



# Cross-species transmission of coronaviruses with a focus on severe acute respiratory syndrome coronavirus 2 infection in animals: a review for the veterinary practitioner

M Dunowska

To cite this article: M Dunowska (2023) Cross-species transmission of coronaviruses with a focus on severe acute respiratory syndrome coronavirus 2 infection in animals: a review for the veterinary practitioner, New Zealand Veterinary Journal, 71:4, 159-171, DOI: [10.1080/00480169.2023.2191349](https://doi.org/10.1080/00480169.2023.2191349)

To link to this article: <https://doi.org/10.1080/00480169.2023.2191349>



© 2023 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group



Published online: 19 Apr 2023.



Submit your article to this journal [↗](#)



Article views: 5080



View related articles [↗](#)



View Crossmark data [↗](#)

# Cross-species transmission of coronaviruses with a focus on severe acute respiratory syndrome coronavirus 2 infection in animals: a review for the veterinary practitioner

M Dunowska 

Tāwharau Ora – School of Veterinary Science, Massey University, Palmerston North, New Zealand

## ABSTRACT

In 2019 a novel coronavirus termed severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) emerged from an unidentified source and spread rapidly among humans worldwide. While many human infections are mild, some result in severe clinical disease that in a small proportion of infected people is fatal. The pandemic spread of SARS-CoV-2 has been facilitated by efficient human-to-human transmission of the virus, with no data to indicate that animals contributed to this global health crisis. However, a range of domesticated and wild animals are also susceptible to SARS-CoV-2 infection under both experimental and natural conditions. Humans are presumed to be the source of most animal infections thus far, although natural transmission between mink and between free-ranging deer has occurred, and occasional natural transmission between cats cannot be fully excluded. Considering the ongoing circulation of the virus among people, together with its capacity to evolve through mutation and recombination, the risk of the emergence of animal-adapted variants is not negligible. If such variants remain infectious to humans, this could lead to the establishment of an animal reservoir for the virus, which would complicate control efforts. As such, minimising human-to-animal transmission of SARS-CoV-2 should be considered as part of infection control efforts. The aim of this review is to summarise what is currently known about the species specificity of animal coronaviruses, with an emphasis on SARS-CoV-2, in the broader context of factors that facilitate cross-species transmission of viruses.

**Abbreviations:** ACE2: Angiotensin-converting enzyme 2; COVID-19: Coronavirus disease 2019; HCoV: Human coronavirus; MERS-CoV: Middle East respiratory syndrome coronavirus; RBD: Receptor-binding domain; SARS: Severe acute respiratory syndrome; SARS-CoV-1: Severe acute respiratory syndrome coronavirus 1; SARS-CoV-2: Severe acute respiratory syndrome coronavirus 2; S: Spike; TGEV: Transmissible gastroenteritis virus

## ARTICLE HISTORY

Received 15 December 2022  
Accepted 14 March 2023  
Published online 17 March 2023

## KEYWORDS

SARS-CoV-2; COVID-19; animal coronaviruses; cross-species transmission; New Zealand

Suspected or confirmed cases of SARS-CoV-2 infection in animals should be notified to the World Organisation for Animal Health through the World Animal Health Information System. For more information on case definition and guidelines for sampling see: [https://www.oie.int/fileadmin/Home/eng/Our\\_scientific\\_expertise/docs/pdf/COV-19/Sampling\\_Testing\\_and\\_Reporting\\_of\\_SARS-CoV-2\\_in\\_animals\\_final\\_7May\\_2020.pdf](https://www.oie.int/fileadmin/Home/eng/Our_scientific_expertise/docs/pdf/COV-19/Sampling_Testing_and_Reporting_of_SARS-CoV-2_in_animals_final_7May_2020.pdf)

## Introduction

In January 2020, the World Health Organisation announced the identification of a novel coronavirus (CoV) associated with a cluster of cases of viral pneumonia in Wuhan, China (Huang *et al.* 2020b; WHO 2020; Zhu *et al.* 2020). The disease was named coronavirus disease 2019 (COVID-2019) and was shown to be caused by a novel coronavirus, named severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2). Since then, the virus has spread among people across the globe causing an unprecedented pandemic with over 680 million infections including 6.8 million

deaths (as of 2 March 2022, <https://www.worldometers.info/coronavirus/>). The origin of SARS-CoV-2 remains obscure, but most researchers agree that the virus crossed into a human population from animals (Holmes *et al.* 2021; Lytras *et al.* 2021). The aim of this review is to summarise what is currently known about the species specificity of SARS-CoV-2 in the broader context of factors that facilitate cross-species transmission of viruses.

## General characteristics of coronaviruses

Coronaviruses are enveloped viruses with a positive sense, non-segmented RNA genome. There are over

**CONTACT** M. Dunowska  [m.dunowska@massey.ac.nz](mailto:m.dunowska@massey.ac.nz)

© 2023 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group  
This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial-NoDerivatives License (<http://creativecommons.org/licenses/by-nc-nd/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited, and is not altered, transformed, or built upon in any way. The terms on which this article has been published allow the posting of the Accepted Manuscript in a repository by the author(s) or with their consent.

2,500 coronavirus sequences available in public databases, which represent coronaviruses from a variety of vertebrate hosts. Based on the similarities in the conserved regions of coronavirus genomes, these viruses are currently classified into 54 species, 28 subgenera, six genera, and three subfamilies within the family *Coronaviridae*, suborder *Cornidovirineae*, and order *Nidovirales* (Woo 2023). SARS-CoV-2 is classified in the species *Severe acute respiratory syndrome-related coronavirus*, subgenus *Sarbecovirus* and genus *Betacoronavirus* (Coronaviridae Study Group of the International Committee on Taxonomy of Viruses 2020). In general, coronaviruses have a predilection for the respiratory or gastrointestinal tract and are usually associated with gastrointestinal or respiratory disease, which is often mild or subclinical (Zappulli *et al.* 2020; Kayode *et al.* 2021). However, selected human and animal coronaviruses can cause severe systemic disease, sometimes with a neurological component. Examples include severe acute respiratory

syndrome (SARS) and COVID-19 in people, feline infectious peritonitis, ferret systemic coronavirus disease, or the cardiovascular and central nervous system presentations that can accompany gastrointestinal disease caused by coronaviruses of swine (Murray *et al.* 2010; Pedersen 2014; Thakor *et al.* 2022). One animal species can serve as a host for several different coronaviruses (Table 1).

All coronaviruses have similar genome organisation and replication strategies (Gorbalenya *et al.* 2006; Pasternak *et al.* 2006). Approximately two-thirds of the genomic RNA encodes two large polyproteins, 1a and 1ab, which are expressed from two overlapping open reading frames located at the 5' end of the genome. These viral polyproteins are further cleaved into 16 non-structural proteins (nsp1 to nsp16) that are involved in virus replication and interactions with the host's immune system (Fang *et al.* 2021). The downstream open reading frame encodes structural viral proteins, which comprise spike (S), envelope,

**Table 1.** Host and disease characteristics of selected coronaviruses that can infect animals that are present in New Zealand, including whether each virus has been identified in New Zealand.

Virus	Genus	Animal host	Disease characteristics	Reference <sup>e</sup>	Present in NZ <sup>f</sup>
Feline enteric coronavirus (FECV) <sup>a,b</sup>	<i>Alphacoronavirus</i>	Cats	GI disease of varying severity	Pedersen (2014)	Yes
Feline infectious peritonitis virus (FIPV) <sup>a,b</sup>	<i>Alphacoronavirus</i>	Cats	Fatal systemic disease	Pedersen (2014)	Yes
Ferret enteric coronavirus	<i>Alphacoronavirus</i>	Ferrets	GI disease of varying severity	Murray <i>et al.</i> (2010)	Unknown
Ferret systemic coronavirus	<i>Alphacoronavirus</i>	Ferrets	Severe systemic disease	Murray <i>et al.</i> (2010)	Unknown
Canine coronavirus (CCoV) <sup>b</sup>	<i>Alphacoronavirus</i>	Dogs	GI disease of varying severity, sometimes severe pantropic disease	Decaro and Buonavoglia (2011)	Yes
Canine respiratory coronavirus (CRCoV) <sup>c</sup>	<i>Betacoronavirus</i>	Dogs	Respiratory disease of varying severity	Erles and Brownlie (2008)	Yes
Alpaca respiratory coronavirus	<i>Betacoronavirus</i>	Alpacas	Respiratory disease	Crossley <i>et al.</i> (2012)	Unknown
Alpaca enteric coronavirus	<i>Betacoronavirus</i>	Alpacas	GI disease of varying severity	Cebra <i>et al.</i> (2003)	Unknown
Equine coronavirus (ECoV) <sup>c</sup>	<i>Betacoronavirus</i>	Horses	Inappetence, depression, colic, ± diarrhoea	Berryhill <i>et al.</i> (2019)	Yes
Bovine coronavirus (BCoV) <sup>c</sup>	<i>Betacoronavirus</i>	Cattle <sup>5</sup>	Gastroenteritis or respiratory disease of varying severity	Vlasova and Saif (2021)	Yes
Transmissible gastroenteritis virus (TGEV) <sup>b</sup>	<i>Alphacoronavirus</i>	Pigs	GI disease of varying severity	Thakor <i>et al.</i> (2022)	No
Porcine respiratory coronavirus	<i>Alphacoronavirus</i>	Pigs	Subclinical or mild respiratory disease	Thakor <i>et al.</i> (2022)	Unknown
Porcine epidemic diarrhoea virus	<i>Alphacoronavirus</i>	Pigs	GI disease of varying severity	Thakor <i>et al.</i> (2022)	No
Porcine deltacoronavirus	<i>Deltacoronavirus</i>	Pigs	GI disease of varying severity	Thakor <i>et al.</i> (2022)	Unknown
Porcine hemagglutinating encephalomyelitis virus (PHEV) <sup>c</sup>	<i>Betacoronavirus</i>	Pigs	Wasting or encephalomyelitis	Thakor <i>et al.</i> (2022)	Unknown
Swine acute diarrhea syndrome coronavirus	<i>Alphacoronavirus</i>	Pigs	GI disease	Thakor <i>et al.</i> (2022)	Unknown
Murine hepatitis virus	<i>Betacoronavirus</i>	Mice	Enteritis, hepatitis or demyelinating encephalomyelitis	Korner <i>et al.</i> (2020)	Unknown
Infectious bronchitis virus (IBV) and other avian coronaviruses <sup>d</sup>	<i>Gammacoronavirus</i>	Birds	Respiratory or GI disease of varying severity, sometimes proventriculitis or nephropathy	de Wit and Cook (2020)	Yes (IBV)
Avian deltacoronaviruses	<i>Deltacoronavirus</i>	Birds	Unknown	Woo <i>et al.</i> (2012)	Unknown

<sup>a</sup>FECV and FIPV are two pathotypes of the same virus.

