

Review

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Review

Influenza A Viruses in Swine Population—A Scientific Review

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Abstract: Influenza viruses are important pathogens that affect human and animal health. The ecology and epidemiology of influenza viruses are very complex because they have a diverse host range. Influenza A viruses are responsible for serious epidemics. Influenza B viruses cause respiratory disease in humans, seals, and pigs. Influenza C viruses are infectious to humans and pigs. Influenza D virus infects cattle, although it was first isolated from a sick pig in 2011. Only influenza A viruses are of clinical importance in pigs. Although influenza A viruses infect a variety of animal species, pigs are one of the natural hosts of these viruses. Swine influenza is a very serious respiratory disease in pigs, and its main causative agents are the H1N1, H1N2, and H3N2 subtypes, which are antigenically related to human influenza viruses. Pigs are susceptible to infection by avian and human influenza viruses and are thought to play a significant role in the ecology of human influenza. This review examines scientific articles on the zoonotic spread of swine influenza A viruses to humans, their circulation in pig populations worldwide, reverse zoonosis from humans to pigs, and the role of pigs in interspecies transmission.

Keywords: swine influenza; reassortment; epizootiology; zoonotic infection; transmission

1. Introduction

Influenza viruses (IVs) belong to the *Orthomyxoviridae* family and have a segmented genome with single-stranded negative-sense RNA. Based on genetic and antigenic differences, IVs are divided into four types: A, B, C, and D, which infect different species of mammals and birds with the four types of IV that occur in pigs. Among the four types of IVs, influenza A viruses (IAVs) are highly significant pathogens and responsible for serious epidemics in humans and domestic animals [1].

The IAV genome consists of eight RNA segments: PB2, PB1, PA, hemagglutinin (HA), NP, neuraminidase (NA), M, and NS [1]. Two surface antigens, HA and NA, are mainly subject to antigenic variability, while internal proteins (NP and M) are relatively conservative. HA and NA play an essential role in the initial stages of cell infection [2]. HA binds to host cell receptors that contain terminal sialic acid residues (-2,6-SA or -2,3-SA). The HA gene is charge of the attachment of viral pieces to the host cell receptor. NA removes the cell surface receptor (sialic acid); this is crucial for the liberation of viral particles from the cell surface and the virus spillover [2].

Based on major antigenic differences in surface proteins (HA and NA), 18 HA subtypes (H1–H18) and 11 NA subtypes (N1–N11) have currently been identified. The H1–H16 and N1–N9 virus subtypes have been identified in waterfowl, which are believed to constitute the natural IAV reservoir [3–5]; while H17–H18 and N10–N11 subtype sequences have been found in bats [6–8]. Only a limited number of subtypes have been found in mammals, such as H1 and H3 subtypes of viruses, which we identified and circulate in both humans and swine [9–16].

The IAV epidemiology and ecology are complicated by its multi-host and segmented genome. IAVs are one of the main pathogens in swine that give rise to acute respiratory infections and cause significant economic losses for pig farms. In addition to swine IAV, human and avian IAVs can also

infect pigs. Pigs are believed to serve as an intermediate “mixing vessel” for generating a variety of novel IVs [17]. Co-infection of pigs with two or more IAV strains can induce reassortment [18,19], which in turn can promote the emergence of new IV strains [20–22]. There are numerous reports of zoonotic infections in humans with swine IAVs and reverse zoonotic infections in pigs with human IAVs [23–27].

2. Ecology of Influenza Virus

The recurrent outbursts and fast spillover differing both genetically and antigenically IAVs pose a serious problem for both the pig production and public health. This issue is considered not only from the point of view of estimating and controlling the presently developing strains in pigs, but also in terms of describing their zoonotic potential [28].

It is considered that IAVs infect various animal species, and pigs (*Sus scrofa*) are one of the natural hosts for these viruses. Swine influenza (SI) is an extremely dangerous respiratory disease in swine. The major causative viruses include H1N1, H1N2, and H3N2 subtypes [29], which are antigenically related to human IV.

The development of IAV proceeds very rapidly due to two key mechanisms called antigenic drift and antigenic shift. Antigenic drift occurs due to the gradual accumulation of mutations in the surface proteins HA and NA, which leads to antigenic changes in IAV. Antigenic drift is responsible for human seasonal influenza viruses. Antigenic shift, otherwise known as reassortment, happens owing to the segmented IV genome. When two or more different IAVs infect a cell or a host, the viral gene segments can be intermixed and reassorted, leading to the appearance of different reassortant viruses. The examples of antigenic shift include the emergence of three of the four pandemic IVs that have occurred in human history, which caused the 1957 H2N2 Asian flu pandemic, the 1968 Hong Kong H3N2 flu pandemic, and the 2009 H1N1 flu pandemic [30,31].

