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Short communication

Genetic characteristics and analysis of a novel rotavirus G3P [22] identified in diarrheic feces of Korean rabbit

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ABSTRACT

Group A rotaviruses (RVAs) are important gastroenteric pathogens that infect humans and animals. This study aimed to analyze the complete genome sequence, i.e., 11 genome segments of the lapine rotavirus (LRV) identified in the intestine of a dead rabbit in the Republic of Korea (ROK) and to describe the genetic relationships between this lapine isolate [RVA/Rabbit-wt/KOR/Rab1404/2014/G3P[22] (Rab1404)] and other lapine isolates/strains. Rab1404 possessed the following genotype constellation: G3-P[22]-I2-R3-C3-M3-A9-N2-T3-E3-H3. The P[22] genotype was found to originate from rabbits and was for the first time identified in the ROK. Phylogenetic analysis showed that Rab1404 possessed VP1-3 and VP7 genes, which were closely related to those of the bat strain LZHP2; NSP1-4 genes, which were closely related to those of the simian strain RRV; and VP4, VP6, and NSP5 genes, which were closely related to the genes obtained from other rabbits. Interestingly, a close relationship between Rab1404 and simian RVA strain RVA/Simian-tc/USA/RRV/1975/G3P[3] for 8 gene segments was observed. RRV is believed to be a reassortant between bovine-like RVA strain and canine/feline RVA strains. Rab1404 and canine/feline RVAs shared the genes encoding VP1, VP3, VP7, NSP3, and NSP4. Additionally, the genome segments VP6 (I2), NSP1 (N2), and NSP5 (H3) of Rab1404 were closely related to those of bovine RVAs. This is the first report describing the complete genome sequence of an LRV detected in the ROK. These results indicate that Rab1404 could be a result of interspecies transmission, possibly through multiple reassortment events in the strains of various animal species and the subsequent transmission of the virus to a rabbit. Additional studies are required to determine the evolutionary source and to identify possible reservoirs of RVAs in nature.

1. Introduction

Group A rotaviruses (RVAs) are major pathogens associated with acute gastroenteritis in various host species, including birds and mammals, throughout the world (Bresee et al., 2005). RVAs belong to the family Reoviridae and have 11 genome segments composed of double-stranded RNA encoding six structural viral proteins (VP1-VP4, VP6, and VP7) and five or six non-structural proteins (NSP1-NSP6) (Estes and Cohen, 1989; Pesavento et al., 2006). The infectious rotavirus particle is composed of three concentric layers (the inner, middle, and outer layers). The outer layer is formed by the two capsid proteins VP7 and VP4, which are most frequently used to classify RVAs into G (for glycoprotein) and P (for protease-sensitive) genotypes, respectively (Abe et al., 2011; Matthijnssens et al., 2006). This dual classification system has accelerated the comparison according to species-specific patterns among various animal species. To date, based on genetic characterization, 32 G and 47 P genotypes have been identified in humans and animals (Li et al., 2016).

Lapine rotavirus (LRV) strains have been isolated in Canada, China, Japan, Italy, Hungary, and the United States (Banyai et al., 2005; Bonica et al., 2015; Ciarlet et al., 1997; Guo et al., 2012; Hoshino et al., 2002; Martella et al., 2003), and those that have been characterized belong to the VP7 G3 genotype. The G3 genotype has been described in various different host species, such as humans, rabbits, pigs, birds, bats, cats, dogs, monkeys, horses, mice, cows, and lambs (Bonica et al., 2015). The P[14] and P[22] genotypes of VP4 have mainly been reported in LRVs (Banyai et al., 2005; Martella et al., 2003; Martella et al., 2005). Additionally, the P[13]/[22] genotype has been identified in porcine (Collins et al., 2010; Tonietti et al., 2013). LRV is recognized as a potential source of human infection (Bonica et al., 2015); however, to date, little is known about the molecular characteristics of rotavirus infection in rabbits in the Republic of Korea (ROK). Moreover, LRV is

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Table 1
Genotype of 11 genome segments of Rab1404, which have been completely sequenced in this study, as well as that of the reference LRV, human, and animal RVA strains together with nucleotide similarity (%) between Rab1404 and other rotavirus strains.

