Understanding Viruses: Philosophical Investigations

Editorial introduction

Thomas Pradeu, Gladys Kostyrka, and John Dupré

Final version published in

***Studies in History and Philosophy of Biological and Biomedical Sciences* (2016):**

http://www.sciencedirect.com/science/article/pii/S1369848616300024

Highlights

- Even though it has been neglected, the study of viruses raises important philosophical questions.
- Questions about viruses (definition, classification, etc.) can be related to classic issues in philosophy of biology and general philosophy.
- The contributions gathered in this special issue address these questions in different and sometimes conflicting ways.

1. Introduction

Viruses have been virtually absent from philosophy of biology. This is a quite surprising situation, because viruses probably constitute the most abundant and diverse biological entities in nature (Rohwer & Barott, 2013; Wasik & Turner, 2013). Viruses also successfully occupy a wide range of niches, are key players in evolutionary and ecological processes (Villarreal 2005; Wasik and Turner 2013), and, last but not least, have long been a matter of concern to medical doctors and epidemiologists. The situation is even more astonishing considering that several biologists have, over the years, produced a rich conceptual reflection on viruses (e.g., Burnet, 1945; Claverie & Abergel, 2010, 2012; Forterre, 2010a; Koonin & Dolja, 2013; López-García, 2012; Lwoff, 1957; Moreira & López-García, 2009; Raoult & Forterre, 2008; Stanley, 1957; Van Regenmortel, 2003), and the philosophy of microbiology more broadly has blossomed in recent years (O'Malley, 2013, 2014; O'Malley & Dupré, 2007a, 2007b). Meanwhile, both virologists and historians of biology have produced a detailed and rich history of virology (e.g., Bos, 1999, 2000; Creager, 2002; Hughes, 1977; Lustig & Levine, 1992; Sankaran, 2010; Summers, 2014; van Helvoort, 1994a, 1994b, 1996; Waterson & Wilkinson, 1978)[1].

Naturally, there have been important exceptions to the near absence of viruses from the domain of philosophy of biology, in particular the work of Gregory Morgan (Morgan, 2001, 2006, 2010; Morgan & Pitts, 2008), as well as a few other contributions by philosophers, or appearing in philosophical journals (e.g., Rohwer & Barott, 2013; Witzany, 2012). Yet it seems fair to say that, overall, the philosophy of virology has remained rather inchoate in recent years, at least in comparison with other branches of philosophy of biology. To our knowledge, the present issue of *Studies in History and Philosophy of Biological and Biomedical Sciences* is the first special issue of a history and philosophy of science journal specifically devoted to philosophical analyses of viruses. Now, in our view, it is all the more important to pay attention to viruses as their study raises crucial conceptual and philosophical questions – in addition to practical questions already discussed extensively in the medias (for example, recently, about Ebola and Zika viruses). In this editorial introduction, we mention some of these conceptual and philosophical questions, and show how the essays gathered in this special issue address them.

2. Philosophical questions raised by the study of viruses

The study of viruses raises pressing conceptual and philosophical questions, several of which can be directly related to classic issues in philosophy of biology, or even general philosophy. With no claims to exhaustiveness, we mention here six problems that seem to us of great philosophical significance. As suggested by **Table 1**, a first general problem, "What are viruses?" can be divided into three more specific problems (definition; individuality; taxonomy), while a second general problem, "What is the place of viruses in the biological world?" can be divided into three other specific problems (life; organismality; non-living biological roles).

[1] This historical work has led to important discussions and controversies. On the tensions and disagreements among historical accounts of virology, see Méthot, this special issue.

<table>
<tr><th colspan="2">Problems for virology and philosophy of virology</th><th>Problems for philosophy of biology and general philosophy</th></tr>
<tr><td rowspan="3">What are viruses?</td><td>1. How to define a virus?</td><td>Are definitions useful in science, and how are they constructed?</td></tr>
<tr><td>2. Individuality and diachronic identity: where and when a virus starts and ends?</td><td>What is a biological individual and what makes its identity through time?</td></tr>
<tr><td>3. What is a virus species?</td><td>What is a biological species? What are “natural kinds” in biology?</td></tr>
<tr><td rowspan="3">What is the place of viruses in the biological world?</td><td>4. Are viruses alive?</td><td>What is life?</td></tr>
<tr><td>5. Is a virus an organism?</td><td>What is an organism?</td></tr>
<tr><td>6. Whether or not considered living, what are the biological (especially evolutionary and ecological) roles of viruses?</td><td>How to articulate the biological and the “living” dimensions? How biotic and abiotic elements interact and what can be the impact of the latter on living processes?</td></tr>
</table>

Table 1.

