

Capsid Morphologies and Predominant Morphotypes in Viruses of Halophilic and Thermophilic Archaea



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WRITERS' COMMENT: I remember that on the first day of UWP 102B, Dr. Carpenter stated a universally true fact: “writing is hard.” But at the same time, he continually emphasized that the most challenging aspect of being a scientist is not conducting the research itself, but instead it is communicating the information to the target audience. So, when the time came for us to draft our review papers, my goal was to choose a topic that thoroughly excites me and then to translate this excitement into a paper in a way that is accessible to all my peers. Growing up being interested in space fiction, astrobiology, which is the study of living organisms in space, was an obvious choice for me. But as I delved deeper, I came across the term “astrovirology” and noticed that viruses are almost completely disregarded in the search for life in space. Consequently, I decided to write about the biosignatures specific to viruses that we can look for to find out if these strange little creatures do indeed exist in space.

INSTRUCTOR'S COMMENT: Winter Quarter 2021 was a difficult quarter for students and instructors alike. We celebrated the one-year anniversary of being in Covid lockdown and even the strongest of us were starting to bend a bit under the compound stressors of online learning and doing literally anything else during the pandemic. In her end-of-the-quarter reflection on the things she learned in this course, Eesha said that “the most useful tip [she] learned was that it is better to start somewhere than to not start at all.” She continued, “Once you start writing and or annotating, it is very convenient to build slowly on

that foundation.” There is a lesson there for all of us: often the hardest part of a task is starting. Once you get the ball rolling, it is easier to keep it moving along, adding, massaging, condensing as you go. Sometimes, in very complex topics, the author can get “lost in the sauce” and lose sight of their goal—in this case, to help a scientifically literate audience understand the intricate relationships between virus morphology (how they are built) and their genetic makeup. By building this knowledge, Eesha believes, we can glean vital information about the origin of viruses on Earth. From there, it is possible that we can develop a biomarker for identifying the presence of viruses in extraterrestrial habitats. During one of our office-hours chats, Eesha talked to me about astrobiology—her passion for the field, for space exploration and the importance of learning about the things that we don’t even know we don’t know. This paper is an excellent example of how Eesha worked to engage her audience with the unknown, then worked to illustrate how we can use genetics and virus morphology on Earth to help us better understand how life could be flourishing on other planets.

Thus, I encourage you, dear reader, to take a bit of advice from Eesha Gupte, no matter how difficult something may seem, it is better to start somewhere than to not start at all. You never know how far that simple start may end up taking you.

—Russ Carpenter, University Writing Program

Abstract

Viruses are abundant life forms and have been involved in the process of evolution of cellular life on Earth. Nevertheless, they are largely ignored by astrobiologists in the search for life in outer space, and consequently no valid virus biosignatures have been identified. This review describes the potential of virus capsid morphology as a biosignature to be used in future missions by examining the commonality of morphotypes in viruses of halophilic and thermophilic archaea and also addresses the influence of environmental factors, genetics, and host on these morphologies. After surveying multiple studies that describe newly discovered viruses of our interest, it was found that in hypersaline environments, most frequently

observed morphotypes are spindle-shaped, pleomorphic, head-tailed, and spherical. In regions with high temperature and acidity filamentous and spindle-shaped morphotypes but also other unique morphotypes are found. While study of some of these indicates that viruses require a cellular host to exist, study of others suggests that viruses evolved before or concurrently with cellular life on Earth. Though this provides a better insight about the origin of life on Earth, current research on viruses of haloarchaea and thermophilic archaea is limited. Therefore, more research is required to identify how genetics, environment, and hosts affect virus capsid morphology and whether it can be used as a viable virus biosignature in the future.