<sup>b</sup>FECV, FIPV, CCoV and TGEV are closely related viruses that are classified within the same species *Alphacoronavirus 1*.

<sup>c</sup>BCoV, ECoV, PHEV, CRCoV, human enteric coronavirus and human coronavirus-OC43 are closely related viruses that are classified within the species *Betacoronavirus 1*. Coronaviruses very similar to BCoV (bovine-like coronaviruses) have also been detected from a number of other ruminants including sheep, goats, llamas, alpacas and deer (Amer 2018).

<sup>d</sup>Avian coronaviruses include infectious bronchitis virus, turkey coronavirus, goose coronavirus, pigeon coronavirus and duck coronavirus. All appear closely related based on available sequence data and classified within one species *Avian coronavirus*. IBV is present in New Zealand; there are no data for other avian coronaviruses.

<sup>e</sup>Selected papers with more detailed information on pathogenesis and clinical signs caused by the viruses listed.

<sup>f</sup>Based on published information (where available) and data available through Official New Zealand Pest Register (accessible through the Ministry of Primary Industries webpage: <https://pierpesterregister.mpi.govt.nz/pests-of-concern/>).

GI = gastrointestinal.

membrane, and nucleocapsid proteins, and several accessory proteins that differ between various coronaviruses (Gorbalenya *et al.* 2006; Pasternak *et al.* 2006).

### Coronavirus entry into the cell

Coronavirus entry into cells is mediated by interactions between the S protein and host receptors, which vary between different coronaviruses (Cheng *et al.* 2021). The receptor used by SARS-CoV-2 is angiotensin-converting enzyme 2 (ACE2) (Jackson *et al.* 2022). Each spike in the “crown” of coronaviruses consists of three copies of the S protein. The S protein of SARS-CoV-2 is cleaved during the assembly within infected cells into two subunits, S1 and S2 (Figure 1). These two subunits remain non-covalently bonded on the surface of the virion and play different roles during SARS-CoV-2 entry into the cell: subunit 1 binds ACE2 through its receptor binding domain (RBD), while subunit 2 anchors the virion to the host cell and mediates membrane fusion (Jackson *et al.* 2022). The changes in the conformation of the S trimer before and after the binding to ACE2 are crucial for the

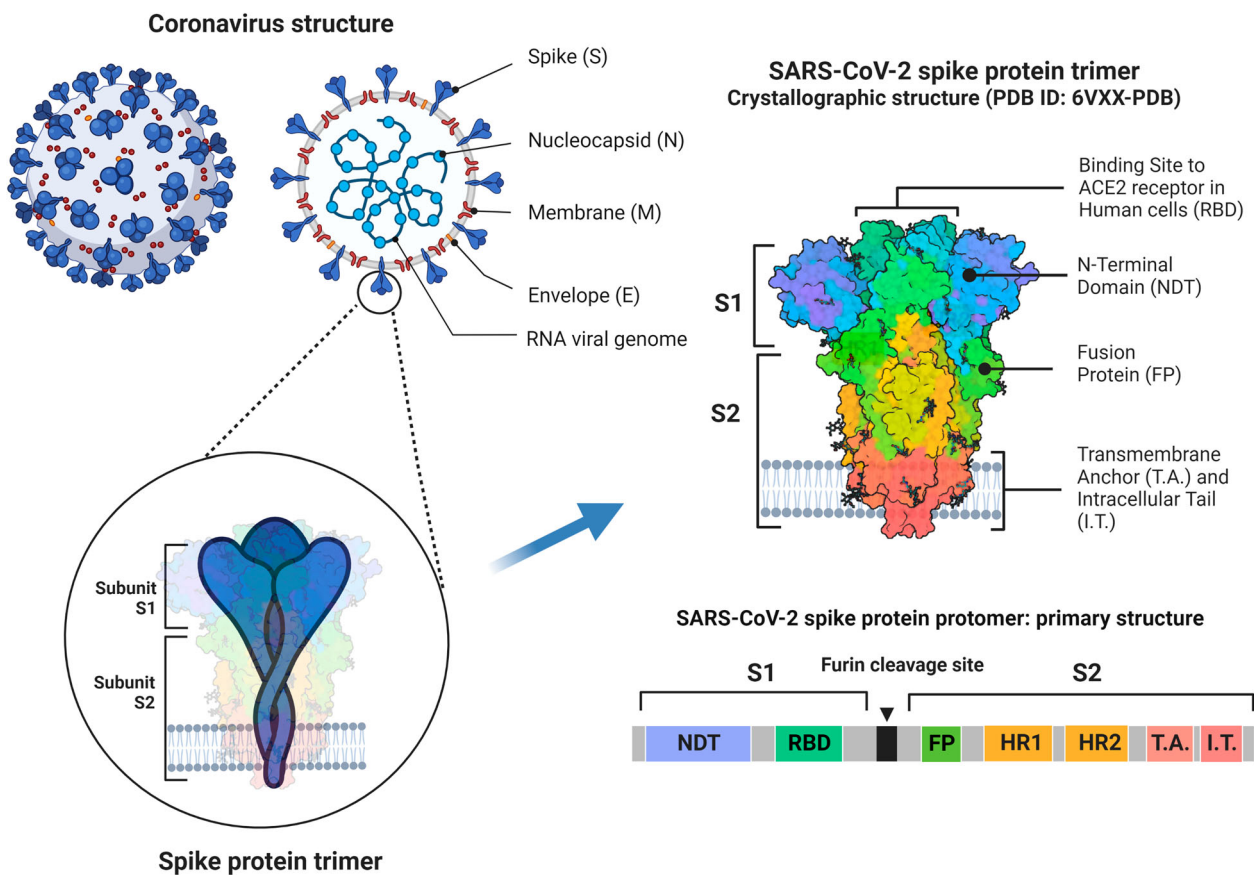
successful entry of the virus into the cell (Jackson *et al.* 2022).

In addition to its role in the virus entry into the host cell, the RBD on the S protein is also the main target for neutralising antibodies during SARS-CoV-2 infection. Although correlates of protective immunity against SARS-CoV-2 are not yet fully elucidated, the levels and specificity of anti-S neutralising antibodies have been used as a proxy for the assessment of levels of protective immunity following natural infection or vaccination (Huang *et al.* 2020a; Gilbert *et al.* 2022).

The sequence of the S protein is one of the crucial determinants for the species- and tissue-specificity of SARS-CoV-2, as well as the virulence of the virus (Gussow *et al.* 2020).

### Human coronaviruses

Four coronaviruses are endemic in human populations worldwide, including New Zealand (CDC 2020). These include two alphacoronaviruses (human coronavirus (HCoV-229E and HCoV-NL63) and two betacoronaviruses (HCoV-HKU1 and HCoV-OC43). Infections with



**Figure 1.** Schematic representation of the structure of a coronavirus including details of the structure of the spike (S) protein of severe acute respiratory coronavirus type 2 (SARS-CoV-2). Each viral spike comprises three S proteins. A single S protein consists of two subunits (S1 and S2) which are separated by a furin cleavage site. These subunits contain different domains and play different roles during virus entry into the cell: S1 binds angiotensin-converting enzyme 2 (ACE2) receptor on the host cell through its receptor binding domain (RBD), while S2 anchors the virion to the host cell and mediates membrane fusion (Jackson *et al.* 2022). Adapted from “An in-depth look into the structure of SARS-CoV-2 spike glycoprotein” by BioRender.com (2023). Retrieved from <https://app.biorender.com/biorender-templates>.

these endemic viruses are typically associated with mild-to-moderate respiratory disease referred to as “common colds” (Kayode *et al.* 2021). Coronaviruses had not attracted much scientific attention until 2002 when the first worldwide outbreak of SARS occurred (Song *et al.* 2019). This was followed by the emergence of Middle East respiratory syndrome (MERS) in 2012 (Guan *et al.* 2003) and finally the current COVID-19 pandemic. Unlike upper respiratory tract infections associated with endemic human coronaviruses, which are typically self-limiting, a comparatively high proportion of people infected with these three emerging coronaviruses go on to develop severe pneumonia. Case fatality rates are estimated to range from < 5% for SARS-CoV-2 (Sreedharan *et al.* 2021) to 35% for MERS-CoV (WHO 2016). Unlike the global spread of SARS-CoV-2, SARS-CoV-1 (the virus responsible for SARS) has not been circulating among humans since 2004, and transmission of MERS-CoV has been limited to the Middle East.

All three recently emerged human coronaviruses are believed to have a zoonotic origin. An overall prevalence of coronavirus infection of 6.8% was found in a recent study of bats ( $n = 1,067$ , from 21 species) from three provinces of China (Lin *et al.* 2017). The researchers identified 73 different coronaviruses among which were 41 betacoronaviruses closely related to the known members of the species *Severe acute respiratory syndrome related viruses*, including SARS-CoV-1 and SARS-CoV-2. This suggests that bats probably had a role as direct or indirect sources of SARS-CoV-1 (Guan *et al.* 2003), MERS-CoV (Drosten *et al.* 2014), and possibly SARS-CoV-2 (Zhou *et al.* 2020), and may also harbour other coronaviruses that may threaten human health. In fact, it has been recently suggested that the “Russian flu” pandemic, which killed an estimated 1 million people (approximately 7% of the human population at the time) between 1889 and 1891, may have been caused by a coronavirus rather than by influenza virus, as has been presumed until now (Brussow and Brussow 2021; Ramassy *et al.* 2022). Coincidentally, results of a phylogenetic analysis suggested that HCoV-OC43 may have originated from a relatively recent zoonotic transmission of bovine coronavirus. The most recent common ancestor of these two viruses was estimated to exist around 1890 (Vijgen *et al.* 2005). Taken together, those findings suggest a possibility that the now endemic HCoV-OC43 originated from cross-species transmission of a bovine coronavirus that coincided with a global pandemic that clinically resembled the current COVID-19 disease, although more research is needed to confirm or refute this theory.

### Animal coronaviruses

Many coronaviruses have been detected from various domestic and wild animals (Haake *et al.* 2020; Stout

*et al.* 2020; Zhang *et al.* 2021). Coronaviruses that can infect animals living in New Zealand are listed in Table 1. Only some of those viruses are known to be present in New Zealand, including canine, feline, equine, bovine and avian coronaviruses. Other coronaviruses have never been detected here. However, only two porcine diseases (transmissible gastroenteritis virus (TGEV) and porcine epidemic diarrhoea) are specified as “absent from New Zealand” by the Ministry for Primary Industries (MPI 2022). As there is no active surveillance for any of the animal coronaviruses in New Zealand, the lack of reports of a specific virus does not equate to absence of that virus in the country.