2.1. What are viruses?

Perhaps the most basic and essential problem raised by virus research concerns the definition of the concept of virus. Indeed, this seemingly naïve question has always been a crucial concern for virologists (Summers, 2014). Though some people include viruses in a very general category of “microbes”, others consider that viruses are very different from microbes. Historically, at the time of what is often described as their discovery at the end of the 19th century, viruses were conceived of as infectious agents that pass through a Chamberland-Pasteur filter, that is, a filter that blocks bacterial agents. In other words, viruses were mainly distinguished from bacteria by their filterability (van Helvoort, 1996). More than half a century later, in his highly influential paper “The Concept of Virus”, André Lwoff famously claimed that “*viruses are viruses*” – a way of stressing “the nature of the difference between viruses and other infectious agents, between viruses and micro-organisms” (Lwoff, 1957, p.

240). In his Nobel lecture in 1965, Lwoff still insisted that there is an "essential difference" between a virus and a microbe, a virus being defined by its capacity to reproduce itself solely from its genetic material (Lwoff, 1966). As has often been emphasized (Summers, 2014; Claverie & Abergel, this special issue), viruses have most of the time been defined *negatively*: viruses are conceived as entities lacking this or that feature (e.g., metabolism or autonomous replication) found in other biological entities, especially bacteria, and it is clearly worth asking whether a positive definition of viruses can be offered.

Today, some biologists (e.g., Claverie and Abergel, Forterre, and Koonin and Starokadomskyy, this special issue) consider that several of the criteria traditionally used to separate viruses from other biological entities have become fragile, or even sometimes obsolete. One aspect of this concerns the degree of "autonomy" exhibited by viruses. A very influential definition of viruses has been that viruses are intracellular obligate parasites, with a strong emphasis on their *dependency* on a host. Yet, the recent understanding that symbioses are ubiquitous in nature, added to the realization that at least certain viruses exhibit some degree of autonomy (Claverie & Abergel, 2010) while many bacteria live as obligate parasites, has led some biologists to adopt a much more *continuous* view of autonomy among biological entities. According to this view, far from distinguishing, in a absolute way, dependent from independent biological entities, the only thing one can do is to distinguish *degrees* of autonomy in the biological world (e.g., Dupré & O'Malley, 2009; Claverie & Abergel 2012).

A related question is whether or not viruses are necessarily harmful. Viruses have generally been described as harmful (most often disease-causing, that is, pathogenic) entities, and it is undeniably true that some viruses can be devastating to their hosts. Nonetheless, recent research has shown that many viruses are neutral or even beneficial to their hosts (see Pradeu, as well as Dupré & Guttinger, this special issue), so harmfulness could hardly be a defining feature of viruses.

Taken together, these observations suggest that it is today both crucial and at the same time extremely difficult to offer a precise and distinctive definition of the notion of virus. In this context, contributions to this special issue raise significant problems, such as to what extent a general definition of virus is possible, whether definitions of virus should necessarily be negative (i.e., descriptions of what viruses lack as compared to other biological entities), what definition of viruses could be compatible with scenarios that give an important role to viruses in the origins of life (Forterre and Kostyrka, this special issue), and what kind of new conceptual distinctions could perhaps shed light on future virological research (e.g., Forterre suggests the distinction between "ribocells" and "virocells"; Claverie and Abergel offer a definition of a virus as any biological entity the genome of which is replicated by a system of macromolecules that it does not entirely encode, and disseminated using a metabolically inert structure the maintenance of which does not require energy; Koonin and Starokadomskyy propose to distinguish different forms and degrees of "replicators", and conceive lytic viruses as extreme selfish replicators; in contrast, van Regenmortel defends a more "orthodox" view on viruses, which according to him is shared by a majority of virologists).

A second major set of problems concerns the individuality and diachronic identity of a virus. Indeed, it is extremely difficult to determine where and when a virus starts and ends, and what it means for one virus to remain the same through time. These seemingly philosophical and rather abstract questions are in fact related to a very practical issue, regularly met by working virologists: is a virus the viral particle (the virion), or is it the whole viral cycle? (See **Figure 1**). Although every virologist takes into account the whole cycle of a virus in order to describe its features and explain how it works, many statements made by virologists about viruses suggest that their focus is most often the virion. For example, two of the traditional criteria of Lwoff, according to which typical cellular organisms contain both DNA and RNA while viruses only contain one type, and all microorganisms are reproduced from the integrated sum of their constituents while viruses are produced solely from their nucleic acid, make sense only if the virus is identified with the virion. Many contributors to this special issue raise the problem mentioned here, and the reader will find strong disagreements between them (see, in particular, Claverie and Abergel, Dupré and Guttinger, Forterre, van Regenmortel, this special issue).

