Exotic rotaviruses in animals and rotaviruses in exotic animals

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Abstract Group A rotaviruses (RVA) are a major cause of viral diarrhea in the young of mammals and birds. RVA strains with certain genotype constellations or VP7–VP4 (G–P) genotype combinations are commonly found in a particular host species, whilst unusual or exotic RVAs have also been reported. In most cases, these exotic rotaviruses are derived from RVA strains common to other host species, possibly through interspecies transmission coupled with reassortment events, whilst a few other strains exhibit novel genotypes/genetic constellations rarely found in other RVAs. The epidemiology and evolutionary patterns of exotic rotaviruses in humans have been thoroughly reviewed previously. On the other hand, there is no comprehensive review article devoted to exotic rotaviruses in domestic animals and birds so far. The present review focuses on the exotic/unusual rotaviruses detected in livestock (cattle and pigs), horses and companion animals (cats and dogs). Avian rotaviruses (group D, group F and group G strains), including RVAs, which are genetically divergent from mammalian RVAs, are also discussed. Although scattered and limited studies have reported rotaviruses in several exotic animals and birds, including wildlife, these data remain to be reviewed. Therefore, a section entitled “rotaviruses in exotic animals” was included in the present review.

Keywords Rotavirus · Diarrhea · Exotic strains · Exotic animals

Introduction

Rotaviruses (RV), members of the family *Reoviridae*, are a major cause of viral diarrhea in humans, animals and birds [24]. Globally, RVs have been associated with more than 100 million infections, 2 million hospitalizations and 600,000 deaths in children <5 years of age every year [106, 145]. Considering the severity of RV disease in humans, two live oral vaccines, Rotarix^{TM} (a monovalent vaccine manufactured by GlaxoSmithKline Biologicals, Belgium) and RotaTeq^{TM} (a pentavalent vaccine manufactured by Merck & Co., USA), have been successfully introduced in national immunization programs throughout the world [59]. RVs cause high rates of mortality and morbidity in farm animals, resulting in significant economic losses to the livestock industry [22, 24, 113]. However, compared with human RVs, studies on animal RVs are scattered and limited, and to date, there is a dearth of global data on RV-related deaths in different animals.

Mature RV particles consist of a triple layer icosahedral capsid enclosing the viral genome [24]. The RV genome is composed of eleven segments of double-stranded RNA encoding six structural (VP1–VP6) and six nonstructural (NSP1–NSP6) proteins [24]. The segmented RV genome exhibits considerable genetic diversity, with some genes found to be more divergent than others [24, 31, 77, 79, 80, 84]. The forces that govern RV genetic diversity include point mutations, reassortment, rearrangement and intra-genic recombination [24, 31]. Among them, accumulation of point mutations may cause genetic/antigenic drift, whilst reassortment events may lead to genetic/antigenic shift [24, 31, 77].

To date, RVs have been classified into at least eight groups/species (designated as RVA–RVH) on the basis of differences in the antigenicity of their middle capsid VP6

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Table 1 Rotavirus group/species detected so far in different mammalian and/or avian host species

Rotavirus group/species	Host species
A	A wide variety of mammalian and avian species
B	Humans, cattle, goats, pigs, rat and sheep
C	Humans, cattle, dogs, goats, juvenile ferrets and pigs
D	Chicken and turkey
E	Pigs
F	Chicken
G	Chicken
H	Humans and pigs

protein and nucleotide sequence identities of the VP6-encoding gene [5, 24, 87]. Among the eight RV groups, RVA, RVB, RVC and RVH are found in both humans and animals, whilst RVD–RVG have been detected only in animals and birds so far (Table 1). RVAs are the most common cause of viral diarrhea in the young of humans and a wide variety of animal species and birds [5]. The current animal and human RV vaccines are directed against RVAs [22, 24, 59, 60, 104, 105]. On the other hand, the other RV groups are detected less frequently [5, 24, 87]. Among them, RVBs have been detected in humans, cattle, goats, pigs, rat and sheep [65, 76, 87, 94, 129, 140]. RVCs have been reported from humans, cattle, dogs, goats, juvenile ferrets and pigs [15, 87, 94, 99, 146]. On the other hand, RVHs have been detected only in humans and pigs so far [87]. To date, RVE have been found only in pigs, whilst RVD, RVF and RVG have been reported only in birds [87].

The outer capsid of infectious RV particles consists of VP7 and VP4 proteins which elicit neutralizing antibodies in the host and confer resistance to virulent strains [24]. Therefore, information on the antigenic diversity of these proteins or on the diversity of the genes encoding them is crucial to devise future vaccine strategies and/or govern the efficacy of the current RV vaccines [24]. Since RVAs are a major cause of viral diarrhea in young mammals, the genetic diversity of their VP7- and VP4-genes have been studied extensively [81, 119]. To date, RVAs have been classified into at least 27 G and 37 P genotypes based on the differences in the nucleotide sequences of their VP7 and VP4 genes, respectively [84, 133, GenBank accession no. AB823215]. However, information on the diversity of the VP7 and VP4 genes may not be sufficient to obtain conclusive data on the overall genetic makeup and complex evolutionary patterns of RV strains, as the 11 segmented RV genome is susceptible to reassortment events [31]. Therefore, the Rotavirus Classification Working Group (RCWG) has introduced a whole-genome-based genotyping scheme, which is based on nucleotide sequence identity

Table 2 Common RVA VP7 (G-) and VP4 (P-) genotypes found in humans, domestic and companion animals

Host species	Typical RVA VP7 and VP4 genotypes
Humans	G1-G4, G9, G12, P[4], P[6], P[8]
Cattle	G6, G8, G10, P[1], P[5], P[11]
Pigs	G3-G5, G9, G11, P[6], P[7]
Horses	G3, G14, P[12]
Cats and dogs	G3, P[3], P[9]

cutoff percentages for each of the 11 RVA gene segments [79, 80, 84]. Under this system, the notation G_x-P_[x]-I_x-R_x-C_x-M_x-A_x-N_x-T_x-E_x-H_x (“x” denotes the genotype number) has been used to represent the complete genotype constellation (VP7–VP4–VP6–VP1–VP2–VP3–NSP1–NSP2–NSP3–NSP4–NSP5 genes, respectively) of a RVA strain. The RCWG genotyping system has proved to be an uniform and reliable platform for comparing the whole genomes of RVAs within and between different host species [31, 84].

