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Dear Dr. González-Ittig:

It is a pleasure to accept your manuscript entitled "The molecular phylogenetics of the genus *Oligoryzomys* (Rodentia: Cricetidae) clarifies rodent host-Hantavirus associations." in its current form for publication in the Zoological Journal of the Linnean Society.

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1
2 **Title:** The molecular phylogenetics of the genus *Oligoryzomys* (Rodentia: Cricetidae) clarifies
3 rodent host-Hantavirus associations.

4

5

6 **Authors:** Raul E. González-Ittig¹, Paula C. Rivera¹, Silvana C. Levis², Gladys E. Calderón²,
7 Cristina N. Gardenal¹

8

9

10 **Affiliations**

11 ¹Instituto de Diversidad y Ecología Animal (CONICET-UNC) and Facultad de Ciencias
12 Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. Argentina. ² Instituto
13 Nacional de Enfermedades Humanas (INEVH), Pergamino, Argentina.

14

15 **Running title:** Rodent host-hantavirus genotypes relationships

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18

19 **Corresponding author:** Raul E. González-Ittig. Instituto de Diversidad y Ecología Animal
20 (CONICET-UNC), Av. Vélez Sarsfield 299. 5000. Córdoba, Argentina. Telephone: 54-351-
21 4332100. Fax: 54-351-4332097. E-mail: raulgonzalezittig@yahoo.com.ar and
22 regonzalez@efn.uncor.edu

23

24

25

1 **Abstract**

2 Several species of the genus *Oligoryzomys* are natural hosts of different hantavirus
3 genotypes affecting humans. The systematics of the genus is confusing, which complicates
4 the identification of the rodent host and hence, the potential endemic areas of Hantavirus
5 Pulmonary Syndrome. In this study, we analyse molecular data to infer phylogenetic
6 relationships among Central and South American specimens of *Oligoryzomys* and compare
7 our results with previously published data on karyotypic, geographic distribution and host-
8 virus associations to solve contradictory taxonomic reports. We identified 25 clades, each one
9 corresponding to a different putative species. The phylogenetic trees show that *O.*
10 *longicaudatus* is strongly related to the *O. flavescens* complex, which comprises four clades;
11 *O. nigripes* is related to *O. stramineus*, *O. vegetus* to *O. fulvescens* from Central America and
12 *O. brendae* is the sister species of *O. aff. destructor*. We identified the following rodent host-
13 hantavirus genotypes relationships: *O. longicaudatus*-Andes, *O. flavescens* “West”-Bermejo,
14 *O. flavescens* “East”-Lechiguanas, *O. nigripes*-Juquitiba, *O. microtis*-Rio Mamore and Rio
15 Mamore-3, *O. chacoensis*-Oran, *O. costaricensis*-Choclo, *O. delicatus*-Maporal, *O.*
16 *utiaritensis*-Castelo dos Sonhos, *Oligoryzomys* sp. RT2012-Rio Mamore-4, *Oligoryzomys* sp.
17 (and not *O. fornesi*)-Anajatuba. This work, besides contributing to develop prevention
18 programs for the hantavirus epidemiology in Latin America, represents a comprehensive
19 update of the systematics of the genus *Oligoryzomys*.

20

21

22

23 **Keywords:** cytochrome b – *Hantavirus* - molecular systematics - natural hosts- *Oligoryzomys*

1 **Introduction**

2 In the Americas, several species of the genus *Hantavirus* (family Bunyaviridae) act as
3 ethiological agents of the Hantavirus Pulmonary Syndrome (HPS), a disease with hundreds of
4 cases recorded each year and with a high rate of mortality (Hjelle & Torres-Pérez, 2010;
5 Blasdell, Henttonen & Buchy, 2012). Since there is no specific treatment available,
6 prevention measures are essential to decrease HPS cases. This requires a detailed knowledge
7 of the hantavirus infection epizootiology as well as of the reservoir population ecology (Mills
8 *et al.*, 1999).

9 The International Committee on Taxonomy of Viruses (ICTV) recognizes the
10 existence of 23 hantavirus species worldwide. Besides, several genotypes have been
11 characterized only by molecular techniques; according to the ICTV these genotypes do not
12 reach the status of species because they have never been isolated. From Mexico to southern
13 South America, most viral species and genotypes are hosted by several rodent species
14 belonging to the genus *Oligoryzomys* Bangs, 1900 (Cricetidae: Sigmodontinae) (Hjelle &
15 Torres-Pérez, 2010, Blasdell *et al.*, 2012). In order to control and prevent human zoonoses,
16 Mills *et al.* (1999) recommended to: a) identify the reservoir host, b) delimit the geographic
17 range of the host and the range of infection by the pathogen within the host range, and c)
18 define the relative risk to humans by determining host and pathogen distribution in distinct
19 habitats.

20 One of the main limitations to define the virus-host relationships is the poorly resolved
21 taxonomy of rodents species associated to Hantavirus in Latin America (Almeida, Bonvicino
22 & Cordeiro-Estrela, 2007; Haag *et al.*, 2007; González-Ittig *et al.*, 2010a; Palma *et al.*, 2010;
23 Hanson, Utrera & Fulhorst, 2011). *Oligoryzomys* is the most speciose genus of the
24 Oryzomyini tribe comprising small-bodied, long-tailed, nocturnal, terrestrial, and frequently
25 arboreal rodents that feed on fruit, seeds, and insects (Carleton & Musser, 1989). The genus

1 presents high chromosomal variation, with diploid numbers ranging from $2n= 46$ to 70 (Silva
2 & Yonenaga-Yassuda, 1997; Andrades-Miranda *et al.*, 2001; Lima, Bonvicino & Kasahara,
3 2003; Weksler & Bonvicino, 2005). The number of species is quite uncertain; for example,
4 Tate (1932) recognized 30 species but Hershkovitz (1966) indicated only one (*Oryzomys*
5 *nigripes*). However, most authors reported between 12 and 18 species (Honacki, Kinman &
6 Koepl, 1982; Reig, 1986; Carleton & Musser, 1989; Musser & Carleton, 1993; Musser &
7 Carleton, 2005; González-Ittig *et al.*, 2010a; Palma *et al.*, 2010, Hanson *et al.*, 2011).
8 González-Ittig *et al.* (2010a) suggested that given the scarcity of captures in several
9 geographic areas of South America it is likely that there could be new undescribed species of
10 *Oligoryzomys*. Regarding the molecular systematic of this genus, the inconsistencies among
11 different studies (González-Ittig *et al.*, 2010a; Palma *et al.*, 2010; Hanson *et al.*, 2011) may be
12 generated by incorrect morphologic and/or morphometric specimen assignments. To avoid
13 this problem, thorough species level revisions including vouchered material from type
14 localities and range documentation would be a major contribution (Musser & Carleton 2005).
15 On the basis of morphological characters, Carleton & Musser (1989) proposed the existence
16 of five groups of species within of the genus (*fulvescens*, *microtis*, *andinus*, *flavescens* and
17 *nigripes*), which has been partially corroborated by molecular studies. For example, Hanson
18 *et al.* (2011) demonstrated that *O. fulvescens* and *O. vegetus* (belonging to the *fulvescens*
19 group) are closely related and Agrellos *et al.* (2012) reported that *O. nigripes* and *O. eliurus*
20 were synonyms (both were included in the *nigripes* group). In contrast, Gonzalez-Ittig *et al.*
21 (2010a) and Firth *et al.* (2012) showed that *O. nigripes*, *O. longicaudatus* and *O. destructor*,
22 all part of the *nigripes* group, are distantly related in the molecular phylogenetic trees.

23 In a study on the phylogenetic relationships among hantaviruses of Latin America and
24 their natural reservoirs, Levis *et al.* (1998) rejected the hypothesis that each species of
25 hantavirus is host-related (Schmaljohn *et al.*, 1985) since the rodent *O. longicaudatus* was

Comentario [pa1]: Problem 1

1 recognized as a reservoir of two viral genotypes: Andes (or Andes South) and Oran (or Andes
2 North). Rivera *et al.* (2007) found, using molecular markers, that several of the previous
3 morphological identifications of rodents reported in Levis *et al.* (1998) were incorrect. For
4 example, specimen OR 22495 from Orán (Salta, Argentina) infected with the Oran hantavirus
5 was in fact *O. chacoensis* and not *O. longicaudatus*. Moreover, specimen OR 22531, from the
6 same locality, infected with the Bermejo virus corresponded to the *O. flavescens* complex (*O.*
7 *flavescens* West), instead of *O. chacoensis*. Rivera *et al.* (2007) concluded that *O.*
8 *longicaudatus* is distributed only in forests and steppes of southern Argentina and Chile, and
9 does not reach the northern regions of Argentina. Except in Palma *et al.* (2012a) where the
10 observations mentioned above were included, most of these taxonomic corrections were not
11 incorporated either into reviews or into other papers recently published on the hantavirus
12 epidemiology. This is the case in Ramsden, Holmes & Charleston (2009), Hjelle & Torres-
13 Pérez (2010), Martínez *et al.* (2010), Londoño, Levis & Rodas (2011), Blasdel *et al.* (2012)
14 and Firth *et al.* (2012).

15 In recent years, phylogenetic studies based on molecular data have helped to resolve
16 several alpha systematic problems of *Oligoryzomys* and to clarify the relationships of its
17 species with different hantavirus genotypes. González-Ittig *et al.* (2010a), using the
18 mitochondrial control region and cytochrome b genes (*Cytb*), corroborated that *O. flavescens*
19 is a complex of at least four lineages, two of which are associated with two different
20 hantavirus genotypes: *O. flavescens* “East” being the reservoir of the Lechiguanas/Central
21 Plata genotype and *O. flavescens* “West” being the host of the Bermejo genotype. Similarly,
22 Hanson *et al.* (2011) went further into the *O. fulvescens*-hantavirus relationships; previously,
23 this species was recognized as the reservoir of two different hantavirus genotypes: Maporal in
24 Venezuela and Choclo in Panamá. These authors, using the *Cytb* gene, demonstrated that
25 several individuals were wrongly classified under the name *O. fulvescens*. They indicated that

1 specimen MSB96073 (GenBank N° EU192164) from the Azuero Peninsula, Panama, infected
2 with Choclo strain 588, corresponded to the species *O. costaricensis*, and specimen FHV-
3 4083 (GenBank N° DQ227457) from Caño Delgadito in Estado Portuguesa, Venezuela,
4 infected with Maporal prototype strain HV 97021050, corresponded to the species *O.*
5 *delicatus*, so *O. fulvescens* has no relationship with any hantavirus genotype. The above-
6 mentioned new hantavirus-host relationships were not included in later reviews by Blasdell *et*
7 *al.* (2012) and Firth *et al.* (2012). In general, epidemiological studies have not taken into
8 account updated taxonomic findings about rodent hosts, even when they mention the
9 importance of a good specimen identification to elucidate rodent host-hantavirus
10 relationships.

11 In this study we perform a new analysis of the phylogenetic relationships among
12 species of *Oligoryzomys* based on molecular data, in order to clarify the associations between
13 *Oligoryzomys* species and hantavirus genotypes in Latin America and to summarize the
14 existing knowledge. We also compare our results with previously published data on
15 karyotypic, geographic distribution and host-virus associations to shed light on contradictory
16 taxonomic reports.

