A CRITICAL APPRAISAL of VIRAL TAXONOMY

R. E. F. Matthews

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PREFACE

By the early 1960s many hundreds of viruses had been found infecting vertebrates, invertebrates, plants, and bacteria. The classification and nomenclature of these agents were in a chaotic state. At a Microbiology Congress in Moscow in 1966 the International Committee for Nomenclature of Viruses was launched. Many problems were encountered, particularly in the early years, but steady progress was made. By 1981, 54 virus families and groups, with a total of 1372 member viruses, had been delineated and had received formal international approval. In spite of this progress many problems remain for the future.

The overall aim of this volume is to review critically the current state of, and future prospects for developments in viral taxonomy. Most of the contributors have recently had substantial periods of service on the Executive Committee and subcommittees of the International Committee on Taxonomy of Viruses (ICTV) as follows:

H. -W. Ackermann (3 years as vice-chairman and 6 years as chairman of the Bacterial Virus Subcommittee); J. G. Atherton (6 years as chairman of the Code and Data subcommittee); K. W. Buck (6 Years as a member of the Fungal Virus subcommittee and 1 year as chairman); R. I. B. Francki (3 years as a member of the Plant Virus subcommittee and 6 years as chairman); J. F. Longworth (3 years as a member of Executive Committee and the Invertebrate Virus subcommittee); R. E. F. Matthews (6 years as President of the ICTV); F. A. Murphy (3 years as vice-chairman and 6 years as chairman of the Vertebrate Virus subcommittee). Chairmen of subcommittees were also *ex officio* members of the Executive Committee.

All these workers except K. W. Buck and J. F. Longworth retired from the ICTV Executive Committee in August 1981. It should be stressed that the views express in each chapter are those of the individual author. They are not necessarily shared either by the editor, or by the ICTV.

In the first chapter I have outlined the historical development of the subject, emphasizing the difficulties along the way and the extent to which these have been overcome. The chapter concludes with a summary of the state of viral taxonomy at August 1981. Chapters 2 to 6 consider past, present, and future problems that are particularly relevant for the taxonomy of viruses infecting vertebrates, plants, bacteria, invertebrates, and fungi. In Chapter 7, J. A. Dodds gives a brief account of the structure and biology of the new viruses and virus-like particles being found in eukaryotic algae and in protozoa. The taxonomy of these agents poses significant problems. Chapter 8 summarizes the progress that has been made in developing a universal system for the collection, and computer-based storage and retrieval of virus data. Last, Chapter 9 outlines my personal views on the future prospects for viral taxonomy, with particular emphasis on the difficult problems associated with the delineation and naming of virus species.

I wish to thank all the contributors for their ready cooperation in the production of this volume. I thank particularly the following colleagues who read and commented upon parts or all of the manuscripts for my own contributions: H. -W. Ackermann, A. R. Bellamy, D. W. Dye, F. Fenner, R. I. B. Francki, A. J. Gibbs, B. D. Harrison, D. W. Kingsbury, J. F. Longworth, J. Maurin, F. A. Murphy. H. G. Pereira, and P. Wildy.

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He has published 130 research papers mainly in the field of plant virology, together with two books in this field. From 1974 to 1981 he was President of the International Committee for Taxonomy of Viruses and was editor of two reports for the committee published in 1979 and 1982. He was made a life member of the organization in 1981. He is a member of the Society for General Microbiology and the Biochemical Society of London. He is a Fellow of the New Zealand Institute of Chemists and the Royal Society of New Zealand. In 1974 he was elected a Fellow of the Royal Society of London.

