

**UNIVERSIDADE FEDERAL DE MINAS GERAIS**  
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**COLEGIADO DO CURSO DE PÓS-GRADUAÇÃO EM CIÊNCIA ANIMAL**

**GENETIC VARIABILITY OF NEW BRAZILIAN PCV2D STRAINS AND THEIR  
RELATION TO COMMERCIAL VACCINES**

**Heloiza Irtes de Jesus Nascimento**

**Belo Horizonte**  
**2021**

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**GENETIC VARIABILITY OF NEW BRAZILIAN PCV2D STRAINS AND THEIR  
RELATION TO COMMERCIAL VACCINES**

Dissertation submitted to the Graduate Program from Escola de Veterinária, Universidade Federal de Minas Gerais, in partial fulfillment of requirement of Master's degree in Veterinary Science.

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“Once you have tasted flight, you will forever walk the earth with your eyes turned skyward, for there you have been, and there you will always long to return.”

— Leonardo da Vinci

## RESUMO

No presente estudo 246 amostras clínicas oriundas de granjas de suínos comerciais nas regiões sul, sudeste e centr-oeste do Brasil, previamente vacinadas contra PCV2 e que apresentavam sinais clínicos compatíveis com PCVD foram submetidas para genotipagem de PCV2. O tipo de material enviado para diagnóstico foram amostras de fluido oral, soro e pool de órgãos linfoides. Das amostras analisadas, 106 (43.09% - 106/246) foram genotipadas, sendo 75.47% (80/106) identificadas como PCV2d e 22.64% (24/106) identificadas como PCV2b. Em 2/106 (1.89%) amostras foram verificadas co-infecção de PCV2b e PCV2d. Não houve detecção do genótipo PCV2a nas amostras analisadas. Dentre as amostras clínicas analisadas, o fluido oral obteve um maior número de amostras genotipadas (40/106-37.74%), seguido de pool de órgãos linfóides e soro, com o mesmo número de amostras genotipadas (33/106-31.13%). Adicionalmente, 51 amostras clínicas brasileiras coletadas em 2019 foram enviadas para sequenciamento genético do gene ORF2, que codifica a proteína do capsídeo viral (Cap). Destas, 25 apresentaram boa qualidade para análise, sendo 8 genotipadas como PCV2b e 17 como PCV2d, confirmando que no Brasil, como descrito mundialmente, houve o aumento do genótipo PCV2d. Para analisar a distribuição temporal dos genótipos e flutuação mundial dos genótipos desde 1993 à 2019, 3,544 sequencias disponíveis no GenBank foram analisadas, demonstrando um considerável aumento do genótipo PCV2d a partir de 2006, sendo hoje, o genótipo mais prevalente no mundo. Para estimar a variabilidade da Cap protein de nossas sequencias de PCV2d, comparamos nossas amostras com outras 1,300 sequencias de PCV2d disponíveis no GenBank. Com o objetivo de avaliar a possível pressão vacinal sobre o o genótipo PCV2d, separamos as sequencias em 4 grupos: (1) Pre vacinação (PreVacD) - sequencias de amostras coletadas antes de 2006; (2) Pós vacinação (PosVacD) - sequencias de amostras coletadas entre 2007 e 2020; (3) sequencias de suínos selvagens ou de vida livre(Wboard) que não sofreram pressão vacinal; e (4) nossas sequencias de PCV2d (TestD), analisadas no presente estudo.. Devido às possíveis falhas vacinais observadas nas granjas de suínos comerciais no Brasil, as amostras de PCV2d sequenciadas no presente estudo foram comparadas com as sequencias da ORF2 disponíveis de três vacinas comerciais utilizadas no Brasil, uma contendo o genótipo PCV2b e duas contendo o genótipo PCV2a. Grande parte dos resíduos de aminoácidos que se encontram dentro de regiões de epítipo são conservadas, sugerindo uma boa reação cruzada entre as amostras vacinais e as amostras de PCV2d analisadas. Contudo, em alguns resíduos de aminoácidos em sítios antigênicos, essenciais para ligação de anticorpos e, conseqüentemente, neutralização viral, foram detectadas mutações entre as sequencias de PCV2d e as sequencias vacinais. Este resultado sugere que estas mutações possam ter importancia em relação à resposta. Porém, mais estudos devem ser realizados para elucidar essas questões, principalmente a implementação de processos de vigilância de genótipos de Circovirus suínos tipo 2 circulantes no Brasil.

Palavras chaves: PCV2, PCV2d, Circovírus Suino tipo 2, Circovirose, Brasil

## ABSTRACT

In the present study, 246 clinical samples from commercial pig farms located in the south, southeast and central-west regions of Brazil previously vaccinated against PCV2 and showing clinical signs compatible with PCVD were submitted for PCV2 genotyping. The type of material sent for diagnosis were samples of oral fluid, serum and lymphoid organs pool. Of the analyzed samples, 106 (43.09% - 106/246) were genotyped, with 75.47% (80/106) identified as PCV2d and 22.64% (24/106) as PCV2b. In 2/106 (1.89%) samples, coinfection of PCV2b and PCV2d was observed. There was no detection of the PCV2a genotype in the analyzed samples. Among the analyzed clinical samples, oral fluid obtained the greater number of genotyped samples (40/106-37.74%), followed by pool of lymphoid organs and serum, with the same number of genotyped samples (33/106-31.13%) . Additionally, 51 Brazilian clinical samples collected in 2019 were sent for genetic sequencing of the ORF2 gene, widely used for genomic/protein analysis, which encodes for the viral capsid protein (Cap). Of these, 25 had good quality for analysis, and 8 were genotyped as PCV2b and 17 as PCV2d, corroborating many other publications around the world that demonstrated the increase of the PCV2d genotype. To analyze the temporal distribution of genotypes and fluctuation of genotypes from 1993 to 2019 worldwide, 3,544 sequences available in GenBank were analyzed, demonstrating a considerable increase in the PCV2d genotype since 2006, today the most prevalent genotype in the world. To estimate the Cap protein variability of our PCV2d sequences, our results were compared to other 1,300 PCV2d sequences available in GenBank. In order to assess the possible pressure of the vaccine against the PCV2d genotype population infection, four groups of samples were defined: (1) Prevaccination (PreVacD) - sequences from samples collected before 2006; (2) Post-vaccination (PosVacD) - sequences of samples collected between 2007 and 2020; (3) sequences from wild or feral pigs (Wboard) that were not vaccinated, and (4) our PCV2d sequences (TestD) analyzed in the present study. Due to possible vaccine failures observed in commercial pig farms in Brazil, the PCV2d sequenced samples in the present study were compared to the ORF2 amino acid sequences available from three commercial vaccines used in Brazil, one containing the PCV2b genotype and 2 containing the PCV2a genotype. Most of the amino acid residues found within epitope regions were conserved, suggesting a good cross-reaction between vaccines and the analyzed PCV2d samples. However, in some amino acid residues in antigenic sites essential for antibody binding and consequently viral neutralization, mutations were detected in PCV2d sequences and in vaccine sequences. This result may suggest that these mutations might be involved in the vaccine immune response. However, further studies must be carried out to elucidate these aspects, especially the implementation of surveillance processes of Porcine Circovirus type 2 genotypes circulating in Brazil.

Key words: PCV2, PV2d, Porcine Circovirus type 2, Circovirose, Brazil

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## LIST OF ABBREVIATIONS

3D - three-dimensional

A - Alanine

aa – Amino acid

Amino acid 3-letter abbreviation 1-letter abbreviation

B-cell - B lymphocytes

C - Cysteine

Cap - Capsid protein

Cryo-EM - Cryo electron microscopy

D - Aspartic acid

DNA – Deoxyribonucleic acid

E - Glutamic acid

ELISA - enzyme-linked immunosorbent assays

EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária

F - Phenylalanine

G - Glycine

H - Histidine

I - Isoleucine

ICTV - International Committee on Taxonomy of Viruses

IFN-gamma - Interferon-gama

IL10 - Interleukin 10

K - Lysine

L - Leucine

LPVA - Department of Preventive Veterinary Medicine

M - Methionine

mAb - monoclonal antibodies

MAFFT - multiple alignment using fast Fourier transform

mPCV2b - mutant PCV2b

N - Asparagine

NA - neutralizing antibodies

NCBI - National Center for Biotechnology  
NJ - Neighbor-Joining  
nt – Nucleotide  
ORF – Open Reading Frame  
P - Proline  
PCR - polymerase chain reaction  
PCV2 - Porcine Circovirus Type 2  
PCV2- AD Associated Disease  
PCV2- SD - PCV2 systemic disease  
PCV2 -SI - PCV2 subclinical infection  
PCV2-ED- PCV2 enteric disease  
PCV2-LD – PCV2 lung disease  
PCV2-RD – PCV2 reproductive disorder  
PCVAD - Porcine Circovirus Associated Disease  
PCVD - Porcine Circovirus Diseases  
PDNS - Porcine dermatitis and nephropathy syndrome  
PMWS - Postweaning multisystemic wasting syndrome  
PosVacD - Pos-Vaccination genotype PCV2d  
PreVacD - Pre-Vaccination genotype PCV2d  
PRRSV- reproductive and respiratory syndrome virus  
Q - Glutamine  
R - Arginine  
S - Serine  
ssDNA - single-stranded DNA  
T - Threonine  
T-cell - T lymphocytes  
TestD – Test genotype PCV2d  
TNF-alfa - Tumor necrosis factor alfa  
UV – Ultra Violet  
V - Valine

W - Tryptophan

WboarD - Wild boar genotype PCV2d

Y - Tyrosine

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## 1. INTRODUCTION

Pork is still the most consumed animal protein in the world (OECD 2021) and Brazil is the fourth biggest pork producer, responsible for 3.88% of the world's production. The first three largest pork producer (China, European Union and United States) together are responsible for 78.49% of global production (USDA 2021).

Brazil has 2.019,356 housed sows and produced 4,436 million tons of pork in 2020 (ABPA 2021). There are 1,024 thousand tons of exported meat (4th place in the world) and an average consumption of 16 kg of pork per capita (ABPA 2021).

The entire relevance of Brazilian swine production justifies the swine herd health concern and the importance of controlling diseases of economic impact such as porcine circovirus diseases (PCVD) caused by Porcine Circovirus type 2 (PCV2).

PCV2 genome is 1766–1777 nucleotides (nt) in length (WEI et al., 2019a), belongs to Circovirus genus of the family Circoviridae and is a single stranded DNA (ssDNA) virus. It contains eleven open reading frames (ORFs) (HAMEL; LIN; NAYAR, 1998) and at least four ORFs were identified as important. ORF1 encodes a protein responsible for genome replication (MANKERTZ, 2001). ORF3 is associated with apoptosis during infection (LIN, 2011). ORF4 encodes a protein capable of blocking PCV2-induced apoptosis (GAO et al., 2014). The protein encoded by ORF2 is the capsid protein (Cap), the only viral structural protein, and it was found to be responsible for its antigenicity and virulence (HAMEL; LIN; NAYAR, 1998; NAWAGITGUL et al., 2000). ORF 2 is also used for analyzing PCV2 genetic diversity (OLVERA; CORTEY; SEGALÉS, 2007)

The first PCV2 diagnosis in Brazil was made in 1999 by Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) swine and poultry team, but the first clinical signs such as postweaning multisystemic wasting syndrome (PMWS), pneumonia and other secondary diseases associated and aggravated by the virus appeared in 2005 (MIELE et al., 2011). Since the emergence of commercial vaccines against circovirus in 2006, Brazilian swine herd has been systematically vaccinated to ensure better production rates, reduction of viremia and excretion of PCV2.

Based on serological studies for PCV2, it is assumed that PCV2 infection is ubiquitous worldwide and is accepted as a multifactorial swine disease, in which PCV2 is the essential infective agent (SEGALÉS; ALLAN; DOMINGO, 2005). It is one of the most important pathogens in Brazilian and worldwide swine production, as it causes important economic losses due to high mortality, high cull rate and delayed performance. PCV2 is an immunosuppressive agent, making pigs more vulnerable to other pathogens of respiratory and enteric tracts (CIACCI-ZANELLA, 2017).

PCV2 has been suggested to play a role in reproductive disorders (reproductive failures, abortion and mummified), is part of the Porcine Respiratory Complex, causes enteritis, porcine nephropathy and dermatitis syndrome, and proliferative and necrotizing pneumonia (OPRIESSNIG; MENG; HALBUR, 2007). However, the subclinical manifestation of the disease is more common than the clinical form of circovirus diseases.

In PCV2 subclinical infection (PCV2-SI) there is decreased average daily gain without any evident clinical sign, or macroscopic lesions. In lymphoid tissues there is no lesion or mild lymphocyte depletion with granulomatous inflammation. There is a low amount of PCV2 found in lymphoid tissues, but it can be detected by the standard PCR technique (SEGALÉS, 2012). All these clinical conditions were referred as PCVD (Porcine Circovirus Diseases) in Europe and PCVAD (Porcine Circovirus “Associated” Diseases) in North América. In 2012, (SEGALÉS, 2012) proposed the unified terminology of porcine circovirus diseases – PCVD, to designate all the aforementioned diseases, including subclinical PCV2 infection and this is the term used in this work.

Interestingly the emergence of PCVD in Europe and North America occurred almost at the same time. This phenome can be explained by the independent emergence of the virus in several regions or by the unique emergence and global spread by the swine trade (FIRTH et al., 2009). This second theory seems more plausible and might explain the rapid spread of PCV2 virus around the world, including new genotypes.

The rate of swine herds vaccinated for PCV2 in Brazil varies between 80-98% (CIACCI-ZANELLA, 2017) and the most used protocol is the vaccination of three-week-old piglets, a time that usually coincides with weaning. Since the massive introduction of vaccination, the health status of farms has changed and

there are currently self-limited subclinical problems, with occasional outbreaks. However, practices inherent to the application of the vaccine (half dose, change of manufacturers' brands, inadequate storage temperature, application in part of the batch) possibly caused the virus (of all genotypes) to continue circulating and causing disease (CIACCI-ZANELLA, 2017).

## 2. OBJECTIVES

- To determine which PCV2 genotypes are circulating in Brazilian vaccinated swine herds.
- Determine which PCV2 strains are more often present in Brazilian vaccinated pig herds from diagnostic samples and determine its genetic diversity
- Analyze samples of PCV2d from NCBI from the periods pre and post launch of vaccines, checking for significant changes on amino acid level.
- To compare the amino acid sequence at antigenic sites among Brazilian PCV2d samples and three currently registered vaccines.

### 3. Literature Review

#### 3.1. Etiology

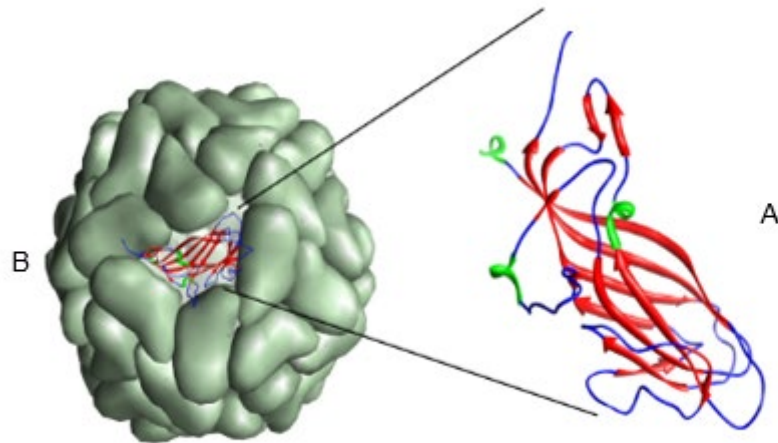
PCV is thought to have originally evolved from a plant nanovirus through host-switch followed by a recombination event with a picorna-like virus in a mammalian host (GIBBS; WEILLER, 1999). FIRTH *et al.* (FIRTH *et al.*, 2009) showed that PCV2 originated within approximately the last 100 years and that PCV2a and PCV2b shared a common ancestor (not that PCV2b evolved from PCV2a) and these two genotypes have been independently circulating since then.

The First report of an outbreak of what came to be called postweaning multisystemic wasting syndrome (PMWS) was reported in West Canada (ALLAN *et al.*, 1998; ELLIS, 2014; HARDING *et al.*, 1998) but the first identification of the virus as a pathogen and its isolation was performed by Dr. Gordon Allan and Brian Meehan in 1997 (ALLAN *et al.*, 1998; MEEHAN *et al.*, 1998)

PCV2 at the time of discovery was challenging because experiments failed while trying to reproduce Koch's postulate (ELLIS, 2014), concluding that PCV2 is the necessary but not sufficient cause of PCVD but could be more severe or even fatal when pigs were coinfecting with another pathogen (KRAKOWKA *et al.*, 2000; OPRIESSNIG; HALBUR, 2012). Nowadays, it is clear that PCV2 is ubiquitous and was present many years prior to the onset of clinical PCVD (PATTERSON; OPRIESSNIG, 2010).

