Viruses of the Archaea

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Advanced article

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Double-stranded deoxyribonucleic acid (DNA) viruses that infect members of the third domain of life, the Archaea, are diverse and exceptional in both their morphotypes and their genomic properties. The majority of characterized species infect hyperthermophilic hosts and carry morphological features which have not been observed for viruses from the other domains of life, the Bacteria and the Eukarya. This exceptional status of the archaeal viruses is reinforced by the finding that a large majority of their predicted genes yield no sequence matches in public sequence databases, and their functions remain unknown. One of the viruses, the bicaudavirus ATV (*Acidianus* two-tailed virus), is quite unique in that it undergoes a major morphological change, growing long tail structures, extracellularly. A small minority of archaeal viruses, which exclusively infect mesophilic or moderately thermophilic hosts, are morphologically similar to head-tail DNA viruses of bacteria.

Introduction

Susceptibility to viral infection and intracellular viral replication are as common to the Archaea, the third domain of life, as they are to the other two domains, the Bacteria and Eukarya. The domain Archaea was discovered as a result of molecular 16S ribosomal ribonucleic acid (RNA) sequence analyses, pioneered by Carl Woese. Its independent phylogenetic status was later confirmed by revealing certain biological features that are exclusive to this domain. Recently it has become clear that the exceptional diversity of double-stranded deoxyribonucleic acid (dsDNA) viruses is another particular trait of the archaeal domain.

The history of research on archaeal viruses is relatively short and we know significantly less about them than about the viruses of the Bacteria and Eukarya. About 40 viral species have been described so far and they all carry dsDNA genomes.

Ecology

Screening for archaeal viruses has been performed mainly in extreme hydrothermal or hypersaline environments. Present results suggest that the composition of viral communities reflects that of their hosts and is similar at different geographical locations with comparable environmental conditions. It has been well established that the diversity of microorganisms in natural environments greatly exceeds that observed under culture conditions. Moreover, this finding has been reinforced in a recent study of archaeal viruses from the family *Fuselloviridae* and there is ongoing work to assess the sequence diversity of other viruses in hot aquatic environments. Acidothermophilic aquatic environments, where the highest morphological diversity of archaeal viruses has been observed, show virus concentrations significantly lower than in other analysed ecosystems. This could be due, for example, to the limited stability of virions at high temperatures and low pH, or to the capacity of most known viruses from such environments to persist stably in the host cell rather than to lyse it. The latter apparently reduces the possibility of direct exposure of a viral population to the harsh environmental conditions.

Morphology and Classification

Despite the relatively small number of isolated species of archaeal viruses, their morphological diversity is astounding and greatly surpasses the morphological diversity of dsDNA viruses of the Bacteria, 96% of which represent tailed bacteriophages. Head-tailed phages resembling bacteriophages are also replicated by the extremely halophilic or methane-producing archaea. However, hyperthermophilic archaea replicate a plethora of viruses with most morphotypes not encountered among dsDNA viruses of either Bacteria or Eukarya. These include fusiforms, filaments, spheres, droplet and bottle shapes, while some virions combine features of these different forms (**Figure 1**).

