DIVERSITÉ GÉNÉTIQUE DE TALPA EUROPAEA ET DE L'HANTAVIRUS NOVA (NVAV) EN FRANCE

GENETIC DIVERSITY OF TALPA EUROPAEA AND NOVA HANTAVIRUS (NVAV) IN FRANCE

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RÉSUMÉ

L'Hantavirus Nova (NVAV) a été identifié chez un spécimen de *Talpa europaea* capturé en Hongrie. L'analyse de 94 spécimens de taupes capturés en France a révélé la présence de NVAV chez 50% des individus. Une étude populationnelle des taupes montre que les individus collectés entre Poitiers et Bordeaux sont génétiquement proches de l'espèce voisine *T. occidentalis*, jusqu'ici supposée être strictement endémique dans la péninsule ibérique. Plusieurs hypothèses permettant d'expliquer ces observations sont discutées : 1) la présence jusqu'ici ignorée de *T. occidentalis* dans le sud-ouest de la France ; 2) l'existence d'un ancien phénomène d'introgression mitochondriale entre les deux espèces, ; 3) la présence d'une zone d'hybridation entre les deux espèces, produisant un phénotype particulier chez certains hybrides ; 4) l'existence d'une espèce nouvelle. NVAV n'ayant été détecté chez aucun des spécimens du Sud-Ouest, la question de l'existence d'un Hantavirus particulier dans cette population et chez la taupe ibérique est posée.

Mots-Clés: *Talpa europaea*, *Talpa occidentalis*, Hantavirus, NVAV, phylogénétique, phylogéographie.

SUMMARY

*Nova hantavirus (NVAV) was first identified in a captured European mole (*Talpa europaea*) in Hungary. Analysis of lung tissues from 94 moles captured in France revealed NVAV in 50% of the animals. Based on the genetic diversity of the cytochrome b mtDNA, moles collected in Poitiers and Bordeaux were more closely related to the Iberian mole (*T. occidentalis*), a species previously assumed to be restricted to the Iberian Peninsula. Several hypotheses are discussed to explain these observations: 1) the presence of hitherto unnoticed* T. occidentalis *in southwestern France; 2) the existence of an ancient mitochondrial introgression phenomenon between the two* Talpa *species, producing a particular phenotype in some hybrids; 3) the existence of a hybrid zone between the two species; and 4) the existence of a new* Talpa *species. NVAV was not detected in the southwestern moles, which raises the question of the possible presence of a particular Hantavirus species in this population and/or in the Iberian moles.*

Key-Words:* Talpa europaea, Talpa occidentalis, *Hantavirus, NVAV, phylogenetics, phylogeography.

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INTRODUCTION

Hantaviruses (family Bunyaviridae), long known to be harbored by rodents (rats, mice, voles, etc.) of the Muridae and Cricetidae families, have been detected in multiple species of shrews (Soricidae) and moles (Talpidae) (Yanagihara *et al.* 2014). More recently, highly divergent lineages of hantaviruses have also been discovered in insectivorous bats (Gu *et al.* 2014b; Guo *et al.* 2013; Yanagihara *et al.* 2014; ***table 1***). In-depth studies of non-rodent hosts, which are heavily represented among micro-mammals all around the world, may provide a better understanding about their evolutionary origins. Since some hantaviruses may infect and cause diseases in humans, such studies may also interest epidemiologists (Pontier & Fouchet, 2013; Reynes, 2013; Tordo *et al.* 2013).

Between October 2012 and March 2013, we sampled European moles, *Talpa europaea*, in various regions of France. The purpose of this investigation was:

1) to verify the presence of Nova hantavirus (NVAV), originally described in a single specimen of *T. europaea* from Hungary (Kang *et al.* 2009);

2) to assess the prevalence and genetic variability of NVAV; and

3) to compare NVAV genetic diversity with mole population genetics.

