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Review

Shrews (Soricidae) and Viruses Identified in Shrews

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Abstract: Shrews (Soricidae) are common small wild mammals with a significant overlap in their habitats with humans and domestic animals. Currently, viruses from 24 families have been identified in shrews, including Adenoviridae, Arenaviridae, Arteriviridae, Astroviridae, Bornaviridae, Caliciviridae, Circoviridae, Coronaviridae, Filoviridae, Flaviviridae, Hantaviridae, Hepadnaviridae, Hepeviridae, Nairoviridae, Orthoherpesviridae, Paramyxoviridae, Parvoviridae, Phenuiviridae, Picornaviridae, Polyomaviridae, Poxviridae, Rhabdoviridae, Sedoreoviridae, and Spinareoviridae, which pose potential threats to humans and domestic animals. This review compiled fundamental information about shrews and provided a comprehensive summary of the viruses that have been detected in shrews, with the aim to facilitating a deeper understanding of shrews and the diversity and risks of their viruses for researchers and the general public.

Keywords: shrew; virus; diversity; domestic animal; human

1. Introduction of Shrews (Soricidae)

Shrews are usually termed long-nosed mice, but they are not rodents. The largest species of shrews, *Suncus murinus* (Asian house shrews) (Figure 1), attains a length of approximately 15 cm and a weight of around 100 g, while *Suncus etruscus* (Etruscan shrews) could represent the smallest extant terrestrial mammals, measuring a mere 3.5 cm in length and weighing approximately 1.8 g [1].



Figure 1. Three Asian house shrews we raised in a barrel with soil.

In taxonomy, shrews are closer in phylogenetics to hedgehogs and moles than to rodents. They are taxonomically classified within the family Soricidae in the order Eulipotyphla. Currently, Soricidae encompasses three subfamilies, 26 genera, and 376 recognized species (Table 1, Figure 2). The three subfamilies are Crocidurinae (white-toothed shrews), Soricinae (red-toothed shrews), and Myosoricinae (African shrews). These three subfamilies comprise nine genera with 210 species, 14 genera with 148 species, and three genera with 18 species, respectively. The genus Crocidura in the subfamily Crocidurinae is the largest genus in Soricidae and covers 172 species. The genus Sorex is the largest genus in Soricidae and covers 77 species. The common names of some shrew species are listed in Table

Table 1. Geographic and viral distribution of 26 shrew genera.			
Shrew Genus	Geographical Distribution	Viral Distribution (Shrew Host Species Were Given in Parentheses)	
Crocidura in the subfamily Crocidurinae covers 172 species	temperate regions of Africa,	Langya virus (Crocidura shantungensis, Crocidura lasiura); Gamak virus and Daeryong virus (Crocidura shantungensis, Crocidura lasiura); Melian virus (Crocidura grandiceps); Denwin virus (Crocidura russula); Beilong virus (Crocidura shantungensis); Bowé virus (Crocidura douceti); Imjin virus (Crocidura lasiura); Jeju virus (Crocidura lasiura); Seoul virus (Crocidura lasiura); Azagny virus (Crocidura obscurior); Bufavirus (Crocidura hirta); Lamusara virus (Crocidura sp.); Lamgora virus (Crocidura sp.); Erve virus (Crocidura russula); Thiafora virus (Crocidura spp.); Usutu virus (Crocidura sp.); Olivier's shrew virus 1 (Crocidura olivieri guineensis); lymphocytic choriomeningitis virus (Crocidura goliath); Borna disease virus (Crocidura leucodon); Ljungan virus (Crocidura leucodon); Monkeypox virus (Crocidura spp.); Shrew herpesviruses (Crocidura spp.); Mokola virus (Crocidura russula); Shrew orthoreovirus (Crocidura hirta) Thottapalayam virus (Suncus murinus); Rotavirus A (Suncus	
Suncus in the subfamily Crocidurinae covers 18 species	^y Distributed in all continents except Oceania	murinus); Porcine Bocavirus G4 (Suncus murinus); adeno- associated virus (Suncus murinus); Japanese encephalitis virus (Suncus murinus); Suncus murinus hepacivirus (Suncus murinus); rat pegivirus (Suncus murinus); Wenzhou virus (Suncus murinus); torque teno virus (Suncus murinus); astroviruses (Suncus murinus); severe fever with thrombocytopenia syndrome virus (Suncus murinus); hepatitis E virus (Suncus murinus); shrew hepatitis B virus (Suncus murinus); Asian house shrew adenovirus (Suncus murinus); Cencurut virus (Suncus murinus); Wénchéng shrew virus (Suncus murinus)	
Sylvisorex in the subfamily Crocidurinae covers 12 species Diplomesodon	Distributed in Africa	Ebola virus (<i>Sylvisorex ollula</i>); Unnamed shrew adenovirus (<i>Sylvisorex sp.</i>)	
in the subfamily Crocidurinae covers 1 species	Distributed in Caspian region	No viruses have been identified in this shrew genus	
Feroculus	Distributed in southern Sri Lanka and southern India	No viruses have been identified in this shrew genus	

in the subfamily Crocidurinae covers 1 species

Distributed in Burundi, the Paracrocidura in the Democratic Republic of the

subfamily Crocidurinae Congo, Rwanda, Uganda, Gabon, No viruses have been identified in this shrew genus

covers 3 species the Central African Republic, and Equatorial Guinea in Africa

Ruwenzorisorex Distributed in Found in Burundi,

in the subfamily the Democratic Republic of the No viruses have been identified in this shrew genus

Crocidurinae covers 1 Congo, Rwanda, and Uganda species

Scutisorex in the subfamily Distributed in the Republic of the

No viruses have been identified in this shrew genus Crocidurinae covers 1 Congo

species Solisorex

Distributed in Sri Lanka and in the subfamily No viruses have been identified in this shrew genus Crocidurinae covers 1 southern India

roboratus); Seewis virus (Sorex araneus); Yakeshi virus (Sorex unguiculatus); Altai virus (Sorex araneus); Artybash virus Sorex Distributed Eurasia and North in the subfamily

