Antibodies to Tacaribe Serocomplex Viruses (Family *Arenaviridae*, Genus *Arenavirus*) in Cricetid Rodents from New Mexico, Texas, and Mexico

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Abstract

Blood samples from 4893 cricetid rodents were tested for antibody (immunoglobulin G) to Whitewater Arroyo virus and Amaparí virus to extend our knowledge of the natural host range and geographical distribution of Tacaribe serocomplex viruses in North America. Antibodies to arenaviruses were found in northern pygmy mice (*Baiomys taylori*), woodrats (*Neotoma* spp.), northern grasshopper mice (*Onychomys leucogaster*), oryzomys (*Oryzomys* spp.), deermice (*Megadontomys nelsoni* and *Peromyscus* spp.), harvest mice (*Reithrodontomys* spp.), and cotton rats (*Sigmodon* spp.) captured in New Mexico, Texas, or Mexico. Comparison of endpoint antibody titers to Whitewater Arroyo virus and Amaparí virus in individual blood samples indicated that the Tacaribe complex viruses enzootic in Texas and Mexico are antigenically diverse.

Key Words: *Arenaviridae*—*Arenavirus*—Cricetidae—Hemorrhagic fever—Mexico—Rodent—Tacaribe serocomplex—Whitewater Arroyo virus.

Introduction

THE TACARIBE SEROCOMPLEX (virus family *Arenaviridae*, genus *Arenavirus*) comprises 7 North American and 15 South American viruses. The North American viruses are Bear Canyon virus (BCNV), Big Brushy Tank virus (BBTV), Catarina virus (CTNV), Skinner Tank virus (SKTV), Tamiami virus (TAMV), Tonto Creek virus (TTCV), and Whitewater Arroyo virus (WWAV) (Table 1). The South American viruses include Junín virus, four other agents of hemorrhagic fever in humans (i.e., Guanarito, Machupo, Sabiá, and Chapare viruses), and Amaparí virus (AMAV).

Specific members of the rodent family Cricetidae (Musser and Carleton 2005) are the principal hosts of the Tacaribe

serocomplex viruses for which natural host relationships have been well characterized (Childs and Peters 1993). For example, the hispid cotton rat (*Sigmodon hispidus*) in southern Florida is the principal host of TAMV (Calisher et al. 1970, Jennings et al. 1970), and the southern plains woodrat (*Neotoma micropus*) in Dimmitt and La Salle counties in southern Texas is the principal host of CTNV (Fulhorst et al. 2002b, Cajimat et al. 2007a). Other natural hosts of Tacaribe serocomplex viruses in North America include the white-throated woodrat (*N. albigula*) in Arizona, Colorado, New Mexico, and Oklahoma, bushy-tailed woodrat (*N. cinerea*) in Utah, Mexican woodrat (*N. mexicana*) in Arizona, Colorado, New Mexico, and Utah, southern plains woodrat in Colorado, Stephen's woodrat (*N. stephensi*) in Arizona and New Mexico, Bryant's

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TABLE 1. NATURAL HOSTS AND GEOGRAPHICAL DISTRIBUTION OF THE SEVEN NORTH AMERICAN TACARIBE SEROCOMPLEX VIRUSES

Virus ^a	Natural host(s)	State	Reference(s)
Bear Canyon	Large-eared woodrat (<i>Neotoma macrotis</i>) and California mouse (<i>Peromyscus californicus</i>)	CA	Fulhorst et al. (2002a) and Cajimat et al. (2007b)
Big Brushy Tank	White-throated woodrat (<i>Neotoma albigula</i>)	AZ	Milazzo et al. (2008)
Catarina	Southern plains woodrat (<i>Neotoma micropus</i>)	TX	Fulhorst et al. (2002b) and Cajimat et al. (2007a)
Skinner Tank	Mexican woodrat (<i>Neotoma mexicana</i>)	AZ	Cajimat et al. (2008)
Tamiami virus	Hispid cotton rat (<i>Sigmodon hispidus</i>)	FL	Calisher et al. (1970) and Jennings et al. (1970)
Tonto Creek	White-throated woodrat (<i>N. albigula</i>)	AZ	Milazzo et al. (2008)
Whitewater Arroyo	White-throated woodrat (<i>N. albigula</i>)	NM	Fulhorst et al. (1996)

^aArenaviruses antigenically and phylogenetically related to Whitewater Arroyo virus have been isolated from Mexican woodrats (*N. mexicana*) captured in New Mexico, a Mexican woodrat and bushy-tailed woodrat (*N. cinerea*) captured in Utah, and woodrats (*Neotoma* spp.) captured in Oklahoma (Fulhorst et al. 2001a).

AZ, Arizona; CA, California; FL, Florida; NM, New Mexico; TX, Texas.

woodrat (*N. bryanti*, formerly *N. lepida*; Patton et al. 2008), dusky-footed woodrat (*N. fuscipes*), large-eared woodrat (*N. macrotis*), brush mouse (*Peromyscus boylii*), California mouse (*P. californicus*), cactus deer mouse (*P. eremicus*), North American deer mouse (*P. maniculatus*), and western harvest mouse (*Reithrodontomys megalotis*) in California, and marsh oryzomys (*Oryzomys palustris*) in Florida (Fulhorst et al. 1996, 2001a, 2002a, Kosoy et al. 1996, Bennett et al. 2000, Calisher et al. 2001, Abbott et al. 2004, Cajimat et al. 2007b, 2008, Milazzo et al. 2008). The aim of this study was to extend our knowledge of the natural host range and geographical distribution of Tacaribe serocomplex viruses associated with cricetid rodents in North America.

