Arch Virol (2016) 161:1095–1099
DOI 10.1007/s00705-015-2728-0

VIROLOGY DIVISION NEWS

Taxonomy of prokaryotic viruses: update from the ICTV bacterial and archaeal viruses subcommittee

Mart Krupovic[1] · Bas E. Dutilh[2,3,4] · Evelien M. Adriaenssens[5] · Johannes Wittmann[6] · Finn K. Vogensen[7] · Mathew B. Sullivan[8,9] · Janis Rumnieks[10] · David Prangishvili[1] · Rob Lavigne[11] · Andrew M. Kropinski[22] · Jochen Klumpp[12] · Annika Gillis[13] · Francois Enault[14,15] · Rob A. Edwards[16] · Siobain Duffy[17] · Martha R. C. Clokie[18] · Jakub Barylski[19] · Hans-Wolfgang Ackermann[20] · Jens H. Kuhn[21]

Received: 10 December 2015 / Accepted: 12 December 2015 / Published online: 5 January 2016

The prokaryotic virus community is represented on the International Committee on Taxonomy of Viruses (ICTV) by the Bacterial and Archaeal Viruses Subcommittee. In 2008, the three caudoviral families *Myoviridae, Podoviridae*, and *Siphoviridae* included only 18 genera and 36 species. Under the able chairmanship of Rob Lavigne (KU Leuven, Belgium), major advances were made in the classification of prokaryotic viruses and the order *Caudovirales* was expanded dramatically, to reflect the genome-based relationships between phages. Today, the order includes six subfamilies, 80 genera, and 441 species. This year, additional changes in prokaryotic virus taxonomy have been brought forward under the new subcommittee chair, Andrew M. Kropinski (University of Guelph, Canada). These changes are:

1. **replacement of "*phage*" with "*virus*" in prokaryotic virus taxon names.** In recognition of the fact that phages are first and foremost genuine viruses, and to adhere to ICTV's International Code of Virus Classification and Nomenclature (ICVCN), the word "*phage*" will disappear from taxon names, but not from phage names. For instance, the current taxon *Escherichia phage T4* will be renamed *Escherichia virus T4*, while the name of this taxon's member will remain unchanged (*Escherichia* phage T4). It is

The content of this publication does not necessarily reflect the views or policies of the US Department of Health and Human Services, or the institutions and companies affiliated with the authors. The taxonomic changes summarized here have been submitted as official taxonomic proposals to the International Committee on Taxonomy of Viruses (ICTV) (www.ictvonline.org) and are by now accepted, but not yet ratified. These changes therefore may differ from any new taxonomy that is ultimately approved by the ICTV.

✉ Andrew M. Kropinski
Phage.Canada@gmail.com

Jens H. Kuhn
kuhnjens@mail.nih.gov

[1] Unit of Molecular Biology of the Gene in Extremophiles, Department of Microbiology, Institut Pasteur, 25 rue du Dr Roux, 75015 Paris, France

[2] Theoretical Biology and Bioinformatics, Utrecht University, Utrecht, The Netherlands

[3] Centre for Molecular and Biomolecular Informatics, Radboud University, Medical Centre, Nijmegen, The Netherlands

[4] Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

[5] Department of Genetics, Centre for Microbial Ecology and Genomics, University of Pretoria, Private Bag X20, Hatfield, Pretoria 0028, South Africa

[6] Leibniz-Institut DSMZ-Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Inhoffenstraße 7B, 38124 Braunschweig, Germany

[7] Department of Food Science, University of Copenhagen, Rolighedsvej 26, 1958 Frederiksberg C, Denmark

[8] Department of Microbiology, Ohio State University, 496 W 12th Ave, Columbus, OH 43210, USA

[9] Department of Civil, Environmental, and Geodetic Engineering, Ohio State University, 470 Hitchcock Hall, 2070 Neil Avenue, Columbus, OH 43210, USA

[10] Latvian Biomedical Research and Study Center, Rātsupītes 1, Riga, LV 1067, Latvia

[11] Laboratory of Gene Technology, KU Leuven, Kasteelpark Arenberg 21-box 2462, 3001 Leuven, Belgium