Strain	VP7	VP4	VP6	VP1	VP2	VP3	NSP1	NSP2	NSP3	NSP4	NSP5
RVA/Rabbit-wt/KOR/Rab1404/2011/G3P[22]	G3	P[22]	I2	R3	C3	M3	A9	N2	T3	E3	H3
RVA/Rabbit-tc/ITA/30-96/1996/G3P[14]	G3	P[14]	I2	R2	C2	M3	A9	N2	T6	E5	H3
	84.3		95.9			80.0	82.25	94.3			93.2
RVA/Rabbit-tc/CHN/N5/1992/G3P[14]	G3	P[14]	I17	R3	C3	M3	A9	N1	T1	E3[a]	H2
	88.8			85.3	90.1	87.8	88.2			94.2	
RVA/Rabbit-tc/NLD/K1130027/2011/G6P[11]	G6	P[11]	I2	R2	C2	M2	A13	N2	T6	E2	H3
			90.3				50.4	89.8			89.8
RVA/Human-wt/BEL/B4106/2000/G3P[14]	G3	P[14]	I2	R2	C2	M3	A9	N2	T6	E5	H3[a]
	84.9		96.7			80.6	82.8	97.8			98.4
RVA/Human-wt/BEL/BE5028/2012/G3P[14]	G3	P[14]	I2[a]	R2	C2	M3	A9	N2[a]	T6	E5	H3
	84.1		97.3			80.0	82.4	98.0			98.1
RVA/Simian-tc/USA/RRV/1975/G3P[3]	G3	P[3]	I2	R2	C3	M3[a]	A9[a]	N2	T3[a]	E3	H6
	89.4		90.0		90.7	88.2	92.0	90.7	94.7	93.5	
RVA/Bat-wt/CHN/LZHP2/2015/G3P[3]	G3[a]	P[3]	I3	R3[a]	C3	M3	A9	N3	T3	E3	H6
	91.3			95.7	90.1	87.2	87.6		86.5	92.9	
RVA/Bat-tc/CHN/MYAS33/2013/G3P[10]	G3	P[10]	I17	R3	C3	M3	A9	N3	T3	E3	H6
	91.0			86.4	93.2[a]	86.3	87.5		85.6	86.8	
RVA/Horse-wt/ARG/E3198/2008/G3P[3]	G3	P[3]	I3	R3	C3	M3	A9	N3	T3	E3	H6
	91.1			86.4	93.0	86.7	89.5		92.9	93.3	
RVA/Dog-tc/USA/CU-1/1982/G3P[3]	G3	P[3]	I3	R3	C2	M3	A9	N2	T3	E3	H6
	84.9			85.9		82.3	83.1	83.9	84.0	83.8	
RVA/Cat-tc/AUS/Cat97/1984/G3P[3]	G3	P[3]	I3	R3	C2	M3	A9	N2	T3	E3	H6
	85.0			86.0		81.9	82.6	84.8	84.1	84.3	
RVA/Human-tc/USA/HCR3A/1984/G3P[3]	G3	P[3]	I3	R3	C2	M3	A9	N2	T3	E3	H6
	84.7			86.0		82.2	83.5	84.3	85.3	83.8	
RVA/Human-wt/AUS/RCH272/2012/G3P[14]	G3	P[14]	I2	R3	C3	M3	A9	N2	T6	E2	H3
	88.0		88.9	84.8	86.0	81.3	85.8	88.8			90.4
RVA/Cow-wt/ZAF/1603/2007/G6P[5]	G6	P[5]	I2	R2	C2	M2	A3	N2	T6	E2	H3
			89.9					87.0			90.5
RVA/Cat-wt/ITA/BA222/2005/G3P[9]	G3	P[9]	I2	R2	C2	M2	A3	N1	T3	E2	H3
	80.7		87.1						85.2		90.5
RVA/Rhesus-tc/USA/TUCH/2002/G3P[24]	G3	P[24]	I9	R3	C3	M3	A9	N1	T3	E3	H6
	77.4			86.6	87.1	85.6	86.2		87.9	83.4	
RVA/Rabbit/ITA/160-01/2002/G3P[22]	G3	P[22]	–	–	–	–	–	–	–	E5	–
	82.7	88.8									
RVA/Rabbit/ITA/229-01/2002/G3P[22]	G3	P[22]	–	–						E5	–
	82.6	89.4									
RVA/Rabbit/ITA/308-01/2002/G3P[22]	G3	P[22]	–	–	–	–	–	–	–	E5	–
	83.5	87.7									
RVA/Rabbit/HUN/3489-3/2004/G?P[22]	–	P[22][a]	–	–	–	–	–	–	–	–	–
		97.8									
RVA/Porcine-wt/ARG/A46/1994/G5P[22]	G5	P[22]									
		82.1									

VP, viral protein: NSP, non-structural protein.
Shaded cells indicate strains with the same genotype as RVA/Rabbit-wt/KOR/Rab1404/2011/G3P[22].
"-": no sequence data available for analysis.
[a] Strains within each genotype having the highest nucleotide similarity to RVA/Rabbit-wt/KOR/Rab1404/2011/G3P[22].

reportedly capable of direct interspecies transmission (Matthijnssens et al., 2009; Parreno et al., 2004; Schoondermark-van de Ven et al., 2013). The objective of this study was to analyze an LRV isolated from the intestine of a dead rabbit in 2014 in the ROK by performing a complete genomic sequence analysis of the 11 genome segments and to characterize the phylogenetic relationships between our isolate and other lapine isolates/strains.

2. Materials and methods

2.1. Sample origin

In 2014, 20 young rabbits died of acute enteritis in a flock of approximately 1000 rabbits. A domesticated rabbit that died suddenly was sent to the Animal Disease Diagnostic Division, Animal and Plant Quarantine Agency, ROK, for post-mortem examination, where routine bacterial examination of the intestinal content was also performed. Rabbit enteritis-related virological examination was performed, and rotavirus was detected using RT-PCR. The rabbit rotavirus RVA/Rabbit-wt/KOR/Rab1404/2014/G3P[22] (Rab1404) was isolated from the intestinal content of the rabbit.

2.2. RNA extraction and RT-PCR

Viral RNA was extracted from fecal suspensions using a RNeasy Mini Kit (Qiagen, Hilden, Germany) according to the manufacturer's instructions. The total RNA was eluted in 50 μL of RNase-free water and stored at −80 °C until use. RT-PCR was performed using 2× One-Step RT-PCR Smart Mix (Solgent, Daejeon, Korea). The primers used for amplifying VP1-VP4, VP6, VP7, and NSP1-NSP5 were as described previously (De Leener et al., 2004; Matthijnssens et al., 2006; Zeller et al., 2012). Briefly, RNA was denatured at 95 °C for 3 min and quenched on ice. Reverse transcription was performed at 50 °C for 30 min, followed by 95 °C for 15 min, and then 35 cycles of amplification [at 94 °C for 30 s, 45 °C for 30 s (VP4, VP6, VP7, and NSP2-NSP5), 47 °C for 30 s (VP1-VP3 and NSP1), 72 °C for 6 min (VP1-VP4 and NSP1) and 72 °C for 2 min (VP6, VP7, and NSP2-NSP5)], and a final extension step at 74 °C for 10 min (VP1-VP4 and NSP1) and 75 °C for 10 min (VP6, VP7, and NSP2-NSP5).

2.3. Nucleotide sequencing and phylogenetic analysis

Each PCR product was purified using the Accupower PCR Purification Kit (Bioneer, Daejeon, Korea). PCR amplicons were directly cloned into pGEM®-T Easy vector (Promega, Madison, WI, USA), which was then used for direct sequencing (Macrogen Inc., Daejeon, Korea). The obtained sequence data were analyzed using the Basic Local Alignment Search Tool of the National Center for Biotechnology Information database. Homologous sequences were analyzed using the Chromas software (version 2.33, http://www.technelysium.com.au/chromas.html) and aligned using ClustalX (version 1.8). Phylogenetic trees were constructed based on the 11 genome segments of LRV using the maximum-likelihood method and a Kimura 2-parameter (Kimura, 1980) substitution model by employing MEGA7 software (Kumar et al., 2016). To construct each phylogenetic tree, additional sequences were obtained from GenBank (http://www.ncbi.nlm.nih.gov). The complete nucleotide sequences of the 11 genome segments of Rab1404 obtained in this study were assigned the accession numbers MK893920 and MK751428-MK751437.