The study revealed the presence of NVAV in France and the existence of a genetic variability of the virus linked to the localities where the moles were captured (Gu *et al.* 2014a). Analysis of the cytochrome *b* mtDNA produced an unexpected finding: that is, although only one mole species (*T. europaea*) was considered to be present in France, some moles collected in the southwestern part of the country were genetically more closely related to *T. occidentalis*, a different species previously believed to be endemic to the Iberian Peninsula. Details of these results are presented and discussed.

MATERIAL AND METHODS

Collecting moles

Approximately 350 moles were captured in different localities in France ***(figure 1)*** from October 2012 to March 2013, using Putange traps and following a protocol approved by French professional mole catchers (Dormion, 2012).

Research of hantavirus

A subset of 94 moles captured either in the Golf of Ozoir-la-Ferrière (48.7700°N, 2.6800°E), or in the Beauvais agreement park called « *Le Plan d'eau du Canada* » (49°452698 N, 2°058234 E), were studied. We also analyzed 24 mole specimens collected between Bordeaux and Poitiers and genetically different from *T. europaea*. After capture, moles were frozen at -20°C; for tissue dissection, moles were partially thawed and lung tissues were removed using ethanol-cleaned instruments and placed in RNAlater® RNA Stabilization Reagent (Qiagen Inc., Valencia, CA).

Hantavirus detection and sequencing

Total RNA was extracted from mole lung tissues, using the PureLink Micro-to-Midi total RNA purification kit (Invitrogen, San Diego, CA), and cDNA was prepared using the SuperScript III First-Strand Synthesis System (Invitrogen) and random hexamers. PCR was performed as described previously using oligonucleotide primers designed from NVAV and other soricomorph-borne hantaviruses (Song *et al.* 2007; Arai *et al.* 2008) and DNA sequencing was performed using an ABI Prism 377XL Genetic Analyzer (Applied Biosystems, Foster City, CA).