[12] Institute of Food, Nutrition and Health, ETH Zurich, Schmelzbergstrasse 7, 8092 Zurich, Switzerland

important that the community remembers the ICVCN distinction between viral taxa (such as species, genera, families, or orders) and their members, the actual viruses/phages: "viruses are real physical entities produced by biological evolution and genetics, whereas virus species and higher taxa are abstract concepts produced by rational thought and logic";

2. **elimination of the infix "*like*" from prokaryotic virus genus names.** The naming of phage taxa has been an evolving process with genus names in the form "P22-like virus", which was always considered to be a stop-gap measure, being replaced by *P22likevirus*. However, the latter convention is also problematic since it was only applied to genera included in the order *Caudovirales*, and the infix "*like*" was unnecessary since the grouping of viruses in genera implies *per se* that their constituent members are alike. Consequently, the infix "*like*" will be removed from the names of phage genera and genus names such as *Lambdalikevirus* and *T4likevirus* will become *Lambdavirus* and *T4virus*, respectively. It will of course remain correct to refer to "lambda-like viruses" and "T4-like phages" during discussions regarding specific groups of phages classified in these taxa. There have also been discussions in the Subcommittee whether all prokaryotic virus genera should adopt the system used for some archaeal and eukaryotic viruses, in which names of genera are created from the root of the corresponding family name with sequentially appended transliterated Greek letters (e.g., *Alphabaculovirus*, *Betabaculovirus,* etc.). However, it was decided that recognition of new genus names is of paramount importance and that further drastic changes in one setting might overly confuse the community. Thus, in most cases, the infix "*like*" was merely removed and the name of the founding member of the genus was retained as a root of the taxon name;
3. **discontinuation of the use of "*Phi*" and other transliterated Greek letters in the naming of new prokaryotic virus genera.** Since some scientists are under the impression that "*Phi*" in its various forms (phi, φ, Φ) indicates a phage, over the years, many phages were given names containing the prefix "*Phi*". However, the prefix "*Phi*" adds no informational value when naming phage genera. Consequently, the Subcommittee decided that, unless there was sufficient historical precedent (e.g., Φ29 or ΦX174), *Phi* would no longer be added to genus names. In addition, Greek letters can create problems in electronic databases, as exemplified by a PubMed search for references on *Bacillus* phage Φ29 [1], which retrieved articles on phi 29, phi29, Phi 29, Phi29, 29 phi, {phi}29, φ29, and *φ*29 phages. Therefore, the Subcommittee strongly discourages phage scientists from using *Phi* or any other Greek letter in virus and virus taxon names in the future;
4. **elimination of hyphens from taxon names.** The ICVCN discourages hyphens in virus taxon names. Accordingly, taxon names such as *Yersinia phage L-413C* have been renamed (in this instance to *Yersinia virus L413C*). However, hyphens are retained when appearing in a number string: *Thermus phage P2345* becomes *Thermus virus P23-45* (its correct name) [2].
5. **inclusion of the isolation host name in the taxon name.** On several occasions, terms such as "*Enterobacteria*" or "*Pseudomonad*" have been used in phage taxon names. However, such terms do not refer to a specific bacterial host; nor do they indicate whether the phage in question was tested upon a variety of members of the particular host group. To improve the situation, terms such as "*Enterobacteria*"

[13] Laboratory of Food and Environmental Microbiology, Université catholique de Louvain, Croix du Sud 2, L7.05.12, 1348 Louvain-la-Neuve, Belgium

[14] Clermont Université, Université Blaise Pascal, Laboratoire "Microorganismes: Génome et Environnement", Clermont-Ferrand, France

[15] CNRS UMR 6023, LMGE, Aubière, France

[16] Bioinformatics Lab, Department of Computer Science, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182-7720, USA

[17] Department of Ecology, Evolution and Natural Resources, Rutgers University, 14 College Farm Rd, New Brunswick, NJ 08901, USA

[18] Department of Infection, Immunity and Inflammation, University of Leicester, University Road, Leicester LE1 9HN, UK

[19] Department of Molecular Virology, Institute of Experimental Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznan, Poland

