Discovery of Novel Viruses in Arachnids

by

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ABSTRACT

Arachnids belong to the phylum Arthropoda, the largest phylum in the animal kingdom. Ticks are blood-feeding arachnids that vector numerous pathogens of significant medical and veterinary importance, while scorpions have become a common concern in urban desert cities due to the high level of toxicity in their venom. To date, viruses associated with arachnids have been under sampled and understudied. Here viral metagenomics was used to explore the diversity of viruses present in ticks and scorpions. American dog ticks (*Dermacentor variabilis*) and blacklegged ticks (*Ixodes scapularis*) were collected in Pennsylvania while one hairy scorpion (*Hadrurus arizonensis*) and four bark scorpions (*Centruroides sculpturatus*) were collected in Phoenix. Novel viral genomes described here belong to the families *Polyomaviridae, Anelloviridae, Genomoviridae,* and a newly proposed family, Arthropolviridae.

Polyomaviruses are non-enveloped viruses with a small, circular double-stranded DNA (dsDNA) genomes that have been identified in a variety of mammals, birds and fish and are known to cause various diseases. Arthropolviridae is a proposed family of circular, large tumor antigen encoding dsDNA viruses that have a unidirectional genome organization. Genomoviruses and anelloviruses are ssDNA viruses that have circular genomes ranging in size from 2–2.4 kb and 2.1–3.8 kb, respectively. Genomoviruses are ubiquitous in the environment, having been identified in a wide range of animal, plant and environmental samples, while anelloviruses have been associated with a plethora of animals.

Here, 16 novel viruses are reported that span four viral families. Eight novel polyomaviruses were recovered from bark scorpions, three arthropolviruses were recovered from dog ticks and one arthropolvirus from a hairy scorpion. Viruses belonging to the families *Polyomaviridae* and Arthropolviridae are highly divergent. This is the first more extensive study of these viruses in arachnids. Three genomoviruses were recovered from both dog and deer ticks and one anellovirus was recovered from deer ticks, which are the first records of these viruses being recovered from

ticks. This work highlights the diversity of dsDNA and ssDNA viruses in the arachnid population and emphasizes the importance of performing viral surveys on these populations.

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CHAPTER 1

AN OVERVIEW OF ARACHNID-ASSOCIATED VIRAL SEQUENCE DATA

Abstract

Advancements in high-throughput sequencing have led to the rapid discovery and characterization of novel viruses, however, much of this work has been done on mammal and environmental samples leading to a skewed and incomplete view of the viral landscape. Recently studies have begun to unearth the pronounced levels of unexplored diversity of both RNA and DNA viruses in invertebrates. Ticks are blood-feeding arachnids that vector numerous pathogens of significant medical and veterinary importance while scorpions have become a common concern in urban desert cities due to the high level of toxicity in their venom. While there is a large body of work surrounding known vector borne viruses associated with ticks, other members of the virome remain undocumented and uncharacterized. In order to gauge the known diversity of viruses circulating in these animals this review examines the available complete viral genomes associated with ticks and scorpions. There are 623 complete viral genome sequences associated with these important arachnids are available in public databases. Continued studies utilizing viral metagenomics to explore the virome of these species will likely identify known and novel viruses, highlight viral diversity and provide further insights into the evolutionary history of some viral lineages.

1. Introduction

It has been estimated that there are 10^{31} virus particles on earth, most of which infect bacteria, making them the most abundant entity on the planet (Breitbart and Rohwer, 2005). Despite their ubiquity and ecologically important role in the environment, less than 1% of viral diversity has been documented (Geoghegan and Holmes, 2017). Furthermore, the vast majority of our understanding comes from viruses that are medically or economically important and can be cultured. This leaves an expansive gap in knowledge between characterized viruses and the virome. Recent advances in high-throughput (HTS) sequencing technologies are helping to close this gap as costs continue to decrease, and output data quality and accuracy increases. Due to high viral diversity and the lack of universal genes in viruses, HTS is an ideal tool to identify and characterize viral diversity

without prior knowledge of the nucleic acid sequences present. In general, RNA viruses are more widely studied and well characterized as many are economically or medically important infectious agents to humans, animals and plants. At present, most studies bias screening of vertebrate and plant samples for known viruses have produced a narrowed understanding of virus evolution and diversity. This is particularly true for groups, such as arthropods, were few studies have examined the viral diversity within these animals.

Arachnids belong to the phylum Arthropoda, which is the largest phylum in the animal kingdom housing ~80% of all known animal species (Zhang, 2013). Few studies have been undertaken to identify and describe the viruses associated with these animals and most have focused on blood feeding arachnids (Junglen and Drosten, 2013). In an attempt to shed light on the viral diversity associated with arthropods, several recently published surveys have described the viromes associated with non-blood feeding arachnids. Li et al published 112 novel RNA viruses from 70 arthropod species in 2015 which was followed in 2016 by Shi et al published nearly 1500 ssRNA virus genomes that were identified from 220 different invertebrate species collected from a small number of sites in China (Li et al., 2015; Shi et al., 2016a). Shi's study resulted in the establishment of several new genera and families, increased the overall knowledge of ssRNA viruses and eluded to the true scale of the virosphere. Rosario et al explored ssDNA viruses associated with arthropods in 2018 and reported 44 viral genomes from three major lineages of terrestrial arthropods (Rosario et al., 2018). These results highlight the viral diversity within arthropods that remains to be explored. To date, the viruses associated with arachnids have been undersampled and therefore understudied. This review will summarize the available complete genome sequences of tick and scorpion associated viruses in GenBank.

1.1. Ticks

Ticks are hematophagous ectoparasites that belong to the subclass Acari, order Ixodida. They feed on mammals, birds, reptiles and amphibians (Anderson and Magnarelli, 2008). There are 907 species subdivided into three families: Ixodidae or "hard ticks" (692 species), Argasiae "soft ticks"

(186 species) and Nuttallielidae (1 species) (Barker and Murrell, 2004; Bowman and Nuttall, 2008). Ticks are chelicerates, which means they have segment bodies (two instead of three like many other arthropods), no antennae but with a chitin exoskeleton that is molted and jointed legs (Sonenshine and Roe, 2013). Hard ticks possess a unique sclerotized scutum, also called a cuticle, that covers the entire dorsal surface of the male and one third of the female which acts as a moisture barrier to keep the tick from drying up and is molted between life stages allowing for a larger cuticle to form (Bowman and Nuttall, 2008). Since hard ticks must remain attached during cuticle formation, feeding is a slow process (Sonenshine and Roe, 2013). Soft ticks possess a thick, folded, leathery cuticle which hinders expansion but allows for rapid feeding (Sonenshine and Roe, 2013).

Ticks have distinct active life cycles that take up to six years to be completed (Labuda and Nuttall, 2008). In order to transition to the next stage, ticks require a blood meal (Labuda and Nuttall, 2004). Hard ticks have three active stages: larvae, nymphs and adults. Depending on the species, soft ticks have two or more nymphal stages which are directly related to slower developmental cycles (Sonenshine and Roe, 2013). The duration and number of blood meals varies between the ticks in different families, with hard ticks taking one blood meal, lasting between 3 to 6 days, per life stage, and soft ticks taking several shorter meals lasting 30-60 minutes (Bowman and Nuttall, 2008). Their ability to successfully overwinter without feeding is a major contributor to the long life span and this makes ticks an excellent reservoir and vector for tick-borne viruses (Bowman and Nuttall, 2008).

Most ticks have a wide host range, which makes them an effective vector. The method by which ticks take a blood-meal is important for disease transmission. Ticks are pool feeders. They attach to the host skin using their chelicerae and toothed hypostome (Nuttall and Labuda, 2008). Hard ticks feed for days to weeks at a time and cement their mouthparts into the skin. Ticks carry an array of tools to increase the chances of taking a successful blood meal. Their saliva is composed of anti-hemostatic, vasodilatory, anti-inflammatory and immunosuppressive compounds (Kazimirova and Stibraniova, 2013). Viruses transmitted by this route enter a vertebrate skin where

the host immune system is inefficient at the site as saliva modulates the complement and natural killer cells, antibody production and T-lymphocyte proliferation and function facilitating viral infection (Nuttall and Labuda, 2008).

1.2. Community impact and public health concern

Globally, ticks are the second most important vector of human pathogens that cause disease, only surpassed by mosquitos (Goodman et al., 2005). Ticks are responsible for causing significant burden to public health throughout the world as they transmit a broader range of infectious agents than any other vector (Kazimirova et al., 2017). In North America, however, they are considered to be the most significant vector for human and animal pathogens (De La Fuente et al., 2017a). In 2014 ~95% of the 50,000 reportable cases of vector-borne diseases were vectored by ticks (Eisen et al., 2017). Ticks are capable of transmitting bacteria, viruses and parasites that affect humans, livestock and companion animals (Jongejan and Uilenberg, 2004). Approximately 10% of the currently known species (soft ticks: genera *Ornithodoros, Carios*, and *Argas, and hard ticks: genera Ixodes, Haemaphysalis, Hyalomma, Amblyomma, Dermacentor*, and *Rhipicephalus* (Kazimirova et al., 2017) are of significant medical and veterinary importance (de la Fuente et al., 2017b; Kazimirova et al., 2017) (Figure 1.1). Interestingly, numerous viruses such as colorado tick fever virus and heartland virus that result in serious disease are not required to be reported in the US, which demonstrates this number is not an accurate reflection of the impact of tick-borne viruses. In recent years, a notable increase in medical and veterinary impacts have been documented as the geographical spread of ticks increase due to socio-economic and climatic conditions as well as a lack of overall control measures (Kazimirova et al., 2017). Vaccines and antivirals for tick-borne viruses are lacking and tick control efforts have proved to be difficult to implement and are often associated with high financial costs (Ginsberg and Stafford III, 2005; Kazimirova et al., 2017). Current tick management methods include, tick avoidance, self-protective precautions such as wearing protective clothing and using repellents like DEET, manipulation of tick habitat, breeding tick resistant cattle, lowering host populations and applying acaricides (Ginsberg and Stafford III,

2005). Despite control efforts nearly all tick-borne diseases have persisted in the population and most have increased geographic range in recent years (Ginsberg and Stafford III, 2005).

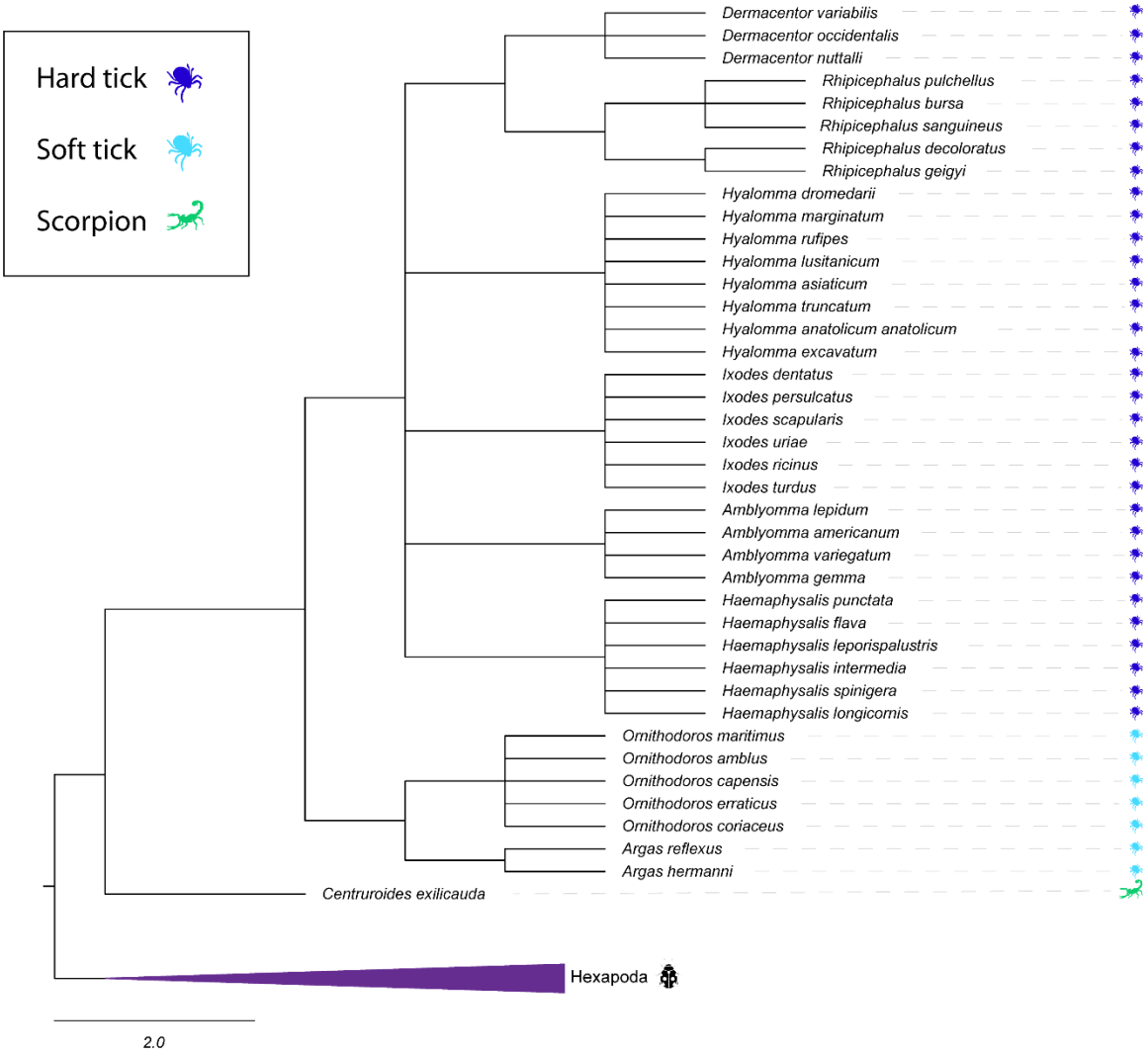

Figure 1.1: Phylogenetic relationship of tick and scorpion species complete viral genomes have been recovered from. Tree was generated using PhyloT and host names were collated from GenBank records. The subphylum Hexapoda was used to root the cladogram.

1.3. Arboviruses

Arthropod-borne viruses (arboviruses) are defined as viruses maintained in nature through continuous transmission between vertebrate hosts and hematophagous arthropods or through vertical transmission mechanisms. Arboviruses replicate and cause disease in vertebrate hosts but

are also able to replicate in arthropod tissues. Therefore, an environment that allows for the virus, vector and host to be present during synchronized time period is required for viral transmission (Brackney and Armstrong, 2016). All known arboviruses, except African swine fever virus (dsDNA), have RNA genomes (Labuda and Nuttall, 2004). Tick-borne arboviruses belong to 11 virus families and have a unique genome structure and replication strategies. Arboviruses are an extremely successful group of viruses with the unique evolutionary advantage of replicating in two distinct hosts and are the largest biological group of vertebrate-infecting viruses (Labuda and Nuttall, 2008).

Viruses are maintained in tick population in several ways: 1) vertical transmission (infected female to egg) plays a role in several tick-borne viruses, however, it appears to happen at low frequency in nature (Labuda and Nuttall, 2004) and it has been suggested that vertical transmission is not a significant factor in ecology and epidemiology of tick-borne viruses (Mansfield et al., 2017); 2) Horizontal transmission, when a naïve tick feeds on an infected host, results in a significant number of infected ticks (Labuda et al., 1993); 3) Co-feeding transmission can occur when an uninfected tick feeds in close proximity to an infected tick. Larvae from one egg mass will quest together with several attaching to the same host there by enabling a higher propensity for vertically acquired viruses to be spread via co-feeding (Labuda and Nuttall, 2008). Of importance, once infected a tick is infected for life and is capable of transmitting the virus to vertebrate hosts or other ticks. Additionally, vertebrate hosts can become infected by ingesting infected ticks, consuming unpasteurized dairy products from infected animals, butchering and ingestion of infected meats and blood transfusions (Brackney and Armstrong, 2016).

Ticks present unique challenges for arboviruses especially in regards to blood feeding, blood meal digestion and molting. Many viruses have evolved with ticks in such a way that the viral life cycle is coordinated with the tick's feeding cycle (Labuda and Nuttall, 2004). While virus lifecycle in ticks are not completely understood it is suggested that during feeding on an infected host the tick ingests infected blood that is pumped into the midgut epithelial cells where the virus is able to replicate. It is thought that some viruses utilize specific cell receptors while others passively enter digestive

cells during blood uptake (Brackney and Armstrong, 2016). In order to be transmitted the virus must disseminate to distal tissues (mouth parts). Again, little is known about this process, but it has been suggested that the viruses are able to circulate in the hemolymph by infecting hemocytes prior to molting.

With limited information on viral diversity in ticks available, the development and application of metagenomics to tick populations has led to the identification of novel tick associated viruses (Shi et al., 2016a). This is important as many arboviruses do not cause overt signs of infection in arthropod host and do not infect laboratory animals. Molecular detection has been an applicable method to detect known and novel viruses (Shi et al., 2016a).

1.4. Tick-borne virus diversity

In order to gain a comprehensive picture of the genetic information available on tick-associated viruses, an extensive review of tick associated viral sequences was performed. All sequence data presented in tables 1.1-1.6 was collated from the public database, GenBank, and for the purpose of this review partial sequences were omitted and only complete genome recovered from ticks were reported below (considered to be complete as of February 20, 2019). A summary of tick associated viruses is provided in Figure 1.2. Accession numbers for sequence data are listed in the appendix. In order to compare the depth of knowledge between tick-derived viral sequences and host derived viral sequences, the total number of complete genomes recovered from non-tick hosts are listed for each virus species.

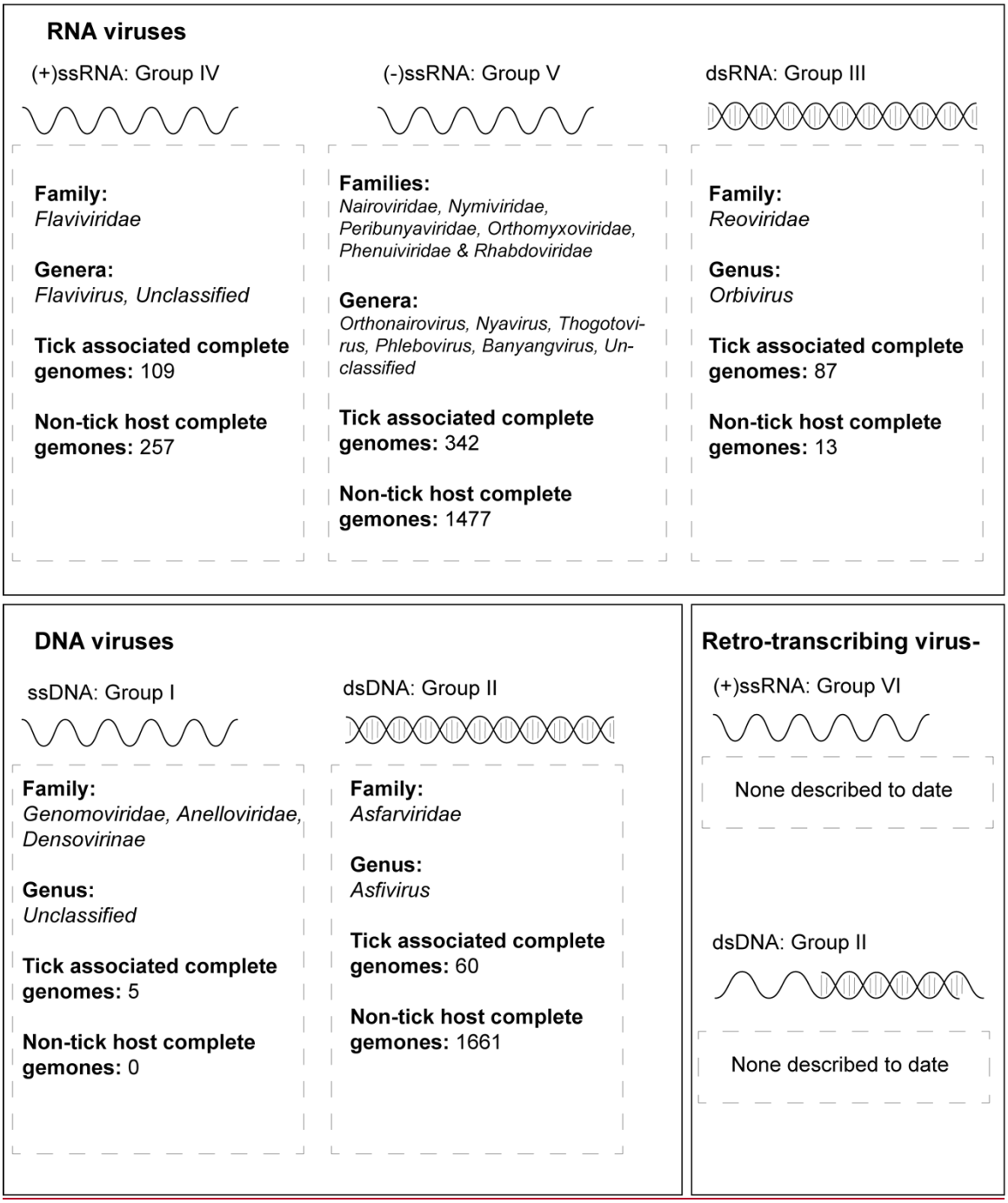

Figure 1.2: Groups, families and genera containing tick associated complete sequence records.

1.5 RNA viruses

1.5.1 Positive-sense single-stranded RNA viruses

1.5.1.1 Flaviviridae

The family *Flaviviridae* consist of enveloped positive sense (+) single-stranded (ss) RNA viruses with a genome size ranging from 9 to 12 kb. This viral family has four genera: *Flavivirus, Hepacivirus, Pegivirus, Pestivirus* (Simmonds et al., 2017). Tick-borne viruses are primarily vectored by ixodid ticks but have also been recovered from argasid ticks. They fall into the genus *Flavivirus* and are classified into the mammalian tick-borne virus group (M-TBFV) or the seabird tick-borne virus group (S-TBFV) (Grard et al., 2007; Labuda and Nuttall, 2004). The M-TBFV are encephalitic viruses with the exception of and Kyasanur forest disease virus, which are hemorrhagic fever viruses. With the exception of *Tyuleniy virus*, S-TBFV have only been recovered in the Old World (Grard et al., 2007). Flaviviruses are distributed world-wide but individual species are restricted to endemic areas (Simmonds et al., 2017) (Table 1.1).

Table 1.1: Tick-associated (+) ssRNA viruses complete genome sequences

Family	Genus	Species	Complete sequences tick host	Complete genome sequences non-tick host
Flaviviridae	*Flavivirus*	*Tick-borne encephalitis virus*	67	152
	Flavivirus	*Powassan virus*	17	35
	Flavivirus	*Kyasanur forest disease virus*	10	41
	Unclassified	*Alkhumra hemorrhagic fever virus*	7	15
	Unclassified	*Deer tick virus*	2	1
	Flavivirus	*Tyuleniy virus*	2	1
	Flavivirus	*Louping ill virus*	1	7
	Flavivirus	*Karshi virus*	2	2
	Flavivirus	*Langat virus*	1	3
Total (+) ssRNA tick associated viral sequences			109	257

1.5.2 Negative-sense ssRNA viruses

1.5.2.1 Nairoviridae

Nairoviridae is a proposed family in the proposed order *Bunyavirales* that has a single genus *Orthonairovirus* (Adams et al., 2017; Kuhn et al., 2016). This family is unique as all known viruses are transmitted by hard or soft ticks. These enveloped viruses are distributed worldwide, have three segments with complementary 3' and 5' ends; the small (S) segment (structural nucleoprotein (NP), medium (M) segment (glycoprotein precursor (GPC)), and large (L) segment (RNA-dependent RNA

polymerase) and are approximately 18.8 kb in length (S ~1.7 kb; M ~4.9 kb and L ~12.2 kb) (Kuhn et al., 2016). Crimean-Congo hemorrhagic fever virus is the most medically relevant virus from this family as it causes a lethal viral hemorrhagic fever in Africa, the Balkans, Southern Europe and Western Asia (Kuhn et al., 2016). However, other members of the family are known to cause no disease or mild-to-severe febrile illness in humans and livestock (Walker et al., 2016). Nairobi sheep disease virus is of veterinary importance as it causes hemorrhagic gastroenteritis in sheep and goats with up to 90% mortality rates (Walker et al., 2016). Of additional importance, the vertebrate hosts for the majority of nairoviruses have yet to be identified and it is possible some may not replicate in vertebrates at all (Lasecka and Baron, 2014). Genomic sequence data for this family of viruses is increasing, however, available data is still limited (Table 1.2).

