Iranian Journal of Virology 2018;12(1): 52-62
©2018, Iranian Society of Virology

Review Article

Bacteriophages: An Illustrated General Review

Ramin Mazaheri Nezhad Fard [1,2*]

1. Department of Pathobiology, School of Public Health, Tehran University of Medical Sciences, Tehran, Iran.
2. Food Microbiology Research Center, Tehran University of Medical Sciences, Tehran, Iran.

Table of Contents

Bacteriophages: An Illustrated General Review……..……..52

Abstract.....52

Introduction.....53

Background.....53

History.....53

Taxonomy.....55

Morphology.....55

Conclusions.....59

Acknowledgments.....59

References.....59

Abstract

Bacteriophages are the most widespread entities on earth, which are able to invade prokaryotes. Bacteriophages play roles in dynamics of bacterial population, pathogenicity, epidemics and evolution. Bacteriophages are taxonomically categorized into two major orders of Caudovirales and Ligamenvirales, five families, nine subfamilies, 145 genera and 684 species; from which, family members of Siphoviridae, Myoviridae, Podoviridae and Inoviridae are the most widespread bacteriophages in nature. Bacteriophages are morphologically categorized into two main categories of tailed and polyhedral, filamentous or pleomorphic bacteriophages. They can have a single or double stranded DNA or RNA genome. The current review generally introduces bacteriophages using illustrations.

Keywords: Bacteriophage, prokaryote, bacteria, virus, morphology, taxonomy

[Downloaded from journal.isv.org.ir on 2026-09-17]

Introduction

Background

Bacteriophages (simply phages) are viruses that infect prokaryotes, including eubacteria and archaea (1). In other words, bacteriophages dramatically hunt prokaryotes as their prey (bacteriophagy). This term means bacterial eating in Latin. These predators are more abundant on earth (approx. population of 1031) than any other biological entities (2–4).

They are found everywhere, in soil, water, food and even saliva. The bacteriophage population is estimated as being ten times greater than the bacterial population (5). The infection rate of bacteria by the bacteriophages is approximated 1025 per second, ongoing at least for the last three billion years.

Bacteriophages destroy a significant portion (1/5) of bacterial populations every two days and are more important in adoption of pathogens to new hosts than any other mechanism, with new strains emerging and epidemics occurring (6–8). Therefore, host-pathogen interaction is redefined by a novel concept "host-pathogen-phage interaction".

History

Bacteriophages were first discovered in the late 1800s. In 1896, Ernest Hankin, an English chemical examiner and bacteriologist, inactivated Vibrio cholerae using filtrates of water from the Ganges and Yamuna Rivers in northern India (Figure 1) (9). This was repeated later in 1898 by Nikolay Gamaleya, a Russian physician and scientist, while working with Bacillus subtilis. In 1915, Frederick Twort, an English bacteriologist, suggested that the causative agent was a "bacterial virus" (Figure 2) (10). In 1917, Felix d'Herelle, a French-Canadian microbiologist, used a plaque method and reported the first bacterial lysis (Figures 3 and 4) (11). He named the causative agent a "bacteriophage", which means bacteria eater in Greek. Most of the early applied knowledge of the bacteriophages are results of his studies (Figure 5). Clark and Clark (1927) made the first successful isolation of a streptococcal bacteriophage (12).

Enterococcal bacteriophages were firstly isolated from sewage by Evans (1934) and later by Rakieten and Tiffany (1938), Tiffany and Rakieten (1939) and Evans (1941) (13–16).

Fig. 1. Ernest Hanbury Hankin, St. John's College, ca 1900 (public domain file from Wikipedia).

Fig. 2. Frederick William Twort, ca 1900 (public domain file from Wikipedia).

Fig. 3. Felix d'Herelle, 1910 (public domain file from Wikipedia)

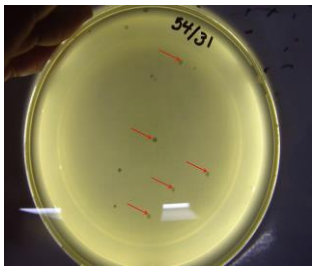
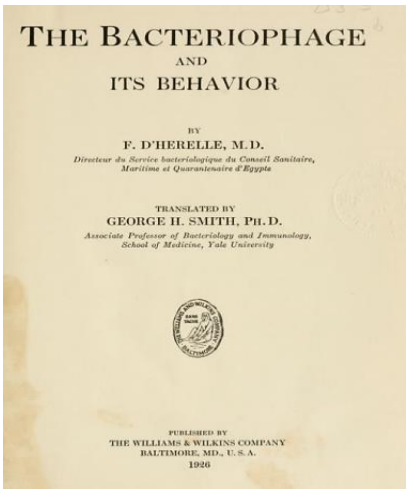


Fig. 4. Enterococcal bacteriophage plaques on TSA plate (courtesy of R. Mazaheri Nezhad Fard).

***Corresponding author**: Ramin Mazaheri Nezhad Fard
Assistant Professor in Medical Bacteriology,
Email: r-mazaherinf@sina.tums.ac.ir,
Office: +98-21-42933208, Mobile: +98-9129303788,
Address: Department of, Pathobiology, School of Public Health, Tehran, University of Medical Sciences, Pour Sina St., Keshavarz Blvd., Tehran, Iran

[Downloaded from journal.isv.org.ir on 2026-09-17]


THE BACTERIOPHAGE
AND
ITS BEHAVIOR

BY
F. D'HERELLE, M.D.
Directeur du Service bacteriologique du Conseil Sanitaire, Maritime et Quarantenaire d'Egypte

TRANSLATED BY
GEORGE H. SMITH, PH.D.
Associate Professor of Bacteriology and Immunology, School of Medicine, Yale University

PUBLISHED BY
THE WILLIAMS & WILKINS COMPANY
BALTIMORE, MD., U. S. A.
1926

Fig. 5. D'Herelle, F. and G. H. Smith, The bacteriophage and its behavior, Baltimore: Williams & Wilkins, 1926 (digital scan from Open Library).