Materials and Methods

Rodents

Blood samples from 4893 rodents, representing at least 65 species in the family Cricetidae, were tested for antibodies (immunoglobulin G [IgG]) to WWAV and AMAV (Table 2). The rodents were captured from January 1995 through June 2008 for studies on the biodiversity of mammals in New Mexico, Texas, and Mexico. This survey included 163 rodents from 4 localities in Otero County, New Mexico, 2677 rodents from 44 localities in 27 counties in Texas, and 2053 rodents from 97 localities in 79 municipalities in 20 states in Mexico (Fig. 1; Appendix 1).

The rodents were captured in livetraps set on transects and baited with sunflower seeds or a mixture of cracked corn, wheat, milo, and rolled oats. Blood samples were collected from a retro-orbital venous plexus or body cavity at necropsy and then dried on Nobuto Blood Filter Strips (Toyo Roshi Kaisha, Ltd., Tokyo, Japan). Voucher specimens (skins, skulls, and solid tissues) from the 163 rodents captured in New Mexico, 2643 of the 2677 rodents captured in Texas, and more than 1850 of the 2053 rodents captured in Mexico were deposited into the Museum of Texas Tech University, M. L. Bean Life Science Museum at Brigham Young University, Angelo State Natural History Collection, or Colección de Mamíferos del Centro de Educación Ambiental e Investigación Sierra de Huautla, Universidad Autónoma del Estado de Morelos.

Antibody assay

The blood samples were tested for antibodies (IgG) to WWAV and AMAV, using an enzyme-linked immunosorbent assay (ELISA). We note that WWAV and AMAV represent the two major antigenic groups in the Tacaribe serocomplex in ELISA (Fulhorst et al. 1996); IgG to BCNV, BBTv, SKTV, TTCV, and TAMV in naturally infected rodents can be highly reactive against WWAV in ELISA (M.L. Milazzo, unpublished data); and IgG to Junín virus and the other arenaviruses associated with hemorrhagic fever in South America can be highly reactive against AMAV in ELISA (Fulhorst et al. 1996). The WWAV antigen was a lysate of Vero E6 cells infected with WWAV strain AV 9310135, the AMAV antigen was a lysate of Vero E6 cells infected with AMAV strain BeAn 70563, and the control (comparison) antigens were lysates of uninfected Vero E6 cells. The working concentration of the WWAV antigen was determined by box-titration against sera from white-throated woodrats experimentally infected with strain AV 9310135. The working concentration of the AMAV antigen was determined by box-titration against sera from captive-bred hispid cotton rats experimentally infected with strain BeAn 70563. Serial fourfold dilutions (from 1:80 through 1:5120) of each blood sample were tested against the WWAV antigen, AMAV antigen, and control antigens. Antibody bound to antigen was detected using a mixture of goat anti-Rat IgG peroxidase conjugate and goat anti-*Peromyscus leucopus* IgG peroxidase conjugate (Kirkegaard and Perry Laboratories, Gaithersburg, MD) in conjunction with the ABTS (2,2'-azino-di[3-ethyl-benzthiazoline sulfonate (6)]) Microwell Peroxidase Substrate System (Kirkegaard and Perry Laboratories). Optical densities (ODs) at 410 nm (reference = 490 nm) were measured with a Dynatech MRX II microplate reader (Dynatech Industries, Inc., McLean, VA). The adjusted OD (AOD) of a blood sample-antigen reaction was the OD of the well coated with the test antigen less the OD of the well coated with the corresponding control antigen.

Data analysis

A blood sample was considered antibody-positive if the AOD at 1:80 was >0.200, the AOD at 1:320 was >0.200, and the sum of the AOD for the series of fourfold dilutions (from

TABLE 2. PREVALENCE OF ANTIBODIES TO ARENAVIRUSES IN 4893 CRICETID RODENTS CAPTURED IN NEW MEXICO, TEXAS, OR MEXICO, 1995–2008

