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Full genome analysis of a novel adenovirus from the South Polar skua (Catharacta maccormicki) in Antarctica

Yon Mi Park a, Jeong-Hoon Kim b, Se Hun Gu a, Sook Young Lee a, Min-Goo Lee c, Yoon Kyoo Kang d, Sung-Ho Kang b, Hak Jun Kim b, c, Jin-Won Song a,⁎

a Department of Microbiology, College of Medicine, Korea University, 5-ga, Anam-dong, Seongbuk-gu, Seoul 136-705, Republic of Korea
b Korea Polar Research Institute, Incheon 406-840, Republic of Korea
c Department of Physiology, College of Medicine, Korea University, 5-ga, Anam-dong, Seongbuk-gu, Seoul 136-705, Republic of Korea
d Department of Physical Medicine & Rehabilitation, College of Medicine, Korea University Anam Hospital, 5-ga, Anam-dong, Seongbuk-gu, Seoul 136-705, Republic of Korea
e Department of Polar Sciences, University of Science and Technology, Incheon 406-840, Republic of Korea

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A B S T R A C T

Adenoviruses have been identified in humans and a wide range of vertebrate animals, but not previously from the polar region. Here, we report the entire 26,340-bp genome of a novel adenovirus, detected by PCR, in tissues of six of nine South Polar skuas (Catharacta maccormicki), collected in Lake King Sejong, King George Island, Antarctica, from 2007 to 2009. The DNA polymerase, penton base, hexon and fiber genes of the South Polar skua adenovirus (SPSAdV) exhibited 68.3%, 75.4%, 74.9% and 48.0% nucleotide sequence similarity with their counterparts in turkey hemorrhagic enteritis virus. Phylogenetic analysis based on the entire genome revealed that SPSAdV belonged to the genus Ichtadenovirus, family Adenoviridae. This is the first evidence of a novel adenovirus, SPSAdV, from a large polar seabird (family Stercorariidae) in Antarctica.

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Introduction

Adenoviruses have linear, non-segmented, double-stranded DNA genomes, which range between 26 and 43 kb and are generally characteristic of each genus (Davison et al., 2003; Klempa et al., 2009; Kovács and Benkö, 2011; Mase et al., 2009).

The family Adenoviridae is comprised of five genera: Mastadenovirus, Aviadenovirus, Atadenovirus, Siadenovirus and Ichtadenovirus (Houng et al., 2006; Kovács and Benkö, 2011; Kovács et al., 2010; Lehmkuhl and Hobbs, 2008; Wellehan et al., 2004), which infect a wide range of vertebrate species (Davison et al., 2003; Morrison et al., 1997). Mastadenovirus has been identified in mammals, including human, sea lion, canine, bovine, porcine, murine and bat (Aggarwal and Mittal, 2000; Goldstein et al., 2011; Klempa et al., 2009; Kovács et al., 2004; Li et al., 2010; Morrison et al., 1997; Rux and Burnett, 2004). Aviadenovirus contains falcon and other fowl adenoviruses (Davison et al., 2000). Atadenovirus has been found in snake, marsupial and ruminants (Dan et al., 1998; Farkas et al., 2008; Thomson et al., 2002). Siadenovirus has been detected in frog, raptor and turkey (Beach et al., 2009; Davison and Harrach, 2002; Davison et al., 2000; Kovács and Benkö, 2009). A new genus, Ichtadenovirus, has been identified recently in fish (Benkö et al., 2005).

Typically, adenovirus infection in most species is characterized by enteritis and respiratory disease (Beach et al., 2009; Russell, 2009; Rux and Burnett, 2004; Schrenzel et al., 2005). However, other clinical manifestations have been observed. For example, turkey hemorrhagic enteritis virus (THEV) causes inclusion body hepatitis, depression, splenomegaly, immunosuppression and death (Beach et al., 2009; Jucker et al., 1996; Pitcovski et al., 1998); falcon adenovirus also causes hepatitis (Schrenzel et al., 2005); and agamid adenovirus infection can be subclinical or lethal (Wellehan et al., 2004).