Kjems (1955) found evidence of lysogeny and isolated four strains of bacteriophages from Group D streptococci, including Streptococcus faecalis and S. faecium (17). Further isolations were carried out by Bleiweis and Zimmerman (1961), Brock et al. (1963) and Brock (1964) (18–20). Furthermore, the golden era of bacteriophage research has begun from 1938 when Max Delbruck, a German physicist and biologist, started a series of studies on physiology and ecology of the bacteriophages at the California Institute of Technology, USA. Soon, Italian Salvadore Luria and American Al Hershey joined him and carried out some most interesting genetic studies on bacteriophages. The genetic studies were continued by Luria and Human (1952) and Arber and Dussoix (1962) and many other researchers worldwide (21, 22).

Table 1. Taxonomy and classification of bacteriophages

Order	Family	Specifications				
		Head	Tail	Env.	Gen.	Other
Caudovirales	Myoviridae, A1	Isometric	Contractile	No	Linear dsDNA	
Caudovirales	Myoviridae, A2	Elongated	Contractile	No	Linear dsDNA	Head L/W ratio = 1.3−1.8
Caudovirales	Myoviridae, A3	Elongated	Contractile	No	Linear dsDNA	Head L/W ratio ≥ 2
Caudovirales	Podoviridae, C1	Isometric	Short, noncontractile	No	Linear dsDNA	
Caudovirales	Podoviridae, C2	Elongated	Short, noncontractile	No	Linear dsDNA	Head L/W ratio = 1.4
Caudovirales	Podoviridae, C3	Elongated	Short, noncontractile	No	Linear dsDNA	Head L/W ratio ≥ 2.5
Caudovirales	Siphoviridae, B1	Isometric	Long, noncontractile	No	Linear dsDNA	
Caudovirales	Siphoviridae, B2	Elongated	Long, noncontractile	No	Linear dsDNA	Head L/W ratio = 1.2−2
Caudovirales	Siphoviridae, B3	Elongated	Long, noncontractile	No	Linear dsDNA	Head L/W ratio ≥ 2.5
Ligamenvirales	Lipothrixviridae	PFP	PFP	Yes	Linear dsDNA	Filaments, lipids
Ligamenvirales	Rudiviridae	PFP	PFP	No	Linear dsDNA	Helical rods
No order	Corticoviridae			No	Circular supercoiled dsDNA	Icosahedral capsid, lipids
No order	Cystoviridae	PFP	PFP	Yes	3× linear dsRNA	Icosahedral capsid, lipids
No order	Guttaviridae	PFP	PFP	Yes	Circular dsDNA	Pleomorphic capsid, protrusions, beard of long fibers
No order	Fuselloviridae	PFP	PFP	Yes	Circular supercoiled dsDNA	Pleomorphic capsid, lipids, protrusions, short tail-like fibers
No order	Inoviridae: Inovirus	PFP	PFP	No	Circular ssDNA	Long filaments with helical symmetry
No order	Inoviridae: Plectrovirus	PFP	PFP	No	Circular ssDNA	Short rods with helical symmetry
No order	Leviviridae	PFP	PFP	No	Linear ssRNA	Quasi-icosahedral capsid
No order	Microviridae	PFP	PFP	No	Circular ssDNA	Icosahedral capsid
No order	Plasmaviridae	PFP	PFP	Yes	Circular supercoiled dsDNA	Pleomorphic, no capsid, lipids,
No order	Tectiviridae	PFP	PFP	No	Linear dsDNA,	Icosahedral capsid with inner lipoprotein vesicle, tail is produced for DNA injection
Unassigned	Salterprovirus	PFP	PFP	Yes	Linear dsDNA	Pleomorphic capsid, lemon-shaped, short tail-like fibers

[Downloaded from journal.isv.org.ir on 2026-09-17]

Taxonomy

Since research on bacteriophages is a fast developing trend worldwide and because much genetic data from bacteriophages are published every year, bacteriophage taxonomy changes regularly. Like other viruses, bacteriophages are classified based on general criteria, including type of genetic material (DNA or RNA, single or double stranded, linear or circular, segmented or non-segmented), morphology (e.g. symmetry versus asymmetry, presence or absence of the tail), capsid components (e.g. existence of envelope, lipid molecules), virion dimensions and the bacteriophage life cycle and strategies (23).

Of these criteria, the first criterion is critical in Baltimore classification. Currently, the International Committee on Taxonomy of Viruses (ICTV) classifies bacteriophages in two orders (Caudovirales and Ligamenvirales), five families, nine subfamilies, 145 genera and 684 species and further unassigned families mostly belong to archaea (Table 1) (24, 25).

Bacteriophage families are alphabetically listed as follows: Corticoviridae, Cystoviridae, Fuselloviridae, Guttaviridae, Inoviridae, Leviviridae, Lipothrixviridae, Microviridae, Myoviridae, Plasmaviridae, Podoviridae, Rudiviridae, Siphoviridae and Tectiviridae.

