# The overlooked small terrestrial mammal taxa (Rodentia, Eulipotyphla, and Lagomorpha) in the evolution of coronaviruses

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## Abstract

Coronaviruses have been extensively detected in bats over the past few decades. However, increasing evidence suggests that other taxa, such as Rodentia, Eulipotyphla, and Lagomorpha, may have played a significant role in the ecology and evolution of some coronaviruses. Here, we compile recent contributions illuminating these mammals' enigmatic role in coronavirus evolution. We highlight how taxonomic and technical biases in coronavirus surveillance may have diminished the perceived importance of these animals in the ecology and evolution of certain coronaviruses and propose future directions to uncover the role of these small terrestrial mammals in coronavirus circulation. Additionally, we examine ecological factors that drive the maintenance and circulation of coronaviruses within small mammal populations and explore the importance of host dynamics on viral circulation within these groups. Furthermore, we address the potential risk small terrestrial mammals pose as sources or intermediate hosts for newly emergent human and livestock pathogenic coronaviruses. We address the under-investigation of specific taxa like Eulipotyphla in coronavirus evolution, emphasizing the need for comprehensive surveillance and research efforts. By recommending these future directions, we aim to enhance our understanding of coronavirus ecology and improve our ability to manage potential zoonotic threats.

## Coronaviruses: origin, classification and hosts

*Coronaviridae* was one of the two original families classified within the order *Nidovirales* in 1996. Since 2018, progressive revisions driven by advances in sequencing technologies have expanded the order, which by 2025 comprises eight suborders and 14 recognized viral families ([1]; ICTV). The *Orthocoronavirinae* subfamily is subdivided into four genera: alpha-coronavirus (α-CoV), beta-coronavirus (β-CoV), delta-coronavirus (δ-CoV) and gamma-coronavirus (γ-CoV), and is found in various mammal and bird species (**Figure 1**) [2–5]. Multiple studies have tried to identify the origin of coronaviruses (CoVs) and to estimate the most recent common ancestor for different CoV clades over the past decades [6–9], with a first timing of the most recent common ancestor (tMRCA) for the four CoV genera around 10,000 years ago [6]. In 2013, Wertheim et al. estimated the most probable emergence time of CoVs to be around 293 (95% CI, 190 to 489) million years ago [8]. More recently, in 2021, Hayman & Knox calibrated their analysis using the a priori coevolutionary relationship between orthocoronaviruses and their bat or bird hosts. By using the splitting times of hosts as constraints, they proposed that the tMRCA dates for orthocoronaviruses are between 133 and 391 million years ago [10].

For a long time, the δ- and γ-CoVs were considered avian in origin, whereas α- and β-coronaviruses were considered bat-derived [2]. However, the discovery of *Nidovirales* sequences in insects has raised questions about the origin of this order [1,11–13] and how insectivorous mammals, such as shrews and hedgehogs, might have been critical hosts shaping the evolution and radiation of some *Coronaviridae* subgenera [5]. A similar evolutionary history has already been hypothesized for other RNA viruses hosted by a large diversity of insectivorous mammals [14]. For example, the former *Bunyavirales* order (now referred to as the *Bunyaviricetes* class, split into two orders, *Elliovirales* and *Hareavirales*) contains arthropod-borne pathogens responsible for viral hemorrhagic fevers in humans and animals, such as Rift Valley fever virus and Crimean-Congo hemorrhagic fever virus [15]. All bunyaviruses are transmitted by arthropod

vectors, except for the viruses from the *Mammantavirinae* subfamily *(Elliovirales* order, *Hantaviridae* family) and from the *Mammarenavirus* genus (*Hareavirales* order, *Arenaviridae* family) which are carried by small mammals such as bats, shrews, and rodents [16,17]. The genomic and phylogenetic analyses of bunyaviruses suggest that ancient arthropod tropism in the *Mammantavirinae* subfamily has been lost in favor of vertebrate monotropism [14]. Marklewitz et al. further hypothesize that this shift may have occurred in the ancestors of bats and small terrestrial mammals, which frequently interact with arthropods through their diet [14]. This raises the question of whether small insectivorous terrestrial mammals may represent an important connecting link in the evolution of CoVs [5] (**Figure 1**).

## Evolution of small terrestrial mammal-borne coronaviruses

Phylogenetic and genomic analyses can help investigate the evolution of viruses and host-virus interactions[18,19]. These analyses provide insights into how viruses have adapted and diversified over time, their potential for cross-species transmission, and their evolutionary trends.

The phylogenetic reconstruction of partial nucleotide sequences encoding the RNA-dependent RNA polymerase (RdRp) of representative α- and β-CoVs highlights distinct host-associated clades among small terrestrial mammals, underscoring evolutionary divergence and host specificity within and between CoV genera (**Figure 2**). Both α- and β-CoVs have been detected in the orders Rodentia and Lagomorpha (Leporidae and Ochotonidae families). Within the order Eulipotyphla, α-CoVs have only been detected in the family Soricidae (shrews) while β-CoVs are only associated with the family Erinaceidae (hedgehogs).

The study of the evolutionary history of α-CoVs through both phylogenetic and genomic analyses suggests that all rodent α-CoVs have originated from a single common ancestor, with a long-term association between α-CoVs and rodents[20]. Alpha-CoVs detected in rodents form

a monophyletic group with similar topologies based on partial nucleotide sequences encoding the RdRp and the nucleocapsid (ORF1b and N) genes, supporting the coevolutionary hypothesis [20]. However, the analysis of the spike (S) gene suggests an ancient recombination history of these α-CoVs with β-CoVs [20]. For example, the phylogenetic analysis of Lucheng Rn rat CoV (LNRV) from *Rattus norvegicus* captured in China in 2015 showed that the position of the sequence in the phylogeny varies depending on the considered genes, suggesting recombination events [21,22].

To date, shrew coronaviruses have only been identified within the *Alphacoronavirus* genus, with no β-CoVs reported from this host group. Shrew-borne α-CoVs are currently classified into three subgenera: *Soracovirus* and *Sunacovirus*, both composed exclusively of sequences isolated from shrews, and potentially *Luchacovirus*, which includes a mixture of sequences isolated from shrews, rodents, rabbits, pikas, and carnivorous animals such as foxes, fishers, and bobcats (**Figure 2**) [23–25]. The host-restricted pattern in two subgenera, together with the broader composition of the third, underscores the unique role of shrews as reservoirs of α-CoVs and highlights their potential long-term contribution to coronavirus evolution.

The *Embecovirus* subgenus (previously β-CoV lineage A) groups multiple CoV sequences from hosts such as humans, pigs, cows, horses, rabbits, and rodents [1]. In 2015, the discovery of a new β-CoV HKU24 in Norway rats (*Rattus norvegicus*) in China provided important insights into the host diversity of this subgenus [4]. In 2020, an even greater diversity of HKU24-related CoVs has been identified in 15 rodent species across five genera (*Apodemus*, *Eothenomys* , *Niviventer*, *Rattus*, and *Rhabdomys*) [21]. Based on the analysis of the evolutionary associations between rodent-borne CoVs and their hosts, no strong host or geographical restriction pattern has been identified [21]. Similarly, in 2023, the metagenomic screening of a diversity of small mammals, pangolins, and zoo animals revealed the first β-CoVs in pikas (*Ochotona cansus* and *Ochotona*

*curzoniae*) from the Ochotonidae family (order Lagomorpha) [26]. The phylogenetic reconstruction based on amino acid sequences of the RdRp gene suggests that these pika-derived viruses occupy a distinct basal position within the *Embecovirus* subgenus [26].

The *Merbecovirus* subgenus (previously β-CoV lineage C) includes CoVs isolated from bats, camels, humans, and hedgehogs [1]. In 2014, Corman et al. discovered four strains of a novel β-CoV related to the Middle East Respiratory Syndrome Coronavirus in European hedgehogs (*Erinaceus europaeus)* [27]. The Bayesian phylogenetic analysis, including all ORFs, revealed that this *Erinaceus* CoV (EriCoV) is at a basal position of the *Merbecovirus* subgenus. Since then, multiple detections of EriCoV have been reported in European hedgehogs in Germany, Italy, France, Portugal, Poland, and Great Britain, and in Amur hedgehogs (*Erinaceus amurensis*) in China [24,28–36].

## Diversity of small terrestrial mammalian hosts for coronaviruses

Rodents, like bats, are known to harbor a high diversity of viruses, with more than 33 viral families detected in each of these two taxa since 1995 [37,38]. Nevertheless, recent studies suggest that they may not be exceptional viral reservoirs compared to other taxa, and that the diversity of viruses with zoonotic potential in mammals rather correlates with the species richness of individual orders and not with specific traits [39–41].

