

Prokaryote viruses studied by electron microscopy

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Abstract This review summarizes the electron microscopical descriptions of prokaryote viruses. Since 1959, nearly 6300 prokaryote viruses have been described morphologically, including 6196 bacterial and 88 archaeal viruses. As in previous counts, the vast majority (96.3 %) are tailed, and only 230 (3.7 %) are polyhedral, filamentous, or pleomorphic. The family *Siphoviridae*, whose members are characterized by long, noncontractile tails, is by far the largest family (over 3600 descriptions, or 57.3 %). Prokaryote viruses are found in members of 12 bacterial and archaeal phyla. Archaeal viruses belong to 15 families or groups of family level and infect members of 16 archaeal genera, nearly exclusively hyperthermophiles or extreme halophiles. Tailed archaeal viruses are found in the Euryarchaeota only, whereas most filamentous and pleomorphic archaeal viruses occur in the Crenarchaeota. Bacterial viruses belong to 10 families and infect members of 179 bacterial genera, mostly members of the Firmicutes and γ -proteobacteria.

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Introduction

Prokaryote viruses include archaeal and bacterial viruses. The latter, commonly named “phages” or bacteriophages, occur in enormous numbers everywhere in nature and probably constitute the most common entities in the living world [11, 31]. They occur in the oceans and freshwater, the rhizosphere, on plants and food, in industrial fermentations, and on the outside and in the body cavities of humans and animals. In addition, most cultivable bacteria carry prophages, which may be complete and infectious or represent fragments of viral genomes. Bacterial viruses have been observed in great numbers and constitute the largest of all virus groups. The first archaeal viruses, also named archeoviruses, were described in 1974 in batch cultures of *Halobacterium halobium* [32]. They are generally found in extreme environments, whether hypersaline, anaerobic, or hyperthermic, which are difficult to reproduce in the laboratory. As a result, archaeal viruses have been relatively little studied, but their investigation has been rewarded by the discovery of a wealth of novel and indeed exceptional virus types.

This study is an update of earlier virus counts. We intend to present a reasonably complete and exact account of prokaryote viruses studied by electron microscopy and to report the frequency of virus isolations per host genus or group. The first phage survey was published in 1967 [12]. It listed 111 negatively stained viruses, mostly tailed phages, but also phage ϕ X174 (*Microviridae*), two ssRNA phages or *Leviviridae*, and nine filamentous phages of the family *Inoviridae*. The latest surveys were published in 1996, 2001, and 2007, featuring 4551, 5136, and 5568 viruses, respectively [1, 2, 4]. Archaeal viruses were then still counted as “phages”, partly because several of them had the characteristic head-tail morphology of most bacterial

viruses. In all surveys, over 96 % of phages were tailed and belonged to the same three families, the *Myoviridae*, *Siphoviridae*, and *Podoviridae*. In the last 20 years, the rate of bacterial and archaeal virus descriptions has remained constant, at approximately 100 per year (Fig. 1). This trend is likely to continue in the future.

This survey is based on the authors' personal files. It starts in 1959 with the introduction of negative staining by Brenner, Horne and their coworkers [9, 10]. The survey encompasses negatively stained viable or potentially viable, lytic and lysogenic viruses from regular publications (periodicals, books, theses). Series of mutants are counted as a single virus each. The survey does not cover shadowed or sectioned viruses and those few illustrated by atomic force microscopy; known defective phages; "particulate bacteriocins" and "killer particles"; unpublished viruses from oral communications, congress reports, patent applications, and databases; phages with unidentified hosts (e.g., unclassified marine bacteria); uncultured virus-like particles without host (e.g., observed in environmental studies of water and soil); lump descriptions of unspecified numbers of viruses; and finally, a small number of individual, unidentifiable entities illustrated by very poor micrographs. The reader is referred to a recent overview of archaeal viruses [21] and a prokaryote virus bibliography with 31,000 references for the years 1965 to 2011 (Félix d'Herelle Reference Center, <http://www.phage.ulaval.ca>). A list of 5000 phage names is available on the Internet (<http://www.phage.org/names.htm>). For sequenced genomes of prokaryote viruses, we refer the reader to a recent review [18].

