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Review of global rotavirus strain prevalence data from six years post vaccine licensure surveillance: Is there evidence of strain selection from vaccine pressure?

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Abstract

Comprehensive reviews of pre licensure rotavirus strain prevalence data indicated the global importance of six rotavirus genotypes, G1P[8], G2P[4], G3P[8], G4P[8], G9P[8] and G12P[8]. Since 2006, two vaccines, the monovalent Rotarix (RV1) and the pentavalent RotaTeq (RV5) have been available in over 100 countries worldwide. Of these, 60 countries have already introduced either RV1 or RV5 in their national immunization programs. Post licensure vaccine effectiveness is closely monitored worldwide. This review aimed at describing the global changes in rotavirus strain prevalence over time. The genotype distribution of the nearly 47,000 strains that were characterized during 2007–2012 showed similar picture to that seen in the preceding period. An intriguing finding was the transient predominance of heterotypic strains, mainly in countries using RV1. Unusual and novel antigen combinations continue to emerge, including some causing local outbreaks, even in vaccinated populations. In addition, vaccine strains have been found in both vaccinated infants and their contacts and there is evidence for genetic interaction between vaccine and wild-type strains. In conclusion, the post-vaccine introduction strain prevalence data do not show any consistent pattern indicative of selection pressure resulting from vaccine use, although the increased detection rate of heterotypic G2P[4] strains in some countries following RV1 vaccination is unusual and this issue requires further monitoring.

Keywords

Surveillance; Rotarix; RotaTeq; Genotype; Rotavirus

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1. Introduction

From 2006 onward, two rotavirus vaccines, the monovalent Rotarix (RV1) and the pentavalent Rotateq (RV5) have been licensed in >100 countries worldwide and have been recommended by the World Health Organization (WHO) for routine immunization of all children worldwide (Dennehy, 2008; WHO, 2009a). As of May 2014, 60 countries worldwide have introduced either RV1 and/or RV5 into their national childhood immunization programs (PATH, 2014). RV1 is a monovalent vaccine composed of a single human-derived rotavirus strain of G1P[8] specificity, whereas RV5 is a pentavalent vaccine containing bovine-human reassortant rotaviruses expressing human surface antigens of G1–G4 and P[8] (Parashar et al., 2006; Cortese et al., 2009). Whereas the composition of RV1 and RV5 is different, the multiple vaccine doses administered a few weeks apart imitate the role of sequential natural rotavirus infections in infants and young children, which stimulate the development of both type specific (i.e. homotypic) and heterotypic protective immunity against a variety of group A rotavirus (RVA) strains (Velazquez et al., 1996).

Efficacy, safety and strain-specific effectiveness of RVA vaccines are being closely monitored in post licensure surveillance. Rotavirus strain surveillance targets the characterization of both neutralization antigens, VP7 or G and VP4 or P, of RVAs. Previous reviews on rotavirus strain prevalence (using G and P type data) focused on the pre vaccine licensure period. Three major reviews reported global prevalence data and several regional reviews summarized relevant information from a continent or a WHO region (Gentsch et al., 2005; Santos and Hoshino, 2005; Bányai et al., 2012; Usonis et al., 2012; Ogilvie et al., 2011; Khoury et al., 2011; Todd et al., 2010; Castello et al., 2004; Sanchez-Padilla et al., 2009). The largest data set analyzed so far included over 100,000 strains between 1996 and 2007 to provide baseline data for evaluation of any possible changes in strain distribution following vaccine introduction (Bányai et al., 2012). That study listed >70 individual G–P antigen combinations from 281 studies and 100 countries worldwide, and, together with other major reviews, highlighted the spatiotemporal fluctuation of genotype prevalence in various populations without vaccine pressure. During the 1990s and 2000s at least 2 novel strains, G9P[8] and G12P[8], emerged to become medically important globally in addition to the historically well known four endemic strains, G1P[8], G2P[4], G3P[8], and G4P[8]. In fact, the emerging variants of G9 and G12 strains were inferred to have spread worldwide over the course of a decade to become, respectively, the 5th and 6th most commonly reported RVA strains (Matthijnssens et al., 2010). In addition to these six globally important genotypes, some strains have been demonstrated to be locally or regionally important. Historical examples include G5P[8] strains in South America and G8P[6] strains in parts of Africa (Cunliffe et al., 2000, 2010; Alfieri et al., 1996; Gouvea et al., 1994).

With the availability of vaccines and the observation that newly emerging RVAs may reshape the global landscape of medically important strains, it has become even more important to monitor strain prevalence to assess vaccine effectiveness against various RVA strains. Strain surveillance will also allow studies of the evolution and epidemiology of field strains under vaccine immune selective pressure, to identify possible breakthrough events and genetic interplay between vaccine and field strains. The objective of this review is to gather information about spatial and temporal changes in strain prevalence and summarize reports

about possible vaccination associated changes during the first six years of vaccine use. To obtain the required information, we reviewed studies reporting RVA prevalence data from 2007 onward and abstracted data on reported G–P combinations. In addition, strain characterization studies (such as those reporting whole genome sequences or sequencing and phylogenetic analyses of neutralization antigens) were also evaluated and combined with prevalence surveys if background information suggested that data from different sources could be merged.

2. Medically important RVA strains

From 2007 to 2012 the genotypes of 46,967 RVA strains were reported from a total of 81 countries (Table 1). Of the whole data set, 8224 strains were characterized in the WHO African region (AFR), 2341 in the Eastern Mediterranean region (EMR), 6756 in the Americas region (AMR), 14,438 in the European region (EUR), 5728 in the South East Asia region (SEAR), and 9480 in the Western pacific region (WPR) (Fig. 1). Among the 60 countries with a national RV immunization program, 15 were found to have reported post licensure prevalence data. Globally, the most commonly reported six strains were found in ~73% of the samples (G1P[8], 31.2%; G2P[4], 13.0%; G3P[8], 10.7%; G9P[8], 10.2%; G4P[8], 5.0%; G12P[8], 2.7%), or in ~87% of specimens (out of 39,403) when non-typeable strains and mixed infections were removed before the calculation.