The discussion as to whether the virus should be equated with the virion or the whole viral cycle also has significant ontological consequences. In a series of recent publication, Dupré has been arguing in favour of a process-based, rather than thing-based, biological ontology, suggesting that what is prior in the biological world is change, not stability (see Dupré, 2012 for an overview). Viruses might offer a very convincing example in favour of this view, both because considering viruses as processes seems to be a good way to properly take into account the whole viral life cycle, and because the choice between defining viruses as virions or as whole life cycles has important practical consequences on some controversies of direct interest to virologists, such as the possibility to say that viruses might have metabolism after all (Dupré and Guttinger, this special issue; see also Claverie and Abergel, this special issue).

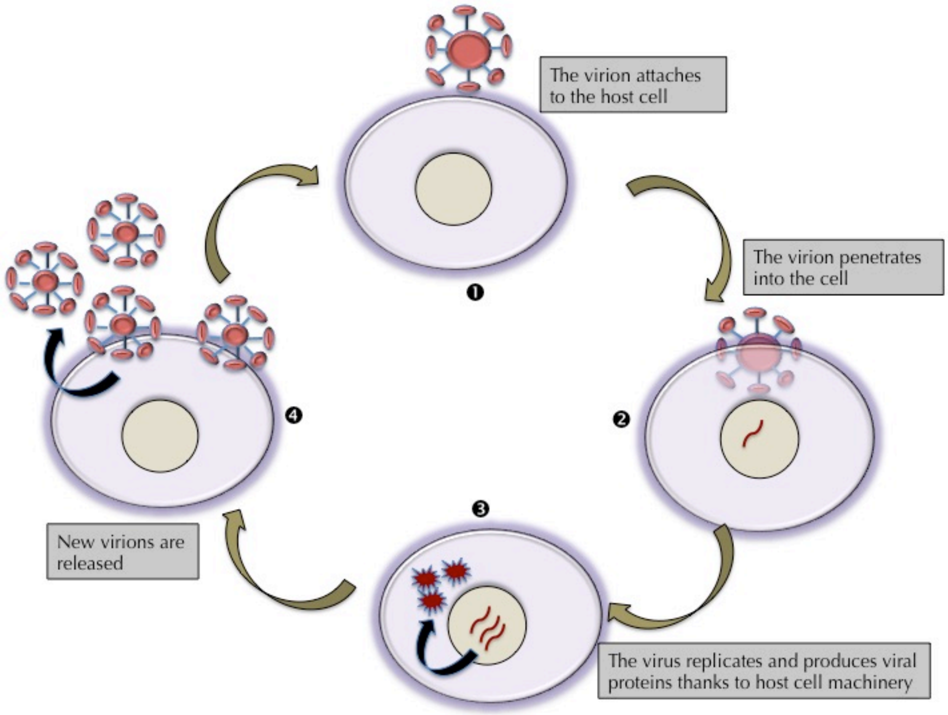

Figure 1. Highly schematic and simplified representation of a viral cycle.

(1) The virion (virus particle) attaches to the host cell. (2) The virion enters the cytoplasm via endocytosis, and is then uncoated. (3) In the nucleus, viral nucleic acid is replicated, and newly synthesized viral messenger RNAs migrate to the cytoplasm, where they are translated into viral proteins. (4) The newly formed virions bud from the infected cell and are released, sometimes killing the host cell. The actual details of the cycle vary considerably depending on the type of virus; the present figure offers only a schematic and oversimplified view.

Problems regarding biological individuality and identity, including about where and when biological entities start and end, have been highly debated in philosophy of biology. They have been raised about a large diversity of living things, including plants, fungi, colonial and social organisms, as well as symbiotic associations (Bouchard & Huneman, 2013; Buss, 1987; Godfrey-Smith, 2009; Michod, 1999; Pradeu, 2012), but, in light of the discussions presented in this special issue, viruses could constitute a particularly challenging "borderline" case for those problems, and one that could be particularly useful to discuss for philosophers of biology.

A third problem is how to classify viruses and whether or not it is possible to define viral species. Determining what counts as one species in the world of microbes is already a difficult task (O'Malley, 2014, p. 45-94), as recognized early by key actors in the debate over the definition of biological species (Mayr, 1953). But establishing a viral taxonomy is even more challenging. In the 1990s, especially under the influence of van Regenmortel (1989), the International Committee on the Taxonomy of Viruses (ICTV) developed a phylogenetic approach to viruses, in contrast with previous classifications, which were mainly based on structural characteristics of viruses (see also van Regenmortel, 2003). Nevertheless, as shown by Morgan (this special issue), this phylogenetic approach faces many challenges, in particular the possibility of extensive horizontal gene transfers (HGTs) among viruses. This suggests that, instead of a tree-like structure, the history of viruses is better represented by a reticulated network, and that only a pluralistic approach to virus taxonomy may be satisfactory.

2.2. What is the place of viruses in the biological world?

The question "Are viruses alive?" has been raised repeatedly throughout the history of virological research. Of course, this question is directly related to another question, "What is life?". Answering this question is notoriously difficult, and it has often been emphasized that conceptions of life have regularly changed in the last decades, making any answer to this question even more delicate. Of course, one possibility is to examine the distinction between the living and the non-living from a historical point of view, by characterizing the origins of life, but this is also a very arduous task (Maynard Smith & Szathmáry, 1999).