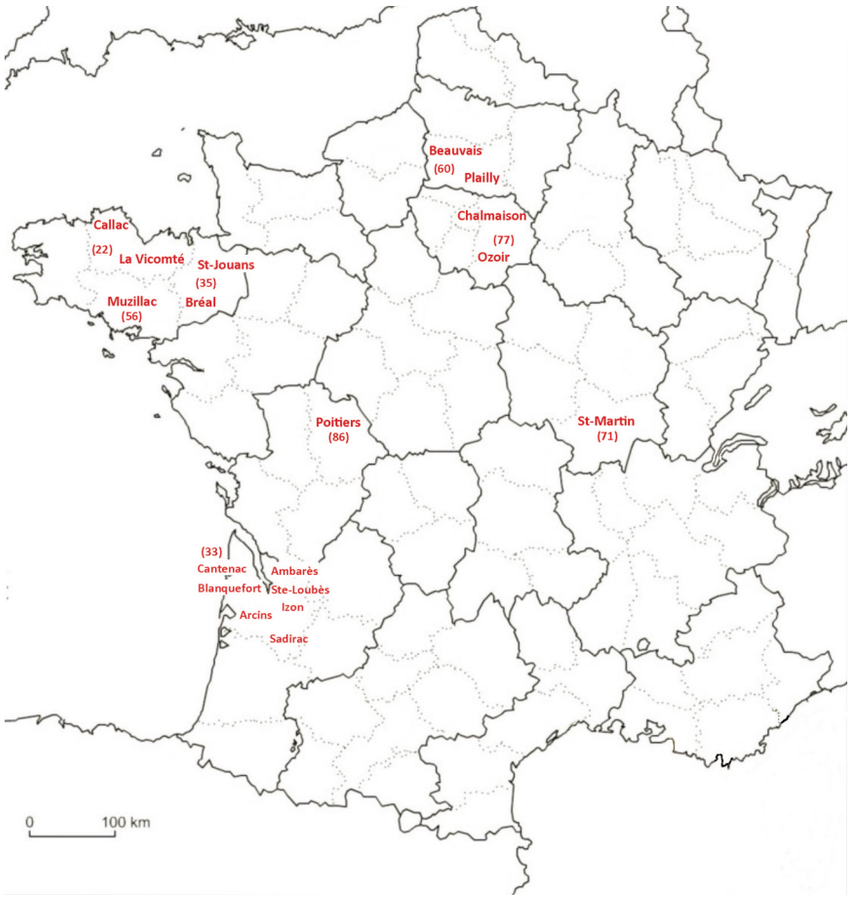

Figure 1. Map of collection localities.
Map of France, showing localities where European moles were captured during October 2012 to March 2013. The results presented in this manuscript were obtained from specimens collected in the localities indicated in red (Blanquefort, St-Loubès, Sadirac, Ambarès, Arcins and Izon are small cities situated on either side of the Gironde estuary, in the vicinity of Bordeaux).

	Virus name	Logo	Host species	Host family	Biorealm	Country	Collection year	Publication year	Genbank
1	Thottapalayam	TPMV	*Suncus murinus*	Soricidae	Oriental	India	1964	1971	AY526097
2	Tanganya	TGNV	*Crocidura theresae*	Soricidae	Ethiopian	Guinea	2004	2007	EF050455
3	Cao Bang	CBNV	*Anourosorex squamipes*	Soricidae	Oriental	Vietnam	2006	2007	EF543524
4	Ash River	ARRV	*Sorex cinereus*	Soricidae	Nearctic	USA	1994	2008	EF650086
5	Amga	MGAV	*Sorex caecutiens*	Soricidae	Palearctic	Russia	2006	2008	-
6	Jemez Spring	JMSV	*Sorex monticolus*	Soricidae	Nearctic	USA	1996	2008	FJ593499
7	Kenkeme	KKMV	*Sorex roboratus*	Soricidae	Palearctic	Russia	2006	2009	GQ306148
8	Kathmandu	TPMV	*Suncus murinus*	Soricidae	Oriental	Nepal	1996	2011	HQ831363
9	Imjin	MJNV	*Crocidura lasiura*	Soricidae	Palearctic	South Korea	2004	2009	EF641804
10	Qian Hu Shan	QHSV	*Sorex cylindricauda*	Soricidae	Palearctic	China	2005	2014	GU566023
11	Asagny	AZGV	*Crocidura obscurior*	Soricidae	Ethiopian	Côte d'Ivoire	2009	2011	JF276226
12	Longwan	TPMV	*Suncus murinus*	Soricidae	Palearctic	China	2009	2011	JF784177
13	Uluguru	ULUV	*Myosorex geata*	Soricidae	Ethiopian	Tanzania	1996	2014	JX193695
14	Kilimanjaro	KMJV	*Myosorex zinki*	Soricidae	Ethiopian	Tanzania	2002	2014	JX193698
15	Seewis	SWSV	*Sorex araneus*	Soricidae	Palearctic	Switzerland	2006	2007	EF636024
16	Jeju	JJUV	*Crocidura shantungensis*	Soricidae	Palearctic	South Korea	2007	2012	HQ834695
17	Bowé	BOWV	*Crocidura douceti*	Soricidae	Ethiopian	Guinea	2012	2013	KC631782
18	Lianghe	CBNV	*Anourosorex squamipes*	Soricidae	Palearctic	China	2011	2013	JX465395
19	Yakeshi	YKSV	*Sorex isodon*	Soricidae	Palearctic	China	2006	2013	JX465423
20	Asikkala	ASIV	*Sorex minutus*	Soricidae	Palearctic	Germany	2010	2013	KC880343
21	Boginia	BOGV	*Neomys fodiens*	Soricidae	Palearctic	Poland	2011	2013	-
22	Asama	ASAV	*Urotrichus talpoides*	Talpidae	Palearctic	Japan	2008	2008	EU929070
23	Nova	NVAV	*Talpa europaea*	Talpidae	Palearctic	Hungary	1999	2009	FJ539168
24	Oxbow	OXBV	*Neurotrichus gibbsii*	Talpidae	Nearctic	USA	2003	2009	FJ539166
25	Dahonggou Creek	DHCV	*Scaptonyx fusicaudus*	Talpidae	Palearctic	China	1989	-	HQ616595
26	Rockport	RKPV	*Scalopus aquaticus*	Talpidae	Nearctic	USA	1986	2011	HM015223
27	Magboi	MGBV	*Nycteris hispida*	Nycteridae	Ethiopian	Sierra Leone	2010	2012	-
28	Mouyassué	MOYV	*Neoromicia nanus*	Vespertilionidae	Ethiopian	Côte d'Ivoire	2011	2012	-
29	Xuan Son	XSV	*Hipposideros pomona*	Hipposideridae	Oriental	Vietnam	2012	2013	KF704712
30	Longquan	LQUV	*Rhinolophus spp*	Rhinolophidae	Palearctic	China	2011	2013	JX465422
31	Huangpi	HUPV	*Pipistrellus abramus*	Vespertilionidae	Palearctic	China	2011	2013	JX473273