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Chapter I

THE HISTORY OF VIRAL TAXONOMY

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I. INTRODUCTION

Viruses have been found in almost all the major groups of prokaryotic and eukaryotic organisms. The number of distinct viruses that have been described cannot be ascertained with any precision, but the total must be several thousand. There are over 2000 descriptions of viruses infecting bacteria alone. Man has an innate desire to classify and name all of the natural objects which he studies, and viruses are no exception. However, there are many different possible ways of classifying and naming biological objects, and judgments must be made that do not have a strictly scientific basis. Thus there is ample room for differences of opinion, emotional attachment to a particular point of view, and unwillingness to compromise. For these reasons the development of viral taxonomy has been marked by some stormy interludes. In this introductory chapter the development of viral taxonomy over the past half century or so will be outlined and the state the subject had reached at the end of the Fifth International Congress for Virology in Strasbourg, 1981, will be summarized.

The historical development can usefully be divided into four periods as follows:

1. The period up to 1961. This period was characterized by premature efforts on the part of individual virologists to establish their particular scheme, accompanied by slow-moving and largely ineffective international cooperation.
2. 1962-1966. In this period important events took place which led up to the meetings held during the International Congress for Microbiology in Moscow in 1966, and to the establishment of the International Committee on Nomenclature of Viruses (I.C.N.V.).
3. 1966-1970. The first period of I.C.N.V., under the 4-year presidency of Wildy, was a critical one. The policy decisions made and the taxonomic work carried out laid the foundations for further development of a universal taxonomy of viruses based on international and interdisciplinary cooperation.
4. 1971-1981. This period was mainly one of development and consolidation.

II. THE PERIOD UP TO 1961

From the very beginnings of virology, names have been given to viruses as they were discovered and described. For viruses infecting animals and plants most of these names were trivial or vernacular, and commonly included an important host or an important disease symptom as part of the name. Bacterial viruses were commonly given code symbols such as T1 or C16 sometimes in a quite haphazard fashion. However, some workers in this period provided their viruses with more high-sounding names. For example d'Herelle[1] applied the name *Bacteriophagum intestinale* to a culture of a bacterial virus (or viruses) which he studied, but names such as this were seldom of any lasting significance.

As far as virus classification was concerned in this period, the custom developed of grouping viruses according to the kind of host—animal, plant, or bacterial. The reasons for this were mainly historical and practical. Most virologists worked with viruses replicating (or thought to replicate) in only one kind of host. Doubts concerning this system arose in the 1940s when it became apparent that some plant viruses could replicate in their insect vectors. During the period up to 1961 attempts were made both by individuals and by organizations to introduce more detailed systems of classification and nomenclature. I will deal first with efforts made by individual virologists. I can find no record of any phage worker attempting a comprehensive classification of bacterial viruses in this period.

A. Individual Plant Virologists

Johnson[2] made the first approach to the problem of classifying plant viruses. He was well aware of the problem. He wrote: "A system of nomenclature for plant viruses is greatly

needed. The present system of applying names on the basis of host attacked or symptoms exhibited is quite inadequate for present needs." He confined his attention to a set of 11 viruses affecting tobacco and other solanaceous hosts. The separation and classification of the viruses described was based on the symptoms (if any) produced on 10 or more different host species, their longevity in vitro, thermal death points, lethal effects of chemicals, and such properties as relative infectivity and length of incubation period. He suggested that properties of the virus in vitro would be more reliable criteria than disease symptoms. He named the viruses with the English name of the host followed by a number, e.g., Tobacco virus 1, Tobacco virus 2, etc.

Using the same naming system, Johnson and Hoggan[3] compiled a descriptive key based on five characters — modes of transmission, natural or differential hosts, longevity in vitro, thermal death point, and distinctive or specific symptoms. About 50 viruses were identified and placed in groups.

Smith[4] outlined a scheme in which the known viruses or virus diseases were divided into 51 groups. Viruses were named and grouped according to the generic name of the host in which they were first found. Successive members in a group were given a number. For example, tobacco mosaic virus was *Nicotiana virus* 1, and there were 15 viruses in the *Nicotiana* virus group. Viruses that were quite unrelated in their basic properties were given names that might have been thought to imply that they were related. Although Smith's list served for a time as a useful catalogue of the known plant viruses, it was not a classification.

