Diversity in Indian equine rotaviruses: Identification of G10, P6[1] and G1 type and a new VP7 genotype (G16) strains in diarrheic foals in India

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ABSTRACT

Rotaviruses causing severe diarrhea in foals in two organized farms in northern India, during the period 2003 to 2005, were characterized by electropherotyping, serotyping and sequence analysis of the genes encoding the outer capsid proteins. Of 137 specimens, 47 (34.31%) were positive for rotavirus and exhibited at least 5 different electropherotypes (E), E1-E5. Strains belonging to different electropherotypes exhibited either a different serotype/genotype specificity or a lack of reactivity to typing MAbs used in this study. Strains belonging to E1, E2 and E5 exhibited G10, P6[1], G3 and G1 type specificities and accounted for 19.0, 42.9 and 9.5% of the isolates, respectively. The E1 strains, though possessed G10 type VP7, exhibited high reactivity with the G6-specific MAb suggesting that the uncommon combination of the outer capsid proteins altered the specificity of the conformation-dependent antigenic epitopes on VP7. E3 and E4 strains accounted for 28.6% of the isolates and were untypeable. Sequence analysis of VP7 from E4 strains (Erv92, Erv99) revealed that they represent a new VP7 genotype, G16. Detection of unexpected bovine rotavirus-derived G10, P6[1] reassortants, G1 serotype and a new genotype G16 strains in two distant farms reveals interesting epidemiological situation and diversity of equine rotaviruses in India.

Running title: Diversity in Indian equine rotaviruses

Keywords: Equine rotavirus, serotype, genotype, electropherotype, diarrhea, reassortants
INTRODUCTION

Rotaviruses, members of the family *Reoviridae*, are the major etiologic agents of severe, acute dehydrating diarrhea in the young of many mammalian species, including humans, calves and foals (43). Recent estimates indicate an annual death toll of approximately 600,000 infants due to rotavirus, besides inflicting staggering economic burden worldwide (54). Flewett, et al., in 1975 (22) first detected and described the presence of group A rotavirus in stools of foals. Equine group A rotavirus is the main cause of diarrhea in foals up to 3 months of age, causing severe economic loss due to morbidity and mortality in studs (4, 36, 38).

Rotavirus genome consists of 11 segments of double-stranded (ds) RNA that encodes six structural and six non-structural proteins. The genome is enclosed in a triple-layered protein capsid (21). VP4 and VP7, the two proteins comprising the outer capsid, are encoded by gene segments 4 and 7, 8, or 9 (depending on the strain), respectively (20, 43). VP6, encoded by gene segment 6, constitutes the intermediate capsid and VP2, encoded by RNA segment 2, forms the inner capsid (21, 26).

Based on the antigenic epitopes present on the intermediate capsid protein VP6, rotaviruses are classified into groups and subgroups. Seven groups termed A to G have been identified of which group A rotaviruses are the major pathogens of humans and animals (43). Four subgroups I, II, I and II, non I/II have been identified among Group A rotaviruses (26). Rotaviruses can also be classified as ‘long’ and ‘short’ electropherotypes (E) based on the ‘fast’ or ‘slow’ electrophoretic mobility, respectively, of gene segment 11 in polyacrylamide gels. While human rotaviruses with ‘short’ RNA pattern generally exhibit subgroup I specificity, those with ‘long’ RNA pattern possess subgroup II VP6. In contrast, ‘long’ RNA pattern and subgroup I specificity are commonly associated with animal rotaviruses (43). Rotaviruses (RV) have been classified into G and P serotypes based on the antigenic specificity of outer capsid proteins VP7 (glycoprotein) and VP4 (protease sensitive), respectively (20). So far 15 G serotypes/genotypes have been recognized and of these, several serotypes are shared between humans and animals (43, 53). Serotypes G1-G4 are most widespread in humans (43). Serotypes G6, G8, and G10 are major pathogens in cattle (27, 58, 63), but strains belonging to these serotypes are being frequently detected in humans in recent years (3, 8, 14, 15, 17, 23, 24, 30, 41, 43,
Serotype G3 strains appear to have the broadest host range and were observed in humans and many animal species (43). Three widely separated regions, A (amino acid 87-101), B (amino acid 143-152), and C (amino acid 208-223), have been identified as major antigenic determinants on VP7 and were suggested to form complex, functionally related and operationally overlapping conformational epitopes that determine the serotype and neutralization specificities of rotaviruses (16, 18-20, 34, 44, 47, 61). Due to lack of appropriate antibody reagents, a dual P typing system (P serotypes and P genotypes) is being used to characterize rotaviruses (20). However, genotypes do not always correlate with serotypes (45, 46). So far only 11 P serotypes have been characterized, and at least 26 P genotypes are identified (21, 43). Strains sharing ≥89% aa sequence identities are considered to belong to the same genotype (21). In this typing system, the P serotype is represented by a number immediately after the letter P and the genotype is denoted by a number in square brackets (20).

