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Taxonomy of bacterial viruses: establishment of tailed virus genera and the order *Caudovirales*

J. Maniloff[1] and **H.-W. Ackermann**[2]

[1] Department of Microbiology and Immunology, University of Rochester, School of Medicine and Dentistry, Rochester, New York, U.S.A.
[2] Félix d'Hérelle Reference Center for Bacterial Viruses, Département de Biologie Médicale, Université Laval, Faculté de Médecine, Cité Universitaire, Québec, Canada

Summary. Bacterial viruses have been classified into 13 families and 1 unassigned genus. A new order, *Caudovirales*, has now been established, comprising the three families of tailed bacterial viruses, based on similarities in tailed virus morphology, replication, and assembly. In addition, genera have been established for some species in each tailed virus family, based on properties involving viral DNA replication and packaging, and on some features specific to particular genera (e.g., DNA-termini linked proteins, virus-encoded polymerases, and ability to establish temperate infections). At present, there are six genera in the family *Myoviridae* (viruses with contractile tails), six in the family *Siphoviridae* (viruses with long, noncontractile tails), and three in the family *Podoviridae* (viruses with short noncontractile tails). In recognition that the definitions of tailed virus genera represent a "work in progress" and to keep the nomenclature flexible, tailed virus genera have been assigned vernacular names based on their type species.

Introduction

Over the past three decades, the Bacterial Virus Subcommittee of the International Committee on Taxonomy of Viruses (ICTV) has developed a taxonomic system for bacterial viruses. "Bacterial virus" is used here as a generic term for viruses infecting hosts in the domains *Bacteria* and *Archaea*. The Bacterial Virus Subcommittee usually has consisted of 15–20 members, representing different specialities in bacterial virology, and a variety of *ad hoc* study groups formed to examine specific issues and formulate taxonomic proposals. Subcommittee organization and international membership have provided input from many bacterial virologists, and led to an evolving taxonomy paralleling advances in viral molecular biology and phylogeny. The classification and nomenclature of bacterial viruses is reviewed in regularly published ICTV Reports, most recently in 1995 [27].

The latest compilation of bacterial viruses (data up to 1995) includes 4551 published descriptions, with 96% being tailed viruses [1]. A small fraction of these viruses have been characterized in sufficient detail to allow their classification into 13 families and 1 unas-

signed genus (Table 1). This taxonomy is reviewed and updated here to include ICTV decisions as of spring 1998.

The ICTV recently established the order *Caudovirales*, comprising the three families of bacterial tailed viruses: the families *Myoviridae* (viruses with contractile tails), *Siphoviridae* (viruses with long, noncontractile tails), and *Podoviridae* (viruses with short noncontractile tails) (Table 1). In addition, genera were established for some species in each tailed virus family. To denote the putative nature of these genera, tailed virus genera have been given vernacular names instead of more formal Latinized ones.

The other bacterial virus taxa contain viruses with cubic, helical, or no obvious symmetry (Table 1), and differ from the tailed viruses in the breadth of their host range. Tailed virus families contain species that infect hosts on most branches of the bacterial phylogenetic tree, while other bacterial virus families typically contain viruses with limited host ranges (Table 1) [1]. Of particular interest, two of the three tailed virus families (*Myoviridae* and *Siphoviridae*) include species that infect *Bacteria* and species that infect *Archaea*, suggesting tailed viruses may have originated before divergence of the *Bacteria* and *Archaea* phylogenetic branches.

