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Multiple reassortment and interspecies transmission events contribute to the diversity of feline, canine and feline/canine-like human group A rotavirus strains

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ABSTRACT

RNA–RNA hybridization assays and complete genome sequence analyses have shown that feline rotavirus (FRV) and canine rotavirus (CRV) strains display at least two distinct genotype constellations (genogroups), represented by the FRV strain RVA/Cat-tc/AUS/Cat97/1984/G3P[3] and the human rotavirus (HRV) strain RVA/Human-tc/JPN/AU-1/1982/G3P3[9], respectively. G3P[3] and G3P[9] strains have been detected sporadically in humans. The complete genomes of two CRV strains (RVA/Dog-tc/ITA/RV198-95/1995/G3P[3] and RVA/Dog-tc/ITA/RV52-96/1996/G3P[3]) and an unusual HRV strain (RVA/Human-tc/ITA/PA260-97/1997/G3P[3]) were determined to further elucidate the complex relationships among FRV, CRV and HRV strains. The CRV strains RV198-95 and RV52-96 were shown to possess a Cat97-like genotype constellation. However, 3 and 5 genes of RV198-95 and RV52-96, respectively, were found in distinct subclusters of the same genotypes, suggesting the occurrence of reassortment events among strains belonging to this FRV/CRV/HRV genogroup. Detailed phylogenetic analyses of the HRV strain PA260-97 showed that (i) 8 genome segments (VP3, VP4, VP6, VP7 and NSP2-5) clustered closely with RV198-95 and/or RV52-96; (ii) 2 genome segments (VP1 and VP2) were more closely related to HRV AU-1; and (iii) 1 genome segment (NSP1) was distantly related to any other established NSP1 genotypes and was ratified as a new NSP1 genotype, A15. These findings suggest that the human strain PA260-97 has a history of zoonotic transmission and is likely a reassortant among FRV/CRV strains from the Cat97 and AU-1-like genogroups. In addition, a potential third BA222-05-like genogroup of FRV and HRV strains should be recognized, consisting of rotavirus strains with a stable genetic genotype constellation of genes also partially related to bovine rotavirus (BRV) and bovine-like rotaviruses. The detailed phylogenetic analysis indicated that three major genotype constellations exist among FRV, CRV and feline/canine-like HRV strains, and that reassortment and interspecies transmission events contribute significantly to their wide genetic diversity.

1. Introduction

Group A rotaviruses are the most frequently detected viral cause of diarrhea in children worldwide causing approximately 527,000 deaths in children under 5 years of age, mainly in developing countries (Parashar et al., 2006, 2009). Rotavirus possesses a genome of 11 segments of dsRNA encoding 6 structural (VP) and 5 or 6 non-structural (NSP) proteins (Estes and Kapikian, 2007). The two outer capsid proteins VP7 and VP4 are the basis for a widely used dual classification system defining G- and P-types, respectively. Currently, at least 25 G-genotypes and 33 P-genotypes have been published

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(Abe et al., 2009, 2011; Collins et al., 2010; Esona et al., 2010; Matthijnssens et al., 2008a; Schumann et al., 2009; Solberg et al., 2009; Trojnar et al., 2009; Ursu et al., 2009). However, only a limited number of G/P-genotype combinations are found frequently in humans, such as G1P[8], G2P[4], G3P[8], G4P[8], G9P[8], and more recently the G12 genotype in combination with P[8] or P[6] (Matthijnssens et al., 2008c, 2009a; Santos and Hoshino, 2005). An extended group A rotavirus classification and nomenclature system was established to encompass all 11 genome segments, defining genotypes for each genome segment (Matthijnssens et al., 2008a). The classification scheme Gx-P[x]-Ix-Rx-Cx-Mx-Ax-Nx-Tx-Ex-Hx represents genotypes of, respectively, the VP7-VP4-VP6-VP1-VP2-VP3-NSP1-NSP2-NSP3-NSP4-NSP5 encoding genome segments, with x indicating the numbers of the corresponding genotypes (Matthijnssens et al., 2008a). The use of the new classification system has enabled the identification of reassortment and interspecies transmission events, highlighting the role of animals as a source of rotavirus infection in humans (Ghosh et al., 2010; Iturriza-Gómara et al., 2004; Matthijnssens et al., 2006a,b, 2008a,d, 2009b, 2010; Rahman et al., 2007; Trojnar et al., 2009; Tsugawa and Hoshino, 2008). A Rotavirus Classification Working Group (RCWG) was created to preserve the classification system and to assign new genotypes that are identified for any of the 11 genome segments (Matthijnssens et al., 2008b). The comprehensive classification system revealed genetic relationships among rotaviruses from different host species, including evidence that human rotavirus (HRV) strains belonging to the Wa-like genogroup have a common origin with porcine rotavirus strains while those belonging to the DS-1-like genogroup have a common origin with bovine rotavirus (BRV) strains (Matthijnssens et al., 2008a). In addition, the RCWG recently proposed a novel standardized system to name RV strains according to the following scheme: RV group/species of origin/country of identification/common name/year of identification/G- and P-type (Matthijnssens et al., in press).

