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4	The origin and evolution of life as continuing expansion of viral hosts
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40 Abstract
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42 Emergence of life on Earth, presumably beginning from "cosmic chemistry" and culminating in
43 the last universal common ancestor, likely involved a complicated evolution of the primeval residues via
44 basic intermediate forms capable of self-replication. These primordial replicators could have further
45 evolved into archaic virus-like structures, which in turn became the precursors of the cellular life forms.
46 The hypothesis presented in this article suggests that viruses were not only predecessors of the first

47 cellular life forms, but that *their hosts themselves emerged and evolved as factories and reservoirs for* 48 *virus production and dissemination*. In other words, it expands the role of viruses as not only originators 49 of cellular life forms and the selfish driving force behind their evolution, but as the primary reason for

50 their existence and biological heterogeneity.

51 Keywords: viruses; evolution of life; virus hosts; evolutionary force

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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, 2006). There also are several hypotheses on the origins of life, including the RNA world, primordial virus, abiogenesis, and extraterrestrial sources (panspermia), (Bada and Lazcano, 2003; Forterre and Gribaldo, 2007; Koonin, 2009a; Wesson, 2010; Pross and Paskal, 2013; Higgs and Lehman, 2015). At least two of them, the RNA world (Higgs and Lehman, 2015) and primordial virus (Koonin, 2009a) assume a possible role of virus-like structures in the origin and evolution of early life.

Present-day research reinforces the idea that building blocks leading to the emergence of life on Earth may have originated from outer space (Callahan et al. 2011; Pizzarello et al., 2011; Glavin et al. 2025). In view of this data, the last universal common ancestor (LUCA) and successive genesis of life could trace their origin from organic molecules initially delivered from the cosmos. If that was the case, the life-building process beginning from "cosmic chemistry" and culminating in LUCA, was not brief
(de Duve, 2003) and likely involved a complicated evolution of the primeval residues via basic
intermediate forms (Forterre, 2006).

69 Among these transitional forms could have been primitive RNA molecules possessing catalytic 70 activities and capable of self-replication (Forterre, 2006; Krupovic et al. 2019; Tjhung et al. 2020). In 71 turn, these RNA replicators (Higgs and Lehman, 2015) could have evolved into primordial virus-like 72 structures, which transitioned to a DNA-RNA-protein world, compartmentalized, and became potential 73 precursors of cellular life forms. This initial compartmentalization could have been as uncomplicated as 74 the enclosure and packaging of virus-like elements within a single capsid protein (Koonin, 2009a). 75 Specifics of each of these consecutive steps are outside the scope of this short note and were described 76 elsewhere in great detail (Claverie, 2006; Glavin et al. 2015; Krupovic et al. 2019; Koonin, 2009, 2014, 77 2022; deDuve, 2003; Forterre, 2006; Forterre and Gribaldo, 2007; Forterre, 2010; Higgs and Lehman, 78 2015; Tjhung et al. 2020; Wesson et al. 2010).

The hypothesis presented in this article builds upon suggestions that these virus-like precellular organisms actively captured and repurposed all elements needed for their multiplication and subsequent distribution from the primordial 'RNA world' that included genetic elements, selfish replicators, primitive 'RNA cells', ancestral proteins, and possibly early cellular ancestors (Forterre, 2006; Koonin, 2009; Krupovic et al. 2019; Koonin et al. 2022).

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2. Main text

However, the proposed hypothesis goes a step further to argue that viruses were not only predecessors of the first cellular life forms, but their hosts themselves emerged and evolved as factories for virus assembly, production and further dissemination. In other words, all living organisms may have originated as highly specialized reservoirs for viral evolutionary expansion, i.e. viruses are not only the evolutionary drivers, but the primary reason for the existence of modern life forms. Indeed, 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). 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 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 living organisms into three forms of life (Claverie, 2006).

97 Thus, it is hardly surprising that some of the many scenarios of the advent of the nucleus in LECA 98 (last eukaryotic common ancestor), (Wilson and Dawson, 2011), describe its origin by way of 'viral 99 eukaryogenesis', the viral factories of a large DNA virus (Bell, 2001, 2020; Claverie, 2006), or symbiotic 100 contact of the ancestral poxvirus with an archaebacterium (Takemura, 2001). Furthermore, it is beyond 101 doubt that both constituents of the first endosymbionts, Asgard archaean and alphaproteobacteria 102 (Zaremba-Niedzwiedzka et al. 2017; Bennet et al. 2024; Koonin, 2015), were hosts to viral infections 103 (Rambo et al. 2022; Hyde et al. 2023). The former was recently found to have a broad array of unique 104 antiviral defense systems affirming its ancestral coevolution with viruses (Leao et al., 2024). 105 Reconstructed viromes of LECA and LUCA suggest complex representation of different groups of 106 viruses: of bacterial origin in LECA and of bacterial and archaeal origin in LUCA (Krupovic et. al. 2020; 107 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). These and numerous other studies support the idea of viruses as originators and principal evolutionary drivers of their hosts.

