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50 years of the International Committee on Taxonomy of Viruses: progress and prospects

Michael J. Adams[1] · **Elliot J. Lefkowitz**[2] · **Andrew M. Q. King**[3] ·
Balázs Harrach[4] · **Robert L. Harrison**[5] · **Nick J. Knowles**[6] · **Andrew M. Kropinski**[7] ·
Mart Krupovic[8] · **Jens H. Kuhn**[9] · **Arcady R. Mushegian**[10] · **Max L. Nibert**[11] ·
Sead Sabanadzovic[12] · **Hélène Sanfaçon**[13] · **Stuart G. Siddell**[14] ·
Peter Simmonds[15] · **Arvind Varsani**[16] · **Francisco Murilo Zerbini**[17] ·
Richard J. Orton[18] · **Donald B. Smith**[19] · **Alexander E. Gorbalenya**[20,21] ·
Andrew J. Davison[18]

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Abstract We mark the 50th anniversary of the International Committee on Taxonomy of Viruses (ICTV) by presenting a brief history of the organization since its foundation, showing how it has adapted to advancements in our knowledge of virus diversity and the methods used to characterize it. We also outline recent developments, supported by a grant from the Wellcome Trust (UK), that are facilitating substantial changes in the operations of the ICTV and promoting dialogue with the virology community. These developments will generate improved online resources, including a freely available and regularly updated ICTV Virus Taxonomy Report. They also include a series of meetings between the ICTV and the broader community focused on some of the major challenges facing virus taxonomy, with the outcomes helping to inform the future policy and practice of the ICTV.

✉ Michael J. Adams
mike.adams.ictv@gmail.com

[1] 24 Woodland Way, Stevenage, Herts SG2 8BT, UK

[2] Department of Microbiology, University of Alabama at Birmingham (UAB), BBRB 276, 845 19th ST South, Birmingham, AL 35294-2170, USA

[3] Sunfield, Dawney Hill, Pirbright, Woking, Surrey GU24 0JB, UK

[4] Institute for Veterinary Medical Research, Centre for Agricultural Research, Hungarian Academy of Sciences, Hungária krt. 21, 1143 Budapest, Hungary

[5] Invasive Insect Biocontrol and Behavior Laboratory, USDA, 10300 Baltimore Avenue, Bldg 007 Barc-West, Beltsville, MD 20705, USA

[6] The Pirbright Institute, Ash Road, Pirbright, Surrey GU24 0NF, UK

[7] Departments of Food Science, Molecular and Cellular Biology and Pathobiology, University of Guelph, Guelph, ON N1G 2W1, Canada

[8] Department of Microbiology, Institut Pasteur, 25 rue du Dr Roux, 75015 Paris, France

[9] NIH/NIAID/DCR Integrated Research Facility at Fort Detrick (IRF-Frederick), B-8200 Research Plaza, Fort Detrick, Frederick, MD 21702, USA

[10] Division of Molecular and Cellular Biosciences, National Science Foundation, Arlington, VA 22230, USA

[11] Department of Microbiology and Immunobiology, Harvard Medical School, 77 Ave Louis Pasteur, Boston, MA 02115, USA

[12] Department of Biochemistry, Molecular Biology, Entomology and Plant Pathology, Mississippi State University, 100 Old Hwy 12 Mail Stop 9775, Starkville, MS 39762, USA

[13] Summerland Research and Development Centre, Agriculture and Agri-Food Canada, 4200 Highway 97, Summerland, BC V0H 1Z0, Canada

[14] School of Cellular and Molecular Medicine, Faculty of Biomedical Sciences, University of Bristol, University Walk, Bristol BS8 1TD, UK

[15] Nuffield Department of Experimental Medicine, University of Oxford, Peter Medawar Building, South Parks Road, Oxford OX1 3PS, UK

[16] The Biodesign Center for Fundamental and Applied Microbiomics, School of Life Sciences, Center for Evolution and Medicine, Arizona State University, P.O. Box 874701, Tempe, AZ 85287-4701, USA

[17] Departamento de Fitopatologia/BIOAGRO, Universidade Federal de Viçosa, Viçosa, MG 36570-900, Brazil

Introduction

From the beginnings of virology more than a hundred years ago, viruses were often named by researchers after the diseases they caused. The development of various methods to characterise viruses (physicochemical methods, tissue culture, electron microscopy, serology, etc.) led to a steady increase in the number known and helped demonstrate some relationships among them. As a result, the need for oversight of virus nomenclature and classification was recognized, and this led eventually to the founding of the International Committee on Nomenclature of Viruses (ICNV) in 1966. The ICNV changed its name to the International Committee on Taxonomy of Viruses (ICTV) in 1975, reflecting the fact that the ICTV regulates both the creation and the naming of taxa. To mark the 50th anniversary of the organisation, we now provide a brief historical overview and describe some recent significant developments that are helping it adapt to the future.