At the level of WHO regions, the combined prevalence of the six common genotypes ranged from 62.7% (AFR) to 96.9% (EUR). G1P[8] strains predominated in all but one WHO region; the only exception was AMR, where G2P[4] strains were relatively more commonly reported. On the contrary, among the globally common strains, the prevalence of G4P[8] and G12P[8] strains was negligible in several regions (e.g., WPR: G4P[8], 0.8%; G12P[8], 0.1%; EMR: G12P[8], 0.2%; SEAR: G4P[8], not detected). All other common genotypes had >1% prevalence (regional ranges in the whole study period: G1P[8], 20.4–47.7%; G2P[4], 10.0–29.2%; G3P[8], 2.6–34.4%; G4P[8], up to 15.5%; G9P[8], 7.9–16.6%; G12P[8], 0.1–10.1%). Furthermore, in the AFR an additional seven genotypes were found at a prevalence greater than 1%, including G2P[6] (8.2%), G1P[6] (6.0%), G3P[6] (5.5%), G12P[6] (3.5%), G8P[6] (1.7%), G8P[4] (1.8%), and G1P[4] (1.1%). These data demonstrate that genotype P[6] RVA strains continue to circulate at marked prevalence in the AFR. Somewhat less genotype diversity among medically important strains was seen in the AMR (G1P[6], 2.1%; G9P[6], 2.2%; G9P[4], 1.7%), in the EMR (G2P[6], 3.9%; G1P[6], 3.8%; G1P[4], 1.8%; G9P[6], 1%), in the SEAR (G12P[6], 14.9%; G9P[4], 1.6%; G1P[6], 1.2%; G9P[6], 1.1%), and in the WPR (G4P[6], 2.4%; G3P[4], 1%). No additional prevalent strains were found in EUR. Of note is that several of the regionally common strains were reported from single countries that contributed a disproportionately large number of strains to the regional total. Thus, the regional prevalence data may be somewhat biased by the relative significance of unusual strains reported from countries with greater sample size analyzed.

In order to study annual fluctuation of RVA strains within and between countries, data were summarized at the level of study sites of reporting countries whenever possible. With this approach temporal and spatial changes were observed both in countries with and without a rotavirus vaccination program (Fig. 2). Predominance and sustained circulation of G1P[8]

strains was observed in parts of North America, and many countries in the EMR and the EUR and even in selected countries within the AFR and the WPR, where G1P[8] strains were otherwise regionally not prevalent. Genotype G2P[4] was predominant in many countries utilizing RV1 in their childhood immunization program, including Latin American countries and Belgium and Austria in Europe (Braeckman et al., 2012; Gurgel et al., 2009; Nakagomi et al., 2008; Paulke-Korinek et al., 2013; Peláez-Carvajal et al., 2014). However, territories in Australia using RV5 as well as several countries worldwide with low vaccine usage also reported high G2P[4] prevalence that was sustained over consecutive years (Fig. 2). Among the historically important genotypes, G3P[8] was reported to prevail in several study sites in the United States and Australia using RV1 and RV5 vaccine, but this genotype was also prevalent in several countries without universal rotavirus vaccination programs including Thailand, Germany, Argentina and the Reunion Island, as well as some SEAR countries (e.g., China, Japan, and Vietnam), where it has been prevalent over consecutive years (Breiman et al., 2012; Caillère et al., 2013; Chen et al., 2013; Ngo et al., 2009; Hull et al., 2011; Kamiya et al., 2011; Kuzuya et al., 2014; Kirkwood et al., 2007, 2008, 2009, 2010, 2011; Li et al., 2009; Maiklang et al., 2012; Stupka et al., 2012; Pietsch et al., 2009, 2011; Thongprachum et al., 2013; Wang et al., 2009, 2011; Zeng et al., 2010). Genotype G4P[8] strains were reported to prevail in a few countries worldwide (e.g., Ivory Coast, Estonia, Greece, Hungary, and Russia) typically during a single epidemic season, and G4P[8] strains were also predominant at some Australian RV1 sites (Akoua-Koffi et al., 2014; Karamoko and Dabonne, 2013; Kirkwood et al., 2007, 2008, 2009, 2010, 2011; Koukou et al., 2011; László et al., 2012; Soeorg et al., 2012; Trimis et al., 2011; Zhirakovskaya et al., 2012). Finally, many countries worldwide reported transient increase in the frequency of genotypes G9P[8] and G12P[8] that emerged during the 1990s, including some high vaccine coverage areas within the USA (Fig. 2).

3. Minority and novel wild-type RVA strains

No globally emerging new strains were identified in the past six years, but several locally or regionally important strains were recognized including some with partially or fully heterotypic serotypes compared to the two vaccines (Fig. 2). One example is G9P[4] strains identified in Guatemala and Bangladesh during 2009–2010 and 2011, respectively (Quaye et al., 2013; Afrad et al., 2013). G12P[6] strains predominated in Nepal between 2007 and 2011 and in Malawi in 2007, G1P[6] and/or G2P[6] prevailed in some study years in Columbia, Gambia and Iraq, and G4P[6]s were locally important in some regions of Hungary and South Korea during 2008 (Ahmed et al., 2013; Ansari et al., 2013; Gauchan et al., 2013; Jeong et al., 2011; Kwambana et al., 2014; László et al., 2012; Peláez-Carvajal et al., 2014; Sherchand et al., 2009, 2012; Steele et al., 2012). Another example of a regionally emerging genotype is G6P[6], recently reported in several African countries among genotyped strains (prevalence range 3.4–17.6%) (Nordgren et al., 2012a,b; Page et al., 2014). In addition, phylogenetic analyses identified a possible epidemiological linkage between African and European G6P[6] strains (Nordgren et al., 2012b; Ianiri et al., 2013). A bovine RVA related human strain, G10P[14], was described in several individuals of an aboriginal population in Australia vaccinated with RV1 (Cowley et al., 2013).

Two VP4 genotypes, P[6] and P[11], were originally associated with asymptomatic infections on neonatal wards (Das et al., 1994; Gentsch et al., 1993; Dunn et al., 1993; Sukumaran et al., 1992; Gorziglia et al., 1986). Subsequent studies, however, found P[6] to be very common among pathogenic strains. The most salient example is the high prevalence of genotype P[6] among RV patients in many sub-Saharan countries of Africa (Todd et al., 2010). RVA strains bearing genotype P[11], have been also detected in children with diarrhea in several countries worldwide, including India, Pakistan, Estonia, Slovenia, and Italy (Table 2).

In previous comprehensive reviews which collected and published data from the pre licensure period, at least 74 G–P combinations were identified. In studies of published data for the 2007–2012 period, an additional 11 new antigen combinations were identified, each from sporadic cases. These included a G14P[24] strain from the USA that contained simian-, equine- and bovine RVA related genes in the whole genomic configuration, a G3P[25] strain and a G5P[19] from Taiwan both carrying porcine RVA related genes in their genomes, two G6P[1] strains from Pakistan closely related to bovine RVA strains in their VP4 and VP7 genes, a G10P[15] rotavirus identified in China that shared over 99% VP4 and VP7 gene sequence identities with ovine rotaviruses, two G8P[9] detected in Australia, a G2P[3] strain from Turkey, a G2P[14] strain from Gambia, a G3P[24] from the USA, a G1P[5] strain from Bangladesh, and a G2P[5] strain from Mali (Breiman et al., 2012; Hwang et al., 2012; Kirkwood et al., 2011; Kwambana et al., 2014; Staat et al., 2011; Tamim et al., 2013; Tapisiz et al., 2011; Weinberg et al., 2013; Zhang et al., 2012). Some of the rare strains were detected from diarrheic patients during vaccine trials and the shared genotypes with vaccine strains indicate a possible vaccine strain origin (Table 2).