3. Results and discussion

The intestinal content of the rabbit was tested and found to be positive for rotavirus alone. No other enteric pathogens, such as *E. coli* and coronavirus, were detected. The nucleotide sequences of the 10 genome segments of Rab1404 were completely identified, whereas the VP3 gene (1825 bp) of Rab1404 was partially sequenced. Based on the nucleotide sequence identities, the VP7, VP4, VP6, VP1-3, and NSP1-5 genome segments of Rab1404 were observed to possess G3-P[22]-I2-R3-C3-M3-A9-N2-T3-E3-H3, which is different from the constellation observed in previously characterized LRV strains (Table 1). On comparison of the genotype of Rab1404 with that of the Italian lapine strain 30–96, Chinese lapine strain N5, and the Dutch lapine strain K1130027, differences were found in five (VP1-2, VP4, NSP3, and NSP4), five (VP4, VP6, NSP2, NSP3, and NSP5), and eight genes (VP1-4, VP7, NSP1, NSP3, and NSP4), respectively (Table 1). Interestingly, Rab1404 shared eight identical genes with RCH272 (VP1-3, VP6-7, NSP1-2, and NSP5) and RRV (VP2-3, VP6-7, and NSP1-4). Furthermore, Rab1404 shared seven genotypes with the canine strain CU-1, canine-like human strain HCR3A, bat strain LZHP2 isolated in China, and equine strain E3198 (Table 1).

The sequences of 11 genome segments of Rab1404 were analyzed and the genetic relationships between Rab1404 and other known LRVs as well as RVAs were compared. The VP7 genome segment of Rab1404 was most closely related to the Chinese bat strains, MYAS33 (91.0%) and LZHP2 (91.3%), and the Argentine horse strain E3198 (91.1%) but not to the LRVs (Fig. 1 and Table 1). The VP4 sequence was compared with the currently known representative rabbit strains. The VP4 gene of Rab1404 exhibited a maximum nucleotide similarity of 97.8% with the lapine strain 3489-3 from Hungary followed by 89.4%, 88.8%, and 87.7% similarity with the 229-01, 160-01, and 308-01 Italian rabbit strains; phylogenetic analysis revealed that the VP4 gene from Rab1404 clustered in the P[22] genotype with LRVs (Fig. 1 and Table 1). The VP6 gene of Rab1404 clustered most closely with the lapine strain 30–96 (95.9%) as well as with the human lapine-like strains B4106 (96.7%) and BE5028 (97.3%), which were previously demonstrated to have a lapine origin (Matthijnssens et al., 2006); this VP6 gene of either simian, bovine, or human origin belonged to the I2 genotype (Fig. 1). The VP1 gene of Rab1404 was closely related to LZHP2 (95.7%) belonging to the R3 genotype. The VP2 gene of Rab1404 belonged to the C3 genotype and included bat, simian, and equine RVA strains. Rab1404 clustered most closely with the bat strain MYAS33 (93.2%). The VP3 gene segment of Rab1404 was closely related to RRV (88.2%, Table 1). The NSP1, NSP3, and NSP4 genes of Rab1404 were closely related to RRV (92.0%, 94.7%, and 95.3%) and E3198 (89.5%, 92.9%, and 93.3%) and belonged to the A9, T3, and E3 genotypes, respectively. The NSP1 gene segment of Rab1404 clustered in the A9 genotype with RRV (92.0%). The NSP3 and NSP4 genes of Rab1404 showed genetic relatedness to RRV (94.7% and 93.5%) and LZHP2 (85.6% and 92.9%), whereas the NSP3 and NSP4 genes of the lapine strain 30–96 and the human lapine-like strains B4106 and BE5028 clustered in the T6 and E5 genotypes, respectively. The NSP2 and NSP5 genes of Rab1404 clustered in the N2 and H3 genotypes and were closely related to the strains 30–96 (94.3% and 93.2%), K1130027 (both genes 89.8%), B4106 (97.8% and 98.4%), and BE5028 (98.0% and 98.1%), respectively (Fig. 1 and Table 1). Although K1130027 originated in a rabbit, it was completely divergent from the N5 strain and shared three genotypes with Rab1404 and six with the 30–96 strain (Fig. 1).

To date, 32 G and 47 P genotypes of rotavirus have been identified (Li et al., 2016). Among them, G3 has been detected in a broad spectrum of host species, including humans, indicating that G3 is more likely to undergo interspecies transmission than G1, G2 and G4. Additionally, G3 is the only genotype identified in rabbits having VP7-specificity (Banyai et al., 2005; Guo et al., 2012; Martella et al., 2003). P[14] for VP4 has been found in humans, goats, and rabbits (Martella et al., 2003; Matthijnssens et al., 2009; Parreno et al., 2004). Previous studies have also identified P[14] in the lapine-like human strains B4106 and BE5028 and in the human bovine-like strain RCH272 (Bonica et al., 2015; Donato et al., 2014). Consequently, P[14] specificity in humans may be attributed to interspecies transmission. However, recently, P[14] rotaviruses have rarely been reported in humans. Moreover, P[22] has mainly been found in rabbits in Hungary and Italy (Banyai et al., 2005; Martella et al., 2005) and also identified in porcine (Collins et al., 2010; Tonietti et al., 2013). This seems to be related to virus evolution. Our results revealed that the P[22] genotype was detected in a rabbit for the first time in the ROK, suggesting that P[22] has greater species specificity than P[14]. Because little LRV sequencing data are available, further studies are necessary to investigate the presence of the P[22] genotype in other animal species in the ROK.