Table 1. Classification of bacterial viruses

Order Family Genus	Description of order/family	Type species
	Double-stranded DNA viruses	
Caudovirales	tailed phages, genome linear dsDNA	
Myoviridae	contractile tails	
"T4-like viruses"		coliphage T4
"P1-like viruses"		coliphage P1
"P2-like viruses"		coliphage P2
"Mu-like viruses"		coliphage Mu
"SP01-like viruses"		Bacillus phage SP01
"ΦH-like viruses"[a]		Halobacterium phage ΦH
Siphoviridae	long, noncontractile tails	
"λ-like viruses"		coliphage λ
"T1-like viruses"		coliphage T1
"T5-like viruses"		coliphage T5
"L5-like viruses"		Mycobacterium phage L5
"c2-like viruses"		Lactococcus phage c2
"ψM1-like viruses"[a]		Methanobacterium phage ψM1
Podoviridae	short, noncontractile tails	
"T7-like viruses"		coliphage T7
"P22-like viruses"		enterobacteria phage P22
"ϕ29-like viruses"		Bacillus phage ϕ29
Tectiviridae	lipid-containing, double icosahedral capsids, produce tail-like tube upon nucleic acid ejection, genome linear dsDNA	
Tectivirus		polyvalent phage PRD1

Table 1 (*continued*)

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Order Family Genus	Description of order/family	Type species
Corticoviridae	lipid-containing, icosahedral capsid, genome circular dsDNA	
Corticovirus		Alteromonas phage PM2
Plasmaviridae	enveloped, pleomorphic, genome circular dsDNA	
Plasmavirus		Acholeplasma phage L2
Lipothrixviridae[a]	enveloped, rod-shaped, genome linear dsDNA	
Lipothrixvirus		Thermoproteus virus TTV1
Rudiviridae[a]	nonenveloped, rod-shaped, genome linear dsDNA	
Rudivirus		Thermoproteus virus TTV4
Fuselloviridae[a]	nonenveloped, lemon-shaped, genome circular dsDNA	
Fusellovirus		Sulfolobus virus SSV1
Unassigned Genus SNDV[a]	droplet-shaped, genome circular dsDNA	Sulfolobus virus SNDV
	Single-stranded DNA viruses	
Inoviridae	nonenveloped, filamentous or rod-shaped, genome circular ssDNA	
Inovirus		coliphage Ff[b]
Plectrovirus		Acholeplasma phage L51
Microviridae	nonenveloped, icosahedral, genome circular ssDNA	
Microvirus		coliphage ϕX174
Spiromicrovirus		Spiroplasma phage SpV4
Bdellomicrovirus		Bdellovibrio phage MAC1
Chlamydiamicrovirus		Chlamydia phage Chp1
	Double-stranded RNA viruses	
Cystoviridae	enveloped, icosahedral, genome segmented linear dsRNA	
Cystovirus		Pseudomonas phage ϕ6
	Positive-sense, single-stranded RNA viruses	
Leviviridae	nonenveloped, icosahedral, genome linear ssRNA	
Levivirus		enterobacteriophage MS2
Allolevirus		enterobacteriophage Qβ

[a] Infect *Archaea* spp.
[b] Collective designation for coliphages M13, f1, and fd

Tailed virus species

Although electron microscopic observation of a virus is frequently sufficient for preliminary assignment to a specific family, additional physical, chemical, and biological properties are needed to define a species. The ICTV definition of a virus species is [27, 35]: "A virus species is a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche." This means that members of a species must have a number of properties in common, but no single property need be shared by all members of the species.

Common criteria used to define tailed virus species are morphology, protein composition, DNA structure, base sequence similarity, host range, and infection characteristics [4]. These properties are generally adequate to identify a virus or group of viruses as distinct from other virus species. The 1995 ICTV Report lists several hundred species of tailed bacterial viruses [27]. However, as for other viruses, there is an element of judgment in deciding whether a particular bacterial virus should be considered a species or a strain. In addition, all levels of bacterial virus taxonomy are confounded by the exceptional diversity of viral genotypes and phenotypes [3, 21].

Tailed virus genera

The ICTV definition of a virus genus is [27]: "A virus genus is a group of species sharing certain common characters." Criteria for grouping tailed virus species into genera have emerged only over the last few years, with increasing data on viral genomes and the molecular biology of viral replication and assembly. Unfortunately, such data are available, at present, only for a relatively small number of tailed viruses.