Species	Antibody prevalence ^a	Map location(s) ^b	Species	Antibody prevalence ^a	Map location(s) ^b
<i>Baiomys musculus</i>	0/57		<i>Peromyscus gratus</i>	0/10	
<i>Baiomys taylori</i>	8/167	9, 12	<i>Peromyscus hooperi</i>	0/6	
<i>Habromys ixtlani</i>	0/5		<i>Peromyscus hylocetes</i>	0/8	
<i>Habromys schmidlyi</i>	0/2		<i>Peromyscus leucopus</i>	11/432	1, 2, 5, 10, 13, 14
<i>Habromys</i> sp.	0/1		<i>Peromyscus levipes</i>	0/64	
<i>Hodomys alleni</i>	0/1		<i>Peromyscus maniculatus</i>	9/145	4, 6, 18, 22
<i>Megadontomys cryophilus</i>	0/4		<i>Peromyscus megalops</i>	1/61	24
<i>Megadontomys nelsoni</i>	1/12	23	<i>Peromyscus melanocarpus</i>	0/15	
<i>Megadontomys thomasi</i>	0/16		<i>Peromyscus melanophrys</i>	2/28	17
<i>Neotoma albigula</i>	0/63		<i>Peromyscus melanotis</i>	1/135	22
<i>Neotoma floridana</i>	0/1		<i>Peromyscus merriami</i>	0/6	
<i>Neotoma leucodon</i>	12/42	15–17	<i>Peromyscus mexicanus</i>	4/56	26, 27
<i>Neotoma mexicana</i>	1/26	17	<i>Peromyscus nasutus</i>	0/16	
<i>Neotoma micropus</i>	19/154	1, 3, 5, 6, 14	<i>Peromyscus ochraeater</i>	0/11	
<i>Neotoma</i> sp.	0/1		<i>Peromyscus pectoralis</i>	0/442	
<i>Neotomodon alstoni</i>	0/7		<i>Peromyscus schmidlyi</i>	0/1	
<i>Oligoryzomys fulvescens</i>	0/27		<i>Peromyscus spicilegus</i>	0/31	
<i>Onychomys arenicola</i>	0/4		<i>Peromyscus truei</i>	0/2	
<i>Onychomys leucogaster</i>	3/61	1, 12	<i>Peromyscus zarhynchus</i>	0/2	
<i>Onychomys torridus</i>	0/3		<i>Peromyscus</i> spp.	7/293	19–21, 24
<i>Oryzomys alfaroi</i>	0/6		<i>Reithrodontomys bakeri</i>	0/3	
<i>Oryzomys chapmani</i>	0/25		<i>Reithrodontomys fulvescens</i>	0/76	
<i>Oryzomys couesi</i>	1/43	25	<i>Reithrodontomys gracilis</i>	0/2	
<i>Oryzomys melanotis</i>	0/4		<i>Reithrodontomys megalotis</i>	0/94	
<i>Oryzomys palustris</i>	7/185	11	<i>Reithrodontomys mexicanus</i>	0/48	
<i>Oryzomys rostratus</i>	0/1		<i>Reithrodontomys microndon</i>	0/4	
<i>Oryzomys</i> spp.	0/64		<i>Reithrodontomys montanus</i>	0/11	
<i>Osgoodomys banderanus</i>	0/15		<i>Reithrodontomys sumichrasti</i>	2/82	24
<i>Peromyscus attwateri</i>	3/443	5, 8	<i>Reithrodontomys</i> spp.	1/56	4
<i>Peromyscus aztecus</i>	0/25		<i>Sigmodon alleni</i>	0/1	
<i>Peromyscus beatae</i>	0/34		<i>Sigmodon hispidus</i>	2/627	5, 8
<i>Peromyscus boylii</i>	3/314	7	<i>Sigmodon mascotensis</i>	0/52	
<i>Peromyscus difficilis</i>	0/10		<i>Sigmodon ochrognathus</i>	0/13	
<i>Peromyscus eremicus</i>	0/75		<i>Sigmodon toltecus</i>	2/71	28
<i>Peromyscus fuscus</i>	0/53		<i>Sigmodon</i> spp.	0/32	
<i>Peromyscus gossypinus</i>	0/5		<i>Tylomys</i> sp.	0/1	
			Total	100/4893	

^aNumber positive/number tested for antibody (immunoglobulin G) to arenaviruses.

^bThe numbers indicate the locations of the antibody-positive counties and municipalities in the map in Figure 1.

1:80 through 1:5120) was >0.750. These criteria for positivity were based on the results of a study on the pathogenesis of WWAV strain AV 9310135 infections in experimentally infected white-throated woodrats (Fulhorst et al. 2001b). The endpoint titer in a positive sample in this study was the reciprocal of the highest dilution for which the AOD was >0.200. Titers <320 were 160 in comparisons of titers to WWAV and AMAV in individual blood samples.

Results

Antibody (IgG) to WWAV or AMAV was found in 100 (2.0%) of 4893 cricetid rodents: 8 (4.8%) of 167 northern pygmy mice (*Baiomys taylori*), 1 (8.3%) of 12 Nelson's big-toothed deer mice (*Megadontomys nelsoni*), 12 (28.6%) of 42 white-toothed woodrats (*N. leucodon*), 1 (3.8%) of 26 Mexican woodrats. Woodrats (*N. leucodon*), 1 (3.8%) of 26 Mexican woodrats (*N. mexicana*), 19 (12.3%) of 154 southern plains

woodrats (*N. micropus*), 3 (4.9%) of 61 northern grasshopper mice (*Onychomys leucogaster*), 1 (2.3%) of 43 Coues' oryzomys (*Oryzomys couesi*), 7 (3.8%) of 185 marsh oryzomys (*O. palustris*), 3 (0.6%) of 443 Texas deer mice (*Peromyscus attwateri*), 3 (1.0%) of 314 brush deer mice (*P. boylii*), 11 (2.5%) of 432 white-footed mice (*P. leucopus*), 9 (6.2%) of 145 North American deer mice (*P. maniculatus*), 1 (1.6%) of 61 broad-faced deer mice (*P. megalops*), 2 (7.1%) of 28 plateau deer mice (*P. melanophrys*), 1 (0.7%) of 135 black-eared deer mice (*P. melanotis*), 4 (7.1%) of 56 Mexican deer mice (*P. mexicanus*), 7 (2.4%) of 293 other deer mice (*Peromyscus* spp.), 2 (2.4%) of 82 Sumichrast's harvest mice (*Reithrodontomys sumichrasti*), 1 (1.8%) of 56 other harvest mice (*Reithrodontomys* spp.), 2 (0.3%) of 627 hispid cotton rats (*Sigmodon hispidus*), and 2 (2.8%) of 71 Toltec cotton rats (*S. toltecus*) (Table 2).