1.5.2.2 Nyamiviridae

The family *Nyamiviridae* contains spherical, enveloped viruses with single negative-sense (-) ssRNA genomes that are 11 to 12 kb in length and have similar genome organization to other viruses in the order *Mononegavirales* (Kuhn et al., 2013). The genus *Nyavirus* comprises tick-borne viruses that have been recovered from islands in the Central Pacific and Japan from soft ticks (Mihindukulasuriya et al., 2009) (Table 1.2).

1.5.2.3. Peribunyaviridae

Peribunyaviridae is a family in the proposed order *Bunyavirales* that has a single genus Orthobunyavirus that is comprised mainly of arboviruses (Shi et al., 2018). Virions are enveloped, spherical and contain three linear (-) ssRNA segments that total between 11 and 20 kb in length. All tick-borne viruses in *Peribunyaviridae* are vectored by/associated with hard ticks but vertebrate host disease states have yet to be linked with these viruses (Shi et al., 2018) (Table 1.2).

1.5.2.4. Orthomyxoviridae

Orthomyxoviridae contains six genera of viruses known to cause respiratory diseases including Influenzavirus A-C and Thogotovirus, which contains the tick-borne viruses. Thogotovirus virions

are spherical, enveloped, and contain six or seven linear, (-) ssRNA segments which total around 10kb in length (https://talk.ictvonline.org/ictv-reports/ictv_9th_report/negative-sense-rna-viruses-2011/w/negrna_viruses/209/orthomyxoviridae). The fourth largest segment encodes a glycoprotein that is unrelated to any influenza protein but has homology with a baculovirus surface protein which is likely the factor that allows members of this genus to replicate in tick cells. Reassortment of genome sequences during infection have been demonstrated but the role it plays in epidemiology is yet to be determined. These viruses are vectored by ixodid ticks and have a wide geographic distribution across the Americas, Africa, and Europe (Weber et al., 1996) (Table 1.2).

1.5.2.5. Phenuiviridae

The family *Phenuiviridae* contains four genera. The virions are enveloped and spherical encapsidating three linear (-) ssRNA segments with a total genomes size of 10.5 kb. Viruses within this family are primarily arboviruses and have been associated with ixodid ticks (Shi et al., 2018; Yun et al., 2017). They have been recovered worldwide and several members of this family, including severe fever with thrombocytopenia virus, are known to cause disease in the vertebrate hosts (Shi et al., 2018) (Table 1.2).

1.5.2.6. Rhabdoviridae

Virions of this family are bullet shaped, covered with glycoproteins, and contain a single, linear, (-) ssRNA genome that is approximately 10-16 kb (Ghedin et al., 2013). The 2016 ICTV report breaks *Rhabdoviridae* into 18 genera and most rhabdoviruses are arboviruses, however, only a few species have been associated with ticks. One species has been associated with hard ticks in Africa and the remainder are found in various species of hard ticks along the eastern coast of the United States (Ghedin et al., 2013; Tokarz et al., 2018). (Table 1.2)

Table 1.2: Tick-associated (-) ssRNA viruses

Family	Genus	Species	Complete sequences tick host	Complete genome non-tick host
Nairoviridae	*Orthonairovirus*	*Crimean-Congo hemorrhagic fever orthonairovirus*	85	425
	Orthonairovirus	*Dugbe virus*	26	7
	Orthonairovirus	*Nairobi sheep disease virus*	19	10
	Orthonairovirus	*Avalon virus*	6	-
	Orthonairovirus	*Dera Ghazi Khan virus*	6	-
	Orthonairovirus	*Farallon virus*	6	-
	Orthonairovirus	*Tofla virus*	6	-
	Orthonairovirus	*Zirqa virus*	6	-
	Orthonairovirus	*Abu Hammad virus*	3	-
	Orthonairovirus	*Avalon Bres virus*	3	-
	Orthonairovirus	*Clo Mor virus*	3	-
	Orthonairovirus	*Ganjam virus*	3	-
	Orthonairovirus	*Great Saltee virus*	3	-
	Orthonairovirus	*Hughes virus*	3	-
	Orthonairovirus	*Khasan virus*	3	-
	Orthonairovirus	*Punta Salinas virus*	3	-
	Orthonairovirus	*Qalyub virus*	6	-
	Orthonairovirus	*Soldado virus*	3	-
	Orthonairovirus	*Tillamook virus*	3	-
	Orthonairovirus	*Tunis virus*	3	-
	Orthonairovirus	*Raza virus*	2	-
Nyamiviridae	*Nyavirus*	*Midway nyavirus*	1	-
	Nyavirus	*Nyamanini nyavirus*	1	-
	Nyavirus	*Sierra Nevada virus*	1	-
Peribunyaviridae	*Unclassified*	*Hunter Island virus*	6	-
	Unclassified	*Komandory virus*	3	-
	Unclassified	*Lone Star Virus*	3	-
Orthomyxoviridae	*Thogotovirus*	*Thogoto virus*	6	9
Phenuiviridae	*Phlebovirus*	*Severe fever with thrombocytopenia virus*	40	980
	Phlebovirus	*Blacklegged tick phlebovirus*	12	-
	Phlebovirus	*Uukuniemi virus*	8	3
	Phlebovirus	*Zaliv Terpeniya virus*	12	3
	Unclassified	*Bhanja virus*	9	6
	Phlebovirus	*American dog tick phlebovirus*	4	-
	Unclassified	*Forecariah virus*	3	-
	Banyangvirus	*Guertu virus*	3	-
	Unclassified	*Kaisodi virus*	3	-
	Unclassified	*Kismayo virus*	3	-
	Phlebovirus	*Mukawa virus*	3	-
	Phlebovirus	*Palma virus*	3	3
	Phlebovirus	*Rukutama virus*	3	-
	Unclassified	*Silverwater virus*	3	-
	Phlebovirus	*Huaiyangshan virus*	3	31
	Phlebovirus	*Pacific coast tick phlebovirus*	2	-
	Phlebovirus	*Gissar virus*	1	-
Rhabdoviridae	*Unclassified*	*Long Island tick rhabdovirus*	1	-
	Unclassified	*Blacklegged tick chuvirus*	1	-
	Ledantevirus	*Kolente virus*	1	-
	Unclassified	*Dog tick rhabdovirus*	1	-
	Unclassified	*Connecticut virus*	1	-
	Unclassified	*New Minto virus*	1	-
	Unclassified	*Sawgrass virus*	1	-
	Unclassified	*Zahedan virus*	1	-
Total (–)ssRNA tick associated viral sequences			342	1477

1.5.3. Double-stranded RNA viruses

1.5.3.1 Reoviridae

Virus particles in the large family of *Reoviridae* have between 9 and 12 linear dsRNA segments, a protein capsid organized as one, two or three concentric layers, which has an icosahedral symmetry (ICTV 9th report). Viruses from the genera *Orbiviruses*, *Coltiviruses* and *Seadornaviruses* have been shown to replicate in both vertebrate hosts and arthropods vectors. Viruses from this family have been recovered from hard ticks. (Table 1.3)

Table 1.3: Tick-associated dsRNA virus sequences

Family	Genus	Species	Complete sequences tick host	Complete genome non-tick host
Reoviridae	*Orbivirus*	*Wad Medani virus*	47	-
	Orbivirus	*Muko virus*	20	-
	Orbivirus	*Baku virus*	20	-
	Orbivirus	*Chobar Gorge Virus*	10	-
	Orbivirus	*Kemerovo virus*	10	13
Total dsRNA tick associated viral sequences			107	13

1.6.DNA Viruses

1.6.1 Double-stranded DNA viruses

1.6.1.1. Asfarviridae

The family *Asfarviridae* contains a single genus, *Asfivirus*, and a single species *African swine fever virus* which is the only known DNA arbovirus. Isolates from this species have a linear dsDNA genome that range in size from 170-194 kb, have an internal lipid layer, icosahedral capsid and an outer lipid envelope. Symptoms in domestic pigs include hemorrhagic fever leading to death in some cases. This virus has been shown to be transmitted by a soft tick of the genus *Ornithodoros* and is endemic to Africa where warthogs and bush pigs are reservoirs. In 2007, isolates were recovered in Europe and outbreaks are actively occurring in Russia, Poland, Czech Republic, Romania and several surrounding areas (Mansfield et al., 2017). Virus isolates differ in virulence and may produce a variety of signs ranging from acute to chronic, or they may produce asymptomatic infections. Virulent isolates can cause 100% mortality in 7–10 days. Less virulent isolates may produce a mild disease from which a number of infected swine recover and become carriers (Vinuela, 1985; Salas, 1994). A striking feature of African swine fever virus infections is the

absence of neutralizing antibody production. This has severely hampered attempts to produce an effective vaccine although the use of gene deleted virus strains has shown promise in protecting against virulent strains (Gibbs, 2001). (Table 1.4)

Table 1.4: Tick-associated dsDNA virus sequences

Family	Genus	Species	Complete sequences tick host	Complete genome non-tick host
Asfarviridae	*Asfivirus*	*African swine fever virus*	60	1661
Total sequences			60	1661

1.6.2 Single-stranded DNA viruses

1.6.2.1. Genomoviridae

Genomoviridae is a family of viruses that have circular ssDNA genomes of approximately 2 kb in length that encode a replication-associated protein and a capsid protein. They have been identified from multiple animal and environmental samples (Krupovic et al., 2016). Recently, the first isolates of genomoviruses associated with ticks have been recovered. Those were isolated from ixodid ticks in Pennsylvania, USA (Waits et al., 2018). (Table 1.5)

1.6.2.2. Anelloviridae

The family *Anelloviridae* is a large group of small, non-enveloped viruses that contain circular ssDNA genomes that range in size from 2 to 4 kb (Manzin et al., 2015). They have been recovered from a variety of mammals, mosquitoes and one genome has been associated with a hard tick (Waits et al., 2018). (Table 1.5)

Table 1.5: Tick-associated ssDNA virus sequences

Family	Genus	Virus	Complete sequences tick host	Complete genome non-tick host
Genomoviridae	*Unclassified*	*Genomovirus*	3	-
Anelloviridae	*Unclassified*	*Torque teno virus*	1	-
Densovirinae	*Unclassified*	*Lone star tick densovirus*	1	-
Total ssDNA tick associated viral sequences			5	0

1.7. Scorpion biology

Scorpions are one the oldest terrestrial arthropods with fossil records dating back 450 million years (Lourenco, 2018). While their morphology has been greatly conserved, they are highly adaptive in

regards to their ecology, behavior and physiology as demonstrated by their success despite environmental changes since the Middle Siluarian (Shi et al., 2013). They are venomous, nocturnal, predatory animals that belong to the class Arachnida. Nearly 2200 species are recognized worldwide as scorpions found in wide range of ecosystems including deserts, grasslands, savannahs, deciduous forests, pine forests, intertidal zones, rain forests and caves (Lourenco, 2018). Their bodies are separated into two segments a cephalothorax and an abdomen that includes the tail and stinger, four pairs of legs and pedipals with plier-like pinchers (Polis, 1990). Similar to ticks, scorpions have a hard exoskeleton that is molted several times during its lifecycle in order to grow and the time to maturity ranges from 6 months to 8 years (Polis, 1990).

1.8. Scorpion associated viral sequence data

Sequence data presented in table 6 was collected from GenBank, and for the purpose of this review only complete genomes recovered from scorpions were reported below (considered to be complete as of February 20, 2019). Accession numbers for sequence data are listed in the appendix.

1.8.1. Polyomaviridae

Polyomaviridae is family of small dsDNA viruses with circular genomes ranging in size from 3.9 to 7.4 kb with an average of ~5 kb. They are known to have oncogenic properties and after their discovery in the mid-1950s have been recovered from numerous mammal, avian and fish species. While a full genome has yet to be recovered from arthropods, one nearly complete genome was assembled from WGS data providing the first evidence that these viruses might be circulating in invertebrate hosts. (Table 1.6)

Table 1.6: Scorpion-associated dsDNA virus sequences

Family	Genus	Species	Complete sequences scorpion host	Complete sequences non-scorpion host
Polyomaviridae	*Unclassified*	*California bark scorpion polyomavirus*	1	-
Total dsDNA scorpion associated viral sequences			1	0

1.9. Effects of climate change on tick and scorpion habitat range

Climate change and direct anthropogenic factors have facilitated the expansion of tick distribution globally and thereby tick-borne zoonotic diseases are emerging in temperate parts of the world, representing an increasing public health risk (Jongejan and Uilenberg, 2004). The last few decades have seen a steadily increasing number of reported tick-borne disease cases. Some of this is attributed to an expanded geographic range of many tick vectors and the discovery of novel tick-borne induced diseases (Eisen et al., 2017). In the US the deer ticks, *I. scapularis* and *I. pacificus*, are found in dense brush and heavily forested woodlands and requirements for high humidity prevent both from inhabiting the Rocky Mountains or Inter-Mountain West with *I. scapularis* distributed in eastern states and *I. pacificus* distributed western states (Eisen et al., 2016). Tick populations and distributions declined throughout the late 1800s – early 1900s due mainly to deforestation and reduced deer populations, which are their main host. Reforestation, rebounding deer populations and increasing temperatures during the last half of the 20th century produced ecological conditions ideal for the reemergence of *I. scapularis*. The abundance of *I. scapularis* has continued to increase and the number of counties *I. scapularis* is considered established has doubled from 1996 to 2015 with the greatest increase seen in north central and northeastern states (Eisen et al., 2017). These trends can be expanded to other tick species as increasing geographical distribution of ticks (mainly *Ixodes sp.)* have been reported in Europe, Africa, Asia, South America, Australia (Medlock et al., 2013; Yamaji et al., 2018)

Studies on scorpion biogeography began in the late 1800s with most recent work being completed in the 1980s (Lourenco, 2018) so it is unclear at the present time if climate change is impacting the habitat range of these arachnids. In the last 40 years nearly 1500 distinct species have been described as this number is expected to climb as new habitats are explored (Lourenco, 2018). They

are presently found on all major land masses except Antarctica and based on the increased distribution of other arachnids it is plausible that this hearty animal will also be able to tolerate increasing temperatures and expand outside its present geographic range.

1.10. Conclusions and future research

Viral metagenomic approaches have led to a significant increase in viral discovery over the past decade. While many of these novel viruses come from mammal and environmental samples, recent studies have shown that arthropods harbor a wide diversity of viruses (Li et al., 2015; Rosario et al., 2018; Shi et al., 2016a). Given the relatively small number of complete tick associated viral genomes available in GenBank and the number of viruses being documented from other invertebrates, it stands to reason that the tick virome is not well known and there is a wide array of viral diversity waiting to be explored. In total, there are 623 complete viral sequences recovered from ticks available in GenBank. All positive sense ssRNA tick associated viruses are members of the family *Flaviviridae* and 109 complete genomes have been categorized. Negative sense ssRNA viruses are more widely distributed with 342 genomes being classified into six families, *Nairoviridae, Nyamiviridae, Peribunyaviridae, Orthomyxoviridae, Phenuiviridae, or Rhabdoviridae*. Meanwhile, 107 full genomes have been recovered from ticks that fall within the family of dsRNA *Reoviridae*. Due to its veterinary relevance, 60 complete genome of African swine fever virus, a dsDNA virus belonging to the family *Asfarviridae*, have been sequenced. Finally, five complete genomes of ssDNA viruses from the families *Genomoviridae, Anelloviridae, and Densovirinae* have also been recovered from ticks. The number of sequences recovered from non-tick hosts is significantly greater than those recovered from tick in all viral families with the exception of *Reoviridae* (dsRNA) and ssDNA families providing further evidence of biased sampling as known human and animal pathogens such as *African swine fever virus, Crimean-Congo hemorrhagic fever orthonairovirus* and *Severe fever with thrombocytopenia virus* are extensively studied in their vertebrate hosts. In total *African swine fever virus* has 1721 complete genome records however only 60 of those were isolated from tick hosts. Similar trends can be seen for *Severe fever with thrombocytopenia virus* and *Crimean-Congo hemorrhagic fever orthonairovirus* which respectively

have 1020 and 219 complete genome records with only 40 and 67 coming from ticks hosts. In total there are 3408 complete sequence records in GenBank with only 623 coming from tick hosts. This highlights the need to further explore the tick virome and vector enable metagenomics will provide a reliable method for identifying and classifying known and novel viruses from ticks.

As tick geographical distribution continues to expand it will become increasingly important to explore the tick virome to characterize the relationship between viruses and their hosts as well as the viral diversity associated with the arachnids. Future work should be aimed at determining the molecular mechanisms by which arboviruses are able to replicate in both invertebrate and vertebrate systems, identifying molecules that facilitate transmission and characterizing tick-virus-vertebrate interactions. Such insights could be utilized for vaccine development and to improve control measures above personal protection. Additionally, viral metagenomics could be used identify how many viruses a tick can harbor at a given time, aid in determining how many viruses can co-replicate in a tick and identify viral mutations that contribute to overall virulence, fitness and other adaptations.

Presently, there is only one viral sequences associated with scorpions in GenBank, which is a polyomavirus that was assembled from WGS data and have not been recovered for sequence confirmation from the original host, California bark scorpion (*Centruroides exilicauda*). Even though this sequence has yet to be confirmed, it begins to help unravel the evolutionary history of polyomaviruses by providing the first evidence of an arthropod lineage. It is imperative to continue to explore the scorpion virome as the discovery of known and novel of viruses will help elucidate the evolutionary history of viral species by providing valuable information on a lineage that branched from other polyomaviruses a long time ago.

Metagenomics is a relatively unbiased way to characterize viral diversity within a sample. As more arthropod species are investigated, the viral diversity is expected to rapidly expand. One exciting avenue of exploration lies in unraveling the evolution of viral families once thought to infect only

vertebrates, such as polyomaviruses, by studying newly characterized viral lineages. The work involved with generating a more complete understanding of viral evolution and ecology in arthropods will be great but the knowledge gained will provide valuable insights into viral evolution.

CHAPTER 2

ARIZONA SCORPION REVEALS A NOVEL LINEAGE OF POLYOMAVIRUSES

Abstract

Polyomaviruses are non–enveloped viruses with circular dsDNA genomes that range in size from ~3.9–7.3 kb. Initially identified in mammals, polyomaviruses have now been documented in birds and a few fish species. In general, polyomaviruses are host specific showing strong evidence of host-virus co-evolution. Their evolutionary history has remained somewhat unresolved partly due to the bias in sampling of polyomaviruses from largely terrestrial vertebrates. Identification of polyomaviruses in a broader host range across the animal kingdom would certainly go a long way in addressing this. Scorpions are predatory animals that belong to the class Arachnida and are among the oldest terrestrial arthropods and thus far, viruses in arachnids have been under–sampled and understudied. Here, high–throughput sequencing in conjunction with traditional molecular techniques were utilized to explore the diversity of DNA viruses associated with bark scorpions (*Centruroides sculpturatus*) from the greater Phoenix area, Arizona, USA. Novel polyomaviruses were identified and the genomes of eight polyomaviruses were recovered and characterized. This is the first group of polyomaviruses recovered from invertebrates and are shown to be highly divergent from other polyomaviruses. Phylogenetic analyses provides further evidence co-divergence with their hosts, suggest that the last common ancestor of arthropods and invertebrates harbored at least one polyomavirus and provides important key information that will help inform polyomavirus evolution.

2.1. Introduction

2.1.1. Scorpions

Scorpions are one the oldest terrestrial arthropods, with fossil records dating back 450 million years. They are venomous, predatory animals that belong to the class Arachnida. Nearly 2200 species are recognized worldwide as scorpions are found in wide range of ecosystems including deserts, grasslands, savannahs, deciduous forests, pine forests, intertidal zones, rain forests and

caves (Lourenco, 2018). Their bodies are separated into two segments a cephalothorax and an abdomen that includes the tail and stinger, four pairs of legs and pedipals with plier–like pinchers (Polis, 1990). Bark scorpions (*Centruroides sculpturatus*) are nocturnal, (generalist) predators that consume a wide variety of insects, spiders, centipedes and other scorpions, They inhabit arid desert and riparian regions in south–western North America (Webber et al., 2015). Although these scorpions are desert adapted, water is a limiting factor, so they are most commonly found in riparian areas, which has caused the bark scorpion to become an surprising common concern in urban desert cities (Bibbs et al., 2014).

2.1.2. Polyomaviruses

The first polyomavirus was discovered in the mid-1950s as a filterable agent and was shown to induce multiple tumors when injected into animal models which led to the name poly (multiple) oma (tumors) (Buck et al., 2016). Since then polyomaviruses have been recovered from a variety of mammals including humans, dolphins, bats and rodents, and diverse genomes recently reported in an assortment of birds and fish (Buck et al., 2016; Van Doorslaer et al., 2018).

Polyomaviruses have a conserved genome organization that consists of an early region and late region separated by a non–coding control region (NCCR). Polyomavirus genomes encode at least two regulatory proteins, a large (LT) and small tumor (ST) antigen in the early region and two structural proteins, capsid proteins VP1 and VP2 in the late region (Moens et al., 2017). The NCCR contains the origin of replication and regulatory sequences for early and late transcription. Replication and transcription of the genome occurs in the nucleus and is regulated by the NCCR. Transcription of the early region initiates prior to viral replication and the late region after viral replication. Transcription of all genes is mediated by host polymerase II and host factors. The early promoter contains a TATA–box and multiple binding sites for LT and cellular transcription factors (Van Ghelue 2012). At high concentrations the LT binds to motifs downstream of the TATA box and prevents transcription. Early transcripts are generated via mRNA splicing from a single transcript. The main products generated from this splicing event are the LT and ST proteins. The LT is the only protein required for viral replication and is the major viral protein responsible for

regulation of the host replication machinery in a way that leads to tumorigenesis. It has three conserved domains, DnaJ which includes the HPDKGG and LXCXE motif, the origin binding domain and a Helicase/ATPase domain. The DnaJ domain stimulates ATPase activity of Hsc70 and the energy released in the conversion of ATP to ADP is used to break the pRB:E2F complex which allows S phase progression and results in uncontrolled cell growth (An et al., 2012).

Polyomaviruses are host specific, however, co-divergence does not fully explain polyomavirus evolution. A growing body of evidence suggests an ancient and relatively stable association of polyomaviruses with their hosts. This long–standing association implicates co–divergence as the main driver of polyomavirus evolution, however, there are deviations that indicate additional factors contributed to the evolutionary history including, host switching, intra-host lineage duplication (viral speciation within the same host species), and incomplete lineage sorting (persistence of viral polymorphism during successive host divergence events) (Buck et al., 2016). These have all led to inconsistencies between viral and host phylogenies. Since most polyomaviruses show very strong host specificity, it is unclear whether natural host switching occurs as it has not been convincingly documented. However, spillover infection between closely related species has to be considered as recombination between polyomaviruses is possible (Woolford et al., 2007). Lineage duplication appears to happen more frequently as seen by the presence of 13 human polyomaviruses and eight chimpanzee polyomaviruses that appear in three of the four established genera. Lineage sorting based on recent duplications is difficult to access as it is likely the entire polyomavirome has yet to be sampled from hosts (Buck et al., 2016). Determining the individual impact of each of these factors is difficult due to incomplete and biased sampling of both host and virus.

Viral metagenomics and molecular techniques, such as PCR and rolling circle amplification (RCA), are enabling the identification and recovery of polyomaviruses from novel hosts at an increased frequency, which has allowed for a deeper understanding of polyomavirus evolutionary history. Biased sampling of mammalian hosts has been moderately mediated by divergent sequences recovered from fish and a whole genome sequence (WGS) derived assembly from a California bark

scorpion (Buck et al., 2016). This has aided in generating the currently accepted model of intra-host divergence. In this model, polyomaviruses diverge at a slightly faster rate than the host, which allows for the emergence of viruses that sit in separate clades to share the same host (Buck et al., 2016). The acquisition of additional highly divergent sequences will help further resolve the evolutionary history of polyomaviruses and help generate taxonomic framework that can be utilized to accurately categorize novel viruses in such a way that sequence similarities and differences could be used by researchers and clinicians to aid in predicting hosts, tissue tropism and disease states.

