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Review

Viruses associated with Antarctic wildlife: From serology based detection to identification of genomes using high throughput sequencing

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ABSTRACT

The Antarctic, sub-Antarctic islands and surrounding sea-ice provide a unique environment for the existence of organisms. Nonetheless, birds and seals of a variety of species inhabit them, particularly during their breeding seasons. Early research on Antarctic wildlife health, using serology-based assays, showed exposure to viruses in the families *Birnaviridae*, *Flaviviridae*, *Herpesviridae*, *Orthomyxoviridae* and *Paramyxoviridae* circulating in seals (Phocidae), penguins (Spheniscidae), petrels (Procellariidae) and skuas (Stercorariidae). It is only during the last decade or so that polymerase chain reaction-based assays have been used to characterize viruses associated with Antarctic animals. Furthermore, it is only during the last five years that full/whole genomes of viruses (adenoviruses, anelloviruses, orthomyxoviruses, a papillomavirus, paramyoviruses, polyomaviruses and a togavirus) have been sequenced using Sanger sequencing or high throughput sequencing (HTS) approaches. This review summaries the knowledge of animal Antarctic virology and discusses potential future directions with the advent of HTS in virus discovery and ecology.

1. Introduction

Among Earth's oceans, those in the Polar Regions are the smallest and most constrained, the Arctic Ocean encircled by landmasses and the Southern Ocean by the Antarctic Circumpolar Current (ACC). The latter ocean is bounded to its north by the Antarctic Polar Front (APF), a well-known faunal barrier, and has a high degree of endemism among both vertebrates and invertebrates (e.g. Briggs, 1995; Eastman, 2013). Owing to dramatic annual cycles of heat and light, the productivity of the Southern Ocean is highly constrained on a seasonal basis, a characteristic that provides a generally challenging environment for the existence of organisms. Moreover, the high latitude Southern Ocean, i.e. that portion south of the Southern Boundary of the ACC (SBACC), is covered by sea ice for much of the year, in some places the entire year. Most of the birds and seals of a variety of species that inhabit that zone are endemic and resident, the most unvarying species assemblage found in Southern Hemisphere oceans; only a few migrant species augment that assemblage during summer (Ribic and Ainley, 1989). The species comprising this assemblage breed either on Antarctic islands (birds) or the sea ice that surrounds the continent (seals). In contrast, waters north of the SBACC host a much more speciose, seasonally varying seabird and marine mammal assemblage composed of species breeding on low latitude islands bordering the APF (Antarctic and sub-Antarctic) as well as seasonal migrants from more temperate regions (e.g. Ainley et al., 1994; Laws, 1977a,b; Ribic and Ainley, 1989; Ribic et al., 2011). In accord with trends of diversity varying inversely with latitude, overall diversity of vertebrate species is low in the Southern Ocean, especially south of the SBACC, but populations are immense (e.g. Laws, 1977a,b).

Inhabiting the pack-ice surrounding Antarctica is a unique assemblage of pagophilic seals, crabeater (*Lobodon carcinophaga*), leopard (*Hydrurda leptonyx*), Ross (*Ommatophoca rossii*) and Weddell seal (*Leptonychotes weddellii*). Weddell seals colonize near-shore fast-ice regions feeding mainly on fish, while other Antarctic seals remain year round in the pack-ice composed of individual, often compacted floes. Crabeater seals feed principally on krill (*Euphausia* spp.), and Ross seals mostly on squid. Unlike the other Antarctic seals, leopard seals are solitary and highly predatory feeding on penguins and other seals as well as fish, krill and cephalopods (Siniff, 1981). Southern elephant seals (*Mirounga leonina*) occupy sub-Antarctic islands for breeding, then

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migrate south to Antarctica, some hauling out on land for moulting; Antarctic fur seals (*Arctocephalus gazella*) breed on peri-Antarctic islands, such as Macquarie, South Georgia and South Sandwich, as well as islands of the northern Antarctic Peninsula, around which they also hunt for krill and fish (Siniff et al., 2008).

Confined to pack-ice affected waters south of the SBACC are the Adélie (*Pygoscelis adeliae*) and emperor (*Aptenodytes forsteri*) penguins; north of that boundary are three other penguin species: gentoo (*P. papua*), chinstrap (*P. antarctica*) and macaroni (*Eudyptes chrysolophus*) (Williams, 1995). While mostly distributed to the north, populations of chinstrap, gentoo and macaroni penguins breed on islands of the northwestern Antarctic Peninsula, overlapping with Adélie penguins. Gentoo penguins are distributed as far as temperate waters surrounding the Falkland Islands, while macaroni penguins mainly colonize Heard and South Georgia islands in proximity to the APF (Trathan et al., 2016). Colonies of king penguins (*A. patagonicus*), royal penguins (*E. schlegeli*) and rockhopper penguins (*E. chrysocome*) are found on sub-Antarctic islands and do not inhabit the coastal Antarctic continent. Flying birds inhabiting Antarctica and sub-Antarctic regions include skuas, petrels, terns, gulls and Albatross (Brooke, 2004; Murphy, 1936).

In addition to the two penguins endemic to the sea ice zone are the endemic snow (*Pagodroma nivea*) and Antarctic petrels (*Thalassoica antarctica*), this pagophilic community increased only in summer by a few other flighted seabirds: skuas, albatross and a few petrel species. The peri-Antarctic and sub-Antarctic islands, and surrounding ice-free ocean, are densely populated by many more petrel and albatross species, with sparse inclusion of skuas and larid species (Brooke, 2004; Murphy, 1936).

2. Early reports of mass mortality in Antarctic animals

Due to its zoogeographical isolation, introduction of pathogens and parasites to these populations of Antarctic wildlife, particularly the endemics of high latitude, may have detrimental effects. Understanding these potential effects required a knowledge of the entities circulating in the ecosystem. This concern drove interest toward detecting viruses, bacteria and parasites among Antarctic animals providing insight to their health. There have been a few reported cases of mass mortality where the disease-causing agent was undetermined. In 1971, several hundred gentoo penguin chicks at a Signey Island colony, South Orkneys, were found dead (MacDonald and Conroy, 1971). Although symptoms were described as similar to puffinosis coronavirus infection, no isolation of the disease agent was possible (Barbosa and Palacios, 2009). In 1972, about 65% of Adélie penguin chicks were reported dead in a colony near Mawson Station. In this case, penguins were found face down and apparently unable to walk or stand properly (Kerry et al., 2009). The cause of this disease was not determined. The only mass mortality reported in seals was the death of over 1500 crabeater seals in a colony around Crown Prince Gustav Channel, Antarctic Peninsula in 1955 (Laws and Taylor, 1957). Interestingly, Weddell seals in the area were unaffected and while the nature of this disease was unknown, a viral infection was suggested. Laws and Taylor (1957) noted that the population of seals in this area was almost ten times higher than normal and predicted that this crowding and partial starvation likely contributed to the effects of the disease.

3. Viruses associated with Antarctic animals

Only within the last ten years has an increase in knowledge of the viral diversity been evident among Antarctic wildlife at a genome level. Early work, beginning in the mid-1970s, on identifying viruses associated with Antarctic animals relied on serology-based assays (Table 1). The research then was particularly focused around detecting pathogens posing a risk to animal health due to concerns regarding the impact of increased anthropogenic activity, e.g. research, tourism, on birds and marine mammals (Kerry and Riddle, 2009). During the early period of Antarctic virus research, paramyxoviruses, orthomyxoviruses, birnaviruses, herpesviruses and flaviviruses were serologically detected (Table 1, Fig. 1). Subsequently, between 2000 and 2010, probe based assays using polymerase chain reaction (PCR) were used to detect paramyxoviruses, orthomyxoviruses and a poxvirus (Table 2, Fig. 1). Finally, in the last decade, advancements in high throughput sequencing (HTS) approaches are beginning to have an impact on our knowledge of Antarctic animal virology. For example, in the last five years using viral metagenomic based approaches with HTS, various novel viruses have been identified and characterized at a genomic level (Table 2, Fig. 1). These include adenoviruses, anelloviruses, orthomyxoviruses, papillomaviruses, polyomaviruses and paramyxoviruses.