17

18 **Material and Methods**

19 We updated the *Cytb* gene matrix of González-Ittig *et al.* (2010a) by incorporating the
20 following sequences of *Oligoryzomys* presented in recently published studies (in this section
21 we use the names given by the respective authors, which do not necessarily coincide with
22 those resulting from the analysis here performed): a) from Palma *et al.* (2010): *O. microtis*
23 (EU192172), *Oligoryzomys* sp 1 (EU192167, EU192168, EU192169), *O. flavescens*
24 (EU192170), *O. destructor* (EU192171), *O. nigripes* (EU192161), *O. delticola* (EU192162),
25 *O. eliurus* (EU192163); b) from Hanson *et al.* (2011): *O. costaricensis* (GU393988,

1 GU393989, EU192164, EU258539), *O. delicatus* (GU393996, GU393995, GU393994,
 2 GU393997, GU126529, GU393993, DQ227457), *O. andinus* (GU393999), *O. destructor*
 3 (GU393992, GU393991, GU393990), *O. messorius* (EU258546, EU258537), *O. microtis*
 4 (FJ374766, EU258549); c) from Agrellos *et al.* (2012): *O. utiaritensis* (JQ013748, JQ013761,
 5 JQ013760, JQ013757, JQ013762, JQ013776), *O. rupestris* (JQ013763, JQ013764); d) from
 6 Rocha *et al.* (2011): *O. fornesi* (HM594619, HM594620, HM594621, HM594622,
 7 HM594623), *Oligoryzomys* sp RR2010a (HM594618); e) from Miranda *et al.* (2009): *O.*
 8 *fornesi* (DQ826022, DQ826023), *O. moojeni* (DQ826017, DQ826016); f) from Rogers *et al.*
 9 (2009): *O. destructor* (EU258544), *O. vegetus* (EU258538); g) from Richter *et al.* (2010): *O.*
 10 *microtis* (FJ374766); h) from Firth *et al.* (2012): *O. microtis* (JX443647, JX443648), *O.*
 11 *utiaritensis* (JX443655, JX443664), *Oligoryzomys* sp RT2012 (JX443663, JX443662,
 12 JX443666, JX443657). The voucher number and the geographic location of all specimens
 13 studied here are shown in Table 1 and in Figure 1. We rooted the trees using sequences of the
 14 following outgroups: *Pseudoryzomys simplex* (GU185899), *Holochilus chacarius*
 15 (GU185898), *Euryoryzomys russatus* (DQ826028), *Microryzomys minutus* (EU258535) and
 16 *Neacomys minutus* (EU258536).

17 The *Cytb* matrix was analyzed using maximum parsimony (MP), maximum likelihood
 18 (ML) and Bayesian methods. The best-fitting model of sequence evolution was selected using
 19 jModeltest 0.1.1 (Posada, 2008) in which likelihood scores for 88 different models were
 20 computed. The HKY+I+G model was selected using the Bayesian information criterion (BIC)
 21 and the following starting parameters were used subsequently: a base frequency of A =
 22 0.3287, C = 0.3218, G = 0.0822, T = 0.2673; a transition/transversion ratio of 3.3623; a
 23 proportion of invariable sites of 0.2630; a gamma distribution with alpha = 0.5280. Bayesian
 24 inferences (BI) were performed using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) with
 25 two independent Markov chain Monte Carlo (MCMC) runs, with one cold and three heated

Comentario [pa2]: Problem 3

1 chains each. Runs were performed for ten million generations and trees were sampled every
2 1000 generations. Mixing, convergence to stable values and Effective Sample Size (ESS)
3 were checked with Tracer v1.5 (Rambaut & Drummond, 2007). The two runs converged on
4 very similar posterior estimates with an average standard deviation of split frequencies of
5 0.006. We discarded the first 25% of the samples as “burn in” and used ESS and probability
6 distribution values for all parameters greater than 500. ML trees were constructed using the
7 on line version of program PhyML ver 3.0 (<http://www.atgc-montpellier.fr/phyml/>) (Guindon
8 *et al.*, 2010). We used the HKY85 model and the parameters described above for the analyses;
9 1000 bootstrap replicates were performed.

10 MP was performed with TNT ver 1.1. (Goloboff, Farris & Nixon, 2008). Characters
11 were unordered and equally weighted; no gaps were detected in the dataset. A heuristic search
12 of 1000 iterations of random taxon addition was performed using the TBR (tree bisection-
13 reconnection) branch swapping algorithm. The most parsimonious trees resulting from the
14 MP analysis were summarized in a strict consensus tree. Nonparametric bootstrap support
15 values were calculated based on 1000 replicate searches. To evaluate possible explanatios for
16 the anomalous behaviour of sequences with unresolved phylogenetic positions, a second
17 analysis was performed with TNT options ‘Tree’, ‘Comparisons’, and ‘Pruned trees’ to detect
18 “unstable” taxa in the trees. This method prunes taxa of the cladograms, and shows the nodes
19 gained on the strict consensus, helping to identify floating terminals (Goloboff *et al.*, 2008).

Comentario [pa3]: Problem 2

21 **Results**

22 The Bayesian consensus tree identifying 25 clades is shown in Fig. 2; most individuals
23 group as in González-Ittig *et al.* (2010a), where 18 clades were recovered. Although the ML
24 and MP trees yielded polytomies in the nodes close to the root, they show identical terminal
25 taxa clustering as in the BI tree. The results shown in Fig. 2 confirm the relationships obtained

1 in previous studies by González-Ittig *et al.* (2010a), Hanson *et al.* (2011), Agrellos *et al.*
 2 (2012) and Firth *et al.* (2012), for example, the association of *O. longicaudatus* (clade E)/*O.*
 3 *magellanicus* (clade F) with the *O. flavescens* complex (clades A-D), the relationship of *O.*
 4 *nigripes* (clade G), *O. stramineus* (clade H) and *O. chacoensis* (clade I), the links between *O.*
 5 *utiaritensis* (clade O) and *O. moojeni* (clade P) and between *O. fulvescens* (clade S) and *O.*
 6 *vegetus* (clade R) (Fig. 2).

Comentario [G4]: Problem 4

Eliminado: the one

7 We also detected misidentifications in specimen assignments with respect to their
 8 original studies (Table 1). For example, the sequences GU393999 (Hanson *et al.*, 2011) and
 9 AY452200 (Palma *et al.*, 2005) identified in GenBank as *O. andinus* clustered within the *O.*
 10 *flavescens* West clade (clade D), with a bootstrap support of 0.9BI/83MP/92ML. The

Comentario [pa5]: Problem 2

11 sequence L37400 (clade V) considered *O. andinus* in Myers, Lundrigan & Tucker (1995) do
 12 not cluster with any other sequence and has an unresolved phylogenetic position in the trees,
 13 regardless the different approaches used, BI, MP and ML (Fig 2). Given that this sequence is
 14 short (401pb) we explored possible explanations to its anomalous behaviour by the pruning
 15 procedure implemented in TNT, which identified as a floating terminal. The alternative
 16 positions are marked with a symbol in Fig 2. However, it never clustered within clade D (Fig
 17 2), as did sequences GU393999 and AY452200. We also performed a third analysis with MP
 18 and ML, constraining the grouping of the three sequences into a single clade. It resulted in
 19 much more mutational steps (from 1823 in the normal MP analysis to 1844 in the constrained
 20 one) and a lower likelihood (from -ln 11078.043 to -ln 11130.1819, respectively), indicating
 21 that forcing the monophyly of *O. andinus* a statistically unsupported tree is obtained. It is

Comentario [pa6]: Problem 8

22 interesting to point out that two closely related sequences, EU192170 and EU192171, were
 23 assigned in Palma *et al.* (2010) to *O. flavescens* and to *O. destructor*, respectively. In our
 24 present study these two sequences form the clade U with sequence L37402, referred to as
 25 *Oligoryzomys* sp. in Myers *et al.* (1995). None of these sequences are related to any of the

1 clades corresponding to the *O. flavescens* complex (clades *A-D*) (Fig. 2). Another group of
2 sequences (clade *Q*) from Ecuador would belong to *O. destructor* according to Hanson *et al.*
3 (2011); however, they are not associated to the sequence EU192171 included in Palma *et al.*
4 (2010).

5 Sequences EU192167, EU192168 and EU192169 from Catamarca, Argentina,
6 considered *Oligoryzomys* sp.1 by Palma *et al.* (2010), are part of the clade *T*, that grouped
7 sequences of specimens of *O. brendae* from northern Argentina (bootstrap support values of
8 1.00BI/98MP/99ML) (Fig. 2). Our present results also show that the name *O. messorius* was
9 used for two clearly unrelated lineages: one forming clade *K* (Miranda *et al.* 2009) and the
10 other forming clade *N* (Hanson *et al.*, 2011). In most previous studies, *O. microtis* appears as
11 the sister species of all the others of the genus; however, our tree does not show this
12 relationship; instead, the sequences of *O. microtis* form the clade *W* that is closely related to
13 the clades *X* and *Y* composed of four sequences of *Oligoryzomys* sp. RT2012 and a sequence
14 of *Oligoryzomys* sp. RR2010a, respectively; a similar result was obtained by Firth *et al.*
15 (2012). A group of sequences forming the most basal clade in the present study (HM594622,
16 HM594620, HM594619, HM594623, HM594621, DQ826022 and DQ826023) was named *O.*
17 *fornesi* by Miranda *et al.* (2009) and Rocha *et al.* (2011). Nevertheless, they are not related to
18 the sequences belonging to *O. fornesi* (clade *B*) defined previously in González-Ittig *et al.*
19 (2010a).

20

21 **Discussion**

22 *Species identification and geographic distribution of Oligoryzomys species not associated*
23 *with Hantavirus*

24 An increasing number of phylogenetic studies of *Oligoryzomys* have recently been
25 published. Nonetheless, the generated information remains scattered, pointing to an urgent

1 need of an integrative approach to achieve a better understanding of the rodent
 2 host/*Hantavirus* relationships. In our initial systematic studies of *Oligoryzomys* in Argentina
 3 (González-Ittig *et al.*, 2002; Rivera *et al.*, 2007) we used the mitochondrial DNA control
 4 region as molecular marker; for that reason, those studies were not comparable with previous
 5 ones that used *Cytb* as molecular marker. Later, in González-Ittig *et al.* (2010a) we combined
 6 the data of Argentina with the available *Cytb* sequences from the rest of Latin America to
 7 perform the most complete phylogenetic analysis of the genus *Oligoryzomys* up to that date.

8 In the present study we integrate our previous data with the information generated by
 9 other authors since González-Ittig *et al.* (2010a) until now, obtaining a more complete
 10 *Oligoryzomys* phylogeny. Our results indicate that sequences from several taxa fail to form
 11 monophyletic clades and we have hypothesized associations between sequences and taxon
 12 names based on our phylogenetic analysis (Fig. 2) and geographic localities from which
 13 sequences were obtained (Table 1). Future work should include sequencing of material
 14 collected from near type localities or examining vouchered materials with type specimens to
 15 test these hypotheses.

16 Miranda *et al.* (2009) and Hanson *et al.* (2011) apply the name *O. messorius* to two
 17 clearly separated lineages (clades *K* and *N*, respectively). The species *O. messorius* was
 18 considered a subspecies of *O. fulvescens* (Musser & Carleton, 2005), but the studies of Rogers
 19 *et al.* (2009) and Hanson *et al.* (2011) suggest that *O. fulvescens* is distributed only in Mexico.

20 Thomas (1901) identified the type locality of *O. messorius* as the Kanaku Mountains, Guyana
 21 (a pentagon in Fig. 1). The individual sequenced by Miranda *et al.* (2009) was captured about
 22 150 Km (locality 49; Fig 1) from the type locality whereas the clade N sequences are from
 23 individuals obtained from 420 to 1000 Km (localities 50-52) from the Kanaku Mountains.
 24 Although a complete morphological description is needed –this is given in Thomas (1901),
 25 since the specimen analyzed in Miranda *et al.* (2009) is close to the type locality, the sequence

Comentario [pa7]: Problem 5

Eliminado: accurate

Comentario [pa8]: Problem 6

Eliminado: The type locality of *O. messorius* is the Kanaku

Eliminado: The individual analyzed in Miranda *et al.* (2009) was captured about 150 km from this area (locality 49; Fig. 1). The clade *N* grouped sequences from individuals obtained at about 1000 km, 420 km and 900 km from the Kanaku mountains (localities 50, 51 and 52, respectively; Fig 1).

