BioSystems 257 (2025) 105609

Contents lists available at ScienceDirect

BioSystems

journal homepage: www.elsevier.com/locate/biosystems

The origin and evolution of life as continuing expansion of viral hosts

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A R T I C L E I N F O

Keywords:
Viruses
Evolution of life
Virus hosts
Evolutionary force

A B S T R A C T

The emergence of life on Earth likely involved a complicated evolution of the primeval residues via basic intermediate forms capable of self-replication. These primordial replicators could have further evolved into archaic virus-like structures, which in turn became the precursors of the cellular life forms. If viruses were indeed the predecessors of the first cellular life forms as suggested by the 'primordial virus world' and 'virus-first' scenarios, could their hosts themselves emerged and evolved predominantly as factories and reservoirs for virus production and dissemination? In other words, is that hypothetically possible that viruses were not only the originators of cellular life forms and the selfish driving force behind their evolution, but the fundamental reason for both their existence and biological heterogeneity? A short note presented here deliberates on this not entirely unfeasible course of events.

1. Introduction

There are several self-explanatory hypotheses on the origin of viruses, obligate parasites that cannot exist without their hosts: virus-first, cellular escape, and reduction scenarios (Forterre, 2006a). Briefly, the virus-first hypothesis assumes that viruses are older than cells and originated in the prebiotic world; the cellular escape hypothesis proposes that viruses were parts of the cell genomes eventually escaping living cells and becoming autonomous; and reduction or regression hypothesis suggests that viruses originated from cellular organisms which degraded, losing their complexity and adapting to a parasitic lifestyle (Forterre, 2006a; Krupovic et al., 2019). There also are several hypotheses on the origin of life, including the RNA world and primitive replicons, abiogenesis, and extraterrestrial sources (Gilbert, 1986; Bada and Lazcano, 2003; Forterre and Gribaldo, 2007; Koonin, 2009, 2014; Wesson, 2010; Koonin and Dolja, 2013; Pross; Paskal, 2013; Domingo, 2019; Higgs and Lehman, 2015). Some of them suggest a possible role of viruses, as descendants of primitive replicating entities, in the origin and evolution of early life (Forterre, 2006a, 2006b; Koonin, 2009, 2014; Koonin and Martin, 2005; Domingo, 2019).

The life-building process culminating in the last universal common ancestor (LUCA) was not brief (de Duve, 2003) and likely involved a complicated evolution of primeval residues via basic, intermediate forms (Forterre, 2006a; Domingo, 2019). Among these transitional forms could have been primitive RNA molecules possessing catalytic activities, capable of self-replication, and, possibly, of compartmentalization, likely in the form of membranous vesicles (Koonin, 2014; Forterre, 2006a; Krupovic et al., 2019; Matsumura et al., 2016; Orgel, 1992; Szostak, 2012; Tjhung et al., 2020). Hypothetically, these RNA replicators could have further optimized and evolved into primordial virus-like structures (Krupovic et al., 2019; Domingo, 2019) that subsequently transitioned from the unstable RNA world relying on self-replicating RNA molecules (Gilbert, 1986) to the RNA-protein stage (Forterre and Gribaldo, 2007) and finally to the modern, more complex and chemically stable DNA-RNA-protein world (Forterre, 2006b; Koonin et al., 2022), becoming potential precursors of the cellular life forms (Koonin and Martin, 2005). Specifics of each of these consecutive steps are outside the scope of this brief note and were described elsewhere in great detail (Krupovic et al., 2019; Koonin, 2009, 2014, 2022; Koonin and Martin, 2005; Forterre, 2006a, 2006b, 2010; Forterre and Gribaldo, 2007; Higgs and Lehman, 2015; Domingo, 2019; Tjhung et al., 2020).

Building upon suggestions that the virus-like entities may have actively captured and repurposed all elements needed for their multiplication and subsequent distribution from the primordial RNA world, which could have included genetic elements, selfish replicators, RNA polymerases, primitive 'RNA cells' and possibly ancestral proteins (Forterre, 2005; Krupovic et al., 2019; Wolf and Koonin, 2007; Koonin et al., 2022), would it be reasonable to speculate that they could eventually give rise to cellular life forms and trigger all life's successive manifestations?