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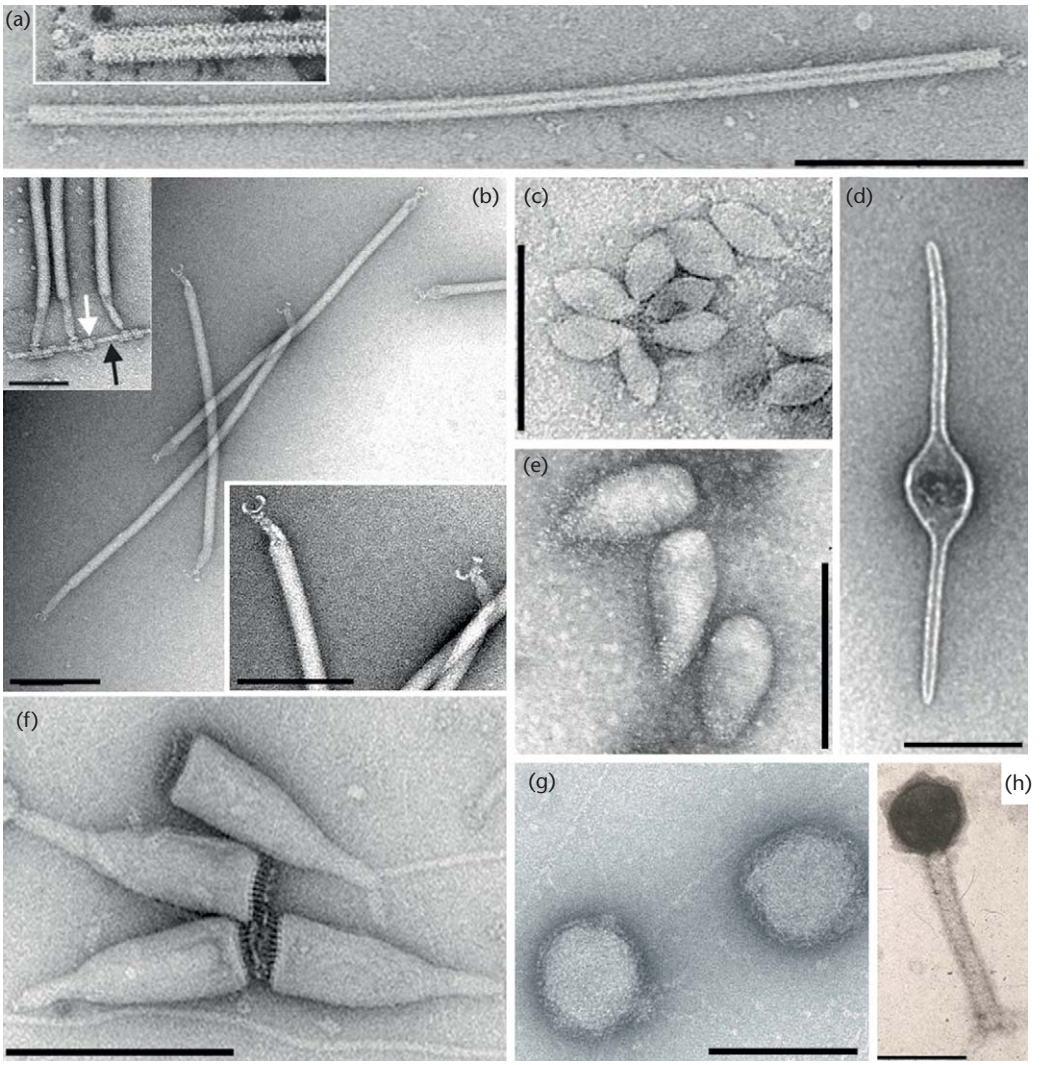

Figure 1 Electron micrographs of viruses of the Archaea. (a) *Sulfolobus islandicus* rod-shaped virus 1, SIRV1; (b) *Acidianus* filamentous virus 1, AFV1; in insets claw-like structures are shown in 'open' and 'closed' conformation, white arrow indicates a 'claw' clamped around host pili and separated from the virion body, and black arrow indicates pili-like appendices of the host cell. (c) *Sulfolobus shibatae* virus 1, SSV1; (d) *Acidianus* two-tailed virus, ATV; (e) *Sulfolobus neozealandicus* droplet-shaped virus, SNDV; (f) *Acidianus* bottle-shaped virus, ABV; (g) *Pyrobaculum* spherical virus, PSV; (h) *Sulfolobus* turreted icosahedral virus, STIV and (i) Haloarchaeal virus ÖH. Scale bars represent 200 nm except in g, h, i and insets where it represents 100 nm. Figures 1a, 1c, 1e and 1i are courtesy of the late Wolfram Zillig. Figure 1b was published in *Virology*, **315**, Bettsetter *et al*, 68–79, copyright Elsevier (2003). Reproduced with permission. Figure 1f was reproduced with permission from the American Society for Microbiology from Haring *et al*., 2005, *Journal of Virology*, **79**: 9904–9911. Figure 1g was publsihed in *Virology*, **323**, Haring *et al*, 233–242, copyright Elsevier (2004). Reproduced with permission. Figure 1h is courtesy of Mark Young.