3.1. Positive sense RNA viruses

3.1.1. Flaviviridae

Flaviviridae is a family of enveloped positive sense RNA viruses with four genera: *Flavivirus*, *Hepacivirus*, *Pegivirus* and *Pestivirus*. Their genomes range in length from 8.9–13 kb (Simmonds et al., 2017b). While no genomic information is available for flaviviruses circulating in Antarctic animals, neutralizing antibodies to a flavivirus were detected in the serum of South Polar skuas (*Stercorarius maccormicki*) around Davis station, East Antarctica (Miller et al., 2008). As lower latitude seabirds are infested with ticks (e.g. Lee and Baust, 1987), which are known to carry flaviviruses, this may indicate the transmission of tick-borne flaviviruses to seabirds, especially given the fact that a flavivirus was isolated from seabird ticks (*Ixodes uriae*) infecting king penguins on Macquarie Island (Major et al., 2009).

3.1.2. Togaviridae

The family *Togaviridae* consist of enveloped positive sense RNA viruses with a genome length of about 11–12 kb in length. Togaviruses are classified into two genera, *Alphavirus* and *Rubivirus* (Power et al., 2017). While the human pathogenic virus, rubella virus, is the only known member of the single species in the genus *Rubivirus* to date (species *Rubella virus*), all animal togaviruses are classified as alphaviruses (Power et al., 2017). The life cycle of alphaviruses requires an arthropod vector, either a mosquito or tick, for transmission to their vertebrate host. The first instance of alphaviruses found in marine mammals was shown in southern elephant seals of Macquarie Island. Initially the seal alphavirus was isolated from the blood-sucking louse (*Lepidophthirus macrorhini*) that is widespread among southern elephant seals. However, a high seroprevalence of antibodies against the southern elephant seal alphavirus strongly indicated its transmission from lice to seals (La Linn et al., 2001). The full genome of this alphavirus (Southern elephant seal virus) was determined in a later study (Forrester et al., 2012).

3.2. Negative sense RNA viruses

3.2.1. Orthomyxoviridae

Viruses in the family *Orthomyxoviridae* have enveloped, negative sense RNA genomes that consist of 6–8 segments. Seven genera are established in this family (*Influenzavirus A, Influenazavirus B, Influenzavirus C, Influenzavirus D, Isavirus, Quaranjavirus* and *Thogotovirus*) (McCauley et al., 2011). *Influenza A virus* is the only species in the genus *Influenzavirus A*, consisting of several pathogenic strains infecting humans, horses, pigs, whales, seals, birds and mink (McCauley et al., 2011). Influenza A virus strains are transmissible to humans and have caused worldwide endemics. This zoonotic nature of influenza viruses has led to extensive research on Influenza A virus. Antarctica continues to provide an interesting environment to study Influenza A viruses, especially in the case of migratory birds. For example, the South Polar skuas that breed on the Antarctic continent in the summer but move north, well into the Northern Hemisphere during the non-breeding season (Weimerskirch et al., 2015), thus act as

Table 1
Summary of Antarctic bird- and mammal-associated viruses detected through serological approaches.

	Virus taxonomy					Notes				
ID	**Order**	**family**	**genus**	**Virus**	**Host**	**Method**	**Sample**	**Location**	**Year of collection**	**Reference**
1	*Mononegavirales*	*Paramyxoviridae*	*Avulavirus*	Avian paramyxovirus	Adelie penguins (*Pygoscelis adeliae*)	Hemagglutination-inhibition, immunodiffusion tests, morphology	2/42 serum samples with antibodies to NDV, cloacal swabs	Wilkes base	–	Morgan and Westbury (1981)
2						Hemagglutination-inhibition, immunodiffusion tests, morphology	serum, 2 APMV viruses isolated from 550 cloacal swabs	Peterson Island, Midgley Island, Shirley Island, Cameron Island, d'Urville (Casey station)	–	Morgan and Westbury (1981)
3						Virus isolation, Haemagglutination test	Serum samples and cloacal swabs	Vestfold Hills	December 1981	Morgan and Westbury (1988)
4						Indirect ELISA, electron microscopy	Cloacal swab, serum	Ross Island	1978	Austin and Webster (1993)
5					Royal penguins (*Eudyptes chrysolophus*)	Hemagglutination-inhibition, immunodiffusion tests, morphology	Cloacal samples	Macquarie Island	–	Morgan et al. (1981)
5					King penguin (*Aptenodytes patagonicus*)	Hemagglutination-inhibition, immunodiffusion tests, morphology	Cloaca samples	Macquarie Island	–	Morgan et al. (1981)
7					South Polar skua (*Stercorarius maccormicki)*	Indirect ELISA, electron microscopy	Serum	Ross Island	1978, 1986	Austin and Webster (1993)
8						Haemagglutination-inhibition test	Serum samples and cloacal swabs	Davis station	November/December 1999	Miller et al. (2008)
9			*Morbillivirus*	Canine distemper virus	Leopard seal (*Hydrurda leptonyx*)	CDV-like antibodies detected through microneutralization test using two CDV strains and a phocine distemper virus isolate	2/3 serum samples tested positive	Antarctic peninsula	1989	Bengtson et al. (1991)
10					Crabeater seal (*Lobodon carcinophaga*)	CDV-like antibodies detected through microneutralization test using two CDV strains and a phocine distemper virus isolate	35% serum samples tested positive for CDV	Antarctic peninsula	January/March 1989	Bengtson et al. (1991)
11	Unassigned	*Orthomyxoviridae*	*Influenzavirus*	Influenza A virus	Adelie penguins (*Pygoscelis adeliae*)	Hemagglutination-inhibition, immunodiffusion tests	Serum	Peterson Island (Casey)	–	Morgan et al. (1981)
12						Hemagglutination-inhibition, Neuraminidase-inhibition tests	Serum	Ross Island	1978	Austin and Webster (1993)
13						Hemagglutination-inhibition test against H1N1, H3N2, H5N1, and H7N2 antigens	Serum	Hope Bay	December–March, 1998, 2001, and 2002	Baumeister et al. (2004)

(*continued on next page*)

Table 1 (*continued*)