Recently, several biologists have claimed that a series of new discoveries, primarily the discovery of a growing number of "giant" viruses (viruses visible under the light microscope, often with a large double-stranded DNA genome, and a large gene content) since 2003 (La Scola et al., 2008), had the potential to radically modify our views about the living or non-living status of viruses (mainly because it has become very difficult to draw a boundary between some cellular organisms strongly dependent on their host and harbouring less than a minimal genome and the giant viruses that encode many genes and exhibit some degree of autonomy (Claverie & Abergel, 2010; this special issue)) and/or the role viruses could have played in the origins of life (Forterre, 2010b; Raoult & Forterre, 2008). These views have been met with scepticism by many other virologists (López-García, 2012; López-García & Moreira, 2012; Moreira & López-García, 2009), giving rise to a strong controversy (see, e.g., (Villarreal, 2004), (Villarreal & Witzany, 2010); see also Claverie and Abergel, Forterre, as well as van Regenmortel, this special issue).

A related problem is to determine to what extent viruses could be considered as organisms (with the thought that all organisms are living things but not all living things are organisms). The answer to this question will naturally depend on the definition of organism one adopts, but many biologists, for several of the reasons mentioned above such as the dependency on a host and the absence of an autonomous metabolism, have considered that viruses were not organisms. The notion of organism is usually considered as more precise than the wider notion of a living thing, because it is associated with the idea of a very high degree of functional organization and cooperation, with strong interactions among parts (e.g., Huneman, 2006; Pradeu, 2010; Sober, 2000). From that point of view, the suggestion that viruses might belong to the category of organisms after all is surprising, but some contributors to this special issue do examine it, if somewhat marginally[2].

Some people, however, doubt that the question "Are viruses alive?" (and the question "Are viruses organisms?") is a crucial one, whether because they think the discrimination between the living and the non-living does not fit well the specific case of viruses, or that this question is altogether ill-conceived. To a large extent, the answer to the question whether viruses are alive will depend on the pre-existing conceptions of "life" of each participant in the debate. In particular, those who see life first and foremost as a metabolic process tend to exclude viruses from the living world, while those who see life as primarily an evolutionary process are much more prone to say that viruses belong to the living world. Yet, even those sceptical of the question of the living status of viruses usually consider that the wider issue of the place of viruses in the biological world is worth exploring. Indeed, regardless of their inclusion or exclusion from the category of living things, viruses necessarily appear as major biological entities from several key points of view. They are Darwinian entities, replicating themselves, and subject to evolutionary processes such as natural selection and drift, while in turn exerting selective pressure on their hosts. They are also involved in fundamental ecological processes (see O'Malley, this special issue), for example in marine food webs (Rohwer & Thurber, 2009). All this suggests that the question of what viruses do (the different evolutionary, ecological, and physiological phenomena in which they are involved) is in fact at least as important as the question of what they are (that is, their living or non-living status).

Thus, the study of viruses raises fundamental issues, having to do with the definition of life, biological individuality and identity, the notion of organism, and the ontology of living things or processes. In this context, it seems urgent for philosophers of biology – and perhaps even for all philosophers – to start paying attention to viruses. This integration of viruses into philosophy of biology will certainly be facilitated by the remarkably rich conceptual reflection built by virologists themselves over the years and the welcome inclination of many

[2] Forterre (this special issue) explores arguments that have to do with the degree of organization of some viruses in the "virocell" stage (see also (Raoult & Forterre, 2008)), while Pradeu (this special issue) mentions the possibility that even viruses might possess an immune system, a feature that could perhaps be associated with the category of organism.

of them to interact with philosophers, as exemplified by this special issue, but also previous publications (e.g., Claverie & Abergel, 2012; López-García, 2012; Rohwer & Barott, 2013).

3. Structure of this special issue

To address the conceptual and philosophical problems raised by present-day virology, the present special issue gathers the contributions of biologists, philosophers, and historians. When we solicited papers from biologists, our aim has been to focus on controversial discussions occurring in present-day virology rather than more consensual points. As a consequence, several papers of this special issue express strong personal views, which are not necessarily shared by, and representative of, virologists in general, and all readers should be aware that they will not find here any neutral and consensual description of the current state of virology research, but rather a reflection of the often confrontational debates that have animated that field in recent years.