RVA strains with certain genotype constellations, or VP7–VP4 (G–P) genotype combinations are commonly found in a particular host species, such as G1P[8], G2P[4], G3P[8], G4P[8], G9P[8] and to a lesser extent G12P[8] RVAs in humans, G6, G8 and G10 RVAs in combination with P[1], P[5] or P[11] in cattle, or G3–G5, G9 and G11 RVAs in conjunction with P[6] or P[7] in pigs [31, 77, 79–81, 84, 104, 105, 119] (Table 2). However, RVA strains with uncommon G–P combinations, often referred to as “exotic rotaviruses”, have also been detected in these and other host species [31, 73, 77, 79–81, 84, 104, 119]. In most cases, these exotic rotaviruses are derived from RV strains that are common to other host species, possibly through interspecies transmission coupled with reassortment events, such as bovine-like G6P[14] strains or porcine-like G5P[7] strains in humans [31, 73, 77, 79–81, 84, 119]. Barring a few exceptions, most of these exotic RVs have failed to spread effectively in the alien host species, pointing towards a fairly stringent host restriction [77]. On the other hand, some other RV strains are considered unusual because they possess unique genotypes/genetic constellation rarely found in nature, such as novel group RVs (RVH) or RVAs with rare genotypes [31, 84, 87].

The epidemiology and evolutionary patterns of exotic RVs in humans have been thoroughly reviewed by us [31] and other colleagues [18, 73, 81, 84, 87, 102, 119]. On the other hand, there is no comprehensive review article devoted to exotic rotaviruses in domestic animals and birds so far. The present review focuses on the exotic/unusual rotaviruses detected in livestock (cattle and pigs), horses and companion animals (cats and dogs). Avian RVs (RVD, RVF and RVG), including RVAs, which are genetically

divergent from mammalian RVAs, are also discussed. Although scattered and limited studies have reported rotaviruses in several exotic animals and birds, including wildlife, these data remain to be compiled and reviewed. Therefore, a section entitled “rotaviruses in exotic animals” was included in the present article.

Exotic/unusual rotaviruses in livestock, horses and companion animals

Cattle

G6, G8 or G10 RVAs possessing P[1], P[5] or P[11] are commonly found in cattle, with G6P[5] being the most predominant genotype combination among bovine RVAs [22, 104] (Table 2). In addition, RVA strains belonging to other VP7 genotypes (G1–G4, G5, G11, G12, G15, G17, G21 and G24) and VP4 genotypes (P[3], P[6], P[7], P[14], P[17], P[21], P[29] and P[33]) have been reported occasionally in cattle [91, 104]. Some of these genotypes are commonly detected in human RVAs (G1–G4, G12 and P[6]) and porcine RVAs (G3–G5, G11, P[6] and P[7]), whilst some others are avian-like (G17P[17]) or novel bovine genotypes (G15, G21, G24, P[21], P[29] and P[33]) [80, 91, 95, 104]. Unfortunately, only a few of these exotic bovine RVA strains have been analyzed for the whole or partial genome so far, providing limited insights into the complex evolutionary patterns of these unusual strains (Table 3).

Partial genomic analysis (VP4 [VP8*], VP6, VP7, NSP4 and NSP5 genes) of the bovine G3P[3] strains provided evidence for multiple reassortment events involving ruminant and simian strains [34]. By whole genomic analysis, bovine G5P[7] strains, isolated from cattle herds in South Korea, was found to be genetically closely related to porcine RVAs, including those from Korea, providing compelling evidence for porcine-to-bovine interspecies transmission events [47, 109]. Interestingly, during cross-species pathogenicity studies, the bovine G5P[7] strain induced diarrhea in calves and piglets, whilst its porcine counterpart caused diarrhea in piglets, but not in calves [109]. Since the whole genomes of both the strains were nearly identical, some of the mutations in these strains were thought to be associated with the differences observed in RVA pathogenicity [109]. In another whole genome-based study, two Korean bovine G5 strains were found to possess bovine RVA-like VP3 and VP4 genes on a porcine RVA genetic backbone [79, 107]. G6P[7] and G8P[7] RVA strains derived from multiple reassortment events involving bovine, porcine and human RVAs have also been reported from South Korea [108].

To date, P[14] RVAs have been detected in combination with one of the three major bovine VP7 genotypes (G6, G8

or G10) in different artiodactyl host species (ruminants and camelids) and in zoonotic human strains [73, 77, 82, 84]. However, in cattle, only G8P[14] and G10P[14] RVAs have been detected so far [13, 29, 104]. Although the whole genome of the bovine P[14] strains remain to be analyzed, whole genomic analyses of several other P[14] strains have revealed the existence of an overall consensus genotype constellation [(G6/G8)–P[14]–I2–(R2/R5)–C2–M2–(A3/A11)–N2–T6–(E2/E12)–H3] that might be circulating among ruminants, including common bovine RVAs, and other artiodactyl host species [82, 84]. Partial genomic analysis of the unusual bovine G18P[17] strain RVA/Cow-tc/DEU/993/83/1983/G18P[17] provided evidence for avian-to-bovine interspecies transmission events [57, 79, 80, 84, 117].

Among the bovine RVAs with novel genotypes, the G21P[29] and G24P[33] strains were isolated from asymptomatic cows [2]. Both strains shared eight genotypes with those of typical bovine RVAs, whilst their VP4, VP7 and NSP3 genes were assigned to new genotypes. Phylogenetically, within the VP6–I2 and NSP2–N2 RVA genotypes, strains RVA/Cow-wt/JPN/Azuk-1/2006/G21P[29] and RVA/Cow-wt/JPN/Dai-10/2007/G24P[33] strains appeared to be more closely related to simian or canine/feline rotaviruses than bovine rotaviruses, pointing towards possible interspecies transmission and multiple reassortment events involving bovine, simian and canine/feline RVAs. Interestingly, partial genomic analysis of two rare bovine G15P[21] RVAs also revealed VP6 genes that were more closely related to simian RVAs than bovine RVAs, whilst the NSP4 and NSP5 genes of these strains were of bovine origin [35]. By whole genomic analysis, bovine G15P[11] strain RVA/Cow-wt/ARG/B383/1998/G15P[11] exhibited a typical bovine RVA genotype constellation, except for the VP1, VP7, NSP1 and NSP4 genes, and shared a common origin with other ruminants and artiodactyls (Table 3) [82].