Rab1404 shared three genes with two LRVs (30–96 and N5), namely VP7 (G3 genotype), VP3 (M3 genotype), and NSP1 (A9 genotype), whereas the remaining eight genes (VP1, VP2, VP4, VP6, NSP2, NSP3, NSP4, and NSP5) were different from each other (Table 1). Considering the lapine origin, the reason underlying differences in genotypes remains unclear. It is therefore presumed that its ancestor/origin is different. Interestingly, of the 11 genotypes, Rab1404 shares eight identical genotypes with RRV and RCH272. However, RCH272 showed $\leq$90% sequence identify for a majority of Rab1404 gene segments. RRV, which was isolated from a juvenile rhesus macaque with diarrhea, shared 6 gene segments (VP2, VP6, NSP1-4) and showed $\geq$90% sequence identity with Rab1404. RRV was most closely related to Rab1404 with regard to the VP3, NSP1, and NSP3 genes (Fig. 1 and Table 1). Additionally, RRV shared eight genotypes with the canine strain CU-1, feline strain Cat97, and canine-like human strain HCR3A (Mino et al., 2013; Tsugawa and Hoshino, 2008) and three genotypes with the bovine-like RVA strain (VP1, VP6, and NSP2) (Matthijnssens et al., 2010) (Table 1). RRV may present strong evidence for reassortment among different animals RVA strains via interspecies transmission. RRV appears to have undergone reassortment a long time ago. So far, the infection source and host origin of Rab1404 remains unknown. These results indicate that Rab1404 is most closely related to the canine/feline ancestor of RRV.

Our genomic analysis showed that Rab1404 was more related to other animal strains, such as simian, bat, and equine, than rabbit. This implies that RVAs can easily cross between different host species and are able to spread successfully and cause diseases in a new host. Several studies have reported that human and animal RVAs originate from complex animal-human reassortment or interspecies transmission events, presumably because of the close proximity of humans to livestock and companion animals (Banyai et al., 2009a; Banyai et al., 2009b; Ghosh et al., 2010; Guo et al., 2012; Matthijnssens et al., 2009; Matthijnssens et al., 2006). Rab1404 shared the following genes with

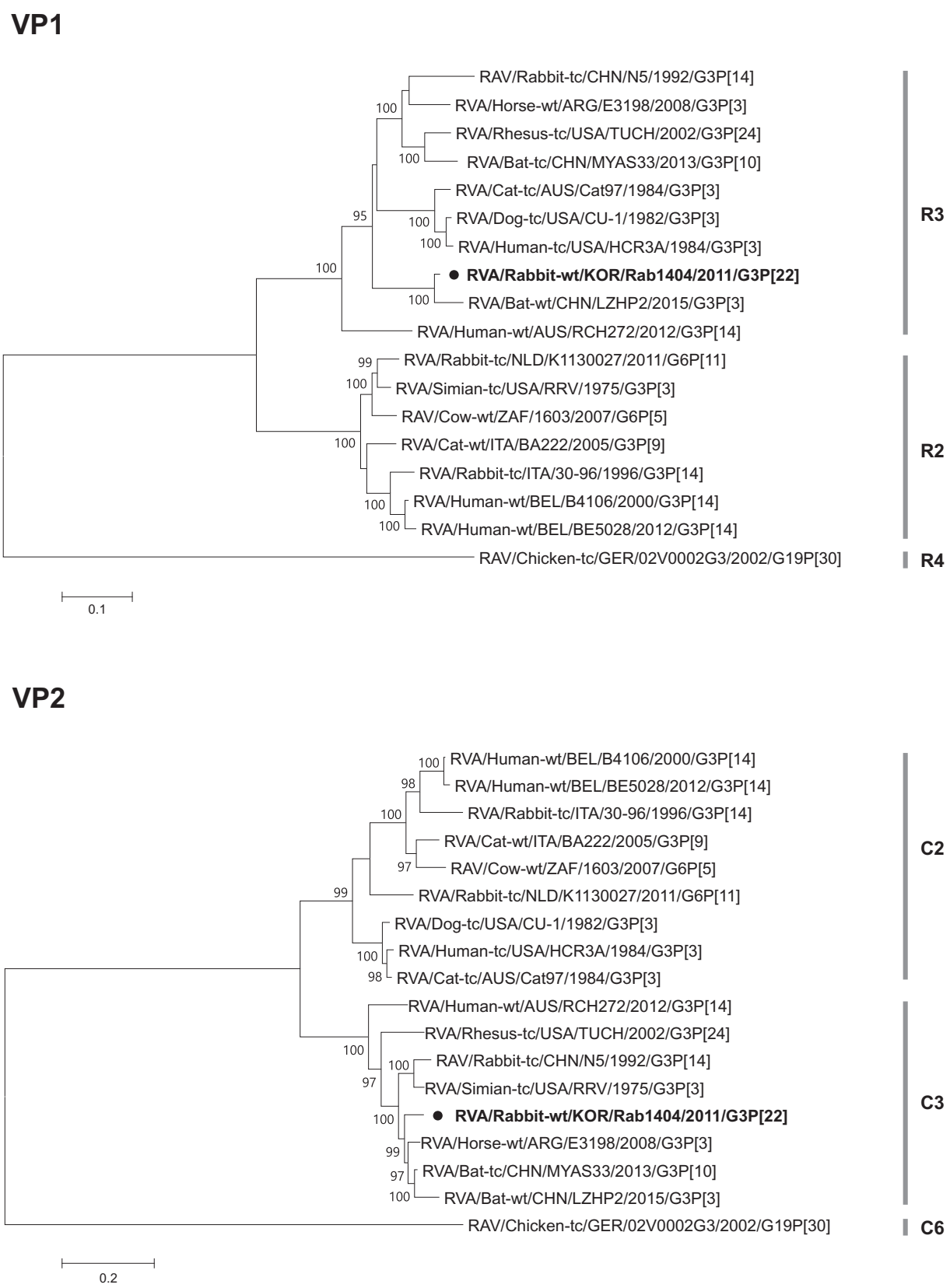
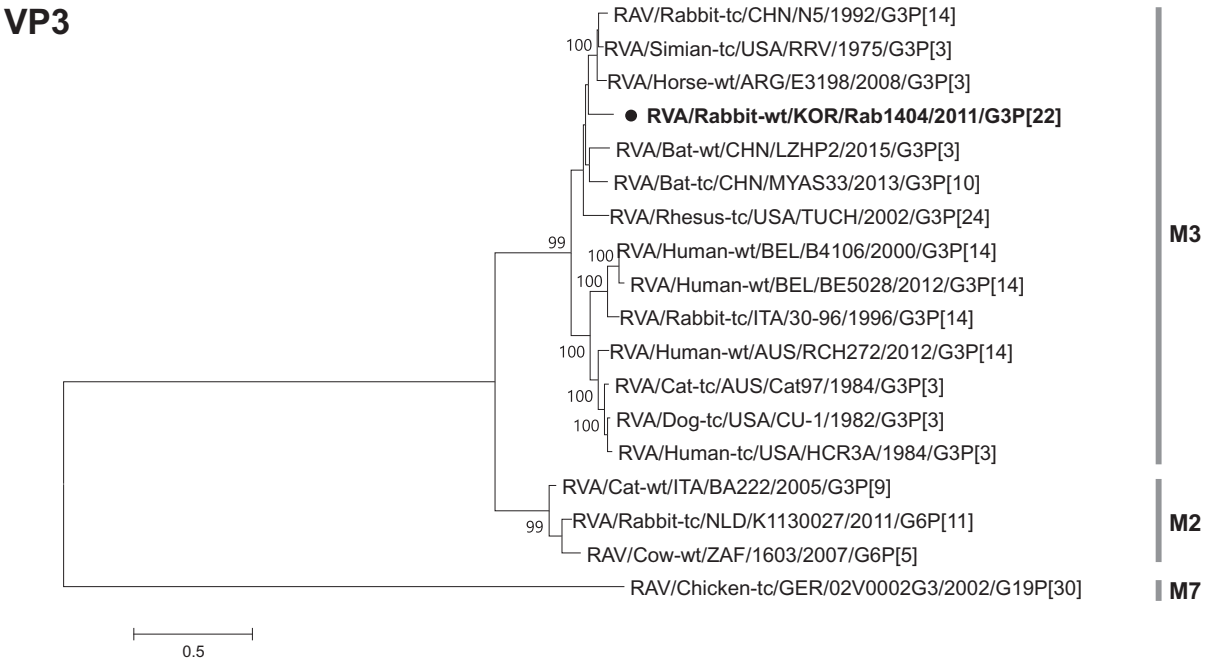


