Virus Research 272 (2019) 197717

Contents lists available at ScienceDirect

Virus Research

journal homepage: www.elsevier.com/locate/virusres

Short communication

Co-circulation of distinct shrew-borne hantaviruses in the far east of Russia

Liudmila N. Yashina[a,*], Mikhail Yu Kartashov[a], Wen Wang[b], Kun Li[b], Nina I. Zdanovskaya[c], Leonid I. Ivanov[c], Yong-Zhen Zhang[b,*]

[a] State Research Center of Virology and Biotechnology "Vector", Russia
[b] State Key Laboratory for Infectious Disease Prevention and Control, Department of Zoonoses, National Institute for Communicable Disease Control and Prevention, Chinese Center for Disease Control and Prevention, Changping, Beijing, China
[c] Khabarovsk Antiplague Station, Russia

ARTICLE INFO

Keywords:
Hantavirus
Novel viruses
Shrews
Co-circulation
Russia

ABSTRACT

Insectivores are the new emerging reservoir of hantaviruses. Here, we describe Lena virus (LENV), a novel hantavirus harbored by the Laxmann`s shrew (*Sorex caecutiens*), which is also the host of Artybash virus (ARTV). Genetic analysis of the complete genomic sequence shows that LENV is in distant relation to ARTV and other *Sorex*-borne hantaviruses, suggesting that LENV has emerged from cross-species transmission. Additionally, new genetic variant of ARTV, designated as ARTV-St, was identified in tundra shrews (*Sorex tundrensis*). Finally, distinct insectivore-borne hantaviruses are co-circulating in the same localities of far eastern Russia: LENV, ARTV and Yakeshi in the forest site, while ARTV, ARTV-St, and Kenkeme virus in the meadow field site.

Hantaviruses (genus *Orthohantavirus*, family *Hantaviridae*) have long been considered rodent-borne pathogens of humans. However, the host range of hantaviruses has expanded with the ongoing discovery of more and more novel hantaviruses in shrews, moles, and bats over the past decade (Yanagihara et al., 2014). Rodent-borne hantaviruses cause either hemorrhagic fever with renal syndrome or hantavirus cardiopulmonary syndrome (Jonsson et al., 2010). Recently, antibodies against shrew-borne hantaviruses were detected in human patients, suggesting that shrew-borne hantaviruses can also infect humans (Heinemann et al., 2016). The genome of hantaviruses is comprised of three negative-sense RNA segments: small (S), medium (M), and large (L), encoding a nucleocapsid (N) protein, glycoproteins (GPC), and an RNA-dependent RNA polymerase, respectively. Currently, known hantaviruses have classified into four genera: *Orthohantavirus*, *Loanvirus*, *Mobatvirus*, and *Thottimvirus* (Maes et al., 2019).

Since the discovery of the first *Sorex*-borne hantavirus (Seewis virus, SWSV) in the Eurasian common shrews (*Sorex araneus*) (Song et al., 2007), multiple of genetically distinct shrew-borne hantaviruses have been identified in other *Sorex* species, including Ash River virus (ARRV) in the North American masked shrew (*S. cinereus*) and Jemez Springs virus (JMSV) in the dusky shrew (*S. monticolus*) (Arai et al., 2008), Kenkeme virus (KKMV) in the Asian flat-skulled shrew (*S. roboratus*) (Kang et al., 2010), Asikkala virus (ASIV) in the Eurasian pygmy shrew (*S. minutus*) (Radosa et al., 2013), Yakeshi virus (YKSV) in the taiga shrew (*S. isodon*) (Guo et al., 2013), Qian Hu Shan virus (QHSV) in the striped-back shrew (*S. cylindricauda*) (Zuo et al., 2014), Artybash virus (ARTV) in the Laxmann`s shrew (*S. caecutiens*) (Arai et al., 2016a), and Altai virus (ALTV) in the Eurasian common shrew (GenBank accession numbers EU424341, KP657656).