(Sorex caecutiens); Artybash virus (Sorex caecutiens); Ash River virus (Sorex cinereus) Jemez Springs virus (Sorex America monticolus); Puumala virus (Sorex araneus); Qian hu shan virus (Sorex cylindricauda); common shrew coronavirus Tibet-2014 (Sorex araneus); Ljungan Virus (Sorex antinorii); Hepatitis A virus (sorex araneus); human polyomavirus 12 (sorex araneus, sorex coronatus, sorex minutus); cowpox virus (Sorex araneus); tick-borne encephalitis virus (Sorex araneus)

Ninorex virus (Sorex minutus); Lena mobatvirus (Sorex caecutiens, Sorex roboratus); Asikkala virus (Sorex minutus); Asikkala virus (Sorex minutus); Kenkeme virus (Sorex

Anourosorex

species

species

species

species

Soricinae covers 77

species

species

in the subfamily Distributed in China, Taiwan, Cao Bang virus (Anourosorex squamipes); Lianghe virus Soricinae covers 4 India, and Indochina (Anourosorex squamipes); Xinyi virus (Anourosorex yamashinai)

Blarinella in the subfamily Distributed in India, China, and

Camp Ripley virus (Blarina brevicauda); Powassan virus type 2 (Blarina brevicauda) Soricinae covers 3 Myanmar

Neomys in the subfamily Distributed in Europe and

Boginia virus (Neomys fodiens) Soricinae covers 3 northern Asia

Blarina in the subfamily Soricinae covers 4

Distributed in North America No viruses have been identified in this shrew genus

Distributed in North America Cryptotis No viruses have been identified in this shrew genus and Central America

in the subfamily Soricinae covers 30 species Chimarrogale in the subfamily Distributed in Asia No viruses have been identified in this shrew genus Soricinae covers 6 species Chodsigoa in the subfamily Distributed in Asia No viruses have been identified in this shrew genus Soricinae covers 8 species **Episoriculus** in the subfamily Distributed in Asia No viruses have been identified in this shrew genus Soricinae covers 4 species Nectogale in the subfamily Distributed in India and China No viruses have been identified in this shrew genus Soricinae covers 1 species Nesiotites in the subfamily Distributed in Europe and North No viruses have been identified in this shrew genus Soricinae covers 2 Africa species Soriculus in the subfamily Distributed in Asia No viruses have been identified in this shrew genus Soricinae covers 1 species Megasorex in the subfamily Distributed in the United States No viruses have been identified in this shrew genus Soricinae covers 1 and Mexico species Notiosorex in the subfamily Distributed in the United States No viruses have been identified in this shrew genus Soricinae covers 4 and Mexico species Myosorex in the subfamily Kilimanjaro virus (Myosorex geata); Uluguru virus (Myosorex Distributed in Africa Myosoricinae covers 14 zinki) species Surdisorex in the subfamily Distributed in Kenya No viruses have been identified in this shrew genus Myosoricinae covers 2 species Congosorex Distributed in Gabon, Central in the subfamily African Republic, Democratic No viruses have been identified in this shrew genus Myosoricinae covers 2 Congo, Cameroon, Tanzania species

Table 2. The common names of some shrew species.

Common Name of Shrews	Species Name of Shrews
American water shrew	Sorex palustris

Asian lesser white-toothed shrews

bicolored shrews

Chinese mole shrews

Asian house shrews

Doucet's musk shrews

dusky shrews

Eurasian pygmy shrews

Eurasian common shrews

Eurasian water shrews

flat-skulled shrews

Geata mouse shrews

Goliath shrews

greater forest shrews

greater white-toothed shrews

Kilimanjaro mouse shrews

large-headed shrews

Laxmann's shrews

lesser red musk shrews

long-clawed shrews

masked shrews

Millet's shrews

northern short-tailed shrews

Olivier's shrews

stripe-backed shrews

Taiwanese mole shrews

Ussuri white-toothed shrews

Valais shrews

West African pygmy shrews

Suncus murinus

Crocidura shantungensis

Crocidura leucodon

Anourosorex squamipes

Crocidura douceti

Sorex monticolus

Sorex minutus

Sorex Araneus

Neomys fodiens

0 1 1

 $Sorex\ roboratus$

Myosorex geata

Crocidura goliath

Sylvisorex ollula

Crocidura russula

Myosorex zinki

Crocidura grandiceps

Sorex caecutiens

Crocidura hirta

Sorex unguiculatus

Sorex cinereus

Sorex coronatus

Blarina brevicauda

Crocidura olivieri guineensis

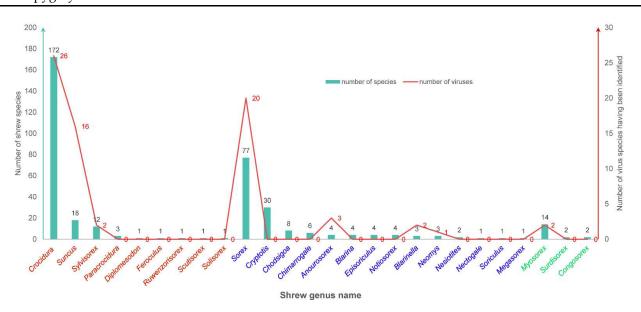
Sorex cylindricauda

Anourosorex yamashinai

Crocidura lasiura

Sorex antinorii

Crocidura obscurior



It is worth emphasizing that tree shrews, otter shrews, elephant shrews, West Indies shrews, and marsupial shrews are not shrews, because they do not fall within the *Soricidae* family [2].

Shrews are distributed globally across major tropical and temperate landmasses (Table 1), with notable exceptions in New Guinea, Australia, and New Zealand, where indigenous shrew populations are absent. In South America, shrews are confined to the northern Andes region and were introduced during the Great American Interchange.

