

---

# Animal Reservoirs and Hosts for Emerging Alphacoronaviruses and Betacoronaviruses

Ria R. Ghai, Ann Carpenter, Amanda Y. Liew, Krystalyn B. Martin, Meghan K. Herring, Susan I. Gerber, Aron J. Hall, Jonathan M. Sleeman, Sophie VonDobschuetz, Casey Barton Behravesh

The ongoing global pandemic caused by coronavirus disease has once again demonstrated the role of the family *Coronaviridae* in causing human disease outbreaks. Because severe acute respiratory syndrome coronavirus 2 was first detected in December 2019, information on its tropism, host range, and clinical manifestations in animals is limited. Given the limited information, data from other coronaviruses might be useful for informing scientific inquiry, risk assessment, and decision-making. We reviewed endemic and emerging infections of alphacoronaviruses and betacoronaviruses in wildlife, livestock, and companion animals and provide information on the receptor use, known hosts, and clinical signs associated with each host for 15 coronaviruses detected in humans and animals. This information can be used to guide implementation of a One Health approach that involves human health, animal health, environmental, and other relevant partners in developing strategies for preparedness, response, and control to current and future coronavirus disease threats.

Coronaviruses are a family of RNA viruses whose large genomes, propensity for mutation, and frequent recombination events have resulted in a diversity of strains and species that are capable of rapid adaptation to new hosts and ecologic environments (1). This viral plasticity has garnered widespread concern because of zoonotic potential and the consequences of new emergence events in both human and animal populations. The emergence of a new strain of severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), which causes coronavirus disease

(COVID-19) has once again demonstrated the role of the family *Coronaviridae* in causing human disease outbreaks. SARS-CoV-2, a novel betacoronavirus, was identified in human patients from Wuhan, China, during December 2019 and has resulted in a global pandemic, an unprecedented public health emergency, and untold economic and societal repercussions worldwide. Similar to the 2002–2003 severe acute respiratory syndrome (SARS) epidemic, a live animal market where hundreds of animal species were sold is suspected to be associated with the emergence or early spread of COVID-19 in humans (2).

Although COVID-19 is novel in the breadth of the human outbreak, several pathogenic alphacoronaviruses and betacoronaviruses have shown similar patterns of emergence. As early as the 1930s, coronaviruses pathogenic to livestock, companion animals, and laboratory animals were identified (3). During the 1960s, 2 human coronaviruses, HCoV-229E and HCoV-OC43, were detected in patients who had common colds (4,5). Although it is speculated that HCoV-OC43 might also have emerged through a global pandemic in the late 1800s (6), the 2002–2003 SARS outbreak is the first known global epidemic caused by a coronavirus. The SARS epidemic triggered research within this viral family (3). This research led to detection of 2 new human coronaviruses, HCoV-NL63 and HCoV-HKU1 (7,8). HCoV-229E, HCoV-OC43, HCoV-NL63, and HCoV-HKU1 are now accepted as globally endemic common cold species that are typically associated with mild-to-moderate respiratory illness. In 2012, the most deadly human coronavirus to date was detected in the Arabian Peninsula: Middle East respiratory syndrome coronavirus (MERS-CoV) (9). A cumulative body of research on these and other coronaviruses has shown that most alphacoronaviruses and betacoronaviruses infecting humans have come from animal hosts and that both historic patterns and coronavirus biology establish an urgent ongoing threat to human and animal health (10).

---

Author affiliations: Centers for Disease Control and Prevention, Atlanta, Georgia, USA (R.R. Ghai, A. Carpenter, A.Y. Liew, K.B. Martin, M.K. Herring, S.I. Gerber, A.J. Hall, C. Barton Behravesh); Emory University, Atlanta (A.Y. Liew, K.B. Martin, M.K. Herring); US Geological Survey, Madison, Wisconsin, USA (J.M. Sleeman); Food and Agriculture Organization of the United Nations, Rome, Italy (S. VonDobschuetz)

DOI: <https://doi.org/10.3201/eid2704.203945>

Although coronaviruses are divided into 4 viral genera, namely alphacoronaviruses, betacoronaviruses, gammacoronaviruses, and deltacoronaviruses, we focus on alphacoronaviruses and betacoronaviruses because all known human coronaviruses are from these genera, and they may therefore pose an increased risk for causing future pandemics.

This review is intended to compile data to inform a One Health approach to combatting emerging alphacoronaviruses and betacoronaviruses. One Health is a collaborative, multisectoral, and transdisciplinary approach—working at the local, regional, national, and global levels—with the goal of achieving optimal health outcomes recognizing the interconnection between humans, animals, plants, and their shared environment (11). For example, in Qatar, a One Health approach for MERS-CoV prevention and control has been implemented since early in the outbreak, and is associated with improvements in coordination, joint outbreak response rates, and diagnostic capacity (12). Similarly, in the United States, establishment of the One Health Federal Interagency COVID-19 Coordination Group has been instrumental in ensuring an efficient and coordinated all-of-government response by creating a mechanism to communicate, share timely updates, and align messaging (13). More generally, the One Health approach is endorsed as an effective means of combatting zoonotic diseases internationally by the Tripartite international health organizations, consisting of the Food and Agriculture Organization of the United Nations, the World Health Organization, and the World Organisation for Animal Health (14).

As with other zoonotic diseases, effective implementation of a One Health approach for emerging coronaviruses requires an understanding of the transmission dynamics and human and animal hosts associated with the pathogen. Therefore, this review summarizes information from other coronavirus emergence events, which might be useful in identifying trends, establishing baselines, and informing decision-making by using a One Health approach around the current COVID-19 pandemic and future emerging coronavirus threats. Specifically, we provide information on the receptor used by each current or previously emerging coronavirus because tropism can help predict host susceptibility (Table 1) for all known hosts of each coronavirus and their host category (i.e., reservoir, intermediate, spillover, susceptible through experimental infection, or nonsusceptible through experimental infection) (Table 2, <https://wwwnc.cdc.gov/EID/article/27/4/20-3945-T2.htm>) and clinical signs associated with

coronavirus infection (Table 3, <https://wwwnc.cdc.gov/EID/article/27/4/20-3945-T3.htm>)

### Emerging Coronaviruses and Wildlife

More than 70% of zoonotic emerging infectious diseases in humans are caused by pathogens that have a wildlife origin (11). Several mammalian orders are now known to host coronaviruses, including carnivores, lagomorphs, nonhuman primates, ungulates and rodents (3). However, the attention has focused on Chiroptera (bats), which are hypothesized to be the origin host for all alphacoronaviruses and betacoronaviruses, and therefore all human coronaviruses (Table 2) (1,3).

After rodents, bats are the second most diverse and abundant mammalian order, comprising 20% of all mammalian biodiversity worldwide. In the past 2 decades, research has intensified to determine why bats harbor more zoonotic diseases than other mammalian taxa, including pathogens that result in high-consequence infectious diseases, such as Ebola and Marburg filoviruses; Nipah and Hendra paramyxoviruses; and SARS-CoV, SARS-CoV-2, and MERS-CoV, emerging in humans (15). Behavioral and ecologic traits, such as their gregariousness, sympatry with mixed species assemblages in roosts, and long lifespan relative to size, have been suggested explanations for why bats are reservoirs to many viral pathogens (15). Physiologically, bats have comparatively high metabolic rates and typically do not show clinical signs after viral infection. Recently, it has also been shown that bats have several immune characteristics that are unique among mammals and that cumulatively dampen their antiviral responses (16). Those factors also probably contribute to their effectiveness as viral reservoirs.

Coronavirus richness and diversity detected in bats far exceeds those of other mammalian orders;  $\geq 11$  of 18 chiropteran families across 6 continents have tested positive for  $\geq 1$  coronavirus species (3). A study surveying the diversity of wildlife coronaviruses across global disease hotspots identified 100 distinct viruses, of which 91 were detected in bats (10). This study reported that patterns of coronavirus diversity mirrored bat diversity and evolutionary history, reinforcing the idea that bats are the predominant reservoir of zoonotic and emerging coronaviruses (10). On the basis of extrapolations made in the same study, Anthony et al. predicted that bats harbor  $\approx 3,204$  coronaviruses, most of which remain undetected (10). Although much coronavirus diversity remains to be detected, several SARS-like coronaviruses have been detected already in bats,

**Table 1.** Current or previously emerging coronaviruses\*

Pathogen (abbreviation)	Disease (abbreviation)	Viral genus	Receptor (abbreviation) [suspected]
Alphacoronavirus 1 (ACoV1); strain canine enteric coronavirus (CCoV)	Canine coronavirus infection (CCoV)	<i>Alphacoronavirus</i>	Aminopeptidase N (APN, CD13)
Alphacoronavirus 1 (ACoV1); strain feline infectious peritonitis virus (FIPV)	Feline infectious peritonitis virus (FIP)	<i>Alphacoronavirus</i>	Aminopeptidase N (APN, CD13)
Bat coronavirus HKU10	NA	<i>Alphacoronavirus</i>	Unknown
Ferret systemic coronavirus (FRSCV)	Ferret systemic coronavirus (FRSCV)-associated disease	<i>Alphacoronavirus</i>	Unknown
Human coronavirus NL63	Common cold	<i>Alphacoronavirus</i>	Angiotensin-converting enzyme 2 (ACE2)
Human coronavirus 229E	Common cold	<i>Alphacoronavirus</i>	Human aminopeptidase N (hAPN, CD13)
Porcine epidemic diarrhea virus (PEDV)	Porcine epidemic diarrhea (PED)	<i>Alphacoronavirus</i>	[Aminopeptidase N (APN, CD13)]
Rhinolophus bat coronavirus HKU2; strain swine acute diarrhea syndrome coronavirus (SADS-CoV)	Swine acute diarrhea syndrome (SADS)	<i>Alphacoronavirus</i>	Unknown
Betacoronavirus 1; strain bovine coronavirus	NA	<i>Betacoronavirus</i>	Human leukocyte antigen class I (HLA-1)
Betacoronavirus 1; strain canine respiratory coronavirus	Canine infectious respiratory disease (CIRD)	<i>Betacoronavirus</i>	Human leukocyte antigen class I (HLA-1)
Betacoronavirus1; strain human coronavirus OC43	Common cold	<i>Betacoronavirus</i>	Human leukocyte antigen class I (HLA-1)
Human coronavirus HKU1	Common cold	<i>Betacoronavirus</i>	Human leukocyte antigen class I (HLA-1)
Middle East respiratory syndrome coronavirus (MERS-CoV)	Middle East respiratory syndrome (MERS)	<i>Betacoronavirus</i>	Dipeptidyl peptidase 4 (DPP4, CD26)
Severe acute respiratory syndrome coronavirus (SARS-CoV)	Severe acute respiratory syndrome (SARS)	<i>Betacoronavirus</i>	Angiotensin-converting enzyme 2 (ACE2)
Severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2)	Coronavirus disease (COVID-19)	<i>Betacoronavirus</i>	Angiotensin-converting enzyme 2 (ACE2)

\*All coronaviruses are described in Tables 2 and 3, including the receptor used for viral entry. NA, not available.

including viruses that use the same human cellular receptor molecule as SARS-CoV and SARS-CoV-2, and might therefore pose an increased risk for future emergence from bats to humans (17).