An understanding of virus diversity in wildlife provides epidemiological and ecological information about potential pathogens and may lead to the identification of newly emerging microbial threats. A previous study reported that some Antarctic avifauna is infected with various viruses, which may have been spread by Antarctic birds (Austin and Webster, 1993; Stannard et al., 1998). The South Polar skua (Catharacta maccormicki, previously known as Stercorarius maccormicki), which migrates for their breeding season (Yogui and Sericano, 2009), is an important top predator, exhibiting piratical behavior throughout the year.

In the present study, we examined various organs from carcasses of South Polar skuas, collected in Antarctica during 2007 to 2009, for evidence of adenovirus infection. The genetic and phylogenetic analyses of a newfound South Polar skua adenovirus (SPSAdV) are reported.

⁎ Corresponding author. Fax: +82 2 923 3645.
E-mail address: jwsong@korea.ac.kr (J.-W. Song).
Table 1
Oligonucleotide primers for full genome amplification of South Polar skua adenovirus.

| Gene   | Primer           | Nucleotide sequence (5′–3′) | Polarity |
|--------|------------------|----------------------------|----------|
| ITR    | Adv-ITR_EcoR I   | 5′-GAA TTC CA ATC AAT ATA TAT ACC-3′ | +/-      |
| IVA2   | Adv-IVA2R2926    | 5′-ACC TAG ATCA TCA ACA ATC A-3′ | -        |
| Polyomavirus | Adv-polV1     | 5′-CTG TCK TGR TCD CCA TA-3′ | +        |
|         | Adv-PolFinder_ku| 5′-TCT GAG GIB GAC GAT GTY ACC C-3′ | -        |
|         | Adv-Pol707R     | 5′-GAT ACC CAA CCT AAC TAG CA-3′ | -        |
|         | Adv-Pol4052     | 5′-TGC TCA CAG TAT AGA TAG TC-3′ | +        |
|         | Adv-Pol2452     | 5′-TAC AGG ATT TCG AAG AT-3′ | +        |
|         | Adv-Pol3992     | 5′-AGA CTG TCA GTA TCA-3′ | +        |
| pTP    | Adv-pTP6783R    | 5′-ACT AAG ACC ACC AAG ATG A-3′ | -        |
| 52K    | Adv-52KR686R    | 5′-TAC TGG TTA TAA CTA GA-3′ | -        |
|        | Adv-52K9279R    | 5′-TAT GTC TAC AAA CTA GA-3′ | +        |
| Penton | Adv-Pen1116R    | 5′-GAA TGA TCT TTA TCA TCA T-3′ | -        |
|         | Adv-Pen241F     | 5′-GAT AAG ACC GCV ADT ATG AT-3′ | +        |
|         | Adv-Pen597R     | 5′-TCA ATA ADC TCA TT-3′ | -        |
|         | Adv-Pen826R     | 5′-ATT RAR TAT GAT GA-3′ | +        |
| Hexon  | Adv-Hex13700R   | 5′-AAT CTA CGA TAT CTC ATG A-3′ | -        |
|        | Adv-Hex16F      | 5′-ATG GAY ATW TCA AAT GCT AC-3′ | +        |
|        | Adv-Hex409R     | 5′-ATT GAG CTC AGC GAG C-3′ | -        |
|        | Adv-Hex1359R    | 5′-TGG AAY AAV CCA GGT GTA-3′ | -        |
| DBP    | Adv-DBP17722F   | 5′-ATG GAA GCA TCA GTA-3′ | +        |
| 100K   | Adv-100K1931R   | 5′-ATG CTC TCA ACC AT-3′ | -        |
|        | Adv-100K19813F  | 5′-AGC TTT ACA CAA TAA-3′ | -        |
|        | Adv-100K19278F  | 5′-TGA ATG ATG GTG AAG C-3′ | -        |
|        | Adv-100K19955R  | 5′-TTC TCA GCA TAA TCC A-3′ | -        |
| E3     | Adv-E321275     | 5′-AGC CAA CCA GCC GCA CCA-3′ | -        |
| Fiber  | Adv-Fiber23068R | 5′-ATC CAA GAT CAT TAC CAA-3′ | -        |
|        | Adv-Fiber23030F | 5′-CTG GTA TCC TTA GTG TGA-3′ | +        |

Sequence analysis

The positions and coding directions of the 24 genes and open reading frames (ORF) are shown in the schematic genome map (Fig. 2). The locations, as well as lengths of each gene (nucleotide and amino acid) and their G+C content, are indicated in Table 3. The ITR regions were located on left and right ends. IVA2, polyomavirus, protein precursor (pTP), DNA binding protein (DBP), U exon and ORF8 were transcribed leftward, and sialidase, ORF4, 52K, pVII, pVIII (penton), pVII, pX, pVI, hexon, protease, 100K, 22K, 33K, pVIII, E3 region, fiber and ORF7 were transcribed rightward.

