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Research in Veterinary Science 89 (2010) 275–278

Contents lists available at ScienceDirect

Research in Veterinary Science

journal homepage: www.elsevier.com/locate/rvsc

Characterisation of canine parvovirus strains isolated from cats with feline panleukopenia

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ARTICLE INFO

Article history:
Accepted 2 March 2010

Keywords:
Cat
Feline panleukopenia
Canine parvovirus
Strain characterisation

ABSTRACT

Unlike the original canine parvovirus type 2 (CPV-2), CPV-2 variants have gained the ability to replicate in vivo in cats but there is limited information on the disease patterns induced by these variants in the feline host. During 2008, two distinct cases of parvoviral infection were diagnosed in our laboratories. A CPV-2a variant was identified in a 3-month-old Persian kitten displaying clinical sign of feline panleukopenia (FPL) (acute gastroenteritis and marked leukopenia) and oral ulcerations, that died eight days after the onset of the disease. Two pups living in the same pet shop as the cat were found to shed a CPV-2a strain genetically identical to the feline virus and were likely the source of infection. Also, non-fatal infection by a CPV-2c strain occurred in a 2.5-month-old European shorthair kitten displaying non-haemorrhagic diarrhoea and normal white blood cell counts. By sequence analysis of the major capsid protein (VP2) gene, the feline CPV-2c strain showed 100% identity to a recent canine type-2c isolate. Both kittens had been administered multivalent vaccines against common feline pathogens including FPL virus. Whether and to which extent the FPL vaccines can protect cats adequately from the antigenic variants of CPV-2 should be assessed.

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Feline panleukopenia (FPL) is a contagious disease of cats caused by feline panleukopenia virus (FPLV), a member of the feline parvovirus subgroup within the *Parvovirus* genus (family *Parvoviridae*) together with canine parvovirus type 2 (CPV-2) and parvoviruses of wild carnivores. While FPLV has been known since 1920, CPV emerged as dog pathogen in the late 1970s most likely as host variant of the feline virus (Truyen, 2006). FPLV has maintained a certain genetic stability (Decaro et al., 2008c), whereas CPV-2 has displayed higher rates of nucleotide changes (Shackelton et al., 2005; Pereira et al., 2007; Hoelzer et al., 2008; Decaro et al., 2009). Few years after its onset, the original CPV-2 was replaced by two antigenic variants, CPV-2a and 2b, differing in 5–6 amino acids in the main capsid protein VP2 (Parrish et al., 1985, 1991). A third variant CPV-2c was detected in 2000 in Italy (Buonavoglia et al., 2001) and found to spread quickly in all continents (Martella et al., 2004; Nakamura et al., 2004; Decaro et al., 2005a, 2006b,c, 2007b; Perez et al., 2007; Hong et al., 2007; Calderon et al., 2009; Nandi et al., 2010).

Unlike the original type 2, the antigenic variants are able to infect cats causing a disease undistinguishable from that induced by true FPLV strains in natural (Mochizuki et al., 1993; Truyen et al., 1996; Ikeda et al., 2000; Battilani et al., 2006) and experimental conditions (Nakamura et al., 2001b; Gamoh et al., 2003a). There are several reports on the detection of CPV-2a/2b in cats affected by FPL (Mochizuki et al., 1993; Truyen et al., 1996; Ikeda et al., 2000) but only one report on infection by CPV-2c (Battilani et al., 2006). Also, a unique mutation (Gly-300 to Asp), related to the loss of the canine host range *in vitro* (Parker and Parrish, 1997), has been identified in some feline CPV-2a/2b isolates (Ikeda et al., 2000), suggesting that CPV-2 variants may have started a process of adaptation to the new feline host.

In this note, two distinct cases of FPL caused by CPV-2a and 2c in cats are described.