To date, four shrew-borne hantaviruses (SWSV, ARTV, ALTV, and KKMV) have been discovered in Russia. Geographically, SWSV has been found to be present in the vast territory of western and eastern Siberia (Yashina et al., 2010). Although ARTV was originally identified in Altai region of western Siberia, it also has been found in eastern Siberia and even in Japan (Arai et al., 2016a, 2016b). Notably, ALTV was first discovered in *S. araneus* sampled from the Altai Republic of western Siberia, while later ALTV-like virus was found in *S. araneus* from Finland (Ling et al., 2014), as well as in *S. caecutiens* from eastern Siberia (GenBank KM362174) and Sakha Republic (GenBank KM361048, KM361053, KM361061). Additionally, KKMV was detected in *S. roboratus* sampled from Sakha Republic, which is located in the northeastern part of Russia (Kang et al., 2010). Finally, six rodent-borne hantaviruses are also endemic in Far-eastern Russia: Hantaan virus [genetic variants HTNV and Amur (AMRV)], Seoul virus (SEOV), Puumala virus [genetic variant Hokkaido (HOKV)], Khabarovsk virus (KHAV) and Vladivostok virus (VLAV) (Horling et al., 1996; Kariwa et al., 2012; Yashina et al., 2001, 2004). All these data indicate the remarkable diversity of hantaviruses in Russia.

During 2007–2009, 2011 and 2016–2017, 183 shrews representing five species were captured according to protocols described previously

* Corresponding authors.
E-mail addresses: yashina@vector.nsc.ru (L.N. Yashina), zhangyongzhen@icdc.cn (Y.-Z. Zhang).

https://doi.org/10.1016/j.virusres.2019.197717
Received 5 April 2019; Received in revised form 14 August 2019; Accepted 14 August 2019
Available online 15 August 2019

Table 1
Prevalence of hantavirus infection, as determined by RT-PCR, in shrews by species and location in Khabarovsk Krai.

	Khekhtsir					Galkino				
Species	2007	2008	2009	2011	2016	2007	2008	2016	2017	Total
Sorex caecutience	1/13[a]	1/7	0/3	4/17	1/3	2/28	0/11	0/2	0/1	9/85
S. isodon	1/12	1/11	0/2	0/11	0/2	0/3	0/2	–	–	2/43
S. roboratus	–	–	–	–	–	–	–	1/1	–	1/1
S. tundrensis	–	–	–	–	–	10/32	4/13	1/1	1/3	16/49
Crocidura lasiura	–	–	–	–	–	–	–	0/5	–	0/5
Total	2/25	2/18	0/5	4/28	1/5	12/63	4/26	2/9	1/4	28/183

Note: "-" means that no animals were captured.
[a] Number of hantavirus RNA positive shrews/number captured. Hantavirus RNA was detected by RT-PCR, using L-segment specific primers.

(Mills et al., 1995) at two different natural foci: forest site located 20 km south of Khabarovsk city, Bolshekhekhtsirsky nature reserve (site Khekhtsir), and meadow-field site (Galkino), located 20 km east of Khabarovsk city in agricultural zone (Table 1 and Supplementary Fig. S1). RNA was extracted from shrew lung tissues using the RNeasy MiniKit (Qiagen), and cDNA was synthesized using Expand reverse transcriptase (Roche). All samples were screened for hantaviruses by nested RT-PCR targeting the conserved region of the L segment (Klempa et al., 2007). Consequently, hantaviral RNA (346 base pairs) were identified in nine *S. caecutiens*, 16 *S. tundrensis*, two *S. isodon*, and one *S. roboratus* (Table 1). All recovered viral sequences were deposited in GenBank (accession numbers: KJ742934-KJ742935, MG860917-MG860925, MG888356-MG888368, MG888374, MG888376). Finally, the whole genome (two strains), complete S and M segments (two strains), complete S segments (three strains) sequences were recovered from seven positive samples to better understand the taxonomy of these newly identified strains (MH499470-MH499473, MG888402-MG888405, MG913806-MG913808, MH422500-MH422501) (Supplementary Table S1). Primers for amplifying and sequencingthe full genomes were designed based on consensus regions of other available hantaviruses. For highly diverged genome, primer identity was modified based on output sequences.