	Virus taxonomy				Notes				
ID	Order	family	genus	Virus	Host	Method	Sample	Location	Year of collection	Reference
14					South Polar skua (*Stercorarius maccormicki*)	Indirect ELISA, Hemagglutination-inhibition tests	Serum	Ross Island	1978, 1986	Austin and Webster (1993)
15						Capture ELISA	Serum and cloacal swabs	Davis station	November/December 1999	Miller et al. (2008)
16						Hemagglutination inhibition test against H1N1, H3N2, H5N1, and H7N2 antigens	Serum	Potter peninsula and Hope Bay	December–March, 1998, 2001, and 2002	Baumeister et al. (2004)
17					Chinstrap penguins (*Pygoscelis antarctica*)	Hemagglutination inhibition test against H1N1, H3N2, H5N1, and H7N2 antigens	Serum	Potter peninsula	December-March, 1998, 2001, and 2002	Baumeister et al. (2004)
18					Gentoo penguins (*Pygoscelis papua*)	Hemagglutination inhibition test against H1N1, H3N2, H5N1, and H7N2 antigens	Serum	Potter peninsula	December-March, 1998, 2001, and 2002	Baumeister et al. (2004)
19						Influenzavirus type A virus antibody ELISA kit		Bird Island	1996	
20					Giant petrel (*Macronectes giganteus*)	Hemagglutination inhibition test against H1N1, H3N2, H5N1, and H7N2 antigens	Serum	Potter peninsula and Harmony peninsula	December–March, 1998, 2001, and 2002	Baumeister et al. (2004)
21		*Birnaviridae*	*Avibirnavirus*	Infectious bursal disease virus	Adelie penguins (*Pygoscelis adeliae*)	Virus neutralization tests, IBDV serotype 1 and 2 antibodies	High titer of neutralizing antibodies detected in 2.6% or 133 penguins	Mawson station	1995/96 summer	Gardner et al. (1997)
22						Virus neutralization tests to measure antibody titers to IBDV serotype 1	Seroprevalence 7.7%, no significant difference between locations or years. Highly significant titres were obtained from 1.8% of birds	Mawson coast, Davis Coast, Terra Nova Bay	November–February 1996-2002	Watts et al. (2009)
23					Emperor penguin (*Aptenodytes forsteri*)	Virus neutralization tests, IBDV serotype 1 and 2 antibodies	High titer of neutralizing antibodies detected in 65.4% of 53 penguins	Mawson station	1995/96 summer	Gardner et al. (1997)
24						Virus neutralization tests to measure antibody titers to IBDV serotype 1		Auster Rookery, Amanda Bay rookery, Cape Washington rookery	November–February 1996–2001	Watts et al. (2009)
25					King penguin (*Aptenodytes patagonicus*)	Virus neutralization tests, IBDV serotype 1 and 2 antibodies, cough and conjunctivitis clinical signs	Serum of adults and chicks	sub-Antarctic Iles Crozet	November 1996-February 1997	Gauthier-Clerc et al. (2002)
26					South Polar skua (*Stercorarius maccormicki*)	Antibody neutralization test	Serum and cloacal swab	Davis station	November/December 1999	Miller et al. (2008)

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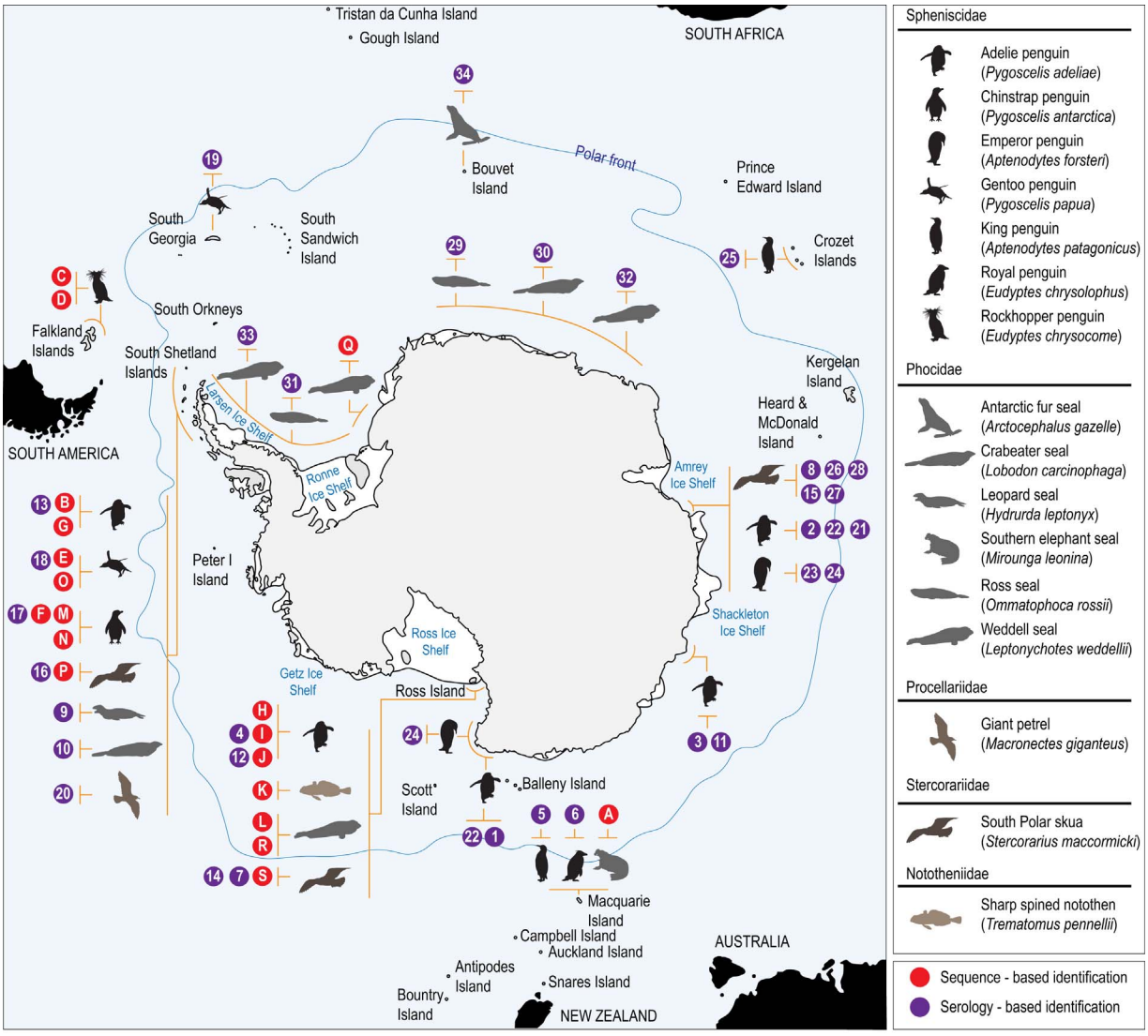
Table 1 (*continued*)

ID	Virus taxonomy				Host	Notes				
	Order	family	genus	Virus		Method	Sample	Location	Year of collection	Reference
27						Virus neutralization tests to measure antibody titers to IBDV serotype 1	Antibodies detected in 11.8% of individuals, Significant difference in prevalence between sample years	Vestfolds, Davis station	November–February 1999–2002	Watts et al. (2009)
28		*Flaviviridae*	*Flavivirus*	–	South Polar skua (*Stercorarius maccormicki)*	Capture ELISA	Serum samples and cloacal swabs	Davis station	November/December 1999	Miller et al. (2008)
29	*Herpesvirales*	*Herpesviridae*	*Varicellovirus*	Phocid alphaherpesvirus 1	Ross seal (*Ommatophoca rossii*)	Indirect ELISA using PhHV-1 as antigen, serum neutralization test	Serum	Queen Maud Land	2001	Tryland et al. (2012)
30					Crabeater seal (*Lobodon carcinophaga*)	Indirect ELISA using PhHV-1 as antigen, serum neutralization test	Serum	Queen Maud Land	2001	Tryland et al. (2012)
31						Testing for neutralizing antibodies against phocine, feline and canine herspevirus using either microneutralization or by neutralizing peroxidase-linked antibody assay	Serum	Weddell Sea	1990	Harder et al. (1991)
32					Weddell seal (*Leptonychotes weddellii*)	Indirect ELISA using PhHV-1 as antigen, serum neutralization test (SNT)	Serum	Queen Maud Land	2001	Tryland et al. (2012)
33						Testing for neutralizing antibodies against phocine, feline and canine herspevirus using either microneutralization or by neutralizing peroxidase-linked antibody assay	Serum	Weddell Sea	1990	Harder et al. (1991) and Stenvers et al. (1992)
34					Antarctic fur seal (*Arctocephalus gazelle*)	Indirect ELISA using PhHV-1 as antigen	Serum	Bouvet Island	2000–2001, 2001–2002	Tryland et al. (2012)

CDV: Canine distemper virus.
ELISA: Enzyme-linked immunosorbent assay.
IBDV: Infectious bursal disease virus.