Rodentia, Chiroptera, and Eulipotyphla are the three most diverse orders of mammals. According to the IUCN (2024), the order Rodentia comprises 2,338 species, making it the most species-rich mammalian order, followed by Chiroptera with 1,326 species and Eulipotyphla with 491 species. These three orders encompass approximately 66% of all extant mammal species, highlighting their critical role in global biodiversity. Although a large diversity of viral

families has been described in rodents [38], CoVs represent only 8.3 % of this viral diversity, with about 1600 sequences generated, while they represent nearly 44.6 % of the viral diversity detected in bats, with over 10,000 sequences [38]. Overall, CoVs have been isolated from rodents belonging to eight families (Chinchillidae, Cricetidae, Dipodidae, Heteromyiidae, Hystricidae, Muridae, Sciuridae, Spalacidae), encompassing more than 20 genera and 40 species (**Table S1)** [38]. In bats, CoVs have been detected in at least 14 families (Emballonuridae, Hipposideridae, Megadermatidae, Miniopteridae, Molossidae, Mormoopidae, Mystacinidae, Nycteridae, Rhinolophidae, Rhinonycteridae, Phyllostomidae, Pteropodidae, Rhinopomatidae, Vespertillionidae), about 79 genera and more than 245 species [38].

The order Eulipotyphla encompasses four families: Soricidae (shrews), Erinaceidae (hedgehogs), Talpidae (moles), and Solenodontidae (solenodons). Despite their diverse species composition, Eulipotyphla remain relatively understudied in terms of viral diversity compared to Rodentia and Chiroptera. Viral diversity studies have identified at least 24 viral families in Soricidae (totaling 2,217 sequences), 17 in Erinaceidae (364 sequences), and two in Talpidae (471 sequences), while no sequences have yet been reported for Solenodontidae. CoVs have been detected exclusively within the Soricidae (in three genera and four species) and Erinaceidae families (in one genus and two species). Of the 3,052 viral sequences cataloged on GenBank for Eulipotyphla, CoVs constitute 9% (283 sequences), with 227 originating from hedgehogs and 56 from shrews.

Similarly, the order Lagomorpha, comprising the families Leporidae (rabbits, jackrabbits, hares) and Ochotonidae (pikas), has been less studied for CoVs. There are 2,913 viral sequences from Lagomorpha hosts in GenBank, representing 31 viral families. Specifically, 53 CoV sequences have been identified in Lagomorpha: seven in Ochotonidae (from one genus, two

148 species) and 46 in Leporidae (from three genera, three species). This highlights significant
149 research gaps in understanding CoVs within these mammalian orders.

150

151 ## Technical detection bias

152 The identification of CoVs relies on using molecular biology tools, specifically Polymerase
153 Chain Reaction (PCR) systems. These PCR systems enable the detection of CoV RNA in
154 biological samples and, therefore, allow testing whether the animal was carrying CoVs at the
155 time of sampling. Over the past few decades, various detection systems have been developed,
156 some of which target highly conserved regions shared among all CoV genera across a wide
157 range of animal species[42]. A systematic review and meta-analysis of CoV sampling and
158 surveillance in bats revealed that approximately 95% of studies utilized PCR techniques
159 targeting the RdRp gene [43]. The analysis of the primer sequences in pan-CoV protocols targeting
160 this gene reveals that most systems align and amplify the same region, indicating an overall
161 limited diversity among these detection systems [42].

162 Similarly to the wide range of PCR systems employed for CoV detection in bats, there is no
163 consensus on the most effective one for detecting CoVs in other taxonomic groups (Table 2).
164 Between 2008 and 2024, over 20,200 Rodentia, 1,570 Eulipotyphla, and 274 Lagomorpha
165 samples were tested for the presence of coronaviruses (CoVs) (**Table S3**). Multiple detection
166 systems have been used to screen these mammalian orders, with most primers targeting the
167 same CoV genomic regions as those used for bats (**Table S2**). Interestingly, some studies have
168 reported detection failure with specific systems while succeeding with others. For example,
169 Wasberg et al. (2022) failed to detect CoVs in bank voles with a PCR system targeting part of
170 the RdRp gene but succeeded when screening the same samples using their in-house PCR
171 method targeting the spike protein gene, designed based on previous virome investigation of

Swedish bank voles [44]. Furthermore, the PCR systems that have successfully detected CoVs in rodents in some studies were not as successful in others, for example, with the Quan and Watanabe primer sets. Huong et al. (2020) detected α- and β-CoVs in 23% of their rodent samples (266/1131) in Vietnam, McIver et al. (2020) detected β-CoVs in 1.4% of their rodent samples (12/851) in Laos and Kumakamba et al. (2021) detected α-CoVs in 0.1% (2/1347) of their rodent samples in the Democratic Republic of the Congo and the Republic of Congo [45–47]. Using the same primer sets, no rodent samples tested positive for CoVs in Cameroon (0/2740), but one α-CoV was detected in one shrew (1/159) [48].

Geographical and ecological variations may influence the prevalence and distribution of CoVs among small mammal populations. Understanding these factors is essential for accurately interpreting and comparing detection rates across different studies and regions. For example, when using the Quan and Watanabe PCR systems to analyze 10,038 small terrestrial mammals, significantly more positive cases were found in Asia (13.4%) compared to Africa (0.05%) for similar sample types. It is thus essential to investigate whether these differences are due to the specific testing systems used or if they are associated with the geographic origin of CoV sequences from small terrestrial mammals. Most PCR systems for CoV detection have been developed using sequences derived from Asian mammalian hosts. However, the genetic diversity and evolutionary paths of CoVs in African rodents could be significantly different from those in Asian rodents, potentially affecting the accuracy of PCR assays designed primarily based on Asian sequences. Therefore, it is crucial to prioritize the development of systems that consider the broader genetic diversity of CoVs and the ecological contexts in which they circulate.

As next-generation sequencing becomes more accessible, we can anticipate an increase in the untargeted detection of CoVs in small terrestrial mammals. The metagenomic screening of

different biological samples (organs and feces) from 41 wild Qinghai voles (*Microtus fuscus)* uncovered a diversity of viruses, including a few α-CoVs [49]. Interestingly, only the fecal library contained contigs from *Coronaviridae* but not the tissue libraries (liver, lung, spleen, intestine) [49]. In 2023, Cui et al. used metagenomics to investigate the viromes in blood, feces, pharyngeal and anal swabs of 1497 bats, 363 rodents, 58 pikas, 18 pangolins, 45 insectivorous animals, and 194 zoo animals collected in eight provinces of south China [26]. In brief, CoVs reads were present in 49/214 libraries from bats, 11/123 libraries from rodents, 7/56 libraries from pangolins, and 9/18 libraries from pikas, with detection of both α- and β-CoVs in bats and rodents [26].

The investigation of CoVs in bats over the last decades has highlighted a higher detection rate in fecal, rectal, and intestinal samples than in oropharyngeal samples, pooled swabs/samples, and pooled tissue [43,45]. Unfortunately, few comprehensive studies have compared CoV detection rates depending on the type of samples examined. In 2014, Corman et al. tested the difference in CoV detection in different sample types of 12 positive hedgehogs [27]. The results showed no statistical difference in detection between feces and intestines. However, the mean viral concentrations were at least 10-fold lower in other organs (brain, heart, lung, liver, kidney, spleen), urine, and blood. Another challenge in comparing the efficiency of different studies in CoV detection lies in the varied testing units utilized . Some studies involve pooling individuals or organs from the same or different species, complicating the interpretation of results (**Table S3**).

## Ecological factors facilitating CoV maintenance in small mammal taxa

As previously discussed, rodents and bats are not exceptional taxa for harboring viruses, which is primarily related to their species' diversity [40]. However, we propose that some taxa also

possess unique ecological traits, making them more suitable, efficient hosts for CoVs. Thus, to understand the factors that facilitate the circulation of CoVs, it is crucial to investigate the specific ecology of CoV-positive species and their community structures. Analyzing how particular species interact within their environments and how their social structures influence pathogen transmission can provide insights into the dynamics of viral spread [50]. By examining the broader ecological patterns and the specific behaviors of infected species, researchers can better identify the conditions that promote the maintenance and circulation of CoVs in rodent and bat populations.