Two types of criteria have been used to define tailed virus genera. The first are properties related to DNA replication and packaging, and are applicable to all viruses. The second are specific features a virus may or may not have, and are limited to particular genera.

For the first type of criteria, the coupling of viral DNA replication and packaging mechanisms generates a set of overlapping properties linking DNA structure, replication, and packaging [8]. First, unit length progeny viral DNA can be packaged from either concatemeric or non-concatemeric DNA. Second, concatemeric DNA can be produced by either recombination between linear DNAs or rolling circle replication. Third, progeny viral DNA can be cleaved and packaged from concatemeric DNA at: (1) unique sites to produce identical DNA molecules; (2) *pac* sites to produce DNA molecules with limited circular permutation and terminal redundancy; or (3) random sites to produce circularly permuted, terminally redundant DNA molecules. The first option, cleavage at a unique site, generates DNA molecules with either cohesive ends (*cos* sites or "sticky ends") or blunt end termini. Terminal sequences of progeny DNA molecules produced this way are either unique or have terminal repeats.

The second type of criteria are features a virus genus may or may not have, such as: (1) DNA termini-linked proteins to prime DNA replication; (2) virus-encoded type A or B DNA polymerase; (3) virus-encoded RNA polymerase; (4) single-stranded DNA nicks; (5) unusual DNA bases; (6) DNA replication via transposition; and (7) the ability to establish a temperate infection, with the prophage either integrated into the host chromosome or persisting as a plasmid. Host range is also a useful taxonomic character (e.g.,

Bacteria or *Archaea*, Gram-positive or Gram-negative eubacteria). Although these properties have more limited applicability, they provide distinctive taxonomic markers in defining certain genera [2].

Using these criteria, six genera have been established in the family *Myoviridae* (Table 2), six in the family *Siphoviridae* (Table 3) and three in the family *Podoviridae* (Table 4). The type species of these genera are illustrated in Fig. 1.

Table 2. Distinguishing features of *Myoviridae* genera[a]

Property	Feature
	"T4-like phages"
Infection	virulent
Genome	about 170 kbp, with circular permutation and terminal repeats, cytosine replaced by 5-hydroxymethylcytosine
DNA replication	concatemer formation via recombination
DNA packaging	headful packaging and random cleavage from concatemers
Phage-encoded polymerases	type B DNA polymerase
Hosts	entero- and related bacteria (*Acinetobacter*, *Aeromonas*, *Pseudomonas*, *Vibrio*)
	"P1-like phages"
Infection	temperate, with prophage persisting as plasmid
Genome	about 100 kbp, with limited circular permutation and terminal repeats
DNA replication	via θ structures followed by rolling circle replication to form concatemers
DNA packaging	headful packaging processively from *pac* sites in concatemers
Phage-encoded polymerases	no activity reported
Hosts	entero- and related bacteria (*Aeromonas*, *Vibrio*)
	"P2-like phages"
Infection	temperate, with prophage integrated into host chromosome by site-specific recombination
Genome	about 33 kbp, unique genome with cohesive ends (*cos* sites)
DNA replication	via θ structures to form covalently closed circular DNA
DNA packaging	covalently closed circular molecules cleaved at *cos* site and packaged
Phage-encoded polymerases	none
Hosts	entero- and related bacteria (*Hemophilus*)
	"Mu-like phages"
Infection	temperate, with prophage integrated at random locations in host chromosome by nonreplicative and replicative mechanisms

Table 2 (*continued*)

Table 2 (*continued*)