2. Main text

In other words, is it safe to assume that viruses were not only

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https://doi.org/10.1016/j.biosystems.2025.105609
Received 21 August 2025; Received in revised form 18 September 2025; Accepted 3 October 2025

predecessors of the first cellular life forms, but their hosts themselves emerged and evolved as factories for virus assembly, production and further dissemination? In this way, all living organisms would have originated as highly specialized reservoirs for viral evolutionary expansion, with viruses not merely as the evolutionary drivers, but the primary reason for the existence of modern life forms. An examination of the simple facts before drawing any definite conclusions could facilitate more insightful answers to these complex questions.

Viruses are found everywhere, from deep-sea creatures and marine microorganisms (Suttle, 2005, 2007) to permafrost and extreme thermal environments (Legendre et al., 2014; Rice et al., 2001). According to the virolithopanspermia hypothesis, viruses could even have withstood damaging space exposure when transported to Earth from other planets inside the rocks (Bushman, 2025). There are estimated 10^6 to 10^9 (one million to one billion) virus particles per milliliter of sea water (Kristensen et al., 2009). The plant virome contains on average 9.2×10^7 (92 million) virus particles per gram of leaf tissue (Park et al., 2025). As ubiquitous and prolific biological entities which constitute a significant - if not the most abundant - part of the biosphere (Forterre, 2010; Koonin, 2015; Suttle, 2007), viruses apparently have the power to affect all life forms and essential processes on Earth, perhaps even major evolutionary developments (Greene and Reid, 2013; Koonin and Dolja, 2013; Koonin, 2016) and the partition of biological organisms into three forms of life (Claverie, 2006). Infecting all existent living beings, viruses transform their cells into 'viral organisms' or 'virocells' that are taking on an entirely new role - to produce virions and disseminate viral genes (Forterre, 2011, 2013).

It is hardly surprising that some of the many scenarios of the advent of the nucleus in LECA (last eukaryotic common ancestor), (Wilson and Dawson, 2011), describe its origin by way of viral eukaryogenesis that took place when the eukaryotic nucleus evolved from a complex DNA virus (Bell, 2001, 2020), the cell-like viral factories of a large DNA virus (Claverie, 2006), or a symbiotic contact of the ancestral poxvirus with an archaebacterium (Takemura, 2001).

Furthermore, it is beyond doubt that both constituents of the first endosymbionts implicated in the formation of eukaryotic cells, Asgard archaeon and alphaproteobacteria (Zaremba-Niedzwiedzka et al., 2017; Bennett et al., 2024; Koonin, 2015), were hosts to viral infections (Rambo et al., 2022; Hyde et al., 2024). The former was recently found to have a broad array of unique antiviral defense systems affirming its ancestral coevolution with viruses (Leao et al., 2024). Reconstructed viromes of LECA and the last universal cellular ancestor suggest complex representation of different groups of viruses: of bacterial origin in LECA and of bacterial and archaeal origin in LUCA (Krupovic et al., 2020; Krupovic et al., 2023).

In green algae, the ancestor of modern land plants (Graham et al., 2000), viruses played a multitude of roles, taking part in pathways encompassing host fermentation, metabolic, behavioral, gene transfer, genome endogenization, adaptation, population regulation, and distribution processes, thus comprehensively shaping host evolution (Rozenberg et al., 2020; Cai et al., 2023; Schvarcz et al., 2018; Moniruzzaman et al., 2020). Likewise, recent findings indicate that giant viruses of the *Mimiviridae* lineage infect choanoflagellates reorganizing host physiology and energy transfer in these marine protists (Needham et al., 2019). Choanoflagellates, widespread predators related to metazoans, are thought to be the closest unicellular ancestors of Animalia (Ros-Rocher et al., 2021).

It is accurate to state that these and numerous other studies at the very least do not oppose the idea of viruses as evolutionary drivers of their hosts. But going a few steps further, could the manifold diversity of life on Earth stem from infectious microorganisms and owe its very existence to their selfish expansion? Especially given that viruses are obligate intracellular parasites and would not be able to reproduce without a host at the precellular stage?