Presentation of data

As in the preceding surveys [1, 2, 4], viruses are listed by families or, in the case of those awaiting further classification, "groups". Phage classification started in 1967 when Bradley [8] defined six basic morphotypes of bacteriophages

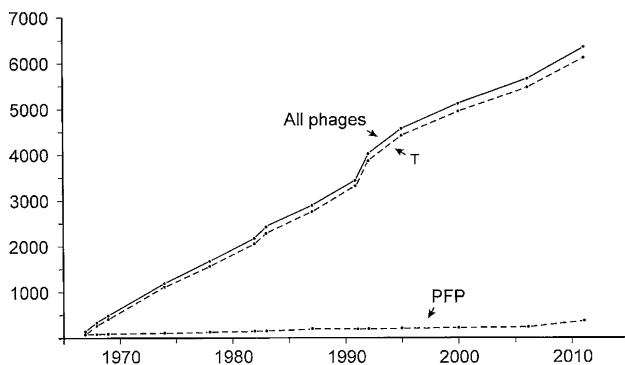


Fig. 1 Cumulative numbers of prokaryote virus descriptions from 1967 to 2011; modified from [4]. PFP, polyhedral, filamentous and pleomorphic viruses; T, tailed viruses

by gross morphology and type of nucleic acid, termed A-F, corresponding to the present phage families *Myoviridae* (tail contractile), *Siphoviridae* (tail long and noncontractile), *Podoviridae* (tail short), and *Microviridae*, *Leviviridae*, and *Inoviridae*, respectively (Fig. 2). New types were added over time. The present ICTV bacteriophage classification [16] includes one order, *Caudovirales*, which encompasses tailed phages, and seven other families that are all very small and sometimes have a single member only (Table 1). These taxa have been described in detail elsewhere [3, 16]. Archaeal viruses are listed according to the same principles. Some of them have been officially classified by the ICTV; others are still awaiting classification.

Prokaryote viruses (Table 1, Fig. 2) can be tailed, polyhedral, filamentous, or pleomorphic (PFP). They contain single-stranded or double-stranded DNA or RNA. Tailed viruses, grouped in the order *Caudovirales*, have icosahedral heads or prolate capsids that have additional rows of subunits in their central parts. PFP viruses are not yet grouped into orders, although similarities are apparent in some taxa of archeoviruses (see below). Polyhedral viruses are icosahedra or closely related bodies (e.g., tricontahedra in the case of leviviruses). Some contain lipids in an internal lipoprotein vesicle (*Tectiviridae*, SH1- and STIV-groups) or even as part of the capsid itself (*Corticoviridae*). Pleomorphic viruses cover a broad range of forms, including fusiform, bacilliform, spherical shapes, and particles resembling bottles and droplets. Many of the pleomorphic viruses and certain filamentous viruses (*Lipothrixviridae*) have lipid envelopes. Lipid-containing viruses are generally chloroform-sensitive.

In Tables S1 and S2, viruses are listed by host genus because both bacterial and archaeal viruses are essentially host-genus-specific in infection and replication. Enterobacteria are so closely related – and cross-genus reactions are so frequent in them – that they constitute, from the phage viewpoint, a single host “genus.” A few more polyvalent phages exist in the family *Tectiviridae* [5] and are found among viruses of the archaeal genera *Haloarcula* and *Halorubrum* [22], but this does not invalidate the general observation that most prokaryote viruses are genus-specific. The list of bacterial hosts was verified on the Internet at the site of the National Center of Biotechnology Information (NCBI, <http://www.ncbi.nlm.nih.gov/Taxonomy>) in Bethesda, MD. It is noteworthy that bacterial taxonomy and nomenclature have remained essentially stable during the last five years.

Virus frequency and distribution

Approximately 6300 prokaryote viruses have been studied by electron microscopy. This makes them arguably the