It was discovered that pig tissues express both α -2,6-SA (human IAV receptor preference) and α -2,3-SA (avian IAV receptor preference) [17]. Genetic reassortment between human and/or avian and/or swine IAVs can take place in pigs. A prime example of this reassortment is the 2009 influenza pandemic caused by H1N1swine influenza reassortant virus containing the NA and M genes from the Eurasian swine virus and 6 remaining genes from the North American triple- reassortant virus [32,33]. The possibility of creating novel IAVs has led to the fact that pigs became known as “mixing vessels” [21,31,34]. However, whether pigs are necessary intermediate hosts for bird-to-human infections is a debatable matter, because people and certain land birds have also been found to express both types of sialic acids [35–37]. At the same time, pigs play a major role in the IAV ecology, and this is especially true of the human-pig interactions. Infection in pigs can nevertheless cause viruses to acquire the adaptation needed either to maintain infection inside pigs, thereby ensuring an additional reservoir for human infection, or to provide the mutations necessary for transmission to humans, which will lead to the establishment of that virus in the human population [24,38–40].

3. Geographical Distribution of Swine Influenza Viruses

There is a huge variety of H1N1/N2 and H3N2 IAV subtypes in swine throughout the world, and it has been established that different lineages are circulating in various regions of the Earth. A common characteristic of swine IAV ecology is the periodic spread of seasonal human viruses. Introduction of seasonal H1N1 and H3N2 IAVs from humans to pigs at different times and in various geographical areas has led to the establishment of novel IAV lineages in swine host and contributed to the genetic and antigenic diversity of influenza observed in pigs [24,41–43].

Swine surveillance level has increased around the world following the emergence of the pandemic H1N1 virus (H1N1pdm09) as well as still detectable IAV and/or novel gene lineages not previously recognized in swine, in the regions not belonging to IAV-endemic [19,22,44,45]

3.1. Circulation of Swine Influenza Viruses in North America

SI was first identified as a swine respiratory infection in the U.S. in 1918, coinciding in time with the Spanish human influenza pandemic [46,47]. IAV was first isolated from pigs in 1930 by Schope, who demonstrated that the virus caused a respiratory illness similar to human influenza in pigs [48]. Phylogenetic analysis of this virus, named the classical H1N1 (cH1N1) SIV, showed that the cH1N1 lineage was closely related to the 1918 H1N1 Spanish IVs [49] and other isolated human IAVs after discovery SI virus (SIVs) in the 1930s. The cH1N1 virus was circulating among pigs in the U.S. for almost 80 years with minimal genetic changes [37]. However, in the late 1990s, a triple reassortant IAV was discovered. It contained the HA, NA, and PB1 genes derived from seasonal human H3N2; PB2 and PA - from avian IAV, and NP, M and NS - from IAV cH1N1 of pigs [50].

Several outbreaks of respiratory diseases occurred in 1998 among pig herds in North Carolina, Texas, Minnesota, and Iowa. The disease was caused by H3N2 IAVs. Molecular genetic analyses showed that the origin of these SIVs appeared in two diverse ways. The isolate from North Carolina was a product of genetic reassortment and contained segments of the IAV H3N2 gene of human origin (PB1, HA, NA) circulating in 1995 and segments of gene the cH1N1 porcine lineage (PB2, PA, NP, M, NS). The strains isolated in Minnesota, Iowa and Texas constituted the triple reassortants and contained segments of gene cH1N1 SIV (NP, M, NS), the same segments of gene human virus (PB1, HA, NA), and viruses of avian origin (PB2, PA) [51]. This swine IAV genomic composition is known as the triple-reassortant internal gene (TRIG) cassette [22,52–54].

At the end of the 90s of the last century in the United States, in the swine population, in contrast to double reassortant viruses that did not take root, active circulation of triple reassortant viruses was observed [55]. Since H3N2 IAVs were almost non-existent among the U.S. swine population, a question arose of in-depth study of the virus spread extent. For this purpose, 4,382 swine serums collected from 23 states were serologically analyzed using the hemagglutination inhibition (HI) assay [55]. It was established that 28.3% of these animals were exposed to the cH1N1 virus while 20.5% were exposed to the triple-reassortant-like H3N2 viruses. The HI assay results suggested that viruses antigenically related to the double reassortment H3N2 virus have not become widespread among the U.S. swine population. In contrast, serodiagnosis of swine serum samples as well as additional molecular sequencing analysis of six 1999 isolates that had a triple-reassortant genotype, suggested that the H3N2 viruses carrying the avian PA and PB2 genes had spread throughout most of the United States [55].

The presence of avian polymerase genes (PB2 and PA) in the triple reassortant virus provided the major diversity between the two viruses. The epidemiology of IAVs in pigs from the U.S. has drastically changed after 1998, when the triple-reassortant H3N2 viruses containing gene segments from the cH1N1 virus (NP, M, NS), seasonal H3N2 human IAV subtype (PB1, HA, NA), and avian IAV (PB2, RA) successfully emerged in swine population [51,55].