4. Detection and evolution of vaccine strains in patients with diarrhea

The mechanisms of attenuation and potential reversion to regain the virulent phenotype of rotavirus vaccine strains are unknown. A temporal association between vaccination and diarrhea in a low proportion of vaccinees has been documented in large vaccine trials as well as during strain surveillance in the post licensure period (Payne et al., 2010; Bowen and Payne, 2012; Boom et al., 2012; Donato et al., 2012). In addition, vaccine derived strains have been described in contacts of vaccinees and even in patients without history of vaccination or apparent contact with a vaccinated infant. For some of these cases only RV1/RV5 derived strains but no other common enteropathogens were detected, suggesting that the vaccine strains could have (re)gained a pathogenic phenotype.

Concerning putative RV5 derived vaccine strains, several G6 and/or P[5] RVAs were identified in RV5 vaccine trials suggestive of vaccine origin of the identified strains in infants. The G6 VP7 and P[5] VP4 genotypes are components of the RV5 vaccine and are co-expressed with the human-derived P[8] VP4 and G1–G4 VP7 antigens, respectively, as individual reassortants (Fig. 3A). Of note is that in these vaccine trials no further analysis was conducted to provide evidence for the possible bovine parental RVA strain (i.e. WC3) origin of the G6 VP7 or the P[5] VP4 antigens (Breiman et al., 2012). Following the introduction of RV5 in routine vaccination programs, only few authors have reported detailed molecular analysis of vaccine derived strains. For example, Payne et al. (2010) used

a genome sequencing approach to demonstrate that the identified G1P[8] strain detected in a 30 month old US child suffering from diarrhea was fully RV5 vaccine origin. Because both G1 VP7 and P[8] VP4 specificities are expressed on separate reassortants of the pentavalent vaccine, identification of a single G1P[8] strain is consistent with reassortment between two RV5 vaccine strains. Boom et al. (2012) described four RV5 derived vaccine strains by partial genome sequencing (including only VP3, VP4, VP6 and VP7 genes). Donato et al. (2012) described 13 RV5 derived strains from Australian patients by targeting only four genes (VP3, VP4, VP6 and VP7). Of these, four patients were found to shed vaccine derived (vd) G1P[8] reassortants. Hemming and Vesikari (2012, 2014) reported several vdG1P[8] strains in diarrheic patients from Finland by sequencing of selected genes; one report from Finland raised the possibility that vaccine-derived strains may be acquired from the community. Bucardo et al. (2012) demonstrated for the first time the possible rescue of a RV5 origin NSP2 gene in wild-type G1P[8] strains detected in two Nicaraguan children. Altogether, some data indicate that vdG1P[8] reassortants of the RV5 strains might be more transmissible and more virulent in humans than the original vaccine component strains individually.

With regard to RV1 origin strains, Rose et al. (2013) reported several cases from Brazil demonstrating natural reassortment events between the RV1 vaccine strain and wild-type strains (Fig. 3B). Among the reassortants identified were two mono-reassortant strains; one strain carried an RV1 derived VP1 gene on the configuration of a wild-type strain and another strain carried a wild-type derived VP2 gene on the configuration of the RV1 vaccine strain. Another reassortant strain carried the VP2, NSP1 and NSP5 gene from a wild-type strain, whereas the remaining genes were of RV1 vaccine strain origin. In addition, Boom et al. (2012), in their aforementioned paper, reported a RV1 associated case by sequencing of the VP7, VP4 and NSP2 genes, where the affected child was non-vaccinated and had no contact history with a vaccinated child.

5. Concluding remarks

In a previous review, we described the decline of the historically dominant G1P[8] strains over time between 1996 and 2007, and the simultaneous global emergence of G9P[8] and G12P[8] strains (Bányai et al., 2012). Analysis of new data in the vaccine post licensure period indicates the resurgence of G1P[8] strains to become the most prevalent genotype in many countries worldwide although not to levels described in earlier reviews. The sustained predominance of G2P[4] strains reported in the Americas and parts of Europe and Australia, where RV1 vaccine is used in national immunization programs, raised concerns whether this strain that is fully heterotypic to the G1P[8] strain in RV1 was being selected because of vaccine pressure (Grimwood and Kirkwood, 2008; Matthijnssens et al., 2009, 2012). However, contemporary data from other countries in the same regions with low rates of RV1 use as well as from countries using RV5 indicates sustained prevalence of G2P[4] strains in these countries as well, diminishing the initial concern that a fully heterotypic strain may overwhelm a highly vaccinated population. Nevertheless, the very high prevalence of G2P[4] strains reported in some countries after implementation of RV1 vaccination is highly unusual, and this issue requires further monitoring.

Although the emergence and transient predominance of fully heterotypic strains in countries using either RV1 or RV5 were observed, in several instances fully or partially homotypic strains replaced these fully heterotypic strains over several years post-vaccine implementation. Furthermore, many pre-licensure and post-licensure studies have shown that both RV1 and RV5 have high effectiveness against non-vaccine strains (Justino et al., 2011; Yen et al., 2011; Braeckman et al., 2012; Cortese et al., 2013; Patel et al., 2013). Despite these reassuring findings, it is important to note that among the 60 countries which introduced RV1 and/or RV5 in national immunization programs (PATH, 2014), only a few have so far reported detailed, longitudinal strain prevalence data, and thus it is not possible to exclude the possibility of some strain selection related to vaccine pressure over several years after vaccine implementation.

Regardless, an important question that we need to ask is what the implication of a putative vaccine use associated strain selection would be? Currently there is no conclusive evidence associating RVA genotype and disease severity. Furthermore, although from a historical perspective it may be very unusual for genotype G2P[4] to predominate for several years, one needs to remember that a single genotype, G1P[8], predominated over several consecutive years in many countries during the 1980s to late 1990s (Hull et al., 2011; Bányai et al., 2009a,b; Arista et al., 2006). In some studies the long term prevalence of G1P[8] strains was linked to antigenic drift and intra-typic shift leading to new combinations of different co-circulating G1 VP7 and P[8] VP4 variants (lineages) (Bányai et al., 2009a,b; Arista et al., 2006). Natural fluctuation of the common RVA strains during consecutive seasons may attest to their fitness; however, vaccine breakthrough events may result from lineage changes in VP4, VP7 and other rotavirus genes. Recent sequencing studies have identified marked intra-typic heterogeneity even within G2P[4] strains, thus their unusual epidemiology in high vaccine use countries need to be reconsidered in relation to the emergence of the novel genetic and antigenic variants of G2P[4] strains (Do et al., 2014; Dennis et al., 2014; Donato et al., 2014; Giammanco et al., 2014).