A limited number of studies have investigated the molecular characteristics of rotavirus strains in stool specimens of both symptomatic and asymptomatic cats and dogs (Birch et al., 1985; Hoshino et al., 1981; Mochizuki et al., 1997, 2001; Mochizuki and Yamakawa, 1987; Oka et al., 2001), with only a few feline rotavirus (FRV) and canine rotavirus (CRV) strains that have been isolated and partially characterized to date. All FRV strains, RVA/Cat-tc/AUS/Cat2/1984/G3P[9] and RVA/Cat/AUS/Cat97/1984/G3P[3], isolated in Australia (Birch et al., 1985), RVA/Cat-wt/JPN/FRV-1/1985/G3P3[9], RVA/Cat-wt/JPN/FRV72/1989/G3P5[3], RVA/Cat-wt/JPN/FRV73/1989/G3P5[3], RVA/Cat-wt/JPN/FRV317/1993/G3P3[9], RVA/Cat-wt/JPN/FRV64/1989/G3P5[3], RVA/Cat-wt/JPN/FRV70/1989/G3P5[3], RVA/Cat-wt/JPN/FRV303/1993/G3P5[3], RVA/Cat-wt/JPN/FRV348/1993/G3P5[3], RVA/Cat-wt/JPN/FRV381/1993/G3P3[9] and RVA/Cat-wt/JPN/FRV384/1993/G3P3[9], isolated in Japan (Oka et al., 2001), and RVA/Cat-wt/ITA/BA222/2005/G3P[9], isolated in Italy (Martella et al., 2011) have been shown to bear the G3P[3] or G3P[9] specificities. All CRV strains, the Australian RVA/Dog-ct/AUS/K9/1981/G3P[3] (also known as LSU 79C-36) (Fulton et al., 1981), the American RVA/Dog-tc/USA/CU-1/1982/G3P[3] and RVA/Dog-tc/USA/A79-10/1979/G3P[3] (Hoshino et al., 1982, 1983), the Japanese RVA/Dog-tc/JPN/RS15/19XX/G3P5[3] (Mochizuki and Hsuan, 1984), the Korean RVA/Dog-tc/KOR/GC-KS05/XXXX/G3P[3] (Kang et al., 2007), and the Italian RVA/Dog-tc/ITA/RV198-95/1995/G3P[3] and RVA/Dog-tc/ITA/RV52-96/1996/G3P[3] strains (Martella et al., 2001a) have been shown to belong to the G3P[3] genotype combination. Interestingly, some rotavirus strains isolated from humans have been shown to possess feline/canine characteristics. For example, RVA/Human-tc/JPN/AU-1/1982/G3P3[9] was found to be different from the common Wa-like and DS-1-like HRV strains by RNA–RNA hybridization (Nakagomi et al., 1987) and served as the prototype strain of a separate HRV genogroup (Nakagomi et al., 1985). This finding has been recently confirmed upon availability of complete genome sequence data (Matthijnssens et al., 2008a). AU-1-like HRV strains have been also identified occasionally in Japan and Israel (Gollop et al., 1998; Gunasena et al., 1993; Iizuka et al., 1994; Kaga et al., 1994; Nakagomi et al., 1989; Nakagomi and Nakagomi, 1989). In addition, RNA–RNA hybridization analyses of the HRV strain RVA/Human-xx/JPN/K8/XXXX/G1P[9] suggest that this strain is a natural reassortant between AU-1-like and Wa-like rotavirus strains (Nakagomi et al., 1992b). G12P[9] HRV strains, isolated in Thailand, Japan and several South American countries, have been shown to belong to the AU-1 genogroup (Castello et al., 2009; Matthijnssens et al., 2008c, 2009a; Pietruchinski et al., 2006; Pongsuwanna et al., 2002; Shinozaki et al., 2004). Molecular characterization of several additional HRVs has revealed a close