In behaviors, shrews have a lifespan of 12 to 30 months, and they exhibit a relatively high metabolic rate, higher than some mammals of similar body sizes. Consequently, shrews have a relatively large food intake. Shrews do not hibernate but can enter a torpid state. During the winter, many shrews undergo significant changes in morphology, with body weight decreasing by 30% to 50%, and both skeletal and organ sizes noticeably shrinking [3]. Shrews are mostly found in cool and humid environments, with many being terrestrial, while some are semi-aquatic or burrowing. They may be active during both day and night or primarily nocturnal. Shrews are typically solitary creatures, coming together only for mating purposes.

In reproduction, female shrews can give birth to as many as 10 litters each year. In tropical regions, they are capable of mating year-round, while in temperate regions, they cease reproduction during the winter. The gestation period for shrews ranges from 17 to 32 days. Female shrews can become pregnant again within one to two days after giving birth and can lactate and nurse their offspring during pregnancy [4].

Shrews possess two characteristics distinct from most mammals. Firstly, certain shrew species secrete venom [5], which contains various compounds. For example, the venom of American short-tailed shrews can kill 200 mice when administered intravenously. Some shrews in China also produce venom. Secondly, similar to bats and toothed whales, some shrews are capable of echolocation [6]. Currently, two genera, namely *Sorex* (long-tailed shrews) and *Blarina* (blarina shrews) possess echolocation abilities. Species within these two genera include Eurasian water shrews (*Neomys fodiens*), northern short-tailed shrews (*Blarina brevicauda*), and American water shrews (*Sorex palustris*), among others [7].

The viruses in shrews have exhibited a high diversity, and many viruses in shrews have not been identified [8]. Currently, as detailed below and summarized in Figure 2 and Table 3, viruses from 24 families have been identified in shrews, including *Adenoviridae*, *Arenaviridae*, *Arteriviridae*, *Astroviridae*, *Bornaviridae*, *Caliciviridae*, *Circoviridae*, *Coronaviridae*, *Filoviridae*, *Flaviviridae*, *Hantaviridae*, *Hepadnaviridae*, *Hepeviridae*, *Nairoviridae*, *Orthoherpesviridae*, *Paramyxoviridae*, *Parvoviridae*, *Phenuiviridae*, *Picornaviridae*, *Polyomaviridae*, *Poxviridae*, *Rhabdoviridae*, *Sedoreoviridae*, and *Spinareoviridae*.

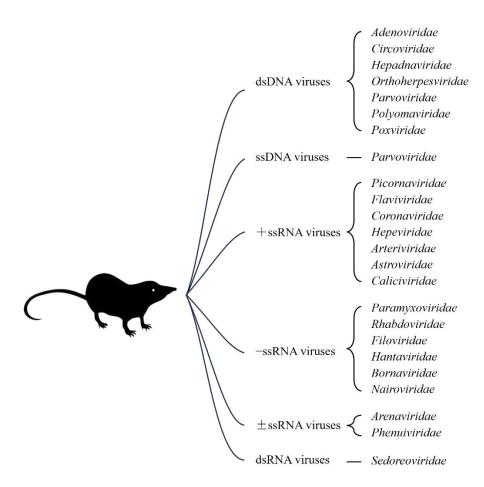


Figure 3. The virus families that contain viruses having been identified in shrews.

2. Paramyxoviruses in Shrews

Paramyxoviridae family contains several important viruses that are pathogenic to both humans and livestock. Viruses within this family are enveloped, approximately spherical or pleomorphic in shape, with a diameter of around 150 nm or larger. The genomes of *Paramyxoviridae* viruses consist of single-stranded, negative-sense RNA that is non-segmented, with a length of approximately 15 to 21 kb. These genomes encode six to ten different proteins, including the nucleocapsid protein (NP), phosphoprotein (P), large polymerase protein (L), matrix protein (M), fusion protein (F), and hemagglutinin-neuraminidase protein (HN) [9].

The International Committee on Taxonomy of Viruses (ICTV) currently classifies the *Paramyxoviridae* into 17 genera. The *Paraavulavirus* genus contains two species of avian viruses. The *Henipavirus* genus comprises 10 mammalian viruses, including the pathogenic Hendra virus, Nipah virus, and Langya virus. The *Jeilongvirus* genus includes 15 mammalian viruses, such as J virus and Beilong virus. Currently, seven species of paramyxoviruses have been identified in shrews, with six belonging to the *Henipavirus* genus and one belonging to the *Jeilongvirus* genus.

Langya virus, a member of the *Henipavirus*, was first reported in China in 2022, with shrews potentially serving as its natural reservoir host, detected in two shrew species, *Crocidura lasiura* (Ussuri white-toothed shrews) and *Crocidura shantungensis* (Asian lesser white-toothed shrews). The study identified 35 acute Langya virus cases among patients in Shandong and Henan provinces, manifesting symptoms such as fever (100%), fatigue (54%), cough (50%), loss of appetite (50%), myalgia (46%), nausea (38%), headache (35%), vomiting (35%), thrombocytopenia (35%), leukopenia (54%), and liver (35%) and kidney dysfunction (8%). Research encompassed 25 wild animal species and indicated a high virus infection rate among shrews (71/262 [27%]). Nevertheless, the virus's distribution in shrews and other animals across diverse Chinese regions remains poorly elucidated [10].

Gamak virus and Daeryong virus, both belonging to the *Henipavirus*, which were discovered in South Korea in 2021 from Ussuri white-toothed shrews and Asian lesser white-toothed shrews, respectively. Gamak virus has the ability to infect and replicate in human lung epithelial cell line A549 cells and rapidly induce the secretion of type I/III interferons, ISGs, and pro-inflammatory cytokines from these cells [11].

The viruses Melian virus and Denwin virus, belonging to the *Henipavirus*, were respectively discovered in 2022 in large-headed shrews (*Crocidura grandiceps*) in Guinea and greater white-toothed shrews (*Crocidura russula*) in Belgium. Further studies on their pathogenicity have not been conducted yet [12].

Ninorex virus, belonging to the *Henipavirus*, were respectively discovered in 2023 in *Sorex minutus* in Belgian. Further studies on their pathogenicity have not been conducted yet [13].

