

**Genome Sequencing and Analysis of a Porcine Delta Coronavirus from Eastern China**

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**Abstract**

Porcine delta coronavirus (PDCoV) has been reported in many countries, including the United States, Canada, South Korea, China, Thailand, Vietnam and Laos. In December 2016, clinical diarrhea similar to that caused by porcine epidemic diarrhea virus (PEDV), but with a lower mortality rate, was reported on a swine farm in Shanghai, China. Six intestine samples were collected from dead suckling piglets (<3 weeks old) with clinical diarrhea, and they were assayed for the presence of swine enteric coronaviruses. Polymerase chain reaction results were positive for PDCoV (6/6), but negative for PEDV (0/6), transmissible gastroenteritis virus (TGEV) (0/6) and porcine rotavirus group A (Rota A) (0/6). The full-length genome sequence of the PDCoV strain SHJS/SL/2016 was determined. Phylogenetic trees demonstrated that PDCoV strain SHJS/SL/2016 belongs to the Chinese clade, which might share a common evolutionary ancestor with United States and South Korean clades, but it clustered separately from Thai and Laoian PDCoV strains. This report describes the complete genome sequence of SHJS/SL/2016, and the data will promote a better understanding of the molecular epidemiology and genetic diversity of PDCoV isolates in China.

**Keywords:** Porcine deltacoronavirus; Full-length genome; Phylogenetics

**Introduction**

Porcine deltacoronavirus (PDCoV) is an enveloped, single-stranded, positive-sense RNA virus that is taxonomically classified within the family Coronaviridae, genus Deltacoronavirus [1]. The virus was first identified through a genomic sequence analysis of avian and pig isolates in Hong Kong in 2012 [2]. PDCoV was first detected in farmed pigs with diarrhea in the United States in early 2014 [3]. PDCoV causes an enteric disease that is characterized by watery diarrhea, dehydration, low mortality in adult pigs, and high mortality in piglets. The clinical symptoms of PDCoV disease are very similar to those of porcine epidemic diarrhea, but PDCoV disease is milder [4]. Since April 2017, disease caused by PDCoV strains has been reported in North America (the United States, Canada, and Mexico) [5-10] and Asia, including South Korea, Mainland China, Thailand, Laos, and Vietnam [11-17].

The PDCoV genome is approximately 25.4 kb in length (excluding the poly(A) tail), and starting from the 5’ end, approximately three-fourths of the viral genome encodes two overlapping open reading frames (ORFs) (ORF1a and ORF1b) that produce up to 15 nonstructural (NS) proteins, although PDCoV lacks the gene encoding NS protein 1 (NS1) [2]. Downstream of ORF1, PDCoV contains six additional ORFs (ORF2 to ORF7) that encode the spike (S), envelope (E), membrane (M), and nucleocapsid (N) structural proteins, as well as NS6 and NS7. The genome is flanked by short 5’ and 3’ untranslated regions (UTRs), with the typical gene order 5’-UTR-ORF1-S-E-M-NS6-N-NS7-3’-UTR [18].

To reveal the characteristics of this virus and determine more precisely its relationships with other PDCoV strains that have been reported in other countries, we determined and analyzed the complete genomic sequence of the SHJS/SL/2016 strain.

**Methods**

In December 2016, an outbreak of diarrhea occurred among piglets in a breeding farm in Shanghai. To determine etiology, 6 intestinal samples from dead suckling piglets (<3 weeks old) were collected. For the extraction of viral RNA from intestinal samples, suspensions were prepared by vortexing 1 g of intestines with 1 ml of phosphate-buffered saline (0.1M, pH 7.2). The suspensions were clarified at 5000×g for 10 minutes at 4°C. 200 μl of clarified supernatants was used to extract viral RNA by Viral RNA minikits (Qiagen, Germany) according to the manufacturer’s instructions. Two pairs of primers (41F: 5’-TTTCAGGTGCTCAAAGCTCA-3’ and 735R: 5’-
GGAAAAAGCATTCCGTAAC-3") were used for the detection of PDCoV nucleocapsid (N) gene with reaction conditions (50°C for 30 min and 95°C for 15 min for the reverse transcription reaction, followed by 40 cycles of PCR amplification at 95°C for 15 s, 55°C for 45 s, and 72°C for 1 min, with a final extension at 72°C for 7 min) [3]. In addition, molecular detection of the three diarrhea-related enteric viruses (Porcine epidemic diarrhea virus, PEDV; Porcine transmissible gastroenteritis virus, TGEV; Porcine rotavirus group A, Rota A) was performed by using the commercial real time RT-PCR kits (Weiboxin, Guangzhou, China) for further evaluation of the possible co-infection status with PDCoV in investigated pig samples. The complete genomic sequence of PDCoV (SHJS/SL/2016) was determined from extracted RNA by RT-PCR and sequenced to obtain a consensus sequence. Sequences were assembled and analyzed using the DNASTAR software package (DNASTAR Inc., Madison, WI, USA). Phylogenetic trees were constructed by the neighbor-joining method using MEGA software version 5 [19]. The topology of the trees based on the nt sequences was obtained by majority-rule consensus using 1,000 bootstrap replicates, which are shown as percentages, and bootstrap values greater than 60% were considered statistically significant for grouping.

