Identification and characterization of a novel paramyxovirus, porcine parainfluenza virus 1, from deceased pigs

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We describe the discovery and characterization of a novel paramyxovirus, porcine parainfluenza virus 1 (PPIV-1), from swine. The virus was detected in 12 (3.1 %) of 386 nasopharyngeal and two (0.7 %) of 303 rectal swab samples from 386 deceased pigs by reverse transcription-PCR, with viral loads of up to 10^6 copies ml^-1. Complete genome sequencing and phylogenetic analysis showed that PPIV-1 represented a novel paramyxovirus within the genus Respirovirus, being most closely related to human parainfluenza virus 1 (HPIV-1) and Sendai virus (SeV). In contrast to HPIV-1, PPIV-1 possessed a mRNA editing function in the phosphoprotein gene. Moreover, PPIV-1 was unique among respiroviruses in having two G residues instead of three to five G residues following the A_6 run at the editing site. Nevertheless, PPIV-1, HPIV-1 and SeV share common genomic features and may belong to a separate group within the genus Respirovirus. The presence of PPIV-1 in mainly respiratory samples suggests a possible association with respiratory disease, similar to HPIV-1 and SeV.

Paramyxoviruses are known to cause systemic, exanthematous, respiratory and neurological diseases in a wide variety of animals, including humans. They are enveloped, negative-stranded RNA viruses that are classified into two subfamilies: Paramyxovirinae and Pneumovirinae. Within the subfamily Paramyxovirinae, there are currently seven genera: Aquaparamyxovirus, Avulavirus, Ferlavirus, Henipavirus, Morbillivirus, Respirovirus and Rubulavirus. Among members of the Paramyxovirinae, measles virus (MeV), mumps virus and human parainfluenza virus 1–4 (HPIV-1–4) are the most well-known human paramyxoviruses that cause outbreaks of respiratory/systemic infections (Lau et al., 2005, 2009; Virtue et al., 2009).

In the last few decades, a number of novel paramyxoviruses belonging to the subfamily Paramyxovirinae have emerged in animals and/or humans, causing severe illness and death. These are best exemplified by Hendra virus (HeV) (Selvey et al., 1995; Young et al., 1996) and Nipah virus (NiV) (Chua et al., 1999, 2000). Fruit bats were subsequently found to be the natural reservoir for both viruses (Enserink, 2000; Halpin et al., 2000; Young et al., 1996); however, human outbreaks due to HeV and NiV have occurred as a result of transmission from horses and pigs, respectively (Chua et al., 1999; Selvey et al., 1995). A number of novel paramyxoviruses have since been identified from various animals and their genomes have been sequenced, including Menangle virus (MenPV) (Bowden et al., 2001), Tioman virus (Chua et al., 2001), Tuhoko virus 1–3 (ThkPV-1–3) (Lau et al., 2010) and Cedar virus (CedPV) (Marsh et al., 2012) from bats, Tupaiia paramyxovirus (TupPV) from tree shrew (Tidona et al., 1999), Salem virus (SaLV) from horse mononuclear cells (Renshaw et al., 2000), Mossman virus (MosPV) (Miller et al., 2003), J virus (JPV) (Jack et al., 2005), Beilong virus (BeiPV) or variant (Li et al., 2006; Woo et al., 2012b) and Tailam virus (TlmPV) (Woo et al., 2011) from rodents or rodent cells, Tursiops truncatus parainfluenza virus 1 from dolphins (Nollens et al., 2008), Sunshine virus

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The GenBank/EMBL/DBJ accession numbers for the nucleotide sequences of the genomes of PPIV-1 determined in this study are JX857409–JX857411.
from snakes (Hyndman et al., 2012) and feline morbillivirus (FmoPV) from domestic cats (Woo et al., 2012a). During the process of centralized slaughtering of pigs carried out to ensure safe pork supply in Hong Kong, deceased pigs are occasionally encountered without any obvious or identified cause of death, and are excluded from further food processing. As pigs are also a known reservoir for a variety of viruses (Lau et al., 2008, 2011), we therefore hypothesized that previously unrecognized paramyxoviruses may be present in our swine population. A novel paramyxovirus, belonging to the genus Respirovirus, was identified, with three complete genome sequences determined. Based on the results, we propose a novel porcine paramyxovirus, porcine parainfluenza virus 1 (PPIV-1), in the genus Respirovirus.

