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5500 Phages examined in the electron microscope

Brief Review

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Summary. "Phages" include viruses of eubacteria and archaea. At least 5568 phages have been examined in the electron microscope since the introduction of negative staining in 1959. Most virions (96%) are tailed. Only 208 phages (3.7%) are polyhedral, filamentous, or pleomorphic. Phages belong to one order, 17 families, and three "floating" groups. Phages are found in 11 eubacterial and archaeal phyla and infect 154 host genera, mostly of the phyla *Actinobacteria*, *Firmicutes*, and *Proteobacteria*. Of the tailed phages, 61% have long, noncontractile tails and belong to the family *Siphoviridae*. Convergent evolution is visible in the morphology of certain phage groups.

Introduction

"Phages" or bacteriophages are prokaryote viruses and include viruses of eubacteria and archaea. They occur in vast numbers everywhere in the biosphere, especially in the oceans [11, 12, 28]. In addition, most cultivable bacteria harbor complete or defective prophages. Phages as a group are extremely diversified and are arguably the oldest and most numerous of all viruses. The numbers of known phages have been expanding for decades at a rate of approximately 100 per year. Novel phages are continually reported in investigations of the environment and industrial fermentations. Keeping track of them is one of the activities of the Félix d'Hérelle Reference Center for Bacterial Viruses.

The first phage survey was published in 1967 and listed 111 negatively stained phages, 99 of which were tailed. Three phages were isometric and nine were filamentous [13]. The latest surveys were made in 1995 and 2000. They included 4551 and 5136 phages, respectively [1, 2]. Over 96% of phages were tailed and belonged to three families, the *Myoviridae*, *Siphoviridae*, and *Podoviridae*.

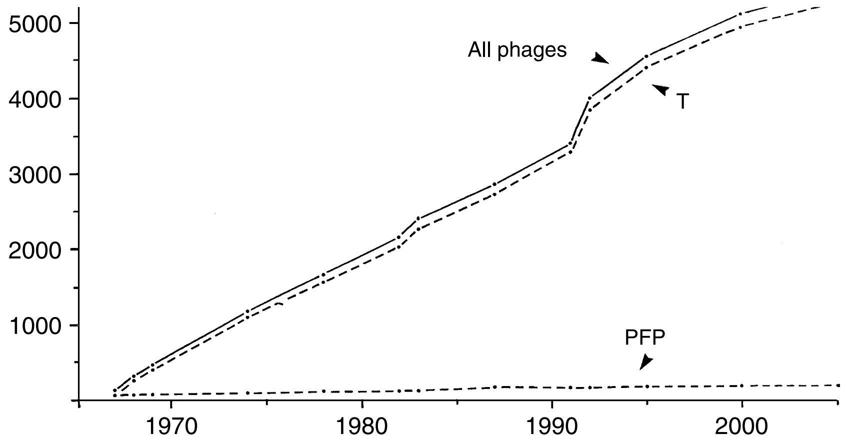

Fig. 1. Cumulative numbers of phage descriptions from 1967 to 2005. *PFP* Polyhedral, filamentous, and pleomorphic phages; *T* tailed phages

Polyhedral, filamentous, and pleomorphic phages represented only 3–4% and belonged to 10 families, some of which were very small. Since the last survey, bacterial classification of has undergone deep rearrangements, and over 400 novel phages have been described, many of them for Archaea from hyperthermophilic habitats (Fig. 1). This survey is based on the author's files and starts in 1959, the year when negative staining was introduced by Brenner and Horne [10]. It covers negatively stained viable or potentially viable, virulent or lysogenic phages from regular publications (periodicals, books, theses). Omitted are: defective and shadowed phages, "particulate bacteriocins," unpublished phages from oral communications and personal databases, phages with unidentified hosts (e.g., unclassified marine bacteria), phage-like particles without hosts (e.g., observed in water and soil samples), and finally a few individual phages illustrated by very poor electron micrographs. Completeness is attempted. References may be obtained from the author. The names of 5000 phages are available on the Web (http://www.phage.org/names.htm).

