

## Adenovirus Diversity in Fur Seal and Penguin Colonies of South America

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**ABSTRACT:** Adenoviruses are medium size non-enveloped viruses with a trend of coevolution with their hosts. We surveyed South American fur seals (*Arctocephalus australis*) and Humboldt penguins (*Spheniscus humboldti*) for adenoviruses at two sites from 2009 to 2012. Despite the common pattern of host specificity, some of the adenoviruses in our study were present in samples from unexpected host species. We identified mastadenoviruses, aviadenoviruses, and siadenoviruses in *A. australis* from Peru and Chile and in *S. humboldti* from Peru. The El Niño Southern Oscillation (ENSO) significantly reduces the productivity of the Humboldt upwelling system, which can change trophic and other ecological interactions, facilitating exposure to new pathogens. One aviadenovirus was detected in both the penguins and the fur seals, an interclass distance. This finding occurred only during the 2009 ENSO and not in 2010 or 2012. Further studies of viral diversity in sites with high-density mixed species populations are necessary to better understand viral evolution and the effect of environmental change on viral evolution and host specificity.

**Key words:** Adenovirus, *Arctocephalus australis*, Chile, El Niño, Humboldt penguin, Peru, Peruvian American fur seal.

The Humboldt Current upwelling system is one of the most productive marine ecosystems in the world, bringing cold, nutrient-rich water from the Antarctic to the west coast of South America (Gutierrez et al. 2016). This system supports diverse marine fauna in Peru and northern-central Chile (Alheit and Niquen 2004). In this region, the El Niño Southern Oscillation (ENSO) cycle results in changes in sea surface temperature, reducing upwelling and primary productivity in the

ocean. These changes have been associated with significant mortalities of apex predators, especially among juveniles (Soto et al. 2006).

The viruses of the family *Adenoviridae* are nonenveloped DNA viruses with high host specificity. Members of the genus *Mastadenovirus* are found in mammalian hosts, while the genus *Aviadenovirus* are found in avian hosts. Host jumping is rarely reported, with exceptions including canine adenovirus 1 (Park et al. 2007), Titi monkey adenovirus (Chen et al. 2011), and California sea lion adenovirus 1 (CSLAdV1; Cortés-Hinojosa et al. 2016). A study from Kohl and colleagues (2012) infers that canine adenoviruses originated from an ancient jump from bats, which could explain the aggressive clinical presentation in multiple carnivore hosts, including Eurasian river otters (*Lutra lutra*; Park et al. 2007). Hepatitis associated with CSLAdV1 has been reported in multiple pinniped species (Cortés-Hinojosa et al. 2016). A recent report of an aviadenovirus in pine marten (*Martes martes*), a terrestrial carnivore, using Next Generation Sequencing further expands the complexity of host jumping of adenoviruses (Walker et al. 2017).

South American fur seals (SAFSs; *Arctocephalus australis*) have an extensive range of distribution along both coasts of South America. A gap of more than 2000 km isolates the Peruvian subspecies found in Peru and northern Chile from the southern subspecies, which ranges from Guafó Island in northern Chilean Patagonia to Rio Grande do Sul in

Brazil (de Oliveira and Brownell 2014; Paves et al. 2016). Humboldt penguins (HPs; *Spheniscus humboldti*) have an overlapping range of distribution from Isla Foca in Peru to Guafo Island. Punta San Juan is one of the most critical breeding rookeries for both species (Mattern et al. 2004) and has been studied for years. Disease surveillance in SAFSs has detected several pathogens (Jankowski et al. 2015), but serology for adenoviruses has not been reported. Serologic testing for an adenovirus in HPs at the Peruvian site found 4/61 positive animals (Smith et al. 2008).

Adenoviruses are nonenveloped and thus more resistant to environmental conditions. Human adenoviruses can persist up to 384 days in groundwater and 77–85 days in seawater at 15 C (Enriquez et al. 1995; Ogorzaly et al. 2010). This environmental persistence results in high risk of exposure for animals, particularly in colonial species like SAFSs and HPs, which cohabit in high population densities. With high resource variability and dense reproductive populations of different species, the Peruvian site represents an ideal situation to evaluate adenoviral diversity and host jumping in a natural system.