Method of identification*	Order	Family	Genus	Species
29 30 31 32 33 34	*Herpesvirales*	*Herpesviridae*	*Varicellovirus*	*Phocid alphaherpesvirus 1*
1 2 3 4 5 6 7 8 B	*Mononegavirales*	*Paramyxoviridae*	*Avulavirus*	*Avian avulavirus 1*
C D	*Mononegavirales*	*Paramyxoviridae*	*Avulavirus*	*Avian avulavirus 10*
E	*Mononegavirales*	*Paramyxoviridae*	*Avulavirus*	unassigned (avian avulavirus 15, -16, -17)
9 10	*Mononegavirales*	*Paramyxoviridae*	*Morbillivirus*	*Canine distemper virus*
A	Unassigend	*Togavirdae*	*Alphavirus*	*Southern elephant seal virus*
M N O	Unassigned	*Adenoviridae*	*Siadenovirus*	*Penguin siadenovirus A*
P	Unassigned	*Adenoviridae*	*Siadenovirus*	*Skua siadenovirus A*
R	Unassigned	*Anelloviridae*	unassigned	unassigned (torque teno Leptonychotes weddelli virus 1, -2)
S	Unassigned	*Anelloviridae*	unassigned	unassigned (torque teno Leptonychotes weddelli virus 1)
21 22 23 24 25 26 27	Unassigned	*Birnaviridae*	*Avibirnavirus*	*Infectious bursal disease virus*
28	Unassigned	*Flaviviridae*	*Flavivirus*	-
11 12 13 14 15 16 17 18 19 20 F G	Unassigned	*Orthomyxoviridae*	*Influenzavirus A*	*Influenza virus A*
H	Unassigned	*Papillomaviridae*	*Treisepsilonpapillomavirus*	*Treisetapapillomavirus 1*
I	Unassigned	*Papillomaviridae*	unassigned	unassigned (pygoscelis adeliae polyomavirus 2)
L	Unassigned	*Polyomaviridae*	*Betapolyomavirus*	*Leptonychotes weddellii polyomavirus 1*
J	Unassigned	*Polyomaviridae*	*Gammapolyomavirus*	*Pygoscelis adeliae polyomavirus 1*
K	Unassigned	*Polyomaviridae*	unassigned	*Trematomus pennellii polyomavirus 1*
Q	Unassigned	*Poxviridae*	*Parapoxvirus*	unassigned (seal poxvirus)

Fig. 1. Distribution of viruses identified among populations of animals of the Antarctic and high latitude sub-Antarctic. Colored circles denote the method of viral identification. Purple indicates serology based identification, number inside circle corresponding to details provided in Table 1. Red circle indicates sequence based identification, letter inside circle corresponding to details provided in Table 2.

potential vectors bringing in new variants and reassortants to Antarctica during each breeding season.

The majority of studies screening for influenza have used hemagglutination-inhibition assays to detect antibodies against several common strains of avian influenza virus circulating among Antarctic animals. Antarctic influenza virus research carried out between 1978

Table 2
Summary of Antarctic bird- and mammal-associated viruses identified through sequencing based approaches, including respective accession numbers of the partial and full genome sequences.

	Virus taxonomy				Notes					
ID	**Family**	**Genus**	**Species & virus**	**Host**	**Method**	**Sample type**	**Location**	**Year of collection**	**Accession #**	**Reference**
A	*Togaviridae*	*Alphavirus*	*Southern elephant seal virus* [Southern elephant seal virus (SES virus)]	Southern elephant seals (*Mirounga leonina*)	Virus cultured in BHK-21 cells virus from blood sucking lice *Lepidophthirus macrorhini* and used in viral neutralization assay for serology. Negative stain electron microscopy. RT-PCR and Sanger sequencing of capsid protein gene.	*Lepidophthirus macrorhini* and serum from southern elephant seal virus	Macquarie Island	–	AF315122 HM147990	Forrester et al. (2012) and La Linn et al. (2001)
B	*Paramyxoviridae*	*Avulavirus*	*Avian avulavirus 1* [New castle disease virus (NDV)]	Adélie penguins (*Pygoscelis adeliae*)	RT-PCR and real-time PCR targeting F gene of NDV, virus culture, haemagglutination test using antigen against B1 NDV strain, Sanger sequencing.	Cloacal/tracheal swabs and serum samples	King George Island	2006	HM143848–HM143850	Thomazelli et al. (2010)
C			*Avian avulavirus 10* [Avian paramyxovirus 10 (APMV10)]	Rockhopper penguins (*Eudyptes chrysocome*)	Real-time RT-PCR, hemagglutination assay, binaxNOW influenza A & B test, hemagglutination inhibition assay, ELISA, electron microscopy, Sanger sequencing.	Cloacal/tracheal swabs and serum samples	Falkland Islands	2007	HM147142, HM755886–HM755888 (updated following the publication of Goraichuk et al. (2017)	Miller et al. (2010)
D				Rockhopper penguins (*Eudyptes chrysocome*)	Complete genome sequencing using Illumina and Sanger sequencing.	Cloacal/tracheal swabs and serum samples	Falkland Islands	2007	HM147142, HM755886–HM755888	Goraichuk et al. (2017)
E			Unclassified [Avian paramyxovirus 15, 16, 17 (APMV15, APMV16, APMV17)]	Gentoo penguins (*Pygoscelis papua*)	Hemagglutination assay, RT-PCR and Sanger sequencing.	Virus isolated from 12 cloacal swabs, 5 confirmed by sequencing	Kopaitic Island	2014 – 2016	KY452442–KY452444	Neira et al. (2017)
F	*Orthomyxoviridae*	*Influenzavirus A*	*Influenzavirus A* [Avian Influenza A virus H5N5]	Chinstrap penguins (*Pygoscelis antarctica*)	RT-PCR, HTS, ELISA using nucleoprotein, hemagglutination assay.	Cloacal/tracheal swabs and serum samples	Antarctic peninsula	2015	GISAID #s [EPI774530-EPI774536, EPI774538-EPI774539]; [EPI774527- EPI774529]	Hurt et al. (2016)
G			*Influenzavirus A* [Avian influenza A virus H11N2]	Adélie penguins (*Pygoscelis adeliae*)	RT-PCR, virus culture, ELISA, whole genome Sanger sequencing.	Cloacal/tracheal swabs and serum samples	Rada Covadonga, Antarctic Peninsula and King George Island	2013	KJ729348–KJ729379	Hurt et al. (2014)
H	*Papillomaviridae*	*Treisepsilonpapillomavirus*	*Treisetapapillomavirus 1* [Pygoscelis adeliae papillomavirus 1]	Adélie penguins (*Pygoscelis adeliae*)	HTS-informed approach, genome recovered by abutting primers, cloned and Sanger sequenced.	Faeces	Cape Crozier, Ross Island	2012/2013	KJ173785	Varsani et al. (2014)
I			Unclassified [Pygoscelis adeliae papillomavirus 2]	Adélie penguins (*Pygoscelis adeliae*)	HTS-informed approach, genome recovered by abutting primers, cloned and Sanger sequenced.	Cloacal swab	Cape Crozier, Ross Island	2014	MF168943	Van Doorslaer et al. (2017)

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Table 2 (*continued*)

