
Geographic Distribution of Hantaviruses Associated with Neotomine and Sigmodontine Rodents, Mexico

Mary L. Milazzo,¹ Maria N.B. Cajimat,¹ Hannah E. Romo, Jose G. Estrada-Franco, L. Ignacio Iñiguez-Dávalos, Robert D. Bradley, and Charles F. Fulhorst

To increase our knowledge of the geographic distribution of hantaviruses associated with neotomine or sigmodontine rodents in Mexico, we tested 876 cricetid rodents captured in 18 Mexican states (representing at least 44 species in the subfamily Neotominae and 10 species in the subfamily Sigmodontinae) for anti-hantavirus IgG. We found antibodies against hantavirus in 35 (4.0%) rodents. Nucleotide sequence data from 5 antibody-positive rodents indicated that Sin Nombre virus (the major cause of hantavirus pulmonary syndrome [HPS] in the United States) is enzootic in the Mexican states of Nuevo León, San Luis Potosí, Tamaulipas, and Veracruz. However, HPS has not been reported from these states, which suggests that in northeastern Mexico, HPS has been confused with other rapidly progressive, life-threatening respiratory diseases. Analyses of nucleotide sequence data from 19 other antibody-positive rodents indicated that El Moro Canyon virus and Limestone Canyon virus are geographically widely distributed in Mexico.

Hantavirus pulmonary syndrome (HPS) is a potentially fatal zoonosis caused by hantaviruses (family *Bunyaviridae*, genus *Hantavirus*) that are principally associated with members of the rodent family Cricetidae, more specifically, members of the subfamily Neotominae or Sigmodontinae (1,2). The viruses known to cause HPS

Author affiliations: University of Texas Medical Branch, Galveston, Texas, USA (M.L. Milazzo, M.N.B. Cajimat, H.E. Romo, J.G. Estrada-Franco, C.F. Fulhorst); Universidad de Guadalajara, Autlán de Navarro, Mexico (L.I. Iñiguez-Dávalos); and Texas Tech University, Lubbock, Texas, USA (R.D. Bradley)

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on the North American continent are Bayou virus, Black Creek Canal virus (BCCV), Choclo virus (CHOV), New York virus, and Sin Nombre virus (SNV) (3–7). Other hantaviruses that are principally associated with neotomine or North American sigmodontine rodents include Carrizal virus (CARV), Catacamas virus, El Moro Canyon virus (ELMCV), Huitzilac virus (HUIV), Limestone Canyon virus (LSCV), Montano virus (MTNV), Muleshoe virus (MULV), Playa de Oro virus, and Rio Segundo virus (RIOSV) (8–14).

Specific rodents (usually 1 or 2 closely related species) are the principal hosts of the hantaviruses, for which natural host relationships have been well characterized. The current principal host relationships of some hantaviruses seem to represent a long-term association between viruses in the genus *Hantavirus* and rodents in the family Cricetidae. Evidence for this ancient relationship includes the association of phylogenetically closely related hantavirus species with phylogenetically closely related allopatric rodent species. For example, Catacamas virus is associated with Coues's rice rat (*Oryzomys couesi*) in Honduras, and Bayou virus is associated with the marsh rice rat (*Oryzomys palustris*) in the southeastern United States (9,15).

The rodent fauna of Mexico comprises the brush mouse (*Peromyscus boylii*), the deer mouse (*P. maniculatus*), the western harvest mouse (*Reithrodontomys megalotis*), the hispid cotton rat (*Sigmodon hispidus*), the fulvous pygmy rice rat (*Oligoryzomys fulvescens*), and 122 other species in the Neotominae or Sigmodontinae (16).

¹These authors contributed equally to this article.

In the southwestern United States, LSCV, SNV, ELMCV, and MULV are principally associated with rodents of the species *P. boylii*, *P. maniculatus*, *R. megalotis*, and *S. hispidus*, respectively (10–12,17), and that in Panama, CHOV is principally associated with *O. fulvescens* (18). Hypothetically, LSCV, SNV, ELMCV, and/or MULV—in association with deer mice (*Peromyscus* spp.), harvest mice (*Reithrodontomys* spp.), or cotton rats (*Sigmodon* spp.)—are widely distributed in northern Mexico, and the hantavirus assemblage of southern Mexico includes CHOV or hantaviruses that are phylogenetically closely related to CHOV.