Fig. 1. Phylogenetic trees constructed from the nucleotide sequences of the VP1-4, VP6-7, and NSP1-5 genes of the rabbit rotavirus isolate, RVA/Rabbit-wt/KOR/Rab1404/2014/G3P[22] (Rab1404), with reference to other group A rotavirus strains. In all trees, the position of the isolate Rab1404 is indicated by a circle symbol and in bold. Bootstrap values of ≥95 are shown.



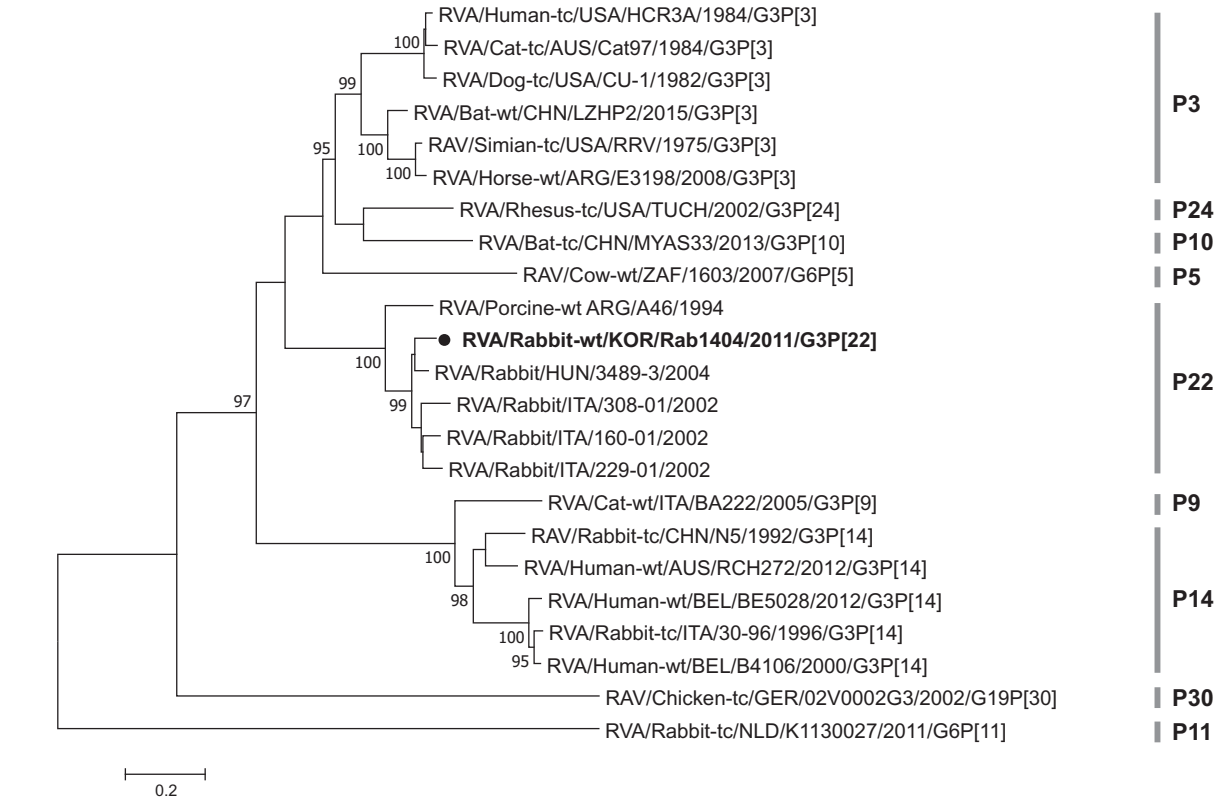
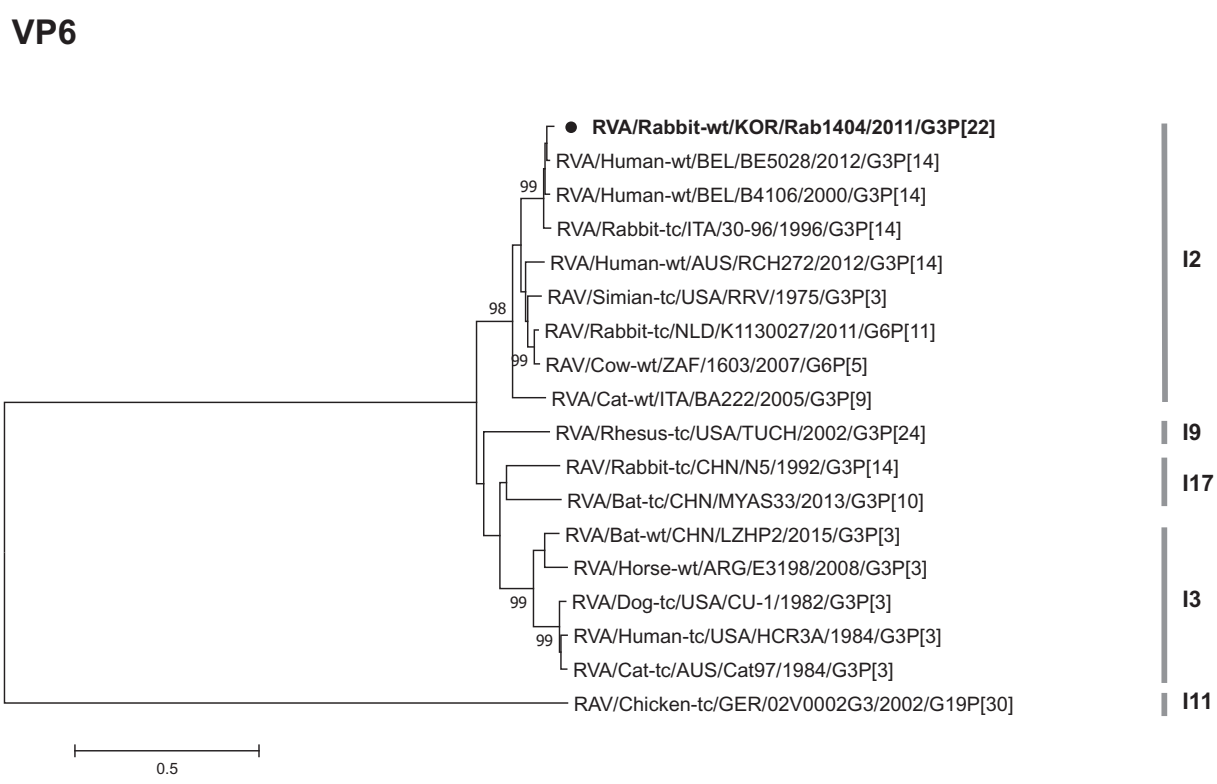