The International committee for the taxonomy of viruses (ICTV) recommends using phylogeny–based taxonomy of the LT to classify sequences into four recognized genera as well as several unclassified species (*Polyomaviridae* Study Group of the International Committee on Taxonomy of et al., 2016). There are four established genera in the family *Polyomaviridae*. Members of the genera *Alphapolyomavirus*, *Betapolyomavirus* and *Deltapolyomavirus* infect mammalian hosts whereas those of the genus *Gammapolyomavirus* infect avian species. The recently identified polyomaviruses from fish have not been assigned to a genus.

The detection of a near complete polyomavirus genome assembled from the WGS data of a California bark scorpion led to investigation of the polyomavirus population within arachnids, specifically the Arizona bark scorpion. Here we report, characterize, describe the phylogeny and highlight the diversity of the first complete polyomavirus genomes recovered from an invertebrate.

2.2. Material and methods

2.2.1. Sample collection and preparation

Four bark scorpions were collected from two locations in Phoenix, Arizona, USA, between August and November 2018 and stored at –80°C. Scorpions were surface sterilized using the following protocol: wash in 95% ethanol for 15 seconds followed by a wash in 10% bleach for 60 seconds and finally rinsed three times in molecular grade water. The specimens were allowed to air dry in a

petri dish lined with sterile filter paper in a laminar flow hood prior to dissection. The stinger was removed and a sterile scalpel used to cut along the side of the body in between the legs and body plate. Sterile forceps were used to remove the top plate so the internal cavity was visible.

The gut and liver were removed and each was placed in a sterile 1.5ml tube and homogenized in 500µl of SM buffer (50mM Tris–HCl, 10mM $MgSO_4$, 0.1M NaCl, pH 7.5). The homogenate was processed as previously described in (Dayaram et al., 2014; Dayaram et al., 2016; Dayaram et al., 2015). Viral DNA was extracted using the Roche high pure viral nucleic acid kit (Roche, USA) according to manufactures instructions and circular DNA was enriched by rolling circle amplification (RCA) with TempliPhi™ amplification kit (GE Healthcare, USA).

2.2.2. High throughput sequencing, de novo assembly and recovery of viral genomes

The RCA DNA was sequenced on an Illumina HiSeq4000 (2×150 bp paired end library) and the reads were *de novo* assembled using SPAdes 3.12 (Bankevich et al., 2012). Contigs of >1000 nts were analyzed using BLASTx (Altschul et al., 1990) against a local viral protein sequence database. Eight *de novo* assembled contigs were identified to have sequence similarities to dsDNA viruses from the family *Polyomaviridae*.

Abutting primers were designed (Table 2.1) to recover the complete circular viral genomes by PCR. For each PCR amplification, 1µl of RCA product was used as a template with specific primer pairs and Kapa Hifi Hotstart Ready Mix (Kapa Biosystems, USA) using the following thermal cycling protocol: initial denaturation at 95°C for 3 min followed by 25 cycles 98°C for 20 s, 60°C for 15 s, 72°C for 6 min, final elongation at 72°C for 6 min and a final renaturation at 4°C for 10 min. The resulting ~5 kb amplicons were resolve on a 0.7% agarose gel, excised, gel purified, ligated into pJET1.2 vector (ThermoFisher, USA) and transformed into XLBlue1 *Escherichia coli* competent cells. The resulting recombinant plasmid were Sanger sequenced at Macrogen Inc. (South Korea)

by primer walking. The Sanger sequence contigs were assembled using Geneious Prime 2019.1.1 (https://www.geneious.com).

Table 2.1: Primer details for each recovered scorpion polyomavirus

Sequence Name	Forward primer	Reverse primer
Bark_scorpion_1_gut_1	CAAATTTTCCCAACCGTAGCCTCCTTTTCCC	GAAAGTCTCCGAGACCATATTGATGGTCGTATC
Bark_scorpion_1_gut_2	CAAATTTTCCCAACCGTAGCCTCCTTTTCCC	GAAAGTCTCCGAGACCATATTGATGGTCGTATC
Bark_scorpion_1_liver_1	CGAGCATACTCTTTCCGGAATTGTAATATCCGG	CACATGCGTTCTCCCAATTATTCGATGCTGTG
Bark_scorpion_3_gut_1	CGAGCATACTCTTTCCGGAATTGTAATATCCGG	CACATGCGTTCTCCCAATTATTCGATGCTGTG
Bark_scorpion_1_liver_2	CGAGCATACTCTTTCCGGAATTGTAATATCCGG	CACATGCGTTCTCCCAATTATTCGATGCTGTG
Bark_scorpion_2_liver_1	CATACGGCGGTCAAGGGCATTACCC	GTCATCTTCGACGACGTCAGAGGGG
Bark_scorpion_3_gut_2	CATACGGCGGTCAAGGGCATTACCC	GTCATCTTCGACGACGTCAGAGGGG
Bark_scorpion_3_liver_1	CATACGGCGGTCAAGGGCATTACCC	GTCATCTTCGACGACGTCAGAGGGG

2.2.3. Total RNA extraction and transcript synthesis

Samples were homogenized in 50µl SM buffer as described above. Total RNA was extracted from the homogenates using the TRIzol Reagent kit (Invitrogen, USA). 500µl of trizol was added to each sample and incubated at room temperature for 5 min. Then 100µl of chloroform was added followed by a 2 min incubation at room temperature. Samples were centrifuged for 15 min at 12,000g at 4°C. The upper aqueous phase was transferred to a sterile tube, 250µl of isopropanol was added to the aqueous phase and incubated at room temperature for 10 min followed by a 10 min centrifugation at 12,000g at 4°C. RNA pellet was resuspended in 500µl 75% ethanol. Mixture was centrifuged for 10min at 9,000g at 4°C. Ethanol was discarded, final pellet was allowed to dry and resuspended in 20µl nuclease free water. To ensure total RNA did not contain DNA, samples were treated with DNAaseI (Ambion, USA) under the following conditions: 1µl 10X DNase I Reaction Buffer, 1µl DNase I and DEPC-treated water up to 30µl were added to ~1µg RNA sample. Samples were incubated at room temperature for 15 min and DNaseI was inactivated by the addition of 1µl of 25 mM EDTA and heating for 10 min at 65°C and immediately used for cDNA synthesis using RevertAid First Strand cDNA Synthesis Kit (Thermo Scientific, USA). 1µl of template RNA, 1µl primer, 6µl of water was heated at 65°C for 5 min, then the following were added 2µl reaction buffer, 0.5µl RiboLock RNase inhibitor, 1µl 10mM dNTP mix, and 0.5µl RevertAid M-MulV RT and was incubated for 60 min at 42°C.

2.2.4. Phylogenetic analysis

A curated dataset that includes representative sequences of all currently known polyomavirus species was downloaded on January 28, 2019 from https://ccrod.cancer.gov/confluence/display/LCOTF/Polyomavirus and used in all proceeding analyses. A maximum–likelihood (ML) phylogenetic tree was constructed using the LT amino acid sequences from eight scorpion derived polyomavirus genomes together with those from available in the public database GenBank. The dataset was aligned using MAFFT (Katoh et al., 2002) and a ML phylogenetic tree inferred using PHYML (Guindon et al., 2010) with the model LG+G+I as determined by ProtTest (Darriba et al., 2011). Branches with <0.5 aLRT branch support were collapsed using TreeGraph 2 (Stöver and Müller, 2010) and the tree were visualized using FigTree v 1.4.3 (Rambaut, 2007).

2.2.5. Pairwise identities

Whole genome nucleotide sequences as well as LT and VP1 amino acid pairwise identity was also determined using sequence demarcation tool (SDT) version 1.2 in MUSCLE mode (Muhire et al., 2014).

2.2.6. Network analysis

LT amino acid sequences were input into EFI – enzyme similarity tool (EST) (Gerlt et al., 2015) and used to generate a sequence similarity network with the following parameters: E–vaule = 5, fraction = 1, alignment score = 105, filter = E–value, convergence ratio = 1. The final network had 164 nodes with 8674 edges and was visualized using Cytoscape 3.7.0 (Lopes et al., 2010).

2.2.7. Host phylogeny

Polyomavirus host scientific names were extracted from curated dataset and uploaded to phyloT (https://phylot.biobyte.de/) with the following tree options: identifier = scientific name, internal nodes

= expanded, polytomy = yes. The cladogram was opened in TreeGraph 2 (Stöver and Müller, 2010) and major clades of mammal, avian and fish sequences were collapsed to aid in visualizations.

2.3. Results and Discussion

2.3.1. Genome organization

Four bark scorpions were collected in Phoenix, Arizona, dissected and analyzed for the presence of polyomaviruses. From three of the samples, eight complete diverse genomes that are consistent in organization and size with other polyomaviruses, were recovered (Figure 2.1). The genomes range in size from 5420 to 5945 bp with open reading frames (ORFs) that are predicted to encode proteins homologous to the LT antigen, VP1 and VP2. The LT antigen contains the conserved DnaJ domain as well as an LXCXE motif (Figure 2.2). Some of the recently described polyomaviruses from fish do not have these conserved regions and it has been suggested that these are common ancestral domains that were lost when perciform fish diverged (Van Doorslaer et al., 2018). The presence of these domains in scorpions supports that the DnaJ domain and LXCXE motif are common ancestral features of polyomaviruses.

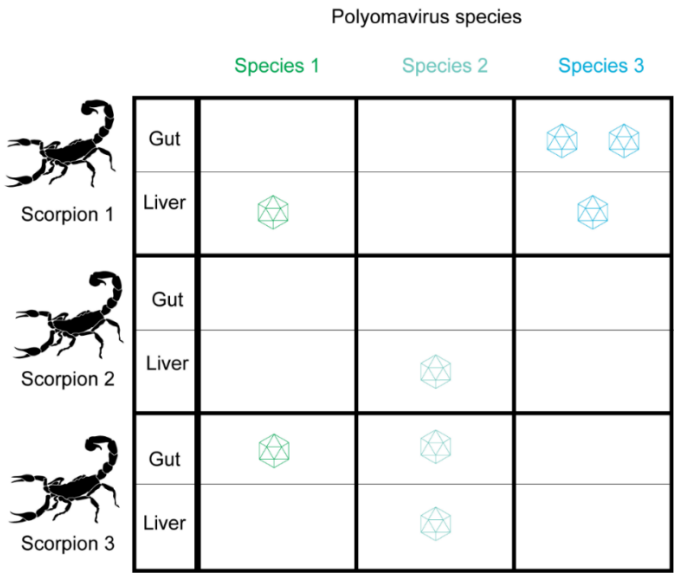

Figure 2.1: Visual summary of polyomavirus isolate recovery by sample tissue. Each scorpion sample (1-3) is broken into sub-samples (gut and liver). Color coded virus cartoons are used to depict where each isolate was recovered.

-

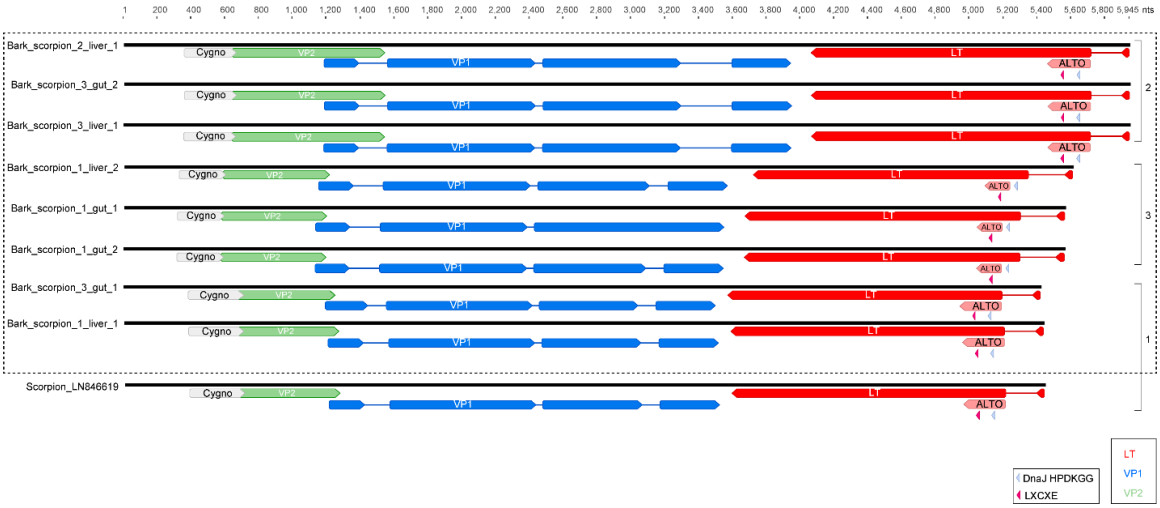

Figure 2.2: Genome organization for each scorpion polyomavirus highlighting the VP2 (green), VP1 (blue) and LT (red) ORFs. Scale at the top is used to show genome length in nucleotides. Genomes are grouped into putative species as noted on the numbered groups on the right hand side.

2.3.2. Similarity comparison

In scorpion sample 1, four polyomaviruses were identified from the gut (n=2) and liver (n=2). The two from the gut share 99% genome-wide identity and the ones from the liver share 74% identity. Overall the four polyomavirus genomes share 73-99% identity (Figure 2.3). These polyomaviruses from the bark scorpions share 73-90% genome-wide identity with the Baja California bark scorpion polyomavirus 1 (LN846619) assembled from the WGS data (Buck et al., 2016).

In scorpion sample 2 only one genome was identified and it is 100% identical to the one identified in scorpion sample 3 (from the liver and gut). In scorpion sample 3, a total of three genomes were recovered from the gut (n=2) and liver (n=1). These share 72-100% genome-wide identity (Figure 2.1, 2.3). 100% identical isolates were recovered from both tissue types.

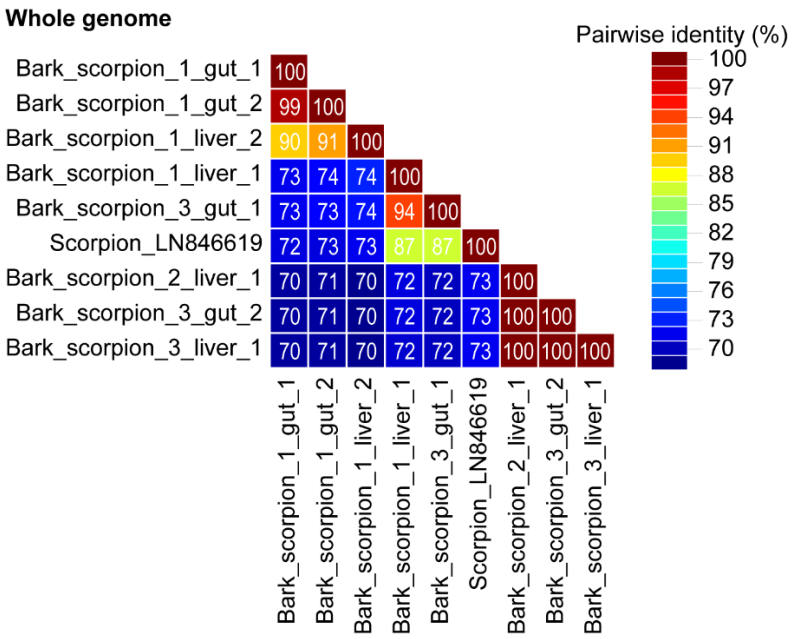

Figure 2.3: Whole genome nucleotide pairwise identity color matrices of scorpion polyomaviruses in this study.

The polyomavirus taxonomy guidelines (*Polyomaviridae* Study Group of the International Committee on Taxonomy of et al., 2016) recommends that polyomaviruses that share <85% LT pairwise nucleotide identity should be considered to belong to distinct viral species. Thus, the genomes recovered from bark scorpions can be assigned to three unique species without a designated genus (Figure 2.4). Polyomavirus sequences recovered from the gut and liver of bark scorpion 1 and 3 along with the CA bark scorpion LN846619 represent species 1. Polyomavirus sequences that represent species 2 were recovered from bark scorpion 2 and 3, from both liver and gut. Species 3 is comprised of sequences from bark scorpion 1 with isolates and both tissue types (Figure 2.4). Identical viruses were recovered from multiple scorpions illustrating that this is endemic to these animals.

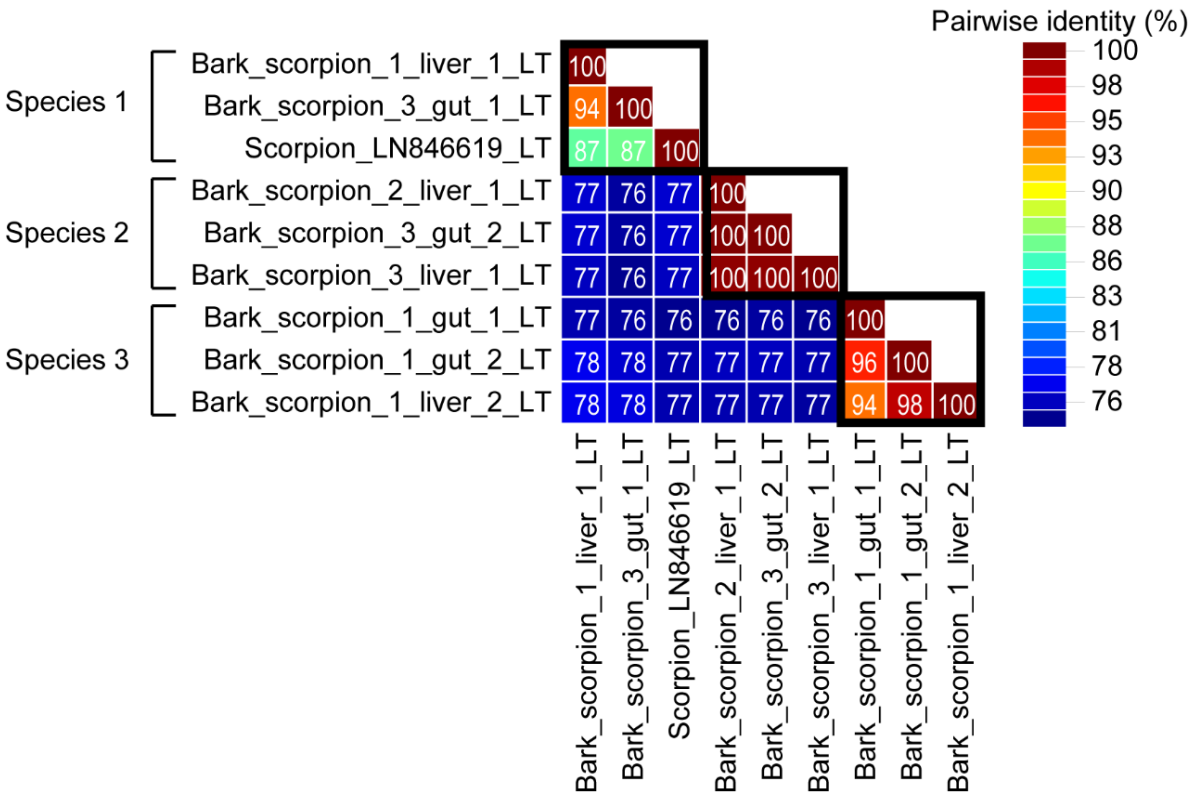

Figure 2.4: LT nucleotide percentage pairwise identity matrix of scorpion polyomaviruses. Sequences are grouped into species as indicated by boxes and text to the left of sequence IDs.

At the nucleotide level, the scorpion polyomaviruses share between 55–61% whole genome pairwise identity with all non-arachnid polyomaviruses (Table 2.2, and Figure 2.3). LT antigens of the scorpion polyomaviruses share between 23–32% amino acid pairwise identity with all other polyomavirus and >80% amongst themselves (Table 2.3 and Figure 2.5A). VP1s show higher diversity sharing between 19–31% amino acid pairwise identity with all other polyomavirus, >56% with each other (Table 2.4 and Figure 2.5B).

Table 2.2: Maximum and minimum whole genome nucleotide percentage pairwise identities to vertebrate polyomavirus sequences in GenBank, California bark scorpion polyomavirus (LN846619) and viruses from the present study.

Genome	Vertebrate polyomavirus	CA bark scorpion	Scorpion polyomavirus
Bark_scorpion_1_gut_1	60% – Chimp2a (HQ385748.1) 55 % – Bullfinch (NC_007923.1)	73%	99% –BS1_gut_2 70% – BS2_liver1 & BS3_liver_1
Bark_scorpion_1_gut_2	60% – Wild goat (MG654480.1) 55% – Bullfinch (NC_007923.1)	73%	99% – BS1_gut_1 71% – BS2_liver_1 & BS3_liver_1
Bark_scorpion_1_liver_2	60% – MWPyV (JQ898291.1) 55 % – Bullfinch (NC_007923.1)	73 %	91% – BS1_gut_2 70% – BS3_liver_1
Bark_scorpion_1_liver_1	61% –STLPyVc (KF525270) 55% – Budgerigar (NC_004764.2)	90%	94.4% – BS3_gut_1 72.1% – BS3_gut_2 & BS3_liver_1
Bark_scorpion_3_gut_1	60% – MWPyV (JQ898291.1) 55% – Adelie penguin (KP033140.1)	90%	100% – BS3_gut_1 72% – BS3_liver_1
Bark_scorpion_2_liver_1	61% – Red panda (KT878838) 55% – Sea bream (KX643371)	72%	100% – BS3_gut2 70% – BS1_liver_2
Bark_scorpion_3_gut_2	60% – Chimp6 (KT184855.1) 55% – Sea bream (KX643371)	72%	100% – BS2_liver_1 70% – BS1_liver_2
Bark_scorpion_3_liver_1	60% – Chimp6 (KT184855.1) 55% – Sea bream (KX643371)	72%	100% – BS3_gut_2 70% – BS1_liver_2

Table 2.3: Maximum and minimum LT amino acid percentage pairwise identities vertebrate polyomavirus sequences in GenBank, California bark scorpion polyomavirus (LN846619) and viruses from the present study.

Genome	Vertebrate polyomavirus	CA bark scorpion	Scorpion polyomavirus
Bark_scorpion_1_gut_1	32% – Budgerigar (NC_004764.2) 24% – Japanese eel (AB543063.1)	83%	99% – BS1_gut2 80% – BS3_liver_1
Bark_scorpion_1_gut_2	32% – Budgerigar (NC_004764.2) 24% – Japanese eel (AB543063.1)	83%	100% – BS1_liver2 81% – BS3_liver_1
Bark_scorpion_1_liver_2	32% – Budgerigar (NC_004764.2) 24% – Japanese eel (AB543063.1)	83%	100% – BS1_gut2 81 % – BS3_liver_1
Bark_scorpion_1_liver_1	32% – Goose (NC_004800.1) & Bullfinch (NC_007923.1) 24% – Bushveld horseshoe bat (LC269978.1)	99%	98% – BS3_gut_1 81% – BS3_liver_1
Bark_scorpion_3_gut_1	32% – Goose (NC_004800.1) 24% – Chmip3 (JX159980.1)	99%	99% – BS3_gut_1 81% – BS3_liver_1
Bark_scorpion_2_liver_1	31% – Little brown bat (NC_011310.1) 23 – Japanese eel (AB543063.1)	81%	100% – BS3_gut2 81%– BS1_gut_1
Bark_scorpion_3_gut_2	31% – Little brown bat (NC_011310.1) 23 – Japanese eel (AB543063.1)	81 %	100% – BS2_liver1 81% – BS1_gut_1
Bark_scorpion_3_liver_1	31% – Little brown bat (NC_011310.1) 23 – Japanese eel (AB543063.1)	81%	100% – BS2_liver_1 80%– BS1_gut_1

Table 2.4: Maximum and minimum VP1 amino acid percentage pairwise identities vertebrate polyomavirus sequences in GenBank, California bark scorpion polyomavirus (LN846619) and viruses from the present study.

