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Current Opinion in Virology

Accelerating expansion of the viral universe

Editorial overview

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Current Opinion in Virology 2013, **3**:542–545

For a complete overview see the Issue

Available online 30th August 2013

http://dx.doi.org/10.1016/j.coviro.2013.08.002

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Valerian V Dolja is a Professor at Oregon State University. His research team works on functional genomics of the plant RNA viruses, virus gene expression and RNA interference vectors, as well as on the mechanisms of membrane transport in plant cells. In addition, his long-term passion is virus origins and evolution, a problem on which he collaborates with Eugene Koonin (NIH) for over two decades.

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Mart Krupovic is a research scientist in the Department of Microbiology at the Pasteur Institute. He has a profound interest in how the virosphere is constructed. His research focuses on the origin of viruses, evolutionary relationships between different viral groups and other types of mobile genetic elements, and exploration of the pathways underlying the diversification of viruses. Beyond that, Mart's research focuses on different aspects of the life cycles of viruses infecting archaea.

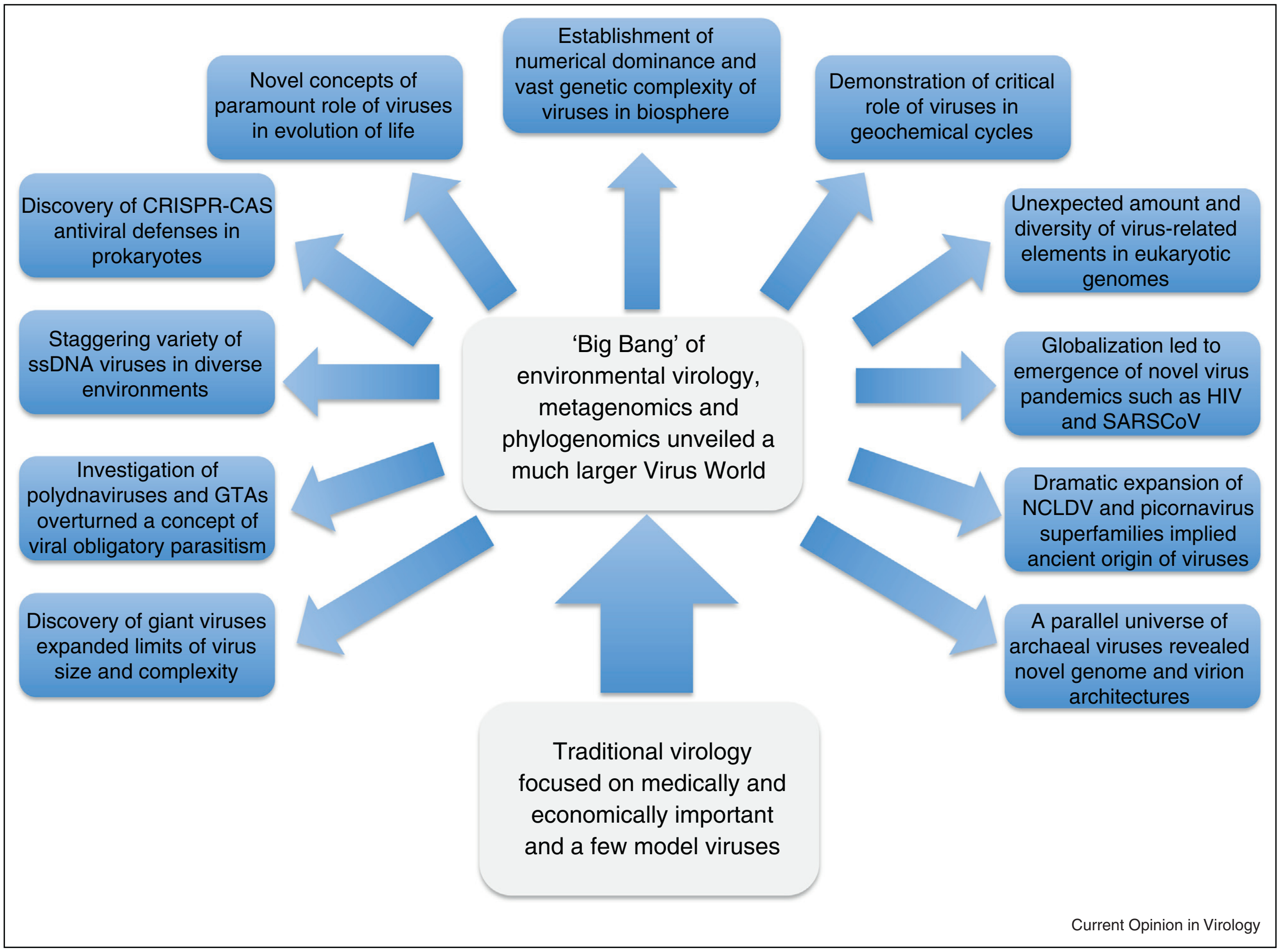
For two decades between 1985 and 2006, the field of virology seemed to be defined by the *Fields Virology* [1] that features encyclopedic coverage of the viruses of humans and other animals, but barely touches on viruses infecting other hosts such as bacteria or plants let alone archaea. Although this book will continue to play a fundamental role in the education and training of virologists, it hardly scratches the surface of the Virus World as we now come to know it: almost every single concept previously held dear by the students of viruses has been challenged or overturned by revolutionary new discoveries (Figure 1).

