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Perspective

Geovirology: viruses and their roles in geological history

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Viruses are the most diverse and abundant type of biological entity on Earth, infecting species from all of life's domains and being found in almost all types of environments. They are gaining increasing attention from scientists, officials and the public due to recent major outbreaks with human health consequences (e.g., AIDS, SARS, COVID-19) and a growing appreciation of the impact viruses have had on the long-term development of both the biosphere and geosphere. The ability to identify viruses in ancient times is of importance in promoting our understanding of viral evolution and the relationships of viruses to their hosts and to paleoclimate conditions, enabling predictions of present and future impacts of the virosphere on life and the climate system.

The study of ancient viruses and the evolutionary history of viruses using genomics has been termed "paleovirology" [1]. It is based largely on analysis of endogenous viral elements (EVEs), which represent the viral components of a host's genome. Paleovirology is now a burgeoning field thanks to the development of advanced metagenomic next-generation sequencing techniques [2]. Its successes include detection of genomic viral signatures in host cells from sediments that are thousands of years old. However, this field has made very limited use of the fossil record of viruses in rocks.

Here, we propose a new field to be known as "geovirology", targeted at the record of ancient viruses in geological materials and on analysis of the effects of viruses on geological systems through time. The term "geovirology" has not been formally discussed in publication, but it was recently proposed at academic meetings (for example, https://agu.confex.com/agu/fm20/meetingapp.cgi/Session/103979). To date, identification of ancient viruses (i.e., paleovirology) in glaciers, permafrost, and corpses has depended primarily on the polymerase chain reaction (PCR) and next-generation sequencing techniques applied to well-preserved DNA. The lack of recovery of viruses from geological materials is due in large measure to the rapid degradation of cell-nuclear genetic material, leaving few traces of viral existence after the death of the host organism. However, as many EVEs were integrated into eukaryotic genomes millions of years ago, they offer a means of bridging the gap between the modern and ancient virospheres. Geovirology can also potentially exploit fossil lipids and minerals in rocks as signatures of ancient viral activity, as discussed below. With regard to their effects on geological systems, it has been inferred that viruses have played important roles in the biogeochemical cycles of carbon, nitrogen, and sulfur. Thus, one facet of geovirology is its focus on long-term interactions among, and coevolution of, viruses, their hosts, and environmental/climatic conditions on Earth. Such investigations are likely to provide essential context to the results of genomic analyses in its sister field, paleovirology. However, paleovirology is different from geovirology, just as paleobiology (i.e., the study of the organismal evolution) differs from geobiology (i.e., the study of life-environment interactions and co-evolutionary processes). Development of geovirology as a field will likely be dependent on breakthroughs on the following two critical issues.

One of the most critical issues for geovirology is to establish the methodology of recognizing viruses and viral infections preserved in rocks. Investigations of ancient organisms preserved in rocks have benefited immensely from innovations in observational and analytic techniques. For example, the development of microscopes was a prerequisite to the study of microfossils such as radiolaria, diatoms, foraminifera, and coccoliths. Later on, the introduction of organic geochemical techniques made it possible to study lipid biomarkers known as molecular fossils, greatly promoting our understanding of bacteria and archaea in ancient times. Nevertheless, the study of viruses in geological materials is fundamentally more challenging than that of bacteria and archaea. Genetic material can be partly, if not wholly, preserved in recent sediments, but is generally lost in rocks that undergo diagenesis, resulting in the complete degradation of DNA. Viruses, most of which consist of strands of genetic material simply enveloped by proteins, are thus rarely preserved in geological records, leading to the focus of the field of paleovirology on genomics [1]. However, geological deposits contain lipids and minerals that may serve as the fingerprints of ancient viral infections, thus providing indirect evidence of viral activity.