	Virus taxonomy				Notes					
ID	**Family**	**Genus**	**Species & virus**	**Host**	**Method**	**Sample type**	**Location**	**Year of collection**	**Accession #**	**Reference**
J	*Polyomaviridae*	*Gammapolyomavirus*	*Pygoscelis adeliae polyomavirus 1* [Adelie penguin polyomavirus (AdPyV)]	Adélie penguins (*Pygoscelis adeliae*)	HTS-informed approach, genome recovered by abutting primers, cloned and Sanger sequenced.	Faeces	Cape Royds, Ross Island	2012/2013	KP033140	Varsani et al. (2015)
K		*unassigned*	*Trematomus pennellii polyomavirus 1* [Sharp-spined notothenia polyomavirus (SspPyV)]	Sharp spined notothen (*Trematomus pennellii*)	HTS-informed approach, genome recovered by abutting primers, cloned and Sanger sequenced.	Stomach and liver samples	Ross Sea	2012/2013	KP768176	Buck et al. (2016)
L		*Betapolyomavirus*	*Leptonychotes weddellii polyomavirus 1* [Weddell seal polyomavirus (WsPyV)]	Weddell seal (*Leptonychotes weddellii*)	HTS-informed approach, genome recovered by abutting primers, cloned and Sanger sequenced.	Kidney	Ross Sea	2014	KX533457	Varsani et al. (2017)
M	*Adenoviridae*	*Siadenovirus*	*Penguin siadenovirus A* [Chinstrap penguin adenovirus (CSPAdV)]	Chinstrap penguins (*Pygoscelis antarctica*)	PCR of protein VI and capsid protein hexon genes.	Lung, liver, kidney, heart, intestine, trachea samples	King George Island	2009/2010	KC593379–KC593386	Lee et al. (2014)
N			*Penguin siadenovirus A* [Chinstrap penguin adenovirus (CSPAdV)]	Chinstrap penguins (*Pygoscelis antarctica*)	RACE PCR, Sanger sequencing of whole genome.	Lung, liver, kidney, heart, intestine, trachea samples	King George Island	2008–2013	KP144329–KP144330	Lee et al. (2016)
O			*Penguin siadenovirus A* [Gentoo penguin adenvirus (GPAdV)]	Gentoo penguins (*Pygoscelis papua*)	RACE PCR, Sanger sequencing of whole genome.	lung, liver, kidney, heart, intestine, trachea, feces	King George Island	2008–2013	KP279746–KP279747	Lee et al. (2016)
P			*Skua siadenovirus A* [South polar skua adenovirus 1 (SPSAdV 1)]	South Polar skua (*Stercorarius maccormicki)*	Nested PCR, RACE PCR, Sanger sequencing of whole genome.	kidney	King George Island	2007–2009	HM585353 (full genome) JM585354-HM585358	Park et al. (2012)
Q	*Poxviridae*	*Parapoxvirus*	Unassigned [Seal poxvirus]	Weddell seal (*Leptonychotes weddellii*)	Electron microscopy, PCR of B2L gene, sequencing of B2L gene.	Neck skin lesion from a single seal	Queen Maud Land	2001	AJ622900	Tryland et al. (2005)
R	*Anelloviridae*	unassigned	Unassigned [Torque teno Leptonychotes weddelli virus 1,-2(TTLwV1 & TTLwV2)]	Weddell seal (*Leptonychotes weddellii*)	HTS-informed approach, genome recovered by abutting primers, cloned and Sanger sequenced.	Vaginal, nasal and faecal samples	Ross Sea	November-February 2014–2015	KY246479–KY246627	Fahsbender et al. (2017)
S			Unassigned [Torque teno Leptonychotes weddelli virus 1 (TTLwV1)	South Polar skua (*Stercorarius maccormicki*)	HTS-informed approach, genome recovered by abutting primers, cloned and Sanger sequenced.	Faecal sample	Ross Sea	November/ December 2014	KY246476–KY246478	Fahsbender et al. (2017)

cDNA: complementary DNA.
ELISA: Enzyme-linked immunosorbent assay.
PCR: Polymerase chain reaction.
HTS: High throughput sequencing.
RACE: Rapid Amplification of cDNA ends.
RT-PCT: Reverse transcription PCR.

and 2002, detected antibodies against several strains of avian influenza virus in South Polar skuas, southern giant petrels (*Macronectes giganteus*), and Adélie, chinstrap and gentoo penguins from various locations around the Antarctic Peninsula, Ross Island and East Antarctica (Table 1, Fig. 1) (Austin and Webster, 1993; Baumeister et al., 2004; Miller et al., 2008; Morgan and Westbury, 1981). Such research has indicated that influenza virus is highly widespread and prevalent in Antarctic birds. However, the pathogenicity of avian influenza virus in these populations is unknown. No genomic information for Influenza A viruses in Antarctic birds was available until Hurt et al. (2014) used HTS approaches to identify influenza A virus (H11N2) in Adélie penguins around the Antarctic Peninsula. A following study around the same area later identified the strain H5N5 among chinstrap penguins (Hurt et al., 2016).

None of the early studies have detected antibodies against influenza A virus strains in Antarctic pinnipeds, although several studies have looked at crabeater and Weddell seals (Austin and Webster, 1993; McFarlane, 2009).

3.2.2. Paramyxoviridae

Paramyxoviridae is a family of enveloped, non-segmented negative sense RNA viruses in the order *Mononegavirales* with genomes of ~15 kb. Paramyxoviruses are divided into seven genera: *Aquaparamyxovirus*, *Ferlavirus*, *Respirovirus*, *Morbillivirus*, *Rubulavirus*, *Henipavirus*, and *Avulavirus*. The genus *Avulavirus* includes of 13 formally classified species of avian paramyxoviruses including avian paramyxovirus 1 (AVPM-1) (Afonso et al., 2016). The genus *Morbillivirus* contains paramyxoviruses infecting mammals.

The majority of research on paramyxoviruses in Antarctica has been based on serological studies using haemagglutination inhibition assay to detect antibodies against paramyxoviruses in serum samples (Table 1). A high prevalence of antibodies to NDV in South Polar skuas has been reported (Miller et al., 2010), whereas low incidences have been found in Adélie and royal penguins around coastal Antarctica and Macquarie Island (Table 1, Fig. 1) (Morgan and Westbury, 1981, 1988). So far, king, gentoo and rockhopper penguin colonies on Macquarie Island have tested negative for AVPM-1 antibodies (Morgan et al., 1981).

Despite serology-based knowledge of these viruses among Antarctic birds, our understanding of their diversity is extremely limited due to the lack of available genomic data. Partial genome sequences of NDV in Adélie penguins has been obtained using HTS approaches (Thomazelli et al., 2010). Most recently, complete genome sequences of avian paramyxovirus 10 (APMV 10) and three novel avulaviruses (APMV 11, 12, 13) have been determined from rockhopper penguins on the Falkland Islands and gentoo penguins sampled on Kopaitic Island, northern tip of the Antarctic Peninsula (Table 1, Fig. 1) (Goraichuk et al., 2017; Neira et al., 2017).

With the use of sled dogs (*Canis familiaris*) during the early Antarctic expeditions, concern of morbillivirus infection among Antarctic pinnipeds drove research in monitoring for this virus in seal populations. Antibodies to canine distemper virus (CDV) have been reported in leopard and crabeater seals around the Antarctic Peninsula (Bengtson et al., 1991) and phocine distemper virus (PDV) in Weddell seals from Vestfold Hills, East Antarctica (McFarlane, 2009). With the exception of crabeater seals, both of these studies revealed low antibody titers against CDV and PDV. Several other studies looking at morbilliviruses in Antarctic seals have failed to detect any antibodies against these viruses (Harder et al., 1991; Osterhaus et al., 1988; Stenvers et al., 1992; Yochem et al., 2009). This may suggest morbilliviruses are not persistent in Antarctic seals or perhaps there are diverse morbilliviruses circulating amongst the pinnipeds that cannot be detected using conventional serology assays but likely to be identified using HTS approaches. Unlike avian paramyxoviruses, no genomic data are available for morbilliviruses from Antarctic seals and therefore impossible to tell if there was a spillover event from the canines to the pinnipeds. Sled dogs are no longer allowed in Antarctica.

