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### Expansion of Microbial Virology by Impetus of the Reduction of Viral Dark Matter

Siddharth Ravindran Krishnamurthy  
*Washington University in St. Louis*

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WASHINGTON UNIVERSITY IN ST. LOUIS

Division of Biology and Biomedical Sciences  
Immunology

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The Reduction of Viral Dark Matter by Expanding of Viral Diversity

by

Siddharth Ravindran Krishnamurthy

A dissertation presented to  
The Graduate School  
of Washington University in  
partial fulfillment of the  
requirements for the degree  
of Doctor of Philosophy

August 2017  
Saint Louis, MO

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## List of Abbreviations

<b>Abbreviation</b>	<b>Full Name</b>
BHI	Blood Heart Infusion
CAT	Chloramphenicol Acetyl Transferase
CLASH	cross-linking, ligation and sequencing hybrids
contigs	Contiguous Sequence
CROC	Concentrated ROC
dsDNA	Double-Stranded DNA
dsRNA	Double-Stranded RNA
HPBV	Human Picobirnavirus
ICTV	International Committee on the Taxonomy of Viruses
ITS	Internal Transcribed Spacer
LB	Lysogeny Broth
NBC	Naïve Bayes Classifier
NCBI	National Center for Biotechnology Information
NEPRC	New England Primate Research Center
nr	Non-redundant protein database
nt	Non-redundant nucleotide database
ORF	Open Reading Frame
OTU	Operational Taxonomic Unit
RACE	Rapid amplification of cDNA ends
RBS	Ribosomal Binding Site
RdRp	RNA dependent RNA Polymerase
ROC	Receiver Operator Characteristic
SDA	Sabouraud Dextrose Agar
SIV	Simian Immunodeficiency Virus
SRA	Sequence Read Archive
ssDNA	Single-stranded DNA
ssRNA	Single-stranded RNA
SVM	Support Vector Machine
TEM	Transmission Electron Microscopy
TNPRC	Tulane Primate Research Center

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I would also like to thank my collaborators and informants outside of the Wang lab complex. Nathan Crook from the Dantas Lab has been invaluable in helping me design and analyze the functional metagenomic screen for RNA phage resistance genes. Dr. Anca Segall from San Diego State University provided critical direction in how to perform bacteriophage assays correctly. Dr. Mario Feldman, Dr. Christina Stallings, and their labs provided useful guidance on bacterial genetics as well as reagents and equipment to perform most of the phage

infection experiments. I would also like to thank Dr. Stephen Beverley for his useful insights on microbial virology.

All of the database scans for novel viruses, (whether RNA bacteriophages, Discovirus or picobirnaviruses) was greatly facilitated by the infrastructure set up and maintained by the Pathogen Discovery Core, namely Guoyan Zhao, Lindsay Droit and Scott Handley. Additionally, the Wang lab has been a great place to work and develop as a scientist.

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I would like to acknowledge my friends, who have been useful throughout my years in graduate school, as well as my family, nuclear and extended, who have always expressed (or at least feigned) excitement about my scientific pursuits.



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*Washington University in Saint Louis*

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## ABSTRACT OF THE DISSERTATION

Expansion of Microbial Virology by Impetus of the Reduction of Viral Dark Matter

by

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Doctor of Philosophy in Biology and Biomedical Sciences

Immunology

Washington University in St. Louis, 2017

Professor David Wang, Chair

Modern metagenomic methods have rapidly accelerated the rate of viral discovery. Currently, to discover a novel virus, deep sequencing reads must align to a known reference virus. While alignment is effective at identifying closely related viruses, highly divergent viruses can often share no discernable sequence alignment with known viruses. Therefore, the accurate classification of viral dark matter – metagenomic sequences that originate from viruses but do not align to any reference virus sequences – is one of the major obstacles in not only discovering novel viruses, but also by extension, comprehensively defining the virome. As viral dark matter results fundamentally from a failure to align sequence reads, two major contributors to viral dark matter include 1) the lack of diversity in specific viral families and 2) the reliance on alignment as a metric to define viral taxonomy. In this dissertation, I address each of these issues. These projects resulted in a massive expansion in understanding of microbial virus diversity, which led me to further interrogate the biology of microbial viruses. Specifically, I attempted to identify novel antiviral mechanisms against RNA bacteriophages and possibly identify a novel family of RNA bacteriophages.

First, I addressed the underrepresentation of viral sequences in databases by identifying a specific underrepresented class of virus, bacteriophages with RNA genomes, and systematically discovered highly divergent novel RNA bacteriophages in previously sequenced data. I identified 161 partial genome sequences from at least 122 RNA bacteriophage phylotypes that are highly divergent from each other and from previously described RNA bacteriophages. These partial genome sequences displayed multiple novel genome organizations previously unknown for RNA bacteriophages, and in aggregate, encoded 91 open reading frames (ORFs) that did not align to any known protein; sequences related to these ORFs would be described as viral dark matter in absence of this systematic discovery effort.

This new level RNA bacteriophage diversity suggested that RNA bacteriophages might be major predators of bacteria in the environment. In turn, this would suggest that there might be active resistance mechanisms in bacteria that specifically antagonize RNA bacteriophages; as of now however, there are no active mechanisms known in bacteria that can antagonize RNA bacteriophages. Therefore, one goal was to identify bacterial genes that can restrict RNA bacteriophage infection. I performed a functional metagenomic screen to identify RNA phage resistance genes. From this, I identified four genes that conferred resistance to the RNA phages, Q $\beta$  and MS2 but not the RNA phage C1.

Additionally, this expansion of RNA bacteriophage diversity suggests that there might be new families of RNA bacteriophages that are unrelated to the previously discovered RNA bacteriophages. One candidate eukaryotic viral family that might in fact be RNA bacteriophages are *Picobirnaviridae*. Picobirnaviruses are bisegmented RNA viruses that are highly prevalent in stool. By analyzing previously sequenced datasets, I discovered multiple new picobirnavirus

segments. From analyzing the upstream regions of the ORFs on these segments, I found that almost all of the ORFs are preceded by a bacterial ribosomal binding sequence. This conservation of bacterial ribosomal binding sequences suggests that these viruses might infect bacteria. I then unsuccessfully tried to show that Human Picobirnavirus can replicate in bacterial cells.

Second, I addressed the reliance on alignment based algorithms by developing a novel alignment-independent algorithm to identify viral sequences. This algorithm, DiscoVir, is a support vector machine (SVM) model that relies on nucleotide k-mer frequencies to discriminate sequences of novel, highly disparate eukaryotic viruses from prokaryotic and fungal sequences. I validated in silico that DiscoVir can identify viruses from novel viral taxa and that it outperforms BLASTx for almost all viral families. When applied to an authentic metagenomic dataset, DiscoVir identified two additional contigs that corresponded to two undetected segments of a novel bunya-like virus. By selectively culturing fungi from this serum sample, I identified an isolate of *Penicillium atramentosum* that contained all three viral RNA segments, thus suggesting that this fungal isolate was in fact the host of this novel virus. I sequenced the whole genome of this novel virus and demonstrated that the terminal nucleotide sequences were conserved between the three segments, and these sequences were consistent with the termini of bunyaviruses in the genera Phlebovirus and Tenuivirus. Thus, application of DiscoVir played a critical role in the identification of the first segmented negative stranded RNA virus infection of a fungus.

Taken together, I have contributed to the systematic reduction of viral dark matter using two different approaches, both of which enable future researchers to identify a much more

diverse repertoire of viruses than previously possible. This increased ability to identify highly divergent viruses will better enable the metagenomics community to accurately identify the role of viruses in larger biological processes, including but not limited to, human disease.

# 1. Introduction

This work has been published in part in *Virus Research* (2017)

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**Abstract:** The accurate classification of viral dark matter –metagenomic sequences that originate from viruses but do not align to any reference virus sequences– is one of the major obstacles in comprehensively defining the virome. Depending on the sample, viral dark matter can make up from anywhere between 40-90% of sequences. This review focuses on the specific nature of dark matter as it relates to viral sequences. We identify three factors that contribute to the existence of viral dark matter: the divergence and length of virus sequences, the limitations of alignment based classification, and limited representation of viruses in reference sequence databases. We then discuss current methods that have been developed to at least partially circumvent these limitations and thereby reduce the extent of viral dark matter.

**Highlights:**

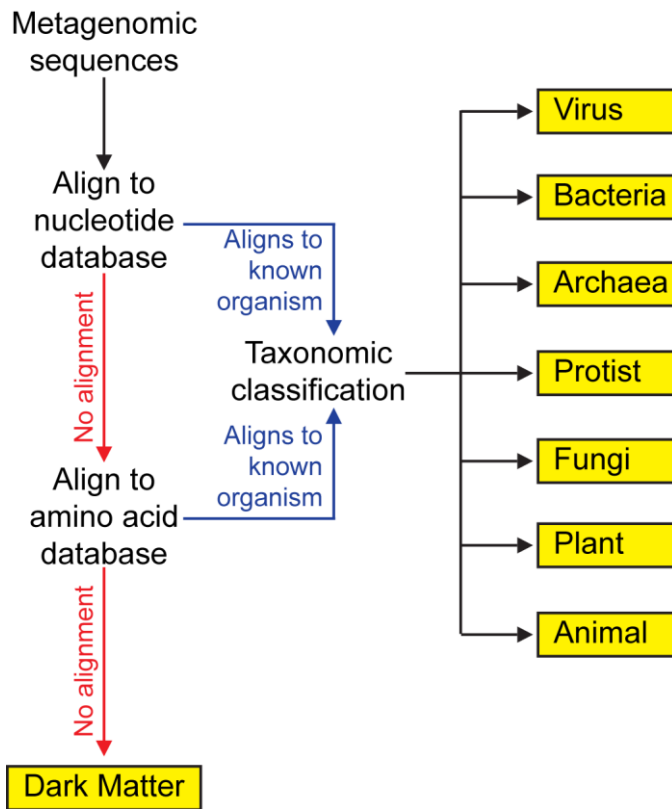
- Primary sequence alignment is the most common method to identify viral sequences
- Alignment methods are limited by low identity query sequences
- Low diversity in viral databases limit alignment based methods
- Experimental methods can specifically enrich viral sequences in sequencing datasets
- Computational methods use virus specific attributes to identify viral sequences

**Introduction**

Next generation sequencing has accelerated the rate at which novel viruses can be discovered. Sequence based viral discovery relies on aligning sequences to known reference genome or protein databases. This approach has been successful in identifying novel viruses that infect hosts from every major taxon of life: e.g. vertebrates <sup>1,2</sup>, arthropods <sup>3</sup>, plants <sup>4</sup>, fungi <sup>5</sup>, bacteria <sup>6,7</sup> and archaea <sup>8</sup>. However, highly divergent viruses may lack any primary sequence similarity to any previously sequenced virus. By comparison to other microbes, the identification of viruses and sub-viral agents pose a particular challenge as they lack a universally conserved gene analogous to the 16S rRNA gene in bacteria or the internal transcribed spacer

(ITS) in fungi<sup>9</sup>. This problem is compounded by the fact that many viruses mutate faster than any cellular organism.

Formally, dark matter is defined negatively: any nucleotide sequence that cannot be taxonomically assigned by alignment to any reference nucleotide or amino acid sequence (Figure 1.1). Viral dark matter is the subset of dark matter that originates from viruses. With total metagenomic data, sequences that do not align to any known organism could be from any organism and need not necessarily be viral. From studies that use experimental techniques to purify viral particles, 40-90% of sequences are unalignable<sup>10-13</sup>. Sequence alignment depends primarily on two variables: the experimental parameters used for sequencing and the computational strategies used for analysis. In this review, we first describe what enables and limits the alignment of sequences to viruses; subsequently, we discuss experimental and computational methods designed to alleviate some of these issues.



**Figure 1.1.** Generic overview of alignment based viral sequence identification



## **Limits of Alignment Based Classification**

Currently, taxonomic classification of a given sequence as being viral in origin is dependent upon statistically significant alignment to known reference virus sequences. There are three fundamental components to aligning a viral sequence accurately to a known virus: the sequence being aligned, the alignment algorithm used, and the database of viral sequences. All three of these components can contribute to the inability of a given sequence to align to known viral sequences.

## **Alignment Algorithms**

In principle, all aligners take in user defined sequences, referred to hereafter as “queries”, and compare them to a database of sequences of known taxonomic origin. Next generation sequencing often relies on short read aligners, such as Bowtie, SOAP or BWA, to efficiently align reads with high nucleotide identity to a known genome<sup>14-16</sup>. However, these aligners by design target nucleic acid sequences and do not generally allow extensive mismatches. Thus, they cannot identify sequences from highly divergent viral species that share only amino acid similarity to reference genomes. Consequently, although computationally slower, BLAST is still the most commonly used algorithm to align sequence reads to nucleotide databases for viral taxonomic classification<sup>17-21</sup>. Even more highly divergent viruses often require translation of these sequences to amino acids and alignment to known viral protein databases. This protein alignment is most often performed by BLASTx<sup>22</sup>. One limitation of protein alignment strategies is that they cannot be employed on the small proportion of agents that do not encode proteins, such as viroids. More rapid amino acid based alignment applications, such as DIAMOND and RAPSearch, have been developed that approximate the sensitivity of BLASTx, making large-scale protein based alignments more computationally feasible<sup>23,24</sup>. DIAMOND and RAPSearch have successfully been used for virus discovery<sup>5,25,26</sup>. Although amino acid alignment algorithms are more sensitive than their nucleotide counterparts, they are dependent upon the quality and completeness of databases of predicted protein

sequences used. Translated nucleic acid alignment algorithms can obviate this need, but they are much more computationally intensive.

### **Profile Based Methods**

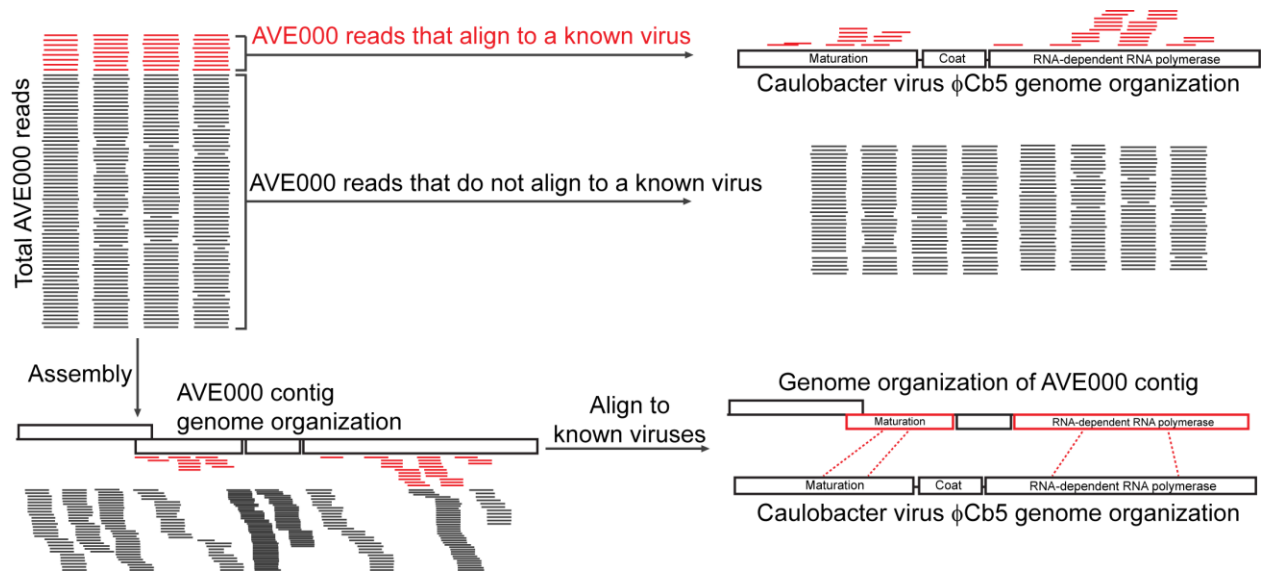
Alignment algorithms calculate distance between two sequences by using a generalized substitution matrix that equally penalizes mismatches at all residues of a sequence. However, from an evolutionary perspective, not all residues in a sequence are equally mutable, with some domains being highly conserved across multiple species; therefore, mutations in these highly conserved domains should be considered more divergent than those in non-conserved regions. Capitalizing on this idea, profile based methods create a substitution matrix specific for each position by integrating position specific information from a multiple sequence alignment of evolutionarily conserved proteins. This idea allows profile methods, including the hidden markov models, Pfam and HMMER, to be more sensitive than direct pairwise alignment<sup>27,28</sup>. Profile models have been used to identify distant homologs of proteins that lack primary amino acid alignment. Recently, groups have mined viral proteins and generated profiles for viral specific proteins and have applied them to identify novel viral sequences<sup>29,30</sup>.

### **Structural alignment algorithms**

Although BLASTn and BLASTx together are most commonly used for the identification of viral sequences, more sensitive methods exist that are not typically used for next generation sequencing applications because their computational intensity makes them largely prohibitive for this function. One such algorithm is Phyre2, which structurally threads amino acid sequences into known structures. In a few studies, Phyre2 has been used to identify structural proteins and polymerases that often have no detectable primary sequence alignment<sup>31-33</sup>.

### **Query Sequences**

As BLAST is the most commonly used method for viral sequence identification, we will limit our discussion of the queries and databases of aligners to BLAST. BLAST based alignment algorithms measure alignment quality using a bit score, a log transformed number that measures the number of similar residues between two sequences. A high bit score can result either from a short alignment of sequence similarity or a very long alignment with low sequence similarity. Thus, shorter reads must have a higher degree of similarity to reference sequences in order to achieve a statistically significant alignment. Given that the length of individual sequence reads of most platforms currently ranges between 50 – 400 nucleotides<sup>34</sup>, for a highly divergent virus, there will likely be many individual reads that cannot be aligned to reference sequences. This problem of short divergent reads, in some instances, can be obviated by assembling these reads into longer contiguous sequences (contigs), and then using those contigs as query sequences (Figure 1.2). In addition to increasing the sensitivity of detection of similarity to reference sequences, the assembly of contigs also enables reads derived from viral genes with no similarity to known viruses to be classified using genomic context; specifically a gene can be inferred as viral if it co-occurs on a contig that has a gene that aligns to a known viral gene. Novel viral genes have been identified this way for many viruses<sup>35-37</sup>. However, assembling contigs is not always possible, specifically with viruses that have lower coverage. Additionally, sequence reads can be misassembled into chimeric contigs, erroneously connecting a viral sequence to a non-viral sequence.



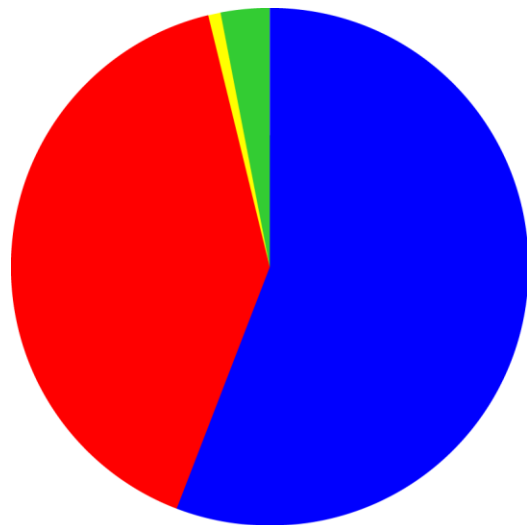
**Figure 1.2.** Assembly can identify more reads from novel viruses than direct alignment. An example virus, AVE000, from real data (PRJEB9503) shows that in this sample, there are more unalignable reads (black lines) than alignable reads (red lines) that map to AVE000. Upon assembly, all of these reads form a single contig that reveal 4 ORFs, two of which align to a known virus, while the other two are inferred as viral by genomic proximity. Aligned regions of AVE000 are represented by red dashed lines.

Viruses with segmented genomes, a common genomic organization characteristic of many families, provide particular challenges to virus discovery. For all segments from a divergent virus to be identified, each viral segment must contain an alignable gene to a known viral reference sequence. There are instances when a highly conserved gene, such as the RNA-dependent RNA polymerase, can be aligned to a reference virus, but viral proteins from other less well conserved genes on distinct viral genome segments cannot be aligned<sup>38,39</sup>. In such cases, only a portion of the novel virus will be identified. Thus, while the most conserved genes can flag the presence of a multi-segmented virus, not all of the viral segments can necessarily be identified through sequence analysis alone.

## Databases

A critical component to identifying viral sequences is a diverse, representative database of viral nucleotide and amino acid sequences. Although there has been a rapid expansion in the number of viral sequences in the Genbank non-redundant database, the sequences are largely biased towards mammalian, plant and bacterial viruses (Figure 1.3). Furthermore, the current limits of known viral diversity as they relate to

hosts and Baltimore classification also likely contribute to the distribution of viral dark matter. Although there are known viruses from every Baltimore classification that infect vertebrates, there are many host types that lack sequenced viruses of specific Baltimore classes (Figure 1.4). Increased metagenomic studies of non-vertebrates have the potential to address this deficiency<sup>40</sup>. One example of this und



- Animal or Plant Viruses (2854)
- Fungal or Protist Viruses (156)
- Bacterial Viruses (2060)
- Archaeal Viruses (39)

**Figure 1.3.** The distribution of viral genomes in RefSeq GenBank as defined by their host species.

	Group I - dsDNA	Group II - ssDNA	Group III - dsRNA	Group IV - ssRNA+	Group V - ssRNA-	Group VI - RNA Retrovirus	Group VII - DNA Retrovirus
Animal	Red	Red	Red	Red	Red	Red	Red
Plant	Red	Red	Red	Red	Red	Red	Red
Fungi	Red	Red	Red	Red	Red	Red	White
Protist	Red	Red	Red	Red	White	White	White
Bacteria	Red	Red	Red	Red	White	White	White
Archaea	Red	Red	White	White	White	White	White

No Viral Family Present
  Viral Family Present

**Figure 1.4.** A presence/absence plot of viral families that infect specific host types from the various Baltimore classification groups.

## **Methods to better identify viral sequences**

Studies of the bacterial and fungal microbiome have benefitted from the fact that all bacteria contain a 16S ribosomal sequence and all fungi contain an ITS sequence, which can be identified by sequencing of DNA. Viruses, however, contain both RNA and DNA genomes and do not have a single gene that is represented in all species. To reduce the amount of background non-viral sequences, many groups have created methods to better identify viral sequences from specific types of viruses. These solutions can be binned broadly into two categories: experimental methods designed to enrich viral sequences in a sequencing dataset and improved computational workflows designed to more sensitively detect viral sequences. The experimental methods address the issue of poor query sequences, while the improved computational workflows address the issue of alignment limitations. As illustrated below, these efforts have been successfully applied to reduce the amount of viral dark matter; however, in most cases, the methods rely on specific attributes of a specific subgroup of viruses and are not generally applicable to all viruses. Nonetheless, these types of approaches are critical to better define all components of the virome.

### **Experimental methods**

These methods use experimental wet lab techniques to specifically enrich viral nucleic acids in a sample so that a higher proportion of viral sequence reads are present in the sequencing dataset. Because a higher percentage of the reads will be from viruses, these viruses are selectively sequenced deeper, with more reads originating from viruses. As each virus will have more reads corresponding to it, assemblers can generate longer viral contigs.

### **Virus Culture**

Propagation of a virus in cell culture is the traditional gold standard to demonstrate a particular sequence is in fact viral in nature, even in the absence of discernable similarity to other known viruses. In terms of sequencing, viral propagation in culture increases the relative abundance of viral nucleic acid to host

nucleic acid, which ultimately can lead to improved assembly and longer contigs as alignment queries. In addition, one class of viruses for which culture is particularly useful is segmented viruses. As described previously, it can be difficult to identify all segments of a highly divergent virus by sequence analysis alone. Identifying viral segments using culture relies on the defined properties of segmented viruses, specifically that the genome of a segmented viruses is defined by the minimal number of segments necessary for viral propagation. Nucleic acids that can co-propagate with viruses but are unnecessary for viral transmission are usually defined as satellites rather than segments. Therefore, given a culture system, one could identify viral segments by performing limiting dilutions of a virus of interest and assess whether the putative segments co-propagate together. Additionally, molecular methods can be used to identify novel segments. Many segmented RNA viral taxa characteristically contain conserved 5' or 3' terminal sequences. These taxa include Bunyaviruses <sup>41</sup>, Emaraviruses <sup>42</sup>, Tenuiviruses <sup>43</sup>, Cystoviruses <sup>44</sup>, Rotaviruses <sup>45</sup>, Cileviruses <sup>46</sup>, and some Orthomyxoviruses <sup>47</sup>. Finding sequences that contain these conserved 5' or 3' motifs among multiple sequences provides strong evidence that these sequences are likely part of the same virus <sup>38,39</sup>.

### **Virus Like Particle (VLP) Purification**

The ability to pass through 0.2 um filters has classically been a defining feature of viruses. Filtering samples through 0.45 um or 0.2 um filters enriches for virions because intact cellular organisms cannot pass through the filter. Since these filtrates can still contain nucleic acid from lysed bacteria or host cells, samples are often treated with RNAses and DNAses to further enrich the samples for viral nucleic acids, which are typically protected from the nucleases within the viral capsids whereas host nucleic acids are not. To more completely remove this nucleic acid, centrifugation through CsCl or other gradients can be performed <sup>48,49</sup>. Because viral particles are encapsidated with protein, they are denser than “naked” nucleic acid and can be separated. However, there is evidence that gradient ultracentrifugation preferentially enriches specific taxa of viruses over others <sup>48</sup>.

There are two major groups of viruses that cannot be enriched using this method. Giant dsDNA viruses including Mimiviruses and specific large viruses like Bacillus G Virus are too large to pass through filters. Secondly, viruses that do not exhibit an extracellular stage are likely to be missed. Viral taxa in this group tend to infect lower eukaryotes and fungi and include *Chrysoviridae*, *Hypoviridae*, *Totiviridae*, *Narnaviridae* and *Endornaviridae*. These viruses are largely transmitted vertically or by cell-cell contact, thus obviating the need for an extracellular phase. Because these viruses largely reside in the cytoplasm of eukaryotes, the viruses will generally co-segregate physically with their hosts, and not pass through a 0.45 um filter. Additionally, viruses that only intermittently exhibit an extracellular phase, such as temperate phages, can often be missed by VLP preps.

### **Viral tagging**

Large dsDNA viruses often have long stretches of sequence containing numerous genes that do not align to any known viral genome. Because of their long length, it is often difficult to assemble a single genomic contig from a large dsDNA virus. This inability to generate a single contig results in multiple contigs assembled from the same virus, with many of these contigs lacking viral specific genes. Therefore, alignment cannot be reliably used to identify all viral derived contigs. Viral tagging is one approach that addresses this problem by capitalizing on the fact that some viruses are permeable to fluorescent dyes that bind DNA <sup>7</sup>. Host cells are grown in isotopically labeled nucleotides, making the host genome labeled with heavy nucleotides. Viruses from an environmental sample can be labeled using a fluorescent dye, incubated with their host, resulting in the fluorescent viral DNA in the host cell. Fluorescent cells are then sorted after which, the DNA is extracted. The intracellular DNA is then centrifuged in a CsCl gradient to separate the light and heavy isotopically labeled DNA. The light DNA is then sequenced. Viral tagging therefore not only enriches viral DNA enabling longer genomic contigs to be assembled, but it also allows for specific phages to be associated with hosts. Currently, viral tagging has been primarily applied to bacteria.



## **dsRNA enrichment**

All non-retroid RNA viruses use a double-stranded RNA (dsRNA) intermediate to replicate their genome. Long stretches of dsRNA are rarely made outside the context of viruses, so much so that mammalian and plant immune systems recognize it as a source of foreign nucleic acid <sup>50</sup>. Thus, physical enrichment of intracellular dsRNA reduces the complexity of the sample and increases the fraction of RNA virus sequences, which increases the likelihood of assembling longer contigs. Before the next generation sequencing era, intracellular dsRNA was enriched using nucleases to identify RNA viral segments from fungal and protozoal viruses <sup>51</sup>. Other methods have also been used to enrich dsRNA, including CF11 cellulose chromatography and dsRNA antibodies <sup>52,53</sup>. Enrichment of dsRNA is particularly useful in the context of plant and fungal viruses, as many of these host organisms do not have genome sequences associated with them, and therefore their host sequences cannot be efficiently subtracted out by alignment.

## **Computational methods**

The following methods address the second limitation in virus identification, the computational limits of sequence alignment. The common thread in these methods is that they identify specific qualities of viral sequences and use them to more specifically identify contigs as putative viruses. While none of these methods can always unequivocally identify viral sequences, they all generate a more compact list of contigs which can later be experimentally validated.

## **PFor**

Many organisms use RNAi as a method to restrict viral infection by generating small RNAs and loading them onto the RISC complex. Because small RNAs are often generated from foreign nucleic acids, they represent a useful enrichment source of viral and sub-viral nucleic acids <sup>54,55</sup>. These sequences can then be assembled into contigs which can be subsequently aligned to viral proteins. Furthermore, these sequences can additionally be analyzed beyond alignment to identify novel viroids. As viroids contain a circular

genome, computationally identifying sequence reads that originate from circular contigs can enrich the likelihood that these reads come from a viroid. This idea is the basis for PFor<sup>56</sup>. PFor identifies reads that are likely to be derived from a circular contig by recognizing that these reads must align to other reads at both the 5' and 3' ends. PFor removes all reads that do not fit this alignment criteria; if an individual read either does not align to any other read or only has reads that align to one terminus of its sequence, it is eliminated from the pool of reads. This process is repeated iteratively on the pool of reads until all the reads contain 5' and 3' alignments to other reads. At this point, the reads are then assembled into contigs. While these contigs cannot be definitively defined as novel viroids, they are likely enriched for viroid sequences, making them more attractive for classical experimentation. PFor and its updated version, PFor2 have identified both known and novel viroids<sup>57,58</sup>.

### **K-mer based classification**

It has been long recognized that genomes from different taxa vary in their dinucleotide composition<sup>59-63</sup>. This idea has been leveraged to develop classifiers that can classify dark matter based on the frequency of nucleotide oligomers, often referred to as k-mers<sup>64-68</sup>. Viral genomes are also known to have specific k-mer compositions, and these variations have previously been shown to correlate with virus host as well as Baltimore classification<sup>69,70</sup>. Studies have shown that altering the dinucleotide composition of a virus can inhibit viral replication, even when no amino acid changes are made<sup>71-78</sup>. Although a mechanistic understanding of the basis for k-mer biases in viruses is still largely unknown, the existence of specific viral k-mer compositions suggest that they could be exploited for taxonomic classification. Currently, there is only one published viral method, the Naïve Bayes Classifier (NBC), that incorporates viral k-mer sequences in its model, although it only includes DNA viral sequences<sup>79-81</sup>. NBC takes in an input sequence and calculates a vector containing k-mer frequencies. Using a pre-computed database of k-mer frequencies of genomes from sequenced organisms, it calculates the probability of getting the input k-mer vector from each genome, and identifies bins the sequence based on whichever genome yields the highest

probability. K-mer based approaches have also been used to classify viral structural proteins based on their amino acid composition<sup>82</sup>. We have developed a method, DiscoVIR, suitable for classification of both DNA and RNA virus k-mer frequencies using a support vector machine (unpublished).