Genome	Vertebrate polyomavirus	CA bark scorpion	Scorpion polyomavirus
Bark_scorpion_1_gut_1	30% – Bat polyomavirus (KX434762) 20% – Vervet (AB767298.1)	61%	100% – BS1_gut_2 56% – BS2_liver_1
Bark_scorpion_1_gut_2	30% – Bat polyomavirus (KX434762) 20% – Badger (NC_026473.1)	63%	100% – BS1_gut_1 58% – BS2_liver_1
Bark_scorpion_1_liver_2	28% – Black capped squirrel monkey (AM748741.2) 20%– Weddell seal (NC_032120.1)	60%	88% – BS2_gut_2 57% – BS2_liver_1
Bark_scorpion_1_liver_1	28% – Notothen (NC_026944) 19% – Delicate grass mouse (MH118579.1)	88%	97% – BS3_gut_1 59% – BS2_liver_1
Bark_scorpion_3_gut_1	28% –Alpaca (NC_034251.1) 19% – Strawcolored fruit bat (JX520660.1)	89%	100% – BS3_gut_1 58% – BS2_liver_1
Bark_scorpion_2_liver_1	31% – Guitarfish (NC_026244) 19% – Giant panda (KY612371.1)	58%	100% – BS3_gut_2 56% – BS1_gut_1
Bark_scorpion_3_gut_2	31% – Guitarfish (NC_026244) 19% – Giant panda (KY612371.1)	58%	100% – BS3_liver_1 56% – BS1_gut_1
Bark_scorpion_3_liver_1	31% – Guitarfish (NC_026244) 19% – Giant panda (KY612371.1)	58%	100% – BS3_gut2 56% – BS1_gut_1

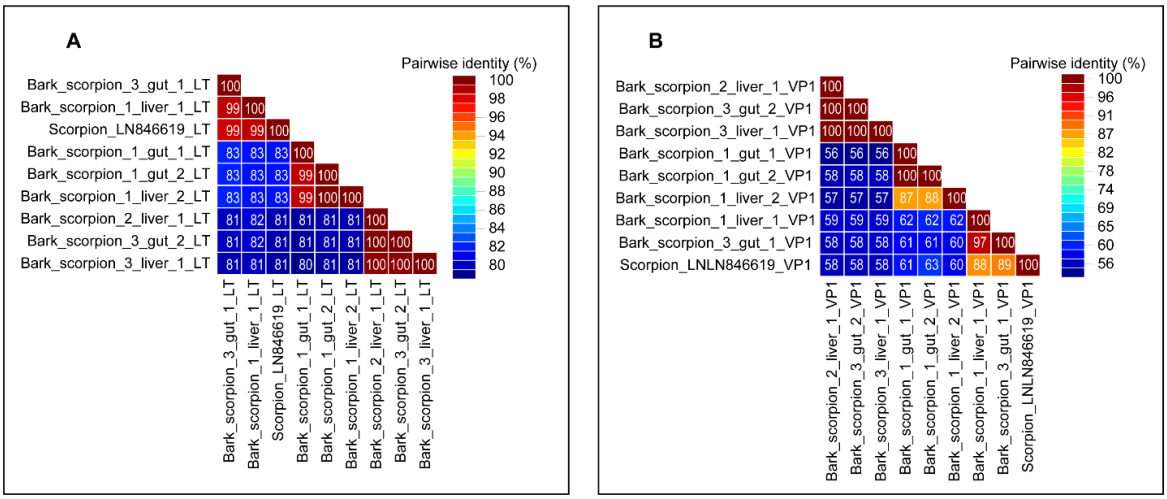

Figure 2.5: Pairwise identity color matrices of scorpion polyomaviruses in this study. **A**. LT amino acid pairwise identity. **B**. VP1 amino acid pairwise identity.

2.3.3. Phylogenetic analysis of LT

To evaluate the phylogenetic relationship between sequences recovered in this study and the GenBank curated polyomavirus dataset, a maximum likelihood phylogenetic tree was constructed from the LT amino acid sequences (Buck et al., 2016). Sequences included in this analysis were available prior to January 2019 and included putative LT sequences from a guitarfish, arowana, Japanese eel, marbled eel, bandicoot and bat feces. The phylogenetic tree (Figure 2.6) shows distinct clades that are consistent with host source of viral sequences. It was possible to completely collapse mammal and avian clades while the clades containing fish sequences were more diverse. Importantly, scorpion derived sequences cluster together and branch from all other polyomavirus sequences. To further support that the sequences reported here are associated with arachnids, network analyses were undertaken using LT amino acid sequences and those derived from all mammal infecting polyomaviruses. The LT protein sequences cluster together respectively with the exception of the recombinant bandicoot LT sequences, and fish sequences. Of the fish polyomaviruses, four sequences cluster together and the remainder are singletons or groups with only one other LT based on the cluster threshold used for this analysis. All scorpion derived sequences cluster together. The LT protein clusters provide some support that the scorpion polyomaviruses have a unique origin which is scorpion specific (Figure 2.7).

2.3.4. Host and LT phylogeny

For additional support that scorpions are the hosts of these viruses the host phylogeny tree, generated with the online tool PhyloT, was compared to that of polyomaviruses. The host tree closely reflects that of the polyomavirus LT protein phylogeny illustration host-virus co-evolution.

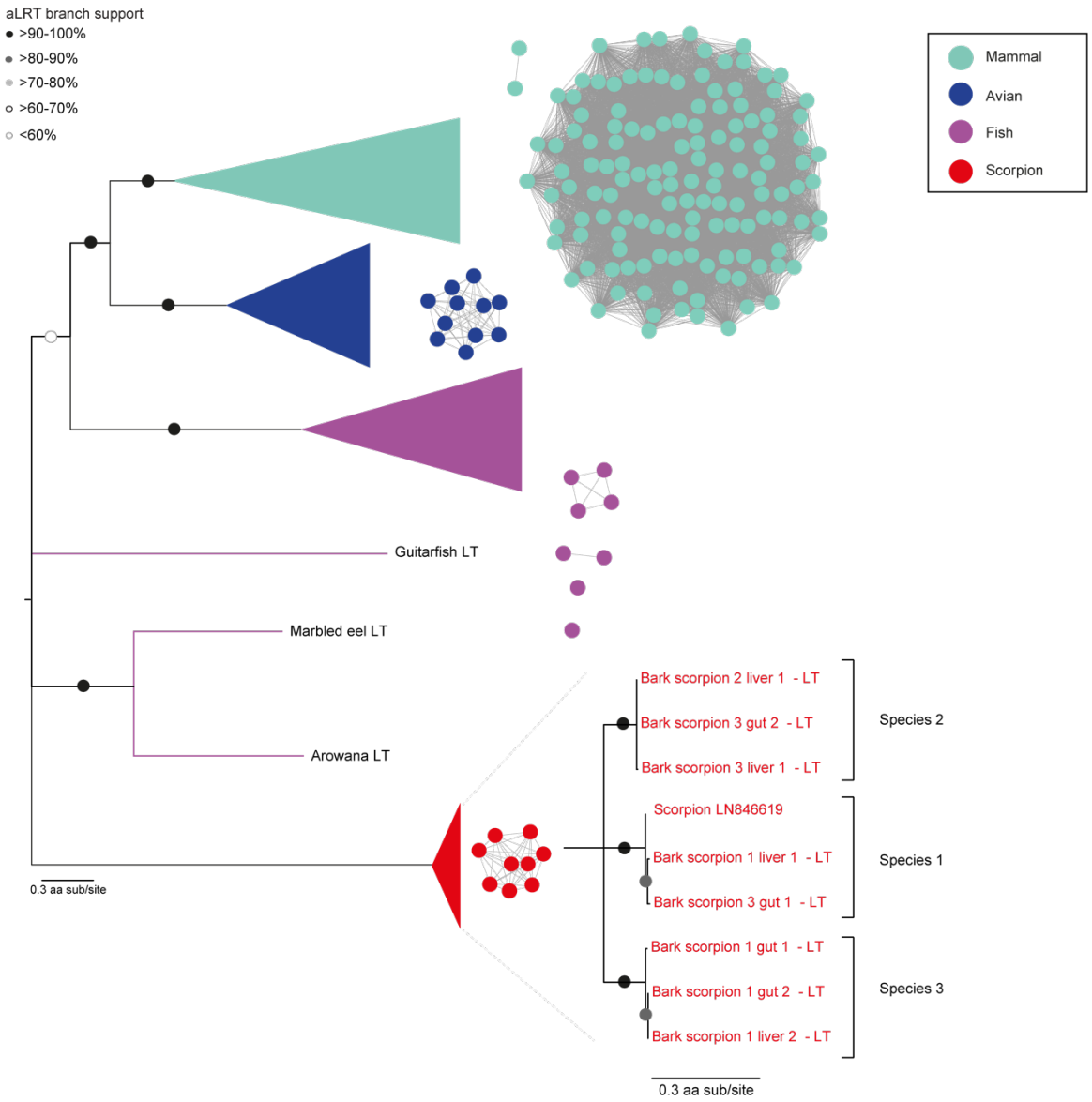

Figure 2.6: Unrooted phylogenetic tree and network analysis inferred from alignments of the LT amino acid sequences of polyomaviruses. Branches were collapsed by host where possible. Each host has a corresponding color with scorpion sequences colored red.

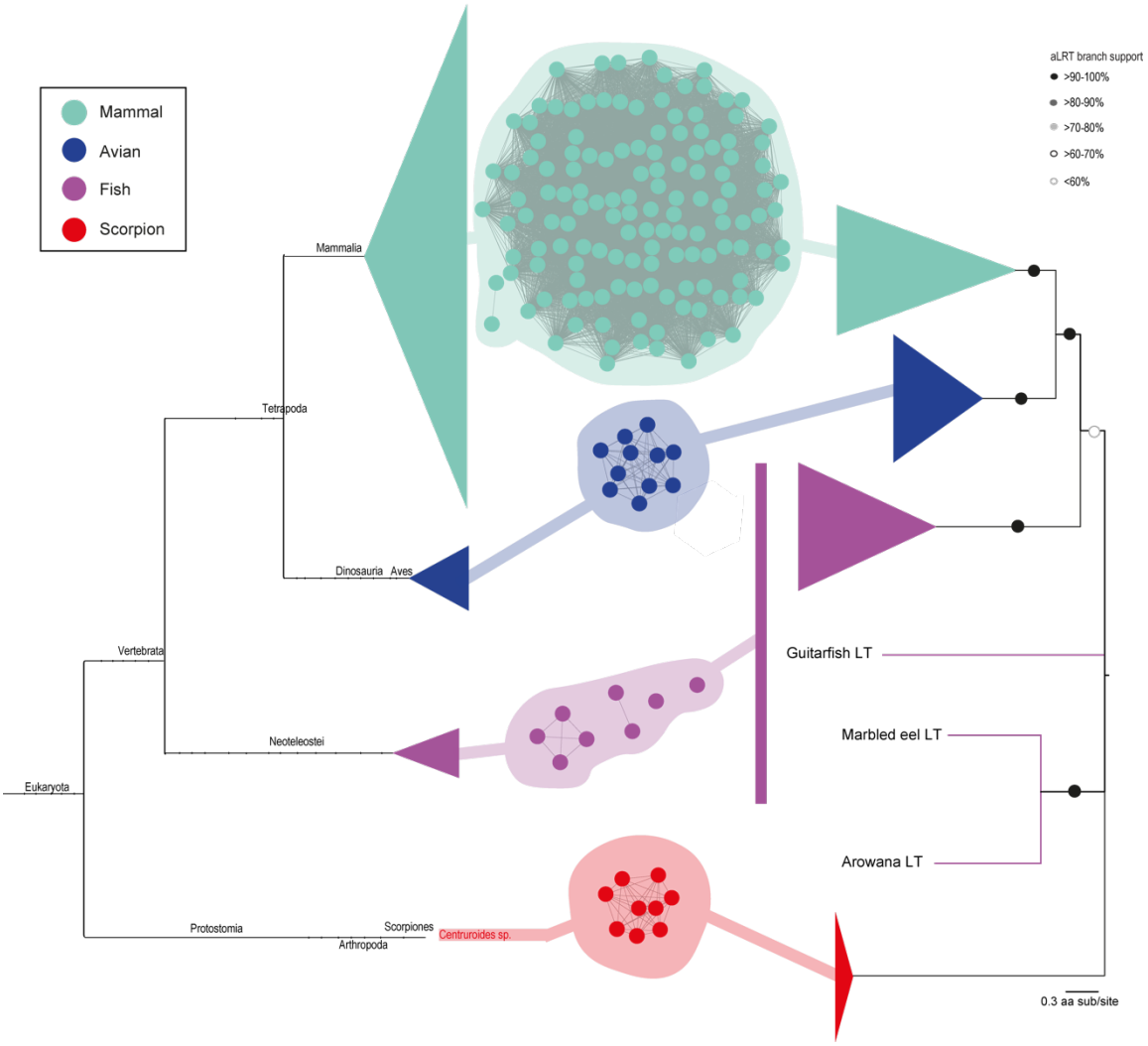

Figure 2.7: Co-phylogenies of polyomaviruses and their hosts. Host phylogeny was generated using PhyloT. Polyomavirus phylogenetic tree and network analysis inferred from LT amino acid sequences. ML tree is unrooted and branches were collapsed into mammal, avian, and fish groups and each has a corresponding color with scorpion sequences in red.

2.3.5 Transcript data

To provide evidence that these polyomaviruses are actively replicating in the scorpion, RNA was extracted from original homogenates and used for transcript detection. A ~600 nucleotide section on the LT was recovered from Bark_scorpion_1_gut_1. The sequence data of the LT transcript cDNA and the viral LT gene were 100% identical. Further work is needed to identify transcripts in other samples and to confirm the putative LT and VP1 splice sites.

2.4. Concluding remarks

Four genomes were recovered from the liver and four were recovered from the gut. All specimens appeared healthy at the time of collection and no investigation into possible associated disease states has been undertaken. In addition to host and LT phylogeny comparisons and identical genomes being identified in multiple scorpions, the recovery of a LT transcript provides evidence that these viruses are replicating and that scorpions are the true host of this novel lineage of polyomaviruses.

This small dataset begins to describe the prevalence and diversity of polyomaviruses within scorpions and it is remarkable. The investigation into four bark scorpions yielded eight genomes separated into three species. Isolates from species 1 and 2 were isolated from two scorpions from both the liver and gut. Isolates from species 3 were recovered from one scorpion, but from both tissue types. Importantly, there are multiple, distinct polyomaviruses circulating in the same animal. Scorpion 1 and scorpion 3 have viruses spanning two species. While it is probable the viruses recovered from the liver infect scorpions, it cannot be ruled out that the genomes recovered from the gut are diet related. Even if scorpions are not the true host, since they prey on other arachnids and insects the viruses are still likely to be associated with an invertebrate.

Further investigation into the virome of scorpions and other arachnids is likely to produce a large range of novel polyomaviruses. The collection and characterization of these genomes will help further elucidate the evolutionary history of polyomaviruses. Recent discoveries of divergent RNA viruses in arthropods has ultimately led to arthropods being identified at the ancestral source of some vertebrate infecting viruses (Shi et al., 2016b). Based on the recovery and characterization of these genomes, it appears that at least one polyomavirus was circulating in the last common ancestor of arthropods and vertebrates.

CHAPTER 3

ARTHROPOLVIRUS: A PROPOSED NEW TAXON OF ARTHROPOD ASSOCIATED POLYOMA-LIKE VIRUSES

Abstract

Viral taxonomy is rapidly undergoing changes to accommodate the new viruses identified through viral metagenomic approaches. In arachnids, namely American dog ticks (n=3) and a hairy scorpion (n=1) four novel viruses ranging in size of 4249 to 5225 bp with unidirectional organized open reading frames (ORFs) were identified. These circular DNA genomes encode contain three large ORFs, one of which is predicted to be homologous to the large tumor (LT) antigen of polyomaviruses. The closest relatives, as determined by BLASTx, are the LT protein sequences of scorpion polyomaviruses (see Chapter 2). Based on their phylogenetic relationships to polyomavirus LT protein sequences, highly divergent VP1 sequences and unidirectional genome organization the viral genomes presented here appear to form a new family and for the purpose of this study have been labelled as arthropolviruses (arthropod associated polyoma-like viruses).

3.1 Introduction

Polyomaviruses and papillomaviruses have circular, double-stranded DNA (dsDNA) genomes and encode a large tumor (LT) antigen protein that is required for viral replication and interacts with host proteins in such a manner than uncontrolled cell growth can lead to tumor formation. The LT has three conserved domains including a DnaJ domain, LXCXE motif and a superfamily 3 helicase domain and is required for viral replication. Recently, genes predicted to encode proteins homologous to LT have been characterized from several novel viral genomes that do not possess classical polyomavirus or papillomavirus genome organization. Woolford et al described two apparent recombinant viruses recovered from a western barred bandicoot. These viruses encode a polyoma-like LT gene however, the capsid proteins are most closely related to papillomavirus L1 and L2 (Woolford et al., 2007). Similar to the bandicoot genomes, five unidirectional sequences, recovered from eel and fish species, are of particular interest as their genomes are unidirectional, contain an ORF coding for a polyoma-like LT however other ORFs are most closely related to

adenoviruses (Mizutani et al., 2011; Okazaki et al., 2016; Welch et al., 2018; Wen et al., 2016). It has been proposed that these viruses create a new family, termed Adomaviridae.

Arthropoda is the largest phylum in the animal kingdom and over the recent years metagenomic studies investigating the virome of arthropods have described numerous novel viruses associated with these animals indicating there is a rich population of viruses circulating in this population (Li et al., 2015; Rosario et al., 2018; Shi et al., 2016a). Studies exploring the tick-borne viruses are often focused on medically or veterinary important diseases and therefore neglect to investigate novel viruses associated with these arachnids (Tokarz et al., 2019). Additionally, studies that aim to characterize novel viruses, the vast majority focus on RNA viruses (Brinkmann et al., 2018; Harvey et al., 2019). As a result, little is known about the dsDNA virus populations circulating in ticks. As part of an ongoing project to characterize the DNA virome of arachnids, we report three viruses that have a polyoma-like LT associated with *Dermacentor variabilis* (American dog tick) and one associated with *Hadrurus arizonensis* (hairy scorpion) that have been tentatively assigned to Arthropolviridae.

3.2 Materials and Methods

3.2.1 Sample collection and preparation

D. variabilis female ticks were collected in the Lehigh Valley region of Pennsylvania, USA, over two summer seasons between April and July 2015 and 2018 by dragging a white fabric flag through grassy habitats (Edwards et al., 2015). Ticks collected in 2015 were stored in 70% ethanol and kept at 4°C while ticks collected in 2018 stored at -80°C until processing. Prior to isolation of viral DNA, samples stored in ethanol were air dried in a petri dish lined with filter paper for several hours. Additionally, a single hairy scorpion (*Hadrurus arizonensis*) was collected from Phoenix, Arizona, USA, and stored at –80°C until processing. All samples were surface sterilized under the following conditions: 15 second wash in 95% ethanol, followed by a 60 second wash in 10% bleach and the three consecutive rinses in molecular grade water. Samples were air dried for several hours in a petri dish lined with sterile filter paper in a laminar flow hood. Approximately 15 dried *D. variabilis*

female ticks, collected in 2015, were dissected lengthwise with sterile scalpel blade, pooled and homogenized in 500µl of SM buffer (50mM Tris–HCl, 10mM $MgSO_4$, 0.1M NaCl, pH 7.5). Ticks collected in 2018 were separated into 20 pools of 10 ticks and processed in the same manner.

The hairy scorpion was dissected by first removing the stinger then a sterile scalpel blade was used to cut along the side of the body in between the legs and body plate. Sterile forceps were used to remove the top plate so the internal cavity was visible. The gut and liver were removed and each was placed in a sterile 1.5ml tube and homogenized in 500µl of SM buffer. The homogenates were processed as previously described in (Dayaram et al., 2016).

3.2.2. High throughput sequencing, de novo assembly and recovery of viral genomes

Viral DNA was extracted using the Roche high pure viral nucleic acid kit (Roche, USA) according to manufactures instructions and circular DNA was amplified by rolling circle amplification (RCA) with TempliPhi™ amplification kit (GE Healthcare, USA). The RCA amplified DNA from ticks collected in 2015 was sequenced on an Illumina NextSeq500 (2 x 125bp paired end library) and the reads were *de novo* assembled using ABySS v1.9 (Simpson et al., 2009). The RCA amplified DNA from ticks collected in 2018 was sequenced on an Illumina HiSeq4000 (2 x 150bp paired end library) and the reads were *de novo* assembled using SPAdes 3.12.0 (Bankevich et al., 2012). Contigs of >1000 nts were analyzed using BLASTx against a local viral protein database curated from GenBank RefSeq sequence data. From the tick and scorpion *de novo* assembled contigs, three contigs were identified to have sequence similarities to the LT protein sequence of dsDNA viruses of the family *Polyomaviridae*. Based on the sequences of these two contigs, abutting primers were designed (Table 3.1) to recover the three complete circular viral genomes by PCR. For each PCR amplification, 1µl of RCA product was used as a template with specific primer pairs and Kapa Hifi Hotstart Ready Mix (Kapa Biosystems, USA) using the following thermal cycling protocol: initial denaturation at 95°C for 3 min followed by 25 cycles 98°C for 20 sec, 60°C for 15 sec, 72°C for 3 min, final elongation at 72°C for 5 min and a final renaturation at 4°C for 10 min.

The resulting ~5 kb amplicons were resolved on a 0.7% agarose gel, excised, gel purified, ligated into pJET1.2 vector (ThermoFisher, USA) and transformed into DH5α *Escherichia coli* competent cells. Clones were Sanger sequenced at Macrogen Inc. (South Korea) by primer walking. The Sanger sequence contigs were assembled using Geneious Prime 2019.1.1 (https://www.geneious.com).

Table 3.1: Abutting primers used to recovered arthropolviruses from arachnids.

Sequence name	Forward primer	Reverse primer
Dog_tick_DT4_2015	GATGAACTAGGTAGTGTTGTACAG	GATACCAAACTCCGTTAACTCTAC
Dog_tick_SP29_2015	CCTGTGATAGACCAGACTGTTCCAAAGATCAC	GGTCAGCTAGATGGGCATATTCATACATGAGG
Dog_tick_SP29_2018	CCTGTGATAGACCAGACTGTTCCAAAGATCAC	GGTCAGCTAGATGGGCATATTCATACATGAGG
Hairy_scorpion_liver	CAGAATTTATGCGCTACTGTGTCACTGTTTTTGAAG	GTTTAACAGTGAGGCAATTGCAATAGACCAGTG

3.2.3 Phylogenetic analysis

To evaluate the phylogenetic relationship of the LTs of arthropolviruses, scorpion polyomaviruses and those in GenBank curated polyomavirus dataset (Buck et al., 2016), a maximum likelihood phylogenetic tree was constructed from aligned LT amino acid sequences using the substitution model LG+G+I. Sequences included in this analysis were those available prior to January 2019 and included putative LT sequences from a guitarfish adomavirus (~21kb, circular genome), arowana fish adomavirus (~17kb, circular genome), Japanese eel adomavirus (~15kb, circular genome), marbled eel adomavirus (~16kb, circular genome), bandicoot (polyomavirus/papillomavirus recombination) and bat feces (likely arthropod derived) (Buck et al., 2016; Van Doorslaer et al., 2018; Welch et al., 2018) as well as LT sequences from eight bark scorpion derived polyomavirus genomes, one assembled from WGS data of Baja California bark scorpion (Chapter 2) together with the three from ticks and hairy scorpion. The dataset was aligned using MAFFT (Katoh et al., 2002) and a ML phylogenetic tree inferred using Seaview 4 (Gouy et al., 2010) with the model LG+G+I as determined by ProtTest (Darriba et al., 2011). Clades corresponding to host type were collapsed and the tree was rooted visually in FigTree v 1.4.3 (Rambaut, 2007).

3.2.4 Pairwise identities

Pairwise identities were determined for the full genome sequences, and the LT and VP1 amino acid using sequence demarcation tool (SDT) version 1.2 in MUSCLE mode (Muhire et al., 2014).

3.2.5 Network analysis

LT amino acid sequences were input into EFI – enzyme similarity tool (EST) (Gerlt et al., 2015) and used to generate a sequence similarity network that was visualized in Cytoscape 3.7.0 (Lopes et al., 2010). SSN was generated with the following parameters: E–value = 5, fraction = 1, alignment score = 105, filter = E–value, convergence ratio = 1. The final network had 168 nodes with 8821 edges.

3.3 Results and discussion

3.3.1 Genome organization and similarity comparison

Dog ticks (n=215) were collected over the summer seasons of 2015 and 2018 in Pennsylvania, USA and one hairy scorpion was collected from Phoenix, Arizona, USA and analyzed various DNA viruses. This effort resulted in the recovery of four complete, highly divergent genomes that encode three putative proteins, one of which is most closely related to the LT of polyomaviruses. The genomes of these viruses are organized with unidirectional ORFs (Figure 3.1).