The geographical distribution of the antibody-positive rodents included Otero County, New Mexico, 10 counties in Texas, and 17 municipalities in nine states in Mexico (Fig. 1).

FIG. 1. Map showing the locations of the counties and municipalities included in this study. The open circles indicate the antibody-positive counties and municipalities. (1) Otero County, New Mexico (NM). In Texas (TX): (2) Hall County, (3) Motley County, (4) Lubbock County, (5) Dickens County, (6) Ward County, (7) Jeff Davis County, (8) Kimble County, (9) Gillespie County, (10) Matagorda County, and (11) Galveston County. In Mexico: (12) Municipality of Janos, Chihuahua; (13) Municipality of Apodaca, Nuevo León; (14) Municipality of San Fernando, Tamaulipas; (15) Municipality of Catorce, San Luis Potosí; (16) Municipality of Cedral, San Luis Potosí; (17) Municipality of Doctor Arroyo, Nuevo León; (18) Municipality of General Zaragoza, Nuevo León; (19) Municipality of Pátzcuaro, Michoacán; (20) Municipality of Santa Clara, Michoacán; (21) Municipality of Morelia, Michoacán; (22) Municipality of Perote, Veracruz; (23) Municipality of Xico, Veracruz; (24) Municipality of Malinaltepec, Guerrero; (25) Municipality of Putla de Guerrero, Oaxaca; (26) Municipality of Ocozocoautla de Espinosa, Chiapas; (27) Municipality of Berriozábal, Chiapas; and (28) Municipality of Emiliano Zapata, Tabasco. The small filled circles indicate the counties and municipalities that were antibody-negative in this study. The filled squares indicate counties in which arenavirus-positive woodrats were captured in previous studies: (A) McKinley County, NM; (B) Socorro County, NM; (C) Cimarron County, Oklahoma (OK); (D) Dimmitt and La Salle Counties, TX. Whitewater Arroyo virus (WWAV) was isolated from white-throated woodrats (*Neotoma albigula*) captured in McKinley County (Fulhorst et al. 1996), arenaviruses antigenically and phylogenetically closely related to WWAV were isolated from woodrats (*Neotoma* spp.) captured in Socorro County and Cimarron counties (Fulhorst et al. 2001a), and Catarina virus was isolated from southern plains woodrats (*Neotoma micropus*) captured in Dimmitt and La Salle counties (Cajimat et al. 2007a).

New Mexico

The antibody-positive rodents from Otero County were 6 (20.7%) of 29 southern plains woodrats (*N. micropus*), 1 (9.1%) of 11 northern grasshopper mice (*O. leucogaster*), and 2 (10.5%) of 19 white-footed mice (*P. leucopus*).

Texas

Dickens County: 6 (23.1%) of 26 southern plains woodrats (*N. micropus*), 1 (11.1%) of 9 Texas deer mice

(*P. attwateri*), 2 (4.7%) of 43 white-footed mice (*P. leucopus*), and 1 (1.8%) of 55 hispid cotton rats (*S. hispidus*).

Galveston County: 7 (4.3%) of 163 marsh oryzomys (*O. palustris*).

Gillespie County: 3 (21.4%) of 14 northern pygmy mice (*B. taylori*).

Hall County: 1 (4.3%) of 23 white-footed mice (*P. leucopus*).

Jeff Davis County: 3 (1.1%) of 269 brush deer mice (*P. boylii*).

Kimble County: 2 (1.8%) of 114 Texas deermice (*P. attwateri*) and 1 (14.3%) of 7 hispid cotton rats (*S. hispidus*).
 Lubbock County: 2 (3.4%) of 59 North American deermice (*P. maniculatus*) and 1 (3.2%) of 31 harvest mice (*Reithrodontomys* spp.).
 Matagorda County: 1 (9.1%) of 11 white-footed deermice (*P. leucopus*).
 Motley County: 4 (36.4%) of 11 southern plains woodrats (*N. micropus*).
 Ward County: 2 (40.0%) of 5 southern plains woodrats (*N. micropus*) and 3 (27.3%) of 11 North American deermice (*P. maniculatus*).

Mexico

Chiapas, Municipality of Berriozábal: 1 (5.6%) of 18 Mexican deermice (*P. mexicanus*).
 Chiapas, Municipality of Ocozacoautla de Espinosa: 3 (23.1%) of 13 Mexican deermice (*P. mexicanus*).
 Chihuahua, Municipality of Janos: 5 (19.2%) of 26 northern pygmy mice (*B. taylori*) and 2 (9.1%) of 22 northern grasshopper mice (*O. leucogaster*).
 Guerrero, Municipality of Malinaltepec: 1 (3.1%) of 32 broad-faced deermice (*P. megalops*), 1 (3.6%) of 28 other deermice (*Peromyscus* spp.), and 2 (11.1%) of 18 Sumichrast's harvest mice (*R. sumichrasti*).
 Michoacán, Municipality of Morelia: 1 (12.5%) of 8 deermice (*Peromyscus* spp.).
 Michoacán, Municipality of Pátzcuaro: 4 (26.7%) of 15 deermice (*Peromyscus* spp.).