Holmes[5] published a classification of plant viruses based primarily on host reactions and methods of transmission. He used a Latin binomial-trinomial system of naming. For example tobacco mosaic virus became *Marmor tabaci*, Holmes. His classification was based on diseases rather than the viruses. The viruses were split into 10 families. The family *Marmoraceae* (the Mosaic group) had a single genus *Marmor* which included 53 of the 89 viruses considered as species by Holmes. This genus contained viruses known even at the time to differ widely in their properties (e.g., tobacco mosaic and tomato bushy stunt viruses). Nevertheless, the Latin binomial system appealed to a number of workers and various modified schemes were put forward.[6-11] The Holmes system received the blessing of the Nomenclature Committee of the American Phytopathological Society.[12] Subsequently Holmes[13] put forward a revised scheme which was published as a supplement in the sixth edition of *Bergey's Manual of Determinative Bacteriology*, which covered all viruses. This version still contained many groupings that were even then obviously inappropriate. These are discussed further below in relation to animal viruses. Hansen[14-16] was the most recent and probably the last individual plant virologist to propose a system for nomenclature and classification. His system for deriving generic names was based on characters of the virus particle, the diseases caused, and the methods of transmission. His system of pseudo-Latinized names would have provided the generic names for a Latinized binomial system.

While the Holmes and similar systems received some support from plant virologists particularly in the U.S., in the main they were ignored. Bawden[17] was a leading critic of the use of disease symptoms in classification. He made an important contribution by suggesting that any permanent classification must be based on the peculiarities of the viruses themselves and not on those of the host plants. He emphasized the importance of serological relationships. He pointed out the widespread existence of virus strains which although closely related on both the physical and chemical properties of the particle and serologically, may cause markedly different diseases. He stated, "it would seem as reasonable to expect to classify flowering plants because of their reactions to a number of viruses as it is to classify viruses by the symptoms they produce in a given number of hosts."

Bawden[17] and Valleau[21] made the useful, but unheeded suggestion that while well-studied viruses might be usefully classified, little-studied entities should be placed aside in a category equivalent to the Fungi Imperfecti. Nevertheless Bawden's published comments and criti-

cisms undoubtedly helped to slow the rush of many plant virologists in the 1940s towards premature classification and nomenclature.

One of the few useful specific contributions made to plant virus taxonomy in this period was that of Brandes and Wetter.[22] They classified elongated rod-shaped plant viruses into 12 groups on the basis of particle morphology, and in particular on the "modal" length of the rods. While some of their subdivisions turned out to be too fine, seven of the groups have survived in the present taxonomy of plant viruses.

B. Individual Animal Virologists

Over the period up to 1961 animal virologists appear not to have felt the necessity to erect comprehensive systems of orderly classification and nomenclature. Would-be taxonomists were warned by Andrewes[23] who wrote, "judgment must be suspended...in the case of the invisible viruses or so-called 'filter-passing' organisms. Here our ignorance is almost complete; they are possibly a heterogeneous group but in the case of creatures which we cannot see and whose very existence is, in many cases, a matter of inference only, it is idle to talk of classification in the usual sense."

However some attempts were made and those classifications that were devised used tissue affinities as the main criterion. Thus Levaditi and Lépine[24] classified some viruses infecting vertebrates into the following eight groups, (1) Ectodermoses (foot-and-mouth disease virus, vesicular stomatitis, ectromelia, vaccinia); (2) Ecto-endodermoses (canary-pox, laryngotracheitis); (3) Mesodermo-endodermoses (fowl plague, and Newcastle disease); (4) Ectodermoses neurotropes (a number of purely neurotropic virus infections); (5) Endodermoses neurotropes (yellow fever); (6) Mesodermoses (lymphogranuloma venereum); (7) Septicémies (influenza, Rift valley fever); (8) Ultravirus neoformatif (Rous sarcoma). This and similar classifications of the period met with little favor.