Property	Feature
Genome	about 40 kbp, consisting of phage genome with cell DNA at both termini
DNA replication	via replicative transposition of phage genome to random sites in host genome
DNA packaging	from integrated phage DNA by cleavage about 100 bp from left end, headful packaging, and cleavage about 2 kbp from right end
Phage-encoded polymerases	no activity reported
Hosts	enterobacteria
	"SP01-like phages"
Infection	virulent
Genome	140–160 kbp, unique genome with short terminal repeats, thymine replaced by 5-hydroxymethyluracil
DNA replication	concatemer formation, probably by annealing single-stranded 3'-ends of terminal repeats of daughter molecules
DNA packaging	data not available, but genome structure suggests headful packaging from concatemers with site-specific cleavage and DNA synthesis to duplicate terminal repeats
Phage-encoded polymerases	type A DNA polymerase
Hosts	*Bacillus* spp.
	"ΦH-like viruses"
Infection	temperate, with provirus persisting as plasmid
Genome	about 59 kbp linear ds DNA, with limited circular permutation and terminal repeats
DNA replication	data not available
DNA packaging	data not available, but genome structure suggests headful packaging processively from *pac* sites in concatemers
Phage-encoded polymerases	data not available
Hosts	*Halobacterium* (*Archaea*)

[a] References: T4 [6, 9, 20], P1 [9, 37], P2 [7, 9], Mu [9, 13, 34], SP01 [32], ΦH [33]

Table 3. Distinguishing features of *Siphoviridae* genera[a]

Property	Feature
	"λ-like phages"
Infection	temperate, with prophage integrated into host chromosome by site-specific recombination
Genome	about 49 kbp, unique with cohesive ends (*cos* sites)
DNA replication	via θ structures followed by rolling circle replication to produce concatemers
DNA packaging	progeny DNA cut from concatemers at *cos* sites
Phage-encoded polymerases	none
Hosts	enterobacteria
	"T1-like phages"
Infection	virulent
Genome	about 49 kbp, with limited circular permutation and terminal repeats
DNA replication	concatemers formed via recombination
DNA packaging	headful packaging processively from *pac* sites in concatemers
Phage-encoded polymerases	no activity reported
Hosts	enterobacteria
	"T5-like phages"
Infection	virulent
Genome	about 121 kbp, unique with (10 kbp terminal repeats) and 5 site-specific single-strand nicks
DNA replication	DNA injection by 2-step transfer process, concatemers formed
DNA packaging	data not available, but genome structure suggests headful packaging from concatemers with site-specific cleavage and DNA synthesis to duplicate terminal repeats
Phage-encoded polymerases	type A DNA polymerase
Hosts	entero- and related bacteria (*Vibrio*)
	"L5-like phages"
Infection	temperate, with prophage integrated into host chromosome by site-specific recombination
Genome	about 52 kbp, unique with cohesive ends (*cos* sites)
DNA replication	data not available
DNA packaging	progeny DNA cut at *cos* sites
Phage-encoded polymerases	type A DNA polymerase
Hosts	*Mycobacterium* spp.
	"c2-like phages"
Infection	virulent
Genome	about 22 kbp, unique with cohesive ends (*cos* sites)
DNA replication	data not available, putative recombinase gene with possible function in concatemer formation
DNA packaging	progeny DNA cut at *cos* sites

Table 3 (*continued*)

Table 3 (*continued*)

Property	Feature
Phage-encoded polymerases	putative type B DNA polymerase
Hosts	*Lactococcus* spp.
	"ψM-like viruses"
Infection	virulent
Genome	about 30 kbp linear ds DNA, with circular permutation and terminal repeats
DNA replication	data not available
DNA packaging	data not available, but genome structure suggests headful packaging and random cleavage from concatemers
Phage-encoded polymerases	data not available
Hosts	*Methanobacterium thermoautotrophicum*

[a] References: λ [9, 10, 16], T1 [12], T5 [25], L5 [14], c2 [18, 19, 23], ψM [33]

The tailed virus genera described here represent a "work in progress." There will certainly be genera additions, deletions, modifications, and rearrangements as more viruses are studied and more data become available. To keep this putative taxonomy flexible and open to revision, tailed virus genera have been given provisional vernacular names. As the degree of confidence in specific established genera increases, formal Latinized names for those genera will be proposed. Until then, the vernacular tailed virus genus names are easy to remember and use, acknowledge the tentative nature of this level of classification, and should facilitate further discussion of bacterial virus taxonomy and phylogeny.