## **VirSorter**

Taxonomic classification of DNA bacteriophages poses several challenges. One difficulty is that many bacteriophage genes share homology with host bacterial genes making it difficult to discern the true origin of a sequence that aligns to both reference bacteriophages and bacteria. Another challenge is that many bacteriophage defining genes, such as structural genes, share no primary sequence alignment to known phage genes in the database. VirSorter solves the lack of alignment of structural genes by constructing a specifically curated database of only bacteriophage defining protein sequences, most of which are structural genes such as “major capsid protein,” “portal,” “terminase large subunit,” “spike,” “tail,” “virion formation” or “coat”<sup>83</sup>. Additionally, VirSorter identifies additional bacteriophage defining proteins by alignment of the initial derived set to publically available viromes, and includes those virome derived sequences in their database. Using these expanded sequences for bacteriophage defining sequences, VirSorter defines amino acid profile HMMs and uses these profiles to search new protein sequences against these profiles. Finally, VirSorter can identify bacteriophage sequences completely independent of alignment, scoring sequences for having bacteriophage genomic signatures, such as an enrichment for short genes and uncharacterized genes, a depletion of non-phage genes or segments of DNA that do not change the coding strand. The output of VirSorter is a confidence score that identifies contigs likely to be phage derived. VirSorter has been applied to public sequencing databases and has been successful in classifying a large proportion of dark matter as phage derived<sup>84</sup>.

## **Conclusions and Future Directions**

The discovery of highly divergent viruses will greatly advance our understanding of biology in the context of immunity, molecular biology, ecology and human disease. Broadening viral diversity creates

the evolutionary and genomic context to study these viral systems to understand these concepts. Here, I show how discovering highly divergent viruses can be used to expand biological understanding by using microbial viruses, specifically, the RNA bacteriophages, as an example case. RNA bacteriophages were highly underrepresented among known sequenced bacteriophages. Previously, only 16 known bacteriophages with RNA genomes were known, all of which were derived from two families, the *Leviviridae* and *Cystoviridae*<sup>32</sup>. This underrepresentation is not an accurate reflection of their importance in biology or utility, as many fundamental concepts in molecular biology have been discovered using RNA bacteriophages<sup>85,86</sup>.

I address the underrepresentation of viral sequences in databases by identifying a specific underrepresented class of virus, bacteriophages with RNA genomes and systematically discovering highly divergent viruses in publically deposited sequencing data. This massive expansion of RNA bacteriophages created the context for us to ask whether there were any genes that could actively restrict RNA bacteriophages. Additionally, this expansion of RNA bacteriophages made us ask whether we could identify any novel families of RNA bacteriophages, unrelated to the known families. I then addressed the reliance on alignment based algorithms by developing a novel alignment-independent algorithm to identify viral sequences, DiscoVir. I applied DiscoVir to an authentic metagenome to aid in discovering the first segmented negative stranded RNA virus infecting a fungus.

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## 2. Hyperexpansion of RNA Bacteriophage Diversity

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## **Abstract**

Bacteriophage modulation of microbial populations impacts critical processes in ocean, soil, and animal ecosystems. However, the role of bacteriophages with RNA genomes (RNA bacteriophages) in these processes is poorly understood, in part because of the limited number of known RNA bacteriophage species. Here, we identify partial genome sequences of 122 RNA bacteriophage phylotypes that are highly divergent from each other and from previously described RNA bacteriophages. These novel RNA bacteriophage sequences were present in samples collected from a range of ecological niches worldwide, including invertebrates and extreme microbial sediment, demonstrating that they are more widely distributed than previously recognized. Genomic analyses of these novel bacteriophages yielded multiple novel genome organizations. Furthermore, one RNA bacteriophage was detected in the transcriptome of a pure culture of *Streptomyces avermitilis*, suggesting for the first time that the known tropism of RNA bacteriophages may include gram-positive bacteria. Finally, reverse transcription PCR (RT-PCR)-based screening for two specific RNA bacteriophages in stool samples from a longitudinal cohort of macaques suggested that they are generally acutely present rather than persistent.

## **Author Summary**

Bacteriophages (viruses that infect bacteria) can alter biological processes in numerous ecosystems. While there are numerous studies describing the role of bacteriophages with DNA genomes in these processes, the role of bacteriophages with RNA genomes (RNA

bacteriophages) is poorly understood. This gap in knowledge is in part because of the limited diversity of known RNA bacteriophages. Here, we begin to address the question by identifying 122 novel RNA bacteriophage partial genome sequences present in metagenomic datasets that are highly divergent from each other and previously described RNA bacteriophages.

Additionally, many of these sequences contained novel properties, including novel genes, segmentation, and host range, expanding the frontiers of RNA bacteriophage genomics, evolution, and tropism. These novel RNA bacteriophage sequences were globally distributed from numerous ecological niches, including animal-associated and environmental habitats. These findings will facilitate our understanding of the role of the RNA bacteriophage in microbial communities. Furthermore, there are likely many more unrecognized RNA bacteriophages that remain to be discovered.

## **Introduction**

Bacteria play key roles in metabolic and immunological processes; however, at this time many of the factors that define the composition of a given microbial population are still unknown<sup>1-4</sup>. Bacteriophages are abundant in many environments, and because they can lyse bacteria or transfer genes, bacteriophages likely play a role in shaping the specific composition of microbial populations. The currently recognized bacteriophages employ highly diverse lifestyles, especially in regards to host range specificity and potential to induce cell lysis, and therefore, bacteriophages from different taxa may uniquely impact the microbial composition of a given

niche<sup>5,6</sup>. One particularly understudied area of bacteriophage diversity is that of RNA bacteriophages. While many recent studies have aimed to characterize DNA bacteriophage communities in microbial populations, the RNA bacteriophage component of these communities is poorly defined<sup>7-10</sup>.

DNA bacteriophages are currently classified by the International Committee for the Taxonomy of Viruses (ICTV) into eight separate families with a total of 494 species, 55 single-stranded DNA (ssDNA), and 439 double-stranded DNA (dsDNA) bacteriophage species. These species derive from a diverse group of host bacteria; additionally, there are over 1,000 genomic sequences of DNA bacteriophage species in GenBank. By contrast, according to the latest (2014) report of the ICTV, only two official families of RNA bacteriophages are recognized: the single-stranded RNA (ssRNA) bacteriophage family *Leviviridae* that includes four recognized species (Enterobacteria phage Q $\beta$ , Enterobacteria phage F1, Enterobacteria phage MS2, and Enterobacteria phage GA) and the segmented, double-stranded RNA (dsRNA) family *Cystoviridae* that contains a single recognized species (Pseudomonas phage  $\phi$ 6)<sup>11,12</sup>. There are complete sequences of 11 ssRNA and five dsRNA bacteriophages in the GenBank “Genomes” database as of 20 October 2015, inclusive of the five ICTV-recognized RNA bacteriophage species. In contrast to the DNA bacteriophages, in which bacteriophages have been characterized from a variety of bacterial phyla, all 16 of these bacteriophages are thought to infect hosts within the phylum Proteobacteria, with 15 that infect hosts within the class  $\gamma$ -proteobacteria. In addition, three highly divergent, sewage-derived ssRNA bacteriophage genomes, with unknown host tropisms, were recently deposited in Genbank<sup>13</sup>. For the analyses in this paper, we will refer to these 14 ssRNA bacteriophage sequences and five dsRNA bacteriophages sequences as the “reference RNA bacteriophages.” For some of these RNA bacteriophages, there are additional

partial and/or full genomic sequences of closely related variants (share > 66% nucleotide identity to the reference sequences) also available in Genbank.

Bacteriophage identification has historically relied on culture-based methods<sup>14-18</sup>. Given that the majority of bacterial species cannot be cultured in the laboratory, alternative culture-independent methods are necessary to describe bacteriophage diversity<sup>19</sup>. In recent years, metagenomic sequencing has been applied to define bacteriophage populations in the human gut<sup>20-25</sup>, skin<sup>26</sup>, serum<sup>27</sup>, and in the environment<sup>7</sup>. Additionally, computational mining of metagenomic datasets has been valuable for identifying additional novel taxa of DNA bacteriophages<sup>28,29</sup>. However, the vast majority of these studies focused on sequencing and analysis of DNA only and therefore could not evaluate known or novel RNA bacteriophages that may be present. Of the studies that did examine RNA viruses in the environment, only one recent metagenomic study of sewage reported the presence of two novel RNA bacteriophages related to leviviruses<sup>13</sup>.

Here, by mining multiple metagenomic datasets that were generated such that RNA could be evaluated, we identify partial genomes of over 120 highly diverse RNA bacteriophage phylotypes that are highly divergent from each other and all of the known RNA bacteriophage genomes. This expansive diversity enabled us to identify new dimensions of RNA bacteriophage biology, including bacteriophages with novel genome organizations, numerous open reading frames (ORFs) that contain novel genes with no detectable homology to known bacteriophage genes, presence in novel ecological niches, and the first data in support of a RNA bacteriophage infection of a gram-positive bacterium. We additionally assess the prevalence of two novel RNA bacteriophages in a cohort of macaques, presenting the first description of the ecological dynamics of these novel RNA bacteriophages. Our results critically illuminate an unexamined

dimension of molecular and ecological bacteriophage diversity and fundamentally establish a necessary framework that enables a more accurate dissection of RNA bacteriophage modulation of microbial populations.

## **Results and Discussion**

### **Identification of RNA Bacteriophage Sequences in Local Metagenomic Datasets**

To detect RNA bacteriophages, we initially queried multiple metagenomic nucleotide sequence datasets with protein sequences from the known leviviruses and cystoviruses. We focused on datasets generated by our laboratory that contained cDNA sequences derived from RNA in the original material and that represented ecological niches known to support DNA bacteriophages, such as the vertebrate gastrointestinal tract and sewage. Cystovirus protein queries yielded no significant alignments (e-value  $< 10^{-4}$ ). In contrast, multiple nucleotide sequences in datasets from stool-associated and sewage specimens were identified that, following translation to amino acid sequences, aligned to leviviral proteins. The four studies of relevance, which were previously generated by our laboratory, included a study of raw sewage<sup>30</sup>, two distinct studies of simian immunodeficiency virus (SIV) infection in nonhuman primates<sup>31,32</sup>, and a study of astrovirus infection in mice. Any single dataset that had at least ten sequence reads that yielded significant alignments (e-value  $< 10^{-4}$ ) was selected for assembly. Using a National Center for Biotechnology Information (NCBI) conserved-domain search (e-value  $< 10^{-3}$ ) or Phyre2 (confidence  $> 90\%$ ), partial genomes of RNA bacteriophage phylotypes were defined as any assembled sequence greater than 750 nucleotides in length that contained a translated frame with a recognizable RNA bacteriophage-specific domain, such as a

bacteriophage-specific RNA-dependent RNA polymerase (RdRp), capsid, maturation protein, or packaging nucleoside triphosphatase (NTPase)<sup>33,34</sup>.

In order to focus our analyses on truly unique RNA bacteriophage phylotypes, any partial genomes that shared > 70% nucleotide identity in either the RdRp or the maturation gene were defined as belonging to a single phylotype. The longest partial genome for a given phylotype was selected as the representative sequence for that phylotype in all downstream analyses. By these criteria, partial genomes of 20 unique RNA bacteriophage phylotypes were identified in 17 distinct specimens. Five partial genomes were assembled from metagenomic data from sewage specimens, 14 were from rhesus macaque stool data, and one was from mouse stool data. Additional partial genomes that shared 85%–97% nucleotide identity to these 20 unique partial genomes were also identified in multiple other specimens in these studies, but they did not represent novel phylotypes by our criteria and therefore were not analyzed further. Based on the sequence diversity of each of these assembled partial genomes within a single phylotype, we believe it is unlikely that these RNA bacteriophages originate from laboratory contamination. The 20 unique bacteriophage phylotypes were sequentially named based on whether it was identified from an environmental or animal specimen, followed by a two-letter descriptor of the ecological niche.

### **Experimental Confirmation of Partial Genome Assembly and 3' Termini**

To confirm the partial genome assemblies, the eight longest partial genomes (range 3.5–5.0 kb) out of the 20 identified were experimentally validated by generating multiple overlapping reverse transcription PCR (RT-PCR) amplicons followed by Sanger sequencing. The average



length of the amplicons was ~1.8 kb. In addition, the 3' ends of AVE000, AVE001, and AVE003 were extended using rapid amplification of cDNA ends (RACE).

**Table 2.1:** List of novel ssRNA phage artial genomes

Phage	Partial Genome Length	Phage Source	Geographic Location	Nucleotide Database	Accession Number	Sequence confirmed by PCR	Amino Acid Identity to Closest Levivirus	Closest Known Leviviral Member	ssRNA Phage Maturation Domain (mat)	ssRNA Phage Coat Domain (Levi_Coat)	MS2 Lysin Domain (Lys)	ssRNA Phage Replicase Domain (rep)
AIN000	3675	Insect Pool	Hubei, China	SRA	SRR1745803	No	No	Enterobacteria C-1	X	X		X
AIN001	3635	Insect Pool	Hubei, China	SRA	SRR1745803	No	No	Enterobacteria QB	X			X
AIN002	3846	Insect Pool	Hubei, China	SRA	SRR1745803	No	No	Enterobacteria C-1	X	X		X
AIN003	3929	Insect Pool	Hubei, China	SRA	SRR1745803	No	No	Enterobacteria Hga1	X	X		X
AIN004	1209	Crab and Barnacle Pools	Zhejiang, China	SRA	SRR1745809	No	No	Enterobacteria F1				X
AIN005	924	Millipedes	Hubei, China	SRA	SRR1745810	No	No	Caulobacter phiCb5				X
AIN006	1032	Stylissa carteri sponge	Thuwal, Saudi Arabia	SRA	SRR1038495	No	No	Enterobacteria BZ13	X			
AIN007	1684	Stylissa carteri sponge	Thuwal, Saudi Arabia	SRA	SRR1038495	No	No	Enterobacteria Hga1				X
AIN008	1054	Insect Pool	Hubei, China	SRA	SRR1745803	No	No	Caulobacter phiCb5				X
AIN009	832	Crab and Barnacle Pools	Zhejiang, China	SRA	SRR1745809	No	No	Enterobacteria M11				X
AIN010	1647	Insect Pool	Hubei, China	SRA	SRR1745803	No	No	Enterobacteria C-1				X
AVE000	4977	Primate Stool	Boston, USA	ENA	PRJEB9503	Yes	Yes	Caulobacter phiCb5	X			X
AVE001	5022	Primate Stool	Boston, USA	ENA	PRJEB9503	Yes	Yes	Pseudomonas PP7	X			X
AVE002	4220	Primate Stool	Boston, USA	ENA	PRJEB9503	Yes	Yes	Enterobacteria F1	X			X
AVE003	3957	Murine Stool	Saint Louis, USA	SRA	PRJNA291303	Yes	Yes	Enterobacteria C-1	X			X
AVE004	3776	Primate Stool	New Orleans, USA	ENA	PRJEB9503	Yes	Yes	Pseudomonas PRR1	X			X
AVE005	3709	Primate Stool	Boston, USA	ENA	PRJEB9503	Yes	Yes	Enterobacteria SP	X			X
AVE006	3609	Primate Stool	New Orleans, USA	ENA	PRJEB9503	Yes	Yes	Enterobacteria M11	X			X
AVE007	3580	Primate Stool	Boston, USA	ENA	PRJEB9503	Yes	Yes	Pseudomonas PRR1	X			X
AVE008	2565	Primate Stool	Boston, USA	ENA	PRJEB9503	No	No	Enterobacteria QB				X
AVE009	2094	Primate Stool	Boston, USA	ENA	PRJEB9503	No	No	Enterobacteria M	X			
AVE010	1753	Primate Stool	Boston, USA	ENA	PRJEB9503	No	No	Enterobacteria F1	X			
AVE011	1422	Primate Stool	Boston, USA	ENA	PRJEB9503	No	No	Enterobacteria M	X			
AVE012	1053	Primate Stool	Boston, USA	ENA	PRJEB9503	No	No	Enterobacteria F1	X			
AVE013	946	Primate Stool	Boston, USA	ENA	PRJEB9503	No	No	Enterobacteria QB				X
AVE014	798	Primate Stool	Boston, USA	ENA	PRJEB9503	No	No	Enterobacteria fr				X
AVE015	4385	Grass Carp Intestine	Unknown	SRA	DRR013899	No	No	Enterobacteria BZ13	X			X
AVE016	4198	ETEC Associated Feces	Unknown	SRA	SRR901903	No	No	Enterobacteria M	X			X
AVE017	3483	Grass Carp Intestine	Unknown	SRA	DRR013891	No	No	Enterobacteria BZ13	X	X	X	X
AVE018	3746	Cow Rumen	Beijing, China	SRA	SRR1604866	No	No	Enterobacteria F1				X
AVE019	3737	Cow Rumen	Beijing, China	SRA	SRR594642	No	No	Enterobacteria QB	X			X
AVE020	4729	Cow Rumen	Beijing, China	SRA	SRR594654	No	No	Enterobacteria F1	X			X
AVE021	3362	Cow Rumen	Beijing, China	SRA	SRR1604865	No	No	Enterobacteria QB	X			X
AVE022	3124	Cow Rumen	Beijing, China	SRA	SRR1604865	No	No	Pseudomonas PRR1	X			X
AVE023	3023	Cow Rumen	Beijing, China	SRA	SRR1604865	No	No	Enterobacteria M11				X

AVE024	2663	Cow Rumen	Beijing, China	SRA	SRR1604865	No	No	Enterobacteria QB					X
AVE025	1925	Cow Rumen	Beijing, China	SRA	SRR594642	No	No	Pseudomonas PRR1					X
AVE026	1727	Cow Rumen	Beijing, China	SRA	SRR1604866	No	No	Enterobacteria F1	X				
AVE027	1132	Grass Carp Intestine	Unknown	SRA	DRR013891	No	No	Pseudomonas PRR1					X
AVE028	798	Cow Rumen	Beijing, China	SRA	SRR594670	No	No	Enterobacteria M					X
AVE029	1591	Wild Shrew Feces	Mpungu, Zambia	SRA	DRR023333	No	No	Enterobacteria BZ13					X
AVE030	987	Cow Rumen	Beijing, China	SRA	SRR1604865	No	No	Enterobacteria F1	X				
AVE031	965	Cow Rumen	Beijing, China	SRA	SRR1604865	No	No	Enterobacteria F1	X				
AVE032	965	Cow Rumen	Beijing, China	SRA	SRR1604865	No	No	Enterobacteria QB					X
AVE033	1818	Cow Rumen	Beijing, China	SRA	SRR1604866	No	No	Caulobacter phiCb5					X
AVE034	866	Cow Rumen	Beijing, China	SRA	SRR1604866	No	No	Enterobacteria SP					X
AVE035	811	Cow Rumen	Beijing, China	SRA	SRR1604866	No	No	Enterobacteria M					X
AVE036	769	Cow Rumen	Beijing, China	SRA	SRR1604866	No	No	Enterobacteria F1					X
AVE037	1163	Nasopharyngeal Viromes	Unknown	SRA	SRR466446	No	No	Enterobacteria C-1	X				
AVE038	1350	Nasopharyngeal Viromes	Unknown	SRA	SRR466446	No	No	Enterobacteria C-1					X
AVE039	2469	Cow Rumen	Beijing, China	SRA	SRR594642	No	No	Enterobacteria QB	X				
EMM000	2478	Microbial Mat	Rennes, France	SRA	ERR435911	No	No	Pseudomonas PRR1					X
EMM001	1193	Microbial Mat	Rennes, France	SRA	ERR435911	No	No	Enterobacteria SP	X				
EMM002	1062	Microbial Mat	Rennes, France	SRA	ERR435911	No	No	Enterobacteria M11					X
EMM003	976	Microbial Mat	USA	SRA	SRR1283110	No	No	Enterobacteria QB					X
EMS000	2751	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Enterobacteria SP					X
EMS001	3229	Sulfur Spring Sediment	Mountain View, USA	SRA	SRR064197	No	No	Enterobacteria M11					X
EMS002	2572	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Enterobacteria Hgal1	X				X
EMS003	2391	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Enterobacteria QB					X
EMS004	1980	Sediment	Wadden Sea	SRA	SRR2012732	No	No	Enterobacteria QB					X
EMS005	1750	Sediment	Wadden Sea	SRA	SRR2012732	No	No	Enterobacteria M	X				
EMS006	1679	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Enterobacteria F1					X
EMS007	1535	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Caulobacter phiCb5	X				
EMS008	1313	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Pseudomonas PP7					X
EMS009	1221	Sulfur Spring Sediment	Mountain View, USA	SRA	SRR064284	No	No	Caulobacter phiCb5					X
EMS010	1218	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Pseudomonas PRR1	X				
EMS011	1161	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Enterobacteria M11	X				
EMS012	1109	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Pseudomonas PRR1					X
EMS014	3843	Sulfur Spring Sediment	Mountain View, USA	SRA	SRR064197	No	No	Enterobacteria Hgal1	X		X		X
EMS016	912	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Caulobacter phiCb5					X
EMS017	880	Benthic Cold Seep Sediment	Barbados	SRA	SRR1822316	No	No	Enterobacteria SP	X				
EOC000	3303	Cyanobacterial Mat	Champs-sur-Marne, France	SRA	SRR1283306	No	No	Enterobacteria QB	X				X
EOC001	1670	Marine Environment	Baltic Sea	SRA	SRR072888	No	No	Pseudomonas PRR1					X
EOC002	1285	Plume	Amazon River	SRA	SRR1199286	No	No	Enterobacteria M					X
EOC004	1344	Ocean	West Mediterranean Sea	SRA	ERR550396	No	No	Enterobacteria M	X				
EOC005	1435	Watershed	British Columbia, Canada	SRA	SRR2089023	No	No	Enterobacteria BZ13	X				
EOC006	1037	Watershed	British Columbia, Canada	SRA	SRR2089023	No	No	Enterobacteria MS2	X				

E0C007	976	Watershed	British Columbia, Canada	SRA	SRR2089023	No	No	Enterobacteria MS2					X
ESE000	3426	Sewage	Pittsburgh, USA	SRA	SRR315458	No	No	Enterobacteria Hga1	X				X
ESE001	1862	Sewage	Pittsburgh, USA	SRA	SRR315458	No	No	Enterobacteria F1	X				
ESE002	1451	Sewage	Pittsburgh, USA	SRA	SRR315458	No	No	Acinetobacter Phage AP205	X				
ESE003	1366	Sewage	Barcelona, Spain	SRA	SRR315457	No	No	Enterobacteria MS2					X
ESE004	1290	Sewage	Pittsburgh, USA	SRA	SRR315458	No	No	Enterobacteria C-1	X				
ESE005	4407	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1611147	No	No	Pseudomonas PRR1	X				X
ESE006	3469	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1611147	No	No	Pseudomonas PRR1	X				X
ESE007	3294	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1427729	No	No	Pseudomonas PRR1	X	X			X
ESE008	4187	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1611150	No	No	Caulobacter phiCb5	X				X
ESE009	1917	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1046681	No	No	Enterobacteria SP					X
ESE010	1852	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1611150	No	No	Enterobacteria M	X				X
ESE011	1598	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1611150	No	No	Enterobacteria F1					X
ESE012	1550	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1611147	No	No	Enterobacteria MS2					X
ESE013	950	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1046681	No	No	Enterobacteria C-1					X
ESE014	896	Luxemburg Sewage	Schifflange, Luxemburg	SRA	SRR1046681	No	No	Caulobacter phiCb5					X
ESE015	3805	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Caulobacter phiCb5	X				X
ESE016	3692	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Caulobacter phiCb5					X
ESE017	3604	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria MS2	X				X
ESE018	3502	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria fr	X				X
ESE019	3608	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB	X				X
ESE020	3727	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria F1	X				X
ESE021	3547	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB	X				X
ESE022	2915	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Caulobacter phiCb5					X
ESE023	3666	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB	X				X
ESE024	2671	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB	X				X
ESE025	2383	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria F1					X
ESE026	2128	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Caulobacter phiCb5	X				
ESE027	1851	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria M11					X
ESE028	1635	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Caulobacter phiCb5					X
ESE029	3655	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria C-1	X				X
ESE030	1789	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria M	X				
ESE031	914	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB					X
ESE032	903	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Pseudomonas PP7					X
ESE033	951	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria fr					X
ESE034	1433	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB					X
ESE035	755	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB					X
ESE036	1464	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria MS2					X
ESE037	1224	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria Hga1	X				
ESE038	1000	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB					X
ESE039	796	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria MS2	X				
ESE040	1012	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB					X

ESE041	1877	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria QB	X				
ESE042	1431	Ulpandan Sewage	Singapore	SRA	SRR1027978	No	No	Enterobacteria BZ13	X				
ESE043	1272	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1427729	No	No	Enterobacteria fr	X				
ESE044	1135	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1427729	No	No	Enterobacteria BZ13					X
ESE045	1731	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1427729	No	No	Enterobacteria M11					X
ESE046	1703	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1427729	No	No	Enterobacteria M12	X	X			
ESE048	1677	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1544599	No	No	Enterobacteria F1					X
ESE049	1067	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1544599	No	No	Enterobacteria C-1	X				
ESE050	752	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1544599	No	No	Acinetobacter AP205					X
ESE051	1147	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1611147	No	No	Enterobacteria F1	X				
ESE052	915	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1611147	No	No	Enterobacteria QB					X
ESE053	1192	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1611147	No	No	Caulobacter phiCb5					X
ESE054	818	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1611147	No	No	Enterobacteria BZ13	X				
ESE055	764	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1611150	No	No	Caulobacter phiCb5					X
ESE056	1301	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1611150	No	No	Enterobacteria MS2	X				
ESE057	984	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1611150	No	No	Enterobacteria Hgall					X
ESE058	3620	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1611150	No	No	Enterobacteria Hgall	X				X
ESE047	971	Luxemburg Sewage	Schliffange, Luxemburg	SRA	SRR1611150	No	No	Enterobacteria F1	X				
ES0000	4110	Arctic Peat Soil	Svalbard	SRA	SRR1509497	No	No	Caulobacter phiCb5	X				X
ES0001	3968	Arctic Peat Soil	Svalbard	SRA	SRR1509497	No	No	Caulobacter phiCb5	X				X
ES0002	3819	Arctic Peat Soil	Svalbard	SRA	SRR1509497	No	No	Caulobacter phiCb5	X				X
ES0003	3679	Anoxic Bulk Soil of Rice Paddy	Vercelli, Italy	SRA	SRR1013758	No	No	Enterobacteria M11	X				X
ES0004	1662	Arctic Peat Soil	Svalbard	SRA	SRR1509498	No	No	Pseudomonas PRR1					X
ES0005	874	Anoxic Bulk Soil of Rice Paddy	Vercelli, Italy	SRA	SRR1013758	No	No	Enterobacteria fr					X
ES0006	831	Anoxic Bulk Soil of Rice Paddy	Vercelli, Italy	SRA	SRR1013758	No	No	Pseudomonas PRR1	X				
ES0007	1301	Anoxic Bulk Soil of Rice Paddy	Vercelli, Italy	SRA	SRR1013758	No	No	Enterobacteria QB	X				
ES0008	1760	Arctic Peat Soil	Svalbard	SRA	SRR1509497	No	No	Caulobacter phiCb5					X
ES0009	1514	Arctic Peat Soil	Svalbard	SRA	SRR1509497	No	No	Caulobacter phiCb5					X
ES0010	3612	Arctic Peat Soil	Svalbard	SRA	SRR1509497	No	No	Enterobacteria SP	X				X
ES0011	1284	Arctic Peat Soil	Svalbard	SRA	SRR1509497	No	No	Enterobacteria SP					X
ES0012	1198	Arctic Peat Soil	Svalbard	SRA	SRR1509498	No	No	Enterobacteria F1	X				
ES0013	988	Arctic Peat Soil	Svalbard	SRA	SRR1509498	No	No	Enterobacteria MS2					X
ES0014	1484	Arctic Peat Soil	Svalbard	SRA	SRR1509498	No	No	Enterobacteria MS2					X
ES0015	1176	Arctic Peat Soil	Svalbard	SRA	SRR1509518	No	No	Enterobacteria M11					X
ES0016	904	Arctic Peat Soil	Svalbard	SRA	SRR1509518	No	No	Enterobacteria QB					X
ES0017	948	Arctic Peat Soil	Svalbard	SRA	SRR1509518	No	No	Enterobacteria MS2					X
ES0018	1240	Arctic Peat Soil	Svalbard	SRA	SRR1509518	No	No	Caulobacter phiCb5					X
ES0019	1521	Rhizosphere	Norfolk, United Kingdom	SRA	ERR566379	No	No	Caulobacter phiCb5					X
ES0020	1292	Rhizosphere	Norfolk, United Kingdom	SRA	ERR566379	No	No	Caulobacter phiCb5	X				

## RNA Bacteriophages Are Prevalent in Publicly Available Metagenomic Datasets

To expand our search space, we analyzed publicly deposited sequencing datasets—generated by other laboratories—that sequenced RNA (>10,000 Sequence Read Archive [SRA] datasets associated with >2,000 publications). These included transcriptomic and RNA-inclusive metagenomic studies. The metagenomic data analyzed were derived from environmental sources, such as oceans, sewage, and soil, and animal-associated sources, including stool. We aligned amino acid sequences from the 20 novel and 19 reference RNA bacteriophages against sequences in these datasets, following six-frame translation, using tBLASTn. Out of 2,765 RNA-inclusive metagenomes and 7,309 transcriptomic datasets examined, 115 contained at least ten sequences with significant alignments (e-value <  $10^{-4}$ ). The complete sequencing data from each of these 115 datasets were assembled, and RNA bacteriophage partial genomes were defined as above (length > 750 nt, <70% identity to any other partial or complete genome). We identified 138 unique partial genomes that contained ssRNA bacteriophage domains and five unique partial genomes that contained characteristic dsRNA bacteriophage motifs (Table 2.1; Table 2.2). Thus, including the initial identification of the 20 novel ssRNA bacteriophages, we identified a total of 158 unique ssRNA bacteriophage motif-containing partial genomes. For the partial genomes that contained ssRNA bacteriophage-associated domains, 119 contained RdRp domains, and 81 contained maturation domains (42 contained both maturation and RdRp domains). Three partial genomes contained dsRNA bacteriophage RdRp domains. As RNA viruses are not known to encode multiple RdRp genes, we conservatively estimated the number of novel RNA bacteriophage phylotypes based on the number of partial genomes that contain unique RdRp domains. Based on this criterion, we have identified at least 122 novel RNA bacteriophage phylotypes, greatly increasing the known RNA bacteriophage diversity. Furthermore, it is

possible that some of the partial genomes that contained only maturation domains may derive from additional novel RNA bacteriophages, so this is likely an underestimation.

