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Phylogeographic characteristics of vesicular stomatitis New Jersey viruses circulating in Mexico from 2005 to 2011 and their relationship to epidemics in the United States

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ABSTRACT

We analyzed the phylogenetic and time–space relationships (phylodynamics) of 181 isolates of vesicular stomatitis New Jersey virus (VSNJV) causing disease in Mexico and the United States (US) from 2005 through 2012. We detail the emergence of a genetic lineage in southern Mexico causing outbreaks in central Mexico spreading into northern Mexico and eventually into the US. That emerging lineage showed higher nucleotide sequence identity (99.5%) than that observed for multiple lineages circulating concurrently in southern Mexico (96.8%). Additionally, we identified 58 isolates from Mexico that, unlike previous isolates from Mexico, grouped with northern Central America clade II viruses. This study provides the first direct evidence for the emergence and northward migration of a specific VSNJV genetic lineage from endemic areas in Mexico causing VS outbreaks in the US. In addition we document the emergence of a Central American VSNJV genetic lineage moving northward and causing outbreaks in central Mexico.

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Introduction

Vesicular stomatitis (VS) is the most common vesicular disease affecting livestock throughout the Americas (Rodriguez, 2002). Clinical signs of VS in cattle and pigs are indistinguishable from foot and mouth disease (FMD), one of the most devastating viral infections of livestock. Thus, VS causes alarm and economic losses associated to animal quarantines and trade embargoes when it occurs in FMD-free areas and the occurrence of VS greatly exacerbates the inherent difficulties involved in the control of FMD in South America (Valbuena et al., 2000). Horses can also be infected by VS viruses (VSV) and outbreaks typically result in quarantines and stop-movement measures that cause disruption to horse shows and trade (Bridges et al., 1997).

The causal agents of VS are members of the family Rhabdoviridae and the genus Vesiculovirus (Wagner and Rose, 1996). Two main serotypes of VSV have been described: New Jersey (VSNJV) and Indiana (VSIV). These viruses are endemic from northern South America (Colombia, Venezuela, Ecuador, and Peru) to southern Mexico, with VSNJV being responsible for roughly 80% of the clinical cases reported annually (Hanson et al., 1968). In endemic areas, VS outbreaks are seasonal, often associated to the transitions between the rainy and dry seasons (Hanson, 1981). In Mexico and the US, the NJ serotype has been responsible for the great majority of VS cases for at least the last 2 decades with the last published report of an IN outbreak in Mexico dating back to 1997 and 1998 in the US (Rodriguez et al., 2000).

Phylogenetic analysis of VSNJV isolates suggests an evolutionary pattern in which geographic rather than temporal factors influence the evolution of the virus (Nichol et al., 1989). There is evidence that ecological factors (typically dictated by geography), rather than immune selection, are the main selective forces influencing VSNJV evolution in endemic areas. Within these endemic areas, specific viral genetic lineages can be maintained for many years (decades) with little genetic change. This genetic stability within endemic regions allows

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the use of phylogenetic analysis to infer the geographical and, in some cases, ecological zone from which viral strains originate (Rodriguez et al., 1996).

Vesicular stomatitis is endemic in the southern states of Mexico along the Isthmus of Tehuantepec where multiple genetic viral lineages are maintained on a yearly basis. In contrast, in Mexico's central and northern states VS has cyclic epidemic occurrence, usually associated with only a single genetic lineage (Arroyo et al., 2011). In the US, VS epidemics occur in sporadic cycles of 8–10 year intervals, starting usually in the border states of Arizona, New Mexico or Texas and spreading as far north as Colorado and Wyoming (Perez et al., 2010; Rainwater-Lovett et al., 2007). The factors responsible for the cyclic epidemics of VS in central and northern Mexico as well as in the southwestern US remain unclear. However, there is evidence that viral strains causing outbreaks in the southwestern US are monophyletic and are genetically closely related to specific viral lineages occurring in endemic areas of Mexico (McCluskey et al., 2003; Rainwater-Lovett et al., 2007; Rodriguez et al., 2000). Currently, two hypotheses exist regarding the natural cycle of VS in the southwestern US. The first proposes that VS has an endemic transmission cycle in reservoir species from which the virus periodically infects domestic animals (Webb et al., 1987). The second hypothesis maintains that each VS outbreak is an introduction of the virus into the US from endemic areas elsewhere (Rodriguez et al., 2000). The latter hypothesis is consistent with data obtained from recent outbreaks in the US, where the viral strain involved in the outbreak was genetically related to viral strains circulating in Mexico (Rainwater-Lovett et al., 2007; Rodriguez et al., 2000). Although there is no evidence of long term maintenance of VSNJV in the US, there is evidence that under certain conditions, viruses from Mexico introduced into the US may over-winter for up to consecutive three years (Perez et al., 2010).