Several animal coronaviruses evolved through mutations and recombinations (Focosi and Maggi 2022). Those events can lead to changes in hosts or the virulence of the virus. Examples include the emergence of TGEV in pigs and feline coronavirus in cats, which are believed to represent cross-species transfer of canine coronavirus to pigs and cats, respectively (Licitra *et al.* 2014).

### SARS-CoV-2 infection of animals

Direct transmission of SARS-CoV-2 between people occurs via respiratory droplets produced during coughing, sneezing or talking, or through contact with body fluids and secretions, such as faeces or saliva (Chan *et al.* 2020a; Wang *et al.* 2020; Bahl *et al.* 2022). The contribution of airborne transmission by aerosols has been suggested, although views on the importance of that route in the global spread of the virus vary (Bushmaker *et al.* 2022; Tellier 2022). Indirect transmission may occur through contact with fomites such as contaminated objects or common-use surfaces. Viable SARS-CoV-2 virus can survive for up to 4 days on various surfaces, depending on the environmental conditions and type of surface (Guo *et al.* 2020; Pastorino *et al.* 2020; van Doremalen *et al.* 2020).

Similar routes of infection would be expected to exist between humans and domesticated animals, especially those in close contact with people (pets or livestock). There is no indication that domesticated animals have played a role in the current pandemic spread of SARS-CoV-2 among people. However, SARS-CoV-2 can experimentally infect a wide range of animals including cats (Bosco-Lauth *et al.* 2020; Gaudreault *et al.* 2020; Halfmann *et al.* 2020), ferrets (Shi *et al.* 2020; Kutter *et al.* 2021), mink (Virtanen *et al.* 2022), hamsters (Chan *et al.* 2020b; Osterrieder *et al.* 2020), rabbits (Mykytyn *et al.* 2021), raccoon dogs (*Nyctereutes procyonoides*; Freuling *et al.* 2020), tree shrews (*Tupaia belangeris*; Zhao *et al.* 2020), white-tailed deer (*Odocoileus virginianus*; Martins *et al.* 2022) and non-human primates (Trichel 2021). Dogs appeared partially refractory to experimental infection as only some, but not all, became infected with the virus, and the infection was not passed on further to susceptible

dogs (Shi *et al.* 2020). Pigs, chickens and ducks were not susceptible to experimental infection with SARS-CoV-2 (Schlottau *et al.* 2020; Suarez *et al.* 2020). There are currently no data available on the susceptibility of horses to experimental infection with SARS-CoV-2, but horses were refractory to experimental infection with MERS-CoV-1 (Vergara-Alert *et al.* 2017).

The susceptibility to experimental infection cannot be used to directly extrapolate the likelihood of natural infection in the same species. To exemplify this, cats experimentally infected with SARS-CoV-2 transmitted the virus to one of three uninfected cats housed in adjacent cages (Shi *et al.* 2020). The experimental conditions (high load of the inoculated virus and prolonged indirect exposure of naïve cats to infected cats) would be unlikely to be replicated in real life and hence, the ability of SARS-CoV-2 to be transmitted from naturally infected cats to other cats, or to humans, needs to be further investigated.

Natural infection with SARS-CoV-2 has, however, been reported to the World Organisation for Animal Health for 26 different animal species (WOAH 2022) including domestic cats and several species of wild felids, dogs and red foxes (*Vulpes vulpes*), several mustelid spp., non-human primates including both apes and monkeys, several species of deer, and a variety of other mammals across widely diverse orders. As of 31 December 2022, a total of 699 outbreaks (one or more epidemiologically linked cases) of SARS-CoV-2 infection in animals have been reported from 36 countries in the Americas, Africa, Asia and Europe. There is also serological evidence suggesting that a pet rabbit (Fritz *et al.* 2022) and a horse (Pusterla *et al.* 2022) may have become infected with the virus. However, nasal secretions from 667 horses with acute onset of fever and respiratory signs that were submitted to a diagnostic laboratory in California (USA) from January to December 2020 were all negative for SARS-CoV-2 by quantitative PCR (Lawton *et al.* 2022). In addition, 633 serum samples from 587 healthy racing Thoroughbred horses from California, collected between July and September 2020 during the time of a confirmed circulation of SARS-CoV-2 among the racetrack personnel, were also negative for SARS-CoV-2 antibodies. Altogether, these data suggest that SARS-CoV-2 infection of the horse is rare. Similarly, there are no reports of SARS-CoV-1 infection of horses, even though both the SARS-CoV-1 and SARS-CoV-2 spike was shown to bind to the equine ACE2 receptor *in vitro*, albeit with lower affinity than to human ACE2 (Lan *et al.* 2022).

This underscores the ability of the virus to infect a variety of hosts, despite its clear preference for humans. Most of the natural SARS-CoV-2 infections in animals were linked to contact with infected people and hence most likely represented “reverse zoonosis,” defined as human-to-animal spread (Barrs *et al.* 2020;

Musso *et al.* 2020; Segalés *et al.* 2020). The frequency of such reverse zoonotic transmissions is not well understood but has likely been low (Kannekens-Jager *et al.* 2022). However, the ability of the virus to evolve and adjust to the new hosts may occasionally lead to sustained animal-to-animal transmission, as presumably occurred among farmed mink in Europe (Rasmussen *et al.* 2021; Wolters *et al.* 2022) and free-ranging deer in the USA (Hale *et al.* 2022; Kuchipudi *et al.* 2022; Roundy *et al.* 2022).

### **SARS-CoV-2 infection of dogs and cats**

Among domesticated animals that have close contact with people, cats have been most frequently reported to be naturally infected with SARS-CoV-2 based on both virological and serological data. The frequency of detection of SARS-CoV-2 antibodies in cats differed between different studies (Table 2). Those discrepancies most likely reflect differences in the sampled populations, sampling strategies, the type of serological tests employed, and interpretation of the results obtained.

The most likely source of SARS-CoV-2 infection in cats was people, although other sources cannot be fully excluded (e.g. cat-to-cat or environmental contamination). Blood samples for various studies were collected from cats during the pandemic spread of SARS-CoV-2 among people in the same geographical area, but the level of contact between cats and SARS-CoV-2 infected people was unknown in most studies (Table 2). When such data for individual animals were available, the frequency of infection among cats with known exposure to SARS-CoV-2 was higher than the frequency of infection among cats with unknown exposure to the virus. This can be exemplified by a French study where 10/47 (21%) cats from COVID-19 households were positive for SARS-CoV-2 antibodies as compared to 1/16 (6%) cats from households with unknown COVID-19 status (Fritz *et al.* 2021).

The serological tests employed differed between studies. Several authors employed more than one test, and only sera that tested positive for SARS-CoV-2 antibodies in all tests used were considered positive (Dileepan *et al.* 2021; Fritz *et al.* 2021). While such an approach increased the specificity of results, it also decreased sensitivity, so the number of seropositive cats was likely to be underestimated in some of the studies. Similar issues have been described for serological testing for SARS-CoV-2 exposure in people. In one study, antibodies to S protein were detectable for longer than neutralising antibodies to the nucleocapsid protein after SARS-CoV-2 infection (Fenwick *et al.* 2021). As a result, serological tests based on detection of the S and nucleocapsid proteins produced similar results during the acute phase of infection, but the latter considerably underestimated the level of

**Table 2.** Seroprevalence of SARS-CoV-2 antibody among cats.

Source of samples	Dates of collection	Country	Direct contact with SARS-CoV-2-infected people	Proportion positive (%)	Reference
Shelters/veterinary clinics	Jan–Mar 2020	China (Wuhan)	15 from COVID-19-infected owners, rest unknown	15/102 (14.7%)	Zhang <i>et al.</i> (2020)
Veterinary students	March 2020	France	Confirmed COVID-19-infected or symptomatic close contacts	0/9 (0%)	Temmam <i>et al.</i> (2020)
Veterinary clinics	Mar–May 2020	Italy	Unknown	11/191 (5.8%)	Patterson <i>et al.</i> (2020)
Veterinary clinics	Apr–Sep 2020	Germany	Unknown	6/920 (0.7%)	Michelitsch <i>et al.</i> (2020)
Unknown	Early stages of pandemic	China (not specified)	Unknown	0/87 (0%)	Deng <i>et al.</i> (2020)
Veterinary clinic	Apr–Jun 2020	USA (Minnesota)	Unknown	19/239 (8%)	Dileepan <i>et al.</i> (2021)
Private owners	May–June 2020	France	34 from COVID-19-infected households 16 unknown	8/34 (24%) 1/16 (6%)	Fritz <i>et al.</i> 2021
Veterinary clinics and private owners	Feb–June 2020	Croatia (various)	Unknown	1/131 (0.8%)	Stevanovic <i>et al.</i> (2021)
Private owners, longitudinal study	Jun–Sep 2020	USA (Texas)	COVID-19-affected	7/16 (43.8%)	Hamer <i>et al.</i> (2021)
Veterinary clinics	Sep–Feb 2021	Germany	Unknown	16/1173 (1.4%)	Michelitsch <i>et al.</i> (2021)
Veterinary clinics	Jul–Nov 2020	Brazil (various)	Unknown	40/547 (7.3%)	de Oliveira-Filho <i>et al.</i> (2022)
Stray cats	Jan–Oct 2020	Spain	Unknown	4/114 (3.51%)	Villanueva-Saz <i>et al.</i> (2022a)
Stray cats	Oct 2020–Jan 2022	Spain	Unknown	4/254 (1%)	Villanueva-Saz <i>et al.</i> (2022b)
Shelters and veterinary clinics	Apr 2021–Jan 2022	Korea (various)	Unknown	18/346 (5.2%)	Bae <i>et al.</i> (2022)

seropositive individuals in the general population with various histories of SARS-CoV-2 exposure.

Several studies demonstrated that dogs can also be naturally infected with SARS-CoV-2. In most of those studies, the prevalence of SARS-CoV-2 antibodies was lower in dogs than in cats from the same geographical area (Dileepan *et al.* 2021; Fritz *et al.* 2021; Hamer *et al.* 2021), in agreement with results of experimental transmission studies (Bosco-Lauth *et al.* 2020; Shi *et al.* 2020).

Overall, the available data indicate that both dogs and cats can be naturally infected with SARS-CoV-2 and that the most likely source of infection is SARS-CoV-2-infected people. The reported frequency of infection with SARS-CoV-2 in pets owned by COVID-19-affected people varied between studies, which most likely reflects factors such as the variant of the virus involved, the level of close contact between infected people and their pets, and individual differences between pets (e.g. breed, age, presence of concurrent infections, etc.).