Despite the risks associated with bat-origin coronaviruses, bats play integral roles in ecosystems, including insect suppression through predation, prey for numerous predators, pollinators for economically and ecologically useful plants, and seed dispersal for countless tropical trees and shrubs (18). Therefore, mitigating the risks of future emergence events from bats would benefit from minimizing close interaction between humans and bats and other wildlife, by reducing or stopping wildlife sales at wet markets, wildlife hunting, and encroachment on wildlife habitat.

Although further research on bats might help to understand the origins of coronaviruses, other wildlife species are intermediate hosts for human emerging coronaviruses. Intermediate hosts might not only add complexity to coronavirus transmission dynamics, but might also amplify viral spillover to new hosts by closing gaps in interaction frequency between species, and by increasing transmissibility and/or infectiousness through viral adaptation (19). A canonical example is SARS-CoV, whose intermediate host is

accepted to be palm civets (Table 2; Appendix, <https://wwwnc.cdc.gov/EID/article/27/4/20-3945-App1.pdf>). In this instance, close interaction between humans and civets sold through wildlife markets probably facilitated transmission to humans, and passage and ongoing recombination in civet intermediate hosts is believed to have played a critical role in human receptor tropism (19,20) (Table 1).

Some wildlife species are at risk for human coronavirus spillover. Wild great apes, all species of which are endangered, are a taxonomic group vulnerable to spillover from humans, at least in part because they are our closest living relatives. Several documented respiratory outbreaks that resulted in clinical signs ranging from mild illness to death in chimpanzee and gorilla populations originated from a human source (21,22). The human betacoronavirus HCoV-OC43 was reported as the causative agent of mild-to-moderate respiratory illness among wild chimpanzees in Côte D'Ivoire in late 2016 and early 2017 (Table 2; Appendix), suggesting the susceptibility of these chimpanzees to human coronaviruses. As the COVID-19 pandemic continues, there is concern that susceptible wildlife, such as great apes, might be exposed to the virus through human contact, resulting in a new host reservoir, which could pose a risk for perpetuating

enzootic transmission and zoonotic transmission into recovering human populations.

Wildlife infections with SARS-CoV-2 have already occurred; the first natural infection of SARS-CoV-2 in a wild animal, and the first confirmed animal cases in the United States, were in tigers (n = 5) and lions (n = 3) at a zoo in New York, NY (Table 2; Appendix). Unlike most other asymptomatic animal cases reported previously, the large cats demonstrated respiratory signs that included coughing and wheezing but ultimately made a full recovery (Table 3). SARS-CoV-2 infection in wild felids in captivity highlights the complex interactions humans might have with wildlife, including the potential for human-to-wildlife transmission. Given these interlinkages, framing risk by using a One Health approach might more comprehensively address the socioeconomic and environmental drivers of disease emergence, leading to potentially novel, mutually beneficial solutions. For example, risks could be reduced by improving wildlife importation, trade and market regulations, and sanitary standards, which would not only protect public health and animal health but also result in positive wildlife conservation outcomes.

### Emerging Coronaviruses and Livestock

Some coronaviruses naturally infect livestock and can have devastating economic consequences, such as swine acute diarrhea syndrome coronavirus (SADS-CoV), porcine epidemic diarrhea virus (PEDV), and betacoronavirus 1. Although recent studies suggest that pigs are not susceptible hosts for SARS-CoV-2 infection (23,24), pigs are a common host for alphacoronaviruses and betacoronaviruses; 6 viral species cause disease (25) (Table 2). Of these species, the enteric alphacoronavirus PEDV is considered reemerging, and the enteric alphacoronavirus SADS-CoV (a strain of the *Rhinolophus* bat coronavirus HKU2) is considered emerging (25). Although PEDV was detected in China in the 1970s, a highly pathogenic variant caused considerable losses to the United States pork industry in 2013–2014 (26). SADS-CoV is highly pathogenic in swine and was detected in Guangdong Province in China during 2016–2017, causing the death of nearly 25,000 piglets (27) (Table 3). SADS-CoV emerged within 100 km of the accepted locale of the SARS index case, and like SARS-CoV and SARS-CoV-2, SADS-CoV is suspected to originate in horseshoe bats (*Rhinolophus* spp.) (Table 2; Appendix). However, unlike SARS-CoV and SARS-CoV-2, SADS-CoV has not been detected outside China (25).

Among betacoronaviruses, a strain of betacoronavirus 1 also infects pigs (25). Porcine hemagglutinating encephalomyelitis virus has been circulating for decades and causes rapid death in piglets (25) (Table 3). Unlike other coronaviruses, betacoronavirus 1 is a unique species complex, in that its distinct strains are host-specific to a range of different species, including wild and domestic ungulates, rabbits, and canines (19,28) (Table 2; Appendix). Perhaps the most well-studied strain of betacoronavirus 1 is bovine coronavirus (BCoV), which has a major economic role because it can be associated with a suite of clinical disease in calves and cattle, including calf diarrhea, winter dysentery, and respiratory infection (28) (Table 3). BCoV also infects several other livestock species, including horses, sheep, and camels (19,28) (Table 2).

Livestock have also been intermediate hosts in the emergence of 3 human coronaviruses. An unknown ungulate species, speculated to be cattle, is accepted as the intermediate host of HCoV-OC43 (6,29), a strain of betacoronavirus 1 (Table 2). On the basis of molecular clock calculations, HCoV-OC43 is predicted to have jumped from livestock to humans around 1890, a timeframe coincident with pandemics of respiratory disease in cattle (which resulted in widespread culling) and humans (although this outbreak is historically attributed to influenza) (6). Dromedary camels are accepted as established hosts of MERS-CoV and are believed to be associated with the emergence of HCoV-229E in humans on the basis of closely related viruses found in camelids (Table 2; Appendix). Dromedary camels inhabit the Middle East and northern Africa and comprise 90% of extant camels on earth. In much of their range, dromedaries are a major livestock species that are used as racing and working animals, as well as for their milk, meat, and hides.

Livestock can also be spillover hosts of human coronavirus infection. After the 2002–2003 SARS outbreak, a study conducted on farms in Xiqing County, China, tested livestock (pigs, cattle, chickens, and ducks) and companion animals (dogs and cats), leading to detection of 1 pig that was positive for SARS-CoV by antibody test and reverse transcription PCR (30) (Table 2). A larger and more complex series of livestock outbreaks of SARS-CoV-2 has been unfolding since April 2020. Mink farms across Europe and North America have reported outbreaks of SARS-CoV-2 (Tables 2, 3). In most outbreaks, farmed mink were suspected to be initially infected by COVID-19–positive farm employees (31,32). Findings from the Netherlands have

also identified instances of spillback from mink to humans through ongoing investigations (33). National surveillance and control efforts have been implemented in several countries, many of which have subsequently identified other SARS-CoV-2-positive species living on or nearby mink farms, including cats, dogs, and escaped or wild mink (32). Several countries have implemented mandatory reporting of any virus-positive animals and depopulation or quarantine of affected farms (32). In Europe, several million mink have been culled, and a moratorium has been placed on the mink industry in some countries; such early and coordinated One Health actions are needed to prevent bidirectional transmission of zoonotic diseases (32).

### Emerging Coronaviruses and Companion Animals

Companion animals are members of many households and can improve the physical and mental well-being of their owners (34). In the United States,  $\approx 71.5$  million households (57%) own  $\geq 1$  companion animal (35). Among households with companion animals, dogs (67%) and cats (44%) are the most commonly owned (35). Despite the many benefits of pet ownership, close interactions with pets pose risks for zoonotic disease transmission (34). Zoonotic diseases that are spread between humans and companion animals include rabies, salmonellosis, campylobacteriosis, and hookworm (34,36,37). Companion animals are estimated to be a source of  $>70$  human diseases (38), and the burden of zoonotic diseases attributed to interactions with companion animals is substantial. For example, rabies kills  $\approx 59,000$  persons per year globally, and 99% of human rabies cases originate from rabid dogs (37).

Several common coronaviruses have been detected in companion animals, although none of the coronaviruses that are endemic to companion animal populations are zoonotic. One of the most common respiratory diseases in dogs is canine infectious respiratory disease, or kennel cough, which typically causes cough and nasal discharge in puppies and dogs (39,40). Although kennel cough can be caused by several pathogens, most frequently the bacterium *Bordetella bronchiseptica*, canine respiratory coronavirus (CRCoV) is a contributing pathogen to this syndrome (39,41) (Table 1). CRCoV is believed to originate from BCoV through a common ancestor, host variant, or a host species shift and is therefore considered a strain of betacoronavirus 1 (39,41). Regardless of how CRCoV and BCoV are genetically related, experimental studies have shown that dogs challenged

with BCoV can become infected and transmit the virus to other dogs, although they do not exhibit clinical signs of disease (Tables 2, 3; Appendix).

Canine enteric coronavirus (CCoV) is an alphacoronavirus often associated with mild enteritis in puppies and dogs, especially in group housing situations (42). However, during 2005, a novel, highly pathogenic variant strain of CCoV-II, CB/05, was identified (43) (Table 2). This new variant is now pantropic, and results in a mortality rate up to 100% in isolated outbreaks in puppies (43) (Table 3). Because of its increased pathogenicity and changes in tissue tropism, CCoV is considered an emerging pathogen (42).

Although CCoV is generally considered to be specific to dogs, cats experimentally challenged with the virus can be infected with CCoV and mount an anamnestic response to further exposure, although they do not develop clinical signs of illness (Table 3; Appendix). In addition, although there are 2 serotypes of feline coronavirus (FCoV), FCoV type I and FCoV type II, type II is hypothesized to have originated from a recombination event between FCoV type I and CCoV, which suggests co-infections of coronaviruses among companion animals might yield opportunity for emergence of new disease (44).

Companion animals might also act as spillover hosts for human coronaviruses. A study after the 2002–2003 SARS outbreak showed that pet cats living in a Hong Kong, China, apartment complex were naturally infected with SARS during the epidemic (45). After the epidemic, challenge experiments in cats and ferrets found that both species could be experimentally infected and transmit the infection to immunologically naive animals of the same species they were housed with (45) (Table 2). In this experiment, cats did not show clinical signs of illness, although ferrets became lethargic, showed development of conjunctivitis, and died on days 16 and 21 postinfection. However, unlike human cases, there was no evidence that SARS-CoV-associated pneumonia was a cause of death (Table 3). Rather, the main findings in deceased ferrets were marked hepatic lipidosis and emaciation (45).