Sheep and goats

To date, only a few caprine and ovine RVA strains have been molecularly characterized [22]. Whole genomic analysis of a Chinese ovine strain RVA/Sheep-tc/CHN/Lamb-NT/XXXX/G10P[15] revealed the presence of novel VP4 (P[15]) and VP6 (I10) genotypes on an artiodactyl RVA-like genetic backbone [12] (Table 3). By whole genome sequencing, the unusual ovine P[14] strain RVA/Sheep-tc/ESP/OVR762/2002/G8P[14] was found to share a largely conserved genotype constellation with those of other artiodactyl RVAs [82]. The whole genome of only a single caprine RVA strain, RVA/Goat-tc/BGD/GO34/1999/G6P[1], has been analyzed so far, revealing a close evolutionary relationship with artiodactyl RVAs [36]. On the other hand, partial genomic analysis of an unusual Korean

Table 3 Genotype constellations of avian RVAs, RVAs from exotic animals, and unusual RVA strains detected in livestock and companion animals with those of selected common bovine, canine/feline, equine, human and porcine RVA strains

Strain	Genotypes										
	VP7	VP4	VP6	VP1	VP2	VP3	NSP1	NSP2	NSP3	NSP4	NSP5
Humans											
<i>RVA/Human-tc/USA/Wa/1974/G1P1A</i> [8]	G1	P[8]	I1	R1	C1	M1	A1	N1	T1	E1	H1
<i>RVA/Human-tc/USA/DS-1/1976/G2P1B</i> [4]	G2	P[4]	I2	R2	C2	M2	A2	N2	T2	E2	H2
<i>RVA/Human-tc/JPN/AU-1/1982/G3P3</i> [9]	G3	P[9]	I3	R3	C3	M3	A3	N3	T3	E3	H3
Cattle											
<i>RVA/Cow-tc/USA/NCDV/1967/G6P6</i> [1]	G6	P[1]	I2	R2	C2	M2	A3	N2	T6	E2	H3
<i>RVA/Cow-wt/IND/RUBV3/200X/G3P</i> [3]	G3	P[3]	I2	–	–	–	–	–	–	E2	H3
<i>RVA/Cow-wt/KOR/K5/2005/G5P</i> [7]	G5	P[7]	I5	R1	C1	M1	A1	N1	T1	E1	H1
<i>RVA/Cow-tc/KOR/KJ44/200X/G5P</i> [1]	G5	P[1]	I1	R1	C1	M2	A1	N1	T1	E1	H1
<i>RVA/Cow-tc/KOR/KJ75/200X/G5P</i> [5]	G5	P[5]	I1	R1	C1	M2	A1	N1	T1	E1	H1
<i>RVA/Cow-tc/KOR/KJ9-1/200X/G6P</i> [7]	G6	P[7]	I2	R2	C1	M2	A1	N2	T1	E2	H1
<i>RVA/Cow-tc/KOR/KJ9-2/200X/G6P</i> [7]	G6	P[7]	I2	R2	C2	M2	A3	N2	T6	E2	H3
<i>RVA/Cow-tc/KOR/KJ25-1/200X/G8P</i> [7]	G8	P[7]	I5	R1	C1	M2	A1	N1	T1	E1	H1
<i>RVA/Cow-wt/IND/BRV-68/200X/G8P</i> [14]	G8	P[14]	I2	–	–	–	–	–	–	E2	–
<i>RVA/Cow-wt/IND/RUBV81/200X/G10P</i> [14]	G10	P[14]	I2	–	–	–	–	–	–	E2	–
<i>RVA/Cow-wt/ARG/B383/1998/G15P</i> [11]	G15	P[11]	I2	R5	C2	M2	A13	N2	T6	E12	H3
<i>RVA/Cow-wt/IND/RUBV117/200X/G15P</i> [21]	G15	P[21]	I2	–	–	–	–	–	–	E2	H3
<i>RVA/Cow-tc/DEU/993/83/1983/G18P</i> [17]	G18	P[17]	I4	–	–	–	–	–	–	–	–
<i>RVA/Cow-wt/JPN/Azuk-1/2006/G21P</i> [29]	G21	P[29]	I2	R2	C2	M2	A13	N2	T9	E2	H3
<i>RVA/Cow-wt/JPN/Dai-10/2007/G24P</i> [33]	G24	P[33]	I2	R2	C2	M2	A13	N2	T9	E2	H3
Sheep/goat											
<i>RVA/Goat-tc/BGD/GO34/1999/G6P</i> [1]	G6	P[1]	I2	R2	C2	M2	A11	N2	T6	E2	H3
<i>RVA/Goat-tc/KOR/GRV/1998/G3P5</i> [3]	G3	P[3]	–	–	–	–	–	–	–	E3	–
<i>RVA/Sheep-tc/ESP/OVR762/2002/G8P</i> [14]	G8	P[14]	I2	R2	C2	M2	A11	N2	T6	E2	H3
<i>RVA/Sheep-tc/CHN/Lamb-NT/XXXX/G10P</i> [15]	G10	P[15]	I10	R2	C2	M2	A11	N2	T6	E2	H3
Pigs											
<i>RVA/Pig-tc/USA/OSU/1975/G5P9</i> [7]	G5	P[7]	I5	R1	C1	M1	A1	N1	T1	E1	H1
<i>RVA/Pig-tc/MEX/YM/1983/G11P9</i> [7]	G11	P[7]	I5	R1	C1	M1	A8	N1	T1	E1	H1
<i>RVA/Pig-wt/CHN/sh0902/2007/G1P</i> [7]	G1 ^a	P[7]	–	–	–	–	–	–	–	E1	–
<i>RVA/Pig-wt/SVN/P21-5/2004/G1P</i> [27]	G1	P[27]	–	–	–	–	–	–	–	E9	–
<i>RVA/Pig-wt/THA/CMP034/2000/G2P</i> [27]	G2	P[27]	I5	–	–	–	–	–	–	E9	H1
<i>RVA/Pig-wt/CAN/AB82/2006/G2P</i> [34]	G2 ^b	P[34]	I5/14	R1	C1	M1	A8	N1	T7	E9	H1
<i>RVA/Pig-tc/VEN/A131/1998/G3P9</i> [7]	G3	P[7]	I5	R1	C2	M1	A1	N1	T1	E1	H1
<i>RVA/Pig-wt/THA/CMP29/08/2008/G3P</i> [13]	G3	P[13]	I5	R1	C1	M1	A8	N1	T1	E1	H1
<i>RVA/Pig-wt/THA/CMP48/08/2008/G3P</i> [23]	G3	P[23]	I5	R1	C1	M1	A8	N1	T1	E1	H1
<i>RVA/Pig-wt/IND/HP140/2002/G6P</i> [13]	G6	P[13]	I2	–	–	–	–	–	–	E1	H1
<i>RVA/Pig-wt/THA/CMP45/08/2008/G9P</i> [23]	G9	P[23]	I5	R1	C1	M1	A8	N1	T7	E1	H1
<i>RVA/Pig-wt/VEN/A253/1998/G11P9</i> [7]	G11	P[7]	R1	C2	M1	A1	N1	T1	E1	H1	R1
<i>RVA/Pig-wt/IND/RU172/2002/G12P</i> [7]	G12	P[7]	I5	R1	C1	M1	A1	N1	T1	E1	H1
Horses											
<i>RVA/Horse-wt/IRL/03V04954/2003/G3P</i> [12]	G3	P[12]	I6	R2	C2	M3	A10	N2	T3	E2	H7
<i>RVA/Horse-wt/ARG/E403/2006/G14P</i> [12]	G14	P[12]	I2	R2	C2	M3	A10	N2	T3	E12	H7
<i>RVA/Horse-wt/ARG/E3198/2008/G3P</i> [3]	G3	P[3]	I3	R3	C3	M3	A9	N3	T3	E3	H6
<i>RVA/Horse-tc/JPN/HH-22/1989/G3P</i> [12]	G3	P[12]	I6	R2	C2	M3	A10	N2	T3	E2	H7
<i>RVA/Horse-tc/GBR/H-1/1975/G5P9</i> [7]	G5	P[7]	I5	R1	C1	M1	A8	N1	T1	E1	H1
<i>RVA/Horse-tc/JPN/OH-4/1982/G6P</i> [5]	G6	P[5]	I2	R2	C2	M2	A13	N2	T6	E2	H3