We collected dry nasal swabs (2009–10) and paired nasal and fecal swabs (2011–12) placed in RNAlater (Thermo Fisher, Gaithersburg, Maryland, USA) from SAFSs. We collected 83 samples at Punta San Juan, Peru (15°22'S, 75°12'W) and 35 at Guafo Island, Chile (43°35'34.9"S, 74°42'48.53"W; Fig. 1 and Table 1). Additionally, dry swabs were collected from conjunctiva, choana, and cloaca of 81 HPs at the Peruvian site in 2011–12 (Table 1) and then stored at –80 C until extractions were carried out in a Maxwell 16 automated extractor (Promega, Madison, Wisconsin, USA). Adenoviruses were detected using a previously described PCR protocol for the DNA-dependent DNA polymerase gene (Wellehan et al. 2004). Host verification was carried out using PCR for the *cyclooxygenase 1* gene (Ward et al. 2005). Fragments of the expected size were sequenced using ABI 3130 DNA sequencers (Applied Biosystems, Foster City, California, USA). Bayesian and maxi-

mum likelihood phylogenetic analyses were carried out as previously described (Cortés-Hinojosa et al. 2015, 2016).

Several novel adenoviruses were identified, including five mastadenoviruses, four aviadenoviruses, and one siadenovirus in SAFSs, and three mastadenoviruses, two aviadenoviruses, and three siadenoviruses in HPs. One aviadenovirus and one siadenovirus were detected in both HPs and SAFSs in Peru (Table 1 and Supplementary Material Table S1). There are no previous reports of mastadenoviruses in birds or aviadenoviruses in marine mammals. The host *cyclooxygenase 1* gene sequence results confirmed that the adenovirus positive samples corresponded to the host species from which the sample had been taken.

Chi-square analyses revealed statistically significant differences in the prevalence of aviadenoviruses ( $P=0.002$ ), but not mastadenoviruses ( $P=0.67$ ), in Peruvian SAFS pups between 2009 and 2010. Increased adenoviral pathogenicity occurs with high host densities and immunosuppressed hosts and when stressful conditions exist (Sanchez et al. 2015). The Humboldt Current along the Pacific coast of Peru and Chile supports an extremely high density of marine wildlife, but it is periodically disrupted by naturally occurring ENSO, creating stressful conditions for marine predators (Trillmich and Limberger 1985).

We detected four aviadenoviruses in SAFS pups (SAFS-Avia1 to 4) in 2009 during an ENSO event. One of these novel aviadenoviruses (SAFS-Avia2) was detected in three SAFS nasal swabs and 22 HP samples. Given that aviadenoviruses are usually found in avian hosts, and this virus was found in HPs with greater prevalence than any other adenovirus, the HP is the most likely endemic host for this virus (Table 1). The other three SAFS aviadenoviruses were detected solely in SAFSs and, given that we did not find them in HPs, are most likely endemic in other sympatric avian hosts, such as *Sula variegata*, *Pelecanus thagus*, or *Phalacrocorax bougainvillii*, which were not surveyed. Lack of primary prey species caused by ENSO may cause shifts toward avian predation or co-