With continued enhanced RVA surveillance in the post-licensure period additional new genotypes were identified in humans, most typically from sporadic cases. Sequencing of several genes or the full genomes of many of these strains often uncovered relationships with animal RVAs. Animal origin RVAs identified, for example, were the bovine/ovine origin G6, G8, and P[14] specificities (de Rougemont et al., 2011; Wu et al., 2012; Swiatek et al., 2010; Steyer et al., 2009; Cowley et al., 2013; Mullick et al., 2013), the porcine origin G5, P[6], and P[19] genotypes (Mladenova et al., 2012; Komoto et al., 2013; Hwang et al., 2012; Wu et al., 2011b), the feline/canine origin G3, P[3] and P[9] specificities (Luchs et al., 2012; Hwang et al., 2011), and more interestingly the putative equine origin G14 specificity (Weinberg et al., 2012, 2013). Phylogenetic analyses of sporadic rare strains in the respective studies were not consistent with regard to the epidemiological relationships among the spatially isolated cases. For example, human RVA strains carrying the P[3] and P[9] VP4 genotype specificities detected in different locations appear to be more similar to each other and often to the putative canine and feline hosts (Luchs et al., 2012; Hwang et al., 2011), whereas bovine/ovine-like P[14] or porcine-like P[6], P[19] and P[25] strains detected at various geographic locations appear to be more diverse genetically (Wu et al., 2011a,b; Mladenova et al., 2012). So far, very few strains have been characterized in

sufficient detail; therefore one cannot make conclusions about possible differences in the driving forces of these specificities in their respective host species. Nonetheless, all these findings raise the possibility that rare RVA genotypes detected in humans originate from local gene pools harbored by one or multiple animal host species with humans merely a heterologous dead end host for these rare strains, whereas other strains might have some limited potential for human-to-human transmissibility and thus, are able more readily to disperse geographically.

Whereas the mechanisms and the potential implications of possible selection of heterotypic strains by vaccine pressure, including those that are currently considered uncommon remain to be understood, evidence has been published that vaccine strains may exchange genetic material with wild type strains (Bucardo et al., 2012; Rose et al., 2013). Such mechanisms were identified for both vaccines indicating that either single-gene or multi-gene reassortment could lead to new strains potentially pathogenic to infants. Although mechanisms of attenuation and reversion still await exploration, the detection of vaccine strain derived genes in virulent reassortant wild-type strains during the post licensure surveillance period has implications for routine surveillance methods. The laboratory protocol recommended for strain monitoring relies on amplified fragment length polymorphism driven by genotype specific primers (WHO, 2009b). However, currently used primer cocktails do not contain some of the genotype specificities expressed by RV5. Furthermore, this approach cannot be used to differentiate vaccine and wild-type strains. Alternative methods may be needed, particularly because typing primers may cross react with heterotypic strains and emergence of new sequence variants may lead to reduced reactivity with the homotypic primer. Furthermore, the number of individual typing primers in a cocktail is another limiting factor. One possible alternative to address these issues is to use unbiased massively parallel sequencing of whole genomes to obtain new insight into mechanisms of evolution within and between field RVA strains and vaccine strains.

In conclusion, the post-vaccine introduction strain prevalence data in countries using either RV1 or RV5 do not show any consistent pattern indicative of selection pressure resulting from vaccine use. The six genotype combinations responsible for a majority of infections in most of the world remained medically important during 2007–2012. Only a few putative novel candidates for possible new pandemics were identified, including some rapidly spreading genotypes, such as G6P[6] and G9P[4], in Africa and Latin America, respectively, whose genetically closely related counterparts have been identified in several continents. The question of whether strain evolution over the long term will result in declining vaccine effectiveness to particular types or whether escape mutants due to completely novel gene constellations will emerge is still open. The observed dominance of the fully heterotypic G2P[4] strains in some countries in some years following RV1 vaccination is unusual, however, and this issue requires further monitoring. As more post-vaccine implementation data on strain diversity become available from many low-income countries in Africa that have recently introduced either RV1 or RV5 in routine childhood immunization programs and from high and middle income countries that have been using for vaccines for several years, further evidence of vaccine selection pressure on circulating rotavirus strains should be examined.

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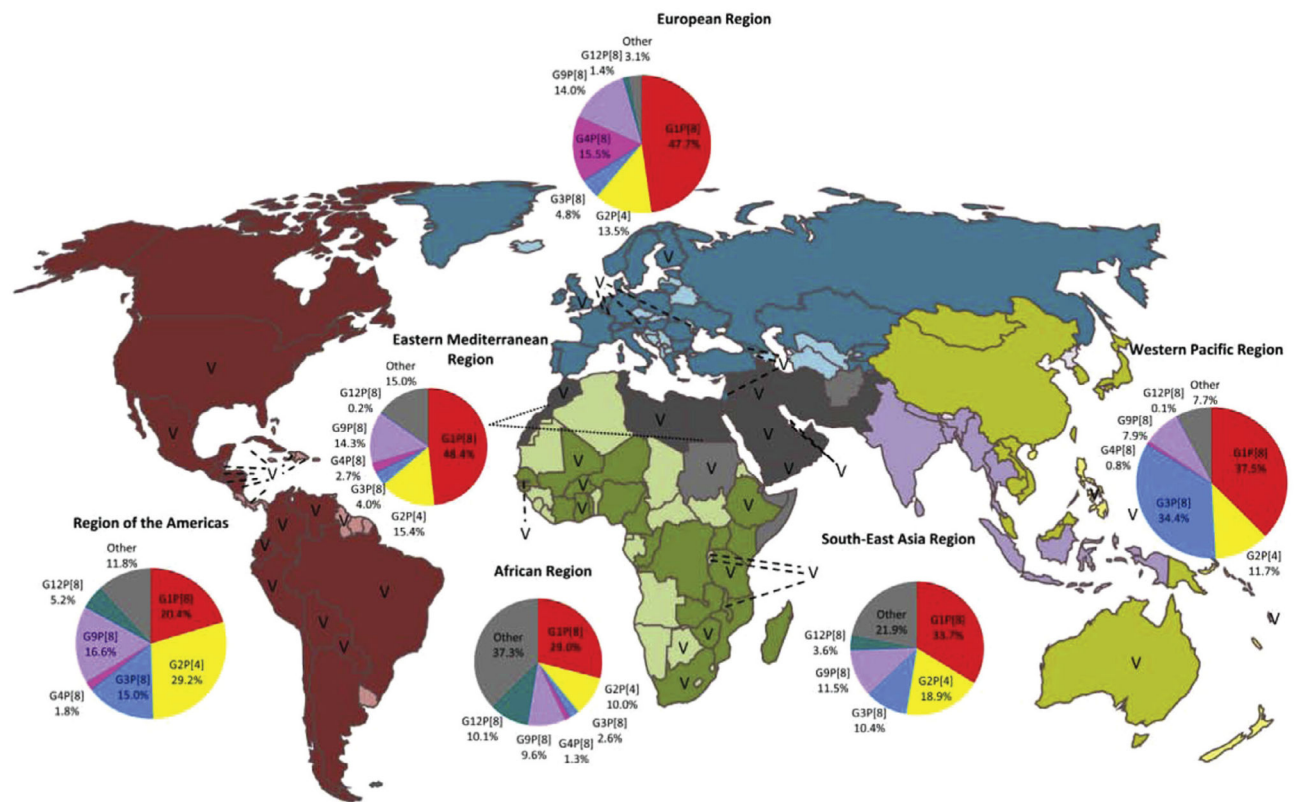
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**Fig. 1.**

Geographical distribution of medically important RVA strains between 2007 and 2012.