(1) *Lipid biomarkers.* Lipid biomarkers from cell membranes are one of the most critical and fascinating records of bacteria and archaea in rocks. Most viruses lack membranes, leading to difficulty in making use of lipids to explore viruses in geological materials. However, viruses need substantial amounts of compounds

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such as fatty acids to complete their life cycles, making it promising to use lipids as diagnostic tools of viral infection. In particular, viruses are known to contain a high abundance of auxiliary metabolic genes (AMGs), which rewire various metabolic pathways in the infected host cell [3], possibly resulting in identifiable changes in lipid composition. These genes are thought to be an expression of viruses that boost the metabolic capabilities of the infected host [3]. Such viruses may release new metabolites or develop other biochemical features that can serve as unique fingerprints of viral infection. Of importance is that remodeling of the host's primary metabolism toward lipid biosynthesis was found to be critical for successful infections by some viruses [3].

The alga *Emiliania huxleyi*, which is cosmopolitan in the modern ocean, is known to be infected by the *E. huxleyi* Virus (EhV, a large double-stranded DNA virus). The EhV infection causes massive changes in the metabolome and lipidome of infected cells due to extensive remodeling of the transcriptome (Fig. 1), including *de novo* fatty acid synthesis, introduction of triacylglycerols (TAGs), and rewiring of sphingolipid biosynthesis [3]. Virus-derived glycosphingolipids (vGSLs) were found to be central components of the EhV membranes, having a structural role as a signaling lipid as well as inducing programmed host cell death [4]. These lipids are produced exclusively during viral infection and can be used as an effective metabolic biomarker to detect viral infection during natural blooms of *E. huxleyi* in the ocean [4].

Further study of the metabolic basis of host-virus interactions during blooms of *E. huxleyi* led to the finding of massive introduction of C15:0-based lipids during lytic infection in diverse lipid classes, suggesting a systemic-level metabolic shift towards a C15:0-based lipidome [5]. This fingerprint of the presence of the EhV infection is potentially preservable in sediments or even in sedimentary rocks. In addition, the widespread cyanophage AMG, encoding for a fatty acid desaturase (Δ9 lipid desaturase), has been found in some cyanobacteria [6]. This desaturase can catalyze desaturation at carbon 9 in C_{16} fatty acid chains, modulating the fluidity of the host's membrane, a fundamental stress response in living cells [6]. Consequently, vGSLs, fatty acids, TAGs and their diagenetic products have the potential to reveal the presence of viruses infecting microorganisms in sediments or rocks. However, there have been very few studies to date of lipid biomarkers related to viral infection; further studies of this type in the future will constitute one of the most promising avenues for geovirological research.

Virally-influenced microbial metabolic pathways may cause large isotopic fractionations, and isotopic records are potentially one of the most important archives for study of viral effects in ancient times. For example, our preliminary observational data suggest changes in the deuterium content of fatty acids in cyanophages. However, the isotopic effects of viruses have received little attention to date. Future isotopic investigations should target AMG-encoded lipids.

(2) *Biogenic mineral nanospheres*. Interaction of microbes with minerals is a major vector of research in geomicrobiology, leading to extensive investigation of microbially influenced sediments. However, less is known about virus-mineral interactions and the role of viruses in organomineralization, which may represent important processes for preservation of viral influences in geological materials [7].

Viruses can play direct or indirect roles in mineral precipitation (Fig. 2). Free viruses and/or cell debris resulting from cell lysis can serve as nucleation sites for mineral precipitation [7]. Ionic equilibria are also affected by viral lysis of the host cell [8]. Recently, viral lysis of cyanobacteria was shown to promote the precipitation of carbonate minerals, including amorphous calcium carbonate and aragonite [8]. Mineral precipitation was also experimentally observed both in free viruses from living mats of a hypersaline lake and in cell debris resulting from cell lysis [7]. Viruses can be initially permineralized by amorphous magnesium silicates, which then alter to magnesium carbonate nanospheres during diagenesis, concomitant with the formation of successive mineral layers within the microbialite [7]. Virus-induced biomineralization may result in a direct correlation between organic material and biogenic silicate or carbonate minerals, leaving some fingerprints of viral infection in rocks. Viral calcification not only offers new perspec-