Foal rotaviruses exhibit RNA electropherotypes that are distinct from those of strains from calves, pig, mouse, deer and humans (59). Most of the equine rotaviruses exhibit an RNA electrophoretic migration pattern of 4:2:3:2 characteristic of group A rotavirus (13). Reverse transcriptase (RT)-PCR assay (64) and ELISA (7) have been developed for G-typing and hybridization assays with specific probes have been used in P-typing of equine group A rotaviruses (35, 39). Strains belonging to G3, P4[12] serotype are the most prevalent in diarrheic foals, followed by those belonging to G14, P4[12] serotypes (4, 5, 7, 13, 28, 33, 36, 37, 39, 50, 64). Single isolates each belonging to G5, P9[7] (H-1) (12, 28, 32), G8 P6[1] (Eq/26/94) (39), G10 P8[11] (Eq/R-22) (35) and G13 P[18] (L338) (6) genotypes/serotypes have been reported from young horses suffering from diarrhea. G14 equine rotavirus strains had an overall genomic RNA constellation that was highly conserved not only with contemporary and earlier G3 strains isolated in Japan but also with prototype G3 and G14 strains identified in U.S.A (50). An inactivated vaccine (HO-5 strain, G3, P[12]) has been recently developed in Japan to immunize mares and thereby protecting foals against rotavirus diarrhea through passive immunity (38).

To date, there exists no information on equine group A rotaviruses in India. This limited epidemiological study was undertaken to determine the serotypic / genotypic
nature of rotaviruses circulating in diarrheic foals. Here, we describe for the first time, identification and characterization of G10 P6[1] rotaviruses that are likely to be reassortants between G10 and P6[1] type bovine strains, G1 strains as well as strains representing a new VP7 genotype (G16) in diarrheic foals in two equine farms from northern India.

**MATERIALS AND METHODS**

**Viruses, virus isolation and adaptation to cell culture.** Fecal samples from young horses below the age of 3 months, suffering from severe diarrhea, were collected from two equine farms in Hisar (Haryana) and Hapur (Uttar Pradesh) in northern India between March and July during the years 2003 to 2005. A total of 137 stool specimens were processed as described earlier (60). Some of the samples that were positive for rotavirus and showed good quality RNA are Erv2, Erv3, Erv25, Erv28, Erv58, Erv64, Erv75, Erv77, Erv80, Erv92, Erv94, Erv95, Erv96, Erv97, Erv101, Erv104, Erv105, Erv108, Erv155, Erv165. Of these isolates, Erv2-28 were collected during the year 2003 from the equine farm in Hisar and Erv58-165 were collected during 2004 and 2005 from Hapur farm. The established prototype rotavirus strains Wa (SGII, P1A[8], G1); S2 (SGI, P1B[4], G2); RRV (SG1, P5[3], G3); ST3 (SGII, P2A[6], G4); NCDV (SGI, P6[1], G6) and I321 (SGI, P8[11], G10) were grown in MA104 cells for use as controls in subgrouping and serotyping ELISA.