PCV2 genome is 1766–1777 nucleotides (nt) in length (WEI *et al.*, 2019a) making them the smallest autonomously replicating pathogen. It belongs to *Circovirus* genus of the family *Circoviridae*, is a single-stranded DNA (ssDNA) and is a nonenveloped icosahedral virus. It contains eleven open reading frames (ORFs) (HAMEL; LIN; NAYAR, 1998) and at least four ORFs were identified as important. ORF1 encodes a protein responsible for genome replication (Rep) (MANKERTZ; HILLENBRAND, 2001), ORF3 is associated with apoptosis during infection (Wei-Li Lin, 2011) and ORF4 protein is capable of blocking PCV2-induced apoptosis (GAO *et al.*, 2014). The protein encoded by ORF2 is the capsid protein (Cap) and the only viral structural protein and was found to be responsible for its antigenicity and virulence (HAMEL; LIN; NAYAR, 1998; NAWAGITGUL *et al.*, 2000). ORF 2 is also used for analyzing PCV2 genetic

diversity (OLVERA; CORTEY; SEGALÉS, 2007) and the virion is a structure containing 60 copies of the capsid protein (CROWTHER et al., 2003).



**Figure 1: PCV2 Cap subunit model structure and assembly into a viral capsid.** The ribbon model of the Cap subunit (A) with helices, loops and sheets shown in green, blue and red, respectively. Panel B shows a CP subunit placed in the context of the viral capsid. The remaining 59 Cap subunits are depicted in gray. **Source:** TRIBLE; ROWLAND, 2012.

### 3.2. Epidemiology

Phylogenetic analysis around the world identified PCV2 viruses as very similar (nucleotide sequences identity higher than 93%) to each other (OLVERA; CORTEY; SEGALÉS, 2007) but with application of bioinformatic tool, many research groups started to report the emergence of different genetic groups which later came to be called genotypes (SEGALÉS et al., 2008).

Nowadays the genotyping methodology proposed by (FRANZO; SEGALÉS, 2018) of maximum intra-genotype p-distance of 13% (calculated on the ORF2 gene), bootstrap support at the corresponding internal node higher than 70% and at least 15 available sequences. This method has been used for PCV2 genotyping and allows the definition of 8 genotypes (PCV2a to PCV2h).

PCV2a, PCV2b and PCV2d has been widely diagnosed worldwide while

PCV2c was described in Denmark (DUPONT et al., 2008), in Brazil on feral pigs (FRANZO et al., 2015) and wild boars (SATO et al., 2017). PCV2e was first described in Mexico and USA (HARMON et al., 2015), PCV2f (BAO et al., 2018) and PCV2h (YAO et al., 2019) were described in China few years ago. In 2020 a new genotype, PCV2i, isolated from a USA pig was proposed by Wang (WANG et al., 2020).

In the early 2000s, more severe clinical diseases were observed in pigs and PCVD became present worldwide. The most prevalent genotype identified and associated with the disease at the time was PCV2b (FIRTH et al., 2009; FRANZO; SEGALÉS, 2018).

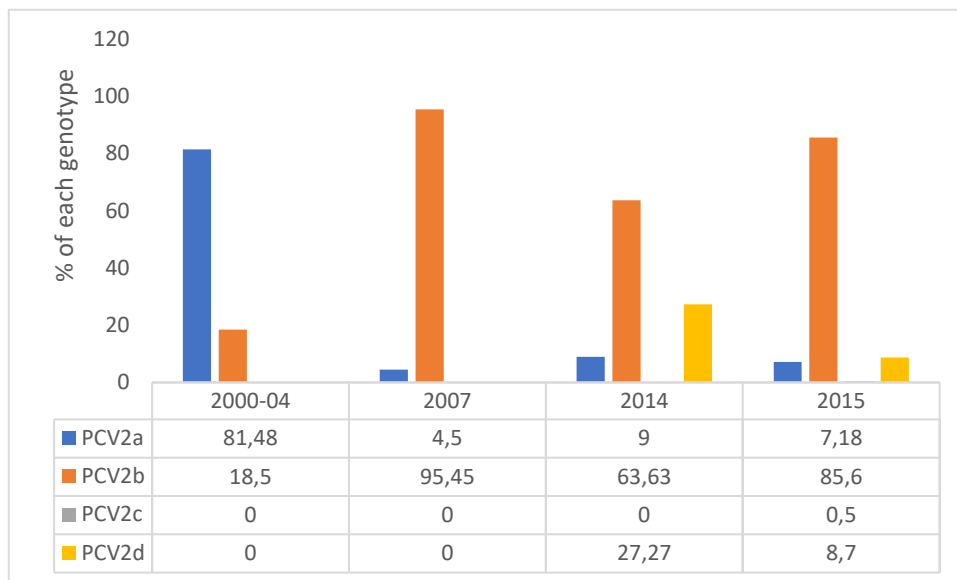
The first global shift in the predominance of subtype was pointed to occur from PCV2a to PCV2b prior to 2003 (DUPONT et al., 2008) and few years after this first genotype prevalence shift, commercial PCV2a-based vaccines become widely used worldwide and these vaccines seemed to be highly efficacious against PCV2 infection (CHAE, 2012; OPRIESSNIG et al., 2009). However, in 2012 new PCVD outbreaks started to be reported in vaccinated farms in the USA and an emerging mutant PCV2b (mPCV2b) strain was identified (OPRIESSNIG et al., 2013). This mPCV2b found was very similar to the strain previously reported in 2010 in China (GUO et al., 2010) and later was designated as PCV2d. Since then, there has been an increase in the deposition of PCV2d sequences, indicating its predominance in Asia, Europe, North and South America (KHAYAT et al., 2010). This change could be, at least in part, induced by PCV2 vaccination pressure (REINER; HOFMEISTER; WILLEMS, 2015).

PCV2d shows an elongation of ORF2 by one Lysine (K) (XIAO; HALBUR; OPRIESSNIG, 2012). In addition to the nucleotide differences, structure-based sequence comparison demonstrate that each genotype possesses a unique combination of amino acids located on the surface of the capsid that undergo substitution (KHAYAT et al., 2010).

In the comparison of virulence, the Chinese PCV2d strain caused more serious disease compared to the PCV2a and PCV2b strains while the Korean and North American PCV2d strain exhibited similar virulence to PCV2a and PCV2b strains (CHO et al., 2020; GUO et al., 2012; OPRIESSNIG et al., 2014). Another study aiming to compare virulence between PCV2a, PCV2b and PCV2d, although concluding they have similar virulence. Animals infected with PCV2d had a

significantly higher amount of PCV2 DNA and lymphoid lesions consistent with PCVD (OPRIESSNIG et al., 2014). Also PCV2d showed a significant higher virulence when coinfecting with other pathogen, such as PRRSV (SUH et al., 2021).

This new mutant strain had its first identification in Brazil in 2014 (SALGADO et al., 2014). The strain was isolated from vaccinated pigs suffering of PMWS. Many authors in Brazil reported the presence of different PCV2 genotype along the years providing information that PCV2b until now, seemed to be the predominant genotype (Figure 2).



**Figure 2: Percentage of the genotyped samples in the years 2000-04, 2007, 2014 and 2015.** Data from: (CHIARELLI-NETO et al., 2009; DE CASTRO et al., 2008, 2012; FRANZO et al., 2015; GAVA et al., 2018; RODRIGUES; CRUZ; ARAÚJO JÚNIOR, 2018; SALGADO et al., 2014; SATO et al., 2017; SCHAEFER et al., 2015).

### 3.3. Pathogenesis, Clinical Signs and Lesions

PCV2 is the primary causative agent of PCVD, however it has been difficult to reproduce the disease under experimental conditions (FENAUX et al., 2002; OPRIESSNIG; HALBUR, 2012; OPRIESSNIG; MENG; HALBUR, 2007) and coinfections with other swine pathogens or immunostimulant are usually necessary to reproduce PCVD (OPRIESSNIG; HALBUR, 2012).

Clinical signs are usually present on pig with 8-16 weeks of age and a variety of symptoms can be associated to PCV2 as PCV2 systemic disease (PCV2-SD), PCV2

lung disease (PCV2-LD), PCV2 enteric disease (PCV2-ED), PCV2 reproductive disease (PCV2-RD) and Porcine dermatitis and nephropathy syndrome (PDNS) (SEGALÉS, 2012). All denominations are summarized on table 1. Nowadays PCV2 disease complex is collectively named Porcine Circovirus Diseases (PCVD) and designates all the above-mentioned conditions, including the PCV2 subclinical infection and PMWS (SEGALÉS, 2012).

Transmission of PCV2 is thought to occur through direct contact via oronasal, fecal, semen and urinary routes (OPRIESSNIG; MENG; HALBUR, 2007). The virus can be found in semen (LAROCHELLE et al., 2000), and vertical intrauterine transfer of PCV2 results in viremic or persistently infected piglets at birth (JOHNSON et al., 2002; O'CONNOR et al., 2001). PCV2 uses heparan sulfate and chondroitin sulfate B, glycosaminoglycans as receptors for its attachment and internalization to host cells (MISINZO et al., 2006).

Despite most of the pig population are infected with PCV2, a high percentage of animals shows no clinical signs of disease, indicating a subclinical infection (OPRIESSNIG et al., 2020). PCV2 subclinical infection (PCV2-SI) can be described as showing decreased average daily gain without any evident clinical sign, lack of notorious clinical signs, none or minimal histopathological lesions, low amount of PCV2 in tissues and also has been linked to decreased vaccine efficacy (OPRIESSNIG et al., 2006; SEGALÉS, 2012).

PMWS or PCV2-SD pigs have marked depletion of lymphocytes from lymphoid tissue and the replacement with histiocytes and macrophages (KRAKOWKA et al., 2002). These include depletion of B and T lymphocytes combined with decrease on IgM+ (DARWICH et al., 2002). The depletion of lymphocytes has been suggested to be a result of apoptosis, but the evidence for this theory is still lacking (WIKSTROM, 2008). Proposal mechanism that may enhance PCV2 replication during coinfection includes alteration of the host cytokine response to create a more favorable environment for PCV2 (increase of IFN-gamma and chemokines like IL10 and TNF-alfa) and initiation of host cell replication, necessary for the S-phase-dependent PCV2 replication (ELLIS, 2014; SEGALÉS; ALLAN; DOMINGO, 2005). PCV2-LD has a potential diagnostic overlapping with PCV2-SD since respiratory clinical signs can be easily present in cases of systemic disease (OPRIESSNIG; MENG; HALBUR, 2007; TICO; SEGALÉS; MARTI, 2013).

In cases of nephropathy syndrome (PDNS), extremely high PCV2 antibody

amount triggers the development of fibrinous deposits (immune complexes) in kidney tissue. This immune complex can initiate an inflammatory process when deposited within the vascular or glomerular capillary walls added to an increased number of CD8+ cells in kidneys. This might be an explanation for the severe renal lesions (WELLENBERG; STOCKHOFE-ZURWIEDEN; JONG, 2004).

PCV2-ED is characterized by granulomatous inflammation and lymphoid depletion in the Peyer's patches in the small and large intestines (infiltrates of epithelioid cells and giant multinucleated cells), presence of intracytoplasmic inclusion bodies and some animal can show multifocal necrosis and ulceration with fibrin and neutrophils exuding from the ulcerated areas into the lumen (KIM et al., 2004)

PCV2-RD can be described as clinical manifestations of abortions, stillbirths, fetal mummification and increased preweaning mortalities (OPRIESSNIG; MENG; HALBUR, 2007). Affected herds are typically gilt startups or new populations. Nonsuppurative to necrotizing or fibrosing myocarditis associated with abundant PCV2 antigen is the hallmark lesion in stillborn and neonatal pigs from field cases (O'CONNOR et al., 2001; WEST et al., 1999). PCV2-associated microscopic lesions have not been reported in dams with PCV2-associated reproductive failure, and reproductive organs and placental sections are usually normal (RITTERBUSCH et al., 2012).

**Table 1:** Summary of denomination, gross and microscopic lesions on PCVD. Adapted from (SEGALÉS, 2012)

PCVD	Gross Lesions	Microscopic lesions
PCV2 subclinical infection (PCV2-SI)	None	None or slight lymphocyte depletion with granulomatous inflammation of lymphoid tissues
PCV2 systemic disease (PCV2-SD)  Replaced terminology: Postweaning multisystemic wasting syndrome (PMWS), Porcine circovirus, PCV2-associated systemic infection	Long rough hair coat, prominent backbone and relatively oversized head; Lymph node enlargement; Lack of pulmonary collapse. White spots on kidney's cortices; Atrophic and discolored liver, slightly, rough hepatic surface. Catarrhal enteritis with or without mesenteric edema; Occasional spleen infarcts.	Moderate to severe lymphocyte depletion with granulomatous inflammation of lymphoid tissues; possible presence of intracytoplasmic botryoid inclusion bodies; Lymphohistiocytic to granulomatous interstitial pneumonia; occasionally, peribronchiolar fibroplasia, mild to severe necrotizing bronchiolitis and/or proliferative and necrotizing pneumonia. Interstitial nephritis. Variable degree of lymphohistiocytic hepatitis, with apoptotic bodies, disorganization of hepatic plates, and/or perilobular fibrosis. Granulomatous enteritis. Possibility of lymphohistiocytic inflammation in virtually whatever tissue.
PCV2 lung disease (PCV2-LD)  Replaced terminology: PCV2-associated respiratory disease Proliferative and necrotizing pneumonia (PNP)	Lack of pulmonary collapse and tan-mottled lungs	Granulomatous bronchointerstitial pneumonia with or without bronchiolitis and bronchiolar fibrosis. Lack of PCV2-SD hallmark lesions in lymphoid tissues.
PCV2 enteric disease (PCV2-ED)  Replaced terminology: PCV2-associated enteritis	Catarrhal enteritis with or without mesenteric edema. Intestinal mucosa thickened. Enlargement of mesenteric lymph nodes.	Granulomatous enteritis. Lymphocyte depletion with granulomatous inflammation in Peyer's patches but not in other lymphoid tissues.
PCV2 reproductive disease (PCV2-RD)  Replaces Terminology: PCV2-associated reproductive failure	Fetal mummification or edematous fetuses. Fetal hepatic enlargement and congestion. Fetal cardiac hypertrophy with multifocal areas of myocardial discoloration. Ascites, hydrothorax and hydropericardium in fetuses	Non-suppurative to necrotizing or fibrosing myocarditis of fetuses. Chronic, passive, hepatic congestion in fetuses. Mild pneumonia in fetuses.
Porcine dermatitis and nephropathy syndrome (PDNS)	Irregular, red-to-purple macules and papules in the skin; subcutaneous hemorrhages and edema of affected areas. Enlarged lymph nodes, mainly inguinal superficial one.	Systemic necrotizing vasculitis Fibrino-necrotizing glomerulitis with non-purulent interstitial nephritis. Chronic, fibrous interstitial nephritis with glomerulosclerosis in animals that recovered from the acute phase. From none to mild/moderate lymphocyte depletion with mild granulomatous inflammation of lymphoid tissues.

	<p>Cutaneous scars in animals that recovered from the acute phase. Bilaterally enlarged kidneys, small cortical petechiae and edema of the renal pelvis. Occasional spleen infarcts.</p>	
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### 3.4. Diagnostic

The complexity of PCV2D diagnosis relies on the fact that the sole detection of PCV2 in serum or tissues of a pig, even in the presence of clinical signs compatible with PCV2D, is not conclusive to establish a diagnosis (PUIG, 2009). At present, three diagnostic criteria must be fulfilled to establish an individual diagnosis of PCVD (SEGALÉS; ALLAN; DOMINGO, 2005):

- 1) Presence of clinical signs such as wasting, weight loss, and respiratory disease;
- 2) Presence of the hallmark PCV2-associated microscopic lesions (lymphoid depletion and/or histiocytic replacement of follicles in lymphoid tissues), and
- 3) PCV2 antigen or nucleic acids associated with the microscopic lesions as determined by immunohistochemistry or ISH.

Some techniques might be useful to refine PMWS diagnosis but cannot be used alternatively to histopathology and detection of PCV2 in tissues. This techniques includes PCV2 load quantification in sera of  $10^7$  DNA copies/ml (OLVERA et al., 2004) and serological tests (FORT; OLVERA; SIBILA, 2007).

Subclinical PCV2 infection is established when, although PCV2 is detected in blood and/or tissues, the amount of viral load is low and associated with no or minimal lesions (OPRIESSNIG; MENG; HALBUR, 2007).

### 3.5. Immune Response

Cell mediated immune response and neutralizing antibodies (NA) are important for protection against PCV2 (DARWICH; MATEU, 2012) and the presence of NA is important in controlling virus replication (MEERTS et al., 2006). A decrease in viraemia coincides with an increase in NA titers in pigs inoculated with PCV2 suggesting that NAs represent an important mechanism for viral clearance and recovery from infection (FORT; OLVERA; SIBILA, 2007).

The immunogenic epitopes of the PCV2 capsid protein have been mapped and the residue 47 to 84, 113 to 131, 156 to 208 and 228 to 233 have been demonstrated as important neutralizing epitopes (HUANG et al., 2011; KHAYAT

et al., 2011; LEKCHAROENSUK et al., 2004; MAHÉ et al., 2000; SHANG et al., 2009; TRUONG et al., 2001). Amino acid mutations were found in these regions suggesting that important antigenic differences may occur between genotypes and strains (HUANG et al., 2011; MENG, 2013; SAHA et al., 2012; WEI et al., 2019b).