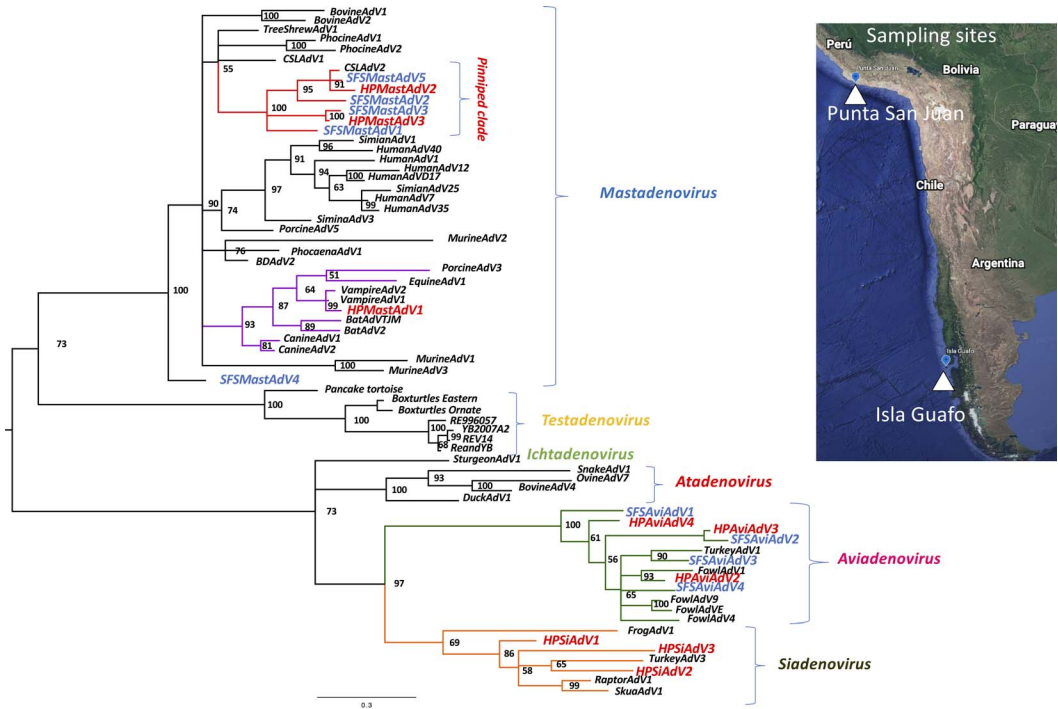


FIGURE 1. Bayesian analysis phylogram depicting the relationship of the novel adenoviruses from Humboldt penguins (*Spheniscus humboldti*) and South American fur seals (*Arctocephalus australis*) sampled at two sites in Peru, 2009–12, to representatives from each of the genera in the family *Adenoviridae*, based on partial amino acid sequences for the adenoviral DNA-dependent DNA polymerase gene (93 AA characters including gaps and poorly aligned sequence) using the LG+G model of evolution. Numbers at each node represent the posterior probability. Branch lengths are based on the number of inferred substitutions, as indicated by the scale (accession numbers for adenoviruses used in this figure are located in Supplementary Material Table S1). Each adenovirus genus is indicated by brackets; novel penguin adenoviruses start with “HP” in the label, and novel SAFS adenoviruses start with “SFS” in the label. Figure shows South America with each sample site indicated with a white triangle.

prophagy in SAFSs. Though SAFSs do not generally prey on birds, avian predation is reported in other pinniped species (Rogers and Bryden 1995). Direct transmission through contact with seabird guano is also possible. No aviadenoviruses were detected in samples of SAFSs from the Chilean site, where several bird species interact closely with fur seal pups (Seguel et al. 2017). This finding may be related to sample collection occurring during non-ENSO years, and because this colony is located at a southern latitude where ENSO impact on the environment is milder, further study is needed to investigate this (Gutierrez et al. 2016).

The most common mastadenovirus, SAFS-Masta2, was sequenced in both Peruvian and

Chilean SAFS populations. However, SAFS-Masta1, 3, and 5 were present only at the Peruvian site, and SAFS-Masta4 only at in the Chilean site (Table 1). This difference in adenovirus distribution could indicate limited pathogen flow between SAFS populations, which may be due to the 2000 km gap in the distribution range between subspecies, unlike HPs, which have a continuous population across this range. Future analyses of more variable regions of SAFS-Masta2 may help clarify the evolutionary history of SAFSs.

Three mastadenoviruses were detected in HPs (HP-Masta1 to 3). Both HP-Masta2 and HP-Masta3 cluster in a pinniped host clade, consistent with crossovers from a pinniped to HPs; however, we did not detect either HP-

TABLE 1. Findings of adenoviruses from Humbolt penguins (*Spheniscus humboldti*) and South American fur seals (*Arctocephalus australis*) sampled at two sites in Peru, 2009–12, showing locations and years of sampling. Adenoviruses were detected with PCR.<sup>a</sup>

Virus (sample type)	Peru 2009 (SAFS n=30)	Peru 2010 (SAFS n=30)	Peru 2011 (HP n=48)	Chile 2011 (SAFS n=35)	Peru 2012 (SAFS n=23, HP n=33)
SAFS-Masta1 (resp.)	1	0	0	0	1 SAFS
SAFS-Masta2 (resp. and fecal)	0	2	0	9	0
SAFS-Masta3 (resp.)	1	2	0	0	1 SAFS
SAFS-Masta4 (resp.)	0	0	0	1	0
SAFS-Masta5 (fecal)	0	0	0	0	1 SAFS
SAFS-Avia1 (resp.)	5	0	0	0	0
SAFS Avia2 (resp.)–HP-Avia1 (mix)	3	0	13	0	9 HPs
SAFS-Avia3 (resp.)	1	0	0	0	0
SAFS-Avia4 (resp.)	1	0	0	0	0
HP-Masta1 (mix)	—	—	1	—	2 HPs
HP-Masta2 (mix)	—	—	1	—	0
HP-Masta3 (mix)	—	—	2	—	0
HP-Avia2 (mix)	—	—	1	—	2 HPs
HP-Avia3 (fecal)	—	—	0	—	3 HPs
HP-Avia4 (fecal)	—	—	0	—	1 HP
HP-Sia1 (mix)	—	—	1	—	2 HPs
HP-Sia2 (mix)	—	—	3	—	6 HPs, 1 SAFS
HP-Sia3 (mix)	—	—	1	—	0

<sup>a</sup> SAFS = South America fur seal; HP = Humbolt penguin; resp. = choanal (HP) or nasal swab (SAFS); fecal = cloacal (HP) or rectal swab (SAFS); mix = conjunctival-choanal-cloacal swab; — = no data.