**Electropherotype analysis.** Rotavirus in the specimens was first detected by polyacrylamide gel electrophoresis (PAGE) of genomic dsRNA as previously described (15, 29, 60). Two or three isolates representing different electropherotypes (E or E-types) were adapted to growth in MA104 cells (67). Differences in RNA patterns were confirmed by co-electrophoresis of the genomic RNAs from two strains belonging to different E-types. **Subgroup and serotype analysis.** Subgrouping and serotyping ELISA was carried out as described earlier (1, 25, 51, 60). In subgrouping ELISA, hyperimmune anti-RRV antiserum R2, the SG I-specific monoclonal antibody (MAb) 255/60 and SG II-specific MAb 631/9 were used (25). MAb specific for G1 (5E8), G2 (2F1), G3 (4F8), G4 (ST-2G7), G6 (1C3) and G10 (B223/N27), used in serotyping ELISA, were reported earlier (1, 51) and were generously provided by Dr. H. B. Greenberg (Stanford University School of Medicine, Stanford, CA).
cDNA Cloning, comparative sequence and phylogenetic analysis of VP4 and VP7
genes of equine isolates. Viral genomic dsRNA purified from fecal samples was used for
RT-PCR using AMV-reverse transcriptase and Taq DNA polymerase as described
previously (53). Gene-specific primers were used for cDNA synthesis and PCR
amplification. The VP4 gene-specific 5’ and 3’ primers were 5’-CTAAGCTTCCCCGCTATAAAATGC/GC/GTTC-3’ and 5’-CTAAGCTTCCCCGGG
TCACATCC/TT-3’, respectively. The respective sequences for VP7 gene primers were
5’-CTTCCCCGGCTTTAAAAAGA/CGAGAAT-3’ and 5’-CTTCCCCGGGTACA/G
T/AC/CATACA-3’. Primers contained sites for specific restriction enzymes at the 5’
ends. Rotavirus gene-specific nucleotide (nt) sequences in the primers are underlined.
The PCR amplified DNAs were digested with appropriate restriction endonucleases and
cloned into either pUC18 or pBlueScript (KS+) vectors. Sequencing of the cloned VP4
and VP7 genes was carried out by Macrogen, Korea. To rule out PCR-mediated
nucleotide substitutions, sequences of both strands of at least two clones for each gene
from Erv2, Erv101, Erv80, Erv105, Erv92, Erv99 strains, obtained from two independent
PCR products (a total of four clones), were determined using vector-specific as well as
gene-specific internal primers. The sequence of only about 776 nt from the 5’ and 3’ ends
of the VP4 gene from Erv2 and Erv101 was determined. The nucleotide and deduced
amino acid (aa) sequences of VP4 and VP7 genes were analyzed and compared with the
previously published corresponding rotavirus gene sequences representing all the
established serotypes/genotypes. Phylogram was constructed by MEGA 3.1 program
using the p-distances and neighbour-joining method (56). The distance is the proportion
of amino acid differences by the total number of sites compared. The GenBank accession
numbers for the equine VP7 gene sequences are: Erv2/Erv28/Erv105, DQ981476; Erv80,
DQ981477; Erv92/Erv99, DQ981478; Erv105, DQ981479.

RESULTS
Electropherotypes and serotypes. Of 137 samples, 47 (34.31%) were found to be
positive for rotavirus both by RNA-PAGE and ELISA. All the equine strains, without
exception, showed long RNA pattern (Fig. 1) and subgroup I specificity. Among the 47
isolates, at least 5 distinct E patterns (E1-E5) were observed. Among the five E-types,
major differences were observed in the migration patterns of RNA segments 2, 3 and 4, 5
and 6, 7, 8 and 9, and segment 11 (Fig. 1). Co-electrophoresis of the RNAs from strains representing different E-types clearly established the differences among the five electropherotypes (data not shown). The E5 pattern is not shown due to poor quality of RNA. Of the 47 rotavirus-positive samples, 21 isolates that exhibited good quality RNA and representing each of the five electropherotypes were serotyped using available MAbs specific for serotypes G1-G4, G6 and G10. As shown in table 1, strains belonging to different E patterns showing differences in the migration of the RNA segments 7, 8 and 9, exhibited either different serotype specificity or a lack of reactivity with the typing MAbs. Of note, E1 strains represented by Erv2 (Table 1 and 2), showed high reactivity with the MAb specific for G6 (1C3) compared with the G10 MAb B223/N7 and these strains accounted for 19.0% of the characterized isolates. Thus, by serotype analysis, the E1 strains appear to belong to G6 serotype. E2 strains, represented by Erv80 (Table 1 and 3), accounted for 42.9% of the isolates and reacted only with G3-specific MAb 4F8 indicating that this group of strains belongs to G3 serotype. As reported in previous studies, G3 serotype is the most prevalent among equine strains (4, 5, 28, 36, 37, 39, 64). Strains belonging to E3 and E4, representing 28.6% of the isolates, did not show any reactivity with the typing MAbs, though good amount of viral RNA was detectable in these samples. E5 strains, represented by Erv155 and Erv165, accounted for 9.5% of the isolates and exhibited high reactivity only with the G1-specific MAb 5E8, suggesting that these isolates represent G1 serotype.