Table 1: Checklist of the hantaviruses hosted by Soricomorpha and Chiroptera. *Since the report of Thottapalayam virus in 1971, more than 30 other hantavirus strains have been detected either from Soricomorpha (Soricidae, Talpidae) or Chiroptera, from: the Palearctic (19), Nearctic (5), Oriental (3) or Ethiopian (7) Biorealms, respectively. Accession numbers in GenBank are given when the short gene sequence (S) of the corresponding hantavirus strain is available.*

Mitochondrial DNA sequencing

DNA was extracted from ethanol-preserved tissues by the CTAB method (Winnepenninckx *et al.*, 1993). The cytochrome b gene was amplified from 40 mole specimens using polymerase chain reaction (PCR) primers L14723 and H15915 (Ducroz *et al.* 2001; Nicolas *et al.* 2008).

Sequence alignment

Alignment of the coding region of the hantavirus S segment, or the cytochrome *b* of the moles was performed using CLUSTAL-X automatic procedure (Thompson *et al.* 1994) then improved manually using SEAL v2.0a11 (Rambaut, 1996) and validated using the amino acid translation.

Phylogenetic analyses

Evolutionary relationships among sequences were estimated by constructing phylogenetic trees using maximum parsimony (MP) and Bayesian Markov chain Monte Carlo phylogenetic analyses (MCMC). MP analysis was performed with PAUP 4b10 (Swofford, 2001) and Bayesian analysis with MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001). The MP analysis was performed with tree-bisection-reconnection (TBR) branch swapping option and 10 random addition replicates. We estimated the robustness of internal nodes by 1,000 bootstrapping replicates (each with a single replication of random addition of taxa). An equal weighting of character-state transformations was applied. In all MCMC analyses three heated chains and one single cold chain were employed, and runs were initiated with random trees. Two independent MCMC runs were conducted with six million generations per run; trees (and parameters) sampled every 100 generations. Stationarity was assessed by: examining the average standard deviation of split frequencies and, the Potential Scale Reduction Factor (Ronquist *et al.* 2005). For each run, the first 25% of sampled trees were discarded as burn-in. A consensus tree was computed using the "halfcompat" option, equivalent to the 50% majority rule and rooted using the "midpoint root" option. Proportion values of posterior probability of bipartition were used for evaluation of robustness of the nodes.

RESULTS

Prevalence of NVAV in moles

Hantavirus RNA was detected in 47 moles (50%) by RT-PCR. Of 36 and 28 moles captured in Ozoir-la-Ferrière on October 18, 2012 and February 21, 2013, 15 and 14, respectively, were positive, while 18 of 30 moles captured in Beauvais on March 3, 2013 were positive (Gu *et al.* 2014a). NVAV was not detected in the 24 southwestern moles.