[20] L'Institut de biologie intégrative et des systems, Université Laval, Pavillon Charles-Eugène-Marchand, 1030, avenue de la Médecine, Quebec, QC G1V 0A6, Canada

[21] Integrated Research Facility at Fort Detrick, National Institute of Allergy and Infectious Diseases, National Institutes of Health, Fort Detrick, Frederick, MD 21702, USA

[22] Departments of Food Science, Molecular and Cellular Biology, and Pathobiology, University of Guelph, 50 Stone Rd E, Guelph, ON N1G 2W1, Canada

Table 1 Taxonomy proposals describing new taxa (genera, subfamilies, families) submitted to the ICTV in 2015

New genus	Family	Subfamily	Type species	Number of genus-included species
Ap22virus	*Myoviridae*		*Acinetobacter virus AP22*	4
Secunda5virus	*Myoviridae*		*Aeromonas virus 25*	5
Biquartavirus	*Myoviridae*		*Aeromonas virus 44RR2*	1
Agatevirus	*Myoviridae*		*Bacillus virus Agate*	3
B4virus	*Myoviridae*		*Bacillus virus B4*	5
Bastillevirus	*Myoviridae*		*Bacillus virus Bastille*	2
Bv431virus	*Myoviridae*		*Bacillus virus Bc431*	4
Cp51virus	*Myoviridae*		*Bacillus virus CP51*	3
Nit1virus	*Myoviridae*		*Bacillus virus NIT1*	3
Wphvirus	*Myoviridae*		*Bacillus virus WPh*	1
Cvm10virus	*Myoviridae*		*Escherichia virus CVM10*	2
Kpp10virus	*Myoviridae*		*Pseudomonas virus KPP10*	3
Pakpunavirus	*Myoviridae*		*Pseudomonas virus PAKP1*	6
Rheph4virus	*Myoviridae*		*Rhizobium virus RHEph4*	1
Vhmlvirus	*Myoviridae*		*Vibrio virus VHML*	3
Tg1virus	*Myoviridae*		*Yersinia virus TG1*	2
P100virus	*Myoviridae*	*Spounavirinae*	*Listeria virus P100*	1
Kayvirus	*Myoviridae*	*Spounavirinae*	*Staphylococcus virus K*	7
Silviavirus	*Myoviridae*	*Spounavirinae*	*Staphylococcus virus Remus*	2
Rb49virus	*Myoviridae*	*Tevenvirinae*	*Escherichia virus RB49*	3
Rb69virus	*Myoviridae*	*Tevenvirinae*	*Escherichia virus RB69*	4
Js98virus	*Myoviridae*	*Tevenvirinae*	*Escherichia virus JS98*	5
Sp18virus	*Myoviridae*	*Tevenvirinae*	*Shigella virus SP18*	5
S16virus	*Myoviridae*	*Tevenvirinae*	*Salmonella virus S16*	2
Cc31virus	*Myoviridae*	*Tevenvirinae*	*Enterobacter virus CC31*	2
Cr3virus	*Myoviridae*	*Vequintavirinae* (new)	*Cronobacter virus CR3*	3
V5virus	*Myoviridae*	*Vequintavirinae* (new)	*Escherichia virus V5*	4
Se1virus	*Myoviridae*	*Vequintavirinae* (new)	*Salmonella virus SE1*	4
Pagevirus	*Podoviridae*		*Bacillus virus Page*	5
Cba41virus	*Podoviridae*		*Cellulophaga virus Cba41*	2
G7cvirus	*Podoviridae*		*Escherichia virus G7C*	8
Lit1virus	*Podoviridae*		*Pseudomonas virus LIT1*	3
Vp5virus	*Podoviridae*		*Vibrio virus VP5*	3
Kp34virus	*Podoviridae*	*Autographivirinae*	*Klebsiella virus KP34*	5
Slashvirus	*Siphoviridae*		*Bacillus virus Slash*	4
Cba181virus	*Siphoviridae*		*Cellulophaga virus Cba181*	3
Cbastvirus	*Siphoviridae*		*Cellulophaga virus ST*	1
Nonagvirus	*Siphoviridae*		*Escherichia virus 9g*	4
Seuratvirus	*Siphoviridae*		*Escherichia virus Seurat*	2
P70virus	*Siphoviridae*		*Listeria virus P70*	5
Psavirus	*Siphoviridae*		*Listeria virus PSA*	2
Ff47virus	*Siphoviridae*		*Mycobacterium virus Ff47*	2
Sitaravirus	*Siphoviridae*		*Paenibacillus virus Diva*	5
Septima3virus	*Siphoviridae*		*Pseudomonas virus 73*	5
Nonanavirus	*Siphoviridae*		*Salmonella virus 9NA*	2
Sextaecvirus	*Siphoviridae*		*Staphylococcus virus 6ec*	2
Ssp2virus	*Siphoviridae*		*Vibrio virus SSP002*	2