Nucleotide sequence analysis of VP7 and VP4 genes. The VP7 gene from all the strains was 1062 nt in length and encoded a protein of 326 aa. Comparison of the gene sequences from the two E1 strains Erv2 and Erv28 with each other revealed complete identity indicating that the isolates from two different farms belonging to E1 electropherotype represent a single strain. Comparative analysis of the nucleotide and deduced amino acid (aa) sequences of the VP7 gene from Erv2 and Erv28 with the corresponding gene sequences from the prototype strains representing the known 15 G serotypes/genotypes revealed 86.4% and 96.3% identity, respectively, with the VP7 gene from the G10 serotype bovine strain B223. The nt and aa sequence identities with VP7 from other serotypes ranged between 65.5 and 77.7% and 62.1 and 84.4%, respectively (Table 2). These results indicate that the electropherotype E1 strains, though appeared to
represent G6 serotype based on reactivity with the G6-specific MAb, in fact belong to G10 genotype. To determine the VP4 genotype of the E1 strains, the sequence of 776 nt from the 5’ and 3’ ends was compared with the corresponding gene sequences from all the known VP4 serotypes/genotypes. Of significance, both the 5’ and 3’ end sequences of the VP4 gene from Erv2 and Erv28 showed 96.3% identity with the P6[1] type VP4 gene from the bovine NCDV strain (data not shown), indicating that the E1 strains represented by Erv2 and Erv28 possess G10, P6[1] serotype/genotype specificities.

Comparison of the VP7 gene sequences from E2 strains Erv80 and Erv105 showed 87.3% nt and 95.6% aa identity between themselves suggesting that they belong to the same genotype but exhibit limited genetic diversity. Comparison with VP7 sequences from other serotypes revealed that both strains shared greatest homology to the prototype serotype G3 simian strain SA11, exhibiting 95.4% aa identity. The nt sequence identities were 82.4 and 83.1%, respectively. The aa sequence identity of VP7 from Erv80 with that from other G3 equine strains ranged between 92.9 and 93.6%. However, VP7 from Erv105 showed slightly higher amino acid identity with other equine G3 strains, ranging between 94.8 and 95.4%. Of significance, the VP7 from both strains also showed 87.4 to 89% aa identity with that from G9, G11 and G14 strains BA201, YM and JE91, respectively (Table 2). The aa identities with VP7 from other serotypes ranged from 59.8 to 85.0%. These results indicate that the E2 strains, represented by Erv80 and Erv105, belong to serotype G3.

The VP7 gene sequence from the E4 strains Erv92 and Erv99 was identical, suggesting that both isolates represent a single strain. Comparison with the VP7 sequences representing all the 15 G serotypes/genotypes showed aa sequence identities ranging between 59.5 and 85.3% (Table 2). The predicted 85.3% aa identity with G3 strain SA11 is less than the required ≥89% identity for assigning a strain to a specific G serotype/genotype. The major antigenic determinant regions A, B and C of the E4 strains also showed very high sequence diversity from those of all the established 15 G serotypes/genotypes (Fig. 3), suggesting that the strains Erv92 and Erv99 represent a new Genotype. Phylogenetic analysis also revealed Erv99 as a new genotype that is distinct from the known G genotypes (Fig. 4). The VP7 gene from the E3 strains represented by Erv25, Erv58 and Erv64 could not be PCR amplified with the primers used. Although the
E5 strains represented by Erv155 and Erv165 were assigned to G1 serotype based on their high reactivity with G1-specific MAb, the sequence of VP7 and VP4 genes need to be determined. Efforts are directed towards cloning the VP7 gene from E3 and E5 strains as well as the VP4 gene from strains belonging to E2 –E5. Serotype and nucleotide sequence analyses revealed a general correspondence between electropherotypes and serotypes/genotypes as summarized in Table 3.