Companion animals, specifically dogs and cats, are among the most commonly infected groups of animals in the ongoing COVID-19 pandemic. Natural cases of suspected human-to-animal transmission have been confirmed in dogs and cats from several countries, and the earliest reports date back to March 2020 in Hong Kong (32). As of January 2021, there are  $\approx 100$  confirmed cases of SARS-CoV-2 infections in dogs and cats in the United States; most of those

cases resulted from exposure to owners who had COVID-19 (46). Experimental challenge studies additionally suggest that similar to SARS-CoV, several companion animals, including cats, ferrets, and golden hamsters, are all susceptible to SARS-CoV-2 infection under laboratory conditions (Table 2; Appendix). Furthermore, studies in cats, hamsters, and ferrets showed that they are capable of direct and indirect transmission to healthy animals of the same species in experimental settings (23,24,47,48), which underscores the need for infection prevention and control practices for humans and companion animals (49).

The global prevalence of companion animal ownership underscores the need for better understanding of pathogens, such as coronaviruses, that can infect pets. Because companion animals harbor endemic coronaviruses and might also be at risk for spillover for some human zoonotic coronaviruses, there is potential for coronavirus recombination events and new viral emergence to occur within these hosts. Therefore, ensuring that persons understand how to safely interact with their companion animals is essential for ensuring that persons and companion animals stay healthy while also protecting animal welfare.

## Conclusions

A considerable number of mammalian species, including wildlife, livestock, and companion animals, are susceptible to infection with alphacoronaviruses and betacoronaviruses. The propensity of alphacoronaviruses and betacoronaviruses to jump to new hosts, coupled with their relatively large host ranges, suggests that a One Health approach could be used to develop strategies to mitigate the effects of current and future coronavirus emergence events. During the COVID-19 pandemic, One Health collaboration between public health and veterinary sectors has already bolstered critical healthcare resources and infrastructure, leading to improvements in diagnostic testing capacity and human resource availability (50). In the United States, the One Health Federal Interagency COVID-19 Coordination Group has developed risk communication and messaging for companion animals, livestock, and wildlife and has been instrumental in coordinating joint outbreak response and diagnostic testing in animals. As these examples highlight, integration of the One Health approach into preparedness planning, joint epidemiologic investigations, surveillance, laboratory diagnostics, risk assessment, and field research is not only beneficial but a useful approach to safeguard the health, welfare and safety of humans, animals, and their shared environment.

## Acknowledgments

We thank members of the COVID-19 One Health Working Group of the Centers for Disease Control and Prevention, the One Health Federal Interagency Coordination Group, and state and local partners for providing valuable contributions and insights for this manuscript.

The opinions expressed by authors contributing to this journal do not necessarily reflect the opinions of the Centers for Disease Control and Prevention, Emory University, or the Food and Agriculture Organization of the United Nations, but do represent the views of the US Geological Survey.

## About the Author

Dr. Ghai is an associate service fellow in the One Health Office, National Center for Emerging and Zoonotic Infectious Diseases, Centers for Disease Control and Prevention, Atlanta, GA. Her primary research interests include One Health, disease ecology, and zoonotic diseases.

## References

1. Woo PC, Lau SK, Huang Y, Yuen K-Y. Coronavirus diversity, phylogeny and interspecies jumping. *Exp Biol Med* (Maywood). 2009;234:1117-27. <https://doi.org/10.3181/0903-MR-94>
2. Huang C, Wang Y, Li X, Ren L, Zhao J, Hu Y, et al. Clinical features of patients infected with 2019 novel coronavirus in Wuhan, China. *Lancet*. 2020;395:497-506. [https://doi.org/10.1016/S0140-6736\(20\)30183-5](https://doi.org/10.1016/S0140-6736(20)30183-5)
3. Drexler JF, Corman VM, Drosten C. Ecology, evolution and classification of bat coronaviruses in the aftermath of SARS. *Antiviral Res*. 2014;101:45-56. <https://doi.org/10.1016/j.antiviral.2013.10.013>
4. Hamre D, Procknow JJ. A new virus isolated from the human respiratory tract. *Proc Soc Exp Biol Med*. 1966;121:190-3. <https://doi.org/10.3181/00379727-121-30734>
5. McIntosh K, Dees JH, Becker WB, Kapikian AZ, Chanock RM. Recovery in tracheal organ cultures of novel viruses from patients with respiratory disease. *Proc Natl Acad Sci U S A*. 1967;57:933-40. <https://doi.org/10.1073/pnas.57.4.933>
6. Vijgen L, Keyaerts E, Moës E, Thoelen I, Wollants E, Lemey P, et al. Complete genomic sequence of human coronavirus OC43: molecular clock analysis suggests a relatively recent zoonotic coronavirus transmission event. *J Virol*. 2005;79:1595-604. <https://doi.org/10.1128/JVI.79.3.1595-1604.2005>
7. van der Hoek L, Pyrc K, Jebbink MF, Vermeulen-Oost W, Berkhout RJ, Wolthers KC, et al. Identification of a new human coronavirus. *Nat Med*. 2004;10:368-73. <https://doi.org/10.1038/nm1024>
8. Woo PC, Lau SK, Chu CM, Chan KH, Tsoi HW, Huang Y, et al. Characterization and complete genome sequence of a novel coronavirus, coronavirus HKU1, from patients with pneumonia. *J Virol*. 2005;79:884-95. <https://doi.org/10.1128/JVI.79.2.884-895.2005>
9. Zaki AM, van Boheemen S, Bestebroer TM, Osterhaus AD, Fouchier R. Isolation of a novel coronavirus from a man with pneumonia in Saudi Arabia. *N Engl J Med*. 2012;367:1814-20. <https://doi.org/10.1056/NEJMoa1211721>

10. Anthony SJ, Johnson CK, Greig DJ, Kramer S, Che X, Wells H, et al.; PREDICT Consortium. Global patterns in coronavirus diversity. *Virus Evol.* 2017;3:vex012. <https://doi.org/10.1093/ve/vex012>
11. Centers for Disease Control and Prevention. One Health. 2020 [cited 2020 Jul 15]. <https://www.cdc.gov/onehealth/index.html>
12. Farag E, Nour M, Islam MM, Mustafa A, Khalid M, Sikkema RS, et al. Qatar experience on One Health approach for Middle East respiratory syndrome coronavirus, 2012–2017: a viewpoint. *One Health.* 2019;7:100090. <https://doi.org/10.1016/j.onehlt.2019.100090>
13. Newman A, Smith D, Ghai RR, Wallace RM, Torchetti MK, Loiacono C, et al. First reported cases of SARS-CoV-2 infection in companion animals – New York, March–April 2020. *MMWR Morb Mortal Wkly Rep.* 2020;69:710–3. <https://doi.org/10.15585/mmwr.mm6923e3>
14. World Health Organization, Food and Agriculture Organization of the United Nations, World Organisation for Animal Health. Taking a multisectoral, One Health approach: a tripartite guide to addressing zoonotic diseases in countries. Geneva: The Organization; 2019.
15. Luis AD, Hayman DT, O’Shea TJ, Cryan PM, Gilbert AT, Pulliam JR, et al. A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? *Proc Biol Sci.* 2013;280:20122753. <https://doi.org/10.1098/rspb.2012.2753>
16. Banerjee A, Baker ML, Kulcsar K, Misra V, Plowright R, Mossman K. Novel insights into immune systems of bats. *Front Immunol.* 2020;11:26. <https://doi.org/10.3389/fimmu.2020.00026>
17. Ge X-Y, Li J-L, Yang X-L, Chmura AA, Zhu G, Epstein JH, et al. Isolation and characterization of a bat SARS-like coronavirus that uses the ACE2 receptor. *Nature.* 2013;503:535–8. <https://doi.org/10.1038/nature12711>
18. Kasso M, Mundanthra B. Ecological and economic importance of bats (order Chiroptera). *Int Sch Res Notices.* 2013;2013:187415 [cited 2021 Jan 22]. <https://www.hindawi.com/journals/isrn/2013/187415>
19. Corman VM, Muth D, Niemeyer D, Drosten C. Hosts and sources of endemic human coronaviruses. In: Kielian M, Mettenleiter TC, Roossinck MJ, editors. *Advances in Virus Research.* New York: Academic Press; 2018. p. 163–88.
20. Song H-D, Tu C-C, Zhang G-W, Wang S-Y, Zheng K, Lei L-C, et al. Cross-host evolution of severe acute respiratory syndrome coronavirus in palm civet and human. *Proc Natl Acad Sci U S A.* 2005;102:2430–5. <https://doi.org/10.1073/pnas.0409608102>
21. Köndgen S, Schenk S, Pauli G, Boesch C, Leendertz FH. Noninvasive monitoring of respiratory viruses in wild chimpanzees. *EcoHealth.* 2010;7:332–41. <https://doi.org/10.1007/s10393-010-0340-z>
22. Scully EJ, Basnet S, Wrangham RW, Muller MN, Otali E, Hyeroba D, et al. Lethal respiratory disease associated with human rhinovirus C in wild chimpanzees, Uganda, 2013. *Emerg Infect Dis.* 2018;24:267–74. <https://doi.org/10.3201/eid2402.170778>
23. Shi J, Wen Z, Zhong G, Yang H, Wang C, Huang B, et al. Susceptibility of ferrets, cats, dogs, and other domesticated animals to SARS-coronavirus 2. *Science.* 2020;368:1016–20. <https://doi.org/10.1126/science.abb7015>
24. Schlottau K, Rissmann M, Graaf A, Schön J, Sehl J, Wylezich C, et al. Experimental transmission studies of SARS-CoV-2 in fruit bats, ferrets, pigs and chickens. *Lancet Microbe.* 2020;1:e218–25. [https://doi.org/10.1016/S2666-5247\(20\)30089-6](https://doi.org/10.1016/S2666-5247(20)30089-6)
25. Wang Q, Vlasova AN, Kenney SP, Saif LJ. Emerging and re-emerging coronaviruses in pigs. *Curr Opin Virol.* 2019;34:39–49. <https://doi.org/10.1016/j.coviro.2018.12.001>
26. Lee C. Porcine epidemic diarrhoea virus: An emerging and re-emerging epizootic swine virus. *Virol J.* 2015;12:193. <https://doi.org/10.1186/s12985-015-0421-2>
27. Zhou P, Fan H, Lan T, Yang X-L, Shi W-F, Zhang W, et al. Fatal swine acute diarrhoea syndrome caused by an HKU2-related coronavirus of bat origin. *Nature.* 2018;556:255–8. <https://doi.org/10.1038/s41586-018-0010-9>
28. Amer HM. Bovine-like coronaviruses in domestic and wild ruminants. *Anim Health Res Rev.* 2018;19:113–24. <https://doi.org/10.1017/S1466252318000117>
29. Vijgen L, Keyaerts E, Lemey P, Maes P, Van Reeth K, Nauwynck H, et al. Evolutionary history of the closely related group 2 coronaviruses: porcine hemagglutinating encephalomyelitis virus, bovine coronavirus, and human coronavirus OC43. *J Virol.* 2006;80:7270–4. <https://doi.org/10.1128/JVI.02675-05>
30. Chen W, Yan M, Yang L, Ding B, He B, Wang Y, et al. SARS-associated coronavirus transmitted from human to pig. *Emerg Infect Dis.* 2005;11:446–8. <https://doi.org/10.3201/eid1103.040824>
31. Oreshkova N, Molenaar R-J, Vreman S, Harders F, Oude Munnink BB, Hakze-van der Honing RW, et al. SARS-CoV-2 infection in farmed minks, the Netherlands, April and May 2020. *Euro Surveill.* 2020;25:2001005. <https://doi.org/10.2807/1560-7917.ES.2020.25.23.2001005>
32. World Organisation for Animal Health. COVID 19 portal events in animals; 2020 [cited 2020 Jul 13]. : <https://www.oie.int/en/scientific-expertise/specific-information-and-recommendations/questions-and-answers-on-2019-novel-coronavirus/events-in-animals>
33. Oude Munnink BB, Sikkema RS, Nieuwenhuijse DF, Molenaar RJ, Munger E, Molenkamp R, et al. Transmission of SARS-CoV-2 on mink farms between humans and mink and back to humans. *Science.* 2021;371:172–7. <https://doi.org/10.1126/science.abe5901>
34. Centers for Disease Control and Prevention. Healthy pets, healthy people, 2020 [cited 2020 Jul 13]. <https://www.cdc.gov/healthypets/index.html>
35. American Veterinary Medical Association. Pet ownership and demographics sourcebook. Schaumburg (IL): The Association; 2018.
36. Smith K, Boxrud D, Leano F, Snider C, Braden C, Montgomery S, et al.; Centers for Disease Control and Prevention (CDC). Outbreak of multidrug-resistant *Salmonella typhimurium* associated with rodents purchased at retail pet stores – United States, December 2003–October 2004. *MMWR Morb Mortal Wkly Rep.* 2005; 54:429–33.
37. Hampson K, Coudeville L, Lembo T, Sambo M, Kieffer A, Atlan M, et al.; Global Alliance for Rabies Control Partners for Rabies Prevention. Estimating the global burden of endemic canine rabies. *PLoS Negl Trop Dis.* 2015;9:e0003709. <https://doi.org/10.1371/journal.pntd.0003709>
38. Stull JW, Brophy J, Weese JS. Reducing the risk of pet-associated zoonotic infections. *CMAJ.* 2015;187:736–43. <https://doi.org/10.1503/cmaj.141020>
39. Erles K, Toomey C, Brooks HW, Brownlie J. Detection of a group 2 coronavirus in dogs with canine infectious respiratory disease. *Virology.* 2003;310:216–23. [https://doi.org/10.1016/S0042-6822\(03\)00160-0](https://doi.org/10.1016/S0042-6822(03)00160-0)
40. Erles K, Brownlie J. Canine respiratory coronavirus: an emerging pathogen in the canine infectious respiratory disease complex. *Vet Clin North Am Small Anim Pract.*