The special issue starts with the contribution of Gregory J. Morgan (Stevens Institute of Technology, USA) who, as emphasized above, is probably the only philosopher of biology whose recent research has dealt specifically with viruses. Morgan asks what a virus species is, and defends what he calls a "radical Pluralism" in viral taxonomy. He reconstructs the history of virus classification since early attempts in the 1960s, showing how virologists have moved from phenetic to an increasingly evolutionary approach to virus species, with the current International Committee on the Taxonomy of Viruses (ICTV) defining viral species in terms of monophyly. Morgan rejects the latter view, arguing that the existence of extensive horizontal genetic transfer (HGT) among various groups of viruses presents a challenge to this definition. To avoid the difficulties met by past approaches, Morgan defends a radical pluralism, which says that some viruses can be members of more than one species, while others do not form species at all and should be classified using new reticulate categories.

Maureen O'Malley (University of Bordeaux, France) shows that, since the late 1980s, a growing stream of micrographic, experimental, molecular, and model-based (theoretical) research has been investigating how and why viruses should be understood as important ecological actors. Viruses, especially phage, participate in the planet's most crucial food webs. They also constitute regulators of planetary biogeochemistry, controlling cycles on which all life depends (carbon, nitrogen and phosphorus). O'Malley argues that viruses are probably ecological actors of equal in importance to organismal actors, and that ecological agency should therefore be distinguished from standard interpretations of biological agency.

Thomas Pradeu (CNRS & University of Bordeaux, France) shows that, although viruses have generally been characterized by their harmful effects, many examples of mutualistic viruses (i.e. viruses that can increase the host fitness) exist. He explains how the idea of mutualistic viruses has been defended in recent virology, and explores four conceptual and practical consequences, asking to what extent this research modifies the way scientists might search for new viruses, our notion of how the host immune system interacts with microbes, the development of new therapeutic approaches, and, finally, the role played by the criterion of autonomy in our understanding of living things. He concludes that the recognition of mutualistic viruses plays a major role in a wider ongoing revision of the concept of virus.

Jean-Michel Claverie and Chantal Abergel (University of Mediterranée School of Medicine, France) use the epistemological approach of Gaston Bachelard – especially his idea that the advancement of science is often made through the breaking of "epistemological barriers" – to shed light on the reasons why the discovery of giant viruses occurred only in 2003, even though everything had been in place for their identification for over a century. Mimivirus was discovered in 2003, quickly followed by the identification of unrelated families of giant viruses such as the Pandoraviruses, the Pithoviruses and most recently Mollivirus, eliciting many questions about the definition of viruses and the exact nature of their differences with bacteria. Claverie and Abergel examine to what extent the giant viruses challenge previous definitions of viruses, the diversity of forms they can take, and how they might have evolved from extinct ancestral cellular lineages. They offer a new definition of viruses, which emphasizes that they do not encode a single universally shared macromolecule or biochemical function.

Patrick Forterre (Institut Pasteur & Paris-Sud University, France) argues that during the last decades three major discoveries have profoundly modified our perception of the viral world: (i) molecular ecologists have shown that viral particles are more abundant than cells in all environments; (ii) structural biologists have shown that some viruses from the three domains of life, Bacteria, Eukarya and Archaea, are evolutionarily related, revealing that viruses have most likely predated the last universal common ancestor, LUCA, and (iii) microbiologists have discovered giant viruses that rival cells in terms of size and gene content. Forterre discusses the scientific and philosophical impact of these discoveries on the debates over the definition, nature (living or not), and origin of viruses. He suggests that, even though viruses have often been considered non-living because they are traditionally assimilated to their virions, the term "virus" actually describes a biological process that integrates all aspects of the viral reproduction cycle. He insists on the importance of the intracellular part of this cycle, what he calls "virocell", when the viral information is actively expressed and reproduced, allowing the emergence of new viral genes. He claims that the virocell concept theoretically removes roadblocks that prevent defining viruses as living organisms, while admitting that defining a "living organism" remains an outstanding challenge. He concludes by offering new clues to address the question of what viruses are and whether or not they can be considered as living entities.

John Dupré and Stephan Guttinger (University of Exeter, UK) suggest that the conception of life as composed of distinct entities with well-defined boundaries has been undermined in recent years by the realisation of the near omnipresence of symbiosis. This has not only presented severe problems for our traditional understanding of biological individuality but has also led some to claim that we need to switch to a process ontology to be able adequately to understand biological systems. They note, however, that a large group of biological entities has been excluded from these discussions, namely viruses. Dupré and Guttinger develop two lines of argument to show that, despite common belief, viruses fit well with the integrated and collaborative picture of nature implied by symbiosis. First, viruses can be "nice" and collaborate with their hosts, meaning that they form parts of integrated biological systems and processes. Second, there are various reasons why viruses should be seen as processes rather than things, or substances. They conclude with some reflections on the debate as to whether viruses should be seen as living, and argue that there are good reasons for an affirmative answer to this question.