Table 3 continued

Strain	Genotypes										
	VP7	VP4	VP6	VP1	VP2	VP3	NSP1	NSP2	NSP3	NSP4	NSP5
RVA/Horse-tc/GBR/L338/1991/G13P[18]	G13	P[18]	I6	R9	C9	M6	A6	N9	T12	E14	H11
Cats											
<i>RVA/Cat-tc/AUS/Cat97/1984/G3P[3]</i>	G3	P[3]	I3	R3	C2	M3	A9	N2	T3	E3	H6
RVA/Cat-wt/ITA/BA222/2005/G3P[9]	G3	P[9]	I2	R2	C2	M2	A3	N1	T3	E2	H3
RVA/Cat-tc/AUS/Cat2/1984/G3P[9]	G3	P[9]	I3	R3	C2	M3	A3	N1	T6	E3	H3
Birds											
RVA/Turkey-tc/IRL/Ty-3/1979/G7P[17]	G7	P[17]	I4	–	–	–	–	–	–	E11	–
RVA/Turkey-tc/IRL/Ty-1/1979/G17P[17]	G17	P[17]	I4	–	–	–	–	N4	–	E4	–
RVA/Pigeon-tc/JPN/PO-13/1983/G18P[17]	G18	P[17]	I4	R4	C4	M4	A4	N4	T4	E4	H4
RVA/Chicken-tc/DEU/02V0002G3/2002/G19P[30]	G19	P[30]	I11	R6	C6	M7	A16	N6	T8	E10	H8
RVA/Chicken-tc/DEU/06V0661/2006/G19P[31]	G19	P[31]	I11	–	–	–	–	–	–	–	H8
RVA/Turkey-tc/DEU/03V0002E10/2003/G22P[39]	G22	P[35]	I4	R4	C4	M4	A16	N4	T4	E11	H4
RVA/Pheasant-tc/DEU/10V0112H5/2010/G23P[37]	G23	P[37]	I4	R4	C4	M4	A16	N10	T4	E4	H4
Exotic animals											
Non-human primates											
RVA/Simian-tc/ZAF/SA11-H96/1958/G3P5B[2]	G3	P[2]	I2	R2	C5	M5	A5	N5	T5	E2	H5
RVA/Simian-tc/ZAF/SA11-Both/1958/G3P5B[2]	G3	P[2]	I2	R2	C5	M5	A5	N2	T5	E2	H5
RVA/Simian-tc/ZAF/SA11-30/19/1958/G3P[1]	G3	P[1]	I2	R2	C5	M5	A5	N5	T5	E2	H5
RVA/Simian-tc/ZAF/SA11-5S/1958/G3P[1]	G3	P[1]	I2	R2	C5	M5	A5	N5	T5	E2	H5
RVA/Simian-tc/USA/RRV/1975/G3P[3]	G3	P[3]	I2	R2	C3	M3	A9	N2	T3	E3	H6
RVA/Macaque-tc/USA/YK-1/XXXX/G3P[3]	G3	P[3]	–	–	–	–	–	–	–	E3	–
RVA/Rhesus-tc/USA/TUCH/2002/G3P[24]	G3	P[24]	I9	R3	C3	M3	A9	N1	T3	E3	H6
RVA/Macaque-tc/PTRV/1990/G8P[1]	G8	P[1]	I2	R2	C2	M2	A3	N2	T6	E2	H3
Hoofed mammals											
RVA/Antelope-wt/ZAF/RC-18/08/2008/G6P[14]	G6	P[14]	I2	R2	C2	M2	A11	N2	T6	E2	H3
RVA/Guanaco-wt/ARG/Rio_Negro/1998/G8P[1]	G8	P[1]	I2	R5	C2	M2	A11	N2	T6	E12	H3
RVA/Guanaco-wt/ARG/Chubut/1999/G8P[14]	G8	P[14]	I2	R5	C2	M2	A3	N2	T6	E12	H3
RVA/Vicuna-wt/ARG/C75/2010/G8P[14]	G8	P[14]	I2	R2	C2	M2	A?	N2	T6	E3	H?
Bats											
RVA/Bat-tc/CHN/MSLH14/2012/G3P[3]	G3	P[3]	I8	R3	C3	M3	A9	N3	T3	E3	H6
RVA/Bat-tc/KEN/KE4852/07/2007/G25P[6]	G25	P[6]	I15	R8 ^c	C8	M?	A?	N8	T11	E2	H10
Rodents											
RVA/Mouse-tc/USA/EB-Po/1982/G16P[16]	G16	P[16]	I7	R7	C7	M8	A7	N7	T10	E7	H9
RVA/Mouse-tc/USA/ETD_822/XXXX/G16P[16]	G16	P[16]	I7	R7	C7	M8	A7	N7	T10	E7	H9
RVA/Mouse-tc/BRA/EHP/1981/G16P[20]	G16	P[20]	–	–	–	–	A7	–	–	E7	–
Rabbits											
RVA/Rabbit-tc/CHN/N5/1992/G3P[14]	G3	P[14]	I17	R3	C3	M3	A9	N1	T1	E3	H2
RVA/Rabbit-tc/ITA/30/96/1996/G3P[14]	G3	P[14]	I2	R2	C2	M3	A9	N2	T6	E5	H3
Giant panda											
RVA/Giant panda-tc/CHN/CH-1/2008/G1P[7]	G1 ^a	P[7]	I5	R1	C1	M1	A1	N1	T1	E1	H1

The common bovine, canine/feline, equine, human and porcine RVA strains are italicised

^a The VP7 genes of strains sh0902 and CH-1 were most closely related to each other, and shared low nucleotide sequence identities (< 90 %) with those of other G1 strains [46, 148]

^b The porcine G2 VP7 gene was found to be genetically distinct from those of human G2 strains, and has been referred to as G2-like [16, 17, 61, 71, 75]

^c Only partial nucleotide sequence of the VP1 gene of strain KE4852/07 was obtained, which could not be assigned to any of the known VP1-R genotypes, and therefore, was tentatively designated as R8 [23]

“–” indicates that no nucleotide sequence data were available in the GenBank database

caprine G3P[3] strain, RVA/Goat-tc/KOR/GRV/1998/G3P5[3], provided evidence for reassortment events and/or interspecies transmission of canine, feline and/or simian RVAs [66].