In each genus, a species for which considerable data are available has been designated the type species and used in the genus name (Table 1). As noted by Van Regenmortel et al. [35]: "It should be stressed that the type species is not, and never could be, one which is most typical of the properties of all species in a genus." The species in each genus will be listed in the next ICTV Report, to be published in 1999.

Tailed virus families

The ICTV definition of a virus family is [27]: "A family is a group of genera sharing certain common characters." The three families of tailed viruses were originally established as groups of species with similar tail morphology, comprising viruses with contractile tails (family *Myoviridae*); long, noncontractile tails (family *Siphoviridae*); and short noncontractile tails (family *Podoviridae*). These tail morphologies reflect major differences in viral genome complexity and mode of infection, and in virion assembly and maturation. The structure of contractile versus noncontractile tails means significant differences in gene number and function, and in the mechanism of DNA injection during infection. The assembly of long versus short noncontractile tails involves differences in assembly pathways: long tails are completely assembled and then added onto completed heads, while short tails are sequentially assembled onto completed heads.

There is extensive variation in tail fine structure and size, head morphology and size (ranging from isometric to prolate, elongated icosahedra) and DNA content within each

Table 4. Distinguishing features of *Podoviridae* genera[a]

	"T7-like phages"
Infection	virulent
Genome	about 40 kbp, unique with short terminal repeats
DNA replication	semi-conservative replication of linear molecules, with concatemers formed by annealing single-stranded 3'-ends of terminal repeats of daughter molecules
DNA packaging	packaging from concatemers with mechanism for site-specific cleavage and DNA synthesis to duplicate terminal repeats
Phage-encoded polymerases	type A DNA polymerase and RNA polymerase
Hosts	entero- and related bacteria (*Kluyvera*, *Pseudomonas*, *Vibrio*)
	"P22-like phages"
Infection	temperate, with prophage integrated into host chromosome by site-specific recombination
Genome	about 43 kbp, with limited circular permutation and terminal repeats
DNA replication	via θ structures followed by rolling circle replication to produce concatemers
DNA packaging	headful packaging processively from *pac* sites in concatemers
Phage-encoded polymerases	type A DNA polymerase
Hosts	enterobacteria
	"ϕ29-like phages"
Infection	virulent
Genome	about 19 kbp, unique with short inverted terminal repeats and protein covalently linked to 5'-termini
DNA replication	primed by protein at 5'-termini, proceeds from both termini by strand displacement to produce linear monomeric daughter molecules
DNA packaging	linear daughter molecules packaged
Phage-encoded polymerases	type B DNA polymerase
Hosts	*Bacillus* and *Streptococcus* spp.

[a] References: T7 [9, 15], P22 [28], ϕ29 [26,30]

tailed virus family [3]. Also, *Myoviridae* and *Siphoviridae* are the only bacterial virus families with species infecting *Bacteria* and *Archaea* hosts, suggesting ancestral tailed viruses may have evolved before the phylogenetic separation of these two prokaryote domains [3, 38].

Tailed virus order

The ICTV definition of a virus order is [27]: "An order is a group of families sharing certain common characters." The first two virus orders were established for animal viruses based on similarities in genome organization and replicative strategies [11, 29].