3.3. Double stranded RNA viruses

3.3.1. Birnaviridae

Viruses in the family *Birnaviridae* have non-enveloped capsids that encapsidate two linear double stranded segments of RNA, each ~2.3–3 kb in length. Four genera have been established in this family: *Avibirnavirus*, *Aquabirnavirus*, *Blosnavirus* and *Entomobirnavirus* (Delmas et al., 2011). Infectious bursal disease virus is the only characterized virus belonging to genus *Avibirnavirus*. Since its initial identification as virus responsible for a highly infectious disease among chickens, infectious bursal disease virus (IBDV) has widely been isolated from other birds in the poultry industry including ducks and turkeys, however, disease has only been identified in chickens. Between 1995–2002 neutralization assays identified high titers of antibodies against IBDV in Adélie penguin at colonies around Mawson and Davis stations, and Terra Nova Bay, East Antarctica; and emperor penguin at the Auster, Amanda and Cape Washington colonies, also in East Antarctica (Table 1, Fig. 1) (Gardner et al., 1997; Watts et al., 2009). Highest seroprevalence has been detected among emperor penguin colonies with no difference between sampled locations or years (Watts et al., 2009). South Polar skuas around Vestold Hills and Davis Station, East Antarctica, have also had high titer of antibodies against IBDV (Miller et al., 2008; Watts et al., 2009), however, a significant difference in seroprevalence between sampling periods during 1999–2002 was observed. A low titer and prevalence of antibodies to IBDV has been detected in king penguins around Possession Island, among the Crozet Islands along the APF (Gauthier-Clerc et al., 2002). High-titers of IBDV neutralizing antibodies detected in distant populations of penguins and South Polar skua around Antarctica suggests it is unlikely IBDV was introduced through disposal of chicken products around Mawson Station as previously suggested by Gardner et al. (1997). Given that IBDV infection has been commonly detected in other wild avian populations (Hollmén et al., 2000; Kasanga et al., 2008; Ogawa et al., 1998), this virus may be naturally occurring among Antarctic birds (Watts et al., 2009). It is worth noting, however, that IBDV has yet to be isolated from Antarctic birds despite several studies detecting neutralizing antibodies. Therefore, it is difficult to address any questions about the diversity, evolution or transmission of this virus among Antarctic birds.

3.4. Double stranded DNA viruses

3.4.1. Adenoviridae

Adenoviruses are a family of non-enveloped double stranded DNA viruses with a genome length of ~26–45 kb. The diversification of these viruses is thought to have occurred through several animal hosts including mammals, reptiles, birds, fish and amphibians. The family *Adenoviridae* has been divided into five genera: *Mastadenovirus*, *Aviadenovirus*, *Atadenovirus*, *Siadenovirus*, *Ichtadenovirus* (Harrach et al., 2011).

Most adenovirus research has focused on the implications of human-associated adenoviruses, likely due to the known clinical significance in causing respiratory disease and gastroenteritis. However, the first adenoviruses from Antarctic animals have only recently been identified among South Polar skua (*Skua siadenovirus A*) (Park et al., 2012), as well as chinstrap, Adélie and gentoo penguins (*Penguin siadenovirus A*) (Table 2, Fig. 1) (Lee et al., 2014; Lee et al., 2016). This provides important insight to monitoring penguin health in Antarctica, as adenoviruses have been known to cause severe disease among animals.

Whole genomes for these adenoviruses were confirmed using HTS approaches and subsequent phylogenetic analyses of the genomic sequences provide support for the classification of the South Polar skua and penguin adenoviruses in the genus *Siadenovirus*. Despite this classification, penguin adenovirus genomes are unique in that they lack a putative sialidase gene that is characteristic of other genomes in this

genus (Lee et al., 2016).

It is likely that there exits adenoviruses associated with Antarctic seals based on the fact that adenoviruses has been identified in California sea lion (*Zalophus californianus*), Fur seals (*Arctocephalus* spp.) and South American sea lion (*Otaria flavescens*) (Chiappetta et al., 2017; Cortes-Hinojosa et al., 2016; Cortes-Hinojosa et al., 2015; Goldstein et al., 2011; Inoshima et al., 2013).

3.4.2. Herpesviridae

Herpesviridae is a large family of enveloped viruses with a linear, double stranded DNA genome about 120–240 kb in length. This family has been divided into three subfamilies (*Alphaherpesvirinae*, *Betaherpesvirinae* and *Gammaherpesvirinae*). Herpesviruses belonging to two species, based on partial genome sequencing of conserved regions, have been found among pinnipeds in the Northern Hemisphere (Harder et al., 1996): phocid alphaherpesvirus-1 (PhHV-1, species *Phocid alphaherpesvirus 1*) belonging to the *Varicellovirus* genus of the *Alphaherpesvirinae* subfamily and phocid gammaherpesvirus-2 (PhHV-2, *Phocid gammaherpesvirus 2*) belonging to the *Gammaherpesvirinae* subfamily. Both PhHV-1 and PhHV-2 have been identified in several non-Antarctic pinniped species around the world from free-ranging populations as well as captive populations in zoos and aquaria (Bellehumeur et al., 2016; Goldstein et al., 2004; Osterhaus et al., 1985).

Among Antarctic pinnipeds, herpesvirus has not been confirmed by molecular methods, however, several studies over the years have shown high levels of PhHV-1 neutralizing antibodies in Antarctic fur seals among sub-Antarctic islands, and Ross, Weddell and crabeater seals off East Antarctica (Table 1, Fig. 1) (Harder et al., 1991; Stenvers et al., 1992; Tryland et al., 2012). Thus, it is highly likely that herpesvirus is widespread and persistent among pinnipeds. However, genomic data is required to confirm this virus among Antarctic pinnipeds as the serological data has only indicated infection of a herpesvirus antigenically similar to PhHV-1.

3.4.3. Papillomaviridae

Papillomaviridae is a large family of non- enveloped, circular, double stranded DNA viruses with ~7–8 kb genomes and are known to infect skin, squamous and mucosal epithelial cells. All papillomavirus genomes have a very similar organization that can be divided into three regions encoding replication associated and regulatory proteins, structural proteins, and a long control region. While research on human papillomaviruses has been extensive due its clinical significance, relatively few studies have looked at non-human papillomaviruses. Papillomaviruses are found in a range of hosts including mammals, birds, reptiles and fish. It is a well-supported hypothesis that they have co-evolved with their hosts given their diversity and host specificity, with supporting phylogenetic analyses that track diversification of papillomaviruses to the evolution of their host (Bernard et al., 2010; de Villiers et al., 2004).

Two novel papillomavirus, Pygoscelis adeliae papillomavirus 1, −2 (PaPV1, −2), was recently identified in Antarctica from feces and cloacal swab of Adélie penguins at Cape Crozier, Ross Island (Table 2, Fig. 1) using a HTS-informed approach (Van Doorslaer et al., 2017; Varsani et al., 2014). PaPV1 and −2 are related to other avian papillomaviruses, PaPV1 has been assigned to the genus *Treisepsilonpapillomavirus* whereas PaPV2 is currently unclassified and shares ~64% genome-wide pairwise identity with PaPV1. These PaPVs are the first papillomaviruses to be discovered in Antarctic animals and are part of the few known avian papillomaviruses.