Beilong virus, belonging to the *Jeilongvirus*, has also been detected in shrews, although it was initially found in rodents. A study conducted between September 2013 and May 2019, covering eleven provinces in China, examined small mammals. The PCR testing showed a positivity rate of 28.57% (2/7) in the Asian lesser white-toothed shrews and 17.57% (13/74) in the *Suncus murinus*. Currently, there is no evidence of human infection with Beilong virus, but its potential risk to humans and livestock should not be underestimated [14].

3. Hantaviruses in Shrews

Hantaviridae family includes many pathogenic viruses for both humans and animals. These viruses are enveloped and are typically spherical or tubular, with a diameter ranging from 120 to 160 nm. The viral genome is a single-stranded negative-sense RNA virus (-ssRNA) with a size ranging from approximately 10,000 to 15,000 nucleotides. It consists of three segments: large (L), medium (M), and small (S), which collectively encode at least four structural proteins [15]. The largest segment (L) of the viral genome encodes an RNA-dependent RNA polymerase (RdRp). The medium segment (M) encodes a glycoprotein precursor (GPC), which is co-translationally cleaved by host cell signal peptidases in the endoplasmic reticulum to produce two envelope glycoproteins (Gn and Gc, or G1 and G2). The small segment (S) encodes the nucleocapsid protein (N), responsible for assembling the viral genomic RNA [16].

Hantaviridae is currently classified into seven genera. The *Orthohantavirus* genus has 38 mammalian viruses, including 15 that are zoonotic. The *Mobatvirus* genus contains 5 animal viruses. The *Thottimvirus* genus contains 2 mammalian viruses.

Lena mobatvirus, belonging to the *Mobatvirus*, was discovered in 2021 in the *Sorex caecutiens* and *Sorex roboratus* in the Siberian and Far Eastern regions of Russia. Its zoonotic potential has not been analyzed [17].

Asikkala virus, belonging to the *Orthohantavirus*, was discovered in 2010 in Eurasian pygmy shrews (*Sorex minutus*) in Finland. Subsequently, partial L segment sequences of three new hantaviruses were obtained in the Czech Republic and Germany. Genetic evolutionary analysis indicated that all of these hantaviruses belong to the Asikkala virus group, originally identified in Finland [18].

Bowé virus, belonging to the *Orthohantavirus*, was discovered in 2012 in the muscle tissue of the Doucet's musk shrews (*Crocidura douceti*) in southwestern Guinea. It shares a common ancestor with the unclassified Tanganya virus, and its zoonotic potential is currently unknown [19].

Cao Bang virus, a member of the *Orthohantavirus*, was discovered in 2006 in the lung tissue of the Chinese mole shrews (*Anourosorex squamipes*) in China. Sequencing of the M and partial S segments revealed that it is genetically distantly related to hantaviruses carried by rodents and other mole shrews hantaviruses. Its zoonotic potential is currently unknown [20].

Imjin virus, a member of the *Orthohantavirus*, was discovered in 2009 in Ussuri white-toothed shrews in South Korea. Its zoonotic potential is currently unknown [21].

Jeju virus, a member of the *Orthohantavirus*, was discovered in 2012 in Ussuri white-toothed shrews on Jeju Island, South Korea. Genetic evolution analysis revealed that it is distantly related to

the previously discovered Imjin virus in South Korea, making it a new member of the *Orthohantavirus*. Its zoonotic potential is currently unknown [22].

Kenkeme virus, a member of the *Orthohantavirus*, was discovered in 2010 on *Sorex roboratus* in the northeastern part of the Sakha Republic, Siberia. Sequence analysis of the full-length S segment and partial M and L segments indicated that Kenkeme virus represents a novel *Orthohantavirus* in terms of its genetic makeup and phylogenetic relationship. Kenkeme virus exhibits distinct differences in terms of genetics and phylogeny when compared to other hantaviruses found in Eurasian common shrews, as well as in other rodents, shrews, and moles. Its zoonotic potential is currently unknown [23].

Seewis virus, a member of the *Orthohantavirus*, was discovered in 2006 in Eurasian common shrews (*Sorex araneus*) in Switzerland. Phylogenetic analysis of the complete S segment and partial M and L segments of Seewis virus revealed that it is genetically distant from hantaviruses found in rodents but more closely related to hantaviruses found in shrews. The zoonotic potential of Seewis virus is currently unknown [24].

Yakeshi virus, a member of the *Orthohantavirus*, was discovered in 2013 on long-clawed shrews (*Sorex unguiculatus*) in China. Lianghe virus, an unclassified virus within the *Orthohantavirus*, was found in Chinese mole shrews (*Anourosorex squamipes*). The zoonotic potential of these viruses is currently unknown [25].

Seoul virus, a member of the *Orthohantavirus*, was first reported in 2014 in Ussuri white-toothed shrews in China. This virus is known to be infectious to humans [26].

Altai virus, an unclassified member of the *Orthohantavirus*, was amplified from the tissue of an Eurasian common shrew in the Altai Republic in 2007. Initially, this virus was classified as Seewis virus, but subsequent findings indicated that it did not align with the host shrew species and geographical location. Through nucleotide pairing comparisons and analysis of a 300-nucleotide region of the L segment, it was confirmed to be a unique Hantavirus species [27].

Artybash virus, an unclassified member of the *Orthohantavirus*, was detected in a very limited manner in the *Sorex caecutiens* captured near Lake Teletskoye in the Altai Republic of Western Siberia in 2006. Initially referred to as the Amga virus, genetic and phylogenetic analysis of both partial and complete genome sequences identified it as a genetic variant of the Artybash virus. Its zoonotic potential remains unknown [28].

Xinyi virus, an unclassified member of the *Orthohantavirus*, was reported in 2016 and discovered in the *Anourosorex yamashinai*. Phylogenetic analysis based on the S segment, M segment, and L segment sequences suggests that Xinyi virus shares a common ancestor with the Cao Bang virus. Their pathogenicity to humans and animals is currently unknown [29].