### **Clinical signs in animals infected with SARS-CoV-2**

Little is known about clinical disease associated with SARS-CoV-2 infection in animals. Experimental infection with SARS-CoV-2 produced no clinical signs in dogs and adult cats (Bosco-Lauth *et al.* 2020). Juvenile cats were more likely to develop disease than adult cats based on severity of pathological lesions described (Shi *et al.* 2020). In agreement with those studies, SARS-CoV-2 RNA has been detected in samples from naturally infected, clinically healthy cats and dogs (Sit *et al.* 2020; Calvet *et al.* 2021;

Hamer *et al.* 2021). The clinical signs observed in mink on SARS-CoV-2-infected farms were mostly restricted to watery nasal discharge, although some animals developed severe respiratory disease (Oreshkova *et al.* 2020). There are, however, some reports of SARS-CoV-2 detection in pets that displayed clinical signs resembling those of COVID-19 infection in people, including lethargy, anorexia, diarrhoea, vomiting, breathing difficulties, and cough (Sailleau *et al.* 2020; Calvet *et al.* 2021; Hamer *et al.* 2021). Similar clinical signs were reported in SARS-CoV-2-infected large cats (tigers and lions) in zoos (McAloose *et al.* 2020; Grome *et al.* 2022). These clinical signs are non-specific and can be induced by several infectious or non-infectious causes. Hence, such reports should be evaluated with caution, as it is difficult to conclusively establish a causal link between SARS-CoV-2 infection and disease for an individual naturally infected animal.

### **Factors affecting cross-species transmission of viruses**

Successful cross-species transmission of a virus from an animal to a person, with subsequent person-to-person spread, as has occurred with SARS-CoV-2, is fortunately a rare event. Several well-timed coincidences need to happen for this to occur (Parrish *et al.* 2008; Plowright *et al.* 2017). These are briefly outlined below.

#### ***Vicinity of the infected host animal to a potential new host***

To start with, the infected animal needs to find itself in close vicinity to the prospective new host. A major

source of new emerging infections for humans are viruses that circulate in wildlife among animals that rarely, if ever, find themselves near people (Epstein and Anthony 2017). Human expansion coupled with activities such as deforestation, urbanisation, illegal wildlife, or bushmeat trade all tip this balance in favour of potential “spillover” events to occur (Parrish *et al.* 2008; Hassell *et al.* 2017; Plowright *et al.* 2017). It is probably not a coincidence that the emergence of both SARS-CoV-1 and SARS-CoV-2 has strong epidemiological links to live-animal markets (Lytras *et al.* 2021). A variety of animals, both farmed and caught locally from the wild, are sold at such markets. In addition, carcasses of wildlife that were either caught or farmed elsewhere can be transported to the markets using established cold chains, both legal and illegal (Lytras *et al.* 2021). High levels of stress among animals at the market, coupled with crowded conditions, create a perfect opportunity for a cross-species transfer of viruses between animals or from animals to humans. During the 2003 SARS-CoV-1 outbreak, 66/508 (13%) animal traders from three markets in the Guangdong province of China were positive for SARS-CoV-1 antibodies with the seroprevalence reaching 16/22 (73%) among traders of palm civets (*Paradoxurus hermaphroditus*; CDC 2003). Only 4/137 (3%) hospital workers sampled at the same time had SARS-CoV-1 antibodies, supporting the view that close contact with live animals at the market was a significant risk factor for SARS-CoV-1 infection. While the first cases of SARS-CoV-2 infection were also epidemiologically linked to a live-animal market in China, similar serological data to support this connection are not available, most likely due to the rapid spread of SARS-CoV-2 and presumed lack of appropriate samples from the early phases of the outbreak.

### **Intermediate and reservoir hosts**

Transmission of viruses from wildlife to humans can occur directly or indirectly via domesticated animals. Livestock and some pet animals (e.g. cats or hunting dogs) have more opportunities to come into close contact with potentially infected wildlife than do humans. At the same time, domesticated animals are frequently handled by people, and can therefore act as intermediate hosts for human infection. If the virus establishes itself in the population of domesticated animals, they can also become new reservoir hosts for that virus and be a source of future infections for people. The two terms (reservoir and intermediate host) are not synonymous. This may be exemplified by the role of civet cats in the transmission of SARS-CoV-1 to people during the 2003 outbreak, which was believed to initially occur through contact with infected civet cats at the market (Wang and Eaton 2007). Although the rates of SARS-CoV-1 infection

among palm civets at the Quandong markets was high, palm civets at the neighbouring farms or from the wild were mostly negative for the virus or virus-specific antibodies (Tu *et al.* 2004; Kan *et al.* 2005; Poon *et al.* 2005). This suggests that infected palm civets were a likely immediate source for human infection (intermediate host) but they were probably infected at the market from other animals, and were unlikely to be the natural wildlife reservoir host for the virus. In contrast, a large proportion of healthy camels in Saudi Arabia were positive for MERS-CoV (Drosten *et al.* 2014). The virus most likely originated in bats and was transmitted at some point in the past to camels, but by the time MERS-CoV was detected in people, the virus circulated endemically among camels in the Arabian Peninsula without causing any overt clinical illness. The camels were the source of infection for people (intermediate hosts), but they also became the reservoir host for the virus.

At present, neither an intermediate nor reservoir host for SARS-CoV-2 has been conclusively determined. Bats are considered to be the most likely reservoir host based on the fact that they harbour a large number of diverse coronaviruses (Lin *et al.* 2017). However, none of the viruses identified from bats thus far is similar enough to SARS-CoV-2 to be considered a direct source of the zoonotic transmission to people (Lytras *et al.* 2021). In addition, the 2019 outbreak was epidemiologically linked to wet animal markets in Wuhan, which is geographically distant from Yunnan, where bat viruses similar to SARS-CoV-2 were identified. Finally, bats were hibernating at the time of SARS-CoV-2's emergence and no bats were sold at the Wuhan market. Pangolins (*Manis javanica*) have been suggested as an alternative intermediate host (Lytras *et al.* 2021). While sequence similarity of SARS-CoV-2-like viruses obtained from pangolins to human SARS-CoV-2 is lower than that of bat viruses over the full genome length, their RBD on the S protein is very similar to that of human SARS-CoV-2 (Lytras *et al.* 2021). In fact, pangolin viruses bind to human ACE *in vitro* better than SARS-CoV-2 (Dicken *et al.* 2021). This led to a suggestion that pandemic SARS-CoV-2 may have arisen by recombination between bat and pangolin SARS-CoV-2-like viruses within an unidentified intermediate host (Lytras *et al.* 2022). Recombination between coronaviruses that leads to emergence of new pathogens has been described before (Focosi and Maggi 2022). An example may be an intertwined history of several events of the emergence of new viruses through recombination between canine coronaviruses, feline coronaviruses, and porcine TGEV (Pratelli *et al.* 2021). While most of those recombinant viruses were identified in dogs or cats, one was detected in hospitalised children in Malaysia, further highlighting the ability of coronaviruses to cross species barriers (Vlasova *et al.* 2022).

### **Availability of suitable receptors on the new host's cells**

Following a chance encounter with a non-natural host, the virus must be able to enter appropriate tissues and establish productive infection in those tissues. The binding between the virus and its receptor is a prerequisite for infection, so this single factor plays an important role in the species-specificity of any virus. Viruses that utilise molecules that are conserved between various animal species or viruses that can utilise more than one receptor for entry tend to have a broader host range than viruses that enter through a highly species-specific receptor. The results of the comparative genomic, evolutionary and structural analysis of ACE2 orthologs from 410 vertebrate species including selected species of fish, amphibians, birds, reptiles and mammals suggested that the SARS-CoV-2 receptor on ACE has very high (18 species), high (28 species) or medium (57 species) likelihood of being able to bind to SARS-CoV-2 S protein (Damas *et al.* 2020). The species with very high and high similarity to human ACE included old-world primates, great apes, other primates, old-world monkeys, some rodents, and cervids, as well as whales and dolphins. Several domesticated animals were within the medium likelihood group, including dog, cat, hamster, cattle, sheep, alpaca, horse and donkey. The predicted binding capacity differed between species from the same order. For example, 9/43 carnivorans scored medium, 9/43 scored low, and 25/43 scored very low, with all medium-scoring carnivorans being felids.

While such analyses can help to assess the theoretical likelihood of cross-species transmission of SARS-CoV-2, they cannot replace the data derived either from transmission studies or from investigations of field cases. To exemplify this, ACE from ferret, American mink (*Neovison vison*) and European mink (*Mustela nivalis*) all scored very low for the likelihood of binding SARS-CoV-2, and yet all three animal species are susceptible to SARS-CoV-2 infection, with outbreaks of SARS-CoV-2 among farmed American mink reported on 400 mink farms in six European countries (Boklund *et al.* 2021). In agreement with the importance of RBD for successful cross-species transfer, the viruses that circulated among mink had mutations within the RBD of the S protein that increased the efficiency of viral RBD binding to mink ACE, highlighting the propensity of coronaviruses for change not only through recombination but also through mutations (Su *et al.* 2022).

### **On-going transmission between new hosts**

Finally, for the virus to establish itself in a new host species, enough infectious virus needs to be generated to allow infection to be propagated to another

individual from that species. This is not easy for the virus to accomplish, as there are several host- and virus-related restrictions that prevent effective establishment of infection in a non-natural host (Parrish *et al.* 2008; Plowright *et al.* 2017). In addition to the availability of suitable cellular receptors for the virus entry, these include restrictions at various steps of intracellular virus replication or innate immune responses. Even if successful, the virus typically needs to adjust to its new host to allow for a sustained spread between the new hosts (Parrish *et al.* 2008; Plowright *et al.* 2017). Viruses that are highly virulent in the new host may not spread further, as the host is killed before transmission can occur. In the opposite scenario, infection may be initially established only briefly, without overt clinical disease and without further transmission of the virus, as was observed in dogs experimentally infected with SARS-CoV-2 (Shi *et al.* 2020). Such undetected, sporadic spill-over events are likely to occur on a regular basis whenever there is frequent direct or indirect contact between wildlife and people or domesticated animals, for example in rural areas or among people with occupational exposure to wildlife. If some ongoing transmission between the new hosts does occur, the virus can accumulate mutations that are necessary for adaptation to specific restriction factors, with the possibility of subsequent epidemic or pandemic spread within an immunologically naïve population. This is what has been observed with SARS-CoV-2's spread among people and, on a smaller scale, among farmed mink. Factors such as density of the new hosts in the given area and the frequency of direct or indirect contact between them are likely to be important for the successful adaptation of a virus to the new population.