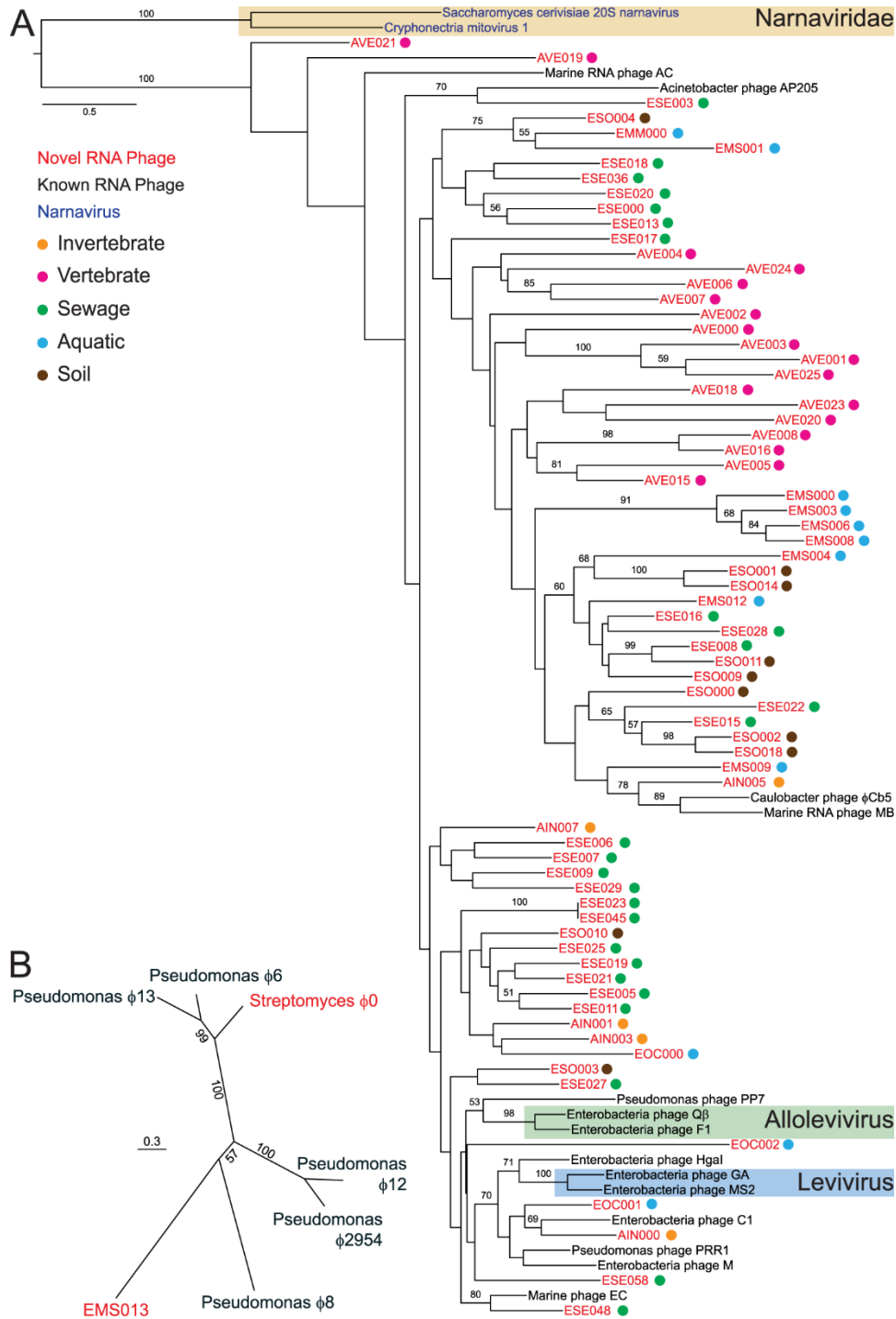
**Table 2.2:** List of novel dsRNA bacteriophage partial genomes

Phage	Segment	Contig Size	Phage Source	Geographic Location	Nucleotide Database	Accession Number	Closest Known Cystovirus	dsRNA Motifs
EMS013	L	11089	Sulfur Spring Sediment	Mountain View, USA	SRA	SRR064283	$\phi 8$	RdRp, NTPase, Muramoyl-Dipeptide Carboxypeptidase
EOC003	L	950	Oxygen Minimum Zone	Iquique, Chile	SRA	SRR1617598	$\phi 6/\phi 13$	RdRp
Streptomyces phage $\phi 0$	L	6775	Soil	Canada	SRA	SRX1090146	$\phi 6$	P7 Assembly, P2 RdRp, P4 Packaging NTPase, P1 Procapsid Shell
Streptomyces phage $\phi 0$	M	3397	Soil	Canada	SRA	SRX1090146	$\phi 6$	P3 Host Attachment Protein, P6 Membrane Fusion Protein
Streptomyces phage $\phi 0$	S	3211	Soil	Canada	SRA	SRX1090146	$\phi 13$	P8, Lysozyme Related Gene

### Novel RNA Bacteriophage Genomes Are Highly Divergent from Known Genomes

To elucidate the evolutionary relationships between the novel and known RNA bacteriophages, we next performed phylogenetic analysis. Of the 119 novel ssRNA RdRp-domain-containing partial genomes, we limited the analysis to the 71 partial genomes that encompassed all five conserved motifs of the RdRp palm domain<sup>35</sup>. In addition, we included the 14 “reference ssRNA bacteriophages.” We included an outgroup containing the RdRp palm domains of the two type species of *Narnaviridae*, as their polymerases are most closely related to those of leviviruses<sup>36</sup>. While bootstrap support for some portions of the tree is limited, it nonetheless demonstrated that the partial genomes were highly divergent from each other and from the known RNA bacteriophages (Figure 2.1A). For the dsRNA bacteriophage-domain-

containing partial genomes, two unique partial genomes contained the entire RdRp gene, and both were clearly distinct (Figure 2.1B).



**Figure 2.1.** Phylogenetic analyses of novel RNA bacteriophages discovered in metagenomic sequencing datasets. (A) ssRNA RdRp domain-based tree. Colored dots represent the ecological niche from which each partial genome was identified. Bootstrap

values under 50 are not displayed. The current ICTV taxonomic classification for RNA bacteriophages and eukaryotic viruses is shaded. (B) Phylogenetic analysis based on RdRp of EMS013 and Streptomyces bacteriophage  $\phi$ 0 with known cystoviruses.

There are currently no official ICTV criteria for defining species among RNA bacteriophages. For many other viral taxa, strictly molecular criteria are used<sup>37,38</sup>. For example, marine picornaviruses have previously been identified by sequence alignment and classified based on phylogenetic distance<sup>38</sup>. Taxonomy of DNA bacteriophages has traditionally relied on bacteriophage morphology but now is largely determined using sequence-based criteria, in that phages that share a certain percentage of genes are considered the same species<sup>39,40</sup>. One possible classification strategy for RNA bacteriophage would be to infer sequence-based criteria based on the current ICTV-recognized species. Distinct ssRNA bacteriophage species within ICTV-recognized genera (levivirus and allolevivirus) share <60% amino acid identity (51% and 55% amino acid identity in the RdRp, respectively). By extension, if membership in a species is defined as sharing  $\geq 60\%$  amino acid identity in the RdRp, the 158 ssRNA RNA bacteriophage phylotypes would represent 111 novel RNA bacteriophage species. Even using a 50% amino acid identity threshold (which would collapse currently recognized distinct species into one species) would still result in 53 novel ssRNA bacteriophage species (Table 2.3). Regardless of the final criteria used for classification by the ICTV, the RNA bacteriophage phylotypes identified in this study dramatically expand the known sequence diversity of RNA bacteriophages.

**Table 2.3.** Number of ssRNA bacteriophage species based on varying amino acid identity cut-offs.

Amino acid identity	Number of Species
70	117
60	111



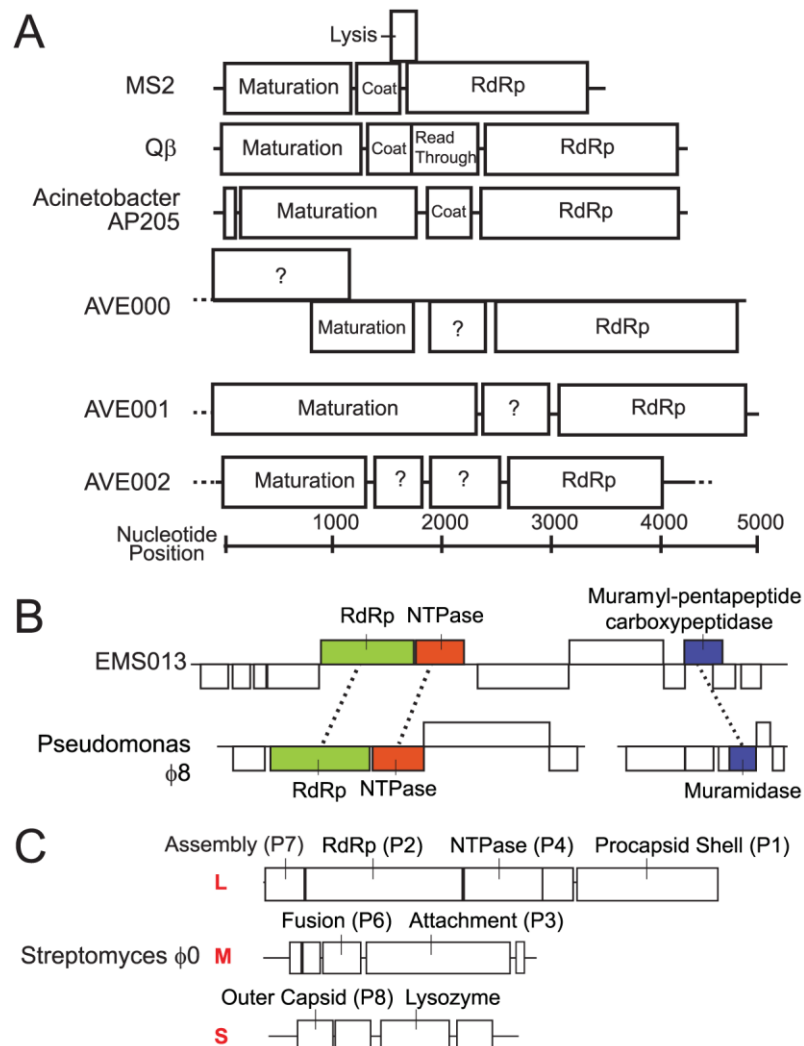
50	53
40	9

The family *Cystoviridae* has a single genus, the only ICTV-recognized species of which is *Pseudomonas* phage  $\phi 6$ <sup>12</sup>. The four additional fully sequenced dsRNA bacteriophage species in Genbank, which are not officially classified in the genus *Cystovirus*, encode polymerase proteins that share 20%–51% amino acid identity to that of *Pseudomonas* phage  $\phi 6$ . A species defining criterion of 50% amino acid identity would classify the three novel dsRNA bacteriophage phylotypes as three species. A threshold of 40% amino acid identity, which would collapse four distinctly recognized species into two, would result in two novel dsRNA species.

### **Multiple Novel Genome Organizations for RNA Bacteriophages Identified**

Following gene prediction and annotation of all the novel RNA bacteriophages, multiple novel genome organizations were identified. Two of the novel RNA bacteriophage partial genomes, both of which were confirmed by RT-PCR and Sanger sequencing, were much longer than all sequenced leviviruses, which range from 3.73–4.27 kb in length<sup>41</sup>. The genome of AVE000 had at least a 4.95 kb genome; this longer genome can be attributed to the presence of a novel >1.20 kb ORF of unknown function that is 5' to and partially overlaps the maturation protein by 259 nucleotides (Figure 2.2A). AVE001 also has an expanded genome of at least 5.02 kb, due to the presence of a strikingly large 2.39 kb ORF containing the maturation domain, which is larger than all of the reference ssRNA bacteriophages maturation genes, which on average are 1.27 kb and range from 1.17–1.60 kb. In addition, AVE002 is the first RNA bacteriophage described to contain two nonoverlapping ORFs between the RdRp and maturation

genes; neither of the two ORFs has discernable similarity to known proteins. While one of these ORFs likely represents the coat protein, the other ORF might represent a novel lysin or have homologous function to the Q $\beta$  read-through protein. From the 119 ssRNA partial genomes, there were 100 ORFs predicted exclusive of the RdRp and maturation genes. Aside from eight ORFs that had predicted leviviral coat domains and one that had a MS2 lysin domain, none of the other 91 ORFs had primary sequence alignment to any known bacteriophage coat or lysin protein. These ORFs may encode proteins that are coat or lysin orthologs that are unrecognizable because of the greater evolutionary divergence of those genes as compared to the RdRp or maturation protein, or they could have completely novel functionalities. Even in the former case, the extreme evolutionary divergence may result in novel host tropisms or novel mechanisms of bacterial lysis. Further elaboration of these bacteriophage genomes will likely identify additional novel genome organizations and additional novel ORFs of unknown function.



**Figure 2.2.** Unique characteristics of novel RNA bacteriophage. (A) Genome organizations of three novel RNA bacteriophage partial genomes compared to prototypical RNA bacteriophage. (B) EMS013 and (C) Streptomyces bacteriophage  $\phi 0$  genome organizations. ORFs were annotated using protein alignment, conserved domain searching, and structural alignment.

The cystovirus protein sequence queries of public sequencing datasets identified partial genomes that provided evidence of an RNA bacteriophage with a novel genomic organization. All five reference cystoviruses are trisegmented, with a ~6.4 kb L segment encoding both the RdRp and packaging NTPase and a ~2.9 kb S segment separately encoding a peptidoglycan degradation enzyme. We identified EMS013, a single 11.2 kb assembled sequence from a metatranscriptomic sample, originally isolated from the Zodletone sulfur spring, containing three individual ORFs that were annotated with these three functions (Figure 2.2B). Two additional

samples from this sulfur spring in the same study also contained sequences that aligned to this partial genome. An assembled sequence that contains both a cystoviral L and S genes is notable as there is ongoing debate as to the evolutionary origin of cystoviruses<sup>42</sup>. One model suggests that cystoviruses share a common eukaryote-infecting ancestor with segmented eukaryotic RNA viruses. The competing model suggests that cystoviruses originate from an unsegmented bacteria-infecting dsRNA bacteriophage. While this partial genome is based solely on in silico assembly, a provocative hypothesis is that this bacteriophage could represent evidence of an unsegmented cystovirus ancestor.

### **Identification of a RNA Bacteriophage in a Gram-Positive Bacteria Transcriptome Study**

As the majority of the novel RNA bacteriophage partial genomes were detected in metagenomic datasets derived from complex microbial communities, the host bacterium of each bacteriophage could not be explicitly determined by our analyses in most cases. One notable exception was the detection of three dsRNA motif-containing assembled sequences in a publically available bacterial transcriptomic study derived from pure culture of *Streptomyces avermitilis*<sup>43</sup>. This bacteriophage had the traditional genome organization of cystoviruses, although many ORFs could not be definitively annotated by either sequence or structural alignment (Figure 2.2C). This was named *Streptomyces* bacteriophage  $\phi 0$ , keeping with nomenclature conventions of other cystoviruses. The study was composed of two conditions with three replicates each, and five out of six samples contained sequences from the RNA bacteriophage. The presence of sequences in each of the specimens in this experiment, combined with the annotation of the study as being derived from bacterial monoculture, strongly suggests that *S. avermitilis* represents the true host for this bacteriophage. As the known RNA

bacteriophages are only believed to infect proteobacteria, Streptomyces bacteriophage  $\phi 0$ , if experimentally confirmed to infect *S. avermitilis*, would represent the first RNA bacteriophage known to infect bacteria in a phylum other than the proteobacteria. Moreover, it would be the first RNA bacteriophage known to infect a gram-positive bacteria, thereby dramatically broadening the known bacterial host range of RNA bacteriophages.

### **RNA Bacteriophages Inhabit Multiple Novel Biogeographies**

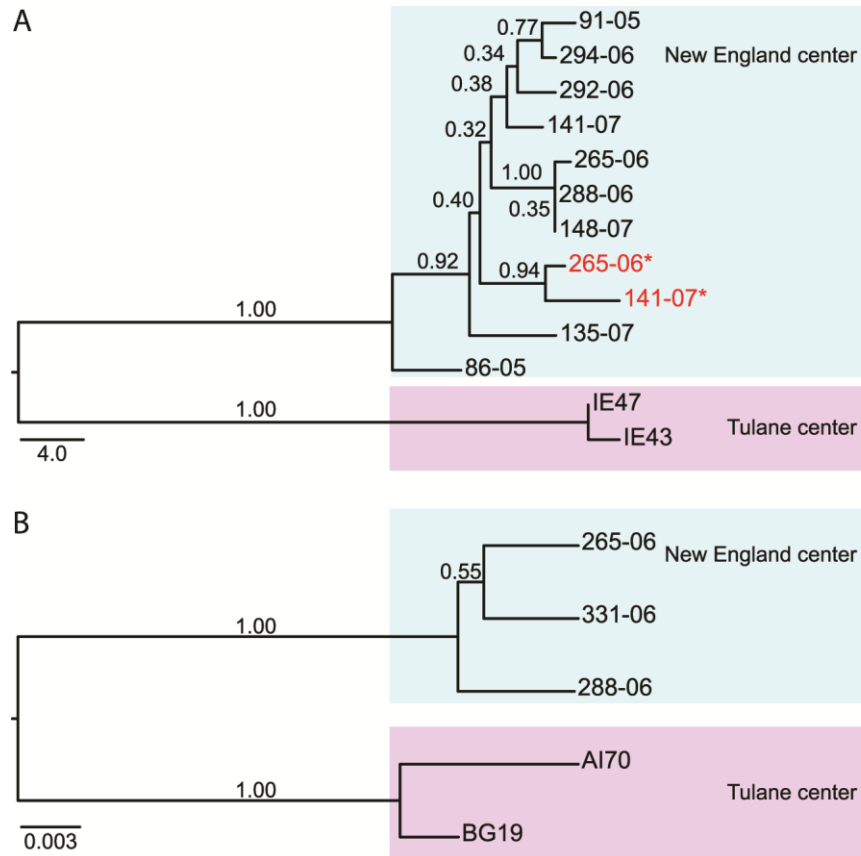
While many bacteriophages were found from ecologies known to harbor RNA bacteriophages, namely mammalian stool and sewage, we identified numerous bacteriophages from novel ecological niches (Table 2.1). Interestingly, we identified numerous bacteriophages that originated from microbial communities of invertebrate hosts, including pools of insects and aquatic invertebrates such as crabs, sponges, and barnacles. Additionally, bacteriophages were identified from microbial sediments associated with extreme aquatic environments, such as sulfur springs and benthic cold seeps.

### **RNA Bacteriophages Are Acutely Present in the Microbiome**

In order to evaluate spatial and temporal trends associated with novel RNA bacteriophages, we defined the prevalence of RNA bacteriophages in stool from previously described cohorts<sup>32</sup> of rhesus macaques collected at the Tulane National Primate Research Center (TNPRC) and the New England Primate Research Center (NEPRC) using both metagenomic and RT-PCR-based approaches. Specimens from NEPRC were available at two separate time points, 24 and 64 wk post SIV infection. Based on metagenomic sequencing data, 34 out of 120 specimens had at least one sequence from one novel RNA bacteriophage, with ten

specimens containing at least one sequence from two or more novel RNA bacteriophages (Figure 2.3). To independently assess the prevalence of a subset of these RNA bacteriophages, we screened this cohort using two sets of PCR primers: one set for AVE000 and another for AVE001. We detected AVE000 in five out of 120 rhesus macaques and detected AVE001 in 13 specimens. The AVE000-positive amplicon sequences shared 95%–99% nucleotide identity with each other, while AVE001-positive amplicons shared 84%–100% nucleotide identity with each other. Phylogenetic analysis demonstrated that there was apparent geographic segregation of both AVE000 and AVE001, as sequences from each primate research center formed distinct clusters (Figure 2.4, Table 2.4, Table 2.5). All specimens positive by metagenomic sequencing for AVE000 or AVE001 were confirmed to be RT-PCR positive. In addition, four specimens that were negative by metagenomic sequencing were RT-PCR positive, most likely because of the increased sensitivity of the RT-PCR assay compared to metagenomic sequencing. The geographic clustering of the amplicon sequences combined with their observed diversity strongly argues against the possibility of laboratory contamination, as all of these specimens were prepared using the same protocol and reagents. From the RT-PCR analysis, we found only two macaques were positive for the same RNA bacteriophage at two separate time points, suggesting that AVE000 and AVE001 generally do not persist (Figure 2.4). Similarly, from the metagenomic analysis, the vast majority of the RNA bacteriophages were only present at a single time point. This acute presence of these RNA bacteriophages is in stark contrast to the persistent nature in the primate gut of lytic DNA bacteriophages, specifically the *Microviridae* bacteriophages<sup>23</sup>.





**Figure 2.4.** Maximum-likelihood phylogenetic analysis of (A) AVE001- and (B) AVE000-positive amplicons. Red text and asterisks indicate samples from the second time point.

**Table 2.4.** Nucleotide alignment identities of AVE001 amplicons from the screening of Rhesus Macaque Study 1. Top half: pairwise nucleotide identity. Bottom half: number of mismatched nucleotides.

Location	Time Point	Specimen	265-06	141-07	135-07	141-07	147-07	265-06	91-05	86-05	294-06	288-06	148-07	IE43	IE47
NEPRC	64	265-06		0.99	0.97	0.98	0.98	0.98	0.97	0.97	0.98	0.98	0.98	0.84	0.84
NEPRC	64	141-07	6		0.97	0.97	0.97	0.97	0.97	0.96	0.97	0.97	0.97	0.84	0.84
NEPRC	24	135-07	12	16		0.98	0.98	0.97	0.98	0.97	0.98	0.97	0.97	0.84	0.85
NEPRC	24	141-07	10	14	11		0.99	0.98	0.99	0.97	0.99	0.99	0.99	0.85	0.85
NEPRC	24	147-07	10	14	11	6		0.98	0.99	0.97	0.99	0.99	0.99	0.84	0.85
NEPRC	24	265-06	10	14	13	8	8		0.97	0.96	0.98	1	1	0.84	0.84
NEPRC	24	91-05	12	14	11	6	6	12		0.96	0.99	0.98	0.98	0.84	0.85
NEPRC	24	86-05	15	17	14	15	15	17	17		0.97	0.97	0.97	0.86	0.86
NEPRC	24	294-06	11	15	8	5	5	11	3	14		0.98	0.98	0.84	0.85
NEPRC	24	288-06	9	13	12	7	7	1	11	16	10		1	0.84	0.85
NEPRC	24	148-07	9	13	12	7	7	1	11	16	10	0		0.84	0.85
TNPRC	NA	IE43	77	78	76	72	76	77	75	67	75	76	76		1
TNPRC	NA	IE47	75	76	74	70	74	75	73	65	73	74	74	2	



**Table 2.5.** Nucleotide alignment identities of AVE000 amplicons from the screening of Rhesus Macaque Study 1. Top half: pairwise nucleotide identity. Bottom half: number of mismatched nucleotides.

<b>Location</b>	<b>Specimen</b>	<b>265-06</b>	<b>288-06</b>	<b>313-08</b>	<b>AI70</b>	<b>BG19</b>
<b>NEPRC</b>	<b>265-06</b>		0.99	0.99	0.95	0.95
<b>NEPRC</b>	<b>288-06</b>	5		0.99	0.95	0.95
<b>NEPRC</b>	<b>313-08</b>	4	5		0.95	0.95
<b>TNPRC</b>	<b>AI70</b>	23	22	23		0.99
<b>TNPRC</b>	<b>BG19</b>	20	21	20	5	

In this study, we have vastly increased the number of known RNA bacteriophage phylotypes and demonstrated their presence in a wide range of habitats worldwide. However, this is clearly an underestimate of the total number of RNA bacteriophage species, as there are undoubtedly many more novel RNA bacteriophages that remain undiscovered. While our work has clearly identified a much greater diversity of RNA bacteriophages, there are still obvious taxonomic groups that are missing. For example, RNA bacteriophages that contain negative-sense genomes or helical capsids have still not been identified, both of which underscore some of the many remaining gaps left in our understanding of RNA bacteriophage diversity. Some of these novel RNA bacteriophages may be present in existing metagenomic datasets that simply cannot be currently recognized because of a lack of primary sequence alignment. Furthermore, the vast majority of metagenomic studies are still heavily DNA-centric. With the increased recognition of the importance of RNA bacteriophages and RNA eukaryotic viruses, the number of RNA-inclusive metagenomic datasets will surely grow, leading to additional discoveries of novel RNA bacteriophages. Critically, the multitude of RNA bacteriophages already identified in this study provide a unique opportunity to define their natural contributions to ecology, explore novel aspects of their life cycle, and potentially exploit them as novel tools for bacteriophage therapy.

## Methods

### Ethics Statement

Mouse experiments yielding metagenomic data were performed with the approval of the Washington University IACUC, under protocol #20140244.

### Metagenomic Studies Mined for RNA Bacteriophages

**Rhesus Macaque Study 1.** We analyzed 120 stool specimens that had been previously sequenced using 454 FLX Titanium technology from a previously published study (MG-RAST Project 1449, 1451, 1452)<sup>32</sup>. Briefly, rhesus macaques were either pathogenically infected with SIV or served as controls. They were housed at NEPRC or TNPRC. Macaques at NEPRC were sampled at two time points, 24 and 64 wk post SIV infection, whereas macaques at TNPRC were sampled once.

**Rhesus Macaque Study 2.** From 36 primates that were a subset of a previously published SIV vaccination cohort, 79 stools were collected<sup>31</sup>. Stools were processed as previously described<sup>32</sup>. Stools were diluted 1:6 in PBS, filtered through 0.45 µm filter, and extracted on a COBAS Ampliprep Instrument (Roche). Nucleic acids were subjected to random cDNA synthesis and then amplification TruSeq library (Illumina). Libraries were sequenced on an Illumina MiSeq Platform<sup>44</sup>. All sequences were uploaded to the European Nucleotide Archive under the project PRJEB9503.

**Murine study.** Stool pellets combined from two mouse cages infected with murine astrovirus were metagenomically analyzed as previously described<sup>45,46</sup>. Briefly, stool was diluted in 1:6 in PBS and filtered through a 0.45 µm membrane to minimize recovery of intact

bacteria. Total nucleic acid was extracted from the filtrate, subjected to random-priming cDNA synthesis and amplification, and sequenced by 454 FLX Titanium pyrosequencing. The sequences from this specimen are deposited in NCBI SRA under PRJNA291303.

**Sewage study.** The sewage sequencing reads have been previously described and are deposited in NCBI SRA (Accession SRA040148)<sup>30</sup>. Briefly, untreated wastewater was obtained from Pittsburgh, Pennsylvania, United States; Barcelona, Spain; and Addis Ababa, Ethiopia, and then virions were concentrated using organic flocculation. Both RNA and DNA were isolated and subsequently sequenced using the 454 FLX Titanium pyrosequencing.

**tBLASTn query of previously sequenced databases.** Nucleotide databases were constructed using either 454 FLX Titanium or Illumina MiSeq sequencing reads from specimens from the above studies. We constructed nucleotide databases from 454 sequencing-based reads that did not align to any known protein within the Genbank non-redundant (nr) database, as determined by VirusHunter<sup>47</sup>. Illumina MiSeq-based nucleotide databases were constructed from sequencing reads that did not align to any known human or eukaryotic viral protein in the non-redundant database, at an e-value of  $10^{-3}$ . We downloaded complete reference genomes of all 11 *Leviviridae* and five *Cystoviridae* species, as defined by NCBI Taxonomy, and isolated amino acid sequences of all annotated ORFs. These amino acid sequences were then queried against the described databases using tBLASTn (non-default parameters: -evalue 1e-4 – num\_descriptions 100000 –num\_alignments 100000 –outfmt 7).

**tBLASTn query of SRA deposited databases.** Using the command line NCBI SRA tBLASTn, amino acid sequences were queried against deposited nucleotide databases that were annotated as having sequenced RNA. SRA was searched for datasets using the key terms “stool,” “feces,” “sewage,” “wastewater,” “metatranscriptome,” “ocean,” “viromes,” or “freshwater;” the

resulting datasets were further filtered to select those that were annotated to sequence RNA. Similarly, all SRA datasets from individual bacteria were identified by querying the NCBI Taxonomy database with the bacteria taxonomic identification number (taxid2) and then filtering for sequencing of RNA. As these latter studies often contained many specimens, we randomly selected, using a random number generator, a single specimen from each study for analysis; if a specimen had reads that aligned to RNA bacteriophage, every specimen from that study was subsequently analyzed for RNA bacteriophage reads. These datasets were queried using amino acid sequences derived from the 19 reference RNA bacteriophage and 20 novel RNA bacteriophage we identified from initial analysis of our own metagenomic datasets using tBLASTn with the same parameters as above.

**Partial genome assembly.** For every specimen that had more than ten reads that aligned with an e-value  $< 10^{-4}$ , all deposited reads from the specimen were then assembled with IDBA using default parameters<sup>48</sup>. Specimen datasets larger than 8 GB were split into files smaller than 8 GB for assembly, with each smaller file individually assembled. The contiguous sequences (contigs) resulting from these individually assembled files were then combined into one file and batch assembled together using IDBA. Only contigs longer than 750 nucleotides were selected for further analysis. Because there are no official guidelines from the ICTV for defining a species for RNA bacteriophages, we selected 70% nucleotide identity in the RdRp or maturation gene as a cutoff for defining unique phylotypes in this study, as this cutoff represented the trend from known leviviral species, in which strains can vary as low as 72% nucleotide identity across the RdRp and maturation genes. Therefore, we defined contigs that BLASTn determined to share greater than 70% nucleotide identity across the RdRp or maturation genes as the same phylotype.

The longest contig that contained RNA bacteriophage domains from these total assemblies were used as the partial genome.

**Novel RNA bacteriophage nomenclature.** Novel RNA bacteriophages were named based on the ecology from which they were identified. The first letter designates whether the bacteriophage was identified from an animal (A) or an environmental (E) specimen. The second two letters designate a more specific ecological designation, where IN = invertebrate, VE = vertebrate, SE = sewage, SO = soil, MS = microbial sediment, MM = microbial mat, and OC = ocean. The three letters were followed by a three-digit number.