Pigs

RVA strains exhibiting G3–G5, G9 or G11 in combination with P[6] or P[7] are prevalent in pigs [104] (Table 2). Although several other VP7 genotypes (G1, G2, G6, G8, G10, G12 and G26) and VP4 genotypes (P[5], P[8], P[11], P[13], P[14], P[19], P[23], P[26], P[27], P[32] and P[34]) have been detected sporadically in porcine RVA strains [91, 104], the genomes of only a handful of these unusual RVAs have been analyzed so far. Several novel VP4 genotypes have been identified in porcine RVAs, such as P[13], P[19], P[23], P[26], P[27], P[32] and P[34]. Interestingly, many of these (G1P[27], G2P[23], G2P[27], G2P[32], G2P[34]) have been reported in combination with common human VP7 genotypes [75, 84, 104]. However, the porcine G2 VP7 gene was found to be genetically distinct from those of human G2 strains, and has been referred to as G2-like [16, 17, 61, 71, 75]. The whole genomes of a few of the porcine strains with novel VP4 genotypes (G2P[34], G3P[13], G3P[23] and G9P[23] strains) have been analyzed so far, and these strains were found to share most of their genotypes with those of typical porcine RVAs, although evidences for intragenotype and intergenotype reassortment events have also been obtained [63, 75, 97, 121] (Table 3).

G12 RVAs are rapidly emerging as important human pathogens [81]. On the other hand, G12 RVAs have rarely been reported in pigs so far [32, 91]. To date, the whole genome of only a single porcine G12 RVA strain RVA/Pig-wt/IND/RU172/2002/G12P[7] has been analyzed [32, 37]. Strain RU172 was hypothesized to be derived from porcine–human reassortment events, or alternatively, it was believed that the Wa-like human and porcine G12 strains might have originated from a common ancestor, and eventually evolved (by genetic drift and shift) with time [37]. The VP7 gene of a porcine G1P[7] RVA strain RVA/Pig-wt/CHN/sh0902/2007/G1P[7] was found to be more closely related (nucleotide sequence identity of 98.5 %) to that of a giant panda RVA strain CH-1 and shared low nucleotide sequence identities (<90 %) with those of other G1 strains, whilst its VP4 and NSP4 genes of sh0902 were closely related to porcine or porcine-like RVA strains [148].

Although bovine RVA-like VP7 (G6, G8 and G10) and VP4 (P[1], P[5] and P[11]) genotypes have been reported in porcine RVAs [33, 62, 70, 91, 104, 110, 112], information on the overall genetic makeup of these atypical strains are lacking so far. However, partial genomic analysis of two porcine G6P[13] RVA strains, RVA/Pig-wt/

IND/HP113/2002/G6P[13] and RVA/Pig-wt/IND/HP140/2002/G6P[13] revealed bovine-like VP6 and VP7 genes and porcine-like NSP4 and NSP5 genes, providing evidence for bovine–porcine reassortment events [33]. Whole genomic analysis of porcine RVA strains RVA/Pig-tc/VEN/A131/1998/G3P9[7] and RVA/Pig-wt/VEN/A253/1998/G11P9[7] revealed a bovine RVA-like VP2 gene on a porcine RVA genetic backbone [79, 80].

Horses

G3P[12] and G14P[12] RVA strains have been frequently reported in horses worldwide [105] (Table 2). By whole genomic analysis, several of the common equine RVAs have been found to share a largely conserved genotype constellation (G3/G14–P[12]–I2/I6–R2–C2–M3–A10–N2–T3–E2/E12–H7) [40, 86]. RVAs with unusual G–P combinations, such as G3P[3], G5P[7], G6P[1], G6P[5], G8P[1], G10P[1], G10P[11] and G13P[18], have also been detected in horses on single occasions [10, 14, 30, 39, 40, 44, 54–56, 92, 128]. The whole genomes of a few of these unusual equine RVAs have been determined so far, providing interesting insights into animal-to-animal interspecies transmission and reassortment events (Table 3).

Equine G3P[3] RVA strain RVA/Horse-wt/ARG/E3198/2008/G3P[3] was shown to originate from interspecies transmission event(s), possibly coupled with one or more reassortment events, involving feline, canine or related host species [92]. All the eleven gene segments of equine G5P[7] strain RVA/Horse-tc/GBR/H-1/1975/G5P9[7] were found to be closely related to porcine or porcine-like RVAs, suggesting porcine-to-equine interspecies transmission events [39]. The whole genome of equine RVA strain RVA/Horse-tc/JPN/OH-4/1982/G6P[5], exhibiting a bovine RVA-like G6P[5] genotype combination, was found to be more closely related to those of bovine and bovine-like human RVA strains, providing conclusive evidence for bovine-to-equine interspecies transmission events [40]. Equine RVA strain RVA/Horse-tc/JPN/HH-22/1989/G3P[12] was shown to possess a bovine RVA-like NSP4 gene on a typical equine RVA genetic backbone, pointing towards possible reassortment events involving bovine and equine RVAs [40]. The unusual equine G3P[18] RVA strain RVA/Horse-tc/GBR/L338/1991/G13P[18] exhibited a unique genotype constellation (G13–P[18]–I6–R9–C9–M6–A6–N9–T12–E14–H11), and is thought to be derived from interspecies transmission events involving unknown host species [86].

Cats and dogs

Most feline RVAs have been found to belong to the G3P[3] or G3P[9] genotype combination, whilst most canine

RVAs exhibit G3P[3] specificities [85] (Table 2). The whole genomes of a limited number of feline RVAs, canine RVAs and canine/feline-like human RVAs have been sequenced so far, revealing the presence of at least three genogroups (based on genotype constellations) among these strains, designated as Cat-97-like (G3–P[3]–I3–R3–C2–M3–A9–N2–T3–E3–H6), AU-1-like (G3–P[9]–I3–R3–C3–M3–A3–N3–T3–E3–H3) and BA222-05-like (G3–P[9]–I2–R2–C2–M2–A3–N1/N2–T6/T3–E2–H3) [85]. Most of the canine and feline strains were found to belong to the stable feline/canine Cat-97-like genogroup [85]. On the other hand, feline G3P[9] RVA strain RVA/Cat-wt/ITA/BA222/2005/G3P[9] was found to possess several genes related to artiodactyl or artiodactyl-like human RVAs, and a human RVA-like NSP2 gene belonging to the N1 genotype [74, 85]. However, several preliminary studies have reported strains which could belong to the BA222-05-like genogroup, suggesting that the BA222-05-like genotype constellation might be truly circulating in feline and canine/feline-like human RVAs worldwide [85]. Another feline strain, RVA/Cat-tc/AUS/Cat2/1984/G3P[9], was speculated to be derived from multiple reassortment events involving canine, feline, human and bovine RVAs [134], and later shown to be a reassortant between RVAs of the Cat-97-like and BA222-05-like genogroups [85].