Presentation of data

As in the preceding surveys [1, 2], phages are listed by phage group (family, genus, morphotype) and host genus. The first six basic phage morphotypes were defined in 1967 by gross morphology and nature of nucleic acid. They corresponded to the present phage families *Myoviridae*, *Siphoviridae*, *Podoviridae*, *Inoviridae*, and *Leviviridae*, respectively [9]. New morphotypes and phage families were added over the years. The present edifice of ICTV phage classification includes one order, the *Caudovirales* or tailed phages, 13 families, and the "floating genus" *Salterprovirus*. These taxa are described in detail elsewhere [3, 4, 14]. Phages are either tailed or polyhedral, filamentous, or pleomorphic. The latter are subsequently designated as PFP phages. Bacteriophages contain double- or single-

Table 1. Overview of phage families

Shape	Nucleic acid	Virus group	Particulars	Example
Tailed	DNA, 2, L	*Myoviridae*	tail contractile	T4
		Siphoviridae	tail long, noncontractile	λ
		Podoviridae	tail short	T7
Polyhedral	DNA, 1, C	*Microviridae*	conspicuous capsomers	φX174
	2, C, S	*Corticoviridae*	complex capsid, lipids	PM2
	2, L	*Tectiviridae*	inner lipid vesicle, pseudotail	PRD1
	2, L	SHI, group*	inner lipid vesicle	SH1
	2, C	STV1 group*	turret-shaped protrusions	STIV
	RNA, 1, L	*Leviviridae*	poliovirus-like	MS2
	2, L, seg	*Cystoviridae*	envelope, lipids	φ6
Filamentous	DNA, 1, C	*Inoviridae*	a. long filaments	fd
			b. short rods	MVL1
	2, L	*Lipothrixviridae*	envelope, lipids	TTV1
	2, L	*Rudiviridae*	TMV-like	SIRV-1
Pleomorphic	DNA, 2, C, S	*Plasmaviridae*	envelope, lipids, no capsid	L2
	2, C, S	*Fuselloviridae*	same, lemon-shaped	SSV1
	2, L, S	*Salterprovirus*	same, lemon-shaped	His1
	2, C, S	*Guttaviridae*	droplet-shaped	SNDV
	2, L	*Ampullaviridae**	bottle-shaped	ABV
	2, C	*Bicaudaviridae**	two-tailed, growth cycle	ATV
	2, L	*Globuloviridae**	paramyxovirus-like	PSV

C Circular; *L* linear; *S* superhelical; *seg* segmented; *1* single-stranded; *2* double-stranded
*Awaiting classification

stranded DNA or RNA. The three families of tailed phages constitute the order *Caudovirales*. Polyhedral phages have "cubic" symmetry and are icosahedra or similar polyhedra (leviviruses). The various families of PFP phages are not grouped into orders. A few of them have lipid envelopes or contain lipids as parts of internal vesicles (*Tectiviridae*) or the capsid (*Corticoviridae*). In addition to phages of established families, a number or archaeal phages have recently been described. They still await classification by the ICTV, but differ profoundly from other known phages and clearly represent novel virus families. The total number of high-ranking phage taxa of family or equivalent rank is thus 20 (Table 1 and Fig. 2).

Phages are listed by host genera because they are essentially host genus-specific in replication. However, enterobacteria are so closely related that polyvalent phages are common there, especially in the *coli-Shigella-Klebsiella* group. Enterobacteria are thus considered here as a single host "genus". Other polyvalent phages exist in tectiviruses [1, 2, 4] and in archaebacteria (*infra*, see *Salterprovirus* and *Globuloviridae*).

Recent changes in bacterial classification are accounted for. The largely phenetic classification of Bergey's Manual [18] has progressively been replaced