The length of the ITR region differed depending on the adenovirus species. For example, the ITR of the ITR region (AY849321) was 40 bp, whereas that of HAdV-1 (AC000017) was 103 bp. By contrast, the ITR of SPSAdV was 31 bp, whereas the lengths of the 5′ and 3′ terminal ends were the same as those of other species.

The sialidase of SPSAdV, located immediately downstream of the ITR region, was composed of ORF1, ORF2 and ORF3. In SPSAdV, ORF4, located immediately next to the sialidase, was identified as hydrophobic, as in RAdV-1, THEV and FrAdV-1. IVA2, a delayed early gene located downstream of the polymerase gene, was slightly shorter than that in the avirulent turkey enteritis virus (10′04 bp) and its G+C content of 29.69% was lower than that of other genes. The E2 region, containing the genes for DNA polymerase, pTP and DBP, consisted of two cleavage sites. The penton base, encoding a major capsid protein of adenovirus, was located between the pilla and pVII. And the hexon gene, encoding a capsid protein with a penton base and a fiber knob, had a G+C content of 34.36%.

The protease gene encoded one of the most conserved proteins among all adenovirus genes (Russell, 2009; Weber, 2007). The length of the E3 gene was 891 bp, and the 1389-nucleotide fiber gene encoded a 462-amino acid capsid protein, which was located between the U exon and ORF 7 (22,600–23,988) and transcribed in the rightward direction. ORF7 and ORF8 were genus specific, existing only in Siaadenovirus.

Phylogenetic analysis

The viral genome and phylogenetic analysis showed that SPSAdV belonged to genus Siaadenovirus in the family Adenoviridae (Fig. 3). At the nucleotide level, the SPSAdV pol, penton base and hexon genes exhibited somewhat higher sequence similarity of 73.8%, 72.9% and 77.5% with RAdV-1 and THEV, respectively. Compared with other genera, the pol, penton base and hexon genes of SPSAdV shared <61% nucleotide sequence similarity, that of Mastadenovirus, Atadenovirus and Aiviadeno virus. The nucleotide and amino acid sequences of the pol, penton base, and fiber genes showed nearly equi-distant differences between SPSAdV and other siadenoviruses.

In Fig. 4, trees were based on the polymerase and hexon genes. Only Siaadenovirus and Aiviadeno virus sequences were compared. These trees, which also included siadenoviruses from great tit, pitta cinea and Sulawesi tortoise, showed that SPSAdV was most closely related to RAdV-1.

Discussion

Only a limited number of viruses have hitherto been discovered among animals in the Polar region. Infectious bursal disease virus (IBDV) and poxvirus were detected in penguins (Gauthier-Clerc et al., 2002; Stannard et al., 1998) and serum antibodies to influenza A viruses and paramyxoviruses were reported in skua and Adelie

Table 2
Detection of South Polar skua adenovirus in various tissues by PCR.

| Animal no. | Accession no. | Genome/gene(s) | Detected tissue                  |
|------------|---------------|----------------|----------------------------------|
| SPS T03    | HM585353      | Complete (26,340 bp) | Heart, Lung, Liver, Kidney, Intestine, Trachea |
| SPS T01    | HM585354      | Polyomavirus, Penton, Hexon | Liver, Kidney, Intestine |
| SPS T02    | HM585355      | Polyomavirus, Penton, Hexon | Liver, Intestine, Trachea |
| SPS T06    | HM585356      | Polyomavirus, Penton, Hexon | Lung, Liver, Kidney |
| SPS T08    | HM585357      | Penton           | Liver                            |
| SPS T09    | HM585358      | Polyomavirus, Penton, Hexon | Lung, Kidney, Intestine |
penguin in the Ross Sea in Antarctica (Austin and Webster, 1993). In this study, viruses were targeted for discovery in Antarctic birds. Although no evidence of influenza virus and coronavirus was found, a novel adenovirus was detected by PCR in the South Polar skua, a predatory seabird species whose migratory route includes Antarctica.