WHO regions are highlighted by various colors; dark shade shows countries providing data from any given region. In addition to the six globally common G–P combinations, regionally common, unusual and rare strains are also shown and referred to as ‘Other’. Mixed infection with multiple G and/or P types and non-typeable strains were not included in the calculations.

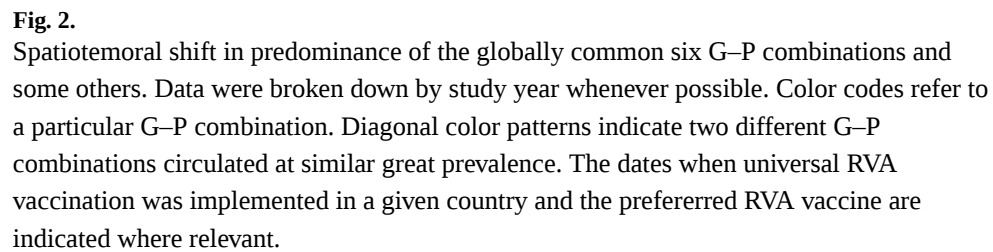


Fig. 2. Spatiotemoral shift in predominance of the globally common six G–P combinations and some others. Data were broken down by study year whenever possible. Color codes refer to a particular G–P combination. Diagonal color patterns indicate two different G–P combinations circulated at similar great prevalence. The dates when universal RVA vaccination was implemented in a given country and the preferred RVA vaccine are indicated where relevant.

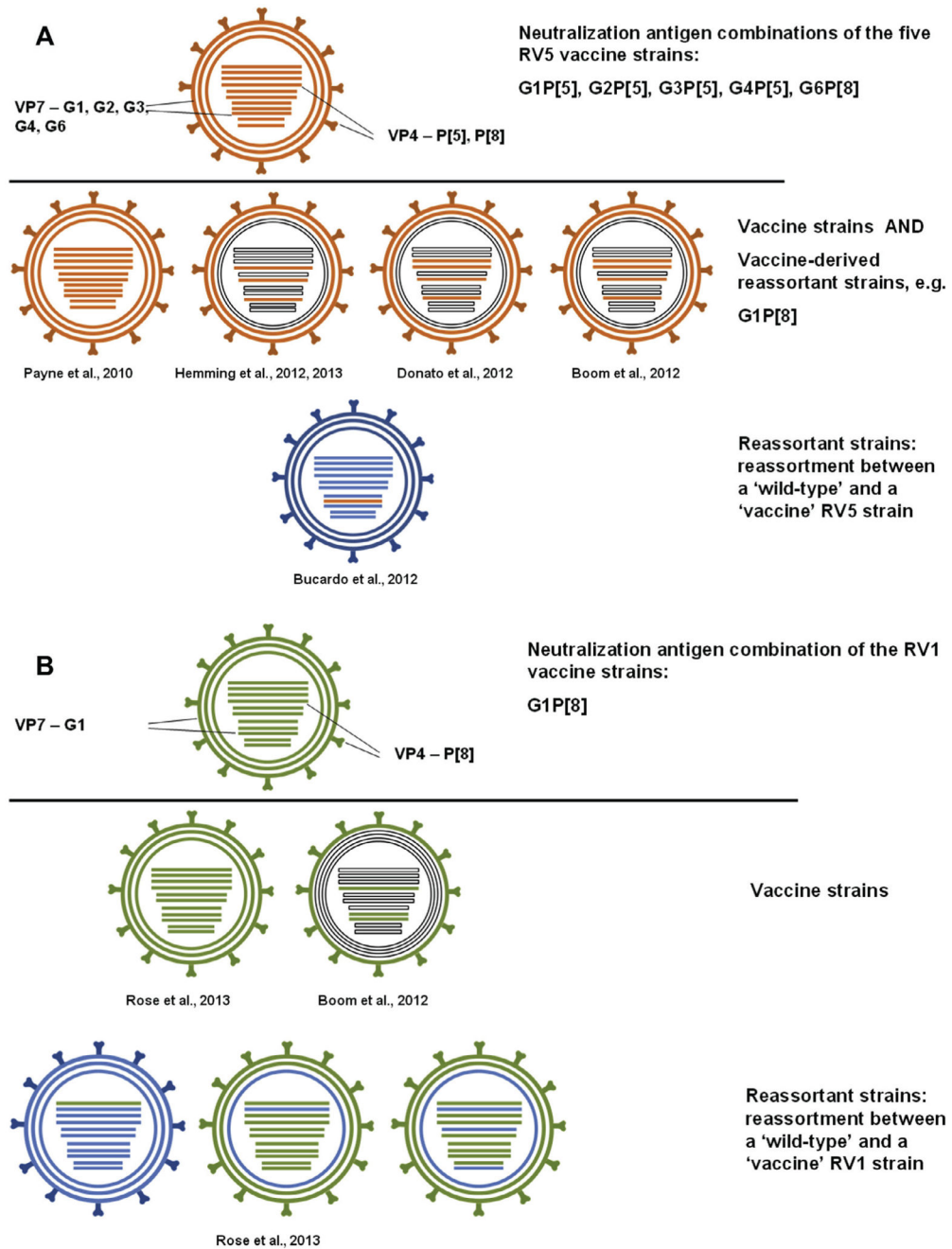


Fig. 3. Evolution of RV vaccines. The virions and the parental genomic constellations of RV1 and RV5 are shown in orange and green, respectively. Wild type strains are represented by blue color. Missing sequence information is shown as empty bars.

Table 1

Countries reporting RVA strain prevalence in humans, 2007–2012.