As far as nomenclature is concerned Goodpasture[25] proposed a generic name *Borreliota* for the Pox group and three specific names within that genus. Apart from such occasional small-scale attempts there was little activity in nomenclature until Holmes[13] proposed his comprehensive system for all viruses. This was an expanded version of his earlier scheme for plant viruses and bacteriophages.[5]

Although the generic and specific names proposed by Holmes were often quite suitable, the scheme was almost completely ignored and rejected by vertebrate virologists. This was because the classification was so bad. Five of the six families in the suborder *Zoophagineae* were based almost entirely on tissue tropisms and symptomatology. These families grouped together viruses with widely differing properties. For example the family *Borreliotaceae* was characterized as follows, "viruses of the Pox group, inducing diseases characterized in general by discrete primary and secondary lesions of the nature of macules, papules, vesicles, or pustules." It included poxviruses, herpes viruses, and viruses of the foot-and-mouth disease virus group.

Andrewes[26] in a discussion on virus classification wrote, "Dr. Holmes is the credit for stimulating great interest in virus taxonomy and nomenclature; his action has also been invaluable — and here I am still trying to be polite — as a glaring example of how not to classify viruses."

In spite of such severe criticisms of Holmes' classification by many leading virologists, others published similar schemes or formal revisions of Holmes.[13] For example, Zhdanov[27] published a classification scheme similar to that of Holmes but omitted the names he used. Breed and Petraitis[28] gave a summary translation in English. Van Rooyen[29] published a formal revision and extension of Holmes' classification of animal viruses. These publications were almost totally ignored by other virologists.

In the period leading up to 1961 Cooper[30] was the last to suggest a basis for the classification of animal viruses. He made an important contribution by suggesting that properties of the

virus particle that are inherently genetically stable should be used to make the primary groupings of viruses. His primary division was on the basis of genome nucleic acid type — DNA or RNA. The DNA viruses were further subdivided on the basis of size and then on ether sensitivity (presence of a lipoprotein membrane). The RNA viruses were further subdivided on the basis of ether sensitivity. This use of properties of the virus particle foreshadowed the classification proposed by Lwoff et al.[31] which is discussed in a later section.

C. Attempts at International Cooperation

I will now turn to the attempts that were made to achieve international cooperation concerning viral taxonomy in the period up to 1961. The earliest attempts were made in conjunction with International Congresses of Botany in 1930 and Microbiology in 1939.

In 1930 an appeal was made before the Fifth International Botanical Congress meeting in Cambridge, England for an internationally agreed-upon viral classification and nomenclature.[32] A committee of five members was formed under the chairmanship of Johnson to propose a standard system of nomenclature with the objective of preventing further wide proliferation and use of synonyms.

A tentative system of nomenclature based on the name of the host with appropriate numbers to indicate the virus species and letters for strain designation was presented to phytopathologists at the Sixth Botanical Congress in Amsterdam in 1935. The report was adopted "in principle" by the Congress, but it was never officially published. The committee was empowered to continue working and to put forward a more complete proposal at the next Congress due to be held in Stockholm in 1940. Six additional virologists were appointed to the committee and by 1939 a 32-page mimeographed prospectus had been circulated to many virus workers for comments and suggestions.

The committee met with the International Microbiological Congress in New York City in September 1939, in the hope that some joint system of virus nomenclature could be agreed upon by animal and plant virologists attending the Congress. On the day of the meeting war was declared in Europe, bringing to an end any attempt at international cooperation concerning viral nomenclature.

The Seventh International Botanical Congress, planned for Stockholm in 1940, was never held. Bawden[18] criticized the apparent inactivity of Johnson's committee. Johnson[33] defended its work. He pointed out that at the time World War II began, bringing the activity of the committee to a halt, substantial progress had been made in securing world-wide adoption of its plan for the nomenclature of plant viruses. He stated, "had the committee anticipated more closely the oncoming chaos in both virus nomenclature and world politics, it might have proceeded with more speed and dictatorial methods, but perhaps with less caution and diplomacy."