Table 1 continued

New genus	Family	Subfamily	Type species	Number of genus-included species
K1gvirus	*Siphoviridae*	*Guernseyvirinae* (new)	*Escherichia virus K1G*	4
Jerseyvirus (existing)	*Siphoviridae*	*Guernseyvirinae* (new)	*Salmonella virus Jersey*	6
Sp31virus	*Siphoviridae*	*Guernseyvirinae* (new)	*Salmonella virus SP31*	1
T1virus (existing)	*Siphoviridae*	*Tunavirinae* (new)	*Escherichia virus T1*	4
Tlsvirus	*Siphoviridae*	*Tunavirinae* (new)	*Escherichia virus TLS*	3
Rtpvirus	*Siphoviridae*	*Tunavirinae* (new)	*Escherichia virus Rtp*	2
Kp36virus	*Siphoviridae*	*Tunavirinae* (new)	*Klebsiella virus KP36*	3
Rogue1virus	*Siphoviridae*	*Tunavirinae* (new)	*Escherichia virus Rogue1*	8
Alpha3microvirus	*Microviridae*	*Bullavirinae* (new)	*Escherichia virus alpha3*	8
G4microvirus	*Microviridae*	*Bullavirinae* (new)	*Escherichia virus G4*	3
Phix174microvirus	*Microviridae*	*Bullavirinae* (new)	*Escherichia virus phiX174*	1
Alphapleolipovirus	*Pleolipoviridae* (new)		*Halorubrum virus HRPV-1*	5
Betapleolipovirus	*Pleolipoviridae* (new)		*Halorubrum virus HRPV-3*	2
Gammapleolipovirus	*Pleolipoviridae* (new)		*Haloarcula virus His2*	1

or "*Pseudomonad*" in taxon names will be replaced with the isolation host genus name: for instance, *Enterobacteria phage T7* will become *Escherichia virus T7*. In addition, host species names will be eliminated from taxon names. For example, *Thermus thermophilus phage IN93* will become *Thermus virus IN93*.

Further considerations

DNA-DNA relatedness is the gold standard in the classification of all prokaryotes [3–7], and efforts are underway to move towards a completely genomic taxonomy in that field [8]. The Bacterial and Archaeal Viruses Subcommittee has previously used overall proteome similarity to define genera and subfamilies, with 40 % homologous proteins indicating membership in the same genus [9–11]. This has resulted in spurious taxonomic lumping [12–14]. Furthermore, EMBOSS Stretcher [15, 16], which has been used for calculating nucleotide similarities between related phages (e.g., [17]), suffers from certain limitations (in particular the requirement for the genomes to be collinear). Problems with EMBOSS Stretcher are highlighted when an alignment of the phage T7 genome with a randomly shuffled T7 DNA sequence (http://www.bioinformatics.org/sms2/shuffle_dna.html) is attempted. The resulting value, 47.6 % identity, demonstrates that EMBOSS Stretcher values below a certain threshold are meaningless. Accordingly, more recent phage classification efforts have explored alternative approaches. Specifically, BLASTN [19] was found to be superior to EMBOSS Stretcher for identification and quantitative comparison of closely related phages [16]. Indeed, a BLASTN search seeded with the shuffled sequence of phage T7 specifically against "Enterobacteria phage T7" results in no detectable similarity, as expected from a randomized sequence with 48.4 % GC content. Moreover, BLASTN has also been used to determine relationships between phages at larger phylogenetic distances [17, 18], although the meaning of a similarity search hit in the absence of a true-shared ancestry remains unclear. Most of the newer programs that calculate phylogenetic relationships between genome sequences, including CLANS [20], GEGENEES [21], and mVISTA [22], are based upon sequence similarity analyses such as provided by BLASTN [19]. Complete and near-complete viral genome and protein homologies will be the focus of the Bacterial and Archaeal Viruses Subcommittee's attention in 2016 to develop clearer parameters for the molecular definition of genera, subfamilies, and families.