Country	Year of sample collection	No. of strains	G1P[8]	G2P[4]	G3P[8]	G4P[8]	G9P[8]	G12P[8]	OTHERS	NT	Mix	Refs.
<i>African region</i>												
African Rotavirus Surveillance Network (Ghana, Kenya, Uganda, Zambia, Cameroon, Tanzania, Zimbabwe, Ethiopia)	JUN 2006–2012	4638	954	295	129	68	361	293	1330	609	599	Mwenda et al. (2010, 2014)
Burkina Faso	DEC 2009–MAR 2011	156	16	7			66		47	9	11	Nordgren et al. (2012a,b)
Cameroon	2010–2011	135		8	1		1	73	40	7	5	Ndze et al. (2013)
Ethiopia	AUG 2007–MAR 2012	215	44	23			9	37	67	11	24	Abebe et al. (2014)
Gambia	2008–2010	204	52	5					124	19	4	Kwambana et al. (2014)
Ghana	APR 2007–FEB 2011	1015	224	73	7		6	3	249	239	214	Breiman et al. (2012), Enweronu-Laryea et al. (2013)
Ivory Coast	DEC 2007–JUN 2010	90	22	9	8	16	0		19		16	Karamoko and Dabonne (2013), Akoua-Koffi et al. (2014)
Kenya	APR 2007–AUG 2011	246	76	1			62		56	38	13	Breiman et al. (2012), Kiulia et al. (2014)
Madagascar	FEB 2008–MAY 2009	104	15				51		13	25		Razafindratsimandresy et al. (2013)
Malawi	2006–2007	131	25	2			11	6	76	9	2	Cunliffe et al. (2010), Steele et al. (2012)
Mali	APR 2007–MAR 2009	370	201	16			4		127	22		Breiman et al. (2012)
Niger	APR 2010–MAR 2012	449	14	167			16	154	29	39	30	Page et al. (2014)
Nigeria	JUN 2010–JAN 2011	19		1				6	1	11		Japhet et al. (2012)
Réunion Island	AUG 2012–NOV 2012	20			15			4			1	Caillière et al. (2013)
South Africa	2012	123	2	16			7	54	38	2	4	Iyaloo et al. (2013)
Tanzania	JAN 2010–JUN 2012	309	161	2			1		107		38	Hokororo et al. (in press), Moyo et al. (2014)

Country	Year of sample collection	No. of strains	G1P[8]	G2P[4]	G3P[8]	G4P[8]	G9P[8]	G12P[8]	OTHERS	NT	Mix	Refs.
Total		8224	1806	625	160	84	595	630	2323	1040	961	
<i>American region</i>												
Argentina	JAN 2007–DEC 2011	912	67	168	232	23	188	143	9	57	25	Esteban et al. (2010), Mandile et al. (2014), Stupka et al. (2009, 2012)
Bolivia	JAN 2007–JUN 2011	740	16	134	52		253		167	55	63	Patel et al. (2013), Rivera et al. (2013)
Brazil	MAR 2006–MAR 2012	980	87	521	11		64		117	111	69	Assis et al. (2013), Borges et al. (2011), Carvalho-Costa et al. (2009), Cilli et al. (2011), Nakagomi et al. (2008), Dulghero et al. (2012), Gómez et al. (2013), Gurgel et al. (2009), Luchs et al. (2012, 2013), Luchs and Timenetsky (2014), Nozawa et al. (2010), Safadi et al. (2010), Soares et al. (2012, 2014)
Canada	2007–2011	323	192	26	45	5	32		6	5	12	Cherit et al. (2013), McDermid et al. (2012), Ward et al. (2013)
Chile	JUL 2006–MAR 2010	238	12	14			177		15	20		Lucero et al. (2012), O’Ryan et al. (2009)
Colombia	2008–2012	467	1	191	5		26		103	61	80	Peláez-Carvajal et al. (2014)
Cuba	2007–2008	29	14				13		1		1	Ribas et al. (2011)
Guatemala	2007–2010	147	91				15		37		4	Cortes et al. (2012), Quaye et al. (2013)
Honduras	2009–2010	50	25						25			Quaye et al. (2013)
Mexico	MAR 2010–MAY 2010	16							16			Yen et al. (2011)
Nicaragua	FEB 2007–OCT 2009	1095	336	341	39	42			68	266	3	Bányai et al. (2009a,b), Becker-Dreps et al. (2011), Khawaja et al. (2013)
Paraguay	2006–2007	143		69			37		6	23	8	Martínez et al. (2010)
Peru	JAN 2010–DEC 2012	42				2	5	4	19	12		Espejo et al. (2014)
USA	2007–2011	1574	342	230	489	35	157	153	97	29	42	Abdel-Haq et al. (2011), Boom et al. (2010), Cardemil et al. (2012), Clark et al. (2011), Hull et al. (2011), McDonald et al. (2012), Payne et al. (2009, 2013), Staat et al. (2011), Weinberg et al. (2012, 2013)
Total		6756	1183	1694	873	107	967	300	686	639	307	
<i>Western pacific region</i>												
Australia	JUL 2006–SEP 2011	1715	543	635	167	37	106		46	149	32	Cowley et al. (2013), Kirkwood et al. (2007, 2008, 2009, 2010, 2011)
China	2006–2011	2516	534	78	1245	6	103		137	299	114	Chen et al. (2013), Dong et al. (2013), Li et al. (2009), Shen et al. (2013), Wang et al. (2009,

Country	Year of sample collection	No. of strains	G1P[8]	G2P[4]	G3P[8]	G4P[8]	G9P[8]	G12P[8]	OTHERS	NT	Mix	Refs.
Fiji	JAN 2006–DEC 2007	116	1		98		1		2	14		2011, 2013), Zeng et al. (2010), Zhang et al. (2012)
Japan	JUL 2006–AUG 2012	682	268	23	295	1	80		15			Jenney et al. (2009)
Malaysia	SEP 2007–DEC 2007	12	4				5			3		Chan-it et al. (2011), Dey et al. (2009), Kamiya et al. (2011), Komoto et al. (2013), Kuzuya et al. (2014), Thongprachum et al. (2013), Yamamoto et al. (2011);
Papua New Guinea	APR 2008–NOV 2010	244	122	20	56		2	6	2	8	28	Zuridah et al. (2010)
Singapore	SEP 2005–APR 2008	320	125	49	61	1	68			16		Horwood et al. (2012)
South Korea	2006–2012	1398	507	38	125	18	77	1	364	172	96	Phua et al. (2013)
Taiwan	JAN 2005–DEC 2010	1831	891	111	347		214		18	250		Han et al. (2010), Jeong et al. (2011), Park et al. (2011), Shim et al. (2010, 2011), Than et al., 2013
Vietnam	SEP 2006–NOV 2008	646	106	11	450	1			38	12	28	Hwang et al. (2012), Wu et al. (2011a,b, 2012)
Total		9480	3101	965	2844	64	656	7	638	907	298	Breiman et al. (2012), Matsushima et al. (2012), Ngo et al. (2009), Tra My et al. (2011)
<i>South East Asian region</i>												
Bangladesh	2007–2009	439	120	85			112	19	54	24	25	Afrad et al. (2013), Breiman et al. (2012), Rahman et al. (2011)
India	2007–2012	3424	788	540			296	97	346	1090	267	Kang et al. (2013), Mangavarkarasi et al. (2012), Mathew et al. (2014), Mukherjee et al. (2009, 2012, 2013), Mullick et al. (2013), Reesu et al. (2013)
Nepal	NOV 2006–SEP 2011	849	40	91			36	23	498	66	95	Ansari et al. (2013), Gauchan et al. (2013), Sherchand et al. (2009, 2012)
Thailand	2007–MAY 2013	1016	454	71	431		36	11	13			Chaimongkol et al. (2012), Chieochansin et al. (2014), Khananurak et al. (2010), Maiklang et al. (2012)
Total		5728	1402	787	431	0	480	150	911	1180	387	
<i>E. mediterranean region</i>												
Bahrain	APR 2006–APR 2007	16	10	2			2		2			Musawi et al. (2013)