In December 1939 an attempt to rescue and develop the work of Johnson's committee was made by the American Phytopathological Society. It appointed a Standing Committee on Virus Nomenclature. As Johnson[33] describes, this committee was composed mainly of individualists who cherished, and published, their own particular schemes leading to further chaos.

At the First International Congress for Microbiology held in Paris in 1930, an International Committee on Bacteriological Nomenclature was set up. At the Fourth International Congress in Copenhagen in 1947, it was decided that viruses came within the field of jurisdiction of the Microbiological Code. The following wording was authorized: "Bacteriological nomenclature considers bacteria, related organisms and the viruses."

Some important and influential recommendations were made at the Fifth International Congress of Microbiology held at Rio de Janeiro in August 1950. Before this meeting Andrewes had been asked to convene an unofficial committee which was given official status at Rio de Janeiro under the International Nomenclature Committee.[34] The committee

was no doubt spurred on by the unilateral publication of Holmes[13] classification as a supplement to *Bergey's Manual of Determinative Bacteriology*. Before the meeting opinions were sought by correspondence from 120 virologists in 22 countries.[34] Over 80 replies were received from plant and animal virologists in about equal numbers. Plant virologists were evenly divided as to whether they wanted binomial nomenclature, while about two out of three animal virologists believed that a binomial system would be appropriate. However the verdict was almost unanimously against Holmes' system.

Of the eight members of Andrewes' virus subcommittee meeting at Rio de Janeiro, only one was a plant virologist. For this reason the committee was unwilling to make far-reaching recommendations concerning plant viruses. As a result of submissions made by the committee, the following resolutions were endorsed unanimously by the Plenary session of the Congress.

1. That consideration of the starting date for scientific nomenclature of viruses be deferred to the next Congress,
2. That until studies on viruses now in progress have advanced further, the use of any comprehensive system of scientific nomenclature for them is unwise. The cooperation of all virologists is requested in assisting the subcommittee now studying the nomenclature and classification of viruses.

The Virus Subcommittee considered and agreed upon a set of principles upon which the classification of animal viruses should be based. These were

1. Morphology and methods of reproduction
2. Chemical composition and physical properties
3. Immunological properties
4. Susceptibility to physical and chemical agents
5. Natural methods of transmission
6. Host, tissue, and cell tropisms
7. Pathology, including inclusion-body formation
8. Symptomatology (symptomatology is purposely placed last, as of minor importance)

The Plant Diseases section of the Congress asked the Virus Subcommittee to divide into sections to consider separately the viruses attacking animals, plants, and bacteria, these sections to deliberate together at a later date.

The Virus Subcommittee considered that a start could be made on the taxonomy of certain animal virus groups. These were

1. Psittacosis-lymphogranuloma group (Chlamydozoaceae)
2. Insect-pathogenic viruses
3. Pox group
4. Influenza group (influenza, mumps, fowl-plague)
5. Insect-borne encephalitides

Convenors for each of these five groups were appointed, and suggestions were made for small groups of working specialists. This working separation of animal, plant, and bacterial virologists and the setting up of small international groups of specialists foreshadowed the organization adopted by the International Committee for Nomenclature of Viruses some 16 years later. In spite of this activity in 1950, a proposal at the International Botanical Congress at Stocknolm in 1951 that the nomenclature of plant viruses become the responsibility of microbiologists was not approved. This decision appears to have had little impact on subsequent events.

In January 1952 the New York Academy of Sciences through its section on Biology provided for an International Conference on Virus and Rickettsial Classification and Nomenclature under the chairmanship of Sir McFarlane Burnet.[35]

Most speakers agreed that a system of classification that relied heavily on symptomatology would be unsatisfactory, and that it would be wise to proceed slowly and deal at first only with those groups of viruses about which there was sufficient knowledge. This plan which became known as the 'Rio Approach' received general support. Some individual speakers foreshadowed later trends.