A third order has now been established for bacterial tailed viruses, the order *Caudovirales* (caudo: from Latin *cauda*, "tail") comprising the families *Myoviridae*, *Siphoviridae*, and *Podoviridae* (Table 1). Unlike the previous two orders, similar genome organization and sequences are not useful properties for defining higher order bacterial virus taxa, and different criteria are required to evaluate the deep taxonomic and phylogenetic relationships

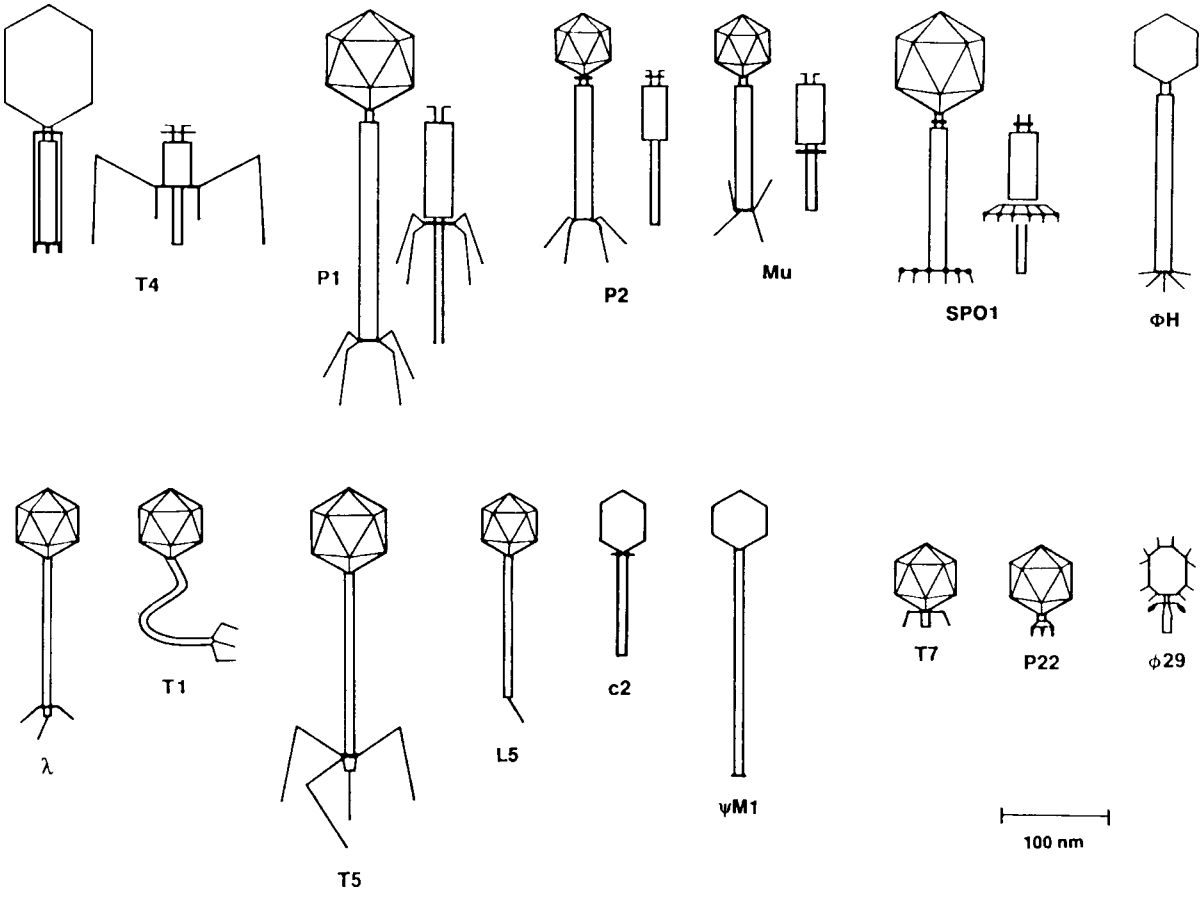

Fig. 1. Morphology of tailed virus genera type species

amongst bacteria and viruses. Many traces of bacterial and viral phylogenetic relationships appear to have been obscured by great geological age [31], large population sizes and ecological diversity [24], and extensive horizontal gene transfer [2, 5, 10, 17, 22].