***Density/ gregariousness***

The spread of pathogens within animal communities is significantly impacted by factors such as population density and social behavior [50]. Species that inhabit densely populated areas, engage in large social gatherings, or exhibit indiscriminate mating practices are particularly prone to sharing infectious diseases, primarily due to the heightened proximity and frequency of contact among individuals [51]. Both rodents and bats display various social and grouping structures that vary considerably between species. Some rodent species, like deer mice, may lead solitary lives or form loose, temporary groups; others, such as voles, can establish more stable and densely packed colonies [52–54]. Reported rodent densities usually range from < 1 to 300 individuals per hectare [53–56] with exceptionally high densities reported for rats, mice, voles, lemmings, and giant pouched rats [55–59]. Similarly, bats exhibit various social behaviors, from solitary roosting to forming vast colonies with multiple species. For example, large bat colonies can host thousands of individuals, while other bat species may roost in smaller, less densely packed groups [60–62]. In New Mexico, colonies of *Tadarida brasiliensis* bats can exceed 700,000 individuals in the same cave [60].

***Multispecies assemblages***

Sympatry (i.e., coexistence of several species in the same habitat) favors the horizontal transmission of intra- and inter-specific viruses and their maintenance in communities [37]. Its effect on viral transmission in chiropterans appears to be 3.9 times greater than in rodents [37]. Numerous species composition and community structure studies have reported the co-occurrence of multiple rodent species within the same habitat [63–66]. For example, in North America, several species of rodents, including deer mice, voles, and chipmunks, can live in sympatry in the same forested areas [66]. Bats can form large colonies, sometimes of several species [62]. In Turkey, the Koyunbaba cave hosts a maternity colony that can include 23,000 bats belonging to 11 different species [61].

***Seasonality***

Differences in the seasonality of reproduction can significantly impact the social dynamics and grouping patterns within mammalian species, particularly in the context of maternity colonies and reproductive contact frequencies [67,68]. In species with seasonal reproduction, reproduction is concentrated within specific times of the year. This seasonality can lead to significant changes in social grouping patterns. Rodents often have a higher average number of reproductive seasons in a year, with some species reproducing non-seasonally throughout the year [69]. However, the overall social units of species can vary in different populations or seasons [53]. In contrast, bats typically exhibit synchronized reproduction, with one or two reproductive seasons annually, during which they gather in maternity colonies to give birth and nurse their young [70]. Additionally, seasonal migrations involving thousands of bats from various colonies or regions result in high-density gatherings and increased interactions. This convergence significantly enhances opportunities for pathogen exchange, facilitating the spread of viruses within and between bat species and increasing the likelihood of zoonotic spillover.[71].

Despite the valuable insights gained from studying rodents and bats, our understanding of transmission ecology within Eulipotyphla and Lagomorpha remains incomplete[72–76]. These groups are less studied, and further investigation into their ecology, social and behavioral patterns could reveal critical factors influencing the circulation of CoVs. By addressing these knowledge gaps, we can enhance our understanding of how these viruses are maintained and transmitted within animal populations, thereby improving our ability to predict and manage potential zoonotic threats.

## Host dynamics and viral circulation

Multiple studies on bat colonies have reported a relationship between bat population structure and infection dynamics of viruses from different families (e.g. *Paramyxoviridae*, *Filoviridae*, *Coronaviridae*) [77–85]. The circulation of CoVs in bat colonies has been reported to be seasonal, following the population structure dynamic [78,81,85–87]. CoV shedding increases during the aggregation of pregnant bats in the same roosting colony and when juveniles become weaned, possibly because of the potential waning of maternal antibodies in juvenile bats [78,81,85–87]. This temporal dynamic in bat colonies may increase the circulation and spillover opportunities between bat species during these periods, with the dispersion of viruses with juveniles' dispersion. In summary, the aggregation of hundreds to thousands of animals in low physiological conditions and the input of a population of susceptible individuals with juveniles represent two important ecological factors facilitating CoV persistence in bat populations [71,84,88]. In contrast, very little is known about the ecology of CoVs in small terrestrial mammals.

In rodent populations, the circulation of viruses from other families (e.g., *Hantaviridae*, *Arenaviridae*, *Paramyxoviridae*) also seems to exhibit seasonal patterns, with a strong effect of host density [89–92]. For orthohantaviruses, the temporal dynamics of Puumala virus in bank voles

(*Clethrionomys glareolus)* in Europe, Sin Nombre virus in deer mice (*Peromyscus maniculatus*) in North America and Hantaan virus in striped field mice (*Apodemus agrarius*) in Asia is primarily influenced by population density and associated fluctuations in contact rates [89–91,93–95]. Interestingly, high rodent density does not always lead to higher prevalence (or seroprevalence) in host species [96]. Rodent population structure will likely also play a role in virus transmission, as in bats. Age and sex have been identified as important factors that affect orthohantavirus prevalence [89]. Indirectly, the dynamic of the viruses also depends on environmental factors, with changes in climate and precipitation patterns strongly influencing the resource availabilities and, therefore, the host population survival and reproduction [95,97,98]. Similar mechanisms have been reported for the temporal dynamics of mammarenaviruses. Seasonal Morogoro virus seroprevalence cycles have been observed in multimammate mice (*Mastomys natalensis)* in Tanzania and are positively correlated with host density [92]. Observed seasonal patterns and mathematical transmission models suggest that the temporal dynamics of this arenavirus in a highly fluctuating population can be best explained by a combination of density-dependent vertical and horizontal transmission [92]. The persistence of this virus within the rodent population during low-density periods seems to rely on a few chronically infected individuals [92].

While specific interactions between shrew population dynamics and viral circulation are not extensively documented, initial studies suggest that Eulipotyphla, like other taxa, display temporal and geographical viral patterns [99–102]. The bicolored white-toothed shrew (*Crocidura leucodon*) has been identified as a reservoir for Borna disease virus 1 (BoDV-1), a zoonotic neurotropic virus responsible for fatalities in sheep, horses, alpacas and humans in Europe [101,103,104]. A detailed long-term study monitoring naturally infected shrews revealed persistent BoDV-1 shedding from multiple routes [105]. The epidemiology of Borna disease closely corresponds to the ecological patterns of *C. leucodon*, particularly in Bavaria, where the virus's

prevalence correlates with the distribution of these shrews [99–101]. Annual variations in Borna disease cases among incidental hosts, such as horses and sheep, are assumed to be linked to fluctuations in shrew populations and habitat changes, often driven by modern agricultural practices. Also, the limited dispersal and high inbreeding rates in *C. leucodon* likely contribute to the virus's localized presence within endemic regions. In 2023, a comprehensive epidemiological study was conducted on the family members of 20 patients with PCR-confirmed BoDV-1 encephalitis who died between 1996 and 2021 in Germany. All cases resided in rural areas with a natural distribution of *C. leucodon* and 13 out of 20 cases confirmed the peridomestic presence of shrews. Since none of the interviewed individuals reported direct contact with shrews, these findings support the notion of environmental transmission of BoDV-1 [106]. In 2023, De Sabato et al. tested fecal samples from 102 captive European hedgehogs for the partial RdRp CoV gene using real-time PCR [102]. CoV was circulating within the hedgehog population, with 42% of animals testing positive. The mean viral shedding duration was 22.8 days, lasting up to 62 days, indicating that the virus not only circulates but also persists within the population, making hedgehogs a suitable reservoir for the virus. Overall, apart from the above studies, there is limited information regarding virus circulation in Eulipotyphla and Lagomorpha, necessitating further research to fully understand these dynamics and their implications.

## Dispersion ability

Bats are the only mammals capable of active flight and have a unique capacity for long-distance migration. However, true migration (*i.e.*, seasonal movements greater than 50 km) has been reported in less than 3% of extant bat species [107,108]. These migrations may occur seasonally during the animal's life cycle (reproduction) or episodically to escape a disturbed environment (loss of food sources or habitats), whether or not induced by human activity [71,109–111]. Some bat

species can migrate several hundred kilometers in a few months [112–114]. For example, a study of the migrations of fruit bats (*Eidolon helvum*) in Zambia showed that they could travel more than 2,000 km in 3 months. This migratory behavior can significantly enhance the spread of infectious agents and thus favor transmission to other susceptible species [109,115,116].

Small terrestrial mammals generally exhibit less natural dispersal ability compared to bats. Rodents typically have more restricted movement patterns, confining them to relatively smaller territories. Consequently, the spread of rodent-borne diseases would tend to be more localized. This theoretically limited mobility reduces their likelihood of spreading diseases over large geographic areas. However, human activities such as trade, travel, and urbanization can inadvertently facilitate the dispersal of small terrestrial mammals over long distances, thereby increasing the potential for disease transmission beyond their natural ranges [117–119]. In such cases, small terrestrial mammals can serve as vectors for disease dissemination on a broader scale, highlighting the intricate interplay between ecological factors, human behavior, and the spread of infectious agents [117–119].

## Small terrestrial mammal-borne coronaviruses: risk as a source or intermediate host for emergent human/ livestock pathogenic coronaviruses?