In the tree based on the L segment sequences, the viral sequences recovered from one Laxmann`s shrew *S. caecutiens* (strain Khekhtsir-Sc67), are most closely related to those of yet unpublished ALTV-like viruses, which were initially identified in Laxmann`s shrews sampled from Sakha Republic near Lena River (GenBank KM361057, KM361061) and eastern Siberia (GenBank KM362174). Genetic analysis of complete L or M and S sequences, revealed 80–90% nucleotide and 99–100% amino acid sequence identity between newly and previously discovered strains, but far different from ALTV and other shrew-borne hantaviruses both at the nucleotide (> 27%) and amino acid (> 28%) levels (Supplementary Table S2). However, the strain Khekhtsir-Sc67 was closely related to members of *Mobatvirus* genera in both the M and L phylogenetic trees (Fig. 1). Notably, the strain occupied the basal position of mobatvirus and loanvirus phylogroups in the S tree. The different clustering in these trees suggest the occurrence of ancient reassortment events or are due to the limited sequences available for viruses within the genera *Mobatvirus* and *Loanvirus*, as it was suggested for QZNV (Arai et al., 2016b). In sum, our data suggest that it may represent a new hantavirus. Here, novel ALTV-like virus (prototype strain Khekhtsir-Sc67) is designated as Lena River virus (LENV) according to the initial capture site.

The partial L segment sequences recovered from the remaining eight Laxmann`s shrew exhibited 0–9.9% divergence. However, they were far distinct from LENV, while they showed a close evolutionary relationship to those of ARTV (12.1–22.6% nucleotide and 1.7–4.4% amino acid sequence divergence) identified previously in *S. caecutiens* from western Siberia of Russia and Hokkaido of Japan (Arai et al., 2017). Hence, further efforts are needed to know whether Laxmann`s shrew is the true host of LENV or LENV was just jumped from other hosts. Finally, the complete S and M segment sequences recovered from two positive samples, representing forest (Khekhtsir-Sc1126) and meadow-field (Galkino-Sc2712) sites respectively, were closely related to each other, with less then 2.5% nucleotide and 0.2% amino acid sequence divergence.

The viral sequences recovered from 16 tundra shrews captured in the meadow-field site were closely related to each other, with less than 2.3% divergence for partial L segment nucleotide sequences. Complete S segment sequences obtained from two positive samples also demonstrated similar level of sequence divergence (2.9%). These complete S segment sequences showed 19.1–19.4% nucleotide (6.5% amino acid) divergence to the prototype strain Mukawa-AH301 of ARTV. Fortunately, we recovered the whole genome sequence from one of 16 positive samples (reference strain Galkino–St2714). Comparison of the S and M segments of strain Galkino-St2714 with ARTV strains, which were identified in the same meadow-field locality (Galkino-Sc2712) and in the nearest forest locality (strain Khekhtsir-Sc1126), showed 21.2% and 20.1% nucleotide, 7.7% and 6.3% amino acid sequence divergence, respectively. Hence, the newly discovered viruses may represent a new genetic variant of ARTV (Fig. 1). Here, we call the two genetic variants of ARTV as ARTV-St and ARTV-Sc respectively. Similar definition is also appeared in Dobrava/Belgrad virus (DOBV) variants harbored by distinct rodent species (Klempa et al., 2013).

The viral sequences recovered from two *S. isodon* showed higher level of both nucleotide sequence divergence (17.2% for partial L segments, and 10.0% for complete S segments) and amino acid sequence divergence (4.0 and 2.4%). Notably, these sequences demonstrated comparable level of sequence divergence with the closest YKSV strain (Yakeshi-Si-210) which was identified in Yakeshi of China (Guo et al., 2013), more than 850 km away from Khekhtsir site of Russia. In addition, new partial L sequence from *S. roboratus* is most closely related to those of KKMV strains sampled from China (Wang et al., 2014) and Sakha Republic of Russia (Kang et al., 2010).

It is well known that far-eastern biotic communities are the natural foci of multiple hantaviruses. Previously, co-circulation of rodent-borne hantaviruses was described in the same sites: AMRV genotype of HTNV and HOKV genotype of PUUV in the forest site Khekhtsir; HTNV and KHAV in the meadow-field site Galkino (Horling et al., 1996; Kariwa et al., 2012; GenBank AB677484). In addition to rodent-borne hantaviruses, this study demonstrates the co-circulation of three distinct shrew-borne hantaviruses LENV, ARTV-Sc and YKSV in the same forest locality, as well as ARTV-Sc, ARTV-St and KKMV in the meadow-field locality. Four species of hantaviruses in rodents and shrews were found in the same locality of Altai Republic, Russia: HOKV, SWSV, ARTV and ALTV (Yashina et al., 2010, 2015; Arai et al., 2016a, 2016b). The co-circulation of HTNV, KHAV and KKMV in rodents and shrews was also reported in China (Wang et al., 2014), as well as the co-circulation of SWSV and ALTV-like in shrews in Finland (Ling et al., 2014). The future studies are needed to clarify whether there is an evolutionary basis for the phenomena of multiple hantaviruses in a local small mammal community.