The basis for classification of many archaeal viruses was originally their diverse and unique morphological features, which led to the introduction of seven novel viral families (**Table 1**). The current morphological classification is supported by results of genome analyses (see the section Genomics).

Fusiform viruses

Fusiform viruses appear to be ubiquitous in hypersaline and hot environments where archaea predominate. They are associated with a broad range of hosts: the hyperthermophiles, the extreme halophiles and presumably also the anaerobic methane-producers. Virions of the fusiform viruses are broader in the middle and they taper towards the ends terminating with one or two tails. Those which have been studied carry host-derived lipids. Organization of the core structure is unknown and the structural basis for the unusual virion shape is unclear. Owing to the significant differences in virion structure and genomic properties, the known fusiform viruses were assigned to the *Fuselloviridae* (Wiedenheft *et al*., 2004), the proposed family *Bicaudaviridae* (Haring *et al*., 2005b) and the genus *Salterprovirus* (Bath *et al*., 2006), while some remain unclassified (**Table 1**).

The best-studied fusiform virus is the *Sulfolobus shibatae* virus 1, SSV1, from the family *Fuselloviridae* (**Figure 1c**). The

Table 1 Viruses of Archaea

Family, species	Host	Genome details	Accession number of genome sequences
Rod-shaped and filamentous viruses			
Rudiviridae			
SIRV1	*Sulfolobus islandicus*	L, 32 308	AJ414696
SIRV2	*S. islandicus*	L, 35 450	AJ344259
ARV1	*Acidianus pozzuoliensis*	L, 24 655	AJ875026
Lipothrixviridae			
TTV1[a]	*Thermoproteus tenax*	L, 15 900	X14855
SIFV	*S. islandicus*	L, 40 852	AF440571
AFV1	*Acidianus hospitalis*	L, 21 080	AJ567472
AFV2	*Acidianus* sp.	L, 311 787	AJ854042
Fusiform viruses			
Fuselloviridae			
SSV1	*Sulfolobus shibatae* *Sulfolobus solfataricus*	C, 15 465	XO7234
SSV2	*S. islandicus* *S. solfataricus*	C, 14 796	AY370762
SSV-K1	*S. solfataricus*	C, 17 385	AY423772
SSVRH	*S. solfataricus*	C, 16 473	AY388628
Floating genus *Salterprovirus*			
His1	*Haloarcula hispanica*	L, 14 900[b]	AF191796
His2	*Haloarcula hispanica*	L, 16 100	AF191797
Bicaudaviridae[*]			
ATV[*]	*Acidianus convivator*	C, 62 730	AJ888457
Unclassified			
STSV1	*Sulfolobus tengchongensis*	C, 75 294	AJ783769
Droplet- and bottle-shaped viruses			
Guttaviridae			
SNDV[a]	*Sulfolobus neozealandicus*	C, 20 000[b]	nd
Ampullaviridae[*]			
ABV	*A. convivator*	L, 23 900[b]	EF432053
Spherical and icosahedral viruses			
Globuloviridae[*]			
PSV	*Pyrobaculum* sp. *T. tenax*	L, 28 337	AJ635161
TTSV1	*T. tenax*	L, 20 933	AY722806
Unclassified			
SH1	*Haloarcula hispanica*	L, 30 898	AY95080
STIV	*Sulfolobus* sp.	C, 17 663	AY569307
Head-tail viruses[c]			
Myoviridae			
ΦH	*Halobacterium salinarum*	L, 59 000[b]	Available for genome fragments
ΦCh1	*Natrialba magadii*	L, 58 498	AF440695