The unclassified Ash River virus and Jemez Springs virus, both members of the *Orthohantavirus*, were discovered in 2008 on masked shrews (*Sorex cinereus*) and dusky shrews (*Sorex monticolus*) in the United States. Their pathogenicity to humans and animals is currently unknown [30].

The unclassified Camp Ripley virus, a member of the *Orthohantavirus*, was discovered in 2007 in the northern short-tailed shrews in the United States. Its pathogenicity to humans and animals is currently unknown [31].

The unclassified Boginia virus, a member of the *Orthohantavirus*, was reported in 2013 in Eurasian water shrews in Poland. Its pathogenicity to humans and animals is currently unknown [32].

The unclassified Azagny virus, a member of the *Orthohantavirus*, was discovered in 2011 in West African pygmy shrews (*Crocidura obscurior*) in Azagny Park, Côte d'Ivoire. Its pathogenicity to humans and animals is currently unknown [33].

The unclassified Puumala virus, a member of the *Orthohantavirus* genus, was discovered in 2014 in Eurasian common shrews in Finland. Its pathogenicity to humans and animals is currently unknown [34].

The unclassified Kilimanjaro virus and Uluguru virus, members of the *Orthohantavirus*, were discovered in 2014 in the *Myosorex geata* and *Myosorex zinki* in West Africa. Their pathogenicity to humans and animals is currently unknown [35].

(

The unclassified Qian hu shan virus, a member of the *Orthohantavirus*, was detected in the lung tissue of stripe-backed shrews (*Sorex cylindricauda*) in China in 2014. Its pathogenicity to humans and animals is currently unknown [36].

Thottapalayam virus (TPMV), a member of the *Thottimvirus*, was first isolated in 1965 from Asian house shrews in India. This virus represents the earliest isolation of a hantavirus from shrews [37].

4. Sedoreoviruses in Shrews

The viruses in *Sedoreoviridae* family include numerous pathogens for humans and animals. These viruses lack an envelope, have an icosahedral shape, and measure approximately 60 to 100 nm in diameter [38]. The genome of *Sedoreoviridae* consists of 10 to 12 linear double-stranded RNA segments, with a total length ranging from 18 to 26 kilobase pairs (kp). Individual segments vary in length from 0.6 to 5.8 kp. Each double-stranded positive-sense RNA carries a type 1 cap structure at the 5' end but lacks a 3' polyadenylated tail. Virus RNAs are typically monogenic and feature relatively short 5' and 3' non-coding regions, although some segments may contain a second or third functional open reading frame [39].

Sedoreoviridae is currently classified into six genera. The *Orbivirus* genus contains a total of 22 animal viruses, including 16 mammalian viruses such as Bluetongue virus; the *Rotavirus* genus contains 9 rotaviruses, including 3 that are pathogenic to humans, 3 to birds, and 3 to other mammals.

Rotavirus A, belonging to the *Rotavirus*, was detected in Asian house shrews in 2016. This virus can infect humans, causing severe diarrhea in infants and young children. It can also infect domestic and wild mammals as well as birds [40].

Bluetongue virus, a member of the *Orbivirus*, was discovered in an unknown shrew species in Africa in 1994. This virus primarily infects sheep and various ruminant animals, with a very high fatality rate in sheep [41].

5. Parvoviruses in Shrews

The *Parvoviridae* family contains several significant viruses that can cause diseases in humans and animals. Viruses in this family are non-enveloped and typically have small, symmetrical icosahedral shapes with a diameter of approximately 23 to 28 nm [42]. The genome of parvoviruses consists of a linear, non-circular, single-stranded DNA molecule with a length ranging from 4 to 6 kb. The capsid is composed of sixty VP proteins that assemble into a nested arrangement, usually encoded by a single structural gene. This gene includes the entire coding sequence for VP1, which typically ranges from 75 to 100 kDa. Additionally, there are one or more smaller forms (VP2-5) that share a common C-terminal sequence but have varying lengths of N-terminal truncation [43].

Parvoviridae is currently classified into 14 genera. The *Bocaparvovirus* genus encompasses 31 mammalian viruses. The *Dependoparvovirus* genus comprises 13 animal viruses, including 3 avian viruses and 8 mammalian viruses. The *Protoparvovirus* genus includes 18 mammalian viruses, such as canine parvovirus, porcine parvovirus, and 3 human parvoviruses.

Bufavirus, a member of the *Protoparvovirus*, was discovered in the lesser red musk shrews (*Crocidura hirta*) in Zambia in 2015. This virus is capable of infecting humans, primarily causing diarrhea in children [44].

Porcine bocavirus G4, a member of the *Bocaparvovirus*, was discovered in Asian house shrews in 2019 in China. This virus can infect pigs, leading to respiratory and gastrointestinal diseases [45].

Adeno-associated virus (AAV), a member of the *Dependoparvovirus*, was discovered in Asian house shrews in 2020 in China. The Infection status in humans and other animals is unknown [46].

6. Nairoviruses in Shrews

The *Nairoviridae* family includes various significant viruses that are harmful to both humans and animals. Viruses in this family are enveloped, spherical in shape, with a diameter of 80-120 nm. The envelope is covered with glycoproteins Gn and Gc. The isolated ribonucleoprotein (RNP) complex

consists of segmented genomic RNA, each wrapped in nucleoprotein (N) [47]. The Nairovirus genome comprises three single-stranded negative-sense RNA molecules, with these three genomic segments labeled as L (large), M (medium), and S (small). These RNAs code for proteins on the viral complementary strands, including N, glycoprotein precursor (GPC), and L (containing RdRp, helicase, and nuclease domains) [48].

Nairoviridae is currently classified into three genera. The *Orthonairovirus* genus comprises 55 animal viruses.

The *Orthonairovirus* Lamusara virus and Lamgora virus were discovered in *Crocidura* sp. in Gabon, Central Africa, in 2022. Their pathogenicity to humans and animals is currently unknown [49].