## SYNOPSIS

- 2008;38:815–25, viii. <https://doi.org/10.1016/j.jcvsm.2008.02.008>
41. Erles K, Shiu K-B, Brownlie J. Isolation and sequence analysis of canine respiratory coronavirus. *Virus Res.* 2007; 124:78–87. <https://doi.org/10.1016/j.virusres.2006.10.004>
42. Licitra BN, Duhamel GE, Whittaker GR. Canine enteric coronaviruses: emerging viral pathogens with distinct recombinant spike proteins. *Viruses.* 2014;6:3363–76. <https://doi.org/10.3390/v6083363>
43. Buonavoglia C, Decaro N, Martella V, Elia G, Campolo M, Desario C, et al. Canine coronavirus highly pathogenic for dogs. *Emerg Infect Dis.* 2006;12:492–4. <https://doi.org/10.3201/eid1203.050839>
44. Pratelli A. Genetic evolution of canine coronavirus and recent advances in prophylaxis. *Vet Res.* 2006;37:191–200. <https://doi.org/10.1051/vetres:2005053>
45. Martina BE, Haagmans BL, Kuiken T, Fouchier RA, Rimmelzwaan GF, Van Amerongen G, et al. Virology: SARS virus infection of cats and ferrets. *Nature.* 2003;425:915. <https://doi.org/10.1038/425915a>
46. US Department of Agriculture. Cases of SARS-CoV-2 in animals in the United States, 2020 [cited 2020 Dec 20]. [https://www.aphis.usda.gov/aphis/ourfocus/animalhealth/sa\\_one\\_health/sars-cov-2-animals-us](https://www.aphis.usda.gov/aphis/ourfocus/animalhealth/sa_one_health/sars-cov-2-animals-us)
47. Kim Y-I, Kim S-G, Kim S-M, Kim E-H, Park S-J, Yu K-M, et al. Infection and rapid transmission of SARS-CoV-2 in ferrets. *Cell Host Microbe.* 2020;27:704–709.e2. <https://doi.org/10.1016/j.chom.2020.03.023>
48. Halfmann PJ, Hatta M, Chiba S, Maemura T, Fan S, Takeda M, et al. Transmission of SARS-CoV-2 in domestic cats. *N Engl J Med.* 2020;383:592–4. <https://doi.org/10.1056/NEJMc2013400>
49. Centers for Disease Control and Prevention. Toolkit: One Health approach to address companion animals with SARS-CoV-2, 2020 [cited 2020 Dec 20]. <https://www.cdc.gov/coronavirus/2019-ncov/animals/toolkit.html>
50. Lorusso A, Calistri P, Mercante MT, Monaco F, Portanti O, Marcacci M, et al. A “One-Health” approach for diagnosis and molecular characterization of SARS-CoV-2 in Italy. *One Health.* 2020;10:100135. <https://doi.org/10.1016/j.onehlt.2020.100135>

Address for correspondence: Ria R. Ghai, Centers for Disease Control and Prevention, 1600 Clifton Rd NE, Mailstop H116-5, Atlanta, GA 30329-4027, USA; email: ofu9@cdc.gov

## The Public Health Image Library (PHIL)



The Public Health Image Library (PHIL), Centers for Disease Control and Prevention, contains thousands of public health-related images, including high-resolution (print quality) photographs, illustrations, and videos.

PHIL collections illustrate current events and articles, supply visual content for health promotion brochures, document the effects of disease, and enhance instructional media.

PHIL images, accessible to PC and Macintosh users, are in the public domain and available without charge.

Visit PHIL at:  
<http://phil.cdc.gov/phil>



# Animal Reservoirs and Hosts for Emerging Alphacoronaviruses and Betacoronaviruses

## Appendix

**Appendix Table.** Citations for in-text tables, by coronavirus and host category

Pathogen (abbreviation)	Category	Table	Reference
Alphacoronavirus 1 (ACoV1); strain canine enteric coronavirus (CCoV)	Receptor	1	(1)
	Reservoir host(s)	2	(2)
	Spillover host(s)	2	(3–6)
	Clinical manifestation	3	(3–9)
Alphacoronavirus 1 (ACoV1); strain feline infectious peritonitis virus (FIPV)	Receptor	1	(10)
	Reservoir host(s)	2	(11,12)
	Spillover host(s)	2	(13–15)
	Susceptible host	2	(16)
	Clinical manifestation	3	(7,9,17,18)
Bat coronavirus HKU10	Receptor	1	(19)
	Reservoir host(s)	2	(20)
	Spillover host(s)	2	(21)
	Clinical manifestation	3	(9,21)
Ferret systemic coronavirus (FRSCV)	Receptor	1	(22)
	Reservoir host(s)	2	(23)
	Spillover host(s)	2	(24,25)
	Clinical manifestation	3	(9,26)
Human coronavirus NL63	Receptor	1	(27)
	Reservoir host(s)	2	(28)
	Spillover host(s)	2	(29,30)
	Nonsusceptible host(s)	2	(31)
	Clinical manifestation	3	(9,32–34)
Human coronavirus 229E	Receptor	1	(35)
	Reservoir host(s)	2	(28,36,37)
	Intermediate host(s)	2	(38)
	Spillover host(s)	2	(39,40)
	Susceptible host(s)	2	(41)
	Clinical manifestation	3	(9,32,34,38,41–43)
Porcine epidemic diarrhea virus (PEDV)	Receptor	1	(44,45)
	Reservoir host(s)	2	(32,46)
	Spillover host(s)	2	(47)
	Clinical manifestation	3	(7,9,32,48)
Rhinolophus bat coronavirus HKU2; strain swine acute diarrhea syndrome coronavirus (SADS-CoV)	Receptor	1	(49)
	Reservoir host(s)	2	(49)
	Spillover host(s)	2	(49)
	Susceptible host(s)	2	(50)
	Clinical manifestation	3	(9,32)
Betacoronavirus 1 (BCoV1); strain bovine coronavirus	Receptor	1	(51)
	Reservoir host(s)	2	(52)
	Spillover host(s)	2	(53)
	Susceptible host(s)	2	(54)
	Nonsusceptible host(s)	2	(54)
	Clinical manifestation	3	(7,9,52,54)
Betacoronavirus 1 (BCoV1); strain canine respiratory coronavirus	Receptor	1	(51)
	Reservoir host(s)	2	(52)
	Intermediate host(s)	2	(55)
	Spillover host(s)	2	(56)
	Clinical manifestation	3	(7,9,52,56,57)
	Betacoronavirus1 (BCoV1); strain human coronavirus OC43	Receptor	1
Reservoir host(s)		2	(52)
Intermediate host(s)		2	(59)
Spillover host(s)		2	(60,61)
Susceptible host(s)		2	(62)
Clinical manifestation		3	(9,34,52,57,61–63)
Human coronavirus HKU1		Receptor	1
	Reservoir host(s)	2	(65,66)
	Spillover host(s)	2	(67)

Pathogen (abbreviation)	Category	Table	Reference
	Clinical manifestation	3	(9,34,66,68)
Middle East respiratory syndrome coronavirus (MERS-CoV)	Receptor	1	(69)
	Reservoir host(s)	2	(65,70)
	Intermediate host(s)	2	(71)
	Spillover host(s)	2	(72)
	Susceptible host(s)	2	(73–79)
	Nonsusceptible host(s)	2	(76,80–82)
	Clinical manifestation	3	(9,32,73,74,76,79,83,84)
Severe acute respiratory syndrome coronavirus (SARS-CoV)	Receptor	1	(85)
	Reservoir host(s)	2	(19,86–88)
	Intermediate host(s)	2	(89,90)
	Spillover host(s)	2	(87,90–95)
	Susceptible host(s)	2	(87,91,96–101)
	Nonsusceptible host(s)	2	(97)
	Clinical manifestation	3	(9,17,32,84,87,91,92,96–101)
Severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2)	Receptor	1	(102)
	Reservoir host(s)	2	(103)
	Spillover host(s)	2	(104–109)
	Susceptible host(s)	2	(110–125)
	Nonsusceptible host(s)	2	(111,113,126–129)
	Clinical manifestation	3	(103–106,108,110,111,113–119,121,122,124,130)