Results and Discussion

The PCR results demonstrated that all samples were positive for PDCoV (6/6), and none were PCR positive for PEDV (0/6), TGEV (0/6) or Rota A (0/6). After that, the full-length genome sequence of a PDCoV strain (SHJS/SL/2016) was determined.

The newly characterized sequence has been deposited in the GenBank database under the accession number MF041982.

The complete genomic sequence of the SHJS/SL/2016 strain is 25,414 nt in length, excluding the poly(A) tail, and it consists of the 539-nt 5’ UTR, the 18,797-nt replicate gene (nt 540 to 11,408 for 1a and nt 11,408 to 19,336 for 1b), the 3,480-nt S gene (nt 19,318 to 22,797), the 252-nt E gene (nt 22,791 to 23,042), the 654-nt M gene (nt 23,035 to 23,688), the 285-nt NS6 gene (nt 23,688 to 23,972), the 1,029-nt N gene (nt 23,993 to 25,021), the 603-nt NS7 gene (nt 24,087 to 24,689), and the 393-nt 3’ UTR. A pairwise comparison showed that the complete genome shared 97.6%–99.3% nucleotide identities with the other 60 PDCoV strains available in GenBank. The highest level of similarity, shared with strain CHN-JS-2014, was 99.3% (Table 1). A comparison of individual regions indicated that the S gene is the region of the viral genome that varies the most between strain SHJS/SL/2016 and the other PDCoV strains, with nucleotide sequence identities of 96.5%–99.5%, which are more variable than those of the NS7 gene (97.0%–99.0%) (Table 1). Moreover, a subsequent sequence alignment showed that seven PDCoV strains, including three Thai PDCoV strains, two Vietnamese PDCoV strains, one Laotian PDCoV strain, and one Chinese PDCoV strain, contain a 6-nt (TTTGAA) deletion and a 9-nt deletion (CCGGTTGGT) in ORF1a, while the SHJS/SL/2016 and CHN/Tianjin/2016 PDCoV strains only have a 6-nt deletion in ORF1a (Figure 1). Compared with these PDCoV strains, a 3-nt (TAA) deletion was observed in the S gene of PDCoV strain SHJS/SL/2016, and this deletion was also present in most Chinese PDCoV strains, except PDCoV strains HKU15-44 and CHN-AH-2004 (Figure 1). However, this strain has a 1-nt (T) insertion in its 3’ UTR (Figure 1).

Table 1: Percent nucleotide sequence identity of SHJS/SL/2016 to the corresponding sequences of 60 PDCoV strains.

