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Phylogeography and evolutionary history of rodent-borne hantaviruses

W.M. Souza [a,*], G. Bello [b], A.A. Amarilla [c], H.L. Alfonso [c], V.H Aquino [c], L.T.M. Figueiredo [a,*]

[a] Virology Research Center, School of Medicine of Ribeirao Preto of University of São Paulo, Ribeirao Preto, São Paulo, Brazil
[b] Laboratório de AIDS & Imunologia Molecular, Instituto Oswaldo Cruz, FIOCRUZ, Rio de Janeiro, Brazil
[c] Departamento de Análises Clínicas, Toxicológicas e Bromatológicas, Faculdade de Ciências Farmacêuticas, Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil

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ABSTRACT

Hantavirus (Family *Bunyaviridae*) are mostly associated to rodents and transmitted to man by inhalation of aerosolized infected excreta of these animals. The human infection by hantaviruses can lead to severe diseases such as hemorrhagic fever with renal syndrome (HFRS) in Asia and Europe, and pulmonary syndrome (HPS) in the Americas. To determine the origin, spreading and evolutionary dynamics of rodent-borne hantaviruses, 190 sequences of nucleoprotein (*N*) of hantaviruses isolated in 30 countries, from 1985 to 2010, were retrieved from the GenBank and analyzed using the BEAST program. Our evolutionary analysis indicates that current genetic diversity of *N* gene of rodent-borne hantaviruses probably was originated around 2000 years ago. *Hantavirus* harbored by *Murinae* and *Arvicolinae* subfamilies, probably, were originated in Asia 500–700 years ago and later spread toward Siberia, Europe, Africa and North America. *Hantavirus* carried by *Neotominae* subfamily, probably, emerged 500–600 years ago in Central America and spread toward North America. Finally, hantaviruses associated to *Sigmodontinae* occurred in Brazil 400 years ago and were, probably, originated from *Neotominae*-associated virus from northern South America. These data offer subsidies to understand the time-scale and worldwide dissemination dynamics of rodent-borne hantaviruses.

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1. Introduction

Viruses of the genus *Hantavirus*, family *Bunyaviridae*, are enveloped viruses containing three segments of single-stranded and negative-sense RNA genome. These segments are designated based on their size as small (S), medium (M) and large (L) (Jonsson et al., 2010; Vaheri et al., 2013). The S segment encodes both the nucleoprotein (*N*) and a small nonstructural protein (NSs) in an overlapping (+1) open reading frame, the M segment encodes two envelope glycoproteins (Gn and Gc), and the L segment encodes the RNA-dependent RNA polymerase (RdRp) (Jaaskelainen et al., 2007; Vera-Otarola et al., 2012).

Unlike other members of the *Bunyaviridae* family, which are transmitted by arthropods, hantaviruses are transmitted to humans particularly by *Muridae* or *Cricetidae* rodents through inhalation of excreta or aggressive interactions between animals (Jonsson et al., 2010). Nevertheless, novel hantaviruses continue to be described in a wide range of species, including shrews and bats whose cross-species transmission and virus-host co-divergence have played important roles in hantavirus evolution (Arai et al., 2008; Guo et al., 2013; Weiss et al., 2012). The rodent-borne hantaviruses produce emerging infectious diseases that have a substantial impact on public health: the hemorrhagic fever with renal syndrome (HFRS) in Eurasia, and the hantavirus pulmonary syndrome (HPS) in the Americas (Jonsson et al., 2010; Vaheri et al., 2013).

As the phylogenetic inference of the rodent-borne viruses appear to be largely congruent with that of their hosts, hantaviruses were often considered to have co-diverged with rodent hosts over time-scales of millions of years (Hughes and Friedman, 2000; Morzunov et al., 1998; Nemirov et al., 2002). However, recent studies estimated that the *Hantavirus* exhibit a short-term substitution rate too fast (10^{-2} to 10^{-4} substitutions/site/year) and divergence times too recent (<1000 years ago) that are not compatible with a codivergence with their hosts (Ramsden et al., 2009; Ramsden et al., 2008). Thus, it has been proposed that apparent similarities between phylogeny of hantaviruses and that of their mammalian hosts are the result of a more recent history of preferential host switching and local adaptation (Ramsden et al., 2009).