Masta2 or HP-Masta3 in SAFSs. Interestingly, HP-Masta1 clusters in a canine-horse-bat host clade. Vampire bat (*Desmodus rotundus*) feeding on HP chicks has been reported (Luna-Jorquera and Culik 1995). *Desmodus rotundus* adenovirus 1 and 2 (Lacoste et al. 2017) are the closest relatives of HP-Masta1, with sequence homologies of 96% and 94%, respectively, and strong phylogenetic support (Fig. 1 and Supplementary Material Fig. S1) suggests that HP Mastadenovirus-1 may represent a host jump from *D. rotundus*. Exposure of HPs to *D. rotundus* feces is also plausible, particularly by HPs nesting in burrows frequented by bats.

Birds are common hosts for siadenoviruses and aviadenoviruses; we detected two siadenoviruses and three aviadenoviruses in HPs. In addition, we detected a siadenovirus in one SAFS fecal sample, supporting the hypothesis of HP predation by SAFSs (Table 1).

Our data also provide insight into the evolution of adenoviruses in Carnivora. Our

Bayesian analysis shows four possible independent lineages of pinniped adenoviruses. The first lineage includes only CSLAdV1, clustering outside of a canine-bat-equine clade. A second pinniped clade includes most otariid adenoviruses, herein called the “Pinniped clade.” A third clade includes the two known phocid adenoviruses (Phocine adenovirus 1 and 2). SAFS-Masta4 represents a possible fourth clade at the root of the genus *Mastadenovirus* (Fig. 1). Our maximum likelihood analysis does not resolve this pattern clearly, most likely due to poor resolution (Supplementary Material Fig. S1). We detected a low GC% content in most pinniped adenoviruses, which has been hypothesized to correlate with host jumping events in other virus/host systems (Wellehan et al. 2004). Further analyses, including sequence data from Brazil (Chiappetta et al. 2017), more genes, and molecular clock calibration, may help to clarify the history of pinniped adenoviruses. Future studies should include

disease correlations and histologic examination, as well as long-term data sets that include several sample seasons with data from multiple ENSO.

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#### SUPPLEMENTARY MATERIAL

Supplementary material for this article is online at <http://dx.doi.org/10.7589/JWD-D-20-00118>.