Eliminado: Although a complete morphological description is needed

Eliminado: given that

1 in clade K is assigned to *O. aff. messorius* and the sequences assigned to *O. messorius* by
 2 Hanson et al. (2011) (here in clade *N*) were assigned to an unknown species (*Oligoryzomys*
 3 sp. 1).
 4 Several taxonomic conflicts characterize the species *O. destructor*. In González-Ittig et
 5 al. (2010a), we included sequences from specimens we assigned to *O. destructor*, belonging
 6 to the high altitude Yungas Rainforest in northwestern Argentina. Massoia (1998) described a
 7 large-sized species present in this region under the name *Oligoryzomys brendae*. Musser &
 8 Carleton (2005) recognized *O. brendae* as a valid species, but highlighted the fact that the
 9 details for its recognition were skimpy and additional study was needed to illuminate status,
 10 discrimination from other regional forms and distribution. For several years the validity of
 11 this name was questioned, but Teta et al. (2013) re-examined the holotype of *O. brendae*
 12 adding new morphological characters to the species description and concluded that *O.*
 13 *brendae* is a valid name. In addition, Teta et al. (2013) obtained *Cytb* gene sequences of
 14 specimens captured in its type locality (Cerro San Javier, Tucumán, Argentina) and compared
 15 them with those published previously in González-Ittig et al. (2010a), concluding that those
 16 specimens belong to *O. brendae* (here clade *T*; Fig. 2; Table 1). Therefore *O. destructor*
 17 would not be present in the Yungas Rainforest of northwestern Argentina. The type locality of
 18 *O. destructor* is Río Chinchao (Huanuco), in the northern Peru Yungas (Musser & Carleton,
 19 2005). The Yungas biogeographic region is distributed on the eastern slopes of the Andean
 20 and subandean mountains of Colombia, Ecuador, Peru, Bolivia and Argentina (Cabrera &
 21 Willink, 1973). Two studies (Palma et al., 2010; Hanson et al., 2011) applied the name *O.*
 22 *destructor* to sequences that are grouped in distinct clades, neither of which include the
 23 sequences from specimens captured near the type locality. One of these clades is formed by
 24 sequences of three individuals captured in the Bolivian Yungas (clade *U*). In our study, this is
 25 the sister clade of *O. brendae*. The other clade grouped specimens identified as *O. destructor*

Eliminado: we name this individual *O. aff. messorius* (clade *K*)

Eliminado: clade named *O. messorius* by Hanson et al. (2011) is here referred to as *Oligoryzomys* sp. 1 (clade *N*) (Fig. 2; Table 1).

Comentario [pa9]: Problem 7

Eliminado: we included specimens we named *O. destructor*

Eliminado: Besides

Comentario [pa10]: Problem 7

Eliminado: Two studies (Palma et al., 2010; Hanson et al., 2011) applied the name *O. destructor* to clearly separated clades, none of which included specimens captured near the type locality.

1 captured in Ecuador (clade *Q*). Unfortunately, only the sample locality of one of those
 2 specimens is available in western slopes of the Andean mountains in the Pacific biogeographic
 3 region (locality 53; Fig. 1). Based on the distribution of the specimens from which the
 4 sequences in these two clades were obtained and on their phylogenetic position we referred to
 5 the specimens of the Bolivian Yungas (clade *U*) as *O. aff. destructor* (Fig. 2; Table 1). To
 6 confirm that this clade is in fact *O. destructor* it is necessary to analyze specimens from the
 7 type locality in Perú. Regarding the clade *Q*, Hershkovitz (1940) studied specimens captured
 8 in the western Andean slopes of Ecuador and concluded that they corresponded to a new
 9 species named *Oligoryzomys spodiurus*. Musser & Carleton (2005) posed that *O. spodiurus* is
 10 a junior synonym of *O. destructor*. Teta *et al.* (2013) suggested that specimens included in the
 11 study of Hanson *et al.* (2011) matched the description of Hershkovitz (1940); in addition, they
 12 were captured near the type locality of *O. spodiurus*. Both distribution and morphology
 13 suggest that the sequences in clade *Q* could be assigned to *O. spodiurus*, which would make
 14 valid this specific name. Since a sample from its type locality is not available, we refer to
 15 clade *Q* as *O. aff. spodiurus* (Table 1; Fig. 2).

Comentario [pa11]: Problem 7

Eliminado: Based on the distribution of these two clades and on their phylogenetic

Eliminado: , similar to *O. destructor* in external morphology

Eliminado: besides

17 *Species identification and geographic distribution of Oligoryzomys species acting as*
 18 *reservoirs of hantavirus genotypes*

19 While the knowledge of the phylogenetic relationships within the genus *Oligoryzomys*
 20 has an evolutionary interest, it is crucial for virologists to have a correct classification of the
 21 specimens in which viruses are detected. Several studies have contributed to the taxonomic
 22 status of specimens infected with hantaviruses (Rivera *et al.*, 2007; Palma *et al.*, 2010; Hanson
 23 *et al.*, 2011; Agrellos *et al.*, 2012; Firth *et al.*, 2012). As a consequence, some rodent
 24 host/hantavirus relationships have been fully established. However, other species acting as
 25 reservoirs of hantavirus genotypes still deserve additional systematic research.

1 *Oligoryzomys longicaudatus*, a species restricted to southern Chile and Argentina, acts
2 as the reservoir of the Andes hantavirus genotype (Levis *et al.*, 1998; Padula *et al.*, 2004). The
3 historical and ongoing processes determining the level of gene flow of *O. longicaudatus*
4 populations and consequently, the probability of dispersion of the Andes virus within and
5 among Argentina and Chile were evaluated in phylogeographic studies (Palma *et al.*, 2005;
6 Belmar-Lucero *et al.*, 2009; González-Ittig *et al.*, 2010b; Palma *et al.*, 2012b). Besides,
7 Torres-Perez *et al.* (2011) studied the co-divergence between *O. longicaudatus*/Andes
8 hantavirus genotype and reported that while the virus presented strong spatial subdivision in
9 three regions (Mediterranean, Valdivian and Patagonian regions of Chile) the rodent showed a
10 different evolutionary history, with a less evident geographic structuring. Regarding the
11 phylogenetic position of *O. longicaudatus* (2n=56), most authors recovered it as the sister
12 species of *O. magellanicus* (2n=54); this last species is restricted to Harrison Island in
13 southern Chile. In the present study, the *O. longicaudatus*/*O. magellanicus* clade (E-F) is
14 recovered as sister to that of the *O. flavescens* complex (A-D)(Fig. 2). An identical topology
15 was obtained in several other studies (Rivera *et al.*, 2007; Miranda *et al.*, 2009; González-Ittig
16 *et al.*, 2010a; Agrellos *et al.*, 2012; Firth *et al.*, 2012).

17 *Oligoryzomys nigripes* inhabits the Cerrado and the Atlantic Rain Forest domains in
18 Brazil (Weksler & Bonvicino, 2005; Miranda *et al.*, 2009), and the Paranaense Rainforest
19 extending along rivers Paraná, Paraguay and Uruguay (Myers & Carleton, 1981; Francés &
20 D'Elía, 2006; Rivera *et al.*, 2007; Carbajo & Teta, 2009). This rodent is recognized as the
21 natural host of the pathogenic Juitiba hantavirus in southeastern Brazil (Suzuki *et al.*, 2004;
22 Oliveira *et al.*, 2009), in northeastern Argentina (Misiones province; Padula *et al.*, 2007) and
23 in Uruguay (Delfraro *et al.*, 2008). Studies on *O. nigripes* genetic structure in an altitudinal
24 range of about 750 m in southern Brazil showed a high polymorphism and high levels of gene
25 flow among populations occupying different types of habitat (Gonçalves, Marinho & Freitas,

1 2009). Cytogenetic analyses in specimens of *O. nigripes* from Paraguay, Argentina and Brazil
2 revealed a similar karyotype ($2n=62/FN=78-82$) (Myers & Carleton, 1981; Espinosa & Reig,
3 1991; Paresque *et al.*, 2007). Agrellos *et al.* (2012) concluded that *O. eliurus* is a junior
4 synonym of *O. nigripes* on the basis of morphological, cytogenetics and molecular data.
5 Francés & D'Elía (2006) and Rivera *et al.* (2007) by using molecular markers, concluded that
6 *O. delticola* is also a synonym of *O. nigripes*. In the present study, the two sequences obtained
7 by Palma *et al.* (2010) classified as *O. eliurus* (EU192163) and *O. delticola* (EU192162) are
8 clearly part of the clade of *O. nigripes* (clade *G*; Fig. 2). This clade, represented by samples
9 from Argentina, Paraguay and Brazil, is sister to *O. stramineus* (clade *H*; Fig. 2), which is
10 endemic to the Cerrado and the Caatinga domains in Brazil (Andrades-Miranda *et al.*, 2001;
11 Weksler & Bonvicino, 2005). This relationship between *O. nigripes* and *O. stramineus* was
12 also reported by Miranda *et al.* (2009), González-Ittig *et al.* (2010a), Hanson *et al.* (2011),
13 Agrellos *et al.* (2012) and Firth *et al.* (2012). *Oligoryzomys stramineus* has not been
14 associated to any hantavirus genotype.

15 *Oligoryzomys chacoensis* inhabits the Chaco of Argentina, Bolivia and Paraguay and it
16 is the sister species to the clade of *O. nigripes* and *O. stramineus* (clade *I*; Fig. 2). This species
17 has been recognized as the reservoir of the Oran hantavirus genotype (González Della Valle *et*
18 *al.*, 2002; Rivera *et al.*, 2007) and has also been associated to Ñeembucu hantavirus in
19 Paraguay (Chu *et al.*, 2006). This last viral genotype (detected in individual TK64399)
20 clustered with the Bermejo genotype in the phylogenetic tree, which in turn, is associated to
21 *O. flavescens* West (Rivera *et al.*, 2007). In the study by Chu *et al.* (2006), the authors do not
22 mention how the rodents were identified. Besides, their study presents several of the
23 misidentifications later corrected by Rivera *et al.* (2007), such as the wrong relationships *O.*
24 *chacoensis*-Bermejo and *O. longicaudatus*-Oran. A molecular identification of the specimen

1 TK64399 is needed to clarify whether this individual actually belongs to *O. chacoensis* or to
 2 *O. flavescens* West. Therefore, the relationship *O. chacoensis*-Ñeembucu is dubious.

3 Although some progress has been made-regarding the taxonomic identification of
 4 specimens of the *O. flavescens* “complex”, there are still several unresolved relationships. As
 5 demonstrated by Rivera *et al.* (2007) and González-Ittig *et al.* (2010a), this complex includes
 6 four groups: *O. flavescens* East (clade A), *O. fornesi* (clade B), *O. flavescens* Brazil (clade C)
 7 and *O. flavescens* West (clade D). The taxonomic entity denominated *O. flavescens* West is
 8 the reservoir of the Bermejo genotype (Rivera *et al.*, 2007). In our study, this lineage presents
 9 a geographical distribution encompassing a wide altitudinal range, from 100 masl in Villa
 10 Hayes, Paraguay to 3730 masl in Huancaroma, Bolivia (Table 1). The presence of this species

Comentario [pa12]: Problem
8

11 in high altitudes could explain why two individuals captured in the Bolivian Andes belonging
 12 to this lineage (individual MSB55318-NK12051 from Comarapa, Santa Cruz and individual
 13 NK11547 from Huancaroma, Oruro) were misidentified as *O. andinus*. In the eastern flanks
 14 of the Andes mountains, Carleton & Musser (1989) identified several individuals from
 15 Bolivia (AMNH26405 and AMNH26406 from Huancaroma, Oruro; AMNH255946 from
 16 Pocoata, Potosí) and Perú (LSU19253, LSU19254, LSU19255 from Cuzco Department) as *O.*
 17 *andinus*. Unfortunately, none of these specimens have been analyzed using molecular
 18 markers. Given that the specimens from Huancaroma included in the present paper clustered
 19 within the clade of *O. flavescens* West, more studies are needed to clarify if *O. andinus* and
 20 *O. flavescens* West are sympatric at high altitudes. In Perú, specimens of *O. andinus* have
 21 been collected in several localities of the semiarid western slope of the Peruvian Andes (La
 22 Libertad, Lambayeque, Ancash and Lima Departments) (Carleton & Musser, 1989). In
 23 accordance with our present data, we restricted the name *O. andinus* to the sequence L37400,
 24 belonging to a specimen collected in Lima, Perú, relatively close to the type locality
 25 (Hacienda Llagueda, La Libertad). Although the geographic and altitudinal limits of this

1 species are unknown, its distribution would not include lowlands areas. The presence of
2 different lineages of *Oligoryzomys* such as *O. flavescens* West, *O. andinus*, *O. aff destructor*
3 and *O. aff. spodiurus* inhabiting high altitudes stresses the need for further sampling to get a
4 better knowledge of the diversity of *Oligoryzomys* rodents in the Andean region.