Based on genetic and phylogenetic analyses, the newly identified viral sequences from six South Polar skuas could be classified as a novel siadenovirus. Other members of the genus Siadenovirus include THEV (Beach et al., 2009), RAdV-1 (Kovács and Benkő, 2011) and great tit adenovirus (GTAdV) (Kovács et al., 2010), all from avian
hosts, as well as frog adenovirus 1 (FrAdV-1) (Davison et al., 2000), originating from an amphibian host. At first, we assumed that SPSAdV would belong to the Aviadenovirus genus because the South Polar skua is an Antarctic bird. However, phylogenetic analysis revealed that SPSAdV was similar to RAdV-1 and THEV (Pitcovski et al., 1998). Comparison between SPSAdV and its closest relatives (RAdV-1 and THEV) showed 21–43% and 25–52% nucleotide dissimilarity at the pol, penton base, hexon and fiber genes, and 15–56% and 25–71% amino acid difference, respectively. Also, the nucleotide sequences of the pol, penton base, hexon and fiber genes of SPSAdV, compared with FrAdV-1, showed 34–53% dissimilarity. Interestingly, although birds serve as host species of aviadenoviruses (Jiang et al., 1999; Oaks et al., 2005; Schrenzel et al., 2005), Aviadenovirus encodes more distinct proteins than Siadenovirus (Benkö et al., 2000). The G+C content of the SPSAdV (34.2%) is similar with that of the other three siadenoviruses (RAdV-1: 38.5%, TAdV-3: 34.9%, FrAdV-1: 37.9%). The pVII gene of SPSAdV also shows significantly higher G+C content (46.9%). The G+C content does not vary across the genome in a systematic fashion, and this may suggest that a recombination event between disparate viruses did not occur.

| Gene    | Strand | Location   | Nucleotides | Amino acids | G+C content (%) |
|---------|--------|------------|-------------|-------------|-----------------|
| ITR     | Both   | 1–30       | 30          | –           | 40.00           |
| Sialidase | r      | 331–2001   | 1671        | 556         | 38.06           |
| ORF4    | r      | 2028–2351  | 324         | 107         | 44.75           |
| IVA2    | l      | 2402–3499  | 1098        | 365         | 29.69           |
| DNA pol | l      | 3492–6827  | 3336        | 1111        | 31.71           |
| pTP     | l      | 6824–8600; 11,001–11,020 | 1797 | 598 | 34.11 |
| 52K     | r      | 8628–9593  | 876         | 291         | 33.93           |
| pllla   | r      | 9493–11,004 | 1512  | 503         | 32.27           |
| III     | r      | 11,026–12,375 | 1350  | 449         | 33.26           |
| pVII    | r      | 12,375–12,785 | 411  | 136         | 46.96           |
| pVII    | r      | 12,987–13,652 | 177   | 58          | 36.72           |
| Hexon   | r      | 13,661–16,393 | 2733  | 910         | 34.36           |
| Protease| r      | 16,393–17,001 | 609   | 202         | 30.54           |
| DBP     | l      | 17,034–18,131; 18,208–18,240 | 1131  | 376         | 38.73           |
| 100K    | r      | 18,284–20,380 | 2097  | 698         | 33.43           |
| 33K     | r      | 20,274–20,376; 20,601–20,851 | 354   | 117         | 29.38           |
| 22K     | r      | 20,274–20,561 | 288   | 95          | 35.42           |
| pVIII   | r      | 20,944–21,579 | 636   | 211         | 43.24           |
| E3      | r      | 21,425–22,315 | 891   | 296         | 30.98           |
| U exon  | l      | 22,326–22,592 | 267   | 88          | 33.33           |
| Fiber   | r      | 22,560–23,988 | 1389  | 462         | 33.05           |
| ORF 7   | r      | 24,426–25,088 | 663   | 220         | 36.50           |
| ORF 8   | l      | 25,103–25,600 | 498   | 165         | 37.95           |