#### LITERATURE CITED

- Alheit J, Niquen M. 2004. Regime shifts in the Humboldt Current ecosystem. *Prog Oceanogr* 60:201–222.
- Chen EC, Yagi S, Kelly KR, Mendoza SP, Tarara RP, Canfield DR, Maninger N, Rosenthal A, Spinner A, Bales KL, et al. 2011. Cross-species transmission of a novel adenovirus associated with a fulminant pneumonia outbreak in a New World monkey colony. *PLoS Pathog* 7:e1002155.
- Chiappetta CM, Cibulski SP, Lima FES, Varela APM, Amorim DB, Tavares M, Roehle PM. 2017. Molecular detection of circovirus and adenovirus in feces of fur seals (*Arctocephalus* spp.). *EcoHealth* 14:69–77.
- Cortés-Hinojosa G, Doescher B, Kinsel M, Lednicky J, Loeb J, Waltzek T, Wellehan JFX Jr. 2016. Coinfection of California sea lion adenovirus 1 and a novel polyomavirus in Hawaiian monk seal (*Neomonachus schauinslandi*). *J Zoo Wildl Med* 47:427–437.
- Cortés-Hinojosa G, Gulland FMD, Goldstein T, Venn-Watson S, Rivera R, Waltzek TB, Salemi M, Wellehan JF Jr. 2015. Phylogenomic characterization of California sea lion adenovirus-1. *Infect Genet Evol* 31:270–276.
- De Oliveira L, Brownell R. 2014. Taxonomic status of two subspecies of South American fur seals: *Arctocephalus australis australis* vs. *A. a. gracilis*. *Marine Mammal Sci* 30:1258–1263.
- Enriquez CE, Hurst CJ, Gerba CP. 1995. Survival of the enteric adenoviruses 40 and 41 in tap, sea, and waste water. *Water Res* 29:2548–2553.
- Gutierrez O, Panario D, Nagy G, Bidegain M, Montes C. 2016. Climate teleconnections and indicators of coastal systems response. *Ocean Coast Manag* 122: 64–76.
- Jankowski G, Adkesson M, Saliki J, Cardenas-Alayza S, Majluf P. 2015. Survey for infectious disease in the South American fur seal (*Arctocephalus australis*) population at Punta San Juan, Peru. *J Zoo Wildl Med* 46:246–254.
- Kohl C, Vidovsky M, Muhldorfer K, Dabrowski P, Radonic A, Nitsche A, Wibbelt G, Kurth A, Harrach B. 2012. Genome analysis of bat adenovirus 2: Indications of interspecies transmission. *J Virol* 86: 1888–1892.
- Lacoste V, Salmier A, Tirera S, Franc A, Darcissac E, Donato D, Bouchier C, Lavergne A, Thoisy BD, Forrester N. 2017. Virome analysis of two sympatric bat species (*Desmodus rotundus* and *Molossus molossus*) in French Guiana. *PLoS One* 12:e0186943.
- Luna-Jorquiera G, Culik BM. 1995. Penguins bled by vampires. *J Ornithol* 136:471–472.
- Mattern T, Ellenberg U, Luna-Jorquiera G, Davis LS. 2004. Humboldt penguin census on Isla Chañaral, Chile: Recent increase or past underestimate of penguin numbers? *Waterbirds* 27:368–376.
- Ogorzaly L, Bertrand I, Paris M, Maul A, Gantzer C. 2010. Occurrence, survival, and persistence of human adenoviruses and F-specific RNA phages in raw groundwater. *Appl Environ Microbiol* 76:8019–8025.
- Park N, Lee M, Kurkure N, Cho H. 2007. Canine adenovirus type 1 infection of a Eurasian river otter (*Lutra lutra*). *Vet Pathol* 44:536–539.
- Paves H, Schlatter R, Franco-Trecu V, Paez E, Sielfeld W, Araos V, Giesecke R, Batalles L, Cappozzo H. 2016. Breeding season of the South American fur seal (*Arctocephalus australis*, Otariidae: Carnivora): New data for establishing independent evolutionary histories? *Rev Biol Mar Oceanogr* 51:241–253.
- Rogers T, Bryden MM. 1995. Predation of Adelie penguins (*Pygoscelis adeliae*) by leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Antarctica. *Canad J Zool* 73:1001–1004.
- Sanchez JL, Cooper MJ, Myers CA, Cummings JF, Vest KG, Russell KL, Sanchez JL, Hiser MJ, Gaydos CA. 2015. Respiratory infections in the U.S. military: Recent experience and control. *Clin Microbiol Rev* 28:743–800.
- Seguel M, Muñoz F, Montalva F, Perez-Venegas D, Pavés H, Gottdenker N. 2017. Kelp and dolphin gulls cause perineal wounds in South American fur seal pups