Foundation

The ICNV was established on 22 July 1966 in Moscow during the 9th Congress of the International Association of Microbiological Societies (IAMS). A provisional steering committee established three years earlier had invited each of the national microbiological societies affiliated to IAMS to appoint a virology representative, and these became the founding members of the ICNV. An Executive Committee (EC) elected by the members to oversee the ICNV drew up a set of rules that were approved by the National Members at a subsequent meeting during the same congress. Key decisions of these founding meetings were that the ICNV would establish a universal system of classification and nomenclature for viruses (i.e. one for all viruses, irrespective of host), that the bacterial code of nomenclature would not be applied to viruses, and that the rule of priority of publication would not be observed. These principles established a system in which the decisions of the ICNV (and later the ICTV) would determine both the creation and the naming of taxa, and thus set virus taxonomy apart from most biological taxonomy (botanical, zoological, etc.), for which the international codes regulate only the names that are used. The founding meeting of the ICNV also agreed that 'an effort should be made towards a latinized binomial nomenclature'.

To begin its task, the EC created four host-based Subcommittees to propose genera and families for the known viruses of insects, vertebrates, plants and bacteria. Each Subcommittee was chaired by a member of the EC, and consisted of specialists representing each of the major groups of viruses within their remit. These specialists in turn chaired Study Groups to propose a classification and nomenclature in their areas. The taxonomy proposed by the Study Groups was discussed by the relevant Subcommittee and by the EC, and (once agreement had been reached) then required final approval from the entire ICNV. The same basic pattern continues to this day – most taxa and taxon names originate in proposals made by specialist Study Groups, whose work is co-ordinated and overseen by the EC.

The 1st Report of the ICNV was published in 1971 [1] and provided the first indication of progress in virus classification. Most of the vertebrate viruses listed in that Report were classified into 19 genera and two families (*Papovaviridae* and *Picornaviridae*), and the remaining viruses were presented in 24 groups pending further information to determine appropriate classification levels. Each genus or group had a type member and a list of 'other members', all specified using the common (vernacular) name of the virus. A total of 290 viruses were listed as members of these genera or groups, together with a similar number listed as 'possible members'. The taxonomy established by the 1st Report is available at http://www.ictvonline.org/virusTaxonomy.asp?msl_id=1. Each subsequent release of the ICNV/ICTV taxonomy is available at http://www.ictvonline.org/taxonomyReleases.asp.

Consolidation

A process was soon established upon these foundations that lasted for some 25 years. Taxonomic proposals for genera and families (and later a few subfamilies and orders) were prepared (usually) by the Study Groups, discussed and modified where necessary in consultation with the relevant Subcommittee and the EC, and finally presented to the voting membership of the ICTV at a plenary session of the triennial International Congress of Virology (ICV) or occasionally by postal ballot. Voting members consisted of the National Members, the EC members and a small number of honorary Life Members. Changes to taxonomy were sometimes reported as journal articles, and the 2nd to

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[18] MRC, University of Glasgow Centre for Virus Research, Sir Michael Stoker Building, 464 Bearsden Road, Glasgow G61 1QH, UK

[19] Centre for Immunity, Infection and Evolution, Ashworth Laboratories, University of Edinburgh, King's Buildings, West Mains Road, Edinburgh EH9 3JT, UK

[20] Department of Medical Microbiology, Leiden University Medical Center, E4-P, rm. E4-72, P. O. Box 9600, 2300 RC Leiden, The Netherlands

[21] Faculty of Bioengineering and Bioinformatics, Lomonosov Moscow State University, 119899 Moscow, Russia

6th ICTV Reports were published in 1976 [2], 1979 [3], 1982 [4], 1991 [5] and 1995 [6]. The Reports were initially journal supplements but soon became independent publications that were standard reference works, providing the authoritative viral taxonomy and also a comprehensive overview of the properties of the viruses classified. In most cases, the groups listed in the 1st Report were eventually recognised and named as genera, and member viruses (together with separate lists of 'probable members' and sometimes also 'possible members') were listed at the discretion of the respective Study Groups that prepared the chapters. The main efforts were thus directed at the rank of genus and above. The early intention to adopt a latinized binomial nomenclature was abandoned as a result of direct opposition by some virologists and differences of view about the feasibility and merits of recognising virus species [7].