## References

1. Licitra BN, Duhamel GE, Whittaker GR. Canine enteric coronaviruses: emerging viral pathogens with distinct recombinant spike proteins. *Viruses*. 2014;6:3363–76. [PubMed https://doi.org/10.3390/v6083363](https://doi.org/10.3390/v6083363)
2. Binn LN, Lazar EC, Keenan KP, Huxsoll DL, Marchwicki RH, Strano AJ. Recovery and characterization of a coronavirus from military dogs with diarrhea. *Proc Annu Meet US Anim Health Assoc*. 1974;78:359–66. [PubMed](#)
3. Wang Y, Ma G, Lu C, Wen H. Detection of canine coronaviruses genotype I and II in raised Canidae animals in China. *Berl Munch Tierarztl Wochenschr*. 2006;119:35–9. [PubMed](#)
4. Rosa GM, Santos N, Grøndahl-Rosado R, Fonseca FP, Tavares L, Neto I, et al. Unveiling patterns of viral pathogen infection in free-ranging carnivores of northern Portugal using a complementary methodological approach. *Comp Immunol Microbiol Infect Dis*. 2020;69:101432. [PubMed https://doi.org/10.1016/j.cimid.2020.101432](https://doi.org/10.1016/j.cimid.2020.101432)
5. Zarnke RL, Evermann J, Ver Hoef JM, McNay ME, Boertje RD, Gardner CL, et al. Serologic survey for canine coronavirus in wolves from Alaska. *J Wildl Dis*. 2001;37:740–5. [PubMed https://doi.org/10.7589/0090-3558-37.4.740](https://doi.org/10.7589/0090-3558-37.4.740)
6. McArdle F, Bennett M, Gaskell RM, Tennant B, Kelly DF, Gaskell CJ. Induction and enhancement of feline infectious peritonitis by canine coronavirus. *Am J Vet Res*. 1992;53:1500–6. [PubMed](#)
7. American Veterinary Medical Association. *Coronavirus in domestic species*. Schaumburg (IL): The Association; 2020.

8. Pratelli A. Genetic evolution of canine coronavirus and recent advances in prophylaxis. *Vet Res.* 2006;37:191–200. [PubMed https://doi.org/10.1051/vetres:2005053](https://doi.org/10.1051/vetres:2005053)
9. US Department of Agriculture. *Veterinary biological products.* Ames (IA): The Department; 2020.
10. Hohdatsu T, Izumiya Y, Yokoyama Y, Kida K, Koyama H. Differences in virus receptor for type I and type II feline infectious peritonitis virus. *Arch Virol.* 1998;143:839–50. [PubMed https://doi.org/10.1007/s007050050336](https://doi.org/10.1007/s007050050336)
11. Poland AM, Vennema H, Foley JE, Pedersen NC. Two related strains of feline infectious peritonitis virus isolated from immunocompromised cats infected with a feline enteric coronavirus. *J Clin Microbiol.* 1996;34:3180–4. [PubMed https://doi.org/10.1128/JCM.34.12.3180-3184.1996](https://doi.org/10.1128/JCM.34.12.3180-3184.1996)
12. Vennema H, Poland A, Foley J, Pedersen NC. Feline infectious peritonitis viruses arise by mutation from endemic feline enteric coronaviruses. *Virology.* 1998;243:150–7. [PubMed https://doi.org/10.1006/viro.1998.9045](https://doi.org/10.1006/viro.1998.9045)
13. Evermann JF, Heeney JL, Roelke ME, McKeirnan AJ, O'Brien SJ. Biological and pathological consequences of feline infectious peritonitis virus infection in the cheetah. *Arch Virol.* 1988;102:155–71. [PubMed https://doi.org/10.1007/BF01310822](https://doi.org/10.1007/BF01310822)
14. Mwase M, Shimada K, Mumba C, Yabe J, Squarre D, Madarame H. Positive immunolabelling for feline infectious peritonitis in an African lion (*Panthera leo*) with bilateral panuveitis. *J Comp Pathol.* 2015;152:265–8. [PubMed https://doi.org/10.1016/j.jcpa.2014.12.006](https://doi.org/10.1016/j.jcpa.2014.12.006)
15. Foley JE, Swift P, Fleer KA, Torres S, Girard YA, Johnson CK. Risk factors for exposure to feline pathogens in California mountain lions (*Puma concolor*). *J Wildl Dis.* 2013;49:279–93. [PubMed https://doi.org/10.7589/2012-08-206](https://doi.org/10.7589/2012-08-206)
16. Horzinek MC, Osterhaus AD, Wirahadiredja RM, de Kreek P. Feline infectious peritonitis (FIP) virus. III. Studies on the multiplication of FIP virus in the suckling mouse. *Zentralbl Veterinärmed B.* 1978;25:806–15. [PubMed https://doi.org/10.1111/j.1439-0450.1978.tb01056.x](https://doi.org/10.1111/j.1439-0450.1978.tb01056.x)
17. Levy JK. Overview of feline infectious peritonitis. *Merck Veterinary Manual*; 2014 [cited 2021 Jan 22]. <https://www.merckvetmanual.com/generalized-conditions/feline-infectious-peritonitis/overview-of-feline-infectious-peritonitis>
18. Pedersen NC. An update on feline infectious peritonitis: diagnostics and therapeutics. *Vet J.* 2014;201:133–41. [PubMed https://doi.org/10.1016/j.tvjl.2014.04.016](https://doi.org/10.1016/j.tvjl.2014.04.016)
19. Lau SK, Woo PC, Li KS, Huang Y, Tsoi H-W, Wong BH, et al. Severe acute respiratory syndrome coronavirus-like virus in Chinese horseshoe bats. *Proc Natl Acad Sci U S A.* 2005;102:14040–5. [PubMed https://doi.org/10.1073/pnas.0506735102](https://doi.org/10.1073/pnas.0506735102)

20. Woo PC, Wang M, Lau SK, Xu H, Poon RW, Guo R, et al. Comparative analysis of twelve genomes of three novel group 2c and group 2d coronaviruses reveals unique group and subgroup features. *J Virol*. 2007;81:1574–85. [PubMed https://doi.org/10.1128/JVI.02182-06](https://doi.org/10.1128/JVI.02182-06)
21. Lau SK, Li KS, Tsang AK, Shek C-T, Wang M, Choi GK, et al. Recent transmission of a novel alphacoronavirus, bat coronavirus HKU10, from Leschenault's rousettes to pomona leaf-nosed bats: first evidence of interspecies transmission of coronavirus between bats of different suborders. *J Virol*. 2012;86:11906–18. [PubMed https://doi.org/10.1128/JVI.01305-12](https://doi.org/10.1128/JVI.01305-12)
22. Murray J, Kiupel M, Maes RK. Ferret coronavirus-associated diseases. *Vet Clin North Am Exot Anim Pract*. 2010;13:543–60. [PubMed https://doi.org/10.1016/j.cvex.2010.05.010](https://doi.org/10.1016/j.cvex.2010.05.010)
23. Wise AG, Kiupel M, Maes RK. Molecular characterization of a novel coronavirus associated with epizootic catarrhal enteritis (ECE) in ferrets. *Virology*. 2006;349:164–74. [PubMed https://doi.org/10.1016/j.virol.2006.01.031](https://doi.org/10.1016/j.virol.2006.01.031)
24. Garner MM, Ramsell K, Morera N, Juan-Sallés C, Jiménez J, Ardiaca M, et al. Clinicopathologic features of a systemic coronavirus-associated disease resembling feline infectious peritonitis in the domestic ferret (*Mustela putorius*). *Vet Pathol*. 2008;45:236–46. [PubMed https://doi.org/10.1354/vp.45-2-236](https://doi.org/10.1354/vp.45-2-236)
25. Xu Y. Genetic diversity and potential recombination between ferret coronaviruses from European and American lineages. *J Infect*. 2020;80:350–71. [PubMed https://doi.org/10.1016/j.jinf.2020.01.016](https://doi.org/10.1016/j.jinf.2020.01.016)
26. Morrisey JK. Infectious diseases of Ferrets. *Merck Veterinary Manual*; 2013 [cited 2021 Jan 22]. <https://www.merckvetmanual.com/exotic-and-laboratory-animals/ferrets/infectious-diseases-of-ferrets>
27. Hofmann H, Pyrc K, van der Hoek L, Geier M, Berkhout B, Pöhlmann S. Human coronavirus NL63 employs the severe acute respiratory syndrome coronavirus receptor for cellular entry. *Proc Natl Acad Sci U S A*. 2005;102:7988–93. [PubMed https://doi.org/10.1073/pnas.0409465102](https://doi.org/10.1073/pnas.0409465102)
28. Tao Y, Shi M, Chommanard C, Queen K, Zhang J, Markotter W, et al. Surveillance of bat coronaviruses in Kenya identifies relatives of human coronaviruses NL63 and 229E and their recombination history. *J Virol*. 2017;91:e01953–16. [PubMed https://doi.org/10.1128/JVI.01953-16](https://doi.org/10.1128/JVI.01953-16)
29. van der Hoek L, Pyrc K, Jebbink MF, Vermeulen-Oost W, Berkhout RJ, Wolthers KC, et al. Identification of a new human coronavirus. *Nat Med*. 2004;10:368–73. [PubMed https://doi.org/10.1038/nm1024](https://doi.org/10.1038/nm1024)
30. Fouchier RA, Hartwig NG, Bestebroer TM, Niemeyer B, de Jong JC, Simon JH, et al. A previously undescribed coronavirus associated with respiratory disease in humans. *Proc Natl Acad Sci U S A*. 2004;101:6212–6. [PubMed https://doi.org/10.1073/pnas.0400762101](https://doi.org/10.1073/pnas.0400762101)