Arguably, the most dramatic shift in the virology worldview was brought about by environmental virology and metagenomics which revealed the dominance of viruses in biosphere, both in numerical terms (10–100 virions per every cell) and in terms of genomic complexity [2,3]. Comparative analysis of viral genes showed that much of this complexity is represented by ORFans that have no detectable homologs in cellular or other viral genomes and accordingly, in most cases, no predicted function [4]. The viral communities also sport a panoply of genes that were embezzled from cells to facilitate virus reproduction, for example, photosystem gene cassettes in cyanophages [5]. The third category of viral genes includes the core genes that distinguish viruses from cells. There are only a few of these broadly conserved viral hallmark genes, but because they specify key functions of genome replication, expression, packaging and encapsidation, collectively, they define viral infection cycles and, arguably, the state of being a virus [6].

For a long time, viruses infecting prokaryotes and eukaryotes were considered separately and perceived as 'escaped genes', that is, derivatives of their respective cellular hosts. However, owing to the accumulation of genomic and high-resolution structural data on viruses infecting hosts from all three domains of cellular life, clear-cut evolutionary connections were revealed between viruses once considered unrelated [6–8]. This realization together with the likely ancient origin of the viral hallmark genes including replication enzymes and capsid proteins implied that viruses emerged along with the primordial genetic systems predating the last universal cellular ancestor.

A convenient perception of viruses as submicroscopic filterable agents was shattered by a discovery of giant mimiviruses whose virions and genomes are larger than those of smallest cells [9] and very recently of the even bigger Pandoraviruses [10]. It was found later that these viruses themselves are parasitized by virophages [11] and transpovirons [12]. A long-standing belief that the extracellular virions are entirely dormant was challenged by the discovery of an archaeal virus that completes its morphogenesis *ex vivo* [13].

Figure 1



Major developments in the field of Virology.

In general, the recent studies into viruses of archaea revealed previously unimaginable variety of genome architectures and virion shapes from rods with claws to lemons to bottles [14]. A simple concept of a virion as a genome coated by protein capsid (and sometimes membrane overcoat) is no longer universal: there are 'virions' composed of DNA within a lipoprotein vesicle [15] and many capsid-less RNA viruses [16]. Given that some recognized capsid-possessing viruses (*Metaviridae* and *Pseudoviridae*) also double as retrotransposons [17], whereas some self-replicating DNA transposons (polintons/mavericks) encode a typical retroviral integrase along with adenoviral protease and a packaging ATPase [18], the traditional distinction between capsid-possessing viruses and capsid-less selfish elements becomes hardly sustainable.

Even obligatory parasitism, the cornerstone of the virus definition, appears to be crumbling. Characterization of the polydnaviruses that are obligatory symbionts [19], and Gene Transfer Agents (GTAs) that are degraded prophages apparently recruited by bacteria and archaea for horizontal transfer of their own genes [20], show that viruses are amenable to dramatic changes in their life styles. It now seems as if viruses are more about exceptions than the rules: nearly all imaginable combinations of genome or virion architectures, genome replication and expression strategies, virus-host interaction paradigms, and virus evolution scenarios are realized somewhere in a virus universe.

The spectacular discoveries noted above call for a 'new synthesis', an overarching concept that will unify the greatly expanded virus world and define the critical impact of viruses on the origin and evolution of cellular organisms. The two first entries in this section are in response to this call. Eugene Koonin and Valerian Dolja amalgamate the knowledge on the virosphere and the cellular realm into a ''virocentric view'' of life's history. The authors present a broad overview of the virus world, which comprises both *bona fide* viruses and capsid-less