The first case was observed in January 2008 in a pet shop located in the Apulia region, importing purebred dogs and cats from Eastern Europe. A 3-month-old Persian kitten (case no. 1, 11/08), was hospitalized with haemorrhagic diarrhoea, fever (39.8 °C), depression, anorexia, oral ulcers, gingivitis and progressive loss of weight. The animal had already completed the vaccination protocol against FPLV, feline herpesvirus (FeHV-1), feline calicivirus (FCV), *Chlamydophila felis* and rabies. Despite the administration of fluids and antibiotics, the kitten died eight days after the onset of the disease. Blood cell counts obtained from an EDTA–blood sample collected three days before the death showed a slight modification of white blood cell (WBC) counts, with marked

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0034-5288/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.rvsc.2010.03.001

lymphopenia and neutrophil counts within normal ranges (data not shown). At necropsy, the carcass was cachectic with ulcers in the oral and pharyngeal mucosae, haemorrhagic enteritis, areas of necrosis in the liver, enlargement of the spleen and mesenteric lymph nodes that were scattered with haemorrhages. Material from the oral ulcers and the intestinal content were collected at necropsy for virological investigations. Few days before, clinical signs of acute gastroenteritis had appeared in a 1.5-month-old Italian Mastiff dog (12/08-A, born and raised in Italy) and in a 3-month-old German Spitz dog (12/08-B, imported from Romania), that had received one and two doses, respectively, of a tetravalent vaccine against parvovirosis, canine distemper, adenovirosis and leptospirosis. The imported pup had also been vaccinated against rabies. Haematological investigations carried out at day 4 after the onset of clinical signs showed moderate lymphopenia in both pups, with WBC and neutrophil counts being within normal values (data not shown). Both pups were given fluids and antibiotics with a full recover within 8–10 days. Rectal swabs were collected from the two pups at day 4 after the appearance of symptoms.

In June 2008, a 2.5-month-old European shorthair kitten (case no. 2, 234/08) was presented at the veterinarian with non-haemorrhagic diarrhoea, depression and loss of appetite. The cat lived in a household environment with the possibility to wander around the neighbourhood during the day and had been administered two doses of a vaccine containing FPLV, FeHV-1, FCV and *C. felis*. Fluids and antibiotic therapy were given for 1 week until the kitten recovered from the condition. An EDTA–blood sample and a rectal swab were collected at clinical examination. Laboratory investigations did not show significant alterations of the haematological parameters, including total and differential WBC counts (data not shown).

Samples obtained from the intestine and from the ulcerated mucosa of the oral cavity of the dead kitten (case no. 1), rectal swabs of the other kitten (case no. 2) and of the pups were processed to extract nucleic acids using the DNeasy Tissue Kit and QIAamp Viral RNA Mini Kit (QIAGEN S.p.A., Milan, Italy). DNA extracts from the intestinal content and rectal swabs were subjected to a real-time PCR assay able to detect both CPV and FPLV (Decaro et al., 2005a). The DNA and RNA obtained from the canine samples were also tested for canine adenovirus types 1 and 2 and for canine distemper virus (CDV) (Elia et al., 2006), while all RNA extracts were screened by either real-time or conventional RT-PCR assays specific for carnivore coronaviruses (Gut et al., 1999) and caliciviruses (Jiang et al., 1999; Marsilio et al., 2005).

The parvovirus and coronavirus strains detected in the feline and canine samples were characterised by (geno)type-specific real-time PCR or RT-PCR assays. Prediction of the parvovirus type was obtained by a panel of real-time PCR assays using minor groove binder (MGB) probes able to discriminate between: (i) FPLV and CPV (Decaro et al., 2008b); (ii) CPV-2a and 2b or CPV-2b and 2c (Decaro et al., 2006b) and (iii) CPV vaccine and field strains (Decaro et al., 2006a,d). Genotyping of canine coronavirus (CCoV) was carried out by means of two TaqMan assays specific for CCoV types I and II (Decaro et al., 2005b).

Attempts were made to isolate on Crandell feline kidney (CrFK) and canine mammary fibroma (A-72) cells the parvovirus strains identified in the feline and canine samples, as described previously (Desario et al., 2005, 2006c).