Erve virus, belonging to the *Orthonairovirus*, was discovered in greater white-toothed shrews in France in 1989. It can infect humans and various domestic animals, leading to neurological symptoms in humans [50].

Thiafora virus, belonging to the *Orthonairovirus*, was discovered in *Crocidura sp.* in Senegal in 2015. Its pathogenicity to humans and animals is currently unknown [51].

Cencurut virus, belonging to the *Orthonairovirus*, was discovered in Asian house shrews in Singapore in 2023. Its pathogenicity to humans and animals is currently unknown [52].

7. Coronaviruses in Shrews

The *Coronaviridae* family includes various significant viruses that are harmful to both humans and animals. Viruses in this family are enveloped and, in the case of the *Orthocoronavirinae* subfamily, have a spherical shape with a diameter of 80 to 160 nm [53]. The shapes of viruses in the other two subfamilies have not yet been determined. The viral genome is non-segmented, single-stranded RNA, approximately 26 to 32 kb in size. The initial part of the coronavirus genome encodes 16 non-structural proteins, while the remaining portion encodes four essential structural proteins: envelope protein (E), spike glycoprotein (S), matrix (M) protein, and nucleocapsid (N) protein [54].

Coronaviridae is currently classified into six genera. The *Alphacoronavirus* genus includes 27 mammalian viruses, including several common human coronaviruses such as Human Coronavirus 229E and Human Coronavirus NL63, as well as porcine epidemic diarrhea virus.

Wencheng shrew virus, belonging to the *Alphacoronavirus*, was discovered in 2017 in China in Asian house shrews. Its pathogenicity to humans and animals is unknown [55].

A previously unnamed shrew coronavirus in the *Alphacoronavirus* was discovered in 2016 in Eurasian common shrews in the United Kingdom. Phylogenetically, it falls within the same branch as the Lu-cheng virus found in Chinese rats. Its pathogenicity to humans and animals is unknown [56].

Common shrew coronavirus Tibet-2014, belonging to the *Alphacoronavirus*, was identified in Eurasian common shrews in Tibet, China, in 2014. Its pathogenicity to humans and animals is unknown [57].

8. Flaviviruses in Shrews

The *Flaviviridae* family comprises several significant viruses that are harmful to humans and animals. Viruses in this family are enveloped and spherical, with a viral particle diameter ranging from 40 to 60 nm [58]. The viral genome is a positive-sense, single-stranded RNA, with a length of 8.9 to 13.0 kb. It consists of a single large open reading frame (ORF) flanked by 3' and 5' untranslated regions (UTRs), and it possesses a 5' cap structure. This single ORF encodes a polyprotein that undergoes processing and cleavage by viral protease NS2B/NS3 and cellular proteases. This cleavage results in the formation of three structural proteins, including the C protein of the viral capsid, the M (membrane) protein, and the E (membrane) protein. Additionally, seven non-structural proteins play essential roles in viral replication. These proteins are NS1, NS2A, NS2B, NS3, NS4A, NS4B, and NS5 [59].

Flaviviridae is currently classified into four genera. The Orthoflavivirus genus includes 52 animal viruses, including several significant human pathogens such as Yellow Fever virus, Dengue virus,

Zika virus, Japanese Encephalitis virus, West Nile virus, and Tick-Borne Encephalitis virus. It also has pathogenicity for livestock and poultry (turkeys, pigs, horses, and sheep), causing economically important diseases such as encephalitis viruses in various livestock. The *Hepacivirus* genus contains 14 mammalian viruses, with human hepatitis C virus being among those capable of infecting humans. The *Pegivirus* genus comprises 11 mammalian viruses.

Usutu virus, belonging to the *Orthoflavivirus*, was first reported in *Crocidura sp.* in Senegal in 2019. At the time of collection, no pathogenic infection or symptoms were observed in shrews. This virus was initially discovered in 1959 and is associated with Culex mosquitoes as its vectors. Currently, the virus has been isolated from birds, arthropods, and humans in Europe and Africa, and subsequently detected in bats and horses [60].

Powassan virus type 2, classified within the *Orthoflavivirus*, was first discovered in 2021 in *Blarina brevicauda* in the United States. Previously, it had been found primarily in ticks and humans. This virus can lead to encephalitis in humans and is primarily transmitted by arthropod vectors [61].

Tick-borne encephalitis virus, classified within the *Orthoflavivirus*, was first discovered in 1967 in Eurasian common shrews in Slovakia. This virus can infect humans, and when it reaches the central nervous system, neurological symptoms can occur. Infection can manifest as meningitis, encephalitis, or meningoencephalitis. In nature, tick-borne encephalitis virus circulates between ticks and small mammals [62].

Japanese encephalitis virus, classified within the *Orthoflavivirus*, was first discovered to infect Asian house shrews in 1984. This virus can infect humans and various livestock. Infected individuals may exhibit mild symptoms such as fever and headache, or they may be asymptomatic. However, approximately 1 in every 250 infected individuals may develop severe illness. Initial symptoms in children can include abdominal pain and vomiting. Severe illness is characterized by a rapid rise in body temperature, headache, neck stiffness, loss of orientation, coma, seizures, spasmodic paralysis, and may lead to death. The fatality rate for individuals displaying disease symptoms can be as high as 30% [63].

Suncus murinus hepacivirus, belonging to the *Hepacivirus*, was discovered in Asian house shrews in 2016. Currently, its zoonotic potential is unknown [64].

Rat pegivirus, belonging to the *Pegivirus*, was discovered in Chinese Asian house shrews in 2020. This virus primarily targets lymphocytes and causes asymptomatic infections in humans and other animals, presenting as benign [65].

9. Arteriviruses in Shrews

The *Arteriviridae* family comprises several significant veterinary pathogens. The viruses in this family are enveloped and generally spherical, with an estimated diameter ranging from 50 to 74 nm [66]. The viral genome is a linear positive-sense RNA, approximately 12 to 16 kb in length. The infectious genome RNA contains a 5' type I cap structure and a 3' polyadenylate sequence, surrounding multiple and mostly overlapping open reading frames (ORFs). The two largest ORFs closest to the 5' end, known as ORF1a and ORF1b, encode non-structural proteins, while the ORFs at the 3' end encode structural viral proteins.