**DISCUSSION**

The present study on characterization of a limited number of strains revealed high diversity of electropherotypes and serotypes/genotypes in equine rotaviruses isolated from two farms in northern India. Prior to this study, there is no information on the serotypic and genotypic nature of rotaviruses circulating in diarrheic foals in India. At least five distinct electropherotypes each of which represented a distinct G serotype/genotype have been identified. Among the isolates characterized from diarrheic foals, G3, G10, P6[1] and G1 serotypes/genotypes represented 42.9, 19.0 and 9.5%, respectively. E3 and E4 strains, accounting for 28.6% of the isolates, did not react with the serotyping MAbs used in this study. In contrast to the G3 and G10 serotype strains, VP7 from the E4 strains Erv92 and Erv99 exhibited highly divergent antigenic regions A, B and C (Fig. 3) and less than 85.3% aa identity with that of strains representing the established 15 G serotypes/genotypes (Table 2) suggesting that these strains represent a new G genotype, G16. The serotypic/genotypic nature of the E3 strains needs to be determined.

Another observation of significance is the identification of strains that exhibited high reactivity with the typing MAb specific for G1 serotype in diarrheic foals. To date, G1 strains have not been reported to be associated with diarrhea in young horses. It may be noted that though strains belonging to G3, G1 and the new G16 types were detected in only the Hapur farm, their presence in the Hisar farm cannot be precluded because of the limited number of samples characterized from the latter.

The observation that the unusual G10, P6[1] and the E3 untypeable strains are detected in diarrheic foals from two distant farms in India is of epidemiological importance. Recently we have reported very high prevalence of G10, P8[11] strains in diarrheic calves which accounted for 80-85% of the bovine isolates in some farms in
different regions of India (66). Age-old traditions, extensive use of cattle waste as manure and firewood and close proximity of majority of the Indian population with cattle appear to have played a facilitating role in the evolution and persistence of G10, P[11] and G9, P[11] type reassortant asymptomatic/symptomatic stains in newborn children in India (15, 23, 41, 66). Strains that are reassortants between animal-human or animal-animal strains have also been reported both from humans and cattle in India (15, 17, 40, 65, 66). This is the first report of G10, P6[1] type strains in equines and considering the unique epidemiological scenario in India, it is likely that the G10, P6[1] type strains evolved by reassortment in nature between G10, P8[11] and G6, P6[1] type bovine strains and adapted to growth in foals, causing diarrhea.

It is of importance to note that the E1 strains, though possessed G10 VP7, exhibited high reactivity with G6-specific MAb compared with the G10-specific MAb (Table 1). In this context, it should be noted that the natural partner of G10 type VP7 in the outer capsid of bovine strains is P8[11] type VP4 and that of G6 VP7 is P6[1] type VP4. Independent segregation of VP4 and VP7 has also been reported in several strains (31). Further, a single VP4 (P2A[6]) is associated with four VP7 serotypes 1, 2, 3 and 4, in neonatal asymptomatic strains (43). In recent years, reassortants with a wide variety of gene constellations that encode proteins of heterologous parental origin have been reported (43). Though VP4 and VP7 can function as independent protective antigens, several reports indicate that uncommon combination of VP4 and VP7 in some reassortants affects the expression of important viral phenotypes, such as virion stability (11), receptor binding (49), protease sensitivity of VP4 and plaque morphology (9, 62) and expression of conformation-specific neutralization epitopes on both the proteins (9, 10, 16, 52). The neutralizing epitopes on VP7 and VP4 appear to require association and highly specific interactions between VP4 and VP7 (10, 52). The neutralizing epitopes on VP7 are conformation dependent and appear to be complex, unstable and require calcium for stability (16). This could explain for the failure of purified recombinant VP7 to function as an effective protective antigen in animals immunized against rotavirus (2, 42, 48). In this context, it is possible that the association of G10 VP7 with P6[1] VP4, instead of the P8[11] VP4 that is commonly found in the G10 bovine strains, could have resulted in altered antigenic properties leading to high reactivity of the G10 VP7 with the G6
typing MAb. In contrast, the G10, P8[11] asymptomatic neonatal strain I321 showed
reactivity only with the G10-specific MAb suggesting that the high reactivity of all the
E1 strains with G6-specific MAb is in deed due to the antigenic property of the strains
and not due to nonspecific reaction. The present study, though limited, unravelled
interesting epidemiology of equine rotaviruses, with novel genotypes/serotypes
circulating in large numbers in diarrheic foals in two different locations in India.
Identification of two new rotavirus genotypes (G15 and G16) in succession from India
(53, this study) signifies the need to characterize untypeable strains to further identify
novel genotypes/serotypes. Taking into account the unique genetic/antigenic repertoire of
rotaviruses, these findings are of significance in the context of development of an
effective vaccine against equine rotavirus diarrhea in India.