Of these families, four families seem to be more widespread in nature, namely Siphoviridae (Order Caudovirales), Myoviridae (Order Caudovirales), Podoviridae (Order Caudovirales) and Inoviridae (no order) (26, 27). A dilemma is seen here which is linked to the bacteriophage nomenclature. The question is that which prokaryotes (eubacteria or archaea) can be referred as the host of bacteriophages, since Ligamenvirales members have been suggested recently as archaean viruses by ICTV (28). However, most of the bacteriophage families have been reported in eubacteria. Therefore, the current review still virtually uses "bacteriophage" as a general name for all prokaryotic viruses to avoid confliction.

Morphology

Bacteriophages are morphologically categorized to two major categories of tailed (head-tail) and PFP (polyhedral, filamentous or pleomorphic) bacteriophages (Figures 6–14).

A typical structure of tailed bacteriophages consists of an icosohedral head containing the virus capsid (including units of capsomers), genome and sometimes a lipid coat, a neck or collar, a tail (some contain multiple tails) and a baseplate (Figure 15) (29, 30).

The tail includes a core covered by a helical sheath that ends to the base plate, which bears long tail fibers and short tail fibers or tail pins.

The genome of bacteriophages can be composed of either single or double-stranded DNA or RNA and can range in size from a few to several hundred kilobases (2, 31).

The largest bacteriophage genome belongs to Klebsiella Phage vB_KleM-RaK2, including 346 kb (32). Most genes in bacteriophages belong to lysis, replication and regulation, packaging and structural, antibiotic resistance and housekeeping genes. In general, these genes can be classified into two major groups: housekeeping and regulatory genes.

Housekeeping genes encode proteins such as head-tail joining proteins, head-tail adaptor proteins, host specificity proteins, portal proteins, prohead protease, tail component, tail major proteins, tape measure proteins, terminase large subunit and terminase small subunit.

Regulatory genes encode proteins such as amidase, holing, HNH endonuclease and DNA primase (33).

Since 1959, thousands of bacteriophages have been examined by electron microscope (EM) (34). However, the first bacteriophage was observed by Helmut Ruska, a German

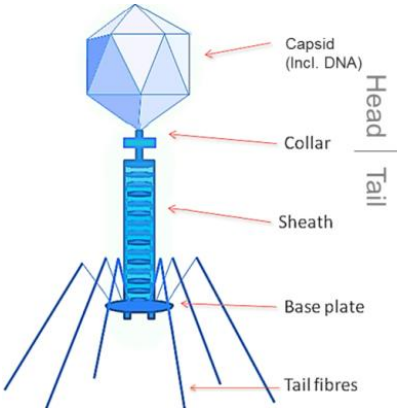


Fig. 15. Schematic of a tailed bacteriophage (modified public domain file from Wikipedia).

[Downloaded from journal.isv.org.ir on 2026-09-17]

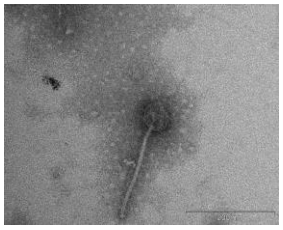


Fig. 6. An isometric head, long tailed bacteriophage (TEM 130,000×) (courtesy of R. Mazaheri Nezhad Fard).

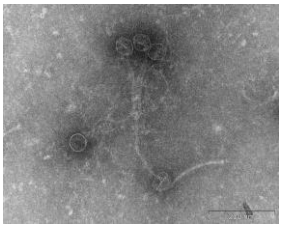


Fig. 7. Isometric head, long tailed bacteriophages (TEM 92,000×) (courtesy of R. Mazaheri Nezhad Fard).

Fig. 8. A tailed bacteriophage (TEM 130,000×). Circular double-stranded genome is removed from the bacteriophage (courtesy of R. Mazaheri Nezhad Fard).

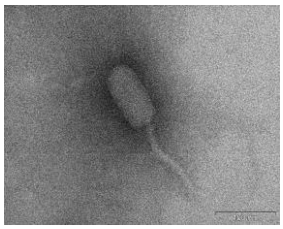


Fig. 9. A long head, long tailed bacteriophage (TEM 180,000×) (courtesy of R. Mazaheri Nezhad Fard).

Fig. 10. An isometric head, long tailed bacteriophage (TEM 92,000×) (courtesy of R. Mazaheri Nezhad Fard).

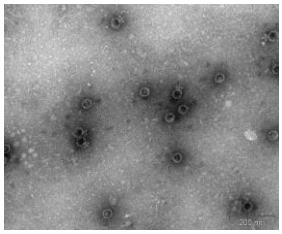


Fig. 11. Isometric head, short tailed bacteriophages (TEM 92,000×) (courtesy of R. Mazaheri Nezhad Fard).

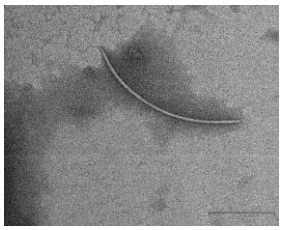


Fig. 12. A filamentous bacteriophage (TEM 92,000×) (courtesy of R. Mazaheri Nezhad Fard).

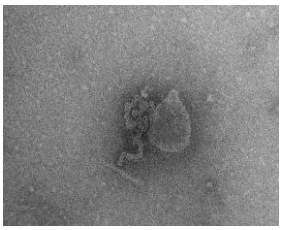


Fig. 13. A droplet shaped (pleomorphic) bacteriophage (TEM 92,000×). Circular double-stranded genome is leaking from the bacteriophage (courtesy of R. Mazaheri Nezhad Fard).