The sequence of the full-length VP2 gene of the identified parvovirus strains was determined in order to track the epidemiology of the viruses at a molecular level. The obtained sequences were assembled, edited and compared with FPLV and CPV reference strains and with a sequence database of parvovirus strains detected in Italy (Decaro et al., 2008c, 2009), using the BioEdit software package, version 7.0.1 (www.mbio.ncsu.edu/BioEdit/bioedit.html). The VP2 gene sequences were deposited in the GenBank database under accession numbers GU362932–GU362935.

The intestinal content/rectal swabs of the cats and dogs tested positive by real-time PCR for carnivore parvoviruses, displaying variable viral titres (Table 1). Molecular characterisation by real-time PCR assays with MGB probes revealed that all the viral strains, including the feline viruses, were CPVs. A CPV-2a strain was identified in the dead kitten (case no. 1, 11/08) and in the pups (12/08-A, 12/08-B) living in the pet shop with the cat, whereas the household kitten (case no. 2, 234/08) tested positive for a CPV-2c strain. FCV was detected in the oral ulcers of cat 11/08 and CCoV type I was identified in the rectal swabs of both dogs.

The CPV strains detected in the two kittens were successfully isolated on feline and canine cell cultures. A cytopathic effect was visible starting from the third or fourth passage on both feline and canine cell lines and the presence of parvovirus antigens in infected cells was detected by an immunofluorescence assay (Desario et al., 2005). By real-time PCR using MGB probes, the feline isolates were characterised as CPV-2a and 2c. A CPV-2a isolates was also made from the stools of pup 12/08-B, containing high viral titres (Table 1).

Sequence analysis of the VP2 gene of the CPV strains confirmed the results of real-time PCR typing. At position 1276–1278 of the VP2 gene there was the codon AAT (residue Asn-426) in the CPV-2a viruses and GAA (Glu-426) in the CPV-2c strain. Residues typical of CPV-2 strains, Leu-87, Thr-101, Gly-300, Tyr-305, and Asp375 were present in the VP2 of all the viruses. The CPV-2a strain 11/08, detected in the dead kitten, displayed 100% nucleotide identity to the canine strains 12/08-A and 12/08-B, whereas the feline CPV-2c strain 234/08 was identical to a canine strain (127/08-B) recently identified in Italy (Decaro et al., 2009).

Cases of FPL caused by CPV-2a or 2b in wild and domestic felids have been reported worldwide (Mochizuki et al., 1993; Truyen et al., 1996; Ikeda et al., 2000; Steinel et al., 2000; Gamoh et al., 2003b). Infection of a cat by the new variant CPV-2c has been documented recently in Italy, although details inherent the clinical signs and outcome of the infection were not reported (Battilani et al., 2006).

In the present study, we have described in detail the clinical signs and evolution of the disease in two cats infected by variants 2a and 2c of CPV-2. The viruses were characterised genetically by mapping single nucleotides polymorphisms in real-time PCR with MGB probes and by sequence analysis of the VP2 protein gene. The severity of the clinical signs and the outcome of the disease varied between the two cats, as the infection was fatal only for the CPV-2a infected cat. The source of infection was tracked for the CPV-2a-infected cat, and it was likely represented by one of the two infected pups housed in the same pet shop. Whether the pup imported from Romania was the index case could be only suspected but not clearly demonstrated, considering that the disease appeared simultaneously in both domestic and imported pups. CPV-2a is epidemiologically predominant in dog populations of Eastern Europe, whereas in Italy CPV-2c appears to be more common (Martella et al., 2004; Decaro et al., 2007b). Importation to Italy of pups from Eastern European countries has been suggested to be the source for emerging or re-emerging pathogens including canine adenovirus type 1 (Decaro et al., 2007a) and the arctic lineage of CDV (Martella et al., 2006). According to this scenario, it is tempting to hypothesize that the type 2a strain detected in the cat 11/08 and dogs 12/08-A and 12/08-B was introduced in the pet shop with animals imported from Romania.