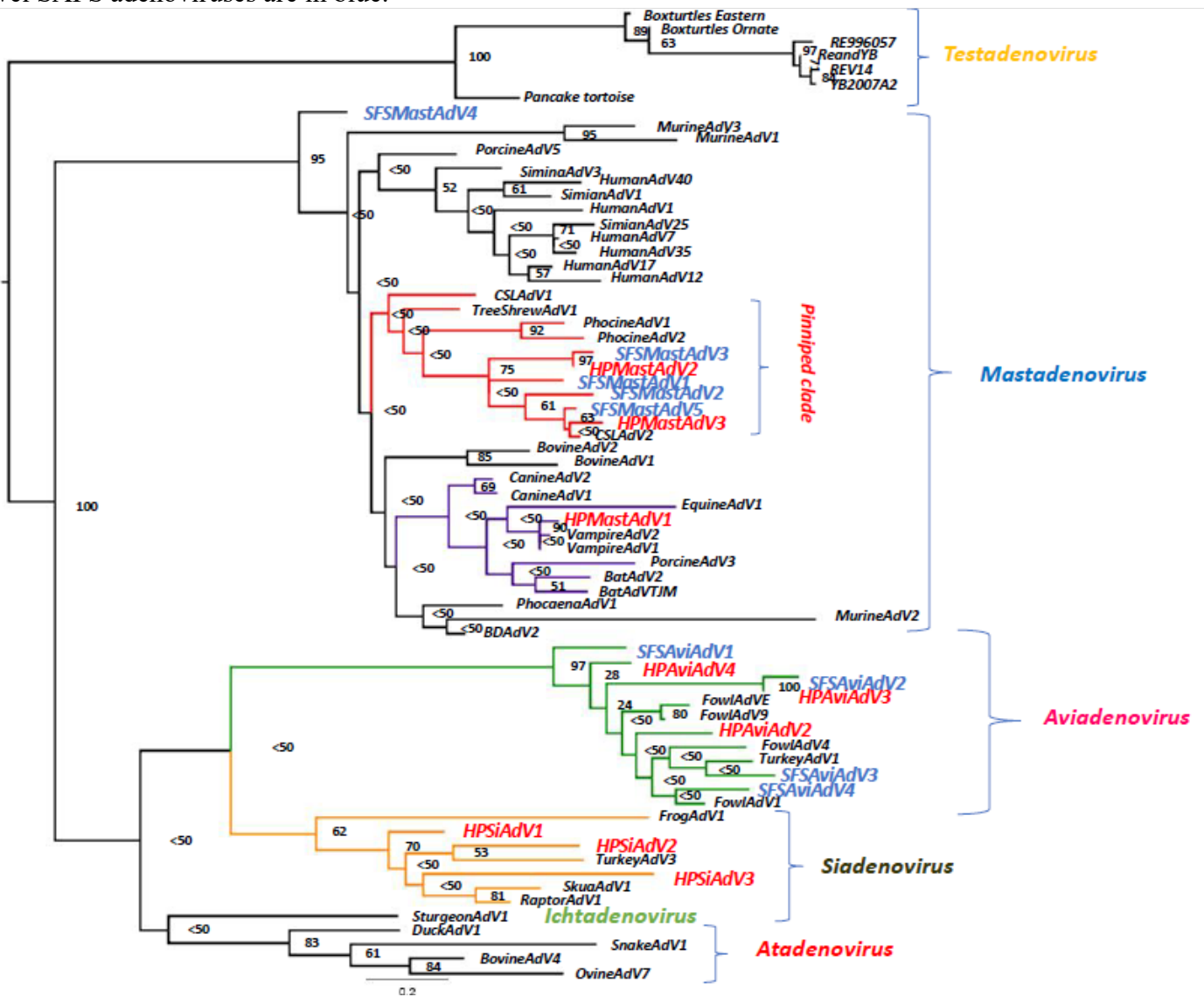
- (*Arctocephalus australis*) at Guafo Island, Chilean Patagonia. *R Soc Open Sci* 4:170638.
- Smith KM, Karesh WB, Majluf P, Paredes R, Zavalaga C, Reul AH, Stetter M, Braselton WE, Puche H, Cook RA. 2008. Health evaluation of free-ranging Humboldt penguins (*Spheniscus humboldti*) in Peru. *Avian Dis* 52:130–135.
- Soto K, Trites A, Arias-Schreiber M. 2006. Changes in diet and maternal attendance of South American sea lions indicate changes in the marine environment and prey abundance. *Mar Ecol Progr Series* 312:277–290.
- Trillmich F, Limberger D. 1985. Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia* 67:19–22.
- Walker D, Gregory WF, Turnbull D, Rocchi M, Meredith AL, Philbey AW, Sharp CP. 2017. Novel adenoviruses detected in British mustelids, including a unique Aviadenovirus in the tissues of pine martens (*Martes martes*). *J Med Microbiol* 66:1177–1182.
- Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PD. 2005. DNA barcoding Australia's fish species. *Philos Trans R Soc Lond B Biol Sci* 360:1847–1857.
- Wellehan JF, Johnson AJ, Harrach B, Benkő M, Pessier AP, Johnson CM, Garner MM, Childress A, Jacobson ER. 2004. Detection and analysis of six lizard adenoviruses by consensus primer PCR provides further evidence of a reptilian origin for the atadenoviruses. *J Virol* 78:13366–13369.

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**Supplemental Figure 1.** Maximum Likelihood analysis phylogram depicting the relationship of novel adenoviruses from Humboldt penguins (*Spheniscus humboldti*) and South American fur seals (*Arctocephalus australis*) in Chile and Peru to representatives from each of the genera in the family *Adenoviridae*, based on partial amino acid sequences for the adenoviral DNA-dependent DNA polymerase gene (93 AA characters including gaps and poorly aligned sequence) using the LG+G model of evolution. Numbers at each node represent the posterior bootstrap values for ML. Branch lengths are based on the number of inferred substitutions, as indicated by the scale (accession number for adenoviruses used in this figure are located on Table S1). Each adenovirus genus is represented by a distinct color; novel penguin adenoviruses are in red and novel SAFS adenoviruses are in blue.



**Table S1:** List of adenoviruses with Genbank accession number and its corresponding host used for phylogenetic analysis.