Viral sequences were recovered from three tick pools, with Dog_tick_SP29 recovered from samples collected in 2015 and 2018 sharing 100% genome-wide identity, and one from the hairy scorpion liver. They range in size from 4249 to 5945 nts. These viruses are referred to from here on as arthropolviruses (arthropod associated polyoma-like viruses). At the nucleotide level they share between 61-63% with each other (Figure 3.2).

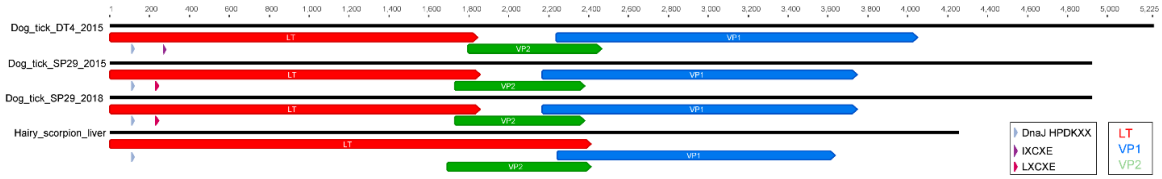

Figure 3.1: Genome organization tick arthropolvirus highlighting the LT (red), VP2 (green), and VP1 (blue) ORFs. The conserved HPDKXX motif of DnaJ and L/IXCXE motif are marked. Scale bar illustrates genome length in nucleotides.

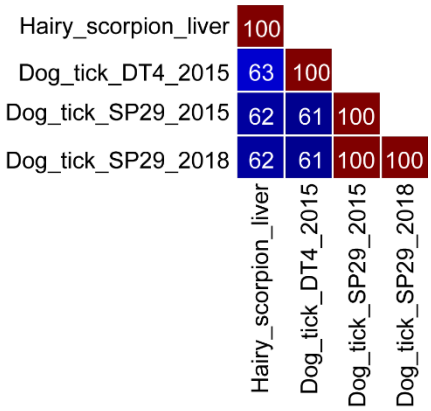

Figure 3.2: Whole genome nucleotide pairwise identity comparison plots of arthropolviruses.

The DnaJ domain of the LT protein is conserved in all sequences of the arthropolviruses, however, the LXCXE motif, which is found in most polyomavirus LTs and interacts with pRB and is involved in altering the cell cycle, is variable (Figure 3.1). The LT of Dog_tick_DT4_2015 contains an IXCXE motif, that of Dog_tick_SP29_2015 and 2018 contain an LXCXE motif and no comparable motif is identified in the LT of hairy scorpion liver derived arthropolvirus The presence of these domains in tick arthropolviruses supports the hypothesis that DnaJ domain and LXCXE/IXCXE motifs are common ancestral features. Previously described unidirectional genomes described from eels also contain a DnaJ domain but do not have a LXCXE motif suggesting the loss of LXCXE occurred some time after arachnids and fish diverge. However, the absence of the LXCXE motif in the hairy scorpion liver arthropolvirus results in an unclear resolution of ancestral components. Additional

arthropolvirus sequences will help to resolve when these motifs were gained and lost and which motifs were present in the ancestral variants.

3.3.2 Putative species demarcation

Given that arthropolviruses encode a LT that is homologous to that of polyomaviruses, if a similar species demarcation criteria is used, i.e. polyomavirus LTs that share <85% LT pairwise nucleotide identity are considered to be distinct viral species, the genomes recovered from these arachnids fall into three distinct species (Figure 3.3). Hairy_scorpion_liver is a member of species 1, Dog_tick_DT4 is the sole member of species 2 and Dog_tick_SP29_2015 and Dog_tick_SP29_2018 belong to species 3.

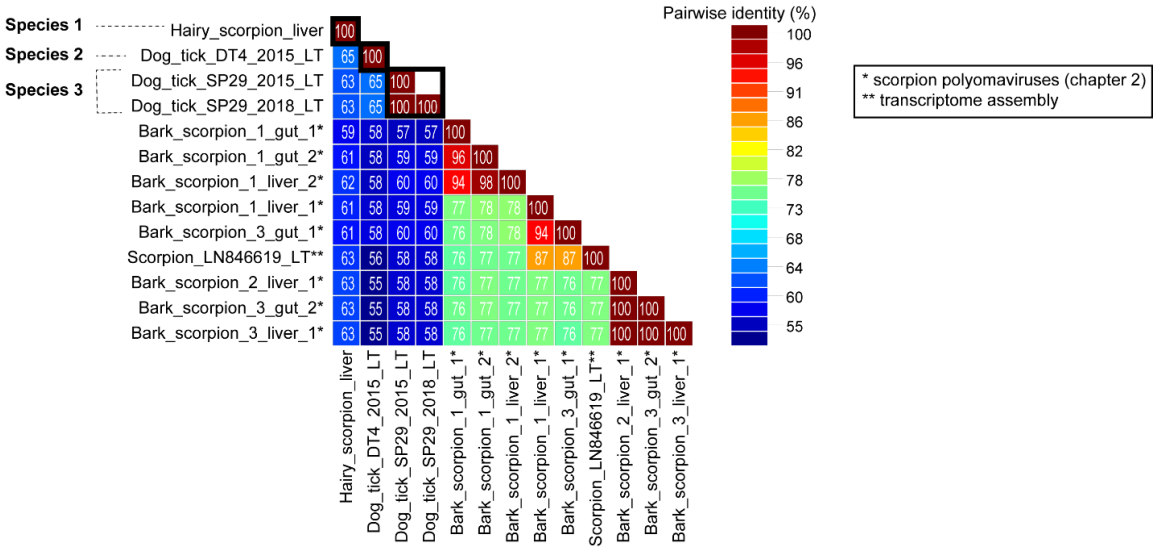

Figure 3.3: LT nucleotide percentage pairwise identities of known scorpion polyomaviruses and dog tick and hairy scorpion arthropolviruses. Suggested species groups are outlined with black boxes.

3.3.3 Similarity comparison

LT antigens of those genomes share between 24–32% amino acid pairwise identity with all other polyomavirus, 32–33% with scorpion polyomaviruses and 43-53% with each other (Table 3.2, Figure 3.4 and Figure 3.5A).

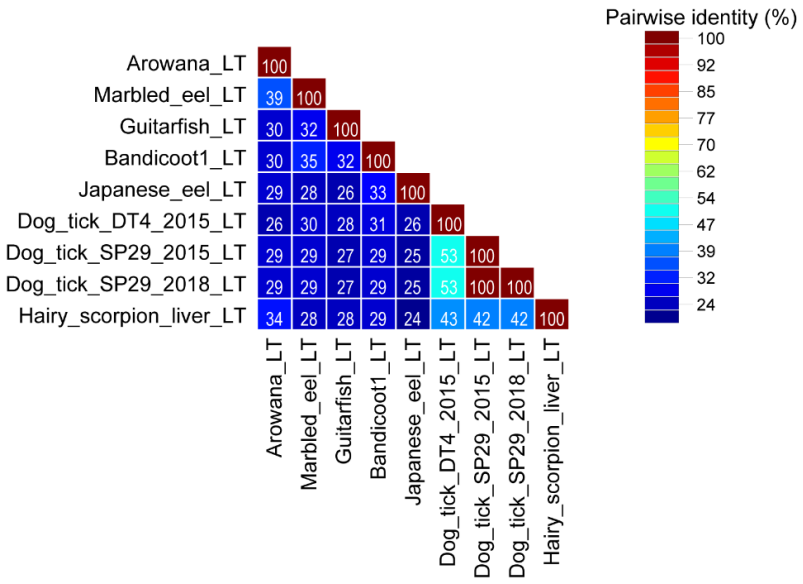

Figure 3.4: LT amino acid pairwise identity from unidirectional genomes.

Table 3.2: Maximum and minimum LT amino acid percentage pairwise identities vertebrate polyomavirus sequences in GenBank and scorpion derived polyomaviruses.

Genome	Vertebrate polyomavirus	Scorpion polyomavirus
Hairy_scorpion_liver	34% - Arowana (MH282863) 21% - Sea bream (KX643371)	34% - BS1_gut_1 30% - CA bark scorpion
Dog_tick_DT4_2015	32% – Squirrel monkey (JX159989) 25% – Notothen (NC_026944)	33% – BS1_liver_1 32% – BS3_liver_1
Dog_tick_SP29_2015	31% – Vesper mouse (MH118579) 24% – Emerald rockcod (MG800627)	34% – BS2_liver_1 32% – BS3_gut_1
Dog_tick_SP29_2018	31% – Vesper mouse (MH118579) 24% – Emerald rockcod (MG800627)	34% – BS2_liver_1 32% – BS3_gut_1

Within the genomes of arthropolviruses two putative capsid protein ORFs, VP1 and VP2, were identified. VP1s show higher diversity sharing between 17-27% amino acid pairwise identity with all other polyomavirus, 18-23% with scorpion polyomaviruses 26-29% with each other (Table 3.3 and Fig 3.5B). There is an extreme amount of diversity within these isolates.

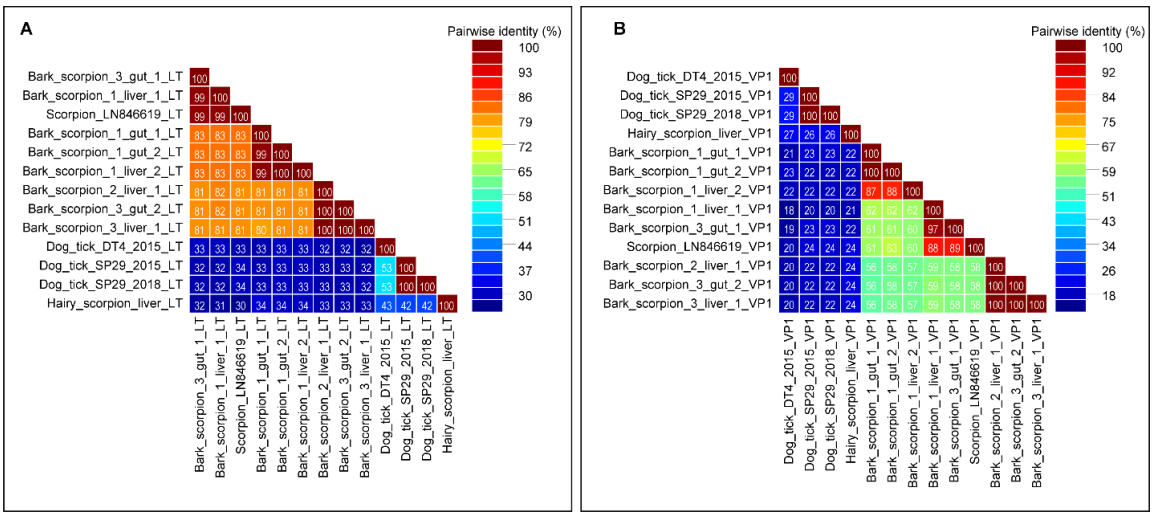

Figure 3.5: Pairwise identity comparison plots of scorpion polyomaviruses and arthropolviruses. A. LT amino acid pairwise identity. B. VP1 amino acid pairwise identity.

Table 3.3: Maximum and minimum VP1 amino acid percentage pairwise identities vertebrate polyomavirus sequences in GenBank and scorpion derived polyomaviruses.

Genome	Vertebrate polyomavirus	Scorpion polyomavirus
Hairy_scorpion_liver	24% - Brazilian free tail bat (KM655868) 14% - Flying fox (AB972942)	24% - BS3_liver_1 21% - BS1_liver_1
Dog_tick_DT4_2015	27% – Guitar fish (NC_026244) 17% – NJPyV (KF954417)	24% – BS1_gut_2 18% – BS1_liver_1
Dog_tick_SP29_2015	25% – Martienssens freetailed bat1 (JX520664) 20% – Vervet (AB767298)	23% – BS1_gut_2 20% – BS1_liver_1
Dog_tick_SP29_2018	25% – Martienssens freetailed bat1 (JX520664) 20% – Vervet (AB767298)	23% – BS1_gut_2 20% – BS1_liver_1

3.3.4 Phylogenetic analysis of LT

Arthropolviruses branch from all other LT encoding viruses, indicating that they are divergent sequences but are closely related to scorpion polyomaviruses (Chapter 2). The phylogenetic tree shows distinct clades that are consistent with host source of viral sequences providing initial supporting dog ticks and hairy scorpions are the hosts of these novel viruses (Figure 3.6).

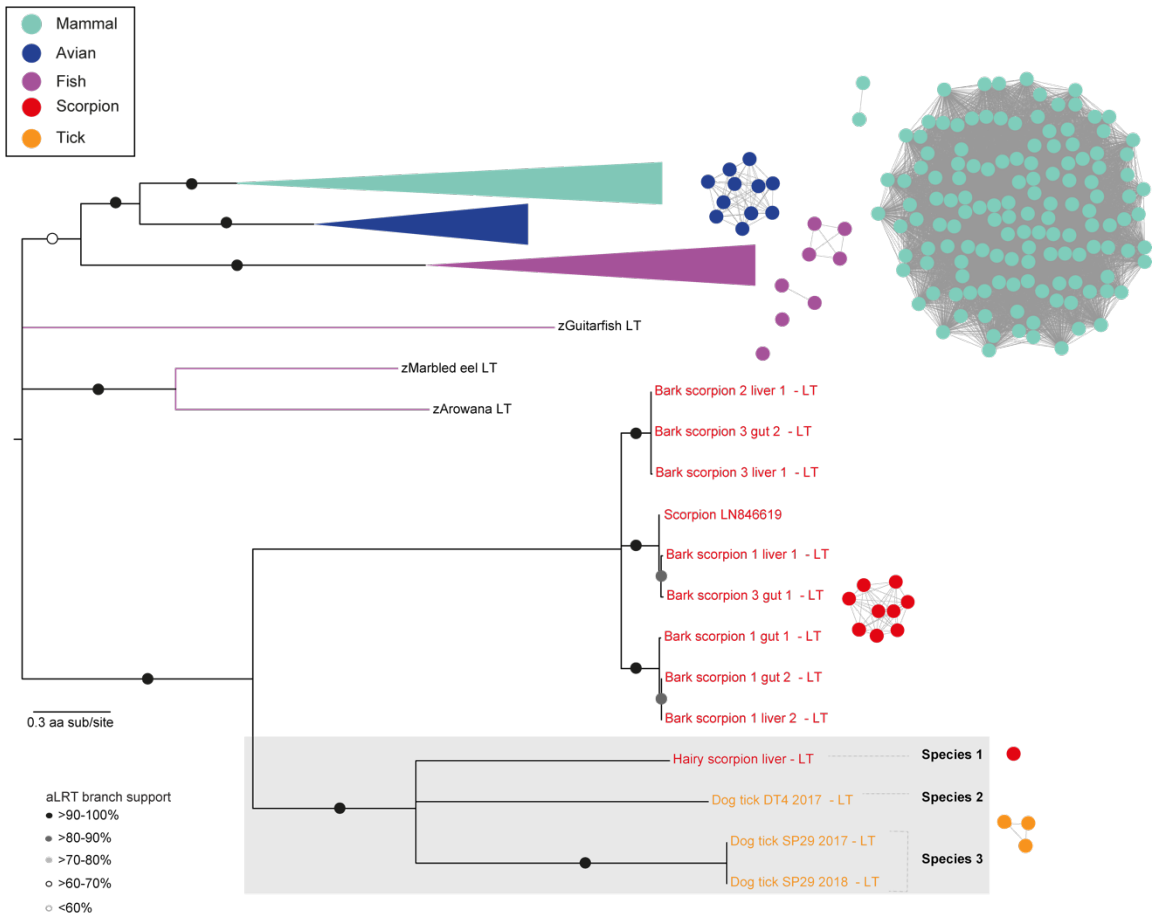

Figure 3.6: Unrooted maximum likelihood phylogenic tree and cluster analysis of LT amino acid sequences of polyomaviruses and arthropolviruses. Each host has a corresponding color. Arthropolviruses are shaded by a grey box.

3.4 Concluding remarks

The investigation into the DNA viruses in dog ticks and a hairy scorpion resulted in the discovery of diverse viral genomes that will likely belong to a new family, tentatively designated as Arthropolvirus. The LT protein encoded by arthropolviruses is most closely related to that encoded by polyomaviruses, however, the VP1 is highly divergent. Arthropolvirus species 3 was identified from samples collected in 2015 and 2018, which begins to highlight that arthropolviruses are persistent temporally within this population. As the virome of various arthropods are studied, it is likely the number of arthropolviruses sequences will increase. These discoveries will help provide more structure to the diversity and host range of these viruses coupled with evolutionary insights.

CHAPTER 4

IDENTIFCATION OF AN ANELLOVIRUS AND GENOMOVIRUSES IN IXODID TICKS

Abstract

Ticks are blood-feeding arachnids that are vectors of several important human and animal pathogens. Little is known about single-stranded DNA (ssDNA) viruses that are associated with these ectoparasites. As part of a pilot study to identify ssDNA viruses present in female American dog ticks (*Dermacentor variabilis*) and blacklegged ticks (*Ixodes scapularis*), were collected in eastern Pennsylvania (USA), and the extracted viral DNA was analyzed using viral metagenomics approaches. Three genomoviruses were recovered from pooled samples of *D. variabilis* (n=2) and *I. scapularis* (n=1); two belonging to the genus *Gemycircularvirus*, sharing <63% pairwise identity with other members within the genus and the third belonging to the genus *Gemykolovirus*, sharing <70% pairwise identity to other gemykoloviruses. Furthermore, a genome of an anellovirus belonging to the sharing 62-65% nucleotide identity with torque teno canis viruses (genus *Thetatorquevirus*) was also recovered from *D. variabilis* pooled sample.

4.1 Introduction

Ixodes scapularis (blacklegged tick) and *Dermacentor variabilis* (American dog tick) are obligate blood-feeders, which ingest a blood meal to transform between stages of development. Larval meals are typically taken from small mammals, particularly white footed mice (*Peromyscus leucopus*), which serve as important reservoirs of several bacterial and protozoan pathogens. At the nymphal and adult female stages, both ticks are opportunistic feeders with a wide range of hosts that can incidentally include humans. This interaction between host and tick can last from a few days up to two weeks (Brackney and Armstrong, 2016). During this time, the host is exposed to a variety of molecules and pathogens present in tick saliva (Brackney and Armstrong, 2016; Labuda and Nuttall, 2004). The transmission cycles of viruses between ticks and their vertebrate hosts are not well understood but it is clear that tick salivary glands play a critical role in pathogen transmission and it is likely that more viruses are circulated than have been identified (Brackney and Armstrong, 2016; Kazimirova and Stibraniova, 2013).

I. scapularis is one of the most important vectors of human disease in eastern North America. *I. scapularis* vector the spirochete bacteria *Borrelia burgdorferi*, which cause Lyme disease. They also serve as vectors for the intracellular bacteria *Anaplasma phagocytophilum*, the causative agent of human granulocytic anaplasmosis and the malaria-like apicomplexan parasite *Babesia microti* that causes human babesiosis. Although human infections are rare, *I. scapularis* is also a known vector of Powassan virus (family *Flaviviridae*) (Eisen et al., 2017). *D. variabilis* is widely distributed east of the Rocky Mountains and in limited regions along the Pacific coast (California and southern Oregon, USA) is an important vector of *Rickettsia rickettsii,* the bacteria that cause potentially lethal Rocky Mountain spotted fever.

While a few important tick-borne viruses such Colorado tick fever virus and African swine fever virus are double-stranded DNA viruses, only a few single-stranded DNA (ssDNA) viruses circulating in ticks have been identified. These include three circular replication associated protein encoding single stranded (CRESS) DNA viruses (GenBank accession #s KU230452, KX987146 and KX987147) and a 1311 nts sequence of an anellovirus (Xia et al., 2015).

As part of a pilot project to identify novel DNA viruses in *D. variabilis* and *I. scapulari*, female ticks were collected in the Lehigh Valley region of Pennsylvania, USA, between April and July 2015 by dragging a white fabric flag through grassy or forested habitats, respectively (Edwards et al., 2015). The ticks were preserved in 70% ethanol at 4°C until processing. Prior to viral DNA processing, the female ticks were air dried in a petri dish lined with filter paper for several hours. Approximately 15 dried *D. variabilis* and *I. scapulari* female ticks were dissected lengthwise with sterile scalpel bladed, pooled based on species and homogenized in 500µl of SM buffer (0.1 M NaCl, 50 mMTris/HCl (Marschang et al.), 10mM $MgSO_4$). The homogenate was processed as previously described in (Dayaram et al., 2014; Dayaram et al., 2016; Dayaram et al., 2015). Viral DNA was extracted using the Roche high pure viral kit (Roche, USA) according to manufactures instructions and circular DNA was amplified by rolling circle amplification (RCA) with TempliPhi™ Amplification

Kit (GE Healthcare, USA). The RCA amplified DNA was sequenced on an Illumina NextSeq500 (2 x 125bp paired end library) and the reads were *de novo* assembled using ABySS v1.9 (Simpson et al., 2009). Contigs of >1000 nts were analyzed using BLASTx against a viral database. Three *de novo* assembled contigs (*D. variabilis*, n=2; *I. scapularis*, n=1) were identified to have sequence similarities to single stranded DNA viruses of the family *Genomoviridae* and one (*D. variabilis*) to those in *Anelloviridae*. Based on the sequences of the contigs, abutting primers were designed (Supplementary Table 1) to recover the four complete circular viral genomes by PCR. For each PCR amplification, 1µl of RCA product was used as a template with specific primer pairs and Kapa Hifi Hotstart Ready Mix (Kapa Biosystems, USA) using the following thermal cycling protocol: initial denaturation at 95°C for 3 min followed by 25 cycles 98°C for 20 s, 60°C for 15 s, 72° for 3 min, final elongation at 72°C for 3 min and a final renaturation at 4°C for 10 min. The resulting ~2–2.5kb amplicons were gel purified, ligated into pJET1.2 vector (ThermoFisher, USA) and transformed into DH5α *Escherichia coli* competent cells. Clones were Sanger sequenced at Macrogen Inc. (South Korea) by primer walking. The Sanger sequence contigs were assembled using DNA Baser sequence assembler V4 (HeracleBioSoft, Romania).

4.2 Results and discussion

An anellovirus genome (MF173068) was recovered from *D. variabilis*. The family *Anelloviridae* encompasses a large group of small, non-enveloped viruses that contain circular ssDNA genomes that vary in size from 2.1 – 3.8 kb (Manzin et al., 2015). Anelloviruses are ubiquitous in nature and have been detected in a variety of mammals, mosquitoes and a partial sequence was identified in a metagenomics study of ticks (*Rhipicephalus* spp) (Xia et al., 2015). A dataset of the ORF1 encoded by 727 anellovirus genomes available in GenBank (10th June 2017) together with the ORF1 sequences from the partial genome of Nayun tick torque virus (KP141758) from China (Xia et al., 2015) and the tick associated torque teno virus from this study was constructed. The ORF1 sequences were codon aligned as describe in Fahsbender et al. (Fahsbender et al., 2017) and alignment was used to infer a ML phylogenetic tree using IQ-TREE (Nguyen et al., 2015). The resulting phylogenetic tree was midpoint rooted and branches with <60% bootstrap support were

collapsed using TreeGraph 2 (Stover and Muller, 2010). For each of visualization of anellovirus taxa, large clades were collapsed in FigTree v1.43 (http://tree.bio.ed.ac.uk/software/figtree/). The ML phylogenetic tree (Figure 1) shows that the ORF1 of tick associated torque teno virus from this study and that of Nayun tick torque virus (KP141758) cluster with those identified in dogs in the species *Torque teno canis virus* from Japan and China (AB076002, GU951508 and KX377522) (Lan et al., 2011; Okamoto et al., 2002) sharing 62-65% pairwise nucleotide identity. Based on the guidelines for classification for the family *Anelloviridae,* tick associated torque teno virus from this study belongs to the genus *Thetatorquevirus* (Biagini, 2009) and is a putative new species as its ORF1 amino acid sequence clusters and shares share 44-55% pairwise amino acid identity with those of torque teno canis viruses from dogs and partial Nayun tick torque virus sequence (Figure 4.1).