Also vaccine trial studies has been extensively demonstrated by Opriessnig and other authors showing that PCV2a based vaccine are efficient against PCV2 infection and PCVD (CHAE, 2012; OPRIESSNIG et al., 2008, 2009, 2010, 2011; SEGALÉS et al., 2009; SINHA et al., 2010). But the lack of a consistent, precise and reproducible model of PCVD is one of the main obstacles to establishing clear parameters for the experimental evaluation of PCV2 vaccines (CHAE, 2012).

With the use of immuno-informatic tools, increased genetic diversity in epitope regions between field isolates and vaccines has been demonstrated and a fully protection might not be reached by current available products (BANDRICK et al., 2020; CONSTANS et al., 2015) what was demonstrated by (KANG et al., 2020), showing that sera from a commercial PCV2a based vaccine had a lower activity against PCV2d viruses.

The increase in the number of in silico analyzes, genetic diversity in epitope regions between field isolates and vaccines has been demonstrated. T- and B-cell epitopes in a PCV2a vaccine strain were not identified as epitopes in PCV2b and PCV2d field strains, indicating a difference in their antigenicity or binding affinity to receptors (CONSTANS et al., 2015). Also it was demonstrated that vaccines based only on PCV2a strain shared less T-cell epitopes with PCV2 field strains current circulating and that more than one genotype in vaccines are necessary for a better protection against PCV2 (BANDRICK et al., 2020; SEGALÉS, 2015).

## **4. MATERIALS AND METHODS**

### **4.1. Samples sent to the laboratory used in this study**

A total of 246 clinical samples from Southeast (Minas Gerais-MG State), South (Paraná-PR, Santa Catarina-SC Rio Grande do Sul-RS States), and Midwest (Mato Grosso-MT, Mato Grosso do Sul-MS, Goiás-GO, Distrito Federal-DF States) regions of Brazil were obtained. Oral fluids, lymphoid organ and sera were received for routine diagnostic at the Laboratório de Pesquisa em Virologia Animal (LPVA), Department of Preventive Veterinary Medicine, School of Veterinary Medicine of the Universidade Federal de Minas Gerais (UFMG) from 2019 to 2021. These samples were originated from pig farms previously vaccinated against PCV2 and showing PCVD-like symptoms. The pigs were vaccinated against PCV2 with one out seven PCV2 vaccines available in Brazil, according to the farm's choice (Table 4). The state that sent the highest number of samples was Minas Gerais with 122 of 246 samples (49.5%), followed by Paraná (n= 33, 13.4%), Mato Grosso (n=22, 8.9%), Rio Grande do Sul (n=21, 8.54%), Santa Catarina (n=12, 4.88%), Mato Grosso do Sul (n=9, 3.6%), Goiás (n=4, 1.63%), Distrito Federal (n=1, 0.40%) and (n=22, 9.94%) samples had no identification of origin. The most frequent clinical specimens received for PCV2 genotyping was lymphoid organ pool (n=90, 36.58%), followed by oral fluid (n=82, 33.33%) and serum (n=74, 30.08%). Fifty-eight samples were received in 2019 (n=44, 75.86% oral fluid; n=10, 7.24% lymphoid organ pool and n=4, 6.90% serum), ninety-one in 2020 (n=24, 26.37% oral fluid; n=55, 60.43% lymphoid organ pool and n=12, 13.19% serum), and ninety-seven in 2021 (n=14, 14.43% oral fluid; n=25, 25.77% lymphoid organ pool and n=58, 59.79% serum). Samples were received in the context of routine diagnosis and some information were missing such as the herd size and age of the animal. This field samples were used for genotyping by polymerase chain reaction (PCR).

### **4.2. PCV2 genotyping**

Total DNA was extracted using mini spin DNA extraction kit (Kasvi, Brasil), according to the manufacturer's instructions, and eluted with 30 µL of nuclease free

water. Two  $\mu\text{L}$  of extracted total DNA was mixed with  $0.5 \mu\text{M}$  of each PCV-2-specific primers,  $1.5 \text{ mM}$  of  $\text{MgCl}_2$ ,  $200 \mu\text{M}$  of each dNTP and  $1.5 \text{ U}$  of Taq DNA polymerase (Phoneutria, Brasil), added up to a final volume of  $25 \mu\text{L}$ . The DNA was stored at  $-80^\circ\text{C}$  until used. For genotyping of PCV2a, PCV2b and PCV2d, specific primers and PCR cycling were used according to Kwon et al (2017). All amplicons were analyzed by electrophoresis on a 1.5% agarose gel, stained by ethidium bromide and visualized in UV transilluminator.

### **4.3. Samples for sequencing**

In addition, a total of 51 samples were used for complete sequencing of Open Reading frame 2 (ORF2) gene. Eighteen came from samples collected in the field from animals with clinical signs compatible with PCVD and 33 positive samples for PCV2 by conventional PCR, kindly provided by Microvet - Microbiologia Veterinária Especial, were used for ORF2 sequencing. All samples used for sequencing were collected in the year 2019. The ORF2 gene encodes for the capsid viral protein (Cap) and were used for genomic/protein analysis. All samples sent by Microvet came from vaccinated commercial pig herds in Brazil as well, and the sequencing was performed by Simbios Biotecnologia laboratory using Sanger method.

### **4.4. Phylogenetic analysis**

Fifty-one samples were sent for sequencing, 34 of them were fully or partially sequenced, after manual polishing of sequences with the removal of important gaps, only 25 of them had enough quality to be analyzed. To estimate the phylogeny of the Brazilian PCV2 isolates, the OR2 gene from 25 Brazilian sequenced strains were aligned with 51 reference sequences described by FRANZO; SEGALÉS, (2018) from PCV2a, PCV2b and PCV2d, obtained in the National Center for Biotechnology information (NCBI) GenBank (Supplementary Figure 1), using MAFFT v7.471 (KATO;STANDLEY, 2013), with globalpair method, adjust direction options and 1,000 iterations. The alignment was manually polished to remove poor-aligned regions with AliView (<https://academic.oup.com/bioinformatics/article/30/22/3276/2391211>)

and used in the phylogeny estimation. Phylogeny was estimated by Neighbor-Joining (NJ) method (SAITOU; NEI, 1987) with 1,000 bootstrap replicates (FELSENSTEIN, 1985), using MEGA X software (KUMAR et al., 2018). The pairwise distance between sequences were estimated by p-distance method under 1,000 bootstrap replications using MEGA X software.

#### 4.5. Sequence dataset

To evaluate the PCV2 isolates fluctuation from 1993 to 2019, a total of 3,544 ORF2 sequences and metadata deposited until March of 2019 were retrieved from NCBI (Table 2). The metadata containing the year of evaluation was used to plot a graph representing their occurrence along the years, using the ggplot library (<https://link.springer.com/book/10.1007/978-3-319-24277-4>) in R (<https://www.R-project.org/>).

**Table 2:** Sequences used in retrospective study

PCV2 Genotype	PosVac	PreVac	Test	WildBoar	Others
2a	275	260	0	17	3
2b	954	476	9	111	6
2c	1	0	0	0	0
2d	1270	9	15	21	3
2e	20	2	0	0	0
2f	19	6	0	0	0
2g	3	1	0	1	0
2h	61	1	0	0	0
Total	2603	755	24	150	12

#### 4.6. Analysis of ORF2 of PCV2d from different strains and vaccines

To estimate the PCV2d ORF2 sequence variability and compare them to three available vaccine sequences, 1,300 PCV2d sequences from NCBI and 17 PCV2d strains from Brazil obtained in the present work were separated into 4 groups: 1 - Pre-Vaccination (PreVacD): PCV2d isolates collected before 2006 and not obtained from wild boars; 2 - Pos-Vaccination (PosVacD): isolates obtained from 2007 to 2020 and not obtained from wild boars; 3 - Test (TestD): PCV2d isolates sequenced in the

present work; and 4 - Wild boar (Wboard): Isolates obtained from wild boars (Table 3 and Addendum). The sequences from each group were aligned with MAFFT v7.471 (KATO; STANDLEY, 2013), with globalpair method, adjust direction options and 1,000 iterations. The alignment was manually polished and translated to amino acid sequences using AliView (<https://academic.oup.com/bioinformatics/article/30/22/3276/2391211>). Then, the consensus sequence of each group was generated in R, using the consensus function from the seqinr library ([https://link.springer.com/chapter/10.1007/978-3-540-35306-5\\_10](https://link.springer.com/chapter/10.1007/978-3-540-35306-5_10)), where sequences that were not identical in > 90% of the isolates in the group were replaced by “-“. Multiple alignment of the amino acid sequences of the capsid protein (encoded by ORF2) of the four consensus groups, PreVacD, PosVacD, Wboard and TestD, and three vaccine strains (tables 3 and 4) were performed using MAFFT v7.471 (KATO; STANDLEY, 2013). The alignment was displayed and edited on Aliview software version 1.27, and the logo representation of the consensus sequence for each group was generated with the library ggseqlogo (<https://academic.oup.com/bioinformatics/article/33/22/3645/3980251>) in R. Alignment are displayed on figure 5.

**Table 3:** Number of PCV2d sequences in each group.

Group	Sequences
Pre-Vaccination	9
Pos-Vaccination	1270
Test	17
Wild boar	21

**Table 4:** Vaccine strains used in our study

Strain	GenBank Access Number	Genotype	Reference
Vac2000-2a	GU049340	PCV2a	(MEEHAN et al., 1998)
cVac2007-2a	AF264042	PCV2a	(BANDRICK et al., 2020)
cVac2009-2b	GU799576	PCV2b	(BANDRICK et al., 2020)

## 5. RESULTS AND DISCUSSION

### 5.1. Genotyping of field samples

From 246 field samples analyzed, 106 of 246 (43.09%) were genotyped by PCR. The amount of PCV2 positive samples for genotyping was 27.59% in 2019, 47.25% in 2020 and 48.45% in 2021 (Table 5). Considering that samples were received until June of 2021 and this amount was higher than in previous years, there was a significant increase in the submission of diagnostic material. This may have been due to the increase in clinical disease in the field, the need for differential diagnosis with other diseases or more PCV2 vaccines sponsoring diagnosis. Regarding genotype, studies in Brazil so far have shown the frequent detection of PCV2b (CASTRO, 2005; DE CASTRO et al., 2008, 2012; FERRARI, 2012; GAVA et al., 2018).

Most of the genotyped samples in this study was identified as PCV2d 80 of 106 (75.47%) followed by PCV2b 24 of 106 (22.64%). Coinfection between PCV2b and PCV2d were detected in 2 of 106 (1.89%) of the samples. No PCV2a was detected. This is the first study demonstrating that PCV2b is not the most present genotype and that PCV2d stood out over PCV2b in Brazil. Data showing year of collection and genotype is presented in Table 5.

**Table 5:** Total genotyped samples by PCR from 2019 to 2021.

Relation of subtyped samples				
Genotypes	2019	2020	2021	Positivity (%)
PCV2a	0/16 (0%)	0/43 (0%)	0/47 (0%)	0/106 (0%)
PCV2b	0/16 (0%)	7/43 (16.28%)	16/47 (34.04%)	23/106 (21.90%)
PCV2d	16/16 (100%)	33/43 (76.74%)	31/47 (65.96%)	80/106 (76.19%)
Coinfection A ESCRITA TEM DE SER CONSISTENTE EM TODA A DISSERTACAO (PCV2b+PCV2d)	0/16 (0%)	2/43 (4.65%)	0/47 (0%)	2/106 (1.89%)
Not genotyped	42/58 (66.6%)	48/91 (52.75%)	50/97 (51.55%)	141/246 (57.32%)
Total genotyped samples	16/58 (27.59%)	42/91 (47.25%)	47/97 (48.45%)	105/246 (43.09%)

Among the clinical specimens analyzed, oral fluid had the highest number of genotyped samples 40 of 106-(37.74%), followed by the pool of organs and serum, which had the same amount, with 33 of 106 (31.13%). Oral fluid sampling is well suited for detecting and monitoring presence of PCV2 and has gained growing interest as an

even more cost and time-saving method while also considering animal welfare (KIM, 2010; NIELSEN et al., 2018; PRICKETT et al., 2011).

Of the 106 genotyped samples, the state with highest positivity was Minas Gerais, with 22 samples, followed by 20 from Mato Grosso, 14 from Paraná, 8 from Rio Grande do Sul, 2 from Santa Catarina, and 11 samples had no identification of origin, as described in the table 6. In all Brazilian States, the occurrence of genotype PCV2d prevailed over PCV2b.

**Table 6:** Number of samples tested and genotyped by Brazilian states from 2019 to 2021.

Brazilian States	Samples tested	Samples genotyped	PCV2a genotype	PCV2b genotype	PCV2d genotype	Mixed infections (PCV2a + PCV2d)
DF	1	0	0	0	0	0
GO	4	0	0	0	0	0
MT	22	20	0	0	19	1
MS	9	0	0	0	0	0
MG	122	51	0	10	41	0
PR	33	14	0	4	9	1
RS	21	8	0	1	7	0
SC	12	2	0	2	0	0
W/I	22	11	0	7	4	0
<b>Total samples</b>	<b>246</b>	<b>106</b>	<b>0</b>	<b>24</b>	<b>80</b>	<b>2</b>

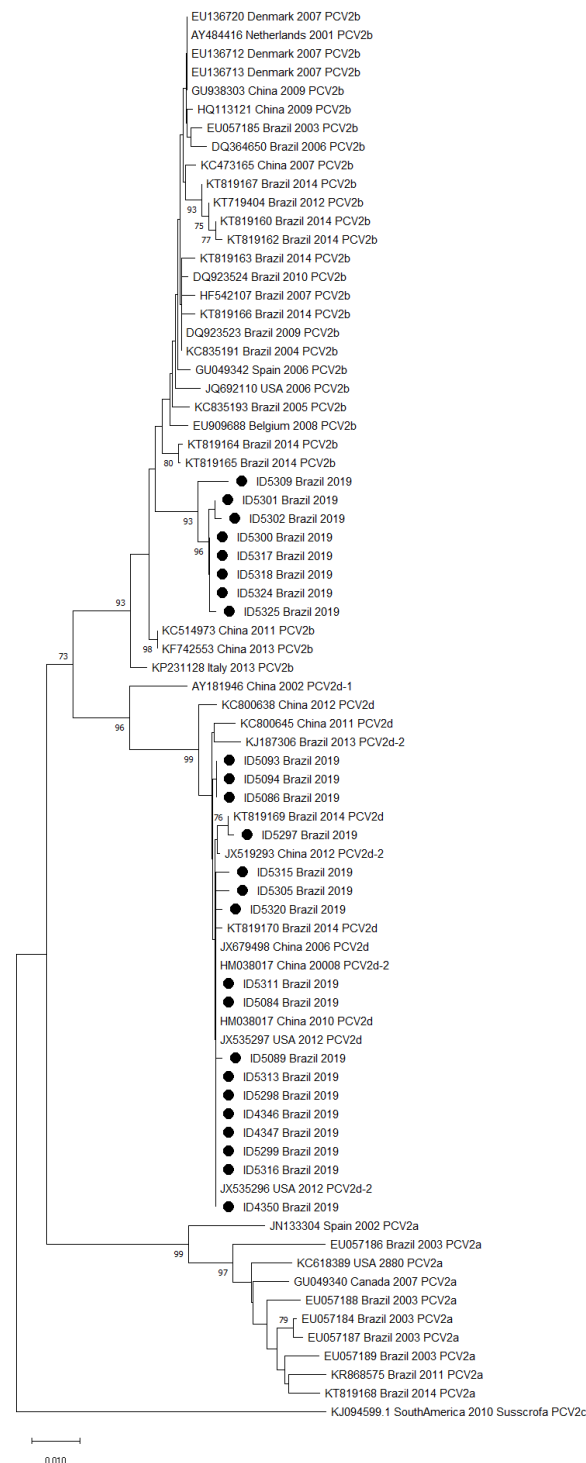
Abreviados: DF=Distrito Federal; GO=Goiás; MT=Mato Grosso; MS=Mato Grosso do Sul; MG=Minas Gerais; PR=Paraná; RS=Rio Grande do Sul; SC=Santa Catarina; W/I= Without identification

In Brazil, the PMWS was first identified in 2000 and retrospective studies have demonstrated PCV2 circulation since 1978 (CIACCI-ZANELLA et al., 2009; da SILVA et al., 2011). Several studies have reported a relevant circulation of PCV2a and PCV2b genotypes in commercial pig herds (CASTRO et al., 2007; 2012; CHIARELLI-NETO et al., 2009; CIACCI-ZANELLA et al., 2009) and wild boars (BARBOSA et al., 2006; (DE CASTRO et al., 2012; FRANZO et al., 2015; SATO et al., 2017) in Brazil. However, the PCV2d genotype was only detected for the first time in 2010 from feral pig samples from Brazilian Pantanal (FRANZO et al., 2015) and in 2013-2014 from samples collected in conventional nursery and fattening commercial herds (SALGADO et al. 2014). The data from this study, associated to the PCR results previously demonstrated, indicates that PCV2d may be the most common genotype circulating in Brazilian herd nowadays.

This data corroborates several authors that concluded that PCV2d has become the most prevalent genotype worldwide (FRANZO et al., 2016a; FRANZO; SEGALÉS, 2018; KHAYAT et al., 2010; QU et al., 2018; XIAO; HALBUR; OPRIESSNIG, 2015; YAO et al., 2019). Due to the relevance of PCV2d as the predominant genotype circulation in Brazilian farms and its association with cases of perceived failure of PCV2 vaccination, this genotype was chosen to be evaluated at the amino acid level

## **5.2. DNA sequencing and ORF2 phylogenetic analysis**

Although the ORF2 gene from 34 out of 51 PCV2 PCR positive samples were sequenced after alignment and exclusion of sequences with important gaps and poor quality, 25 sequences were selected for our phylogenetic tree (Figure 3).