To illustrate these concepts, antibodies to SARS-CoV-1 were retrospectively detected in 17/938 (1.7%) adults tested in Hong Kong, indicating that sporadic infections with SARS-CoV-1-like virus were occurring in Hong Kong at least 2 years before the 2003 pandemic (Zheng *et al.* 2004). Similarly, antibodies reactive with SARS-CoV-2 were retrospectively detected in 8/478 (1.7%) healthy individuals from Saudi Arabia in samples collected between October 2019 and January 2020, i.e. before the pandemic spread of the virus (Mahallawi and Ibrahim 2022). All eight seropositive individuals in that study had a history of travel to China within 4 weeks prior to blood collection. In another study, limited serological evidence indicated that SARS-CoV-2-like viruses may have circulated in Africa before the emergence of COVID-19 in China (Souris *et al.* 2022).

### **Conclusion**

Thus far, the spread of SARS-CoV-2 has been largely mediated by human-to-human transmission. However,

the virus can infect animals of many different species including pets and livestock. With the notable exception of mink and deer, occasional animal infections have not thus far led to sustained animal-to-animal transmission. The source of animal infections has most likely been human-derived virus, although occasional natural transmission between cats cannot be fully excluded. Considering the capacity of the virus to evolve through mutation and recombination, together with close contact between humans and animals, the on-going frequent transmission of the virus between people poses a risk of the emergence of animal-adapted variants. If such variants remain infectious to humans, this could lead to the establishment of animal reservoirs for the virus, which would complicate control efforts. As such, minimising human-to-animal transmission of SARS-CoV-2 should be considered as part of infection control efforts.

## ORCID

M Dunowska  <http://orcid.org/0000-0003-3874-0154>

## References

- Amer HM.** Bovine-like coronaviruses in domestic and wild ruminants. *Animal Health Research Reviews* 19, 113–24, 2018. <https://doi.org/10.1017/S1466252318000117>
- Bae DY, Tark D, Moon SH, Oem JK, Kim WI, Park C, Na KJ, Park CK, Oh Y, Cho HS.** Evidence of exposure to SARS-CoV-2 in dogs and cats from households and animal shelters in Korea. *Animals* 12, 2786, 2022. <https://doi.org/10.3390/ani12202786>
- Bahl P, Doolan C, de Silva C, Chughtai AA, Bourouiba L, MacIntyre CR.** Airborne or droplet precautions for health workers treating COVID-19? *The Journal of Infectious Diseases* 225, 1561–8, 2022. <https://doi.org/10.1093/infdis/jiaa189>
- Barrs VR, Peiris M, Tam KWS, Law PYT, Brackman CJ, To EMW, Yu VYT, Chu DKW, Perera R, Sit THC.** SARS-CoV-2 in quarantined domestic cats from COVID-19 households or close contacts, Hong Kong, China. *Emerging Infectious Diseases* 26, 3071–4, 2020. <https://doi.org/10.3201/eid2612.202786>
- Berryhill EH, Magdesian KG, Aleman M, Pusterla N.** Clinical presentation, diagnostic findings, and outcome of adult horses with equine coronavirus infection at a veterinary teaching hospital: 33 cases (2012–2018). *Veterinary Journal* 248, 95–100, 2019. <https://doi.org/10.1016/j.tvjl.2019.05.001>
- Boklund A, Gortazar C, Pasquali P, Roberts H, Nielsen SS, Stahl K, Stegeman A, Baldinelli F, Broglia A, Van Der Stede Y, et al.** Monitoring of SARS-CoV-2 infection in mus-telids. *European Food Safety Authority Journal* 19, e06459, 2021. <https://doi.org/10.2903/j.efsa.2021.6459>
- Bosco-Lauth AM, Hartwig AE, Porter SM, Gordy PW, Nehring M, Byas AD, VandeWoude S, Ragan IK, Maison RM, Bowen RA.** Experimental infection of domestic dogs and cats with SARS-CoV-2: pathogenesis, transmission, and response to reexposure in cats. *Proceedings of the National Academy of Sciences of the USA* 117, 26382–8, 2020. <https://doi.org/10.1073/pnas.2013102117>
- Brussow H, Brussow L.** Clinical evidence that the pandemic from 1889 to 1891 commonly called the Russian flu might have been an earlier coronavirus pandemic. *Microbial Biotechnology* 14, 1860–70, 2021. <https://doi.org/10.1111/1751-7915.13889>
- Bushmaker T, Yinda CK, Morris DH, Holbrook MG, Gamble A, Adney D, Bushmaker C, van Doremalen N, Fischer RJ, Plowright RK, et al.** Comparative aerosol and surface stability of SARS-CoV-2 variants of concern. *bioRxiv*, 2022. <https://doi.org/10.1101/2022.11.21.517352>
- Calvet GA, Pereira SA, Ogrzewalska M, Pauvolid-Corrêa A, Resende PC, Tassinari WS, Costa AP, Keidel LO, da Rocha ASB, da Silva MFB, et al.** Investigation of SARS-CoV-2 infection in dogs and cats of humans diagnosed with COVID-19 in Rio de Janeiro, Brazil. *PLoS ONE* 16, e0250853, 2021. <https://doi.org/10.1371/journal.pone.0250853>
- \***CDC.** Prevalence of IgG antibody to SARS-associated coronavirus in animal traders – Guangdong Province, China, 2003. *Morbidity and Mortality Weekly Report* 52, 986–7, 2003
- \***CDC.** Coronaviruses. <https://www.cdc.gov/coronavirus/types.html> (accessed 29 November 2022). Centers for Disease Control and Prevention, Atlanta, GA, USA, 2020
- Cebra CK, Mattson DE, Baker RJ, Sonn RJ, Dearing PL.** Potential pathogens in feces from unweaned llamas and alpacas with diarrhea. *Journal of the American Veterinary Medical Association* 223, 1806–8, 2003. <https://doi.org/10.2460/javma.2003.223.1806>
- Chan JF, Yuan S, Kok K, To KK, Chu H, Yang J, Xing F, Liu J, Yip CC, Poon RW, et al.** A familial cluster of pneumonia associated with the 2019 novel coronavirus indicating person-to-person transmission: a study of a family cluster. *The Lancet* 395, 514–23, 2020a. [https://doi.org/10.1016/S0140-6736\(20\)30154-9](https://doi.org/10.1016/S0140-6736(20)30154-9)
- Chan JF, Zhang AJ, Yuan S, Poon VK, Chan CC, Lee AC, Chan WM, Fan Z, Tsoi HW, Wen L, et al.** Simulation of the clinical and pathological manifestations of coronavirus disease 2019 (COVID-19) in a golden Syrian hamster model: implications for disease pathogenesis and transmissibility. *Clinical Infectious Diseases* 71, 2428–46, 2020b. <https://doi.org/10.1093/cid/ciaa325>
- Cheng YR, Li X, Zhao X, Lin H.** Cell entry of animal coronaviruses. *Viruses* 13, 1977, 2021. <https://doi.org/10.3390/v13101977>
- Coronaviridae Study Group of the International Committee on Taxonomy of Viruses.** The species *Severe acute respiratory syndrome-related coronavirus: classifying 2019-nCoV and naming it SARS-CoV-2*. *Nature Microbiology* 5, 536–44, 2020. <https://doi.org/10.1038/s41564-020-0695-z>
- 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* 4, 3689–700, 2012. <https://doi.org/10.3390/v4123689>
- Damas J, Hughes GM, Keough KC, Painter CA, Persky NS, Corbo M, Hiller M, Koepfli KP, Pfenning AR, Zhao H, et al.** Broad host range of SARS-CoV-2 predicted by comparative and structural analysis of ACE2 in vertebrates. *Proceedings of the National Academy of Sciences of the USA* 117, 22311–22, 2020. <https://doi.org/10.1073/pnas.2010146117>
- de Oliveira-Filho EF, de Carvalho OV, Carneiro IO, Fernandes FD, Vaz SN, Pedroso C, Gonzalez-Auza L, Urbietta VC, Kühne A, Mayoral R, et al.** Frequent infection of cats with SARS-CoV-2 irrespective of pre-existing

