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Genesis and genetic constellations of swine influenza viruses in Thailand

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ABSTRACT

Swine influenza virus (SIV) is one of the most important zoonotic agents and the origin of the most recent pandemic virus. Asia is considered to be the epicenter for genetic exchanging of influenza A viruses and Southeast Asia including Thailand serves as a reservoir to maintain the persistence of the viruses for seeding other regions. Therefore, searching for new reassortants in this area has been routinely required. Although SIVs in Thailand have been characterized, collective information regarding their genetic evolution and gene constellations is limited. In this study, whole genomes of 30 SIVs isolated during clinical target surveillance plus all available sequences of past and currently circulating Thai SIVs were genetically characterized based on their evolutionary relationships. All genetic pools of Thai SIVs are comprised of four lineages including classical swine (CS), Eurasian swine (EAs), Triple reassortants (TRIG) and Seasonal human (Shs). Out of 84 isolates, nine H1N1, six H3N2 and one H1N2 strains were identified. Gene constellations of SIVs in Thailand are highly complex resulting from multiple reassortments among concurrently circulating SIVs and temporally introduced foreign genes. Most strains contain gene segments from both EAs and CS lineages and appeared transiently. TRIG lineage has been recently introduced into Thai SIV gene pools. The existence of EAs and TRIG lineages in this region may increase rates of genetic exchange and diversity while Southeast Asia is a persistent reservoir for influenza A viruses. Continual monitoring of SIV evolution in this region is crucial in searching for the next potential pandemic viruses
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1. Introduction

Swine influenza virus (SIV) is an important zoonotic agent posing a threat to human health. Transmission of SIVs to human hosts or vice versa is very common, although in most cases, the transmitted viruses cannot establish their niches in the new host (Vincent et al., 2008). Swine was suspected to be an intermediate host for generating the first (1918 H1N1 Spanish Flu) and probably the second (1957 H2N2 Asian Flu) and third (1968 H3N2 Hong Kong Flu) pandemic viruses since they might circulate in mammalian hosts including swine before each pandemic period, not directly transmitted from avian to human host (Smith et al., 2009a). In addition, epithelium lining pigs' trachea contains receptors for entry of both human and avian influenza viruses (Ito et al., 1998). Thus, pigs serve as mixing vessels for human, avian and swine viruses to generate new reassortants. The mixing vessel

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theory has been recently confirmed since all eight genes of the most recent influenza pandemic, pdmH1N1 2009, are derived directly from swine origin (Smith et al., 2009b).

The pandemic potential of SIV is inherited in characteristics of all influenza A viruses which are classified in genus *influenzavirus* A, family *Orthomyxoviridae*. The virus in this genus contains eight segments of negative-sense, single-stranded RNA genome. The genomic segments 1–8 are polymerase basic 2 (PB2), PB1, polymerase acid (PA), heamagglutinin (HA), nucleoprotein (NP), neuraminidase (NA), matrix (M) and nonstructural protein (NS). Its polymerase lacks proofreading activity which point mutations are introduced into the genome every round of replication resulting in genetic drift (Webster et al., 1992). In addition, the segmented genome allows mixing and exchanging of genetic materials within a cell infected with two or more strains creating new reassortants containing new genetic compositions. This process is called genetic shift. More importantly, influenza A viruses can infect various species of animals which maintain the existence of viruses in the world (Webster et al., 1992). Wide ranges of reservoirs also expand sizes of gene pools and chances for genetic reassortment. The aforementioned factors generate high genetically variable characteristics and genomic complexity of influenza A viruses that benefit their constant adaptation and evolution.