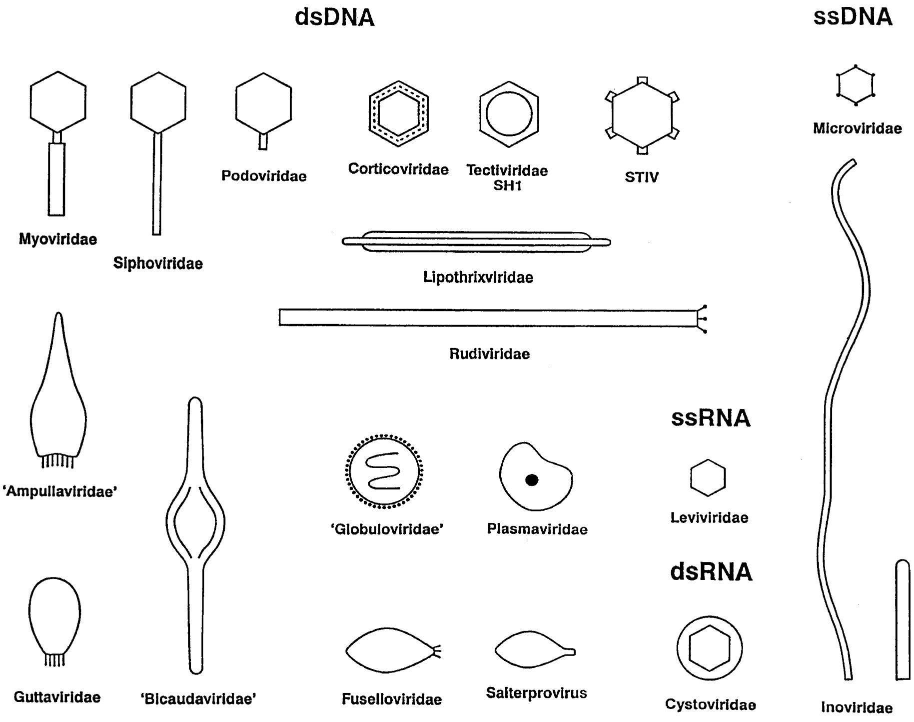

Fig. 2. Morphotypes of bacteriophages. See Table 1 for explanations

by a phylogenetically oriented system based essentially on 16S rRNA which, unfortunately, is not fully available in print. It is still under construction under the auspices of the National Center of Biotechnology Information (NCBI) in Bethesda, MD, and may be found on the Net [8]. In the new bacterial classification, many important phage host genera, e.g., *Bacillus*, *Pseudomonas*, and *Rhizobium*, have been subdivided, and many new actinomycete genera have been defined. In a general way, host species have remained more stable than host genera, which have frequently been subdivided or renamed. This author checked the taxonomic position of each phage host species and arranged phage host genera accordingly. The latter was impossible in some older publications where no host species had been indicated.

Phage frequency and distribution

At least 5568 phages have been examined in the electron microscope since 1959. The overall conclusions of this study confirm those of previous surveys [1, 2]. The vast majority (5360 viruses or 96.2%) are tailed and belong to three families. Polyhedral, filamentous, and pleomorphic phages (PFP) comprise 208 viruses (3.7%) and belong to 17 families or "floating genera", many of which have a single member and are restricted to archaebacteria or unusual eubacteria such as mycoplasmas. Tailed phages fall into three families, the *Myoviridae* (24.5%), *Siphoviridae* (61%), and *Podoviridae* (14%). Approximately 780 tailed

Table 2. Number of phage observations in archaea and eubacteria

Prokaryote phyla	Myoviridae	Siphoviridae	Podoviridae	Tailed phages	PFP
ARCHAEA					
Euryarchaeota					
Haloarcula					2
Halobacterium	6	5		11	
Methanobacterium	1	1		2	
Methanobrevibacter		1		1	
Natronobacterium	1			1	
Pyrococcus					1
Crenarcheota					
Acidianus					6
Pyrobaculum					1
Sulfolobus					14
Thermoproteus					5
EUBACTERIA					
Actinobacteria					
a. Actinomyces	*	3	11	14	
Arcanobacterium		2		2	
Arthrobacter		25	1	26	
Brevibacterum	*	3		3	
Clavibacter		6		6	
Corynebacterium	*	112		112	
Dermatophilus		1		1	
Micrococcus		12	1	13	
Mycobacterium	2	91		93	
Nocardia		4		4	
Oerskovia		1		1	
Promicromonospora		1		1	
Rhodococccus		13		13	
b. Actinoplanes	1	3		4	
Amycolatopsis		4		4	
Dactylosporangium		1		1	
Lechevalieria		1		1	
Micromonospora		9		9	
Nocardioides		2		2	
Propionibacterium		20		20	1
Saccharothrix		1		1	
Saccharomonospora	1	2	1	4	
Saccharopolyspora		38		38	
c. Actinomadura		1		1	
Microtetraspora		1		1	
Nonomuraea		1		1	
Streptomyces	2	132	8	142	