**Figure 3: Phylogenetic analysis of 25 sequences from this study (eight are genotype PCV2b and seventeen are PCV2d) and 51 Reference strains from PCV2a, PCV2b, PCV2c and PCV2d) were used according FRANZO; SEGALÉS (2018).** Sequences from this study are indicated by a solid circle. The phylogenetic tree was constructed based on the nucleotide sequences of the Cap gene (ORF2). The tree was inferred by using the Neighbor-Joining method with 1,000 bootstrap replicates. Only Bootstrap values  $\geq 70\%$  are shown. The division of PCV2d genotype sequences into PCV2d-1 (AY181946) and PCV2d-2 (KJ187306, JX519293, HM038017 and JX535296) was done by (XIAO; HALBUR; OPRIESSNIG, 2015).

Due a high mutation rate (compared to RNA virus such as Influenza virus i.e.,  $10^{-3}$ - $10^{-4}$  substitution/site/year), progressive increase in sequence availability and the discovery of new genetically divergent clades of PCV2 genotypes are not recognized by the International Committee on Taxonomy of Viruses (ICTV). Even if a certain consensus has been achieved on the PCV2 nomenclature below the species level, this is essentially based on the criteria chosen with the main aim of establishing a common and shared language (FRANZO; SEGALÉS, 2018). Thus, in the present work, a new classification proposed by FRANZO; SEGALÉS (2018) was used. This classification allowed defining nine genotypes (PCV2a to PCV2i), based on three criteria: maximum intra-genotype p-distance of 13% (calculated on the ORF2 gene), bootstrap support at the corresponding internal node higher than 70%, using Neighbor-Joining (NJ) method and at least 15 reference sequences described by FRANZO; SEGALÉS (2018). With this classification, 17 of 25 Brazilian sequences clustered with PCV2d (68.00%) and 8 of 17 clustered with PCV2b (32.00%) (Figure 3). No PCV2a genotype was detected. Although other methods of phylogeny are more reliable (Maximum likelihood and Bayesian for example), FRANZO; SEGALÉS, (2018) proposed a simpler model able to be robust and with lasting approach for genotype definition and less susceptible to future database updates.

The eight PCV2b samples sequenced in the present study shared high genetic similarity with each other, ranging from 98.8% to 100% at nucleotide level. All Brazilian PCV2 grouped in a separate sub-cluster within the PCV2b clade supported by strong bootstrap values of 93. When they were compared to reference sequences, they shared high similarity with other Brazilian isolates, with values ranging from 97.3% to 98.3%. *P-distance* data at nucleotide level are shown in Supplementary Table 3.

The seventeen PCV2d sequences in the present study also shared high similarity with each other, ranging from 99.4% to 100% (Supplementary Table 4). The PCV2d genotype presented a clear separation into 2 distinct subclusters, PCV2d-1 and PCV2d-2, with bootstrap support >70%. All Brazilian samples were assigned to the PCV2d-2 subclade. Even though there are some potential subclades in PCV2d-2, they did not present bootstrap support > 70%. Hence, the currently used marker did not have enough discrimination power to segregate the intra-PCV2d-2 clade phylogeny. This division of PCV2d genotype into two subclades, PCV2d-1 and PCV2d-2, has already been reported, with most PCV2d-1 samples circulating during 1999 to 2011, while PCV2d-2 samples were only identified in 2006 (XIAO; HALBUR;

OPRIESSNIG, 2015). In a phylogenetic study of field samples from pigs with clinical signs of PCVD in Belgium collected between 2009 and 2018, it was also demonstrated that PCV2d-1 samples were found in 2009 and 2010, while in 2018 all sequences of PCV2d clustered in the PCVd-2 clade (WEI et al. 2019). Thus, researchers have suggested that PCV2d-1 is possibly an ancestor of PCV2d-2 (XIAO; HALBUR; OPRIESSNIG, 2015).

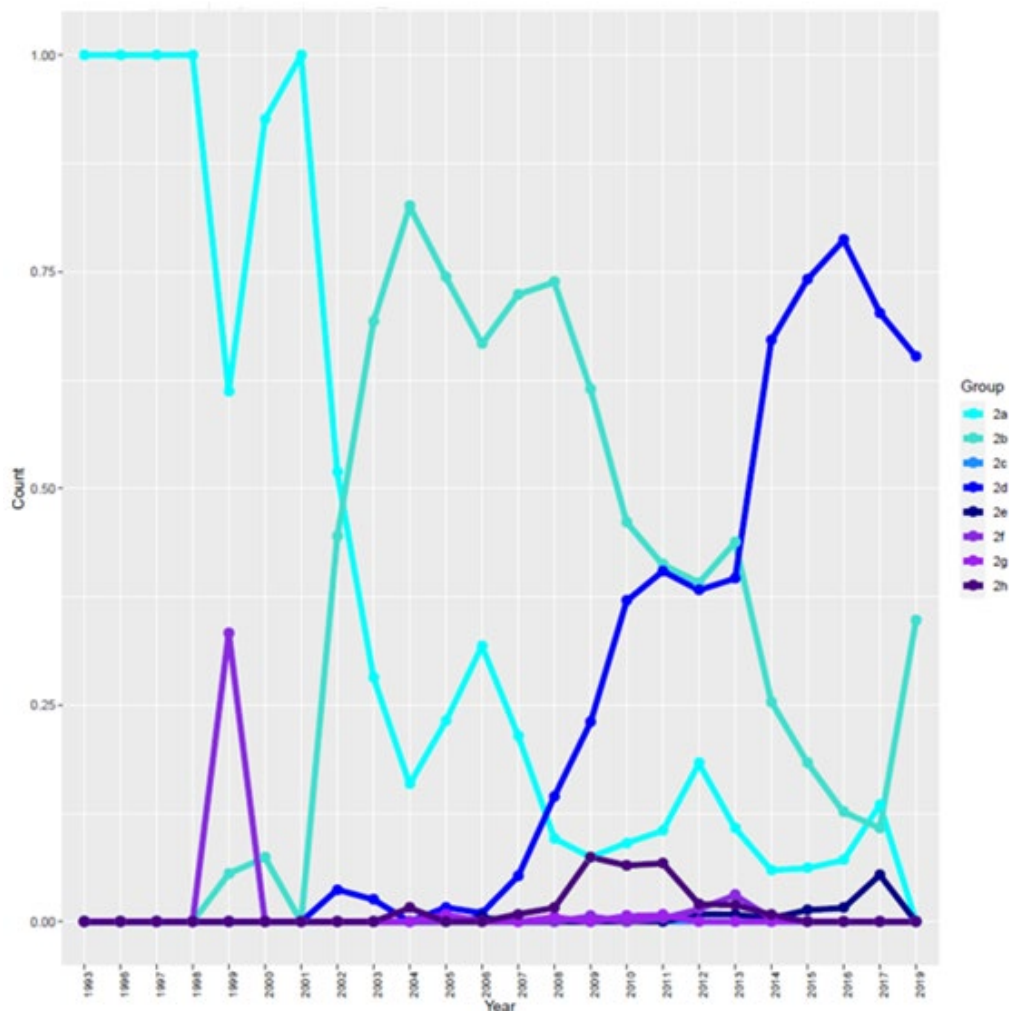
### **5.3. Genotype temporal distribution from 1993 to 2019**

Three thousand five hundred and forty-four PCV2 ORF2 sequences available from GenBank ([www.ncbi.nlm.nih.gov](http://www.ncbi.nlm.nih.gov)) were downloaded in March 2020 to evaluate PCV2 genotypes fluctuation from 1993 to 2019 (Supplementary Figure 1). Retrospective analysis of sequences available showed a clear temporal change in genotypes prevalence over time as previously describe (FRANZO; SEGALÉS, 2018).

The first PCV2 genotype with a considerable percentage of sequences available on GenBank was the PCV2a genotype. Around 2003, a genotype shift occurred and PCV2b became the most available genotype (Figure 4). This first genotype shift (from PCV2a to PCV2b) was described in several countries and was associated with the appearance of a more severe clinical disease outbreaks (FRANZO; SEGALÉS, 2020). From 2013, a second genotype shift (from PCV2b to PCV2d) occurred globally and it has been reported in cases of vaccination failure also associated with clinical disease outbreaks (OPRIESSNIG et al., 2013; XIAO; HALBUR; OPRIESSNIG, 2012). Since then, PCV2d became the genotype with the largest percentage of published sequences available. When evaluating PCV2d sequences deposited over time, two distinct peaks can be observed: a smaller one in the year of 2011, corresponding to approximately 40% of all sequence depositions and a higher peak, comprising approximately 80% of the sequences available, in the year of 2016. According to WEI et al (2019), the origin of PCV2d strains can be traced back to 1998 in Switzerland and is now spread in many countries. The PCV2c, PCV2e, PCV2f, PCV2g, PCV2h and PCV2i genotypes are less prevalent and distributed in limited continents, thereby, there are few sequences deposited in GenBank. PCV2c was considered extinguish or non-detectable for a long time after a retrospective report from Denmark in 1980. PCV2c was again being identified only in feral pigs in Brazilian Pantanal and in domestic pigs

in China (FRANZO et al., 2015; SATO et al., 2017; WANG et al., 2020) . PCV2e was identified in USA and Mexico, PCV2f and PCV2h in China, PCV2g in China, Europe and USA, and PCV2i in USA (WANG et al., 2020). The clinical significance of these genotypes is not known (FRANZO; SEGALÉS, 2018).

The scarce genotyping data in Brazil reflex a small number of sequence deposition in GenBank that does not allow to clear demonstrate the genotype shift reported above. According to the available data, PCV2b was until now the most predominant genotype in Brazil (CASTRO et al., 2007; 2008; FRANZO; SEGALÉS, 2018; GAVA et al., 2018).



**Figure 4: Count of sequences for each year.** Different clusters are identified by color. Number of isolates evaluated per year, percentage of representativeness (for each year, the value on the curve corresponds to how many percent of the subgroup among the samples of the year).

#### **5.4. Amino acid sequence analysis from Brazilian PCV2b and PCV2d genotypes**

The nucleotide sequences of PCV2 ORF2 gene that codified a viral capsid protein (Cap) of all PCV2 Brazilian strains in this study had 695 nucleotides of length, with 231 amino acids. The last amino acids (position 232 to 233), due to the sequencing poor quality on this location, were not reliable and were excluded from the analysis.

Amino acid sequences of Cap protein from this study are conserved within genotypes. When comparing the conserved Brazilian sequences of PCV2b to PCV2d genotypes, there are mutations in 13 positions in the amino acid sequences Y8F, F53I, I57V, R59K, S64T, R89L/I, S90T, S121T, P134N, S169R/G, N207Y, E210D, V215I (displayed on Table 7). Nine of these 13 positions are found in immunogenic regions: 53, 57, 59, 64, 121, 134, 169, 207 and 210, highlighted in gray in Table 7.

At positions 32, 34 and 68, 24 out 25 (96%) sequences were identical, except for samples ID5297, ID5325, IDI15309, ID5297, which had the following mutations at positions P32H, H34N, N68A, 89 and 169, respectively. Of these mutations, only the mutation at position 68 (ID5309) was in an immunogenic region (Table 7).

Most of the polymorphisms between genotypes are presented at epitopes regions. Regions of the virus where interactions with the environment occur and this change may favor the virus to escape the host's immune response.

**Table 7:** Polymorphic sites within PCV2 ORF2 gene sequences from Brazil. Dashes represent amino acid position similar to GenBank accession number AF201311, according to MAHÉ et al., (2000). As a reference PCV2d genotype, The Genbank accession number KT819170, described by GAVA et al. (2018), was used as a reference PCV2d genotype The sequences with 100% amino acid identity were excluded.

Samples	Amino acid position															
	8	32	34	53	57	59	64	68	89	90	121	134	169	207	210	215
<b>PCV2b</b>																
<b>AF201311</b>	Y	P	H	F	V	R	T	A	R	S	S	T	S	Y	E	V
ID5324	-	-	-	-	I	-	S	N	-	-	-	P	-	N	-	-
ID5325	-	-	N	-	I	-	S	N	-	-	-	P	-	N	-	-
ID5309	-	-	-	-	I	-	S	-	-	-	-	P	-	N	-	-
<b>PCV2d</b>																
<b>KT819170</b>	F	-	-	I	-	K	-	N	L	T	T	N	R	-	D	I
ID4346	F	-	-	I	-	K	-	N	L	T	T	N	R	-	D	I
ID5305	F	-	-	I	-	K	-	N	I	T	T	N	R	-	D	I
ID5297	F	H	-	I	-	K	-	N	L	T	T	N	G	-	D	I
ID5320	F	-	-	I	-	K	-	N	L	T	T	N	R	-	D	I

\*The sequences with 100% identity to ID5324 (ID5300, ID5302, ID5317, ID5318, ID5301) and to ID4346 (ID4347, ID4350, ID5084, ID5086, ID5089, ID5093, ID5094, ID5298, ID5299, ID5311, ID5316, ID5315, ID5313) were omitted from the table. Position of the immunogenic domains 53, 57, 59, 64, 68, 121,134, 169,207 and 210 are highlighted in gray.

Compiling all the information described so far by MAHE et al. (2000); TRUONG, et al (2001); LEKCHAROENSUK et al. (2004); SHANG et al. (2009); HUANG et al. (2011); KHAYAT et al. (2011); HUANG et al. (2020), four general antibody recognition regions were identified in Cap protein, labeled A (47 to 94), B (113 to 137), C (156 to 210) and D (230 to 233), in addition to the positions 88 and 228 (Table 9). These immunogenic regions comprise 54,7% (128/234) of all Cap amino acid residues. Generally, most amino acid residues within antigenic regions are similar, providing protection between vaccines. HUANG et al. (2020) analyzed the conservation of the amino acids in the epitope regions. However, some residues are different among genotypes, and there are also differences among strains of the same genotype (SASHA et al., 2012; HUANG et al., 2020). Of these, some single residues located on the outer surface of Cap protein (59, 89, 134 and 210) are responsible for the binding strength within the epitope and differ between PCV2b and PCV2d (LIU et al., 2013). Of these, the amino acids at positions 59 and 134 are involved not only in binding strength but in the difference in efficacy of neutralizing antibodies among monoclonal antibodies (mAb) against PCV2a, PCV2b and PCV2d genotypes (HUANG et al., 2020). According to HUANG et al. (2020), the positions 59 and 134 are moderately conserved among PCV2 strains (approximately 60%). The single mutation in T134 resulted in >50% loss of binding reactivity of mAb, while the mutation in A59 can reduce the binding reactivity of the mAb by approximately 30%.

### **5.5. Evolution before and after the vaccination introduction**

There are many discussions about changes of the Cap protein encoded by ORF2 and the role vaccination can play on PCV2 evolution, immunological and vaccine escapes (KEKARAINEN; GONZALEZ; LLORENS, 2014; LV; GUO; ZHANG, 2014; REINER; HOFMEISTER; WILLEMS, 2015; SHEN; HALBUR; OPRIESSNIG, 2012). Vaccination was introduced in Brazil in 2006 and it was widely adopted after that (FRANZO et al., 2016b). Today there are several vaccines brands available in Brazil (Table 8), all with trial studies demonstrating efficacy (BANDRICK et al., 2020; MARTELLI et al., 2011; OPRIESSNIG et al., 2009, 2019). All currently available vaccines, independently from the production techniques (i.e. inactivation, chimeric PCV1-2 virus, Cap subunit expressed in baculovirus system), contain the

immunogenic Cap protein of the PCV2a or PCV2b. Most of these vaccines are based on PCV2a genotype, one is based on PCV2b genotype and just one is a bivalent vaccine (PCV2a and PCV2b genotypes) (Table 8). The Cap protein, besides being the major immunogen, is more variable region of PCV2 genome thereby the most commonly used for diagnosis and classification purposes (FRANZO et al., 2016b).