**Fig. 3.** Phylogenetic trees, based on the entire amino acid sequences of the polymerase (left), penton base (middle), hexon (right) genes, generated by the neighbor-joining method. Phylogenetic relationships of SPSAdV are shown with raptor adenovirus 1 (RAdV-1, EU715130), avirulent turkey hemorrhagic enteritis virus (THEV, AY849321), hemorrhagic enteritis virus (HEV, AF074946), turkey adenovirus A (TAdV-A, AC000016), frog adenovirus 1 (FrAdV-1, AF224336), psittacine adenovirus (PsAdV, pol, EU053825; hexon, EU627198), Sulawesi tortoises adenovirus (STAdV, EU056826), great tit adenovirus (GTAdV, FJ849795), fowl adenovirus 1 (FAvD-1, U46933), falcon adenovirus (FaAdV, AY863541), duck adenovirus 1 (DAdV-1, Y09558), snake adenovirus 1 (SnAdV-1, DQ106414), ovine adenovirus 7 (OAdV-7, DQ40839), bovine adenovirus 3 (BAdV-3, AC000012), canine adenovirus 2 (CAdV-2, AC000020), porcine adenovirus A (PAvD-A, NC_005869), tree shrew adenovirus (TsAdV, NC_004453), murine adenovirus A (MAdV-A, AC000012), equine adenovirus 2 (EAdV-2, L80007), human adenovirus 1 (HAdV-1, AC000017), human adenovirus 3 (HAdV-3, DQ086466), human adenovirus 4 (HAdV-4, AY458856), human adenovirus 8 (HAdV-8, AB448769), human adenovirus 12 (HAdV-12, X73487), human adenovirus 40 (HAdV-40, NC_001454), simian adenovirus 21 (SAdV-21, AC000010) and white sturgeon adenovirus (WsAdV, AY082701). Branch lengths are proportional to the number of amino acid substitutions, while vertical distances are for clarity only. The numbers at each node are bootstrap probabilities (expressed as percentages), as determined for 1000 iterations by PAUP version 4.0b.
Designation of a novel siadenovirus species is predicated on more than 10% sequence dissimilarity at the nucleotide and amino acid levels and a previously unrecognized host species (Benkö et al., 2000, 2005). Based on these criteria, we conclude that SPSAdV represents a novel adenovirus species in the genus Siadenovirus. Recently, the entire genome of RAdV-1 was obtained by PCR without virus isolation (Kovács and Benkö, 2011). Thus, apart from THEV, RAdV-1 and FrAdV-1, this is the fourth complete viral genome sequence in the genus Siadenovirus. Partial siadenovirus genomes have also been reported from the great tit (Kovács et al., 2010), budgerigar (Katoh and Benkö, 2009), suggesting that the evolutionary history may have major implications for the future studies. Future studies are warranted to ascertain the biology, epizootiology and pathogenic potential of this newfound polar-region siadenovirus.
Materials and methods

Samples

Frozen carcasses of nine South Polar skuas (SPS T01-T09), without readily discernable signs of disease, were collected in Lake King Sejong near King Sejong station (latitude 62° 13′ S and longitude 58° 47′ W) in Antarctica (Fig. 1), when ambient temperatures ranged from −5.6 °C to 2.1 °C. Tissue samples from various organs (heart, trachea, lung, esophagus, intestine, liver, kidney) were obtained using separate sterile instruments from each bird and stored at −70 °C until use. Autopsy was conducted in a BSL2 laboratory.

PCR and DNA sequencing

Total DNA was extracted from blood and tissue samples using the High Pure PCR Template preparation kit (Roche, Indianapolis, IN), according to the manufacturer’s instructions. First and nested PCR were performed in a 50-μl reaction volume containing 1 μl of 10 mM dNTP, 2 μl (10 PM) of each primer, 1 unit of Super-Therm Taq polymerase (JMR Holdings, London, UK) and 2.5 μl (400 ng) of template. Primers used for PCR amplification and sequencing are provided in Table 1.

Initially, adenovirus sequences available in GenBank were aligned using Clustal W, MegAlign program. The identity of the sequences was searched by Blast (Altschul et al., 1990). Phylogenetic trees were constructed, using BioEdit and hexon were performed for the analysis of partially characterized penton base and core protein genes. J. Gen. Virol. 77 (Pt 3), 469–479.

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