Fig. 1. (*continued*)

canine/feline RVAs: VP1 (R3), VP3 (M3), VP7 (G3), NSP3 (T3), and NSP4 (E3). Furthermore, the genes VP6 (I2), NSP1 (N2), and NSP5 (H3) of Rab1404 were closely related to the corresponding bovine genes (Schoondermark-van de Ven et al., 2013). Consequently, these results suggest that Rab1404 may have feline/canine and bovine origin.

A previous phylogenetic analysis revealed that Rab1404 showed a high sequence identity for VP6 (97.3%), NSP2 (98.0%), and NSP5 (98.1%) genes with the human strain BE5028, representing a rabbit to



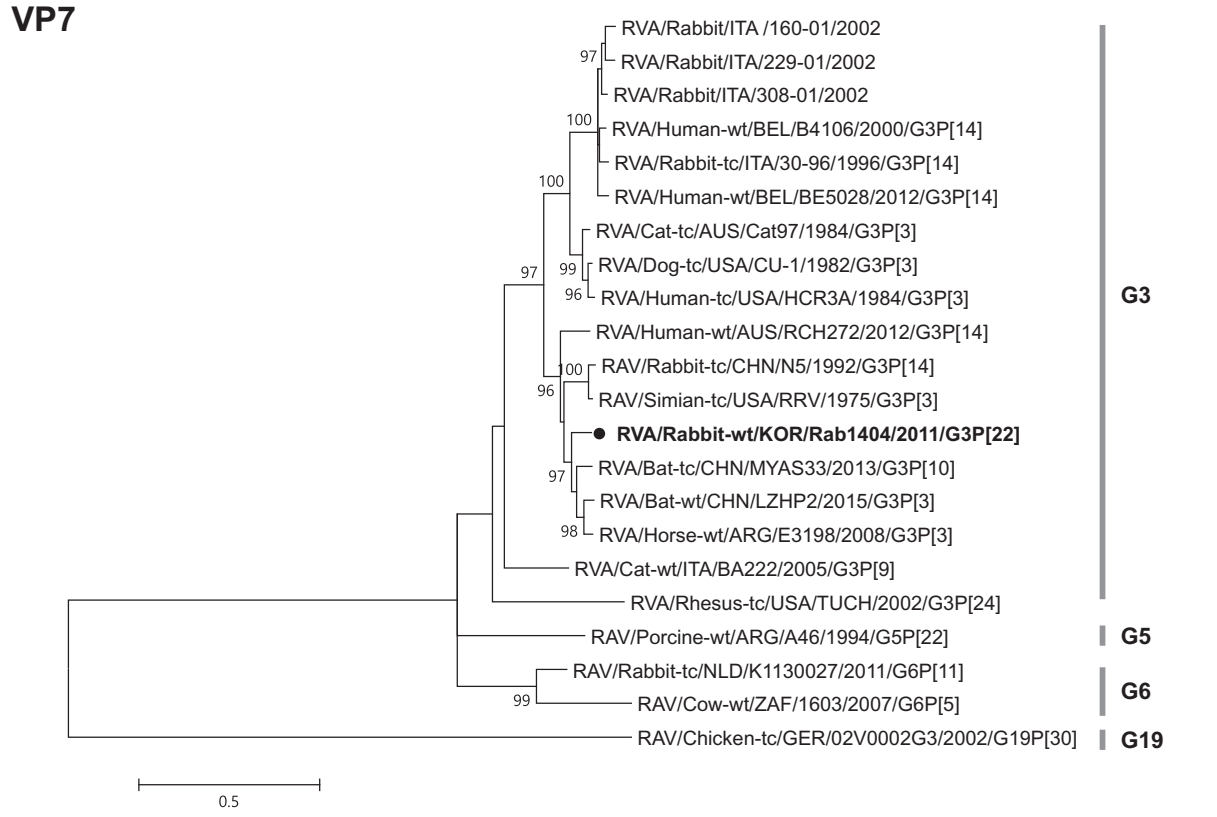


Fig. 1. (*continued*)