Establishment

An important conceptual change occurred with the formal recognition of virus species as proposed by van Regenmortel [8] and adopted by the ICTV in 1991 [9]. This change was largely approved by the community and universally implemented in the 7th Report, which was published in 2000 [10]. From then on, Study Groups classified viruses into species, and taxonomic proposals became necessary for the creation and naming of new species. Each species could include numerous viruses differing antigenically or pathogenically, one of which was designated as the representative isolate. This step-change in virus taxonomy led to drastic revisions in some genera. For example, the 96 viruses that had been listed as independent members of the genus *Enterovirus* in the 6th Report were classified into a mere eight species in the 7th Report. However, in many other cases the lists of species in the 7th Report corresponded largely with the viruses listed as genus members in earlier Reports. To distinguish them as virus species, their names were now printed in italics and with an initial capital letter. Species names to this day have many different styles, often reflecting the differing approaches to naming viruses among researchers working with various virus groups (e.g. bacteriophages, plant viruses, arboviruses, etc.). Efforts continue to be made to achieve consistency of species naming styles within certain genera and families, often incorporating the genus name (e.g. *Enterovirus A* and *Rabies lyssavirus*).

Virus taxa (including species) are usually accepted to be man-made categories (although see [11]). Thus, the decision to create a new species in a particular genus is inevitably a matter of scientific judgement and pragmatism, usually guided by genus- or family-specific criteria established by the relevant Study Group. The formal definition of a virus species has been controversial [12], and there are differing viewpoints on what that definition should contain, whether a universally agreed definition is necessary (botanical taxonomy, for example, does not have one), and what the consequences of adopting different definitions might be. Despite considerable criticism from some eminent virologists [13], the 1991 definition: "A virus species is defined as a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche" was replaced by majority vote in 2013 with: "Species shall be created in accordance with the following definition: A species is the lowest taxonomic level in the hierarchy approved by the ICTV. A species is a monophyletic group of viruses whose properties can be distinguished from those of other species by multiple criteria". The view that the ICTV should have a species definition that endorses the polythetic concept is still being advocated [14].

Growth

The early years of the 21st century have seen significant changes in the rate of virus discovery and characterisation, driven mainly by the explosion in high-throughput sequencing and the development of sophisticated bioinformatic tools. This has resulted in an ever-increasing workload for Study Groups and the EC and in the creation of many more virus taxa. Following the latest (2016) ratification vote [15], an untold number of viruses are classified within 3704 species, 609 genera, 111 families (including 27 subfamilies) and 7 orders. This rapid expansion has only become possible by changes within the EC to increase the numbers of Subcommittees (now six, some of them based on genome type as well as on host) and Study Groups (now 99). Nonetheless, in organisational terms, the ICTV has retained many of its early characteristics. It is now a committee of the Virology Division of the International Union of Microbiological Societies (IUMS; the successor of IAMS), and its governance is determined by Statutes, the latest version of which can be found at http://www.ictvonline.org/statutes.asp. A separate Code containing the rules governing the creation and naming of virus taxa is available at http://www.ictvonline.org/codeOfVirusClassification.asp.

An internet home page for the ICTV was created in 1995, and since then a web presence has become increasingly integral to ICTV operations. It now provides open access to a wealth of information including past and present virus taxonomy, taxonomic proposals under consideration and the opportunity to contribute to discussions. Although Study Groups continue to play a leading role in preparing taxonomic proposals, submissions are welcomed from any virologist, and forms and instructions for this purpose are available at https://talk.ictvonline.org/files/taxonomy-proposal-templates/. The web site includes lists of EC Members, Subcommittee Members, Study Group Members, Life Members (to which the previous President was added recently [16]) and National Members. Study Group chairs were added to the ICTV voting membership in 2005, in recognition of the important role they play in developing virus taxonomy and encouraging the involvement of the wider virology community. The final vote on all proposals approved by the EC has been conducted by an email ballot since 2009, and now takes place annually. The up-to-date list of currently approved virus taxa (the Master Species List) can be downloaded in its entirety from https://talk.ictvonline.org/files/master-species-lists/m/msl/5945, or its contents explored online at http://www.ictvonline.org/virusTaxonomy.asp. An important recent development has provided access to the complete history of all taxonomic changes during the past 50 years and, in many cases, access to the formal proposals that introduced these changes [17]. The web site is also a source of news and information relevant to virus taxonomy, including the annual ICTV newsletter available at https://talk.ictvonline.org/files/ictv_documents/m/newsletters.