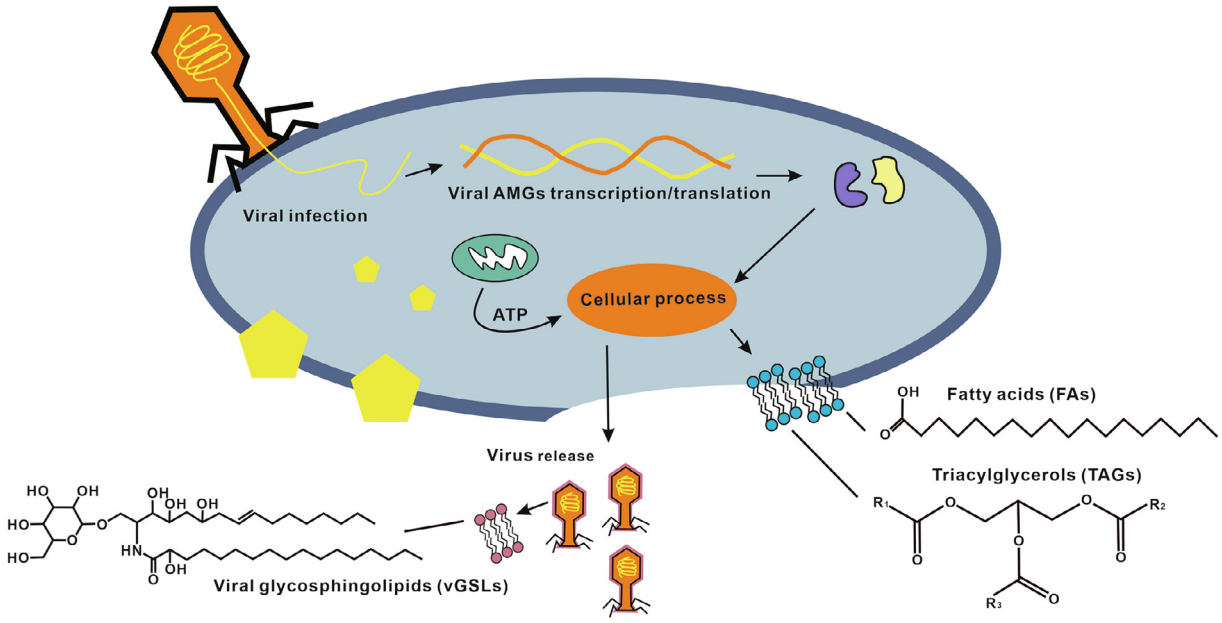

Fig. 1. The principle of specific lipids produced by host (virus) after viral infection. After viral infection, the auxiliary metabolic genes (AMGs) carried by a virus are transcribed and translated, influencing cellular processes through protein-encoding genes of the host, resulting in massive changes in the metabolome and lipidome of infected cells, which can serve as potential fingerprints in geological history. Blue symbols (bottom, right) for fatty acids (FAs), triacylglycerols (TAGs), and other molecules indicate infected-host lipids, and red symbols (bottom, left) for viral glycosphingolipids (vGSLs) indicate the envelope of viral lipids.