5 The type locality of *O. fornesi* is Nainneck in Formosa, Argentina (Massoia, 1973;
6 marked with a star in Fig. 1). Gonzalez-Ittig *et al.* (2010a) obtained a highly supported clade
7 they named *O. fornesi* that included individuals from localities of southern Paraguay and
8 northern Argentina, separated from Nainneck by less than 250 km. In the present study,
9 individual INEVH-36163 (GenBank N° HQ890936) from Colonia Buena Vista (locality 16,
10 Fig. 1), 30 km from Nainneck, is included in the clade of *O. fornesi* (Clade B; Fig. 2) with high
11 statistical support (0.99BI/81MP/88ML). Studies by Massoia (1973), Contreras & Berry
12 (1983), González-Ittig *et al.* (2010a) and a currently ongoing phylogeographic analysis in our
13 laboratory (results not shown) differentiate clearly *O. fornesi* from *O. flavescens sensu stricto*
14 (Clade A; Fig. 2) even when these two species are sympatric in the Chaco domain in
15 Argentina. These species are very similar in external morphology, often causing field
16 misidentifications. For example, individual GD10 was originally considered *O. fornesi* by
17 Palma *et al.* (2005), but then Rogers *et al.* (2009) referred to as *O. flavescens*. In the present
18 study the sequence of this last individual clearly belongs to the *O. fornesi* clade. A proper
19 classification is important in these lineages because *O. flavescens* East is the reservoir of the
20 Lechiguana genotype (Levis *et al.*, 1998) and in Argentina and Paraguay *O. fornesi* has not
21 been associated with any type of hantavirus.

22 In Brazil, specimens from Anajatuba and Santa Rita in Maranhão (locality marked
23 with a triangle in Fig. 1) were infected with the Anajatuba hantavirus (Travassos da Rosa *et*
24 *al.*, 2005, 2010). These individuals were identified as *O. fornesi* without any alpha taxonomic
25 study leading to that species denomination; no *Cytb* sequences of these specimens are

1 available in GenBank. The two localities from Maranhão are about 2800 km away from
2 Naineck (Formosa, Argentina) in a very different biogeographic region, suggesting the
3 specimens captured in Maranhão would correspond to another taxonomic entity different
4 from *O. fornesi*. Furthermore, these localities are outside the indicated distribution for *O.*
5 *fornesi* (Musser & Carleton, 2005). Specimens captured in central Brazil from localities
6 separated from Naineck about 1650 to 2000 km (44, 45, 68, 69 and 70 in Fig. 1) were also
7 identified as *O. fornesi* (Miranda *et al.* 2009; Rocha *et al.* 2011). The sequences of these
8 specimens (HM594622, HM594620, HM594619, HM594623, HM594621, DQ826022 and
9 DQ826023) form a basal group (Fig. 2) that does not include individuals from the Chaco
10 biogeographical region (Paraguay and northern Argentina) where the species was originally
11 described (Massoia, 1973). Besides, sequences of specimens identified as *O. fornesi* by
12 Miranda *et al.* (2009) yielded very different results according to what gene was considered:
13 *Cytb* sequences (DQ826022 and DQ826023) formed a basal clade in the phylogenetic tree
14 while the IRBP sequence (DQ826033), grouped with the sequence of *O. fornesi* AY163610,
15 formed a clade closely related to that of *O. flavescens*. This systematic incongruence
16 prompted González-Iltig *et al.* (2010a) to suggest that sequences DQ826022 and DQ826023
17 could be mitochondrial pseudogenes (Numts). Our present phylogenetic estimation based on
18 *Cytb* (Fig. 2) agrees with this asseveration. In our laboratory (results not shown), we co-
19 amplified Numts in some specimens of *Oligoryzomys* when we used the primer combination
20 MVZ05/MVZ16 (Smith & Patton, 1993). This does not occur when the primer combination
21 Mus14095/Mus15398 (Anderson & Yates, 2000) is used. Rocha *et al.* (2011) and Miranda *et*
22 *al.* (2009) amplified *Cytb* using the primer combination MVZ05/MVZ16, so their sequences
23 that form the basal clade here observed (Fig. 2) could be Numts. A new sequencing of the
24 *Cytb* gene using another primer combination is needed to clarify the taxonomic identification
25 of the specimens in the basal clade. In the study of Firth *et al.* (2012), the authors proposed a

1 geographic distribution for *O. fornesi* that includes the sampling sites of specimens analyzed
2 by Miranda *et al.* (2009) and Rocha *et al.* (2011). They excluded, however, the sampling sites
3 of Maranhão. Therefore, after considering all the available information, we hypothesize that
4 the specimens analyzed by Travassos da Rosa *et al.* (2005, 2010) do not correspond to *O.*
5 *fornesi*, and thus this species would not be the natural reservoir of the Anajatuba genotype.

6 Regarding the species *O. utiaritensis*, it was stated to be the reservoir of the genotype
7 Castelo dos Sonhos (Travassos da Rosa *et al.*, 2011); however, these authors did not publish
8 any *Cytb* GenBank accession number of infected rodents (the authors only published
9 accession numbers to viral strains). Although, *O. utiaritensis* was previously considered a
10 junior synonym of *O. nigripes* (Carleton & Musser, 1989) and of *O. eliurus* (Musser &
11 Carleton, 2005), Agrellos *et al.* (2012) using morphology, morphometry, karyotyping, and
12 molecular phylogenetic data, demonstrated that *O. utiaritensis* is a valid species. Firth *et al.*
13 (2012) sequenced the *Cytb* gene of the infected individuals captured by Travassos da Rosa *et*
14 *al.* (2011). These sequences grouped with those of *O. utiaritensis* obtained by Agrellos *et al.*
15 (2012), confirming that they correspond to this species. In the present study, we include
16 sequences of two of the infected rodents obtained by Firth *et al.* (2012) from Mato Grosso,
17 Brazil (locality 72; Fig. 1); they grouped with sequences of individuals from Mato Grosso and
18 Pará reported in Agrellos *et al.* (2012) (localities 47 and 48; Fig. 1) and formed a
19 monophyletic clade (clade *O*; Fig. 2). In the phylogenetic tree, *O. utiaritensis* appeared to be
20 the sister species of *O. moojeni* Weksler & Bonvicino 2005 (clade *P*), as was reported in
21 Agrellos *et al.* (2012) the two species are distantly related to *O. nigripes*.

22 As we mentioned above, Hanson *et al.* (2011) made an important contribution to the
23 knowledge of rodent host-hantavirus relationships. They demonstrated that *O. costaricensis*
24 and *O. delicatus* are the reservoirs of Choclo and Maporal hantavirus genotypes, respectively,
25 and not *O. fulvescens*. Regarding their phylogenetic relationships, *O. delicatus* (clade *L*)

1 appears in our study as the sister species of *O. rupestris* Weksler & Bonvicino, 2005 (clade
2 *M*) whereas in Hanson *et al.* (2011) it is proposed as the sister species of *O. messorius*. In the
3 case of *O. costaricensis* Hanson *et al.* (2011) recovered it as the sister species to the clade of
4 *O. vegetus* and *O. fulvescens*, a result not supported in our present study when most of the
5 species of the genus are included. Further evidence is needed to clarify the phylogenetic
6 relationships of *O. costaricensis* and *O. delicatus*. Based on the studies of Rogers *et al.* (2009)
7 and Hanson *et al.* (2011) the species *O. fulvescens* would be restricted to Central America
8 (with *O. vegetus* and *O. costaricensis*). In the two studies mentioned above *O. fulvescens*
9 appears as the sister species of *O. vegetus*. In our analysis this relationship was only
10 confirmed in the Bayesian tree (clades *S* and *R*, respectively)

11 The Rio Mamore hantavirus seems to be a complex of several genotypes: Rio Mamore
12 (Bolivia, Peru and Brazil), Rio Mamore-3 (Brazil) and Rio Mamore-4 (Brazil) (Firth *et al.*,
13 2012). The reservoir of Rio Mamore (Bharadwaj *et al.*, 1997; Powers *et al.*, 1999; Richter *et*
14 *al.*, 2010; Casapía *et al.*, 2012) and of Rio Mamore-3 (Firth *et al.*, 2012) is *O. microtis*,
15 recovered here as one of the most basal species of the genus (Fig. 2). Recently, Firth *et al.*
16 (2012) found that the reservoir of Rio Mamore-4 is an unidentified species of *Oligoryzomys*,
17 which is closely related to *O. microtis*. In our phylogenetic analysis, we included specimens
18 TTU76249 and BYU19014, infected with Rio Mamore, and AN683313 infected with Rio
19 Mamore-3; all these individuals belongs to the monophyletic clade of *O. microtis* (clade *W*).
20 The sister clade to *O. microtis* includes four individuals from Rondonia, Brazil (locality 73;
21 Fig. 1) named *Oligoryzomys* sp RT2012 by Firth *et al.* (2012) as well as a specimen from
22 Tocantins, Brazil (locality 68; Fig. 1) named *Oligoryzomys* sp RR2010a by Rocha *et al.*
23 (2011). Based on the level of genetic divergence between *Oligoryzomys* sp RT2012 and
24 *Oligoryzomys* sp RR2010a (7.1%), Firth *et al.* (2012) suggested that they correspond to two
25 different genetic species. In Fig. 2, these two lineages are clearly separated. Since

1 *Oligoryzomys* sp RT2012 has been associated with Rio Mamore-4 hantavirus, its formal
 2 taxonomic description should be performed. It is also important to determine if it is sympatric
 3 with *O. microtis*; *O. microtis* has been captured in the Amazonian domain of Peru, Bolivia
 4 and Brazil (Table 1) whereas *Oligoryzomys* sp RT2012 has been captured only in Rondonia
 5 (Brazil) within the same region.

6 **Summing up**, after re-analysing the information provided by several sources of
 7 evidence, we show in Table 2 the most **current** rodent host-viral genotypes relationships
 8 emerging from those data. Our results suggest that *O. fornesi* is not the reservoir of the
 9 Anajatuba genotype and that the relationship *O. chacoensis*-Ñeembucu genotype is
 10 unsubstantiated. **Besides**, our present work points out several controversial issues on the
 11 phylogenetic relationships in *Oligoryzomys*. **However, to get a comprehensive knowledge of**
 12 **the species boundaries in the genus *Oligoryzomys* and of the distribution of rodent hosts**
 13 **further studies encompassing more sampling sites and the re-examination of voucher**
 14 **specimens of type localities using new molecular as well as morphometrical tools are needed.**

Comentario [pa13]: Problem
9

Eliminado: reliable

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1 **References**

- 2 **Agrellos R, Bonvicino CR, Travassos da Rosa ES, Marques AAR, D'andrea OS,**
3 **Weksler M. 2012.** The taxonomic status of the Castelo dos Sonhos Hantavirus
4 reservoir, *Oligoryzomys utiaritensis* Allen 1916 (Rodentia: Cricetidae:
5 Sigmodontinae). *Zootaxa* **3220**: 1-28.
- 6 **Almeida FC, Bonvicino CR, Cordeiro-Estrela P. 2007.** Phylogeny and temporal
7 diversification of *Calomys* (Rodentia, Sigmodontinae): Implications for the
8 biogeography of an endemic genus of the open/dry biomes of South America.
9 *Molecular Phylogenetic and Evolution* **42**: 449-466.
- 10 **Anderson S, Yates TL. 2000.** A new genus and species of phyllotine rodent from Bolivia.
11 *Journal of Mammalogy* **81**: 18-36.
- 12 **Andrades-Miranda J, Oliveira LFB, Lima-Rosa AV, Nunes AP, Zanchin NIT, Mattevi**
13 **MS. 2001.** Chromosome studies of seven species of *Oligoryzomys* (Rodentia:
14 Sigmodontinae) from Brazil. *Journal of Mammalogy* **82**: 1080-1091.
- 15 **Bangs O. 1900.** List of the mammals collected in the Santa Marta region of Colombia. In:
16 Brown Jr WW, ed. *Proceedings of the New England Zoological Club* **1**: 87-102.
- 17 **Belmar-Lucero S, Godoy P, Ferrés M, Vial P, Palma RE. 2009.** Range expansion of
18 *Oligoryzomys longicaudatus* (Rodentia, Sigmodontinae) in Patagonian Chile, and first
19 record of Hantavirus in the region. *Revista Chilena de Historia Natural* **82**: 265-275.
- 20 **Bharadwaj M, Botten J, Torrez-Martinez N, Hjelle B. 1997.** Rio Mamore virus: genetic
21 characterization of a newly recognized hantavirus of the pygmy rice rat, *Oligoryzomys*
22 *microtis*, from Bolivia. *American Journal of Tropical Medicine and Hygiene* **57**: 368-
23 374.