Arteriviridae is currently classified into 13 genera. The Muarterivirus genus contains only one shrew arterivirus, Olivier's shrew virus 1, which was discovered in 2018 in Olivier's shrews (Crocidura olivieri guineensis) in Guinea. Both phylogenetic analysis and pairwise sequence comparison indicate that this virus is distinctly different from the established arterivirus genera and belongs to a new genus [67].

10. Other Viruses in Shrews

Shrews serve as the hosts for multiple other viruses, such as adenovirus, hepatitis B virus, herpesvirus, Ebola virus, pegivirus, and astrovirus, as listed in Table 2.

Table 2. The taxonomy and zoonotic potential of the viruses having been identified in shrews.

Family	Genus	Virus	Zoonotic Potential	Year / Country / Host Species
Paramyxoviridae	Henipavirus	Langya virus	Infects humans and some other mammals	2022 / China / Crocidura lasiura, Crocidura shantungensis [10]
Paramyxoviridae	Henipavirus	Gamak virus	Unknown	2021 / China / Crocidura lasiura, Crocidura shantungensis [11]
Paramyxoviridae	Henipavirus	Daeryong virus	Unknown	2021 / China / Crocidura lasiura, Crocidura shantungensis [11]
Paramyxoviridae	Henipavirus	Melian virus	Unknown	2022 / Guinea / Crocidura grandiceps [12]
Paramyxoviridae	Henipavirus	Denwin virus	Unknown	2022 / Belgium / <i>Crocidura russula</i> [12]
Paramyxoviridae	Henipavirus	Ninorex virus	Unknown	2023 / Belgian / Sorex minutus [13]
Paramyxoviridae	Jeilongvirus	Beilong virus	Unknown	2019 / China / Crocidura shantungensis, Suncus murinus [14]
Hantaviridae	Mobatvirus	Lena mobatvirus	Unknown	2021 / Siberian and Russia / Sorex caecutiens, Sorex roboratus [17]
Hantaviridae	Orthohantavirus	Asikkala virus	Unknown	2010 / Finland / Sorex minutus [18]
Hantaviridae	Orthohantavirus	Bowé virus	Unknown	2012 / Guinea / Crocidura douceti [19]
Hantaviridae	Orthohantavirus	Cao Bang virus	Unknown	2006 / China / Anourosorex squamipes [20]
Hantaviridae	Orthohantavirus	Imjin virus	Unknown	2009 / South Korea / Crocidura lasiura [21]
Hantaviridae	Orthohantavirus	Jeju virus	Unknown	2012 / South Korea / Crocidura lasiura [22]
Hantaviridae	Orthohantavirus	Kenkeme virus	Unknown	2010 / Sakha Republic, Siberia / Sorex roboratus [23]
Hantaviridae	Orthohantavirus	Seewis virus	Unknown	2006 / Switzerland / <i>Sorex araneus</i> [24]
Hantaviridae	Orthohantavirus	Yakeshi virus	Unknown	2013 / China / Sorex unguiculatus [25]
Hantaviridae	Orthohantavirus	Lianghe virus	Unknown	2013 / China / Anourosorex squamipes [25]
Hantaviridae	Orthohantavirus	Seoul virus	Infects humans	2014 / China / Crocidura lasiura [26]
Hantaviridae	Orthohantavirus	Altai virus	Unknown	2007 / Altai Republic / Sorex araneus [27]
Hantaviridae	Orthohantavirus	Artybash virus	Unknown	2006 / Altai Republic / Sorex caecutiens [28]
Hantaviridae	Orthohantavirus	Xinyi virus	Unknown	2016 / Chian / Anourosorex yamashinai [29]
Hantaviridae	Orthohantavirus	Ash River virus	Unknown	2008 / United States / Sorex cinereus, Sorex monticolus [30]
Hantaviridae	Orthohantavirus	Camp Ripley virus	Unknown	2007 / United States / Blarina brevicauda [31]
Hantaviridae	Orthohantavirus	Boginia virus	Unknown	2013 / Poland / Neomys fodiens [32]
Hantaviridae	Orthohantavirus	Azagny virus	Unknown	2011 / Côte d'Ivoire / <i>Crocidura</i> obscurior [33]
Hantaviridae	Orthohantavirus	Puumala virus	Unknown	2014 / Finland / Sorex araneus [34]
Hantaviridae	Orthohantavirus	Kilimanjaro virus	Unknown	2014 / West Africa / Myosorex geata [35]