| GenBank NO. | Virus          | Complete genome (nt) | Complete Genome | 5’UTR | ORF1a | ORF1b | S     | E     | M     | NS6   | N     | NS7   | 3’UTR |
|------------|----------------|----------------------|----------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| KP757890   | CHN-AH-2004    | 25420                | 98.9           | 99.8  | 98.6  | 99.4  | 98.4  | 98.8  | 99.6  | 98.6  | 95.7  | 99.2  |
| JQ065042   | HKU15-44       | 25430                | 98.9           | 99.8  | 98.4  | 99.2  | 99.1  | 99.6  | 98.6  | 99.3  | 98.9  | 98.3  | 99    |
| JQ065043   | HKU15-155      | 25425                | 99.1           | 99.1  | 98.8  | 99.5  | 99.1  | 99.6  | 98.9  | 99.6  | 99.3  | 99    | 99.5  |
| KT26822    | CH/Sichuan/   | 25404                | 99.2           | 100   | 98.9  | 99.6  | 98.9  | 98.6  | 99.3  | 99.2  | 98.8  | 99    |
|            | SZT/2012       |                      |                |       |       |       |       |       |       |       |       |       |
| KT336560   | CHN-HN-2014    | 25420                | 98.8           | 99.3  | 98.8  | 99.4  | 98.6  | 98.8  | 99.6  | 99    | 99.7  | 99.2  |
| KP757892   | CHN-JS-2014    | 25420                | 99.3           | 99.6  | 98.9  | 99.7  | 99.5  | 99.2  | 98.9  | 99.6  | 99.1  | 98.7  | 99.2  |
| KP757891   | CHN-HB-2014    | 25420                | 99.2           | 99.8  | 99    | 99.6  | 99.2  | 99.6  | 98.6  | 99.3  | 98.8  | 98.2  | 99    |
| KU981059   | NH             | 25420                | 99.6           | 99.6  | 98.7  | 99.5  | 99.1  | 99.2  | 98.9  | 99.8  | 98.5  | 98.7  | 98.7  |
| KR131621   | PDCoV/CHJXN12/2015 | 25438          | 98.9           | 98.7  | 99.2  | 99.1  | 99.2  | 99.8  | 98.6  | 99.9  | 98.5  | 98.2  | 99.7  |
| KT021234   | CH/SXD1/2015   | 25419                | 98.9           | 99.3  | 98.8  | 99.4  | 98.5  | 99.2  | 98.9  | 99.8  | 98.6  | 97.8  | 98.2  |
| KY065120   | CHN-Tianjin/2016 | 25413              | 99.4           | 99.1  | 99    | 98.6  | 99.2  | 98.6  | 98.9  | 98.8  | 98.5  | 97.7  |
| KM820765   | KNU14-04       | 25422                | 98.9           | 99.6  | 98.4  | 99.2  | 99.8  | 99.6  | 98.8  | 98.7  | 98.7  | 98.7  |