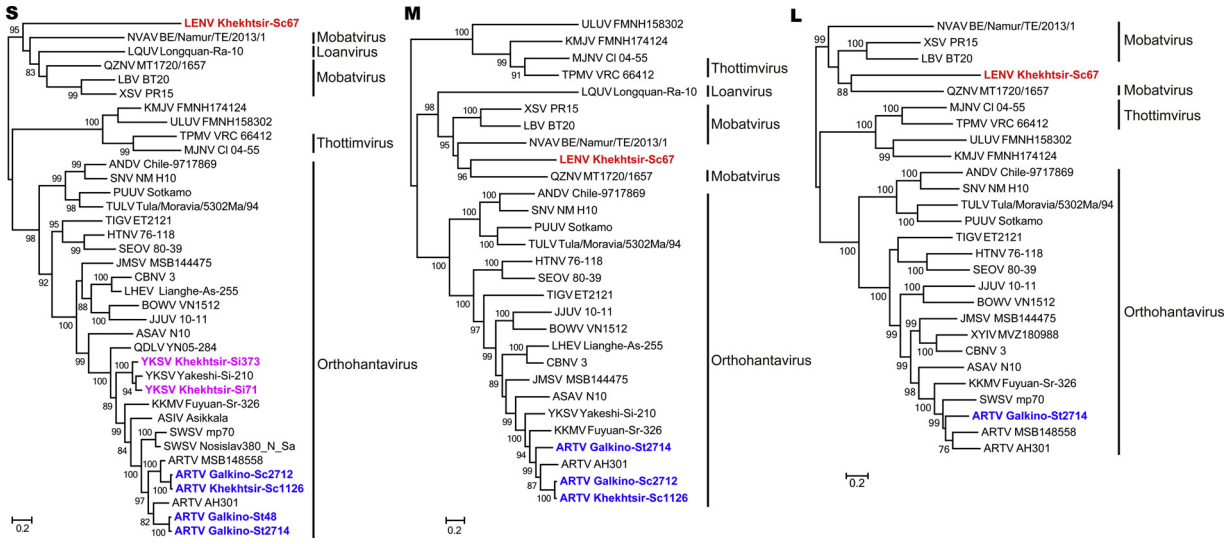

Fig. 1. Phylogenetic trees, generated by maximum-likelihood (ML) methods, were based on the alignment of the complete coding regions of the (S) S-segment, (M) M-segment and (L) L-segment sequences of newfound *Sorex*-borne and other representative hantaviruses. The coding sequences of the S, M and L segments were aligned using MUSCLE implemented in MEGA version 7 (Kumar et al., 2016). Alignment-ambiguous positions were then trimmed using the TrimAl program. The best-fit model of nucleotide substitution was determined by MEGA. Phylogenetic trees were inferred for using the ML approach with the PhyML v3.0 program (Guindon et al., 2010) and employing SPR (Subtree Pruning and Regrafting) branch-swapping. Topologies for each trees were derived, under the best-fit GTR + I + Γ model of evolution. Bootstrap values (> 70%) are shown at relevant nodes. The scale bar depicts the number of nucleotide substitutions per site. Colors highlight newfound viruses. Phylogenetic trees show the positions of insectivore-borne hantaviruses LENV (Lena virus), SWSV (Seewis virus), ARTV (Artybash virus), YKSV (Yakeshi virus), KKMV (Kenkeme virus), CBNV (Cao Bang virus), ASIV (Assikala virus), QDLV (Qian Hu Shan virus), LHEV (Lianghe virus), JMSV (Jemez Spring virus), BOWV (Bowe virus), JJUV (Jeju virus), ULUV (Uluguru virus), KMJV (Kilimanjaro virus), MJNV (Imjin virus), TPMV (Thottapalayam virus), ASAV (Asama virus), BRGV (Bruges virus), NVAV (Nova virus); bat-borne hantaviruses BRNV (Brno virus), QZNV (Quezon virus), LQUV (Longquan virus), LBV (Laibin virus), XSV (Xuan Son virus); rodent-borne hantaviruses PUUV (Puumala virus); HTNV (Hantaan virus), SEOV (Seoul viris), TIGV (Tigray virus), TULV (Tula virus), SNV (Sin Nombre virus), ANDV (Andes virus).