Michoacán, Municipality of Santa Clara: 1 (50.0%) of 2 deermice (*Peromyscus* spp.).
 Nuevo León, Municipality of Apodaca: 2 (6.7%) of 30 white-footed mice (*P. leucopus*).
 Nuevo León, Municipality of Doctor Arroyo: 7 (41.2%) of 17 white-toothed woodrats (*N. leucodon*), a Mexican woodrat (*N. mexicana*), and 2 (22.2%) of 9 plateau deermice (*P. melanophrys*).
 Nuevo León, Municipality of General Zaragoza: 3 (25.0%) of 12 North American deermice (*P. maniculatus*).
 Oaxaca, Municipality of Putla de Guerrero: 1 (25.0%) of 4 Coues' oryzomys (*O. couesi*).
 San Luis Potosí, Municipality of Catorce: 2 (20.0%) of 10 white-toothed woodrats (*N. leucodon*).
 San Luis Potosí, Municipality of Cedral: 3 (100%) of 3 white-toothed woodrats (*N. leucodon*).
 Tabasco, Municipality of Emiliano Zapata: 2 (5.3%) of 38 Toltec cotton rats (*S. toltecus*).
 Tamaulipas, Municipality of San Fernando: 1 (8.3%) of 12 southern plains woodrats (*N. micropus*) and 3 (6.4%) of 47 white-footed mice (*P. leucopus*).
 Veracruz, Municipality of Xico: 1 (20.0%) of 5 Nelson's big-toothed deermice (*M. nelsoni*).
 Veracruz, Municipality of Perote: 1 (20.0%) of 5 North American deermice (*P. maniculatus*) and 1 (1.7%) of 59 black-eared deermice (*P. melanotis*).

Eighty-three (83.0%) of the 100 antibody-positive rodents were positive to WWAV but not AMAV, 10 (10.0%) of the antibody-positive rodents were positive to AMAV but not WWAV, and 7 (7.0%) of the antibody-positive animals were

TABLE 3. FREQUENCY OF ANTIBODY TITERS TO WHITEWATER ARROYO VIRUS AND AMAPARÍ VIRUS IN THE ANTIBODY-POSITIVE RODENTS, BY SPECIES^a

	Number of antibody-positive rodents	Antibody titer to Whitewater Arroyo virus				Antibody titer to Amaparí virus			
		<320	320	1280	≥5120	<320	320	1280	≥5120
<i>B. taylori</i>	8	8	—	—	—	—	4	4	—
<i>M. nelsoni</i>	1	—	1	—	—	1	—	—	—
<i>N. mexicana</i>	1	—	—	—	1	—	1	—	—
<i>N. micropus</i>	19	—	2	3	14	17	2	—	—
<i>O. leucogaster</i>	3	—	2	1	—	3	—	—	—
<i>O. couesi</i>	1	—	1	—	—	1	—	—	—
<i>O. palustris</i>	7	—	4	3	—	7	—	—	—
<i>P. attwateri</i>	3	—	2	1	—	3	—	—	—
<i>P. boylii</i>	3	—	3	—	—	3	—	—	—
<i>P. leucopus</i>	11	—	6	5	—	11	—	—	—
<i>P. maniculatus</i>	9	—	5	3	1	9	—	—	—
<i>P. megalops</i>	1	—	—	1	—	1	—	—	—
<i>P. melanophrys</i>	2	—	2	—	—	2	—	—	—
<i>P. melanotis</i>	1	—	1	—	—	1	—	—	—
<i>P. mexicanus</i>	4	2	2	—	—	—	—	1	3
<i>Peromyscus</i> spp.	7	—	5	2	—	7	—	—	—
<i>R. sumichrasti</i>	2	—	2	—	—	2	—	—	—
<i>Reithrodontomys</i> sp.	1	—	1	—	—	1	—	—	—
<i>S. hispidus</i>	2	—	1	1	—	2	—	—	—
<i>S. toltecus</i>	2	—	2	—	—	2	—	—	—
Total	100	10	42	20	28	83	8	6	3

^aAntibodies (immunoglobulin G) to Whitewater Arroyo virus (WWAV) but not to Amaparí virus (AMAV) were found in 83 rodents, antibodies to AMAV but not to WWAV were found in 10 rodents, and antibodies to WWAV and AMAV were found in 2 white-toothed woodrats (*N. leucodon*), 1 Mexican woodrat (*N. mexicana*), 2 southern plains woodrats (*N. micropus*), and 2 Mexican deermice (*P. mexicanus*).

positive to WWAV and AMAV (Table 3). The antibody titers to WWAV in the 83 animals that were positive to WWAV but not AMAV ranged from 320 to >5120. The antibody titers to WWAV in 48 of these rodents were >1280, indicating that the homologous virus in each was antigenically more closely related to WWAV than AMAV. The antibody titers to AMAV in the 10 animals that were positive to AMAV but not WWAV ranged from 320 to >5120. The antibody titers to AMAV in 7 of these rodents were >1280, indicating that the homologous virus in each was antigenically more closely related to AMAV than WWAV.