Nevertheless, the order *Caudovirales* (grouping the families *Myoviridae*, *Siphoviridae*, and *Podoviridae*) has been established based on relationships amongst tailed viruses still evident in common aspects of their morphology, replication, and assembly [2]:

1. The virion consists of a head, an icosahedron-based protein shell with 5-fold symmetry, containing one molecule of linear dsDNA, and a helix-based protein tail with 6-fold symmetry, for adsorption and DNA injection into host cells. The head and tail are joined by a connector. Some minor dimensions, such as tail width, are remarkably similar suggesting selective advantages for conservation of such structural features. Virions have no envelope and typically contain no lipids.
2. Infection involves DNA injection into host cells, with the virion protein shell remaining on the cell surface. In general, DNA replication proceeds via formation of concatemers. Cleavage of concatemers produces unit-length linear progeny viral DNAs. There are a few alternative ways in which unit-length linear progeny DNA is produced: (1) replication of unit-length linear DNA primed by DNA termini-linked proteins (e.g., Bacillus

phage ϕ29), (2) replicative transposition (e.g., coliphage Mu), or (3) replication of θ structures to form covalently closed circular DNA which is then cleaved at *cos* sites (e.g., coliphage P2). These linear progeny viral DNAs are packaged into viral proheads.

3. The virion capsid is assembled from a precursor prohead, consisting of a protein shell, a portal protein, and internal scaffolding protein or its functional equivalent. Progeny viral DNA enters preformed proheads and head maturation proceeds via proteolytic cleavages of capsid subunits.
4. Virion assembly is completed by addition of a protein tail to, or assembly of a protein tail on, a matured, DNA-filled head. Progeny virus release is by cell lysis, produced by one or two virus-encoded lytic enzymes (lysins and holins).

Conclusions

The taxonomy of the bacterial viruses in the First ICTV Report in 1971 consisted of six genera: viruses with (1) a polyhedral capsid and contractile tail, containing dsDNA (T-even virus types), (2) a polyhedral capsid and noncontractile tail, containing dsDNA (T-odd and λ virus types), (3) an icosahedral capsid containing lipid and dsDNA (PM2 virus), (4) an icosahedral capsid containing ssDNA (ϕX174 virus), (5) an icosahedral capsid containing ssRNA (f2 virus), and (6) a filamentous capsid containing ssDNA (fd virus) [36]. The taxonomy of bacterial viruses in the Seventh ICTV Report, to be published in 1999, consists of 1 order, 13 families, 30 genera, and 1 unassigned genus (Table 1). This taxonomic expansion reflects investigations of bacterial cells and viruses in increasingly diverse habitats and application of advances in molecular biology to the study of bacterial viruses. These change have been extraordinarily rapid.

Although tailed bacterial viruses now have order status, their classification is still in a very early stage, because: (1) most virus isolates are from relatively few extensively studied types of bacteria (e.g., enterobacteria and *Bacillus*), (2) most virus isolates have not yet been classified into species, (3) most virus species have not yet been classified in genera, and (4) most established virus genera represent the few well-studied types of viruses that infect enterobacteria or *Bacillus*. These concerns apply, not only to the tailed bacterial viruses, but to most bacterial virus families. This means that current bacterial virus taxonomy reflects only a fraction of the range of bacterial virus diversity and suggests that more tailed virus genera will be identified as the microbiology of new ecosystems is studied. An indication of the extent of novel viruses yet to be discovered can be seen in the fact that, thus far, limited studies of *Archaea* viruses over the last 10 years already have led to establishment of two new tailed virus genera, three new families, and one new unassigned genus (Table 1).

The classification of bacterial viruses has been developed over several decades by virologists from many countries who have served on ICTV Bacterial Virus Subcommittees and Study Groups. Bacterial virus taxonomy is an evolving structure, and we welcome comments and suggestions from the virology community for improving and extending it.

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Authors' address: Dr. J. Maniloff, Department of Microbiology and Immunology, University of Rochester, Medical Center Box 672, Rochester, NY 14642, U.S.A.