(*Continued*)

Table 1 Continued

Family, species	Host	Genome details	Accession number of genome sequences
Unassigned species in the family			
HF1	*Haloferax volcanii* *Halobacterium salinarum*	L, 75 898	AY190604
HF2	*Halorubrum cariense*	L, 77 670	AF222060
Siphoviridae			
ψM1	*Methanothermobacter marburgensis*	L, 30 400	AF065411 AF065412

Notes: Listed are archaeal viruses with sequenced genomes, except SNDV. nd, not determined; L, linear; C, covalently closed circular and Taxonomic proposals are approved or pending (∗) at the International Committee on Taxonomy of Viruses.
[a]Presently the viruses are not available in laboratory collections.
[b]Approximate values.
[c]Only those with sequenced genomes are listed.

virions are 55 × 80 nm in size and they have a short tail of constant length at one end. Short fibres are inserted into the tail which serve to attach the virus to the host. Studies of SSV1 provided some seminal findings about the biology of archaea. One was the identification of transcriptional promoter sequences on the SSV1 genome that resembled eukaryotic counterparts. Circular DNA of SSV1 provided one of the first known examples of a positively supercoiled DNA in nature. The genome of SSV1 also carries a gene for a functional integrase which facilitates integration of the viral genome in the host chromosome. Integration into a transfer RNA (tRNA) gene results in the partitioning of the integrase gene while the tRNA gene remains intact. It has been demonstrated that the SSV1 integrase is not required for virus replication and maintenance in the host culture. However, integrase deletion mutants seem to be less competitive in co-culture with the wild-type virus. The presence of an integrase on the circular genome is a common trait of fusiform viruses except for the two viruses of the genus *Salterprovirus*, His1 and His2, which have linear genomes. SSV1 does not cause lysis of the host cells during the release of its progeny.

Viral replication can be induced by treatment with UV light or mitomycin C resulting in temporary inhibition of host growth. Although most SSV1 genes are transcribed constitutively, the UV irradiation provokes upregulation of some of them together with appearance of a short RNA molecule that could be involved in initiation of genome replication.

The reproductive cycle of the *Acidianus* two-tailed virus, ATV, has some unique features (Haring *et al*., 2005b). It is the only virus that was shown to be capable of major morphological transformation outside, and independently of, its host cell. When released from the host cell, particles are fusiform (243 × 119 nm in size) but later they gradually develop tails exclusively at the temperatures above 75°C, close to the temperature range of the host habitat. Particles with fully developed tails are approximately 750 nm in length (**Figure 1d**). The tail-protrusion process is host-independent proceeding in the absence of any cofactors, and its molecular mechanisms are currently unknown. However, structural features of the unusual virions have been studied in some detail. The tails are hollow tubes that contain a filament of unknown nature, which exhibits a structural periodicity. The tubes terminate with an anchor-like structure formed by two furled filaments. ATV is the only known virus from hot, acidic environment that causes the lysis of its host cell, and it was suggested that development of tails, specifically at temperatures at which hosts are active, may constitute part of a strategy for viral survival in unstable and hostile environmental conditions.

The process of extracellular tail development maybe shared by other fusiform viruses, e.g. by *Sulfolobus tengchongensis* spindle-shaped virus 1, STSV1, the largest (230 × 107 nm) among them (Xiang *et al*., 2005). The variable length of its tail (0–133 nm) in a virus population may reflect an extracellular development similar to that of ATV.

Bottle- and droplet-shaped viruses

Exceptional morphological features of archaeal viruses are well illustrated by the *Acidianus* bottle-shaped virus, ABV and the *Sulfolobus neozealandicus* virus, SNDV, which are morphologically so unusual that they are classified into two new viral families *Ampullaviridae* and *Guttaviridae* (**Table 1**).