Keywords: Virus, Capsid, Morphology, Archaea, Halophilic, Thermophilic

Introduction

Astrobiology is a multidisciplinary field, and one of its objectives is to find life in outer space. This is done by sending rovers to other planets to look for predetermined biosignatures such as nucleic acids and membrane lipids that are commonly found in all cellular life on Earth. Viruses are the most abundant life forms on Earth—estimated extracellular viruses called virions (Breitbart & Rohwer, 2005)—but are greatly ignored by astrobiologists, and subsequently no valid virus biosignatures have been identified. However, viruses are hypothesized to be crucial in the process of origin and evolution of life on Earth (Koonin et al., 2006). Therefore, it is necessary to identify structures that are common throughout most of the virus population on Earth and can potentially be used as a virus biosignature for future missions.

The significant genetic diversity within viruses and ambiguity regarding their origin and evolution is a major challenge in this process. Nevertheless, the virus capsid morphology is highly conserved despite some notable exceptions (Berliner et al., 2018). Hence, this review will examine the potential of the most common viral capsid morphologies as a biosignature and whether these are influenced by genetics, environmental factors, and hosts. The focus will be on viruses of halophilic and thermophilic archaea since extreme environments are common in outer space and most extremophile hosts on Earth tend to be archaea (Rampelotto, 2013).

1. Virion Structure and Common Morphotypes

A virion is commonly made up of a protein capsid and enclosed genetic material. The genetic material can either be circular or linear and can either comprise single-stranded DNA (ssDNA), double-stranded DNA (dsDNA), or RNA. Since the genome of a virus is extremely small, it encodes only a few types of proteins, out of which some are repeated to form the capsid and are called capsomeres. These capsomeres can assemble in various ways and give rise to the different capsid morphologies which are grouped into multiple morphotypes [see Figure 1]. Most often, helical arrangement of the capsomeres gives rise to long, filamentous viruses, whereas polyhedral arrangement of the capsomere gives rise to icosahedral viruses (Norrby, 1983).

In addition to these morphotypes, there also exist more complex capsid morphotypes, such as pleomorphic haloarchaeal viruses [see












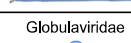



Viral Morphology	Family	Host Species	Notable References
Spindle	 Fuselloviridae	<i>Sulfolobus</i> , <i>Acidianus</i> , <i>Haloarcula</i> , <i>Pyrococcus</i> , <i>Aeropyrum</i> , <i>Stygiolobus</i> and <i>Thermococcus</i>	Krupovic et al. 2014
	 Bicaudoviridae	<i>Acidianus</i>	Haring et al. 2005b
	 Spiraviridae	<i>Aeropyrum</i>	Mochizuki et al. 2012
Spherical	 "Halospaerovirus"	<i>Haloarcula</i> and <i>Halorubrum</i>	Luk et al. 2014 Porter et al. 2013
Pleomorphic	 Pleolipoviruses	<i>Haloarcula</i> , <i>Halorubrum</i> , and <i>Halogeometricum</i>	Pietila et al. 2012
Head and Tail	 Myoviridae	<i>Halorubrum</i> , <i>Natrialba</i> , <i>Halobacterium</i> , <i>Haloarcula</i> , and <i>Methanobacterium</i>	Pietila et al. 2012 Ackerman et al. 2012
	 Podoviridae	<i>Haloarcula</i>	Pietila et al. 2012 Ackerman et al. 2012
	 Siphoviridae	<i>Haloarcula</i>	Pietila et al. 2012 Ackerman et al. 2012
Bottle	 Ampullaviridae	<i>Acidianus</i>	Haring et al. 2005a
Bacilliform	 Clavaviridae	<i>Aeropyrum</i>	Mochizuki et al. 2010
Droplet	 Guttaviridae	<i>Sulfolobus</i> and <i>Aeropyrum</i>	Arnold et al. 2000a Mochizuki et al. 2011
Linear	 Lipothrixviridae	<i>Acidianus</i> and <i>Sulfolobus</i>	Arnold et al. 2000b
	 Rudiviridae	<i>Sulfolobus</i> , <i>Stygiolobus</i> , and <i>Acidianus</i>	Prangishvili et al. 1999 Vestergaard et al. 2005
Spherical	 Globulaviridae	<i>Pyrobaculum</i> and <i>Thermoproteus</i>	Ahn et al. 2006 Haring et al. 2004
Icosahedral	 "Turriviridae"	<i>Sulfolobus</i>	Rice et al. 2004 Happonen et al. 2010

Figure 1. *Capsid morphotypes of archaeal viruses and associated host species (Snyder et al., 2015)*

“Viruses of halophilic archaea” below].