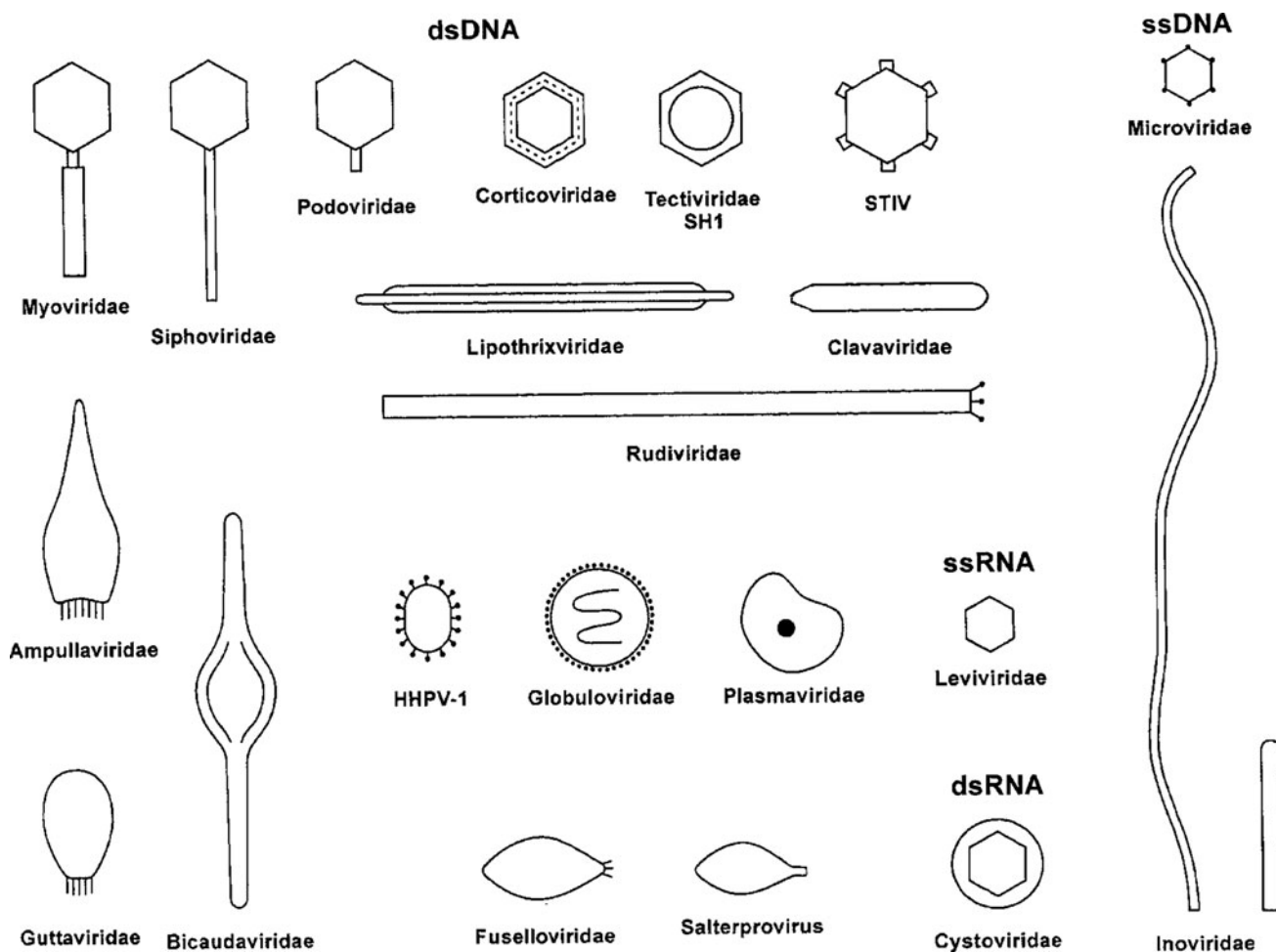


Fig. 2 Morphotypes of prokaryote viruses; modified from [4]. See Table 1 for explanations

largest virus group known. The vast majority are bacterial viruses (98.5 %), but this reflects largely the relative ease of cultivation of bacterial viruses and the overall research effort directed at them. With respect to previous surveys, the general frequency of phage groups has not changed.

Viruses have been found in 12 prokaryote phyla comprising 16 archaeal and 163 bacterial genera (Tables 2, S1, S2). Electron microscopic observations are summarized in Table 2 and compared with the numbers of complete genome sequences of tailed and PFP-type viruses, respectively, recorded in GenBank. Both archaea and bacteria have tailed viruses. They fall into the three basic families *Myoviridae*, *Siphoviridae*, and *Podoviridae* (24.8, 57.3, and 14.2 % of all viruses, respectively) (Fig. 2). Although most capsids are isometric, approximately 15 % of them are prolate. Elongated heads are relatively frequent in enterobacterial and lactococcal phages (up to 29 % in the latter). The frequent practice of ascribing icosahedral symmetry to any isometric capsid or virion with a hexagonal outline

should be abandoned. Indeed, hexagonal capsids may be icosahedra, octahedra, or dodecahedra.

In bacteriophages, tailed viruses predominate overwhelmingly, whereas PFP types are relatively rare. This suggests that the rate of discovery of PFP bacteriophages has reached a ceiling. As in previous surveys, phages of enterobacteria and the host genera *Streptomyces*, *Mycobacterium*, *Bacillus*, *Lactococcus*, *Pseudomonas*, and *Vibrio* predominate. It is noteworthy that the vast majority of actinophages are siphoviruses, whereas enterobacteria have a much more balanced phage population, including relatively numerous podoviruses and polyhedral and filamentous phages. About 10 additional bacterial genera (indicated by asterisks in Table S1) produce headless contractile tails, suggesting that complete myoviruses may be found some day in these bacteria. The prevalence of tailed phages among bacterial viruses is in agreement with observations in nature. In aquatic systems where bacteria dominate, the overwhelming majority of observed