**Experimental confirmation of contig assembly and 3' termini sequencing.** Multiple PCR primers were designed to confirm eight (AVE000, AVE001, AVE002, AVE003, AVE004, AVE005, AVE006, and AVE007) of the assembled partial genomes (Table 2.6). RT-PCR was performed using the Qiagen OneStep RT-PCR kit. Gaps between contigs from the same specimen were closed by designing PCR primers from the existing contigs. Using 3' RACE as previously described, 3' termini were confirmed<sup>47</sup>. Briefly, total nucleic acid was polyadenylated (Ambion), column purified (Qiagen RNEasy), and then used as a template in OneStep RT-PCR (Qiagen), using an Oligo-d(T) primer and the primers specified (Table 2.6). All amplicons were cloned into pCR4-TOPO and Sanger sequenced. Each partial genome was sequenced to >2x coverage by Sanger sequencing. Discrepancies between next-generation sequencing partial genomes and Sanger sequencing reads were resolved with additional Sanger sequencing.

**Table 2.6:** List of primers used to confirm partial genomes by Sanger sequence

PhageSpecies	PrimerName	Sequence
AVE000	SK_MiSeq70_Levivirus_1	TTGCAACGGAAAAAGCCGAG

AVE000	SK_MiSeq70_Levivirus_2	CCTGGTTAACACCAGACCCC
AVE000	SK_MiSeq70_Levivirus_3	GAATCAACCCATTCTGTGCGG
AVE000	SK_MiSeq70_Levivirus_4	AAGTTGCTGGCCTATCGCTT
AVE000	SK_MiSeq70_Levivirus_5	CCCCTCTACTACAATGAAAGGAGTG
AVE000	SK_MiSeq70_Levivirus_6	CATCCGGACTTCGGTCTCAG
AVE000	SK_MiSeq70_Levivirus_7	CTTCGCAGGCCAGCAAAAAT
AVE000	SK_MiSeq70_Levivirus_8	CCTTTTCGACCATGGGGTCA
AVE000	SK_MiSeq70_Levivirus_9	AGTCAACGGATCGTGGAGTC
AVE000	SK_MiSeq70_Levivirus_10	GACCTGAAGCGTGTAGGTGA
AVE000	SK-MiSeq70Broad1	GTGTWCAAARACACACC
AVE000	SK-MiSeq70Broad2	TGWYTCMACWGGGAAAC
AVE000	SK_MiSeq70_3RACE	TCGCAAAGCGATATACAGCGG
AVE000	SK_MiSeq70_3RACE2	TCGAACCGATTCAACGCTCA
AVE000	SK_MiSeq70_3RACE3	CGCAAAGCGATATACAGCGG
AVE001	SK_MiSeq66.5_Levi_1	TGCAATGCGGATAGCGTTTG
AVE001	SK_MiSeq66.5_Levi_2	GACTTTGAGTCCCCTCCCG
AVE001	SK_MiSeq66.5_Levi_3	GTGTGGGTAAGGTGACCTCG
AVE001	SK_MiSeq66.5_Levi_4	TTTTGTAGCTCTGAGGCGCA
AVE001	SK_MiSeq66.5_Levi_5	CTGGGATGAGAGCCTTGGTG
AVE001	SK_MiSeq66.5_Levi_6	ATGCCTTCAGTGTAGCTCCG
AVE001	SK-MiSeq66.5Yokoyama1	AAGGATCGACTMATWACWGTSGAGCCG
AVE001	SK-MiSeq66.5Yokoyama2	AGAACGACTTRGCCSKGTTKACGCGGAAG
AVE001	SK_MiSeq66.5_3RACE	GTCTGTACACTTCTGGAACAG
AVE001	SK_MiSeq66.5_3RACE2	CTGGCCCTTCTTAGTAGAGGG
AVE001	SK_MiSeq66.5_3RACE3	ACGCTCTTTGGTCATCGGTT
AVE001	SK_MiSeq66.5_3RACE4	CTGCGAAGGGGAGAGCATTCA
AVE002	SK_MiSeq69_0_Levi_1	ACCCAGGACACCCTAATCCA
AVE002	SK_MiSeq69_0_Levi_2	GGATCAGCGACCAATGACGA
AVE002	SK_MiSeq69_0_Levi_3	GTACGCAAAGACGAACAGCG
AVE002	SK_MiSeq69_0_Levi_4	ATCTGGTCACGGACTCTCCA
AVE002	SK_MiSeq69_0_Levi_5	GCAGGCCTGATGGGTAAAGT
AVE002	SK_MiSeq69_0_Levi_6	GAACCGTCGGATGCGTAGAT
AVE003	Yokoyama_Levi_1	GCCGAAGACGAAGGTACACA
AVE003	Yokoyama_Levi_2	CCGGCAGCGTTTTAGATTCTG
AVE003	Yokoyama_Levi_3	ACATCAACTCCGGCGCTAAA
AVE003	Yokoyama_Levi_4	GCTAATAGCTCCTCAGGGCG
AVE003	Yokoyama_Levi_5	GCCCTTCGTGACTGATGGAA
AVE003	Yokoyama_Levi_3RACE1	CAACCGGGCTAAGTCGTTT
AVE003	Yokoyama_Levi_3RACE2	CGTATCGCACGGTTTTTCGAC
AVE004	SK_Tulane_IP45_1	GTAATCGCAATCCAAGGAAGGG
AVE004	SK_Tulane_IP45_2	TGCAAGGATTTTCTTACTGTGT
AVE004	SK_Tulane_IP45_3	TTGCAGACCCTTGTGCGTA

AVE004	SK_Tulane_IP45_4	CCACTGGCATAACATCCACCA
AVE004	SK_Tulane_IP45_1_New	GTAATCGCAATCCAAGGAAAGG
AVE005	SK_Contig4_Fwd	GGCATATACCGGAAGCCACA
AVE005	SK_Contig1_Rev	CCACATGGTCGTAACAGGCT
AVE005	SK_Contig2_Fwd	AATGGCTGGACATGGCTCAA
AVE005	SK_Contig3_Rev	GAGCCAGTCTCGATCATCCG
AVE006	SK_IP94_Levivirus_1	TTCCCATTATCGCCAGAGGC
AVE006	SK_IP94_Levivirus_2	GCGAAATGACTGCGTAGCTG
AVE006	SK_IP94_Levivirus_3	GGGCACTCGGCTCTCTATTC
AVE006	SK_IP94_Levivirus_4	GGGTTTCCCACACAGGACAT
AVE006	SK_IP94_Levivirus_5	GCACGATTATTAAGGAGGTGC
AVE006	SK_IP94_Levivirus_6	GGCCAACAGTTACAGGGTCA
AVE006	SK_IP94_Levivirus_7	AGACTATACGCCATGCGAGC
AVE006	SK_IP94_Levivirus_8	AGAGGACTGAAACGCTTCGG
AVE007	SK_MiSeq64_0_Levi_1	AGGAGACAGATATGACTAATC
AVE007	SK_MiSeq64_0_Levi_2	CCTCCACGAAAACATTAGGGT
AVE007	SK_MiSeq64_0_Levi_3	GCCCGTTCAGGACTAAGTGA
AVE007	SK_MiSeq64_0_Levi_4	CCTTCTGTGCGGATGATCC

**Genomic analysis.** ORFs were predicted using ORF Finder from NCBI and subsequently analyzed for conserved domains using the NCBI Conserved-Domain Search. Domain annotation was defined using NCBI conserved domains that had e-values  $< 10^{-3}$  or structural alignments with greater than 90% accuracy using Phyre2. Global alignment of RNA bacteriophage proteins was performed with the MUSCLE algorithm using MEGA6, and pairwise percent identity was calculated based on the p-distance based on the alignment matrix.

**Phylogenetic analysis.** ssRNA bacteriophage phylogeny was determined by acquiring RdRp protein sequences from NCBI GenBank for all reference levivirus genomes (Enterobacteria bacteriophage FI: NC\_004301.1, Acinetobacter bacteriophage AP205: NC\_002700.2, Enterobacteria bacteriophage Q $\beta$ : NC\_001890.1, Caulobacter bacteriophage  $\phi$ Cb5: NC\_019453.1, Pseudomonas bacteriophage PP7: NC\_001628.1, Pseudomonas

bacteriophage PRR1: NC\_008294.1, Enterobacteria bacteriophage MS2: NC\_001417.2, Enterobacteria bacteriophage Hgal1: NC\_019922.1, Enterobacteria bacteriophage C-1 INW-2012: NC\_019920.1, Enterobacteria bacteriophage GA: NC\_001426.1, and Enterobacteria bacteriophage M: NC\_019707.1) as well as three additional known ssRNA bacteriophages: Marine bacteriophage MB: KF510034.2, Marine bacteriophage EC: KF616862.2, and Marine bacteriophage AC: KF616864. Additionally, the two type species of the family *Narnaviridae* (Cryphonectria parasitica mitovirus: NC\_004046.1, and Saccharomyces cerevisiae narnavirus 20S: NC\_004051.1) were included as out-groups. Novel ssRNA bacteriophage that contained all five motifs of the RdRp palm domain as determined by multiple sequence alignment to the known ssRNA bacteriophage were selected for phylogenetic analysis. Amino acid sequences were aligned using 13 iterations of MUSCLE in MEGA6. The palm domain alignment was isolated, and noninformative sequences were trimmed using GBlocks (minimum number of sequences for a conserved position = 20, minimum number of sequences for a flank position = 73, maximum number of contiguous nonconserved positions = 20, minimum length of a block = 4, and allowed gap positions = all) <sup>49</sup>. The final trimmed alignment was manually edited to preserve known conserved RdRp motifs and then used to construct maximum likelihood phylogenetic trees using Blosum62 + F + G + I with 100 bootstrap replicates in PhyML. dsRNA bacteriophage phylogeny was determined by acquiring RdRp protein sequences from NCBI GenBank for all reference cystovirus genomes (Pseudomonas bacteriophage  $\phi$ 6: NC\_003715.1, Pseudomonas bacteriophage  $\phi$ 8: NC\_003299.1, Pseudomonas bacteriophage  $\phi$ 12: NC\_004173.1, Pseudomonas bacteriophage  $\phi$ 13: NC\_004172.1 and Pseudomonas bacteriophage  $\phi$ 2954: NC\_012091.2). Novel dsRNA bacteriophages that contained the full RdRp ORF were also selected for phylogenetic analysis. Amino acid sequences were aligned using six iterations of



MUSCLE and maximum likelihood phylogenetic trees using LG + F + G + I with 100 bootstrap replicates in MEGA6. Phylogenetic trees that examine single phylotype diversity based on RT-PCR screening were constructed using nucleotide sequence alignments using MUSCLE with six iterations in MEGA6. Maximum likelihood trees were constructed using the Kimura 2-parameter model with 100 bootstraps.

**RT-PCR screening of samples in Rhesus Macaque Study 1.** PCR primers designed to detect AVE000 and AVE001 (Table 2.6) were designed. PCR cycling conditions were 50 °C for 45 min, 95 °C for 15 min, and 40 cycles of 95 °C for 30 s, 50 °C for 30 s, and 72 °C for 1 min, followed by 72 °C for 10 min using OneStep RT-PCR (Qiagen).

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### 3. Identification of a novel bunya-like virus using DiscoVir, an alignment independent k-mer algorithm for viral sequence classification

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## Abstract

Alignment of deep sequencing reads to known reference genomes enables metagenomic studies of microbial populations. While this is an effective method of classification for some sequences, many sequences have no significant alignment to any sequenced organism. Here we describe DiscoVir, a support vector machine (SVM) model that relies on nucleotide k-mer frequencies to discriminate sequences of novel, highly disparate eukaryotic viruses from prokaryotic and fungal sequences. We validated *in silico* that the model can identify viruses from novel viral taxa using a leave two taxa out approach. Furthermore, DiscoVir outperforms BLASTx for almost all viral families. When we applied DiscoVir to a metagenomic dataset from which we only could identify one segment of a tripartite bunyavirus by conventional alignment, DiscoVir identified two additional contigs that corresponded to the two undetected segments of the virus. By selectively culturing fungi from this serum sample, we identified an isolate of *Penicillium atramentosum* that contained all three viral RNA segments. Sequencing of these segments demonstrated that the terminal nucleotide sequences were conserved between the three segments, and these sequences were consistent with the termini of viruses in the genera *Phlebovirus* and *Tenuivirus*. We determined that this virus can be vertically transmitted through fungal spores and that every spore isolated contained this virus. Thus, application of DiscoVir played a critical role in the identification of the first segmented negative stranded RNA virus of a fungus. DiscoVir is the first algorithm to identify novel viral sequences without requiring alignment.

## Introduction

The discovery of novel eukaryotic viruses has enhanced our understanding of human disease<sup>1,2</sup>. Next generation metagenomic sequencing has rapidly accelerated the rate of viral discovery. However, despite this rapid progress, highly divergent eukaryotic viruses are still difficult to identify due to the absence of a universally conserved gene among all viruses analogous to the 16S rRNA gene in bacteria<sup>3</sup>. Current metagenomic analysis of viruses is dependent on primary sequence alignment to known reference genome or protein databases in order to assign metagenomic sequences to novel viruses<sup>4</sup>. Highly divergent viruses are particularly challenging because viruses mutate faster than any cellular organism, and thus their genes are less likely to align to known viruses<sup>3</sup>. Therefore, there is a critical need to develop tools that are able to discover highly divergent viruses without requiring sequence alignment. The ability to identify highly divergent viral sequences will increase our understanding of metagenomic communities and help identify novel, potentially disease-causing viruses.

K-mers are contiguous sequences of k elements, most often amino acids or nucleotides in biology. Many alignment-independent methods use k-mer frequencies to compositionally transform a sequence into a vector in which each element represents a specific k-mer frequency. Various vector operations, such as the inner product or Euclidean distance, can then be calculated to measure sequence relatedness. Using this approach, alignment-independent methods such as Phylopythia and RaiPhy can classify bacterial sequences using machine learning models, including support vector machines, developed from compositionally transformed genome fragments from bacteria<sup>5,6</sup>. Furthermore, applications have used k-mers to differentiate noise from true biological signal from metagenomic data<sup>7-9</sup>. Complex site metagenomes such as stool, sewage and oceans are largely dominated by bacterial sequences;

therefore, to better identify viral reads, alignment-independent methods that can specifically separate viral reads from reads originating from other highly diverse organisms, such as bacterial and fungi, are necessary. While many alignment-independent methods can classify bacterial sequences<sup>3,5,6,10-14</sup> and one can classify DNA eukaryotic viral sequences<sup>15</sup>, no algorithm has been described that is broadly applicable for classification of all types of eukaryotic viral sequences (DNA viruses, RNA viruses and retroviruses).

The *Bunyaviridae* viral family contains tri-segmented negative-sense RNA viruses that infect humans, plants and arthropods. Some members of this family, such as Rift Valley fever and Crimean Congo hemorrhagic fever, cause acute febrile illness that can progress to fatal hemorrhagic fever or encephalitis<sup>16</sup>. Their genomes encode a RNA dependent RNA Polymerase (RdRp) on the L segment, envelope glycoproteins genes on the M segment, and a nucleocapsid gene on the S segment, with specific genera of bunyaviruses encoding additional non-structural genes. Multipartite viruses pose a particular difficult challenge for sequence-based identification unlike the situation with monopartite viruses, where a single highly conserved region (e.g. RdRp) may suffice to identify the entire viral genome.

Here, we present DiscoVir, a k-mer based method for discriminating viral sequences from bacterial and fungal sequences. DiscoVir represents sequences as k-mer vectors and uses support vector machines to generate a model that classifies unknown sequences as viral or non-viral. Our *in silico* results demonstrate that DiscoVir is capable of identifying more highly divergent viral sequences than the traditional alignment based BLASTx. Finally, we demonstrate the utility of DiscoVir in real metagenomic data; use of DiscoVir played a critical role in the identification of a novel multi-segmented virus distantly related to known bunyaviruses present in the serum of a patient with unknown febrile illness. Surprisingly, follow up studies



demonstrated that the virus infects a *Penicillium atramentosum* strain present in the patient serum sample. This virus represents the first known segmented negative-sense RNA virus to infect a fungus.

**Results:**

**Parameterization and in silico evaluation of DiscoVir**

The DiscoVir classifier analyzes k-mer transformed sequences using a SVM that discriminates bacterial and viral sequences and a SVM that discriminates fungal and viral sequences. The outputs of these two SVMs are then integrated using a logistic regression, resulting in a log-odds value that evaluate whether a sequence is viral. This log-odds value can then be converted into a probability that a given sequence is viral. To optimize the classification accuracy of both initial SVMs, we evaluated multiple models with varying k-mer and sequence lengths using 5-fold cross validation. We tested a range of values of k ( $2 \leq k \leq 8$ ) and sequence lengths (50, 100, 200 and 400 nucleotides) to identify the optimal parameterization space to enable viral sequence separation. We determined that there were two maxima for viral sequence discrimination from bacteria at  $k = 4$  at a sequence length of 400 nt and  $k = 6$  at a sequence length of 200 nt with area under the curves (AUCs) of receiver operating characteristic (ROC) of 0.81 and 0.83, respectively (Table 3.1). Similar maxima existed for viral sequence discrimination from fungi. Therefore, we established two models of DiscoVir, one using 400 nucleotide length sequences on sequencing data that has sequences 400 base pairs or longer and one utilizing 200 nucleotide length sequences on sequencing data that range between 200-400 nucleotides.

**Table 3.1.** Optimization of DiscoVir parameters. Virus-bacteria and Virus-Fungi SVM models were optimized for k-mer length and sequence length.

	K-mer Length
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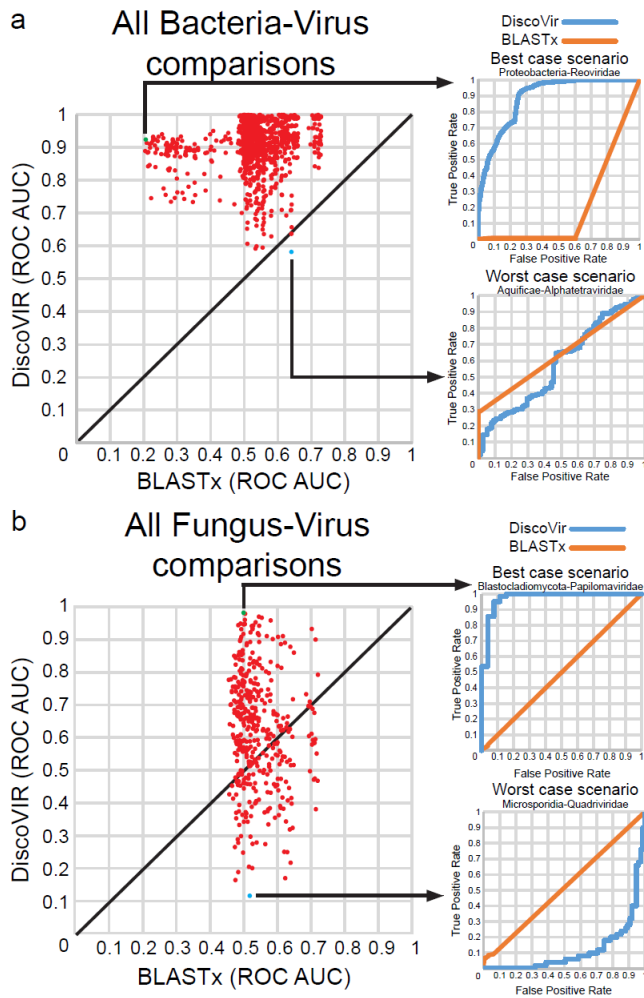
		2	3	4	5	6	7	8	
Sequence Length	Bacteria	50	0.56	0.59	0.61	0.62	0.62	0.62	0.63
		100	0.62	0.65	0.66	0.67	0.68	0.69	0.70
		200	0.75	0.79	0.80	0.82	0.83	0.83	0.83
		400	0.75	0.79	0.81	0.81	0.80	0.79	0.77
	Fungi	50	0.58	0.61	0.64	0.65	0.63	0.66	0.67
		100	0.64	0.69	0.67	0.69	0.70	0.72	0.72
		200	0.74	0.75	0.76	0.79	0.82	0.81	0.81
		400	0.76	0.82	0.84	0.84	0.83	0.82	0.80

### **DiscoVir outperforms BLASTx in identifying sequences from highly divergent viral families**

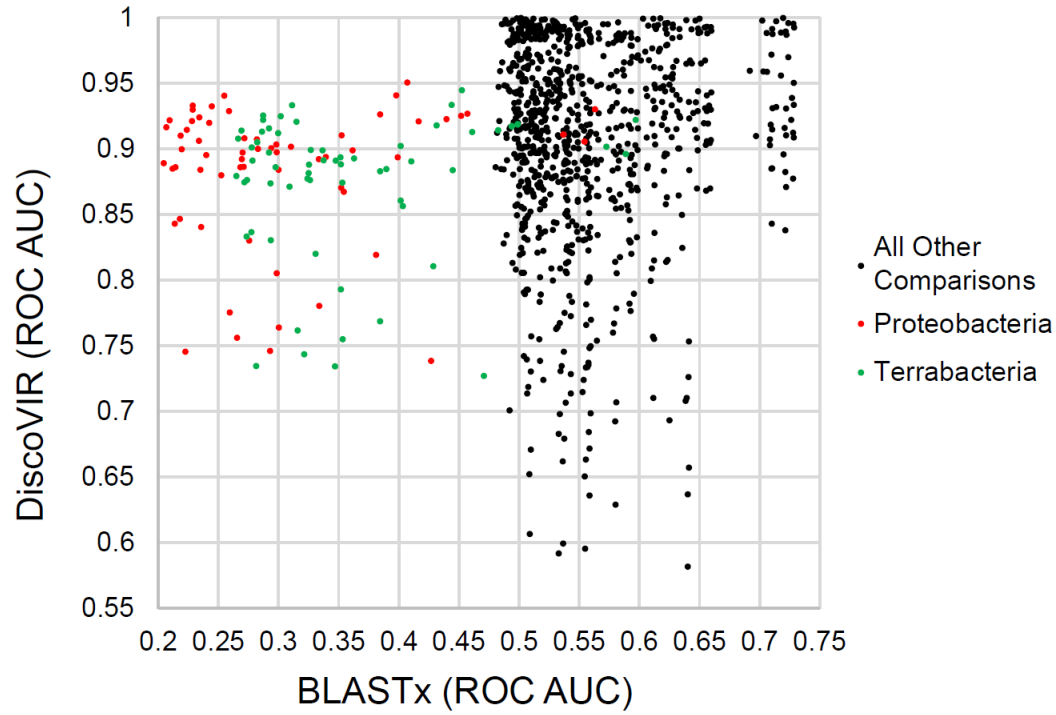
One of the central challenges in viral metagenomics is identifying novel, highly divergent viruses that are members of undiscovered taxa. Therefore, we wanted to test how well DiscoVir could discriminate between sequences from novel viral taxa and novel bacterial or fungal taxa. To evaluate DiscoVir, we simulated a novel virus identification experiment using a leave two taxa out approach. A total of 69 viral taxa, 18 bacterial taxa and 8 fungal taxa were used as input data. In each iteration, all sequences derived from one virus taxon and one non-virus taxon were set aside to be used as test data set. A model was generated from the remaining training set and was assessed for its ability to separate the viral from the non-viral sequences in the test data set. This process was repeated with both SVMs for all combinations of one viral taxa and one non-viral taxa, resulting in 1,794 simulations (Appendix 2). This assessment is more challenging for the classifier than standard cross-validation protocols, because both viral and non-viral sequences in the test set are from taxa the classifier does not see during training. As a performance baseline against which to compare DiscoVir, we also assessed BLASTx in the same protocol. We aligned the held out sequences from the viral and non-viral taxa against protein sequence databases that

were depleted of protein sequences from those taxa. Bitscores were retrieved as measures for alignment and receiver operating characteristic (ROC) curves were constructed.

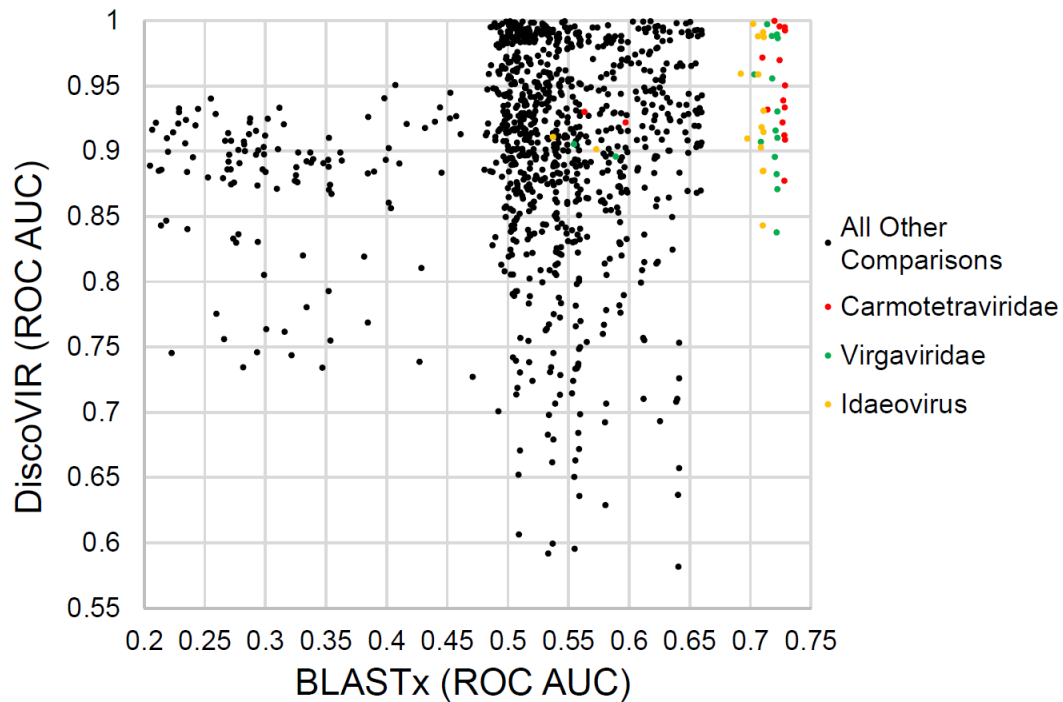
Except for one viral-bacterial taxon comparison (out of 1242), we found that the bacteria-virus SVM performed better than BLASTx at distinguishing viral sequences from bacteria (Figure 3.1a). The average AUC for the 1242 bacteria-virus SVM was 0.9 (range 0.58-1) while for BLASTx the average was 0.53 (range 0.20-0.73). The bacteria-virus SVM performed well, including for bacterial phyla that performed consistently poorly in BLASTx such as *Proteobacteria* and *Terrabacteria*, (Figure 3.2). Novel *Proteobacteria* and *Terrabacteria* sequences might not be inherently difficult to align to other bacterial protein sequences, especially when protein sequences from *Proteobacteria* and *Terrabacteria* are included in the protein database. However, these results demonstrate the idea that in the absence of close relatives, there are sequences from novel bacteria so divergent that they can align better to viral protein sequences than some viral sequences (Figure 3.1a). Even for the best performing viral taxa in the BLASTx analysis, *Carmotetraviridae*, *Virgaviridae* and *Idaeovirus*, the bacteria-virus SVM outperformed BLASTx based on AUC scores (Figure 3.3). The aligned sequences mostly originated from the RNA dependent RNA polymerase genes in these viruses, which are highly conserved with other viral families. Similarly, the fungus-virus SVM outperformed BLASTx in 67% of the comparisons when viral and fungal taxa were removed (Figure 3.1b). The fungus-virus SVM was very sensitive to which phylum of fungus was being used as a comparison, with *Blastocladiomycota* being very well predicted by the SVM while *Microsporidia* were very poorly predicted (Figure 3.1b, Figure 3.4).



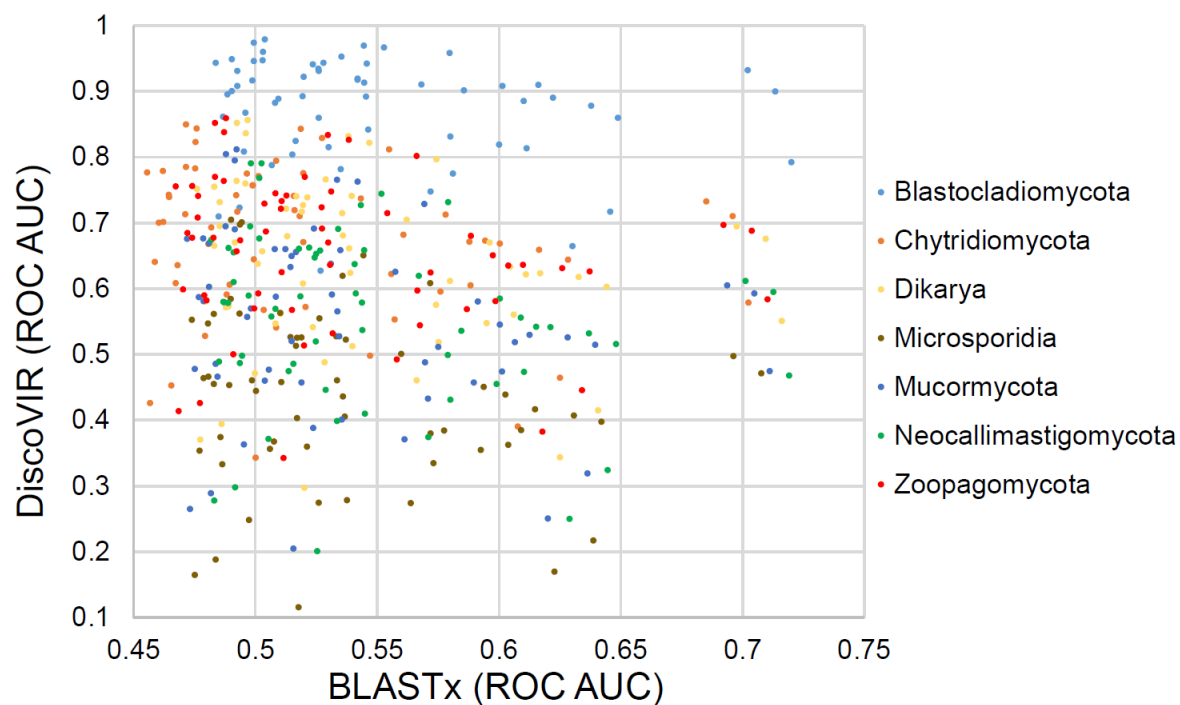
**Figure 3.1.** Performance of DiscoVir compared to BLASTx in a simulated experiment for identifying novel viral sequences. Sequences from one viral and either (a) one bacterial or (b) one fungal top-level taxon were left out of the training data for DiscoVir and were then used as test sets to predict how well DiscoVir could taxonomically classify these sequences. An analogous simulated experiment was performed for BLASTx in which amino acid sequences from the top-level taxa were removed from the protein database, and the sequences from the left out taxa were then used as test sets to assess how well BLASTx could taxonomically classify these sequences. ROC Curves were constructed from both of these experiments and plotted. Example ROC curves are provided of both the best case (upper) and worst case (lower) predictive scenarios.