**Table 8:** Commercial PCV2 vaccines currently registered for use in Brazil, its type and genotype.

Brand	Lab	Vaccine type	Genotype
Circovac®	CEVA	Killed Virus	PCV2a
Fostera Gold PCVMH®	Zoetis	Chimeric virus PCV1 expressing PCV2 ORF2	PCV2a + PCV2b
Ingelvac Circoflex®	Boehringer Ingelheim	Recombinant subunit expressed in the baculovirus	PCV2a
Porcilis PCV®	MSD	Recombinant subunit expressed in the baculovirus	PCV2a
Circunvent PCV®	MSD	Recombinant subunit expressed in the baculovirus	PCV2a
SafeSui®	OuroFino	Recombinant subunit expressed in the baculovirus	PCV2b
Pro-Vac®/Circomaster	Dechra	Recombinant subunit	PCV2a

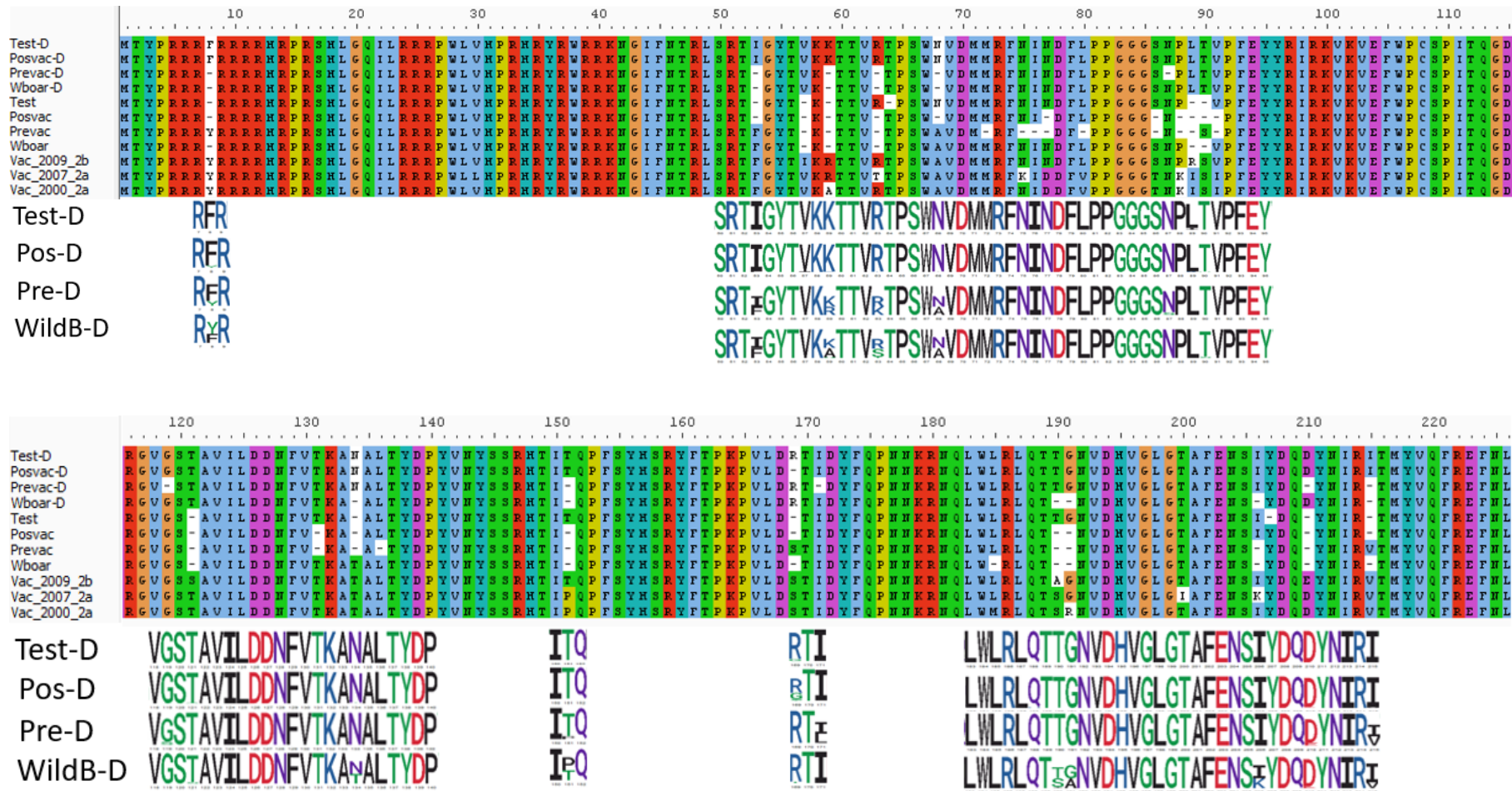
In recent decades, some concerns have been raised about the protection achieved against newly emerged genotypes such as PCV2d. Some publications and field reports attest episodes of vaccine failure in association with PCV2d genotype outbreaks (SALGADO et al., 2014; SEO et al., 2014; XIAO; HALBUR; OPRIESSNIG, 2012) due to presence of decoy epitopes that may affects the antibody neutralizing activity (JIN et al., 2018; TRIBLE; ROWLAND, 2012) or better ability of the virus to bind to host receptors (WEI et al., 2019b) or its higher virulence (GUO et al., 2012). The role of vaccination in the formation of viral evolution has been reported for different diseases that affect both animals and humans. When immunity is not sterilizing, wild strains are able to circulate in a new “challenging” environment made up of less susceptible and immune hosts (FRANZO et al., 2016b; READ et al., 2015).

To evaluate the potential contribution of genotype PCV2a or PCV2b based vaccines over PCV2d genotype evolution, PCV2d amino acid consensus sequences before vaccination (PreVacD), after vaccination (PosVacD), wild boar (Wboard) and PCV2d Brazilian strains from this study (TestD) were compared. Wboard group was included in the study because these animals were not under vaccine pressure, in

addition to represent an important source of genetic variability and/or simply viral exchange (FRANZO et al., 2016).

The amino acid consensus sequences before and after vaccination were divided according to two conservative time points; sequences collected before 2006 were assumed to originate from non-vaccinated animals, while sequences collected after 2007 were considered to originate from vaccinated animals. Although there is no guarantee that all sequences collected after 2007 originated from vaccinated animals, the widespread use of vaccination supported this criterion.

Also, those consensus sequence groups listed above were compared to three vaccine amino acid sequences available, licensed in Brazil (two PCV2a genotype: cVac2007-2a, Vac2000-2a and one PCV2b genotype: cVac2009-2b) (Table 8) and changes on amino acid residues in epitopes region of the Cap protein were analyzed. The alignment is shown on Figure 5.



**Figure 5: Alignment of amino acid from TestD, PosD, PreD and WboarD consensus sequences and amino acid sequences available from 3 vaccines licensed in Brazil. The letters correspond to amino acid residues that have differences between the analyzed groups. Amino Acids not identical in > 90% of the isolates in the group were replaced by “-“.**

The clinical expression of PCVD depends on the final balance between the virus, environmental factors and the host immune response. Different epitope regions have been recognized in the Rep and Cap proteins, but the Cap protein in particular is the main target of the immunity and can elicit antibodies and lymphocyte proliferative responses against PCV2 (TRIBBLE et al., 2011).

Several linear or conformational epitopes within PCV2 ORF2 have been mapped by a set of techniques as: the generation of mutant viruses (PCV1/PCV2 chimeras, recombinant baculoviruses); PEPSCAN analysis for mapping and characterizing epitopes involving the synthesis of overlapping peptides and analysis of the peptides in enzyme-linked immunosorbent assays (ELISAs); development of monoclonal antibodies (mAb) against specific epitope residues from different genotype strains; evaluation of serological reactivity with experimental and natural infection anti-PCV2 antisera and others (MAHÉ et al., 2000; TRUONG, et al. 2001; MISINZO et al., 2006; SHANG et al., 2009; LEKCHAROENSUK et al., 2011; HUANG et a., 2011; KHAYAT et al., 2011; SAHA et al., 2012a,b; LIU et al., 2013; KURTZ et al., 2014; GAVA et al., 2018) (Table 9).

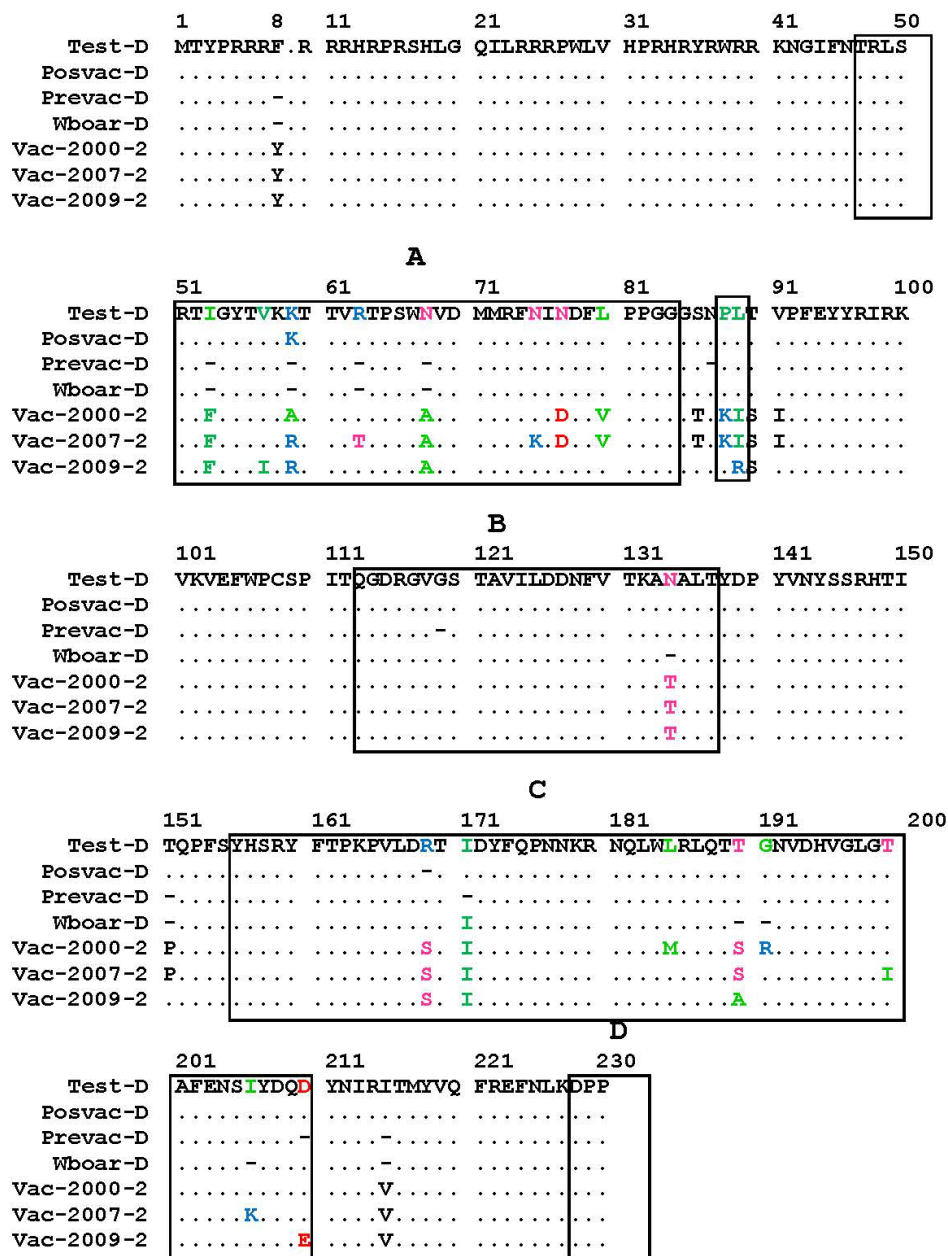
The identification of single amino acids that contributed to the recognition of antibodies within immunodominant Cap epitope regions has also been widely performed by the alanine scanning mutagenesis technique. Furthermore, the use of mAbs with neutralization activity which are specific for unique epitopes within the Cap protein have been used to map the dominant immunological epitopes important for neutralization of different field with biologically relevant differences or mutant strains. The understanding of the ability of specific mAbs to react against different PCV2 genotypes or different biologically relevant PCV2 strains is extremely important, in an attempt to elucidate issues related to how these differences may impact the virulence (SHANG et al., 2009; TRIBBLE et al., 2011; SAHA et al., 2012; LIU et al., 2013; KURTZ et al., 2014; HUANG et al., 2011; 2020). To further explore the neutralization mechanism, predicted three-dimensional (3D) mapping of amino acids in the Cap PCV2 by *in silico* assays and evaluation of cryo electron microscopy (Cryo-EM) structure of virion-mAb complex also have been used (GAVA et al., 2018; HUANG et al., 2020).

**Table 9:** Linear or conformational epitope regions detected in Cap PCV amino acids in reference studies and the analyzed PCV genotypes.

Epitope Residues	PCV genotype analyzed	Reference
47-63	PCV1; PCV2a	LEKCHAROENSUK et al., 2004; HUANG et al., 2011;
55-62	PCV2a; PCV2b; PCV2d	HUANG et al., 2020
68-70	PCV2a; PCV2b; PCV2d	HUANG et al., 2020
165-200	PCV1; PCV2a	LEKCHAROENSUK et al., 2004
230-233	PCV1; PCV2a	LEKCHAROENSUK et al., 2004
69-83	PCV1; PCV2b	MAHE et al., 2000
88	PCV2a; PCV2b; PCV2d	HUANG et al., 2020
55-62	PCV2a; PCV2b; PCV2d	HUANG et al., 2020
128, 131-137	PCV2a, PCV2b, PCV2d	HUANG et al., 2020
117-131	PCV1; PCV2b	MAHE at al., 2000
204	PCV2a, PCV2b, PCV2d	HUANG et al., 2020
189, 231	PCV2a; PCV2b; PCV2d	HUANG et al., 2020
169-183	PCV1; PCV2b	MAHE at al., 2000
195-202	PCV1; PCV2a; PCV2b	SHANG et al., 2009
231-233	PCV1; PCV2a; PCV2b	SHANG et al., 2009
156-162	PCV1; PCV2a; PCV2b	SHANG et al., 2009
175-192	PCV1; PCV2a; PCV2b	SHANG et al., 2009
59, 63, 89, 206, 210, 130, 133	PCV2a; PCV2b	SAHA et al., 2012
117-131	PCV1; PCV2b	TRUONG, et al. 2001
69-83	PCV1; PCV2 <sup>CS*</sup>	KHAYAT et al., 2011
113-127	PCV1; PCV2 <sup>CS*</sup>	KHAYAT et al., 2011
169-183	PCV1; PCV2 <sup>CS*</sup>	KHAYAT et al., 2011
193-207	PCV1; PCV2 <sup>CS*</sup>	KHAYAT et al., 2011

\***PCV2<sup>CS</sup>**: consensus sequence of PCV2 analyzed available in GenBank.

The epitope recognition regions described to date (Table 9) have been combined and classified into four general antibody recognition regions labeled A (47 to 84), B (113 to 137), C (156 to 210) and D (228 to 233) plus positions 88. The consensus sequences PosVacD, PreVacD, WborD, TestD and amino acid sequences available from three vaccines are aligned and the locations of the immunoreactive regions are described in Figure 6.



**Figure 6: Location of the immunoreactive regions in the alignment of amino acid from TestD, PosD, PreD and WboarD consensus sequences and amino acid sequences available from 3 vaccines licensed in Brazil. Sequences that were not identical in > 90% of the isolates in the group were replaced by dashes. The black squares are four general antibody recognition regions labeled A (47 to 84), B (113 to 137), C (156 to 210) and D (228 to 233), plus at position 88. The D epitope was not demonstrated due to the exclusion of the last 3 amino acids of ORF2 from our Brazilian sequences. Dotted are the amino acid sequences identical to the TestD sequence. Colors indicates amino acid chemistry. Red: Acid Polar, Blue: Basic Polar, Pink: Neutral Polar, Green: Nonpolar**

**Table 10:** Different amino acid residues in the Cap protein of PCV2d strains between TestD, PreVacD, Wboard, PosVacD, Wboard groups and vaccine strains. Vaccine strains are cVac2009-2b (GU799576), c2007-2a (AF264042) and Vac2000-2a (GU049340). Colors indicates amino acid chemistry. Red: Acid Polar, Blue: Basic Polar, Pink: Neutral Polar, Green: Nonpolar.

POSITION	EPI TOPE	SEQUENCES				VACCINE STRAIN		
		PreVacD	Wboard	PosVacD	TestD	cVac2009-2b	cVac2007-2a	Vac2000-2a
53	A	F/Y	Y/F	I	I	F	F	F
57	A	V	V	V	V	I	V	V
59	A	K/R	K/A	K	K	R	R	A
63	A	R/K	R/S	R	R	R	T	R
68	A	N/A	N/A	N	N	A	A	A
75	A	N	N	N	N	N	K	N
77	A	N	N	N	N	N	D	D
80	A	L	L	L	L	L	V	V
88	A	P	P	P	P	P	K	K
89	A	L	L	L	L	R	I	I
134	B	N	N	N	N	T	T	T
169	C	R	R	R/G	R	S	S	S
171	C	I/C	I	I	I	I	I	I
185	C	L	L	L	L	L	L	M
190	C	T	T/S	T	T	A	S	S
191	C	G	G/A	G	G	G	G	R
200	C	T	T	T	T	T	I	T
206	C	I	I	I	I	I	K	I
210	C	D/E	D	D	D	E	D	D

Among consensus sequences Wboard, PreVacD (not under vaccine pressure) and PosVacD, epitope regions were analyzed searching for polymorphism. No drastic mutations were observed at the stereochemical level of amino acids between these three groups. But a fixation of some amino acids at epitope position can be observed: K/R/A59/K (fixation of K), RKS/63/R (fixation of R), N/A68/N (fixation of N), I/C171/I (fixation of I), T/S190/T (fixation of T), G/A191/G (fixation of G) and D/E210/D (fixation of D) (Table10). It seems that strains before the use of massive vaccines already were carrying the same amino acids present on current PCV2d samples. These data may suggest that PCV2d, first reported in 1998, already carried characteristics that distinguish it from other genotypes and that vaccines may have an important role on PCV2d evolution. It is known that PCV2a strains changed its viral capsid away from the vaccine antigen after vaccine introduction (FRANZO et al., 2016b). This same “distancing” seems to be a behavior repeated by PCV2d because of its increase on size population. Not only vaccines are able to promote genotype shifts. In the case of the first genotype shift from PCV2a to PCV2b around 2003, it happened before the massive use of vaccines (2007) and this evolution was probably driven by infection immunity present in farms at that time (WEI et al., 2019b). This might be occurring with PCV2d due to its high prevalence on farms nowadays inducing a strong population immunity.