A total of 951 samples from 386 deceased pigs were collected from a slaughter house in Hong Kong from September 2008 to June 2012 using procedures described previously (Lau et al., 2008, 2011). These comprised 386 nasopharyngeal, 303 rectal, 153 blood, 56 lung and 53 liver samples. Viral RNA was extracted using an EZ1 Virus Mini kit or RNeasy Mini kit (Qiagen). Paramyxovirus detection was performed by amplifying a 555 bp fragment of the L gene of respiroviruses using conserved primers (5'-GACTCATCTACTAAGGGNTAYGARA-3' and 5'-CACAACATCTTGCTACTWATDATNGT-3') as described previously (Lau et al., 2010; Woo et al., 2012a). As initial reverse transcription (RT)-PCR revealed a potential novel paramyxovirus, all samples were subject to RT-PCR for PPIV-1 by amplifying a 154 bp fragment of the L gene, using specific primers (5'-TTTGGTGTTCAAGAGATTCCTT-3' and 5'-ACCTTTTGGTCTATGTATAAAGA-3'). Real-time quantitative RT-PCR to detect the L gene of PPIV-1 was performed using FastStart Universal SYBR Green Master (Roche), with specific primers (5'-GACTCATCTACTAAGGGNTAYGARA-3' and 5'-CACAACATCTTGCTACTWATDATNGT-3') as described previously (Lau et al., 2010; Woo et al., 2012a). As initial reverse transcription (RT)-PCR revealed a potential novel paramyxovirus, all samples were subject to RT-PCR for PPIV-1 by amplifying a 154 bp fragment of the L gene, using specific primers (5'-TTTGGTGTTCAAGAGATTCCTT-3' and 5'-ACCTTTTGGTCTATGTATAAAGA-3'). Real-time quantitative RT-PCR to detect the L gene of PPIV-1 was performed using FastStart Universal SYBR Green Master (Roche), with specific primers (5'-GACTCATCTACTAAGGGNTAYGARA-3' and 5'-CACAACATCTTGCTACTWATDATNGT-3') as described previously (Lau et al., 2010; Woo et al., 2012a). Three complete genomes of PPIV-1, from nasopharyngeal samples S033N, S119N and TACAATATATGTGGGTGATCCTTACT-3', were sequenced using previously (Lau et al., 2010; Woo et al., 2012a). Phylogenetic trees were constructed using the maximum-likelihood method by PHYLML 3.0 (Guindon et al., 2010) with a substitution model selected by MODELGENERATOR (Keane et al., 2006).

RT-PCR for a 555 bp fragment of the L gene was positive in two nasopharyngeal samples. Their sequences possessed <76 % nucleotide identities to those of known paramyxoviruses, suggesting a potentially novel paramyxovirus, PPIV-1. Subsequent specific RT-PCR for PPIV-1 was positive in 12 (3.1 %) nasopharyngeal and two (0.7 %) rectal samples. These sequences formed a distinct cluster separate from known respiroviruses upon phylogenetic analysis (data not shown). Quantitative RT-PCR showed that the viral load ranged from 1.3 × 10^2 to 2.7 × 10^6 copies ml^{-1} in positive samples. Attempts to passage PPIV-1 in various cell lines were unsuccessful. The genome of PPIV-1 contained 15396 bases with a G+C content of 37.4–37.5 % and conforms to the rule of six as in other members of the subfamily Paramyxovirinae with similar genome organization. The three sequenced genomes (GenBank accession nos JX857409–JX857411) shared 91.4–96.7 % nucleotide identity. Their predicted gene products showed the highest amino acid identities with those of members of the genus Respirovirus, especially Sendai virus (SeV) and HPIV-1 (Table 1). Phylogenetic trees constructed showed that PPIV-1 was most closely related to SeV and HPIV-1, forming a distinct subgroup among respiroviruses (Fig. 1). Based on the present results, we propose to name the new virus porcine parainfluenza virus 1 (PPIV-1) within the genus Respirovirus.