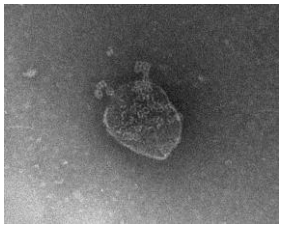


Fig. 14. A lemon shaped (pleomorphic) bacteriophage (TEM 130,000×) (courtesy of R. Mazaheri Nezhad Fard).

physician, biologist, in 1939 using a prototype EM invented by his brother Ernst Ruska (35). Research indicate that approximately 96% of all bacteriophages have a tail; of which, up to 90% feature a single tail while a minority are polyhedral, filamentous or pleomorphic (PFP) (34, 36). Most tailed bacteriophages (nearly 61%) feature long, flexible, noncontractile tails and are categorized in the Siphoviridae family (Order Caudovirales) (37, 38). Some examples include c2, L5, lambda, N15, phiC31, PsiM1, T1 and T5 bacteriophages (Figure 16). This is followed by the members of Myoviridae family (Order Caudovirales) with long, nonflexible, contractile tails (Figure 17) and Podoviridae family (Order Caudovirales) with long, nonflexible, noncontractile tails (Figure 18). Examples of Myoviridae include Bcep781, BcepMu, FelixO1, HP1, I3, KVP40, Mu, P1, P2, PB1, phiCD119, phiH, phiHAP-1, phiKZ, SP01, T4 and Twort bacteriophages and examples of Podoviridae include 44AHJD, BPP-1, epsilon15, LUZ24, N4, P22, phi29, phiEco32, phiKMV, SP6 and T7 bacteriophages. Filamentous bacteriophages are categorized in three families: Inoviridae (no order; e.g. L51, M13, Pf1) (Figure 19), Lipothrixviridae (Order Ligamenvirales; e.g.

[Downloaded from journal.isv.org.ir on 2026-09-17]

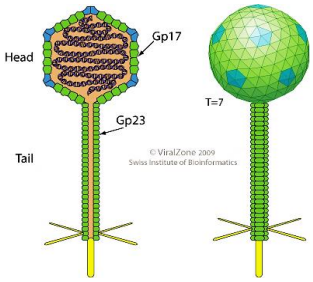


Fig. 16. Schematic of Siphoviridae (from ViralZone, ExPASy).

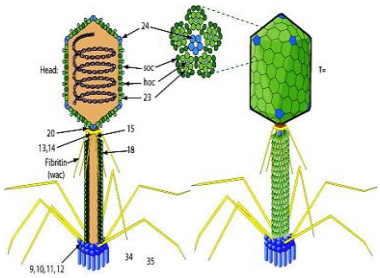


Fig. 17. Schematic of Myoviridae (from ViralZone, ExPASy).

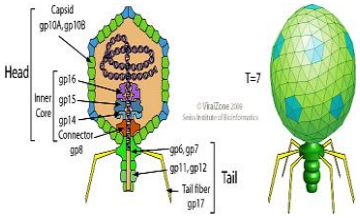


Fig. 18. Schematic of Podoviridae (from ViralZone, ExPASy).

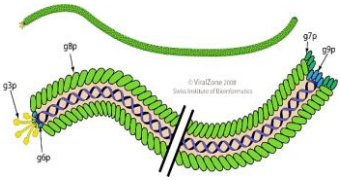


Fig. 19. Schematic of Inoviridae (from ViralZone, ExPASy).

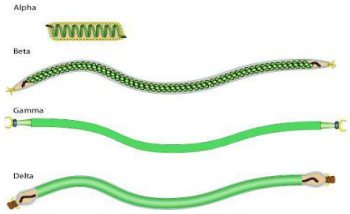


Fig. 20. Schematic of Lipothrixviridae (from ViralZone, ExPASy).

Fig. 21. Schematic of Rudiviridae (from ViralZone, ExPASy).

TTV-1, SIFV, AFV-1, AFV-2) (Figure 20) and Rudiviridae (Order Ligamenvirales; e.g. SIRV-1, SIRV-2) (Figure 21) (39). These bacteriophages are found in both eubacteria (Inoviridae) (40) and archaea (Lipothrixviridae and Rudiviridae) (41). Inoviridae are either long slender tube or short rod bacteriophages with a maximum size of 2 µm and contain a single-stranded circular DNA genome with 4.5–8 kb encoding 4–10 proteins (42).

They are distributed worldwide and can be isolated from a variety of bacteria such as enterobacteria, Vibrio spp., Pseudomonas spp., Xanthomonas spp., Acholeplasma spp. and Spiroplasma spp. Polyphagy is a characteristic of filamentous bacteriophages such as Inoviridae; in which, more than one phage genome are packed in a bacteriophage capsid. Other filamentous bacteriophage families belong to thermophilic and hyperthermophilic archaea. Lipothrixviridae (Order Ligamenvirales) are flexible, enveloped, rod-shaped bacteriophages with 24–38 and 410–1950 nm dimensions (28). The family includes four genera of Alphalipothrixvirus, Betalipothrixvirus, Gammalipothrixvirus and Deltalipothrixvirus (43).

Genome consists of a linear dsDNA genome including 15.9–56 kb. Rudiviridae (Order Ligamenvirales) are rigid, non-enveloped, rod-shaped bacteriophages with three tail fibers at each end (44). The family includes one genus of Rudivirus. Genome consists of a linear dsDNA genome including 32–35 kb and inverted terminal repeats as well as direct repeats at both ends.

