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What is a virus species? Radical pluralism in viral taxonomy

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A R T I C L E I N F O

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A B S T R A C T

Early attempts in the 1960s at constructing a classification scheme for viruses were phenetic and focused on structural properties of the virion. Over time, the International Committee on the Taxonomy of Viruses (ICTV) has refined its definition of a virus species to include an appeal to evolutionary history. The current ICTV definition defines a viral species in terms of monophyly. The existence of prolific horizontal genetic transfer (HGT) among various groups of viruses presents a challenge to this definition. I argue that the proper response to this mode of evolution is to allow for radical pluralism. Some viruses can be members of more than one species; others don't form species at all and should be classified using new reticulate categories.

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1. Introduction

Peterson (2014) suggests three goals for viral taxonomy: organization, stability, and prediction. First, a good classification system should efficiently organize viral diversity. Most biological classification uses the evolutionary history of species—"the tree of life"—to organize biological diversity. Second, it should be stable in the sense that significant revisions are not made too frequently. The third goal is to create a classification that allows for useful predictions. For example, knowing that a virus sample contains members of a pathogenic species might provide guidance in treating a viral infection. The accuracy of these types of predictions has significant consequences, economic and otherwise, in medicine, horticulture, and agriculture. Despite ongoing disagreement about how best to define the species category, for large swaths of macroscopic life, these three goals can be largely satisfied by classifying individual organisms into species. Whether these three goals can be met by classifying all viruses into species is more problematic. The challenges of viral classification can be appreciated by considering the difficulty in defining the nature of viral species.

The species problem is to provide an adequate theoretical definition of biological species (Ereshefsky, 2010a; 2010b). Commonly this problem is approached by considering the utility of various "species concepts." In virology, the problem is to provide an adequate theoretical definition of a viral species. If pluralism about species is true, then different parts of life will require different species definitions (Dupré, 1993; Ereshefsky, 1998; Kitcher, 1984; Mishler & Donohue, 1982). If monism about species is true, then there will be a species definition that covers all parts of the living world. In this case there would be no special problem of viral species. A viral species would be captured by a general definition of species. However, most biologists do not think that monism of this sort is true—definitions that work for eukaryotic life do not work for prokaryotic life and certainly do not work for viral life.

Perhaps the most well-known attempt to define species is Ernst Mayr's biological species concept that defines a species as a population of individuals that can sexually reproduce. Since viruses do not reproduce sexually, Mayr's species concept does not apply to viruses. One response to this asymmetry might be to exclude viruses from the realm of biological classification (See O'Malley, 2014, pp. 76–80 for a discussion of these matters), but this response is unappealing as viruses clearly have genes, adapt to their environments, and evolve. They also interact and co-evolve with their biological hosts. (See Villarreal & Witzany, 2010 for more arguments regarding why viruses should be included in biological classification). In this paper, I will assess the definitions of virus species proposed by the International Committee on Virus Taxonomy (ICTV), the official taxonomic body for the classification of viruses. I

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will argue that the proposed definitions suffer from a variety of problems and that one way to resolve one major problem is to simply accept that many viral groups do not form species. That every biological agent be a member of one and only one species is an intuition that arises from consideration of macroscopic life; microscopic life can be significantly different. Different groups of viruses should be classified using differing systems depending on the level of horizontal gene transfer affecting the evolutionary history of the group. I call this diversity of applicable classificatory systems that includes systems that do not require species, "radical pluralism." I use adjective "radical" to distinguish the view from a more moderate form of pluralism that acknowledges that there is not a single definition of species that covers all of life, but nonetheless holds that any given lifeform is a member of a species.

I previously have argued that since bacteriophages evolve in large part by horizontal (or lateral) gene transfer (LGT or HGT) the most popular classes of species concept fail to properly classify to mosaic bacteriophages (Morgan & Pitts, 2008). Here I examine the approach of the ICTV in more detail.

2. Some background history

The phrase "virus species" was barely used until the 1940s; before then, there were many attempts to define "virus" but few to define "virus species" (Hughes, 1977). Some, such as the plant virologist F. C. Bawden, maintained that viruses were merely chemicals, which implied that they should not be given a biological classification. The modern concept of virus began to emerge in the 1950s (Lwoff, 1957; Van Helvoort, 1994). With the development of negative staining in 1959, which allowed electron microscopists to visualize the subunits of virus capsids, and 1950s developments in x-ray crystallography of viruses, biologists of the 1960s had an increasing amount of data with which to build a robust classification (Morgan, 2003; 2004).