Sometimes, a virus can have a lipid covering, in which case it is then called an enveloped virus. In the absence of the lipid covering, the virus is called a non-enveloped or naked virus. In both of these cases, the entire virus particle, while being infectious and outside the host cell, is termed as the “virion.” Further, only the capsid and the genetic material together are known as the nucleocapsid (Norrby, 1983). Although there is scope for infinite variety of

virion structure, we see that their capsid morphology is highly conserved on Earth. Even the giant viruses with large genomes display the common icosahedral morphotype (Aherfi et al., 2016). Hence, study of the morphotypes in correlation with origin and environmental factors can explain the potential use of capsid morphology as a virus biosignature in extraterrestrial environments.

2. Predominant Morphotypes:

2.1 Viruses of Halophilic Archaea

Halophilic archaea, also known as haloarchaea, thrive in hypersaline environments and only develop in saturation conditions greater than 10 percent salt, and are associated with abundant viruses living in the same environment (Oren, 2014). The haloarchaeal viruses can be classified into six different families but show only four different morphotypes: spindle-shaped, pleomorphic, head-tailed, and spherical. This section will review these four morphotypes and their significance from the perspective of virus evolution or interaction of the virion with environmental factors.

Spindle-shaped/lemon-shaped haloarchaeal viruses have capsids that are wide at the center with tapering ends. Analyses of multiple hypersaline environments have indicated that this is the most frequently observed morphotype in haloarchaeal viruses (Oren et al., 1997; Sime-Ngando et al., 2011). Out of all the observed spindle-shaped viruses, His1 is the only virus that has been isolated and studied. His1 possesses a tail-like structure that allows the virion to anchor onto and inject its genome into the host cell. Further, its non-enveloped capsid displays flexibility as the capsomeres are able to switch conformations in response to changes in the environmental conditions. This capsid morphotype flexibility could be a contributing factor for the resistance of the virus toward extreme environmental conditions (Hong et al., 2015). Consequently, this type of virus hints toward the dependency of the capsid morphology on the environment as opposed to the interaction between the genome and the capsomeres.

Pleomorphic haloarchaeal viruses have been proposed to be grouped into the *Pleolipoviridae* family. Seven of these viruses studied by Pietilä et al. (2012) had the same capsid structure made of lipid membrane and associated membrane and spike proteins, but none of the viruses have more than two or three major structural proteins. This implies that

pleomorphic haloarchaeal virions do not have nucleocapsids and instead rely on the lipids derived unselectively from the host for enveloping their genome. As a result, they are extremely host specific and do not cause host cell lysis, since they are released from the host cell by vesicle formation, inhibiting the growth of the host cell. The genome structures of these viruses vary between linear or circular and ssDNA or dsDNA. However, all of them show similarity in gene organization as well as amino acid sequences as seen in His2, which infects the same host as spindle-shaped His1 but shares amino acid sequences with pleomorphic HRPV-1 and HHPV-1. There is a great variation in the virion size, with HRPV-1 being the smallest with a 40 nm diameter and His2 being the largest with 70 nm diameter (Pietilä et al., 2012). Overall, pleomorphic haloarchaeal viruses display a unique yet common capsid morphology and rely heavily on the interaction between the virus and the host cell for replication as well as formation, and so this morphotype does not seem probable to exist without the presence of a cellular host in the same environment.