Surveillance efforts for CoVs often focus on traditional reservoirs such as bats and certain wild carnivores (e.g. civets), overlooking the significant role of small mammals like rodents, shrews, and lagomorphs. Including these groups in surveillance programs is crucial, given their potential to harbor and transmit CoVs.

Research indicates that human CoVs may share a phylogenetic lineage with CoVs found in rodents, suggesting that rodents could have played a role in their emergence in humans. Studies have identified multiple rodent CoVs within the same phylogenetic clade as HCoV-OC43 and HCoV-HKU1, supporting this hypothesis. Further analysis of the nucleotide sequence

similarity reveals that HCoV-OC43 shows the highest similarity across most of its genes to bovine coronavirus (BCoV) of the *Embecovirus* subgenus, which includes other CoVs such as murine hepatitis virus (MHV) and sialodacryoadenitis virus of rats (SDAV). This genetic similarity points to a potential common origin of HCoV-OC43 and BCoV [120]. Therefore, it is plausible that similar zoonotic transmissions are either happening currently without our awareness or could occur if the right conditions arise.

Like bats, rodents play a pivotal role in zoonotic disease transmission networks [121–124]. These taxa not only occupy central positions in pathogen transmission networks but also harbor a disproportionately high number of zoonotic pathogens compared to other taxa [17–120]. Their adaptability, widespread distribution, and frequent interactions with humans and livestock make them key reservoirs for zoonotic viruses, including CoVs. Understanding their central role and monitoring these species is essential for predicting and preventing future zoonotic outbreaks. Small terrestrial mammal (Rodentia, Eulipotyphla, and Lagomorpha) populations, particularly those in close contact with human habitats, could act as reservoirs or amplifying hosts for CoVs [121,123,125].

Anthropogenic activities such as extensive agriculture, urbanization, and deforestation disrupt natural environments and create new opportunities for wildlife to interact with humans [121]. These changes also generate stable and abundant food sources in villages, crop fields, and urban settings, increasing the likelihood of contact between infected animals and potential new hosts [46]. For example, the presence of rodents near human settlements, coupled with their adaptive behaviors, could facilitate the spillover of pathogens like CoVs from wildlife to humans [121]. Human activities, including wildlife farming and hunting, further elevate the risk of zoonotic spillovers[46]. A 2020 study by Huong et al. explored CoV prevalence in field rats, wildlife farms, and bat roosts near human settlements in southern Vietnam. The study reported high rates of

CoVs in field rats and bats, with prevalence increasing along the wildlife trade supply chain. The highest rates were detected in field rats sold in restaurants, highlighting the substantial risk of zoonotic spillover due to close contact between wildlife and humans.

During SARS-CoV-2 emergence, multiple investigations have been conducted to identify animal hosts of the virus, either to determine the animal reservoir responsible for the emergence or to identify other animals that may be susceptible to the infection [126,127]. Small terrestrial mammals, such as rodents, shrews, and rabbits, have been considered in these investigations. Functional, structural, and genetic analyses of viral receptor ACE2 orthologs, along with experimental *in viv*o and *in vitro* infections, revealed that many rodent species from families such as Cricetidae, Dipodidae, and Muridae, as well as rabbits, were susceptible to the virus [126,127]. Additionally, SARS-CoV-2 has been detected in environments like sewage, raising concerns about its potential spread to rodents and other small mammals through the environment [128]. Altogether, it emphasizes the need to monitor these animals for new viral strains [129].

To effectively manage the risk of CoV emergence, surveillance systems must incorporate monitoring of Rodentia, Eulipotyphla, and Lagomorpha populations. This integration requires several critical components: i) pathogen detection through routine screening of these populations for known and novel CoVs, providing early warnings of possible outbreaks ; ii) ; (ii) genetic and serological analyses to understand the diversity of CoVs in these hosts and assess their potential to infect humans or livestock; and (iii) ecological surveillance to track these small mammals in various environments, especially at the human-animal interface in agricultural and urban settings.

Public health and biosecurity measures should focus on minimizing the risk of CoV transmission between small mammals to humans. Effective strategies include habitat

management to reduce human-rodent interactions by modifying habitats and improving waste management in urban and rural areas; education and awareness campaigns to inform communities about the risks of small mammal infestations and the importance of control measures; and policy and regulation development to support the monitoring and control of small mammal populations in high-risk areas, particularly near food production facilities and urban centers.

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## Data availability

All data supporting the findings of this study are provided in the supplementary materials. Supplementary Tables S1 and S2 are available in full. Supplementary Table S3 is presented as an excerpt containing the first 22 rows of the full dataset to illustrate the structure and variables of the dataset.

The complete version of Table S3 will be released upon formal publication of the manuscript.

**Figure list**

**Figure 1.** Potential origin of *Coronaviridae*.

**Figure 2.** Phylogenetic tree based on the alignment of 118 partial RNA-dependent RNA polymerase gene sequences (614bp).

**Supplementary material**

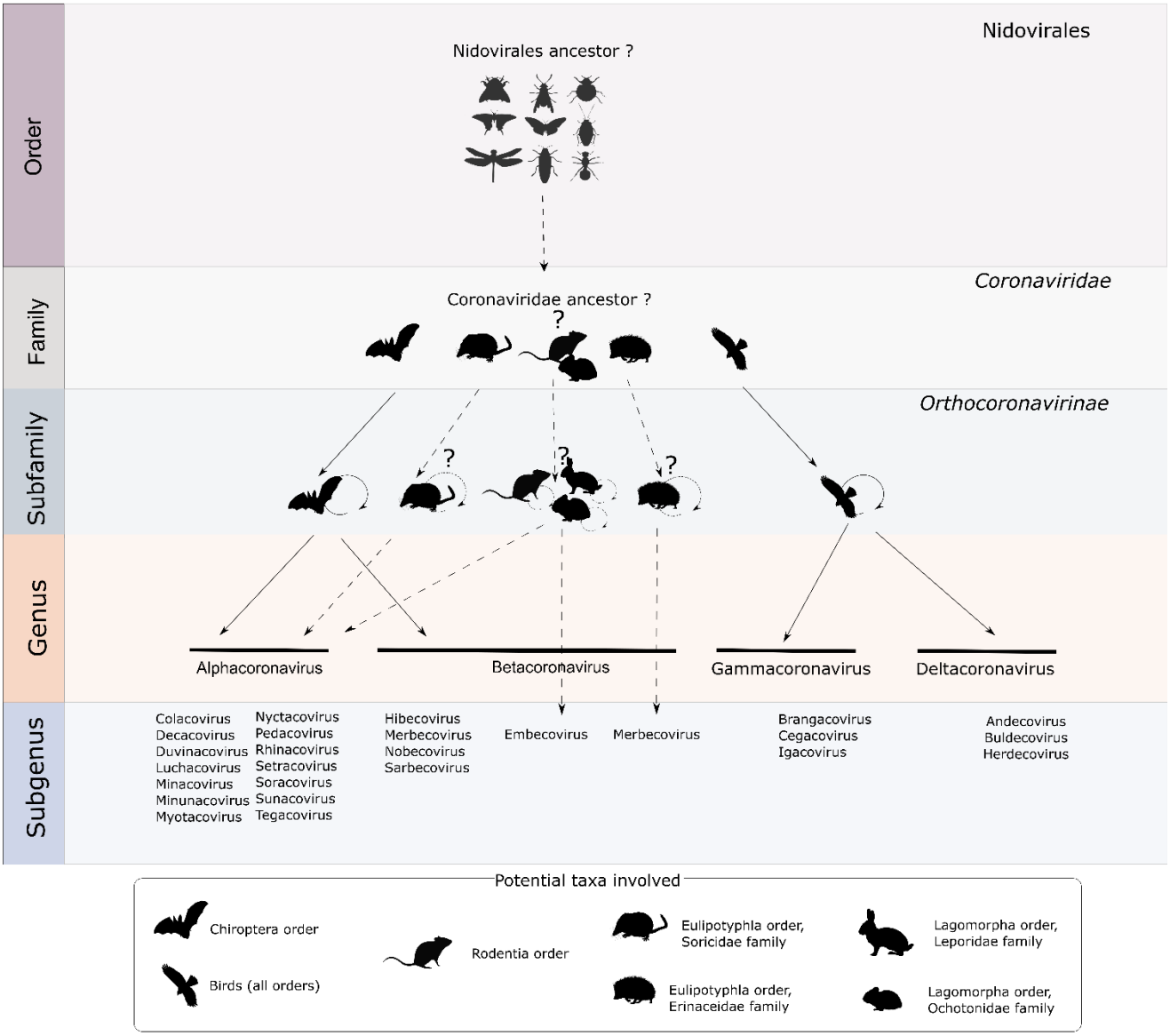
**Table S1**. Number of viral Coronaviridae sequences isolated from rodents by family, species, and geographical origin. ND: Not Determined (update Zover database March 2024/ access 19.09.2024).