The genome of PPIV-1 contained a 12 nt complementary 3' leader and 5' trailer sequence, with the exception of an A→G substitution at the fifth position of the 5' trailer sequence (Fig. 2). Similar to other respiroviruses, as well as henipaviruses and morbilliviruses, PPIV-1 contained characteristic intergenic regions of GAA (genomic sense) trinucleotides. PPIV-1, SeV and HPIV-1 are common in having the trinucleotide AAA at the end of the leader sequence, the trinucleotide GAA at the beginning of the trailer sequence and using coding frame 3 in the fusion (F) and haemagglutinin–neuraminidase (HN) genes. This is in contrast to BPIV-3, SPIV-3 and HPIV-3, which possess the trinucleotide GAA at the end of the leader sequence and the trinucleotide GUA at the beginning of the trailer sequence, and use coding frame 2 in F and HN genes.

Similar to most members of the subfamily Paramyxovirinae, PPIV-1 contains a conserved A₆G₆ editing site in the phosphoprotein (P) gene (Falk et al., 2008; Thomas et al., 1988). In members of the genus Respirovirus, this RNA editing site is present in all viral species except HPIV-1 (Matsuoka et al., 1991). To examine the number of G insertions at the P mRNA editing site, primers (5'-GAAATATAATGGAGAAGGCTGGA-3' and 5'-AATACATGCGCATCTTTGGGAT-3') were used to amplify and clone a 508 bp fragment from strain S206N and the number of G insertions was determined by sequence determination of different clones (Lau et al., 2010; Woo et al., 2012a). Sixty independent clones were obtained, with mRNAs encoding three putative proteins identified: P (mRNA sequence the same as the antigenomic RNA sequence without a G insertion), V (one-G or four-G insertion) and W (two-G insertion) proteins that shared the first 323 aa at the N terminus. Among the 60 clones, 44 (73 %) contained the sequence AAAAAAGG (without a G insertion) (encoding the P protein), 11 (18 %) contained AAAAAAGGGG (one-G insertion) (encoding the V protein), four (7 %) contained AAAAAAGGGGG (four-G insertion) (encoding the V protein) and one (2 %) contained AAAAAAGGGG (two-G insertion) (encoding the W protein). Similar to other respiroviruses, except HPIV-1, the editing site of PPIV-1 contained an A₆G₆ run. However, the number of G residues following (two Gs) and the

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Table 1. Pairwise amino acid identities of predicted gene products of PPIV-1 compared with those of other paramyxoviruses