Hantaviridae	Orthohantavirus	Uluguru virus	Unknown	2014 / West Africa / Myosorex zinki [35]
Hantaviridae	Orthohantavirus	Qian hu shan virus	s Unknown	2014 / China / Sorex cylindricauda [36]
Hantaviridae	Thottimvirus	Thottapalayam virus	Unknown	1965 / India / Suncus murinus [37]
Sedoreoviridae	Rotavirus	Rotavirus A	Infects humans	2016 / China / Suncus murinus [40]
Sedoreoviridae	Orbivirus	Bluetongue virus	Unknown	1994 / Africa / unknown shrew species [41]
Parvoviridae	Protoparvovirus	Bufavirus	Infects humans	2015 / Zambia / Crocidura hirta [44]
Parvoviridae	Bocaparvovirus	porcine bocavirus G4	Infects pigs	2019 / China / Suncus murinus [45]
Parvoviridae	Dependoparvovirus	adeno-associated virus	Unknown	2020 / China / Suncus murinus [46]
Nairoviridae	Orthonairovirus	Lamusara virus	Unknown	2022 / Gabon / <i>Crocidura sp.</i> [49]
Nairoviridae	Orthonairovirus	Lamgora virus	Unknown	2022 / Gabon / <i>Crocidura sp.</i> [49]
Nairoviridae	Orthonairovirus	Erve virus	Unknown	1989 / France / <i>Crocidura russula</i> [50]
Nairoviridae	Orthonairovirus	Thiafora virus	Unknown	2015 / Senegal / Crocidura sp. [51]
Nairoviridae	Orthonairovirus	Cencurut virus	Unknown	2023 / Singapore / Suncus murinus [52]
Coronaviridae	Alphacoronavirus	Wencheng shrew virus	Unknown	2017 / China / Suncus murinus [55]
Coronaviridae	Alphacoronavirus	unnamed shrew coronavirus common shrew	Unknown	2016 / United Kingdom / Sorex araneus [56]
Coronaviridae	Alphacoronavirus	coronavirus Tibet- 2014	Unknown	2014 / China / Sorex araneus [57]
Flaviviridae	Orthoflavivirus	Usutu virus	Infects birds, arthropods humans, bats, and horse	6, 2019 / Senegal / <i>Crocidura sp.</i> [60]
Flaviviridae	Orthoflavivirus	Powassan virus type 2	Infects humans and causes encephalitis	2021 / United States / Blarina brevicauda [61]
Flaviviridae	Orthoflavivirus	tick-borne	Infects humans and	1967 / Slovakia / Sorex araneus [62]
		encephalitis virus	causes encephalitis	
Flaviviridae	Orthoflavivirus	Japanese encephalitis virus	Infects humans and various domestic animals and causes human encephalitis	1984 / Japan / Suncus murinus [63]
Flaviviridae	Hepacivirus	Suncus murinus hepacivirus	Unknown	2016 / China / Suncus murinus [64]
Flaviviridae	Pegivirus	rat pegivirus	Infects humans and other animals without symptoms	2020 / China / Suncus murinus [65]
Arteriviridae	Muarterivirus	Olivier's shrew virus 1	Unknown	2018 / Guinea / Crocidura olivieri guineensis [67]
Caliciviridae	Lagovirus	Rabbit hemorrhagic disease virus	Infects rabbits	2019 / Spain / <i>Crocidura russula</i> [68]
Arenaviridae	Mammarenavirus	Wenzhou virus	Infects humans	2015 / China / Suncus murinus [69,70]

2019 / Zambia / Crocidura hirta [87]

Arenaviridae	Mammarenavirus	lymphocytic choriomeningitis virus	Infects humans and various animals and dangerous to pregnant women and infants Infects humans, horses,	2021 / Gabon / Crocidura goliath [71]
Bornaviridae	Orthobornavirus	Borna disease viru	sheen and various other	: 2006 / Switzerland / Crocidura leucodon [72]
Circoviridae	Anellovirus	torque teno virus	Infects humans and causes various symptoms	2018 / China / Suncus murinus [73]
Picornaviridae	Parechovirus	Ljungan Virus	Infects humans and causes various symptoms	2020 / Italy / Crocidura leucodon, Sorex antinorii [74]
Picornaviridae	Hepatovirus	Hepatitis A virus	Unknown	2015 / Germany / sorex araneus [75]
Polyomaviridae	Betapolyomavirus	human polyomavirus 12	Infects humans	2017 / Germany, Norway / sorex Araneus, sorex coronatus, sorex minutus [76]
Poxviridae	Orthopoxvirus	monkeypox virus	Infects humans and other primates	2015 / Zambia, Congo / Crocidura spp. [77]
Poxviridae	Orthopoxvirus	shrew cowpox virus	Unknown	1998 / Norway / Sorex araneus [78]
Astroviridae	Mamastrovirus	shrew astrovirus	Unknown	2014 / China / Suncus murinus [79]
Filoviridae	Ebolavirus	Ebola virus	Infects humans with a high case fatality rate	1999 / Central Africa / Sylvisorex ollula [80]
Phenuiviridae	Phlebovirus	severe fever with thrombocytopenia syndrome virus	Infects humans with a high case fatality rate	2014 / China / Suncus murinus [81]
Herpesviridae	Unknown	shrew herpesvirus	Unknown	2018 / Central Africa / Crocidura spp. [55]
Rhabdoviridae	Lyssavirus	Mokola virus	Unknown	1968 / Nigeria / Crocidura spp. [82]
Hepeviridae	Paslahepevirus	shrew hepatitis E virus	Unknown	2013 / China / Suncus murinus [83]
Hepadnaviridae	Orthohepadnavirus	shrew hepatitis B virus	Unknown	2019 / China / Suncus murinus [84]
Adenoviridae	Atadenovirus	Asian house shrew adenovirus	Unknown	2016 / China / Suncus murinus [85]
Adenoviridae	Atadenovirus	shrew adenovirus	Unknown	2019 / Cameroon / Sylvisorex sp. [86]
Sninareoviridae	Orthoreovirus	shrew	Unknown	2019 / Zambia / Crocidura hirta [87]

11. Discussion

Orthoreovirus

Spinareoviridae

Shrews share overlapping habitats with humans and livestock, highlighting the importance of shrew virus research for public health and animal welfare. This review shows that shrew populations host at least 24 families of viruses, and 23 species of hantaviruses, seven species of paramyxoviruses, six species of flaviviruses, and five species of nairoviruses in shrews have been identified. 17 species of viruses in 14 families in Asian house shrews (*Suncus murinus*) have been identified. Eight species of viruses in six families in Eurasian common shrews (*Sorex araneus*) have been identified. Six species of viruses in two zoonotic families in Ussuri white-toothed shrews (*Crocidura lasiura*) have been identified. These three species of shrews could host more species of zoonotic viruses than other shrew species.

Unknown

orthoreovirus

Future research should assess the transmission risks of shrew viruses from shrews to humans and domestic animals. Future research should conduct broader surveys to delve into the diversity, evolution, potential pathogenicity, and effective measures of these viruses. This will enhance our capacity to respond swiftly to the potential outbreaks of shrew viruses in humans or domestic animals.

Shrews' small size and ease of husbandry make them ideal for studying viruses of shrews and other animals including humans. Their biological traits, like reproductive cycles, lifespan, and immune systems, are valuable for investigating the transmission, pathogenicity, and potential therapies of viral diseases.

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