#### **5.6. Differences between CAP amino acid sequences of Brazilian PCV2d (TesteD) and vaccine samples (cVac2000-2a, cVac2007-2a and cVac2009-2b)**

Important changes between TestD and vaccine sequences were observed in epitope regions. Seventeen mutations in antigenic regions occurred between TestD and some or all vaccine strains at positions: (Epitope region A): I53F (all vaccine strains), V57I (cVac2009-2b), K59A (Vac2000-2a)/R (cVac2007-2a, cVac2009-2b), R63T (cVac2007-2a), N68A (all vaccine strains), N75K (cVac2007-2b), N77D (Vac2000-2a, cVac2007-2a), L80V (Vac2000-2a, cVac2007-2a); P88K (Vac2000-2a, cVac2007-2a), (L89I (Vac2000-2a, cVac2007-2a)/R (cVac2009-2b); (Epitope region b): N134T (all vaccines). (Epitope region C): R169S (all vaccine strains), L185M (cVac2000-2a), T190S (Vac2000-2a, cVac2007-2a)/A (cVac2009-2b), G191R

(Vac2000-2a), T200I (cVac2007-2a), I206K (cVac2007-2a). Of these 17 positions with mutations in antigenic regions, 13 occurred in cVac2007-2a, 12 in Vac2000-2a and 10 in cVac2009-2b.

Of the 17 mutations that occurred in antigenic sites of the Cap protein between the Brazilian consensus amino acid sequences of PCV2d genotype (TestD) and vaccine samples, 6 (at positions 53, 57, 80, 134, 185 and 210) did not change the physical-chemical property of the amino acids, therefore, they did not cause significant structural changes in the Cap protein. In 12 positions (59, 63, 68, 75, 77, 88, 89, 169, 190, 191, 200 and 206) mutations that altered the stereochemical properties of the amino acids were observed. These mutations are considered the most important for being able to cause significant structural changes in the Cap protein. Among these 12 analyzed mutations (with change on amino acid charge), the vaccine strain with the highest number of mutations was cVac2007-2a, with 8 mutations (at positions R63T, N68A, N75K, N77D, P88K, R169S, T200I, I206K), followed by Vac2000-2a with 6 mutations (at positions K59A, N68A, N77D, P88K, R169S, G191R) and cVac2009-2b, with 4 mutations (at positions N68A, L89R, R169S, T190A). All vaccine strains had an amino acid completely different from the TestD consensus at positions 59, 68, 89, 134, 169 and 190 (Figure 6).

Several authors have reported that within an immunogenic region, some single amino acids are essential for the recognition of specific antibody binding and that mutations in these single amino acids can alter, favoring or inhibiting the recognition of antibodies by the antigenic site. Furthermore, mutations in single amino acids can also determine different levels of viral neutralization by a given mAb, suggesting a crucial role for these amino acids in the differential effectiveness of viral neutralization, between different PCV2 genotypes and even between the same genotype strains with different biological characteristics (SHANG et al., 2009; TRIBLE et al., 2011; SAHA et al., 2012a,b; LIU et al., 2013; KURTZ et al., 2014; HUANG et al., 2011; 2020).

Studies with universal monoclonal antibodies, which react with eight different PCV2 clusters within PCV2a and PCV2b genotypes, have demonstrated that eight amino acids positions are crucial for binding of the different mAbs: at positions 30, 59, 63 (Epitope region A), 89, 130, 133 (Epitope region B) and 206, 210 (Epitope region C) (SAHA et al., et al., 2012). These amino acids are located on the outer surface of a capsid protein. Positions 59 and 63 were in loop BC, position 89 in loop CD, positions 130 and 133 in loop EF; position 206 in loop HI and position 210 in  $\beta$ -strand. The

flexibility of the loops facilitates the binding between the virion and Fab portion of antibodies (SAHA et al., et al., 2012; HUANG et al., 2020). Of these positions, two are considered universal, with similar sharing to all clusters strains: 130 and 133. As expected, our vaccines were identical to the Brazilian samples (TestD) in these two universal positions and also in 2 other positions: 89 and 210. There was a divergence in three positions, when comparing the TestD samples with the vaccines: 59 (all vaccines), 63 (cVac2007-2a) and 206 (cVac2007-2a).

Genotype specific important domains have also been identified using multiple sequence alignment, as six amino acid residues at positions 86 to 91 and four at positions 190, 191, 206 and 210 on the PCV2 Cap SEM SENTIDO (CHEUNG et al., 2011; CHEUNG; GREENLEE, 2011). As expected, since the vaccines have different genotypes (PCV2a or PCV2b) from the Brazilian PCV2d (TestD) samples, mutations were observed at positions 190 (all vaccines), 191 (cVac2000-2a) and 206 (cVac2007-2a).

Although PCV2 infected pigs produce high levels of Cap specific antibody, the onset and severity of PCVD are correlated with the absence or decreased levels of PCV2 neutralizing antibodies, suggesting a crucial role for neutralizing antibodies in the prevention of PCVD (MEERTS et al., 2006). Changes in single amino acids can switch the neutralizing phenotype of PCV2 Cap monoclonal antibodies (SAHA et al., 2012; LIU et al., 2013; KURTZ et al., 2014; HUANG et al., 2020). Studies with mAbs that have different reactivity or neutralization phenotypes have been used to identify these critical amino acids important for PCV2 neutralization being at positions: 59, 60, 131, 151, 190, 191 and the C-terminal area including residues at positions 231 to 233 (SAHA et al., 2012; LIU et al., 2013; KURTZ et al., 2014). Specific mutations in residues R59A, A60T, A151T/P allow the mutant to be recognized and neutralized by monoclonal antibodies, with complete gain of recognition and neutralization of mAbs against PCV2a or PCV2b. Inverse mutations in these regions result in a complete loss of neutralization. Mutations in other amino acid residues have also shown differences in neutralizing activity, such as T190A which result in complete loss of neutralization and mutations T131P and E191R results in partial but significant loss of neutralization (SAHA et al., 2012).

Recently, HUANG et al. (2020) detected by a monoclonal antibody that neutralizes the PCV2a, PCV2b and PCV2d genotypes 18 single amino acids responsible for this neutralization. Ten of these amino acids are completely conserved

(>99%) among all samples deposited in GenBank to date (55Y, 56T, 61T, 62V, 128N, 132K, 135A, 137T, 189T and 231L), and the rest showed variable levels of conservation, with 5 highly conserved (86.89% to 98.33%) at positions 58K, 60T, 131T, 133A and 136L, one moderately conserved (approximately 60%) at 134 position and two highly variable (<25%) at 59A and 88K positions. Most of the amino acids in the epitope regions that neutralizes PCV2a, PCV2b and PCV2d genotypes were conserved among different genotypes, which might explain the relatively broad-spectrum reactivity of a monoclonal antibody with PCV2 strains. However, mutations of some amino acids within the epitope regions had significant effects on the neutralizing activity of this specific mAb. Using cryo-electron microscopy single particle analysis in a complex with mAb Fab fragments and alanine scanning mutagenesis was observed that the single mutations at positions 128, 131, 132, 134, 135, 136 and 189 in the Cap protein resulted in >50% loss of binding reactivity of specific mAb, while the mutation at 59 position reduced the binding reactivity of the mAb by approximately 30%. The binding levels at 56 and 60 position mutations were similar to that of parenteral virus; however, their neutralization activities were significantly lower than that of parenteral virus.

When comparing the Brazilian amino acid sequences with significant effects on the neutralizing activity described of genotype D (TestD) with vaccines, 15 of the 18 positions were completely conserved among them (100%), with differences observed at positions 59, 88 and 134. In the Brazilian samples of PCV2d genotype (TestD), when compared to vaccine samples, the mutations were R (cVac2007-2a, cVac2009-2b/A and cVac2000-2a), 59K, K88P (cVac2000-2a and cVac2007-2a) and T134N (all vaccines). These results are in accordance with HUANG et al. (2020), which demonstrated that these positions were not conserved among different clusters strains, but they were conserved within specific genotypes, indicated that positions were involved in the differential neutralization efficacy of mAb against PCV2a, PCV2b and PCV2d.

In summary, the three vaccines analyzed have a difference in 3 of 8 (37.5%) single nucleotides crucial for monoclonal antibody binding, 3 of 10 (30%) differences among specific genotypes, and 5 of 15 (33.3%) differences among a single amino acid responsible for viral neutralization, without considering the last 3 nucleotides, which were not analyzed. The vaccines that have the greatest variability in important residues for antibody binding within immunogenic regions and neutralization activity

are the PCV2a genotype vaccines (cVac 2007-2a and cVac 2000-2a), followed by the PCV2b genotype vaccine (cVac 2009-2b). The question is how these antigenic differences could be related to vaccine failures observed worldwide, in relation to PCV2d. Reported studies have demonstrated that a set of single amino acids within epitope regions are responsible for differences in neutralization levels between different genotypes or samples of the same genotype that have biological differences. What has been widely sought after is a vaccine that protects against all strains or genotypes of PCV2.

The existence of a specific amino acid genotype in the crucial binding of mAbs may be the reason for somewhat better results in homologous situations. Cross-protection between PCV2 genotypes has been experimentally demonstrated. However, a recent experimental study indicated that a PCV2 vaccine based on the PCV2b genotype was more effective in protecting pigs against the effects of PCV2b or vaccinated with a bivalent PCV2a-PCV2b vaccine, than with a vaccine based on the PCV2a genotype, however that protection against PCV2 is known to be dependent on the generation of neutralizing activity (BANDRICK et al., 2020; OPRIESSNIG et al., 2013) (OPRIESSNIG et al., 2013). When PCV2a vaccinated pigs were challenged with PCV2b, then a higher percentage of animals were positive for viral DNA in nasal and fecal swabs 20 days after challenge than when they were challenged with PCV2a and vice versa (FORT et al., 2008; BEACH et al., 2011). According to the analyzed situations, we suggest that for a more effective neutralizing activity, the vaccine strains should be of the same genotype as the circulating virus, but single amino acids also established as crucial for neutralizing activity, regardless of genotype, should also be considered.

## 6. CONCLUSION

- 1- By the authors' knowledge is the first time that a predominance of PCV2d genotype has been demonstrated in diagnostic samples, suggesting a direct correlation with the genotype circulation on Brazilian commercial swine farms.
- 2- No PCV2a genotype was detected in recent years.
- 3- Contemporary Brazilian isolates of PCV2d had important mutations in immunogenic sites in front of PCV2a and PCV2b-based vaccines that compromise an efficient antibody binding and virus neutralization
- 4- The PCV2a genotype vaccines have more mutations in amino acid residues responsible for antibody binding and neutralizing activity than PCV2b vaccine;
- 5- The success achieved by PV2a and PCV2b-based vaccines is due to the great conservation of amino acid residues in epitope regions, which confers some cross-reaction between genotypes, but the emergence of new PCV2 variants and genotypes should not be neglected;
- 6- Although the viruses sequenced in this study are highly conserved among them, the change in genotype prevalences observed over the years associated with the high mutation rate of PCV2 are reasons for active monitoring of the virus.

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## SUPPLEMENTARY

Supplementary Table 1: Sequences downloaded from GenBank (march, 2020) used as a reference in the construction of the phylogenetic tree.

GU938303_China_2009_PCV2b	KT819168_Brazil_2014_PCV2a
HQ113121_China_2009_PCV2b	EU057184_Brazil_2003_PCV2a
EU136713_Denmark_2007_PCV2b	EU057187_Brazil_2003_PCV2a
EU136712_Denmark_2007_PCV2b	JN133304_Spain_2002_PCV2a
EU136720_Denmark_2007_PCV2b	KJ094599.1_SouthAmerica_2010_Susscrofa_PCV2c
AY484416_Netherlands_2001_PCV2b	
DQ923523_Brazil_2009_PCV2b	
KC835191_Brazil_2004_PCV2b	
DQ923524_Brazil_2010_PCV2b	
GU049342_Spain_2006_PCV2b	
HF542107_Brazil_2007_PCV2b	
JQ692110_USA_2006_PCV2b	
EU057185_Brazil_2003_PCV2b	
KC835193_Brazil_2005_PCV2b	
DQ364650_Brazil_2006_PCV2b	
KP231128_Italy_2013_PCV2b	
KC473165_China_2007_PCV2b	
KT819167_Brazil_2014_PCV2b	
KT719404_Brazil_2012_PCV2b	
KT819160_Brazil_2014_PCV2b	
KT819162_Brazil_2014_PCV2b	
KT819163_Brazil_2014_PCV2b	
KT819164_Brazil_2014_PCV2b	
KT819165_Brazil_2014_PCV2b	
KT819166_Brazil_2014_PCV2b	
KC514973_China_2011_PCV2b	
KF742553_China_2013_PCV2b	
EU909688_Belgium_2008_PCV2b	
KC800638_China_2012_PCV2d	
KC800645_China_2011_PCV2d	
KJ187306_Brazil_2013_PCV2d-2	
KT819169_Brazil_2014_PCV2d	
KT819170_Brazil_2014_PCV2d	
HM038017_China_2010_PCV2d	
HM038017_China_2008_PCV2d-2	
JX535297_USA_2012_PCV2d	
JX535296_USA_2012_PCV2d-2	
JX679498_China_2006_PCV2d	
JX519293_China_2012_PCV2d-2	
AY181946_China_2002_PCV2d-1	
EU057186_Brazil_2003_PCV2a	
EU057188_Brazil_2003_PCV2a	
EU057189_Brazil_2003_PCV2a	
KR868575_Brazil_2011_PCV2a	
KC618389_USA_2880_PCV2a	
GU049340_Canada_2007_PCV2a	

Supplementary Table 2: Sequences Dataset used in this study. Column GenBank corresponds to Access number at NCBI. Country: Country of isolation. Region: Continent of isolation. Year: year of isolation. Subgroup: PCV2 genotype.

<b>GenBank</b>	<b>Country</b>	<b>Region</b>	<b>Year</b>	<b>Subgroup</b>
KX960917	China	Asia	2002	2d
JX679498	China	Asia	2006	2d
KX161690	China	Asia	2006	2d
JQ390467	Taiwan	Asia	2006	2d
GQ404800	China	Asia	2006	2d
AF201897	Netherlands	Europe	2000	2b
AY484411	Netherlands	Europe	2004	2b
AY484413	Netherlands	Europe	2004	2b
DQ220737	Canada	NorthAmerica	2005	2b
HM038016	China	Asia	2005	2b
AY321984	France	Europe	2004	2b
AY321985	France	Europe	2004	2b
EF565357	Denmark	Europe	2003	2b
AY484408	Netherlands	Europe	2004	2b
AY484412	Netherlands	Europe	2004	2b
AY321986	France	Europe	2004	2b
AY188355	China	Asia	2005	2b
AY217743	China	Asia	2003	2b
AY536755	China	Asia	2004	2b
AY322000	France	Europe	2004	2b
AY484416	Netherlands	Europe	2004	2b
AY682990	China	Asia	2004	2b
HM038024	China	Asia	2005	2b
AY321990	France	Europe	2004	2b
AY484415	Netherlands	Europe	2004	2b
AY322002	France	Europe	2004	2b
EF565366	Denmark	Europe	2003	2b
AY484409	Netherlands	Europe	2004	2b
AY969004	China	Asia	2005	2b
EF565364	Denmark	Europe	2003	2b
KF374705	Brazil	SouthAmerica	2005	2b
FJ644919	China	Asia	2002	2b
HM038020	China	Asia	2004	2b
AY321992	France	Europe	2004	2b
AY321994	France	Europe	2004	2b
AY322001	France	Europe	2004	2b
AY604430	China	Asia	2004	2b
AY256457	Hungary	Europe	2003	2b
AY321997	France	Europe	2004	2b
AY321998	France	Europe	2004	2b

HQ831529	Portugal	Europe	2005	2b
DQ233257	Romania	Europe	2003	2b
EF565350	Denmark	Europe	2003	2b
AY321988	France	Europe	2004	2b
AY321989	France	Europe	2004	2b
EF493840	China	Asia	2006	2b
EF493841	China	Asia	2006	2b
EF493842	China	Asia	2006	2b
GU247992	China	Asia	2005	2b
AY321999	France	Europe	2004	2b
HM038021	China	Asia	2006	2b
KC835191	Brazil	SouthAmerica	2004	2b
AY321991	France	Europe	2004	2b
KM604666	China	Asia	2004	2b
AY641542	China	Asia	2004	2b
AY181945	China	Asia	2003	2b
FJ644563	China	Asia	2005	2b
AY291316	China	Asia	2003	2b
EF565367	Denmark	Europe	2003	2b
EF565356	Denmark	Europe	2003	2b
AY424405	Austria	Europe	2003	2b
AY484414	Netherlands	Europe	2004	2b
AY849938	China	Asia	2005	2b
EF565344	Denmark	Europe	2003	2b
FJ158606	China	Asia	2006	2b
KX161698	China	Asia	2006	2b
EF565358	Denmark	Europe	2003	2b
EF565365	Denmark	Europe	2003	2b
EF565361	Denmark	Europe	2003	2b
EF565354	Denmark	Europe	2003	2b
EF565368	Denmark	Europe	2003	2b
EF565346	Denmark	Europe	2003	2b
EF565347	Denmark	Europe	2003	2b
EF565362	Denmark	Europe	2003	2b
EF565363	Denmark	Europe	2003	2b
EF565349	Denmark	Europe	2003	2b
GU049341	Spain	Europe	2006	2b
GU049342	Spain	Europe	2006	2b
DQ017036	China	Asia	2005	2b
FJ905464	SouthKorea	Asia	2005	2b
HQ831521	Portugal	Europe	2004	2b
EF565343	Denmark	Europe	2003	2b
EF565352	Denmark	Europe	2003	2b
EF565353	Denmark	Europe	2003	2b
EF565348	Denmark	Europe	2003	2b
AY321995	France	Europe	2004	2b