117 At first, the hypothesis may seem irrational or even absurd: how could the manifold diversity of 118 life on Earth not only stem from infectious microorganisms, but owe its very existence to their selfish 119 expansion? Especially given that viruses are obligate intracellular parasites and would not be able to 120 reproduce without a host at the precellular stage? On closer look, however, things become clearer and more logical. First, the dependence on host may be a secondary outcome en route to virus-guided 121 122 evolution of unicellular and multicellular life. This means that very early in the evolution of life, 123 primordial replicons could have actively recruited from surrounding prebiotic environment all necessary 124 "machinery" needed to ultimately gather assembly lines for their production (Krupovic et al. 2019). Only 125 after resultant pre-cellular structures could sustain basic viral functions, not before that, they would 126 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 (**Figure 1**). Therefore, maintaining that viruses were the originators of cellular life (Forterre, 2006; Koonin et al. 2009b) and eventual partitioning of living organisms into three existing forms of life (Claverie, 2006), it may be logical to suggest that they were also architects of all life's successive manifestations.

The divergence and progression of life into numerous biological forms would subsequently allow virus adaptation to different environments, unique specializations and, importantly, ensure their infinite survival and preservation of the gene pool.

At some point in evolutionary development, likely after the beginning of eukaryogenesis 137 138 approximately two billion years ago, each of the life's extant lineages began to evolve "co-independently" 139 of viral infections, while carrying on their essential function of being hosts for different types of viruses. 140 Simply put, increasingly diversifying hosts acquired "evolutionary freedom", although still to the benefit 141 of the virus, their evolutionary driver. The evolution of hominids, as descendants of LUCA, would 142 presumably follow the same path of co-independence. The human virome consists of approximately 10^{13} 143 particles per human individual (Liang and Bushman, 2021). That is, at least 10,000,000,000 virions 144 (ten trillion). Every individual human cell would be infected with viruses (Liang and Bushman, 2021). It 145 is hard to imagine that this commanding number assumes anything but a comprehensive exploration of 146 all available anthropoid resources for viral demands. Not surprisingly, even the unique patterns of human 147 evolution, such as emergence of consciousness, may be attributable to viral infections: according to the 148 recent studies, the Arc gene, master regulator of synaptic plasticity responsible for information storage, 149 derived from retrotransposons, ancestors of retroviruses (Pastuzyn et al. 2018; Ashley et al. 2018).

Assuming that virus is 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: survival of the fittest host is advantageous for virus reproduction and expansion.

153 Interestingly, if correct, this hypothesis supersedes a traditional concept of an "arms race" 154 between viruses and their hosts, replacing it with the idea of dynamic coevolution beneficial to both 155 entities: host's antiviral mechanisms increase adaptability of viruses leading to new or more virulent 156 strains which, in turn, promote host to evolve new defense strategies critical for its survival. In this 157 context, killing their hosts does not give viruses any evolutionary advantage: many viruses infect without 158 inflicting any damage or otherwise impair their hosts slowly, without causing instant death, enabling time 159 to spread, adapt, and persist in a new environment (Rouse and Mueller, 2018). Rapid host kills may also 160 be advantageous to the pathogens in large susceptible populations (Legget et al. 2017).

161 The hypothesis presented here also offers an easy explanation why, after ~ 3.5 - 4 billion years 162 since the origin of life, viruses remain the dominant entities in the biosphere (Koonin et al. 2015): it is 163 because they are at the core of the complexity of life that continues to carry and safeguard their gene 164 pool.

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3. Conclusions

The hypothesis detailed in this article argues that all living organisms may have originated as specialized reservoirs for viral evolutionary expansion. Although at first glance appearing similar if not the same as the virus-first and other scenarios on the role of viruses in the evolution of life, it is different in its interpretation and goes further to expand the importance of viruses as not only originators of cellular life forms and the selfish driving force behind their evolution, but as the primary reason for their existence and biological heterogeneity.

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Figure 1

Simplistic representation of the hypothetical origin and evolution of life forms as hosts for virus multiplication and spread. A, Early onset of organic material via extraterrestrial exposure followed by virus-first scenario of the evolution of life. B, Subsequent evolution of LUCA (Last Universal Common Ancestor) and all living organisms as viral hosts.

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204 Ethics approval and consent to participate

205 No human participants were used in this study.

206 **Consent for publication**

207 The author consents to the publication of the manuscript.

208 Conflict of Interest statement

- 209 The author declares that he has no competing interests.
- 210 Data availability
- 211 No datasets were generated or analyzed during the current study.

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