisms of variation. In *Molecular Basis of Virus Evolution*, pp. 426–437. Edited by A. Gibbs, C. H. Calisher & F. Garcia-Arenal. Cambridge: Cambridge University Press.

Pringle, C. R. (1996). Virus taxonomy 1996 – a bulletin from the Xth International Congress of Virology in Jerusalem. *Archives of Virology* **141**, 2251–2256.

Pringle, C. R. (1997). The Order *Mononegavirales* – current status. *Archives of Virology* **142** (in press).

Pringle, C. R. & Easton, A. J. (1997). Monopartite negative strand RNA genomes. *Seminars in Virology* **8**, 49–57.

Randhawa, J. S., Marriott, A. C., Pringle, C. R. & Easton, A. J. (1997). Rescue of synthetic mini-replicons establishes the absence of the NS1 and NS2 genes from avian pneumoviruses. *Journal of Virology* **71**, 9849–9854.

Simon, A. E. & Bujarski, J. J. (1994). RNA–RNA recombination and evolution in virus-infected plants. *Annual Review of Phytopathology* **32**, 337–362.

Van Regenmortel, M. H. V. (1989). Applying the species concept to plant viruses. *Archives of Virology* **104**, 1–17.

Van Regenmortel, M. H. V. (1990). Virus species, a much overlooked but essential concept in virus classification. *Intervirology* **31**, 241–254.

Van Regenmortel, M. H. V., Bishop, D. H. L., Fauquet, C. M., Mayo, M. A., Maniloff, J. & Calisher, C. H. (1997). Guidelines to the demarcation of virus species. *Archives of Virology* **142**, 1505–1518.

Wertz, G. W., Perepelitsa, V. & Ball, L. A. (1997). Attenuation of virulence of a monopartite negative strand RNA virus by rearrangement of gene order. *Cell* (submitted for publication).

Zanotto, P. M. de A., Gibbs, M. J., Gould, E. A. & Holmes, E. C. (1996). A re-evaluation of the higher taxonomy of viruses based on RNA polymerases. *Journal of Virology* **70**, 6083–6096.