- enzootic coronavirus immunity, Brazil 2020. *Frontiers in Immunology* 13, 857322, 2022. <https://doi.org/10.3389/fimmu.2022.857322>
- de Wit JJS, Cook JKA.** Spotlight on avian coronaviruses. *Avian Pathology* 49, 313–6, 2020. <https://doi.org/10.1080/03079457.2020.1761010>
- Decaro N, Buonavoglia C.** Canine coronavirus: not only an enteric pathogen. *Veterinary Clinics of North America: Small Animal Practice* 41, 1121–32, 2011. <https://doi.org/10.1016/j.cvsm.2011.07.005>
- Deng J, Jin Y, Liu Y, Sun J, Hao L, Bai J, Huang T, Lin D, Jin Y, Tian K.** Serological survey of SARS-CoV-2 for experimental, domestic, companion and wild animals excludes intermediate hosts of 35 different species of animals. *Transboundary and Emerging Diseases* 67, 1745–9, 2020. <https://doi.org/10.1111/tbed.13577>
- Dicken SJ, Murray MJ, Thorne LG, Reuschl AK, Forrest C, Ganeshalingham M, Muir L, Kalemera MD, Palor M, McCoy LE, et al.** Characterisation of B.1.1.7 and pangolin coronavirus spike provides insights on the evolutionary trajectory of SARS-CoV-2. *bioRxiv*, 2021. <https://doi.org/10.1101/2021.03.22.436468>
- Dileepan M, Di D, Huang Q, Ahmed S, Heinrich D, Ly H, Liang Y.** Seroprevalence of SARS-CoV-2 (COVID-19) exposure in pet cats and dogs in Minnesota, USA. *Virulence* 12, 1597–609, 2021. <https://doi.org/10.1080/21505594.2021.1936433>
- Drosten C, Kellam P, Memish ZA.** Evidence for camel-to-human transmission of MERS coronavirus. *New England Journal of Medicine* 371, 1359–60, 2014. <https://doi.org/10.1056/NEJMc1409847>
- Epstein JH, Anthony SJ.** Viral discovery as a tool for pandemic preparedness. *Revue Scientifique et Technique* 36, 499–512, 2017. <https://doi.org/10.20506/rst.36.2.2669>
- Erls K, Brownlie J.** Canine respiratory coronavirus: an emerging pathogen in the canine infectious respiratory disease complex. *Veterinary Clinics of North America: Small Animal Practice* 38, 815–25, 2008. <https://doi.org/10.1016/j.cvsm.2008.02.008>
- Fang P, Fang L, Zhang H, Xia S, Xiao S.** Functions of coronavirus accessory proteins: overview of the state of the art. *Viruses* 13, 1139, 2021. <https://doi.org/10.3390/v13061139>
- Fenwick C, Croxatto A, Coste AT, Pojer F, André C, Pellaton C, Farina A, Campos J, Hacker D, Lau K, et al.** Changes in SARS-CoV-2 spike versus nucleoprotein antibody responses impact the estimates of infections in population-based seroprevalence studies. *Journal of Virology* 95, e01828–20, 2021. <https://doi.org/10.1128/JVI.01828-20>
- Focosi D, Maggi F.** Recombination in coronaviruses, with a focus on SARS-CoV-2. *Viruses* 14, 1239, 2022. <https://doi.org/10.3390/v14061239>
- Freuling CM, Breithaupt A, Muller T, Sehl J, Balkema-Buschmann A, Rissmann M, Klein A, Wylezich C, Hoper D, Wernike K, et al.** Susceptibility of raccoon dogs for experimental SARS-CoV-2 infection. *Emerging Infectious Diseases* 26, 2982–5, 2020. <https://doi.org/10.3201/eid2612.203733>
- Fritz M, Rosolen B, Krafft E, Becquart P, Elguero E, Vraskikh O, Denolly S, Boson B, Vanhomwegen J, Gouilh MA, et al.** High prevalence of SARS-CoV-2 antibodies in pets from COVID-19+ households. *One Health* 11, 100192, 2021. <https://doi.org/10.1016/j.onehlt.2020.100192>
- Fritz M, de Riols de Fonclare D, Garcia D, Beurlet S, Becquart P, Rosolen SG, Briend-Marchal A, Leroy EM.** First evidence of natural SARS-CoV-2 infection in domestic rabbits. *Veterinary Sciences* 9, 49, 2022. <https://doi.org/10.3390/vetsci9020049>
- Gaudreault NN, Trujillo JD, Carossino M, Meekins DA, Morozov I, Madden DW, Indran SV, Bold D, Balaraman V, Kwon T, et al.** SARS-CoV-2 infection, disease and transmission in domestic cats. *Emerging Microbes & Infections* 9, 2322–32, 2020. <https://doi.org/10.1080/22221751.2020.1833687>
- Gilbert PB, Donis RO, Koup RA, Fong Y, Plotkin SA, Follmann D.** A COVID-19 milestone attained – a correlate of protection for vaccines. *New England Journal of Medicine* 387, 2203–6, 2022. <https://doi.org/10.1056/NEJMp2211314>
- Gorbalenya AE, Enjuanes L, Ziebuhr J, Snijder EJ.** Nidovirales: evolving the largest RNA virus genome. *Virus Research* 117, 17–37, 2006. <https://doi.org/10.1016/j.virusres.2006.01.017>
- Grome HN, Meyer B, Read E, Buchanan M, Cushing A, Sawatzki K, Levinson KJ, Thomas LS, Perry Z, Uehara A, et al.** SARS-CoV-2 outbreak among Malayan tigers and humans, Tennessee, USA, 2020. *Emerging Infectious Diseases* 28, 833–6, 2022. <https://doi.org/10.3201/eid2804.212219>
- Guan Y, Zheng BJ, He YQ, Liu XL, Zhuang ZX, Cheung CL, Luo SW, Li PH, Zhang LJ, Guan YJ, et al.** Isolation and characterization of viruses related to the SARS coronavirus from animals in southern China. *Science* 302, 276–8, 2003. <https://doi.org/10.1126/science.1087139>
- Guo Z, Wang Z, Zhang S, Li X, Li L, Li C, Cui Y, Fu R, Dong Y, Chi X, et al.** Aerosol and surface distribution of severe acute respiratory syndrome coronavirus 2 in hospital wards, Wuhan, China, 2020. *Emerging Infectious Diseases* 26, 1583–91, 2020. <https://doi.org/10.3201/eid2607.200885>
- Gussow AB, Auslander N, Faure G, Wolf YI, Zhang F, Koonin EV.** Genomic determinants of pathogenicity in SARS-CoV-2 and other human coronaviruses. *Proceedings of the National Academy of Sciences of the USA* 117, 15193–9, 2020. <https://doi.org/10.1073/pnas.2008176117>
- Haake C, Cook S, Pusterla N, Murphy B.** Coronavirus infections in companion animals: virology, epidemiology, clinical and pathologic features. *Viruses* 12, 1023, 2020. <https://doi.org/10.3390/v12091023>
- Hale VL, Dennis PM, McBride DS, Nolting JM, Madden C, Huey D, Ehrlich M, Grieser J, Winston J, Lombardi D, et al.** SARS-CoV-2 infection in free-ranging white-tailed deer. *Nature* 602, 481–6, 2022. <https://doi.org/10.1038/s41586-021-04353-x>
- Halfmann PJ, Hatta M, Chiba S, Maemura T, Fan S, Takeda M, Kinoshita N, Hattori SI, Sakai-Tagawa Y, Iwatsuki-Horimoto K, et al.** Transmission of SARS-CoV-2 in domestic cats. *New England Journal of Medicine* 383, 592–4, 2020. <https://doi.org/10.1056/NEJMc2013400>
- Hamer SA, Pauvolid-Corrêa A, Zecca IB, Davila E, Auckland LD, Roundy CM, Tang W, Torchetti MK, Killian ML, Jenkins-Moore M, et al.** SARS-CoV-2 infections and viral isolations among serially tested cats and dogs in households with infected owners in Texas, USA. *Viruses* 13, 938, 2021. <https://doi.org/10.3390/v13050938>
- Hassell JM, Begon M, Ward MJ, Fèvre EM.** Urbanization and disease emergence: dynamics at the wildlife–livestock–human interface. *Trends in Ecology and Evolution* 32, 55–67, 2017. <https://doi.org/10.1016/j.tree.2016.09.012>
- Holmes EC, Goldstein SA, Rasmussen AL, Robertson DL, Crits-Christoph A, Wertheim JO, Anthony SJ, Barclay WS, Boni MF, Doherty PC, et al.** The origins of SARS-CoV-2: a critical review. *Cell* 184, 4848–56, 2021. <https://doi.org/10.1016/j.cell.2021.08.017>

- Huang AT, Garcia-Carreras B, Hitchings MDT, Yang B, Katzelnick LC, Rattigan SM, Borgert BA, Moreno CA, Solomon BD, Rodriguez-Barraquer I, et al.** A systematic review of antibody mediated immunity to coronaviruses: kinetics, correlates of protection, and association with severity. *Nature Communications* 11, 4704, 2020a. <https://doi.org/10.1038/s41467-020-18450-4>
- Huang C, Wang Y, Li X, Ren L, Zhao J, Hu Y, Zhang L, Fan G, Xu J, Gu X, et al.** Clinical features of patients infected with 2019 novel coronavirus in Wuhan, China. *The Lancet* 395, 15–21, 2020b. [https://doi.org/10.1016/S0140-6736\(20\)30183-5](https://doi.org/10.1016/S0140-6736(20)30183-5)
- Jackson CB, Farzan M, Chen B, Choe H.** Mechanisms of SARS-CoV-2 entry into cells. *Nature Reviews: Molecular Cell Biology* 23, 3–20, 2022. <https://doi.org/10.1038/s41580-021-00418-x>
- Kan B, Wang M, Jing H, Xu H, Jiang X, Yan M, Liang W, Zheng H, Wan K, Liu Q, et al.** Molecular evolution analysis and geographic investigation of severe acute respiratory syndrome coronavirus-like virus in palm civets at an animal market and on farms. *Journal of Virology* 79, 11892–900, 2005. <https://doi.org/10.1128/JVI.79.18.11892-11900.2005>
- Kannekens-Jager MM, de Rooij MMT, de Groot Y, Biesbroeck E, de Jong MK, Pijnacker T, Smit LAM, Schuurman N, Broekhuizen-Stins MJ, Zhao S, et al.** SARS-CoV-2 infection in dogs and cats is associated with contact to COVID-19-positive household members. *Transboundary and Emerging Diseases* 69, 4034–40, 2022. <https://doi.org/10.1111/tbed.14713>
- Kayode AJ, Banji-Onisile FO, Olaniran AO, Okoh AI.** An overview of the pathogenesis, transmission, diagnosis, and management of endemic human coronaviruses: a reflection on the past and present episodes and possible future outbreaks. *Pathogens* 10, 1108, 2021. <https://doi.org/10.3390/pathogens10091108>
- Korner RW, Majjouti M, Alcazar MAA, Mahabir E.** Of mice and men: the coronavirus MHV and mouse models as a translational approach to understand SARS-CoV-2. *Viruses* 12, 880, 2020. <https://doi.org/10.3390/v12080880>
- Kuchipudi SV, Surendran-Nair M, Ruden RM, Yon M, Nissly RH, Vandegrift KJ, Nelli RK, Li L, Jayarao BM, Maranas CD, et al.** Multiple spillovers from humans and onward transmission of SARS-CoV-2 in white-tailed deer. *Proceedings of the National Academy of Sciences of the USA* 119, e2121644119, 2022. <https://doi.org/10.1073/pnas.2121644119>
- Kutter JS, de Meulder D, Bestebroer TM, Lexmond P, Mulders A, Richard M, Fouchier RAM, Herfst S.** SARS-CoV and SARS-CoV-2 are transmitted through the air between ferrets over more than one meter distance. *Nature Communications* 12, 1653, 2021. <https://doi.org/10.1038/s41467-021-21918-6>
- Lan J, Chen P, Liu W, Ren W, Zhang L, Ding Q, Zhang Q, Wang X, Ge J.** Structural insights into the binding of SARS-CoV-2, SARS-CoV, and hCoV-NL63 spike receptor-binding domain to horse ACE2. *Structure* 30, 1432–42, 2022. <https://doi.org/10.1016/j.str.2022.07.005>
- Lawton KOY, Arthur RM, Moeller BC, Barnum S, Pusterla N.** Investigation of the role of healthy and sick equids in the COVID-19 pandemic through serological and molecular testing. *Animals* 12, 614, 2022. <https://doi.org/10.3390/ani12050614>
- Licitra BN, Duhamel GE, Whittaker GR.** Canine enteric coronaviruses: emerging viral pathogens with distinct recombinant spike proteins. *Viruses* 6, 3363–76, 2014. <https://doi.org/10.3390/v6083363>
- Lin XD, Wang W, Hao Z, Wang Z, Guo W, Guan X, Wang M, Wang H, Zhou R, Li M, et al.** Extensive diversity of coronaviruses in bats from China. *Virology* 507, 1–10, 2017. <https://doi.org/10.1016/j.virol.2017.03.019>
- Lytras S, Xia W, Hughes J, Jiang X, Robertson DL.** The animal origin of SARS-CoV-2. *Science* 373, 968–70, 2021. <https://doi.org/10.1126/science.abh0117>
- Lytras S, Hughes J, Martin D, Swanepoel P, de Klerk A, Lourens R, Kosakovsky Pond SL, Xia W, Jiang X, Robertson DL.** Exploring the natural origins of SARS-CoV-2 in the light of recombination. *Genome Biology and Evolution* 14, evac018, 2022. <https://doi.org/10.1093/gbe/evac018>
- Mahallawi W, Ibrahim N.** Unexpected detection of anti-SARS-CoV-2 antibodies before the declaration of the COVID-19 pandemic. *Frontiers in Medicine* 9, 923715, 2022. <https://doi.org/10.3389/fmed.2022.923715>
- Martins M, Boggiatto PM, Buckley A, Cassmann ED, Falkenberg S, Caserta LC, Fernandes MHV, Kanipe C, Lager K, Palmer MV, et al.** From deer-to-deer: SARS-CoV-2 is efficiently transmitted and presents broad tissue tropism and replication sites in white-tailed deer. *PLoS Pathogens* 18, e1010197, 2022. <https://doi.org/10.1371/journal.ppat.1010197>
- McAloose D, Laverack M, Wang L, Killian ML, Caserta LC, Yuan F, Mitchell PK, Queen K, Mauldin MR, Cronk BD, et al.** From people to *Panthera*: natural SARS-CoV-2 infection in tigers and lions at the Bronx Zoo. *mBio* 11, e02220–20, 2020. <https://doi.org/10.1128/mBio.02220-20>
- Michelitsch A, Hoffmann D, Wernike K, Beer M.** Occurrence of antibodies against SARS-CoV-2 in the domestic cat population of Germany. *Vaccines* 8, 772, 2020. <https://doi.org/10.3390/vaccines8040772>
- Michelitsch A, Schon J, Hoffmann D, Beer M, Wernike K.** The second wave of SARS-CoV-2 circulation-antibody detection in the domestic cat population in Germany. *Viruses* 13, 1009, 2021. <https://doi.org/10.3390/v13061009>
- \*MPI. Registers and Lists for Pests and Diseases.** <https://www.mpi.govt.nz/biosecurity/how-to-find-report-and-prevent-pests-and-diseases/registers-and-lists/> (accessed 29 November 2022). Biosecurity New Zealand, Ministry for Primary Industries, Wellington, NZ, 2022
- Murray J, Kiupel M, Maes RK.** Ferret coronavirus-associated diseases. *Veterinary Clinics of North America: Exotic Animal Practice* 13, 543–60, 2010. <https://doi.org/10.1016/j.cvex.2010.05.010>
- Musso N, Costantino A, La Spina S, Finocchiaro A, Andronico F, Stracquadanio S, Liotta L, Visalli R, Emmanuele G.** New SARS-CoV-2 infection detected in an Italian pet cat by RT-qPCR from deep pharyngeal swab. *Pathogens* 9, 746, 2020. <https://doi.org/10.3390/pathogens9090746>
- Mykytyn AZ, Lamers MM, Okba NMA, Breugem TI, Schipper D, van den Doel PB, van Run P, van Amerongen G, de Waal L, Koopmans MPG, et al.** Susceptibility of rabbits to SARS-CoV-2. *Emerging Microbes & Infections* 10, 1–7, 2021. <https://doi.org/10.1080/22221751.2020.1868951>
- Oreshkova N, Molenaar RJ, Vreman S, Harders F, Oude Munnink BB, Hakze-van der Honing RW, Gerhards N, Tolsma P, Bouwstra R, Sikkema R, et al.** SARS-CoV-2 infection in farmed minks, the Netherlands, April and May 2020. *EuroSurveillance* 25, 2001005, 2020. <https://doi.org/10.2807/1560-7917.ES.2020.25.23.2001005>
- Osterrieder N, Bertzbach LD, Dietert K, Abdelgawad A, Vladimirova D, Kunec D, Hoffmann D, Beer M, Gruber AD, Trimpert J.** Age-dependent progression of SARS-