3.4.4. Polyomaviridae

Polyomaviruses represent a family of non-enveloped, circular, double-stranded DNA viruses with a genome length of 5–6 kb, and infect a range of hosts including mammals, birds, reptiles and fish. This family has four genera: *Alphapolyomavirus*, *Betapolyomavirus*, *Deltapolyomavirus*, and *Gammapolyomavirus* with three species unassigned to any of these (Moens et al., 2017; Polyomaviridae Study Group of the International Committee on Taxonomy of Viruses et al., 2016). Phylogenetic analyses have shown that avian polyomaviruses cluster together and have been classified under the genus *Gammapolyomavirus*. Avian polyomaviruses are known to cause inflammatory disease in birds, and can lead to disease of the skin and feathers and mortality in some species. The first polyomavirus identified in Antarctica was found in the feces of Adélie penguins at Cape Royds, Ross Island (Varsani et al., 2015) using a HTS-informed approach. Analysis of this genome shows that it falls in the avian polyomavirus lineage, representing a novel species (*Pygoscelis adeliae polyomavirus 1*).

Following this, two other polyomaviruses have been identified from Antarctic animals: a polyomavirus from the stomach of a sharp-spined notothen (*Trematomus pennellii*) (Buck et al., 2016) and most recently from the kidney of a Weddell seal, both sampled in the Ross Sea (Table 2, Fig. 1) (Varsani et al., 2017). The sharp-spined notothen polyomavirus is one of the three polyomaviruses to be identified associated with fish and all three were identified using HTS approaches (Buck et al., 2016).

Polyomavirus sequences have been identified in three other pinniped species: once in a captive Hawaiian monk seal (*Neomonachus schauinslandi*) (Cortes-Hinojosa et al., 2016), in the placenta of one northern fur seal (*Callorhinus ursinus*) (Duncan et al., 2013) from Alaska and a stranded free-ranging California sea lion (*Zalophus californianus*) (Colegrove et al., 2010). However, until recently the genome of California sea lion polyomavirus (CSLPyV) was the only confirmed pinniped polyomavirus. The recently identified Weddell seal polyomavirus is has been proposed to be classified as the species *Leptonychotes weddellii polyomavirus 1* (https://talk.ictvonline.org/files/proposals/animal_dna_viruses_and_retroviruses/m/animal_dna_ec_approved/6941).

3.4.5. Poxviridae

Poxviruses are a diverse family of double-stranded DNA viruses with a wide host range among vertebrates and arthropods (Skinner et al., 2011). Poxviruses have been extensively studied for their clinical significance in causing highly pathogenic disease among humans and other animals. While sealpox has yet to be formally classified, studies have identified this virus in populations of harbor seals (*Phoca vitulina*) (Muller et al., 2003), gray seals (*Halichoerus grypus*) (Nettleton et al., 1995), Stellar sea lions (*Eumetopias jubatus*), spotted seals (*Phoca largha*) (Bracht et al., 2006), and California sea lions (Nollens et al., 2006), causing severe proliferative lesions on the bodies of infected individuals. Partial sequencing has indicated seal poxvirus falls under the parapoxvirus family of which only four species have been classified.

The only case of poxvirus in Antarctica known to date has been the isolation and detection from a skin lesion of a deceased Weddell seal in Queen Maud Land, East Antarctica (Table 2, Fig. 1) (Tryland et al., 2005). Other Weddell seals in the area were analyzed for seal poxvirus, however, all individuals were negative, suggesting poxviruses may not prevalent in this population. Partial sequencing of the Weddell seal parapoxvirus shows it is closely related to harbor and grey seal poxviruses (Tryland et al., 2005).

Recently a seal parapoxvirus was sequenced using HTS from a skin lesion of a grey seal from the Baltic Sea (Gunther et al., 2017). While poxviruses have been identified in several avian species, very little is known about their diversity and host range. Using HTS technology a novel avipoxvirus genome has been sequenced from an African penguin (*Spheniscus demersus*) (Offerman et al., 2014). It is highly likely that poxviruses will also be recovered from Antarctic penguins through HTS.

3.5. Single stranded DNA viruses

3.5.1. Anelloviridae

Viruses in the family *Anelloviridae* are non-enveloped, circular single stranded DNA viruses with a genome length of about 2–3.9 kb (Biagini

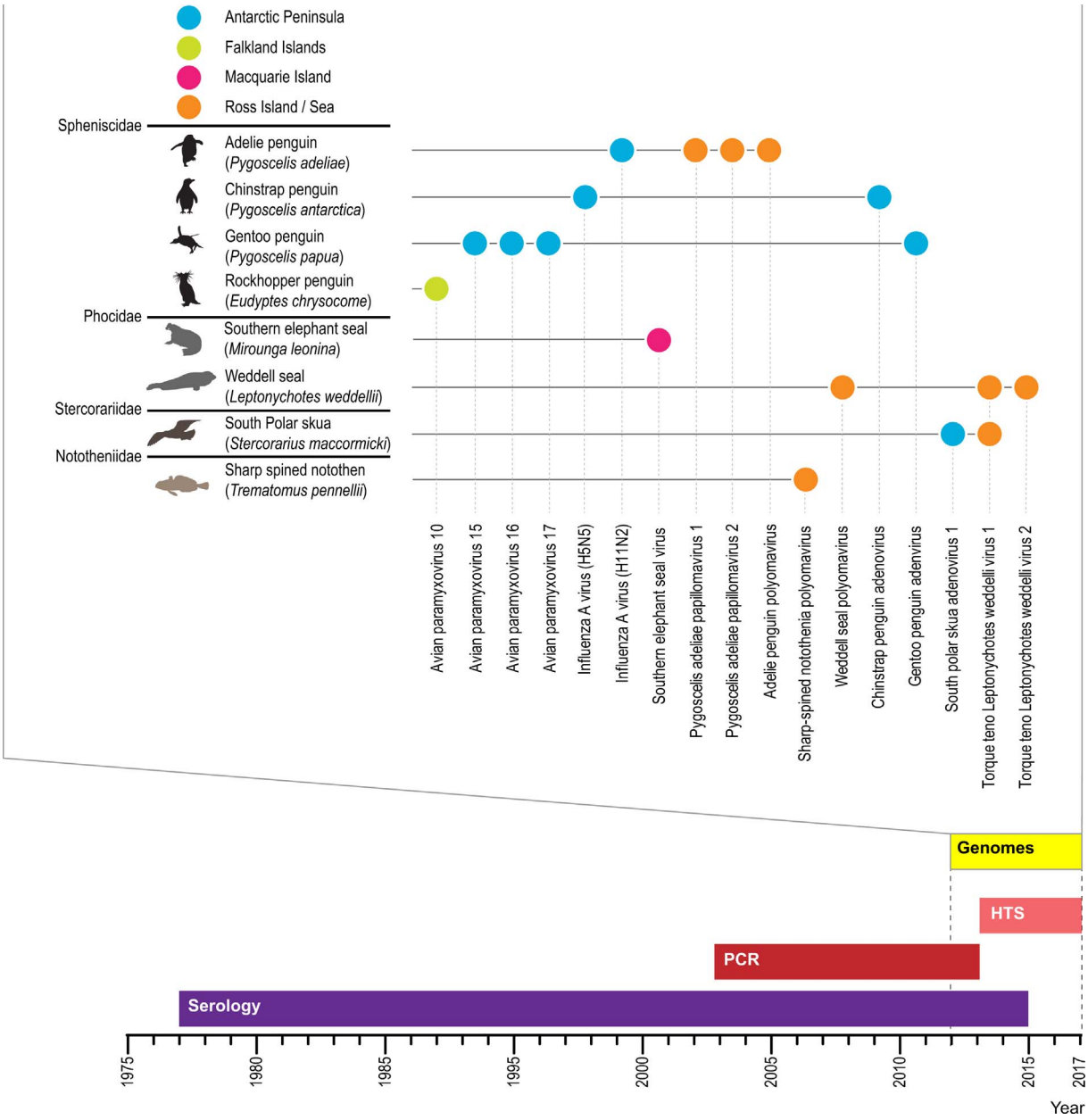

Fig. 2. Timeline,1975-2017 (present), showing the periods of serology- (purple), PCR- (red) and HTS-based (light red) approaches for viral identification. From 2012 onwards, viral genomes are determined by PCR-, Sanger- and HTS-based approaches. Top panel summarizes the determination of complete genomes by either Sanger sequencing and/or HTS from associated Antarctic animals. Colored circles indicating where they were found: Antarctic Peninsula (dark blue), Falkland Islands (green), Macquarie Island (pink) and Ross Island/sea (orange).