The International Association of Microbial Societies formally established the International Committee for Nomenclature of Viruses (ICNV) in 1966 with the objective to create a universal taxonomic system for all viruses. One of the more active participants in the committee was André Lwoff, the winner of the 1965 Nobel Prize for medicine and physiology. He and his supporters proposed a system that applied the taxonomic terms phylum, division, class, order, family, genus, and species to viruses (Lwoff & Tournier, 1966). Focusing on biological structure, they identified four features of the virion to be the most important and definitional of a virus family:

1. The chemical nature of the nucleic acid—either RNA or DNA
2. The symmetry of the capsid—cubic, helical or binal
3. The presence of an envelope
4. The diameter of helical viruses and the triangulation number of icosahedral viruses (Lwoff & Tournier, 1966, p. 53).

This marked a major difference from earlier classification schemes that included symptoms viruses caused in their hosts to make divisions (See Bennett, 1939). Lwoff and Tournier were aware of the importance of connecting the classification to evolutionary history if possible:

> A phylogenetic system, the dream of so many systematicians, must of course, take evolution into account. For a monophyletic group, the hierarchy of subdivisions should correspond to the chronology of evolution: the earlier a given character has appeared, the higher is its hierarchy. For a polyphytetic group, hierarchy is arbitrary. [Our proposed] system is arbitrary, necessarily. (Lwoff & Tournier, 1966, p. 54)

Lwoff took it as unlikely that viruses form a monophyletic group. It is logically possible for viruses as a whole to be polyphyletic, but for the lower taxonomic groups such as virus families to be monophyletic. Lwoff did not discuss this possibility and indeed did not discuss virus species much at all in this proposed viral classification system.

The first President of the ICNV was Peter Wildy, one of the first virologists to use electron microscopy and negative staining to examine virions. Wildy resisted Lwoff's approach and it was not adopted by the ICNV initially even though Lwoff was made a life member of the ICNV (Matthews, 1985, p. 453). Nonetheless, in the first committee report in 1971, Wildy would thank Lwoff for "stimulating" the committee over the last eight years, writing, "[s] ometimes it has seemed that this stimulant was excessively strong but it has been a healthy stimulant" (Wildy, 1971, p. viii). Over the years the committee attempted to classify an increasing number of known viruses—and as Lwoff had proposed, the structural properties of the virion played an important role. In the beginning the ICNV did not define virus species, but rather grouped viruses into different genera. In 1973 the ICNV changed its name to the International Committee for the *Taxonomy* of Viruses (ICTV) to reflect that it was taxonomy and not merely nomenclature with which they were largely concerned. The ICTV produced reports every three years or so.

In 1981 the ICTV published 22 rules governing the nomenclature of viruses. Rule 11 read, "A virus species is a concept that will normally be represented by a cluster of strains, or a population of strains from a particular source, which have in common a set or pattern of correlating stable properties that separates the cluster from other clusters of strains" (Matthews, 1982, p. 23). By adopting this rule, the ICTV adopted a phenetic approach to species that classifies things by similarity. It goes without saying that the definition in rule 11 is vague in not specifying which stable properties are permissible and which are not. Depending on which properties are used, different clusterings can be created. This rule was intended to be helpful in practice, but it has the theoretical weaknesses associated with purely phenetic approaches to viral classification (Morgan & Pitts, 2008).

Kingsbury (1985) argued that the definition implicit in rule 11 was not sufficiently biological as it could be used to classify rocks or any set of objects. Although he did not put it this way, he was arguing against a phenetic approach to species. Arguing that a *biological* definition should include an appeal to genes, he proposed that "A virus species is a population of viruses sharing a pool of genes that is normally maintained distinct from the gene pools of other viruses" (Kingsbury, 1985, p. 67). Like Mayr's biological species concept, Kingsbury's proposal focuses on the cohesion and distinctness of a gene pool. Whereas Mayr took sexual reproduction as the mechanism by which gene pools are shared and barriers to sexual reproduction to mark the edges of species, Kingsbury left open which mechanism(s) keeps viral gene pools distinct from one another. Based on his definition potentially many different mechanisms could play this role. He suggests that an ecological role could be important in many viral species. It is possible by his account that two viral species could have "barely indistinguishable" nucleotide sequences but nonetheless infect two different, distinct hosts, and thus form two distinct gene pools.

In 1991, following Van Regenmortel (1989), the ICTV adopted a new definition: "A virus species is a polythetic class of viruses that constitutes a replicating lineage and occupies a particular ecological niche" (Francki, Fauquet, Knudson, & Brown, 1991). By polythetic they mean that not all of a collection of relevant properties need to be possessed by a virus for it to be a member of the species. For example, in a list of five relevant properties, having four of them