Avian rotaviruses

Rotaviruses have been associated with diarrhea and growth retardation [runting and stunting syndrome (RSS)] in birds [24, 89, 100]. To date, RVA, RVD, RVF and RVG have been reported from avian species [87]. Among them, RVAs are the most prevalent RVs in birds [24, 89, 101, 120]. RVDs have also been frequently detected in avian species, especially in turkeys [89, 101, 115, 132]. On the other hand, avian RVs belonging to RVF and RVG have been detected occasionally [89, 101]. Despite being an important pathogen in birds, there is a dearth of data on the genetic diversity of avian RVs.

Avian RVAs

The complete genomes of only a chicken, a pheasant, a pigeon and a turkey RVA strain have been analyzed so far, revealing genotype constellations that are entirely different from those of mammalian RVAs [57, 131, 133] (Table 3). In addition, the partial genomes (VP4, VP6, VP7 and NSP5 genes) of six chicken and two turkey RVA strains have also been reported [120]. Based on nucleotide and deduced amino acid sequence identities and phylogenetic analyses, the avian RVA strains were found to be more closely related to each other than to those of RVAs from other host species and were genetically divergent from mammalian

RVAs. Interestingly, the VP4 gene of the pheasant RVA strain RVA/Pheasant-tc/DEU/10V0112H5/2010/G23P[37] was found to be more closely related to those of RVAs from pigs, dogs and humans [133]. This gene was assigned a novel VP4 genotype (P[37]), and is believed to be either derived from avian–mammalian reassortment events, or may be an unusual avian VP4 genotype [133]. Several amino acid sequences conserved in mammalian RVAs have been found to be mutated in avian RVA strains [120]. Most of the chicken RVAs were found to lack the putative open reading frame (ORF) encoding the NSP6 protein, which is retained in gene segment 11 of most mammalian RVAs [120]. Limited studies conducted so far have revealed considerable genetic diversity among the avian RVA strains, such as the detection of multiple VP7 (G7, G17–G19, G22 and G23) and VP4 (P[17], P[30], P[31] P[35] and P[37]) genotypes, differences in the complete genotype constellations, especially between the chicken and the pheasant, pigeon and turkey RVA strains, evidence for reassortment events and the presence of insertions into the untranslated regions (UTR) of some of the gene segments [57, 80, 84, 120, 131, 133]. Notable among these insertions is the presence of an adenine-rich insertion (124 nt and 256 nt long, respectively) in the 3'-UTR of the NSP1 gene of the chicken (strain RVA/Chicken-tc/DEU/02V0002G3/2002/G19P[30]) and pheasant (strain 10V0112H5) RVA strains [131, 133]. Interestingly, the NSP1 genes of avian RVAs were found to be more closely related to that of RVD than those of mammalian RVAs [132].

RVAs from heterologous host species have been rarely reported in birds. A study in Brazil reported G6P[1] RVAs with NSP4-E2 genotype and bovine RVA NCDV like electrophoretic migration patterns from turkeys, providing preliminary evidence for bovine-to-avian interspecies transmission events [4]. RVAs exhibiting mammalian (bovine) RVA-like electropherotypes have also been detected in diarrheic chicken in India [142].

Avian RVDs, RVFs and RVGs

RVDs have been detected in chickens and turkeys in different countries [89, 101, 115, 132], and have also been found to induce diarrhea in ringneck pheasant chicks (*Phasianus colchicus*) following experimental inoculation [49]. Unlike avian RVAs, RVDs cannot be propagated in MA104 cells [21]. Whilst avian RVAs have a predilection for the duodenum, RVDs have been shown to have a preference for the cells of the jejunum and ileum [49]. Upon electrophoresis in polyacrylamide gels, RVDs have been found to exhibit a characteristic 5:2:2:2 RNA migration patterns [24]. To date, the complete genome of only a single avian RVD strain has been analyzed [132].

The entire genome sequence of strain RVD/Chicken-wt/DEU/Ch-49/2005/GXP[X] consisted of 18,500 nucleotides. Each of the 11 gene segments was found to contain an open reading frame encoding a protein with homologies to cognate RV proteins. The gene segment 11 lacked an ORF encoding a protein with homologies to the NSP6 protein. Interestingly, the gene segment 10 was found to contain two partially overlapping open reading frames (designated as ORF-1 and ORF-2), with ORF-1 encoding a relatively short NSP4 protein. By phylogenetic analysis, all the 11 gene segments of strain Ch-49 did not cluster consistently with one of the other RV groups, pointing towards a separate evolution of RVDs. However, RVDs appear to share a more common ancestry with RVAs and RVCs than with strains of other RV groups. Many conserved amino acid positions in the functionally important domains of the proteins of RVAs and RVBs were found to be retained in Ch-49. The nucleotide sequences at the termini of all the 11 gene segments of RVD strain Ch-49 were nearly identical to those of RVAs.

RVF and RVG were first detected in chickens in 1984 [90]. Both the groups have been rarely detected in birds and their role in avian diarrhea is unclear [89, 101]. The segmented RNA genomes of RVF and RVG strains exhibit characteristic electrophoretic migration patterns in polyacrylamide gels, which are distinct from those of other RVs [24]. To date, the whole genomes of a single RVF and a RVG strain have been analyzed [64]. The complete genomes of strains RVF/Chicken-wt/DEU/03V0568/2003/GXP[X] and RVG/Chicken-wt/DEU/03V0567/2003/GXP[X] were 18341 bp and 18186 bp long, respectively. All the 11 gene segments of both strains contained open reading frames for the VP1–VP4, VP6, VP7 and NSP1–5 RV proteins. Phylogenetically, RVF was found to cluster with RVA, RVC and RVF, whilst RVG clustered with RVB and RVH. However, considerable genetic diversity was observed between these RV groups within a cluster. The 5'-termini sequences of RVF and RVG were found to be largely conserved with those of other RV groups, whilst different 3'-terminal consensus sequences were observed between RVA/RVD/RVF, RVC and RVB/RVD/RVH.

Rotaviruses in exotic animals and birds

Non-human primates

Rotaviruses or antibodies to rotaviruses have been detected in a wide variety of non-human primate species, such as baboons, chimpanzee, gorillas, hanuman langurs, mangabeys, pygmy marmosets, pig-tailed macaques, rhesus macaques, vervet monkeys and wild cynomolgus monkeys [6, 9, 11, 52, 53, 58, 69, 88, 98, 125, 143, 144]. However, many of these reports are from captive animals. Among the

simian RVAs reported so far, strains RVA/Simian-tc/ZAF/SA11-H96/1958/G3P5B[2] and RVA/Simian-tc/USA/RRV/1975/G3P[3] have been used extensively as standard models to study the replication and pathogenesis of rotaviruses. Moreover, human-simian reassortants derived from RRV formed the basis of the first commercially licensed RVA vaccine (Rotashield™, Wyeth Laboratories) [60]. The whole genomes of only a few simian RVA strains (SA11 and its derivatives, RRV, RVA/Macaque-tc/PTRV/1990/G8P[1] and RVA/Rhesus-tc/USA/TUCH/2002/G3P[24] have been determined so far [83, 124]. Among them, strain SA11-H96 was found to be not closely related genetically to any other known RVAs, except for a human strain B10 from Kenya, which, however, was shown to be a zoonotic rotavirus of possible simian origin [38, 83]. Therefore, SA11-H96 has been considered as the most likely representative of a typical simian RVA genogroup [83]. The different laboratory derivatives of SA11 (SA11-30/19, SA11-5S and SA11-Both) were found to possess bovine RVA genes on a SA11 genetic backbone, possibly resulting from tissue culture contamination of SA11 with the “O” agent, a bovine G8P6[1] RVA strain [124].