AY321996	France	Europe	2004	2b
HQ831527	Portugal	Europe	2006	2b
EF421969	China	Asia	2006	2b
EF565351	Denmark	Europe	2003	2b
FJ935780	Denmark	Europe	2006	2b
KC835190	Brazil	SouthAmerica	2003	2b
FJ158605	China	Asia	2006	2b
HQ831524	Portugal	Europe	2003	2b
FJ644924	China	Asia	2006	2b
GU247991	China	Asia	2006	2b
EF565345	Denmark	Europe	2003	2b
EF565342	Denmark	Europe	2003	2b
DQ141322	China	Asia	2005	2b
KC835192	Brazil	SouthAmerica	2005	2b
EF565355	Denmark	Europe	2003	2b
HM009336	Slovakia	Europe	2005	2b
AY682993	China	Asia	2004	2b
FJ644558	China	Asia	2005	2b
FJ644561	China	Asia	2005	2b
AM086384	China	Asia	2004	2b
AY536756	China	Asia	2004	2b
FJ644925	China	Asia	2006	2b
AY691679	China	Asia	2004	2b
AY256460	Hungary	Europe	2003	2b
AY613854	China	Asia	2004	2b
AY321987	France	Europe	2004	2b
FJ644559	China	Asia	2005	2b
AY651850	China	Asia	2004	2b
AY686764	China	Asia	2004	2b
KM604667	China	Asia	2006	2b
DQ104422	China	Asia	2005	2b
FJ644920	China	Asia	2006	2b
FJ644921	China	Asia	2006	2b
GU247987	China	Asia	2005	2b
FJ905465	SouthKorea	Asia	2005	2b
AY424404	Austria	Europe	2003	2b
FJ644555	China	Asia	2005	2b
FJ905466	SouthKorea	Asia	2005	2b
HM038018	China	Asia	2005	2b
FJ905461	SouthKorea	Asia	2005	2b
HQ831531	Portugal	Europe	2004	2b
AY916791	China	Asia	2005	2b
EF493838	China	Asia	2006	2b
EF493839	China	Asia	2006	2b
EF421968	China	Asia	2006	2b
AY391729	China	Asia	2003	2b

AY686762	China	Asia	2004	2b
EF565359	Denmark	Europe	2003	2b
AY177626	China	Asia	2003	2b
EF421973	China	Asia	2006	2b
AY596823	China	Asia	2004	2b
DQ220738	Canada	NorthAmerica	2005	2b
KC835193	Brazil	SouthAmerica	2005	2b
DQ861895	Brazil	SouthAmerica	2004	2b
DQ861896	Brazil	SouthAmerica	2004	2b
DQ861899	Brazil	SouthAmerica	2003	2b
DQ861897	Brazil	SouthAmerica	2003	2b
DQ861898	Brazil	SouthAmerica	2003	2b
DQ861900	Brazil	SouthAmerica	2002	2b
DQ861901	Brazil	SouthAmerica	2002	2b
DQ861902	Brazil	SouthAmerica	2004	2b
DQ220727	Canada	NorthAmerica	2005	2b
DQ220728	Canada	NorthAmerica	2005	2b
DQ220729	Canada	NorthAmerica	2005	2b
DQ220730	Canada	NorthAmerica	2005	2b
DQ220739	Canada	NorthAmerica	2005	2b
DQ220731	Canada	NorthAmerica	2005	2b
DQ220734	Canada	NorthAmerica	2005	2b
DQ629115	USA	NorthAmerica	2005	2b
EF394777	Canada	NorthAmerica	2005	2b
EF394778	Canada	NorthAmerica	2005	2b
EF394779	Canada	NorthAmerica	2005	2b
HQ148879	Cuba	SouthAmerica	2005	2b
JQ994270	Canada	NorthAmerica	2006	2b
DQ629116	USA	NorthAmerica	2005	2b
FJ218000	USA	NorthAmerica	2006	2b
JF290418	Canada	NorthAmerica	2006	2b
JQ994268	Canada	NorthAmerica	2006	2b
DQ629117	USA	NorthAmerica	2005	2b
DQ629118	USA	NorthAmerica	2005	2b
DQ220735	Canada	NorthAmerica	2005	2b
DQ220736	Canada	NorthAmerica	2005	2b
DQ629119	USA	NorthAmerica	2005	2b
DQ220732	Canada	NorthAmerica	2005	2b
HQ713495	USA	NorthAmerica	2005	2b
EU126887	Canada	NorthAmerica	2006	2b
FJ644923	China	Asia	2006	2b
AY732494	China	Asia	2004	2b
KX161691	China	Asia	2006	2b
KX161692	China	Asia	2006	2b
DQ104420	China	Asia	2005	2b
FJ905462	SouthKorea	Asia	2005	2b

FJ644562	China	Asia	2005	2b
HM038027	China	Asia	2006	2b
EU346945	China	Asia	2004	2b
DQ220733	Canada	NorthAmerica	2005	2b
AY579893	China	Asia	2004	2b
GU247989	China	Asia	2005	2b
HQ831532	Portugal	Europe	2005	2b
HQ831530	Portugal	Europe	2003	2b
FJ644926	China	Asia	2006	2b
EF421970	China	Asia	2006	2b
EF421971	China	Asia	2006	2b
KX161679	China	Asia	2006	2b
EF421972	China	Asia	2006	2b
KX161663	China	Asia	2006	2b
KX161664	China	Asia	2006	2b
EF493837	China	Asia	2006	2b
GU247990	China	Asia	2005	2b
GU233804	China	Asia	2004	2b
HM038019	China	Asia	2005	2b
KX161686	China	Asia	2006	2b
GU247988	China	Asia	2006	2b
FJ644557	China	Asia	2005	2b
FJ158603	China	Asia	2006	2b
FJ905469	SouthKorea	Asia	2005	2b
FJ644556	China	Asia	2005	2b
HQ831528	Portugal	Europe	2006	2b
EU408780	Sweden	Europe	2003	2b
JX506730	VietNam	Asia	2004	2h
AB072301	Japan	Asia	2001	2a
AF381177	China	Asia	2001	2a
AF408635	Canada	NorthAmerica	2001	2a
AB072303	Japan	Asia	2001	2a
AF381175	China	Asia	2001	2a
AF118095	Canada	NorthAmerica	2000	2a
AF118097	Canada	NorthAmerica	2000	2a
EF394775	Canada	NorthAmerica	2005	2a
AY325495	SouthAfrica	Africa	2003	2a
MF964235	SouthKorea	Asia	2004	2a
AY094619	USA	NorthAmerica	2003	2a
EF394774	Canada	NorthAmerica	2005	2a
DQ629113	USA	NorthAmerica	2005	2a
FJ218001	USA	NorthAmerica	2006	2a
DQ629114	USA	NorthAmerica	2005	2a
DQ104421	China	Asia	2005	2a
DQ104423	China	Asia	2005	2a
AY181948	China	Asia	2003	2a

FJ218002	USA	NorthAmerica	2006	2a
EF394776	Canada	NorthAmerica	2005	2a
AF465211	Taiwan	Asia	2002	2a
AF109399	Canada	NorthAmerica	2000	2a
AY256456	Hungary	Europe	2003	2a
AY256458	Hungary	Europe	2003	2a
HM009337	Slovakia	Europe	2005	2a
AY322004	France	Europe	2004	2a
DQ870484	USA	NorthAmerica	2005	2a
AY874165	Hungary	Europe	2002	2a
AY874166	Hungary	Europe	2003	2a
AF381176	China	Asia	2001	2a
AY424401	Austria	Europe	2003	2a
NC005148	Austria	Europe	2003	2a
AY424403	Austria	Europe	2003	2a
AY424402	Austria	Europe	2003	2a
DQ915588	Greece	Europe	2004	2a
EU386606	Sweden	Europe	1993	2a
AB072302	Japan	Asia	2001	2a
EU148506	Denmark	Europe	1993	2a
AF117753	Canada	NorthAmerica	2000	2a
AY874164	Hungary	Europe	2002	2a
AY874169	Hungary	Europe	2003	2a
AY256455	Hungary	Europe	2003	2a
AY256459	Hungary	Europe	2003	2a
AF364094	Taiwan	Asia	2001	2a
AY146991	Taiwan	Asia	2002	2a
FJ483938	China	Asia	2005	2a
AY180397	Taiwan	Asia	2003	2a
AY146993	Taiwan	Asia	2002	2a
AY180396	Taiwan	Asia	2003	2a
JF683387	Taiwan	Asia	2002	2a
JF927978	Taiwan	Asia	2002	2a
JF927979	Taiwan	Asia	2002	2a
AY556474	China	Asia	2004	2a
MF139056	China	Asia	1996	2a
MF139057	China	Asia	1998	2a
MF139071	China	Asia	1998	2a
MF139072	China	Asia	1998	2a
MF139058	China	Asia	1999	2a
MF139062	China	Asia	1998	2a
MF139063	China	Asia	1999	2a
MF139064	China	Asia	1999	2a
MF139065	China	Asia	1999	2a
MF139066	China	Asia	1998	2a
MF139067	China	Asia	1998	2a

MF139068	China	Asia	1997	2a
MF139075	China	Asia	1998	2a
MF139069	China	Asia	1999	2a
MF139070	China	Asia	1998	2a
MF139061	China	Asia	1999	2a
MF139074	China	Asia	1999	2a
MF139059	China	Asia	1999	2a
MF139060	China	Asia	1998	2a
MF139073	China	Asia	1999	2a
MF278779	China	Asia	1999	2f
MF139078	China	Asia	1999	2f
MF278777	China	Asia	1999	2f
MF278778	China	Asia	1999	2f
MF139076	China	Asia	1999	2f
MF139077	China	Asia	1999	2f
FJ998185	China	Asia	2005	2g
KC620553	SouthKorea	Asia	2003	2d
KC620555	SouthKorea	Asia	2005	2d
KC620556	SouthKorea	Asia	2005	2d
KC620554	SouthKorea	Asia	2003	2d
EF421967	China	Asia	2006	2b
DQ915586	Greece	Europe	2002	2b
DQ915587	Greece	Europe	2003	2b
EU136712	Denmark	Europe	2003	2b
EU136720	Denmark	Europe	2002	2b
EU136713	Denmark	Europe	2003	2b
EU136718	Denmark	Europe	2002	2b
EU136716	Denmark	Europe	2003	2b
EU136714	Denmark	Europe	2003	2b
EU136719	Denmark	Europe	2002	2b
EU136715	Denmark	Europe	2003	2b
GQ404801	China	Asia	2006	2b
GQ404798	China	Asia	2006	2b
HM009335	Slovakia	Europe	2006	2b
KC620543	SouthKorea	Asia	2005	2b
KT868345	USA	NorthAmerica	2006	2b
KT868352	USA	NorthAmerica	2006	2b
KC620551	SouthKorea	Asia	2006	2b
KC620547	SouthKorea	Asia	2006	2b
JF683396	Taiwan	Asia	2005	2b
KC620534	SouthKorea	Asia	2002	2b
KC620535	SouthKorea	Asia	2002	2b
KC620541	SouthKorea	Asia	2005	2b
KT868268	USA	NorthAmerica	2006	2b
KT868123	USA	NorthAmerica	2006	2b
KC620538	SouthKorea	Asia	2004	2b

KC620533	SouthKorea	Asia	1999	2b
KC620548	SouthKorea	Asia	2006	2b
KC620552	SouthKorea	Asia	2006	2b
KC620540	SouthKorea	Asia	2005	2b
KC620546	SouthKorea	Asia	2006	2b
KC620549	SouthKorea	Asia	2006	2b
KT868521	USA	NorthAmerica	2006	2b
EU755375	Brazil	SouthAmerica	2005	2b
EU755378	Brazil	SouthAmerica	2005	2b
EU755379	Brazil	SouthAmerica	2005	2b
EU755380	Brazil	SouthAmerica	2005	2b
EU755376	Brazil	SouthAmerica	2005	2b
EU755381	Brazil	SouthAmerica	2005	2b
JF683390	Taiwan	Asia	2002	2b
JF927981	Taiwan	Asia	2003	2b
JF927976	Taiwan	Asia	2002	2b
JF927977	Taiwan	Asia	2002	2b
JF927980	Taiwan	Asia	2003	2b
KC620542	SouthKorea	Asia	2005	2b
KC620544	SouthKorea	Asia	2006	2b
KC620539	SouthKorea	Asia	2005	2b
KC620545	SouthKorea	Asia	2006	2b
KT868062	USA	NorthAmerica	2005	2b
KT868331	USA	NorthAmerica	2005	2b
KT867838	USA	NorthAmerica	2005	2b
KT867840	USA	NorthAmerica	2005	2b
KT867842	USA	NorthAmerica	2005	2b
KT867873	USA	NorthAmerica	2006	2b
KT867880	USA	NorthAmerica	2006	2b
KT867885	USA	NorthAmerica	2006	2b
KT867904	USA	NorthAmerica	2006	2b
KT867908	USA	NorthAmerica	2006	2b
KT867963	USA	NorthAmerica	2006	2b
KT867976	USA	NorthAmerica	2006	2b
KT867978	USA	NorthAmerica	2006	2b
KT867983	USA	NorthAmerica	2006	2b
KT867993	USA	NorthAmerica	2006	2b
KT868003	USA	NorthAmerica	2006	2b
KT868005	USA	NorthAmerica	2006	2b
KT868007	USA	NorthAmerica	2006	2b
KT868015	USA	NorthAmerica	2006	2b
KT868019	USA	NorthAmerica	2006	2b
KT868020	USA	NorthAmerica	2006	2b
KT868021	USA	NorthAmerica	2006	2b
KT868022	USA	NorthAmerica	2006	2b
KT868055	USA	NorthAmerica	2005	2b

KT868061	USA	NorthAmerica	2006	2b
KT868067	USA	NorthAmerica	2006	2b
KT868083	USA	NorthAmerica	2006	2b
KT868085	USA	NorthAmerica	2006	2b
KT868087	USA	NorthAmerica	2006	2b
KT868157	USA	NorthAmerica	2006	2b
KT868161	USA	NorthAmerica	2006	2b
KT868163	USA	NorthAmerica	2006	2b
KT868169	USA	NorthAmerica	2006	2b
KT868178	USA	NorthAmerica	2006	2b
KT868182	USA	NorthAmerica	2006	2b
KT868183	USA	NorthAmerica	2006	2b
KT868189	USA	NorthAmerica	2006	2b
KT868191	USA	NorthAmerica	2006	2b
KT868192	USA	NorthAmerica	2006	2b
KT868193	USA	NorthAmerica	2006	2b
KT868194	USA	NorthAmerica	2006	2b
KT868205	USA	NorthAmerica	2006	2b
KT868221	USA	NorthAmerica	2006	2b
KT868226	USA	NorthAmerica	2006	2b
KT868227	USA	NorthAmerica	2006	2b
KT868228	USA	NorthAmerica	2006	2b
KT868231	USA	NorthAmerica	2006	2b
KT868240	USA	NorthAmerica	2006	2b
KT868241	USA	NorthAmerica	2006	2b
KT868245	USA	NorthAmerica	2006	2b
KT868250	USA	NorthAmerica	2006	2b
KT868261	USA	NorthAmerica	2006	2b
KT868263	USA	NorthAmerica	2006	2b
KT868273	USA	NorthAmerica	2006	2b
KT868275	USA	NorthAmerica	2006	2b
KT868281	USA	NorthAmerica	2006	2b
KT868284	USA	NorthAmerica	2006	2b
KT868297	USA	NorthAmerica	2006	2b
KT868299	USA	NorthAmerica	2006	2b
KT868301	USA	NorthAmerica	2006	2b
KT868306	USA	NorthAmerica	2006	2b
KT868316	USA	NorthAmerica	2006	2b
KT868319	USA	NorthAmerica	2005	2b
KT868320	USA	NorthAmerica	2006	2b
KT868322	USA	NorthAmerica	2006	2b
KT868326	USA	NorthAmerica	2005	2b
KT868328	USA	NorthAmerica	2005	2b
KT868329	USA	NorthAmerica	2006	2b
KT868330	USA	NorthAmerica	2005	2b
KT868342	USA	NorthAmerica	2006	2b