**Table S2.** All PCR primers used for CoV detection in Rodentia, Eulipotyphla, and Lagomorpha from 2008 to 2025.

**Table S3**. Details of the 55 publications screening for CoVs from 2008 to 2025 in Rodentia, Eulipotyphla, and Lagomorpha.

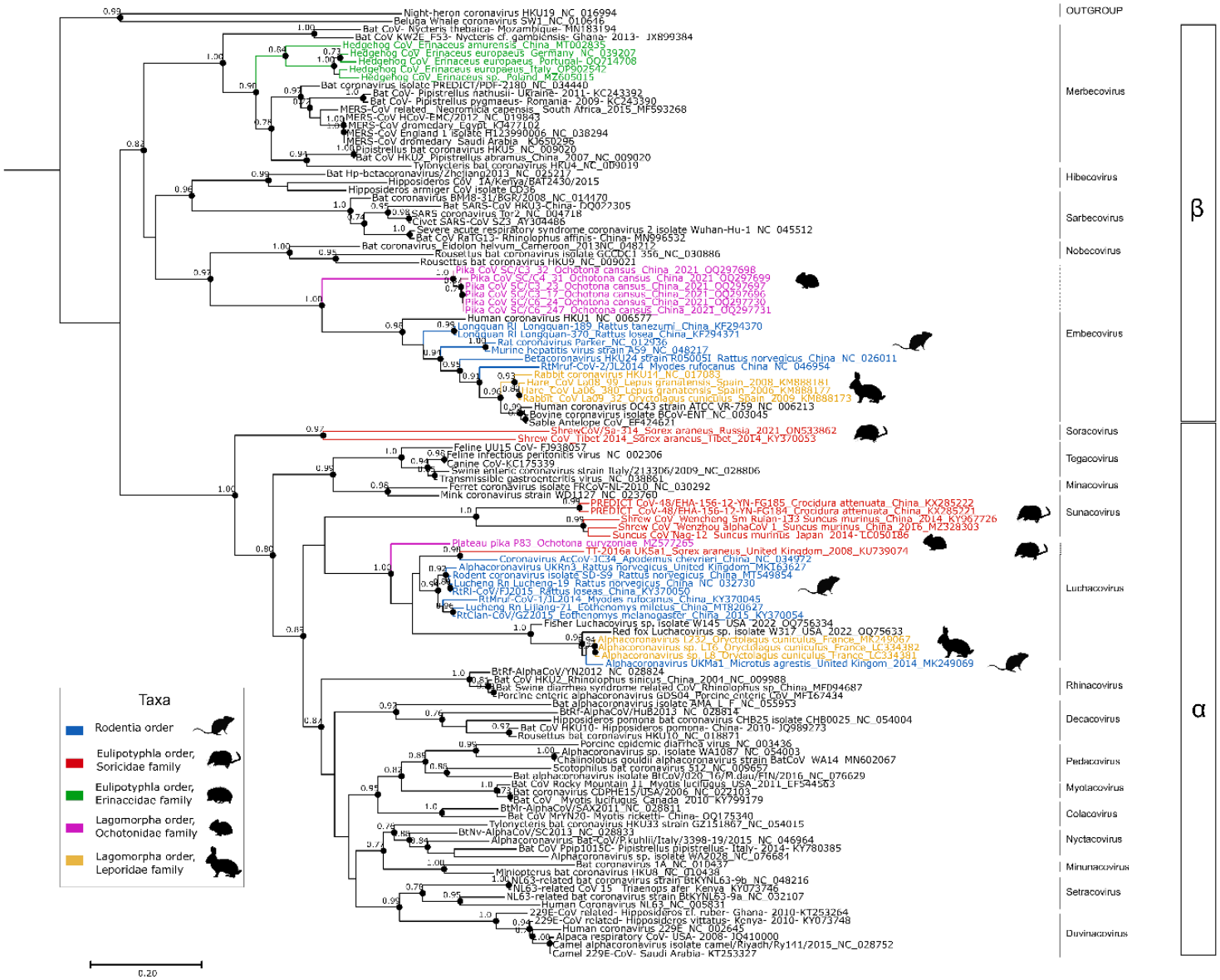
772 **Figure 1**. Potential origin of *Coronaviridae*. Solid arrows: confirmed evolution routes, and

773 dashed arrows with question marks represent hypothetical evolutive routes.




774

**Figure 2.** Phylogenetic tree based on the alignment of 118 partial RNA-dependent RNA polymerase gene sequences (614bp). Fast tree generated in Geneious software; only support values >0.7 are displayed.



# Supplementary information: The overlooked small terrestrial mammal taxa (Rodentia, Eulipotyphla, and Lagomorpha) in the evolution of coronaviruses

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**Literature Search Strategy**

We conducted a systematic literature using two major bibliographic databases: **PubMed** and **Web of Science**. The search aimed to identify studies reporting the detection of coronaviruses in wild small terrestrial mammals, specifically within the orders **Rodentia**, **Lagomorpha**, and **Eulipotyphla**.

Search terms combined taxonomic keywords with virological terms, using Boolean operators to refine results. The following queries were used:

- **PubMed**:
  - (rodent* OR Rodentia*) AND (coronavirus* OR CoV*) → 503 results
  - (rabbit* OR Lagomorpha* OR pikka*) AND (coronavirus* OR CoV*) → 486 results
  - (shrew* OR Eulipotyphla* OR hedgehog*) AND (coronavirus* OR CoV*) → 93 results
  - With additional filters for detection and excluding vaccine-related studies:
    - Rodents: 83 results
    - Lagomorphs: 113 results
    - Eulipotyphla: 19 results

- **Web of Science**:
  - (rodent* OR Rodentia*) AND (coronavirus* OR CoV*) → 4,969 results
  - (rabbit* OR Lagomorpha* OR pikka*) AND (coronavirus* OR CoV*) → 7,523 results
  - (shrew* OR Eulipotyphla* OR hedgehog*) AND (coronavirus* OR CoV*) → 936 results
  - With additional filters for detection and excluding vaccine-related studies:
    - Rodents: 258 results
    - Lagomorphs: 500 results

- Eulipotyphla: 41 results

We also consulted the **ZOVER database**, which yielded 1,613 entries under *Rodents → Coronaviridae*, representing 35 unique references and 936 unpublished sequences.

**Screening and Eligibility Criteria**

After removing duplicates and irrelevant entries, we screened a total of **772 abstracts**. Studies were excluded if they:

- Did not assess coronavirus detection in wild animals,
- Were not written in English,
- Focused solely on serological data or SARS-CoV-2,
- Described laboratory animal experiments or assay development,
- Misused taxonomic terms (e.g., “hedgehog” referring to genes or proteins).

Studies were included if they:

- Reported **PCR-based or metagenomic detection** of coronavirus RNA,
- Provided **quantitative data** on the number of animals, samples, or libraries screened.

Of these, **55 studies** met all inclusion criteria and were retained for data extraction (see Table S3). Each data point in our database corresponds to coronavirus detection results from a specific sample type and host species.

**Genbank sequences data Collection**

We conducted a comprehensive search of viral sequences associated with members of the mammalian families **Soricidae**, **Erinaceidae** (hedgehogs), and **Talpidae** using the NCBI Nucleotide database. Taxonomic queries were constructed to include all relevant genera within each family:

- **Soricidae**: *Crocidura*, *Diplomesodon*, *Feroculus*, *Paracrocidura*, *Ruwenzorisorex*, *Scutisorex*, *Solisorex*, *Suncus*, *Sylvisorex*, *Congosorex*, *Myosorex*, *Surdisorex*, *Anourosorex*, *Blarinella*, *Blarina*, *Cryptotis*, *Chimarrogale*, *Chodsigoa*, *Episoriculus*, *Nectogale*, *Neomys*, *Nesiotites*, *Soriculus*, *Megasorex*, *Notiosorex*, *Sorex*
    - **Filtered for**: species annotated as "Viruses"
    - **Total sequences retrieved**: 2,217
- **Erinaceidae (Hedgehogs)**: *Erinaceus*, *Atelerix*, *Hemiechinus*, *Mesechinus*, *Paraechinus*, and the keyword "hedgehog"
    - **Filtered for**: species annotated as "Viruses"
    - **Initial sequences retrieved**: 598

    - **Excluded**: metagenome-assembled genomes (MAG), TPA_asm entries, phage sequences, and *Cervus timorensis papillomavirus*
    - **Final dataset**: 364 sequences
- **Talpidae**: *Condylura*, *Parascalops*, *Scalopus*, *Scapanulus*, *Scapanus*, *Desmana*, *Galemys*, *Neurotrichus*, *Scaptonyx*, *Euroscaptor*, *Mogera*, *Parascaptor*, *Scaptochirus*, *Talpa*, *Dymecodon*, *Urotrichus*, *Uropsilus*
    - **Filtered for**: species annotated as "Viruses"
    - **Total sequences retrieved**: 471

**Data Processing**

All retrieved sequences were manually curated to remove non-viral entries, duplicates, and irrelevant annotations. Specifically, sequences labelled as MAG, TPA_asm, phages, and unrelated viral taxa (e.g., *Cervus timorensis papillomavirus*) were excluded to ensure dataset specificity.