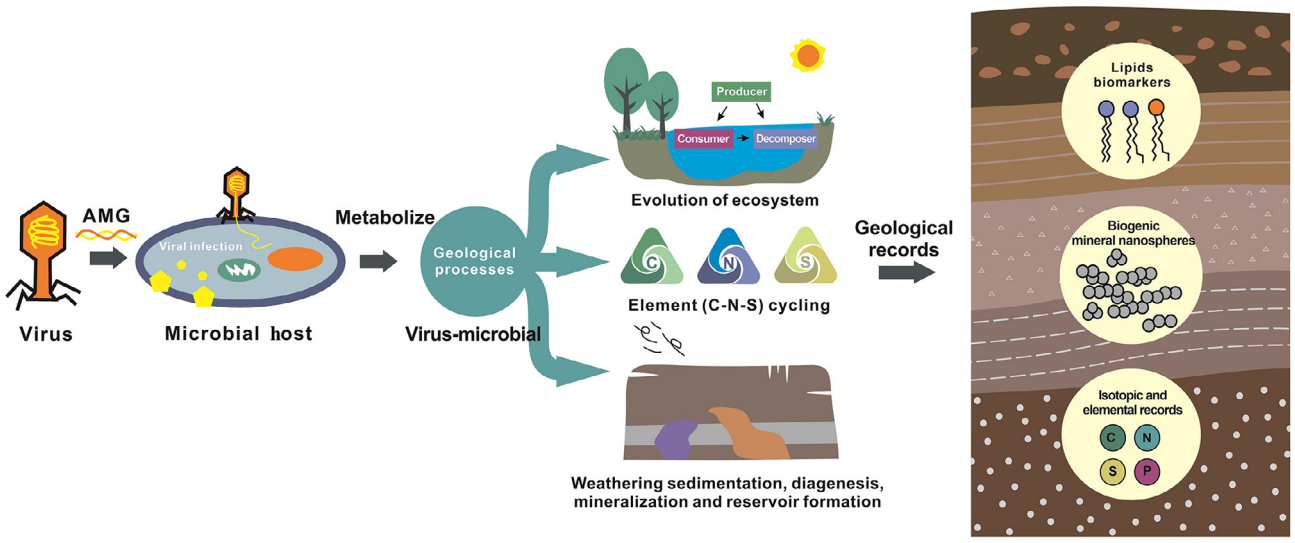

Fig. 2. Potential geological processes and records of virus. After viral infection, the AMGs carried by a virus could participate in, or regulate the metabolic pathway of the host cell, thereby influencing its life activities, with potential impacts on the evolution of ecosystems, elemental (C—N—S) cycling, weathering, sedimentation, diagenesis, mineralization, and reservoir formation. These viral fingerprints may be preserved in rocks or sediments in the form of lipid biomarkers, biogenic mineral nanospheres, and isotopic and elemental records.

tives on mechanisms of carbonate biomineralization but also potentially leaves fingerprints to identify the viral infection through co-precipitation of viral particles and the mineral host phase. The extent to which carbonate nanospheres, which are ubiquitous in the geological record, may be a byproduct of viral infection needs further investigation.

On the basis of limited experimental biomineralization studies, some diagnostic criteria for identification of fossilized viruses in the rock record have been proposed. Key features include a size range of ~20–200 nm, the presence of organic nanospheres, and their association with biogenic sediments (i.e., larger fossil cells or cell-like pseudomorphs, or microbially induced sedimentary structures) [7]. In this regard, detailed investigations are needed of carbonate nanospheres and cyanophages in geological materials deposited during critical periods when cyanobacterial blooms were frequent, such as during the Permian-Triassic boundary crisis or certain Precambrian periods.

In addition to the establishment of the methodology, another critical issue is to investigate viral impacts on biotic evolution and biogeochemical cycles in geological history. Owing to the challenges of recovering viral records from geological materials (Fig. 2), our knowledge of viruses is far better for the modern and historical periods than for the ancient. However, our knowledge of even the modern virosphere is limited. Although viruses were first identified more than a century ago, we know less about their diversity than that of any other biological entity. Most documented animal viruses have been sampled from just two phyla, the Chordata and the Arthropoda, with a strong bias towards viruses that infect humans or animals of economic and social importance, often in association with strong disease phenotypes [2].

(1) *Impact on biotic evolution.* Viruses are believed to have continuously evolved for billions of years and should have left traces of their evolution in their hosts' genomes. Exploring the evolution of a virus can yield information regarding the host's geographic and temporal ranges as well as viral transmission routes. For example, a recent study showed that the integration event of avian hepadnavirus can be traced to at least 19 million years ago, revealing that the ancestry of the hepatoviridae was much deeper than inferred from the merger time of the modern hepadnavirus [9].

Viruses are important agents of genetic exchange and mortality for all life forms, affecting organismal metabolism and immunity, and promoting the evolution of their hosts [7]. Indeed, the evolution of viruses and viroids has occurred in close association with that of their host taxa [2]. For example, viroids, which are only known to infect angiosperms (flowering plants), probably evolved in the late Early Cretaceous, soon after the appearance of the angiosperm clade, and their co-adaptation has continued to the present [10].