Marc van Regenmortel (CNRS & University of Strasbourg, France) argues that the idea that viruses are living is no more than a metaphor. He suggests that virologists often use anthropomorphic metaphors to describe vividly the properties of viruses and this has led some of them to claim that viruses are living microorganisms. The discovery of giant viruses that are larger and have a more complex genome than small bacteria has fostered the interpretation that viral factories, which are the compartments in virus-infected cells where the virus is being replicated, are able to transform themselves into a new type of living viral organism called a "virocell" (see Raoult & Forterre, 2008 and Forterre, this special issue). Van Regenmortel strongly rejects the concept of the living virocell, suggesting that it is based on an over-literal interpretation of a series of metaphors. First, because of the widespread occurrence of horizontal gene transfer, endosymbiosis and hybridization in the evolution of viral genomes, he suggests that it has not been possible to include metaphorical virocells in the so-called Tree of Life, which itself is a metaphor. Van Regenmortel also rejects the metaphor according to which a viral infection process should be seen as a war between host and virus, with the underlying idea that a virus such as the human immunodeficiency virus (HIV) would be able to develop new strategies and mechanisms for escaping protective host immune responses. He concludes by distinguishing two types of metaphors used for describing the behaviour of viruses: an “intentionality metaphor” commonly used for attributing goals and intentions to organisms, and the “living virus” metaphor that considers viruses to be actually living organisms.

Eugene V. Koonin (National Institutes of Health, USA) & Petro Starokadomskyy (UT Southwestern Medical Center, USA) offer a replicator-based approach to viruses. Indeed, they claim that the question whether viruses are alive, despite the considerable debate it has caused over many years, is in fact without substance, because the answer depends entirely on a definition of life bound to be arbitrary. In contrast, they suggest, the status of viruses among biological entities is readily defined within the replicator paradigm. They develop a view in which all biological replicators form a continuum along the selfishness-cooperativity axis, from the completely selfish to fully cooperative forms, and, within this range, typical lytic viruses represent the selfish extreme, whereas temperate viruses and various mobile elements occupy positions closer to the middle of the range. Selfish replicators not only belong to the biological realm, but are intrinsic to any evolving system of replicators. No such system can evolve without the emergence of parasites, and moreover, parasites drive the evolution of biological complexity at multiple levels. Koonin and Starokadomskyy argue that the history of life is a story of parasite-host coevolution that includes both incessant arms races and various forms of cooperation, and all organisms are communities of interacting, coevolving replicators of different classes. They conclude by saying that, even though a complete theory of replicator coevolution remains to be developed, it appears likely that not only the differentiation between selfish and cooperative replicators but the emergence of the entire range of replication strategies, from selfish to cooperative, is intrinsic to biological evolution.

Gladys Kostyrka (CNRS & Paris 1 University, France) examines from a historical point of view the problem of how viruses could have played critical roles in the origin of life if life relies on cellular organization and if viruses are defined as intracellular obligate parasites. How could viruses play a role in the emergence of cellular life if the existence of cells is a prerequisite for the existence of viruses? Building on the work of historian of science Scott Podolsky, Kostyrka argues that disagreements concerning the roles of viruses in origin of life scenarios stem from the different concepts of life and of virus that various scientists defend, and that investigating the roles of viruses in these scenarios not only helps to identify different ways of defining life in the context of origin of life theorizing, but also offers the opportunity to better understand how viruses could be conceptualized.

Finally, Pierre-Olivier Méthot (Université Laval, Canada) offers an analysis of the recent historiography of virology. Whereas aspects of the history of virology from the late nineteenth to the mid-twentieth century have often been recounted through a number of detailed case studies, very few general discussions of the historiography of this discipline have been offered. Looking at the different ways in which the history of virology has been told, Méthot discusses a number of debates among and sometimes between scientists and historians of biology and examines how they are based on a different understanding of notions such as "discipline", of processes such as "scientific discovery" as well as on distinct views about what the history of science is and how it should be written (particularly the opposition between "longue durée" and "micro-history" or between history of "concepts" versus "experimental methods"). This analysis suggests that one way to provide a richer historiography of virology would be to look at the variations over time of the relations between conceptual, technological, and institutional factors that fostered its development at the intersection of several other scientific fields in the life sciences.

Hopefully this special issue will contribute to the emergence of a fully grown philosophy of virology. Because of the very peculiar place viruses have in the biological world, philosophy of virology is interesting in its own right. Moreover, philosophy of virology will be a welcome and very useful addition to the increasingly well-established field of philosophy of microbiology. Finally, the issues raised by virology, in particular the definition of life, individual, organism and autonomy, appear to be of central interest for any philosopher of biology, and even perhaps for any philosopher more generally. As editors, we will be delighted if some readers find that seeing those traditional philosophical questions through viral lens brings novel and important insights.

References

Bos, L. (1999). Beijerinck's work on tobacco mosaic virus: historical context and legacy. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *354*(1383), 675–685.

Bos, L. (2000). 100 years of virology: from vitalism via molecular biology to genetic engineering. *Trends in Microbiology*, *8*(2), 82–87.