**Sequence Quantification**

Following data curation, we quantified the number of viral sequences associated with each taxonomic group. For each family (Soricidae, Erinaceidae, and Talpidae), and each genus within these families, we recorded the total number of viral sequences retrieved from GenBank. This count was used to assess the relative representation of viral diversity across taxa. The same approach was applied to Lagomorpha (families Leporidae and Ochotonidae) to enable comparative analysis. These counts provided the basis for evaluating the distribution of coronavirus (CoV) sequences and identifying taxonomic gaps in current viral surveillance efforts.

**Table S1**. Number of viral Coronaviridae sequences isolated from rodents by family, species and geographical origin. ND: Not Determined (update Zover database March 2024/ access 19.09.2024).

| | Africa | America | Asia | Europe | Oceania | ND | Australia | Bangladesi | Bolivia | Brazil | Cambodia | China | Congo | France | Germany | Indonesia | Laos | Malaysia | Mexico | ND | Nepal | Netherlan | Poland | Russia | Rwanda | Senegal | South Afri | Spain | Sweden | Tanzania | Thailand | Uganda | United Kin | United Sta | Vietnam | (blank) | Grand Tota |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Chinchillidae | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Chinchilla lanigera* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| Cricetidae | 0 | 3 | 12 | 38 | 0 | 0 | | | | | | 10 | | 5 | 25 | | | | | 1 | | 1 | 2 | 2 | | | | | 2 | | | | 3 | 2 | | | 53 |
| *Eothenomys eleusis* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Eothenomys eva* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Eothenomys miletus* | 0 | 0 | 3 | 0 | 0 | 0 | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Lasiopodomys gregali* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Microtus agrestis* | 0 | 0 | 0 | 4 | 0 | 0 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | 3 | | | | 4 |
| *Microtus arvalis* | 0 | 0 | 0 | 7 | 0 | 0 | | | | | | | | | 6 | | | | | | | 1 | | | | | | | | | | | | | | | 7 |
| *Microtus oeconomus* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | 1 |
| *Myodes glareolus* | 0 | 0 | 0 | 27 | 0 | 0 | | | | | | | | 5 | 18 | | | | | | | | 2 | | | | | | 2 | | | | | | | | 27 |
| *Myodes rufocanus* | 0 | 0 | 3 | 0 | 0 | 0 | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Myodes rutilus* | 0 | 0 | 2 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | 1 | | | | | | | | | | | | | 2 |
| *Peromyscus leucopus* | 0 | 1 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 |
| *Peromyscus maniculat* | 0 | 1 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 |
| *Sigmodon* sp. | 0 | 1 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | 1 |
| Dipodidae | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Allactaga sibirica* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| Heteromyidae | 0 | 1 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | 1 |
| *Liomys* sp. | 0 | 1 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | 1 |
| Hystricidae | 0 | 0 | 6 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 6 | 6 |
| *Hystrix brachyurus* | 0 | 0 | 6 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 6 | 6 |
| Muridae | 13 | 24 | 1419 | 28 | 1 | 13 | 1 | 34 | 2 | 1 | 449 | 150 | 1 | 5 | 10 | 67 | 11 | 14 | | 13 | 4 | | | 1 | 2 | 1 | 3 | 11 | | 2 | 57 | 4 | 2 | 21 | 632 | | 1498 |
| *Apodemus* sp. | 0 | 0 | 0 | 5 | 0 | 0 | | | | | | | | 5 | | | | | | | | | | | | | | | | | | | | | | | 5 |
| *Apodemus agrarius* | 0 | 0 | 18 | 2 | 0 | 0 | | | | | | 17 | | | 2 | | | | | | | | | 1 | | | | | | | | | | | | | 20 |
| *Apodemus chevrieri* | 0 | 0 | 25 | 0 | 0 | 0 | | | | | | 25 | | | | | | | | | | | | | | | | | | | | | | | | | 25 |
| *Apodemus draco* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Apodemus flavicollis* | 0 | 0 | 0 | 3 | 0 | 0 | | | | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Apodemus latronum* | 0 | 0 | 3 | 0 | 0 | 0 | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Apodemus peninsulae* | 0 | 0 | 3 | 0 | 0 | 0 | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Apodemus sylvaticus* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| Bandicota sp. | 0 | 0 | 1 | 0 | 0 | 0 | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Bandicota bengalensis* | 0 | 0 | 5 | 0 | 0 | 0 | | 5 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 5 |
| *Bandicota indica* | 0 | 0 | 37 | 0 | 0 | 0 | | 4 | | | 27 | 3 | | | | | | | | | | | | | | | | | | | 1 | | | | 2 | | 37 |
| *Bandicota savilei* | 0 | 0 | 3 | 0 | 0 | 0 | | | | | | | | | | | 1 | | | | | | | | | | | | | | 2 | | | | | | 3 |
| *Bunomys penitus* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | 1 |
| *Leopoldamys edwards* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Leopoldamys neilli* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 |
| *Malacomys longipes* | 1 | 0 | 0 | 0 | 0 | 0 | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Mastomys* sp. | 2 | 0 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 | | | | | 2 |
| *Maxomys surifer* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | 1 |
| *Maxomys whiteheadi* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 1 |
| *Meriones meridianus* | 0 | 0 | 3 | 0 | 0 | 0 | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Mus bufo* | 3 | 0 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | | 3 | | | | | 3 |
| *Mus caroli* | 0 | 0 | 6 | 0 | 0 | 0 | | | | | 4 | 2 | | | | | | | | | | | | | | | | | | | | | | | | | 6 |
| *Mus cervicolor* | 0 | 0 | 7 | 0 | 0 | 0 | | | | | | | | | | | | | | | 1 | | | | | | | | | | 6 | | | | | | 7 |
| *Mus cookii* | 0 | 0 | 2 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | 2 | | | | | | 2 |
| *Mus minutoides* | 1 | 0 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | 1 | | | | | | | 1 |
| *Mus musculus* | 1 | 18 | 7 | 14 | 1 | 9 | 1 | 4 | | 1 | | 3 | | | 3 | | | | | | 9 | | | | | 1 | | 11 | | | | | | 17 | | | 50 |
| *Niviventer* sp. | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | 1 |
| *Niviventer confucianu* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Niviventer eha* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Niviventer fulvescens* | 0 | 0 | 2 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | 1 | | | | | | 2 |
| *Niviventer niviventer* | 0 | 0 | 6 | 0 | 0 | 0 | | | | | | 6 | | | | | | | | | | | | | | | | | | | | | | | | | 6 |
| *Paruromys dominator* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | 1 |
| *Rattus* sp. | 2 | 6 | 517 | 2 | 0 | 4 | | | 2 | | 3 | 6 | | | 2 | 8 | 1 | 5 | | | 4 | | | | 2 | | | | | | 2 | | | 4 | 492 | | 531 |
| *Rattus andamanensis* | 0 | 0 | 2 | 0 | 0 | 0 | | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | 2 |
| *Rattus argentiventer* | 0 | 0 | 508 | 0 | 0 | 0 | | | | | 397 | | | | | 15 | | | | | | | | | | | | | | | | | | | 96 | | 508 |
| *Rattus exulans* | 0 | 0 | 36 | 0 | 0 | 0 | | | | | | | | | | | 9 | | | | | | | | | | | | | | 24 | | | | 3 | | 36 |
| *Rattus flavipectus* | 0 | 0 | 3 | 0 | 0 | 0 | | | | | | 3 | | | | | | | | | | | | | | | | | | | | | | | | | 3 |
| *Rattus hoffmanni* | 0 | 0 | 9 | 0 | 0 | 0 | | | | | | | | | | 9 | | | | | | | | | | | | | | | | | | | | | 9 |
| *Rattus losea* | 0 | 0 | 38 | 0 | 0 | 0 | | | | | 18 | 15 | | | | | | | | | | | | | | | | | | | | | | | 5 | | 38 |
| *Rattus marmosurus* | 0 | 0 | 5 | 0 | 0 | 0 | | | | | | | | | | 5 | | | | | | | | | | | | | | | | | | | | | 5 |
| *Rattus nitidus* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Rattus norvegicus* | 0 | 0 | 74 | 2 | 0 | 0 | | | | | | 43 | | | | | | | | | | | | | | | | | | | | | | 2 | 31 | | 76 |
| *Rattus rattus* | 0 | 0 | 50 | 0 | 0 | 0 | | 18 | | | | 1 | | | | 24 | | 2 | | | | 3 | | | | | | | | | 1 | | | | 1 | | 50 |
| *Rattus tanezumi* | 0 | 0 | 30 | 0 | 0 | 0 | | 2 | | | | 8 | | | | 2 | | | | | | | | | | | | | | | 16 | | | | 2 | | 30 |
| *Rattus xanthurus* | 0 | 0 | 2 | 0 | 0 | 0 | | | | | | | | | | 2 | | | | | | | | | | | | | | | | | | | | | 2 |
| *Rhabdomys pumilio* | 3 | 0 | 0 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | 3 | | | | | | | | | | 3 |
| *Sundamys muelleri* | 0 | 0 | 5 | 0 | 0 | 0 | | | | | | | | | | | | 5 | | | | | | | | | | | | | | | | | | | 5 |
| N/A | 0 | 0 | 12 | 0 | 0 | 1 | | | | | | 6 | | | | | | | | | 1 | 1 | | | | | | | | | 5 | | | | | | 13 |
| unclassified Rodentia | 0 | 0 | 12 | 0 | 0 | 1 | | | | | | 6 | | | | | | | | | 1 | 1 | | | | | | | | | 5 | | | | | | 13 |
| Sciuridae | 0 | 0 | 7 | 0 | 0 | 0 | | | | | | 3 | | | | | 3 | | | | | | | | | | | | | | | | | | 1 | | 7 |
| *Dremomys rufigenis f* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 |
| *Menetes berdmorei* | 0 | 0 | 2 | 0 | 0 | 0 | | | | | | | | | | | 2 | | | | | | | | | | | | | | | | | | | | 2 |
| *Petaurista* sp. | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Ratufa bicolor* | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 |
| *Spermophilus dauricus* | 0 | 0 | 2 | 0 | 0 | 0 | | | | | | 2 | | | | | | | | | | | | | | | | | | | | | | | | | 2 |
| Spalacidae | 0 | 0 | 32 | 0 | 0 | 1 | | | | | | 10 | | | | | | | | | 1 | | | | | | | | | | | | | | 22 | | 33 |
| *Rhizomys* sp. | 0 | 0 | 1 | 0 | 0 | 0 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | | | | | 1 |
| *Rhizomys pruinosus* | 0 | 0 | 29 | 0 | 0 | 0 | | | | | | 7 | | | | | | | | | | | | | | | | | | | | | | | 22 | | 29 |
| *Rhizomys sinensis* | 0 | 0 | 2 | 0 | 0 | 1 | | | | | | 2 | | | | | | | | | 1 | | | | | | | | | | | | | | | | 3 |
| (blank) | 0 | 0 | 0 | 0 | 0 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 |
| (blank) | 0 | 0 | 0 | 0 | 0 | 1 | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | 1 |
| **Grand Total** | 13 | 28 | 1490 | 66 | 1 | 16 | **1** | **34** | **2** | **1** | **449** | **181** | **1** | **10** | **35** | **67** | **14** | **14** | **2** | **15** | **5** | **1** | **2** | **3** | **2** | **1** | **3** | **11** | **2** | **2** | **62** | **4** | **5** | **23** | **661** | **1** | **1614** |