Poliovirus-like (the semi-suffix "like" has recently been removed from the bacteriophage names by ICTV but may still be used in some papers) bacteriophage group belongs to Leviviridae family (no order) of bacteriophages (e.g. MS2, Qbeta) (Figure 22). These polyhedral bacteriophages contain a single-stranded linear molecule of RNA (45). Single-stranded RNA bacteriophages are widely found in bacterial isolates from sewage and feces of mammals but unlikely to be found in avian bacterial species (46). Leviviridae are small bacteriophages with a reported size of 23–30 nm (47, 48). Tectiviridae (no order; e.g. AP50, Bam35, P17-14, PRD1) are non-enveloped, icosahedral bacteriophages with capsid symmetry (Figure 23). Virion size is nearly 66 nm with inner membrane vesicle and 20-nm apical spikes.

Although the bacteriophage is a non-tailed one, a tail is produced for DNA injection during the

[Downloaded from journal.isv.org.ir on 2026-09-17]

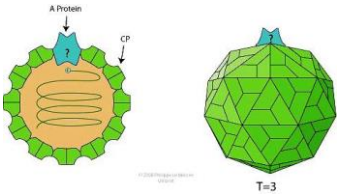


Fig. 22. Schematic of Leviviridae (from ViralZone, ExPASy).

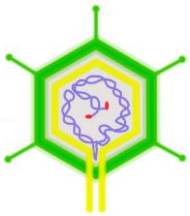


Fig. 24. Schematic of Tectiviridae. The open yellow circle shows a tail produced for DNA injection (modified from Wikimedia Common).

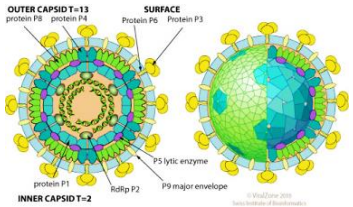


Fig. 26. Schematic of Cystoviridae (from ViralZone, ExPASy).

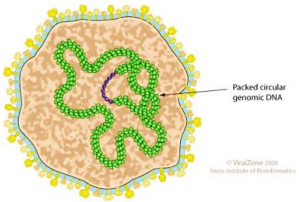


Fig. 28. Schematic of Plasmaviridae (from ViralZone, ExPASy).

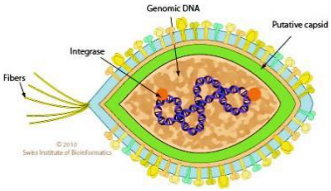


Fig. 30. Schematic of Fuselloviridae (from ViralZone, ExPASy).

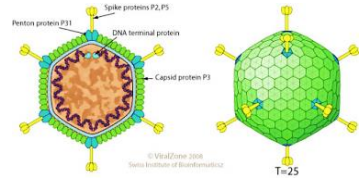


Fig. 23. Schematic of Tectiviridae (from ViralZone, ExPASy).

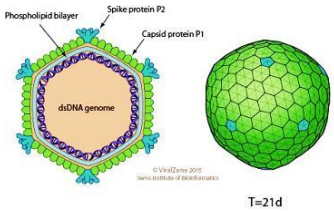


Fig. 25. Schematic of Corticoviridae (from ViralZone, ExPASy).

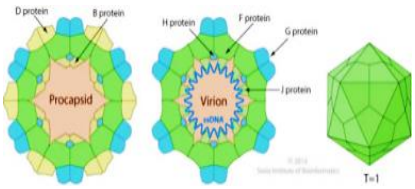


Fig. 27. Schematic of Microviridae (from ViralZone, ExPASy).

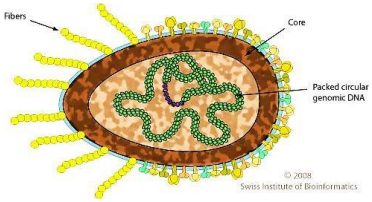


Fig. 29. Schematic of Guttaviridae (from ViralZone, ExPASy).

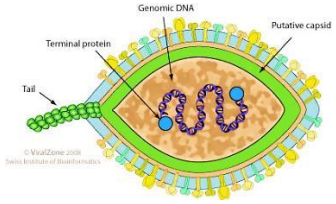


Fig. 31. Schematic of Salterprovirus (from ViralZone, ExPASy).

host infection process (Figure 24). Genome consists of a ~15-kb coiled, linear, dsDNA molecule (49). Corticoviridae bacteriophages (no order; e.g. marine PM2) include ~56-nm icosahedral virions with an internal lipid core and a ~10-kb circular, supercoiled dsDNA genome encoding 21 proteins (Figure 25) (50). There is one genus within the family namely Cortocovirus. Cystoviridae family members (no order; e.g. Phi6– Phi14) are ~85-nm

[Downloaded from journal.isv.org.ir on 2026-09-17]

enveloped, spherical virions with double capsid structure (Figure 26) (51). One genus has been described for the family, namely Cystovirus. The total 13.3-kb genome is segmented, linear dsRNA and contains three segments of large (L), medium (M) and small (S), encoding 12 proteins. Microviridae (no order; e.g. Chp-1, phiMH2K, phiX174, SpV4) includes ~30-nm non-enveloped, round, icosahedral bacteriophages with spikes (Figure 27) (52).