To better understand the origin and the dissemination process of rodent-borne hantaviruses, we have analyzed a comprehensive data set including 252 S gene sequences of hantaviruses detected in humans and rodents worldwide. Spatial and temporal information of sequences were analyzed by a Bayesian method allowing

* Corresponding authors. Address: Virology Research Center, School of Medicine of Ribeirao Preto, University of São Paulo, Av. Bandeirantes, 3900, 14049-900 Ribeirao Preto, São Paulo, Brazil. Tel.: +55 163602 4580; fax: +55 163602 3376.
E-mail addresses: wmarciel@hotmail.com, wmarciel@usp.br (W.M. Souza), ltmfigue@fmrp.usp.br (L.T.M. Figueiredo).

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the reconstruct a time-scale and migration routes of *Hantavirus* infecting *Murinae*, *Arvicolinae*, *Neotominae* and *Sigmodontinae* subfamilies of rodents.

2. Materials and methods

2.1. Sequence dataset

Complete *S* gene sequences (1319 bp) of rodent-borne hantaviruses deposited until November 2012 were retrieved from GenBank (www.ncbi.nlm.nih.gov). Two unpublished sequences of Araraquara virus isolated in Brazil were also included in the study (Supporting Figure 1). Known recombinant sequences were excluded from the analysis. In our initial data set, samples from China were overrepresented ($n = 86$, 34%) when compared to those from other countries ($n \leqslant 21$). To avoid potential biases in the phylogeographic reconstructions (ancestral root location and viral gene flow estimates) due to sampling heterogeneity (Faria et al., 2012; Salemi et al., 2005), we obtained a "non-redundant" representative Chinese subset. Highly similar (identity $\geqslant$ 97%) sequences from China were clustered with the CD-HIT program (Li and Godzik, 2006) using an online web server (Huang et al., 2010) and only one sequence per cluster was selected. It was obtained a final data set of 190 *N* gene sequences identified from 30 countries over the past 25 years (Table 1).

2.2. Evolutionary and phylogeographic analyses

Nucleotide sequences were aligned using the CLUSTAL W program (Thompson et al., 1994) and hand edited. Alignment is available from the authors upon request. Based on this alignment, the spatial–temporal and demographic dynamics of dissemination of rodent-borne hantavirus was reconstructed using the Bayesian Markov Chain Monte Carlo (MCMC) approach using the BEAST 1.7.4 program (Drummond et al., 2012). For these analysis, use the general time reversible GTR + I + G nucleotide substitution model as determined by jModeltest (Posada, 2008), an uncorrelated Lognormal relaxed molecular clock model (Drummond et al., 2006) and a Bayesian skyline coalescent model (Drummond et al., 2005), as previously described (Ramsden et al., 2009). Time-scale was inferred using an informative substitution rate interval (1.0×10^{-4} to 1.0×10^{-3} substitutions/site/year) previously estimated for the *N* gene of rodent-borne hantavirus (Ramsden et al., 2009; Ramsden et al., 2008). Sequences were assigned to 15 geographic locations: China, Japan, South Korea, Southeast Asia (Thailand and Singapore), former URSS (Kazakhstan, Latvia and Russia), Central/Eastern Europe (Croatia, Czech Republic, Germany, Greece, Poland, Serbia and Slovakia), Northern Europe (Denmark, Finland and Sweden), USA, Mexico/Central America (Costa Rica and Panama), Argentina, Brazil, Chile, Bolivia/Paraguay/Peru Venezuela and Guine. Migration events between discrete locations were reconstructed by applying a Bayesian phylogeographic approach that models the unobserved diffusion process as a reversible continuous-time Markov chain process (Lemey et al., 2009). MCMC chain was run for 1×10^8 generations and adequate chain mixing was checked, after excluding an initial 10%, by calculating the effective sample size (ESS) using TRACER v1.4 program (http://www.beast.bio.ed.ac.uk/Tracer). Maximum clade credibility (MCC) trees were summarized from the distribution of trees with TreeAnnotator and were visualized with FigTree v1.4.0 (http://tree.bio.ed.ac.uk/software/figtree).