**Table S2.** All PCR primers used for CoV detection in Rodentia, Eulipotyphla and Lagomorpha from 2008 to 2024.

| Primer set name | Year publication | Gene target | PCR product size | Primer | Sequence | Reference doi |
|---|---|---|---|---|---|---|
| Chu | 2011 | RdRp | 440 | F1 | GGKTGGGAYTAYCCKAARTG | https://doi.org/10.1128/JVI.05838-11 |
| | | | | R1 | TGYTGTSWRCARAAYTCRTG | |
| | | | | F2 | GGTTGGGACTATCCTAAGTGTGA | |
| | | | | R2 | CCATCATCAGATAGAATCATCAT | |
| Adapted from Chu et al, 2011 | 2017 | RdRp | 555 | F1 | GGKTGGGAYTAYCCKAARTG | https://doi.org/10.1128/AEM.01326-17 |
| | | | | R1 | TGYTGTSWRCARAAYTCRTG | |
| | | | | F2 | GGTTGGGACTATCCTAAGTGTGA | |
| | | | | R2 | CCAACAYTTNGARTCWGCCAT | |
| Corman RdRpSeq | 2012 | RdRp | 242 | F | TGC TAT WAG TGC TAA GAA TAG RGC | https://doi.org/10.2807/ese.17.49.20334-en |
| | | | | R | GCA TWG CNC WGT CAC ACT TAG G | |
| Corman Nseq | 2012 | N | 312 | F | CCT TCG GTA CAG TGG AGC CA | https://doi.org/10.2807/ese.17.49.20334-en |
| | | | | R | GAT GGG GTT GCC AAA CAC AAA C | |
| De Sabato | 2020 | spike and ORF3a | 800 | F | TGGATGTGGCACTAGTTGTC | https://doi.org/10.3390/v12121471 |
| | | | | R | CTGGATATTAGGAGCTGTGT | |
| De Souza-Luna | 2007 | RdRp | 494 | Fa, Fb | TTATGGGTTGGGATTATC and TGATGGGATGGGACTATC | https://doi.org/10.1128/jcm.02426-06 |
| | | | | Ra,Rb, Rc | TCATCACTCAGAATCATCA, TCATCAGAAAGAATCATCA, and TCGTCGGACAAGATCATCA | |
| Falcon | 2011 | RdRp | 440 | F1 | CARATGAATYTIAARTAYGC | https://doi.org/10.1007/s00705-011-1057-1 |
| | | | | R1 | TGYTGWGARCAAAAYTCRTG | |
| | | | | F2 | ATGGGWTGGGAYTAYCCIAARTG | |
| | | | | R2 | ACRTTRTTYTGRWARTA | |
| Gouilh | 2011 | RdRp | 438 | F1 | GGTTGGGAYTAYCCWAARTGTGA | 10.1016/j.meegid.2011.06.021 |
| | | | | R1 | CCATCRTCMGAHARAATCATCATA | |
| | | | | F2 | GCNAATWSTGTNTTTAACAT | |
| | | | | R2 | CCATCRTCMGAHARAATCATCATA | |
| Holbrook | 2021 | RdRp | 430 | F1 | GGTGGGAYTAYCCHAARTGYGA | https://doi.org/10.3390/v13040599 |
| | | | | R1 | CCRTCATCAGAHARWATCAT | |
| | | | | F2a, F2b | GAYTAYCCHAARTGTGAYAGA and GAYTAYCCHAARTGTGAYMGH | |
| | | | | R2 | CCRTCATCACTHARWATCAT | |
| Hu | 2018 | RdRp | 668 | F | AARTTYTAYGGHGGYTGG | https://doi.org/10.1016/j.jviromet.2018.02.021 |
| | | | | R | GARCARAATTCATGHGGDCC | |
| Muradrasoli | 2009 | RdRp | 179 | F | TGATGATGSNGTTGTNTGYTAYAA | https://doi.org/10.1016%2Fj.jviromet.2009.04.022 |
| | | | | R | GCATWGTRTGYTGNGARCARAATTC | |
| Poon | 2008 | RdRp | 440 | F1 | AYAACCAAGATCTTAATGG | https://doi.org/10.1007/978-1-59745-181-9_2 |
| | | | | R1 | TGCTTAGAACCCAAAATCAT | |
| | | | | F2 | GGTTGGGACTATCCTAAGTGTGA | |
| | | | | R2 | CCATCATCAGATAGAATCATCATA | |
| Quan | 2010 | RdRp | 400 | F1 | CGTTGGIACWAAYBTVCCWYTICARBTRGG | https://doi.org/10.1128/mBio.00208-10 |
| | | | | R1 | GGTCATKATAGCRTCAVMASWWGCNACNACATG | |
| | | | | F2 | GGCWCCWCCHGGNGARCAATT | |
| | | | | R2 | GGWAWCCCCAYTGYTGWAYRTC | |
| Sabir (UniCoV) | 2015 | RdRp | 442 | F1 | ATGGGTTGGGATTATCCTAAGTGTGA | https://doi.org/10.1126/science.aac8608 |
| | | | | R1 | CATCATCAGATAGAATCATCATAG | |
| | | | | F2 | ATGGGTTGGGATTATCCTAAGTGTGA | |
| | | | | R2 | CCATCATCAGATAGAATCATCAT | |
| Saldanha | 2019 | RdRp | 93 | F | TAATCGCCAATACCATCA | https://doi.org/10.1017%2FS0950268819000207 |
| | | | | R | CAACCACCATAGAACTTAG | |
| Tang | 2006 | RdRp | 440 | F | Not published | https://doi.org/10.1128%2FJVI.00697-06 |
| | | | | R | Not published | |
| Tong | 2009 | RdRp | 200 | F1 | ATGGGITGGGAY TATCCWAARTGTG | https://wwwnc.cdc.gov/eid/article/15/3/08-1013_article |
| | | | | R1 | AATTAT ARCAIACAACISYRTCRTCA | |
| | | | | F2 | ATGGGITGGGAYTATCCWAARTGTG | |
| | | | | R2 | CTAGTICCACCIGGYTTWANRTA | |
| Wang | 2015 | RdRp | 440 | F1 | ATGGGWTGGGAYTAYCCKAARTG | https://doi.org/10.1016/j.virol.2014.10.017 |
| | | | | R1 | CCRTCATCWGANARWATCATCAT | |
| | | | | F2 | GGWTGGGAYTAYCCKAARTG | |
| Wasberg | 2022 | S | 252 | F | GGTCAAACTACTGAATTTATTG | https://doi.org/10.3390/v14061205 |
| | | | | R | AATCCATCAGAACCAACGAC | |
| Watanabe | 2010 | RdRp | 440 | F | TCCTAAGTGTGATAGAGCTATGCC | https://doi.org/10.3201/eid1608.100208 |
| | | | | R | GTGCACACTCATTTGCTAACCG | |
| Woo | 2005 | RdRp | 440 | F | GGTTGGGACTATCCTAAGTGTGA | https://doi.org/10.1128%2FJVI.79.2.884-895.2005 |
| | | | | R | CCATCATCAGATAGAATCATCATA | |
| Woo | 2014 | RdRp | 440 | F | GGTTGGGACTATCCTAAGTGTGA | https://doi.org/10.1128/jvi.02351-13 |
| | | | | R | ACCATCATCNGANARDATCATNA | |