It was established that since 1998 human H3N2 IAVs have been introduced into swine populations at least three times [56,57], resulting in the formation of phylogenetic clusters I, II, and III [58]. Cluster III (C-III) viruses spread actively in North America [59], and then evolved into variants of cluster IV (C-IV) over time [60], which contributed to the conservation and expansion of H3 IAV C-IV [61].

H3N2 viruses subsequently formed reassortants with swine H1N1 IAVs, acquiring the H1N1 or H1N2 subtypes [57,62]. Most of the fully characterized swine viruses contain the TRIG cassette regardless of subtype. Reassortant H1 TRIG viruses, having become endemic, therefore continued to circulate in most swine producing regions of the U.S. and Canada, including other drifting H3N2 variants [55–57,60,63], H1N2 [64] and reassortant IV rH1N1 [57,65–68].

Reassortments observed from 2000 to 2009 are associated with the HA and/or NA protein segments, while remaining the TRIG constellation which comprised swine (M, NP, and NS gene segments), avian (PB2 and PA gene segments), and human IVs (PB1) [52,66,69–71].

The H3N1 viruses were sometimes recognized as bounded outbreaks but were not extensively circulating [72,73]. Furthermore, in 2006 TRIG was demonstrated to have taken the avian HA H2 and N3 variants, resulting in a new triple-reassortant H2N3 SIVs [74]. Yassine et al. [75] have shown that

North American swine TRIG-containing viruses can infect turkeys, which plays a certain role in the IAV epidemiology in swine hosts and human hosts. A number of authors reported that genetically related TRIG-containing swine viruses had also been detected in Korea, Vietnam, and China [76–78].

There are reports on the introduction of IAV with the HA H1 gene of human H1N2 (hu-like H1) seasonal viruses which are both molecularly and genetically different from the SIVs cH1N1 in Canada [79]. Since 2005, TRIG-containing hu-like viruses H1N1 and H1N2 have appeared in the U.S. swine populations [80]. However, their TRIG genes are similar to those found in contemporary triple-reassortant SI viruses.

To better represent the evolution of H1 IAV circulating in North America, a cluster classification was proposed. cH1N1 IAVs, circulating among swine since 1918, evolved, based on the genetic composition of the HA gene, into contemporary a-, b-, and c-clusters, while strains with the H1 HA subtype most similar to seasonal human H1 IAVs form d-cluster [80]. All four HA gene clusters (a, b, c, and d) are found with the NA genes of the N1 or N2 subtype. The HA genes from d-cluster of viruses presumably originated from two different introductions of human seasonal viruses with HA from the H1N2 and H1N1 viruses, phylogenetically differentiated into two subclusters of swine origin, d1 and d2, relatively [66,81]. In strains isolated in the U.S. during 2008–2010, the d-cluster HA genes paired with either the N1 or N2 IAV gene of human origin [82,83]. Until 2009, the H1 IAV evolved as a result of the reassortant formation while maintaining TRIG as the basis and generating genetically and antigenically different viruses [22,66]. Since that moment, H1N1pdm09 has become firmly established in the U.S. pig population with the emergence of subsequent second-generation reassortants [84–86].

A(H1N1)pdm09 IV has also become established in swine in North Carolina and co-circulates with previously enzootic SI virus strains, including avian H1N1 and human-like H1N2 [87]. In 2010, a reassortant IAV (H1N2r) was isolated that caused mild clinical disease in pigs in North Carolina. This reassortant virus has a gene constellation including the internal gene cassette of A(H1N1)pdm09 viruses and the HA and NA genes of swine-origin H1N2 virus. This reassortant virus has been shown to have both zoonotic and reverse zoonotic potential and no apparent increased virulence or transmissibility compared to A(H1N1)pdm09 viruses [88,89].

In the course of swine influenza surveillance in 2012, a reassortant IAV strain containing HA and NA from human seasonal IAV was detected. These viruses subsequently reassorted, maintaining only the human-origin H3, which resulted in a novel lineage of viruses that became the most frequently revealed H3 branch in the U.S. swine (2010.1 HA clade) [61,90,91]. Powell et al. [92] found that compared to the 2010.1 viruses from 2012 and 2014, the 2010.1 strains from the 2015–2017 period led to equivalent macroscopic lung lesions in pigs. A single mutation at amino acid residue 145 in a previously identified HA antigenic motif was associated with a change in antigenic phenotype potentially reducing vaccine effectiveness. The 2010.1 viruses circulating in swine since 2012 were significantly different from both the H3N2 viruses that existed prior to 2012 in swine and human seasonal influenza H3N2 viruses and showed continued evolution within this lineage [92].