The animals that were antibody-positive to WWAV and AMAV were two white-toothed woodrats (*N. leucodon*), one Mexican woodrat (*N. mexicana*), two southern plains woodrats (*N. micropus*), and two Mexican deermice (*P. mexicanus*). The antibody titers to WWAV and AMAV in the white-toothed woodrats, Mexican woodrat, and southern plains woodrats were ≥ 5120 and either 320 or 1280, respectively, indicating that the homologous virus in each of these animals was antigenically more closely related to WWAV than AMAV. The antibody titers to WWAV and AMAV in the Mexican deermice were 320 and ≥ 5120 , respectively, indicating that the homologous virus in each of these animals was antigenically more closely related to AMAV than WWAV. Altogether, AMAV was the apparent homologous virus in eight rodents: three northern pygmy mice (*B. taylori*) captured in Gillespie County, Texas, one northern pygmy mouse from the Municipality of Janos, Chihuahua, and four Mexican deermice (*P. mexicanus*) from Chiapas.

Discussion

This study extends our knowledge of the natural host range of the North American Tacaribe serocomplex viruses from 15 to 28 species in the family Cricetidae and provides the first evidence that a pygmy mouse (*Baiomys* sp.) and grasshopper mouse (*Onychomys* sp.) are natural hosts of Tacaribe serocomplex viruses. Further, this study extends the known geographical distribution of Tacaribe serocomplex viruses in Texas from Dimmitt and La Salle counties (Fulhorst et al. 2002b) to 10 other counties and provides the first evidence that Tacaribe serocomplex viruses are enzootic in Mexico.

Low titers of IgG to Tacaribe serocomplex viruses antigenically distinct from WWAV and AMAV may have been missed in some rodents in this study. Regardless, the results of this study indicate that Tacaribe serocomplex viruses in association with cricetid rodents are geographically widely distributed in Mexico as well as the southwestern United States.

A single cricetid rodent species can be associated with different arenaviruses within a small geographical region. For example, the white-throated woodrat in the southwestern United States is naturally and perhaps principally associated with WWAV, BBTv, and TTCV (Fulhorst et al. 1996, Milazzo et al. 2008). As such, the arenaviruses associated with the southern plains woodrat (*N. micropus*) in Dickens, Motley, and Ward counties in Texas may be different from CTNV (Cajimat et al. 2007a). Additionally, the arenavirus associated with the Mexican woodrat (*N. mexicana*) in Nuevo León may be different from the arenaviruses isolated from Mexican woodrats (*N. mexicana*) captured in Arizona, Colorado, New Mexico, and Utah (Cajimat et al. 2008).

Perhaps the most interesting findings in this study are the high-titered IgG to AMAV in Mexican deermice (*P. mexicanus*) captured in Chiapas and IgG to AMAV but not WWAV in northern pygmy mice (*B. taylori*) captured in Chihuahua and Texas. These findings are the first evidence for an arenavirus in North America that is antigenically more closely related to the Tacaribe serocomplex viruses in South America that cause hemorrhagic fever in humans than to the North American Tacaribe serocomplex viruses described previously (Table 1).

The high-titered IgG to AMAV in Mexican deermice (*P. mexicanus*) captured in Chiapas supports the notion that epidemics of highly lethal hemorrhagic fever(s) in the highlands of Mexico in the 16th century were caused by arenavirus(es) native to Mesoamerica (Acuna-Soto et al. 2000, 2002, 2004, Marr and Kiracofe 2000). We note that human consumption of cricetid rodents is common in the highlands of Mexico. For example, Mexican deermice (*P. mexicanus*), Chiapan deermice (*P. zarhynchus*), and Mexican woodrats (*N. mexicana*) are regularly eaten by Tzeltal Indians in the highlands of Chiapas (Barragán et al. 2007). Clearly, future studies on arenaviruses in North America should include work to assess the human health significance of the Tacaribe serocomplex viruses associated with cricetid rodents in the highlands of Mexico as well as the human health significance of the Tacaribe serocomplex viruses associated with cricetid rodents in rural areas in the southwestern United States. Some of these viruses may cause severe febrile illnesses in humans.

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Disclosure Statement

No competing financial interests exist.