- 1 **Blasdell K, Henttonen H, Buchy P. 2012.** Hantavirus genetic Diversity. In: Morand S,
2 Beaudeau F, Cabaret J, eds. *New frontiers of molecular epidemiology of infectious*
3 *diseases*. Springer Netherlands, 179-216.
- 4 **Cabrera AL, Willink A. 1973.** *Biogeografía de America Latina*. Monografías de la O.E.A.,
5 serie de Biología 13. Washington D.C.
- 6 **Carbajo AE, Teta P. 2009.** Distribution of the hantavirus reservoir *Oligoryzomys nigripes* in
7 Argentina: choosing spatial models for the actual and potential distribution of the
8 black-footed colilargo. *Mammalia* **73**: 313-321.
- 9 **Carleton MD, Musser GG. 1989.** Systematic studies of Oryzomyine rodents (Muridae,
10 Sigmodontinae): a synopsis of *Microryzomys*. *Bulletin of the American Museum of*
11 *Natural History* **191**: 1-83.
- 12 **Carroll DS, Mills JN, Montgomery JM, Bausch DG, Blair PJ, Burans JP, Felices V,**
13 **Gianella A, Iihoshi N, Nichol ST, Olson JG, Rogers DS, Salazar M, Ksiazek TG.**
14 **2005.** Hantavirus Pulmonary Syndrome in central Bolivia: relationships between
15 reservoir hosts, habitats, and viral genotypes. *American Journal of Tropical Medicine*
16 *and Hygiene* **72**: 42-46.
- 17 **Casapía M, Mamani E, García MP, Miraval ML, Valencia P, Quino AH, Álvarez C,**
18 **Donaires LF. 2012.** Síndrome pulmonar por Hantavirus (Virus Río Mamoré) en la
19 Amazonía Peruana. *Revista Peruana de Medicina Experimental y Salud Publica* **29**:
20 390-395.
- 21 **Chu YK, Milligan B, Owen RD, Goodin DG, Jonsson CB. 2006.** Phylogenetic and
22 geographical relationships of Hantavirus strains in Eastern and Western Paraguay.
23 *American Journal of Tropical Medicine and Hygiene* **75**:1127-1134.

- 1 **Contreras JR, Berry LM. 1983.** Notas acerca de los roedores del género *Oligoryzomys* de la
2 Provincia del Chaco, República Argentina (Rodentia, Cricetidae). *Historia Natural*
3 (Argentina) **3**: 145-148.
- 4 **Delfraro A, Tomé L, D'Elía G, Clara M, Achával F, Russi JC, Arbiza Rodonz JR. 2008.**
5 Jujutiba-like Hantavirus from 2 nonrelated rodent species, Uruguay. *Emerging*
6 *Infectious Diseases* **14**: 1447-1451.
- 7 **Espinosa MB, Reig OA. 1991.** Cytogenetics and karyosystematics of South America
8 Oryzomyine rodents (Cricetidae, Sigmodontinae) III. Banding karyotypes of
9 Argentinean *Oligoryzomys*. *Zeitschrift für Säugetierkunde* **56**: 306-317.
- 10 **Firth C, Tokarz R, Simith DB, Nunes MRT, Bhat M, Travassos da Rosa ES, Medeiros**
11 **DBA, Palacios G, Vasconcelos PFC, Lipkin WI. 2012.** Diversity and Distribution of
12 Hantaviruses in South America. *Journal of Virology* **86**: 13756-13766.
- 13 **Francés J, D'Elía G. 2006.** *Oligoryzomys delticola* es sinónimo de *O. nigripes* (Rodentia,
14 Cricetidae, Sigmodontinae). *Mastozoología Neotropical* **13**: 123-131.
- 15 **Goloboff P, Farris S, Nixon K. 2008.** TNT, a free program for phylogenetic analysis.
16 *Cladistics* **24**: 1-13.
- 17 **Gonçalves GL, Marinho JR, Freitas TRO. 2009.** Genetic structure of sigmodontine rodents
18 (Cricetidae) along an altitudinal gradient of the Atlantic Rain Forest in southern
19 Brazil. *Genetics and Molecular Biology* **32**: 882-885.
- 20 **Gonzalez Della Valle M, Edelstein A, Miguel S, Martinez VP, Cortez J, Cacace ML,**
21 **Jurgelenas G, Sosa Estani S, Padula P. 2002.** Andes virus associated with
22 Hantavirus Pulmonary Syndrome in northern Argentina and determination of the
23 precise site of infection. *American Journal of Tropical Medicine and Hygiene* **66**: 713-
24 720.

- 1 **Gonzalez-Ittig RE, Theiler GR, Gardenal CN. 2002.** A contribution to the subgeneric
2 systematics of *Oligoryzomys* (Rodentia, Muridae) from Argentina by means of PCR-
3 RFLP patterns of mitochondrial DNA. *Biochemical Systematics and Ecology* **30**: 23-
4 33.
- 5 **González-Ittig RE, Salazar-Bravo J, Barquez RM, Gardenal CN. 2010a.** Phylogenetic
6 relationships among species of the genus *Oligoryzomys* (Rodentia, Cricetidae) from
7 Central and South America. *Zoologica Scripta* 39: 511-526.
- 8 **Gonzalez-Ittig RE, Rossi-Fraire HJ, Cantoni GE, Herrero ER, Benedetti R, Gallardo**
9 **MH, Gardenal CN. 2010b.** Population genetic structure of long-tailed pygmy rice
10 rats (*Oligoryzomys longicaudatus*) from Argentina and Chile based on the
11 mitochondrial control region. *Canadian Journal of Zoology* **88**: 23-35.
- 12 **Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010.** New
13 algorithms and methods to estimate Maximum-Likelihood phylogenies: assessing the
14 performance of PhyML 3.0. *Systematic Biology* **59**: 307-321.
- 15 **Haag T, Muschner VC, Freitas LB., Oliveira LFB., Langguth AR, Mattevi MS. 2007**
16 Phylogenetic relationships among species of the genus *Calomys* with emphasis on
17 south American lowland taxa. *Journal of Mammalogy* **88**: 769–776.
- 18 **Hanson JD, Utrera A, Fulhorst CF. 2011.** The delicate pygmy rice rat (*Oligoryzomys*
19 *delicatus*) is the principal host of Maporal virus (Family Bunyaviridae, Genus
20 *Hantavirus*). *Vector-Borne and Zoonotic Diseases* **11**: 691-696.
- 21 **Hershkovitz P. 1940.** Four new oryzomyine rodents from Ecuador. *Journal of Mammalogy*
22 **21**: 78-84.
- 23 **Hershkovitz P. 1966.** Mice, land bridges and Latin American faunal interchange. In: Wenzel
24 RL, Tipton VJ, eds. *Ectoparasites of Panama*. Chicago: Field Museum of Natural
25 History, 725-751.

- 1 **Hjelle B, Torres-Pérez F. 2010.** Hantaviruses in the Americas and their role as emerging
2 pathogens. *Viruses* **2**: 2559-2586.
- 3 **Honacki JH, Kinman KE, Koepl JW. 1982.** *Mammal species of the world: A taxonomic*
4 *and geographic reference*. Lawrence, Kansas, Allen Press Inc and The Association of
5 Systematics Collections.
- 6 **Levis S, Morzunov SP, Rowe JE, Enría D, Pini N, Calderón G, Sabattini M, St. Jeor S.**
7 **1998.** Genetic diversity and epidemiology of hantaviruses in Argentina. *Journal of*
8 *Infectious Diseases* **177**: 529-538.
- 9 **Lima JFS, Bonvicino CR, Kasahara S. 2003.** A new karyotype of *Oligoryzomys*
10 (Sigmodontinae, Rodentia) from central Brazil. *Hereditas* **139**: 1-6.
- 11 **Londoño AF, Levis S, Rodas JD. 2011.** Hantavirus como agentes emergentes de importancia
12 en Suramérica. *Biomédica (Colombia)* **31**: 451-464.
- 13 **Martínez VP, Bellomo CM, Cacace ML, Suárez P, Bogni L, Padula PJ. 2010.** Hantavirus
14 Pulmonary Syndrome in Argentina, 1995–2008. *Emerging Infectious Diseases* **16**:
15 1853-1860.
- 16 **Massoia E. 1973.** Descripción de *Oryzomys fornesi*, nueva especie y nuevos datos sobre
17 algunas especies y subespecies argentinas del subgénero *Oryzomys* (*Oligoryzomys*)
18 (Mammalia-Rodentia-Cricetidae). *Revista de Investigaciones Agropecuarias INTA*
19 *Serie I Biología y Producción Animal* **10**: 21-37.
- 20 **Massoia E. 1998.** Roedores vinculados con virosis humanas en la República Argentina.
21 Capítulo 6, Vectores y Reservorios. In: 2do. Congreso Argentino de Zoonosis, 1er
22 Congreso Argentino y Latinoamericano de Enfermedades Emergentes y Asociación
23 Argentina de Zoonosis, eds. *Temas de Zoonosis y Enfermedades Emergentes*. Buenos
24 Aires, Sociedad Argentina de Zoonosis, 243-246.

- 1 **Mills JN, Yates TL, Ksiazek TG, Peters CJ, Childs JE. 1999.** Long-term studies of
2 hantavirus reservoir populations in the southwestern United States: rationale, potential,
3 and methods. *Emerging Infectious Diseases* **5**: 95-101.
- 4 **Miranda GB, Oliveira LFB, Andrades-Miranda J, Langguth A, Callegari-Jacques SM,**
5 **Mattevi M. 2009.** Phylogenetic and phylogeographic patterns in sigmodontine rodents
6 of the genus *Oligoryzomys*. *Journal of Heredity* **100**: 309-321.
- 7 **Musser GG, Carleton MD. 1993. Family Muridae. In: Wilson DE, Reeder DM, eds.**
8 ***Mammal species of the world, a taxonomic and geographic reference. Second Edition.***
9 **Smithsonian Institution Press, Washington DC, USA.**
- 10 **Musser GG, Carleton MD. 2005.** Superfamily Muroidea. In: Wilson DE, Reeder DM, eds.
11 *Mammal Species of the World*. Third Edition. John Hopkins University Press,
12 Baltimore, MD, USA.
- 13 **Myers P, Carleton MD. 1981.** The species of *Oryzomys* (*Oligoryzomys*) in Paraguay and the
14 identity of Azara's "Rat sixième ou Rat á Tarse Noir". *Miscellaneous Publications of*
15 *the Museum of Zoology of the University of Michigan* **161**: 1-41.
- 16 **Myers P, Lundrigan B, Tucker PK. 1995.** Molecular phylogenetics of Oryzomyine rodents:
17 the genus *Oligoryzomys*. *Molecular Phylogenetics and Evolution* **4**: 373-382.
- 18 **Oliveira RC, Teixeira BR, Mello FCA, Pereira AP, Duarte AS, Bonaldo MC, Bonvicino**
19 **CR, D'Andrea PS, Lemos ERS. 2009.** Genetic characterization of a Jucitaba-like
20 viral lineage in *Oligoryzomys nigripes* in Rio de Janeiro, Brazil. *Acta Tropica* **112**:
21 212-218.
- 22 **Padula P, Figueroa R, Navarrete M, Pizarro E, Cadiz R, Bellomo C, Jofre C, Zaror L,**
23 **Rodriguez E, Murúa R. 2004.** Transmission study of Andes hantavirus infection in
24 wild sigmodontine rodents. *Journal of Virology* **78**: 11972-11979.