31. El-Duah P, Meyer B, Sylverken A, Owusu M, Gottula LT, Yeboah R, et al. Development of a whole-virus ELISA for serological evaluation of domestic livestock as possible hosts of human coronavirus NL63. *Viruses*. 2019;11:43. [PubMed https://doi.org/10.3390/v11010043](https://doi.org/10.3390/v11010043)
32. Banerjee A, Kulcsar K, Misra V, Frieman M, Mossman K. Bats and coronaviruses. *Viruses*. 2019;11:41. [PubMed https://doi.org/10.3390/v11010041](https://doi.org/10.3390/v11010041)
33. Abdul-Rasool S, Fielding BC. Understanding human coronavirus HCoV-NL63. *Open Virol J*. 2010;4:76–84. [PubMed https://doi.org/10.2174/1874357901004010076](https://doi.org/10.2174/1874357901004010076)
34. Center for Disease Control and Prevention. Common human coronaviruses. Coronavirus 2020 [cited 2020 Jul 13]. <https://www.cdc.gov/coronavirus/general-information.html>
35. Yeager CL, Ashmun RA, Williams RK, Cardellicchio CB, Shapiro LH, Look AT, et al. Human aminopeptidase N is a receptor for human coronavirus 229E. *Nature*. 1992;357:420–2. [PubMed https://doi.org/10.1038/357420a0](https://doi.org/10.1038/357420a0)
36. Pfefferle S, Oppong S, Drexler JF, Gloza-Rausch F, Ipsen A, Seebens A, et al. Distant relatives of severe acute respiratory syndrome coronavirus and close relatives of human coronavirus 229E in bats, Ghana. *Emerg Infect Dis*. 2009;15:1377–84. [PubMed https://doi.org/10.3201/eid1509.090224](https://doi.org/10.3201/eid1509.090224)
37. Corman VM, Baldwin HJ, Tateno AF, Zerbinati RM, Annan A, Owusu M, et al. Evidence for an ancestral association of human coronavirus 229E with bats. *J Virol*. 2015;89:11858–70. [PubMed https://doi.org/10.1128/JVI.01755-15](https://doi.org/10.1128/JVI.01755-15)
38. Corman VM, Eckerle I, Memish ZA, Liljander AM, Dijkman R, Jonsdottir H, et al. Link of a ubiquitous human coronavirus to dromedary camels. *Proc Natl Acad Sci U S A*. 2016;113:9864–9. [PubMed https://doi.org/10.1073/pnas.1604472113](https://doi.org/10.1073/pnas.1604472113)
39. Crossley BM, Mock RE, Callison SA, Hietala SK. Identification and characterization of a novel alpaca respiratory coronavirus most closely related to the human coronavirus 229E. *Viruses*. 2012;4:3689–700. [PubMed https://doi.org/10.3390/v4123689](https://doi.org/10.3390/v4123689)
40. Hamre D, Procknow JJ. A new virus isolated from the human respiratory tract. *Proc Soc Exp Biol Med*. 1966;121:190–3. [PubMed https://doi.org/10.3181/00379727-121-30734](https://doi.org/10.3181/00379727-121-30734)
41. Barlough JE, Johnson-Lussenburg CM, Stoddart CA, Jacobson RH, Scott FW. Experimental inoculation of cats with human coronavirus 229E and subsequent challenge with feline infectious peritonitis virus. *Can J Comp Med*. 1985;49:303–7. [PubMed https://doi.org/10.3181/00379727-121-30734](https://doi.org/10.3181/00379727-121-30734)
42. Crossley BM, Barr BC, Magdesian KG, Ing M, Mora D, Jensen D, et al. Identification of a novel coronavirus possibly associated with acute respiratory syndrome in alpacas (*Vicugna pacos*) in California, 2007. *J Vet Diagn Invest*. 2010;22:94–7. [PubMed https://doi.org/10.1177/104063871002200118](https://doi.org/10.1177/104063871002200118)

43. McIntosh K. Coronaviruses [cited 2020 Feb 18]. <https://www.uptodate.com/contents/coronaviruses>
44. Liu C, Tang J, Ma Y, Liang X, Yang Y, Peng G, et al. Receptor usage and cell entry of porcine epidemic diarrhea coronavirus. *J Virol*. 2015;89:6121–5. [PubMed https://doi.org/10.1128/JVI.00430-15](https://doi.org/10.1128/JVI.00430-15)
45. Shirato K, Maejima M, Islam MT, Miyazaki A, Kawase M, Matsuyama S, et al. Porcine aminopeptidase N is not a cellular receptor of porcine epidemic diarrhea virus, but promotes its infectivity via aminopeptidase activity. *J Gen Virol*. 2016;97:2528–39. [PubMed https://doi.org/10.1099/jgv.0.000563](https://doi.org/10.1099/jgv.0.000563)
46. Tang XC, Zhang JX, Zhang SY, Wang P, Fan XH, Li LF, et al. Prevalence and genetic diversity of coronaviruses in bats from China. *J Virol*. 2006;80:7481–90. [PubMed https://doi.org/10.1128/JVI.00697-06](https://doi.org/10.1128/JVI.00697-06)
47. Lee C. Porcine epidemic diarrhea virus: An emerging and re-emerging epizootic swine virus. *Virol J*. 2015;12:193. [PubMed https://doi.org/10.1186/s12985-015-0421-2](https://doi.org/10.1186/s12985-015-0421-2)
48. Song D, Moon H, Kang B. Porcine epidemic diarrhea: a review of current epidemiology and available vaccines. *Clin Exp Vaccine Res*. 2015;4:166–76. [PubMed https://doi.org/10.7774/cevr.2015.4.2.166](https://doi.org/10.7774/cevr.2015.4.2.166)
49. Zhou P, Fan H, Lan T, Yang X-L, Shi W-F, Zhang W, et al. Fatal swine acute diarrhoea syndrome caused by an HKU2-related coronavirus of bat origin. *Nature*. 2018;556:255–8. [PubMed https://doi.org/10.1038/s41586-018-0010-9](https://doi.org/10.1038/s41586-018-0010-9)
50. Yang Y-L, Qin P, Wang B, Liu Y, Xu G-H, Peng L, et al. Broad cross-species infection of cultured cells by bat HKU2-related swine acute diarrhea syndrome coronavirus and identification of its replication in murine dendritic cells in vivo highlight its potential for diverse interspecies transmission. *J Virol*. 2019;93:e01448–19. [PubMed https://doi.org/10.1128/JVI.01448-19](https://doi.org/10.1128/JVI.01448-19)
51. Szczepanski A, Owczarek K, Bzowska M, Gula K, Drebot I, Ochman M, et al. Canine respiratory coronavirus, bovine coronavirus, and human coronavirus OC43: receptors and attachment factors. *Viruses*. 2019;11:328. [PubMed https://doi.org/10.3390/v11040328](https://doi.org/10.3390/v11040328)
52. Lau SK, Woo PC, Li KS, Tsang AK, Fan RY, Luk HK, et al. Discovery of a novel coronavirus, China *Rattus* coronavirus HKU24, from Norway rats supports the murine origin of betacoronavirus 1 and has implications for the ancestor of betacoronavirus lineage A. *J Virol*. 2015;89:3076–92. [PubMed https://doi.org/10.1128/JVI.02420-14](https://doi.org/10.1128/JVI.02420-14)
53. Storz J, Stine L, Liem A, Anderson GA. Coronavirus isolation from nasal swab samples in cattle with signs of respiratory tract disease after shipping. *J Am Vet Med Assoc*. 1996;208:1452–5. [PubMed https://doi.org/10.2460/javma.1996.208.1452](https://doi.org/10.2460/javma.1996.208.1452)
54. Ismail MM, Cho KO, Ward LA, Saif LJ, Saif YM. Experimental bovine coronavirus in turkey poults and young chickens. *Avian Dis*. 2001;45:157–63. [PubMed https://doi.org/10.2307/1593023](https://doi.org/10.2307/1593023)

55. Erles K, Shiu K-B, Brownlie J. Isolation and sequence analysis of canine respiratory coronavirus. *Virus Res.* 2007;124:78–87. [PubMed https://doi.org/10.1016/j.virusres.2006.10.004](https://doi.org/10.1016/j.virusres.2006.10.004)
56. Erles K, Toomey C, Brooks HW, Brownlie J. Detection of a group 2 coronavirus in dogs with canine infectious respiratory disease. *Virology.* 2003;310:216–23. [PubMed https://doi.org/10.1016/S0042-6822\(03\)00160-0](https://doi.org/10.1016/S0042-6822(03)00160-0)
57. Erles K, Brownlie J. Canine respiratory coronavirus: an emerging pathogen in the canine infectious respiratory disease complex. *Vet Clin North Am Small Anim Pract.* 2008;38:815–25, viii. [PubMed https://doi.org/10.1016/j.cvsm.2008.02.008](https://doi.org/10.1016/j.cvsm.2008.02.008)
58. Collins AR. HLA class I antigen serves as a receptor for human coronavirus OC43. *Immunol Invest.* 1993;22:95–103. [PubMed https://doi.org/10.3109/08820139309063393](https://doi.org/10.3109/08820139309063393)
59. Vijgen L, Keyaerts E, Moës E, Thoelen I, Wollants E, Lemey P, et al. Complete genomic sequence of human coronavirus OC43: molecular clock analysis suggests a relatively recent zoonotic coronavirus transmission event. *J Virol.* 2005;79:1595–604. [PubMed https://doi.org/10.1128/JVI.79.3.1595-1604.2005](https://doi.org/10.1128/JVI.79.3.1595-1604.2005)
60. Patrono LV, Samuni L, Corman VM, Nourifar L, Röthemeier C, Wittig RM, et al. Human coronavirus OC43 outbreak in wild chimpanzees, Côte d’Ivoire, 2016. *Emerg Microbes Infect.* 2018;7:118. [PubMed https://doi.org/10.1038/s41426-018-0121-2](https://doi.org/10.1038/s41426-018-0121-2)
61. McIntosh K, Dees JH, Becker WB, Kapikian AZ, Chanock RM. Recovery in tracheal organ cultures of novel viruses from patients with respiratory disease. *Proc Natl Acad Sci U S A.* 1967;57:933–40. [PubMed https://doi.org/10.1073/pnas.57.4.933](https://doi.org/10.1073/pnas.57.4.933)
62. Jacomy H, Talbot PJ. Vacuolating encephalitis in mice infected by human coronavirus OC43. *Virology.* 2003;315:20–33. [PubMed https://doi.org/10.1016/S0042-6822\(03\)00323-4](https://doi.org/10.1016/S0042-6822(03)00323-4)
63. Patrono LV, Samuni L, Corman VM, Nourifar L, Röthemeier C, Wittig RM, et al. Human coronavirus OC43 outbreak in wild chimpanzees, Côte d’Ivoire, 2016. *Emerg Microbes Infect.* 2018;7:118. [PubMed https://doi.org/10.1038/s41426-018-0121-2](https://doi.org/10.1038/s41426-018-0121-2)
64. Chan CM, Lau SK, Woo PC, Tse H, Zheng B-J, Chen L, et al. Identification of major histocompatibility complex class I C molecule as an attachment factor that facilitates coronavirus HKU1 spike-mediated infection. *J Virol.* 2009;83:1026–35. [PubMed https://doi.org/10.1128/JVI.01387-08](https://doi.org/10.1128/JVI.01387-08)
65. Wang W, Lin X-D, Guo W-P, Zhou R-H, Wang M-R, Wang C-Q, et al. Discovery, diversity and evolution of novel coronaviruses sampled from rodents in China. *Virology.* 2015;474:19–27. [PubMed https://doi.org/10.1016/j.virol.2014.10.017](https://doi.org/10.1016/j.virol.2014.10.017)