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Appendix 1

RODENTS CAPTURED IN NEW MEXICO, TEXAS, OR MEXICO, 1995–2008, BY SPECIES
AND STATE OR GEOGRAPHICAL REGION IN TEXAS^a

Species	Number of rodents (state or region in Texas)	Antibody prevalence ^b
<i>Baiomys musculus</i>	38 (CH), 3 (JA), 1 (MH), 14 (OA), 1 (VZ)	0/57
<i>Baiomys taylori</i>	20 (TX-CP), 48 (TX-GCP), 18 (TX-HP), 1 (TX-PW), 28 (CI), 1 (GJ), 1 (GR), 29 (JA), 5 (MH), 1 (NL), 4 (PU), 9 (SI), 2 (TM)	8/167
<i>Habromys ixtlani</i>	5 (OA)	0/5
<i>Habromys schmidlyi</i>	2 (EM)	0/2
<i>Habromys</i> sp.	1 (VZ)	0/1
<i>Hodomys alleni</i>	1 (OA)	0/1
<i>Megadontomys cryophilus</i>	4 (OA)	0/4
<i>Megadontomys nelsoni</i>	2 (HG), 10 (VZ)	1/12
<i>Megadontomys thomasi</i>	16 (GR)	0/16
<i>Neotoma albigula</i>	48 (NM), 9 (CI), 6 (SO)	0/63
<i>Neotoma floridana</i>	1 (TX-PW)	0/1
<i>Neotoma leucodon</i>	5 (TX-CP), 22 (NL), 15 (SL)	12/42
<i>Neotoma mexicana</i>	7 (TX-MB), 1 (CH), 3 (GR), 3 (MH), 3 (NA), 2 (NL), 4 (OA), 3 (VZ)	1/26
<i>Neotoma micropus</i>	29 (NM), 6 (TX-CP), 6 (TX-GCP), 58 (TX-HP), 11 (TX-MB), 18 (NL), 26 (TM)	19/154
<i>Neotoma</i> sp.	1 (NL)	0/1
<i>Neotomodon alstoni</i>	6 (EM), 1 (MH)	0/7
<i>Oligoryzomys fulvescens</i>	24 (CH), 1 (SL), 2 (TA)	0/27
<i>Onychomys arenicola</i>	2 (NM), 2 (TX-MB)	0/4
<i>Onychomys leucogaster</i>	11 (NM), 2 (TX-CP), 5 (TX-HP), 8 (TX-MB), 22 (CI), 2 (NL), 3 (SL), 8 (TM)	3/61
<i>Onychomys torridus</i>	3 (SO)	0/3
<i>Oryzomys alfaroi</i>	1 (OA), 2 (PU), 3 (VZ)	0/6
<i>Oryzomys chapmani</i>	5 (CH), 6 (HG), 8 (OA), 6 (VZ)	0/25
<i>Oryzomys couesi</i>	2 (TX-GCP), 10 (CH), 3 (NL), 8 (OA), 14 (TA), 6 (VZ)	1/43
<i>Oryzomys melanotis</i>	4 (SL)	0/4
<i>Oryzomys palustris</i>	185 (TX-GCP)	7/185
<i>Oryzomys rostratus</i>	1 (PU)	0/1
<i>Oryzomys</i> spp.	24 (CH), 4 (GR), 2 (MH), 8 (OA), 3 (PU), 23 (VZ)	0/64
<i>Osgoodomys banderanus</i>	2 (JA), 11 (MH), 2 (NA)	0/15
<i>Peromyscus attwateri</i>	400 (TX-CP), 43 (TX-HP)	3/443
<i>Peromyscus aztecus</i>	3 (CH), 1 (EM), 4 (GR), 2 (HG), 15 (OA)	0/25
<i>Peromyscus beatae</i>	3 (CH), 6 (GR), 21 (OA), 4 (VZ)	0/34
<i>Peromyscus boylii</i>	286 (TX-MB), 3 (CI), 1 (EM), 2 (JA), 11 (NL), 5 (SL), 6 (SO)	3/314
<i>Peromyscus difficilis</i>	1 (OA), 1 (SL), 8 (TL)	0/10
<i>Peromyscus eremicus</i>	10 (NM), 36 (TX-MB), 8 (CU), 13 (NL), 8 (SL)	0/75
<i>Peromyscus furvus</i>	25 (HG), 1 (PU), 27 (VZ)	0/53
<i>Peromyscus gossypinus</i>	5 (TX-PW)	0/5
<i>Peromyscus gratus</i>	5 (JA), 5 (PU)	0/10
<i>Peromyscus hooperi</i>	6 (CU)	0/6
<i>Peromyscus hylocetes</i>	8 (EM)	0/8
<i>Peromyscus leucopus</i>	19 (NM), 78 (TX-CP), 23 (TX-GCP), 152 (TX-HP), 9 (TX-MB), 20 (TX-PW), 60 (NL), 2 (SL), 69 (TM)	11/432
<i>Peromyscus levipes</i>	2 (EM), 2 (GR), 1 (MH), 43 (NL), 16 (SL)	0/64
<i>Peromyscus maniculatus</i>	13 (NM), 9 (TX-CP), 69 (TX-HP), 18 (TX-MB), 22 (NL), 8 (SL), 1 (TL), 5 (VZ)	9/145
<i>Peromyscus megalops</i>	61 (GR)	1/61
<i>Peromyscus melanocarpus</i>	15 (OA)	0/15
<i>Peromyscus melanophrys</i>	5 (GJ), 1 (JA), 9 (NL), 5 (PU), 8 (SL)	2/28
<i>Peromyscus melanotis</i>	75 (EM), 1 (MH), 59 (VZ)	1/135
<i>Peromyscus merriami</i>	6 (SO)	0/6
<i>Peromyscus mexicanus</i>	31 (CH), 9 (OA), 4 (PU), 12 (VZ)	4/56
<i>Peromyscus nasutus</i>	16 (TX-MB)	0/16
<i>Peromyscus ochraventer</i>	11 (SL)	0/11
<i>Peromyscus pectoralis</i>	389 (TX-CP), 21 (TX-MB), 2 (CU), 23 (NL), 6 (SL), 1 (TM)	0/442
<i>Peromyscus schmidlyi</i>	1 (SO)	0/1
<i>Peromyscus spicilegus</i>	24 (JA), 7 (MH)	0/31

(continued)

APPENDIX 1 (CONTINUED)