Our knowledge of the rodent-associated hantaviruses in Mexico includes the following findings: HUIV RNA in a western harvest mouse (*R. megalotis*) captured in Morelos (8); CARV RNA in a Sumichrast's harvest mouse (*R. sumichrasti*) and MTNV RNA in an Orizaba deer mouse (*P. beatae*) from Guerrero (8); Playa de Oro virus RNA in a Mexican oryzomys (*Oryzomys mexicanus*) and Jalisco cotton rat (*S. mascotensis*) from Colima (13); ELMCV RNA and SNV RNA in western harvest mice from Zacatecas (14); antibody against hantavirus in nimble-footed mice (*P. levipes*) captured in Tamaulipas (19); and antibody against hantavirus in a North American deer mouse (*P. maniculatus*), transvolcanic mice (*P. hylocetes*), black-eared mice (*P. melanotis*), and Sumichrast's harvest mouse captured in the state of Mexico (20,21). The purpose of this study was to extend our knowledge of the geographic distribution of hantaviruses associated with neotomine or sigmodontine rodents in Mexico.

Materials and Methods

Blood samples from 876 rodents, representing at least 44 species in the Neotominae and 10 species in the Sigmodontinae, were tested for anti-hantavirus IgG. The 876 rodents were captured during 1998–2008 at 43 localities in 18 states in Mexico (online Appendix Table 1, wwwnc.cdc.gov/EID/article/18/4/11-1028-TA1.htm). Blood samples from all of the rodents and lung samples from the antibody-positive rodents were acquired from the Natural Science Research Laboratory, Museum of Texas Tech University, Lubbock, Texas, USA.

The blood samples were tested for IgG to Caño Delgadito virus (CADV) strain VHV-574 by using an ELISA in which CADV can be highly cross-reactive with SNV, BCCV, and other North American hantaviruses (22). The antibody titers in the antibody-positive blood samples were recorded as 320, 1,280, or $\geq 5,120$.

Samples of lung tissue from the antibody-positive rodents were tested for hantavirus nucleocapsid (N) protein gene RNA. Subsequently, we determined the nucleotide sequences of a 1,078-nt fragment of the glycoprotein precursor (GPC) genes of 11 of the hantaviruses associated

with the antibody-positive rodents. We chose these 11 viruses to represent the geographic distribution and natural host associations of the hantaviruses in Mexico included in this study. Total RNA was isolated from 30 mg to 45 mg of lung tissue by using Tri Reagent (Sigma-Aldrich, St. Louis, MO, USA). First-strand cDNA was synthesized from small (S) segment and medium (M) segment RNA by using SuperScript II RNase H⁻ Reverse Transcriptase (Invitrogen Life Technologies, Inc., Carlsbad, CA, USA) in conjunction with oligonucleotide 5'-GGTGGTTGTGGTAGTAGTAGACTCC-3' (23). The first-round and second-round (hemi-nested) PCR assays used the MasterTaq Kit (Eppendorf North America, Inc., Westbury, NY, USA). (The sequences of the oligonucleotides that were used to prime the PCR are available from the corresponding author.) The sizes of the N protein gene amplicons from the second-round assays ranged from 377 to 545 bp, the sizes of the GPC gene amplicons from the second-round assays ranged from 607 to 631 bp (M1 amplicon) and 571 to 618 bp (M2 amplicon), and the lengths of the overlaps between the M1 and M2 amplicons ranged from 125 to 134 bp. Together, the nucleotide sequences of the M1 and M2 amplicons encoded a 359-aa fragment of the G_C glycoprotein.

The sequences in each dataset were aligned by using the computer program ClustalW version 2.0.12 (24).