Table 1 Overview of prokaryote virus families

Shape	Nucleic acid	Virus group	Particulars	Example		
Tailed	DNA, 2, L	<i>Myoviridae</i>	Tail contractile	T4		
		<i>Siphoviridae</i>	Tail long, noncontractile	λ		
		<i>Podoviridae</i>	Tail short	T7		
Polyhedral	DNA, 1, C 2, C, S 2, L 2, L 2, C RNA, 1, L 2, L, seg	<i>Microviridae</i>	Conspicuous capsomers	ϕ X174		
		<i>Corticoviridae</i>	Complex capsid, lipids	PM2		
		<i>Tectiviridae</i>	Inner lipid vesicle, pseudotail	PRD1		
		SH1, group*	Inner lipid vesicle	SH1		
		STV1 group*	Turret-shaped protrusions	STIV		
		<i>Leviviridae</i>	Poliovirus-like	MS2		
		<i>Cystoviridae</i>	Envelope, lipids	ϕ 6		
Filamentous	DNA, 1, C 2, L 2, L 2, C	<i>Inoviridae</i>	a. Long filaments b. Short rods	fd MVL1		
		<i>Lipothrixviridae</i>	Envelope, lipids	TTV1		
		<i>Rudiviridae</i>	TMV-like	SIRV-1		
		<i>Clavaviridae</i>	Bacilliform rods	APBV1		
		Pleomorphic	DNA, 2, C, S 2, C, S 2, L, S 2, C, S 2, L 2, C 2, L	<i>Plasmaviridae</i>	Envelope, lipids, no capsid	L2
				HHPV-1 group*	Same	HHPV-1
<i>Fuselloviridae</i>	Same, lemon-shaped			SSV1		
<i>Salterprovirus</i>	Same, lemon-shaped			His1		
		<i>Guttaviridae</i>	Droplet-shaped	SNDV		
		<i>Ampullaviridae</i>	Bottle-shaped	ABV		
		<i>Bicaudaviridae</i>	Two-tailed, growth cycle	ATV		
		Globulaviridae	Paramyxovirus-like	PSV		

C circular; L linear; S superhelical; seg segmented; 1 single-stranded; 2 double-stranded

*Awaiting classification

virus-like particles resemble tailed phages [33]. However, this type of virus is rare in habitats where archaea represent the major constituent of microbial communities [23, 30].

Novel families of archaeal viruses

There is a clear divide between viruses of the archaeal phyla Euryarchaeota and Crenarchaeota. The former, which include extreme halophiles, methanogens, and hyperthermophiles, have a considerable number of tailed viruses and relatively few PFP types. The relative frequency of tailed viruses in extreme halophiles does not correspond to the observation of viral morphotypes in hypersaline waters, where tailed viruses are only a minority and particles with unusual shapes, not yet cultured, dominate [23, 30]. One of the reasons for this discrepancy could be a biased method of isolation of haloviruses, strongly favouring the isolation of lytic, tailed viruses [7, 23]. Some spindle-shaped haloviruses are classified as belonging to the genus *Salterprovirus*, while others are awaiting classification (Table S2c). The icosahedral halovirus SH1 and the pleomorphic haloviruses HHPV-1 (Fig. 2) and HRPV-1

also remain unclassified. The latter two have a lipid-containing membrane; however, they differ in the nature of their DNA genome, which is double-stranded in HHPV-1 and single-stranded in HRPV-1 [29].

The cultured members of the Crenarchaeota are exclusively hyperthermophiles growing optimally at temperatures above 80 °C. All of these viruses are of the PFP type and have most unusual shapes and particle designs, including the recently discovered bacilliform [19], bottle-shaped [15], spindle-shaped [20, 27], and ovoid viruses [20]. The morphological diversity of isolated crenarchaeal viruses corresponds to reports on virus-like particles in extreme geothermal environments, where hyperthermophilic archaea are the major component of microbial communities [26, 28, 34, 35]. Due to their exceptional morphological and genomic properties, the Crenarchaeota viruses were assigned by the ICTV to eight novel viral families, comprising fusiform *Fuselloviridae* and *Bicaudaviridae*, bacilliform *Clavaviridae*, filamentous *Rudiviridae* and *Lipothrixviridae*, spherical *Globuloviridae*, bottle-shaped *Ampullaviridae* and droplet-shaped *Guttaviridae* (Table 1). Moreover, it has been proposed to establish a new viral order, “Ligamenvirales”, for two families of