Simian RVA strain PTRV likely originated from interspecies transmission of artiodactyl (bovine) RVAs to a colony of pig-tailed macaques [83]. Most of the gene segments of strains RRV and TUCH exhibited genotypes more typical of canine/feline RVAs [83]. However, within these genotypes, low levels of genetic relatedness were observed between RRV or TUCH and the typical canine/feline or canine/feline-like RVAs, indicating that any possible interspecies transmission of a canine/feline progenitor strain to simian host species did not happen recently. The remaining genes of RRV and TUCH were shown to be derived from reassortment events involving human, bovine, or other RVA strains [83]. The partial genome (VP7, VP4 and NSP5 genes) of another simian RVA strain, RVA/Macaque-tc/USA/YK-1/XXXX/G3P[3], isolated from a 2-year-old immunodeficient pig-tailed macaque with chronic diarrhea, was found to be closely related to that of simian RVA strain RRV [143].

Hoofed mammals

Rotaviruses have been reported in many exotic hoofed mammals, such as alpaca, antelope, bison, boar, deer, desert camel, gazelle, guanaco, gnu, giraffe, impala, okapi, reindeer, wild hog and wild vicuna [3, 7, 9, 25, 48, 82, 93, 96, 103, 114, 116, 122, 135]. However, the genomes of only a few of these RVA strains have been studied so far, providing limited insights into the evolutionary patterns of these viruses. Whole genomic analyses of a sable antelope RVA strain and two guanacos RVA strains provided evidence for common origin of these strains with ovine and

other ruminant RVAs, corroborating the presence of an overall consensus genotype constellation (G6/G8)–P[14]–I2–(R2/R5)–C2–M2–(A3/A11)–N2–T6–(E2/E12)–H3 that might be circulating among ruminants, camelids and other artiodactyl host species [82] (Table 3).

The VP7 and VP4 genes of a giraffe rotavirus strain were found to be closely related to those of bovine RVAs [93]. G9P[23], G4P[23], G9P[13] and G4P[6] RVA strains have been reported from Japanese wild boars (*Sus scrofa leucomystax*) migrating close to human habitats in Japan [96]. Phylogenetic analyses of the VP7 and VP4 genes of these strains with those of co-circulating porcine RVAs provided evidence for natural transmission of rotaviruses between domestic pigs and wild boars. Recently, the whole genome sequence of a camel RVA strain (RVA/Camel-wt/KUW/s21/2010/G10P[15]) has been determined [103]. The VP2, NSP2, NSP3 and NSP5 genes of strain s21 were found to exhibit high nucleotide sequence similarities to those of ovine and bovine RVAs, whilst its VP1 gene shared nucleotide sequence identities of <90 % with those of porcine RVAs. The VP4, VP6 and VP7 genes of the camel RVA strain exhibited nucleotide sequence similarities of <88, <82 and <83 %, respectively, to those of reference strains from ruminants. The NSP4 gene of strain s21 was assigned to a novel genotype, E15.

In another recent study, whole genome of a RVA strain (RVA/Vicuna-wt/ARG/C75/2010/G8P[14]) from a wild vicuna, one of the four species of native South American camelids, was analyzed [7]. Strain C75 exhibited a G8–P[14]–I2–R2–C2–M2–Ax–N2–T6–E3–Hx genotype constellation. Except for the NSP3 gene, the partial genome of C75 was found to share close evolutionary relationships with those of RVAs from other artiodactyl host species, especially with guanaco RVA strain Chubut in at least five gene segments (VP7, VP4, VP2, VP3 and NSP3).

Bats

RVAs have been detected in straw-colored fruit bats (*Eidolon helvum*) and lesser horseshoe bats (*Rhinolophus hipposideros*) [23, 50]. By whole genomic analysis, the VP2, VP6, VP7, NSP2, NSP3 and NSP5 genes of a fruit bat RVA strain (RVA/Bat-tc/KEN/KE4852/07/2007/G25P[6]) were assigned to novel genotypes C8, I15, G25, N8, NSP3 and NSP5, respectively [23]. Only partial nucleotide sequence of the VP1 gene of strain KE4852/07 was obtained, which could not be assigned to any of the known VP1-R genotypes and was genetically distinct from cognate genes of other RVAs [23]. Phylogenetically, the VP2, VP6, VP7, NSP2, NSP3 and NSP5 genes of KE4852/07 were found to share ancestry with other mammalian RVAs, but appeared to be distantly related. The NSP4 gene was closely related to those of bovine, human, ovine and simian

RVAs within the E2 genotype, whilst the VP4 gene shared high sequence identities with human P[6] RVAs. Taken together, strain KE4852/07 was proposed to be derived from multiple reassortment events involving human, animal and bat rotaviruses [23].

In a recent study, another bat RVA strain, RVA/Bat-tc/CHN/MSLH14/2012/G3P[3]), was successfully isolated from lesser horseshoe bats in China [50]. By whole genomic analysis, strain MSLH14 exhibited a G3–P[3]–I8–R3–C3–M3–A9–N3–T3–E3–H6 genotype constellation, similar to those observed in feline/canine-like human and animal RVAs [50]. Phylogenetically, strain MSLH14 appeared to be a distant relative of feline/canine RVAs, and is believed to represent a true bat RVA strain [50]. Strain MSLH14 was found to highly pathogenic to suckling mice [50].

Rodents

Although mice have been used as a reliable animal model to study RV replication and pathogenesis, limited information is available on the overall genetic makeup and genetic diversity of murine RVAs. To date, the whole genomes of only two murine RVA strains, strain RVA/Mouse-tc/USA/EB-Po/1982/G6P[16] (Genbank accession nos. JF309297–JF309307) and strain RVA/Mouse-tc/USA/ETD_822/XXXX/G6P[16] (GenBank accession nos. GQ479947–479957), and the partial genomes of a few other murine RVAs have been sequenced, revealing several novel genotypes (G16/G20–P[16]–I7–R7–C7–M8–A7–N7–T10–E7–H9) not reported in RVAs from other host species so far [84]. Nucleotide sequence identities between cognate gene segments of strains EB-Po and ETD_822 ranged from 89 % (VP4 gene) to 94 % (VP7, NSP4 and NSP5 genes), providing evidence for genetic diversity among the murine RVAs. In a recent study, the NSP5 genes of RVA strains detected from rats in a pig farm in Brazil were found to be closely related to porcine RVAs [20].