Figure 1. Municipalities in Mexico in which rodents positive for antibodies against hantaviruses were captured: 1) Municipality of Santiago, state of Nuevo León; 2) San Fernando, Tamaulipas; 3) Real de Catorce, San Luis Potosí; 4) Doctor Arroyo, Nuevo León; 5) Soto la Marina, Tamaulipas; 6) Santa María del Oro, Nayarit; 7) Ciudad del Maíz, San Luis Potosí; 8) Autlán de Navarro, Jalisco; 9) Uruapan, Michoacán; 10) Ecatepec de Morelos, México; 11) Perote, Veracruz; 12) Chilpancingo de los Bravo, Guerrero; 13) Ocozacoautla de Espinosa, Chiapas; 14) Mapastepec, Chiapas. The states shaded in gray are those in which members of *Peromyscus maniculatus* have been found (28). The star indicates the location in Colima at which rodents infected with Playa de Oro virus were captured in a previous study (13).

Sequence nonidentities were equivalent to uncorrected (p) distances. The phylogenetic analyses of nucleotide sequences were conducted with MRBAYES 3.1.2 (25) and programs in the computer software package PAUP* (26). The Bayesian analyses used the general time reversible + proportion invariant + Γ model and the following options in MRBAYES 3.1.2: two simultaneous runs of 4 Markov chains, 2 million generations, and sample frequency = every 1,000th generation. The first 1,000 trees were discarded after review of the likelihood scores, convergence statistics, and potential scale reduction factors; and a consensus tree (50% majority rule) was constructed from the remaining trees. Probability values in support of the clades were calculated a posteriori, and clades with probability values ≥ 0.95 were considered supported by the data (27).

Results

Antibody (IgG) against hantavirus was found in 35 (4.0%) of 876 rodents captured in 18 states in Mexico (online Appendix Table 1). The antibody-positive rodents were from 16 localities (online Appendix Table 2, wwwnc.cdc.gov/EID/article/18/4/11-1028-TA2.htm) in 14 municipalities in 10 states: Chiapas, Guerrero, Jalisco, México, Michoacán, Nayarit, Nuevo León, San Luis Potosí, Tamaulipas, and Veracruz (Figure 1). None of

the rodents captured in Chihuahua (n = 9), Coahuila (n = 16), Guanajuato (n = 8), Oaxaca (n = 64), Puebla (n = 15), Sinaloa (n = 9), Sonora (n = 22), or Tlaxcala (n = 16) were antibody-positive to CADV strain VHV-574.

Hantavirus N protein gene RNA was detected in samples of lung from 24 (68.6%) of the 35 antibody-positive rodents (Table). The Bayesian analyses of the N protein gene sequences separated the 24 Mexican viruses in this study into 4 groups (Figure 2). Group I included CARV, group 2 included HUIV, group III included LSCV and MTNV, and group IV included SNV strains Convict Creek 74, Convict Creek 107, and NM H10.

Hantavirus GPC gene RNA was detected in each of the 11 rodents assayed for GPC gene RNA (Table). The topology of the GPC gene tree (Figure 3) was essentially identical to the topology of the N protein gene tree (Figure 2) with respect to relationships between the viruses from Mexico in this study, CARV, HUIV, MTNV, and the other hantaviruses found in North America. M0040008, CARV, M0040059, H0460041, HUIV, and ELMCV were monophyletic in the Bayesian analyses of the GPC gene sequence data (Figure 3) and N protein gene sequence data (Figure 2).

Nonidentities among the amino acid sequences of the 359-aa fragment of the G_c glycoproteins of the 11

Table. Hantaviruses found in 24 of 35 antibody-positive rodents captured in Mexico in 1998–2008, by state*†