**Figure 3.2.** Simulated experiment using DiscoVir and BLASTx with comparisons that involve Proteobacteria and Terrabacteria highlighted



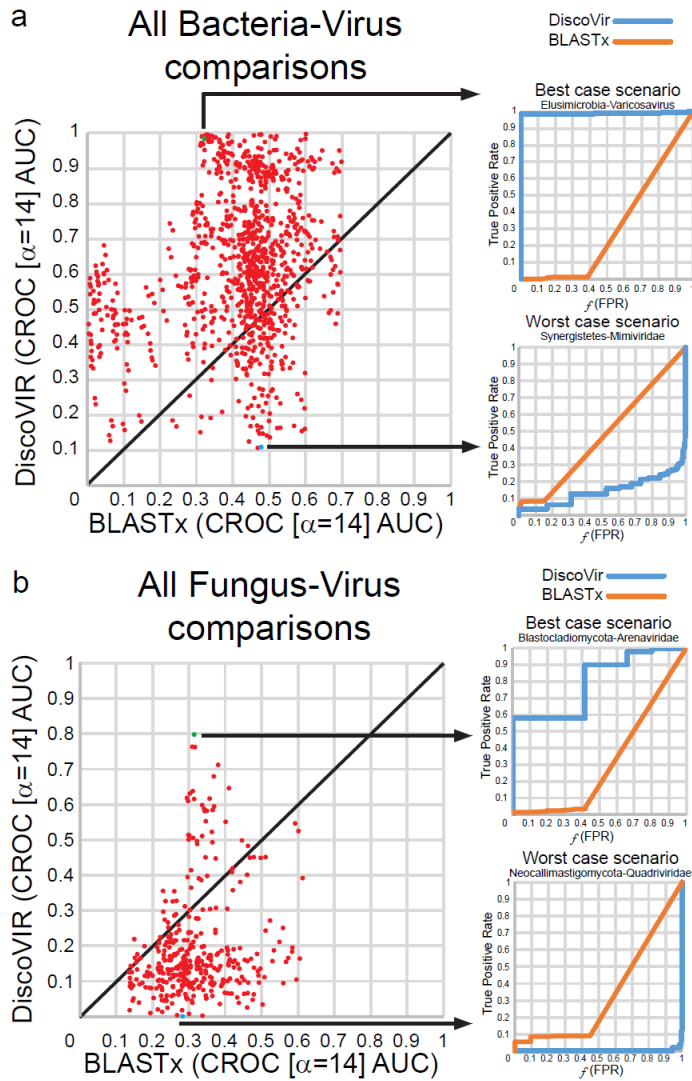
**Figure 3.3.** Simulated experiment using DiscoVir and BLASTx with comparisons that involve Carmotetraviridae, Virgaviridae, and Idaeovirus highlighted



**Figure 3.4.** Simulated experiment using DiscoVir and BLASTx with each fungal taxa highlighted

A common goal of computationally identifying novel viral sequences is to establish candidate sequences for further experimental validation. Experimental validation rarely can be performed on a large set of sequences, therefore it is useful for any viral sequence classifier to have the highest ranked sequences have a very low false positive rate. The proportion of accurately classified sequences at the highest confidence of prediction scores is defined as the early retrieval rate. To compare the early retrieval rate of DiscoVir and BLASTx, we constructed concentrated receiver operating characteristic (CROC) curves based on the leave two taxa out simulated experimental data<sup>17</sup>. We found that the early retrieval rate for the bacteria-virus SVM was generally higher than BLASTx, with 82% of the comparisons resulting in the bacteria-virus SVM having a higher CROC AUC than BLASTx (Figure 3.5). The fungi-virus SVM however,

generally had a worse early retrieval than BLASTx, although both BLASTx and the fungi-virus SVM had a high misclassification rate for early retrieval in general.



**Figure 3.5.** Early retrieval rate was measured for the simulated experiment using CROC curves with an alpha = 14, for both (a) bacterial and (b) fungal taxa, CROC curves are provided of both the best case (left panel) and worst case (right panel) predictive scenarios.

### Novel bunya-like virus identified from human serum

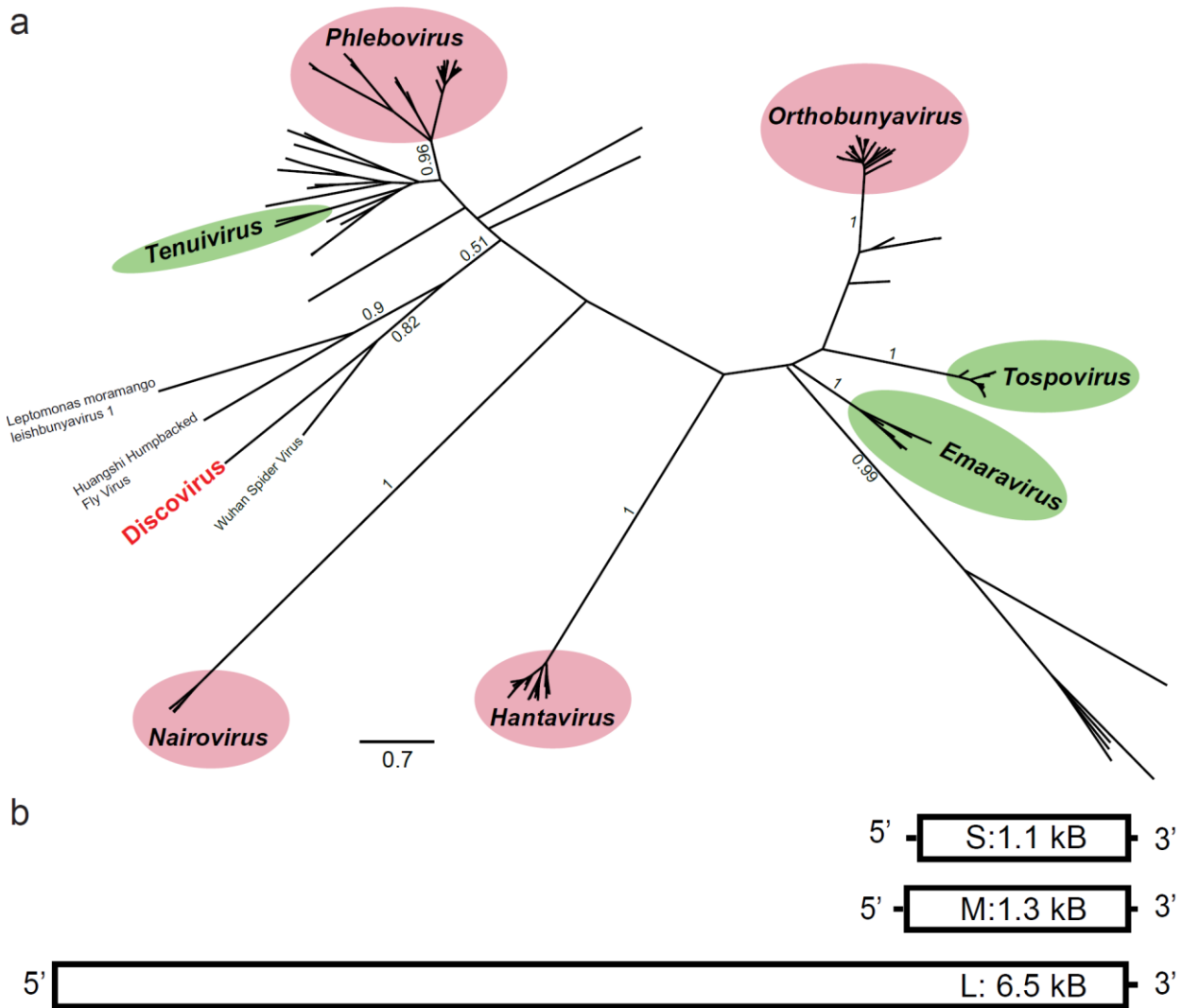
We applied DiscoVir to identify novel viral sequences in an authentic metagenomic dataset derived from a human serum sample. The serum sample originated from a 69 year-old male in Bulgaria who presented with a fever of 39.2°C, shaking, excessive sweating,

lymphadenopathy, hepatomegaly, fatigue, joint pain, muscle soreness and a skin lesion. He was seronegative for etiologic agents of hemorrhagic fever endemic to that geographic region, including Hantaan virus, Puumala virus, Crimean-Congo Hemorrhagic Fever virus, Tick Borne Encephalitis virus and Q-Fever.

The dataset contained a total of 702,502 unique, high quality reads (Illumina MiSeq 2X250 nucleotide length reads). Primary sequence alignment using BLASTx identified reads from numerous viruses in this sample, including 12 reads that aligned to Torque Teno-Like Virus, 41 reads that aligned to Human Adenovirus C and one read that aligned to Durania virus, a bunyavirus. Additionally, over half of the total primary reads contained no translated product that could be aligned to any known protein. This high number could be in part due to the abundance of non-coding nucleic acid in eukaryotic genomes, which would not contain a protein product to align.

Assembly of the primary reads resulted in a total 182 assembled contiguous sequences (contigs) of at least 500 nucleotides, of which 140 contigs aligned to known proteins. Two contigs contained translation products that aligned to known viruses, one aligned to the Human Adenovirus C Fiber protein and another aligned distantly to Durania virus RdRp. No reads or contigs were identified that shared detectable sequence similarity with any M or S segment from any bunyavirus. Phylogenetic analysis based on the predicted bunyaviral RdRp domain demonstrated that it was highly divergent from other bunyavirus RdRps, but was most closely related to those of phleboviruses and tenuiviruses (Figure 3.6A). The novel virus encoding this RdRp was named Discovirus.





**Figure 3.6.** Phylogeny and genome organization of Discovirus. (a) Phylogenetic tree of Discovirus RdRp (b) Genomic organization of Discovirus.

### DiscoVir identified candidate viral sequences among the contigs

As all known viruses in the family *Bunyaviridae* are tri-segmented, we sought to identify the additional genome segments of Discovirus by applying DiscoVir to the 42 contigs in the dataset that did not align to any known proteins. Of these, 5 were predicted to have at least 33% probability of being viral in origin (Table 3.2). Structural modeling using Phyre2 identified one of these five contigs (contig-10) as having significant structural homology to a bunyaviral nucleocapsid protein, suggesting this may be the S segment (Figure 3.6B). Of the remaining four

potential viral contigs, one (contig-7; 1.3 kB in length) had similar sequencing depth coverage as the other two contigs (Table 3.2). Based on these analyses, we hypothesized that these were the two best candidate contigs that might be derived from the additional genome segments of Discovirus.

**Table 3.2.** Assembled contig prediction by DisoVir.

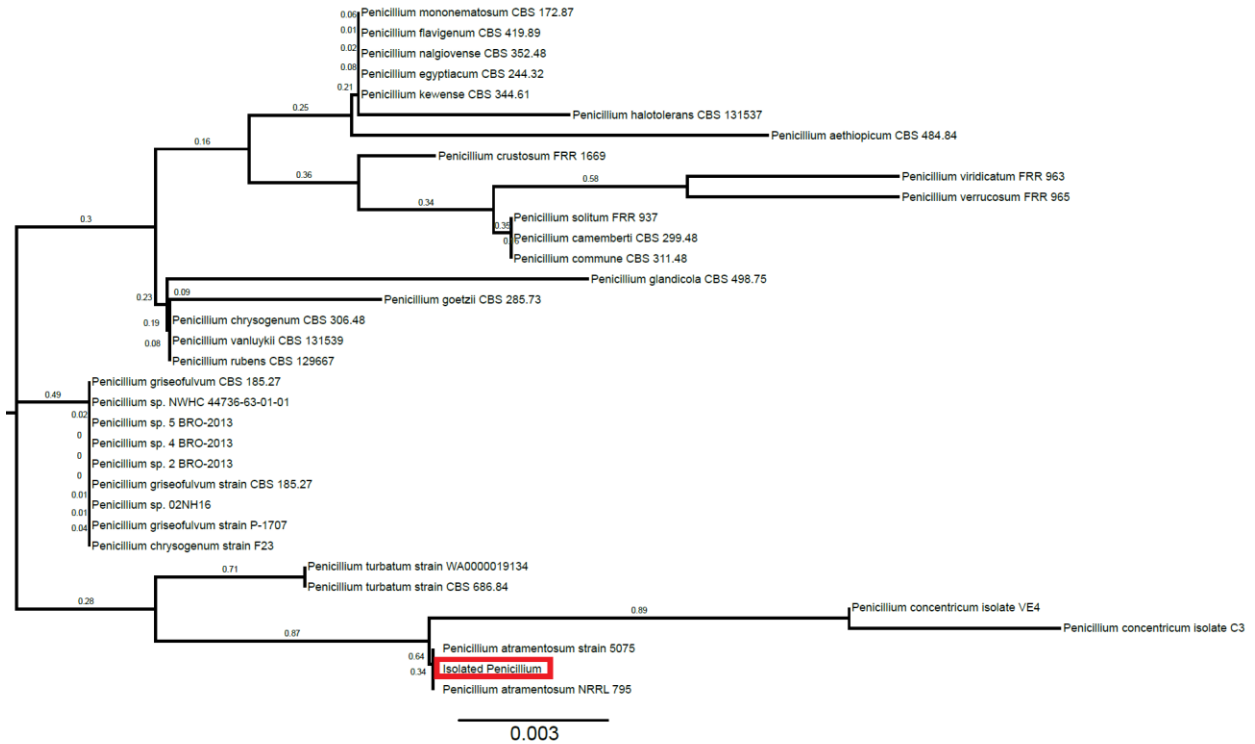
Contig Number	Contig Length	Coverage	Bacteria-Virus SVM Score	Fungal-Virus SVM Score	DiscoVir Score	Probability Sequence is viral	Aligns to Discovirus
174	502	7	0.84	-0.50	0.70	0.669	No
81	646	2	0.80	-0.54	0.47	0.616	No
7	1367	310	0.89	-0.67	0.06	0.514	Yes: M
147	530	4	0.70	-0.77	-0.64	0.346	No
10	1251	210	0.72	-0.78	-0.69	0.334	Yes: S
170	510	2	0.92	-0.85	-0.71	0.329	No
105	594	2	0.94	-0.86	-0.73	0.325	No
166	514	8	0.80	-0.83	-0.76	0.318	No
118	574	2	0.84	-0.85	-0.81	0.307	No
29	932	5	1.34	-1.07	-1.05	0.260	No
28	964	5	0.75	-0.89	-1.12	0.246	No
149	528	3	0.51	-0.82	-1.15	0.241	No
115	577	1	1.25	-1.12	-1.41	0.196	No
101	602	6	0.84	-0.99	-1.42	0.194	No
85	636	2	0.60	-0.92	-1.44	0.191	No
181	500	11	0.93	-1.03	-1.48	0.186	No
25	985	4	0.85	-1.02	-1.52	0.179	No
125	563	2	0.78	-1.00	-1.55	0.175	No
142	535	4	0.54	-0.95	-1.66	0.160	No
52	734	3	0.60	-0.97	-1.67	0.158	No
121	571	1	0.56	-0.96	-1.69	0.155	No
150	527	3	0.62	-0.99	-1.72	0.152	No
98	616	18	0.25	-0.87	-1.74	0.150	No
87	633	3	0.77	-1.04	-1.75	0.149	No
117	575	9	0.80	-1.07	-1.83	0.138	No
163	518	5	0.84	-1.11	-1.92	0.127	No
108	590	30	0.63	-1.06	-1.99	0.120	No
176	501	3	0.05	-0.88	-2.02	0.117	No
144	532	2	0.53	-1.04	-2.07	0.112	No
55	729	3	0.81	-1.15	-2.14	0.105	No
37	817	8	0.50	-1.06	-2.20	0.099	No
110	583	13	-0.17	-0.85	-2.23	0.097	No
40	795	1	0.46	-1.10	-2.42	0.082	No
49	756	2	0.39	-1.09	-2.48	0.077	No
71	672	2	0.34	-1.09	-2.53	0.074	No
112	578	4	0.30	-1.11	-2.70	0.063	No
122	566	1	0.17	-1.09	-2.80	0.057	No
84	641	1	-0.33	-0.98	-2.99	0.048	No
133	550	5	-0.03	-1.17	-3.39	0.033	No
104	600	1	-0.08	-1.17	-3.47	0.030	No
119	574	2	-0.11	-1.19	-3.62	0.026	No
106	591	10	-0.60	-1.14	-4.06	0.017	No

***Penicillium* colonies recovered from patient serum contained Discovirus**

Attempts to culture Discovervirus from the serum sample using Vero, BHK, SW13 and C6/36 cell lines did not yield any detectable cytopathic effect. Additionally, infection in suckling mice did not cause any noticeable pathology (data not shown). These failures combined with the fact that none of the candidate assembled contigs were predicted to contain coding regions expressing transmembrane regions, which are classic features of viral envelope proteins, lead us to ask whether there might be a non-human host for this virus present in the patient serum sample. To address this possibility, we analyzed the non-human and non-viral contigs present in the metagenomic sequencing dataset. The conceptual translation products of 99 assembled contigs aligned to various fungal proteins, many within the *Penicillium* genus with 75-90% amino acid identity. In an effort to culture fungi from this sample, patient serum sample was incubated on Blood Heart Infusion (BHI) and Sabouraud Dextrose agar (SDA) plates. After 4 days at 30°C, fungal colonies of mold morphology were present on both plates (Figure 3.7). The fungal colonies were taxonomically classified by isolating genomic DNA from multiple colonies from the SDA plate and sequencing the Inter-Transcribed Spacer (ITS) region. The ITS region was identical among all the colonies, and clustered among *P. atremetosum* strains (Figure 3.8). We named this isolate *P. atremetosum* St. Louis.



**Figure 3.7.** Discovervirus containing *Penicillium* colony morphology on SDA plate from serum of a patient with acute febrile illness.



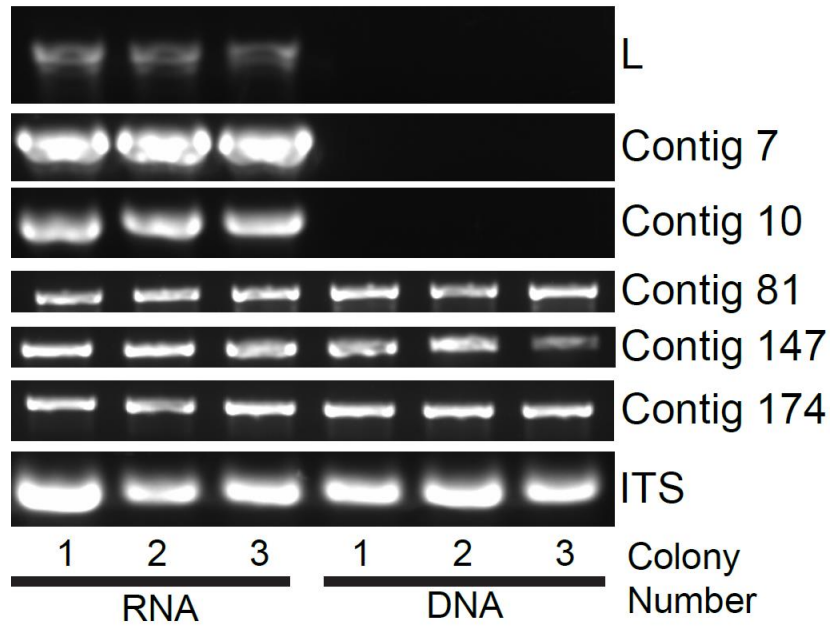
**Figure 3.8.** *Penicillium* discovirus containing fungus phylogenetically clades among *Penicillium* species. Phylogenetic tree was calculated based on ITS sequence

To test for the presence of the L segment of Discovirus in these colonies, we isolated RNA from 3 independent colonies of *P. atrementosum* St. Louis, and the presence of the L was confirmed in each colony by RT-PCR (Figure 3.9A). By contrast, RNA from the reference *Penicillium chrysogenum* strain (ATCC 10106) was negative for L (Figure 3.9B). Next, we tested for the presence of the other five candidate contigs (contigs 7, 10, 81, 147, and 174) by RT-PCR and all five were present in *P. atrementosum* St. Louis but again absent from *Penicillium chrysogenum*. Testing by PCR of DNA extracted from the fungus gave bands for contigs 81, 147 and 174 suggesting they originated from DNA while contigs 7 and 10 were derived from RNA. Because all known bunya-like viruses have RNA genomes and lack a DNA stage, these data support the possibility that contigs 7 and 10 were distinct segments of Discovirus.

Using the isolated total RNA from *P. atremetosum* St. Louis, the L segment and contigs 7 and 10 were extended by RT-PCR and 3' RACE. We determined that both the 3' and 5' termini of all 3 segments contained a conserved (5'-TGGGGTGCTTTGTGT-3') motif. The eight most 5' terminal nucleotides, 5'-CTTTGTGT-3', were shared with both the phleboviruses and tenuiviruses. The conserved terminal nucleotide sequences among the segments is 15 nucleotides in length, consistent with other tenuiviruses and phleboviruses, in which the terminal segment sequences within a specific species share longer conservation than the eight conserved within the genus. Taken together, this suggests that all 3 of these contigs are in fact viral and belong to the same virus. Bunyavirus segments are labeled based on their length, with the longest segment labeled as the L segment, the middle length labeled as the M segment and the smallest segment labeled as the S segment; we use this nomenclature to represent the segments of Discovirus. The L segment is 6494 nucleotides long, the M segment is 1320 nucleotides long, and S segment is 1181 nucleotides long (Genbank Accession numbers MF142458-MF142460). Also, because fungal viruses include their hosts' name, we refer to the virus as "Penicillium discovirus" henceforth.

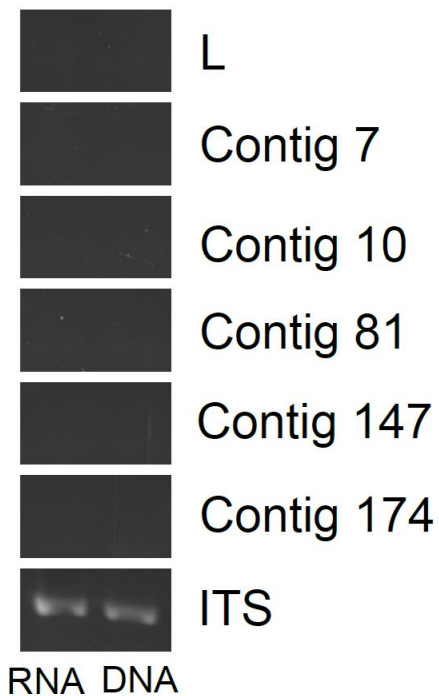
a.

*Penicillium atramentosum* Saint Louis



b.

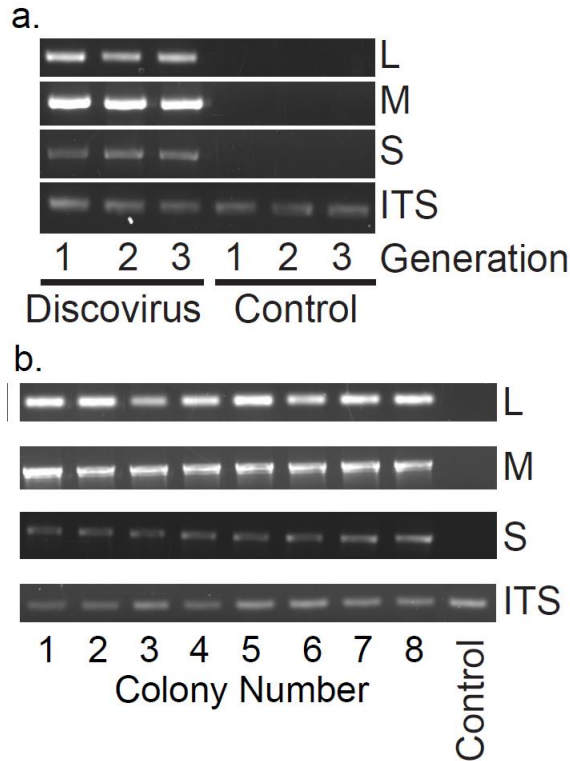
*Penicillium chrysogenum*



**Figure 3.9.** Detection of Discovirus genome segments in isolated *Penicillium* (a) RT-PCR of the Discovirus L segment from multiple colonies of the isolated *Penicillium* fungus and a control reference *Penicillium chrysogenum* strain (b) RT-PCR from RNA and conventional PCR from DNA of putative Discovirus segments

### **Penicillium discovirus is vertically transmitted via sporulation**

As all known bunyaviruses and tenuiviruses are transmitted via arthropod vectors, while most fungal viruses are transmitted vertically, we sought to elucidate the transmission of *Penicillium discovirus*. We assessed whether *Penicillium discovirus* could be vertically transmitted through germination of *P. atremetosum* St. Louis. Spores were isolated and passaged for three generations. Fungal RNA was isolated at each generation, and was assessed for all three segments of *Penicillium discovirus* using RT-PCR. In parallel, we passaged spores of *P. chrysogenum* for three generations and also tested each generation for all three *Penicillium discovirus* segments. Every generation of *P. atremetosum* St. Louis contained detectable levels of each viral segment, whereas no generation of *P. chrysogenum* contained any segment of *Penicillium discovirus* (Figure 3.10A). Although *Penicillium discovirus* is transmitted vertically through spores, it is possible that not every daughter spore carries *Penicillium discovirus*. To assess how frequently *Penicillium discovirus* gets packaged into spores, we performed a limiting dilution assay with the spore filtrate. Eight single spore derived cultures were analyzed by isolating RNA and using RT-PCR to test for all three segments. All eight *Penicillium* colonies contained all three segments of *Penicillium discovirus* (Figure 3.10B).



**Figure 3.10.** Penicillium discovirus is maintained for multiple generations of Penicillium (a) Penicillium spores were filter purified and plated for three generations. Each generation was tested for Penicillium discovirus RNA using RT-PCR. In parallel, Penicillium chrysogenum spores were also passaged for 3 generations, and each generation was tested for Penicillium discovirus (b) Limiting dilution of Penicillium atramentosum spores shows that each spore contained Penicillium discovirus.

### **Viral sequences related to Penicillium discovirus are widespread in fungal and plant**

#### **transcriptome datasets**

Given the extreme sequence divergence of Penicillium discovirus to known viruses and the fact that we were unable to align M or S segment sequence to reference databases using BLAST, we hypothesized that viruses related to Penicillium discovirus were likely to be present in other RNA sequencing datasets but were unrecognized. The logical candidate datasets were fungal RNA transcriptomes, and plant transcriptomic datasets, as fungi can often live inside plants. We queried 9,695 publically available fungal transcriptome and 39,962 plant transcriptome studies from the NCBI sequence read archive by tBLASTn with the amino acid sequences of Penicillium discovirus. From these studies, we identified 14 fungal samples that



contained at least one read that aligned to *Penicillium discovirus*. Two samples from a transcriptome of pathogenic *Pseudogymnoascus* species had over 100 reads that aligned to *Penicillium discovirus* (Table 3.3). In addition 267 plant samples contained at least one read that aligned to *Penicillium discovirus*. To better characterize the genomes of these putative novel Discoviruses, we assembled transcriptomic datasets that contained at least 50 reads that aligned to *Penicillium discovirus*. Twenty-one unique contigs larger than 500 nucleotides (up to 6464 nt) were generated. 13 contigs contained translation frames that aligned to the L segment ORF, 4 contigs contained translation frames that aligned to the M segment ORF and 4 contigs contained translation frames that aligned to the S segment (Table 3.4). Only plant transcriptomic datasets yielded sufficiently long contigs, including some agriculturally important plants<sup>18,19</sup>. These contigs range from 28-76% amino acid identity to *Penicillium Discovirus*, suggesting these are distinct viruses from *Penicillium discovirus*. These viruses were distributed on at least three continents (North America, Europe and Australia), and all the host plants associated with Discoviruses were angiosperms.