	Genbank number	Abbreviation	Host genus	Host species	Host's common name
<b>MASTADENOVIRUS</b>					
Bat adenovirus 2	JN252129.1	BatAdV2	<i>Pipistrellus</i>	<i>pipistrellus</i>	bat
Bat adenovirus TJM	NC_016895.1	BatAdVTJM	<i>Myotis</i>	<i>ricketti</i>	bat
Bovine adenovirus 1	NC_006324.1	BovineAdV1	<i>Bos taurus</i>	<i>taurus</i>	cattle
Bovine adenovirus 2	AC_000001.1	BvineAdV2	<i>Bos taurus</i>	<i>taurus</i>	cattle
Bottlenose dolphin adenovirus 2	ALE15295	BDAdV2	<i>Zalophus</i>	<i>californianus</i>	Bottlenose dolphin
California Sea Lion adenovirus 1	KJ 563221	CSLAdV1	<i>Zalophus</i>	<i>californianus</i>	California sea lion
Canine adenovirus 1	Y07760.1	CanineAdV1	<i>Canis</i>	<i>lupus familiaris</i>	domestic dog
Canine adenovirus 2	U77082.1	CanineAdV2	<i>Canis</i>	<i>lupus familiaris</i>	domestic dog
<i>Desmodus rotundus</i> Adenovirus 1	AOS88389.1	VampyreAdV1	<i>Desmodus</i>	<i>rotundus</i>	vampyre bat
<i>Desmodus rotundus</i> Adenovirus 2	AOS88398.1	VampyreAdV2	<i>Desmodus</i>	<i>rotundus</i>	vampyre bat
Equine adenovirus 1	JN418926	EquineAdV1	<i>Homo</i>	<i>sapiens</i>	humans
Human adenovirus 1	AC_000017.1	HumanAdV1	<i>Homo</i>	<i>sapiens</i>	humans
Human adenovirus 35	AC_000019	HumanAdV35	<i>Homo</i>	<i>sapiens</i>	humans
Human adenovirus 7	AC_000018.1	HumanAdV7	<i>Homo</i>	<i>sapiens</i>	humans
Human adenovirus 12	X73487.1	HumanAdV12	<i>Homo</i>	<i>sapiens</i>	humans
Human adenovirus 17	AF108105.1	HumanAdV17	<i>Homo</i>	<i>sapiens</i>	humans
Human adenovirus 40	L19443	HumanAdV40	<i>Homo</i>	<i>sapiens</i>	humans
Humboldt penguin adenovirus 1	MF175108	HPMastaAdV1	<i>Spheniscus</i>	<i>humboldti</i>	penguin
Humboldt penguin adenovirus 2	MF175109	HPMastaAdV2	<i>Spheniscus</i>	<i>humboldti</i>	penguin
Humboldt penguin adenovirus 3	MF175110	HPMastaAdV3	<i>Spheniscus</i>	<i>humboldti</i>	penguin
Murine adenovirus 2	NC_014899.1	MurineAdV2	<i>Mus</i>	<i>musculus</i>	house mice
Murine adenovirus 3	NC_012584.1	MurineAdV3	<i>Apodemus</i>	<i>agrarius</i>	striped field mouse
Murine adenovirus 1	NC_000942	MurineAdV1	<i>Mus</i>	<i>musculus</i>	house mice
Otarine adenovirus 2	AFS90825.1	(CSLAdV2)	<i>Zalophus</i>	<i>californianus</i>	California sea lion
Phocoena adenovirus 1	AEP16404.1	PhocoenaAdV1	<i>Phocoena</i>	<i>phocoena</i>	harbour porpoise
Phocine adenovirus 1	AFS90827.1	PhocineAdV1	<i>Phoca</i>	<i>vitulina richardsi</i>	harbour seal
Phocine adenovirus 2	AFS90828.1	PhocineAdV2	<i>Phoca</i>	<i>vitulina richardsi</i>	harbour seal
Porcine adenovirus 3	AF083132	PorcineAdV3	<i>Sus</i>	<i>scrofa</i>	pig
Porcine adenovirus 5	AF289262.1	PorcineAdV5	<i>Sus</i>	<i>scrofa</i>	pig
Simian adenovirus 1	NC_006879.1	SimianAdV1	<i>Macaca</i>	<i>fascicularis</i>	cynomolgus monkey
Simian adenovirus 3	NC_006144.1	SimianAdV3	<i>Macaca</i>	<i>mulatta</i>	rhesus monkey
Simian adenovirus 25	AC_000011.1	SimianAdV25	<i>Macaca</i>	<i>mulatta</i>	rhesus monkey
South American fur seal adenovirus 1	MF175103	SFSMastaAdV1	<i>Arctocephalus</i>	<i>australis</i>	South American fur seal
South American fur seal adenovirus 2	MF175104	SFSMastaAdV2	<i>Arctocephalus</i>	<i>australis</i>	South American fur seal
South American fur seal adenovirus 3	MF175105	SFSMastaAdV3	<i>Arctocephalus</i>	<i>australis</i>	South American fur seal