KT868353	USA	NorthAmerica	2006	2b
KT868379	USA	NorthAmerica	2006	2b
KT868421	USA	NorthAmerica	2006	2b
KT868424	USA	NorthAmerica	2006	2b
KT868427	USA	NorthAmerica	2006	2b
KT868474	USA	NorthAmerica	2006	2b
KT868477	USA	NorthAmerica	2006	2b
KT868495	USA	NorthAmerica	2006	2b
KT868520	USA	NorthAmerica	2006	2b
KT867856	USA	NorthAmerica	2006	2b
KT867861	USA	NorthAmerica	2006	2b
KT867889	USA	NorthAmerica	2006	2b
KT867899	USA	NorthAmerica	2006	2b
KT868010	USA	NorthAmerica	2006	2b
KT868011	USA	NorthAmerica	2006	2b
KT868016	USA	NorthAmerica	2006	2b
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GQ358992	China	Asia	2007	2b
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KU960938	China	Asia	2013	2b
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KX161681	China	Asia	2013	2b
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KP231119	Italy	Europe	2011	2b
KP231156	Italy	Europe	2011	2b
KP231158	Italy	Europe	2011	2b
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KF742545	China	Asia	2012	2b
KC823053	China	Asia	2012	2b
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KC514979	China	Asia	2011	2b
GQ358999	China	Asia	2007	2b
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KY305202	China	Asia	2015	2b
KC514980	China	Asia	2011	2b
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EU921256	China	Asia	2008	2b
EU921257	China	Asia	2008	2b
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KX828235	SouthKorea	Asia	2016	2b
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GQ358997	China	Asia	2007	2b
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GQ358998	China	Asia	2007	2b
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JQ181589	VietNam	Asia	2011	2b
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JQ181597	VietNam	Asia	2011	2b
KT336604	VietNam	Asia	2014	2b
HM776442	China	Asia	2009	2b
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KT804910	China	Asia	2015	2d
KC514967	China	Asia	2011	2d
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KR559716	Italy	Europe	2011	2b
KC620519	SouthKorea	Asia	2011	2b
KP768477	Slovakia	Europe	2012	2b
KP768472	Slovakia	Europe	2012	2b
KC620502	SouthKorea	Asia	2011	2b
JN382167	Romania	Europe	2011	2b
JN382184	Romania	Europe	2011	2b
KC620509	SouthKorea	Asia	2010	2b
JN006457	Romania	Europe	2008	2b
JN382168	Romania	Europe	2011	2b
JN382169	Romania	Europe	2011	2b
KC620511	SouthKorea	Asia	2010	2b
KR559710	Italy	Europe	2011	2b
JN382164	Romania	Europe	2011	2b
JN382159	Romania	Europe	2011	2b
JN382175	Romania	Europe	2011	2b
KP768480	Slovakia	Europe	2012	2a
KP768467	Slovakia	Europe	2012	2a
KP768474	Slovakia	Europe	2012	2a
JN006465	Romania	Europe	2010	2a
JN382161	Romania	Europe	2011	2a
JN382162	Romania	Europe	2011	2a
JN382177	Romania	Europe	2011	2a
JN382157	Romania	Europe	2011	2a
JN382160	Romania	Europe	2011	2a
JN382178	Romania	Europe	2011	2a

Supplementary Table 3: Estimates of Evolutionary Divergence between PCV2b Sequences. The number of base differences per site from between sequences are shown. This analysis involved 36 nucleotide sequences. Codon positions included were 1st+2nd+3rd+Noncoding. All ambiguous positions were removed for each sequence pair (pairwise deletion option). There were a total of 693 positions in the final dataset. Evolutionary analyses were conducted in MEGA X (KUMAR et al., 2018)

	GU938303_China_2009_PCV2b	HQ113121_China_2009_PCV2b	EU136713_Denmark_2007_PCV2b	EU136712_Denmark_2007_PCV2b	EU136720_Denmark_2007_PCV2b	AY484416_Netherlands_2001_PCV2b	DQ923523_Brazil_2009_PCV2b	KC835191_Brazil_2004_PCV2b	DQ923524_Brazil_2010_PCV2b	GU049342_Spain_2006_PCV2b	HF542107_Brazil_2007_PCV2b	JG632110_USA_2006_PCV2b	EU057185_Brazil_2003_PCV2b	KC835193_Brazil_2005_PCV2b	
GU938303_China_2009_PCV2b	1,000														
HQ113121_China_2009_PCV2b	0,333	1,000													
EU136713_Denmark_2007_PCV2b	1,000	0,333	1,000												
EU136712_Denmark_2007_PCV2b	1,000	0,333	1,000	1,000											
EU136720_Denmark_2007_PCV2b	1,000	0,333	1,000	1,000	1,000										
AY484416_Netherlands_2001_PCV2b	1,000	0,333	1,000	1,000	1,000	1,000									
DQ923523_Brazil_2009_PCV2b	0,333	0,337	0,333	0,333	0,333	0,333	1,000								
KC835191_Brazil_2004_PCV2b	0,333	0,337	0,333	0,333	0,333	0,333	1,000	1,000							
DQ923524_Brazil_2010_PCV2b	0,337	0,336	0,337	0,337	0,337	0,337	0,333	0,333	1,000						
GU049342_Spain_2006_PCV2b	0,337	0,336	0,337	0,337	0,337	0,337	0,336	0,336	0,334	1,000					
HF542107_Brazil_2007_PCV2b	0,336	0,334	0,336	0,336	0,336	0,336	0,337	0,337	0,336	0,333	1,000				
JG632110_USA_2006_PCV2b	0,334	0,333	0,334	0,334	0,334	0,334	0,333	0,333	0,331	0,331	0,330	1,000			
EU057185_Brazil_2003_PCV2b	0,336	0,334	0,336	0,336	0,336	0,336	0,334	0,334	0,333	0,333	0,331	0,330	1,000		
KC835193_Brazil_2005_PCV2b	0,334	0,333	0,334	0,334	0,334	0,334	0,333	0,333	0,331	0,331	0,330	0,331	0,330	1,000	
DQ364650_Brazil_2006_PCV2b	0,336	0,336	0,336	0,336	0,336	0,336	0,334	0,334	0,333	0,333	0,331	0,330	0,334	0,330	
KP231128_Italy_2013_PCV2b	0,387	0,386	0,387	0,387	0,387	0,387	0,388	0,388	0,387	0,384	0,386	0,384	0,384	0,384	
KC473165_China_2007_PCV2b	0,337	0,336	0,337	0,337	0,337	0,337	0,336	0,336	0,334	0,334	0,333	0,331	0,333	0,333	0,331
KT819167_Brazil_2014_PCV2b	0,334	0,333	0,334	0,334	0,334	0,334	0,336	0,336	0,334	0,331	0,333	0,333	0,333	0,333	0,333
KT719404_Brazil_2012_PCV2b	0,333	0,331	0,333	0,333	0,333	0,333	0,334	0,334	0,333	0,330	0,331	0,331	0,331	0,331	0,331
KT819160_Brazil_2014_PCV2b	0,331	0,330	0,331	0,331	0,331	0,331	0,333	0,333	0,331	0,331	0,331	0,331	0,331	0,331	0,331
KT819162_Brazil_2014_PCV2b	0,330	0,331	0,330	0,330	0,330	0,330	0,331	0,331	0,330	0,331	0,331	0,331	0,331	0,331	0,331
KT819163_Brazil_2014_PCV2b	0,336	0,334	0,336	0,336	0,336	0,336	0,337	0,337	0,336	0,333	0,334	0,330	0,331	0,330	0,330
KT819164_Brazil_2014_PCV2b	0,334	0,333	0,334	0,334	0,334	0,334	0,336	0,336	0,334	0,331	0,333	0,330	0,330	0,330	0,330
KT819165_Brazil_2014_PCV2b	0,336	0,334	0,336	0,336	0,336	0,336	0,337	0,337	0,336	0,333	0,334	0,331	0,331	0,331	0,331
KT819166_Brazil_2014_PCV2b	0,336	0,334	0,336	0,336	0,336	0,336	0,337	0,337	0,336	0,333	0,334	0,330	0,331	0,331	0,331
KC514973_China_2011_PCV2b	0,333	0,331	0,333	0,333	0,333	0,333	0,334	0,334	0,333	0,330	0,331	0,330	0,331	0,331	0,331
KF742553_China_2013_PCV2b	0,333	0,331	0,333	0,333	0,333	0,333	0,334	0,334	0,333	0,330	0,331	0,330	0,331	0,331	0,331
ID5300_Brazil_2019	0,381	0,380	0,381	0,381	0,381	0,381	0,383	0,383	0,381	0,378	0,380	0,378	0,378	0,377	0,378
ID5317_Brazil_2019	0,381	0,380	0,381	0,381	0,381	0,381	0,383	0,383	0,381	0,378	0,380	0,378	0,378	0,377	0,378
ID5318_Brazil_2019	0,381	0,380	0,381	0,381	0,381	0,381	0,383	0,383	0,381	0,378	0,380	0,378	0,378	0,377	0,378
ID5324_Brazil_2019	0,381	0,380	0,381	0,381	0,381	0,381	0,383	0,383	0,381	0,378	0,380	0,378	0,378	0,377	0,378
ID5301_Brazil_2019	0,380	0,378	0,380	0,380	0,380	0,380	0,381	0,381	0,380	0,377	0,378	0,377	0,378	0,377	0,377
ID5302_Brazil_2019	0,378	0,377	0,378	0,378	0,378	0,378	0,380	0,380	0,378	0,375	0,377	0,375	0,377	0,375	0,375
ID5325_Brazil_2019	0,380	0,378	0,380	0,380	0,380	0,380	0,381	0,381	0,380	0,377	0,378	0,377	0,378	0,375	0,377
ID5309_Brazil_2019	0,381	0,380	0,381	0,381	0,381	0,381	0,383	0,383	0,381	0,378	0,380	0,378	0,377	0,377	0,378
EU909688_Belgium_2008_PCV2b	0,334	0,333	0,334	0,334	0,334	0,334	0,333	0,333	0,331	0,331	0,330	0,331	0,331	0,331	0,331

	KC473165_China_2007_PCV2b	KT819167_Brazil_2014_PCV2b	KT719404_Brazil_2012_PCV2b	KT819160_Brazil_2014_PCV2b	KT819162_Brazil_2014_PCV2b	KT819163_Brazil_2014_PCV2b	KT819164_Brazil_2014_PCV2b	KT819165_Brazil_2014_PCV2b	KT819166_Brazil_2014_PCV2b	KC514973_China_2011_PCV2b	KF742553_China_2013_PCV2b	ID5300_Brazil_2019	ID5317_Brazil_2019	ID5318_Brazil_2019	ID5324_Brazil_2019	ID5301_Brazil_2019	ID5302_Brazil_2019	ID5325_Brazil_2019	ID5309_Brazil_2019	EU909688_Belgium_2008_PCV2b	
GU938303_China_2009_PCV2b																					
HQ113121_China_2009_PCV2b																					
EU136713_Denmark_2007_PCV2b																					
EU136712_Denmark_2007_PCV2b																					
EU136720_Denmark_2007_PCV2b																					
AY484416_Netherlands_2001_PCV2b																					
DQ923523_Brazil_2009_PCV2b																					
KC835191_Brazil_2004_PCV2b																					
DQ923524_Brazil_2010_PCV2b																					
GU049342_Spain_2006_PCV2b																					
HF542107_Brazil_2007_PCV2b																					
JG692110_USA_2006_PCV2b																					
EU057185_Brazil_2003_PCV2b																					
KC835193_Brazil_2005_PCV2b																					
DQ364650_Brazil_2006_PCV2b																					
KP231128_Italy_2013_PCV2b																					
KC473165_China_2007_PCV2b	1,000																				
KT819167_Brazil_2014_PCV2b	0,394	1,000																			
KT719404_Brazil_2012_PCV2b	0,393	0,393	1,000																		
KT819160_Brazil_2014_PCV2b	0,391	0,397	0,399	1,000																	
KT819162_Brazil_2014_PCV2b	0,390	0,396	0,397	0,399	1,000																
KT819163_Brazil_2014_PCV2b	0,393	0,393	0,391	0,390	0,390	1,000															
KT819164_Brazil_2014_PCV2b	0,391	0,391	0,390	0,388	0,387	0,393	1,000														
KT819165_Brazil_2014_PCV2b	0,393	0,393	0,391	0,390	0,388	0,394	0,399	1,000													
KT819166_Brazil_2014_PCV2b	0,393	0,393	0,391	0,390	0,388	0,394	0,393	0,394	1,000												
KC514973_China_2011_PCV2b	0,390	0,390	0,388	0,387	0,386	0,391	0,393	0,394	0,391	1,000											
KF742553_China_2013_PCV2b	0,390	0,390	0,388	0,387	0,386	0,391	0,393	0,394	0,391	1,000	1,000										
ID5300_Brazil_2019	0,378	0,378	0,377	0,375	0,374	0,380	0,383	0,383	0,380	0,383	0,383	1,000									
ID5317_Brazil_2019	0,378	0,378	0,377	0,375	0,374	0,380	0,383	0,383	0,380	0,383	0,383	1,000	1,000								
ID5318_Brazil_2019	0,378	0,378	0,377	0,375	0,374	0,380	0,383	0,383	0,380	0,383	0,383	1,000	1,000	1,000							
ID5324_Brazil_2019	0,378	0,378	0,377	0,375	0,374	0,380	0,383	0,383	0,380	0,383	0,383	1,000	1,000	1,000	1,000						
ID5301_Brazil_2019	0,377	0,380	0,378	0,377	0,375	0,378	0,381	0,381	0,378	0,381	0,381	0,393	0,393	0,393	0,393	1,000					
ID5302_Brazil_2019	0,375	0,378	0,377	0,375	0,374	0,377	0,380	0,380	0,377	0,380	0,380	0,397	0,397	0,397	0,397	0,399	1,000				
ID5325_Brazil_2019	0,377	0,377	0,375	0,374	0,373	0,378	0,381	0,381	0,378	0,381	0,381	0,393	0,393	0,393	0,399	0,397	0,396	1,000			
ID5309_Brazil_2019	0,378	0,378	0,377	0,375	0,374	0,380	0,381	0,383	0,381	0,383	0,383	0,391	0,391	0,391	0,391	0,390	0,388	0,390	1,000		
EU909688_Belgium_2008_PCV2b	0,391	0,388	0,387	0,386	0,384	0,390	0,388	0,390	0,390	0,390	0,390	0,378	0,378	0,378	0,378	0,377	0,375	0,377	0,378	1,000	



	ID5313_Brazil_2019	ID5316_Brazil_2019	HM038017_China_20008_PCV2d-2	JX535297_USA_2012_PCV2d	JX535296_USA_2012_PCV2d-2	JX679498_China_2006_PCV2d	ID4350_Brazil_2019	ID5089_Brazil_2019	ID5086_Brazil_2019	ID5093_Brazil_2019	ID5094_Brazil_2019	ID5320_Brazil_2019	ID5305_Brazil_2019	ID5315_Brazil_2019	JX519293_China_2012_PCV2d-2	AY181946_China_2002_PCV2d-1
KC800638_China_2012_PCV2d																
KC800645_China_2011_PCV2d																
KJ187306_Brazil_2013_PCV2d-2																
KT819169_Brazil_2014_PCV2d																
ID5297_Brazil_2019																
KT819170_Brazil_2014_PCV2d																
HM038017_China_2010_PCV2d																
ID4346_Brazil_2019																
ID4347_Brazil_2019																
ID5084_Brazil_2019																
ID5298_Brazil_2019																
ID5299_Brazil_2019																
ID5311_Brazil_2019																
ID5313_Brazil_2019	1,000															
ID5316_Brazil_2019	1,000	1,000														
HM038017_China_20008_PCV2d-2	1,000	1,000	1,000													
JX535297_USA_2012_PCV2d	1,000	1,000	1,000	1,000												
JX535296_USA_2012_PCV2d-2	1,000	1,000	1,000	1,000	1,000											
JX679498_China_2006_PCV2d	1,000	1,000	1,000	1,000	1,000	1,000										
ID4350_Brazil_2019	1,000	1,000	1,000	1,000	1,000	1,000	1,000									
ID5089_Brazil_2019	0,999	0,999	0,999	0,999	0,999	0,999	0,999	1,000								
ID5086_Brazil_2019	0,999	0,999	0,999	0,999	0,999	0,999	0,999	0,997	1,000							
ID5093_Brazil_2019	0,999	0,999	0,999	0,999	0,999	0,999	0,999	0,997	1,000	1,000						
ID5094_Brazil_2019	0,999	0,999	0,999	0,999	0,999	0,999	0,999	0,997	1,000	1,000	1,000					
ID5320_Brazil_2019	0,999	0,999	0,999	0,999	0,999	0,999	0,999	0,997	0,997	0,997	0,997	1,000				
ID5305_Brazil_2019	0,997	0,997	0,997	0,997	0,997	0,997	0,997	0,996	0,996	0,996	0,996	0,996	1,000			
ID5315_Brazil_2019	0,997	0,997	0,997	0,997	0,997	0,997	0,997	0,996	0,996	0,996	0,996	0,994	1,000			
JX519293_China_2012_PCV2d-2	0,999	0,999	0,999	0,999	0,999	0,999	0,999	0,997	0,997	0,997	0,997	0,997	0,996	0,996	1,000	
AY181946_China_2002_PCV2d-1	0,970	0,970	0,970	0,970	0,970	0,970	0,970	0,968	0,971	0,971	0,971	0,968	0,967	0,967	0,968	1,000