Table 2 Numbers of prokaryote viruses (N) and corresponding complete genome sequences available in GenBank

Prokaryote phyla	Tailed phages					PFP	
	<i>Myoviridae</i> , N	<i>Siphoviridae</i> , N	<i>Podoviridae</i> , N	All, N	Genome sequences	Viruses, N	Genome sequences
Archaea							
Euryarchaeota	26	17	1	44	4	7	7
Crenarchaeota						37	33
Bacteria							
Actinobacteria	8	551	22	581	84	1	
Bacteroidetes	39	25	3	67	3	3	
Chlamydia						3	6
Cyanobacteria	32	14	17	63	24		
Deinococcus-Thermus	6	12		18	3	10	
Firmicutes	406	1950	98	2454	133		
Bacilli	305	1873	72	2250	124	11	3
Clostridia, others	101	77	26	204	9	1	
Mollicutes	1	3	10	14	1	21	7
Fusobacteria	3	1	3	7			
Proteobacteria	1023	1030	737	2790	238		
α -Proteobacteria	87	243	165	495	8	9	5
β -Proteobacteria	40	29	12	81	33	4	41
γ -Proteobacteria	820	744	553	2117	191	114	1
δ -Proteobacteria	37	2	7	46	1	9	
ε -Proteobacteria	39	12		51	1		
Spirochaetes	14	2		16			
Total	1558	3605	891	6054	500	230	103

Genome sequences for Firmicutes and Proteobacteria viruses were counted by the authors. All other sequence data are from ref 18

Names in bold indicate supergroups (Firmicutes, Proteobacteria). Numbers in bold indicate the observations made in these supergroups
PFP polyhedral, filamentous and pleomorphic

filamentous viruses, the *Rudiviridae* and *Lipothrixviridae*, because structural and genomic data reveal a robust evolutionary link between members of these two families [24]. A few spindle-shaped and polyhedral viruses still await classification. Despite broad structural similarities to the tectiviruses, the STIV group will probably be assigned to a new family because of the exceptional features of their adsorption structures (apical turrets) and genomes.

Except for tailed viruses, the majority of known archaeal viruses establish a chronic infection in which virions are continuously produced, and the host cell remains alive although its growth rate is usually lower or even null. The best-studied lytic viruses exploit a novel mechanism of egress that is based on formation of a virus-encoded cellular structure that serves as a gate lock for virion release [25].

Outlook

Although the number of archaeoviruses studied by electron microscopy, so far less than 100, is only about 1.5 % of

that of bacterial viruses, their morphological diversity is astounding and significantly surpasses that of bacterial viruses. There are reasons to believe that the exceptional diversity of known archaeal viruses represents no more than the tip of an iceberg. Moreover, archaeal viruses have been isolated from only a few hosts only and a narrow variety of habitats. But even these revealed virus-like particles of a bewildering variety and often unknown nature. Thus, the number of archaeovirus morphotypes is likely to expand in the next years.

By contrast, no new families of bacterial viruses have been found since the 1970s. The last phage families discovered, the *Plasmaviridae* and *Corticoviridae*, were found in 1968 and 1971, respectively [13, 14]. This is likely to remain so, unless little-studied groups of bacteria, for example the phyla *Chloroflexi*, *Nitrospira*, or *Planctomycetes*, are investigated for the presence of viruses. Nevertheless, there is some reason to be optimistic. Not only are prokaryote viruses the most abundant life form on Earth, but (a) viral diversity has been investigated in a few types of environments only, (b) metagenomic studies have shown

that only 10 % of viral genomes in seawater are found in existing databases and suggest that members of hundreds or thousands of virus species may be present in the oceans [6], and (c) there are very few electron microscopical studies on the phage flora outside of Europe and North America. One of them was done by H.W.A., under very imperfect conditions, on Nigerian phages. It yielded only some 14 morphotypes, most of which could be related to known phage species of enterics, pseudomonads, and bacilli [17]. However, this would again indicate that fundamentally new types of bacteriophages are difficult to find.

Some critical comments on phage electron microscopy are necessary. Overall, the quality of micrographs seems to have conspicuously declined in the last five years. Many recent phage images are of poor quality, far inferior to those published over 50 years ago at the very introduction of negative staining [9, 10]. The main problem seems to be lack of contrast. One also notes phage descriptions without micrographs, dimensions, even virus names, mention of the electron microscope, stains, and magnification calibration. At the same time, misdiagnoses abound, in particular, identification of cellular debris as enveloped viruses and confusion of myo-, siph-, and podoviruses. This decline is very regrettable, as electron microscopy often allows instant diagnosis and identification.

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