In 2017, the Iowa State University Veterinary Diagnostic Laboratory detected a reverse zoonotic transmission of seasonal human IAV to swine in Oklahoma. Pairwise comparison between the human H3 IAV (H3.2010.2) HA sequences detected in swine and the most similar 2016–2017 seasonal human H3 sequences revealed 99.9% nucleotide identity [93]. H3.2010.2 is a phylogenetic clade of H3N2 circulating in swine. This clade became established following the spillover of a seasonal human H3N2 virus during the 2016–2017 influenza season. H3.2010.2 transmitted and adapted to the swine host and demonstrated reassortment with the internal genes from strains endemic to pigs, but maintained the human HA and NA. It is genetically and antigenically distinct from H3.2010.1 H3N2, detected earlier in 2010. It was shown that seasonal human-to-swine transmission of IAV became established in the population through adaptation and contributed to the genetic and antigenic diversity of IAV circulating in swine [93].

Exposure to IAV and infectious status of individual pigs assists in the introduction, transmission, and spread of diverse IAVs. Influenza strains circulating among pigs can cause outbreaks in humans. In October 2020, swine-origin H1N2 IAV variant was detected in a person in

Alberta, Canada [94]. The source of the infection was a local pig farm, where a contact person worked in the household. Phylogenetic analysis showed that the isolate was very similar to the strains found on this farm in 2017.

Agricultural fairs also bring humans into close contact with pigs and provide a unique interface for zoonotic transmission of IAVs. Agricultural fairs are held every summer in the United States, where people are exposed to the genetically diverse IAVs circulating among exhibitional swine. As a result of such fairs, more than 450 laboratory-confirmed cases of zoonotic infections have been recorded since 2010 [95].

An understanding of the IAV transmission dynamics through exhibitional swine is therefore critical to reducing the high incidence of various IAV variants registered in connection with agricultural fairs.

3.2. Circulation of Swine Influenza Viruses in South America

IAVs have been found in South American swine populations. Several IAV lineages are circulating among swine populations in Latin America, which apparently existed but remained undetected for many years; however, these lineages were established after the emergence of the seasonal human virus and the global movement of pigs. The emergence of IAV with H1 HA from the classical clade of swine lineage has been reported in Mexico, including viruses with HA that share a common ancestor with the H1N1pdm2009 virus as well as viruses with HA and NA belonging to the H1N1 lineage of Eurasian pigs [96–98]. Two lineages of H3N2 IAVs were also detected in Mexico: one of them was probably resulted due to C-IV H3 importation from North America, and the second as a result of a unique seasonal introduction to humans since the mid-1990s [96].

A report has been received from Argentina in 2009, where a clinical disease and isolation of H1N1pdm IAV were recorded on a commercial pig farm. Later, in 2011, the reassortant H1N1, H1N2, and H3N2 IAVs with internal genes from the H1N1pdm virus were detected. Clinical, pathological, and virological evidence suggested that IV infection spread widely among pig farms in Argentina [99–103].

Since the emergence of H1N1pdm in 2009, IAV outbreaks have also been detected in Brazilian swine herds [96,97,104–114]. A total of 107 strains of H1N1, H1N2, and H3N2 IAVs were characterized during surveillance in swine in Brazil from 2011 to 2020 [115,116]. Phylogenetic analysis based on surface protein segments (HA and NA) showed that since the mid-1980s seasonal human IAVs were introduced at least eight times into swine population in Brazil. The analysis identified three H1 genetic clades within the 1B lineage and an H3 lineage that has diversified into three genetic clades. The N2 segment from seasonal human H1N2 and H3N2 IAVs was detected six times in swine, and the N1 segment from the human H1N1 virus was also once identified. Additional analysis revealed further reassortment with H1N1pdm09 viruses, which confirmed the significant contribution of human IAVs to the genetic diversity of IAV in swine and the need for surveillance for IAV in pigs [115].

Swine H1N2 IAVs which co-circulate with A(H1N1)pdm09-like viruses have been recognized in Chile [117,118]. Genetic analysis based on HA1 domain and antigenic analysis by the HI assay demonstrated the presence of three antigenic clusters, termed as Chilean H1A (ChH1A), Chilean H1B (ChH1B), and A(H1N1)pdm09-like. It was established that the antigenic sites of ChH1A and ChH1B strains differed from those of commercial vaccine strains by 10-60% at the amino acid sequence level. The findings confirmed the importance of antigenic analyses in addition to genetic testing to evaluate control measures such as vaccination. These results emphasized the need for ongoing monitoring to determine further transmission of antigenic variants in Chilean pig populations [96,119,120].

3.3. Circulation of Swine Influenza Viruses in Europe

SIV is one of the most significant primary causative agents of swine respiratory diseases in Europe. Three subtypes of IAVs, H1N1, H1N2 and H3N2, are circulating in the European swine population for decades. These viruses remain endemic in the European swine populations, but they differ in antigenic characteristics from viruses that circulate among swine everywhere.