- 1 **Padula P, Martinez VP, Bellomo C, Maidana S, San Juan J, Tagliaferri P, Bargardi S,**
2 **Vazquez C, Colucci N, Estévez J, Almiron M. 2007.** Pathogenic hantaviruses,
3 northeastern Argentina and eastern Paraguay. *Emerging Infectious Disease* **13:** 1211-
4 1214.
- 5 **Palma RE, Rivera-Milla E, Salazar-Bravo J, Torres-Pérez F, Pardiñas UFJ, Marquet**
6 **PA, Spotorno AE, Meynard AP, Yates TL. 2005.** Phylogeography of *Oligoryzomys*
7 *longicaudatus* (Rodentia: Sigmodontinae) in temperate south America. *Journal of*
8 *Mammalogy* **86:** 191-200.
- 9 **Palma RE, Rodríguez-Serrano E, Rivera-Milla E, Hernandez CE, Salazar-Bravo J,**
10 **Carma MI, Belmar-Lucero S, Gutierrez-Tapia P, Zeballos H, Yates TL. 2010.**
11 Phylogenetic relationships of the pygmy rice rats of the genus *Oligoryzomys* Bangs,
12 1900 (Rodentia: Sigmodontinae). *Zoological Journal of the Linnean Society of London*
13 **160:** 551-566.
- 14 **Palma RE, Polop JJ, Owen RD, Mills JN. 2012a.** Ecology of rodent-associated
15 hantaviruses in the southern cone of South America: Argentina, Chile, Paraguay, and
16 Uruguay. *Journal of Wildlife Diseases* **48:** 267-281.
- 17 **Palma RE, Boric-Bargetto D, Torres-Pérez F, Hernández CE, Yates TL. 2012b.**
18 Glaciation effects on the phylogeographic structure of *Oligoryzomys longicaudatus*
19 (Rodentia: Sigmodontinae) in the Southern Andes. *PLoS ONE* **7:** e32206.
- 20 **Paresque R, de Jesus Silva MJ, Yonenaga-Yassuda Y, Fagundes V. 2007.** Karyological
21 geographic variation of *Oligoryzomys nigripes* Olfers, 1818 (Rodentia, Cricetidae)
22 from Brazil. *Genetics and Molecular Biology* **30:** 43-53.
- 23 **Patton JL, da Silva MNF. 1995.** A review of the spiny mouse genus *Scolomys* (Rodentia:
24 Muridae: Sigmodontinae) with the description of a new species from the western
25 Amazon of Brazil. *Proceedings of the Biological Society of Washington* **108:** 319-337.

- 1 **Percequillo AR, Weksler M, Costa LP. 2011.** A new genus and species of rodent from the
2 Brazilian Atlantic Forest (Rodentia: Cricetidae: Sigmodontinae: Oryzomyini), with
3 comments on oryzomyine biogeography. *Zoological Journal of the Linnean Society of*
4 *London* **161**: 357-390.
- 5 **Posada D. 2008.** jModelTest: phylogenetic model averaging. *Molecular Biology and*
6 *Evolution* **25**: 1253-1256.
- 7 **Powers AM, Mercer D, Watts DM, Guzman H, Fulhorst CF, Popov VL, Tesh RB. 1999.**
8 Isolation and genetic characterization of a hantavirus (Bunyaviridae: Hantavirus) from
9 a rodent *Oligoryzomys microtis* (Muridae), collected in northeastern Perú. *The*
10 *American Journal of Tropical Medicine and Hygiene* **61**: 92-98.
- 11 **Rambaut A, Drummond AJ. 2007.** Tracer, Version 1.5. University of Oxford, Oxford, UK.
12 Available at: <http://tree.bio.ed.ac.uk/software/tracer/>.
- 13 **Ramsden C, Holmes EC, Charleston MA. 2009.** Hantavirus evolution in relation to its
14 rodent and insectivore hosts: no evidence for codivergence. *Molecular Biology and*
15 *Evolution* **26**: 143-153.
- 16 **Reig OA. 1986.** Diversity patterns and differentiation of high Andean rodents. In:
17 Vuilleumier F, Monasterio M, eds. *High altitude tropical biogeography*. New York:
18 Oxford University Press, 404-440.
- 19 **Richter MH, Hanson JD, Cajimat MN, Milazzo ML, Fulhorst CF. 2010.** Geographical
20 range of Rio Mamoré virus (Family Bunyaviridae, Genus Hantavirus) in association
21 with the small-eared pygmy rice rat (*Oligoryzomys microtis*). *Vector-Borne and*
22 *Zoonotic Diseases* **10**: 613-620.
- 23 **Rinehart TA, Grahn RA, Wichman HA. 2005.** SINE extinction preceded LINE extinction
24 in Sigmodontine rodents: implications for retrotranspositional dynamics and
25 mechanisms. *Cytogenetics Genome Research* **110**: 416-425.

- 1 **Rivera PC, González-Ittig RE, Rossi-Fraire HJ, Levis S, Gardenal CN. 2007.** Molecular
2 identification of species of the genus *Oligoryzomys*, putative reservoirs of hantaviruses
3 and phylogenetic relationships among the species present in Argentina. *Zoologica*
4 *Scripta* **36**: 231-239.
- 5 **Rocha RG, Ferreira E, Costa BMA, Martins ICM, Leite YLR, Costa LP, Fonseca C.**
6 **2011.** Small mammals of the mid-Araguaia River in central Brazil, with the
7 description of a new species of climbing rat. *Zootaxa* **2789**: 1-34.
- 8 **Rogers DS, Arenas EA, González-Cózatl FX, Hardy DK, Hanson JD, Lewis-Rogers N.**
9 **2009.** Molecular phylogenetics of *Oligoryzomys fulvescens* based on cytochrome b
10 gene sequences, with comments on the evolution of the genus *Oligoryzomys*. In:
11 Cervantes-Reza FA, Hortelano Moncada Y, Vargas Cuenca J, eds. *60 Años de la*
12 *Colección Nacional de Mamíferos del Instituto de Biología, UNAM. Aportaciones al*
13 *Conocimiento y Conservación de los Mamíferos Mexicanos*. Instituto de Biología,
14 Universidad Nacional Autónoma de México, 179-192.
- 15 **Ronquist F, Huelsenbeck JP. 2003.** MrBayes 3: Bayesian phylogenetic inference under
16 mixed models. *Bioinformatics* **19**: 1572-1574.
- 17 **Schmaljohn CS, Hasty SE, Dalrymple JM, LeDuc JW, Lee HW, von Bonsdorff CH,**
18 **Brummer-Korvenkontio M, Vaheri A, Tsai TF, Regnery HL, Doldgaber D, Lee**
19 **PW. 1985.** Antigenic and genetic properties of viruses linked to hemorrhagic fever
20 with renal syndrome into a newly defined genus of Bunyaviridae. *Science* **227**: 1041-
21 1044.
- 22 **Silva MJ, Yonenaga-Yassuda Y. 1997.** New karyotype of two related species of
23 *Oligoryzomys* genus (Cricetidae, Rodentia) involving centric fusion with loss of NORs
24 and distribution of telomeric (TTAGGG)_n sequences. *Hereditas* **127**: 217-229.

- 1 **Smith MF, Patton JL. 1993.** The diversification of South American murid rodents: evidence
2 from mitochondrial DNA sequence data for the akodontine tribe. *Biological Journal of*
3 *the Linnean Society* **50**: 149-177.
- 4 **Suzuki A, Bisordi I, Levis S, Garcia J, Pereira LE, Souza RP, Sugahara TK, Pini N,**
5 **Enria D, Souza LTM. 2004.** Identifying rodent hantavirus reservoirs, Brazil.
6 *Emerging Infectious Disease* **10**: 2127-2134.
- 7 **Tate GHH. 1932.** The taxonomic history of the South and Central American cricetid rodents
8 of the genus *Oryzomys*. Part 2: subgenera *Oligoryzomys*, *Thallomyscus*, and
9 *Melanomys*. *American Museum Novitates* **580**: 1-16.
- 10 **Teta P, Jayat JP, Ortiz PE, D'Elía G. 2013.** The taxonomic status of *Oligoryzomys brendae*
11 Massoia, 1998 (Rodentia, Cricetidae), with comments on the availability of this name.
12 *Zootaxa* **3641**: 433-447.
- 13 **Thomas O. 1901. On mammals obtained by Mr. Alphonse Robert on the Rio Jordao, Minas**
14 **Geraes. *Annals and Magazine of Natural History*, ser. 7, 8: 526-536.**
- 15 **Torres-Pérez F, Palma RE, Hjelle B, Holmes EC, Cook JA. 2011.** Spatial but not temporal
16 co-divergence of a virus and its mammalian host. *Molecular Ecology* **20**: 4109-4122.
- 17 **Travassos da Rosa ES, Mills JN, Padula PJ, Elkhoury MR, Ksiazek TG, Mendes WS,**
18 **Santos ED, Araujo GCB, Martinez VP, Rosa JFST, Edelstein A, Vasconcelos**
19 **PFC. 2005.** Newly recognized hantaviruses associated with Hantavirus Pulmonary
20 Syndrome in northern Brazil: partial genetic characterization of viruses and serologic
21 implication of likely reservoirs. *Vector-Borne and Zoonotic Diseases* **5**: 11-19
- 22 **Travassos da Rosa ES, Sampaio de Lemos ER, Almeida Medeiros DB, Simith DB, Souza**
23 **Pereira A, Elkhoury MR, Mendes WS, Vidigal JRB, de Oliveira RC, D'Andrea**
24 **PS, Bonvicino CR, Cruz ACR, Nunes MRT, Vasconcelos PFC. 2010.** Hantaviruses

- 1 and Hantavirus Pulmonary Syndrome, Maranhão, Brazil. *Emerging Infectious*
2 *Diseases* **16**: 1952-1955.
- 3 **Travassos da Rosa ES, Medeiros DBA, Nunes MRT, Simith DB, Souza Pereira A,**
4 **Elkhoury MR, Lavocat M, Marques AAR, Via AV, D'Andrea PS, Bonvicino CR,**
5 **Sampaio de Lemos ER, Vasconcelos PFC. 2011.** Pygmy rice rat as potential host of
6 Castelo dos Sonhos Hantavirus. *Emerging Infectious Diseases* **17**: 1527-1530.
- 7 **Weksler M, Bonvicino CR. 2005.** Taxonomy of pigmy rice rats genus *Oligoryzomys* Bangs,
8 1900 (Rodentia, Sigmodontinae) of the Brazilian Cerrado with the description of two
9 new species. *Arquivos do Museu Nacional, Rio de Janeiro (Brazil)* **63**: 113-130.

1 **Legends**

2

3 **Figure 1:** Geographical locations listed in Table 1 for individuals with available *Cytb*
4 sequences in GenBank. The following locations are indicated with an arrow and a symbol:
5 star: Nainock (Formosa, Argentina) the type locality of *O. fornesi*; triangle: area in Maranhão
6 (Brazil) where individuals infected with the Anajatuba hantavirus were captured; pentagon:
7 Kanaku Mountains (Guyana) the type locality of *O. messorius*.

8

9 **Figure 2:** Phylogram of the Bayesian consensus tree obtained from the *Cytb* data set after ten
10 million generations. For each individual the GenBank Accession Number and the country of
11 origin are indicated. Each clade is indicated with a letter and the species name. **:
12 corresponds to specimens infected with different genotypes of Hantavirus. The order of the
13 supporting values of the nodes is: Bayesian posterior probabilities/Maximum
14 Parsimony/Maximum Likelihood. Sequences of *Pseudoryzomys simplex*, *Neacomys minutus*,
15 *Microryzomys minutus*, *Holochilus chacarius* and *Euryoryzomys russatus* were used as
16 outgroups. ⊕ Indicates the alternative positions of the sequence L37400 (*O. andinus*) using
17 the pruning procedure implemented in TNT.

Table 1. List of *Oligoryzomys* taxa with previous classification and that obtained in González-Ittig et al. (2010) and in the present study.