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 citeable, 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.

Bioinformatic resources

To facilitate the development of taxonomy and the involvement of the virology community in this process, the ICTV web site will provide bioinformatic and database resources designed to simplify the processes involved in generating and approving taxonomic proposals. To enhance the rigour with which virus taxonomy is advanced, the web site will also provide information and tools aimed at ensuring data consistency and integrity, including standardised 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.

Focused meetings

A series of focused meetings is providing a much-needed channel through which the expertise of those working in virology, evolutionary biology and bioinformatics will be able to contribute to the work of the ICTV in the short and long terms. The first of these meetings was organized for Study Group chairs and EC Members, and took place on 1-2 February 2016 at Hinxton, near Cambridge (UK), with an attendance of 76 virologists. This very successful workshop gave the opportunity for wide-ranging discussions of the operations of the ICTV, the development of the online Report and the challenges facing virus taxonomy. A summary is available at http://talk.ictvonline.org/meetings/sg_hinxton/w/sg_meeting.

The second meeting, held on 9-11 June 2016 in Boston (USA), was aimed at considering the challenges posed by metagenomics to virus discovery and taxonomy. The 25 attendees included experts in the fields of high-throughput sequencing and virus discovery, along with many EC Members. An important outcome from this meeting was a series of consensus proposals for classifying viruses identified from metagenomic datasets, a summary of which has recently been published [20]. Further focused meetings are planned on other key areas, with the anticipation of again publishing the outcomes and using these to help inform the future policy and practice of the ICTV.

Virus taxonomy in the age of metagenomics

At the EC meeting on 22-24 August 2016 in Budapest (Hungary), the consensus proposals developed at the Boston (USA) meeting were welcomed and thanks were recorded for the stimulating contributions made by the participants to various discussions on the challenges and opportunities posed by increasing volumes of genomic and metagenomic data to virus taxonomy. The EC emphasized that proposals to create taxa on the basis of genomic sequences alone are welcomed, regardless of the technology used to determine those sequences and even in the absence of all other biological data (including host), provided that there is credible evidence for the accuracy of the sequence assembly and that the genome sequence is coding complete. The EC noted that it has been accepting proposals on this basis for some time, at least for species in well-established genera and families, and that it does not believe that any changes to the taxonomic code (including the virus species definition) are required to continue and extend this practice. The EC concluded that species created only on the basis of sequence data should be accommodated in the same classification hierarchy and using the same nomenclatural rules as those created on the basis of traditional biological characterization. The EC recognized that there are additional challenges to the creation of taxa, and particularly higher taxa, where the new viruses are highly diverged from members of currently established taxa, and plans to use expertise within and outside the Committee to develop appropriate methods and standards to meet those challenges.

Prospects

Virus taxonomy, like any biological taxonomy, is never perfect or complete. However, a transparent and functional system for virus classification is essential, particularly in view of the explosion in virus discovery that is currently underway and may continue for the next 50 years. Interest in virus taxonomy is also increasing with the awareness that viruses have a major impact on the health of humans, livestock and crops, and also on the functioning of terrestrial and aquatic ecosystems. Metagenomic studies are revealing the presence of large numbers of distinct viruses that may have little or no adverse effects on their hosts and may even be beneficial to them [21]. The new era of virus discovery poses many exciting challenges and opportunities for virus taxonomists and a motivation for ensuring that formal classification remains relevant to the needs of the community and vital for our understanding of the relationships among viruses. As this brief overview demonstrates, the ICTV is adapting to meet challenges that could not have been foreseen at its foundation. Financial and workload pressures will likely increase, but the EC welcomes the involvement of virologists everywhere to ensure continued progress with this endeavour.

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Compliance with ethical standards

Statement of competing financial interests The authors declare that they have no competing financial interests.

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