Since the mid-twentieth century, cH1N1 IAVs were widely spread in the European swine populations as well as in the North American pig herds. However, in the late 1970s cH1N1 viruses were replaced by avian H1avN1 IAVs, which were transmitted from wild ducks to swine and later spread to Asia [121]. In early 1979, the emergence of avian H1avN1 IAVs has been reported in Belgium [121], later in Germany and France [122–124]. Later, during a long-term 13-year SI surveillance in Germany, the persistent spread of the Eurasian H1avN1 virus was established as well as the emergence of a novel H1N1 reassortant with human HA and avian NA genes. There is a report of a zoonotic infection caused by H1avN1 1C.2.2 IAV and detected in a German child [125]. In addition, the evolution of the A(H1N1)pdm09 antigenic drift variant has been observed [126].

In Serbia, in 2016–2018, during monitoring of IAVs circulation on 13 pig farms, 255 samples were obtained from animals. The IAVs genome was detected in 24 samples. As a result of virological studies, eight strains of IAV were isolated. Sequence studies of the HA and NA genes revealed the circulation of IAVs H1N1 and H3N2. IAVs subtype H1 were classified as 1C.2.1 and 1A.3.3.2. clade. The nucleotide sequences of the genes HA H1 showed that three viruses belong to the H1N1pdm09 lineage, and four belong to the Eurasian “avian-like” lineage H1avN1. Based on their NA gene sequences, these seven viruses belong to the Eurasian avian lineage H1avN1. The HA and NA genes of the H3N2 subtype virus belonged to the A/swine/Gent/1/1984-like H3N2 lineage [127–129].

The genetic diversity of SIVs was investigated in Northern Italy from 2017 to 2020. High genotypic diversity was found among the H1N1 and H1N2 strains, while the H3N2 strains showed a stable genetic pattern. The data obtained confirmed the need for continuous monitoring, since the evolution of IAVs could conduct to the emergence of isolates with zoonotic potential [130].

H1avN1 IAV has therefore become the dominant lineage on both continents, and played a key role in the present-day ecology of endemic viruses, both in these regions and worldwide [131].

The European swine influenza H3N2 viruses of human lineage (A/Hong Kong/1/68) emerged in the 1980s, which differed from the contemporary H3N2 viruses in North America [37,132–134]. They acquired the internal H1avN1 IAV gene cassette as a result of reassortment and had two surface protein genes (HA and NA) from Hong Kong 1968 IAV and six internal genes (M, PB1, PB2, PA, NP, NS) from an endemic avian H1N1 virus [135,136]. However, this virus rapidly disappeared from the European swine population and in 1984 was replaced by another virus with a very similar genetic composition [137]. It has quickly spread in the population of European swine. Epizootics have been recorded in Belgium [136,138], France [139], Germany [140,141], and also England [142], Italy [132,135], Spain [143,144] and the Netherlands [145,146].

H1N2 IAVs, which were first isolated in the UK, became widespread among European pigs in the mid-1990s [147–149]. Swine human-like H1N2 (H1huN2) IAVs retained the genotype of reassortant H3N2 viruses but acquired the H1 gene from the seasonal human H1N1 virus of the 1980s. H1huN2 IAVs later spread in France (1997 and 2000–2018), Italy (1998), Belgium and the Netherlands (1999 and 2014–2019), Germany (2000, 2009, 2014–2015), and Denmark (2011–2014) [126,148–163].

These three subtypes (H1avN1, H3N2, and H1huN2) therefore share internal genes but have clearly distinguishable HAs. All three of these IAV subtypes became established in the European swine populations and gradually replaced previously circulating cH1N1 IAV [45,131].

H1N1pdm09 IAV has also been prevalent in the European pigs since the 2009 pandemic [164–167]. The first reports of H1N1pdm09 IAV came from England and Northern Ireland in 2009 [164]. H1N1pdm09 IAVs were later detected in Finland [168,169] and Germany [166]. A swine reassortant H1N2r IAV was isolated in 2010, which caused mild clinical disease in pigs in the United Kingdom. This reassortant virus had a novel gene constellation, including the internal gene cassette of the H1N1pdm09 viruses and HA and NA genes from swine-origin H1N2 [88]. In 2016, the reports came from Greece about the detection of H1N1pdm09, H1N1, H1N2, and H3N2 IAVs in swine serums collected during 2002–2004 and 2010–2012 [170]. Serological surveillance carried out in Norway from 2009 to 2017 also detected the circulation of H1N1pdm09, H1N1, H1N2, and H3N2 IAVs [171]. Data on zoonotic transmission of H1N1pdm09 IAV from pigs to humans appeared in Germany in 2009–2010 [172], and in France in 2018 [167].