Viruses with head-tailed morphotype are alternatively known as *Caudovirales* and comprise an icosahedral head connected to a flexible tail. Approximately 96 percent of the known prokaryotic viruses are head-tailed, but analyses of haloarchaeal viruses from some hypersaline environments show that only 1 percent of them have this morphotype (Oren et al., 1997; Sime-Ngando et al., 2011; Ackermann & Prangishvili, 2012). The icosahedral head diameter typically ranges from 47–108 nm. All of the known head-tail haloarchaeal viruses fall into the three groups of bacteriophages that possess this morphotype: myovirus (long, contractile tail), siphovirus (long, non-contractile tail) and podovirus (short, non-contractile tail) (Atanasova et al., 2012). In addition to the morphological similarities, these viruses also share genetic similarity to the head-tail bacteriophages, and it has been proposed that head-tailed haloarchaeal viruses either were acquired from ancient halophilic bacterial hosts or existed prior to the evolution of the three domains (Krupovic et al., 2011; Prangishvili et al., 2006; Prangishvili, 2013). In either case, it is unlikely that this morphotype evolved independently in haloarchaea and in bacteria, since there is evidence of genetic elements that are conserved through vertical descent as well as genetic similarities due to horizontal gene exchange (Krupovic et al., 2011). The existence of these homologous genetic sequences spanning different domains suggests that viruses could have predated the last universal common ancestor

(Prangishvili et al, 2006; Prangishvili, 2013), so emergence of this kind of virions without a cellular host is probable.

Spherical haloarchaeal viruses have a lipid membrane inside the tailless icosahedral head, whose diameter can range from 50–80 nm. Analyses of some hypersaline environments revealed that this morphotype was most commonly found along with spindle-shaped morphotype (Oren et al., 1997; Sime-Ngando et al., 2011). However, only five species of haloarchaeal viruses with this morphotype have been discovered: SH1, PH1, HHIV-2, SNJ1 and HCIV-1. All of these belong to the same family: *Sphaerolipoviridae*. SH1, PH1 and HHIV-2 are closely related, share the same host, and have a linear dsDNA, whereas SNJ1 has a circular dsDNA (Atanasova et al., 2015; Porter et al., 2013]. A bacteriophage infecting *T. thermophilus* was discovered to have the same unusual capsid arrangement as these viruses and shared core genes and is proposed to be a part of the *Sphaerolipoviridae* family (Pawlowski et al., 2014). Discovery and description of more spherical haloarchaeal viruses is required to provide more information on the origin and interaction with environmental factors of viruses with this morphotype.

2.2 Viruses of Thermophilic Archaea

Multiple genera of archaea comprise thermophiles that thrive and grow in extremely hot and sometimes also acidic environments. However, the most frequently isolated archaea are from the genus *Sulfolobus*, and consequently, viruses that infect these hosts are the most studied (Rice et al., 2001; *Thermophilic Archaea*, 2020). For this reason, this section will emphasize on the morphologies of viruses that infect members of *Sulfolobus*. The three major families of these viruses where all members of the family have the same morphology are *Rudiviridae*, *Lipothrixviridae*, and *Fuselloviridae* (Rice et al., 2001; Rice et al., 2001). It should be noted that viruses of thermophilic archaea show a large variety of capsid morphologies and do not always have a *Sulfolobus* host or resemble the viruses belonging to these four families. Hence, this section will also briefly present newly discovered and unique morphologies and aim to articulate on the influence of genetic relationships, hosts, and/or environmental conditions on the viruses of thermophilic archaea.

SIRV1 and SIRV2 are the two rudiviruses that specifically infect *Sulfolobus* archaea. They possess a rod-shaped capsid that resembles the filamentous lipothrixviruses, but they have been categorized into a new

family since they lack the lipid envelope (Prangishvili et al., 1999). Further, the 25 nm by 900 nm rod capsids are rigid and have a helical arrangement of capsomeres (Rice et al., 2001). On the other hand, SIFV is the only lipothrixvirus that has a *Sulfolobus* host, since other lipothrixviruses—such as AFV1, AFV2, AFV3, and others—have *Acidianus* hosts, which are also hyperthermophilic archaea (Prangishvili, 2013). These virions have long and flexible 50 nm by 900–1500 nm rod-shaped capsids that are enveloped by lipids derived from the hosts (Rice et al., 2001; Arnold et al., 2000). Hence, just like the pleomorphic haloarchaeal viruses [see “Viruses of halophilic archaea” above], lipothrixviruses show dependency on a cellular host for structural components, and so if these viruses are found, it is likely that cellular life forms also exist in the same environment. *Rudiviridae* and *Lipothrixviridae* have significant structural and genetic similarity and are usually referred as filamentous viruses (Prangishvili et al., 2017). Some studies show that these are the most commonly found morphotypes in hot-spring environments (Liu et al., 2019). It is possible that this is either a result of host availability in these environments or that the helical and filamentous capsid structure provides additional resistance to hot and acidic environments.