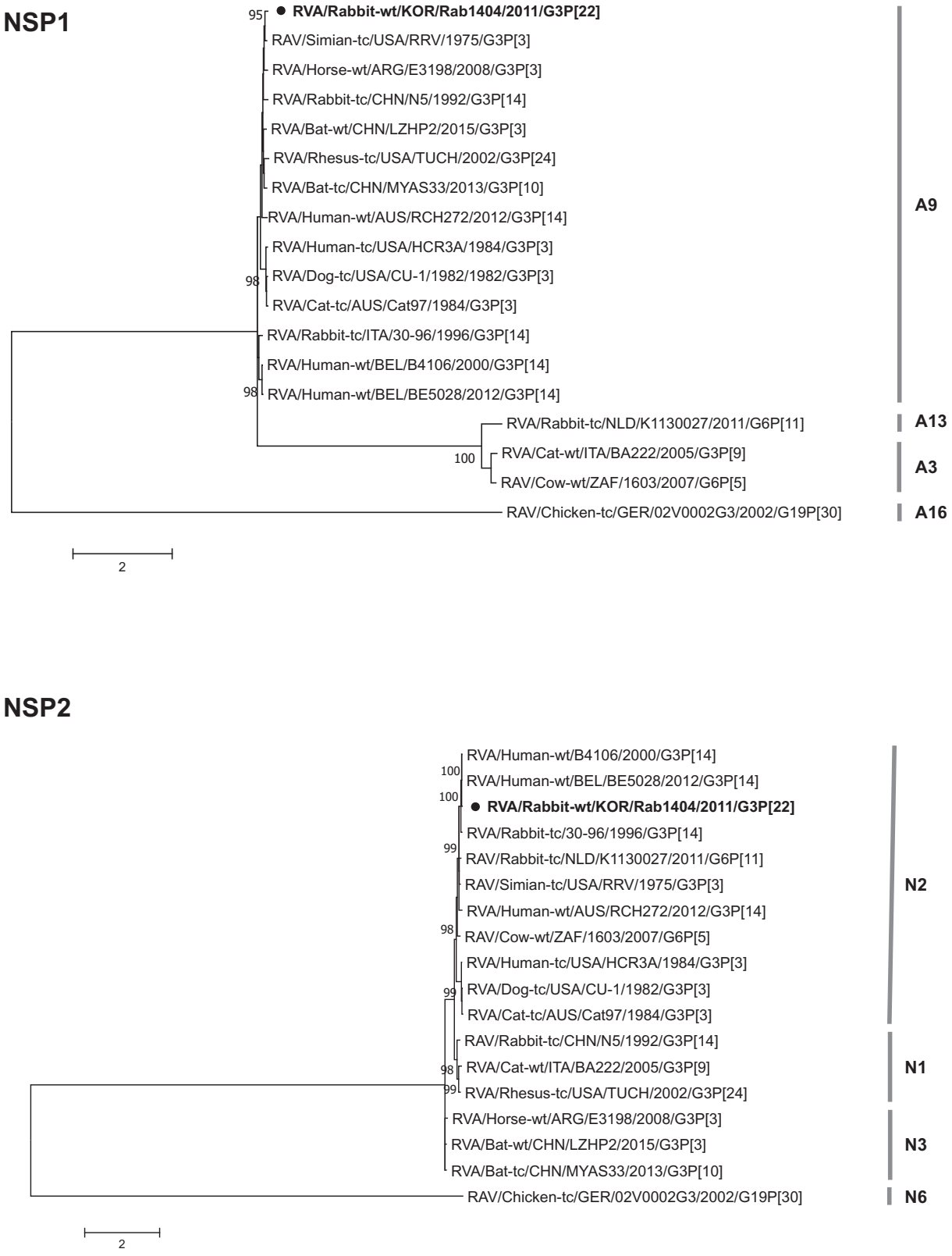
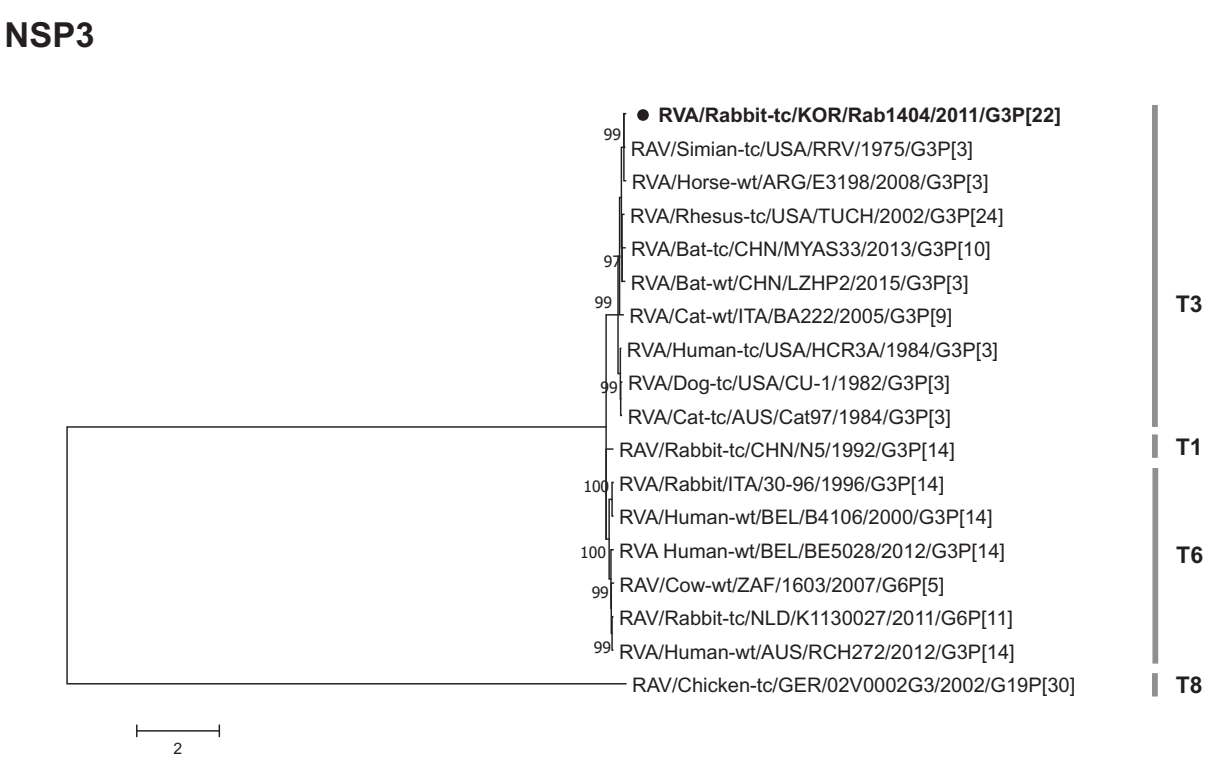