Genome is described as circular ssDNA(+) with 4.5–6 kb in length, encoding A–H and J–K proteins. Plasmaviridae (no order, e.g. L2) is a ~80-nm enveloped, spherical/pleomorphic bacteriophage with one genus of Plasmavirus (Figure 28) (53, 54). Genome of the bacteriophage consists of a ~12-kb low-GC circular, supercoiled dsDNA. Droplet-shaped bacteriophages are classified in the Guttaviridae family (no order; e.g. Sulfolobus newzealandicus droplet-shaped virus) (Figure 29); firstly investigated by Zillig et al. (1998) and described by Arnold et al. (2000) in archaea and later by Mazaheri Nezhad Fard et al. (2010) in eubacteria (55–58). Two genera of Alphaguttavirus and Betaguttavirus are seen in the family. These bacteriophages bear long thin filaments (beard) at one end and contain a dsDNA genome (44, 59). The genome consists of single segment containing a circular dsDNA molecule (app-rox. size of 20 kb) (60–62).

This segment forms a covalently closed circle, which is extensively methylated (60Sau and Deb, 2008; 61). Fuselloviridae family (no order; e.g. SSV-1) represents lemon/spindle-shaped bacterio-phages having peripheral projections and short tail-like fiber(s) attached to one pole (Figure 30) (59, 63, 64). Two genera of Alphafusellovirus and Betafusellovirus are observed within the family.

The bacteriophages contain a single molecule of circular, supercoiled dsDNA with 14.8–17.3 kb encoding 31–37 genes. As with Guttaviridae, Fuselloviridae have mostly been isolated on or from archaea but first reported in eubacteria by Mazaheri Nezhad Fard et al. in 2010 (55, 65, 66).

However, detection of possible archaeal bacteriophages in eubacteria cannot be completely ruled out as other bacteriophage families (Siphoviridae and Myoviridae) are found in both bacterial kingdoms (41, 55). Another lemon-shaped bacteriophage, the unassigned Salterprovirus (e.g. His1 virus, His2 virus), is a pleomorphic, enveloped bacteriophage with short tail-like fibers and a ~14.5-kb linear dsDNA genome (Figure 31) (67). The bacteriophage habitats include high salted waters and lakes (the reason for naming).

Conclusions

In conclusion, bacteriophages are a diverse group of biological entities with great promising potentials of contributions to a variety of sciences. Study of bacteriophages is an interesting challenge, which opens new horizons in front of researchers. Not only are these subjects mostly unknown, they include many useful features from research to treatment which should be explored.

Acknowledgments

The author would like to thank Emeritus Prof. Mary Barton, University of South Australia, and retired A/Prof. Michael Heuzenroeder, University of Adelaide, Australia.

References

1. Mihara T, Nishimura Y, Shimizu Y, Nishiyama H, Yoshikawa G, Uehara H, Hingamp P, Goto S, Ogata H. Linking virus genomes with host taxonomy. Viruses. 2016;8:66.

2. Clokie MRJ, Millard AD, Letarov AV, Heaphy S. Phages in nature. Bacteriophage. 2011;1:31–45.

3. Canchaya C, Fournous G, Brussow H. The impact of prophages on bacterial chromosomes. Mol Microbiol. 2004;53:9−18.

[Downloaded from journal.isv.org.ir on 2026-09-17]