The virions of ABV reveal no helical or icosahedral symmetry and their overall shape resembles a bottle with length of 230 nm and width varying from 4 nm at the pointed end to 75 nm at the broad end (**Figure 1f**; Haring

et al., 2005a). The latter end carries a disc or a ring into which approximately 20 short filaments are inserted. The virions are covered with an envelope which encases the cone-shaped core. The core consists of torroidaly supercoiled nucleoprotein which determines the shape of the virion body. The virion adsorbs to the host cell via its pointed end and the function of the filaments at the opposite, broader end of the virion, is still unclear. The linear viral genome does not integrate into the host chromosome and, apparently, it is replicated by a virus-encoded DNA polymerase that is primed by a protein attached to the genomic termini.

The virion of SNDV has a unique droplet-shaped morphology. The particles measure 110–185 nm in length and 95–70 nm in width and are densely covered by thin fibres at their pointed ends (**Figure 1e**). The core is protected by a beehive-like structure, the surface of which appears to be built-up of helically stacked components.

Rod-shaped and filamentous viruses

The majority of viruses in hot, acidic environments appear to have linear morphology. Those which have been isolated and studied infect hyperthermophilic archaea from the genera *Sulfolobus*, *Acidianus* and *Thermoproteus*. All these viruses have linear dsDNA genomes, and have been assigned into two families: the *Rudiviridae* (Prangishvili *et al*., 1999) and the *Lipothrixviridae* (Arnold *et al*., 2000; **Table 1**).

Virions of the rudiviruses, the *Sulfolobus islandicus* rod-shaped virus 1, SIRV1, the SIRV2 and the *Acidianus* rod-shaped virus 1, ARV1, are nonenveloped stiff rods, 23 nm in width with the length that varies significantly (600–900 nm) and is proportional to the length of genomic DNA. Three thin fibres, 10 nm in length, are attached at the rod termini and are involved in adsorption to the host cell (**Figure 1a**). The virion body represents a nucleoprotein consisting of dsDNA and multiple copies of a single coat protein. The packaged DNA is efficiently protected from degradation in the extremely hot, acidic (pH 1.5–3) natural environment of rudiviruses.

Virions of the lipothrixviruses, the *Thermoproteus tenax* virus 1, TTV1, the *S. islandicus* filamentous virus, SIFV and the *Acidianus* filamentous virus 1, AFV1, are covered by an envelope containing host-derived lipids. However, their core structures appear to be different. For TTV1, the lipid envelope encases a helical core of linear dsDNA covered by multimers of two DNA-binding proteins, whereas the virion of SIFV contains a nucleosome-like core of linear dsDNA wound around a zipper-like array of protein subunits (Arnold *et al*., 2000). The lipothrixviruses exhibit a remarkable diversity in their terminal structures which are always identical at both ends and apparently are involved in host cell adsorption. The virion of SIFV (1950 × 24 nm) tapers towards the termini ending with mop-like structures built of six thin fibres, the virions of AFV1 (24 × 900 nm, **Figure 1b**) carry unusual claw-like structures at the termini, and the virion of AFV2 (24 × 1100 nm) has a complex terminal structure resembling a bottle brush with two sets of filaments arranged in a collar-like manner. For AFV1, adsorption was observed to the pili-like appendices of the host cell and resulted in closing of claw-like pincers maintaining firm contact (**Figure 1b**, inset).

Linear archaeal viruses, with the exception of lytic TTV1, do not cause lysis of the host cell during their replication cycle. Instead, they persist in the cell as a result of equilibrium between cell division and replication of viral genomes. Furthermore, their linear genomes do not integrate into the host chromosome and their replication is not affected by UV irradiation, mitomycin C or other stress factors. Consistent with these fairly unsophisticated virus–host relationships, genomes of the linear viruses lack an integrase gene and reveal a transcription pattern without any pronounced temporal control.