Country	Year of sample collection	No. of strains	G1P[8]	G2P[4]	G3P[8]	G4P[8]	G9P[8]	G12P[8]	OTHERS	NT	Mix	Refs.
Iran	OCT 2006–SEP 2008	69	34			2			4	28	1	Modaress and Rahbarimanesh (2011)
Iraq	JAN 2008–DEC 2008	98	6	5		3		3	49	29	3	Ahmed et al. (2013)
Jordan	JAN 2006–APR 2008	563	299	55	13	8	48		34	85	21	Kaplan et al. (2011), Kareman and Alkafajei (2012), Salem et al. (2011)
Libya	OCT 2007–SEP 2008	176	49	3		5	116		1	1	1	Abugalia et al., 2011
Morocco	JUN 2006–MAY 2009	547	301	50	2	5	62		35	13	79	Benhafid et al., 2013
Oman	JUN 2006–DEC 2007	234	7	60			1		21	123	22	Al Awaidy et al. (2009)
Pakistan	JAN 2008–SEP 2010	290	67	39	3		15		101	52	13	Alan et al. (2013), Ifrikhar et al. (2012), Tamim et al. (2013)
Tunisia	2007–2010	270	74	61	55	27	3		22	3	25	Fredj et al. (2012), Hassine-Zaafraane et al. (2011)
Yemen	NOV 2007–MAR 2009	78	43	9			16	1	7	2		Kirby et al. (2011)
Total		2341	890	284	73	50	263	4	276	336	165	
<i>European region</i>												
Austria	2010–2011	44	10	23	3	3	3			2		Paulke-Korinek et al. (2013)
Belgium	2007–2010	334	86	149	24	26	22	2	19	6		Braeckman et al. (2012), Heylen et al. (2013), Zeller et al. (2010, 2012)
Bulgaria	2007–2008	352	139	88		7	45	1	14	22	36	Mladenova et al. (2010, 2012)
Estonia	JAN 2007–DEC 2008	124	5	43	2	16	5		6	42	5	Soeorg et al. (2012)
Finland	2007–2008	292	214	9	13	38	2			8	8	Räsänen et al. (2011)
France	2007–2009	1380	853	45	46	37	345	8	10		36	De Rougemont et al. (2011)
Germany	JAN 2008–DEC 2010	342	71	13	136	54	59		3		6	Pietsch et al. (2009, 2011)
Greece	JAN 2007–AUG 2010	207	67	41		76	13		2		8	Koukou et al. (2011), Trimis et al. (2011)
Hungary	JAN 2007–DEC 2011	2380	1068	351	22	557	162	15	83	83	39	László et al. (2012)
Ireland	2007–2011	148	106	5	16		11		1		9	Cashman et al. (2012), Gunn et al. (2012)
Israel	NOV 2007–DEC 2009	187	61	50	20	10	10	5	31			Muhsen et al. (2010)

Country	Year of sample collection	No. of strains	G1P[8]	G2P[4]	G3P[8]	G4P[8]	G9P[8]	G12P[8]	OTHERS	NT	Mix	Refs.
Italy	2007–2011	3042	1308	287	88	286	640	1	90	107	235	Finamore et al. (2011), Grassi et al. (2012), Ianaro et al. (2013, 2014), Medici et al. (2011), Ruggeri et al. (2011), Zuccotti et al. (2010)
Kazakhstan	JAN 2007–DEC 2009	446	113	106	65	27	11	3	24	71	26	Vainio et al. (2013)
Kyrgyzstan	JAN 2007–DEC 2009	409	205	52	51	6	6	15	16	25	33	Vainio et al. (2013)
Netherlands	MAY 2008–NOV 2009	54	19	2	8	13	2		4	6		Friesema et al. (2012)
Portugal	JAN 2007–MAR 2007	207	10	142			29		7	8	11	Antunes et al. (2009)
Russia	JAN 2007–MAY 2011	1416	311	90	58	655	7		10	257	28	Zhirakovskaya et al. (2012)
Slovenia	JAN 2007–OCT 2008	823	528	81	19	110	28		15	23	19	Steyer et al. (2009)
Spain	OCT 2006–DEC 2011	1111	443	113	13	6	288	133	14	64	37	Téllez Castillo et al. (2010), Cilla et al. (2010, 2013), Gutiérrez-Gimeno et al. (2010), Sánchez-Fauquier et al. (2013)
Sweden	OCT 2007–OCT 2008	604	467	17	24	36	52			4	4	Rinder et al. (2014)
Switzerland	DEC 2006–JUN 2007	113	59	4	4	4	5		15	22		Lacroix et al. (2010)
Turkey	JAN 2008–JAN 2009	100	7		6	1	19		31	10	26	Tapisiz et al. (2011)
Ukraine, Tajikistan, Georgia	2007	323	102	59	12	59	63	2	8		18	Mirzayeva et al. (2009)
Total		14438	6252	1770	630	2027	1827	185	403	760	584	

Table 2

Detection of rare RVA strains in humans, 2007–2012.

Strain	Country	No./freq.	Comment	Refs.	Strain	Country	No./freq.	Comment	Refs.
G1P[5]	Bangladesh	1/0.6%	Detected during RV5 trial	Breiman et al. (2012)	G6P[1]	Pakistan	2/2.7%	Bovine like	Tamim et al. (2013)
G1P[9]	Pakistan	6/3.5%		Iftikhar et al. (2012)	G6P[4]	Belgium	1/0.9%		Zeller et al. (2010)
	Italy	1/1%		Grassi et al. (2012)	G6P[6]	Burkina Faso	13/23%		Nordgren et al. (2012a)
	Taiwan	1/<0.1%		Hwang et al. (2012)		Burkina Faso	11/11%	Putative bovine-human reassortant G6-P[6]-I2-A2-N2-T2-E2-H2	Nordgren et al. (2012b)
	South Korea	1/0.3%		Shim et al. (2011)		Niger	13/2.9%		Page et al. (2014)
	South Korea	1/0.4%		Park et al. (2011)		Italy	1/N.R.	G6-P[6]-I2-A2-N2-T2-E2-H2	Ianiro et al. (2013)
G1P[10]	Gambia	21/10.2%		Kwambana et al. (2014)	G6P[8]	Belgium	1/0.9%		Zeller et al. (2010)
	Oman	3/1.2%		Al Awaidey et al. (2009)		Bangladesh	1/0.6%	Detected during RV5 vaccine trial	Breiman et al. (2012)
	South Korea	2/0.7%		Park et al. (2011)	G6P[9]	Tunisia	1/0.7%	Feline like	Fredj et al. (2012)
G1P[11]	Estonia	1/0.8%		Soeorg et al. (2012)		France	1/0.1%		de Rougemont et al. (2011)
G2P[3]	Turkey	1/1%		Tapisiz et al. (2011)		Italy	1/N.R.	G6-P[9]-I2-A3-N2-T3-E3-H3	Ianiro et al. (2013)
G2P[5]	Mali	1/0.2%	Detected during RV5 trial	Breiman et al. (2012)		Hungary	7/0.3%		László et al. (2012)
	Australia	1/0.2%	Detected in an RV5 territory (Western Australia)	Kirkwood et al. (2011)		Slovenia	2/0.2%		Steyer et al. (2009)
G2P[9]	South Korea	1/0.2%		Jeong et al. (2011)		Japan	2/N.R.	Possible humanbovine-feline reassortant. G6-P[9]-I2-R2-C2-M2-A3-N2-T3-E3-H3	Yanamoto et al. (2011)
	South Korea	1/0.4%		Park et al. (2011)	G6P[11]	Slovenia	1/0.1%	Bovine like G6-P[11]-I2-R2-C2-M2-A13-N2-T6-E2-H3	Steyer et al. (2009, 2013)
G2P[10]	Oman	3/1.2%		Al Awaidey et al. (2009)	G6P[14]	Spain	1/0.3%		Cilla et al. (2010)
	Italy	2/N.R.		Finamore et al. (2011)		France	1/0.1%		de Rougemont et al. (2011)
	Italy	1/1%		Grassi et al. (2012)		Slovenia	1/0.1%		Steyer et al. (2009)
	Turkey	2/2%		Tapisiz et al. (2011)		India	1/N.R.	Bovine like G6-P[14]-I2-R2-C2-M2-A11-N2-T6-E2-H3	Mullick et al. (2013)