et al., 2011). These viruses have high sequence variability and are highly prevalent in the environment. Despite their ubiquitous nature, the significance of infection and pathogenicity remains unknown. While research has focused on their diversity and significance in humans, anelloviruses have been identified in non-human primates, domesticated animals, rodents and recently in marine mammals. Analysis of lung tissue from a captive California sea lion showing signs of respiratory disease led to discovery of the first anellovirus among pinnipeds, Zalophus californianus anellovirus (ZcAV) (Ng et al., 2009). Since then several novel anellovirus genomes have been recovered in harbor seals (Bodewes et al., 2015; Bodewes et al., 2013). In lung samples of deceased harbor seals along the North American Pacific coast anelloviruses were identified over multiple years demonstrating the persistence of this infection in the population (Ng et al., 2011). Analyses of sub-Antarctic (*Arctocephalus tropicalis*) and South American fur seal (*A. australis*) feces also led to the identification of anellovirus sequences (Kluge et al., 2016).

Anelloviruses circulating in the Antarctic ecosystem have recently been shown following detection by HTS and using pairs of abutting primers in the recovery of 152 genomes from vaginal, nasal and faecal samples of Weddell seals in the Ross Sea during the 2014–2015 summer (Fahsbender et al., 2017). Analyses identified two novel anelloviruses, torque teno Leptonychotes weddellii virus (TTLwV-1, TTLwV-2). T-TLwV-1 was additionally identified in South Polar skua faecal samples and it was thought that this was as a result of skuas feeding on the placenta and dead carcasses of Weddell seals in the area (Fahsbender et al., 2017).

4. Potential vectors of viruses associated with Antarctic wildlife

Both ecto- and endoparasites have been reported among Antarctic animals. While neither appear to be detrimental to animal health, these

organisms may play a significant role as vectors of viruses. Ticks, mites and lice commonly parasitize seals, penguins and other Antarctic birds (Gauthier-Clerc et al., 1998; González-Acuña et al., 2013; McFarlane, 1996). Flaviviruses, orbiviruses, phleboviruses, and nairoviruses have been isolated from seabird ticks (*Ixodes uriae*) associated with king, rockhopper and royal penguins on Macquarie Island (Major et al., 2009). A novel alphavirus has also been isolated and partially sequenced from lice associated with southern elephant seals of Macquarie Island and the high seroprevalence in the southern elephant seal population showed to this virus strongly suggests its transmission by lice (La Linn et al., 2001). Gastrointestinal parasites, particularly cestode and nematode species, are commonly found in Antarctic seals and penguins. Penguins tend to have a low diversity of parasites and similar profiles have been identified among penguins of the same genus (Diaz et al., 2016, 2013; Fonteneau et al., 2011; Kleinertz et al., 2014; Vidal et al., 2012). Of the Antarctic seals, gastrointestinal parasites are most prevalent among Weddell and leopard seals. Given that helminth parasites are strongly associated with the diet of the host they infect, this likely explains the higher abundance of parasites among Weddell and leopard seals compared to other Antarctic seals (McFarlane et al., 2009). The potential for endoparasites to transmit viruses to their host has been demonstrated by two genera of plant viruses, nepoviruses and tobraviruses, transmitted by nematodes (Hull, 2014). While our knowledge of parasites in Antarctic animals remains extremely limited and research in this area has been sporadic, developments in molecular technology will undoubtedly have a strong impact toward revealing relationships between organisms and the movement of viruses in the environment.

Recently, Antarctic penguins have been showing signs of disease of unknown pathology, e.g. unexplained incursions of feather loss in Adélie penguins (Grimaldi et al., 2015) in the Ross Sea (2011–2012) but not the years before or after (personal observation). Furthermore, in 2014 observations of an Adélie penguin colony at Hope Bay, Antarctica identified two chicks showing patches without feathers in two sub colonies (Barbosa et al., 2014). Beak and feather disease virus (family *Circoviridae*) infection in certain psittacines causes feather abnormalities and loss (Pass and Perry, 1984) and hence there is a likelihood that feather loss observed in penguins may be attributed to an unknown circovirus-like agent.

5. Concluding remarks and future directions

Over the last ten years, viral metagenomics has led to a dramatic increase in viral discovery from various environmental and animal samples, for example, Shi et al. (2016) identified ~1400 novel RNA viruses (from over 200 invertebrate species), Brum et al. (2015) identified ~5500 distinct dsDNA virus populations (from 43 surface ocean sites worldwide as part of the Tara Oceans expedition) and Paez-Espino et al. (2016) identified ~120000 partial viral genomes sequences (from ~3000 geographically diverse samples) using HTS. This together with other studies that have identified large datasets of novel viruses using HTS (e.g. Dayaram et al., 2016; Labonte and Suttle, 2013; Rosario et al., 2015) has shown: 1) the HTS enabled identification of large numbers of previously unknown viruses; 2) we have barely scratched the surface of the viral sequence space and thus their diversity; 3) new taxa will need to be created to classify viruses at a rapid rate to match the pace of virus discovery. All this has opened up discussions on viral classification based on sequence data, either derived from Sanger sequencing or HTS, and lead to a consensus statement by Simmonds et al. (2017a) to incorporate these into current viral taxonomy.

HTS has been used to a large extent in Antarctic environmental virology to study soil (Adriaenssens et al., 2017; Zablocki et al., 2014), lake (Aguirre de Cárcer et al., 2016; Lopez-Bueno et al., 2015, 2009; Yau et al., 2011) and marine (Brum et al., 2017; Miranda et al., 2016) viral ecology. Novel viral genomes from various soils and lake samples (Dziewit and Radlinska, 2016; Kerepesi and Grolmusz, 2017; Meiring et al., 2012; Swanson et al., 2012; Zawar-Reza et al., 2014) have been determined using HTS approaches. In contrast, relatively little is known about viruses associated with Antarctic animals and the associated virus ecology despite the advent of HTS. This perhaps can be attributed to the difficulty in accessing/obtaining animal samples and longitudinal sampling for viral ecology studies. Nonetheless, various studies have used HTS to identify viruses associated with Antarctic animals (Table 2, Fig. 2) and we anticipate that the next decade will see a dramatic increase in virology activity and to some extent viral ecology studies of Antarctic animals. Furthermore, it is highly like that large numbers of diverse viruses will be identified using HTS. As sequencing technologies improve, there may be possibility of in-field identification of animal viral pathogens in Antarctica, e.g. using Oxford Nanopore Sequencer (ONS). ONS has been used for metagenomic studies of microbial mats from three lakes in the Antarctic dry valleys (Lakes Fryxell, Lake Vanda and Lake Vida) by Johnson et al. (2017) demonstrating its use in Antarctic field conditions and remote laboratories.

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