Along its evolutionary path, SIVs have changed from a single genotype to be more diverse with more complex gene compositions. Historically, there was only one genotype of SIV subtype H1N1; the so-called classical swine influenza virus (CS). The CS SIV was first isolated from North American pigs in 1930 and appeared to be antigenic closely related to the first H1N1 pandemic virus existing in 1918 (Vincent et al., 2008). It was found not only in North American swine, but also in Eurasian swine populations. In 1979, an avian-like SIV subtype H1N1 with all avian gene segments was introduced into European swine populations and replaced the CS genotype in Europe (Scholtissek et al., 1983). After the third pandemic, a human-like H3N2 virus was introduced into European swine and co-circulated with the avian-like H1N1 SIV in the European swine population. Subsequently, reassortment between the two viruses generated a new virus comprising the human-like H3 and N2 genes plus six internal genes belonging to the avian-like H1N1. This H3N2 reassortant finally replaced the wholly human-like H3N2 viruses (Campitelli et al., 1997). The H3N2 SIV with the avian-like internal genes further reassorted with a human H1N1 virus which existed in the 1980s resulting in H1N2 SIV. This H1N2 virus possessed the newly introduced human H1HA and the remaining genes of the reassortant, SIV subtype H3N2 (Brown et al., 1998). In the 20th century, three subtypes of SIVs, H1N1, H1N2 and H3N2, co-evolved in European swine. Their genetics were more diverse as a result of temporal introduction of new genes from contemporary human viruses in combination with the internal genes of the avian-like SIVs acquired since 1979 (Marozin et al., 2002). Thus, internal genes of the avian-like Eurasian swine (EAs) viruses have contributed to a majority of genetic pools of SIVs.

In North America, the CS virus was the only genotype circulating in swine population from the first pandemic in 1918 until 1998 (Vincent et al., 2008). Around 1997–1998, human H3N2 viruses were introduced into swine population resulting in three types of H3N2 reassortants including wholly human SIV as well as double and triple reassortants. The double reassortants containing human HA, NA and PB1 and the remaining genes of the CS virus emerged in August 1998 in a swine farm in North Carolina (Zhou et al., 1999). The triple reassortants containing genes from avian (PB2 and PA), human (HA, NA and PB1) and classical (NP, M and NS) swine lineages resulting from genetic mixing between the avian, human and CS viruses were reported in several swine herds in the Midwest of the U. S. between November and December 1998. Thereafter, the triple reassortants were widespread in the U. S. and further reassorted with the CS H1N1 virus resulting in rH1N1 and H1N2 SIVs. These reassortants contain H1HA and N1NA from the CS and the N2NA plus internal genes, so-called TRIG, from the triple reassortant H3N2 SIVs (Vincent et al., 2008). In 2003, novel reassortants H1N2 and H1N1 SIVs comprising human H1HA or N1NA and TRIG emerged from genetic mixing between the H1N2 SIV and a human H1N1 virus (Vincent et al., 2009). It was speculated that TRIG may be facilitate the genetic reassortment process of SIVs (Vincent et al., 2008).

To date, SIVs circulating in North American swine are H1N1, H1N2, and H3N2 subtypes. The H1HA gene pool of North American SIVs are classified in to four clusters; α, β, and γ clusters are classified in the classical swine (CS) lineage while the δ cluster was derived from recent seasonal human (Sh) lineage (Vincent et al., 2009). The H3HA gene pool of North American SIVs are divided into four clusters — I, II, III and IV — depending on strains of the temporally distinct human HA such as the HA of cluster III derived from a human H3N2 virus related to A/Wuhan/359/1995 (Webby et al., 2004; Russell et al., 2008; Lekcharoensuk et al., 2010). Thus, before the emergence of the most recent pandemic, genetic sequences of Eurasian swine viruses were not present in the gene pools of North American swine viruses (Smith et al., 2009b). Thereafter, Eurasian swine NA and M genes have been introduced into the gene collection of North American swine viruses. Combinations of TRIG and M gene of EAs lineage may facilitate genetic exchanging between SIV and genes from different hosts (Nelson et al., 2012).

Thus far, three major lineages of SIVs are circulating in swine populations throughout the world; Eurasian avian-like swine (EAs), Classical swine (CS) or North American swine (NAs) and triple reassortant swine (TRIG) (Vijaykrishna et al., 2011). Additionally, seasonal human (Sh) viruses have temporally contributed their H3HA and N2NA genes and to a lesser extent H1HA and N1NA in SIV gene pools resulting in new genetic clusters with antigenically different from the previous existing viruses. All three subtypes, H1N1, H1N2 and H3N2, of SIVs have been also circulating in swine populations in East and Southeast Asia (Guan et al., 1996; Chutinimitkul et al., 2008; Lee et al., 2008). In Southern China and Hong Kong, most of the viruses appeared before 1998 were CS and EAs lineages. TRIG viruses were introduced into the swine population in

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