Here, we report the detection and genomic characterization of a new hantavirus (LENV) in the Laxmann`s shrew, previously recognized as the reservoir of ARTV (Arai et al., 2017). This study shows the co-circulation of two highly distinct hantaviruses in the same host and location. The examples of association of different viruses with the same host species are ALTV and SWSV in *S. araneus* in Altai Republic and Finland (Ling et al., 2014; Yashina et al., 2010; GenBank EU424341), NVAV and Bruges viruses in *Talpa europaea* in Belgium and Germany (Laenen et al., 2018). Based on NVAV and Bruges virus phylogeny, it has been suggested that Bruges virus has emerged from ancient cross-species transmission event. ARTV and LENV fall into orthohantavirus and mobatvirus phylogroups, respectively. Interestingly, orthohantavirus phylogroup also includes most of *Sorex*-borne hantaviruses, while mobatvirus phylogroup contains bat-borne, *Talpidae*-borne, and *Soricidae*-borne hantaviruses, indicating the complexity of hantavirus evolutionary history. Our data can be explained by the host-switch of LENV from ancestral host into Laxmann`s shrew, with the subsequent spread of virus over a large geographical range. Hence, far-eastern territory might be colonized by several streams of migrating shrews, one stream of *S. caecutiens* was associated with LENV, another with ARTV-Sc. Although LENV was detected from a single Laxmann`s shrew captured in the site Khekhtsir of far-eastern Russia, LENV may be present widely throughout the geographic range of *S. caecutiens*, spanning across northern part of Eurasian continent, based on the previous finding of closely related virus sequences from this *Sorex* shrew in distant localities of the Western Siberia and Sakha Republic.

Acknowledgments

This work was supported by the Russian Foundation for Basic Research (grant numbers 16-54-53066 and18-04-00834A) and National Natural Science Foundation of China (grant numbers 81611130073 and81861138003).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.virusres.2019.197717.

References

Arai, S., Bennett, S.N., Sumibcay, L., Cook, J.A., Song, J.-W., Hope, A., Parmenter, C., Nerurkar, V.R., Yates, T.L., Yanagihara, R., 2008. Phylogenetically distinct hantaviruses in the masked shrew (*Sorex cinereus*) and dusky shrew (*Sorex monticolus*) in the United States. Am. J. Trop. Med. Hyg. 78 (2), 348–351.

Arai, S., Kang, H.J., Gu, S.H., Ohdachi, S.D., Cook, J.A., Yashina, L.N., Tanaka-Taya, K., Abramov, S.A., Morikawa, S., Okabe, N., Oishi, K., Yanagihara, R., 2016a. Genetic Diversity of Artybash Virus in the Laxmann's Shrew (*Sorex caecutiens*). Vector Borne Zoonotic Dis. 16 (7), 468–475. https://doi.org/10.1089/vbz.2015.1903.

Arai, S., Taniguchi, S., Aoki, K., Yoshikawa, Y., Kyuwa, S., Tanaka-Taya, K., Masangkay, J.S., Omatsu, T., Puentespina, R., Watanabe, S., Alviola, P., Alvarez, J., Eres, E., Cosico, E., Quibod, M.N.R.M., Morikawa, S., Yanagihara, R., Oishi, K., 2016b. Molecular phylogeny of a genetically divergent hantavirus harbored by the Geoffroy's rousette (Rousettus amplexicaudatus), a frugivorous bat species in the Philippines. Infect. Genet. Evol. 45, 26–32. https://doi.org/10.1016/j.meegid.2016.08.008.

Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W., Gascuel, O., 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Syst. Biol. 59, 307–321. https://doi.org/10.1093/sysbio/syq010.