**Table 3.3.** *Penicillium discovirus* like sequences found in other fungi and plants.

SRA Accession	Kingdom	Species	Number of Reads that Align to		
			L	M	S
SRR1956747	Fungi	<i>Pseudogymnoascus</i> sp. 03VT05	100	57	45
SRR1956737	Fungi	<i>Pseudogymnoascus</i> sp. 03VT05	68	31	24
SRR592710	Fungi	<i>Penicillium digitatum</i>	15	0	1
SRR592713	Fungi	<i>Penicillium digitatum</i>	0	0	13
DRR017631	Fungi	<i>Rhizophagus</i> sp. strain HR1	4	0	2
DRR017627	Fungi	<i>Rhizophagus</i> sp. strain HR1	1	0	2
SRR807362	Fungi	<i>Locusta migratoria</i>	3	0	0
SRR1587811	Fungi	<i>Fabomonas tropica</i>	2	0	0
SRR1066785	Fungi	<i>Aspergillus flavus</i> NRRL3357	0	0	2
SRR1575394	Fungi	<i>Fabomonas tropica</i>	0	2	0
DRR017629	Fungi	<i>Rhizophagus</i> sp. strain HR1	1	0	0
ERR637976	Fungi	<i>Schizosaccharomyces pombe</i>	1	0	0

SRR1695880	Fungi	Pseudophialophora eragrostis	0	1	0
DRR017626	Fungi	Rhizophagus sp. strain HR1	1	0	0
SRR1005294	Plant	Oryza sativa	1795	901	1153
SRR1005257	Plant	Oryza sativa	310	144	220
SRR1005271	Plant	Oryza sativa	155	70	90
ERR1059554	Plant	Vitis vinifera	158	0	57
SRR1005260	Plant	Oryza sativa	99	46	50
ERR777826	Plant	Cleome gynandra	130	0	0
ERR1059557	Plant	Vitis vinifera	81	2	43
ERR1059556	Plant	Vitis vinifera	53	0	61
SRR1005300	Plant	Oryza sativa	50	24	18
SRR3105700	Plant	Lilium	44	0	43
SRR1005312	Plant	Oryza sativa	42	10	34
SRR1005311	Plant	Oryza sativa	28	24	24
SRR1005267	Plant	Oryza sativa	22	26	26
SRR1005301	Plant	Oryza sativa	20	26	21
SRR1005310	Plant	Oryza sativa	24	16	18
SRR1999956	Plant	Nepenthes rafflesiana	29	0	24
SRR1005259	Plant	Oryza sativa	22	22	8
ERR1059555	Plant	Vitis vinifera	41	0	10
SRR1005303	Plant	Oryza sativa	13	10	22
SRR1005296	Plant	Oryza sativa	18	6	20
SRR1005307	Plant	Oryza sativa	22	14	8
SRR1005298	Plant	Oryza sativa	20	8	12
ERR1059553	Plant	Vitis vinifera	29	0	9
SRR1005306	Plant	Oryza sativa	16	9	10
SRR1233165	Plant	Solanum commersonii	14	3	12
SRR1213587	Plant	Oryza sativa Japonica Group	29	0	0
SRR2131364	Plant	Oryza sativa	3	0	25
SRR960254	Plant	Gossypium hirsutum	16	0	12
SRR1005315	Plant	Oryza sativa	8	6	10
SRR960252	Plant	Gossypium hirsutum	14	0	7
SRR3217257	Plant	Panicum virgatum cultivar:Alamo-AP13	19	0	2
SRR1005320	Plant	Oryza sativa	4	12	4
SRR1005317	Plant	Oryza sativa	16	4	0
SRR2131365	Plant	Oryza sativa	1	0	19
SRR1005318	Plant	Oryza sativa	2	8	9
SRR2807659	Plant	Dionaea muscipula	17	0	2
SRR2187589	Plant	Arabidopsis thaliana	19	0	0
SRR1005261	Plant	Oryza sativa	11	2	4
SRR1233161	Plant	Solanum commersonii	8	4	5
SRR1174777	Plant	Oryza glumipatula	13	0	4

SRR2187590	Plant	Arabidopsis thaliana	17	0	0
SRR1005299	Plant	Oryza sativa	6	4	6
SRR1005308	Plant	Oryza sativa	8	4	4
SRR2131352	Plant	Oryza sativa	2	0	14
SRR1724091	Plant	Arabidopsis thaliana	12	0	4
SRR1298983	Plant	Cicer arietinum	12	0	4
SRR1174792	Plant	Oryza meridionalis	6	2	6
SRR2003671	Plant	Brassica rapa	8	4	2
SRR2240273	Plant	Arabidopsis thaliana	14	0	0
SRR2807657	Plant	Dionaea muscipula	13	0	0
ERR748774	Plant	Oryza sativa Japonica Group	13	0	0
SRR1531164	Plant	Heliopsis helianthoides	8	0	4
ERR748773	Plant	Oryza sativa Japonica Group	11	1	0
SRR3217256	Plant	Panicum virgatum	12	0	0
SRR1005280	Plant	Oryza sativa	6	2	3
SRR2240260	Plant	Arabidopsis thaliana	9	0	2
SRR2131363	Plant	Oryza sativa	2	0	9
SRR1005289	Plant	Oryza sativa	6	2	2
SRR1005284	Plant	Oryza sativa	6	4	0
SRR1005258	Plant	Oryza sativa	8	0	2
SRR2807661	Plant	Dionaea muscipula	5	1	4
SRR2131351	Plant	Oryza sativa	1	0	9
SRR1178919	Plant	Oryza granulata	9	0	1
SRR1731532	Plant	Triticum aestivum	8	0	1
SRR1722393	Plant	Triticum aestivum	8	0	1
SRR2807660	Plant	Dionaea muscipula	6	0	3
SRR1302046	Plant	Vitis vinifera	4	0	5
SRR2132800	Plant	Musa acuminata	8	0	1
ERR748777	Plant	Oryza sativa Japonica Group	9	0	0
SRR1005309	Plant	Oryza sativa	4	2	2
SRR1005297	Plant	Oryza sativa	4	2	2
SRR2807662	Plant	Dionaea muscipula	8	0	0
SRR3046431	Plant	Vitis vinifera	6	0	1
ERR1360188	Plant	Triticum aestivum	3	0	4
SRR1778927	Plant	Quercus rubra	7	0	0
SRR3156503	Plant	Citrullus lanatus	7	0	0
SRR1005343	Plant	Oryza sativa	2	2	2
SRR1005276	Plant	Oryza sativa	6	0	0
SRR1005323	Plant	Oryza sativa	6	0	0
ERR260429	Plant	Picea abies	6	0	0
SRR1837885	Plant	Zea mays	4	0	2
SRR926248	Plant	Picea glauca	5	1	0

SRR1562369	Plant	<i>Lindera glauca</i>	6	0	0
SRR1005287	Plant	<i>Oryza sativa</i>	3	2	0
SRR1005277	Plant	<i>Oryza sativa</i>	5	0	0
SRR1005291	Plant	<i>Oryza sativa</i>	5	0	0
SRR2807658	Plant	<i>Dionaea muscipula</i>	2	2	1
SRR1917043	Plant	<i>Dendrobium catenatum</i>	2	1	2
SRR3046430	Plant	<i>Vitis vinifera</i>	4	0	1
SRR1779073	Plant	<i>Juglans nigra</i>	4	0	1
SRR866531	Plant	<i>Vitis vinifera</i>	4	0	1
SRR1005314	Plant	<i>Oryza sativa</i>	2	2	0
SRR1005286	Plant	<i>Oryza sativa</i>	2	2	0
SRR1005273	Plant	<i>Oryza sativa</i>	2	2	0
SRR1005268	Plant	<i>Oryza sativa</i>	2	2	0
SRR1005313	Plant	<i>Oryza sativa</i>	4	0	0
SRR1005292	Plant	<i>Oryza sativa</i>	4	0	0
SRR1005373	Plant	<i>Oryza sativa</i>	2	0	2
SRR1005304	Plant	<i>Oryza sativa</i>	2	2	0
SRR1005263	Plant	<i>Oryza sativa</i>	4	0	0
SRR1506121	Plant	<i>Pinus flexilis</i>	2	0	2
SRR1178935	Plant	<i>Oryza australiensis</i>	3	0	1
SRR1611790	Plant	<i>Hevea brasiliensis</i>	3	0	1
SRR1588453	Plant	<i>Physcomitrella patens</i>	2	2	0
SRR1233164	Plant	<i>Solanum commersonii</i>	2	0	2
SRR1778932	Plant	<i>Quercus rubra</i>	2	0	2
ERR1059552	Plant	<i>Vitis vinifera</i>	3	0	1
SRR3046429	Plant	<i>Vitis vinifera</i>	4	0	0
SRR2127986	Plant	<i>Dipteronia sinensis</i>	4	0	0
SRR2477711	Plant	<i>Orobancha aegyptiaca</i>	4	0	0
SRR1778989	Plant	<i>Quercus rubra</i>	4	0	0
SRR2148997	Plant	<i>Daucus carota</i> subsp. <i>sativus</i>	4	0	0
SRR1778921	Plant	<i>Quercus rubra</i>	4	0	0
SRR1619672	Plant	<i>Narcissus pseudonarcissus</i>	4	0	0
SRR1618547	Plant	<i>Oryza sativa</i>	4	0	0
SRR1257400	Plant	<i>Arabidopsis thaliana</i>	4	0	0
ERR748785	Plant	<i>Oryza sativa Japonica Group</i>	4	0	0
ERR167173	Plant	<i>Quercus suber</i>	4	0	0
SRR1257399	Plant	<i>Arabidopsis thaliana</i>	4	0	0
ERR424752	Plant	<i>Triticum aestivum</i>	4	0	0
SRR960261	Plant	<i>Gossypium hirsutum</i>	4	0	0
ERR493373	Plant	<i>Malus domestica</i>	4	0	0
SRR3208051	Plant	<i>Populus trichocarpa</i>	2	0	1
SRR1162293	Plant	<i>Cleome gynandra</i>	2	0	1

SRR2976057	Plant	Ananas comosus	1	0	2
SRR1778924	Plant	Quercus rubra	2	0	1
SRR1958771	Plant	Triticum aestivum	3	0	0
SRR1162292	Plant	Cleome gynandra	3	0	0
SRR1174772	Plant	Oryza glumipatula	3	0	0
SRR1026209	Plant	Oryza sativa	3	0	0
ERR167181	Plant	Quercus suber	3	0	0
SRR1588171	Plant	Camellia sinensis	3	0	0
SRR1233160	Plant	Solanum commersonii	3	0	0
SRR1212862	Plant	Citrus x paradisi x Citrus trifoliata	3	0	0
SRR1026204	Plant	Oryza sativa	3	0	0
ERR886715	Plant	Sorghum bicolor	3	0	0
SRR1257389	Plant	Arabidopsis thaliana	3	0	0
ERR1360192	Plant	Triticum aestivum	3	0	0
ERR777827	Plant	Cleome gynandra	3	0	0
ERR167179	Plant	Quercus suber	3	0	0
SRR960260	Plant	Gossypium hirsutum	3	0	0
ERR167184	Plant	Quercus suber	3	0	0
SRR1005378	Plant	Oryza sativa	2	0	0
SRR1005266	Plant	Oryza sativa	2	0	0
SRR1005265	Plant	Oryza sativa	2	0	0
SRR3046428	Plant	Vitis vinifera	1	0	1
ERR748784	Plant	Oryza sativa Japonica Group	1	0	1
SRR831704	Plant	Triticum aestivum	1	0	1
SRR3207915	Plant	Populus trichocarpa	2	0	0
SRR1170742	Plant	Oryza barthii	2	0	0
SRR2131361	Plant	Oryza sativa	2	0	0
SRR1186869	Plant	Zea mays	2	0	0
SRR3046433	Plant	Vitis vinifera	2	0	0
SRR2003637	Plant	Arabidopsis thaliana	2	0	0
SRR3046432	Plant	Vitis vinifera	2	0	0
SRR2060956	Plant	Gossypium hirsutum	2	0	0
SRR1822494	Plant	Gossypium hirsutum	2	0	0
SRR1652334	Plant	Gossypium barbadense	2	0	0
SRR1649311	Plant	Panax ginseng	2	0	0
SRR1588170	Plant	Hevea brasiliensis	2	0	0
SRR1287024	Plant	Oryza sativa	2	0	0
SRR1257390	Plant	Arabidopsis thaliana	2	0	0
SRR1233166	Plant	Solanum commersonii	2	0	0
SRR1163705	Plant	Tarenaya hassleriana	2	0	0
SRR1162298	Plant	Cleome gynandra	2	0	0
ERR1025478	Plant	Salix viminalis	2	0	0

SRR1163703	Plant	Tarenaya hassleriana	2	0	0
ERR179753	Plant	Capsicum annuum	2	0	0
SRR3046440	Plant	Vitis quinquangularis	2	0	0
SRR2094397	Plant	Oropetium thomaeum	2	0	0
SRR2081043	Plant	Gossypium hirsutum	2	0	0
SRR1298984	Plant	Cicer arietinum	2	0	0
ERR1360179	Plant	Triticum aestivum	2	0	0
SRR2807652	Plant	Dionaea muscipula	2	0	0
ERR929878	Plant	Primula vulgaris	2	0	0
ERR829294	Plant	Solanum tuberosum	2	0	0
DRR001017	Plant	Secale cereale	2	0	0
SRR3310309	Plant	Cucumis sativus	2	0	0
SRR2676906	Plant	Camellia reticulata	2	0	0
SRR1942951	Plant	Warburgia ugandensis	2	0	0
SRR1797599	Plant	Camellia taliensis	2	0	0
SRR1720767	Plant	Colobanthus quitensis	2	0	0
SRR1413312	Plant	Paphiopedilum callosum	2	0	0
SRR1185546	Plant	Araucaria angustifolia	2	0	0
SRR959508	Plant	Gossypium arboreum	2	0	0
SRR1564725	Plant	Ziziphus jujuba	2	0	0
SRR1162294	Plant	Cleome gynandra	2	0	0
SRR1720760	Plant	Colobanthus quitensis	2	0	0
DRR001451	Plant	Oryza rufipogon	2	0	0
SRR826599	Plant	Helianthus argophyllus	2	0	0
SRR1594527	Plant	Bougainvillea stipitata var. grisebachiana	2	0	0
SRR653057	Plant	Oryza sativa	2	0	0
SRR606404	Plant	Oryza sativa	2	0	0
SRR3110670	Plant	Panicum hallii	1	0	0
SRR3096280	Plant	Festuca pratensis	1	0	0
SRR2477712	Plant	Orobanche aegyptiaca	1	0	0
SRR2040570	Plant	Oryza sativa	1	0	0
SRR1837875	Plant	Zea mays	1	0	0
SRR3204831	Plant	Pisum sativum	1	0	0
SRR3124526	Plant	Camellia oleifera	1	0	0
SRR3112066	Plant	Panicum hallii	1	0	0
SRR3046448	Plant	Vitis quinquangularis	1	0	0
SRR2807630	Plant	Dionaea muscipula	1	0	0
SRR1927120	Plant	Vitis vinifera	1	0	0
SRR1778920	Plant	Quercus rubra	1	0	0
SRR1728120	Plant	Triticum aestivum	1	0	0
SRR1537559	Plant	Oryza sativa	1	0	0
ERR1104413	Plant	Salix purpurea	1	0	0

SRR3207877	Plant	Populus trichocarpa	1	0	0
SRR2807626	Plant	Dionaea muscipula	1	0	0
SRR2240272	Plant	Arabidopsis thaliana	1	0	0
SRR2167610	Plant	Chrysopogon zizanioides	1	0	0
SRR1770420	Plant	Olea europaea	1	0	0
SRR1582386	Plant	Musa acuminata	1	0	0
SRR1537557	Plant	Oryza sativa	1	0	0
SRR1213697	Plant	Oryza sativa Japonica Group	1	0	0
SRR1055109	Plant	Camellia sinensis	1	0	0
SRR1033742	Plant	Citrus x paradisi x Citrus trifoliata	1	0	0
SRR1033317	Plant	Citrus x paradisi x Citrus trifoliata	1	0	0
SRR3105600	Plant	Tulipa gesneriana	1	0	0
SRR2321320	Plant	Festuca arundinacea	1	0	0
SRR2240261	Plant	Arabidopsis thaliana	1	0	0
SRR2120782	Plant	Vitis vinifera	1	0	0
SRR1909493	Plant	Dendrobium catenatum	1	0	0
SRR1537552	Plant	Oryza sativa	1	0	0
SRR1266998	Plant	Howea belmoreana	1	0	0
SRR1026739	Plant	Vitis riparia x Vitis rupestris	1	0	0
SRR1026335	Plant	Vitis riparia x Vitis rupestris	1	0	0
SRR3207796	Plant	Populus trichocarpa	1	0	0
SRR2984592	Plant	Musa acuminata AAA Group	1	0	0
SRR2824359	Plant	Litchi chinensis	1	0	0
SRR2003659	Plant	Arabidopsis thaliana	1	0	0
SRR2003632	Plant	Arabidopsis thaliana	1	0	0
SRR1837717	Plant	Zea mays	1	0	0
SRR1770102	Plant	Zea mays	1	0	0
SRR1724901	Plant	Citrullus lanatus	1	0	0
SRR1724088	Plant	Arabidopsis thaliana	1	0	0
SRR1698111	Plant	Zea nicaraguensis	1	0	0
SRR1267019	Plant	Howea belmoreana	1	0	0
SRR1182649	Plant	Panicum virgatum	1	0	0
SRR1170971	Plant	Solanum tuberosum	1	0	0
SRR1162297	Plant	Cleome gynandra	1	0	0
SRR1026338	Plant	Vitis riparia x Vitis rupestris	1	0	0
SRR3207913	Plant	Populus trichocarpa	1	0	0
SRR1830868	Plant	Araucaria cunninghamii	1	0	0
SRR826644	Plant	Helianthus debilis	1	0	0
SRR912597	Plant	Zea mays	1	0	0
SRR837659	Plant	Brassica rapa	1	0	0
SRR826645	Plant	Helianthus debilis	1	0	0
SRR653062	Plant	Oryza sativa	1	0	0

SRR606409	Plant	Oryza sativa	1	0	0
ERR908395	Plant	Fagus sylvatica	1	0	0
ERR908392	Plant	Fagus sylvatica	1	0	0
ERR690823	Plant	Campanula aff. rotundifolia CAM084	1	0	0
ERR424755	Plant	Triticum aestivum	1	0	0
DRR029010	Plant	Sarracenia purpurea subsp. Venosa	1	0	0
SRR447121	Plant	Oryza sativa Japonica Group	1	0	0
ERR908410	Plant	Fagus sylvatica	1	0	0
ERR789951	Plant	Oryza sativa	1	0	0
ERR748783	Plant	Oryza sativa Japonica Group	1	0	0
ERR424731	Plant	Triticum aestivum	1	0	0
DRR006301	Plant	Allium fistulosum	1	0	0
SRR867435	Plant	Citrus sinensis	1	0	0
ERR260421	Plant	Picea abies	1	0	0
SRR952307	Plant	Notholithocarpus densiflorus var. densiflorus	1	0	0
ERR908403	Plant	Fagus sylvatica	1	0	0
ERR367938	Plant	Hordeum vulgare subsp. spontaneum	1	0	0

**Table 3.4.** Penicillium discovirus like contigs assembled from SRA samples.

Host Kingdom	Host	SRA Accession Number	Number of Contigs that Align to:			Length of Largest Contig (nt)			Amino Acid Percent Identity of Longest Contig to Penicillium discovirus		
			L	M	S	L	M	S	L	M	S
Plant	Oryza Sativa	SRR1005294	1	1	1	6464	1253	1156	76	57	68
Plant	Oryza Sativa	SRR2131364	2	0	0	5360	0	0	27	0	0
Plant	Vitis Vinifera	ERR1059554	1	1	1	2389	1892	894	53	28	35
Plant	Nepenthes rafflesiana	SRR1999956	7	1	1	1232	1960	1126	29	40	44
Plant	Lilium cultivar "McAleese"	SRR3105700	2	1	1	3034	1532	1246	32	35	41

## Discussion

Viral metagenomics has traditionally been dependent upon primary sequence alignment methods to identify highly divergent viruses. While recent reports have shown that nucleotide k-mer based computational methods are sufficient to classify bacterial and other microbial sequences, no method has applied this approach to broadly identify all classes of eukaryotic viral sequences<sup>10</sup>. Here, we present DiscoVir, a k-mer based computation approach capable of identify



viral sequences independent of primary sequence alignment. We show that DiscoVir accurately identifies more viral sequences from highly divergent viral taxa than BLASTx using both *in silico* generated and real sequencing data. DiscoVir provides one modality to address this problem in viral discovery by identifying additional novel viral sequences without alignment. This is an even more challenging problem for certain classes of viruses, such as segmented viruses. For these viruses, independent of sequencing depth, the recovery of one segment does not necessarily lead to the recovery of the full viral genome.

The biological parameters that define k-mer frequencies in viral sequences are not fully understood. There is evidence that some viral taxa partially optimize their codon usage to increase their fitness<sup>20</sup>. As codons are a specific example of a k-mer, codon bias might be in part why DiscoVir can accurately discriminate sequences. Additional factors such as DNA and RNA methylation likely contribute to the k-mer preference of viral sequences.

Finally, we report the discovery of a novel bunya-like virus, of which two segments had no discernable primary sequence alignment to any known virus. Multiple lines of evidence suggest that these segments are part of the same virus. We found that every colony of the initial fungal culture that we tested contained all three segments. After multiple generations of vertical transmission, all three segments were present in each generations of the fungus, once again, with no fungal culture lacking any of the segments. The extracted fungal DNA did not amplify any of the viral segments, demonstrating that all three of the segments were derived from RNA. Finally, the termini of these segments were conserved with each other as well as with the conserved phlebovirus and tenuivirus termini. This virus persistently infects a *Penicillium* fungus species. To our knowledge, no bunya-like virus of fungi have been described. Furthermore, we identified related viral reads and contigs present in an independent fungal and plant sequencing datasets,

suggesting that *Penicillium discovirus* is the prototype of a novel genus of bunya-like viruses that infect fungi.

Bunyaviruses are thought to be transmitted via arthropods to plant or mammalian hosts. However, we demonstrated that *Penicillium discovirus* employed a transmission pattern previously unobserved in bunyaviruses, vertical transmission via fungal sporulation. This finding demonstrates that highly divergent viruses identified using DiscoVir can broaden our understanding of viral biology.

As this *Penicillium* species was found in a patient serum sample, it raises the possibility that this fungus is a novel pathogen of humans; while *Penicillium* fungi are not typically thought to be pathogenic, there is one species, *P. marneffei*, that infects humans in the context of HIV infection<sup>21</sup>. If this *Penicillium* in fact did infect this patient, it is possible *Penicillium discovirus* could represent a virulence factor for this *Penicillium* species, analogous to the Leishmania viruses in *Leishmania major*<sup>22</sup>. Future studies where an isogenic strain of *Penicillium* that lacks this virus is available will not only assist in understanding the phenotypic effects of *Penicillium discovirus* on the fungus, but also will enable a broader understanding of how mammalian host differentially responds to this fungus when co-infected with *Penicillium discovirus*. DiscoVir might elucidate the presence of novel viruses in patient samples, and these viruses might play causative roles in disease.

### **Online Methods:**

#### **Taxonomic defined, reference nucleotide datasets**

DiscoVir is designed to predict viral sequences by training SVMs on sequences of known taxonomic origin, specifically either from eukaryotic viral, bacterial or fungal genomes. Viral and bacterial sequences were retrieved from the NCBI RefSeq Genomes Database on September

2016. Fungal genomes were retrieved from the IMG/M Data Warehouse from the Joint Genome Institute on November 2015<sup>23</sup>. Each genome was taxonomically annotated based on NCBI taxonomic definitions (Appendix 2). For each taxon, a simulated set of short genomic sequences were randomly generated from genomes within that taxon by tiling across each genome, without overlap, and then subsequently using a random number generator to select simulated sequences for each training set. Each simulated sequence was then compositionally transformed into a vector based on the k-mer frequency in the sequence. In the training set, vectors were labeled either as originating from “Eukaryotic Viruses”, “Bacteria”, or “Fungi”. Binary support vector machines (Fungi-Virus and Bacteria-Virus), were implemented with SVM-light using the radial basis function kernel ( $\gamma = 0.001$ ,  $C = 0.051$ )<sup>24</sup>.

### **Parameter estimation**

Bacterial, fungal and viral sequence datasets were each randomly divided into 5 partitions, agnostic of taxonomic representation. Both nucleotide sequence and k-mer length were varied to identify optimal parameters for identifying viral sequences. For each taxon, 50, 100, 200 and 400 nucleotide length sequences were used to simulate short metagenomic sequences. In all cases, a total of 10,000 nucleotides per taxon was used for training (i.e. 25 sequences of 400 nt, 50 sequences of 200 nt, etc). For each length condition, the maximum k-mer lengths used ( $n$ ) to define k-mer spectra ranged  $2 \leq n \leq 8$ . Each k-mer condition was hierarchically parameterized: specifically, given a maximum k-mer length ( $n$ ), the subsequent vector contained the frequencies of all k-mers where  $1 \leq k \leq n$ . Each SVM model condition was then evaluated using the other partitions not used for training.

### **Integrating logistic regression**

Training data from binary SVMs was applied to both the Fungus-Virus and Bacteria-Virus SVM, and the outputs from these SVMs were used as explanatory variables for logistic regression, implemented using generalized linear models in R.

### **Leave two taxa out simulated experiment for support vector machine models**

To assess how well viral sequences from a putative novel family of viruses could be separated from highly divergent bacterial/fungal sequences using DiscoVir, we modeled sequences from novel viral families by defining 69 top-level taxa from viruses using NCBI Taxonomy accessed on September 2016. Viral taxons were generally defined at the family level, unless clear phylogenetic relationships were evident, in which case orders were used. Additionally, we defined 18 top-level taxa for bacteria and 8 top-level taxa for fungi. The bacterial taxa often corresponded to phyla or superphyla while the fungal taxa often corresponded to subkingdoms or divisions (Appendix 2).

We removed a defined viral taxon and bacterial/fungal taxa from the total dataset and trained new Bacteria-Virus or Fungus-Virus SVM models on the remaining data using 200 bp sequences and  $k = 6$ . We then tested the accuracy of the resulting model using the removed viral taxon and non-viral partition by applying the data to the newly trained SVM model, and calculated a ROC curve. This was repeated for all viral taxa and all non-viral taxa. We then combined the total data from all the taxa within a given replicate and constructed a ROC curve to assess the accuracy of the model. ROC curves were constructed in R using the ROCR package<sup>25</sup>. CROC curves were constructed using an alpha = 14 using a CROC package<sup>17</sup>.

### **Leave two taxa out simulated experiment for BLASTx**

All viral, bacterial and fungal protein sequences from the NCBI NR database were downloaded on September 2016. For each test viral taxon and bacterial taxon, a protein database

containing all viral and bacterial protein sequences except for the protein sequences from the test viral and bacterial taxon was constructed. The previously defined test set sequences were then aligned to this new protein database, and the highest bit score generated for each sequence was recorded. This was repeated for all viral taxa as defined by Appendix 2. Bit score values from any sequence that aligned to a viral protein were extracted and a ROC curve was constructed using bit-score as a discriminator.

### **Implementation**

DiscoVir is written in perl, with the exception of the support vector machine implementation, which relies on the pre-compiled SVM-light classifier. Fasta formatted sequences are first transformed into k-mer space and represented in a sparse vector format, using HexanucleotideUnmapped.pl, which creates a text file with the extension “SVMReady”. By default, DiscoVir transforms inputted nucleotide sequences into k-mer space depending on nucleotide length: 200-239 length sequences are processed into a 200 nucleotide length subsequence, 240-399 length sequences are processed into a 200 nucleotide length subsequences using a sliding window approach with a spacing of 40 nucleotides between each subsequence, 400-439 length sequences are processed into 400 nucleotide length subsequences, and sequences that are 440 nucleotides or longer are processed into 400 nucleotide length subsequences using a sliding window approach with a spacing of 40 nucleotides between each subsequence. Each k-mer transformed sequence retains the fasta label of the original sequence, denoted by a pound sign at the line terminus. SVMReady files are then processed with the Bacteria-Virus and Fungi-Virus models using the independently executable SVM-light program, svm\_classify, resulting in a text based output file that contains the SVM score for each sequence. For input sequences between 240-399 nucleotides or longer than 440, the arithmetic mean of the

DiscoVir output score of all the sliding windows is used to define the score of the input sequence. The outputs from both Bacteria-Virus Fungus-Virus SVM models are then combined using a trained logistic regression, outputting a final score, which represents a logit of the probability that a sequence is from virus. Sequences above a user-defined score are then aggregated into a fasta file using the in house script FilterViralReads.pl. DiscoVir and its component parts are available at github.

### **Illumina sequencing and analysis**

Total metagenomic nucleic acid was extracted using Ampliprep (Roche) and subjected to random-priming cDNA synthesis and amplification, and TruSeq (Illumina) libraries were constructed. Libraries were sequenced on an Illumina MiSeq instrument (2 x 250). Reads were filtered for high quality reads (QC30) with Prinseq, clustered using CD-Hit (95% criteria) and aligned to reference protein datasets using BLASTx to known amino acid sequences in the NCBI nr database. Contig assembly on reads was performed with IDBA, with only contigs larger than 500 nucleotides being retained. Contigs that did not align to any known nucleic or amino acid sequence with an e-value  $< 10^{-3}$  were defined to be unassigned. The non-human reads from this dataset are deposited at the NCBI Sequence Read Archive (SRA) under PRJNA295349.

### **Phylogenetic analysis of bunyaviruses and fungi**

All RNA-dependent RNA-polymerase amino acid sequences present in the RefSeq database from the *Bunyaviridae* family and the *Tenuivirus* and *Emaravirus* genera were used for phylogenetic analysis. The bunyaviral RdRp domain, as defined by Pfam (Bunya\_RdRp, PF04196), was extracted from each sequence. Multiple sequence alignment was performed on the isolated domains using the ClustalW algorithm in MEGA6. Maximum Likelihood phylogenies were performed using 100 bootstraps using the model (LG + I +G). For fungal

phylogenies, Internal Transcribed Spacer (ITS) nucleotide sequences from 20 closely related *Penicillium* species were aligned using the ClustalW algorithm in MEGA6. Maximum Likelihood phylogenies were performed using 100 bootstraps.

### **Fungal culture conditions**

Patient serum was plated on Blood-Heart Infusion Agar (BHI) (Remel) and Sabouraud-dextrose agar (SDA) (Remel) at 30°C. Fungal passage in this study was performed by flooding fungal plates with spore solution (15 g/L NaCl in ddH<sub>2</sub>O) and filtering the resulting residue through MiraCloth (EMB Millipore). This spore filtrate was quantified using a hemocytometer, and then 10<sup>5</sup> spores were plated on SDA at 25°C (Sigma). *Penicillium chrysogenum* Thom strain (ATCC 10106) was acquired from ATCC.

### **Fungal nucleic acid isolation, PCR, RT-PCR, termini sequencing**

Fungal RNA was isolated using the Trizol/Chloroform method. 1-step RT-PCR kit (Qiagen) was used for RT-PCR reactions using 0.5 ug of RNA. Both 5' and 3' termini of all segments were sequenced using 3'RACE as previously described<sup>26</sup>. Briefly, total RNA was polyadenylated (Ambion), column purified (Qiagen RNEasy) and then used as a template in 1-step RT-PCR, using an Oligo-d(T) primer and the primers specified (Table 3.5). For ITS sequencing, fungal DNA was isolated using Phenol/chloroform. Accuprime Taq PCR (Life Technologies) was used to amplify gene specific targets from DNA templates.

**Table 3.5.** Primers

<b>Name</b>	<b>Sequence</b>
Contig80_81_F	CAATGCATGGAATGGCCTCG
Contig80_81_R	CGTGGGTGGGGATAGAAGTG
Contig80_174_F	GGCGGGCACTAGGACATTAG
Contig80_174_R	AGGAGGGGACTGAGTTGTGA
Contig80_147_F	GAGGAACCTTGAAGCCCTG
Contig80_147_R	GTTTCATGCGCATCCTGGTG
SK-NewBunya-L-1-Fwd	TGGAGCCTCTGCTGATTGG

SK-NewBunya-L-1-Rev	GGGTGAGGGAATGGTCTTGG
SK-NewBunya-L-2-Fwd	TTGGCCTTGACCCACACAAT
SK-NewBunya-L-2-Rev	GCCTGTGACCTCACTATCCG
SK-NewBunya-L-3-Fwd	CGGATAGTGAGGTCACAGGC
SK-NewBunya-L-3-Rev	GTACCTTGCCAACCACTCCA
SK-NewBunya-L-4-Fwd	ACAATGTGCGGCAGTTTCTG
SK-NewBunya-L-4-Rev	GCCGAAAGTCGACCAAGGTA
SK-NewBunya-L-5-Fwd	GATCGGATCACGGACCATGT
SK-NewBunya-L-5-Rev	TATTGATTGCGGCCTTCCCA
SK-NewBunya-L-6-Fwd	CTGAAGGGCCTAATGGGCAA
SK-NewBunya-L-6-Rev	GGTCCGTGATCCGATCTCTT
SK-NewBunya-S-7-Fwd	TTGCAGGACAAGGCGTGATA
SK-NewBunya-S-7-Rev	CGCGGAGGAGCCAGATTTAT
SK-NewBunya-S-8-Fwd	GGAGCATCTGGCTAGGAGTG
SK-NewBunya-S-8-Rev	TCATTGGCCGTTGATGTTGC
SK-NewBunya-S-Out-1	GCCCTGATTGGTGCCATTAG
SK-NewBunya-S-Out-2	TATCACGCCTTGTCTGCAA
SK-NewBunya-L-Out-1	TCCACCCGGTCTATTGATCCA
SK-NewBunya-L-Out-2	GGGATGAAGAAGCAGACAATGA
SK-Bunya-L-Out-1	TTATACACACGGGGTGCTGC
SK-Bunya-L-7-Fwd	ACTCCTCCTCAGACTCACTCA
SK-Bunya-L-7-Rev	TAGACTTGCCAGACAGGGA
SK-Bunya-L-8-Fwd	AATCTCGCTTTGCTTTCCGC
SK-Bunya-L-8-Rev	CCCAGTGGAGATCCCGAAGA
SK-Bunya-L-9-Fwd	TCCCTGTCTGGCCAAGTCTA
SK-Bunya-L-9-Rev	TCAGGTGTTCGGGTCATTGTT
SK-Bunya-L-Out-4	AACAATGACCCGACACCTGA
SK-Bunya-L-7-Fwd2	CCAAATCAGCAGAGGCTCCA
SK-BunyaM-3RACE	TTTCGAGGGATCAGCAAACGG
SK-BunyaL-3RACE	GCTTCAAGCTCATGAGATGCT
SK-NewBunyaL-3'RACE1	TCCTCAGACATTCTCTCATGGT
SK-NewBunyaL-3'RACE2	AGTGACACCTCACATACTCTCA
SK-NewBunyaL-5'RACE1	GCTGGTGAAGGTGATCAGGAC
SK-NewBunyaL-5'RACE2	ACGCTCTACATGTGACTTCCA
SK-MidNTR-1	AGCGTCGTGGTTCTTCATCC
SK-MidNTR-2	TTCGAGGGATCAGCAAACGG
SK-SmallNTR-1	CCGGATAAAACACGCGAACG
SK-SmallNTR-2	GAGTGAGATCCCAGACGAGC
SK-NewBunya-Mid-ORF1	atggcatcatacacttcagccc
SK-NewBunya-Mid-ORF2	ctaagaaagaatgctccctaacaggg
SK-NewBunya-S-ORF1	atgtctcaaagctctcaacctttgc
SK-NewBunya-S-ORF2	tcaacgacctggtgattatctcac



SK-Bunya-M1Screen	AATCTGAGGCAAAGTGCGGA
SK-Bunya-M2Screen	ACATGGCTGAACTGGATGCT
SK-Bunya-S1Screen	AGCTCGTCTGGGATCTCACT
SK-Bunya-S2Screen	TTTTGACGCTGCAGAACGTG
SK-Bunya-S-5'End	AGTGAGATCCCAGACGAGCT

### **Limiting dilution spore assay**

Spore filtrate of either *P. atrementosum* St. Louis or *P. chrysogenum* was diluted with spore solution to 0.06 spores/uL. 10 uL was subsequently plated on 12 SDA plates, with an additional 2 SDA plates having only 10 uL of spore solution plated. Of the plates that grew *Penicillium* colonies, the fungus was isolated and then cultured in liquid Sabouraud-dextrose medium for 4 days at 30°C. Total RNA was extracted from the liquid cultured fungus for RT-PCR analysis.

