
**Summary**

- So far, all characterized archaeal viruses carry ds[double stranded]DNA genomes and exhibit a wide range of virion morphotypes, strongly surpassing the dsDNA viruses of the Bacteria in their diversity.

- In addition to head-tail viruses, which are common in the Bacteria, the Archaea replicate many viruses with morphologies which have not been observed before for any dsDNA virus. These include fusiforms, droplet and bottle shapes, and linear and spherical virions, with more complex virions combining features of the different forms.

- Genome sequence analyses demonstrate that most of the archaeal viruses are unrelated to other known viruses and indicate that they might have different, and possibly multiple, evolutionary origins.

- Assuming that archaeal head-tail viruses originate from the domain Bacteria (there are many arguments for this suggestion), we are faced with the prospect that each of the three domains of life, the Bacteria, Archaea and Eukarya, was originally characterized by a unique set of associated dsDNA viruses.

- One possible explanation for the existence of three different 'viro-spheres', each associated with a specific domain, is that these viro-spheres were selected when the domains first arose. Therefore, the first evolving organisms of each separate domain could have already been infected by different subsets of viruses from the ancestral virosphere, which predated the last universal common ancestor.

Figure and original caption from the article follows.
Three hypotheses have been proposed to explain the origin of viruses: (a) they originated in a pre-cellular world (the 'virus first' hypothesis); (b) they originated by a reduction from parasitic cells; or (c) they originated from fragments of cellular genetic material that escaped from cellular control and became parasites (the escape hypothesis). Originally, these hypotheses were proposed in the framework of the prokaryote/eukaryote dichotomy. Just as the erroneous concept of the prokaryotes became the paradigm for considering bacterial evolution, the escape hypothesis became the paradigm for explaining the origin of viruses.

In its classical version, the escape hypothesis maintained that bacteriophages originated from bacterial genomes and eukaryotic viruses from eukaryotic genomes. Amazingly, although most archaeal viruses are completely unrelated to bacterial viruses, they are still classified as 'bacteriophages' in this outdated framework. For example, archaeal viruses are illustrated under the heading "Families and genera infecting bacteria" in the latest edition of Virus Taxonomy: Classification and Nomenclature of Viruses (REF. 87). This occurs presumably because the archaeal domain is still not recognized by some biologists.

The problem of virus origin remained deadlocked until recently, when progress in the molecular description of viral proteins caused many scientists to realize that viruses form a world of their own, and that it is futile to continue to speculate on their origin in the framework of the discredited prokaryote/eukaryote dichotomy. The discovery that viruses which are associated with different domains can share similar, and apparently homologous, features strongly suggests that viruses are ancient and that they predated the last universal cellular ancestor (LUCA)93,95.

The early hypotheses for viral origin have now been re-evaluated in the context of this new framework95. Currently, the main debate is between those who suggest a long period of acellular evolution (up to the actual emergence of archaea and bacteria) and those who favour an early appearance of cells. Those who suggest the former have revived the virus-first hypothesis, hypothesis (a) above. For instance, Koonin and Martin recently suggested that viruses emerged from an assemblage of self-replicating elements thriving in a hydrothermal vent, using inorganic compartments as their hosts96. For some of those who favour an early emergence of cellular organisms, viruses are considered to have originated from RNA–protein-based cells, either by reduction from parasitic RNA cells or from genetic material that escaped from the genomes of these cells (variants of hypotheses (b) and (c) above)97. A major question mark is the evolutionary relationship between DNA viruses and RNA viruses: did DNA viruses originate from RNA viruses or from primitive DNA cells, or both95,97? In one hypothesis, DNA itself is considered a viral invention, that is, DNA first appeared in viruses and was later transferred to cells98. In this model, three such independent transfers could have initiated the three modern DNA lineages and the modern virospheres associated with them99.

The figure shows a model of the formation of the three modern virospheres, coincident with the formation of the three domains of life.