As elsewhere, the introduction of H1N1pdm09 into European pigs has resulted in an increase in second-generation reassortants between human H1N1pdm09 and established endemic lineages [173–176]. Circulation of reassortant viruses was reported in the UK [177], Italy [178,179], Germany [154,166,172], France [180], Sweden [181] and Denmark [157,182]. In addition, certain unusual subtypes, such as H3N1 and H1N7 viruses, have been revealed in the European pigs, but they were apparently unable to survive and spread among swine [183–185].

The emergence of H1N1pdm09 and reassortment with endemic swine IAVs therefore significantly diversified the swine IAV ecology in Europe [172,177,178].

3.4. Circulation of Swine Influenza Viruses in Asia

SIV demonstrates high level of diversity in Asian pig populations due to the introduction of viruses from Europe and North America [78,186]. It has been established that first isolation of IAVs in Asia was in 1974 (swine/Hong Kong/1/74), although the first detection of cH1N1 was recorded in Chinese pigs during the Spanish flu pandemic in 1918. SIV observations conducted in Hong Kong and Japan since the mid-1970s have shown that cH1N1 is widely spread in numerous Asian regions and countries [187,188]. The cH1N1s have been discovered in Hong Kong, Japan, India, Taiwan, Singapore, Iran, Thailand, Korea, Vietnam, and Malaysia [178,189–199].

The stock of IAV genetic diversity in swine herds from China, South Korea, Vietnam, and other Asian countries has increased due to the intercontinental movement of swine and their viruses [42,200]. This led to the spread of the European H3N2 and H1avN1 viruses along with North American TRIG viruses introduced in the late 1990s to early 2000s.

The findings of evolutionary studies have shown that cH1N1 SIV and the 1918 pandemic influenza H1N1 virus had a general ancestor or were very closely related to each other [201–203]. The relationship between human and swine H1N1 viruses may be similar to the situation with H1N1pdm09 viruses. Since its appearance, H1N1pdm09 has been time after time transmitted from humans to swine [99,204]. In addition, sporadic isolation of human-like H1N1 viruses has been observed in pigs in Japan [205] and later in China [206,207].

The H1N1pdm09 virus was introduced to swine and reassorted with the endemic subtypes in China [54], Japan [208,209] and Thailand [210]. In many Asian countries, H1N1, H1N2, and H3N2 viruses included different internal gene segments from the H1N1pdm09 virus [54,192,211–224], resulting in numerous highly complex reassortant viruses [78,214,222,224–226].

The avian influenza H1avN1 viruses were detected along with cH1N1 in clinically healthy swine in southern China during 1993 [195,212]. Later, in 2001, H1avN1 viruses that caused the avian influenza Eurasian variant were detected in pigs in Hong Kong and Thailand [42,227].

In Asia, circulation of reassortant H1N1 swine influenza viruses of North American and/or European origin has been recorded among pigs. The reports of the H1N1swine reassortant virus circulation came from Korea [76,228], Thailand [227,229], Malaysia [230]. There is serological evidence for the prevalence of H1N1 SIVs in Cambodian pigs in 2006–2010 [231], H1N1 SIVs have been recorded in Bhutan in 2011–2012 [232]. H1N1 SIVs were detected in Russia in 2016 [233]. Genetic analysis of the H1N1 virus isolate revealed 90% identity of the HA and NA genes with those found in the U.S. humans in the 1980s.

The first outbreak of influenza in swine caused by reassortant H1N2 viruses determined from the human-like variant of swine H3N2 and cH1N1s viruses was observed in Japan in 1978, later the outbreaks were recorded during 1989–1990 [234].

These viruses, having become endemic in Japanese swine populations, established a genetically stable lineage [235]. A similar reassortant H1N2 IAV gene cassette has been detected in pigs in Taiwan [236], China [42,237] and India [238].

Since 2002, a genetically stable line of North American reassortant H1N2 viruses containing HA cH1N1s has become widespread in Korea [76].

Since the 1970s, in Asia H3N2 influenza virus has been transmitted from humans to pigs on multiple occasions, and the first report of the virus being isolated from pigs in Taiwan came a year after the human pandemic in Hong Kong [239]. Outbreaks of viral infection caused by H3N2 IAVs in

pigs have also been reported in Hong Kong, Japan, Korea, India, and Thailand [186,240–247], but these H3N2 viruses could not become established in swine herds [211,248].

In the 1980s, swine H3N2 viruses were isolated in China, containing the human-like HA and NA along with the cH1N1 internal gene segments. At about the same time, two triple reassortant H3N2 viruses were isolated from pigs in China, not genetically related to the North American or European reassortant viruses. In 1999, SIVs appeared in China, which are the European reassortants of human-like H3N2 SIVs. Further reassortment of these viruses with circulating cH1N1 influenza viruses subsequently resulted in the emergence of triple reassortant strains. [211]. In addition, the European reassortant human-like H3N2 SIVs were genetically reassorted with circulating human H1 or H3 strains in Thailand [227,229]. Circulation of the European viruses in swine was confirmed by serological studies in Malaysia [230]. Since 1998, strains of SIVs have been isolated in Korea, which are triple reassortant H3N2 IAVs of the North American swine lineage with three different human-like HAs [76,249]. The pigs showed signs of respiratory disease, but no deaths were recorded. There are also a number of reports on the prevalence of H3N2 virus in swine in Sri Lanka during 2004–2005 [250], in Laos during 2009 [251], in Cambodia during 2011–2012 [252].