The linear viral genomes carry inverted terminal repeats (ITRs) that differ markedly in their lengths. Rudiviruses exhibit large ITRs ranging from approximately 1.5 to 2 kbp, whereas lipothrixviruses have shorter ones approximately 0.5–1 kbp in size. One exception is the lipothrixvirus AFV1 with very short (11 bp) ITRs. However, the terminal sequences of AFV1 genome carry a series of short repeats resembling the telomeres of eukaryotic chromosomes. In SIRV1 and SIRV2 the two DNA strands are covalently linked at the ends, generating a hairpin loop. The presence of such structure has not been demonstrated for lipothrixviral genomes and the nature of their termini remains unclear.

Spherical and icosahedral viruses

Presently, four species of spherical viruses infecting archaea have been isolated and studied. The *Pyrobaculum spherical virus*, PSV, the *T. tenax* spherical virus 1, TTSV1, and the *Sulfolobus* turreted icosahedral virus, STIV, all infect hyperthermophilic archaea, whereas SH1 is replicated by members of the haloarchaeal genera *Haloarcula* and *Halorubrum* (**Table 1**).

Particles of PSV are enveloped spheres approximately 100 nm in diameter (Haring *et al*., 2004; **Figure 1g**). The virion surface contains a variable number of spherical protrusions, approximately 15 nm in diameter, which are probably involved in adsorption to the host cell. The core consists of a tightly packed nucleoprotein with helical symmetry. The linear genome of PSV carries 190 bp ITRs, and its two strands are likely to be covalently linked as for the rudiviral genomes. TTSV1 is similar to PSV in its morphology and genome organization and has been classified as a second member of the family *Globuloviridae*.

The virions of the two other spherical viruses, STIV and SH1, are nonenveloped icosahedra with an internal lipid-containing layer and no detectable tail structures. They strongly resemble virions of the bacteriophages of the family *Tectiviridae* in their morphologies. Furthermore, although at a sequence level their major structural proteins reveal no significant similarity, the crystal structure of the major capsid protein of STIV is very similar to those of the bacterial tectivirus PRD1 and the eukaryal phycondnavirus PBCV-1,

suggesting a common ancestry. The virion structure of STIV has been thoroughly studied and this resulted in the first single particle reconstruction of an archaeal virus revealing unique structural features (Rice *et al*., 2004). These include complex, turret-like appendices regularly arranged at the virion surface, which are probably involved in the adsorption process. STIV persists stably in the host cell in contrast to SH1 which is lytic. The two viruses differ also in the structures of their genomes; they are circular and linear, respectively.

Head-tail viruses

Archaea replicate dsDNA viruses with polyhedral heads and tubular tails of constant length, which in their morphology resemble tailed bacteriophages. They are classified on the basis of their tail structures into the bacteriophage families *Myoviridae*, with contractile tails, or *Sipohoviridae*, with noncontractile tails. Archaeal tailed phages exclusively infect extremely halophilic or methane-producing archaea which are mesophilic or moderately thermophilic (**Table 1**). Sixteen of them have been isolated but only very few were studied beyond a basic description. Archaeal head-tail viruses have also been described in an article on tailed bacteriophages by H. Ackermann. The best-studied myoviruses are *Halobacterium salinarum* phage ΦH (**Figure 1h**) and its close relative ΦCh1, as well as a pair of related haloviruses HF1 and HF2 (**Table 1**). For siphoviruses, best studied are ΨM1 and its deletion mutant ΨM2 from the moderately thermophilic *Methanothermobacter*. **See also**: Bacteriophages: Tailed