Guo, W.P., Lin, X.D., Wang, W., Tian, J.H., Cong, M.L., Zhang, H.L., Wang, M.R., Zhou, R.H., Wang, J.B., Li, M.H., Xu, J., Holmes, E.C., Zhang, Y.Z., 2013. Phylogeny and origins of hantaviruses harbored by bats, insectivores and rodents. PLoS Pathog. 9 (2), e1003159. https://doi.org/10.1371/journal.ppat.1003159.

Heinemann, P., Tia, M., Alabi, A., Anon, J.C., Auste, B., Essbauer, S., Gnionsahe, A., Kigninlman, H., Klempa, B., Kraef, C., Kruger, N., Leendertz, F.H., Ndhatz-Sanogo, M., Schaumburg, F., Witkowski, P.T., Akoua-Koffi, C.G., Kruger, D.H., 2016. Human infections by non-rodent-associated hantaviruses in Africa. J. Infect. Dis. 214 (10), 1507–1511. https://doi.org/10.1093/infdis/jiw401.

Horling, J., Chizhikov, V., Lundkvist, A., Jonsson, M., Ivanov, L., Dekonenko, A., Niklasson, B., Dzagurova, T., Peters, C.J., Tkachenko, E., Nichol, S., 1996. Khabarovsk virus: a phylogenetically and serologically distinct hantavirus isolated from *Microtus fortis* trapped in far-east Russia. J. Gen. Virol. 77, 687–694. https://doi.org/10.1099/0022-1317-77-4-687.

Jonsson, C.B., Figueiredo, L.T., Vapalahti, O., 2010. A global perspective on hantavirus ecology, epidemiology, and disease. Clin. Microbiol. Rev. 23 (2), 412–444. https://doi.org/10.1128/CMR.00062-09.

Kang, H.J., Arai, S., Hope, A.G., Cook, J.A., Yanagihara, R., 2010. Novel hantavirus in the flat-skulled shrew (*Sorex roboratus*). Vector Borne Zoonotic Dis. 10 (6), 593–597. https://doi.org/10.1089/vbz.2009.0159.

Kariwa, H., Yoshikawa, K., Tanikawa, Y., Seto, T., Sanada, T., Saasa, N., Ivanov, L.I., Slonova, R., Zakharycheva, T.A., Nakamura, I., Yoshimatsu, K., Arikawa, J., Yoshii, K., Takashima, I., 2012. Isolation and characterization of hantaviruses in Far East Russia and etiology of hemorrhagic fever with renal syndrome in the region. Am. J. Trop. Med. Hyg. 86 (3), 545–553. https://doi.org/10.4269/ajtmh.2012.11-0297.

Klempa, B., Fichet-Calvet, E., Lecompte, E., Auste, B., Aniskin, V., Meisel, H., Barrier, P., Koivogue, L., Meulen, J., Kruger, D.H., 2007. Novel hantavirus sequences in shrew, Guinea. Emerg. Infect. Dis. 13 (3), 520–522.

Klempa, B., Avsic-Zupanc, T., Clement, J., Dzagurova, T.K., Henttonen, H., Heyman, P., Jakab, F., Kruger, D.H., Maes, P., Papa, A., Tkachenko, E.A., Ulrich, R.G., Vapalahti, O., Vaheri, A., 2013. Complex evolution and epidemiology of Dobrava-Belgrade hantavirus: definition of genotypes and their characteristics. Arch. Virol. 158 (3), 521–529. https://doi.org/10.1007/s00705-012-1514-5.

Kumar, S., Stecher, G., Tamura, K., 2016. MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Mol. Biol. Evol. 33, 1870–1874. https://doi.org/10.1093/molbev/msw054.

Laenen, L., Vergote, V., Kafetzopoulou, L.E., Wawina, T.B., Vassou, D., Cook, J.A., Hugot, J.P., Deboutte, W., Kang, H.J., Witkowski, P.T., Köppen-Rung, P., Krüger, D.H., Licková, M., Stang, A., Striešková, L., Szemeš, T., Markowski, J., Hejduk, J., Kafetzopoulos, D., Van Ranst, M., Yanagihara, R., Klempa, B., Maes, P., 2018. A novel hantavirus of the european mole, Bruges virus, is involved in frequent Nova virus coinfections. Genome Biol. Evol. 10 (1), 45–55. https://doi.org/10.1093/gbe/evx268.