Influenza epizootics among swine represent a serious problem in the Republic of Kazakhstan. In 1984, as a result of a virological examination of piglets with clinical signs of respiratory diseases on pig farms situated in East Kazakhstan, three strains of the A/H1N1 influenza virus were isolated [253]. By the nature of the interaction with a panel of monoclonal antibodies, the Kazakhstan isolates showed similarities with the A/England/333/80 (H1N1) virus. The performed immunological analysis made it possible to classify the strains isolated from pigs as drift variants of the human influenza A(H1N1) virus.

The reassortant A/H3N6 strains have been also isolated from swine in Kazakhstan during 1986. The viruses of this complex were characterized by significant antigenic heterogeneity. The populations of a number of strains contained virions whose enzymatic activity was suppressed by immune serum against NA N6 [253].

In 2008–2009, nine isolates collected from uneven-aged pigs belonging to peasant farms of the Republic of Kazakhstan were identified of which four had A(H1N1), one A(HswN1), and four A/H3N2 antigenic formula. Serological analysis performed to retrospectively confirm the etiological role of influenza viruses showed the presence of antibodies against influenza A/H1N1, A/HswN1, and A/H3N2 viruses in animals, which completely coincided with the results obtained from isolation of viruses in chicken embryos [253].

In 2013–2014, a serological analysis of 492 blood serums collected from pigs belonging to peasant farms in various regions of Kazakhstan was carried out. Data obtained in the study indicated co-circulation of influenza A/H1N1 and A/H3N2 viruses among animals during the specified period [253].

There are data on circulation of H1N1 and H3N2 SIVs among the swine population in Kazakhstan during 2017–2022 [253–256].

Genetic analysis of the H1N1 IAV strain, isolated in Kazakhstan in 2020, showed that it belongs to clade 1A.3.2.2 lineage 1A. This clade has a wide global distribution, which includes the 2009 H1N1 pandemic strains [15]. The findings emphasized the importance of ongoing SIV monitoring to identify the possibility of cross-species transmission of this infectious agent.

Thus, the IVs that infect pigs most frequently belong to the H1N1 subtype, but at the same time the H1N2, H3N1 and H3N2 variants are circulating among them. Sometimes, pigs are infected with more than one virus at the same time, resulting in a reassortant strain containing genes from different sources. Reassortment plays a significant role in the emergence of novel virus variants, in particular in the origin of pandemic strains.

3.5. Circulation of Swine Influenza Viruses in Africa and Australia

H1N1pdm09, H1N1, H3N2 IAVs have been reported in various African countries [257,258], such as Egypt [259,260], Nigeria [261–265], Ghana [266,267], Cameroon [268–270], Kenya [271–273], Réunion Island [274], Uganda [275], Togo [276], and Burkina Faso [277]. In addition to H1N1pdm09,

the circulation of avian influenza viruses such as H5N1, H5N2, and H9N2 has been recorded in Nigeria and Egypt [259,264].

Swine influenza in Australia was first reported in 2009 when a herd of 300 sows was infected with the H1N1pdm09 virus. The outbreak occurred as a result of human-to-swine virus transmission [278,279]. The outbreaks of influenza H1N1pdm were detected on three pig farms located in three different states of Australia. Further analysis of the outbreak in Queensland resulted in the identification of two distinct IAV strains in pigs. Two employees working in the same piggery were also infected with the same two strains found in pigs. Although no reassortment was identified in the above cases, the ability of these viruses to be transmitted between swine and humans was evident, emphasizing the importance of monitoring pigs to identify novel influenza infections [279].

An outbreak of SI occurred in Western Australia in 2012 [280], the infection spread among both pigs and farm workers. Molecular analysis of the isolates revealed the circulation of H1N2, H3N2, H1N1pdm09 IAVs. H1N2, H3N2, and H1N1 SIVs later continued to circulate in Western Australia and southern Queensland right up to 2016 [281]. Public health investigation was carried out that identified an unrecognized zoonotic risk and potential threat of a pandemic in the future [280].

In 2018, there has been a report of a 15-year-old teenage girl from Australia infected with A(H3N2) SIV. The virus contained the HA and NA genes derived from the 1990s-like seasonal human viruses and internal protein genes from H1N1pdm09 IAV, emphasizing the potential risk to human health in Australia [282].