4. Pedulla ML, Ford ME, Houtz JM, Karthikeyan T, Wadsworth C, Lewis JA, Jacobs-Sera D, Falbo J, Gross J, Pannunzio NR, Brucker W, Kumar V, Kandasamy J, Keenan L, Bardarov S, Kriakov J, Lawrence JG, Jacobs Jr WR, Hendrix RW, Hatfull GF. Origins of highly mosaic mycobacteriophage genomes. Cell. 2003;113:171−82.
5. Hendrix RW. Bacteriophages: Evolution of the Majority. Theor Popul Biol. 2002;61:471–80.
6. Ventura M, Canchaya C, Tauch A, Chandra G, Fitzgerald GF, Chater KF, van Sinderen D. Genomics of Actinobacteria: Tracing the evolutionary history of an ancient phylum. Microbiol Mol Biol Rev. 2007;71:495–548.
7. Brussow H, Canchaya C, Hardt W. Phages and the evolution of bacterial pathogens: from genomic rearrangements to lysogenic conversion. Microbiol Mol Biol Rev. 2004;68:560–602.
8. Boyd EF, Brussow H. Common themes among bacteriophage-encoded virulence factors and diversity among the bacteriophages involved. Trends Microbiol. 2002;10:521−9.
9. Hankin EH. L'action bactericide des eaux de la Jumna et du Gange sur le vibrion du cholera. Ann Inst Pasteur (Paris). 1896;10:511–23.
10. Twort FW. An investigation of the nature of ultramicroscopic viruses. The Lancet. 1915;186: 1241–3.
11. d'Herelle F. Sur un microbe invisible antagoniste des bacilles dysenteriques. Comp Rend Acad Sci (Paris). 1917;165:373–5.
12. Clark PF, Clark AS. A bacteriophage active against a virulent hemolytic Streptococcus. Proc Soc Exptl Biol Med. 1927;24:635–9.
13. Evans AC. Technique for the determination of the sensitivity of a strain of Streptococcus to bacteriophage of type A, B, C or D. J Bacteriol. 1941;44:207–9.
14. Tiffany EJ, Rakieten ML. The Absorption of bacteriophage by sensitized enterococci. J Bacteriol. 1939;37:333–50.
15. Rakieten ML, Tiffany EJ. The absorption of Staphylococcus bacteriophages by enterococci. J Bacteriol. 1938;36:155−73.
16. Evans AC. The prevalence of Streptococcus bacteriophage. Science. 1934;80:40–1.
17. Kjems E. Studies on streptococcal bacteriophages, 1. Techniques of isolating phage-producing strains. Acta Pathol Microbiol Scand. 1955;36: 433–40.
18. Brock TD. Host range of certain virulent and temperate bacteriophages attacking Group D streptococci. J Bacteriol. 1964;88:165–71.
19. Brock TD, Peacher B, Pierson D. Survey of the bacteriophages of enterococci. J Bacteriol. 1963; 86:702–7.
20. Bleiweis AS, Zimmerman LN. Formation of two types of osmotically fragile bodies from Streptococcus faecalis var. liquefaciens. Can J Microbiol. 1961;7:363–73.
21. Arber W, Dussoix D. Host specificity of DNA produced by Escherichia coli, 1 Host controlled modification of bacteriophage. J Mol Biol. 1962; 5:516–8.
22. Luria SE, Human ML. A non hereditary host induced variation of bacterial viruses. J Bacteriol. 1952;64:557–62.
23. Weinbauer MG. Ecology of prokaryotic viruses. FEMS Microbiol Rev. 2004;28:127–81.
24. Krupovic M, Dutilh BE, Adriaenssens EM, Wittmann J, Vogensen FK, Sullivan MB, Rumnieks J, Prangishvili D, Lavigne R, Kropinski AM, Klumpp J, Gillis A, Enault F, Edwards RA, Duffy S, Clokie MRC, Barylski J, Ackermann HW, Kuhn JH. Taxonomy of prokaryotic viruses: update from the ICTV bacterial and archaeal viruses subcommittee. Arch Virol. 2016;161(4):1095-9.
25. ICTV International Committee on Taxonomy of Viruses. Virus Taxonomy. 2015; available at http://www.ictvonline.org/virusTaxonomy.asp. Last accessed January 2018.
26. Nelson D. Phage taxonomy: we agree to disagree. J Bacteriol. 2004;186:7029–31.
27. Lawrence JG, Hatfull GF, Hendrix RW. Imbroglios of viral taxonomy: genetic exchange and failings of phenetic approaches. J Bacteriol. 2002;184:4891–905.
28. Prangishvili D, Krupovic M. A new proposed taxon for double-stranded DNA viruses, the order "Ligamenvirales". Arch Virol. 2012;157: 791–795.
29. Fokine A, Rossmann MG. Molecular architecture of tailed double-stranded DNA phages. Bacteriophage. 2014;4:e28281−22.
30. Yap ML, Rossmann MG. Structure and function of bacteriophage T4. Future Microbiol. 2014;9:1319–27.
31. Frost LS, Leplae R, Summers AO, Toussaint A. Mobile genetic elements: the agents of open source evolution. Nature. 2005;3:722−32.
32. Simoliunas E, Kaliniene L, Truncaite L, Zajanckauskaite A, Staniulis J, Kaupinis A, Ger M, Valius M, Meskys R. Klebsiella phage vB_KleM-RaK2—A giant singleton virus of the family Myoviridae. PLoS ONE. 2013;8:e60717.
33. Son JS, Jun SY, Kim EB, Park JE, Paik HR, Yoon SJ, Kang SH, Choi YJ. Complete genome sequence of a newly isolated lytic bacteriophage. EFAP-1 of Enterococcus faecalis, and antibacterial

[Downloaded from journal.isv.org.ir on 2026-09-17]