Virus	Strain	Museum no.	Rodent				GenBank accession no.	
			Species	State	Date captured	Antibody titer	S segment	M segment
ELMCV	M0040008	TK93357	<i>Reithrodontomys sumichrasti</i>	GR (12)	2000 Jul 20	$\geq 5,120$	JN097454	JN097478
ELMCV	M0040010	TK93368	<i>R. sumichrasti</i>	GR (12)	2000 Jul 20	$\geq 5,120$	JN097455	ND
ELMCV	M0040012	TK93370	<i>R. sumichrasti</i>	GR (12)	2000 Jul 20	$\geq 5,120$	JN097456	ND
LSCV	M0040047	TK148818	<i>Peromyscus spicilegus</i>	JA (8)	2008 Jul 22	$\geq 5,120$	JN097457	ND
LSCV	M0040049	TK148820	<i>P. spicilegus</i>	JA (8)	2008 Jul 22	$\geq 5,120$	JN097458	JN097479
LSCV	B0030007	TK78282	<i>P. melanotis</i>	EM (10)	1998 Jun 24	$\geq 5,120$	JN097459	ND
LSCV	B0030008	TK78283	<i>P. hylocetes</i>	EM (10)	1998 Jun 24	$\geq 5,120$	JN097460	JN097480
LSCV	B0030015	TK78290	<i>P. hylocetes</i>	EM (10)	1998 Jun 24	$\geq 5,120$	JN097461	ND
SNV	H0030065	TK137297	<i>P. maniculatus</i>	NL (4)	2005 Aug 6	$\geq 5,120$	JN097462	JN097481
SNV	H0030067	TK137312	<i>P. eremicus</i>	NL (4)	2005 Aug 6	$\geq 5,120$	JN097463	ND
LSCV	H0460002	TK150003	<i>P. levipes</i>	NL (1)	2006 Jul 12	$\geq 5,120$	JN097464	ND
LSCV	H0460005	TK150006	<i>P. levipes</i>	NL (1)	2006 Jul 12	$\geq 5,120$	JN097465	ND
LSCV	H0460008	TK150017	<i>P. levipes</i>	NL (1)	2006 Jul 12	$\geq 5,120$	JN097466	JN097482
SNV	H0020015	TK133396	<i>P. maniculatus</i>	SL (3)	2005 Aug 4	$\geq 5,120$	JN097467	JN097483
LSCV	H0460017	TK150043	<i>P. ochraventer</i>	SL (7)	2006 Jul 13	$\geq 5,120$	JN097468	ND
LSCV	H0460023	TK150086	<i>P. ochraventer</i>	SL (7)	2006 Jul 13	$\geq 5,120$	JN097469	JN097484
SNV	H0030073	TK137359	<i>P. leucopus</i>	TM (2)	2005 Aug 8	$\geq 5,120$	JN097470	JN097485
ELMCV	M0040059	TK150090	<i>R. megalotis</i>	VZ (11)	2006 Jul 15	320	JN097471	JN097486
ELMCV	H0460026	TK150101	<i>R. megalotis</i>	VZ (11)	2006 Jul 15	$\geq 5,120$	JN097473	ND
ELMCV	H0460029	TK150117	<i>P. melanotis</i>	VZ (11)	2006 Jul 16	1,280	JN097472	ND
ELMCV	H0460032	TK150161	<i>R. megalotis</i>	VZ (11)	2006 Jul 15	320	JN097474	ND
ELMCV	H0460035	TK150163	<i>R. megalotis</i>	VZ (11)	2006 Jul 16	320	JN097475	ND
SNV	H0460038	TK150166	<i>P. maniculatus</i>	VZ (11)	2006 Jul 16	$\geq 5,120$	JN097476	JN097487
ELMCV	H0460041	TK150182	<i>R. megalotis</i>	VZ (11)	2006 Jul 16	1,280	JN097477	JN097488

*Numbers in parentheses indicate locations on the map in Figure 1. S, small; M, medium; ELMCV, El Moro Canyon virus; GR, Guerrero; ND, sequences not determined; LSCV, Limestone Canyon virus; JA, Jalisco; EM, México (state); SNV, Sin Nombre virus; NL, Nuevo León; SL, San Luis Potosí; TM, Tamaulipas; VZ, Veracruz.