### **tBLASTn query of SRA deposited databases**

Using the command line NCBI SRA tBLASTn, amino acid sequences were queried against deposited nucleotide databases that were annotated as having sequenced fungal RNA. All SRA datasets from fungi and plants were identified by querying the NCBI Taxonomy database using their taxonomic identification number (taxid 4751 and 33090 respectively) (November 2016) and then filtering for sequencing of RNA. These datasets were queried using amino acid sequences derived from all the three genomic segments of *Penicillium discovirus* using tBLASTn with non-default parameters (Appendix 3).

### **Acknowledgements:**

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## 4. Identifying RNA Phage Resistance Genes

## Introduction:

For almost every major taxonomic clade that has known RNA viruses, there are also counteracting anti-viral mechanisms that hosts encode to antagonize these viruses<sup>1</sup>. These mechanisms include RIG-I/MDA-5 in mammals, and RNAi in plants, arthropods and worms. However, at this time, there are no known mechanisms that inhibit RNA bacteriophages in bacteria. This gap in knowledge is particularly anomalous, as there are numerous well-established bacterial resistance genes effective against DNA phages<sup>2</sup>.

*Escherichia* virus Q $\beta$  and MS2 are the classical RNA bacteriophages used for experimentation<sup>3</sup>. They are part of the ssRNA bacteriophage family the *Leviviridae* and each encode 4 proteins<sup>4</sup>. All leviviruses are thought to use pili to enter bacterial cells; however the receptors for only 3 leviviruses have been identified<sup>5-7</sup>. Although both Q $\beta$  and MS2 use the F-pilus to enter *Escherichia coli* cells, they are distinct species of phages, relying on a number of different host factors for their lifecycle<sup>8</sup>. Although studies have looked for natural bacterial variants that are able to resist phage infection, currently, the only known mechanism by which bacterial cells resist RNA bacteriophage infection is by losing the phage entry receptor, which in the case of Q $\beta$  and MS2 is the F-pilus<sup>9</sup>. Loss of pilus function is thought to come in the form of hypopilation, in which there is lower cell surface expression of pili, or hyperpilation, in which there is a higher density of pili on the cell surface, likely because the pili are unable to retract back into the bacteria<sup>10</sup>.

In this chapter, I detail my efforts on attempting to identify genes that can confer resistance to RNA bacteriophage. To do this, I performed a functional metagenomic screen in which I expressed a library of metagenomic DNA in a susceptible strain of *E. coli* and selected for genes that conferred resistance to Q $\beta$  infection. While we still cannot conclude that any of the genes identified from this study are directly antagonizing RNA bacteriophage infection instead of altering the pilus expression, we certainly have isolated genes that phenotypically do confer an RNA bacteriophage resistance phenotype

to bacteria. These data therefore present an optimistic view that our screening strategy might still be useful in identifying RNA bacteriophage resistance genes.

## **Results:**

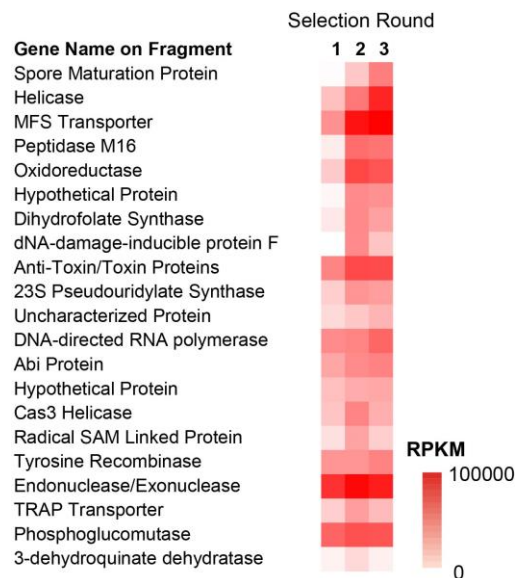
### **A functional metagenomic screen identified antiviral candidate genes**

To identify genes that can restrict RNA bacteriophages, I have employed a functional metagenomics approach. This approach involves extracting and expressing a library of metagenomic DNA fragments within a tractable *E. coli* model (HfrH dhuA) in which each bacterium expresses a sequence fragment from a member of the microbiome. This population can then be challenged with the RNA bacteriophage, Escherichia virus Q $\beta$ , which will lyse non-resistant bacteria and leave only functionally resistant bacteria. The expressed metagenomic DNA fragments conferring functional resistance is then subsequently sequenced, resulting in the identification of metagenomic DNA fragments that confer resistance to RNA bacteriophages. I used a previously generated metagenomic library developed by the Dantas lab, to identify novel RNA bacteriophage resistance genes. To control for fragments that induced cell growth as opposed to conferring phage resistance, I included a set of bacteria that was transformed with the same set of metagenomic fragments but were not infected with Q $\beta$ . Additionally, to ensure any resistance phenotype we observed in the screen was being conferred by the plasmid and not a background mutation on the *E. coli* genome, we performed the Q $\beta$  screen serially three times, isolating the plasmids selected from the previous infection to use in the next one. To account for these controls, multiple inclusion criteria were set to define a metagenomic fragment as possibly antiviral:

- The fragment must be represented in the third selection group
- The fragment must contain be ten times more abundant in the third selection than in the first selection
- The fragment must increase in relative abundance with each subsequent selection

- The fragment must be larger than 500 base pairs

From this screen, we identified 4 fragments that were significantly enriched in the phage treated populations: a spore maturation protein (SpoM) from a *Prevotella* species, a helicase domain containing gene that is distantly related to one from a *Clostridium* species, a Major facilitator superfamily transporter from *Megasphaera eldensii*, and a M16 Peptidase from a *Clostridium* species (Figure 4.1). None of these genes have been previously characterized, but they are related to genes that do have functional annotations.



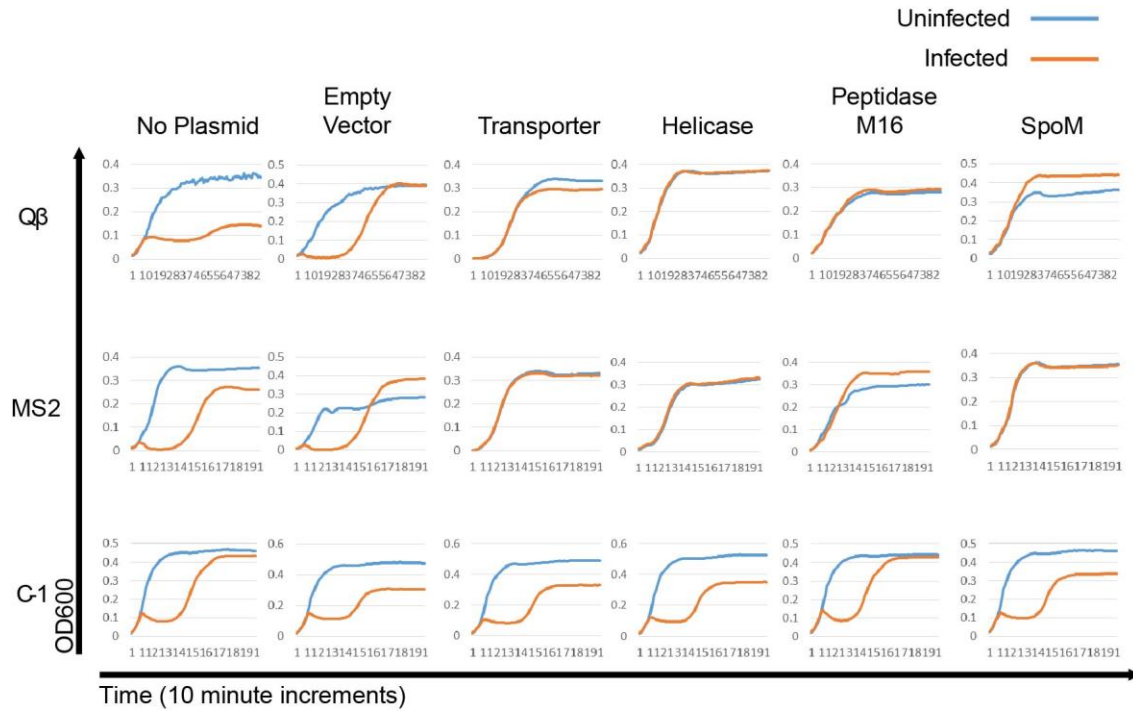
**Figure 4.1.** RPKM abundance of metagenomic fragments in each selection round.

### Metagenomic fragments protect cells from Q $\beta$ and MS2 infection but not C-1

To validate whether these genes could confer a resistance phenotype to *E. coli*, we overexpressed these genes in HfrH dhuA and monitored bacterial density in the context of Q $\beta$  and MS2. Normally, when a susceptible population of bacteria is infected with phage, there is a point at which phage lysis outpaces bacterial cell growth. However, I found that when any of these 4 fragments were overexpressed in *E. coli*, the phage lysis never outpaced cell growth and thus displayed the same growth kinetics as uninfected bacteria (Figure 4.2). This lack of lysis suggests that these genes can confer resistance to Q $\beta$  infection.



We similarly found that all four fragments could confer resistance to MS2 infection. To assess how broadly protective these fragments were to other RNA bacteriophages that did not have the same receptor and host background as Q $\beta$  and MS2, I overexpressed these genes in a different strain of *E. coli*, JE1, that is susceptible to the RNA bacteriophage C-1<sup>11</sup>. I then monitored bacterial density in the context of C-1 phage. None of the four genes provided any resistance to C-1 phage.

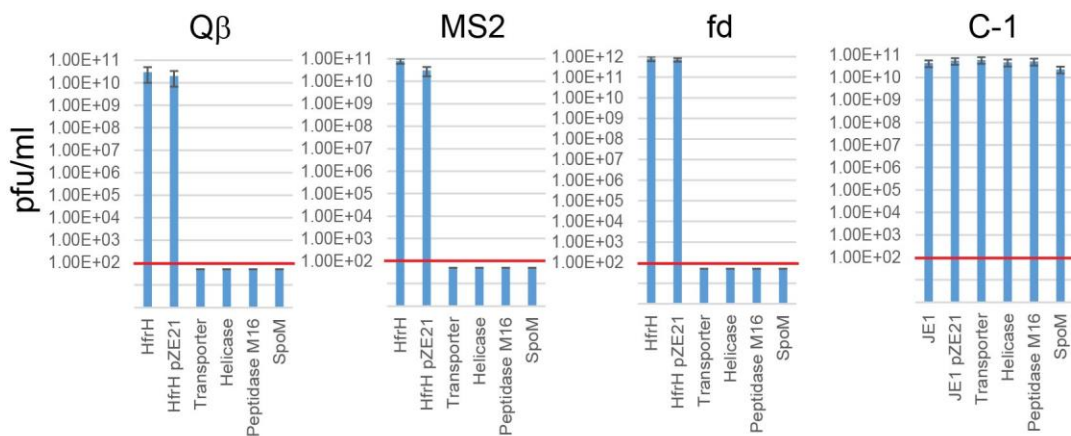


**Figure 4.2.** Q $\beta$ , MS2 and C-1 infection curves with overexpressed metagenomic fragments

### Metagenomic fragments inhibits plaquing of F pilus specific phages but not C-1

To assess whether any of these metagenomic fragments could inhibit the production of infectious RNA bacteriophages, we measured the efficiency of plating of Q $\beta$  and MS2 in the HfrH cells overexpressing these metagenomic fragments. Both Q $\beta$  and MS2 phage production was completely blocked by the overexpression of any of the four fragments (Figure 4.3). Similarly, to assess whether these fragments could inhibit the production of more distantly related phages, we measured the efficiency of plating of C-1 in JE1 cells overexpressing these fragments. We found that none of the fragments

affected the production of C-1 phages from JE1 cells. This complete block in phage production and lysis exclusively in Q $\beta$  and MS2 and not C-1 raised the possibility that these genes might be acting by blocking the proper function of the F pilus rather than targeting an aspect of RNA bacteriophage biology. To begin to decipher whether these fragments were blocking F pilus function, I quantified the efficiency of plating of the non-lytic ssDNA phage, Escherichia virus fd. Like Q $\beta$  and MS2, fd infects *E. coli* cells using the F pilus, but as an ssDNA phage, it has a completely different lifecycle. I found that fd phage production was completely blocked by the overexpression of any of the four fragments.



**Figure 4.3.** Efficiency of plating of Q $\beta$ , MS2, fd and C-1 with overexpressed metagenomic fragments

## Discussion:

Despite the rapid progress in phage resistance mechanisms, an outstanding question in the field is how bacteria resist RNA bacteriophage infection. Here, I attempt to identify the first genes that are capable of conferring resistance to the RNA bacteriophage, Q $\beta$ . By using a functional metagenomic screen, I identified four putative genes that were able to confer a resistance phenotype to both RNA bacteriophages Q $\beta$  and MS2 but not C-1. However, these genes also conferred resistance to the ssDNA phage Fd, which raises the question of whether these genes are specifically resisting RNA bacteriophages or just altering pilus function.

At this time, we cannot definitively state that these genes are altering the F pilus and thus inhibiting phage entry or whether these genes are acting in a direct antiviral fashion. One could argue that because these fragments are effective against only the F specific phages (Q $\beta$ , MS2 and fd) and not C-1 that the most obvious explanation is that the F pilus is somehow altered. This assertion relies on the assumption that it is unlikely that the Q $\beta$ /MS2 are sensitive to the same resistance mechanisms as fd. On the other hand, one could argue that the lack of resistance in C-1 does not necessarily implicate the F pilus, since a different *E. coli* strain (JE1) is used to test C-1. Instead of a receptor, one could argue that the gene carriage of HfrH and JE1 could be fundamentally different, and that these metagenomic fragments might be interacting with genes that are only present in HfrH and not JE1, and thus only effecting their resistance phenotype in HfrH. One could even argue that C-1 phage might have evolved antagonistic proteins that inhibit these resistance genes, and that it is unlikely that any one gene will resist all RNA bacteriophages. The necessary experiment to properly dissect whether these genes are in fact blocking a step in the viral lifecycle post-entry would be to electroporate the genomes of Q $\beta$  and MS2 into HfrH and assess whether overexpression of any of these four fragments inhibits virion production<sup>12</sup>. Because these viruses are all (+)ssRNA viruses, their genomic RNA is naturally infectious and electroporating their genomes into these cells will allow us to test directly how these genes affect translation, replication, assembly and release of these viruses. If Q $\beta$  and MS2 can form the same number of viruses in the control cells and the overexpressed cells, then it would suggest that these genes are blocking entry.

Small improvements could be made to the functional metagenomic screen design in the future to reduce the possibility that we would identify genes that alter pilus function. One very direct improvement that could be made would be to change the host *E. coli* that is used in these experiments. Rather than using an *E. coli* strain that only expresses one receptor on its cell surface, we could construct an *E. coli* strain that both has an F pilus and another compatible pilus that mediates infection of C-1 phage. The

functional metagenomic screen would then be performed using both Q $\beta$  and C-1, thus forcing only metagenomic fragments that could resist both phages to be selected.

### **Materials and Methods:**

**Strains:** HfrH dhuA was a gift from Ryland Young and served as hosts for the functional metagenomic screen, infection curves (for Q $\beta$  and MS2), and lawns for bacteriophage plating (for Q $\beta$ , MS2 and fd). JE1 served as hosts for the C-1 phage infection curves and lawns for C-1 bacteriophage plating. *E. coli* C3000 was used for phage propagation of Q $\beta$ , MS2 and fd. *E. coli* strains were grown under aerobic conditions at 37 uC in standard Luria–Bertani (LB) medium. For infections, this medium was supplemented with 10 mM CaCl<sub>2</sub>. Q $\beta$ , MS2, and fd were all acquired from the American Type Culture Collection and phage C-1 was acquired from the Félix d'Hérelle Reference Center for bacterial viruses of the Université Laval.

**Functional metagenomic screen:** A plasmid library of metagenomic fragments was electroporated into HfrH dhuA. These cells were incubated in SOC media for 1 hour to recover and then transferred to 10 mL of LB supplemented with 10 mM CaCl<sub>2</sub>. These cultures are then either infected with Q $\beta$  at an MOI = 10 or left untreated. After 24 hours, the plasmids from these cultures were extracted using a Qiagen Miniprep kit. As the susceptible host (HfrH dhuA K-12 *E. coli*) is spontaneously resistant to Q $\beta$  infection at a rate of 1:10<sup>4</sup>, I performed 3 serial selections on the population of metagenomic plasmids to ensure any resulting genes identified were in fact conferring phage resistance. The metagenomic inserts were then amplified using conserved primers to the vector backbone. These amplified regions were then constructed into libraries using the NEBNext protocol and sequenced on an Illumina MiSeq 250. Sequencing data was assembled using IDBA and reads were mapped to contigs using Bowtie. RPKM values were calculated using samtools and custom scripts.

**Infection Growth Curve:** Overnight cultures were back diluted, grown to mid-log phase and then back diluted to an OD<sub>600</sub> = 0.1. 100 uL of backdiluted culture was then added to a 96 well plate. Viruses were diluted All infectious were performed at an initial MOI = 0.1.

**Efficiency of Plating Assay:** The double overlay plaque assay was used as previously described<sup>13</sup>.

Briefly, overnight cultures were back diluted grown to mid-log phase and then added to 10 mL of a molten soft agar overlay. 10 uL of a phage suspension serially diluted ranging from  $10^{10}$  pfu/ml to  $10^2$  pfu/ml was then added to the soft agar and bacterial suspension, and then plated onto hard agar. Plates were incubated aerobically overnight at 37 C and plaques were counted manually the next day. Soft agar was made up of LB + 10 mM CaCl<sub>2</sub> and 0.4% agar. Hard agar was made up of LB + 10 mM CaCl<sub>2</sub> and 1% agar.

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5. Picobirnaviruses are a possible novel family of RNA bacteriophages

## Introduction

One of the major limitations of the massive expansion of RNA bacteriophages described previously is that it relied on alignment<sup>1,2</sup>. This reliance on alignment means that all the novel RNA bacteriophages are somehow related to a known, previously cultured, RNA bacteriophage. This reliance is problematic because as mentioned before, only two viral families of RNA phages have been identified, the *Leviviridae* and *Cystoviridae*. The paucity of known RNA viral families of bacteria is somewhat strange, as this trend is not mirrored among the eukaryotic RNA viruses, in which there are over 30 families of RNA viruses. Therefore, I wanted to see if I could identify a novel family of RNA bacteriophages that were unrelated to the previous two families of RNA bacteriophages. There are some ecological and genomic clues we could look for to identify this family. Namely:

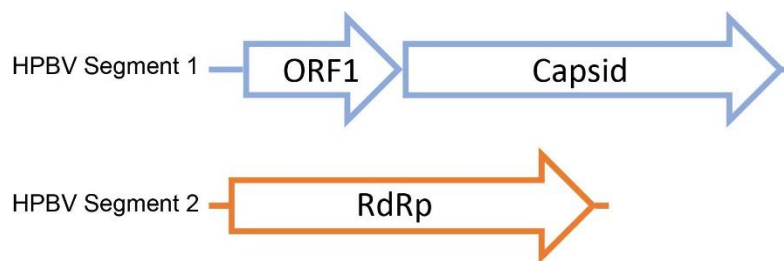
1. Viruses in this putative family would be present in ecological niches that contain or are adjacent to bacteria
2. Viruses in this putative family would be identified in sequencing studies that analyzed RNA and not in those that sequence DNA
3. Viruses in this putative family would ideally contain genomic signatures consistent with bacterial infection
4. Viruses in this putative family would ideally contain viral genes consistent with an RNA virus (an RNA dependent RNA polymerase, etc.)

Through analysis of our previously sequenced data, I identified that a commonly identified viral family, the *Picobirnaviridae*, fulfilled these criteria.

Picobirnaviruses are a family of bisegmented double stranded RNA viruses that are highly prevalent in mammalian stool samples<sup>3-5</sup>. Picobirnaviruses are thought to encode three genes: and RNA-dependent RNA polymerase gene encoded on Segment 2, a capsid gene encoded on Segment 1 and an ORF of unknown function also encoded on Segment 1 (Figure 5.1)<sup>6,7</sup>. Despite their high prevalence in



stool samples of a variety of animals, they have yet to be associated consistently with any disease<sup>8-12</sup>. Currently, it is primarily thought that picobirnaviruses infect mammalian cells; however, this idea is only based on the fact that this virus is primarily found in mammalian stool. No group has cultured this virus in any mammalian cell line. As picobirnaviruses are most closely related to the unicellular eukaryote infecting partitiviruses, some labs have hypothesized that these viruses might infect the unicellular eukaryote cryptosporidium<sup>6</sup>.



**Figure 5.1.** Genome organization of Human Picobirnavirus

Here, we present comparative genomic evidence that picobirnaviruses might be an unrecognized family of RNA bacteriophages. By mining previously sequenced data, I was able to identify 41 novel picobirnavirus sequences. These sequences were highly divergent from each other and in general shared no nucleotide similarity. Through comparative analysis of among the novel and known picobirnavirus genomes, we found that almost all picobirnaviral genomes contained bacterial ribosomal binding site (RBS) sequences upstream of each open reading frame. This prevalence of RBS sequences suggests that picobirnaviruses infect bacteria rather than animals. We aimed to establish whether Human Picobirnavirus (HPBV) can replicate and package in bacteria.

## Results

### Identification of multiple new sequences related to picobirnaviruses

Comparative genomics is strongest when the analysis contains a large number of sequences from highly diverse organisms in the same taxon of interest. Therefore, I wanted to maximize the number of

picobirnavirus sequences I had to analyze. To do this, I mined local datasets for novel picobirnaviruses as previously described for RNA bacteriophages<sup>2</sup>. From this effort, I was able to assemble 41 novel contigs that contained ORFs that aligned to known picobirnaviruses; with 21 contigs containing ORFs that aligned to the RNA dependent RNA polymerase on Segment 2 and the other 20 contigs containing ORFs that aligned to proteins encoded on Segment 1. None of these contigs aligned to any other contig with greater than 75% nucleotide identity across the whole contig, or to any known picobirnavirus genome.

### **Enrichment of bacterial RBS in picobirnaviruses**

Unlike eukaryotic mRNA, bacterial mRNA contains defined nucleotide sequences upstream of each ORF that allows the ribosome to bind and initiate translation<sup>13-15</sup>. In most bacterial this sequence is some 4-mer or greater of the sequence AGGAGG. RNA bacteriophages also encode and conserve these RBS sequences, with the first RBS sequence even being defined in the RNA bacteriophage MS2<sup>15</sup>. Therefore, the presence of a conserved RBS sequence would be suggestive that a family of RNA viruses were in fact bacteriophages. We analyzed the frequency of RBS sequences in all known and novel picobirnaviruses. Excepting ORF1 of Turkey Picobirnavirus, every ORF contained a 5-mer RBS sequence 5' to the predicted methionine start codon (Figure 5.2). This conservation is not an artifact of nucleotide sequence similarity, as the surrounding regions of the RBS sequence are not conserved. We then wanted to see if this enrichment for ribosomal binding sequences was specific to picobirnaviruses or a feature of all eukaryotic RNA and DNA viruses. Therefore, we assessed the prevalence of RBS sequences in known eukaryotic viruses and found that only 117 out of 2585 UTR sequences contained an RBS 5-mer sequence. Under optimal conditions the probability of at least one RBS 5-mer occurring by chance in a random 20 nucleotide sequence is 0.031, which means for 2585 independent sequences, random association would indicate that 80 sequences would have a 5-mer RBS sequence, with an estimated variance of 110. From a viral genomic perspective, no eukaryotic viral genome had more than 50% of their ORFs preceded by 5-mer RBS sequences (Figure 5.3). We additionally wanted to compare

the prevalence of RBS sequences in picobirnaviruses to the prevalence in bona fide bacteriophages. Therefore, we assessed the prevalence of RBS sequences in known bacteriophages and found that predictably, a much higher percentage of bacteriophage ORFs are preceded by RBS sequences. We additionally analyzed eukaryotic virus and bacteriophage genomes for the frequency of 4-mer and 6-mer RBS sequences, and consistently found that prevalence of RBS sequences is an identifying factor for bacteriophage genomes, relative to eukaryotic viruses. Overall, the fact that picobirnaviruses tend to have bacterial RBS sequences suggests that they are more genomically similar to bacteriophage genomes rather than eukaryotic RNA viruses.