<table>
<thead>
<tr>
<th>Virus*</th>
<th>PPIV-1-S206N</th>
<th>PPIV-1-S033N</th>
<th>PPIV-1-S119N</th>
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<tr>
<td></td>
<td>N  P  M  F  A  L</td>
<td>N  P  M  F  A  L</td>
<td>N  P  M  F  A  L</td>
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<tr>
<td>Respirovirus</td>
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<tr>
<td>PPIV-1-S206N</td>
<td>– – – – – –</td>
<td>95.2 85 96 91.4 93.8 96.7</td>
<td>97 91.8 98.8 96.6 98.6 98.7</td>
</tr>
<tr>
<td>PPIV-1-S033N</td>
<td>95.2 85 96 91.4 93.8 96.7</td>
<td>– – – – – –</td>
<td>95.1 84 95.4 91 93.8 96.8</td>
</tr>
<tr>
<td>PPIV-1-S119N</td>
<td>97 91.8 98.8 96.6 98.6 98.7</td>
<td>95.1 84 95.4 91 93.8 96.8</td>
<td>– – – – – –</td>
</tr>
<tr>
<td>SeV</td>
<td>74.5 41.7 76.1 60.5 56.5 77.1</td>
<td>75 42.3 75.9 60.4 56.3 76.6</td>
<td>74.8 41.1 76.4 61.2 56.4 76.9</td>
</tr>
<tr>
<td>HPIV-1</td>
<td>72.5 41.2 75.6 61 57.1 76.5</td>
<td>72.6 41.1 75.3 62 57 76</td>
<td>72.5 40.8 75.3 61.7 56.9 76.4</td>
</tr>
<tr>
<td>BPIV-3</td>
<td>61.8 30.5 62.7 43.6 45.9 61.9</td>
<td>62.1 29.5 62.4 43.1 45.6 61.7</td>
<td>61.6 62.4 43.2 45.7 61.8</td>
</tr>
<tr>
<td>SPIV-3</td>
<td>61.7 28.7 61.8 42.9 46.3 61.6</td>
<td>68.8 28.8 61.5 41.9 46.1 61.6</td>
<td>61.1 28.5 61.5 42.8 46.5 61.5</td>
</tr>
<tr>
<td>HPIV-3</td>
<td>59.3 29.3 62.6 43.7 47.1 62.2</td>
<td>59.1 29.9 62.6 42.9 46.9 61.9</td>
<td>59.1 29.5 61.8 43.2 47 62.2</td>
</tr>
<tr>
<td>Morbillivirus</td>
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<tr>
<td>FMDV</td>
<td>24.2 16.8 34.3 27.7 20.6 38.4</td>
<td>25.2 18.1 34.6 26.9 20.8 38.7</td>
<td>25.5 18.1 34.2 27.6 21.2 38.4</td>
</tr>
<tr>
<td>MeV</td>
<td>24.6 19.3 35.5 27.6 18.8 39.4</td>
<td>25.8 18.2 35.2 27.5 17.8 39.5</td>
<td>24.6 19.2 35 28 18.8 39.5</td>
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<tr>
<td>Avulavirus</td>
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<tr>
<td>APMV-6</td>
<td>20.9 18.5 23.5 28 21.7 27.8</td>
<td>20.4 20.5 23 27.9 22.9 27.9</td>
<td>20.2 18.8 23.4 28 21.7 27.8</td>
</tr>
<tr>
<td>NDV</td>
<td>23.5 17.7 21.3 26.3 25 28</td>
<td>22.6 16.4 20.5 26.5 26.2 27.3</td>
<td>23.3 17.7 21 24.9 25.2 27.7</td>
</tr>
<tr>
<td>Henipavirus</td>
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<tr>
<td>HeV</td>
<td>23.9 17.5 33.3 28.8 23.8 38.1</td>
<td>24.3 18 32.2 28.3 22.3 37.8</td>
<td>23.6 17.7 33.6 28.7 23 37.9</td>
</tr>
<tr>
<td>NiV</td>
<td>23.8 19.4 34.2 29.8 23.6 38.1</td>
<td>24.3 18 33.6 29.3 23.4 38.2</td>
<td>23.7 18.4 34.4 29.6 23.4 38.5</td>
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<tr>
<td>Rubulavirus</td>
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<td></td>
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<tr>
<td>PorPV</td>
<td>22.7 16.1 21.1 25.5 25 30.4</td>
<td>23 17.4 21 26.4 23.3 30.2</td>
<td>22.8 16 21.3 26.1 26 30.3</td>
</tr>
<tr>
<td>MenPV</td>
<td>23.9 17.4 19.8 25.6 18.3 29.4</td>
<td>21.9 19 19.3 25 18.7 29.4</td>
<td>23 17 19.8 25.7 17.9 29.4</td>
</tr>
<tr>
<td>Unclassified</td>
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<tr>
<td>AsaPV</td>
<td>27.5 18 41.7 32.9 37.5 50</td>
<td>28.7 18.9 41.4 33 38.5 49.8</td>
<td>28.3 19.2 41.2 32.8 39 49.6</td>
</tr>
<tr>
<td>BeiPV</td>
<td>25.3 18.4 36.6 29.5 20.3 38.6</td>
<td>25 20.4 36.3 29 21.1 38.6</td>
<td>25.1 20.5 36.3 30.5 20.5 38.4</td>
</tr>
<tr>
<td>FdlPV</td>
<td>24.8 21.1 35.7 29.3 15.4 38.4</td>
<td>24.8 19 35.4 29.3 15.7 38.6</td>
<td>24.5 21 35.4 29.7 15.6 38.2</td>
</tr>
<tr>
<td>JPU</td>
<td>23.8 16.4 37.4 29.6 23.6 38.5</td>
<td>23.8 21.6 37.7 30.1 24.1 38.8</td>
<td>23.6 17 36.6 29.2 23.7 38.7</td>
</tr>
<tr>
<td>MosPV</td>
<td>26.2 18.8 34.8 27.2 20.2 38.5</td>
<td>26.7 16.9 34.5 25.8 20.5 38.3</td>
<td>26 16.6 34.8 26.7 20.7 38.5</td>
</tr>
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<td>TlpPV</td>
<td>24.8 19.1 33.1 29.4 21.9 38.2</td>
<td>25.5 18.3 33.1 27.6 22.4 38</td>
<td>25.1 19.5 32.9 29.7 22.1 38.2</td>
</tr>
<tr>
<td>NarPV</td>
<td>25.1 18.6 36 27.9 20.6 37.9</td>
<td>25.5 17.9 35.4 27.9 21.3 37.7</td>
<td>25.2 18.7 36.3 27.8 20.3 37.8</td>
</tr>
</tbody>
</table>