Bouchard, F., & Huneman, P. (2013). *From Groups to Individuals: Perspectives on*

Biological Associations and Emerging Individuality. Cambridge, MA: MIT Press.
Burnet, F. M. (1945). *Virus as organism: evolutionary and ecological aspects of some human virus diseases*. Cambridge, Mass.: Harvard University Press. Retrieved from http://catalog.hathitrust.org/Record/001556721
Buss, L. W. (1987). *The Evolution of Individuality*. Princeton, N.J.: Princeton University Press.
Claverie, J.-M., & Abergel, C. (2010). Mimivirus: the emerging paradox of quasi-autonomous viruses. *Trends in Genetics: TIG*, *26*(10), 431–437. http://doi.org/10.1016/j.tig.2010.07.003
Claverie, J.-M., & Abergel, C. (2012). The Concept of Virus in the Post-Megavirus Era. In G. Witzany (Ed.), *Viruses: Essential Agents of Life* (pp. 187–202). Springer Netherlands. Retrieved from http://link.springer.com/chapter/10.1007/978-94-007-4899-6_9
Creager, A. N. H. (2002). *The life of a virus : tobacco mosaic virus as an experimental model, 1930-1965*. Chicago: University of Chicago Press.
Dupré, J. (2012). *Processes of Life: Essays in the Philosophy of Biology*. Oxford & New York: Oxford University Press. Retrieved from http://www.oxfordscholarship.com/view/10.1093/acprof:oso/9780199691982.001.0001/acprof-9780199691982
Dupré, J., & O'Malley, M. (2009). Varieties of Living Things: Life at the Intersection of Lineage and Metabolism. *Philosophy & Theory in Biology*, *1*. http://doi.org/http://dx.doi.org/10.3998/ptb.6959004.0001.003
Forterre, P. (2010a). Defining Life: The Virus Viewpoint. *Origins of Life and Evolution of the Biosphere*, *40*(2), 151–160. http://doi.org/10.1007/s11084-010-9194-1
Forterre, P. (2010b). Giant viruses: conflicts in revisiting the virus concept. *Intervirology*, *53*(5), 362–378. http://doi.org/10.1159/000312921
Godfrey-Smith, P. (2009). *Darwinian populations and natural selection*. Oxford: Oxford University Press.
Hughes, S. S. (1977). *The Virus: A History of the Concept*. London: Heinemann Educational Publishers.
Huneman, P. (2006). Naturalising purpose: from comparative anatomy to the "adventure of reason." *Studies in History and Philosophy of Biological and Biomedical Sciences*, *37*(4), 649–674. http://doi.org/10.1016/j.shpsc.2006.09.004
Koonin, E. V., & Dolja, V. V. (2013). A virocentric perspective on the evolution of life. *Current Opinion in Virology*, *3*(5), 546–557. http://doi.org/10.1016/j.coviro.2013.06.008
La Scola, B., Desnues, C., Pagnier, I., Robert, C., Barrassi, L., Fournous, G., … Raoult, D. (2008). The virophage as a unique parasite of the giant mimivirus. *Nature*, *455*(7209), 100–104. http://doi.org/10.1038/nature07218
López-García, P. (2012). The place of viruses in biology in light of the metabolism- versus-replication-first debate. *History and Philosophy of the Life Sciences*, *34*(3), 391–406.
López-García, P., & Moreira, D. (2012). Viruses in Biology. *Evolution: Education and Outreach*, *5*(3), 389–398. http://doi.org/10.1007/s12052-012-0441-y
Lustig, A., & Levine, A. J. (1992). One hundred years of virology. *Journal of Virology*, *66*(8), 4629–4631.
Lwoff, A. (1957). The Concept of Virus. *Journal of General Microbiology*, *17*(2), 239–253. http://doi.org/10.1099/00221287-17-2-239
Lwoff, A. (1966). Interaction among virus, cell, and organism. *Science (New York, N.Y.)*, *152*(3726), 1216–1220.
Maynard Smith, J., & Szathmáry, E. (1999). *The origins of life : from the birth of life to the origin of language*. Oxford ; New York: Oxford University Press.
Mayr, E. (1953). Concepts of classification and nomenclature in higher organisms and microorganisms. *Annals of the New York Academy of Sciences*, *56*(3), 391–397.