Mayr, a zoological taxonomist, considered that, ''virology would avoid many of the nomenclatural difficulties of the zoologists if they would assign the authorship of their scientific names to national or international committees and charge them with the responsibility of issuing a list of official names.''

At the meeting Black described several leafhopper-borne viruses that had been found to multiply in their insect vectors. Their existence served ''to remind us that the separation of viruses into bacterial, plant and animal virus groups is arbitrary and that there exist forms that bridge the gap between two of these three major classes.''

At this meeting two further study groups were set up for viruses related to poliomyelitis and for herpes simplex.

At the Sixth International Congress of Microbiology held in Rome in 1953 the Virus Subcommittee of the International Nomenclature Committee had before it the reports of its study groups. Altogether nine animal virologists and six plant virologists attended the two meetings of the subcommittee.[36-37] They endorsed the conclusion from the 1950 Congress that at present ''the use of systems of classification for, and the application of binomials to viruses as a whole are undesirable and should be discouraged.'' They also recommended that the starting date for valid Linnaean nomenclature for viruses should not yet be determined, and that until this was done names of viruses already proposed should have no standing in bacteriological nomenclature.

However the animal virologists considered that some provisional alternatives to systems such as that of Holmes[13] should be put forward, but that such names should not prejudice future uniformity between animal and plant viruses. They suggested ''non-Linnaean'' binomial names for 20 well-known viruses infecting vertebrates and for 16 viruses infecting insects. The first name was to be a ''group'' name rather than a genus, and end in the suffix ''virus''. The second name would not be a species but a ''group member'' name. For example smallpox virus was named *Poxvirus variolae*. The laws of priority would not be applied and names would not be ascribed to authors. The main International Nomenclature Committee approved publication of the proposals.

Some of the group or generic names such as Poxvirus, Poliovirus, and Myxovirus became widely used but the species names were almost totally ignored.[38] Although the proposed ''non-Linnaean'' binomials never came into general use the idea of using the suffix ''-virus'' for generic names was later adopted by the International Committee for Nomenclature of Viruses.

An important decision at the 1953 Rome meeting concerned the Chlamydozoaceae (Chlamydiae). Up until this time these agents had been classed with the viruses, or were considered as being in a borderland between viruses and bacteria. The Chlamydozoaceae study group held that the agents related to psittacosis were closely related to the Rickettsiae and should be considered with them. This implied that these agents came under the bacterial code, and would no longer be given consideration by virologists. The report was accepted. This decision was important as it made much more evident the gap between bacteria and viruses. Lwoff[39] was able to end his Marjorie Stephenson memorial lecture on ''The concept of virus'' with the now well-known statement, ''viruses should be considered as viruses because viruses are viruses.''

Following the period of activity in the years 1950 to 1953, there appears to have been a slackening of interest in viral taxonomy and nomenclature until 1962. Some papers were published by individuals. For example Andrewes and Sneath[38] discussed the species concept among viruses, while Andrewes et al.[40] and Andrewes[41,42] surveyed the taxonomy of vertebrate viruses and proposed two new names. However there appears to have been very little progress made by the Virus Subcommittee of the International Committee on Bacteriological Nomenclature following the Rome meeting. The reasons for this are not clear. The 1950s and early 1960s were years in which the quality and availability of electron microscopes improved greatly, as did techniques of specimen preparation, and in particular the development of negative staining for studying virus structure.[43] The potential of the negative staining technique for providing basic data for taxonomic purposes was emphasized by the work of Horne and Wildy[44] and Wildy and Watson[45] who studied a series of viruses infecting vertebrates. The history of the application of this technique is given in detail by Horne and Wildy.[46] The impact of this technique for virus classification was immediate: (1) particles could be characterized with respect to size, shape, surface structure, and sometimes symmetry; (2) the method could be applied to viruses infecting all kinds of hosts; and (3) virus particles could be characterized in unpurified material, a considerable advantage for diagnostic purposes. Negative staining and other techniques gave rise to a rapid accumulation of data about the physical and chemical properties of the virions of many viruses. This may have reinforced the idea, already widespread, that to develop a sound taxonomy and nomenclature for viruses, it would be best to make haste slowly.