In this study we report the phylogenetic and time–space relationship (phylodynamics) of VSNJV in Mexico from 2005 to 2011 in terms of evolution, spatial and temporal distribution and the relationship to a recent outbreak in the US in 2012. An unusually large outbreak was detected in the central (non-endemic) states of Mexico (Puebla, Guerrero and Morelos) starting in 2006, which spread progressively through the northern (non-endemic) states of Mexico and eventually affected the southwestern US in 2012. This outbreak was likely caused by a viral genetic lineage circulating endemically in southern Mexico since 2005. Additionally, we identified 58 isolates from Mexico that unlike all previous isolates (hundreds) from Mexico and the US (with exception of the Ogden (Utah, 1949) strain) did not group within the typical North American clade of VSNJV (clade I) (Rainwater-Lovett et al., 2007; Pauszek and Rodriguez, 2012). These 58 isolates grouped within a clade (clade II) comprised of other isolates from northern Central America and the Ogden strain. To the authors' knowledge, this is the first report using phylodynamics to characterize an outbreak that is sourced from an endemic region of Mexico, spreads throughout central and northern Mexico and eventually into the southwestern US. Our data provides direct evidence to support the hypothesis that VS outbreaks in the US originate from viruses circulating in endemic areas of Mexico and cause epidemics in central/northern Mexico en route to the US. We also document the introduction of a novel genetic lineage originating from northern Central America into Mexico causing an increasing number of outbreaks in central Mexico. Monitoring genetic lineages in endemic and non-endemic areas of Mexico might provide an early warning for future VS incursions into the US and allow preventive measures to mitigate the severe economic impacts of these outbreaks.

Results

Phylogenetic analysis

Initial phylogenetic analysis showed the isolates in this study grouping into two of the six clades previously described for VSNJV (Fig. 1) (Pauszek and Rodriguez, 2012). Clade I was comprised exclusively of viruses from North America and clade II includes viruses from North America and northern Central America. Clades IV, V and VI include Central American viruses and clade III includes Central and South American viruses. Of the 181 isolates of VSNJV collected between 2005 and 2012, 176 were collected in 19 states in Mexico and 5 isolates originated from the US (New Mexico). We identified 74 distinct haplotypes, thus 107 of the isolates were identical to at least one other isolate in the hypervariable region of the P gene. The 181 sequences had an average, minimum and maximum percent nucleotide similarity of 92, 89 and 100%, respectively. The dominant haplotype contained 58 isolates and was defined as lineage 1.1. There was high genetic heterogeneity among the isolates from Mexico with an average of 17% nucleotide divergence in the P gene hypervariable region, while the 5 US isolates were almost identical to each other ($<1\%$ nucleotide divergence). Phylogenetic analysis revealed that 123 of the 181 viruses, including the 5 US viruses, grouped with viruses previously found in North America into clade I. The remaining viruses grouped within the northern Central American clade II which

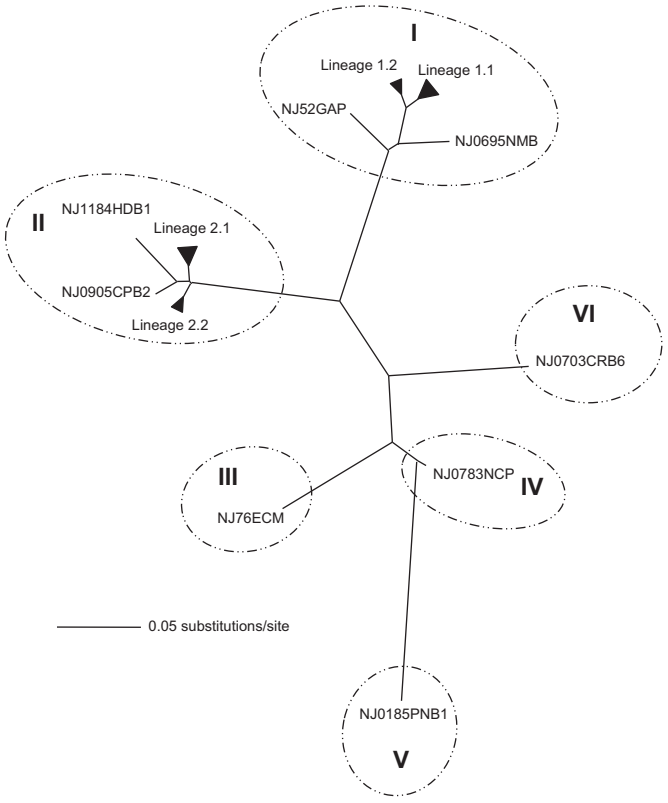

Fig. 1. Unrooted maximum likelihood phylogenetic tree deduced from a fragment of the phosphoprotein gene showing that the isolates from Mexico group into two distinct clades. The previously described six principal clades (I through VI) of VSNJV are encirlced by a broken line and for simplicity, clades II–VI are represented by a single virus. Clade I, the North American clade, is represented by both isolate NJ52GAP from the Southeastern US and isolate NJ0695NMB from the Southwestern US. All viruses in lineage 1.1 ($n=91$) and 1.2 ($n=9$) collected in Mexico and the US, grouped within clade I and are represented by black triangles. Isolate NJ0905CPB2 and all of the lineage 2.1 ($n=42$) and 2.2 ($n=15$) isolates (represented by expanding black triangles) grouped within clade II. Detailed phylogenetic analysis of clade I and clade II isolates from Mexico are shown in Figs. 2–4.

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