In addition to RVAs, RVBs have been detected in rats [140]. The whole genome of a single murine GBR strain, RVB/Rat-tc/USA/IDIR/1984/G1P[X], has been sequenced so far, revealing significant genetic diversity between the murine RVBs and RVBs from other host species (cattle, pigs and humans) [84, 147]. Rotaviruses have also been reported from squirrels [27, 43].

Lapines

RVAs have been detected in rabbits in different countries, and most of these strains are found to belong to G3P[14] or G3P[22] specificities [8, 45, 72, 78, 84]. To date, the whole genomes of only two lapine RVA strains (strains RVA/Rabbit-tc/CHN/N5/1992/G3P[14] and RVA/Rabbit-tc/ITA/30/96/1996/G3P[14]) have been analyzed [45, 78, 79]. Strain

N5 was found to possess a novel VP6 genotype (I17), and is believed to be of canine/feline origin, or was a multiple reassortant involving canine, feline and human rotaviruses [45]. Strain 30/96 belonged to the novel NSP4-E5 genotype, which has been reported in lapine or lapine-like human strains so far, whilst its remaining genes shared genotypes with those of RVAs from other host species, providing evidence for complex interspecies transmission and reassortment events [78, 79, 84]. RVAs have also been detected in hares [67].

Wild carnivores

Rotaviruses or RV antibodies have been reported from a wide variety of wild carnivores, such as badgers, coyote, civet, ferrets, red fox, skunk and wild dogs [1, 26, 28, 130, 138, 146]. The VP7 and VP4 gene sequences of a RVA strain (RVA/Raccoon dog-wt/JPN/RAC-DG5/2004/G3P[9]) from a Japanese raccoon dog and a RVA strain (RVA/Civet-wt/JPN/MP-CIVET66/2005/G3P[9]) from a masked palm civet (*Paguma larvata*) have been analyzed so far, providing preliminary evidence for interspecies transmission from humans or cats [1]. The VP6 gene of one of the RVC strains from juvenile ferrets has been sequenced, and was found to be closely related to bovine RVC strain RVC/Cow-tc/JPN/Shintoku/1991/G2P[3] [146].

In addition to above host species, rotaviruses have also been detected in giant pandas, a wide variety of exotic birds (ducks, emu, love birds, ostrich, partridges, pheasants, reed bunting, velvet scoter and wild pigeon), marsupials (kangaroo, sugar glider and opossum), aquatic mammals (galapagos sea lion), wild bivalve molluscs and wild tree shrews [19, 41, 42, 46, 51, 68, 84, 111, 123, 126, 127, 136, 137, 139, 141]. The VP7 gene of a RVA strain (RVA/Pheasant-wt/HUN/Phea14246/2008/G23P[X]) from a pheasant was assigned to a novel genotype G23 [136], whilst the VP7 and VP4 genes of the sugar glider RVA strain (RVA/Sugarglider-wt/JPN/SG33/2010/G27P[36]) was found to belong to novel genotypes G27 and P[36], respectively [84, GenBank accession no. AB823215]. Recently, the whole genome of a RVA strain (RVA/Giant panda-tc/CHN/CH-1/2008/G1P[7]) isolated from a giant panda has been sequenced, revealing a G1–P[7]–I5–R1–C1–M1–A1–N1–T1–E1–H1 genotype constellation [46]. Rotavirus-like particles have been isolated from aquatic animals, such as striped bass (*Morone saxatilis*), turbot (*Scophthalmus maximus*), smelt (*Osmerus mordax*) and Atlantic salmon (*Salmo salar*) in North America and Europe [118].

Conclusions

The present study is the first of its kind to exclusively review the detection and genetic diversity of unusual

rotaviruses in animals and rotaviruses in exotic animals. The detection of unusual rotavirus strains has always aroused interest among researchers. To date, the genomes of a significant number of exotic human rotavirus strains have been analyzed, providing a plethora of information on animal-to-human interspecies transmission and reassortment events [31, 77, 84]. On the other hand, as evident from this review, studies on unusual rotaviruses from livestock, horses and companion animals are limited and the genomes of only a handful of these strains have been analyzed so far. Genomic analyses of these unusual animal rotavirus strains have greatly expanded our understanding of the complex genetic diversity of rotaviruses. Several novel genotypes and/or genotype constellations were identified and evidence for rare interspecies transmission and reassortment events were obtained. Rotaviruses have also been detected in a wide variety of exotic animals/wildlife, and to date, conclusive evidence for simian-to-human and lapine-to-human interspecies transmission events have been obtained by whole genome-based studies [38, 78]. Molecular characterization of RVs from different exotic animals/birds/wildlife have revealed complex evolutionary patterns, including detection of several novel RV groups/species and genotypes, contributing significantly to the existing knowledge on genetic diversity of RVs. However, the genomes of only a few of the RVs from exotic animals and birds have been analyzed so far. Considering the above, future research should lay emphasis on the following aspects:

1. Although RVA strains with certain G–P combinations are commonly found in a particular animal host species, whilst others are considered unusual to that host, it should be noted that these observations are based on limited studies. Approximately ~110,000 human RVA strains were genotyped from 1996 to 2008, whilst only ~1,100 porcine and ~3,200 bovine RVAs have been genotyped over the last three decades [104]. Therefore, extensive surveillance studies may be required to monitor the actual prevalence of the various RVA genotypes, including those now considered as unusual, in different animals and birds. In humans, genotypes, such as G9 and G12, initially thought to be unusual, were later shown to be widely prevalent globally by extensive surveillance studies [81].
2. The whole genome-based-genotype classification system has provided a reliable platform for comparing the whole genomes of RVAs from different host species [31, 84]. Although RVA strains have been detected in a wide variety of animal and avian species, the whole genomes of only a limited number of these strains have been analyzed so far, revealing volumes of new data

on the overall genetic diversity of RVAs. Therefore, efforts should be made to perform large-scale whole genomic analysis of common and unusual RVAs from different animals and birds.

3. RVAs have been detected in a wide variety of exotic animals/wildlife. Therefore, constant surveillance and whole genomic analysis of RVAs from different species of exotic animals/wildlife should be performed to investigate the possibilities of interspecies transmission of RVs from wildlife to humans and domestic animals. Moreover, as evident from previous reports (compiled under section “Rotaviruses in exotic animals and birds”), such studies would yield novel data on the genetic diversity of RVAs.
4. Most of the studies on animal and avian rotaviruses have focused on surveillance and genetic diversity of RVAs, whilst limited data is available on the non-RVA rotaviruses. Efforts should be made to study the prevalence and overall genetic diversity of animal and avian RVs belonging to the other groups, i.e., RVB-RVH strains.

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