Some studies present that tailed spindle-shaped morphotype of viruses belonging to *Fuselloviridae* is the most common in hot and acidic environments (Rice et al., 2001). These viruses typically form structures called ‘rosettes’ outside the host cell by sticking to other virions at one end, and hence this is a distinguishing feature of fuselloviruses. Interestingly, there are many fuselloviruses that infect *Sulfolobus* archaea, but only ASV1 infects *Acidianus* archaea. This indicates that viruses with this morphotype have a strong host specificity and are unlikely to be found without the host. However, more research is needed to infer whether fusellovirus mutants could be resistant to host switching. Further, it should be noted that while SSV6 and ASV1 are genetically related to the other fuselloviruses, they are more pleomorphic than the others and can have multiple capsid shapes. These two also never form the characteristic ‘rosettes,’ perhaps owing to the difference in their tail fibers (Redder et al., 2009). This is particularly interesting because even though they have genetic similarities with other fuselloviruses, their capsid morphology is different, which means that host-virus interaction and environmental factors could be significantly influential in determining capsid morphology. Additional research on these two viruses that compare change in environment to

change in the morphology could address whether researchers can predict virus morphologies based on geological information.

Apart from the three families of most common *Sulfolobus* archaeal viruses, additional research of hyperthermophilic viruses having unique capsid morphologies has led to the proposal of new families like *Turriviridae* and *Guttaviridae* with *Sulfolobus* archaea host, as well as *Ampullaviridae* and *Bicaudaviridae* with *Acidianus* archaea host (Redder et al., 2009). Guttaviruses are droplet-shaped, ampullaviruses are bottle-shaped, bicaudaviruses are two-tailed spindle-shaped, whereas turriviruses are icosahedral. The turrivirus STIV is of the most interest to researchers currently due to its striking similarity to the proteins, lipids, and carbohydrates of some eukaryotic and bacterial viruses. Conservation of such structural components across domains despite genetic differences is promising because it fortifies the idea that virus capsids are restricted to a few morphotypes on Earth. STIV, just like haloarchaeal *Caudovirales* [see “Viruses of halophilic archaea” above], hints toward the existence of viruses before the divergence of the three domains of life and perhaps even the last universal common ancestor (Maaty et al., 2020). Therefore, discovery and description of such extremophile viruses with unique morphologies is vital for acquiring a deeper understanding of the origin of viruses on Earth and how the different capsid morphologies are affected by the interplay of genetic and environmental factors.

Conclusion

Certain archaeal virus morphotypes are more common in specific environments. In hypersaline environments, we most frequently observe spindle-shaped, pleomorphic, head-tailed, and spherical morphotypes. Whereas in regions with high temperature and acidity, we find filamentous and spindle-shaped morphotypes, along with a large variety of other unique morphotypes. While study of the pleomorphic haloarchaeal viruses and lipothrixviruses emphasizes the dependency of viruses on hosts to exist, study of head-tail viruses and the turrivirus STIV indicates that originally viruses could have evolved before or concurrently with cellular life forms. The conservation of morphotypes in specific extreme environments and these derived implications about the origin of viruses on Earth can prove to be extremely insightful from the perspective of astrobiology, since it provides a better sense about the origin of life on Earth. Additional research on how environmental factors, hosts, and viral

genetics interplay to determine virus morphology and development in better imaging technology that can be used in space will allow future researchers to use morphology as a virus biosignature and expand the potential of search for life in space.