As a consequence of the detection of CPV-2 variants in the feline host, a debate has now arisen on the efficacy of FPLV-based vaccines against infections by CPV variants 2a, 2b and 2c. In a recent study (Gamoh et al., 2005), an FPLV-based vaccine was able to cross-protect against a challenge with a virulent CPV-2b strain. However, in that study only two vaccinated cats were used and the animals were challenged shortly after the administration of

Table 1
Results of virological investigations carried out on the feline and canine samples.

Identification no.	Animal	Parvovirus titre[a]	95% CI	CPV type	Other pathogens
11/08	Cat	8.09×10^7	7.80×10^7–8.38×10^7	2a	FCV
12/08-A	Dog	1.24×10^2	5.65×10^1–1.91×10^2	2a	CCoV type I
12/08-B	Dog	4.72×10^6	4.60×10^6–4.84×10^6	2a	CCoV type I
234/08	Cat	6.74×10^6	6.29×10^6–7.19×10^6	2c	None

CI, confidence interval.
[a] Parvovirus titres are expressed as viral DNA copy numbers per milligram of faeces.

the second vaccine dose. A similar protocol has been employed to demonstrate protection by type 2-based vaccines against the CPV-2 variants in dogs (Spibey et al., 2008; Larson and Schultz, 2008) although this approach does not mimic adequately what happens under field conditions (Decaro et al., 2008a). There are no studies evaluating long-term protection induced by the original type 2 against its variants, when type 2 specific antibody titres could not be adequate to prevent infection and disease caused by field strains. Indeed, the neutralizing antibodies elicited by the original type of CPV-2 appear to recognize the antigenic variants 2a, 2, and 2c less effectively than the original type 2, thus suggesting that even a few amino acid changes in strategic epitopes of the capsid are able to affect markedly virus recognition by protective antibodies (Pratelli et al., 2001; Cavalli et al., 2008). Using cross-neutralisation studies, the antigenic differences between FPLV vaccines and CPV-2 variants appear to be much more marked, reflecting the number of mutations scattered throughout the VP2 protein (Parrish et al., 1991; Nakamura et al., 2001a).

The findings of this study provide firm evidence that the CPV-2 variants, including the novel 2c variant, may represent a threat to the cat populations, thus warranting efforts to increase the epidemiological surveillance and to assess the efficacy of the current vaccines.

Acknowledgements

This work was supported by grants from University of Bari, Italy, Ricerca di Ateneo 2009, project "Epidemiologia molecolare del parvovirus del cane nei carnivori domestici e selvatici" and contribution to PRIN07, project "Infezione da parvovirus nei carnivori: aspetti molecolari, patogenetici ed immunologici".