*BPIV, bovine parainfluenza virus; SPIV, swine parainfluenza virus; APMV, avian paramyxovirus; NDV, Newcastle disease virus; PorPV, porcine rubulavirus; AsaPV, Atlantic salmon paramyxovirus; FdlPV, fer-de-lance virus; NarPV, Nariva virus; see text for other abbreviations.
sequence preceding (ATTGGT) the A6 run were different from other respiroviruses. In addition to the P, V and W proteins, the P gene of PPIV-1 also encoded a 204 aa putative C protein by alternative translation initiation similar to other respiroviruses. This putative C protein was initiated at the second AUG codon in the P/V/C genes, at the +2 frame relative to P. SeV and HPIV-1 possess a nested set of C proteins, called C9, C, Y1 and Y2, which are initiated at four different translation starting sites but share a common C-terminal end (Faisca & Desmecht, 2007; Newman et al., 2002). Such conserved initiation codons were not found in PPIV-1 (Fig. 2).

Similar to SeV and HPIV-1, the F protein of PPIV-1 possessed a single-basic protein cleavage site followed by a highly conserved fusion peptide. This is in contrast to the F proteins of HPIV-3, BPIV-3 and SPIV-3, which possess multi-basic protein cleavage, furin recognition sites (R-X-K/R-R) that allow intracellular cleavage in trans-Golgi membranes (Morrison, 2003). It has been suggested that F proteins with a single-basic cleavage site, as observed in HPIV-4, must be cleaved by an extracellular host enzyme usually found exclusively in the respiratory tract, rendering infections limited to the respiratory tract (Morrison, 2003).

In this study, a novel porcine paramyxovirus, PPIV-1, was discovered, which was phylogenetically most closely related to SeV and HPIV-1. However, in contrast to HPIV-1, which does not possess a mRNA editing function, the P gene of PPIV-1 is able to produce P, V and W proteins as a result of mRNA editing, and the C protein by alternative translation initiation. Moreover, PPIV-1 is different from...
other respiroviruses in having two G residues instead of three to five G residues following the A<sub>g</sub> run at the editing site. These results support the idea that PPIV-1 represents a novel paramyxovirus within the genus *Respirovirus*.