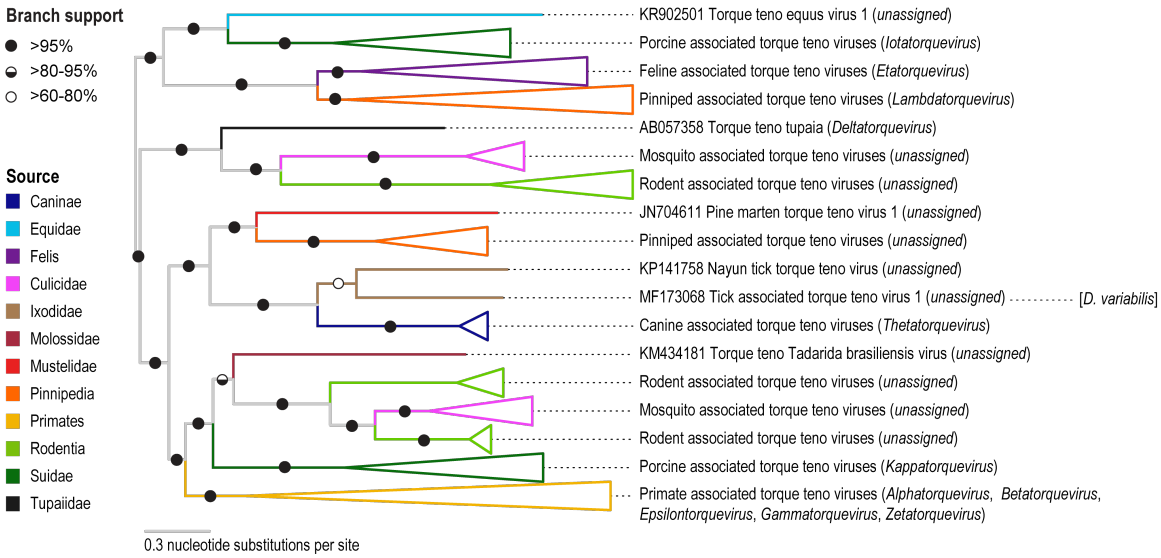

Figure 4.1: Maximum likelihood phylogenetic tree of the ORF1 nucleotide sequences (codon-aligned sequences) of anelloviruses inferred using IQ-TREE with GTR + I + G4 nucleotide substitution model. The tree is midpoint rooted, and branches with < 60% bootstrap support have been collapsed. The anellovirus ORF1 sequence identified in this study from D. variabilis is labeled with the GenBank accession number MF173068

Two genomovirus genomes (2196 and 2373 nts) were recovered from *D. variabilis* and one (2238 nts) from *I. scapularis*. *Genomoviridae* is a recently established family of ssDNA viruses with

circular genomes (~2kb) that encode a replication associated protein (Rep) in the complementary sense strand and a capsid protein (CP) in the virion sense strand (Krupovic et al., 2016; Varsani and Krupovic, 2017). To date, genomoviruses have been identified in animal samples including, abdomen (insects), faeces, blood, cerebrospinal fluid, cervical sample, and serum, buccal, cloacal pharyngeal and rectal swabs (Varsani and Krupovic, 2017). They have also been identified in plants, river sediments and samples from a sewage oxidation pond (Varsani and Krupovic, 2017).

A dataset was constructed of the genomes and the Rep amino acid sequences of genomoviruses (n=130) available in GenBank (10th June 2017) together with the three from this study. The Rep sequence dataset also included representative sequences of Reps of geminiviruses as an outgroup. These were aligned with MUSCLE (Edgar, 2004) and Maximum likelihood (ML) phylogenetic trees were inferred using IQ-TREE (Nguyen et al., 2015). Branches with less than 60% bootstrap support were collapsed with TreeGraph2 (Stover and Muller, 2010). Pairwise identities of the genome and Rep sequences were determined using SDT v1.2 (Muhire et al., 2014). Based on the guidelines for classification for the family *Genomovirdae* by Varsani and Krupovic (2017), one genomovirus each from *D. variabilis* (MF173065) and *I. scapulari* (MF173067) belong to the genus *Gemycircularvirus*, and one from *D. variabilis* (MF173066) to *Gemykolovirus* (Figure 4.2). The two gemycircularviruses share 73% pairwise identity with each other and less than 63% with all other gemycircularviruses and hence these represent two new species for which we propose the names tick associated gemycircularvirus 1 and 2. The Reps of these two viruses share 82% amino acid identity and are most closely related to two virus sequences (KT862249, KT862251) described by Steel et al. (Steel et al., 2016) in the species *Sheep associated gemycirularvirus 1*. The gemykolovirus shares <70% pairwise identity with all other gemykoloviruses and thus this represents a new species for which we propose the name tick associated gemykolovirus 1. The Rep sequence of tick associated gemykolovirus 1 shares 62-76% identity with two unclassified gemykoloviruses recovered from common beans (Lamas et al., 2016) and thrips (Kraberger et al., 2017) and three classified viruses recovered from Pacific flying fox

(*Pteropus tonganus*) faeces in the species *Pteropus associated gemykolovirus* 1 and 2 (KT732798 - KT732800) described by Male et al. (Male et al., 2016).

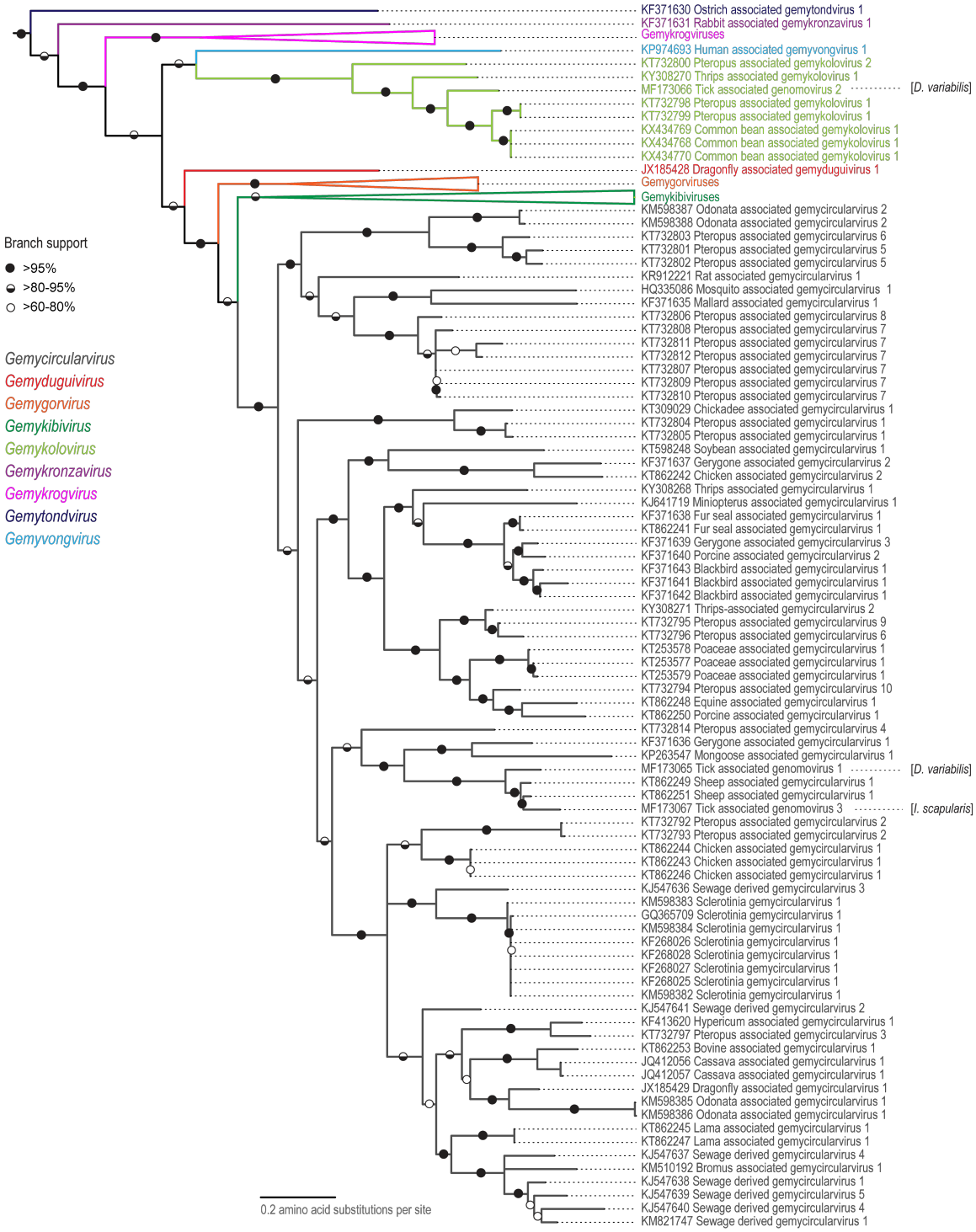

Figure 4.2: Maximum likelihood phylogenetic tree of the Rep amino acid sequences of genomoviruses inferred using IQ-TREE with VT + F + I + G4 amino acid substitution model. The tree is rooted with Rep sequences of geminiviruses, and branches with < 60% bootstrap support have been collapsed. The gemycircularvirus Rep sequences identified in D. variabilis and I. scapularis are labeled with the GenBank accession numbers MF173065 and MF173067, respectively. The gemykolovirus Rep sequence identified in D. variabilis is labeled with the GenBank accession number MF173066

4.3. Concluding remarks

Information about the viruses found in ticks can allow for a better understanding of their role in the ecosystem, especially related to viral acquisition and transmission. This is the first report of genomoviruses in ticks and here we provide the first complete genome of an anellovirus identified in ticks. The anellovirus recovered from ticks is most similar to the torque teno canis viruses found in dogs in Japan (Okamoto et al., 2002) which highlights the importance of viral surveys since ticks can act as vectors for viruses. Viral metagenomic approaches to monitor ticks and insect vectors is ideal for identifying known and novel viruses circulating in ecosystems and for better informed management of vector borne viral diseases.

CHAPTER 5

CONCLUSION

Ticks and scorpions are arachnids that belong to the largest phylum in the animal kingdom, Arthropoda. Both have a broad geographic distribution and can be found broadly across the globe. There are approximately 2200 and 900 species of scorpions and tick, respectively. Ticks are blood feeding arachnids that require a blood meal, taken from mammals, birds, reptiles or amphibians, to transform to the next stage of life. Due to their status as an important vector, ticks have been well studied and as a result the viruses associated with ticks that cause disease in humans and livestock have also been relatively well characterized. However, the other members of their virome remain underrepresented as only a handful of studies have explored novel viruses associated with ticks. The viruses associated with scorpions are all but unknown. While there is genomic data on viruses spanning multiple families that were identified and recovered from ticks, there is only one scorpion-associated viral genome available in GenBank. This highlights the huge gap in knowledge on arachnid-associated viruses and continued work to identify, recover and characterize viruses from arachnids will yield important data that can be used, not only to identify potentially pathogen viruses is tick populations, but allow for a better understanding of the role these important arachnids play in the ecosystem in regards to viral dynamics and transmission.

Polyomaviruses are circular dsDNA viruses of medical and veterinary important. Since the 1950s a remarkable diversity of viruses has been identified in a wide range of mammal, avian and fish hosts. Initially documented as an oncogenic viruses, polyomaviruses have also been shown to cause diseases such as nephropathy, progressive multifocal leukoencephalopathy, trichodysplasia spinulosa and in birds these viruses can cause feather loss. SV40, a polyomavirus known to infect monkeys, has been well documented to be a contaminant of certain batches of polio vaccine and due to public health concerns the molecular biology of these viruses has been well studied. Our understanding of their evolutionary history has some shorts falls, primary due to the biased sample of terrestrial vertebrates. Until recently, it was thought that polyomaviruses only infected mammal and avian species. Metagenomic studies have begun to identify the presence of these viruses in

other populations including the identification of novel polyomaviruses in various fish species. The discovery of divergent polyomaviruses in fish prompted a whole genome sequence data mining project that used fish LT as bait to scan GenBank for other similar sequences. This work resulted in several LT-like sequences being identified from spider transcriptome datasets and a nearly complete genome was assembled from a California bark scorpion WGS dataset. This discovery led to the question, are polyomaviruses also present in arachnids?

The work described in this thesis (Chapter 2) reports the genomes of eight novel polyomaviruses recovered from bark scorpions. The polyomaviruses reported here are the first to be recovered from invertebrates, and, although a relatively small sample set, has revealed a remarkable diversity of polyomaviruses in these animals. Three novel polyomavirus species were recovered from four bark scorpions, with the same species being found in multiple scorpions, in addition two scorpions harbored multiple polyomavirus species. Furthermore, LT-encoding novel viruses were identified (Chapter 3) that have been tentatively named arthropolviruses genomes in American dog ticks and a hairy scorpion samples. The four genomes represent three species. Further exploration of the arachnid virome is likely to produce a diverse range of novel viruses which will contribute to understanding the mechanisms of evolution of polyomaviruses and arthropolviruses. Novel genomes will also begin to shed light on key genomic features that were part of the ancestral virus. While not all sequences described here include the conserved motifs in the LT, scorpion derived sequences contain both the DnaJ and LXCXE suggesting that the motifs were part ancestral LT protein and have since been lost in some fish and arachnid lineages. VP1 sequences are divergent, even within sequences derived from the same host, which maybe be explained by the fact that VP1 is not essential for replication and therefore has more room to explore sequence space. Future studies should aim to scan a wide range of arthropods for LT encoding viruses. Characterization of these genomes will provide clarity of the presence and diversity of these viruses in invertebrate hosts. As additional sequences are determined, the evolutionary history between these viral families will become more defined.

This work also resulted in the identification of four novel ssDNA viruses (Chapter 4) from the viral families *Genomoviridae* and *Anelloviridae* from of *Dermacentor variabilis* and *Ixodes scapularis.* Genomoviruses have small (~2 kb) circular genomes that encode a replication associated protein in the complementary sense and a capsid protein in the virion sense. These viruses have been recovered from a wide range of animal, plant and environmental samples and it has been well documented that they are ubiquitous in the environment. Anelloviruses have circular genomes that range in size from 2.1 – 3.8 kb and are also present in a wide variety of animal and a hand full of insect samples (likely derived from a blood meal). In total three genomoviruses were recovered, two belonging to the genus *Gemycircularvirus* and one to the genus *Gemykolovirus* from pooled samples of *D. variabilis* (n=2) and *I. scapularis* (n=1). Additionally, a single anellovirus was recovered from the *D. variabilis* pool and is most closely related to *Torque teno canis virus*. This is the first report of genomoviruses and anelloviruses being recovered in ticks. It highlights the limited amount of data available on ssDNA viruses circulating in tick populations and how metagenomics can be used to characterize novel viruses associated with these arachnids.

The lack of conserved viral genes has complicated the study of viral evolution, however, viral metagenomics has proven to be an good method for exploring viral sequence space as no prior knowledge of nucleic acid sequence is necessary. Here, 16 novel genomes are reported from tick and scorpion samples which begin to describe the viral diversity present in arachnids and allow for generation of clearer picture of the evolutionary history of DNA viruses.

Future directions

Over the past decade, metagenomics studies have enabled the characterization of viruses primarily from environmental and mammal samples which has created a skewed view of the viral landscape towards economically and medically important viruses found in these sample types. There are more than 3000 species of tick and scorpions currently known and as various arachnid species are analyzed for viral communities, the described viral diversity in arachnids will expand rapidly. It is

clear that arachnids harbor diverse viruses and as we are just beginning to scratch the surface of the characterizing some of these viruses associated with arachnids. Future work should look to identified viruses not only in ecologically important species such as ticks, but also species that are part of the local ecosystem. For novel viruses, work should be undertaken to determine the host, pathogenicity, prevalence in the population, biological role, modes of transmission and host range. Future discoveries will lead to the establishment of new viral families, continue to highlight to diversity of viruses in arachnids and allow for the a more complete development of evolutionary history from viral families once thought to be associated only with vertebrate species as experienced with polyomaviruses.

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APPENDIX A

CO-AUTHOR PERMISSION TO USE PREVIOUSLY PUBLISHED WORK

Chapter 4, Identification of an anellovirus and genomoviruses in ixodid ticks, was published in 2018. All listed co-authors have given permission to use this work as a chapter in my thesis.

Waits (Schmidlin), K., Edwards, M. J., Cobb, I. N., Fontenele, R. S., & Varsani, A. (2018). Identification of an anellovirus and genomoviruses in ixodid ticks. *Virus genes*, *54*(1), 155-159.

APPENDIX B

ACCESSION NUMBERS TICK-BORNE VIRUSES

Accession number	Organism	Host
positive ssRNA viral sequences		
HM440560.1	Powassan virus	Ixodes scapularis
HM440561.1	Powassan virus	Ixodes scapularis
HM440562.1	Powassan virus	Ixodes scapularis
KJ746872.2	Powassan virus	Ixodes scapularis
MG647779.1	Powassan virus	Ixodes scapularis
MG647780.1	Powassan virus	Ixodes scapularis
MG647783.1	Powassan virus	Ixodes scapularis
MG647781.1	Powassan virus	Ixodes scapularis
MG647782.1	Powassan virus	Ixodes scapularis
HM440563.1	Powassan virus	tick
KT224350.1	Powassan virus	Ixodidae tick
KT224351.1	Powassan virus	Ixodidae tick
HM440559.1	Powassan virus	Ixodes scapularis
KU886216.1	Powassan virus	Ixodes scapularis
MG652438.1	Powassan virus	Ixodes persulcatus
EU770575.1	Powassan virus	Dermacentor silvarum (tick)
HM440558.1	Powassan virus	Ixodes scapularis
MG720093.1	Kyasanur forest disease virus	tick
MG720100.1	Kyasanur forest disease virus	tick
MG720084.1	Kyasanur forest disease virus	tick
MG720109.1	Kyasanur forest disease virus	tick
MG720090.1	Kyasanur forest disease virus	tick
MG720119.1	Kyasanur forest disease virus	tick
MG720122.1	Kyasanur forest disease virus	tick
MG720120.1	Kyasanur forest disease virus	tick
MG720116.1	Kyasanur forest disease virus	tick
JF416959.1	Kyasanur forest disease virus	Haemaphysalis spinigera
KF815939.1	Tyuleniy virus	Ixodes uriae
KT224356.1	Tyuleniy virus	Ixodes uriae (tick)
DQ462443.1	Karshi virus	Ornithodoros caniceps
MH688511	Karshi virus	Hyalomma asiaticum
KJ746903.2	Deer tick virus	Ixodes scapularis
KM048317.1	Deer tick virus	Ixodes scapularis
EU790644.1	Langat virus	Ixodes granulatus
KT224354.1	Louping ill virus	Hyalomma marginatum (tick)
U27491.1	Tick-borne encephalitis virus	Ixodes ricinus
LC171402.1	Tick-borne encephalitis virus	Ixodes ricinus
GQ266392.1	Tick-borne encephalitis virus	Ixodes ricinus (tick)
MG210945.1	Tick-borne encephalitis virus	Ixodes ricinus
MG210946.1	Tick-borne encephalitis virus	Ixodes ricinus
MG210947.1	Tick-borne encephalitis virus	Haemophysalis concinna
MG210948.1	Tick-borne encephalitis virus	Ixodes ricinus
FJ968751.1	Tick-borne encephalitis virus	Ixodes pavlovskyi
JQ429588.1	Tick-borne encephalitis virus	Ixodes persulcatus
KT069219.1	Tick-borne encephalitis virus	Ixodes persulcatus
KU761571.1	Tick-borne encephalitis virus	Ixodes persulcatus
KU761573.1	Tick-borne encephalitis virus	Ixodes persulcatus
KP345889.1	Tick-borne encephalitis virus	Ixodes scapularis
MF774565.1	Tick-borne encephalitis virus	Ixodes pavlovskyi
DQ401140.3	Tick-borne encephalitis virus	Ixodes ricinus
JX534167.1	Tick-borne encephalitis virus	Ixodes persulcatus
KF826914.1	Tick-borne encephalitis virus	Ixodes persulcatus
U27495.1	Tick-borne encephalitis virus	Ixodes ricinus
LC017691.1	Tick-borne encephalitis virus	Ixodes persulcatus
LC017692.1	Tick-borne encephalitis virus	Ixodes persulcatus
LC017693.1	Tick-borne encephalitis virus	Ixodes persulcatus
LC440459.1	Tick-borne encephalitis virus	Ixodes ovatus
KC835595.1	Tick-borne encephalitis virus	Ixodes ricinus
KY069123.1	Tick-borne encephalitis virus	Ixodes persulcatus
KY069121.1	Tick-borne encephalitis virus	Ixodes persulcatus
EF469661.1	Tick-borne encephalitis virus	Ixodes persulcatus

DQ989336.1	Tick-borne encephalitis virus	tick
KY069122.1	Tick-borne encephalitis virus	Ixodes persulcatus
KC835596.1	Tick-borne encephalitis virus	Ixodes ricinus
KF880805.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
KF880804.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
KF880803.1	Tick-borne encephalitis virus	Haemaphysalis concinna Koch
KP844726.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
KP844727.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
KJ626343.1	Tick-borne encephalitis virus	Ixodes persulcatus
KP844724.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
KP844725.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
KF823822.1	Tick-borne encephalitis virus	Ixodes persulcatus
KP331441.1	Tick-borne encephalitis virus	Ixodes persulcatus
KP331442.1	Tick-borne encephalitis virus	Ixodes persulcatus
KP331443.1	Tick-borne encephalitis virus	Ixodes persulcatus
KX966398.1	Tick-borne encephalitis virus	Ixodes ricinus
KX966399.1	Tick-borne encephalitis virus	Ixodes ricinus
KT001070.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
KT001071.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
KT001072.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
MG589940.1	Tick-borne encephalitis virus	Ixodes ricinus
KT224357.1	Tick-borne encephalitis virus	Ixodes ricinus (ticks)
MG589938.1	Tick-borne encephalitis virus	Ixodes ricinus
KT224353.1	Tick-borne encephalitis virus	Ixodes persulcatus (tick)
KJ701416.1	Tick-borne encephalitis virus	Ixodes persulcatus
KF991107.1	Tick-borne encephalitis virus	Ixodes ricinus
KX268728.1	Tick-borne encephalitis virus	Ixodidae
KP869172.1	Tick-borne encephalitis virus	Ixodes persulcatus Schulze
MH021184.1	Tick-borne encephalitis virus	Ixodes ricinus
HM859894.1	Tick-borne encephalitis virus	Ixodes persulcatus
HM859895.1	Tick-borne encephalitis virus	Ixodes persulcatus
KF991106.1	Tick-borne encephalitis virus	Ixodes ricinus
KJ739730.1	Tick-borne encephalitis virus	Ixodes persulcatus
KJ755186.1	Tick-borne encephalitis virus	Ixodes persulcatus
KY069124.1	Tick-borne encephalitis virus	Ixodes persulcatus
KY069125.1	Tick-borne encephalitis virus	Ixodes persulcatus
KY069126.1	Tick-borne encephalitis virus	Ixodes persulcatus
JQ693478.1	Tick-borne encephalitis virus	ixodid tick
MF398818.1	Tick-borne encephalitis virus	Dermacentor silvarum
MF398819.1	Tick-borne encephalitis virus	Dermacentor silvarum
MF398820.1	Tick-borne encephalitis virus	Dermacentor silvarum
JF416961.1	Alkhumra hemorrhagic fever virus	Hyalomma dromedarii
JF416962.1	Alkhumra hemorrhagic fever virus	Ornithodoros savignyi
JF416963.1	Alkhumra hemorrhagic fever virus	Ornithodoros savignyi
JF416964.1	Alkhumra hemorrhagic fever virus	Ornithodoros savignyi
JF416965.1	Alkhumra hemorrhagic fever virus	Ornithodoros savignyi
JF416966.1	Alkhumra hemorrhagic fever virus	Ornithodoros savignyi
JF416967.1	Alkhumra hemorrhagic fever virus	Ornithodoros savignyi
AF253419	Langat virus	non-tick
AF253420	Langat virus	non-tick
MF374484	Langat virus	non-tick
AY863002	Karshi virus	non-tick
DQ235147	Karshi virus	non-tick
KP144331	Louping ill virus	non-tick
KF056331	Louping ill virus	non-tick
MH537791	Louping ill virus	non-tick
Y07863	Louping ill virus	non-tick
KJ495985	Louping ill virus	non-tick
LIV369T2	Louping ill virus	non-tick
LC227566	Louping ill virus	non-tick
AB001026	Tick-borne encephalitis virus	non-tick
AB062063	Tick-borne encephalitis virus	non-tick
AB062064	Tick-borne encephalitis virus	non-tick
AB753012	Tick-borne encephalitis virus	non-tick
AF069066	Tick-borne encephalitis virus	non-tick
AF091005	Tick-borne encephalitis virus	non-tick
AF091006	Tick-borne encephalitis virus	non-tick