relationship with FRV or CRV strains genetically unrelated to AU-1. The HRV strain RVA/Human-tc/ISR/Ro1845/1985/G3P[3], isolated in Israel, was shown to be closely related to the FRV strain Cat97 (Nakagomi et al., 1990). Strain RVA/Human-tc/USA/HCR3A/1984/G3P[3], isolated from an asymptomatic child in Philadelphia, was shown to be related to FRV and CRV strains (Gouvea et al., 1990; Li et al., 1993; Nakagomi and Nakagomi, 2000). Three unusual HRV strains (RVA/Human-wt/ITA/PAF96/1994/G3P[9], RVA/Human-wt/ITA/PAH136/1996/G3P[9] and RVA/Human-wt/ITA/PAI58/1996/G3P[9]), isolated in Italy between 1994 and 1996, were shown to possess feline-like VP7, VP4 and VP6 genome segments and a DS-1-like NSP4 genome segment (De Grazia et al., 2008). Several other investigators have reported feline/canine-like rotavirus strains in epidemiological studies in humans (Bányai et al., 2009a; Cao et al., 1999; Ch'ng et al., 2011; Griffin et al., 2002; Iturriza-Gómara et al., 2009, 2010; Kaga et al., 1994; Laird et al., 2003; Shif et al., 1994; Vonsover et al., 1993). Recently, the complete genome sequences of some FRV, CRV and HRV strains with feline/canine characteristics have been reported (De Grazia et al., 2010; Martella et al., 2011; Tsugawa and Hoshino, 2008). FRV strain Cat97, CRV strains CU-1, K9 and A79-10, and HRV strains Ro1845 and HRC3A were shown to contain nearly identical genes, while the FRV strain Cat2 might be the result of multi-reassortment between FRV, CRV, HRV and BRV strains (Tsugawa and Hoshino, 2008). Two unusual HRV strains, PAH136-96 and PAI58-96, that shared neutralization antigen specificities with AU-1 possessed FRV-, BRV- and HRV-like genome segments based on complete genome sequence analyses (De Grazia et al., 2010), and the FRV strain BA222-05 seemed to be closely related to HRV strains PAH136-96 and PAI58-96 (Martella et al., 2011).

In this study, we describe the complete molecular characterization of two CRV strains, RV198-95 and RV52-96, isolated from dog pups with diarrhea (De Grazia et al., 2007; Martella et al., 2001a,b), and the unusual HRV strain PA260-97, exhibiting canine characteristics, isolated from a two year old child in Palermo, Italy (De Grazia et al., 2007). The complete genomes of these three strains were compared to other completely sequenced FRV and CRV strains in an attempt to elucidate their genetic relationships with each other and with other rotavirus strains isolated from several host species, especially cats and dogs.

2. Materials and methods

2.1. Strain collection

CRV strains RV198-95 and RV52-96 (both G3P[3]) were isolated from two pups, 2.5 and 6 months of age, with gastroenteritis symptoms in 1995 and 1996, respectively (Martella et al., 2001a), and the G3P[3] HRV strain PA260-97 was isolated from a 2 year old hospitalized child with severe diarrhea in Palermo, Italy in 1997 (De Grazia et al., 2007). Partial VP7, VP4, VP6 and NSP4 sequences