4. Circulation of Avian Influenza Viruses

Mainly H1N1 and H3N2 IAVs circulate among swine populations in North America, Europe, and Asia. However, there have been no cases of transmission of the 1957 Asian pandemic H2N2 virus to pigs. There is also cross-species transmission of avian viruses to pigs on these continents. The reassortant SIVs which are presently circulating have at least one component of avian virus gene. Although natural infection of pigs with avian influenza viruses has been reported in numerous parts of the world, only the European avian H1avN1 virus became adapted to pigs [163,283–285]. Other subtypes of avian influenza virus have been found sporadically in pigs in North America or Asia. There are reports of sporadic isolation of atypical H1N7 and H3N1 IAVs from pigs in Europe [183,284] and the H4N6, H3N3, H3N1, and H2N3 subtypes in North America [72,74,286]. Numerous interspecies transmission of H9N2 viruses from host birds to swine occurred in Asia [287]. H9N2 IAVs isolated from pigs in Hong Kong in 1998 were fully avian IAV variants [246,287,288]. However, since 2003, reassortant avian strains have emerged with certain genes closely associated with highly pathogenic avian influenza (HPAI) H5N1 virus [289–293]. Infection with the avian H5N1 virus was also detected in pigs in Indonesia [294] and Vietnam [228]. The avian H5N2 virus has been transmitted from wild migratory birds to Korean pigs [295].

H3N1 SIV, which is a reassortant virus with genes of the human-like H3N2 isolate and circulating cH1N1SIVs, have been isolated from pigs in Taiwan [236]. There are data on the circulation of H3N1 SIVs in Indonesia and Korea [296]. H3N1 SIVs circulating in Korea represented a reassortment of co-circulating North American reassortant H1N1 and H3N2 viruses [296].

The equine-like H3N8 SIVs were also isolated from pigs in central China [297].

Thus, some avian IAVs such as H9N2, H5N1, H5N2, H4N8, and H6N6 as well as equine H3N8 IAV have been sporadically detected in pigs from certain Asian countries [78,186,297–299]. The simultaneous circulation of so many genetically diverse IAVs in pigs explains the very complex ecology of swine IAVs in Asia.

5. Conclusions

SIVs are respiratory viral pathogens that can cause serious health problems in both pigs and humans worldwide. Pigs are one of the major hosts of IAVs and play an important role in formation of the present-day influenza ecology. Although waterfowl are considered to be the major natural reservoir of IAVs, pigs are the carriers of a limited but dynamic array of viruses [5].

Swine serve as “mixing vessels” for influenza strains of human, avian, and swine origin because they have specific avian and human influenza receptors in the tracheal epithelium [300]. Co-circulation of different IV strains in pigs may promote the generation of novel variants that could potentially pose a threat to public health [246]. For example, influenza A(H1N1)pdm09 is thought to have been present in pig herds for several months before it became a pandemic strain in humans [32].

The epidemiology of IAVs in swine involves a complex interaction between viruses of human, avian, and swine evolutionary origin. The numerous IAV subtypes of human and avian origin, including H1, H2, H3, H4, H5, H7, and H9 have been discovered in pig populations [301]. Swine play an important role as intermediate hosts in reassortment and/or adaptation processes leading to the development of IVs with human pandemic potential [5,302]. IV human-to-swine transmission however takes place far more frequently than swine-to-human transmission and occupies a central place in the global swine population with new viral diversity[27]. Despite the genetic diversity of SIVs found in the swine population, only H1 and H3 IAVs formed stable lineages and in this respect, they are similar to human IVs. The nature of the H1 and H3 viruses nevertheless differs between the two host populations. In addition, the distribution of subtypes and genotypes of endemic IAVs varies greatly by geographic region due to the repeated introduction of avian and human influenza viruses. An exception is H1N1pdm09, which is widespread mainly as a result of multiple from humans-to-swine reintroduction [54,99,164,173,303,304]. H1N1pdm09 IAV arose from reassortment between North American and Eurasian lineages of IAVs [32,33]. This virus was antigenically distinct from previously known viruses circulating in swine. In addition, it has reassorted widely with almost all regional swine IAVs, which contributed to the further spread of novel IAV genotypes and resulted in a more complex epidemiological picture [24,25,41–43,166,174,219,220,305–309]. Understanding of the transmission modes is of decisive importance for developing effective control strategies and making reasonable surveillance recommendations.

The degree of virulence, epidemiological and epizootological activities of different virus variants appears to be far from the same and directly depends on the molecular biological properties of the strains. Continuous monitoring and genome-wide genetic characterization of SIVs make it possible to obtain a complete picture of the infectious disease process, predict the epidemiological and epizootic situation, and choose the right strategy and tactics for preventive and anti-epidemic measures.

This study may provide information needed to develop a more effective method for monitoring SIVs and selecting countermeasures to prevent the interspecies transmission, which could become a potential pre-pandemic in the future.

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