### RNA-dependent RNA Polymerase

Species	5' UTR
Human Picobirnavirus 0	AGGAGGT-TT-A-CT--ATG
Human Picobirnavirus 1	AGGAGGT-TT-A-CT--ATG
Human Picobirnavirus 2	AGGAGG--CTTCATT--ATG
Human Picobirnavirus 3	AGGAGG--ACTACTT--ATG
Human Picobirnavirus 4	AGGAGG--ACTACTT--ATG
Human Picobirnavirus 5	AGGAGGT-CATTGAC--ATG
Human Picobirnavirus 6	AGGAGGT-TACGATT--ATG
Human Picobirnavirus 7	AGGAGGT-TATTCTT--ATG
Human Picobirnavirus 8	AGGAGG--CTTCTA--ATG
Monkey Picobirnavirus 0	AGGAGGT-TAGTCT--ATG
Monkey Picobirnavirus 1	AGGAGGT-TAGTCT--ATG
Equine Picobirnavirus 0	AGGAGGT-TAGG-TT--ATG
Equine Picobirnavirus 1	AGGAGGT-TAAG-CT--ATG
Fox Picobirnavirus	AGGAGG--CTATCAC--ATG
Bovine Picobirnavirus	AGGAGGA-CTACAA--ATG
Otarine Picobirnavirus	AGGAGG--CCTATCAC-ATG
Turkey Picobirnavirus	AGGAGGT-CATTGATG
Novel Picobirnavirus	AGGAGGT-TTCTT--ATG
Novel Picobirnavirus	AGGAGGT-GCTACTCTAG
Novel Picobirnavirus	-GGAGG--AGTAAACCATG
Novel Picobirnavirus	AGGAGGT-TTACT--ATG
Novel Picobirnavirus	AGGAGGT-TATT--ATG
Novel Picobirnavirus	AGGAGG--CACATA--ATG
Novel Picobirnavirus	AGGAGG--AGAAA--ATG

### Known Picobirnaviruses Novel Picobirnaviruses

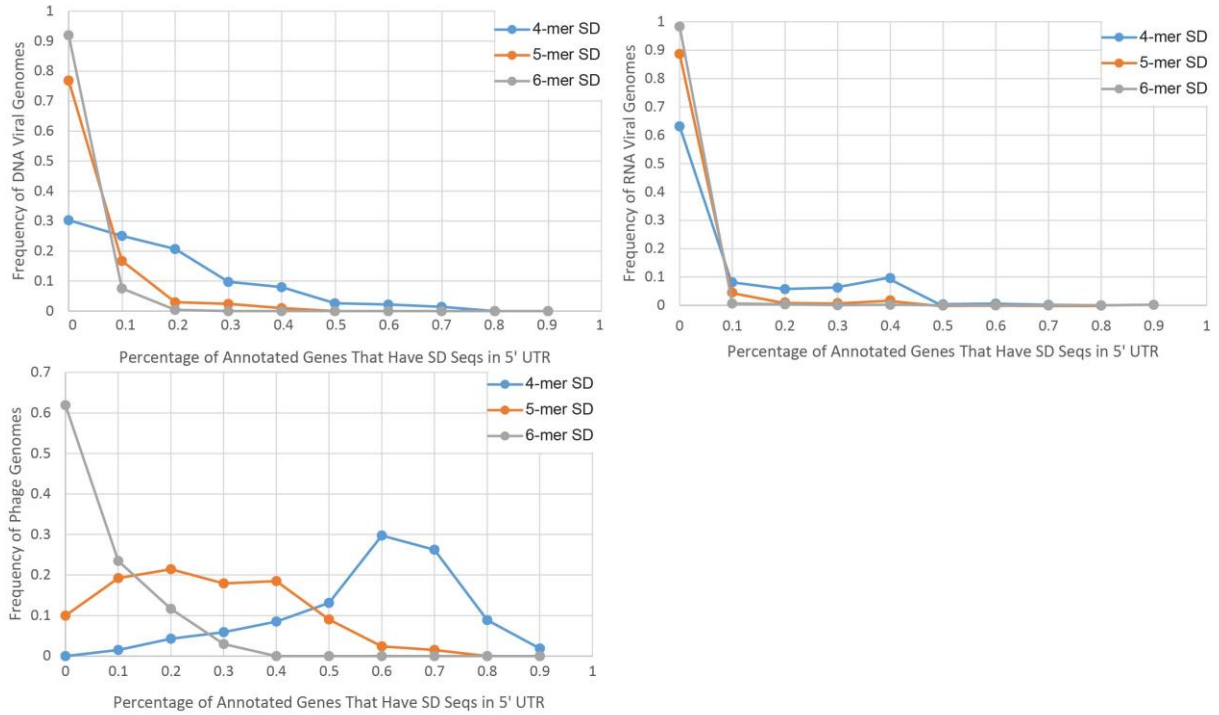
### Capsid Species

Species	5' UTR
Human Picobirnavirus 0	AGGAGGT-AATA-AAT--ATG
Human Picobirnavirus 1	AGGAGGT-T--T-ATC--ATG
Human Picobirnavirus 2	AGGAGGT-T--C-AAA--ATG
Equine Picobirnavirus 0	AGGAGG--ATTG--ATG
Equine Picobirnavirus 1	AGGAGGT-ATTGATT--ATG
Porcine Picobirnavirus 0	-GGAGG-CT--AAT--ATG
Porcine Picobirnavirus 1	AGGAGGT-A-TA-ATT--ATG
Porcine Picobirnavirus 2	AGGAGGT-A-TA-ATT--ATG
Turkey Picobirnavirus	-GGAGG--AATTATCG--ATG
Fox Picobirnavirus	AGGAG--CCT-A-ATT--ATG
Rabbit Picobirnavirus	AGGAGGT-A--A-AT--ATG
Novel Picobirnavirus	AGGAGGT-TCAT--ATG
Novel Picobirnavirus	AGGAGGG-CATACC--ATG
Novel Picobirnavirus	AGGAGGT-AATATA--ATG
Novel Picobirnavirus	AGGAG--AATTATTAT--ATG
Novel Picobirnavirus	AGGAGGT-CCATTACG--ATG
Novel Picobirnavirus	AGGAGGT-CTATA--ATG
Novel Picobirnavirus	AGGAGGT-AGTATA--ATG
Novel Picobirnavirus	AGGAGGG-TATACC--ATG
Novel Picobirnavirus	AGGAG--AGTCTAGT--ATG
Novel Picobirnavirus	AGGAG--AAAVPAAT--ATG
Novel Picobirnavirus	AGGAGGT-TACT--ATG
Novel Picobirnavirus	AGGAGGT-AGACAA--ATG
Novel Picobirnavirus	AGGAGGT-ACTGTT--ATG
Novel Picobirnavirus	AGGAGG--ACTTACA--ATG
Novel Picobirnavirus	AGGAG--TGCTTAT--ATG
Novel Picobirnavirus	AGGAGGT-CAGTCG--ATG
Novel Picobirnavirus	AGGAGGT-ATAGTAAT--ATG
Novel Picobirnavirus	AGGAGGT-TAAAC--ATG

### ORF1

Species	5' UTR
Human Picobirnavirus 1	AGGAGGT---TATTTA---ATG
Human Picobirnavirus 2	AGGAGGT-GGTAATC---ATG
Equine Picobirnavirus 1	AGGAGG--AACCTAATA--ATG
Equine Picobirnavirus 2	AGGAGG--AAAG--ATG
Turkey Picobirnavirus	AGGAATG-GACAAC--ATG
Porcine Picobirnavirus 1	AGGAGGT-GAAAGTT---ATG
Porcine Picobirnavirus 2	AGGAGGT---ATATT---ATG
Porcine Picobirnavirus 3	AGGAGGT---ATATT---ATG
Fox Picobirnavirus	AGGAGGT---ATTCTA---ATG
Rabbit Picobirnavirus	AGGAGGT-GTCAATG---ATG
Novel Picobirnavirus	AGGAGGT-TGCT---ATG
Novel Picobirnavirus	AGGAGG--AATCATTT---ATG
Novel Picobirnavirus	AGG--GT-GTACAGAT--ATG
Novel Picobirnavirus	AGGAGAT-GTCTTATT---ATG
Novel Picobirnavirus	AGGAGG--AAATCTAAGG-ATG
Novel Picobirnavirus	AGGAGGT-CTT-----ATG
Novel Picobirnavirus	AGGAGGT-AAGAAC-----ATG
Novel Picobirnavirus	AGGAGG--ATGCCTA---TTG
Novel Picobirnavirus	-GGAGG--ATCAGTC---ATG
Novel Picobirnavirus	AGGAGG--AAACTCACAC-ATG
Novel Picobirnavirus	AGGAGG--AGAT-----ATG
Novel Picobirnavirus	AGGAGG-AACTCAC-----ATG

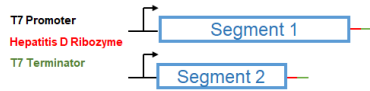
Figure 5.2. Alignment of RBS sequences among known and novel picobirnaviruses



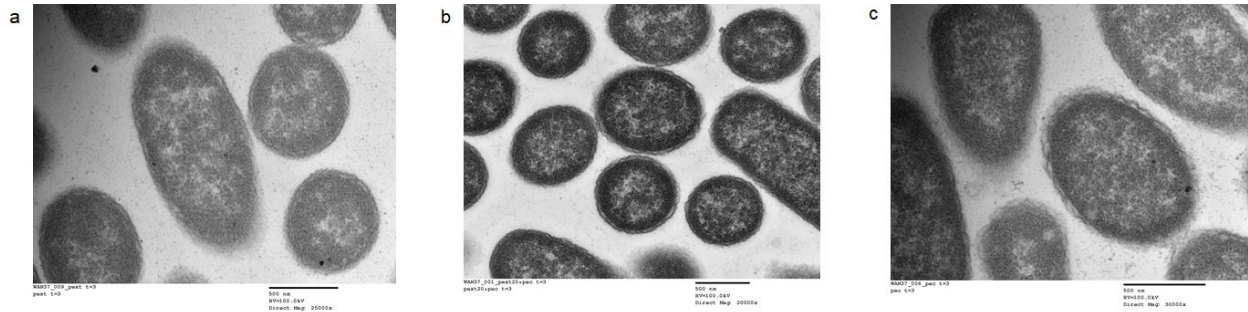
**Figure 5.3.** RBS sequence enrichment among eukaryotic DNA and RNA viral sequences and bacteriophages

### Construction of a HPBV reverse genetic system

We then wanted to assess whether we could demonstrate picobirnaviruses could undergo steps within its lifecycle in a bacterial cell. To do this, we constructed a reverse genetic system for the prototype picobirnavirus, Human Picobirnavirus (HPBV). The reverse genetic system consisted of two plasmids that each contained a viral segment under the control of the T7 promoter and with the 3' end under the control of the hepatitis D ribozyme and T7 terminator (Figure 5.4). We transformed these plasmids into the *E. coli* strain BL-21(DE3), as this strain expresses the T7 RNA polymerase under the lac promoter. To assess packaging, we induced BL-21(DE3) cells transformed with either HPBV Segment 1, HPBV Segment 2, or both HPBV Segment 1 and 2 and then attempted to visualize viral like particles by transmission electron microscopy (TEM) after inducing these cells with IPTG. We visualized no VLPs (Figure 5.5).



**Figure 5.4.** Schematic of initial HPBV reverse genetics system

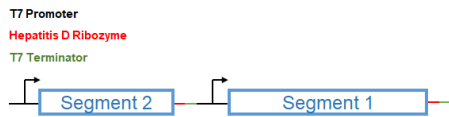


**Figure 5.5.** Transmission electron microscopy of the overexpressed picobirnaviral segments. a) Segment 1 b) Segment 2 c) Segment 1 and Segment 2

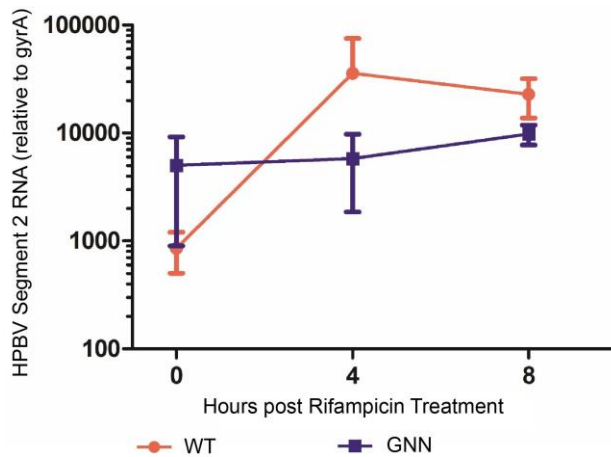
### **Enhanced HPBV genomic replication cannot be detected in *E. coli* cells**

To assess whether HPBV could replicate its genome, we measured HPBV RNA levels in bacterial cells by qRT-PCR. To do this, we wanted to perform a form of pulse-chase experiment, in which we induce bacterial cells to express the HPBV genome, block host cell transcription and then assess whether HPBV RNA levels continue to increase. As the wildtype genomic RNA levels are contributed to both by the transcription of RNA from the plasmid, the stability of the RNA in the cell, as well as RNA replication by the virus, we included a mutant HPBV Segment 2 that contains two mutations in the RdRp at the catalytic GDD residues converting them to GNN. This mutant RdRp will be unable to replicate RNA and any RNA detected in this mutant will be completely from plasmid transcription. Additionally, we needed to move the reverse genetic constructs into the low copy plasmid, pMLBAD, as the RNA extracted from cells containing the high copy plasmids was also routinely contaminated with plasmid DNA, confounding any measurement of RNA from these cells. This construct now contains both segments on the same plasmid in tandem, maintaining the T7 promoters, HDV ribozyme and T7 Terminator control structures (Fig 6). Finally, to reduce the amount of de novo transcription occurring

from the plasmids, we treated the cells with the antibiotic rifampicin, which inhibits the host RNA polymerase. Therefore, HPBV Segment 2 RNA levels should be primarily determined by the RNA dependent RNA polymerase. We transformed both wildtype and GNN mutant constructs into BL-21(DE3) cells and induced the cells with IPTG to initiate transcription for 15 minutes, washed the cells twice with LB and treated the cells with rifampicin. We did not observe consistently higher levels of RNA in the wildtype cells over the mutant virus.



**Figure 5.6.** Schematic of low copy HPBV reverse genetics system

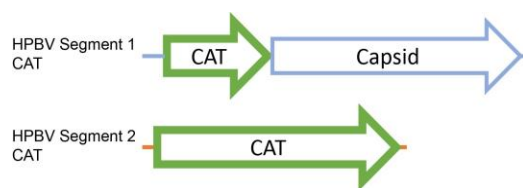


**Figure 5.7.** HPBV2 WT Segment 2 does not decrease slower than the catalytically dead mutant

### Construction of a HPBV replication reporter system

Because we could not assess replication directly by measuring transcript, we wanted to test whether we could indirectly prove that HPBV was replicating by constructing a replicon system. What this would involve is constructing a carrier state bacterium, in which the viral RNA replicates as a stable episome in the host bacterium while expressing reporter genes such as chloramphenicol resistance<sup>16</sup>. To do this, we constructed new constructs of the HPBV viral segments, placing chloramphenicol acetyl-

transferase (CAT) into the HPBV genome in place of either the RNA-dependent RNA polymerase on Segment 2 or ORF1 on Segment 1 (Fig 8). Expression of both of these constructs stably in *E. coli* BL-21(DE3) cells yielded chloramphenicol resistant colonies, suggesting that expression of these RNA segments is sufficient to make cells chloramphenicol resistant. To construct the carrier state, we put these constructs on a pi-dependent plasmid, which can transcribe RNA in *E. coli* but will not replicate in cells that lack the Pi replication factor (including BL-21(DE3) cells). This system allows us to temporarily express the modified genome fragments and have the plasmid lost. This way, any maintenance of the modified genomic RNA and chloramphenicol resistance must be maintained by viral replication. Transformation of these segments in combination with the HPBV Segment 2 wildtype yielded no chloramphenicol resistant colonies.



**Figure 5.8.** Schematic of HPBV constructs containing chloramphenicol resistance genes

## Discussion

It is possible that there are additional RNA bacteriophage families that have yet to be discovered. The viral family of *Picobirnaviridae* could be one of those families. Here, we use a comparative genomic approach to show that picobirnavirus genomes are enriched for a bacterial specific signature, specifically, the RBS sequence. We show that this enrichment is specifically found in picobirnaviruses and not generally in eukaryotic RNA viruses and that this sequence is also enriched in bacteriophage genomes. We then unsuccessfully try to demonstrate that a prototypical picobirnavirus, HPBV, can replicate in bacterial cells.

The inability to show that HPBV can replicate in *E. coli* is not evidence that picobirnaviruses are eukaryotic viruses, as there are numerous reasons why we might not detect any sign of HPBV replication. One such assumption that this line of experimentation relies on is that all the host factors required for HPBV replication are conserved and present in *E. coli*. There is supporting literature that this conservation might be true for the other families of RNA phages, in which only a compatible receptor determines susceptibility of a bacteria to a phage<sup>16,17</sup>. However, these experiments have largely only been done within one taxon: the  $\gamma$ -proteobacteria. It is unknown whether the genes of more distantly related bacteria are conserved sufficiently to support viral replication.

The ultimate evidence to demonstrate that picobirnaviruses are in fact RNA phages would be to identify a bacterium that could propagate any individual picobirnavirus. Identifying such a host is methodologically challenging for a variety of reasons. A majority of the bacteria in the gut are not culturable, which by extension also means their phages are also not culturable. If picobirnaviruses infect one of these non culturable bacteria, then even a systematic screen of all culturable gut bacteria will not identify the host of a picobirnavirus. As a way to narrow down bacterial strains to screen, it is tempting to suggest that 16S rRNA data can be mined to identify bacterial operational taxonomic units (OTUs) that are correlated with picobirnavirus presence. However, this reasoning relies on the assumption that bacteriophages in the stool are sampled from the same space as their bacterial hosts, namely the colon. It is possible that even though the majority bacterial species in stool are sampled from the colon, bacteriophages in stool might be more evenly sampled from all parts of the GI tract. Therefore, the host of picobirnavirus might not even be present in a microbiome sequencing dataset.

There is, however, precedent for systematically identifying hosts of bacteriophages from complex microbial communities. One group constructed a limiting dilution system with microfluidics and used digital PCR to screen, in a high throughput fashion, individual bacterial cells for the presence of a specific DNA phage<sup>18</sup>. By isolating single cells and fluorescently amplifying both the 16S rRNA gene and their



viral marker gene of interest, they can rapidly identify wells that have both a bacteria and their virus of interest, and sequence the 16S rRNA amplicon to identify which bacterium was in that well. Although this was done using a DNA phage as a viral target, one could probably re-engineer this system to work with RNA phages.

## **Materials and Methods**

**Identification of Novel Picobirnaviral Sequences:** Novel picobirnavirus sequences were identified as previously described for other RNA bacteriophages, except the query sequences were the amino acid sequences of all known picobirnaviruses. The sequences used were ORFs derived from the following accessions: KR902502.1, KR902506.1, KF861768.1, KJ495689.1, AB186897.1, KF861772.1, JQ776552.1, AB828072.1, KJ495690.1, AB517734.1, AF246940.1, KF823811.1, KM573790.1, KM573787.1, KM573780.1, KM573789.1, KC692366.1, KJ663814.1, AB517736.1, AB517732.1, KM573800.1, GU968924.1, KM573801.1, KM573802.1, KM573795.1, AB517733.1, AB517735.1, AB517737.1, KM573794.1, KM573799.1, KM573781.1, AB517739.1, KM573785.1, AB517738.1, AF246941.1, KM573782.1, KF823810.1, KM573779.1, KM573798.1, KM573791.1, KM573808.1, KM573786.1, KJ206569.1, KM573804.1, HM070240.1, KM573807.1, NC\_007026.1, NC\_007027.1

**Analysis of RBS Presence in Picobirnaviruses:** The proximal 20 nucleotides of the 5'UTR relative to the start codon of each ORF (RdRp, Capsid, ORF1) was isolated from a manually curated list of picobirnaviral sequences. Using custom scripts I analyzed the sequences for the presence of RBS 4-mers (AGGA|GGAG|GAGG), 5-mers (AGGAG|GGAGG) or 6-mers (AGGAGG).

**Analysis of RBS Presence in Phages and Eukaryotic RNA Viruses:** Genbank files were retrieved from all deposited viruses within established eukaryotic RNA viral families and established bacteriophage taxa. The proximal 20 nucleotides of the 5'UTR relative to the annotated start codon of each ORF was retrieved and analyzed for the presence of RBS 4-mers (AGGA|GGAG|GAGG), 5-mers (AGGAG|GGAGG) or 6-mers (AGGAGG).

**HPBV reverse genetic system:** Both genomic segments of HPBV were ordered from IDT as gBlocks, with T7 promoter directly 5' to the genome segments, and the HDV ribozyme and T7 terminator directly 3'. HPBV Segment 1 was cloned into the high-copy plasmid pEXT20 (ampicillin resistant) and HPBV Segment 2 was cloned into the medium-copy plasmid pEC (kanamycin resistant). Expression of these plasmids was performed in BL-21(DE3) cells. For the low copy reverse genetic system, HPBV segment 2 and segment 1 were cloned between the KpnI and HindIII in the pMLBAD vector. The chloramphenicol acetyl transferase gene (CAT) was cloned into the pEXT-HPBV-Segment2 and pEC-HPBV-Segment1.

**HPBV VLP visualization:** BL-21(DE3) cells were transformed with their respective plasmid set and grown overnight in LB with appropriate antibiotics. These cultures were then back-diluted to an OD<sub>600</sub> = 0.1 and grown to mid-log phase, at which point they were induced with 0.1 mM of IPTG for 2 hours. Cells were then pelleted and negatively stained with uranyl acetate and visualized on using a transmission electron microscope.

**HPBV Segment 2 replication assays:** BL-21(DE3) cells were transformed with their respective plasmid set and grown overnight in LB with appropriate antibiotics. These cultures were then back-diluted to an OD<sub>600</sub> = 0.1 and grown to mid-log phase, at which point they were induced with 0.1 mM of IPTG for 15 minutes, washed the cells twice with LB and treated the cells with 0.1 mg/ml rifampicin. Intracellular RNA was isolated using Trizol-Chloroform and measured HPBV segment 2 was measured using qRT-PCR and normalized to the housekeeping gene *gyrA*. HPBV2 primers were as follows, Forward: TAGCATGGAAGCTGTTGATAGG, Reverse: CACTCTGGCACGTTGGATTA, Probe: /56-FAM/ACAGACTTC/ZEN/TCCAAGTTCGACCAGC/3IABkFQ/. *gyrA* primers were as follows, Forward: CAG GAT ATG GTC GTG GGT ATT C, Reverse: CTC TCA CCA GGG TTA CGT TAA G, Probe: /56-FAM/AG ATT TAC C/Zen/T TTC CCG CCA CGA CG/3IABkFQ/. qRT-PCR was performed with the Taqman Fast Virus 1-step mastermix.

**Chloramphenicol reporter assay:** Chloramphenicol resistance was measured by the ability to for cells to grow on LB/agar plates supplemented with 25  $\mu\text{g/mL}$ .

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## 6. Conclusions and Future Directions

With the recognition that communities of highly diverse viruses are associated with mammals, the next step is to understand how these viral communities impact mammals. However, to completely understand the role of the virome, it is critical to be able to identify as many viral sequences as possible. The ability to identify all viruses within the virome remains a major challenge in identifying the role of the virome in health and disease<sup>1,2</sup>. Although numerous challenges still are present on the experimental side, there are still computational challenges in identifying viruses from deep sequencing data. These challenges include the lack of diversity among the microbial viruses as well as the reliance on amino acid and nucleotide based alignment metrics to identify viruses. Here, I address these computational limitations to massively expand the diversity of microbial viruses, and then use this massive expansion as a justification to pursue broader experimental questions related to microbial virology.

I recognized the under representation of known RNA bacteriophages, and by directly mining previously sequenced data, I was able to identify 122 novel RNA bacteriophages<sup>3</sup>. Although it is unclear why the RNA bacteriophages were so vastly underrepresented, there might be methodological biases in previous bacteriophage discovery studies. Classically, bacteriophages were discovered through the use of enrichment cultures and plaque assays. When samples are collected to propagate virus, they often undergo numerous steps to purify VLPs before they are used to plaque virus. These steps include enrichment on susceptible hosts, concentration by tangential flow filtration or centrifugation, filtration through 0.2 um filters, and chloroform treatments to reduce bacterial contamination<sup>4-14</sup>. Any of these steps, but particularly the chloroform treatment and culture enrichment, might reduce the ability to culture of RNA bacteriophages. This idea is especially relevant since I know one family of RNA bacteriophages,

the *Cystoviridae*, are enveloped virus, which means that they would be inactivated by chloroform treatment<sup>15</sup>. Methods that do not excessively alter environmental samples are likely to enable the culture of novel, diverse viruses. This principle has been demonstrated by the culture of novel, aggregating large dsDNA viruses, which were cultured by directly plating soil, without any processing or removal of contaminating bacteria, into top agar<sup>16,17</sup>. The expansion of bacteriophage culture systems as well as the expansion of hosts that are being used to propagate bacteriophages will lead to more diverse bacteriophages being cultured, perhaps even viruses from the family *Picobirnaviridae*.

With the expansion of RNA bacteriophages, I attempted to identify genes that could restrict RNA bacteriophage infection. Although I were not able to definitively identify any genes that could directly restrict RNA bacteriophages, my functional metagenomics screen did identify genes that did prevent bacterial cells from being lysed by RNA bacteriophages. While I could theoretically continue to screen metagenomic fragments to find a bona fide RNA bacteriophage restriction gene, I could take more classic approaches to identify these genes. One such approach would be taking large banks of bacterial isolates and identify bacterial isolates that are resistant to RNA bacteriophage infection. Once these bacterial isolates are isolated, I could identify the bacterial genes mediating this resistance by performing transposon mutagenesis.

I then try to move beyond alignment to discover novel viruses by creating an alignment independent algorithm that identifies viral sequences using k-mer frequencies, DiscoVir. I then applied DiscoVir to an authentic metagenomic dataset to identify viral segments from a novel bunya-like virus, which I call Discovirus. Discovirus represents the first segmented negative-stranded RNA virus present in a fungus, which fundamentally expands the virological diversity

recognized within fungi. Although in my study, I used DiscoVir to identify a novel virus within my own dataset, there is no reason why I could not apply DiscoVir to public metagenomic datasets to identify sets of contigs that are likely to originate from viruses. The major issue in this approach, however, is validating that these contigs are in fact from viruses, through more classical systems like culture. This necessity to culture novel viruses with genomes that do not align to known viruses is especially problematic, because the organisms that host of these viruses will not necessarily be clear.

A common challenge that has recurred throughout multiple parts of my dissertation has been the ability to identify a host for a specific novel virus and set up a culture system for that virus. This challenge manifested itself during the identification of Discovirus, during which I needed to culture Discovirus in order to demonstrate that it in fact was a virus. Additionally, during my studies on picobirnaviruses, although I suggested that picobirnaviruses might infect bacteria, it would have been greatly advantageous to actually know which species of bacteria any individual picobirnavirus infected. This knowledge would have allowed me to do more targeted culture experiments to try to propagate picobirnavirus. Going forward, I believe the community will need to develop new experimental tools to more rapidly not only identify novel viruses but also identify the hosts of novel viruses, in a high throughput fashion. This necessity is unique to viruses relative to the other components of the microbiomes, because the role of viruses are generally effected through their hosts. Mammalian viruses directly alter the gene expression of mammalian cells and have the potential to directly cause human disease<sup>18,19</sup>. Bacterial viruses directly alter the physiology of bacteria and can modulate microbial populations<sup>20,21</sup>. These efforts to rapidly identify viral hosts are already underway, with studies that use Hi-C to



crosslink extrachromosomal elements to their host chromosomes. By sequencing these crosslinked samples, groups have been able to identify the hosts of plasmids by identifying plasmid sequences that are concatenated to host sequences<sup>22,23</sup>. As many viruses replicate inside their hosts as plasmids, a direct extension of this method could be used to identify bacteriophage genomes in a high throughput manner. The underlying philosophy of crosslinking viral genomes to host nucleic acid can also likely be translated to RNA viruses, by using a version of RNA cross-linking, ligation and sequencing hybrids (CLASH)<sup>24</sup>. The knowledge of what a virus infects allows not only the practical advantage of being able to experimentally manipulate the virus, but it can also lead to better hypotheses on its role in the virome.

The ultimate goal of identifying novel viruses is to understand their role biological processes, including ecology and human disease. With this broader appreciation of the diversity of viruses, future studies focused on the interaction between the virome and mammalian host will hopefully take into account the more diverse set of microbial viruses presented here.

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## Appendix I. List of SRA Files Scanned for RNA Bacteriophages

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## Appendix II. Taxonomy Breakdown for DiscoVir Analysis

## **Viruses**

Adenoviridae, Alphetetraviridae, Alvernaviridae, Amalgaviridae, Anelloviridae, Arenaviridae, Ascoviridae, Asfarviridae, Astroviridae, Baculoviridae, Barnaviridae, Benyviridae, Bidnaviridae, Birnaviridae, Bromoviridae, Bunyaviridae, Caliciviridae, Carmotetraviridae, Caulimoviridae, Chrysoviridae, Cilevirus, Circoviridae, Closteroviridae, Emaravirus, Endornaviridae, Flaviviridae, Geminiviridae, Hepadnaviridae, Hepeviridae, Herpesvirales, Higrevirus, Hypoviridae, Idaeovirus, Iridoviridae, Luteoviridae, Marseillevirus, Mimiviridae, Mononegavirales, Nanoviridae, Narnaviridae, Nidovirales, Nimaviridae, Nodaviridae, Nudiviridae, Ophioviridae, Orthomyxoviridae, Ourmiavirus, Papillomaviridae, Partitiviridae, Parvoviridae, Permutotetraviridae, Phycodnaviridae, Picobirnaviridae, Picornavirales, Polydnviridae, Polyomaviridae, Potyviriidae, Poxviridae, Quadriviridae, Reoviridae, Retroviridae, Sobemovirus, Tenuivirus, Togaviridae, Tombusviridae, Totiviridae, Tymovirales, Varicosavirus, Virgaviridae

## **Bacteria**

Acidobacteria, Aquificae, Chrysiogenetes, Deferribacteres, Dictyoglomi, Elusimicrobia, FCB Group, Fusobacteria, Nitrospinae, Nitrospirae, Proteobacteria, PVC Group, Spirochaetes, Synergistetes, Tectomicrobia, Terrabacteria, Thermodesulfobacteria, Thermotogae

## **Fungi**

Blastocladiomycota, Chytridiomycota, Cryptomycota, Dikarya, Microsporidia, Mucoromycota, Neocallimastigomycota, Zoopagomycota

## Appendix III. List of SRA Files Searched for Novel Discovirus Sequences

ERR260429, SRR2187590, SRR2187589, SRR3046431, SRR2807659, SRR3046429, SRR1005276, SRR2240273, SRR2127986, SRR2807661, SRR2807660, SRR1999956, SRR1174777, SRR1005306, SRR1005261, SRR3105700, SRR2240260, SRR1837885, SRR1724091, SRR1005298, SRR1005291, SRR1005258, SRR1005312, SRR1005310, SRR1005300, SRR3046430, SRR1778927, SRR1731532, SRR1722393, SRR1233161, SRR1174792, SRR1005317, SRR1005296, SRR1005267, SRR1005263, SRR926248, ERR1059554, SRR2807662, SRR2477711, SRR2132800, SRR1779073, SRR1531164, SRR1233165, SRR1213587, SRR1005308, SRR1005271, ERR1059553, SRR3217256, SRR1302046, SRR1005307, SRR1005257, SRR3156503, SRR1778989, SRR1005309, SRR866531, SRR2807657, SRR2148997, SRR1778921, SRR1562369, SRR1005311, SRR1005260, SRR960254, ERR1059555, ERR748785, ERR748773, ERR167173, SRR2003671, SRR1619672, SRR1298983, SRR1178919, ERR1059557, ERR748777, SRR1618547, SRR1257400, SRR1005303, SRR1005294, SRR1005277, SRR1005297, SRR960252, ERR1059556, SRR3217257, ERR424752, SRR1005301, ERR777826, SRR1257399, SRR1005315, ERR748774, SRR1005259, SRR960261, ERR493373, SRR2131364, SRR1958771, SRR1162292, SRR1178935, SRR1005299, SRR1005313, SRR1005287, ERR167181, SRR1611790, SRR1005292, SRR1005284, ERR886715, SRR1174772, SRR1026209, SRR1588171, SRR1233160, SRR1212862, SRR1026204, SRR1257389, SRR1005323, SRR1005280, ERR777827, ERR1360192, ERR1059552, ERR1360188, ERR167179, SRR960260, ERR167184, SRR3207915, SRR1170742, SRR1005320, SRR2131361, SRR1186869, SRR3046433, SRR2003637, SRR1506121, ERR179753, SRR3046432, SRR2131352, SRR2060956, SRR1822494, SRR1652334, SRR1649311, SRR1588170, SRR1287024, SRR1257390, SRR1233166, SRR1233164, SRR1163705, SRR1162298, SRR1005343, SRR1005314, SRR1005265, ERR1025478, SRR3208051, SRR1163703, SRR1005266, ERR929878, ERR829294, DRR001017, SRR3046440, SRR2131363, SRR2094397, SRR2081043, SRR1588453, SRR1298984, SRR959508, ERR1360179, SRR2807658, SRR2807652, SRR1778932, SRR1162293, SRR1005378, SRR3310309, SRR2676906, SRR1942951, SRR1797599, SRR1720767, SRR1413312, SRR1185546, SRR1005373, DRR001451, SRR1917043, SRR1778924, SRR1564725, SRR1162294, SRR1005318, SRR826599, SRR1720760, SRR1005273, SRR1005304, SRR653057, SRR606404, SRR1594527, SRR3110670, SRR3096280, SRR2477712, SRR2040570, SRR1837875, SRR3204831, SRR3124526, SRR3112066, SRR3046448, SRR2807630, SRR1927120, SRR1778920, SRR1728120, SRR1537559, SRR1005289, ERR1104413, SRR3207877, SRR3046428, SRR2807626, SRR2240272, SRR2167610, SRR1770420, SRR1582386, SRR1537557, SRR1213697, SRR1055109, SRR1033742, SRR1033317, SRR1005268, SRR3105600, SRR2976057, SRR2321320, SRR2240261, SRR2131365, SRR2131351, SRR2120782, SRR1909493, SRR1537552, SRR1266998, SRR1026739, SRR1026335, SRR826644, SRR3207796, SRR2984592, SRR2824359, SRR2003659, SRR2003632, SRR1837717, SRR1770102, SRR1724901, SRR1724088, SRR1698111, SRR1267019, SRR1182649, SRR1170971, SRR1162297, SRR1026338, SRR1005286, SRR912597, SRR837659, SRR826645, SRR653062, SRR606409, ERR908395, ERR908392, ERR690823, ERR424755, DRR029010, SRR3207913, SRR1830868,

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