On closer look, this possibility may not be as absurd as it seems. First, the dependence on host may be a secondary outcome en route to virus-guided evolution of unicellular and multicellular life. Very early in the evolution of life, primordial replicons could have actively recruited from surrounding prebiotic environment all the necessary "machinery" needed to ultimately gather assembly lines for their production (Krupovic et al., 2019). Among the molecules acquired from the RNA World at the early stages of cellular evolution there were likely elements that could assemble peptides without a genetic code, such as minihelix precursors of tRNA bearing CCA segment alone and capable of conducting aminoacylation in a rudimentary, noncoded form of protein synthesis (Fox, 2010; Tamura and Schimmel, 2004); proto-mRNAs binding to the anticodon loops of tRNA pairs and possibly playing a structural role in facilitating non-templated peptide synthesis (Bernhardt and Tate, 2010); and ancestral ribosomal components. The latter could have hypothetically evolved in various ways, for instance, from the protoribosome functioning as an RNA replicase/triplicase (Poole ret al. 1998), by catalytic activities of ribozymes (Wolf and Koonin, 2007), by repetitive accretion of rRNA fragments in the form of expansion segments (Petrov et al., 2015), or by different, yet to be discovered processes.

At this point, it is likely that "RNA cells" already coexisted with virus-like entities in a complex, coevolving relationship (Forterre, 2005) throughout which primordial virus-like replicators may have prompted the development and utilized for their benefit ancestral protein-synthesizing machineries, thus influencing the evolution of the ribosome (Krupovic et al., 2019; Forterre, 2005; Miller et al., 2020). Furthermore, the virus-like genetic entities might have been instrumental in the development and optimization of the genetic code via horizontal flow of genetic information between communities of primordial replicators (Vetsigian et al., 2006; Koonin and Novozhilov, 2009). Speculatively, as the major theories on the origin of the genetic code are generally agreeable with the "frozen accident" hypothesis (Crick, 1968) as the initial step for the evolution of the code (Wolf and Koonin, 2007), the primordial virus-like replicator could have been that common ancestor or "a single organism" (Crick, 1968), that originated the standard genetic code (Koonin and Wolf, 2007) and from which "all life evolved" (Crick, 1968).

The primordial RNA World would also hypothetically contain the so-called "palm-domain" related to the RNA-recognition motif (RRM) and characteristic of many polymerases, including the RNA-dependent RNA polymerase (RdRp) (Koonin et al., 2006). Acquiring enzymatic functions, the RRM may have subsequently evolved into the RdRp needed for the replicative autonomy of the primordial viruses (Krupovic et al., 2019). Only after the resultant pre-cellular structures could sustain basic viral functions, not before that, they would become essential requisites, or hosts, for virus survival.

Second, once these initial, rudimentary virus factories were conceived, they continued to evolve and develop into more sophisticated hosts required for virus evolution and spread – LUCA, Bacteria, Archaea, FECA (first eukaryotic common ancestor), LECA, followed by the integrated unicellular and multicellular hosts, Eukaryota. Indeed, archaeoviruses, bacterioviruses and eukaryoviruses not only share some proteins, indicating they evolved from a common ancestral virus likely existing before LUCA times (Forterre and Gribaldo, 2007), but apparently share a large number of universal protein domains with their hosts in *Archaea*, *Bacteria*, and *Eukarya* thus supporting co-existence of viral and cellular ancestors (Malik et al., 2017) and their co-evolution. New metagenomic data increasingly demonstrate that this coevolution involved horizontal gene transfer and evolutionary repurposing leading to the ecological and evolutionarily intertwining between hosts and viruses that continuously evolved to exploit cellular life (Koonin et al., 2022; Harris and Hill, 2021). As per Harris and Hill (2021), "If viruses are truly inseparable from the evolutionary history of cellular life, how can we, in principle, deny them access to the Tree of Life"?

Therefore, maintaining that viruses could be the potential originators of cellular life (Forterre, 2006a, 2006b; Koonin and Martin, 2005; Koonin et al., 2009), and eventual partitioning of living organisms into three existing forms of life (Claverie, 2006), it would only be logical to speculate that they were also architects of all life's successive manifestations. Indeed, the divergence and progression of life into numerous biological forms would allow viruses to adapt to different environments, to acquire unique specializations and, more importantly, would ensure infinite survival and preservation of their gene pool.