- CoV-2 infection in Syrian hamsters. *Viruses* 12, 779, 2020. <https://doi.org/10.3390/v12070779>
- Parrish CR, Holmes EC, Morens DM, Park EC, Burke DS, Calisher CH, Laughlin CA, Saif LJ, Daszak P.** Cross-species virus transmission and the emergence of new epidemic diseases. *Microbiology and Molecular Biology Reviews* 72, 457–70, 2008. <https://doi.org/10.1128/MMBR.00004-08>
- Pasternak AO, Spaan WJM, Snijder EJ.** Nidovirus transcription: how to make sense ...? *Journal of General Virology* 87, 1403–21, 2006. <https://doi.org/10.1099/vir.0.81611-0>
- Pastorino B, Touret F, Gilles M, de Lamballerie X, Charrel RN.** Prolonged infectivity of SARS-CoV-2 in fomites. *Emerging Infectious Diseases* 26, 2256–7, 2020. <https://doi.org/10.3201/eid2609.201788>
- Patterson EI, Elia G, Grassi A, Giordano A, Desario C, Medardo M, Smith SL, Anderson ER, Prince T, Patterson GT, et al.** Evidence of exposure to SARS-CoV-2 in cats and dogs from households in Italy. *Nature Communications* 11, 6231, 2020. <https://doi.org/10.1038/s41467-020-20097-0>
- Pedersen NC.** An update on feline infectious peritonitis: virology and immunopathogenesis. *Veterinary Journal* 201, 123–32, 2014. <https://doi.org/10.1016/j.tvjl.2014.04.017>
- Plowright RK, Parrish CR, McCallum H, Hudson PJ, Ko AI, Graham AL, Lloyd-Smith JO.** Pathways to zoonotic spillover. *Nature Reviews: Microbiology* 15, 502–10, 2017. <https://doi.org/10.1038/nrmicro.2017.45>
- Poon LL, Chu DK, Chan KH, Wong OK, Ellis TM, Leung YH, Lau SK, Woo PC, Suen KY, Yuen KY, et al.** Identification of a novel coronavirus in bats. *Journal of Virology* 79, 2001–9, 2005. <https://doi.org/10.1128/JVI.79.4.2001-2009.2005>
- Pratelli A, Buonavoglia A, Lanave G, Tempesta M, Camero M, Martella V, Decaro N.** One world, one health, one virology of the mysterious labyrinth of coronaviruses: the canine coronavirus affair. *Lancet Microbe* 2, e646–7, 2021. [https://doi.org/10.1016/S2666-5247\(21\)00282-2](https://doi.org/10.1016/S2666-5247(21)00282-2)
- Pusterla N, Chaillon A, Ignacio C, Smith DM, Barnum S, Lawton KOY, Smith G, Pickering B.** SARS-CoV-2 seroconversion in an adult horse with direct contact to a COVID-19 individual. *Viruses* 14, 1047, 2022. <https://doi.org/10.3390/v14051047>
- Ramassy L, Oumarou Hama H, Costedoat C, Signoli M, Verna E, La Scola B, Aboudharam G, Barbieri R, Drancourt M.** Paleoserology points to coronavirus as possible causative pathogens of the 'Russian flu'. *Microbial Biotechnology* 15, 1943–5, 2022. <https://doi.org/10.1111/1751-7915.14058>
- Rasmussen TB, Fonager J, Jorgensen CS, Lassaunière R, Hammer AS, Quaade ML, Boklund A, Lohse L, Strandbygaard B, Rasmussen M, et al.** Infection, recovery and re-infection of farmed mink with SARS-CoV-2. *PLoS Pathogens* 17, e1010068, 2021. <https://doi.org/10.1371/journal.ppat.1010068>
- Roundy CM, Nunez CM, Thomas LF, Auckland LD, Tang W, Richison III JJ, Green BR, Hilton CD, Cherry MJ, Pauvolid-Corrêa A, et al.** High seroprevalence of SARS-CoV-2 in white-tailed deer (*Odocoileus virginianus*) at one of three captive cervid facilities in Texas. *Microbiology Spectrum* 10, e0057622, 2022. <https://doi.org/10.1128/spectrum.00576-22>
- Sailleau C, Dumarest M, Vanhomwegen J, Delaplace M, Caro V, Kwasiorski A, Hourdel V, Chevaillier P, Barbarino A, Comtet L, et al.** First detection and genome sequencing of SARS-CoV-2 in an infected cat in France. *Transboundary and Emerging Diseases* 67, 2324–8, 2020. <https://doi.org/10.1111/tbed.13659>
- Schlottau K, Rissmann M, Graaf A, Schon J, Sehl J, Wylezich C, Hoper D, Mettenleiter TC, Balkema-Buschmann A, Harder T, et al.** SARS-CoV-2 in fruit bats, ferrets, pigs, and chickens: an experimental transmission study. *Lancet Microbe* 1, e218–25, 2020. [https://doi.org/10.1016/S2666-5247\(20\)30089-6](https://doi.org/10.1016/S2666-5247(20)30089-6)
- Segalés J, Puig M, Rodon J, Avila-Nieto C, Carrillo J, Cantero G, Terrón MT, Cruz S, Parera M, Noguera-Julián M, et al.** Detection of SARS-CoV-2 in a cat owned by a COVID-19-affected patient in Spain. *Proceedings of the National Academy of Sciences of the USA* 117, 24790–3, 2020. <https://doi.org/10.1073/pnas.2010817117>
- Shi J, Wen Z, Zhong G, Yang H, Wang C, Huang B, Liu R, He X, Shuai L, Sun Z, et al.** Susceptibility of ferrets, cats, dogs, and other domesticated animals to SARS-coronavirus 2. *Science* 368, 1016–20, 2020. <https://doi.org/10.1126/science.abb7015>
- Sit THC, Brackman CJ, Ip SM, Tam KWS, Law PYT, To EMW, Yu VYT, Sims LD, Tsang DNC, Chu DKW, et al.** Infection of dogs with SARS-CoV-2. *Nature* 586, 776–8, 2020. <https://doi.org/10.1038/s41586-020-2334-5>
- Song Z, Xu Y, Bao L, Zhang L, Yu P, Qu Y, Zhu H, Zhao W, Han Y, Qin C.** From SARS to MERS, thrusting coronaviruses into the spotlight. *Viruses* 11, 59, 2019. <https://doi.org/10.3390/v11010059>
- Souris M, Tshilolo L, Parzy D, Lobaloba Ingoba L, Ntoui F, Kamgaing R, Ndour M, Mbongi D, Phoba B, Tshilolo MA, et al.** Pre-pandemic cross-reactive immunity against SARS-CoV-2 among central and west African populations. *Viruses* 14, 2259, 2022. <https://doi.org/10.3390/v14102259>
- Sreedharan J, Nair SC, Muttappallymyalil J, Gopakumar A, Eapen NT, Satish KP, Manda V.** Case fatality rates of COVID-19 across the globe: are the current draconian measures justified? *Journal of Public Health* 30, 2575–83, 2021. <https://doi.org/10.1007/s10389-021-01491-4>
- Stevanovic V, Vilibic-Cavlek T, Tabain I, Benvin I, Kovac S, Hruskar Z, Mauric M, Milasincic L, Antolasic L, Skrinjaric A, et al.** Seroprevalence of SARS-CoV-2 infection among pet animals in Croatia and potential public health impact. *Transboundary and Emerging Diseases* 68, 1767–73, 2021. <https://doi.org/10.1111/tbed.13924>
- Stout AE, André NM, Jaimes JA, Millet JK, Whittaker GR.** Coronaviruses in cats and other companion animals: where does SARS-CoV-2/COVID-19 fit? *Veterinary Microbiology* 247, 108777, 2020. <https://doi.org/10.1016/j.vetmic.2020.108777>
- Su C, He J, Han P, Bai B, Li D, Cao J, Tian M, Hu Y, Zheng A, Niu S, et al.** Molecular basis of mink ACE2 binding to SARS-CoV-2 and its mink-derived variants. *Journal of Virology* 96, e0081422, 2022. <https://doi.org/10.1128/jvi.00814-22>
- 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. *Emerging Infectious Diseases* 26, 3074–6, 2020. <https://doi.org/10.3201/eid2612.202989>
- Tellier R.** COVID-19: the case for aerosol transmission. *Interface Focus* 12, 20210072, 2022. <https://doi.org/10.1098/rsfs.2021.0072>
- Temmam S, Barbarino A, Maso D, Behillil S, Enouf V, Huon C, Jarraud A, Chevallier L, Backovic M, Perot P, et al.** Absence of SARS-CoV-2 infection in cats and dogs in close contact with a cluster of COVID-19 patients in a veterinary campus. *One Health* 10, 100164, 2020. <https://doi.org/10.1016/j.onehlt.2020.100164>
- Thakor JC, Dinesh M, Manikandan R, Bindu S, Sahoo M, Sahoo D, Dhawan M, Pandey MK, Tiwari R, Emran TB, et al.** Swine coronaviruses (SCoVs) and their emerging threats to swine population, inter-species transmission, exploring the susceptibility of pigs for SARS-CoV-2 and zoonotic concerns. *Veterinary Quarterly* 42, 125–47, 2022. <https://doi.org/10.1080/01652176.2022.2079756>