References

Battilani, M., Bassani, M., Forti, D., Morganti, L., 2006. Analysis of the evolution of feline parvovirus (FPV). Veterinary Research Communications 30, 223–226.
Buonavoglia, C., Martella, V., Pratelli, A., Tempesta, M., Cavalli, A., Buonavoglia, D., Bozzo, G., Elia, G., Decaro, N., Carmichael, L.E., 2001. Evidence for evolution of canine parvovirus type-2 in Italy. Journal of General Virology 82, 1555–1560.
Calderon, M.G., Mattino, N., Bucafusco, D., Fogel, F., Rumorini, P., La Torre, J., 2009. Molecular characterization of canine parvovirus strains in Argentina: detection of the pathogenic variant CPV2c in vaccinated dogs. Journal of Virological Methods 159, 141–145.
Cavalli, A., Martella, V., Desario, C., Camero, M., Bellacicco, A.L., De Palo, P., Decaro, N., Elia, G., Buonavoglia, C., 2008. Evaluation of the antigenic relationships among canine parvovirus type 2 variants. Clinical and Vaccine Immunology 15, 534–539.
Decaro, N., Elia, G., Martella, V., Desario, C., Campolo, M., Di Trani, L., Tarsitano, E., Tempesta, M., Buonavoglia, C., 2005a. A real-time PCR assay for rapid detection and quantitation of canine parvovirus type 2 DNA in the feces of dogs. Veterinary Microbiology 105, 19–28.
Decaro, N., Martella, V., Ricci, D., Elia, G., Desario, C., Campolo, M., Cavaliere, N., Di Trani, L., Tempesta, M., Buonavoglia, C., 2005b. Genotype-specific fluorogenic RT-PCR assays for the detection and quantitation of canine coronavirus type I and type II RNA in faecal samples of dogs. Journal of Virological Methods 130, 72–78.
Decaro, N., Elia, G., Desario, C., Roperto, S., Martella, V., Campolo, M., Lorusso, A., Cavalli, A., Buonavoglia, C., 2006a. A minor groove binder probe real-time PCR assay for discrimination between type 2-based vaccines and field strains of canine parvovirus. Journal of Virological Methods 136, 65–70.
Decaro, N., Elia, G., Martella, V., Campolo, M., Desario, C., Camero, M., Cirone, F., Lorusso, E., Lucente, M.S., Narcisi, D., Scalia, P., Buonavoglia, C., 2006b. Characterisation of the canine parvovirus type 2 variants using minor groove binder probe technology. Journal of Virological Methods 133, 92–99.
Decaro, N., Martella, V., Desario, C., Bellacicco, A.L., Camero, M., Manna, L., D'aloja, D., Buonavoglia, C., 2006c. First detection of canine parvovirus type 2c in pups with haemorrhagic enteritis in Spain. Journal of Veterinary Medicine B, Infectious Diseases and Veterinary Public Health 53, 468–472.
Decaro, N., Martella, V., Elia, G., Desario, C., Campolo, M., Buonavoglia, D., Bellacicco, A.L., Tempesta, M., Buonavoglia, C., 2006d. Diagnostic tools based on minor groove binder probe technology for rapid identification of vaccinal and field strains of canine parvovirus type 2b. Journal of Virological Methods 138, 10–16.
Decaro, N., Campolo, M., Elia, G., Buonavoglia, D., Colaianni, M.L., Lorusso, A., Mari, V., Buonavoglia, C., 2007a. Infectious canine hepatitis: an "old" disease reemerging in Italy. Research in Veterinary Science 83, 269–273.
Decaro, N., Desario, C., Addie, D.D., Martella, V., Vieira, M.J., Elia, G., Zicola, A., Davis, C., Thompson, G., Thiry, E., Truyen, U., Buonavoglia, C., 2007b. Molecular epidemiology of canine parvovirus, Europe. Emerging Infectious Diseases 13, 1222–1224.
Decaro, N., Desario, C., Elia, G., Martella, V., Mari, V., Lavazza, A., Nardi, M., Buonavoglia, C., 2008a. Evidence for immunisation failure in vaccinated adult dogs infected with canine parvovirus type 2c. New Microbiologica 31, 125–130.