Ling, J., Sironen, T., Voutilainen, L., Hepojoki, S., Niemimaa, J., Isoviita, V.M., Vaheri, A., Henttonen, H., Vapalaht, O., 2014. Hantaviruses in Finnish soricomorphs: Evidence for two distinct hantaviruses carried by*Sorex araneus* suggesting ancient host-switch. Infect. Genet. Evol. 27, 51–61. https://doi.org/10.1016/j.meegid.2014.06.023.

Maes, P., Adkins, S., Alkhovsky, S.V., Avšič-Županc, T., Ballinger, M.J., Bente, D.A., Beer, M., Bergeron, E., Blair, C.D., Briese, T., et al., 2019. Taxonomy of the order Bunyavirales: Second update 2018. Arch. Virol. 164, 927–941. https://doi.org/10.1007/s00705-018-04127-3.

Mills, J.N., Childs, J.E., Ksiazek, T.G., Peters, C.J., 1995. Methods for Trapping and Sampling Small Mammals for Virologic Testing. US Department of Health and Human Services, Center for Disease Control and Prevention, Atlanta.

Radosa, L., Schlegel, M., Gebauer, P., Ansorge, H., Heroldová, M., Jánová, E., Stanko, M., Mošanský, L., Fričová, J., Pejčoch, M., Suchomel, J., Purchart, L., Groschup, M.H., Krüger, D.H., Ulrich, R.G., Klempa, B., 2013. Detection of shrew-borne hantavirus in Eurasian pygmy shrew (*Sorex minutus*) in Central Europe. Infect. Genet. Evol. 19, 403–410. https://doi.org/10.1016/j.meegid.2013.04.008.

Song, J.-W., Gu, S.H., Bennett, S.N., Arai, S., Puorger, M., Hilbe, M., Yanagihara, R., 2007. Seewis virus, a genetically distinct hantavirus in the Eurasian common shrew (*Sorex araneus*). Virol. J. 4, 114–119.

Wang, C.Q., Gao, J.H., Li, M., Guo, W.P., Lu, M.Q., Wang, W., Hu, M.X., Li, M.H., Yang, J., Liang, H.J., Tian, X.F., Holmes, E.C., Zhang, Y.Z., 2014. Co-circulation of Hantaan, Kenkeme, and Khabarovsk hantaviruses in Bolshoi Ussuriysky Island. China. Virus Res. 191, 51–58. https://doi.org/10.1016/j.virusres.2014.07.021.

Yanagihara, R., Gu, S.H., Arai, S., Kang, H.J., et al., 2014. Hantaviruses: rediscovery and new beginnings. Virus Res. 187, 6–14. https://doi.org/10.1016/j.virusres.2013.12.038.

Yashina, L., Mishin, V., Zdanovskaya, N., Schmaljohn, C., Ivanov, L., 2001. A newly discovered variant of a hantavirus in Apodemus peninsulae, Far Eastern Russia. Emerg. Infect. Dis. 7, 912–913.

Yashina, L.N., Slonova, R.A., Oleinik, O.V., Kuzina, I.I., Kushnareva, T.V., Kompanets, G.G., Simonov, S.B., Simonova, T.A., Netesov, S.V., Morzunov, S.P., 2004. A new genetic variant of the Puumala virus from the Maritime Territory and its natural carrier red-gray vole Clethrionomys rufocanus (in Russian). Vopr. Virusol. 49 (6), 34–37.

Yashina, L.N., Abramov, S.A., Gutorov, V.V., Dupal, T.A., Krivopalov, A.V., Panov, V.V., Danchinova, G.A., Vinogradov, V.V., Luchnikova, E.M., Hay, J., Kang, H.J., Yanagihara, R., 2010. Seewis virus: phylogeography of a shrew-borne hantavirus in Siberia, Russia. Vector Borne Zoonotic Dis. 10, 585–591. https://doi.org/10.1089/vbz.2009.0154.

Zuo, S.Q., Gong, Z.D., Fang, L.Q., Jiang, J.F., Zhang, J.S., Zhao, Q.M., Cao, W.C., 2014. A new hantavirus from the stripe-backed shrew (*Sorex cylindricauda*) in the People's Republic of China. Virus Res. 184, 82–86. https://doi.org/10.1016/j.viruses.2014.02.004.