(*continued*)

Table 2 (*continued*)

Prokaryote phyla	Myoviridae	Siphoviridae	Podoviridae	Tailed phages	PFP
Thermobifida		7		7	
Thermopseudosporangium[a]		3		3	
d. Bifidobacterium		1		1	
Bacteroidetes					
Bacteroides	3	21	1	25	
Cytophaga	29	2		31	
Flavobacterium	2			2	2
Saprospira	1			1	
Sporocytophaga	*				
Chlamydia/Verrucomicrobia					
Chlamydia					3
Cyanobacteria					
Anabaena	2		5	7	
Nostoc	1			1	
Plectonema	1			1	
Phormidium		1		1	
Prochlorococcus	2		1	3	
Spirulina	*				
Synechococcus[b]	20	6	6	32	
Deinococcus-Thermus					
Thermus	4	3		7	10
Firmicutes					
Bacilli					
a. Alicyclobacillus	1			1	1
Aneurinibacillus	1	1		2	
Bacillus	136	203	31	370	8
Brevibacillus		1		1	
Brochothrix	5	16		21	
Caryophanon	1	3		4	
Geobacillus		13		13	
Kurthia			8	8	
Listeria	5	109		114	
Paenibacillus	14	8	1	23	
Staphylococcus	28	183	4	215	
Thermoactinomyces		3	1	4	
b. Carnobacterium	1			1	
Enterococcus	9	24	3	36	
Lactobacillus	70	120		190	
Lactococcus	3	687	10	700	

(*continued*)

Table 2 (*continued*)

Prokaryote phyla	Myoviridae	Siphoviridae	Podoviridae	Tailed phages	PFP
Leuconostoc	5	21		26	
Oenococcus		50		50	
Pediococcus		3		3	
Streptococcus	2	276	12	290	
Tetragenococcus	1	2		3	
Clostridia					
Butyrivibrio		*			
Clostridium	93	60	21	174	1
Eubacterium		1		1	
Ruminococcus		1	2	3	2
Selenomonas	1	2		3	
Veillonella		2	2	4	
Mollicutes					
Acholeplasma				1	18
Mycoplasma	1	1		4	1
Spiroplasma		2	10	12	2
Erysipelothrix[c]		1		1	
Fusobacteria					
Fusobacterium	3	1	3	7	
PROTEOBACTERIA					
α-Proteobacteria					
Acidiphilium		1		1	
Acidomonas	8			8	
Agrobacterium	3	31	1	35	
Ancalomicrobium		3		3	
Aquaspirillum					1
Asticcacaulis		25		25	
Azospirillum		2		2	
Bartonella			1	1	
Bosea			1	1	
Bradyrhizobium	1	1	5	7	
Brucella			43	43	
Caulobacter	4	40	3	47	8
Chromobacterium	*				
Gluconacetobacter	7			7	
Gluconobacter	5		1	6	
Hyphomicrobium	4	25	11	40	
Mesorhizobium		3		3	
Methylocystis			1	1	
Methylosinus			13	13	
Rhizobium	36	39	25	100	
Rhodobacter	3	6	2	11	

(*continued*)

Table 2 (*continued*)

Prokaryote phyla	Myoviridae	Siphoviridae	Podoviridae	Tailed phages	PFP
Rhodopseudomonas			1	1	
Rickettsia			1	1	
Roseobacter			1	1	
Starkeya	1			1	
Sinorhizobium (Ensifer)	14	38	5	57	
Sphingomonas	2	3	10	15	
Aquaspirillum (unclassified)	*				
Caedibacter[c]			1	1	
α-Proteobacterium sp.		1		1	
β-Proteobacteria					
Achromobacter[d]	14	5	3	22	
Alcaligenes	1	8		9	
Bordetella	1	4	3	8	
Burkholderia	3	2		5	
Comomonas	1			1	
Delftia	1			1	
Hydrogenophaga	2	4		6	
Janthinobacterium	1			1	
Methylophilus			2	2	
Neisseria	2			2	
Ralstonia	1	1	1	3	
Sphaerotilus		1		1	
Variovorax	1			1	
γ-Proteobacteria					
Acinetobacter	31	11	5	47	1
Acirtosiphon[e]			1	1	
Aeromonas	33	7	3	43	
Azotobacter	12	2	6	20	
Enterobacteriaceae	344	297	265	906	76
Haemophilus	12	3		15	
Halomonas		3		3	
Listonella		1		1	
Mannheimia	1	1		2	
Methylobacter			2	2	
Methylomonas	1			1	
Pasteurella	10	9	7	26	
Photobacterium	1			1	
Piscirickettsia		1		1	
Pseudoalteromonas	11	7	4	22	3
Pseudomonas	139	241	119	499	12
Salinivibrio	2			2	
Shewanella	2			2	
Stenotrophomonas	1	2		3	