Decaro, N., Desario, C., Lucente, M.S., Amorisco, F., Campolo, M., Elia, G., Cavalli, A., Martella, V., Buonavoglia, C., 2008b. Specific identification of feline panleukopenia virus and its rapid differentiation from canine parvoviruses using minor groove binder probes. Journal of Virological Methods 147, 67–71.
Decaro, N., Desario, C., Miccolupo, A., Campolo, M., Parisi, A., Martella, V., Amorisco, F., Lucente, M.S., Lavazza, A., Buonavoglia, C., 2008c. Genetic analysis of feline panleukopenia viruses from cats with gastroenteritis. Journal of General Virology 89, 2280–2289.
Decaro, N., Desario, C., Parisi, A., Martella, V., Lorusso, A., Miccolupo, A., Mari, V., Colaianni, M.L., Cavalli, A., Di Trani, L., Buonavoglia, C., 2009. Genetic analysis of canine parvovirus type 2c. Virology 385, 5–10.
Desario, C., Decaro, N., Campolo, M., Cavalli, A., Cirone, F., Elia, G., Martella, V., Lorusso, E., Camero, M., Buonavoglia, C., 2005. Canine parvovirus infection: which diagnostic test for virus? Journal of Virological Methods 121, 179–185.
Elia, G., Decaro, N., Martella, V., Cirone, F., Lucente, M.S., Lorusso, E., Di Trani, L., Buonavoglia, C., 2006. Detection of canine distemper virus in dogs by real-time RT-PCR. Journal of Virological Methods 136, 171–176.
Gamoh, K., Shimazaki, Y., Makie, H., Senda, M., Itoh, O., Inoue, Y., 2003a. The pathogenicity of canine parvovirus type-2b, FP84 strain isolated from a domestic cat, in domestic cats. Journal of Veterinary Medical Science 65, 1027–1029.
Gamoh, K., Shimazaki, Y., Senda, M., Makie, H., Itoh, O., Inoue, Y., 2003b. Antigenic type distribution of parvovirus isolated from domestic cats in Japan. The Veterinary Record 153, 751–752.
Gamoh, K., Senda, M., Inoue, Y., Itoh, O., 2005. Efficacy of an inactivated feline panleucopenia virus vaccine against a canine parvovirus isolated from a domestic cat. The Veterinary Record 157, 285–287.
Gut, M., Leutenegger, C.M., Huder, J.B., Pedersen, N.C., Lutz, H., 1999. One-tube fluorogenic reverse transcription-polymerase chain reaction for the quantitation of feline coronaviruses. Journal of Virological Methods 77, 37–46.
Hoelzer, K., Shackelton, L.A., Parrish, C.R., Holmes, E.C., 2008. Phylogenetic analysis reveals the emergence, evolution and dispersal of carnivore parvoviruses. Journal of General Virology 89, 2280–2289.
Hong, C., Decaro, N., Desario, C., Tanner, P., Pardo, M.C., Sanchez, S., Buonavoglia, C., Saliki, J.T., 2007. Occurrence of canine parvovirus type 2c in the United States. Journal of Veterinary Diagnostic Investigation 19, 535–539.
Ikeda, Y., Mochizuki, M., Naito, R., Nakamura, K., Myazawa, T., Mikami, T., Takahashi, E., 2000. Predominance of canine parvovirus (CPV) in unvaccinated cat populations and emergence of new antigenic types of CPVs in cats. Virology 278, 13–19.
Jiang, X., Huang, P.W., Zhong, W.M., Farkas, T., Cubitt, D.W., Matson, D.O., 1999. Design and evaluation of a primer pair that detects both Norwalk- and Sapporo-like caliciviruses by RT-PCR. Journal of Virological Methods 83, 145–154.
Larson, L.J., Schultz, R.D., 2008. Do two current canine parvovirus type 2 and 2b vaccines provide protection against the new type 2c variant? Veterinary Therapeutics 9, 94–101.
Marsilio, F., Di Martino, B., Decaro, N., Buonavoglia, C., 2005. Nested PCR for the diagnosis of calicivirus infections in the cat. Veterinary Microbiology 105, 1–7.