66. Corman VM, Muth D, Niemeyer D, Drosten C. Hosts and sources of endemic human coronaviruses. In: Kielian M, Mettenleiter TC, Roossinck MJ, editors. *Advances in Virus Research*. New York: Academic Press; 2018. p. 163–88.
67. Woo PC, Lau SK, Chu CM, Chan KH, Tsoi HW, Huang Y, et al. Characterization and complete genome sequence of a novel coronavirus, coronavirus HKU1, from patients with pneumonia. *J Virol*. 2005;79:884–95. [PubMed https://doi.org/10.1128/JVI.79.2.884-895.2005](https://doi.org/10.1128/JVI.79.2.884-895.2005)
68. Esper F, Weibel C, Ferguson D, Landry ML, Kahn JS. Coronavirus HKU1 infection in the United States. *Emerg Infect Dis*. 2006;12:775–9. [PubMed https://doi.org/10.3201/eid1205.051316](https://doi.org/10.3201/eid1205.051316)
69. Meyerholz DK, Lambertz AM, McCray PB Jr. Dipeptidyl peptidase 4 distribution in the human respiratory tract: implications for the Middle East respiratory syndrome. *Am J Pathol*. 2016;186:78–86. [PubMed https://doi.org/10.1016/j.ajpath.2015.09.014](https://doi.org/10.1016/j.ajpath.2015.09.014)
70. Anthony SJ, Gilardi K, Menachery VD, Goldstein T, Ssevide B, Mbabazi R, et al. Further evidence for bats as the evolutionary source of Middle East respiratory syndrome coronavirus. *MBio*. 2017;8:e00373–17. [PubMed https://doi.org/10.1128/mBio.00373-17](https://doi.org/10.1128/mBio.00373-17)
71. Reusken CB, Raj VS, Koopmans MP, Haagmans BL. Cross host transmission in the emergence of MERS coronavirus. *Curr Opin Virol*. 2016;16:55–62. [PubMed https://doi.org/10.1016/j.coviro.2016.01.004](https://doi.org/10.1016/j.coviro.2016.01.004)
72. Zaki AM, van Boheemen S, Bestebroer TM, Osterhaus AD, Fouchier RA. Isolation of a novel coronavirus from a man with pneumonia in Saudi Arabia. *N Engl J Med*. 2012;367:1814–20. [PubMed https://doi.org/10.1056/NEJMoa1211721](https://doi.org/10.1056/NEJMoa1211721)
73. Adney DR, Bielefeldt-Ohmann H, Hartwig AE, Bowen RA. Infection, replication, and transmission of Middle East respiratory syndrome coronavirus in alpacas. *Emerg Infect Dis*. 2016;22:1031–7. [PubMed https://doi.org/10.3201/eid2206.160192](https://doi.org/10.3201/eid2206.160192)
74. Falzarano D, de Wit E, Feldmann F, Rasmussen AL, Okumura A, Peng X, et al. Infection with MERS-CoV causes lethal pneumonia in the common marmoset. *PLoS Pathog*. 2014;10:e1004250. [PubMed https://doi.org/10.1371/journal.ppat.1004250](https://doi.org/10.1371/journal.ppat.1004250)
75. Johnson RF, Via LE, Kumar MR, Cornish JP, Yellayi S, Huzella L, et al. Intratracheal exposure of common marmosets to MERS-CoV Jordan-n3/2012 or MERS-CoV EMC/2012 isolates does not result in lethal disease. *Virology*. 2015;485:422–30. [PubMed https://doi.org/10.1016/j.virol.2015.07.013](https://doi.org/10.1016/j.virol.2015.07.013)
76. Vergara-Alert J, van den Brand JMA, Widagdo W, Muñoz M V, Raj S, Schipper D, et al. Livestock susceptibility to infection with Middle East respiratory syndrome coronavirus. *Emerg Infect Dis*. 2017;23:232–40. [PubMed https://doi.org/10.3201/eid2302.161239](https://doi.org/10.3201/eid2302.161239)



77. de Wit E, Rasmussen AL, Falzarano D, Bushmaker T, Feldmann F, Brining DL, et al. Middle East respiratory syndrome coronavirus (MERS-CoV) causes transient lower respiratory tract infection in rhesus macaques. *Proc Natl Acad Sci U S A*. 2013;110:16598–603. [PubMed](#) <https://doi.org/10.1073/pnas.1310744110>
78. Yao Y, Bao L, Deng W, Xu L, Li F, Lv Q, et al. An animal model of MERS produced by infection of rhesus macaques with MERS coronavirus. *J Infect Dis*. 2014;209:236–42. [PubMed](#) <https://doi.org/10.1093/infdis/jit590>
79. Haagmans BL, van den Brand JM, Provacia LB, Raj VS, Stittelaar KJ, Getu S, et al. Asymptomatic Middle East respiratory syndrome coronavirus infection in rabbits. *J Virol*. 2015;89:6131–5. [PubMed](#) <https://doi.org/10.1128/JVI.00661-15>
80. Raj VS, Smits SL, Provacia LB, van den Brand JM, Wiersma L, Ouwendijk WJ, et al. Adenosine deaminase acts as a natural antagonist for dipeptidyl peptidase 4-mediated entry of the Middle East respiratory syndrome coronavirus. *J Virol*. 2014;88:1834–8. [PubMed](#) <https://doi.org/10.1128/JVI.02935-13>
81. de Wit E, Prescott J, Baseler L, Bushmaker T, Thomas T, Lackemeyer MG, et al. The Middle East respiratory syndrome coronavirus (MERS-CoV) does not replicate in Syrian hamsters. *PLoS One*. 2013;8:e69127. [PubMed](#) <https://doi.org/10.1371/journal.pone.0069127>
82. Cockrell AS, Peck KM, Yount BL, Agnihothram SS, Scobey T, Curnes NR, et al. Mouse dipeptidyl peptidase 4 is not a functional receptor for Middle East respiratory syndrome coronavirus infection. *J Virol*. 2014;88:5195–9. [PubMed](#) <https://doi.org/10.1128/JVI.03764-13>
83. Baseler L, de Wit E, Feldmann H. A comparative review of animal models of Middle East respiratory syndrome coronavirus infection. *Vet Pathol*. 2016;53:521–31. [PubMed](#) <https://doi.org/10.1177/0300985815620845>
84. Precision Vaccinations. Coronavirus vaccines. 2020 [cited 2021 Jan 22]. <https://www.precisionvaccinations.com/vaccines/coronavirus-vaccines>
85. Li W, Moore MJ, Vasilieva N, Sui J, Wong SK, Berne MA, et al. Angiotensin-converting enzyme 2 is a functional receptor for the SARS coronavirus. *Nature*. 2003;426:450–4. [PubMed](#) <https://doi.org/10.1038/nature02145>
86. Li W, Shi Z, Yu M, Ren W, Smith C, Epstein JH, et al. Bats are natural reservoirs of SARS-like coronaviruses. *Science*. 2005;310:676–9. [PubMed](#) <https://doi.org/10.1126/science.1118391>
87. Wang L-F, Shi Z, Zhang S, Field H, Daszak P, Eaton BT. Review of bats and SARS. *Emerg Infect Dis*. 2006;12:1834–40. [PubMed](#) <https://doi.org/10.3201/eid1212.060401>
88. Hu B, Ge X, Wang L-F, Shi Z. Bat origin of human coronaviruses. *Virol J*. 2015;12:221. [PubMed](#) <https://doi.org/10.1186/s12985-015-0422-1>

89. Wang M, Yan M, Xu H, Liang W, Kan B, Zheng B, et al. SARS-CoV infection in a restaurant from palm civet. *Emerg Infect Dis.* 2005;11:1860–5. [PubMed https://doi.org/10.3201/eid1112.041293](https://doi.org/10.3201/eid1112.041293)
90. Guan Y, Zheng BJ, He YQ, Liu XL, Zhuang ZX, Cheung CL, et al. Isolation and characterization of viruses related to the SARS coronavirus from animals in southern China. *Science.* 2003;302:276–8. [PubMed https://doi.org/10.1126/science.1087139](https://doi.org/10.1126/science.1087139)
91. Martina BE, Haagmans BL, Kuiken T, Fouchier RA, Rimmelzwaan GF, Van Amerongen G, et al. Virology: SARS virus infection of cats and ferrets. *Nature.* 2003;425:915. [PubMed https://doi.org/10.1038/425915a](https://doi.org/10.1038/425915a)
92. World Health Organization. Consensus document on the epidemiology of severe acute respiratory syndrome (SARS). Geneva: The Organization; 2003.
93. Chen W, Yan M, Yang L, Ding B, He B, Wang Y, et al. SARS-associated coronavirus transmitted from human to pig. *Emerg Infect Dis.* 2005;11:446–8. [PubMed https://doi.org/10.3201/eid1103.040824](https://doi.org/10.3201/eid1103.040824)
94. Xu R-H, He J-F, Evans MR, Peng G-W, Field HE, Yu D-W, et al. Epidemiologic clues to SARS origin in China. *Emerg Infect Dis.* 2004;10:1030–7. [PubMed https://doi.org/10.3201/eid1006.030852](https://doi.org/10.3201/eid1006.030852)
95. Lee SH. The SARS epidemic in Hong Kong. *J Epidemiol Community Health.* 2003;57:652–4. [PubMed https://doi.org/10.1136/jech.57.9.652](https://doi.org/10.1136/jech.57.9.652)
96. Fouchier RA, Kuiken T, Schutten M, van Amerongen G, van Doornum GJ, van den Hoogen BG, et al. Aetiology: Koch’s postulates fulfilled for SARS virus. *Nature.* 2003;423:240. [PubMed https://doi.org/10.1038/423240a](https://doi.org/10.1038/423240a)
97. Weingartl HM, Copps J, Drebot MA, Marszal P, Smith G, Gren J, et al. Susceptibility of pigs and chickens to SARS coronavirus. *Emerg Infect Dis.* 2004;10:179–84. [PubMed https://doi.org/10.3201/eid1002.030677](https://doi.org/10.3201/eid1002.030677)
98. Roberts A, Vogel L, Guarner J, Hayes N, Murphy B, Zaki S, et al. Severe acute respiratory syndrome coronavirus infection of golden Syrian hamsters. *J Virol.* 2005;79:503–11. [PubMed https://doi.org/10.1128/JVI.79.1.503-511.2005](https://doi.org/10.1128/JVI.79.1.503-511.2005)
99. Wu D, Tu C, Xin C, Xuan H, Meng Q, Liu Y, et al. Civets are equally susceptible to experimental infection by two different severe acute respiratory syndrome coronavirus isolates. *J Virol.* 2005;79:2620–5. [PubMed https://doi.org/10.1128/JVI.79.4.2620-2625.2005](https://doi.org/10.1128/JVI.79.4.2620-2625.2005)
100. Roberts A, Paddock C, Vogel L, Butler E, Zaki S, Subbarao K. Aged BALB/c mice as a model for increased severity of severe acute respiratory syndrome in elderly humans. *J Virol.* 2005;79:5833–8. [PubMed https://doi.org/10.1128/JVI.79.9.5833-5838.2005](https://doi.org/10.1128/JVI.79.9.5833-5838.2005)
101. Qin C, Wang J, Wei Q, She M, Marasco WA, Jiang H, et al. An animal model of SARS produced by infection of *Macaca mulatta* with SARS coronavirus. *J Pathol.* 2005;206:251–9. [PubMed https://doi.org/10.1002/path.1769](https://doi.org/10.1002/path.1769)