Table 1
Nucleotide sequences of rodent-borne hantavirus analyzed in the study.

Region	Country	*N*	Sampling dates
South America	Argentina	11	1997–1999
	Bolivia	4	1992–2008
	Brazil	15	2001–2006
	Chile	4	1997–1999
	Paraguay	4	1995–2000
	Peru	1	1996
	Venezuela	1	1994
Central and North America	Costa Rica	1	1989
	Panama	1	2000
	Mexico	8	2006
	USA	11	1985–2006
Europe	Croatia	1	2000
	Czech Republic	1	1995
	Denmark	1	2000
	Finland	3	1991–2000
	Germany	15	1997–2008
	Greece	3	1999
	Poland	2	1995
	Latvia	5	2000–2008
	Serbia	1	1997
	Slovakia	6	2001–2004
	Sweden	16	2004–2005
	Russia	21	1993–2005
Asia	China	25	1999–2007
	Kazakhstan	1	1995
	Japan	10	1995–2010
	Russia	21	1993–2005
	South Korea	10	1997–2009
	Singapore	4	2006
	Thailand	2	1998–2004
Africa	Guinea	2	2004
4	30	190	1985–2010

3. Results

The Bayesian phylogenetic analysis of 190 hantavirus *S* gene sequences confirmed the existence of two highly supported (Posterior Probability [*PP*] = 1) monophyletic clades associated with the rodent host families *Muridae* (subfamily *Murinae*) and *Cricetidae* (subfamilies *Arvicolinae*, *Neotominae* and *Sigmodontinae*) (Fig. 1A). Viruses included in the *Cricetidae* family were subdivided in two reciprocally monophyletic clades (*PP* = 1) related to *Arvicolinae* and *Neotominae*/*Sigmodontinae* subfamilies. The *Sigmodontinae* hantaviruses branched in a well-supported (*PP* = 1) monophyletic subcluster that was nested within the paraphyletic group of *Neotominae* hantaviruses. The analysis also suggest a subdivision of hantaviruses into genus or tribe of their rodent hosts (Fig. 1B). *Muridae*-borne hantaviruses adapted to rodents of genus *Apodemus* and *Rattus*. The *Arvicolinae*-associated viruses were mostly found in hosts of the genus *Myodes* or *Microtus*. *Neotominae*-associated hantaviruses adapted to genus *Peromyscus* and *Reithrodontomys* (both belong to *Reithrodontomyini* tribe). The *Sigmodontinae* hantaviruses were found principally in *Oryzomyini* and *Akodontini* tribes.

The estimated rate of nucleotide substitutions per site per year for the *N* gene of hantavirus was 6.8×10^{-4}. The 95% HPD interval of such estimate (2.5×10^{-4} to 1×10^{-3} subst./site/year) almost coincided with the informative prior interval (1.0×10^{-4} to 1.0×10^{-3} subst./site/year), thus indicating a correlation between both data. According to this estimated rate, the most recent common ancestor (T_{MRCA}) for all rodent-borne hantaviruses occurred 1915 years before present (ybp) (95% HPD: 5541–922 ybp); whereas the major hantaviruses subfamily clades emergerded around 500–600 ybp: *Murinae* (573 ybp, 95% HPD 1644–339 ybp), *Arvicolinae* (628 ybp, 95% HPD 1782–384 ybp) and *Neotominae/Sigmodontinae* (549 ybp, 95% HPD 1555–341 ybp) (Fig. 1A).

The posterior root state probability (*PRSP*) distributions at the nodes of the rodent subfamilies clades in the Bayesian tree, allowed to infer on the spreading of hantaviruses around the world

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