AF091007	Tick-borne encephalitis virus	non-tick
AF091008	Tick-borne encephalitis virus	non-tick
AF091010	Tick-borne encephalitis virus	non-tick
AF091011	Tick-borne encephalitis virus	non-tick
AF091012	Tick-borne encephalitis virus	non-tick
AF091013	Tick-borne encephalitis virus	non-tick
AF091014	Tick-borne encephalitis virus	non-tick
AF091015	Tick-borne encephalitis virus	non-tick
AF091016	Tick-borne encephalitis virus	non-tick
AF091017	Tick-borne encephalitis virus	non-tick
AF091018	Tick-borne encephalitis virus	non-tick
AF091019	Tick-borne encephalitis virus	non-tick
AF091020	Tick-borne encephalitis virus	non-tick
AF527415	Tick-borne encephalitis virus	non-tick
AH002418	Tick-borne encephalitis virus	non-tick
AY169390	Tick-borne encephalitis virus	non-tick
AY182009	Tick-borne encephalitis virus	non-tick
AY217093	Tick-borne encephalitis virus	non-tick
DQ153877	Tick-borne encephalitis virus	non-tick
DQ486861	Tick-borne encephalitis virus	non-tick
DQ862460	Tick-borne encephalitis virus	non-tick
EF469662	Tick-borne encephalitis virus	non-tick
EU444079	Tick-borne encephalitis virus	non-tick
EU816450	Tick-borne encephalitis virus	non-tick
EU816451	Tick-borne encephalitis virus	non-tick
EU816452	Tick-borne encephalitis virus	non-tick
EU816453	Tick-borne encephalitis virus	non-tick
EU816454	Tick-borne encephalitis virus	non-tick
EU816455	Tick-borne encephalitis virus	non-tick
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FJ402886	Tick-borne encephalitis virus	non-tick
FJ572210	Tick-borne encephalitis virus	non-tick
FJ906622	Tick-borne encephalitis virus	non-tick
FJ997899	Tick-borne encephalitis virus	non-tick
GQ228395	Tick-borne encephalitis virus	non-tick
GU121642	Tick-borne encephalitis virus	non-tick
GU183379	Tick-borne encephalitis virus	non-tick
GU183380	Tick-borne encephalitis virus	non-tick
GU183381	Tick-borne encephalitis virus	non-tick
GU183382	Tick-borne encephalitis virus	non-tick
GU183383	Tick-borne encephalitis virus	non-tick
GU183384	Tick-borne encephalitis virus	non-tick
HM120875	Tick-borne encephalitis virus	non-tick
HM535610	Tick-borne encephalitis virus	non-tick
HM535611	Tick-borne encephalitis virus	non-tick
HQ201303	Tick-borne encephalitis virus	non-tick
HQ901366	Tick-borne encephalitis virus	non-tick
HQ901367	Tick-borne encephalitis virus	non-tick
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JF316708	Tick-borne encephalitis virus	non-tick
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JN003206	Tick-borne encephalitis virus	non-tick
JN003207	Tick-borne encephalitis virus	non-tick
JN003208	Tick-borne encephalitis virus	non-tick
JN003209	Tick-borne encephalitis virus	non-tick
JN229223	Tick-borne encephalitis virus	non-tick
JQ650522	Tick-borne encephalitis virus	non-tick
JQ650523	Tick-borne encephalitis virus	non-tick
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JQ825144	Tick-borne encephalitis virus	non-tick
JQ825145	Tick-borne encephalitis virus	non-tick
JQ825146	Tick-borne encephalitis virus	non-tick
JQ825147	Tick-borne encephalitis virus	non-tick
JQ825148	Tick-borne encephalitis virus	non-tick
JQ825149	Tick-borne encephalitis virus	non-tick
JQ825150	Tick-borne encephalitis virus	non-tick

JQ825151	Tick-borne encephalitis virus	non-tick
JQ825152	Tick-borne encephalitis virus	non-tick
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JQ825154	Tick-borne encephalitis virus	non-tick
JQ825155	Tick-borne encephalitis virus	non-tick
JQ825156	Tick-borne encephalitis virus	non-tick
JQ825157	Tick-borne encephalitis virus	non-tick
JQ825158	Tick-borne encephalitis virus	non-tick
JQ825159	Tick-borne encephalitis virus	non-tick
JQ825160	Tick-borne encephalitis virus	non-tick
JQ825161	Tick-borne encephalitis virus	non-tick
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JQ825164	Tick-borne encephalitis virus	non-tick
JX498939	Tick-borne encephalitis virus	non-tick
JX498940	Tick-borne encephalitis virus	non-tick
JX968560	Tick-borne encephalitis virus	non-tick
KC414090	Tick-borne encephalitis virus	non-tick
KC422663	Tick-borne encephalitis virus	non-tick
KC422667	Tick-borne encephalitis virus	non-tick
KC806252	Tick-borne encephalitis virus	non-tick
KC835597	Tick-borne encephalitis virus	non-tick
KF151173	Tick-borne encephalitis virus	non-tick
KF826915	Tick-borne encephalitis virus	non-tick
KF826916	Tick-borne encephalitis virus	non-tick
KF951037	Tick-borne encephalitis virus	non-tick
KJ000002	Tick-borne encephalitis virus	non-tick
KJ633033	Tick-borne encephalitis virus	non-tick
KJ739729	Tick-borne encephalitis virus	non-tick
KJ739731	Tick-borne encephalitis virus	non-tick
KJ744034	Tick-borne encephalitis virus	non-tick
KJ914682	Tick-borne encephalitis virus	non-tick
KJ914683	Tick-borne encephalitis virus	non-tick
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KJ922513	Tick-borne encephalitis virus	non-tick
KJ922514	Tick-borne encephalitis virus	non-tick
KJ922515	Tick-borne encephalitis virus	non-tick
KJ922516	Tick-borne encephalitis virus	non-tick
KM019545	Tick-borne encephalitis virus	non-tick
KM019546	Tick-borne encephalitis virus	non-tick
KP644245	Tick-borne encephalitis virus	non-tick
KP716971	Tick-borne encephalitis virus	non-tick
KP716972	Tick-borne encephalitis virus	non-tick
KP716973	Tick-borne encephalitis virus	non-tick
KP716974	Tick-borne encephalitis virus	non-tick
KP716975	Tick-borne encephalitis virus	non-tick
KP716976	Tick-borne encephalitis virus	non-tick
KP716977	Tick-borne encephalitis virus	non-tick
KP716978	Tick-borne encephalitis virus	non-tick
KP938507	Tick-borne encephalitis virus	non-tick
KT001073	Tick-borne encephalitis virus	non-tick
KT224352	Tick-borne encephalitis virus	non-tick
KT321430	Tick-borne encephalitis virus	non-tick
KU761567	Tick-borne encephalitis virus	non-tick
KU761568	Tick-borne encephalitis virus	non-tick
KU761569	Tick-borne encephalitis virus	non-tick
KU761570	Tick-borne encephalitis virus	non-tick
KU761572	Tick-borne encephalitis virus	non-tick
KU761574	Tick-borne encephalitis virus	non-tick
KU761575	Tick-borne encephalitis virus	non-tick
KU761576	Tick-borne encephalitis virus	non-tick
KU885457	Tick-borne encephalitis virus	non-tick
KY069119	Tick-borne encephalitis virus	non-tick
KY069120	Tick-borne encephalitis virus	non-tick
L40361	Tick-borne encephalitis virus	non-tick
LC227565	Tick-borne encephalitis virus	non-tick
LC440460	Tick-borne encephalitis virus	non-tick

MF043953	Tick-borne encephalitis virus	non-tick
MF043954	Tick-borne encephalitis virus	non-tick
MF043955	Tick-borne encephalitis virus	non-tick
MF374487	Tick-borne encephalitis virus	non-tick
MG589937	Tick-borne encephalitis virus	non-tick
MG589939	Tick-borne encephalitis virus	non-tick
MG599476	Tick-borne encephalitis virus	non-tick
MG599477	Tick-borne encephalitis virus	non-tick
MH094241	Tick-borne encephalitis virus	non-tick
TEU39292	Tick-borne encephalitis virus	non-tick
Y08863	Tick-borne encephalitis virus	non-tick
AF310909	Powassan virus	non-tick
AF310910	Powassan virus	non-tick
AF310911	Powassan virus	non-tick
AF310912	Powassan virus	non-tick
AF310913	Powassan virus	non-tick
AF310914	Powassan virus	non-tick
AF310915	Powassan virus	non-tick
AF310916	Powassan virus	non-tick
AF310917	Powassan virus	non-tick
AF310918	Powassan virus	non-tick
AF310919	Powassan virus	non-tick
AF310920	Powassan virus	non-tick
AF310921	Powassan virus	non-tick
AF310922	Powassan virus	non-tick
AF310937	Powassan virus	non-tick
AF310938	Powassan virus	non-tick
AF310939	Powassan virus	non-tick
AF310940	Powassan virus	non-tick
AF310941	Powassan virus	non-tick
AF310942	Powassan virus	non-tick
AF310943	Powassan virus	non-tick
AF310944	Powassan virus	non-tick
AF310945	Powassan virus	non-tick
AF310946	Powassan virus	non-tick
AF310947	Powassan virus	non-tick
AF310948	Powassan virus	non-tick
AF310949	Powassan virus	non-tick
AF310950	Powassan virus	non-tick
EU543649	Powassan virus	non-tick
EU670438	Powassan virus	non-tick
HQ231414	Powassan virus	non-tick
HQ231415	Powassan virus	non-tick
LC227572	Powassan virus	non-tick
MF374486	Powassan virus	non-tick
PWARPT	Powassan virus	non-tick
AF331718	Alkhumra hemorrhagic fever virus	non-tick
JF416949	Alkhumra hemorrhagic fever virus	non-tick
JF416950	Alkhumra hemorrhagic fever virus	non-tick
JF416951	Alkhumra hemorrhagic fever virus	non-tick
JF416952	Alkhumra hemorrhagic fever virus	non-tick
JF416953	Alkhumra hemorrhagic fever virus	non-tick
JF416954	Alkhumra hemorrhagic fever virus	non-tick
JF416955	Alkhumra hemorrhagic fever virus	non-tick
JF416956	Alkhumra hemorrhagic fever virus	non-tick
JF416957	Alkhumra hemorrhagic fever virus	non-tick
JN860200	Alkhumra hemorrhagic fever virus	non-tick
JX271892	Alkhumra hemorrhagic fever virus	non-tick
JX271893	Alkhumra hemorrhagic fever virus	non-tick
KU884971	Alkhumra hemorrhagic fever virus	non-tick
LC227576	Alkhumra hemorrhagic fever virus	non-tick
HM055369	Kyasanur Forest disease virus	non-tick
JF416958	Kyasanur Forest disease virus	non-tick
MG720079	Kyasanur Forest disease virus	non-tick
MG720080	Kyasanur Forest disease virus	non-tick
MG720081	Kyasanur Forest disease virus	non-tick
MG720082	Kyasanur Forest disease virus	non-tick

MG720083	Kyasanur Forest disease virus	non-tick
MG720086	Kyasanur Forest disease virus	non-tick
MG720087	Kyasanur Forest disease virus	non-tick
MG720088	Kyasanur Forest disease virus	non-tick
MG720089	Kyasanur Forest disease virus	non-tick
MG720091	Kyasanur Forest disease virus	non-tick
MG720092	Kyasanur Forest disease virus	non-tick
MG720095	Kyasanur Forest disease virus	non-tick
MG720097	Kyasanur Forest disease virus	non-tick
MG720098	Kyasanur Forest disease virus	non-tick
MG720101	Kyasanur Forest disease virus	non-tick
MG720102	Kyasanur Forest disease virus	non-tick
MG720103	Kyasanur Forest disease virus	non-tick
MG720104	Kyasanur Forest disease virus	non-tick
MG720105	Kyasanur Forest disease virus	non-tick
MG720106	Kyasanur Forest disease virus	non-tick
MG720108	Kyasanur Forest disease virus	non-tick
MG720110	Kyasanur Forest disease virus	non-tick
MG720111	Kyasanur Forest disease virus	non-tick
MG720112	Kyasanur Forest disease virus	non-tick
MG720114	Kyasanur Forest disease virus	non-tick
MH013226	Kyasanur Forest disease virus	non-tick
MH013227	Kyasanur Forest disease virus	non-tick
MG720077	Kyasanur Forest disease virus	non-tick
MG720078	Kyasanur Forest disease virus	non-tick
MG720085	Kyasanur Forest disease virus	non-tick
MG720094	Kyasanur Forest disease virus	non-tick
MG720096	Kyasanur Forest disease virus	non-tick
MG720099	Kyasanur Forest disease virus	non-tick
MG720107	Kyasanur Forest disease virus	non-tick
MG720113	Kyasanur Forest disease virus	non-tick
MG720117	Kyasanur Forest disease virus	non-tick
JF416960	Kyasanur Forest disease virus	non-tick
AY323490	Kyasanur Forest disease virus	non-tick
EU480689	Kyasanur Forest disease virus	non-tick
AF311056	deer tick virus	non-tick
DQ235148	Tyuleniy virus	non-tick
negative ssRNA viral sequences		
KU343142.1	Abu Hammad virus	Argas hermanni
KU343143.1	Abu Hammad virus	Argas hermanni
KU343144.1	Abu Hammad virus	Argas hermanni
KU343145.1	Avalon virus	Ixodes uriae
KU343146.1	Avalon virus	Ixodes uriae
KU343147.1	Avalon virus	Ixodes uriae
KU925440.1	Avalon virus	Ixodes uriae (putus)
KU925441.1	Avalon virus	Ixodes uriae (putus)
KU925442.1	Avalon virus	Ixodes uriae (putus)
KU343139.1	Clo Mor virus	Ixodes uriae
KU343140.1	Clo Mor virus	Ixodes uriae
KU343141.1	Clo Mor virus	Ixodes uriae
AF467768.2	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma excavatum
AF481799.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
AY277672.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum
AY675240.2	Crimean-Congo hemorrhagic fever orthonairovirus	tick
AY900141.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum (tick)
AY900144.1	Crimean-Congo hemorrhagic fever orthonairovirus	Alveonasus lahorensis (tick)
AY900145.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum (tick)
DQ211612.1	Crimean-Congo hemorrhagic fever orthonairovirus	Rhipicephalus bursa
DQ211613.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma truncatum
DQ211615.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum rufipes
DQ211625.1	Crimean-Congo hemorrhagic fever orthonairovirus	Rhipicephalus bursa
DQ211626.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma truncatum
DQ211628.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum rufipes
DQ211638.1	Crimean-Congo hemorrhagic fever orthonairovirus	Rhipicephalus bursa
DQ211639.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma truncatum
DQ211641.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum rufipes

DQ227495.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
DQ227496.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
FJ562093.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
FJ562094.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
FJ562095.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
GU477492.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
GU477493.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
GU477494.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KF793333.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma sp. (tick)
KF793334.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma sp. (tick)
KF793335.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma sp. (tick)
KR814833.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum (tick)
KR814834.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum (tick)
KU161583.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KU161585.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KU161587.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KU707898.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma dromedarii
KU707899.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma anatolicum
KU707900.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma dromedarii
KU707901.1	Crimean-Congo hemorrhagic fever orthonairovirus	Rhipicephalus sanguineus
KX013453.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013454.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013455.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013456.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013457.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013458.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013459.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013460.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013461.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013462.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013463.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013464.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013465.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013466.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013467.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013468.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013469.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013470.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013471.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013472.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013473.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013474.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013475.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KX013476.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KY354080.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KY354081.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KY354082.1	Crimean-Congo hemorrhagic fever orthonairovirus	tick
KY484025.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma truncatum
KY484026.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma truncatum
KY484027.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma truncatum
KY484031.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum
KY484032.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum
KY484033.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum
KY484034.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma excavatum
KY484035.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma excavatum
KY484036.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma excavatum
KY484037.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma anatolicum
KY484038.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma anatolicum
KY484039.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma anatolicum
KY484043.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum
KY484044.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum
KY484045.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma marginatum
MF511236.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma rufipes
MF547415.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma lusitanicum
MF547416.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma lusitanicum
MF547417.1	Crimean-Congo hemorrhagic fever orthonairovirus	Hyalomma lusitanicum
MG516211.1	Crimean-Congo hemorrhagic fever orthonairovirus	Rhipicephalus bursa

MG516212.1	Crimean-Congo hemorrhagic fever orthonairovirus	Rhipicephalus bursa
MG516213.1	Crimean-Congo hemorrhagic fever orthonairovirus	Rhipicephalus bursa
KU343151.1	Dera Ghazi Khan orthonairovirus	Hyalomma dromedarii
KU343152.1	Dera Ghazi Khan orthonairovirus	Hyalomma dromedarii
KU343153.1	Dera Ghazi Khan orthonairovirus	Hyalomma dromedarii
KU925452.1	Dera Ghazi Khan orthonairovirus	Hyalomma dromedarii
KU925453.1	Dera Ghazi Khan orthonairovirus	Hyalomma dromedarii
KU925454.1	Dera Ghazi Khan orthonairovirus	Hyalomma dromedarii
FJ422213.2	Dugbe orthonairovirus	Amblyomma variegatum
FJ422214.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422215.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422216.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422217.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422218.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422219.1	Dugbe orthonairovirus	Rhipicephalus pulchellus
FJ422220.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422221.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422222.1	Dugbe orthonairovirus	Amblyomma variegatum
FJ422223.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422224.1	Dugbe orthonairovirus	Amblyomma lepidum
FJ422225.1	Dugbe orthonairovirus	Rhipicephalus pulchellus
FJ422226.1	Dugbe orthonairovirus	Amblyomma variegatum
FJ422227.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422228.1	Dugbe orthonairovirus	Amblyomma lepidum
FJ422229.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422230.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422231.1	Dugbe orthonairovirus	Amblyomma variegatum
FJ422232.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422233.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422234.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422235.1	Dugbe orthonairovirus	Amblyomma variegatum
FJ422236.1	Dugbe orthonairovirus	Amblyomma gemma
FJ422237.1	Dugbe orthonairovirus	Amblyomma variegatum
FJ422238.1	Dugbe orthonairovirus	Amblyomma gemma
KU343154.1	Farallon virus	Ornithodoros sp.
KU343155.1	Farallon virus	Ornithodoros sp.
KU343156.1	Farallon virus	Ornithodoros sp.
KU925461.1	Farallon virus	Ornithodoros capensis
KU925462.1	Farallon virus	Ornithodoros capensis
KU925463.1	Farallon virus	Ornithodoros capensis
KU925464.1	Ganjam virus	Haemaphysalis intermedia
KU925465.1	Ganjam virus	Haemaphysalis intermedia
KU925466.1	Ganjam virus	Haemaphysalis intermedia
KU925467.1	Great Saltee virus	Ornithodoros maritimus
KU925468.1	Great Saltee virus	Ornithodoros maritimus
KU925469.1	Great Saltee virus	Ornithodoros maritimus
KU925470.1	Hughes orthonairovirus	Ornithodoros capensis group
KU925471.1	Hughes orthonairovirus	Ornithodoros capensis group
KU925472.1	Hughes orthonairovirus	Ornithodoros capensis group
EU697949.1	Nairobi sheep disease virus	Haemaphysalis sp.
EU697950.1	Nairobi sheep disease virus	Haemaphysalis sp.
HM991291.1	Nairobi sheep disease virus	Hyalomma intermedia
HM991297.1	Nairobi sheep disease virus	Hyalomma intermedia
HM991299.1	Nairobi sheep disease virus	Hyalomma intermedia
HM991301.1	Nairobi sheep disease virus	Hyalomma intermedia
HM991329.1	Nairobi sheep disease virus	Hyalomma intermedia
HQ286603.1	Nairobi sheep disease virus	Haemaphysalis intermedia
HQ286604.1	Nairobi sheep disease virus	Haemaphysalis intermedia
HQ286605.1	Nairobi sheep disease virus	Haemaphysalis intermedia
HQ286606.1	Nairobi sheep disease virus	Haemaphysalis intermedia
HQ286608.1	Nairobi sheep disease virus	Haemaphysalis intermedia
HQ286609.1	Nairobi sheep disease virus	Haemaphysalis intermedia
KM464724.1	Nairobi sheep disease virus	tick
KM464725.1	Nairobi sheep disease virus	tick
KM464726.1	Nairobi sheep disease virus	tick
MH791449.1	Nairobi sheep disease virus	tick
MH791450.1	Nairobi sheep disease virus	tick

MH791451.1	Nairobi sheep disease virus	tick
KU925473.1	Punta Salinas virus	Ornithodoros amblus
KU925474.1	Punta Salinas virus	Ornithodoros amblus
KU925475.1	Punta Salinas virus	Ornithodoros amblus
KU343160.1	Qalyub orthonairovirus	Ornithodoros erraticus
KU343161.1	Qalyub orthonairovirus	Ornithodoros erraticus
KU343162.1	Qalyub orthonairovirus	Ornithodoros erraticus
KU925476.1	Qualyub virus	Ornithodoros erraticus
KU925477.1	Qualyub virus	Ornithodoros erraticus
KU925478.1	Qualyub virus	Ornithodoros erraticus
KU925479.1	Raza virus	Carios denmarki
KU925481.1	Raza virus	Carios denmarki
KU925488.1	Soldado virus	Ornithodoros capensis
KU925489.1	Soldado virus	Ornithodoros capensis
KU925490.1	Soldado virus	Ornithodoros capensis
KU925494.1	Tillamook virus	Ixodes uriae
KU925495.1	Tillamook virus	Ixodes uriae
KU925496.1	Tillamook virus	Ixodes uriae
LC008510.1	Tofla virus	Haemaphysalis flava (Tick)
LC008511.1	Tofla virus	Haemaphysalis flava (Tick)
LC008512.1	Tofla virus	Haemaphysalis flava (Tick)
LC030113.1	Tofla virus	Haemaphysalis formsensis
LC030114.1	Tofla virus	Haemaphysalis formsensis
LC030115.1	Tofla virus	Haemaphysalis formsensis
KU925497	Tunis virus	Pigeon
KU925498	Tunis virus	Pigeon
KU925499	Tunis virus	Pigeon
KU343169.1	Zirqa virus	Ornithodoros muesebecki
KU343170.1	Zirqa virus	Ornithodoros muesebecki
KU343171.1	Zirqa virus	Ornithodoros muesebecki
KU925500.1	Zirqa virus	Ornithodoros (Alectorobius) muesebecki
KU925501.1	Zirqa virus	Ornithodoros (Alectorobius) muesebecki
KU925502.1	Zirqa virus	Ornithodoros (Alectorobius) muesebecki
KJ746901	American dog tick phlebovirus	Dermacentor variabilis
KJ746902	American dog tick phlebovirus	Dermacentor variabilis
KM048311	American dog tick phlebovirus	Dermacentor variabilis
KM048312	American dog tick phlebovirus	Dermacentor variabilis
JX961616.1	Bhanja virus	Rhipicephalus decoloratus
JX961617.1	Bhanja virus	Rhipicephalus decoloratus
JX961618.1	Bhanja virus	Rhipicephalus decoloratus
JX961619.1	Bhanja virus	Haemaphysalis intermedia
KC521440.1	Bhanja virus	Haemaphysalis intermedia
JX961620.1	Bhanja virus	Haemaphysalis intermedia
KC521441.1	Bhanja virus	Haemaphysalis intermedia
JX961621.1	Bhanja virus	Haemaphysalis intermedia
KC521442.1	Bhanja virus	Haemaphysalis intermedia
MF360789	Blacklegged tick chuvirus-2	Ixodes scapularis
KX184200	Blacklegged tick phlebovirus 1	Ixodes scapularis
KX184201	Blacklegged tick phlebovirus 1	Ixodes scapularis
KU230449	Blacklegged tick phlebovirus 3	Ixodes scapularis
KU230450	Blacklegged tick phlebovirus 3	Ixodes scapularis
KM048313	Blacklegged tick phlebovirus 1	Ixodes scapularis
KM048314	Blacklegged tick phlebovirus 1	Ixodes scapularis
KJ746873	Blacklegged tick phlebovirus 1	Ixodes scapularis
KJ746875	Blacklegged tick phlebovirus 1	Ixodes scapularis
KM048315	Blacklegged tick phlebovirus 2	Ixodes scapularis
KM048316	Blacklegged tick phlebovirus 2	Ixodes scapularis
KJ746874	Blacklegged tick phlebovirus 2	Ixodes scapularis
KJ746876	Blacklegged tick phlebovirus 2	Ixodes scapularis
KM205020.1	Connecticut virus	Ixodes dentatus
MF360791	Dog Tick rhabdovirus-1	Ixodes scapularis
JX961625.1	Forecariah virus	Rhipicephalus geigyi
JX961626.1	Forecariah virus	Rhipicephalus geigyi
JX961627.1	Forecariah virus	Rhipicephalus geigyi
KJ425425.1	Gissar virus	Argas reflexus (tick)
KT328593.1	Guertu virus	Dermacentor nuttalli
KT328592.1	Guertu virus	Dermacentor nuttalli