(*continued*)

Table 2 (*continued*)

Prokaryote phyla	Myoviridae	Siphoviridae	Podoviridae	Tailed phages	PFP
Vibrio	86	67	74	227	13
Xanthomonas	9	25	1	35	7
δ-Proteobacteria					
Archangium	*				
Bdellovibrio	4			4	9
Desulfovibrio	1	1	1	3	
Myxococcus	12		5	17	
Polyangium	*				
ε-Proteobacteria					
Campylobacter	21	10		31	
Helicobacter		2		2	
Spirochaetes					
Borrelia	3	1		4	
Brachyspira (Serpulina)	3			3	
Leptospira	4			4	
Spirochaeta	1			1	
Treponema	1	1		1	
Total	1320	3269	771	5360	208

PFP polyhedral, filamentous, and pleomorphic

*Contractile tails; [a]not listed by NCBI; [b]including former Anacystis; [c]incertae sedis; [d]poorly defined; [e]listed by NCBI as a member of the enterobacteria

Survey concluded on May 1, 2006

phages (14.5% regardless of the family) have elongated heads. Prolate heads are relatively frequent in mycobacteria and streptomycetes, lactococci (29%), and enterobacteria (20%). Their high frequency in lactococci and enterobacteria is due to the prevalence of phages of the c2 and T4 genera, respectively [14, pp 43 and 63].

Phages have been found in 10 archaeal and 144 eubacterial genera (Tables 2–4, Figs. 3 and 4), 14 enterobacterial genera being listed as a single "genus." The enterobacteria include such exotics as the genus *Xenorhabdus*. The bacterial genera with the most phage observations are enterobacteria (906 phages), *Lactococcus* (700), *Bacillus* (380), and *Streptococcus* (290). Approximately 240 *Streptococcus* phages infect one host species, *S. thermophilus*, and are, with a few exceptions, morphologically identical. Most of them are probably related or reisolates of one and the same phage. The high number of *Lactococcus* and *S. thermophilus* phages reflects current research interest in dairy phages. Several bacterial genera (*Archangium*, *Butyrivibrio*, *Chromobacterium*, *Polyangium*, *Spirulina*, *Sporocytophaga*) carry morphologically defective lysogenic phages (Table 2, not counted). This suggests that complete phages will some day be found in these bacteria.

Table 3. Number of observations of polyhedral, filamentous, and pleomorphic phages; **a**. Eubacterial viruses

Host phylum	Genus	Virus family or genus									
		Corticoviridae	Cystoviridae	Inoviridae		Leviviridae	Microviridae	Plasmaviridae	Tectiviridae	?	Total
				Inovirus	Plectrovirus						
Actinomycetes	Propionibacterium			1							1
Bacteroidetes	Flavobacterium*									2	2
Chlamydia-Verrucomicrobia	Chlamydia						3				3
Deinococcus-Thermus	Thermus			6					4		10
Firmicutes	Alicyclobacillus								1		1
	Bacillus								8		8
	Clostridium			1							1
	Ruminococcus			2							2
Mollicutes	Acholeplasma				13			5			18
	Mycoplasma				1						1
	Spiroplasma				1		1				2
Proteobacteria, α subdivision	Aquaspirillum									1	1
	Caulobacter					8					8
γ subdivision	Acinetobacter					1					1
	Enterobacteria			19		25	26		6		76
	Pseudoalteromonas	1								2	3
	Pseudomonas		3	3		4				2	12
	Vibrio			12						1	13
	Xanthomonas			7							7
δ subdivision	Bdellovibrio						8			1	9
Total		1	3	51	15	38	38	5	19	9	179