References

- Ackermann, W-H., & Prangishvili, D. (2012). Prokaryote Viruses Studied by Electron Microscopy. *Archives of Virology*, 157(10), 1843–1849. doi.org/10.1007/s00705-012-1383-y
- Aherfi, S., Colson, P., La Scola, B., & Raoult, D. (2016). Giant Viruses of Amoebas: An Update. *Frontiers in microbiology*, 7, 349. doi.org/10.3389/fmicb.2016.00349
- Arnold, H. P., Zillig, W., Ziese, U., Holz, I., Crosby, M., Utterback, T., Weidmann, J., Kristjanson, J. K., Klenk, H. P., Nelson, K. E., Frazer, C. M. (2000). A Novel Lipothrixvirus, SIFV, of the Extremely Thermophilic Crenarchaeon *Sulfolobus*. *Virology*, 267(2), 252–266. doi.org/10.1006/viro.1999.0105
- Atanasova, N. S., Bamford, D. H., & Oksanen, H. M. (2015). Haloarchaeal virus morphotypes. *Biochimie*, 118, 333-343. doi.org/10.1016/j.biochi.2015.07.002
- Atanasova, N. S., Roine, E., Oren, A., Bamford, D. H., & Oksanen, H. M. (2012). Global network of specific virus-host interactions in hypersaline environments. *Environmental Microbiology*, 14(2), 426–440. doi.org/10.1111/j.1462-2920.2011.02603.x
- Berliner, A. J., Mochizuki, T., & Stedman, K. M. (2018). Astrovirology: Viruses at Large in the Universe. *Astrobiology*, 18(2), 207–22. doi.org/10.1089/ast.2017.1649
- Breitbart, M., & Rohwer, F. (2005). Here a Virus, There a Virus, Everywhere the Same Virus? *Trends in Microbiology*, 13(6), 278–284. doi.org/10.1016/j.tim.2005.04.003

- Hong, C., Pietilä, M. K., Fu, C. J., Schmid, M. F., Bamford, D. H., & Chiu, W. (2015). Lemon-shaped halo archaeal virus His1 with uniform tail but variable capsid structure. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(8), 2449–2454. doi.org/10.1073/pnas.1425008112
- Koonin, E. V., Senkevich, T. G. & Dolja, V. V. (2006). The ancient Virus World and evolution of cells. *Biology Direct*, *1*(1), 29. doi.org/10.1186/1745-6150-1-29
- Krupovic, M., Spang, A., Gribaldo, S., Forterre, P., & Schleper, C. (2011). A thaumarchaeal provirus testifies for an ancient association of tailed viruses with archaea. *Biochemical Society Transactions*, *39*(1), 82–88. doi.org/10.1042/bst0390082
- Liu, Y., Brandt, D., Ishino, S., Ishino, Y., Koonin, E. V., Kalinowski, J., Krupovic, M., & Prangishvili, D. (2019). New archaeal viruses discovered by metagenomic analysis of viral communities in enrichment cultures. *Environmental Microbiology*, *21*(6), 2000–2014. doi.org/10.1111/1462-2920.14479
- Maaty, W. S. A., Ortmann, A. C., Dlakić, M., Schulstad, K., Hilmer, J. K., Liepold, L., Weidenheft, B., Khayat, R., Douglas, T., Young, M. J., & Bothner, B. (2020). Characterization of the Archaeal Thermophile *Sulfolobus* Turreted Icosahedral Virus Validates an Evolutionary Link among Double-Stranded DNA Viruses from All Domains of Life. *Journal of Virology*, *80*(15). doi.org/10.1128/JVI.00522-06
- Norrby E. (1983). The morphology of virus particles. Classification of viruses. *Textbook of Medical Virology*, 4–16. doi.org/10.1016/B978-0-407-00253-1.50007-4
- Oren, A. (2014). Taxonomy of halophilic Archaea: current status and future challenges. *Extremophiles*, *18*(5), 825–834. doi.org/10.1007/s00792-014-0654-9
- Oren, A., Bratbak, G., & Heldal, M. (1997). Occurrence of Virus-like Particles in the Dead Sea. *Extremophiles*, *1*(3), 143–149. doi.org/10.1007/s007920050027
- Pawlowski, A., Rissanen, R., Bamford, J. K. H., Krupovic, M., & Jalasvuori, M. (2014). *Gammasphaerolipovirus*, a newly proposed