†Antibody-positive, hantavirus RNA–negative rodents (species, location, antibody titer): TK78287 (*P. melanotis*, EM, 1,280); TK93383 (*P. megalotis*, GR, $\geq 5,120$); TK148439 (*Peromyscus* sp., Nayarit, 1,280); TK148793 (*Baiomys taylori*, JA, 320); TK148836 (*R. microdon*, Michoacán, 1,280); TK148842 (*R. sumichrasti*, Michoacán, 320); TK148845 (*R. sumichrasti*, Michoacán, 1,280); TK148984 (*P. leucopus*, Tamaulipas, $\geq 5,120$); TK150045 (*P. levipes*, SL, $\geq 5,120$); TK150515 (*B. musculus*, Chiapas, 320); and TK150518 (*Oryzomys couesi*, Chiapas, 1,280).

hantaviruses from Mexico in this study, CARV, HUIV, and MTNV ranged from 0% to 18.4% (online Appendix Table 3, wwwnc.cdc.gov/EID/article/18/4/11-1028-TA3.htm). Nonidentities between the sequences of the 359-aa fragment of the G_c glycoproteins of these 14 hantaviruses and the sequences of the homologous fragment of the G_c glycoproteins of the other hantaviruses found in North America ranged from 1.1% (H0030073 and SNV strain Blue River-Oklahoma) to 18.9% (M0040049 and BCCV strain SPB 9408076).

Discussion

The Eighth Report of the International Committee on Taxonomy of Viruses sets forth the criteria for species demarcation in the genus *Hantavirus* (1). One of these criteria is that strains of different species must exhibit at least a 7% difference in amino acid sequence identity in comparisons of complete N protein sequences and in comparisons of complete GPC sequences.

ELMCV was first described in 1994 (10); LSCV was described in 2001 (11); and CARV, HUIV, and MTNV were described in 2011 (8). In a previous study (8), the amino acid sequence of the N protein of MTNV was 5.8% different from the amino acid sequence of the N protein of LSCV strain 68273, and the amino acid sequence of the N protein of CARV was 3.7% different from the amino acid sequence of the N protein of ELMCV strain RM-97 and 8.4% different from the amino acid sequence of the N protein of RIOSV strain RMx·Costa·1. The amino acid sequence of the N protein of HUIV was 1.4% different from the amino acid sequence of the N protein of ELMCV strain RM-97 and 8.4% different from the amino acid sequence of the N protein of RIOSV strain RMx·Costa·1. Accordingly, MTNV should be considered a strain of LSCV, and CARV and HUIV could be considered strains of ELMCV or RIOSV. Alternatively, CARV and HUIV could be considered members of a species complex that includes ELMCV, RIOSV, and other hantaviruses that are naturally associated with harvest mice (*Reithrodontomys* spp.). There is presumptive evidence for RIOSV or hantavirus(es) that are genetically closely related to RIOSV in Sumichrast's harvest mice, a Mexican harvest mouse (*R. mexicanus*), and a Chiriqui harvest mouse (*R. creper*) captured in Panama (29).

Collectively, the results of the Bayesian analyses of N protein gene sequence data (Figure 2), Bayesian analyses of the GPC gene sequence data (Figure 3), and pairwise comparisons of G_c sequences (online Appendix Table 3) indicate that H0020015, H0030065, H0030073, and H0460038 are strains of SNV. The results of these analyses also indicate that M0040008, M0040059, and H0460041 are strains of ELMCV or RIOSV and that B0030008, H0460008, H0460023, and M0040049 are strains of LSCV.