Previous classification and its citation	Classification of González Ittig et al (2010a) and the present results	Accession Number	Voucher Number	Capture sites (letters in parentheses correspond to squares in Fig. 1)
<i>O. flavescens</i> East (González-Ittig et al. 2010a)	<i>O. flavescens</i> East (clade A)	GU185921	PV27	(5) Uruguay, San José, Puntas de Valdez
<i>O. flavescens</i> East (González-Ittig et al. 2010a)	<i>O. flavescens</i> East (clade A)	GU185922	PV32	(5) Uruguay, San José, Puntas de Valdez
<i>O. flavescens</i> East (González-Ittig et al. 2010a)	<i>O. flavescens</i> East (clade A)	GU185924	UP51	(6) Argentina, Buenos Aires, La Balandra
<i>O. flavescens</i> East (González-Ittig et al. 2010a)	<i>O. flavescens</i> East (clade A)	GU185925	BA850	(7) Argentina, Buenos Aires, La Plata
<i>O. flavescens</i> East (González-Ittig et al. 2010a)	<i>O. flavescens</i> East (clade A)	GU185923	PL32022	(8) Argentina, La Pampa, Reserva Provincial Parque Luro
<i>O. flavescens</i> East (González-Ittig et al. 2010a)	<i>O. flavescens</i> East (clade A)	GU185920	OI9-MACN22830	(9) Argentina, Chaco, Parque Nacional Chaco
<i>O. flavescens</i> East (González-Ittig et al. 2010a)	<i>O. flavescens</i> East (clade A)	GU185919	OI15-MACN22835	(9) Argentina, Chaco, Parque Nacional Chaco
<i>O. fornesi</i> (González-Ittig et al. 2010a)	<i>O. fornesi</i> (clade B)	GU185918	OI40-MACN22837	(9) Argentina, Chaco, Parque Nacional Chaco
<i>O. fornesi</i> (González-Ittig et al. 2010a)	<i>O. fornesi</i> (clade B)	GU185917	OI14-MACN22834	(9) Argentina, Chaco, Parque Nacional Chaco
<i>O. fornesi</i> (this study)	<i>O. fornesi</i> (clade B)	HQ890936	INEVH36163	(16) Argentina, Formosa, Colonia Buena Vista
<i>O. fornesi</i> (Palma et al. 2005), but <i>O. flavescens</i> (Rogers et al. 2009)	<i>O. fornesi</i> (clade B)	AY452199	GD010	(17) Paraguay, Misiones, Hotel Centú Cue
<i>O. fornesi</i> (Myers et al. 1995)	<i>O. fornesi</i> (clade B)	L37391	UMMZ133816	(18) Paraguay Caaguazú, Carayaó
<i>O. flavescens</i> Brazil (Miranda et al. 2009)	<i>O. flavescens</i> Brazil (clade C)	DQ826012	LF2106	(19) Brazil, Rio Grande do Sul, Mostardas, Capão do Leão
<i>O. flavescens</i> Brazil (Miranda et al. 2009)	<i>O. flavescens</i> Brazil (clade C)	DQ826014	MN37722	(20) Brazil, Rio Grande do Sul, Charqueadas
<i>O. flavescens</i> Brazil (Miranda et al. 2009)	<i>O. flavescens</i> Brazil (clade C)	DQ826013	MN37699	(21) Brazil, Rio Grande do Sul, Tainhas
<i>O. flavescens</i> West (González-Ittig et al. 2010a)	<i>O. flavescens</i> West (clade D)	GU185916	SLBCH	(10) Argentina, Córdoba, Pampa de San Luis
<i>O. flavescens</i> West (González-Ittig et al. 2010a)	<i>O. flavescens</i> West (clade D)	GU185915	CE11	(11) Argentina, Córdoba, Capilla de los Remedios
<i>O. flavescens</i> West (González-Ittig et al. 2010a)	<i>O. flavescens</i> West (clade D)	GU185913	Or22531	(12) Argentina, Salta, Orán
<i>O. flavescens</i> West (González-Ittig et al. 2010a)	<i>O. flavescens</i> West (clade D)	GU185914	Or22523	(12) Argentina, Salta, Orán
<i>O. fornesi</i> (Myers et al. 1995)	<i>O. flavescens</i> West ((clade D)	L37392	UMMZ133833	(13) Paraguay, Presidente Hayes, Villa Hayes
<i>O. andinus</i> (Palma et al. 2010; Agrellos et al. 2012)	<i>O. flavescens</i> West (clade D)	AY452200	NK11547	(14) Bolivia, Oruro, Huancaroma
<i>O. andinus</i> (Hanson et al. 2011)	<i>O. flavescens</i> West (clade D)	GU393999	MSB55318-NK12051	(15) Bolivia, Santa Cruz, 28 km NW of Comarapa
<i>O. longicaudatus</i> (Palma et al. 2005)	<i>O. longicaudatus</i> (clade E)	AY452198	NK105650	(2) Chile, Magallanes, Torres del Paine
<i>O. longicaudatus</i> (Palma et al. 2005)	<i>O. longicaudatus</i> (clade E)	AY452197	NK105649	(2) Chile, Magallanes, Torres del Paine
<i>O. longicaudatus</i> (Smith & Patton 1993)	<i>O. longicaudatus</i> (clade E)	U03535	MVZ155842	(3) Argentina, Río Negro, Bariloche

<i>O. longicaudatus</i> (González-Ittig et al. 2010a)	<i>O. longicaudatus</i> (clade E)	GU185912	Bar23403	(3) Argentina, Río Negro, Bariloche
<i>O. longicaudatus</i> (González-Ittig et al. 2010a)	<i>O. longicaudatus</i> (clade E)	GU185911	Bar23404	(3) Argentina, Río Negro, Bariloche
<i>O. longicaudatus</i> (Palma et al. 2005)	<i>O. longicaudatus</i> (clade E)	AY275703	UP374	(4) Argentina, Buenos Aires, Bahía San Blas
<i>O. magellanicus</i> (Palma et al. 2005)	<i>O. magellanicus</i> (clade F)	AY275705	CZIP1025	(1) Chile, Magallanes, Río Penitente
<i>O. nigripes</i> (González-Ittig et al. 2010a)	<i>O. nigripes</i> (clade G)	GU185908	UP45	(6) Argentina, Buenos Aires, La Balandra
<i>O. nigripes</i> (González-Ittig et al. 2010a)	<i>O. nigripes</i> (clade G)	GU185909	UP46	(6) Argentina, Buenos Aires, La Balandra
<i>O. nigripes</i> (González-Ittig et al. 2010a)	<i>O. nigripes</i> (clade G)	GU185905	Roro040	(22) Argentina, Chaco, Selvas de Río Oro
<i>O. nigripes</i> (González-Ittig et al. 2010a)	<i>O. nigripes</i> (clade G)	GU185910	LIF122	(23) Argentina, Chaco, Camino Isla Cerrito
<i>O. nigripes</i> (González-Ittig et al. 2010a)	<i>O. nigripes</i> (clade G)	GU185906	CP007	(24) Argentina, Misiones, Cuñapirú
<i>O. nigripes</i> (González-Ittig et al. 2010a)	<i>O. nigripes</i> (clade G)	GU185907	OI105-MACN22262	(25) Argentina, Misiones, Reserva Provincial Urugua-í
<i>O. nigripes</i> (Myers et al. 1995)	<i>O. nigripes</i> (clade G)	L37393	UMMZ133836	(18) Paraguay Caaguazú, Carayaó
<i>O. fornesi</i> (Rinehart, Grahn & Wichman, 2005)	<i>O. nigripes</i> (clade G)	AY041196	NK22527	(26) Paraguay, Amambay, Parque Nacional Cerro Corá
<i>O. nigripes</i> (Miranda et al. 2009)	<i>O. nigripes</i> (clade G)	DQ826005	ZE72	(21) Brazil, Rio Grande do Sul, Tainhas
<i>O. nigripes</i> (Miranda et al. 2009)	<i>O. nigripes</i> (clade G)	DQ826004	UFPB357	(27) Brazil, Espírito Santo, Monte Verde
<i>O. nigripes</i> (Palma et al. 2010)	<i>O. nigripes</i> (clade G)	EU192161	GD547	(74) Paraguay, Paraguairí, Costa del Río Tebuicary
<i>O. delticola</i> (Palma et al. 2010)	<i>O. nigripes</i> (clade G)	EU192162	GD569	(75) Uruguay, Depto Rivera, Lunarejo (propiedad Sr. Abelenda)
<i>O. eliiurus</i> (Palma et al. 2010)	<i>O. nigripes</i> (clade G)	EU192163	NK42266	(76) Brazil, Sao Paulo, Guariba
<i>O. stramineus</i> (Miranda et al. 2009)	<i>O. stramineus</i> (clade H)	DQ826026	UFPB1825	(42) Brazil, Goias, Mambai
<i>O. stramineus</i> (Miranda et al. 2009)	<i>O. stramineus</i> (clade H)	DQ826027	UFPB1827	(42) Brazil, Goias, Mambai
<i>O. chacoensis</i> (González-Ittig et al. 2010a)	<i>O. chacoensis</i> (clade I)	GU185902	JY1332	(28) Argentina, Jujuy, San Salvador de Jujuy
<i>O. chacoensis</i> (Myers et al. 1995)	<i>O. chacoensis</i> (clade I)	L37387	UMMZ124208	(29) Paraguay, Chaco, Madrejón
<i>O. chacoensis</i> (Myers et al. 1995)	<i>O. chacoensis</i> (clade I)	L37401	AMNH247773	(30) Bolivia, Santa Cruz, Ingenio Mora
<i>O. chacoensis</i> (González-Ittig et al. 2010a)	<i>O. chacoensis</i> (clade I)	GU185903	Or22496	(12) Argentina, Salta, Orán
<i>O. chacoensis</i> (González-Ittig et al. 2010a)	<i>O. chacoensis</i> (clade I)	GU185904	Or22498	(12) Argentina, Salta, Orán
<i>O. costaricensis</i> (Hanson et al. 2011)	<i>O. costaricensis</i> (clade J)	EU258539	MVZ155316-LSUMZ4745	(61) Costa Rica, Cartago, 2km NE Cartago city
<i>O. costaricensis</i> (Hanson et al. 2011)	<i>O. costaricensis</i> (clade J)	EU192164	MSB96073-NK101588	(62) Panamá, Santos, Las Tablas
<i>O. costaricensis</i> (Hanson et al. 2011)	<i>O. costaricensis</i> (clade J)	GU393989	TK163370	(63) Panamá, Gamboa
<i>O. costaricensis</i> (Hanson et al. 2011)	<i>O. costaricensis</i> (clade J)	GU393988	TK163369	(63) Panama, Gamboa
<i>O. messorius</i> (Miranda et al. 2009)	<i>O. aff. messorius</i> (clade K)	DQ826024	MN37751	(49) Brazil, Roraima, Surumú

<i>Oligoryzomys</i> sp 2 (González-Ittig et al. 2010a); <i>O. delicatus</i> (Hanson et al. 2011)	<i>O. delicatus</i> (clade L)	DQ227457	FHV4083-TK138080	(54) Venezuela, Portuguesa, Caño Delgadito, Hato Maporal
<i>O. fulvescens</i> (Percequillo, Weksler & Costa, 2011)	<i>O. delicatus</i> (clade L)	GU126529	AMNH257262	(55) Venezuela, Sucre, 9.7 km SE of Guaraúnos
<i>O. delicatus</i> (Hanson et al. 2011)	<i>O. delicatus</i> (clade L)	GU393997	AMNH257263-HGC773	(55) Venezuela, Sucre, 9.7 km SE of Guaraúnos
<i>O. delicatus</i> (Hanson et al. 2011)	<i>O. delicatus</i> (clade L)	GU393994	FHV3977-TK139248	(56) Venezuela, Cojedes, near Caño Hondo
<i>O. delicatus</i> (Hanson et al. 2011)	<i>O. delicatus</i> (clade L)	GU393995	FHV3968-TK138247-	(56) Venezuela, Cojedes, near Caño Hondo
<i>O. delicatus</i> (Hanson et al. 2011)	<i>O. delicatus</i> (clade L)	GU393996	FHV4110-TK138249	(54) Venezuela, Portuguesa, Caño Delgadito, Hato Maporal
<i>O. delicatus</i> (Hanson et al. 2011)	<i>O. delicatus</i> (clade L)	GU393993	TK21065	Suriname, capture site not available
<i>O. rupestris</i> (Agrellos et al. 2012)	<i>O. rupestris</i> (clade M)	JQ013763	MN50322	(46) Brazil, Goiás, Alto Paraíso de Goiás
<i>O. rupestris</i> (Agrellos et al. 2012)	<i>O. rupestris</i> (clade M)	JQ013764	MN50326	(46) Brazil, Goiás, Alto Paraíso de Goiás
<i>Oligoryzomys</i> sp. (Miranda et al. 2009)	<i>Oligoryzomys</i> sp. 1 (clade N)	DQ826025	MN37756	(50) Brazil, Amapá, Tartarugalzinho
<i>O. messorius</i> (Hanson et al. 2011)	<i>Oligoryzomys</i> sp. 1 (clade N)	EU258546	CM76892-TK17858	(51) Suriname, Nickerie, Sipaliwini Airstrip
<i>O. messorius</i> (Hanson et al. 2011)	<i>Oligoryzomys</i> sp. 1 (clade N)	EU258537	ACUNHC275	(52) Venezuela, Amazonas, Pozon, 50 km NE of Puerto Ayacucho"
<i>O. utiaritensis</i> (Agrellos et al. 2012)	<i>O. utiaritensis</i> (clade O)	JQ013748	MN75596	(47) Brazil: Mato Grosso, Sapezal, Fazenda Begolim
<i>O. utiaritensis</i> (Agrellos et al. 2012)	<i>O. utiaritensis</i> (clade O)	JQ013757	MN75597	(47) Brazil: Mato Grosso, Sapezal, Fazenda Begolim
<i>O. utiaritensis</i> (Agrellos et al. 2012)	<i>O. utiaritensis</i> (clade O)	JQ013760	MN75598	(47) Brazil: Mato Grosso, Sapezal, Fazenda Begolim
<i>O. utiaritensis</i> (Agrellos et al. 2012)	<i>O. utiaritensis</i> (clade O)	JQ013761	MN75613-	(48) Brazil, Pará, Altamira, Castelo dos Sonhos
<i>O. utiaritensis</i> (Agrellos et al. 2012)	<i>O. utiaritensis</i> (clade O)	JQ013762	MN75609	(48) Brazil, Pará, Altamira, Castelo dos Sonhos
<i>O. utiaritensis</i> (Agrellos et al. 2012)	<i>O. utiaritensis</i> (clade O)	JQ013776	MN75612	(48) Brazil, Pará, Altamira, Castelo dos Sonhos
<i>O. utiaritensis</i> (Firth et al. 2012)	<i>O. utiaritensis</i> (clade O)	JX443655	AN717307/BRA299	(72) Brazil, Mato Grosso, Campo Novo dos Parecis
<i>O. utiaritensis</i> (Firth et al. 2012)	<i>O. utiaritensis</i> (clade O)	JX443664	AN717313/BRA300	(72) Brazil, Mato Grosso, Campo Novo dos Parecis
<i>O. moojeni</i> (Miranda et al. 2009)	<i>O. moojeni</i> (clade P)	DQ826016	MN36220	(43) Brazil, Goiás, 20 km NW of Colinas do Sul
<i>O. moojeni</i> (Miranda et al. 2009)	<i>O. moojeni</i> (clade P)	DQ826017	MN36357	(43) Brazil, Goiás, 20 km NW of Colinas do Sul
<i>O. moojeni</i> (Miranda et al. 2009)	<i>O. moojeni</i> (clade P)	DQ826019	MN36832	(44) Brazil, Goiás, 40 km SW of Minaçú, Ríó Tocantinzinho,
<i>O. moojeni</i> (Miranda et al. 2009)	<i>O. moojeni</i> (clade P)	DQ826020	MN37282	(45) Brazil, Goiás, 40 km NE of Uruaçú
<i>O. moojeni</i> (Miranda et al. 2009)	<i>O. moojeni</i> (clade P)	DQ826021	MN37441	(45) Brazil, Goiás, 40 km NE of Uruaçú
<i>O. destructor</i> (Hanson et al. 2011)	<i>O. aff. spodiurus</i> (clade Q)	GU393990	TEL1482	Ecuador, capture site not available
<i>O. destructor</i> (Hanson et al. 2011)	<i>O. aff. spodiurus</i> (clade Q)	GU393991	TEL1481	Ecuador, capture site not available