KT328591.1	Guertu virus	Dermacentor nuttalli
JF906057.1	Huaiyangshan virus	Haemaphysalis longicornis
JF906058.1	Huaiyangshan virus	Haemaphysalis longicornis
JF906056.1	Huaiyangshan virus	Haemaphysalis longicornis
KM198925.1	Hunter Island virus	Ixodes eudyptidis
KM198926.1	Hunter Island virus	Ixodes eudyptidis
KM198927.1	Hunter Island virus	Ixodes eudyptidis
KF848980.1	Hunter Island virus	Tasmanian tick
KF848981.1	Hunter Island virus	Tasmanian tick
KF848982.1	Hunter Island virus	Tasmanian tick
MG581739.1	Kaisodi virus	Haemaphysalis spinigera
MG581740.1	Kaisodi virus	Haemaphysalis spinigera
MG581741.1	Kaisodi virus	Haemaphysalis spinigera
KF892046.1	Khasan virus	Haemaphysalis longicornis (tick)
KF892047.1	Khasan virus	Haemaphysalis longicornis (tick)
KF892048.1	Khasan virus	Haemaphysalis longicornis (tick)
KM114252.1	Kismayo virus	Rhipicephalus pulchellus
KM114253.1	Kismayo virus	Rhipicephalus pulchellus
KM114254.1	Kismayo virus	Rhipicephalus pulchellus
KC984953.1	Kolente virus	Amblyomma (Theileriella) variegatum
KF892049.1	Komandory virus	Ixodes uriae (tick)
KF892050.1	Komandory virus	Ixodes uriae (tick)
KF892051.1	Komandory virus	Ixodes uriae (tick)
KX774632.1	Lone star tick densovirus 1	Amblyomma americanum
KX774635.1	Lone star tick nodavirus	Amblyomma americanum
KX774634.1	Lone star tick nodavirus	Amblyomma americanum
KC589005.1	Lone Star virus	Amblyomma americanum
KC589006.1	Lone Star virus	Amblyomma americanum
KC589007.1	Lone Star virus	Amblyomma americanum
MG554172.1	Lymphocytic choriomeningitis mammarenavirus	Haemaphysalis longicornis; ZDW 31
FJ554525.1	Midway nyavirus	Ornithodoros capensis (pooled ticks)
LC063770	Mukawa virus	
LC063768	Mukawa virus	
LC063769	Mukawa virus	
KM205009.1	New Minto virus	Haemaphysalis leporispalustris
FJ554526.1	Nyamanini nyavirus	pooled ticks
KU933936	Pacific coast tick phlebovirus	Dermacentor occidentalis
KU933937	Pacific coast tick phlebovirus	Dermacentor occidentalis
JX961628.1	Palma virus	Haemaphysalis punctata
JX961629.1	Palma virus	Haemaphysalis punctata
JX961630.1	Palma virus	Haemaphysalis punctata
KF892052.1	Rukutama virus	Ixodes uriae (tick)
KF892053.1	Rukutama virus	Ixodes uriae (tick)
KF892054.1	Rukutama virus	Ixodes uriae (tick)
KM205013.1	Sawgrass virus	Dermacentor variabilis
KF791962.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791957.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791952.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791959.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791954.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791949.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791960.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791955.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791950.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791961.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791956.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KF791951.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KR230765.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KR230785.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KR230805.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KR230766.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KR230786.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KR230806.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KR230767.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KR230787.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KR230807.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KT890280.1	Severe fever with thrombocytopenia virus	tick

KT890281.1	Severe fever with thrombocytopenia virus	tick
KT890282.1	Severe fever with thrombocytopenia virus	tick
KC473540.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KC473541.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KC473542.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
JQ684871.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
JQ684872.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
JQ684873.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
MF045954.1	Severe fever with thrombocytopenia virus	tick
MF045967.1	Severe fever with thrombocytopenia virus	Tick
KY773990.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KY773991.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KY773992.1	Severe fever with thrombocytopenia virus	Haemaphysalis longicornis
KY273136.1	Severe fever with thrombocytopenia virus	tick
KY273137.1	Severe fever with thrombocytopenia virus	tick
KY273138.1	Severe fever with thrombocytopenia virus	tick
MH177014.1	Severe fever with thrombocytopenia virus	TICK-Haemaphysalis longicornis female
MH049431.1	Severe fever with thrombocytopenia virus	Tick-Haemaphysalis longicornis,unfeeded female
KF530058.1	Sierra Nevada virus	Ornithodoros coriaceus
KM114257.1	Silverwater virus	Haemaphysalis leporispalustris
KM114255.1	Silverwater virus	Haemaphysalis leporispalustris
KM114256.1	Silverwater virus	Haemaphysalis leporispalustris
LC010984.1	Thogoto thogotovirus	Haemaphysalis longicornis
LC010986.1	Thogoto thogotovirus	Haemaphysalis longicornis
LC010985.1	Thogoto thogotovirus	Haemaphysalis longicornis
LC010983.1	Thogoto thogotovirus	Haemaphysalis longicornis
LC010982.1	Thogoto thogotovirus	Haemaphysalis longicornis
LC010981.1	Thogoto thogotovirus	Haemaphysalis longicornis
KM114246.1	Uukuniemi virus	Ixodes ricinus
KM114247.1	Uukuniemi virus	Ixodes ricinus
KM114248.1	Uukuniemi virus	Ixodes ricinus
KM114249.1	Uukuniemi virus	Ixodes uriae
KM114250.1	Uukuniemi virus	Ixodes uriae
KM114251.1	Uukuniemi virus	Ixodes uriae
KX219594.1	Uukuniemi virus	tick
KX219593.1	Uukuniemi virus	tick
KJ830812.1	Zahedan rhabdovirus	Hyalomma anatolicum anatolicum
HM566191.1	Zaliv Terpenia virus	tick
HM566193.1	Zaliv Terpenia virus	tick
HM566192.1	Zaliv Terpenia virus	tick
KF892040.1	Zaliv Terpenia virus	Ixodes uriae (tick)
KF892041.1	Zaliv Terpenia virus	Ixodes uriae (tick)
KF892042.1	Zaliv Terpenia virus	Ixodes uriae (tick)
KF892043.1	Zaliv Terpenia virus	Ixodes uriae (tick)
KF892044.1	Zaliv Terpenia virus	Ixodes uriae (tick)
KF892045.1	Zaliv Terpenia virus	Ixodes uriae (tick)
KF767463.1	Zaliv Terpenia virus	Ixodes uriae (tick)
KF767464.1	Zaliv Terpenia virus	Ixodes uriae (tick)
KF767465.1	Zaliv Terpenia virus	Ixodes uriae (tick)
AB069669	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AB069670	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AB069671	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AB069672	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AB069673	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AB069674	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AB069675	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AF338470	Crimean-Congo hemorrhagic fever virus strain BA88166	non-tick host
AF350448	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AF350449	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AF354296	Crimean-Congo Hemorrhagic Fever virus strain China	non-tick host
AF358784	Crimean-Congo Hemorrhagic Fever virus strain China	non-tick host
AF362080	Crimean-Congo Hemorrhagic Fever virus strain China	non-tick host

AF415236	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AF428144	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AF467769	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AF481802	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AF527810	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY029157	Crimean-Congo Hemorrhagic Fever virus strain China	non-tick host
AY049083	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY179961	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY179962	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY223475	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY223476	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY277676	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY297691	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY297692	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY389361	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY389508	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY422208	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY422209	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY675511	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY720893	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY900142	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY900143	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY900144	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY947890	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY947891	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
AY995166	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
CCU04958	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
CHU39455	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
CHU88410	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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CHU88416	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
DQ019222	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
DQ076412	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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DQ133507	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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DQ211650	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
DQ217602	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
DQ446212	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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EF123122	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
EU037902	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
EU044832	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
EU871766	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
GQ337053	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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JN173797	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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KJ027521	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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KJ196326	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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KR814861	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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KR814871	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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KR814880	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
KR814881	Crimean-Congo hemorrhagic fever orthonairovirus	non-tick host
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AF434161	Dugbe orthonairovirus	non-tick host
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DUGNPAA	Dugbe orthonairovirus	non-tick host
DVU15018	Dugbe orthonairovirus	non-tick host
AF004985	Thogoto thogotovirus	non-tick host
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THOGP75A	Thogoto thogotovirus	non-tick host
THORNA3	Thogoto thogotovirus	non-tick host
HM991306	Nairobi sheep disease virus	non-tick host
HM991328	Nairobi sheep disease virus	non-tick host
HQ286599	Nairobi sheep disease virus	non-tick host
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HQ286602	Nairobi sheep disease virus	non-tick host
AF504293	Nairobi sheep disease virus	non-tick host
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EU697951	Nairobi sheep disease virus	non-tick host
EU697952	Nairobi sheep disease virus	non-tick host
KT869018	Nairobi sheep disease virus	non-tick host
LC325234	Severe fever with thrombocytopenia virus	non-tick host
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KR612088	Severe fever with thrombocytopenia virus	non-tick host
KU664007	Severe fever with thrombocytopenia virus	non-tick host
KU664008	Severe fever with thrombocytopenia virus	non-tick host
KU664009	Severe fever with thrombocytopenia virus	non-tick host
KU664010	Severe fever with thrombocytopenia virus	non-tick host
KU664011	Severe fever with thrombocytopenia virus	non-tick host
KU664012	Severe fever with thrombocytopenia virus	non-tick host
KU664013	Severe fever with thrombocytopenia virus	non-tick host
KU664014	Severe fever with thrombocytopenia virus	non-tick host
KU664015	Severe fever with thrombocytopenia virus	non-tick host
KU664016	Severe fever with thrombocytopenia virus	non-tick host
KU664017	Severe fever with thrombocytopenia virus	non-tick host
UUKLRNAP	Uukuniemi virus	non-tick host
UUKGPM	Uukuniemi virus	non-tick host
UUKNNSA	Uukuniemi virus	non-tick host
KF767460	Zaliv Terpenia virus	non-tick host
KF767461	Zaliv Terpenia virus	non-tick host
KF767462	Zaliv Terpenia virus	non-tick host
JQ956376	Bhanja virus	non-tick host
JQ956377	Bhanja virus	non-tick host
JQ956378	Bhanja virus	non-tick host
JX961622	Bhanja virus	non-tick host
JX961623	Bhanja virus	non-tick host
JX961624	Bhanja virus	non-tick host
JQ956379	Palma virus	non-tick host
JQ956380	Palma virus	non-tick host
JQ956381	Palma virus	non-tick host
HQ171186	Huaiyangshan virus	non-tick host
HQ171187	Huaiyangshan virus	non-tick host
HQ171188	Huaiyangshan virus	non-tick host
HQ171189	Huaiyangshan virus	non-tick host
HQ171190	Huaiyangshan virus	non-tick host
JF951393	Huaiyangshan virus	non-tick host
JF951394	Huaiyangshan virus	non-tick host
HQ171191	Huaiyangshan virus	non-tick host
HQ171192	Huaiyangshan virus	non-tick host
HQ171193	Huaiyangshan virus	non-tick host
HQ171194	Huaiyangshan virus	non-tick host
HQ171195	Huaiyangshan virus	non-tick host
HQ419226	Huaiyangshan virus	non-tick host
HQ419227	Huaiyangshan virus	non-tick host
HQ419228	Huaiyangshan virus	non-tick host
HQ419229	Huaiyangshan virus	non-tick host
HQ419230	Huaiyangshan virus	non-tick host
HQ419231	Huaiyangshan virus	non-tick host
HQ419232	Huaiyangshan virus	non-tick host
HQ419233	Huaiyangshan virus	non-tick host
HQ419234	Huaiyangshan virus	non-tick host
HQ419236	Huaiyangshan virus	non-tick host
HQ419237	Huaiyangshan virus	non-tick host
HQ419238	Huaiyangshan virus	non-tick host
HQ419235	Huaiyangshan virus	non-tick host
HQ419239	Huaiyangshan virus	non-tick host
HQ419240	Huaiyangshan virus	non-tick host
HQ419241	Huaiyangshan virus	non-tick host
HQ419242	Huaiyangshan virus	non-tick host
HQ419243	Huaiyangshan virus	non-tick host
HQ419244	Huaiyangshan virus	non-tick host
dsRNA viral sequences		
LC019131	Muko virus	Ixodes turdus
LC158842	Muko virus	Ixodes turdus
LC019132	Muko virus	Ixodes turdus
LC158843	Muko virus	Ixodes turdus
LC158844	Muko virus	Ixodes turdus
LC019133	Muko virus	Ixodes turdus
LC019134	Muko virus	Ixodes turdus

LC158845	Muko virus	Ixodes turdus
LC019135	Muko virus	Ixodes turdus
LC158846	Muko virus	Ixodes turdus
LC019136	Muko virus	Ixodes turdus
LC158847	Muko virus	Ixodes turdus
LC019137	Muko virus	Ixodes turdus
LC158848	Muko virus	Ixodes turdus
LC019138	Muko virus	Ixodes turdus
LC158849	Muko virus	Ixodes turdus
LC019139	Muko virus	Ixodes turdus
LC158850	Muko virus	Ixodes turdus
LC019140	Muko virus	Ixodes turdus
LC158851	Muko virus	Ixodes turdus
KP268784.1	Chobar Gorge virus	Ornithodoros sp.
KP268785.1	Chobar Gorge virus	Ornithodoros sp.
KP268786.1	Chobar Gorge virus	Ornithodoros sp.
KP268787.1	Chobar Gorge virus	Ornithodoros sp.
KP268788.1	Chobar Gorge virus	Ornithodoros sp.
KP268789.1	Chobar Gorge virus	Ornithodoros sp.
KP268790.1	Chobar Gorge virus	Ornithodoros sp.
KP268791.1	Chobar Gorge virus	Ornithodoros sp.
KP268792.1	Chobar Gorge virus	Ornithodoros sp.
KP268793.1	Chobar Gorge virus	Ornithodoros sp.
KC288130.1	Kemerovo virus	Ixodes persulcatus
KC288131.1	Kemerovo virus	Ixodes persulcatus
KC288132.1	Kemerovo virus	Ixodes persulcatus
KC288133.1	Kemerovo virus	Ixodes persulcatus
KC288134.1	Kemerovo virus	Ixodes persulcatus
KC288135.1	Kemerovo virus	Ixodes persulcatus
KC288136.1	Kemerovo virus	Ixodes persulcatus
KC288137.1	Kemerovo virus	Ixodes persulcatus
KC288138.1	Kemerovo virus	Ixodes persulcatus
KC288139.1	Kemerovo virus	Ixodes persulcatus
KJ425427	Wad Medani virus	Hyalomma asiaticum (tick)
KJ425429	Wad Medani virus	Hyalomma asiaticum (tick)
KJ425432	Wad Medani virus	Hyalomma asiaticum (tick)
KP268804	Wad Medani virus	Rhipicephalus sp.
KP268805	Wad Medani virus	Rhipicephalus sp.
KP268806	Wad Medani virus	Rhipicephalus sp.
KP268807	Wad Medani virus	Rhipicephalus sp.
KP268808	Wad Medani virus	Rhipicephalus sp.
KP268809	Wad Medani virus	Rhipicephalus sp.
KP268810	Wad Medani virus	Rhipicephalus sp.
KP268811	Wad Medani virus	Rhipicephalus sp.
KP268812	Wad Medani virus	Rhipicephalus sp.
KP268813	Wad Medani virus	Rhipicephalus sp.
MF521567	Wad Medani virus	Hyalomma asiaticum (tick)
MF521568	Wad Medani virus	Hyalomma asiaticum (tick)
MF521570	Wad Medani virus	Hyalomma asiaticum (tick)
MF521571	Wad Medani virus	Hyalomma asiaticum (tick)
MF521572	Wad Medani virus	Hyalomma asiaticum (tick)
MF521573	Wad Medani virus	Hyalomma asiaticum (tick)
MF521574	Wad Medani virus	Hyalomma asiaticum (tick)
MF521575	Wad Medani virus	Hyalomma asiaticum (tick)
MF521576	Wad Medani virus	Hyalomma asiaticum (tick)
MF521577	Wad Medani virus	Hyalomma asiaticum (tick)
MF521578	Wad Medani virus	Hyalomma asiaticum (tick)
MF521580	Wad Medani virus	Hyalomma asiaticum (tick)
MF521581	Wad Medani virus	Hyalomma asiaticum (tick)
MF521582	Wad Medani virus	Hyalomma asiaticum (tick)
MF521583	Wad Medani virus	Hyalomma asiaticum (tick)
MF521584	Wad Medani virus	Hyalomma asiaticum (tick)
MF521591	Wad Medani virus	Hyalomma asiaticum (tick)
MF521592	Wad Medani virus	Hyalomma asiaticum (tick)
MF521593	Wad Medani virus	Hyalomma asiaticum (tick)
MG770338	Wad Medani virus	tick
MG770339	Wad Medani virus	tick

MG770340	Wad Medani virus	tick
MG770341	Wad Medani virus	tick
MG770342	Wad Medani virus	tick
MG770345	Wad Medani virus	tick
MG770346	Wad Medani virus	tick
MH571965	Wad Medani virus	Hyalomma sp. (tick)
MH571967	Wad Medani virus	Hyalomma sp. (tick)
MH571968	Wad Medani virus	Hyalomma sp. (tick)
MH571969	Wad Medani virus	Hyalomma sp. (tick)
MH571970	Wad Medani virus	Hyalomma sp. (tick)
MH571971	Wad Medani virus	Hyalomma sp. (tick)
MH571972	Wad Medani virus	Hyalomma sp. (tick)
MH571973	Wad Medani virus	Hyalomma sp. (tick)
KY023339.1	Baku virus	Ornithodoros coniceps (tick)
KY023340.1	Baku virus	Ornithodoros coniceps (tick)
KY023341.1	Baku virus	Ornithodoros coniceps (tick)
KY023342.1	Baku virus	Ornithodoros coniceps (tick)
KY023343.1	Baku virus	Ornithodoros coniceps (tick)
KY023344.1	Baku virus	Ornithodoros coniceps (tick)
KY023345.1	Baku virus	Ornithodoros coniceps (tick)
KY023346.1	Baku virus	Ornithodoros coniceps (tick)
KY023347.1	Baku virus	Ornithodoros coniceps (tick)
KY023348.1	Baku virus	Ornithodoros coniceps (tick)
KY023349.1	Baku virus	Ornithodoros capensis (tick)
KY023350.1	Baku virus	Ornithodoros capensis (tick)
KY023351.1	Baku virus	Ornithodoros capensis (tick)
KY023352.1	Baku virus	Ornithodoros capensis (tick)
KY023353.1	Baku virus	Ornithodoros capensis (tick)
KY023354.1	Baku virus	Ornithodoros capensis (tick)
KY023355.1	Baku virus	Ornithodoros capensis (tick)
KY023356.1	Baku virus	Ornithodoros capensis (tick)
KY023357.1	Baku virus	Ornithodoros capensis (tick)
KY023358.1	Baku virus	Ornithodoros capensis (tick)
HM543481	Kemerovo virus	non-tick host
HQ266591	Kemerovo virus	non-tick host
HM543482	Kemerovo virus	non-tick host
HQ266592	Kemerovo virus	non-tick host
HQ266593	Kemerovo virus	non-tick host
HQ266594	Kemerovo virus	non-tick host
HQ266595	Kemerovo virus	non-tick host
HQ266596	Kemerovo virus	non-tick host
HM543483	Kemerovo virus	non-tick host
HQ266597	Kemerovo virus	non-tick host
HQ266598	Kemerovo virus	non-tick host
HQ266599	Kemerovo virus	non-tick host
HQ266600	Kemerovo virus	non-tick host
dsDNA viral sequences		
AF050111.1	African swine fever virus	Ornithodoris tick
HM745336.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745337.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745338.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745339.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745340.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745341.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745342.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745343.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745344.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745345.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745323.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745324.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745325.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745326.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745327.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745328.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745329.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745330.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)

HM745331.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
HM745332.1	African swine fever virus	Ornithodorus porcinus porcinus (tick)
AY261361.1	African swine fever virus	Ornithodoros sp.
AY261362.1	African swine fever virus	Ornithodoros sp.
FJ174425.1	African swine fever virus	Ornithodoros sp.
AY261363.1	African swine fever virus	Ornithodoros porcinus porcinus
AY261365.1	African swine fever virus	tick
KC662383.1	African swine fever virus	tick
KF015859.1	African swine fever virus	tick
KC662379.1	African swine fever virus	tick
KC662382.1	African swine fever virus	tick
KF015871.1	African swine fever virus	tick
KF015860.1	African swine fever virus	tick
KC867508.1	African swine fever virus	tick
KF015900.1	African swine fever virus	tick
KF015927.1	African swine fever virus	tick
KF736414.1	African swine fever virus	tick
KF736443.1	African swine fever virus	tick
KF736425.1	African swine fever virus	tick
KC535552.1	African swine fever virus	tick
KC535546.1	African swine fever virus	tick
KF015882.1	African swine fever virus	tick
KF015930.1	African swine fever virus	tick
KF015928.1	African swine fever virus	tick
KF736415.1	African swine fever virus	tick
KF015932.1	African swine fever virus	tick
KF015929.1	African swine fever virus	tick
KF015898.1	African swine fever virus	tick
KF015931.1	African swine fever virus	tick
KC867522.1	African swine fever virus	tick
KF015857.1	African swine fever virus	tick
KC867501.1	African swine fever virus	tick
KF015903.1	African swine fever virus	tick
KF015906.1	African swine fever virus	tick
KF015910.1	African swine fever virus	tick
KF736427.1	African swine fever virus	tick
KF015963.1	African swine fever virus	tick
KF015973.1	African swine fever virus	tick
KF015892.1	African swine fever virus	tick
KF015890.1	African swine fever virus	tick
KF015889.1	African swine fever virus	tick
KF015974	African swine fever virus	non-tick host
KC867515	African swine fever virus	non-tick host
KF015924	African swine fever virus	non-tick host
KF015867	African swine fever virus	non-tick host
AY261360	African swine fever virus	non-tick host
FJ174384	African swine fever virus	non-tick host
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FJ174387	African swine fever virus	non-tick host
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FJ238536	African swine fever virus	non-tick host
GQ410767	African swine fever virus	non-tick host
GQ410768	African swine fever virus	non-tick host
GQ410771	African swine fever virus	non-tick host
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JN590915	African swine fever virus	non-tick host
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JX857505	African swine fever virus	non-tick host
JX857506	African swine fever virus	non-tick host
JX857507	African swine fever virus	non-tick host
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KF303302	African swine fever virus	non-tick host
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KJ195685	African swine fever virus	non-tick host
KJ380910	African swine fever virus	non-tick host
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KJ626193	African swine fever virus	non-tick host
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KJ627186	African swine fever virus	non-tick host
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KJ627192	African swine fever virus	non-tick host
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KM609342	African swine fever virus	non-tick host
KM609362	African swine fever virus	non-tick host
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AM712239	African swine fever virus Benin 97/1	non-tick host
FN557520	African swine fever virus E75	non-tick host
FR682468	African swine fever virus Georgia 2007/1	non-tick host
AM712240	African swine fever virus OURT 88/3	non-tick host
LN846619.1	California bark scorpion polyomavirus	California bark scorpion
ssDNA viral sequences		
MF173065.1	Tick-associated genomovirus 1 isolate tick24_7, complete genome	Dermacentor variabilis
MF173066.1	Tick-associated genomovirus 2 isolate tick24_130, complete genome	Dermacentor variabilis
MF173067.1	Tick-associated genomovirus 3 isolate tick25_VL-10, complete genome	Ixodes scapularis
MF173068.1	Tick associated torque teno virus	Dermacentor variabilis
KX774632.1	Lone star tick densovirus	Amblyomma americanum