The changes described here were formalized and submitted in more than 40 ICTV taxonomic proposals (TaxoProps) for consideration by the ICTV Executive Committee (http://www.ictvonline.org/). One new archaeal virus family (*Pleolipoviridae*), four new bacterial subfamilies (*Guernseyvirinae* [*Salmonella* phage Jersey], *Vequintavirinae* [*Escherichia* phage rV5], *Tunavirinae* [*Escherichia* phage T1], and *Bullavirinae* [*Escherichia* phage ΦX174]), and 59 new genera including 232 species are covered in these proposals (summarized in Table 1).

While the Bacterial and Archaeal Viruses Subcommittee is delighted with the progress described here, some 400–600 new genomes of novel phages are deposited to

GenBank annually. Many of these may have to be assigned to novel species or higher taxa via the ICTV TaxoProp process. Phage classification will therefore remain a highly demanding and daunting process, unless a genomic taxonomy for viruses is embraced (see [8]). Although a taxonomy that is based on the genome sequence alone might be incorrect due to rampant genomic rearrangements in viruses [23], such an approach may turn out to be the only scalable solution.

Compliance with ethical standards

Funding This work was funded in part through Battelle Memorial Institute's prime contract with the US National Institute of Allergy and Infectious Diseases (NIAID) under Contract No. HHSN272200700016I. A subcontractor to Battelle Memorial Institute who performed this work is: J.H.K., an employee of Tunnell Government Services, Inc. B.E.D. was supported by the Netherlands Organization for Scientific Research (NWO) Vidi Grant 864.14.004 and CAPES/BRASIL.