Phylogenetic analysis of hantavirus found in micro-mammals

Phylogenetic analysis, using Bayesian methods ***(figure 2)*** showed that:

1) NVAV from France and prototype NVAV from Hungary grouped together in a particular lineage;

2) NVAV strains from France segregated along geographic-specific lineages;

3) NVAV clade was strongly associated with another clade, comprising hantaviruses detected in insectivorous bats;

4) other hantaviruses hosted by soricomorphs were distributed into two separate clades:
   i) the most divergent included seven strains from shrews captured in India, South Korea, China and Tanzania;
   ii) the second clade included strains from moles and shrews captured in North America, China, Japan and Europe, and associated with hantaviruses hosted by Murinae rodents;

5) two other clades grouping hantaviruses hosted by Sigmodontinae-Neotominae and Arvicolinae rodents, respectively;

6) a single mole-borne hantavirus, Rockport virus from the eastern mole in North America, was situated between the Sigmodontinae and Arvicolinae clades. All the basal nodes of the cladogram had the maximum posterior probability of bipartition value (= 1).

Genetic affinities within the Family Talpidae

Phylogenetic analysis, using Bayesian methods, of all available sequences from Talpidae species ***(figure 3)*** showed that:

1) the genus *Talpa* may be considered a monophyletic group, in which each different species is recognized as a distinct clade;

2) *T. europaea* and *T. occidentalis* are sister taxa;

3) specimens captured in Brittany, Northern France and Saône-et-Loire clustered with strains identified as *T. europaea* and collected from different European countries (Sweden, Denmark, Switzerland, Hungary, Germany, Italy and Greece);

4) specimens captured in the vicinity of Bordeaux, or Poitiers, clustered with specimens captured either from Spain or Portugal and identified as *T. occidentalis*, the Iberian mole. All the nodes of the cladogram corresponding to a particular mole species had the maximum posterior probability of bipartition value (= 1).

DISCUSSION

Mole infection

Prevalence of anti-viral antibodies and/or viral antigens in rodent species known to harbor disease-causing hantaviruses generally varies from less than 1% to more than 25%, depending on seasonal factors, reservoir population density, geographical area and ecological diversity (Lee *et al.*1978; Dobly *et*