Viruses are major vectors of disease. The most favorable conditions for viral pandemics involve the advent of an abundant, widespread, and genomically uniform host [11]. Both *E. huxleyi* in the oceans and *Homo sapiens* on land have experienced myriad viral attacks because they share these characteristics [11]. However, other factors can also contribute to viral outbreaks. Bats and birds are warm-blooded vertebrates that display high species-level biodiversity, roosting and migratory behavior, and a unique adaptive immune system, which are favorable characteristics for asymptomatic shedding, dissemination, and mixing of different viruses for the generation of novel mutant, recombinant, or reassortant RNA viruses [12].

Although the role of viruses in biological mass death can rarely if ever be tested directly, patterns of mortality and extinction offer clues regarding the importance of viral agents during some major events in Earth history. In contrast to mass extinctions in which many species are eliminated simultaneously, a "focused extinction" involving the disappearance of a single taxon is unlikely to be a response to externally driven environmental perturbations, and, in the absence of other apparent factors, a viral cause is distinctly possible [11]. In this context, virus-induced species losses can generally be regarded as part of the "background" extinction rate [11]. However, it is possible that the loss during a viral pandemic of a "keystone species" that plays a critical ecological role might trigger large-scale collapse of an ecosystem.

Whereas global-scale environmental disturbances have typically been the trigger of the largest mass extinctions in Earth history, viruses may nonetheless have played an important role—particularly through increases in viral abundance within weakened ecosystems, creating a positive feedback on mortality during such events. While this hypothesis has not been tested to date for any

ancient mass extinction, it is clear that viruses thrive under disturbed conditions, as in the modern world. This has led to a large increase in the frequency of viral epidemics, despite the best efforts of humans to control the virosphere.

Viral attacks are host-specific, and, although evidence is lacking, mass extinctions of cellular organisms are hypothesized to have resulted in proportional extinctions in the virosphere, as viral hosts have disappeared. Although direct evidence of viral extinction is lacking, a recent study showed that the blood-feeding ectoparasites of two deinocrotonids causing disease in Mesozoic feathered dinosaurs went extinct along with their dinosaur hosts during the end-Cretaceous crisis [13].

(2) *Impact on biogeochemical cycles.* Viruses are likely to have affected microbially-induced geological processes, including Earth's long-term surface oxygenation, greenhouse gas concentrations, mineral precipitation, and weathering and erosion of rocks (Fig. 2). They have the potential to influence or even control primary production through their effects on photosynthetic metabolisms and/or mortality of planktic heterotrophs, which would almost certainly impact the carbon cycle, and thus climate. Because fossilized viruses have not yet been identified in geological materials, their roles in modulating global biogeochemical cycles remain largely unknown. However, research on modern viruses in the ocean and on land supports the inference that viruses have the potential to substantially alter global biogeochemical cycles.

Some viruses with AMGs may have been actively involved not only in the carbon cycle but also in the biogeochemical cycles of nitrogen and sulfur in ancient times. For example, many genomic sequences of double-stranded DNA viruses have been reported to infect sulfur-oxidizing bacteria, and they contain AMGs for the alpha and gamma subunits of reverse dissimilatory sulfite reductase (rDsr), which oxidizes elemental sulphur [14]. This observation sheds new light on the importance of viruses as a key agent in the sulfur cycle. Genomically and ecologically distinct Thaumarchaeota virus populations have also been shown to encode thaumarchaeal ammonia monooxygenase genes (*amoC*) [15]. Of importance is the finding that viral *amoC* AMGs comprise up to half of total *amoC* DNA copies in cellular metagenomes [15]. This finding highlights the potential impact of viruses on nitrogen cycling through time. Although these are limited examples, further investigation is likely to throw greater light on the role of viruses in modulating the Earth's biogeochemical cycles.

Conflict of interest

The authors declare that they have no conflict of interest.

Acknowledgments

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Appendix A. Supplementary materials

Supplementary materials to this perspective can be found online at https://doi.org/10.1016/j.scib.2023.02.001.

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