102. Zhang H, Penninger JM, Li Y, Zhong N, Slutsky AS. Angiotensin-converting enzyme 2 (ACE2) as a SARS-CoV-2 receptor: molecular mechanisms and potential therapeutic target. *Intensive Care Med.* 2020;46:586–90. [PubMed https://doi.org/10.1007/s00134-020-05985-9](https://doi.org/10.1007/s00134-020-05985-9)
103. Zhou P, Yang X-L, Wang X-G, Hu B, Zhang L, Zhang W, et al. A pneumonia outbreak associated with a new coronavirus of probable bat origin. *Nature.* 2020;579:270–3. [PubMed https://doi.org/10.1038/s41586-020-2012-7](https://doi.org/10.1038/s41586-020-2012-7)
104. Newman A, Smith D, Ghai RR, Wallace RM, Torchetti MK, Loiacono C, et al. First reported cases of SARS-CoV-2 infection in companion animals—New York, March–April 2020. *MMWR Morb Mortal Wkly Rep.* 2020;69:710–3. [PubMed https://doi.org/10.15585/mmwr.mm6923e3](https://doi.org/10.15585/mmwr.mm6923e3)
105. World Organisation for Animal Health. COVID 19 portal events in Animals; 2020 [cited 2020 Jul 13]. : <https://www.oie.int/en/scientific-expertise/specific-information-and-recommendations/questions-and-answers-on-2019novel-coronavirus/events-in-animals>
106. Sit TH, Brackman CJ, Ip SM, Tam KW, Law PY, To E, et al. Infection of dogs with SARS-CoV-2. *Nature.* 2020;586:776–8. [PubMed https://doi.org/10.1038/s41586-020-2334-5](https://doi.org/10.1038/s41586-020-2334-5)
107. Zhu N, Zhang D, Wang W, Li X, Yang B, Song J, et al.; China Novel Coronavirus Investigating and Research Team. A novel coronavirus from patients with pneumonia in China, 2019. *N Engl J Med.* 2020;382:727–33. [PubMed https://doi.org/10.1056/NEJMoa2001017](https://doi.org/10.1056/NEJMoa2001017)
108. Oreshkova N, Molenaar R-J, Vreman S, Harders F, Oude Munnink BB, Hakze-van der Honing RW, et al. SARS-CoV-2 infection in farmed minks, the Netherlands, April and May 2020. *Euro Surveill.* 2020;25:2001005. [PubMed https://doi.org/10.2807/1560-7917.ES.2020.25.23.2001005](https://doi.org/10.2807/1560-7917.ES.2020.25.23.2001005)
109. Molenaar RJ, Vreman S, Hakze-van der Honing RW, Zwart R, de Rond J, Weesendorp E, et al. Clinical and pathological findings in SARS-CoV-2 disease outbreaks in farmed mink. *Vet Pathol.* 2020;57:653–7. [PubMed https://doi.org/10.1177/0300985820943535](https://doi.org/10.1177/0300985820943535)
110. Rockx B, Kuiken T, Herfst S, Bestebroer T, Lamers MM, Oude Munnink BB, et al. Comparative pathogenesis of COVID-19, MERS, and SARS in a nonhuman primate model. *Science.* 2020;368:1012–5. [PubMed https://doi.org/10.1126/science.abb7314](https://doi.org/10.1126/science.abb7314)
111. Shi J, Wen Z, Zhong G, Yang H, Wang C, Huang B, et al. Susceptibility of ferrets, cats, dogs, and other domesticated animals to SARS-coronavirus 2. *Science.* 2020;368:1016–20. [PubMed https://doi.org/10.1126/science.abb7015](https://doi.org/10.1126/science.abb7015)
112. Halfmann PJ, Hatta M, Chiba S, Maemura T, Fan S, Takeda M, et al. Transmission of SARS-CoV-2 in domestic cats. *N Engl J Med.* 2020;383:592–4. [PubMed https://doi.org/10.1056/NEJMc2013400](https://doi.org/10.1056/NEJMc2013400)

113. Schlottau K, Rissmann M, Graaf A, Schön J, Sehl J, Wylezich C, et al. Experimental transmission studies of SARS-CoV-2 in fruit bats, ferrets, pigs and chickens. *Lancet Microbe*. 2020;1:e218–25. [PubMed](#)  
[https://doi.org/10.1016/S2666-5247\(20\)30089-6](https://doi.org/10.1016/S2666-5247(20)30089-6)
114. Kim Y-I, Kim S-G, Kim S-M, Kim E-H, Park S-J, Yu K-M, et al. Infection and rapid transmission of SARS-CoV-2 in ferrets. *Cell Host Microbe*. 2020;27:704–709.e2. [PubMed](#)  
<https://doi.org/10.1016/j.chom.2020.03.023>
115. Cross RW, Agans KN, Prasad AN, Borisevich V, Woolsey C, Deer DJ, et al. Intranasal exposure of African green monkeys to SARS-CoV-2 results in acute phase pneumonia with shedding and lung injury still present in the early convalescence phase. *Virology*. 2020;17:125. [PubMed](#) <https://doi.org/10.1186/s12985-020-01396-w>
116. Lu S, Zhao Y, Yu W, Yang Y, Gao J, Wang J, et al. Comparison of nonhuman primates identified the suitable model for COVID-19. *Signal Transduct Target Ther*. 2020;5:157. [PubMed](#)  
<https://doi.org/10.1038/s41392-020-00269-6>
117. Xu L, Yu DD, Ma YH, Yao YL, Luo RH, Feng XL, et al. COVID-19-like symptoms observed in Chinese tree shrews infected with SARS-CoV-2. *Zool Res*. 2020;41:517–26. [PubMed](#)  
<https://doi.org/10.24272/j.issn.2095-8137.2020.053>
118. Shuai L, Zhong G, Yuan Q, Wen Z, Wang C, He X, et al. Replication, pathogenicity, and transmission of SARS-CoV-2 in minks. *National Science Review*. 2020;nwaa291. <https://doi.org/10.1093/nsr/nwaa291>
119. Mykytyn AZ, Lamers MM, Okba NM, Breugem TI, Schipper D, van den Doel PB, et al. Susceptibility of rabbits to SARS-CoV-2. *Emerg Microbes Infect*. 2021;10:1–7. [PubMed](#)  
<https://doi.org/10.1080/22221751.2020.1868951>
120. Bosco-Lauth AM, Hartwig AE, Porter SM, Gordy PW, Nehring M, Byas AD, et al. Experimental infection of domestic dogs and cats with SARS-CoV-2: pathogenesis, transmission, and response to reexposure in cats. *Proc Natl Acad Sci U S A*. 2020;117:26382–8. [PubMed](#) <https://doi.org/10.1073/pnas.2013102117>
121. Bertzbach LD, Vladimirova D, Dietert K, Abdelgawad A, Gruber AD, Osterrieder N, et al. SARS-CoV-2 infection of Chinese hamsters (*Cricetulus griseus*) reproduces COVID-19 pneumonia in a well-established small animal model. *Transbound Emerg Dis*. 2020;Sep 18:2020. [PubMed](#)  
<https://doi.org/10.1111/tbed.13837>
122. Chan JF-W, Zhang AJ, Yuan S, Poon VK-M, Chan CC-S, Lee AC-Y, et al. Simulation of the clinical and pathological manifestations of coronavirus disease 2019 (COVID-19) in golden Syrian hamster model: implications for disease pathogenesis and transmissibility. *Clin Infect Dis*. 2020;71:2428–46. [PubMed](#)  
<https://doi.org/10.1093/cid/ciaa644>

123. Sia SF, Yan L-M, Chin AW, Fung K, Choy K-T, Wong AY, et al. Pathogenesis and transmission of SARS-CoV-2 in golden hamsters. *Nature*. 2020;583:834–8. [PubMed https://doi.org/10.1038/s41586-020-2342-5](https://doi.org/10.1038/s41586-020-2342-5)
124. Freuling CM, Breithaupt A, Müller T, Sehl J, Balkema-Buschmann A, Rissmann M, et al. Susceptibility of raccoon dogs for experimental SARS-CoV-2 infection. *Emerg Infect Dis*. 2020;26:2982–5. [PubMed https://doi.org/10.3201/eid2612.203733](https://doi.org/10.3201/eid2612.203733)
125. Richard M, Kok A, de Meulder D, Bestebroer TM, Lamers MM, Okba NM, et al. SARS-CoV-2 is transmitted via contact and via the air between ferrets. *Nat Commun*. 2020;11:3496. [PubMed https://doi.org/10.1038/s41467-020-17367-2](https://doi.org/10.1038/s41467-020-17367-2)
126. Bao L, Deng W, Huang B, Gao H, Liu J, Ren L, et al. The pathogenicity of SARS-CoV-2 in hACE2 transgenic mice. *Nature*. 2020;583:830–3. [PubMed https://doi.org/10.1038/s41586-020-2312-y](https://doi.org/10.1038/s41586-020-2312-y)
127. Hall JS, Knowles S, Nashold SW, Ip HS, Leon AE, Rocke T, et al. Experimental challenge of a North American bat species, big brown bat (*Eptesicus fuscus*), with SARS-CoV-2. *Transbound Emerg Dis*. 2020;Dec 9:2020. [PubMed https://doi.org/10.1038/s41467-020-17367-2](https://doi.org/10.1038/s41467-020-17367-2)
128. Ulrich L, Wernike K, Hoffmann D, Mettenleiter TC, Beer M. Experimental infection of cattle with SARS-CoV-2. *Emerg Infect Dis*. 2020;26:2979–81. [PubMed https://doi.org/10.3201/eid2612.203799](https://doi.org/10.3201/eid2612.203799)
129. Suarez DL, Pantin-Jackwood MJ, Swayne DE, Lee SA, DeBlois SM, Spackman E. Lack of susceptibility to SARS-CoV-2 and MERS-CoV in poultry. *Emerg Infect Dis*. 2020;26:3074–6. [PubMed https://doi.org/10.3201/eid2612.202989](https://doi.org/10.3201/eid2612.202989)
130. Munster VJ, Feldmann F, Williamson BN, van Doremalen N, Pérez-Pérez L, Schulz J, et al. Respiratory disease in rhesus macaques inoculated with SARS-CoV-2. *Nature*. 2020;585:268–72. [PubMed https://doi.org/10.1038/s41586-020-2324-7](https://doi.org/10.1038/s41586-020-2324-7)