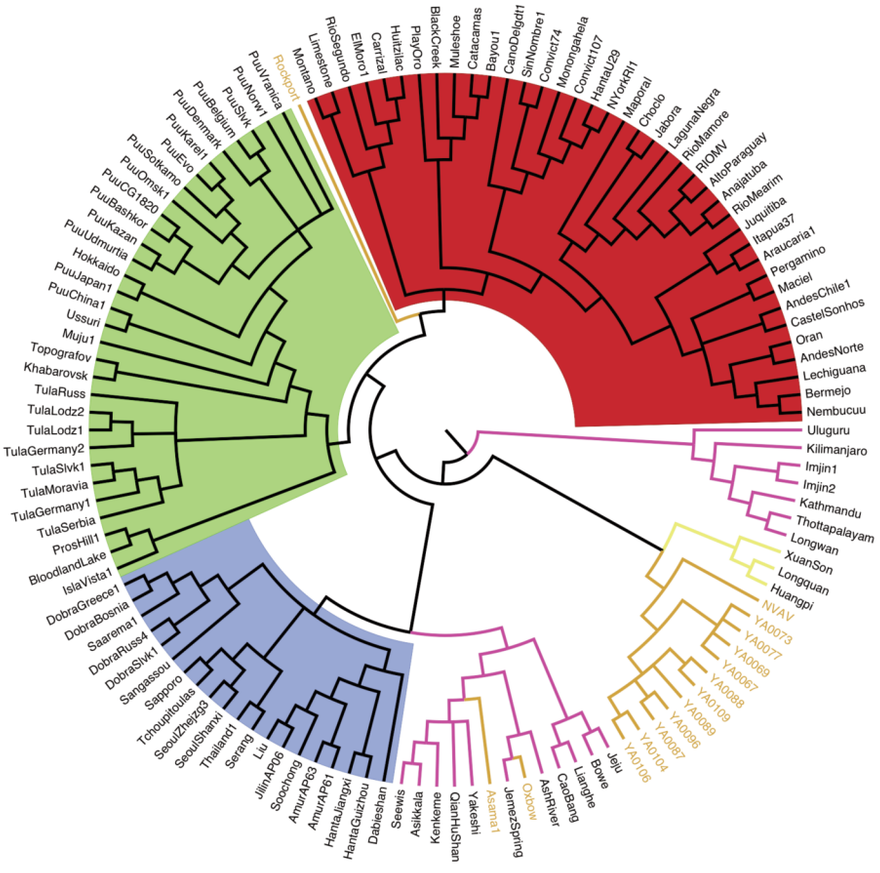

Figure 2: Phylogeny of hantaviruses hosted by Chiroptera, Soricomorpha or Rodents.

Cladogram resulting of Bayesian (MCMC) analysis (GTR+I+G model), based on the entire coding region of the S gene (nucleotides 43–1341). Hantaviruses hosted by different host groups are highlighted in: red (Sigmodontinae-Neotominae), green (Arvicolinae), blue (Murinae), pink (Soricidae), light brown (Talpidae) and yellow (Chiroptera). The analysis used 1) an extent data set of the S gene coding region available on GenBank, including most of the hantavirus strains detected either in rodents or non-rodent mammals (Soricomorpha and Chiroptera), and 2) 11 complete S-segment sequences from moles captured either in Ozoir (4) or Beauvais (7). GenBank accession numbers: FJ539168, NVAV from Hungary; KF010573–KF010576, NVAV strains from Ozoir-la-Ferrière; KF010565–KF010571, NVAV strains from Beauvais. For Chiroptera and Soricomorpha hosts, see Table 1; for rodent hosts, see Herbreteau et al., *2007, Table 16.1.*