? Polyhedral, unknown affiliation
*Uncertain identification

Table 3. b. Archaeal viruses[a]

Host phylum	Host genus	Virus family or genus										
		Ampullaviridae	Bicaudaviridae	Fuselloviridae	Globuloviridae	Guttaviridae	Lipothrixviridae	Rudiviridae	Salterprovirus	SH1	STIV	Total
Euryarchaota	Haloarcula								1	1		2
	Pyrococcus			1								1
Crenarchaota	Acidianus	1	1	1			2	1				6
	Pyrobaculum				1							1
	Sulfolobus		1	8		1	1	2			1	14
	Thermoproteus				1		4					5
Total		1	2	10	2	1	7	3	1	1	1	29

[a] Excluding noncultured round or fusiform virus-like particles found in the euryarchaeota, *Methanococcus voltae* and *Pyrococcus woesei* [29, 31]

Table 4. Summary of phage observations

Prokaryote phyla	Myoviridae	Siphoviridae	Podoviridae	Tailed phages	PFP
Archaea	8	7		15	29
Eubacteria					
Actinobacteria	6	501	22	529	1
Bacteroidetes	35	23	1	59	2
Chlamydia					3
Cyanobacteria	26	7	12	45	
Deinococcus-Thermus	4	3		7	10
Firmicutes	377	1743	105	2275	33
Fusobacteria	3	1	3	7	
α-Proteobacteria	88	218	126	432	9
β-Proteobacteria	28	25	9	62	
γ-Proteobacteria	695	677	487	1859	112
δ-Proteobacteria	17	1	6	24	
ϵ-Proteobacteria	21	12		33	9
Spirochaetes	12	1		13	
Total	1320	3269	771	5360	208

PFP polyhedral, filamentous, and pleomorphic

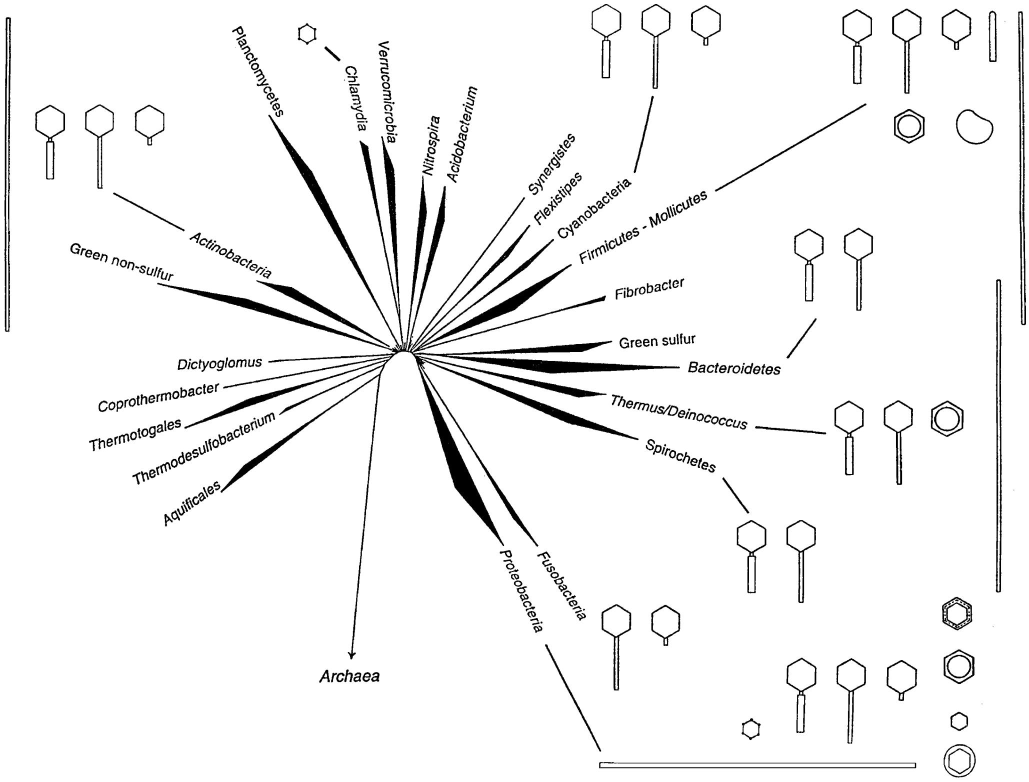

Fig. 3. Observations of phage morphotypes in eubacterial phyla. Adapted from Ref. [18]. With permission of the American Society for Microbiology and N.R. Pace