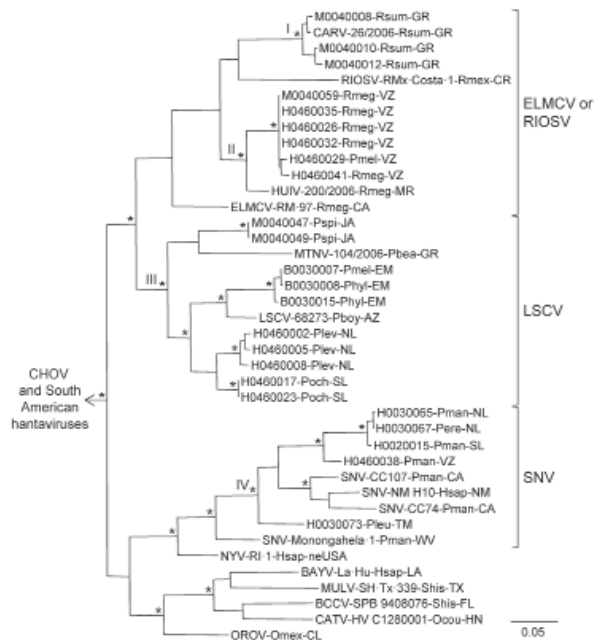


Figure 2. Results of the Bayesian analyses of the nucleotide sequences of a fragment of the nucleocapsid protein genes of the 24 hantaviruses found in Mexico in this study and 22 other hantaviruses naturally associated with members of the Neotominae or Sigmodontinae. An asterisk at a node indicates that the probability values in support of the clade were ≥ 0.95 . Scale bar indicates substitutions per site. The Roman numerals indicate the phylogenetic groups represented by the hantaviruses from Mexico in this study. The branch labels include (in the following order) virus, strain, host species, and state or country. BAYV, Bayou virus, strain LA-Hu (GenBank accession no. L36929); BCCV, Black Creek Canal virus, SPB 9408076 (L39949); CARV, Carrizal virus, 26/2006 (AB620103); CATV, Catacamas virus, HV C1280001 (DQ256126); CHOVI, Choclo virus, 588 (DQ285046); ELMCV, El Moro Canyon virus, RM-97 (U11427); HUIV, Huitzilac virus, 200/2006 (AB620106); LSCV, Limestone Canyon virus, 68273 (AF307322); MTNV, Montano virus, 104/2006 (AB620100); MULV, Muleshoe virus, SH-Tx-339 (U54575); NYV, New York virus, RI-1 (U09488); OROV, Playa de Oro virus (EF534079); RIOSV, Rio Segundo virus, RMx·Costa·1 (U18100); and SNV, Sin Nombre virus strains Convict Creek 74 (CC74), Convict Creek 107 (CC107), Monongahela-1, and NM H10 (L33816, L33683, U32591, and L25784, respectively). The viruses found in South America were Andes virus, strain Chile-9717869 (GenBank accession no. AF291702); Caño Delgadito virus, VHV-574 (DQ285566); Laguna Negra virus, 510B (AF005727); Maporal virus, HV 97021050 (AY267347); and Rio Mamoré virus, HTN-007 (FJ532244). Locations: AZ, Arizona; CA, California; CL, Colima; CR, Costa Rica; EM, México (state); FL, Florida; GR, Guerrero; HN, Honduras; JA, Jalisco; LA, Louisiana; MR, Morelos; NL, Nuevo León; NM, New Mexico; neUSA, northeastern United States (New York or Rhode Island); SL, San Luis Potosí; TM, Tamaulipas; TX, Texas; VZ, Veracruz; WV, West Virginia. Species: Hsap, *Homo sapiens*; Pbea, *Peromyscus beatae*; Pboy, *P. boylii*; Pere, *P. eremicus*; Phyl, *P. hylocetes*; Plev, *P. leucopus*; Plev, *P. levipes*; Pman, *P. maniculatus*; Pmel, *P. melanotis*; Poch, *P. ochraventer*; Pspi, *P. spicilegus*; Ocou, *Oryzomys couesi*; Omex, *O. mexicanus*; Rmeg, *Reithrodontomys megalotis*; Rmex, *R. mexicanus*; Rsum, *R. sumichrasti*; Shis, *Sigmodon hispidus*. The designated outgroup was Andes virus strain Chile-9717869.