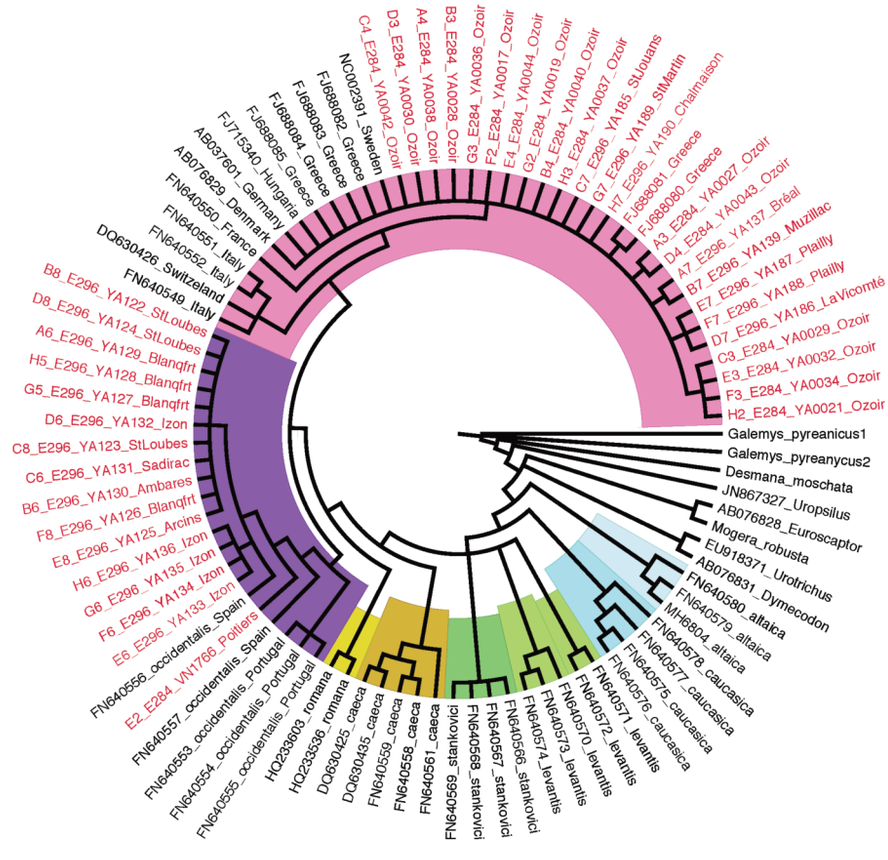

Figure 3. Phylogenetic analysis of Talpa spp. and closely related taxa

Bayesian (MCMC) analysis (GTR+I+G model) based on the entire coding region of the cytochrome b gene. The analysis was rooted using as outgroups several taxa included within the Talpidae: Urotrichus, Dymecodon, Mogera, Euroscaptor, Uropsilus, Desmana *and* Galemys. *All the sequences available in GenBank for these taxa or for* Talpa *spp. were included. The tip labels indicate the GeneBank accession number and the name of the species (for the* Talpa *spp.), the name of the genus for the other taxa. Our own mole samples are labeled using the field collection number + the name of the locality of capture and highlighted in red.*

al. 2012). Recently, a similarly high prevalence of NVAV infection, as evidenced by RT-PCR and confirmed by DNA sequencing, has been found in European moles captured in central Poland, suggesting that NVAV is widespread throughout the vast distribution of *T. europaea* (Gu *et al*. 2014a). The high prevalence of this hantavirus suggests that the mechanisms of transmission between individuals are very efficient.

NVAV was not detected in the southwestern moles, but few specimens (24) were available and the RNA quality was suboptimal. Thus, future studies are warranted to ascertain if NVAV or NVAV-related hantaviruses are harbored by moles in southwestern France. These investigations will be extended to mole specimens collected from different parts of the Iberian Peninsula.

Until now no human infection due to NVAV has been recorded. However, moles have a high propensity to occupy arable fields, deciduous woodland and permanent pastures, and hantavirus are known to be able to survive for prolonged periods (12-15 days) in external environment (Kallio *et al*. 2006; Hardestam *et al*. 2007). Any unusual clinical syndromes, recorded among individuals reporting contact with European moles, should be thoroughly studied by physicians and public health workers.

Host and hantavirus coevolution

Hantaviruses were traditionally considered to have codiverged (co-speciatiated) with their rodent hosts (Herbreteau *et al*. 2006, 2007; Hentonnen *et al*. 2008; Guo *et al*. 2013; Yanagihara *et al*. 2014) and some evidence for such codivergence is apparent here. In particular, rodent-borne hantaviruses clustered according to whether their hosts were members of the Murinae, Arvicolinae or Sigmodontinae-Neotominae subfamilies. However, codivergence alone cannot explain the clustering of hantaviruses hosted by Soricomorpha and Chiroptera, which exist in several paraphyletic clades with no correspondence between the association of the viruses, their geographic origin and/or host taxonomy (***figure 2***; Tordo *et al*. 2013).

Presence of genetically distinct moles in France

Identification of two genetically divergent mole lineages in France was unexpected. Until now, only *T. europaea* was considered to be present in France. In the Iberian Peninsula, the situation is quite different and two species have been recorded for a long time. *T. europaea* is present in Northeast Spain (Catalunya, Navarra and the Eastern part of Pais Vasco) while the closely related *T. occidentalis* is present in the Northwest and South of Spain and in Portugal (Palomo *et al*. 2007).