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| Accession | Strain Details | Coverage Values |
|-----------|----------------|-----------------|
| KU051641  | PDCoV/Swine/Thailand/S5011/2015 | 97.6, 99.1, 97.4, 98.1, 96.5, 99.6, 98.2, 98.2, 97.3, 97.5, 96.7 |
| KU051649  | PDCoV/Swine/Thailand/S5015L/2015 | 97.6, 99.3, 97.4, 98.1, 96.5, 99.6, 98.2, 98.2, 97.3, 97.5, 96.7 |
| KJ884334  | TT_1115 | 97.6, 99.1, 97.4, 98.1, 96.6, 99.6, 97.9, 98.2, 98, 97, 98.7 |
| KX834351  | PDCoV/Swine/Vietnam/HaNoi6/2015 | 97.9, 99.4, 97.7, 98.3, 96.9, 99.2, 98.8, 98.6, 98.5, 97.8, 98.2 |
| KX834352  | PDCoV/Swine/Vietnam/Binh21/2015 | 97.9, 99.4, 97.7, 98.3, 96.9, 99.2, 98.8, 98.6, 98.5, 97.8, 98.2 |
| KX118627  | P1_16_BTL_0115/PDCoV/2016/Lao | 97.6, 99.1, 97.4, 98.1, 96.7, 99.6, 97.9, 98.2, 98.7, 97.3, 96.7 |
| KR265853  | USA/Minnesota/2013 | 99, 99.6, 98.6, 99.4, 98.9, 99.2, 98.5, 99.6, 99, 98.8, 99 |
| KJ481931  | PDCoV/USA/Illinois121/2014 | 98.9, 99.4, 98.6, 99.4, 99, 99.2, 98.5, 99.6, 98.7, 98.5, 99.2 |
| KR265865  | USA/Iowa459/2014 | 98.9, 99.4, 98.6, 99.4, 99, 99.2, 98.5, 99.6, 98.9, 98.8, 99.2 |
| KJ601777  | PDCoV/USA/Illinois133/2014 | 99, 99.6, 98.6, 99.5, 98.9, 99.2, 98.5, 99.3, 98.9, 98.7, 99 |
| KJ601778  | PDCoV/USA/Illinois134/2014 | 99, 99.6, 98.6, 99.5, 98.9, 99.2, 98.5, 99.3, 98.9, 98.7, 99 |
| KJ601779  | PDCoV/USA/Illinois136/2014 | 98.9, 99.4, 98.6, 99.4, 99, 99.2, 98.5, 99.6, 98.7, 98.5, 99.2 |
| KJ601780  | PDCoV/USA/Ohio137/2014 | 99, 99.6, 98.6, 99.4, 99, 99.2, 98.5, 99.6, 98.9, 98.7, 99.2 |
| KJ462462  | OH1987 | 99, 99.4, 98.6, 99.4, 99.2, 98.3, 99.6, 98.9, 98.7, 99.2 |
| KR265861  | USA/Nebraska210/2014 | 99, 99.4, 98.6, 99.5, 98.9, 99.2, 98.3, 99.3, 98.8, 98.7, 99 |
| KR265860  | USA/Nebraska209/2014 | 99, 99.4, 98.6, 99.5, 98.9, 99.2, 98.3, 99.3, 98.9, 98.7, 99 |
| KR265859  | USA/Minnesota159/2014 | 99, 99.6, 98.6, 99.5, 99.1, 99.2, 98.3, 99.6, 99, 98.8, 99 |
| KJ584355  | IL2768 | 99, 99.6, 98.6, 99.4, 99, 99.2, 98.5, 99.3, 99, 98.8, 99 |
| KJ569769  | IN2847 | 99, 99.4, 98.6, 99.4, 98.9, 99.2, 98.5, 99.3, 99, 98.8, 99 |
| KJ584358  | PA3148 | 99, 99.4, 98.6, 99.4, 99, 99.2, 98.2, 99.6, 99, 98.8, 99 |
| KJ584356  | SD3424 | 98.9, 99.6, 98.6, 99.4, 98.9, 99.2, 98.3, 99.6, 98.7, 98.5, 98.7 |
| KJ567050  | 8734/USA-IA/2014 | 98.9, 99.6, 98.6, 99.4, 98.9, 98.8, 98.5, 99.3, 98.9, 98.7, 99 |
| KJ584359  | NE3579 | 99, 99.4, 98.6, 99.5, 98.9, 99.2, 98.3, 99.3, 98.9, 98.7, 99 |
| KR265857  | USA/Illinois273/2014 | 98.9, 99.6, 98.6, 99.4, 99, 98.8, 98.3, 99.6, 98.9, 98.7, 99.2 |
| KR265856  | USA/Illinois272/2014 | 98.9, 99.6, 98.6, 99.4, 99, 98.8, 98.3, 99.6, 98.9, 98.7, 99.2 |
| KJ769231  | SdCV/USA/OhioCVM1/2014 | 98.9, 99.6, 98.6, 99.4, 98.9, 99.6, 98.3, 99.6, 98.5, 98.2, 99.2 |
| Accession Number | Country/State | Date | 25394 | 98.9 | 99.4 | 98.6 | 99.5 | 98.9 | 98.2 | 99.6 | 98.7 | 98.5 | 98.7 |
|------------------|---------------|------|-------|------|------|------|------|------|------|------|------|------|------|
| KR265847         | USA/ Minnesota 442/2014 | 25394 | 98.9 | 99.4 | 98.6 | 99.5 | 98.9 | 98.2 | 99.6 | 98.7 | 98.5 | 98.7 | 98.7 |
| KJ584357         | KY4813         | 25422 | 99   | 99.6 | 98.6 | 99.5 | 99   | 99.2 | 98.5 | 99.6 | 99   | 98.8 | 98.7 |
| KR265848         | USA/ Minnesota 214/2014 | 25396 | 98.9 | 99.6 | 98.6 | 99.5 | 98.9 | 99.2 | 98.2 | 99.6 | 98.7 | 98.5 | 98.7 |
| KR265864         | USA/ Minnesota 292/2014 | 25395 | 98.9 | 99.4 | 98.6 | 99.4 | 99   | 99.2 | 98.3 | 99.6 | 98.9 | 98.8 | 99   |
| KM012168         | Michigan/ 8977/2014 | 25411 | 98.9 | 99.6 | 98.6 | 99.5 | 98.9 | 99.2 | 98.3 | 99.6 | 98.9 | 98.8 | 99   |
| KJ620016         | MI6148         | 25422 | 99   | 99.6 | 98.6 | 99.4 | 99   | 99.2 | 98.3 | 99.3 | 99   | 98.8 | 99.2 |
| KR265862         | USA/ Ohio 444/2014 | 25394 | 98.9 | 99.4 | 98.6 | 99.4 | 99.2 | 98.3 | 99.6 | 98.8 | 97.7 | 99.2 | 99.2 |