**Table S3 (excerpt).** Example of the details of the 55 publications screening for CoVs from 2012 to 13/02/2025 in Rodentia, Eulipotyphla, and Lagomorpha. The full dataset will be released upon publication.

| Web Of Science | Study N° | First author | Year | Method | Order tested | Country | Primer set used | N individual tested | N samples | N libraries | N CoV positive | N α-CoV detected | N β-CoV detected | Sample type tested | Screening level | Sample type poitive | *Species tested* | doi |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| NO | 1 | Anthony | 2017 | PCR | Rodentia and Eulipotyphla | World | Quan et al, 2010 ; Watanabe et al, 2010 | 3387 | | | **11** | | | Swabs (e.g. oral, urine, rectal), fluids (e.g. saliva, blood), and tissues | not specified | Oral swabs, rectal swab, blood | *Mus bufo, Mus cervicolor, Mastomys sp.* | https://doi.org/10.1093%2Fve%2Fvaa012 |
| NO | 1 | Anthony | 2017 | PCR | Rodentia and Eulipotyphla | World | Quan et al, 2010 ; Watanabe et al, 2010 | NA | | | **2** | | | Swabs (e.g. oral, urine, rectal), fluids (e.g. saliva, blood), and tissues | not specified | Oral swabs, rectal swab, blood | *Mus bufo* | https://doi.org/10.1093%2Fve%2Fvaa012 |
| NO | 1 | Anthony | 2017 | PCR | Rodentia and Eulipotyphla | World | Quan et al, 2010 ; Watanabe et al, 2010 | NA | | | **1** | | | Swabs (e.g. oral, urine, rectal), fluids (e.g. saliva, blood), and tissues | not specified | Oral swabs, rectal swab, blood | *Mus cervicolor* | https://doi.org/10.1093%2Fve%2Fvaa012 |
| NO | 1 | Anthony | 2017 | PCR | Rodentia and Eulipotyphla | World | Quan et al, 2010 ; Watanabe et al, 2010 | NA | | | **2** | | | Swabs (e.g. oral, urine, rectal), fluids (e.g. saliva, blood), and tissues | not specified | Oral swabs, rectal swab, blood | *Mastomys sp.* | https://doi.org/10.1093%2Fve%2Fvaa012 |
| YES | 2 | Apaa | 2023 | PCR | Eulipotyphla | Great Britain | Woo et al, 2005 | 5 | | | | | | Feces | Individual | | | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 2 | Apaa | 2023 | PCR | Rodentia | Great Britain | Woo et al, 2005 | | 108 | | | | | fecal sample | Individual | | *Arvicola amphibius* | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 2 | Apaa | 2023 | PCR | Rodentia | Great Britain | Woo et al, 2005 | | 7 | | | | | lung | Individual | | *Myodes glareolus* | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 2 | Apaa | 2023 | PCR | Rodentia | Great Britain | Woo et al, 2005 | | 32 | | | | | fecal sample | Individual | | *Myodes glareolus* | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 2 | Apaa | 2023 | PCR | Rodentia | Great Britain | Woo et al, 2005 | | 5 | | | | | lung | Individual | | *Microtus agrestis* | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 2 | Apaa | 2023 | PCR | Rodentia | Great Britain | Woo et al, 2005 | | 5 | | | | | fecal sample | Individual | | *Microtus agrestis* | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 2 | Apaa | 2023 | PCR | Rodentia | Great Britain | Woo et al, 2005 | | 10 | | | | | fecal sample | Individual | | *Apodemus sylvaticus* | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 2 | Apaa | 2023 | PCR | Eulipotyphla | Great Britain | Woo et al, 2005 | | 1 | | | | | fecal sample | Individual | | *Sorex araneus* | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 2 | Apaa | 2023 | PCR | Eulipotyphla | Great Britain | Woo et al, 2005 | | 2 | | | | | fecal sample | Individual | | *Sorex minutus* | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 2 | Apaa | 2023 | PCR | Eulipotyphla | Great Britain | Woo et al, 2005 | | 2 | | | | | fecal sample | Individual | | *Erinaceus europaeus* | https://pubmed.ncbi.nlm.nih.gov/38056499/ |
| YES | 3 | Arteaga | 2023 | PCR | Rodentia | Argentina | Chu et al, 2011 | 13 | | | | | | oropharyngeal swabs | Individual | | *Rattus norvegicus* | https://doi.org/10.1007/s00705-022-05703-x |
| YES | 3 | Arteaga | 2023 | PCR | Rodentia | Argentina | Chu et al, 2011 | 29 | | | **2** | 2 | | feces | individual | feces | *Rattus norvegicus* | https://doi.org/10.1007/s00705-022-05703-x |
| YES | 3 | Arteaga | 2023 | PCR | Rodentia | Argentina | Chu et al, 2011 | 3 | | | | | | feces | pool | | *Rattus norvegicus* | https://doi.org/10.1007/s00705-022-05703-x |
| YES | 3 | Arteaga | 2023 | PCR | Rodentia | Argentina | Chu et al, 2011 | 48 | | | | | | tissue | Individual | | *Rattus norvegicus* | https://doi.org/10.1007/s00705-022-05703-x |
| YES | 4 | Berto | 2018 | PCR | Rodentia | Vietnam | Poon et al, 2008 | 8 | | | | | | Feces | Individual | Feces | *Bandicota indica* | https://doi.org/10.1111%2Fzph.12582 |
| YES | 4 | Berto | 2018 | PCR | Rodentia | Vietnam | Poon et al, 2008 | 234 | | | **12** | | 12 | Feces | Individual | Feces | *Rattus argentiventer* | https://doi.org/10.1111%2Fzph.12582 |
| YES | 4 | Berto | 2018 | PCR | Rodentia | Vietnam | Poon et al, 2008 | 20 | | | | | | Feces | Individual | | *Rattus losea* | https://doi.org/10.1111%2Fzph.12582 |
| YES | 4 | Berto | 2018 | PCR | Rodentia | Vietnam | Poon et al, 2008 | 8 | | | | | | Feces | Individual | | *Rattus tanezumi* | https://doi.org/10.1111%2Fzph.12582 |

An excerpt of Supplementary Table S3 (22 rows) is included to demonstrate the format and variables. The complete dataset will be deposited in a public repository and linked in the final published version