- bacteriophage genus, unifies viruses of halophilic archaea and thermophilic bacteria within the novel family *Sphaerolipoviridae*. *Virology Division News*, 159(6), 1541–1554. doi.org/10.1007/s00705-013-1970-6
- Pietilä, M. K., Atanasova, N. S., Manole, V., Liljeroos, L., Butcher, S. J., Oksanen, H. M., & Bamford, D. H. (2012). Virion Architecture Unifies Globally Distributed Pleolipoviruses Infecting Halophilic Archaea. *Journal of Virology*, 86(11), Article 6384. doi.org/10.1128/JVI.00861-12
- Porter, K., Tang, S. L., Chen, C. P., Chiang, P. W., Hong, M. J., & Dyal-Smith, M. (2013). PH1: An archaeovirus of *Haloarcula hispanica* related to SH1 and HHIV-2. *Archaea*, 2013, Article 456318. doi.org/10.1155/2013/456318
- Prangishvili, D. (2013). The Wonderful World of Archaeal Viruses. *Annual Review of Microbiology*, 67, 565–585. doi.org/10.1146/annurev-micro-092412-155633
- Prangishvili, D., Arnold, H. P., Götz, D., Ziese, U., Holz, I., Kristjansson, J. K., & Zillig, W. (1999). A novel virus family, the Rudiviridae: Structure, virus-host interactions and genome variability of the sulfobolus viruses SIRV1 and SIRV2. *Genetics*, 152(4), 1387–1396. doi.org/10.1093/genetics/152.4.1387
- Prangishvili, D., Bamford, D. H., Forterre, P., Iranzo, J., Koonin, E. V., & Krupovic, M. (2017). The enigmatic archaeal virosphere. *Nature Reviews Microbiology*, 15(12), 724–739. doi.org/10.1038/nrmicro.2017.125
- Prangishvili, D., Forterre, P., & Garrett, R. A. (2006). Viruses of the Archaea: A unifying view. *Nature Reviews Microbiology*, 4(11), 837–848. doi.org/10.1038/nrmicro1527
- Rampelotto P. H. (2013). Extremophiles and extreme environments. *Life (Basel, Switzerland)*, 3(3), 482–485. doi.org/10.3390/life3030482
- Redder, P., Peng, X., Brügger, K., Shah, S. A., Roesch, F., Greve, B., She, Q., Schleper, C., Forterre, P., Garrett, R. A., & Prangishvili, D. (2009). Four newly isolated fuselloviruses from extreme geothermal environments reveal unusual morphologies and a possible intervirial recombination mechanism. *Environmental Microbiology*, 11(11),

2849–2862. doi.org/10.1111/j.1462-2920.2009.02009.x

Rice, G., Stedman, K., Snyder, J., Wiedenheft, B., Willits, D., Brumfield, S., McDermott, T., & Young, M. J. (2001). Viruses from extreme thermal environments. *Proceedings of the National Academy of Sciences of the United States of America*, 98(23), 13341–13345. doi.org/10.1073/pnas.231170198

Sime-Ngando, T., Lucas, S., Robin, A., Tucker, K. P., Colombet, J., Bettarel, Y., Desmond, E., Gribaldo, S., Forterre, P., Breitbart, M., & Prangishvili, D. (2011). Diversity of virus-host systems in hypersaline Lake Retba, Senegal. *Environmental Microbiology*, 13(8), 1956–1972. doi.org/10.1111/j.1462-2920.2010.02323.x

Snyder, J. C., Bolduc, B., & Young, M. J. (2015). 40 Years of archaeal virology: Expanding viral diversity. *Virology*, 479–480, 369–378. doi.org/10.1016/j.virol.2015.03.031

Thermophilic Archaea. (2020). National Parks Service, U.S. Department of the Interior, Retrieved 2021 from www.nps.gov/yell/learn/nature/thermophilic-archaea.htm