Strain	Country	No./freq.	Comment	Refs.	Strain	Country	No./freq.	Comment	Refs.
	China	1/0.1%		Li et al. (2009)	G8P[1]	Ghana	1/0.7%	Detected during RV5 trial	Breinan et al. (2012)
	South Korea	1/0.4%		Park et al. (2011)	G8P[9]	Australia	2/0.4%		Kirkwood et al. (2011)
G2P[14]	Gambia	1/0.5%		Kwambana et al. (2014)	G8P[14]	Spain	1/0.3%		Cilla et al. (2010)
G3P[3]	Brazil	1/N.R.	Canine like	Luchs et al. (2012)		France	1/0.1%	Bovine like	de Rougemont et al. (2011)
G3P[9]	Madagascar	1/0.9%	Feline like	Razafindratsimandresy et al. (2013)		Greece	1/0.8%		Koukou et al. (2011)
	USA	1/0.4%		Abdel-Haq et al. (2011)		Spain	1/0.8%		Sánchez-Fauquier et al. (2013)
	USA	1/1.2%		Cardemil et al. (2012)		Taiwan	1/<0.1%	Bovine like	Hwang et al. (2012), Wu et al. (2012)
	USA	1/0.5%		Hull et al. (2011)		Australia	1/0.8%		Kirkwood et al. (2009)
	Canada	1/7.6%	Feline like	Ward et al. (2013)		Australia	1/33%	Bovine like	Swiatek et al. (2010)
	Libya	1/0.6%		Abugalia et al. (2011)	G9P[9]	Tunisia	1/0.8%		Hassine-Zafrane et al. (2011)
	Hungary	9/0.4%		László et al. (2012)		Portugal	2/0.9%		Antunes et al. (2009)
	Taiwan	1/<0.1%	Feline like	Hwang et al. (2011, 2012)		Bulgaria	1/0.3%		Mladenova et al. (2010)
	China	1/0.1%		Li et al. (2009)		Slovenia	1/0.1%		Steyer et al. (2009)
	South Korea	1/0.3%		Shim et al. (2011)		Kazakhstan	1/0.2%		Vainio et al. (2013)
	China	1/N.R.	G3-P[9]-I3-R3- C3-M3-A3-N3- T3-E3-H6; Feline/Canine like	Wang et al. (2013)		South Korea	1/0.4%		Park et al. (2011)
	China	2/0.5%	Feline like	Wang et al. (2009)	G9P[10]	Oman	1/0.4%		Al Awaidey et al. (2009)
G3P[10]	India	1/N.R.	G3-P[10]-I2-R2- C2-M5-A2-N5- T5-E2-H3; Simian and caprine like	Mukherjee et al. (2012)		Pakistan	8/4.6%		Ifrikhar et al. (2012)
	South Africa	1/0.8%		Enweronu-Laryea et al. (2013)		Turkey	4/4%		Tapisiz et al. (2011)
G3P[19]	Taiwan	3/0.2%	Porcine like	Wu et al. (2011b)	G9P[11]	Pakistan	2/1.1%	Diarrheic children	Ifrikhar et al. (2012)
G3P[24]	USA			Saat et al. (2011)		Italy	1/N.R.	Diarrheic child	Finamore et al. (2011)
G3P[25]	Taiwan	1/<0.1%	Porcine like	Wu et al. (2011a)	G9P[19]	Taiwan	1/<0.1%	Porcine like	Hwang et al. (2012)
G4P[9]	Portugal	1/0.5%		Antunes et al. (2009)	G10P[14]	Slovenia	6/0.7%	Bovine like	Steyer et al. (2009)
G4P[10]	Gambia	1/0.5%		Kwambana et al. (2014)		Australia	6/N.R.	G10-P[14]-I2-R2-C2-M2- A11-N2-T6-E2-H3 Bovine/ovine like	Cowley et al. (2013)
	Turkey	1/1%		Tapisiz et al. (2011)	G10P[15]	China	1/N.R.	Ovine like	Zhang et al. (2012)

Strain	Country	No./freq.	Comment	Refs.	Strain	Country	No./freq.	Comment	Refs.
G5P[6]	Bulgaria	1/N.R.	G5-P[6]-I1-R1-C1-M1-A8-N1-T1-E1-H1; possible porcine-human reassortant	Mladenova et al. (2012)	G11P[25]	India	1/N.R.	Porcine like G11-P[25]-I12-R1-C1-M1-A1-N1-T1-E1-H1	Mullick et al. (2013)
	Japan	1/N.R.	Porcine like G5-P[6]-I5-R1-C1-M1-A8-N1-T1-E1-H1	Komoto et al. (2013)		South Korea	1/N.R.	Porcine-human reassortant G11-P[25]-I12-R1-C1-M1-A1-N1-T1-E1-H1	Than et al. (2013)
	Taiwan	1/<0.1%	Porcine like	Hwang et al. (2012)	G12P[9]	Paraguay	1/1.6%		Martínez et al. (2010)
G5P[8]	Turkey	2/2%		Tapisiz et al. (2011)		Slovenia	2/0.2%		Steyer et al. (2009)
G5P[19]	Taiwan	1/<0.1%	Porcine like	Wu et al. (2011b)	G14P[24]	USA	1/N.R.	Possible equinehuman-bovine reassortant G14-P24-I9-R2-C3-M3-A9-N3-T3-E3-H6	Weinberg et al. (2013)