South American fur seal adenovirus 4	MF175106	SFSMastaAdV4	<i>Arctocephalus</i>	<i>australis</i>	South American fur seal
South American fur seal adenovirus 5	MF175107	SFSMastaAdV5	<i>Arctocephalus</i>	<i>australis</i>	South American fur seal
Tree shrew adenovirus 1	AF258784.1	ShrewAdVA	<i>Tupaia</i>	<i>spp</i>	Tree shrew
<b>ATADENOVIRUS</b>					
Bovine adenovirus 4	AF036092	BovineAdV4	<i>Bos taurus</i>	<i>taurus</i>	cattle
Duck adenovirus 1	AC_000004.1	DuckAdV1			duck and quail
Ovine adenovirus 7	U40839	OvineAdV7	<i>Ovis</i>	<i>aries</i>	sheep
Snake adenovirus 1	NC_009989.1	SnakeAdV1	<i>Pantherophis</i>	<i>guttatus</i>	corn snake
<b>AVIADENOVIRUS</b>					
Fowl adenovirus 1	NC_001720.1	FowlAdV1			multiple avian species
Fowl adenovirus 4	NC_015323	FowlAdV4			multiple avian species
Fowl adenovirus 9	AF083975	FowlAdV9			multiple avian species
Fowl adenovirus 8	NC_014969.1	FowlAdVE			multiple avian species
Humboldt penguin adenovirus 4	MF175115	HPAviadeno2	<i>Spheniscus</i>	<i>humboldti</i>	Humboldt penguin
Humboldt penguin adenovirus 5	MF175116	HPAviadeno3	<i>Spheniscus</i>	<i>humboldti</i>	Humboldt penguin
Humboldt penguin adenovirus 6	MF175117	HPAviadeno4	<i>Spheniscus</i>	<i>humboldti</i>	Humboldt penguin
South American fur seal adenovirus 6	MF175111	SFSAviadeno1	<i>Arctocephalus</i>	<i>australis</i>	South American fur seal/ Humboldt penguin
South American fur seal adenovirus 7	MF175112	SFSAviadeno2	<i>Arctocephalus</i>	<i>australis</i>	South American fur seal
South American fur seal adenovirus 8	MF175113	SFSAviadeno3	<i>Arctocephalus</i>	<i>australis</i>	South American fur seal
South American fur seal adenovirus 9	MF175114	SFSAviadeno4	<i>Arctocephalus</i>	<i>australis</i>	South American fur seal
Turkey adenovirus 1	NC_014564	TurkeyAdV1	<i>Meleagris</i>	<i>gallopavo</i>	turkey
<b>SIADENOVIRUS</b>					
Frog adenovirus 1	AF224336	FrogAdV1	<i>Rana</i>	<i>pipiens</i>	leopard frog
Humboldt penguin adenovirus 7	MF175118	HPSiadeno1	<i>Spheniscus</i>	<i>humboldti</i>	Humboldt penguin
Humboldt penguin adenovirus 8	MF175119	HPSiadeno2	<i>Spheniscus</i>	<i>humboldti</i>	Humboldt penguin
Humboldt penguin adenovirus 9	MF175120	HPSiadeno3	<i>Spheniscus</i>	<i>humboldti</i>	Humboldt penguin
Raptor adenovirus 1	NC_015455	RaptorAdV1			raptors
Turkey adenovirus 3	NC_001958	TurkeyAdV3	<i>Meleagris</i>	<i>gallopavo</i>	turkey
<b>TESTADENOVIRUS</b>					
Eastern Box turtle adenovirus	AFP53937.1	Box turtles Eastern	<i>Terrapene</i>	<i>carolina carolina</i>	eastern box turtle
Box turtle adenovirus 1	ACJ09760.1	Boxturtles Ornate	<i>Terrapene</i>	<i>ornata ornata</i>	box turtle
Pancake tortoise adenovirus	AFP53933.1	Pancake_Tortoise	<i>Malacochersus</i>	<i>tornieri</i>	pancake tortoise
Red eared slider adenovirus	AFP53938.1	RE996057	<i>Trachemys</i>	<i>scripta elegans</i>	red eared slider
Red eared slider adenovirus	AGA95497.1	REV14	<i>Trachemys</i>	<i>scripta elegans</i>	red eared slider
Red eared slider adenovirus	AFP53935.1	REandYB	<i>Trachemys</i>	<i>scripta</i>	red eared and yellow-bellied sliders
Yellow-bellied slider adenovirus	AFP53931.1	YB2007A2	<i>Trachemys</i>	<i>scripta scripta</i>	yellow-bellied slider

ICHTADENOVIRUS					
White sturgeon adenovirus 1		SturgeonAdV1	<i>Acipenser</i>	<i>transmontanus</i>	white sturgeon