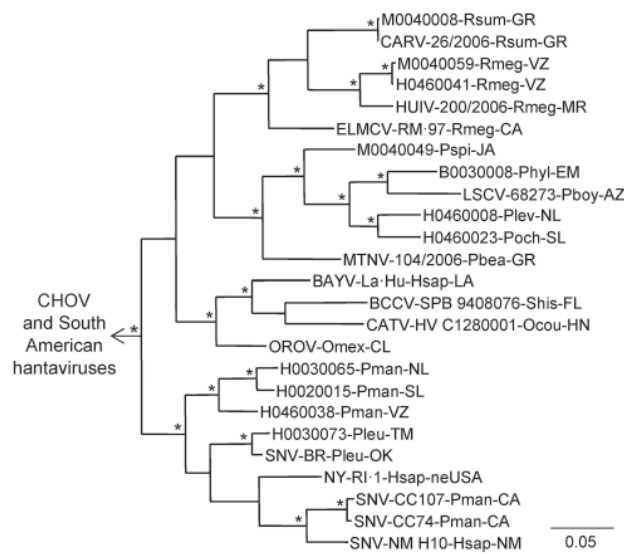


Figure 3. Results of the Bayesian analyses of the nucleotide sequences of a 1,078-nt fragment of the glycoprotein precursor genes of 11 of the 24 hantaviruses found in Mexico in this study and 20 other hantaviruses naturally associated with members of the Neotominae or Sigmodontinae. An asterisk at a node indicates that the probability values in support of the clade were ≥ 0.95 . Scale bar indicates substitutions per site. The branch labels include (in the following order) virus, strain, host species, and state or country. BAYV, GenBank accession no. L36930; BCCV, L39950; CARV, AB620104; CATV, DQ177347; CHO, DQ285047; ELMCV, U26828; HUIV, AB620107; LSCV, AF307323; MTNV, AB620101; NYV, U36801; OROV, EF534080; SNV—strains BR (AF030552), CC74 (L33684), CC107 (L33474), and NM H10 (L25783). The viruses from South America were Andes virus, GenBank accession no. AF291703; Caño Delgado virus, DQ284451; Laguna Negra virus, AF005728; Maporal virus, AY363179; and Rio Mamoré virus, FJ608550. The designated outgroup was Andes virus strain Chile-9717869.

Accordingly, the N protein gene RNA-positive rodents in this study (Table) were infected with SNV, ELMCV, RIOSV, or LSCV.

Specific knowledge of the natural host relationships of LSCV previously was limited to LSCV RNA in 6 brush mice (*P. boylii*) captured in northern Arizona (11). The results of this study indicate that the transvolcanic mouse (*P. hylocetes*) and the black-eared mouse (*P. melanotis*) in the state of México, the nimble-footed mouse (*P. levipes*) in Nuevo León, the El Carrizo deer mouse (*P. ochraverter*) in San Luis Potosí, and the gleaning mouse (*P. spicilegus*) in Jalisco are natural but not necessarily principal hosts of LSCV.

HPS was first recognized as a distinct clinical entity in the southwestern United States in 1993 (30). Through 2009, a total of 510 HPS cases were reported to the National Notifiable Diseases Surveillance System or registered

by the Centers for Disease Control and Prevention (31). Most of these cases occurred in the southwestern United States, 92 (33.7%) of 273 HPS cases that occurred in the southwestern United States before 2010 were fatal, and all of the cases from the southwestern United States through 2009 were attributed to SNV.

The results of this study indicate that SNV is widely distributed in northeastern Mexico. The geographic distribution of deer mice (*P. maniculatus*) in Mexico includes 23 states (28), and ≈ 20 million persons lived in rural areas in this 23-state region in 2010 (32). Yet, to our knowledge, no cases of HPS have been reported from northeastern Mexico or elsewhere in Mexico.

We hypothesize that HPS caused by SNV in Mexico has been confused with other rapidly progressive, life-threatening respiratory diseases (e.g., plague, tularemia, pneumococcal pneumonia, influenza). Alternatively, SNV in Mexico is substantially less virulent than SNV in the western United States, or human contact with SNV-infected rodents in Mexico is less frequent or less intimate than human contact with SNV-infected rodents in the western United States.

Laboratory confirmation of the diagnoses of most HPS cases in the United States before 2010 was based on the results of serologic assays in which ELMCV and LSCV can be highly cross-reactive with SNV (31). Thus, in all likelihood, some of the HPS cases from the western United States were actually caused by ELMCV or LSCV, and these viruses as well as SNV are etiologic agents of HPS in Mexico.

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Ms Milazzo is a senior research associate at the University of Texas Medical Branch, Galveston. Her scientific interests include the epidemiology and ecology of New World rodent-borne RNA viruses.

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Address for correspondence: Charles F. Fulhorst, The University of Texas Medical Branch, 301 University Blvd, Galveston, TX 77555-0609, USA; email: cfulhors@utmb.edu