<i>O. destructor</i> (Hanson et al. 2011)	<i>O. aff. spodiurus</i> (clade Q)	GU393992	ACUNHC899-TEL1526	Ecuador, capture site not available
<i>O. destructor</i> (Rogers et al. 2009)	<i>O. aff. spodiurus</i> (clade Q)	EU258544	ACUNHC898-TEL1479	(53) Ecuador, Pichincha, 60 km N of Quito, Tandayapa valley
<i>O. vegetus</i> (Myers et al. 1995)	<i>O. vegetus</i> (clade R)	L37386	UMMZ116911	(57) Panama, Chiriqui, Rio Chiriqui Viejo
<i>O. vegetus</i> (Rogers et al. 2009)	<i>O. vegetus</i> (clade R)	EU294249	BYU15218	(58) Costa Rica, Cartago, Instituto Costarricense de Electricidad, Rio Macho
<i>O. vegetus</i> (Rogers et al. 2009)	<i>O. vegetus</i> (clade R)	EU294252	BYU15215	(59) Costa Rica, Alajuela Prov, San Isidro, 3Km N of Laguna Fraijanes
<i>O. vegetus</i> (Rogers et al. 2009)	<i>O. vegetus</i> (clade R)	EU294251	BYU15217	(59) Costa Rica, Alajuela Prov, San Isidro, 3Km N of Laguna Fraijanes
<i>O. vegetus</i> (Rogers et al. 2009)	<i>O. vegetus</i> (clade R)	EU258538	ROM112192	(60) Nicaragua, Rivas, Rivas
<i>O. fulvescens</i> (Rogers et al. 2009)	<i>O. fulvescens</i> (clade S)	EU294234	ASNHC1666	(64) Mexico, Chiapas, 12 km N of Berriozabal,
<i>O. fulvescens</i> (Rogers et al. 2009)	<i>O. fulvescens</i> (clade S)	EU294232	ASNHC1670	(65) Mexico, Chiapas, 9.5 km S of Palenque,
<i>O. fulvescens</i> (Rogers et al. 2009)	<i>O. fulvescens</i> (clade S)	EU294248	CNMA34236	(66) Mexico, Veracruz, 18 km NE of Teocelo
<i>O. fulvescens</i> (Rogers et al. 2009)	<i>O. fulvescens</i> (clade S)	EU294235	BYU15797	(67) Mexico, Puebla, 10 km N of Zacapoaxtla
<i>O. destructor</i> (González-Ittig et al. 2010a)	<i>O. brendae</i> (clade T)	GU185900	PIDBA 986	(31) Argentina, Salta, Metán
<i>O. destructor</i> (González-Ittig et al. 2010a)	<i>O. brendae</i> (clade T)	GU185901	JY1245	(28) Argentina, Jujuy, San Salvador de Jujuy
<i>Oligoryzomys sp.1</i> (Palma et al. 2010)	<i>O. brendae</i> (clade T)	EU 192167	MIC210	(32) Argentina, Catamarca Province, Dept Ambato, Las Juntas
<i>Oligoryzomys sp.1</i> (Palma et al. 2010)	<i>O. brendae</i> (clade T)	EU192168	MIC211	(32) Argentina, Catamarca Province, Dept Ambato, Las Juntas
<i>Oligoryzomys sp.1</i> (Palma et al. 2010)	<i>O. brendae</i> (clade T)	EU192169	MIC203	(32) Argentina, Catamarca Province, Dept Ambato, Las Juntas
<i>Oligoryzomys sp.</i> (Myers et al. 1995)	<i>O. aff. destructor</i> (clade U)	L37402	AMNH263838	(33) Bolivia, Chuquisaca, Río Limon
<i>O. flavescens</i> (Palma et al. 2010)	<i>O. aff. destructor</i> (clade U)	EU192170	NK21532	(34) Bolivia, Depto Chuquisaca, 9 km by road N of Padilla
<i>O. destructor</i> (Palma et al. 2010)	<i>O. aff. destructor</i> (clade U)	EU192171	NK22846	(35) Bolivia, Depto Cochabamba, 17 km E of Totora
<i>O. andinus</i> (Myers et al. 1995)	<i>O. andinus</i> (clade V)	L37400	AMNH230986	(41) Peru, Lima, Casapalca.
<i>O. microtis</i> (Carroll et al. 2005)	<i>O. microtis</i> (clade W)	AY439000	BYU19014	(36) Bolivia, Santa Cruz, Dinamarca
<i>O. microtis</i> (Palma et al. 2010)	<i>O. microtis</i> (clade W)	EU192172	NK13425	(37) Bolivia, Depto Beni, 3 km S of Rurrenabaque
<i>O. microtis</i> (Patton & da Silva 1995)	<i>O. microtis</i> (clade W)	U58381	MNFS1321	(38) Brazil, Acre, Igarapé Porangaba
<i>O. microtis</i> (Hanson et al. 2011)	<i>O. microtis</i> (clade W)	EU258549	MVZ193858	(39) Brazil, Amazonas, Jaiu
<i>O. microtis</i> (Richter et al. 2010)	<i>O. microtis</i> (clade W)	FJ374766	TTU76249	(40) Peru, Loreto, Iquitos, Zona Marina, Hospital Iquitos II
<i>O. microtis</i> (Firth et al. 2012)	<i>O. microtis</i> (clade W)	JX443647	AN683313/BRA271	(71) Brazil, Amazonas, Itacoatiara
<i>O. microtis</i> (Firth et al. 2012)	<i>O. microtis</i> (clade W)	JX443648	AN683316/BRA273	(71) Brazil, Amazonas, Itacoatiara
<i>Oligoryzomys sp</i> RT2012 (Firth et al. 2012)	<i>Oligoryzomys sp</i> RT2012 (clade X)	JX443663	AN693292/BRA293	(73) Brazil, Rondonia, Alto Paraíso

<i>Oligoryzomys</i> sp RT2012 (Firth et al. 2012)	<i>Oligoryzomys</i> sp RT2012 (clade X)	JX443662	AN693288/BRA292	(73) Brazil, Rondonia, Alto Paraíso
<i>Oligoryzomys</i> sp RT2012 (Firth et al. 2012)	<i>Oligoryzomys</i> sp RT2012 (clade X)	JX443666	AN693247/BRA286	(73) Brazil, Rondonia, Alto Paraíso
<i>Oligoryzomys</i> sp RT2012 (Firth et al. 2012)	<i>Oligoryzomys</i> sp RT2012 (clade X)	JX443657	AN693307/BRA295	(73) Brazil, Rondonia, Alto Paraíso
<i>Oligoryzomys</i> sp RR2010a (Rocha et al. 2011)	<i>Oligoryzomys</i> sp RR2010a (clade Y)	HM594618	UFES1442	(68) Brazil: Tocantins, Pium
<i>O. fornesi</i> (Rocha et al. 2011)	--- ^a	HM594622	UFES1440	(68) Brazil: Tocantins, Pium
<i>O. fornesi</i> (Rocha et al. 2011)	--- ^a	HM594620	UFES1373	(69) Brazil: Tocantins, Lagoa da Confusão
<i>O. fornesi</i> (Rocha et al. 2011)	--- ^a	HM594619	UFES1372	(69) Brazil: Tocantins, Lagoa da Confusão
<i>O. fornesi</i> (Rocha et al. 2011)	--- ^a	HM594623	UFES1441	(70) Brazil: Pará, Santana do Araguaia
<i>O. fornesi</i> (Rocha et al. 2011)	--- ^a	HM594621	UFES1371	(70) Brazil: Pará, Santana do Araguaia
<i>O. fornesi</i> (Miranda et al. 2009)	--- ^a	DQ826022	MN36746	(44) Brazil, Goiás, 40 km SW of Minaçú, Ríó Tocantinzinho,
<i>O. fornesi</i> (Miranda et al. 2009)	--- ^a	DQ826023	MN36928	(45) Brazil, Goiás, 40 km NE of Uruaçú

a: possible pseudogenes or Numts.

Table 2. Species of *Oligoryzomys* acting as reservoirs of different hantavirus genotypes and geographic distribution of rodent natural hosts.

Rodent Species	Host distribution	Hantavirus genotype	References
<i>O. longicaudatus</i>	Southern Argentina and Chile	Andes/Andes South	Levis et al. (1998), Padula et al. (2004)
<i>O. flavescens</i> “West”	W and NW Argentina, SW Bolivia and W Paraguay	Bermejo	Rivera et al. (2007), González-Ittig et al. (2010a)
<i>O. flavescens</i> “East” or <i>sensu stricto</i>	E Argentina and S Uruguay	Lechiguanas/Central Plata	Rivera et al. (2007), González-Ittig et al. (2010a)
<i>O. nigripes</i>	NE Argentina, E Paraguay and S Brazil	Juquitiba	Suzuki et al. (2004), Padula et al. (2007), Delfraro et al. (2008)
<i>O. microtis</i>	NE Bolivia, E Perú and W Brazil	Rio Mamore and Rio Mamore-3	Richter et al. (2010)
<i>O. chacoensis</i>	N Argentina, SE Bolivia and Paraguay	Oran/Andes North	González Della Valle et al. (2002), Rivera et al. (2007), González-Ittig et al. (2010a)
<i>O. costaricensis</i>	West Panama and Costa Rica	Choclo	Hanson et al. (2011)
<i>O. delicatus</i>	Venezuela and Surinam	Maporal	Hanson et al. (2011)
<i>O. utiaritensis</i>	Central-western Brazil	Castelo dos Sonhos	Agrellos et al. (2012), Firth et al. (2012).
<i>Oligoryzomys</i> sp. RT2012	Rondonia in Brazil	Rio Mamore-4	Firth et al. (2012)
<i>Reservoir not properly identified</i>	Maranhão in Brazil	Anajatuba	This study