All archaeal tailed viruses replicate lytically with the burst size of 170 particles for ΦH and approximately 6 for ΨM1. ΦH and ΦCh1 are both capable of establishing true lysogeny but they differ in the form of the proviral DNA. The genome of ΦH is not integrated into host chromosomes but persists in host cells in a circular form, whereas the genome of ΦCh1 is integratable. The lysogeny can be interrupted by subjecting host cells to suboptimal salt concentrations. In the course of replication, the genomes of ΦH and ΨM1 form concatamers which are packaged by a head-full mechanism from the *pac* site. The packaging is relatively unspecific and their genomes were shown to be redundant and circularly permuted. Halovirus HF2 seems to employ a different replication mechanism because its genome has no terminal redundancy and it contains a 306-bp direct terminal repeat. The nucleic acid content of some viruses is unusual. Thus, virions of the myovirus ΦCh1, along with the genomic dsDNA, contain uncharacterized, host-encoded RNA species of 80–700 nucleotides in length. In the virions of the siphovirus ΨM1, only 85% of the DNA is the phage genome, while the remainder is head-to-tail multimers of the cryptic plasmid of approximately 4.5 kbp from *Methanothermobacter*.

Archaeal head-tail viruses resemble bacteriophages also in having mosaic genomes which can undergo extensive genetic exchange. The genome of ΦH is highly variable due to recombination with the host genome, as well as duplication and inversion of one part of the viral genome. High levels of recombination also occur among the myoviruses HF1 and HF2. The genome of ΦCh1 contains an invertible region that encodes a recombinase and structural proteins which is reminiscent of the invertible genome segments of the bacteriophage-like Mu or P1. As for the latter, inversion of the segment results in variation of the structure of virion proteins, indicating that this mechanism for generating variability is shared by myoviruses across the domains Archaea and Bacteria.

Transcription has only been studied in some detail for ΦH and HF2 and has been found to be strictly time-dependent – early, intermediate and late transcripts are clearly distinguishable. Early transcription has been found to be essential for the expression of the intermediate and late genes. For ΦH, transcription is regulated by a viral transcription repressor, which prevents the formation of the major early lytic transcript T4. The promoters of the repressor (*rep*) and T4 genes are adjacent but inversely oriented similarly to the configuration of the *cI* and *cro* promoters in bacteriophage λ. In addition, it has been shown that ΦH employs regulation of gene expression based on antisense RNA which, in lysogens, mediates the removal of the ribosome-binding site from a transcript involved in the lytic cycle.

It is becoming increasingly clear that relatively high numbers of isolated tailed phages which infect methanogens and halophiles do not reflect the true picture of archaeal viral diversity. Tailed phages are rarely observed in hot terrestrial aquatic environments where archaea represent the dominant cellular form. Furthermore, the most common morphotypes observed in hypersaline environments rich in haloarchaea are spindles, spheres and star-shaped virus-like particles. Thus, the current situation arose from a major bias in virus isolation methods.

Genomics

The most prominent features of genomes of known crenarchaeal viruses are the extremely low number of genes coding for proteins with homologues in the public sequence databases. With the current coverage of viral and cellular genomes, a large majority of viral genes have no detectable homologues other than in closely related viral species (**Figure 2**). The only exception is the archaeal tailed phages viruses which carry genes with homologues in genomes of bacterial cells and bacteriophages from the families *Myoviridae* and *Siphoviridae*. For ΦCh1, ΨM1/2, HF1 and HF2 homologous genes were detected encoding proteins involved in virion assembly, capsid and tail formation and DNA modification, as well as transcriptional regulators, adenosine triphosphatases (ATPases) and nucleases.