If that was the case, at some point of evolutionary development, likely after the emergence of the three domains of life ~3.5 billion years ago (Feng et al., 1998), each of the life's extant lineages would begin to evolve "co-independently" of viral ontogenesis, while carrying on their essential function of being virus hosts. Simply put, increasingly diversifying hosts acquired "evolutionary freedom", although still to the benefit of the virus, their evolutionary driver.

The evolution of hominids, as descendants of LUCA, would presumably follow the same path of co-independence. The human virome consists of approximately 10^{13} particles per human individual (Liang and Bushman, 2021). That is, at least 10,000,000,000,000 virions (ten trillion). Every individual human cell would be infected with viruses (Liang and Bushman, 2021) and potentially transformed into a 'virocell' (Forterre, 2011, 2013). It is therefore hard to imagine that this commanding number assumes anything but a comprehensive exploitation of all available anthropoid resources for viral demands. Not surprisingly, even the unique patterns of human evolution, such as the emergence of consciousness, may be attributable to viruses: according to recent studies, the *Arc* gene, master regulator of synaptic plasticity responsible for information storage, derived from retrotransposons, ancestors of retroviruses (Ashley et al., 2018; Pastuzyn et al., 2018).

Assuming that viruses are indeed a driving force of evolution, how does the natural selection slot in the frame of this hypothesis? It would inevitably appear to do so: while viral hosts followed the path of natural selection, survival of the fittest host was always advantageous for virus reproduction and expansion. And furthermore, why would cells evolve solely for the benefit of viruses without inherent selective advantages? From the viewpoint presented here, viruses are drivers of cellular evolution, and hence they benefit from the evolution they cause. That is to say when cells evolve and acquire useful traits through natural selection, this process is beneficial to viruses.

Interestingly, if true, this hypothesis may supersede a traditional concept of an "arms race" between viruses and their hosts as an escalating coadaptation, replacing it with the idea of a more comprehensive, dynamic coevolution beneficial to both entities, when the seemingly adversarial virus/host relationship becomes part of the basic developmental process.

Moreover, this hypothesis offers a straightforward explanation why, after ~4 billion years since the origin of life, viruses remain the dominant entities in the biosphere (Koonin et al., 2015): it is because they are at the core of the complexity of life that continues to carry and safeguard their gene pool.

3. Discussion

This opinion presents an unconventional view on the origin and evolution of life, speculating that all living organisms could have originated as specialized reservoirs for viral evolutionary expansion. The seemingly adversarial virus/host relationship could then be viewed as a basic biological regulatory process in which viruses are recognized as obligatiory companions profoundly affecting their hosts at many levels rather than mere pathogens (Feschotte and Gilbert, 2012; Roosinck, 2015).

Although at first glance appearing similar to the virus-first and other scenarios on the role of viruses in the evolution of life, this viewpoint offers different interpretation and goes further to expand the importance of viruses as not only potential originators of cellular life forms and the selfish driving force behind their evolution, but as the primary reason for their existence and biological heterogeneity.

The question inevitably remains if this hypothesis is experimentally testable. Although verifying it would be challenging and "we may never truly know how cells evolved" (Koonin, 2014), in essence, many recent findings and conceptual undertakings on this subject, including those cited here, make it reasonable. Moreover, to some extent, they can be considered as the exploratory models obtained by logical reasoning and based on the currently available data. Further testing of this hypothesis would likely require examining the co-evolutionary dynamics between viruses and their hosts across different scales and using various biological and computational methods, for instance, model systems of experimental evolution (Pal et al., 2007; McDonald, 2019) or computational approaches, such as protein fold analysis (Nasir and Caetatno-Anolles, 2015; Romei et al., 2022).

Despite still at the cumulative stage, this promising field of research, centering on the role of viruses in the evolution of life, is approaching a breakthrough, even if the meaning and direction of the breakthrough, beyond exciting quests, is not entirely clear. This viewpoint offers one possible, although unconventional, path to bring all these fascinating discoveries and ideas to a biologically significant outcome.

Ethics approval and consent to participate

No human participants were used in this study.

Consent for publication

The author consents to the publication of the manuscript.

Funding

This study was supported by the United States Department of Agriculture, the Agricultural Research Service, CRIS number 8042-21500-003-000D.

Declaration of competing interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The author would like to thank Sam Grinstead for editing, thoughtful suggestions and helpful criticism.

Data availability

No datasets were generated or analyzed during the current study.

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