PPIV-1 is likely to be associated with respiratory disease in swine, although its pathogenicity remains to be ascertained. Paramyxoviruses are known for their potential to cross species barriers and cause severe disease epidemics or epizootics in the new hosts. Whilst HeV and NiV are known to cause encephalitis in humans, most of the recently identified paramyxoviruses have been isolated from healthy animals or cell lines, and hence their pathogenicity is largely unknown. Nevertheless, at least two cases of human MenPV infection with influenza-like illness have been demonstrated in close contact with infected pigs using serological studies (Bowden et al., 2001; Chant et al., 1998). Recently, a novel morbillivirus, FmoPV, was isolated from the urine of domestic cats, which was associated with tubulointerstitial nephritis (Woo et al., 2012a). This suggests that paramyxoviruses may cause various diseases in different organs of infected animals. In the present study, PPIV-1 was detected mainly in nasopharyngeal swabs of deceased pigs with a positive detection rate of 3.1%. Whilst the causes of deaths in the sampled pigs were unknown, the presence of PPIV-1 in a significant proportion of nasopharyngeal samples with high viral loads suggested its possible association with respiratory disease, similar to its close counterparts, HPIV-1 and SeV (Karron & Collins, 2007). The absence of PPIV-1 in the available lung samples could be due to the relatively small sample size compared with nasopharyngeal samples or the possibility that the viral replication was limited mainly to the upper respiratory tract. However, it is well known that porcine viruses, such as swine influenza viruses and porcine reproductive and respiratory syndrome virus, may play an important role in respiratory illness in swine with secondary infection by bacteria such as *Mycoplasma hyopneumoniae* through virus–bacteria interaction (Fablet et al., 2012; Lau et al., 2008). Further studies on co-infections, serology and cell culture isolation may provide better insights into the pathogenicity of PPIV-1.

Under the genus *Respirovirus*, PPIV-1, HPIV-1 and SeV may belong to a separate group of viruses, ‘group 1’, distinct from another group, ‘group 3’, comprising SPIV-3, BPIV-3 and HPIV-3. PPIV-1 possessed the highest amino acid identities to HPIV-1 and SeV in their predicted proteins. Phylogenetic analysis also showed clustering of the three viruses separate from ‘group 3’ viruses (Fig. 1). It has been shown that HPIV-1 and its murine counterpart, SeV, share high sequence homology and antigenic cross-reactivity (Lyn et al., 1991). Therefore, PPIV-1 may share antigenic cross-reactivity with HPIV-1 and SeV. The three ‘group 1’ viruses also possess another common genome features distinct from ‘group 3’ viruses. These include the presence of an A→G substitution at the fifth position of the 5′ trailer sequence, the trinucleotide AAA at the beginning of the leader sequence, the trinucleotide GAA at the end of the trailer sequence, the use of coding frame 3 in the F and HN genes, and a single basic protein cleavage site in the F protein. Given that they may be associated with respiratory tract infections in their hosts, HPIV-1, PPIV-1 and SeV are likely to be closely related viruses with similar pathogenicity.

The present results support a diversity of paramyxoviruses circulating in swine populations. Paramyxoviruses belonging to four of the seven paramyxovirus genera, including *Avulavirus*, *Henipavirus*, *Respirovirus* and *Rubulavirus*, have been reported to infect swine (Chant et al., 1998; Chua et al., 1999, 2000; Heinen et al., 1998; Ishida & Homma, 1978; Janke et al., 2001; Lipkind et al., 1986; Moreno-López et al., 1986). For respiroviruses, pigs were involved in the epizootic infection by SeV, the mouse parainfluenza virus.
paramyxoviruses in causing new zoonotic epidemics. Human (Woo et al., 2010). In contrast to SPIV-3, we believe that PPIV-1 represents a novel respirovirus with swine as its major reservoir, as positive samples were detected throughout the study period. Given that cross-species transmission of various viruses has continued to occur from swine to human (Woo et al., 2012c), continuous surveillance of swine is important in predicting the potential of porcine paramyxoviruses in causing new zoonotic epidemics.

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