Species	Number of rodents (state or region in Texas)	Antibody prevalence ^b
<i>Peromyscus truei</i>	1 (CI), 1 (TM)	0/2
<i>Peromyscus zarhynchus</i>	2 (CH)	0/2
<i>Peromyscus</i> spp.	11 (TX-CP), 21 (TX-GCP), 24 (CI), 7 (EM), 28 (<u>GR</u>), 4 (HG), 11 (JA), 54 (<u>MH</u>), 27 (NA), 12 (NL), 16 (OA), 61 (PU), 1 (SL), 16 (VZ)	7/293
<i>Reithrodontomys bakeri</i>	3 (GR)	0/3
<i>Reithrodontomys fulvescens</i>	1 (TX-CP), 27 (TX-GCP), 20 (TX-HP), 2 (TX-MB), 9 (TX-PW), 1 (CI), 3 (JA), 4 (NL), 1 (OA), 1 (PU), 5 (SL), 2 (VZ)	0/76
<i>Reithrodontomys gracilis</i>	2 (CH)	0/2
<i>Reithrodontomys megalotis</i>	11 (NM), 31 (TX-HP), 16 (TX-MB), 4 (EM), 4 (JA), 4 (NL), 11 (PU), 5 (SL), 7 (TL), 1 (TM)	0/94
<i>Reithrodontomys mexicanus</i>	1 (HG), 7 (JA), 17 (MH), 1 (PU), 1 (SL), 21 (VZ)	0/48
<i>Reithrodontomys microdon</i>	3 (MH), 1 (OA)	0/4
<i>Reithrodontomys montanus</i>	10 (TX-HP), 1 (TX-MB)	0/11
<i>Reithrodontomys sumichrasti</i>	3 (CH), 36 (<u>GR</u>), 7 (HG), 16 (MH), 9 (PU), 11 (VZ)	2/82
<i>Reithrodontomys</i> spp.	32 (<u>TX-HP</u>), 7 (EM), 1 (GR), 1 (JA), 15 (VZ)	1/56
<i>Sigmodon alleni</i>	1 (JA)	0/1
<i>Sigmodon hispidus</i>	20 (NM), 80 (<u>TX-CP</u>), 141 (TX-GCP), 279 (<u>TX-HP</u>), 3 (TX-MB), 22 (TX-PW), 5 (CI), 41 (NL), 5 (PU), 2 (SL), 29 (TM)	2/627
<i>Sigmodon mascotensis</i>	11 (CH), 2 (GJ), 1 (GR), 21 (JA), 2 (MH), 1 (NA), 14 (OA)	0/52
<i>Sigmodon ochrognathus</i>	12 (TX-MB), 1 (CI)	0/13
<i>Sigmodon toltecus</i>	1 (CH), 1 (NL), 38 (<u>TA</u>), 1 (TM), 30 (VZ)	2/71
<i>Sigmodon</i> spp.	23 (CH), 5 (MH), 4 (OA)	0/32
<i>Tylomys</i> sp.	1 (CH)	0/1
Total		100/4893

^aNM, New Mexico (Otero County); TX-CP, Central Plains of Texas (Blanco, Brown, Coleman, Dimmit, Gillespie, Kerr, Kimble, Mason, and McMullen counties); TX-GCP, Gulf Coastal Plains of Texas (Brazoria, Cameron, Galveston, and Matagorda); TX-HP, High Plains of Texas (Cottle, Dickens, Donley, Hall, Lubbock, Lynn, and Motley); TX-MB, Mountains and Basins of Texas (Brewster, Jeff Davis, and Ward); TX-PW, Piney Woods of Texas (Anderson, Bowie, Lamar, and Morris); CH, Chiapas (municipalities of Berriozábal, Mapastepec, Ocozacoautla de Espinosa, Pijijiapan, and Zinacantán); CI, Chihuahua (Cusihuiachi and Janos); CU, Coahuila (Monclova); EM, Estado de México (Ecatepec de Morelos, Toluca, Villa del Carbón, and Zacualpan); GJ, Guanajuato (Allende); GR, Guerrero (Chilpancingo de los Bravo and Malinaltepec); HG, Hidalgo (Agua Blanca); JA, Jalisco (Autlán de Navarro, Cocula, Jocotepec, and Ojuelos de Jalisco); MH, Michoacán (Coalcomán, Dos Aguas, Morelia, Múgica, Pátzcuaro, Santa Clara, Uruapan, Zinapécuaro, and Zitácuaro); NA, Nayarit (San Blas and Santa María del Oro); NL, Nuevo León (Allende, Apodaca, Aramberri, Ciénega de Flores, Doctor Arroyo, Galeana, General Escobedo, General Zaragoza, Iturbide, Lampazos de Naranjo, Linares, Los Aldama, Mina, Monterrey, Salinas Victoria, and Santiago); OA, Oaxaca (Agua Fria Juxtlahuaca, Concepción Guerrero, Concepción Pápalo, Guichicovi, Oaxaca de Juárez, Putla de Guerrero, San Pedro Mixtepec, and Santo Domingo Zanatepec); PU, Puebla (Las Margaritas, Tehuacán, Vicente Guerrero, and Zacatlán); SL, San Luis Potosí (Catorce, Cedral, Ciudad del Maíz, and Matehuala); SI, Sinaloa (Rosario); SO, Sonora (Navjoa and Yocora); TA, Tabasco (Emiliano Zapata); TL, Tlaxcala (Tepetitla de Lardizabal); TM, Tamaulipas (Ciudad Guerrero, San Fernando, La Pesca, and Matamoros); VZ, Veracruz (Acajete, Coatzacoalcos, Minatitlán, Perote, Poza Rica, Puerto del Aire, San Andrés Tuxtla, Sontecomapan, and Xico). The antibody-positive rodents were from the states or regions that are underlined.

^bNumber positive/number tested for antibody (immunoglobulin G) to arenaviruses.