Michod, R. E. (1999). *Darwinian dynamics : evolutionary transitions in fitness and individuality*. Princeton, NJ: Princeton University Press.
Moreira, D., & López-García, P. (2009). Ten reasons to exclude viruses from the tree of life. *Nature Reviews. Microbiology*, *7*(4), 306–311. http://doi.org/10.1038/nrmicro2108
Morgan, G. J. (2001). Bacteriophage Biology and Kenneth Schaffner's Rendition of Developmentalism. *Biology and Philosophy*, *16*(1), 85–92. http://doi.org/10.1023/A:1006742931958
Morgan, G. J. (2006). Why there was a useful plausible analogy between geodesic domes and spherical viruses. *History and Philosophy of the Life Sciences*, *28*(2), 215–235.
Morgan, G. J. (2010). Laws of biological design: a reply to John Beatty. *Biology & Philosophy*, *25*(3), 379–389. http://doi.org/10.1007/s10539-009-9181-y
Morgan, G. J., & Pitts, W. B. (2008). Evolution without Species: The Case of Mosaic Bacteriophages. *The British Journal for the Philosophy of Science*, *59*(4), 745–765. http://doi.org/10.1093/bjps/axn038
O'Malley, M. A. (2013). Philosophy and the microbe: a balancing act. *Biology & Philosophy*, *28*(2), 153–159. http://doi.org/10.1007/s10539-013-9360-8
O'Malley, M. A. (2014). *Philosophy of Microbiology*. Cambridge University Press.
O'Malley, M. A., & Dupré, J. (2007a). Size doesn't matter: towards a more inclusive philosophy of biology. *Biology & Philosophy*, *22*(2), 155–191. http://doi.org/10.1007/s10539-006-9031-0
O'Malley, M. A., & Dupré, J. (2007b). Towards a philosophy of microbiology. *Studies in History and Philosophy of Biological and Biomedical Sciences*, *38*(4), 775–779. http://doi.org/10.1016/j.shpsc.2007.09.002
Pradeu, T. (2010). What is an organism? An immunological answer. *History and Philosophy of the Life Sciences*, *32*, 247–268.
Pradeu, T. (2012). *The Limits of the Self: Immunology and Biological Identity*. New York: Oxford University Press.
Raoult, D., & Forterre, P. (2008). Redefining viruses: lessons from Mimivirus. *Nature Reviews. Microbiology*, *6*(4), 315–319. http://doi.org/10.1038/nrmicro1858
Rohwer, F., & Barott, K. (2013). Viral information. *Biology & Philosophy*, *28*(2), 283–297. http://doi.org/10.1007/s10539-012-9344-0
Rohwer, F., & Thurber, R. V. (2009). Viruses manipulate the marine environment. *Nature*, *459*(7244), 207–212. http://doi.org/10.1038/nature08060
Sankaran, N. (2010). The bacteriophage, its role in immunology: how Macfarlane Burnet's phage research shaped his scientific style. *Studies in History and Philosophy of Biological and Biomedical Sciences*, *41*(4), 367–375. http://doi.org/10.1016/j.shpsc.2010.10.012
Sober, E. (2000). *Philosophy of Biology* (2nd edition). Westview Press.
Stanley, W. M. (1957). Penrose Memorial Lecture. On the Nature of Viruses, Cancer, Genes, and Life-A Declaration of Dependence. *Proceedings of the American Philosophical Society*, *101*(4), 317–324.
Summers, W. C. (2014). Inventing Viruses. *Annual Review of Virology*, *1*(1), 25–35. http://doi.org/10.1146/annurev-virology-031413-085432
van Helvoort, T. (1994a). History of virus research in the twentieth century: the problem of conceptual continuity. *History of Science; an Annual Review of Literature, Research and Teaching*, *32*(2), 185–235.
van Helvoort, T. (1994b). The construction of bacteriophage as bacterial virus: linking endogenous and exogenous thought styles. *Journal of the History of Biology*, *27*(1), 91–139.
van Helvoort, T. (1996). When Did Virology Start? *ASM News*, *62*(3), 142–145.
van Regenmortel, M. H. V. (1989). Applying the species concept to plant viruses. *Archives of Virology*, *104*(1-2), 1–17.

van Regenmortel, M. H. V. (2003). Viruses are real, virus species are man-made, taxonomic constructions. *Archives of Virology*, *148*(12), 2481–2488. http://doi.org/10.1007/s00705-003-0246-y
Villarreal, L. P. (2004). Are viruses alive? *Scientific American*, *291*(6), 100–105.
Villarreal, L. P., & Witzany, G. (2010). Viruses are essential agents within the roots and stem of the tree of life. *Journal of Theoretical Biology*, *262*(4), 698–710. http://doi.org/10.1016/j.jtbi.2009.10.014
Wasik, B. R., & Turner, P. E. (2013). On the biological success of viruses. *Annual Review of Microbiology*, *67*, 519–541. http://doi.org/10.1146/annurev-micro-090110-102833
Waterson, A. P., & Wilkinson, L. (1978). *An introduction to the history of virology*. Cambridge ; New York: Cambridge University Press.
Witzany, G. (Ed.). (2012). *Viruses: Essential Agents of Life*. Dordrecht: Springer Netherlands. Retrieved from http://link.springer.com/10.1007/978-94-007-4899-6