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

References

1. Salas M (2012) My life with bacteriophage phi29. J Biol Chem 287(53):44568–44579. doi:10.1074/jbc.X112.433458
2. Yu MX, Slater MR, Ackermann HW (2006) Isolation and characterization of *Thermus* bacteriophages. Arch Virol 151(4):663–679
3. Auch AF, Klenk HP, Göker M (2010) Standard operating procedure for calculating genome-to-genome distances based on high-scoring segment pairs. Stand Genomic Sci 2(1):142–148. doi:10.4056/sigs.541628
4. Colston SM, Fullmer MS, Beka L, Lamy B, Gogarten JP, Graf J (2014) Bioinformatic genome comparisons for taxonomic and phylogenetic assignments using *Aeromonas* as a test case. MBio 5(6):e02136. doi:10.1128/mBio.02136-14
5. Lee I, Kim YO, Park SC, Chun J (2015) OrthoANI: An improved algorithm and software for calculating average nucleotide identity. Int J Syst Evol Microbiol. doi:10.1099/ijsem.0.000760
6. Richter M, Rosselló-Móra R, Glöckner FO, Peplies J (2015) JSpeciesWS: a web server for prokaryotic species circumscription based on pairwise genome comparison. Bioinformatics pii: btv681 **[Epub ahead of print]**
7. Caputo A, Merhej V, Georgiades K, Fournier PE, Croce O, Robert C, Raoult D (2015) Pan-genomic analysis to redefine species and subspecies based on quantum discontinuous variation: the *Klebsiella* paradigm. Biol Direct 10:55. doi:10.1186/s13062-015-0085-2
8. Thompson CC, Amaral GR, Campeão M, Edwards RA, Polz MF, Dutilh BE, Ussery DW, Sawabe T, Swings J, Thompson FL (2015) Microbial taxonomy in the post-genomic era: rebuilding from scratch? Arch Microbiol 197(3):359–370. doi:10.1007/s00203-014-1071-2
9. Lavigne R, Seto D, Mahadevan P, Ackermann HW, Kropinski AM (2008) Unifying classical and molecular taxonomic classification: analysis of the *Podoviridae* using BLASTP-based tools. Res Microbiol 159(5):406–414. doi:10.1016/j.resmic.2008.03.005
10. Lavigne R, Darius P, Summer EJ, Seto D, Mahadevan P, Nilsson AS, Ackermann HW, Kropinski AM (2009) Classification of *Myoviridae* bacteriophages using protein sequence similarity. BMC Microbiol 9:224. doi:10.1186/1471-2180-9-224
11. Adriaenssens EM, Edwards R, Nash JH, Mahadevan P, Seto D, Ackermann HW, Lavigne R, Kropinski AM (2015) Integration of genomic and proteomic analyses in the classification of the *Siphoviridae* family. Virology 477:144–154. doi:10.1016/j.virol.2014.10.016
12. Eriksson H, Maciejewska B, Latka A, Majkowska-Skrobek G, Hellstrand M, Melefors Ö, Wang JT, Kropinski AM, Drulis-Kawa Z, Nilsson AS (2015) A suggested new bacteriophage genus, "Kp34likevirus", within the *Autographivirinae* subfamily of *Podoviridae*. Viruses 7(4):1804–1822. doi:10.3390/v7041804
13. Niu YD, McAllister TA, Nash JH, Kropinski AM, Stanford K (2014) Four *Escherichia coli* O157:H7 phages: a new bacteriophage genus and taxonomic classification of T1-like phages. PLoS One 9(6):e100426. doi:10.1371/journal.pone.0100426
14. Wittmann J, Klumpp J, Moreno Switt AI, Yagubi A, Ackermann HW, Wiedmann M, Svircev A, Nash JH, Kropinski AM (2015) Taxonomic reassessment of N4-like viruses using comparative genomics and proteomics suggests a new subfamily—"Enquartavirinae". Arch Virol. 160(12):3053–3062. doi:10.1007/s00705-015-2609-6
15. Rice P, Longden I, Bleasby A (2000) EMBOSS: the European Molecular Biology Open Software Suite. Trends Genet 16(6):276–277
16. Ceyssens PJ, Glonti T, Kropinski NM, Lavigne R, Chanishvili N, Kulakov L, Lashkhi N, Tediashvili M, Merabishvili M (2011) Phenotypic and genotypic variations within a single bacteriophage species. Virol J 8:134. doi:10.1186/1743-422X-8-134
17. Rohwer F, Edwards R (2002) The Phage Proteomic Tree: a genome-based taxonomy for phage. J Bacteriol 184(16):4529–4535
18. Mizuno CM, Rodriguez-Valera F, Kimes NE, Ghai R (2013) Expanding the marine virosphere using metagenomics. PLoS Genet 9(12):e1003987. doi:10.1371/journal.pgen.1003987
19. Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. J Mol Biol 215(3):403–410
20. Asare PT, Jeong TY, Ryu S, Klumpp J, Loessner MJ, Merrill BD, Kim KP (2015) Putative type 1 thymidylate synthase and dihydrofolate reductase as signature genes of a novel Bastille-like group of phages in the subfamily *Spounavirinae*. BMC Genomics 16:582. doi:10.1186/s12864-015-1757-0
21. Agren J, Sundström A, Håfström T, Segerman B (2012) Gegenees: fragmented alignment of multiple genomes for determining phylogenomic distances and genetic signatures unique for specified target groups. PLoS One 7(6):e39107. doi:10.1371/journal.pone.0039107
22. Frazer KA, Pachter L, Poliakov A, Rubin EM, Dubchak I (2004) VISTA: computational tools for comparative genomics. Nucleic Acids Res; 32(Web Server issue): W273–W279
23. Krupovic M, Prangishvili D, Hendrix RW, Bamford DH (2011) Genomics of bacterial and archaeal viruses: dynamics within the prokaryotic virosphere. Microbiol Mol Biol Rev 75(4):610–635. doi:10.1128/MMBR.00011-11