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Serological and genomic characterization of L338, a novel equine group A rotavirus
novel group A rotavirus G serotype: serological and genomic characterization of


FIGURE LEGENDS

FIG. 1.
Electropherotype analysis of the genomic dsRNA of the equine rotavirus strains.

FIG. 2.
Comparison of the deduced amino acid sequences of the major antigenic variable regions A, B and C of VP7 from equine rotavirus strains with those from strains representing all the established G serotypes/genotypes. Note that the antigenic regions of the E4 strains represented by Erv99 are highly divergent from those of all other G serotypes. The accession numbers for the gene sequences compared in this study are Wa, P03532; HU5, P04328; SA11, P03533; Hochi, BAB032864; OSU, P08406; NCDV, Q65699; Ch2, P29821; R291, AY855064; BA201, AY695811; B223, P17700; YM, P17466; L26, M58290; L338, D13549; JE91, BAB40366 and Hg18, AF237666.

FIG. 3.
Phylogenetic tree of the deduced aa sequences of VP7 representing all the established G serotypes / genotypes and the equine strains representative of the three electropherotypes E1, E2 and E4. The phylogram was constructed by MEGA 3.1 program using the p-distances and the neighbour joining method.

TABLE 1.
Serotype analysis of equine isolates by ELISA using serotype-specific MAbs. Data shown here are the average OD$_{405}$ x 1000 of 3 wells each of 2 experiments. *, Serotype based on reactivity to G6 MAb in ELISA. (However, sequence and phylogenetic analyses clearly reveal that these strains belong to G10 genotype (See Fig. 3).

TABLE 2.
Comparison of the nt and deduced aa sequence identities of the VP7 gene from the equine strains with strains representing the established 15 G serotypes/genotypes. Erv2/Erv28, Erv80/Erv105 and Erv92/Erv99 represent electropherotypes E1, E2 and E4, respectively.

TABLE 3.
Summary of electropherotypes and serotypes/genotypes of the equine rotavirus isolates. *, serotype/genotype revealed by nt sequence analysis; R, reactivity with G6 MAb; −, no reactivity with typing MAbs.
### Table 1

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G:
- nt: number of transcribed nucleotides
- aa: number of amino acids

**Note:** The values in bold indicate significant differences.
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Fig. 2.
Fig 3
RETRACTION

Diversity in Indian Equine Rotaviruses: Identification of Genotype G10,P6[1] and G1 Strains and a New VP7 Genotype (G16) Strain in Specimens from Diarrheic Foals in India


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Volume 45, no. 3, p. 972–978. Recently, a mistake in comparative sequence analysis in our paper was recognized. One of the authors had unknowingly used accession number Q65669, which pertains to the bovine G8 genotype NCDV-cody strain, thinking that the number represented the G6 genotype NCDV strain, and concluded on that basis that the equine strain Erv99 represented a new genotype. Sequence analysis using the NCDV sequence revealed Erv99 to be highly related to the G6 genotype. Incorporation of this correction in the data presented in the article would require a change in the title as well as changes in some sections of the text. Hence, we retract the current version of the paper and sincerely apologize for the inconvenience caused to readers.