To explain this presence of mitochondrial haplotypes related to *T. occidentalis* in the Southwest of France, the simplest hypothesis is to admit that *T. occidentalis* was able to cross the mountains, leaving Spain and partly colonizing a territory extending from the Pyrenees to the river Loire. However, this hypothesis doesn't fit well with the comparison of the morphology of the different populations. ***Table 2*** shows that:

i) if the measurements of the specimens clustering with the other European moles fit with the values attributed to *T. europaea* (Palomo *et al*. 2007; Aulagnier *et al*. 2008); conversely,

ii) the comparison of the measurement of the southwestern mole specimens with the values attributed to *T. occidentalis* (Palomo *et al*. 2007; Aulagnier *et al*. 2008) are incompatible;

	Weight	H & Body	Tail	Foot	Head
MAX	118,0	166,0	40,1	30,8	49,0
MIN	48,0	122,8	14,0	16,6	31,6
MOY	78,0	145,5	26,8	20,8	43,6
330 moles from different sites in France					
Talpa europaea					
MAX	130,0	165,0	51,0	25,0	38,0
MIN	36,0	100,0	20,0	16,0	30,0
MOY	83,0	132,5	35,5	20,5	34,0

	Weight	H & Body	Tail	Foot	Head
MAX	147,0	165,0	35,0	26,0	49,0
MIN	69,0	141,0	19,0	19,0	39,0
MOY	92,5	153,2	27,5	21,3	45,8
24 moles from Southwest of France					
Talpa occidentalis					
MAX	70,0	135,0	35	18,0	32,0
MIN	30,0	90,0	16	14,0	28,0
MOY	50,0	112,5	25,5	16,0	30,0

Table 2: *Comparison of the measurements of the moles captured in France, following their genetic affinities*
The measurements shown are those currently used when trapping mammals. In the upper part of the table are given the values collected from our captures : 24 moles (20 females and 4 males) in the vicinity of Bordeaux and Poitiers ; 330 (173 females and 157 males) from other localities in France. In the lower part are given the measurements of T. europaea *and* T. occidentalis *found in the bibliography (Palomo* et al.*, 2007 ; Aulagnier* et al.*, 2008).*

iii) comparison between the two data sets identified in France shows that moles captured in the southwest reach the highest size values recorded for *T. europaea* and are significantly heavier. Thus, moles from southwestern France may be considered as giant specimens while *T. occidentalis* from Iberia may be considered as a dwarf species. These morphological results do not support the simplest hypothesis of the presence of *T. occidentalis* in France.

To interpret our observations, three alternative hypotheses could be raised:

1) an ancient phenomenon of mitochondrial introgression occurred between the two species;

2) existence of a hybrid zone between the two species; and,

3) existence of a new undescribed *Talpa* species in southwestern France.

To better understand the presence of mitochondrial haplotypes related to *T. occidentalis* in this part of France, it would be necessary to perform additional molecular analyses, especially of more specimens from various other localities in France and in the Iberian Peninsula and also to sequence nuclear markers. These new investigations will be accompanied by concurrent research on the presence of NVAV, or another related hantavirus species, in moles genetically identified as *T. occidentalis*.

CONCLUSIONS

Our work confirms the presence of NVAV in France, in association with its specific host, *T. europaea*. This result and the high prevalence observed in the analyzed specimens give additional evidence for the probable distribution of NVAV throughout the geographic range of *T. europaea*. Although NVAV infection has not been recorded yet in humans, the presence and abundance of this hantavirus increase the likelihood of human exposure and should alert medical practitioners and public health workers to be vigilant for unusual clinical syndromes that may be caused by NVAV.

Hantaviruses are found in small mammals all around the World with the exception of the Australian and Antartica Biorealms. An extended phylogenetic analysis of the hantavirus strains hosted by rodents, soricomorphs or bats suggests coevolution between hantavirus and their hosts and implicates complex mechanisms including codivergence (cophylogeny), host switching and/or geographic isolation. The presence in France of two genetically different mole lineages begs the question of the taxonomic position of the southwestern moles and, also, of the potential circulation of a novel hantavirus species in the Iberian mole (*T. occidentalis*). Further investigations are warranted to clarify this possibility.

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