| KR265863         | USA/ Ohio 445/2014 | 25394 | 98.9 | 99.4 | 98.6 | 99.4 | 98.6 | 99.2 | 98.3 | 99.6 | 98.7 | 98.5 | 99.2 |
| KR265850         | USA/ Michigan 448/2014 | 25394 | 99   | 99.6 | 98.6 | 99.5 | 98.9 | 99.2 | 98.5 | 99.6 | 99   | 98.8 | 99   |
| KR265849         | USA/ Michigan 447/2014 | 25393 | 99   | 99.6 | 98.6 | 99.5 | 98.9 | 99.2 | 98.5 | 99.6 | 99   | 98.8 | 99   |
| KR265852         | USA/ Illinois 449/2014 | 25394 | 99   | 99.6 | 98.6 | 99.4 | 99   | 99.2 | 98.5 | 99.3 | 99   | 98.8 | 99   |
| KR265858         | USA/ North Carolina 452/2014 | 25394 | 98.9 | 99.6 | 98.5 | 99.4 | 99.2 | 98 | 99.6 | 99   | 98.8 | 99   |
| KT381613         | OH11846        | 25422 | 99   | 99.6 | 98.6 | 99.4 | 99   | 99.2 | 98.5 | 99.6 | 99   | 98.8 | 99.2 |
| KR265851         | USA/ Indiana 453/2014 | 25394 | 99   | 99.6 | 98.6 | 99.5 | 99   | 99.2 | 98.2 | 99.6 | 98.9 | 98.7 | 99   |
| KR265855         | USA/ Minnesota 455/2014 | 25394 | 98.9 | 99.6 | 98.6 | 99.4 | 99.8 | 99.2 | 98.5 | 99.6 | 98.9 | 98.7 | 99.2 |
| KR265854         | USA/ Minnesota 454/2014 | 25394 | 99   | 99.6 | 98.6 | 99.5 | 99.9 | 99.2 | 98.5 | 99.6 | 98.9 | 98.7 | 99.2 |
| KP981396         | USA/ IL/ 2014/026PDV_P1 | 25422 | 98.9 | 99.6 | 98.6 | 99.5 | 99.9 | 99.2 | 98.3 | 99.6 | 98.9 | 98.8 | 99   |
| KR150443         | USA/ Arkansas 61/2015 | 25398 | 98.9 | 99.6 | 98.5 | 99.4 | 99.9 | 99.2 | 98.5 | 99.6 | 98.9 | 98.7 | 99.2 |
| KX022602         | PDCoV/USA/ Iowa 136/2015 | 25382 | 98.9 | 99.4 | 98.5 | 99.4 | 99.8 | 99.2 | 98 | 99.6 | 98.9 | 98.7 | 98.7 |
| KX022604         | PDCoV/USA/ Nebraska 137/2015 | 25382 | 98.9 | 99.4 | 98.5 | 99.4 | 99.9 | 99.2 | 98.2 | 99.6 | 98.8 | 98.7 | 98.9 |
| KX022603         | PDCoV/USA/ Minnesota 140/2015 | 25394 | 98.9 | 99.4 | 98.5 | 99.4 | 99.9 | 99.2 | 98.2 | 99.6 | 98.9 | 98.7 | 98.7 |
| KX022605         | PDCoV/USA/ Nebraska 145/2015 | 25320 | 98.9 | 99.4 | 98.5 | 99.4 | 98.8 | 99.2 | 98.2 | 99.6 | 98.9 | 98.7 | 98.1 |
A pairwise comparison of the nucleotide identities of 61 global PDCoV strains is summarized in Table 1. Moreover, the S, M, and N genes were further analyzed. The S gene encodes a predicted protein of 1,159 amino acids. It contains 3,480-nt and, therefore, it is 3-nt shorter than that of the PDCoV reference strain HKU15-44. Based on the S gene, the SHJS/SL/2016 strain is 99.1%–99.4% closely related to Chinese PDCoVs, with 98.4%–99.5% and 99.1%–99.4% nucleotide and amino acid sequence identities, respectively (Table 1). It also shared sequence similarity with US PDCoV strains, with 98.8%–99.1% and 99.1%–99.3% identities at the nucleotide and amino acid levels, respectively (Table 1). The SHJS/SL/2016 PDCoV strain shared the lowest nucleotide homologies (96.5%–96.6%) with Thai PDCoV strains (Table 1). A phylogenetic analysis demonstrated that the PDCoV strains from the United States and South Korea clustered into a large clade, whereas PDCoV strain SHJS/SL/2016 clustered with other PDCoV strains detected in China since 2014, which suggests that the United States and South Korean clades might share a common evolutionary ancestor with the Chinese clade (Figure 2A). Interestingly, the PDCoV strains from Thailand, Laos, and Vietnam clustered in a distinct clade (Figure 2A). These findings are similar to those of previous studies [11,14,20].

The M gene is 654 nt long, and it encodes a protein of 217 amino acids. It has no nt deletions or insertions, but it does contain point mutations. The SHJS/SL/2016 PDCoV strain shared the highest nucleotide homologies (98.3%–98.9%) with the Chinese PDCoV strains, and the lowest nucleotide homologies (97.9%–98.2%) with the Thai PDCoV strains (Table 1). As shown in Figure 2B, the topology of the phylogenetic tree constructed using the M gene sequences of strain SHJS/SL/2016 and the other PDCoV strains was identical to that obtained with the S gene sequences.
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