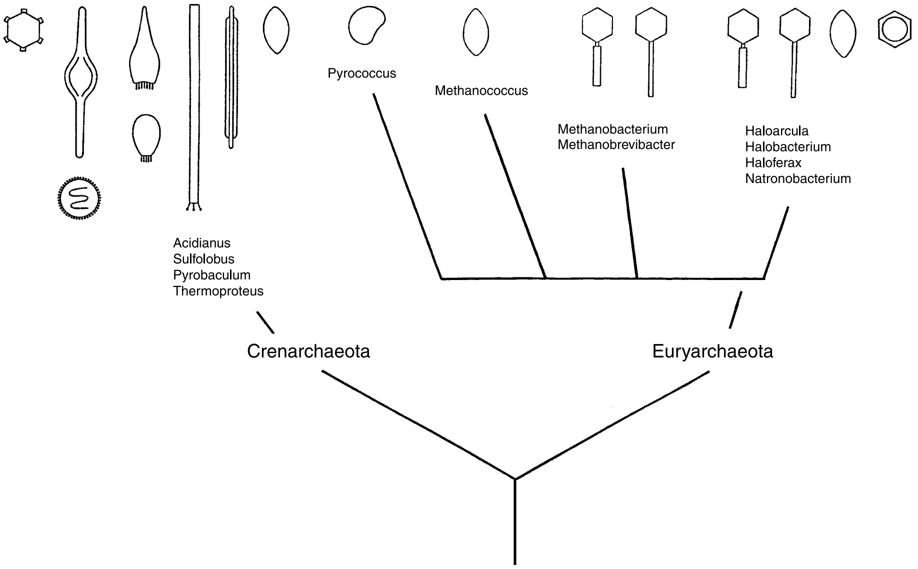

Fig. 4. Observations of phage morphotypes in archaebacterial phyla

Novel phage families

Five types of archaeal viruses were found recently, mostly in volcanic hot springs [23, 25, 26]. They so far have no taxonomic status and remain to be classified by the ICTV. Latinized names have been proposed for three of them (Table 3b).

1. SH1, from "Serpentine-Lake-Hispanica" (polyhedral, dsDNA)
   Particles have the same structure as tectiviruses and contain lipid. The only known representative of this group was found in a hypersaline lake in Australia, resembles tectiviruses in the presence of an inner vesicle and DNA anatomy, and infects halobacteria of the genera *Halorubrum* and *Haloarcula*. Tail-like tubes were not reported [6, 22].
2. STIV, from "*Sulfolobus*-turreted-icosahedral-virus" (polyhedral, dsDNA)
   The single known member infects a hyperthermophilic archaeon, *Sulfolobus solfataricus*, and was found in a hot spring in the Yellowstone National Park (U.S.A.). Viruses are built on a T = 31 icosahedral lattice and characterized by apical protrusions, oddly resembling World War II sea mines. STIV has structural relationships to tectiviruses, adenoviruses, and phycodnaviruses [20, 27].
3. *Ampullaviridae* (pleomorphic, dsDNA)
   Their structure is unique in the viral world. Particles consist of a bottle-shaped mantle, a cone-shaped inner body, a helical nucleocapsid, and polar fibers at the large end. The viruses were isolated from Italian hot springs and infect *Acidianus convivator* [16].
4. *Bicaudaviridae* (pleomorphic, dsDNA)
   The predominant feature of these viruses is an extracellular development cycle. Particles start as oval or arrow-shaped entities which contain a helical

nucleocapsid and grow tail-like appendages at both ends. This occurs at 75–90 °C and does not require the presence of the host cell. Bicaudaviruses are the largest of all archaeal viruses. The first isolate known was found in volcanic hot springs of Italy [17, 24, 25]. A similar isolate, named STSV1 and superficially fusellovirus-like, was found later in acidic hot springs of a geothermal area in China [30] but has no apparent genomic relationships to virus ATV [23].