For hyperthermophilic archaeal viruses detailed analyses of their genomic sequences revealed a set of 15 proteins or protein families with homologues in public databases, other than in closely related archaeal viruses (Prangishvili *et al*., 2006). Among them the most prominent functional

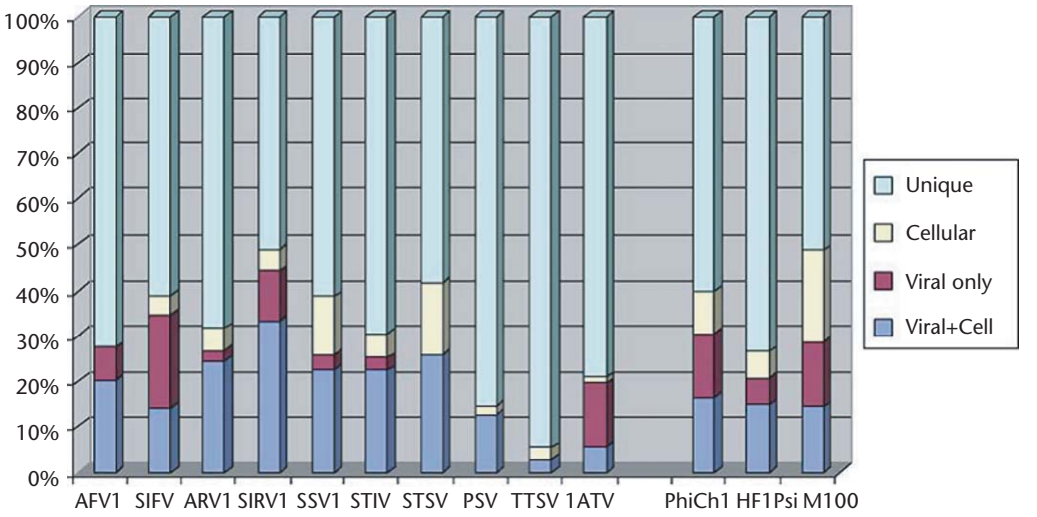

Figure 2 Proportions of different sets of genes in genomes of archaeal viruses. Viral+Cell, genes with homologues in other viruses and cellular life forms; viral only, genes with homologues detectable only in other viruses; cellular, genes with homologues detectable only in cellular life forms; unique, genes without detectable homologues. This figure was prepared by Eugene Koonin and published in *Virus Research*, **117**, Prangishvili *et al*, 52–67, copyright Elsevier (2006). Reproduced with permission.

groups are transcriptional regulators, proteins involved in DNA replication, DNA precursor metabolism and DNA packaging, as well as proteins implicated in virion morphogenesis and modification of the host cell wall. In addition to sequence homology searches, structural studies of some proteins from SSV1, STIV and AFV3 have resulted in prediction of their functions including DNA-binding proteins and an adaptor protein (Ortmann *et al*., 2006).

Evolutionary relationships between viruses can be assessed by determining the sets of shared orthologous genes (Prangishvili *et al*., 2006). Results of the search for such genes in hyperthermophilic archaeal viral genomes are in remarkable accord with evolutionary relationships originally postulated on the basis of morphological features. The analysis revealed that very few orthologous genes are shared between members of different viral families. One exception is provided by members of the *Rudiviridae* and *Lipothrixviridae*, which share a significant number of orthologous genes suggesting a common ancestry for these two families.

Origin and Evolution

The origin and nature of the remarkable biodiversity of archaeal viruses raise intriguing evolutionary questions. This diversity is especially striking in hot habitats in contrast to the relative uniformity of the viral landscape in aquatic environments at moderate and low temperatures, which is dominated by head-tail phages. One possibility is that such diversity was once normal in all environments but was later reduced by the successful expansion of bacteria and their bacteriophages in biotopes with moderate and low temperatures, whereas hot environments still remain a refuge for multiple unusual viral forms.

On the whole, comparative genomic analyses clearly indicate that viruses of hyperthermophilic archaea, as distinct replicating entities, are unrelated to any other viruses and have an unique origin or, more likely, multiple origins (Prangishvili *et al*., 2006). The finding that capsid protein of the icosahedral archaeal virus STIV is homologous to the jelly-roll capsid proteins that are nearly universal among icosahedral viruses from all domains of life supports the notion of the primordial, common pool of viral genes reaching across domain boundaries.

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