III. THE PERIOD LEADING UP TO THE MOSCOW CONFERENCE (1962-1966)

This period was dominated by the activities of Lwoff. To many he appeared as a strong willed and charismatic figure. At the Cold Spring Harbor Symposium of 1962 Lwoff, Horne, and Tournier[31] proposed "a system of viruses" that could embrace all known viruses. This was a further development of the proposals put forward by Cooper.[30] It was an hierarchical system based on arbitrarily chosen characters, as follows: the first subdivision was according to type of nucleic acid — DNA or RNA; the second according to capsid symmetry — helical, cubic, or both; the third — presence or absence of an envelope; and fourth, for helical capsids diameter of the particle, and for cubic capsids the number of capsomeres. This gave rise to 16 groups of viruses. The proposals led to considerable discussion and debate right up to and after the Moscow conference.

Also in 1962, the Virus Subcommittee of the International Nomenclature Committee met in Montreal, with Andrewes as chairman. The subcommittee decided that it would be most useful to define and name major groups of viruses and not to propose any further specific names for individual viruses.[47] Thus they proposed no immediate move towards a binomial system. The major groups would be defined on the basis of (1) nucleic acid composition, (2) sensitivity to ether, (3) presence of a limiting membrane, (4) symmetry whether cubic or helical, and (5) number of capsomers. Thus the criteria used were virtually the same as those used by Lwoff et al.[31] but the objective was much more limited. It was to delineate a few well-described virus groups, and not to erect an all-embracing virological hierarchy. The groups they named and described were *Picornavirus* (replacing the name *Enterovirus*), *Myxovirus*, *Herpesvirus*, *Adenovirus*, *Reovirus*, and *Papovavirus*.

There were only a few plant virologists at the 1962 Montreal meeting and no proposals concerning plant viruses were put forward. Bacterial virologists were not represented.

In 1963 the chairman of the Virus Subcommittee, after consultation with members, submitted a formal proposal to the President of the International Association of Microbiological

Societies (IAMS) requesting that the committee should be dissolved and that a new Virus Committee should be appointed by the Executive Committee of IAMS.

Because of lack of agreement, very few specific nomenclatural or taxonomic proposals had been sent forward to the Judicial Commission in the period since 1950. Most of the proposals had been merely tentative. However, the main reason for this requested change was that many members of the Virus Subcommittee considered that viruses differ so much from bacteria that they needed separate taxonomic treatment. The implication of the request was that the proposed Virus Committee would rank equally with the Committee on Bacteriological Nomenclature and would report directly to the Executive Committee of IAMS.

The Executive Committee of IAMS met in Paris in July 1963 and approved the establishment of an International Committee on Nomenclature of Viruses (ICNV).[48]

It was decided that the members of ICNV should be nominated by the National Societies, and that the first official meeting would be held in Moscow during the Ninth International Microbiological Congress in 1966. However preliminary work before the Congress was needed. For this purpose a Provisional Committee on Nomenclature of Viruses (PCNV) was set up. This committee discussed the problems extensively by correspondence and then met once only, in Paris in June 1965 under the chairmanship of Andrewes. Lwoff was a major contributor to the setting up and subsequent work of the PCNV. In spite of the fact that committee members came from widely differing fields of virology, and had diverging views, substantial agreement was reached on many matters. The main proposals published by the PCNV[49] can be summarized as follows.