5. *Globuloviridae* (pleomorphic, dsDNA)
   Virions consist of a spherical, lipid-containing envelope and a helical nucleocapsid. Except that they contain DNA, they resemble paramyxoviruses. The single known member of this group was found in an Italian hot spring and infects *Pyrobaculum* and *Thermoproteus* [15].

Convergent evolution

Many phages, including novel archaeal viruses, show an uncanny resemblance to apparently unrelated viruses. This resemblance cannot be explained by horizontal gene transfer or phylogenetic relationships and likewise results from independent developments, thus convergent evolution. The best-known example is that of the ssRNA phages of the family *Leviviridae*. Indeed, in the beginnings of virus classification, they were classified, together with polioviruses and ssRNA plant viruses, in the former family *Napoviridae* [21]. Another remarkable case is the “tail” of tailed phages and tectiviruses. In both virus groups, it is a tube evolved for the purpose of DNA transfer into a bacterial host. In tailed phages, the tube is permanent and proteinic, has fixed dimensions, and it built of subunits forming transverse striations. By contrast, the “tail” of tectiviruses is a smooth tube of variable length, does not exist in normal particles, and is produced from an internal lipoprotein vesicle during phage adsorption to the host or after chloroform treatment. Other examples of convergent evolution are found in archaeal rudiviruses and globuloviruses. Rudiviruses are morphologically indistinguishable from the tobacco mosaic virus (genus *Tobamovirus*), but differ from it by the presence of dsDNA instead of ssRNA. Similarly, the dsDNA-containing globuloviruses resemble paramyxoviruses (ssRNA) in size, shape, and presence of an envelope, spikes, and a helical nuclocapsid.

True phylogenetic relationships seem to exist between tailed phages and herpesviruses. Both virus groups have broadly similar genome sizes and share numerous physiological properties related to replication, capsid maturation, portal proteins, DNA packaging, and latency [3]. Other evolutionary links may exist between phages and vertebrate or protozoal viruses sharing double-barrel coat proteins, e.g., tectiviruses, adenoviruses, phycodnaviruses, iridoviruses [7], and the STIV type of archaeal phages [20, 26]. Still more phylogenetic relationships are evident in the lifestyle and capsid structure of dsRNA-containing viruses, namely the *Cystoviridae* phages of pseudomonads and eukaryote viruses belonging to the families *Reoviridae* and *Birnaviridae* [5].

Trends and predictions

The investigation of archaeal phages and extreme habitats, such as volcanic hot springs and hypersaline lagoons, has led to the discovery of no less than five potentially new virus families and a wealth of virus-like particles that possibly represent more novel families [25, 27]. Simultaneously, phages carrying toxin genes, phages of lactic acid bacteria, and marine phages have been intensively investigated. It is probable that these activities will continue and that novel phages will be described, as in the past, at a rhythm of approximately 100 per year (Fig. 1). The relative frequency of phage families is to remain stable. Most novel phages, regardless of their geographical origin, are likely to be tailed and only a minority will be polyhedral, filamentous, or pleomorphic. However, many "novel" phages, especially of enterobacteria, are likely to be reisolates of known phages because novelty is often claimed without experimental proof and sufficient literature research. Another trend is a general and sharp decline, manifest since 10–15 years, in the quality of electron microscopical phage descriptions. The main reason of this seems to be the examination of crude, non-purified specimens. This inevitably leads to poor, "dirty" pictures which sometimes cannot be interpreted at all.

There is no end in sight to the discovery of novel phages. (i) Only a fraction of bacterial phyla has been investigated for the presence of phages (Figs. 3 and 4). (ii) Phages are probably the most abundant life form on Earth [11, 28]. (iii) Viral metagenomics indicates that the environment, especially the sea, contains vast uncultured viral communities [12]. Although marine phages are frequently detected by genomics and electron microscopy, their isolation is generally not attempted. (iv) Some phage habitats have been scarcely investigated, for example the deep sea, industrial fermenters, and mining effluents. (vi) Most phage descriptions come from a handful of developed countries. To my knowledge, no phages have been reported from large geographic areas such as tropical Africa and Siberia. In phage ecology, as in so many fields, we are still at the threshold of human knowledge.

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