Fig. 1. (*continued*)

human interspecies transmission which can cause disease development in humans; Rab1404 was closely related to the bovine strain (Bonica et al., 2015). Another LRV strain, K1130027, has a genotype constellation identical to that of a bovine strain, which was isolated from a 5-month-old boy with gastroenteritis in Slovenia (Steyer et al., 2013). Interestingly, lapine and lapine-like strains have been derived from a population of previously characterized bovine strains and bovine-like ancestral strains, suggesting a past reassortment event between a bovine and lapine. Rab1404 was closely related to the bat strain LZHP2 with regard to VP1 (95.7%), VP2 (90.1%), VP7 (91.3%), and NSP4



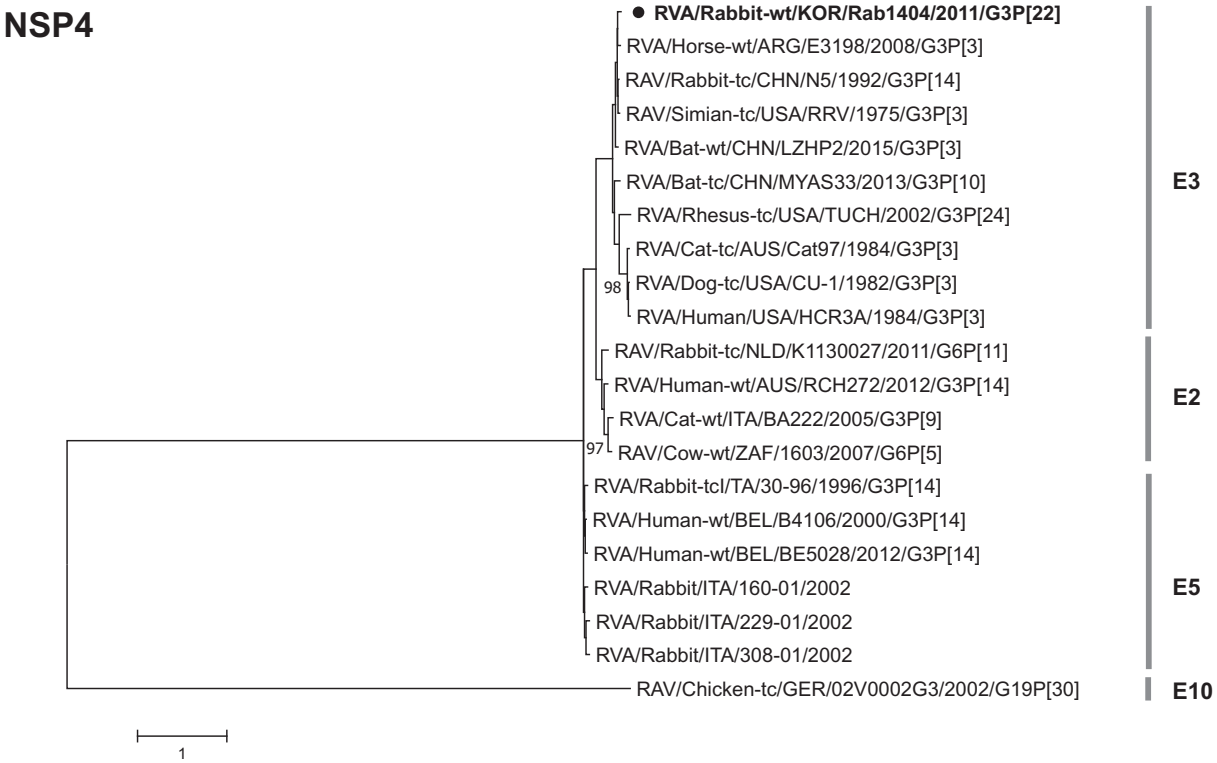


Fig. 1. (*continued*)

Fig. 1. (*continued*)

(92.9%) genes. However, numerous genes of bat strains possessed canine/feline characteristics. Bats may be important zoonotic reservoirs that readily transmit animal RVAs, facilitating reassortment events. The present results indicate that Rab1404 possesses genes derived from various host species; however, it was impossible to accurately determine the host species that transmitted Rab1404. Therefore, Rab1404 identified in the ROK may have originated from other animal strains, instead of rabbits, as a result of multiple reassortment events.

In conclusion, the present findings suggest that Rab1404 is closely related to the simian strain RRV and not LRVs. G3P[22] identified in this study has newly emerged in rabbits in the ROK and may have more species specificity. The results revealed that Rab1404 is an interspecies-transmitted virus, which may have developed owing to multiple reassortments among canine, feline, and bovine hosts and subsequent transmission to a rabbit. The results of this study reinforce the important role of animals in the ecology and evolution of RVAs as well as highlight the potential of this virus to cross between species. Additional studies should emphasize on the importance and the need for continued surveillance of RVAs in animals.

Conflict of interests

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

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