activity of its endolysin EFAL-1. J Appl Microbiol. 2010;108:1769–79.
34. Ackermann HW. 5500 Phages examined in the electron microscope. Arch Virol. 2007;152:227–43.
35. Kruger DH, Schneck P, Gelderblom HR. Helmut Ruska and the visualisation of viruses. Lancet. 2000;355:1713–7.
36. Ackermann HW. Frequency of morphological phage descriptions in the year 2000. Arch Virol. 2001;146:843–57.
37. Mazaheri Nezhad Fard R, Barton MD, Arthur JL, Heuzenroeder MW. Whole genome sequencing and gene mapping of a newly isolated lytic enterococcal bacteriophage EFRM31. Arch Virol. 2010a; 155:1887–91.
38. Mazaheri Nezhad Fard R, Barton MD, Heuzenroeder MW. Bacteriophage-mediated transduction of antibiotic resistance in enterococci. Lett Appl Microbiol. 2011;52:559–64.
39. Ackermann HW. Bacteriophage observations and evolution. Res Microbiol. 2003;154:245–51.
40. Campos J, Martinez E, Suzarte E, Rodriguez BL, Marrero K, Silva Y, Ledon T, del Sol R, Fando R. VGJΦ, a novel filamentous phage of Vibrio cholerae, integrates into the same chromosomal site as CTXΦ. J Bacteriol. 2003;185:5685–96.
41. Geslin C, Le Romancer M, Erauso G, Gaillard M, Perrot G, Prieur D. PAV1, the first virus-like particle isolated from a hyperthermophilic euryarchaeote, "Pyrococcus abyssi". J Bacteriol. 2003; 185:3888−94.
42. Klieve AV, Bain PA, Yokoyama MT, Ouwerkerk D, Forster RJ, Turner AF. Bacteriophages that infect the cellulolytic ruminal bacterium Ruminococcus albus AR67. Lett Appl Microbiol. 2004;38:333–8.
43. Haring M, Vestergaard G, Brugger K, Rachel R, Garrett RA, Prangishvili D. Structure and genome organization of AFV2, a novel archaeal lipothrixvirus with unusual terminal and core structures. J Bacteriol. 2005;187:3855–3858.
44. Prangishvili D, Arnold HP, Gotz D, Ziese U, Holz I, Kristjansson JK, Zillig W. A novel virus family, the Rudiviridae: Structure, virus-host interactions and genome variability of the Sulfolobus viruses SIRV1 and SIRV2. Genetics. 1999;152:1387–96.
45. Vinje J, Oudejans SJG, Stewart JR, Sobsey MD, Long SC. Molecular detection and genotyping of male-specific coliphages by Reverse Transcription-PCR and Reverse Line Blot Hybridization. Appl Environ Microbiol. 2004;70:5996–6004.
46. Bollback JP, Huelsenbeck JP. Phylogeny, genome evolution, and host specificity of single-stranded RNA bacteriophage (Family Leviviridae). J Mol Evol. 2001;52:117–28.
47. Love DC, Vinje J, Khalil SM, Murphy J, Lovelace GL, Sobsey MD. Evaluation of RT-PCR and reverse line blot hybridization for detection and genotyping F+ RNA coliphages from estuarine waters and molluscan shellfish. J Appl Microbiol. 2008;104:1203–12.
48. Klovins J, Overbeek GP, van den Worm SHE, Ackermann HW, van Duin J. Nucleotide sequence of a ssRNA phage from Acinetobacter: kinship to coliphages. J Gen Virol. 2002;83:1523–33.
49. Krupovic M, Cvirkaite-Krupovic V, Bamford DH. Identification and functional analysis of the Rz/Rz1-like accessory lysis genes in the membrane-containing bacteriophage PRD1. Mol Microbiol. 2008;68:492–503.
50. Krupovic M, Bamford DH. Putative prophages related to lytic tailless marine dsDNA phage PM2 are widespread in the genomes of aquatic bacteria. BMC Genomics. 2007;8:236.
51. Silander OK, Weinreich DM, Wright KM, O'Keefe KJ, Rang CU, Turner PE, Chao L. Widespread genetic exchange among terrestrial bacteriophages. PNAS. 2005;102:19009–14.
52. Rokyta DR, Burch CL, Caudle SB, Wichman HA. Horizontal gene transfer and the evolution of microvirid coliphage genomes. J Bacteriol. 2006; 188:1134–42.
53. Maniloff J, Kampo GJ, Dascher CC. Sequence analysis of a unique temperature phage: mycoplasma virus L2. Gene. 1994;141:1–8.
54. Dybvig K, Maniloff J. Integration and lysogeny by an enveloped mycoplasma virus. J Gen Virol. 1983;64:1781–5.
55. Mazaheri Nezhad Fard R, Barton MD, Heuzenroeder MW. Novel bacteriophages in Enterococcus spp. Curr Microbiol. 2010b;60:400− 6.
56. Liu B, Zhou F, Wu S, Xu Y, Zhang X. Genomic and proteomic characterization of a thermophilic Geobacillus bacteriophage GBSV1. Res Microbiol. 2009;160:166−71.
57. Lipps G. Plasmids and viruses of the thermoacidophilic crenarchaeote Sulfolobus. Extremophiles. 2006;10:17–28.
58. Vestergaard G, Haring M, Peng X, Rachel R, Garrett RA, Prangishvili D. A novel rudivirus, ARV1, of the hyperthermophilic archaeal genus Acidianus. Virology. 2005;336:83–92.
59. Prangishvili D, Stedman K, Zillig W. Viruses of the extremely thermophilic archaeon Sulfolobus. Trends Microbiol. 2001;9:39−43.
60. Sau K, Deb A. Temperature influences synonymous codon and amino acid usage biases in the

[Downloaded from journal.isv.org.ir on 2026-09-17]

phages infecting extremely thermophilic prokaryotes. ISB. 2008;9:1−9.
61. Prangishvili D, Garrett RA. Exceptionally diverse morphotypes and genomes of crenarchaeal hyperthermophilic viruses. Biochem Soc Trans. 2004;32:204−8.
62. Rice G, Stedman K, Snyder J, Wiedenheft B, Willits D, Brumfield S, McDermott T, Young MJ. Viruses from extreme thermal environments. Proc Natl Acad Sci USA. 2001;98:13341−5.
63. Kraft P, Oeckinghaus A, Kummel D, Gauss GH, Gilmore J, Wiedenheft B, Young M, Lawrence CM. Crystal structure of F-93 from Sulfolobus spindle-shaped virus 1, a winged-helix DNA binding protein. J Virol. 2004;78:11544−50.
64. Wiedenheft B, Stedman K, Roberto F, Willits D, Gleske AK, Zoeller L, Snyder J, Douglas T, Young M. Comparative genomic analysis of hyperthermophilic archaeal Fuselloviridae viruses. J Virol. 2004;78:1954−61.
65. Xiang X, Chen L, Huang X, Luo Y, She Q, Huang L. Sulfolobus tengchongensis spindle-shaped virus STSV1: virus-host interactions and genomic features. J Virol. 2005;79:8677−86.
66. Stedman KM, She Q, Phan H, Arnold HP, Holz I, Garrett RA, Zillig W. Relationships between fuselloviruses infecting the extremely thermophilic archaeon Sulfolobus: SSV1 and SSV2. Res Microbiol. 2003;154:295−302.
67. Bath C, Cukalac T, Porter K, Dyall-Smith ML. His1 and His2 are distantly related, spindle-shaped haloviruses belonging to the novel virus group, Salterprovirus. Virology. 2006;350:228–39.

[Downloaded from journal.isv.org.ir on 2026-09-17]