With respect to *Principles* the following points were made:

1. An International Nomenclature of Viruses is necessary. Viruses cannot be left in a taxonomic vacuum.
2. The only way to achieve an International Nomenclature of Viruses is by a binomial system.
3. The code of nomenclature of bacteria cannot be applied to viruses.
4. Virologists will therefore have to build their own code.

With respect to naming of taxa the committee made 16 recommendations, the more significant of which were as follows:

1. No taxon should be named from a person
2. Anagrams, siglas, hybrids of names, nonsense names, should be prohibited
3. Names should preferentially be Latin or Latinized Greek names
4. A species shall be selected to typify each genus
5. Specific names can be names or letters or numerals
6. The names of all viral genera end in "virus", e.g., *Poliovirus*
7. A genus shall be selected to typify each family
8. A family is named from its type genus, e.g., Poxvirus, Poxviridae
9. The suffix for the family is *idae*. Therefore all virus families end in *viridae*
10. The name of a taxon whatever its rank is not followed by the name of the author who proposed it

The PCNV proposed a list of names which should be conserved together with a list of new genera. There were 21 families and 39 genera with type species given latinized names. For example genera in the Poxviridae were as follows:

Genus	Type species	Common name
1. *Poxvirus* (type genus)	*variolae*	Variola

2. *Dermovirus*	*orfi*	Contagious pustular dermatitis
3. *Pustulovirus*	*ovis*	Sheep pox
4. *Avipoxvirus*	*galli*	Fowl pox
5. *Fibromavirus*	*myxomatosis*	Rabbit myxoma
6. *Molluscovirus*	*hominis*	Molluscum contagiosum

Finally the PCNV boldly proposed that a scheme for classification of viruses into subphyla, classes, orders, suborders, and families should be adopted. The scheme was the one proposed by Lwoff et al.[31]

The PCNV proposals for Latin binomial names were influenced by the past proposals of the defunct Virus Subcommittee. The overall scheme of classification was clearly influenced by Lwoff's ideas.

The proposals generated a substantial controversy both before and during the Moscow meetings. Lwoff and Tournier[50] gave an expanded account of, and justification of their all-embracing hierarchical scheme. Gibbs, Harrison, Watson, and Wildy[51] opposed the arbitrary decisions on the relative importance of different virus characters that were essential in any hierarchical classification. They considered it essential to follow the principles of Adanson[52] who suggested that all available information should be used in classification and that all characters should be given equal weight. At least 60 characters are needed for each virus to give a satisfactory classification of this sort. They pointed out that while computers make the task relatively easy, not enough information was available for most viruses. One of the main points made by Gibbs et al.[51] was that any temporary measures should not prejudice the later development of a more satisfactory classification.

As far as nomenclature is concerned, Gibbs et al.[51] introduced the idea of the cryptogram. They suggested that virus names should consist of two parts. The first part would be the vernacular name now in use and would be invariant. The second part would consist of a cryptogram which was essentially a coded summary of eight characters. These were considered to be the minimum set of characters that distinguished between most of the obvious groups of viruses known at that time. They were set out in pairs as follows:•

$$\frac{\text{Type of nucleic acid}}{\text{Strandedness}} : \frac{\text{MW of nucleic acid}}{\text{Percent of nucleic acid}} : \frac{\text{Outline of particle}}{\text{Shape of nucleocapsid}} : \frac{\text{Hosts}}{\text{Vector}}$$

Letters and numbers were used to code the information, with an asterisk indicating data not available. For example the cryptogram for influenza virus A was given as:

$$\frac{R}{1} : \frac{2}{1} : \frac{S}{E} : \frac{V}{O}$$

meaning

$$\frac{\text{RNA}}{\text{Single stranded}} : \frac{2 \times 10^6 \text{ MW}}{1\% \text{ of particle weight}} : \frac{\text{Spherical particle}}{\text{Elongated nucleocapsid}} : \frac{\text{Vertebrate hosts}}{\text{No vector known}}$$

For many viruses much of the information was missing in 1966. For example the cryptogram for beet curly top virus was