Martella, V., Cavalli, A., Pratelli, A., Bozzo, G., Camero, M., Buonavoglia, D., Narcisi, D., Tempesta, M., Buonavoglia, C., 2004. A canine parvovirus mutant is spreading in Italy. Journal of Clinical Microbiology 42, 1333–1336.

Martella, V., Cirone, F., Elia, G., Lorusso, E., Decaro, N., Campolo, M., Desario, C., Lucente, M.S., Bellacicco, A.L., Blixenkrone-Møller, M., Carmichael, L.E., Buonavoglia, C., 2006. Heterogeneity within the hemagglutinin genes of canine distemper virus (CDV) strains detected in Italy. Veterinary Microbiology 116, 301–309.

Mochizuki, M., Harasawa, R., Nakatani, H., 1993. Antigenic and genomic variabilities among recently prevalent parvoviruses of canine and feline origin in Japan. Veterinary Microbiology 38, 1–10.

Nakamura, K., Ikeda, Y., Miyazawa, T., Tohya, Y., Takahashi, E., Mochizuki, M., 2001a. Characterisation of cross-reactivity of virus neutralising antibodies induced by feline panleukopenia virus and canine parvoviruses. Research in Veterinary Science 71, 219–222.

Nakamura, K., Sakamoto, M., Ikeda, Y., Sato, E., Kawakami, K., Miyazawa, T., Tohya, Y., Takahashi, E., Mikami, T., Mochizuki, M., 2001b. Pathogenic potential of canine parvovirus types 2a and 2c in domestic cats. Clinical and Diagnostic Laboratory Immunology 8, 663–668.

Nakamura, M., Tohya, Y., Miyazawa, T., Mochizuki, M., Phung, H.T., Nguyen, N.H., Huynh, L.M., Nguyen, L.T., Nguyen, P.N., Nguyen, P.V., Nguyen, N.P., Akashi, H., 2004. A novel antigenic variant of canine parvovirus from a Vietnamese dog. Archives of Virology 149, 2261–2269.

Nandi, S., Chidri, S., Kumar, M., Chauhan, R.S., 2010. Occurrence of canine parvovirus type 2c in the dogs with haemorrhagic enteritis in India. Research in Veterinary Science 88, 169–171.

Parker, J.S., Parrish, C.R., 1997. Canine parvovirus host range is determined by the specific conformation of an additional region of the capsid. Journal of Virology 71, 9214–9222.

Parrish, C.R., O'Connel, P.H., Evermann, J.F., Carmichael, L.E., 1985. Natural variation of canine parvovirus. Science 230, 1046–1048.

Parrish, C.R., Aquadro, C.F., Strassheim, M.L., Evermann, J.F., Sgro, J.-Y., Mohammed, H.O., 1991. Rapid antigenic-type replacement and DNA sequence evolution of canine parvovirus. Journal of Virology 65, 6544–6552.

Pereira, C.A., Leal, E.S., Durigon, E.L., 2007. Selective regimen shift and demographic growth increase associated with the emergence of high-fitness variants of canine parvovirus. Infection, Genetics and Evolution 7, 399–409.

Perez, R., Francia, L., Romero, V., Maya, V., Lopez, I., Hernandez, M., 2007. First detection of canine parvovirus type 2c in South America. Veterinary Microbiology 124, 147–152.

Pratelli, A., Cavalli, A., Martella, V., Tempesta, M., Decaro, N., Carmichael, L.E., Buonavoglia, C., 2001. Canine parvovirus (CPV) vaccination: comparison of neutralizing antibody responses in pups after inoculation with CPV2 or CPV2b modified live virus vaccine. Clinical and Diagnostic Laboratory Immunology 8, 612–615.

Shackelton, L.A., Parrish, C.R., Truyen, U., Holmes, E.C., 2005. High rate of viral evolution associated with the emergence of carnivore parvovirus. Proceedings of the National Academy of Sciences of the United States of America 102, 379–384.

Spibey, N., Greenwood, N.M., Sutton, D., Chalmers, W.S., Tarpey, I., 2008. Canine parvovirus type 2 vaccine protects against virulent challenge with type 2c virus. Veterinary Microbiology 128, 48–55.

Steinel, A., Munson, L., Van Vuuren, M., Truyen, U., 2000. Genetic characterization of feline parvovirus sequences from various carnivores. Journal of General Virology 81, 345–350.

Truyen, U., 2006. Evolution of canine parvovirus – a need for new vaccines? Veterinary Microbiology 117, 9–13.

Truyen, U., Platzer, G., Parrish, C.R., 1996. Antigenic type distribution among canine parvoviruses in dogs and cats in Germany. The Veterinary Record 138, 365–366.