- Trichel AM.** Overview of nonhuman primate models of SARS-CoV-2 infection. *Comparative Medicine* 71, 411–32, 2021. <https://doi.org/10.30802/AALAS-CM-20-000119>
- Tu C, Cramer G, Kong X, Chen J, Sun Y, Yu M, Xiang H, Xia X, Liu S, Ren T, et al.** Antibodies to SARS coronavirus in civets. *Emerging Infectious Diseases* 10, 2244–8, 2004. <https://doi.org/10.3201/eid1012.040520>
- van Doremalen N, Bushmaker T, Morris DH, Holbrook MG, Gamble A, Williamson BN, Tamin A, Harcourt JL, Thornburg NJ, Gerber SI, et al.** Aerosol and surface stability of SARS-CoV-2 as compared with SARS-CoV-1. *New England Journal of Medicine* 382, 1564–7, 2020. <https://doi.org/10.1056/NEJMc2004973>
- Vergara-Alert J, van den Brand JM, Widagdo W, Muñoz MT, Raj S, Schipper D, Solanes D, Cerdón I, Bensaïd A, Haagmans BL, et al.** Livestock susceptibility to infection with Middle East respiratory syndrome coronavirus. *Emerging Infectious Diseases* 23, 232–40, 2017. <https://doi.org/10.3201/eid2302.161239>
- Vijgen L, Keyaerts E, Moes E, Thoelen I, Wollants E, Lemey P, Vandamme AM, Van Ranst M.** Complete genomic sequence of human coronavirus OC43: molecular clock analysis suggests a relatively recent zoonotic coronavirus transmission event. *Journal of Virology* 79, 1595–604, 2005. <https://doi.org/10.1128/JVI.79.3.1595-1604.2005>
- Villanueva-Saz S, Giner J, Tobajas AP, Pérez MD, González-Ramírez AM, Macías-León J, González A, Verde M, Yzuel A, Hurtado-Guerrero R, et al.** Serological evidence of SARS-CoV-2 and co-infections in stray cats in Spain. *Transboundary and Emerging Diseases* 69, 1056–64, 2022a. <https://doi.org/10.1111/tbed.14062>
- Villanueva-Saz S, Martínez M, Giner J, González A, Tobajas AP, Pérez MD, Lira-Navarrete E, González-Ramírez AM, Macías-León J, Verde M, et al.** A cross-sectional serosurvey of SARS-CoV-2 and co-infections in stray cats from the second wave to the sixth wave of COVID-19 outbreaks in Spain. *Veterinary Research Communications*, 1–15, 2022b. <https://doi.org/10.1007/s11259-022-10016-7>
- Virtanen J, Aaltonen K, Kegler K, Venkat V, Niamsap T, Kareinen L, Malmgren R, Kivelä O, Atanasova N, Österlund P, et al.** Experimental infection of mink with SARS-COV-2 Omicron variant and subsequent clinical disease. *Emerging Infectious Diseases* 28, 1286–8, 2022. <https://doi.org/10.3201/eid2806.220328>
- Vlasova AN, Saif LJ.** Bovine coronavirus and the associated diseases. *Frontiers in Veterinary Science* 8, 643220, 2021. <https://doi.org/10.3389/fvets.2021.643220>
- Vlasova AN, Diaz A, Dantje D, Xiu L, Toh TH, Lee JS, Saif LJ, Gray GC.** Novel canine coronavirus isolated from a hospitalized patient with pneumonia in east Malaysia. *Clinical Infectious Diseases* 74, 446–54, 2022. <https://doi.org/10.1093/cid/ciab456>
- Wang LF, Eaton BT.** Bats, civets and the emergence of SARS. *Current Topics in Microbiology and Immunology* 315, 325–44, 2007. [https://doi.org/10.1007/978-3-540-70962-6\\_13](https://doi.org/10.1007/978-3-540-70962-6_13)
- Wang W, Xu Y, Gao R, Lu R, Han K, Wu G, Tan W.** Detection of SARS-CoV-2 in different types of clinical specimens. *Journal of the American Medical Association* 323, 1843–4, 2020. <https://doi.org/10.1001/jama.2020.3786>
- \*WHO.** WHO MERS-CoV Global Summary and Risk Assessment. World Health Organization, Geneva, Switzerland, 2016
- \*WHO.** *Origins of SARS-CoV-2.* [https://apps.who.int/iris/bitstream/handle/10665/332197/WHO-2019-nCoV-FAQ-Virus\\_origin-2020.1-eng.pdf](https://apps.who.int/iris/bitstream/handle/10665/332197/WHO-2019-nCoV-FAQ-Virus_origin-2020.1-eng.pdf) (accessed 29 November 2022). World Health Organization, Geneva, Switzerland, 2020
- \*WOAH.** SARS-CoV-2 in Animals – Situation Report 20. <https://www.woah.org/app/uploads/2023/01/sars-cov-2-situation-report-20.pdf> (accessed 6 March 2023). World Organisation for Animal Health, Paris, France, 2022
- Wolters WJ, de Rooij MMT, Molenaar RJ, de Rond J, Vernooij JCM, Meijer PA, Oude Munnink BB, Sikkema RS, van der Spek AN, Spierenburg MAH, et al.** Manifestation of SARS-CoV-2 infections in mink related to host-, virus- and farm-associated factors, the Netherlands 2020. *Viruses* 14, 1754, 2022. <https://doi.org/10.3390/v14081754>
- Woo PC, Lau SK, Lam CS, Lau CC, Tsang AK, Lau JH, Bai R, Teng JL, Tsang CC, Wang M, et al.** Discovery of seven novel mammalian and avian coronaviruses in the genus *Deltacoronavirus* supports bat coronaviruses as the gene source of *Alphacoronavirus* and *Betacoronavirus* and avian coronaviruses as the gene source of *Gammacoronavirus* and *Deltacoronavirus*. *Journal of Virology* 86, 3995–4008, 2012. <https://doi.org/10.1128/JVI.06540-11>
- Woo PYC.** Family: *Coronaviridae.* <https://ictv.global/report/chapter/coronaviridae/coronaviridae> (accessed 13 March 2023). International Committee on Taxonomy of Viruses, 2023
- Zappulli V, Ferro S, Bonsembiante F, Brocca G, Calore A, Cavicchioli L, Centelleghè C, Corazzola G, De Vreese S, Gelain ME, et al.** Pathology of coronavirus infections: a review of lesions in animals in the One-Health perspective. *Animals* 10, 2377, 2020. <https://doi.org/10.3390/ani10122377>
- Zhang Q, Zhang H, Gao J, Huang K, Yang Y, Hui X, He X, Li C, Gong W, Zhang Y, et al.** A serological survey of SARS-CoV-2 in cat in Wuhan. *Emerging Microbes & Infections* 9, 2013–9, 2020. <https://doi.org/10.1080/22221751.2020.1817796>
- Zhang G, Li B, Yoo D, Qin T, Zhang X, Jia Y, Cui S.** Animal coronaviruses and SARS-CoV-2. *Transboundary and Emerging Diseases* 68, 1097–110, 2021. <https://doi.org/10.1111/tbed.13791>
- Zhao Y, Wang J, Kuang D, Xu J, Yang M, Ma C, Zhao S, Li J, Long H, Ding K, et al.** Susceptibility of tree shrew to SARS-CoV-2 infection. *Scientific Reports* 10, 16007, 2020. <https://doi.org/10.1038/s41598-020-72563-w>
- Zheng BJ, Wong KH, Zhou J, Wong KL, Young BW, Lu LW, Lee SS.** SARS-related virus predating SARS outbreak, Hong Kong. *Emerging Infectious Diseases* 10, 176–8, 2004. <https://doi.org/10.3201/eid1002.030533>
- Zhou P, Yang X, Wang X, Hu B, Zhang L, Zhang W, Si H, Zhu Y, Li B, Huang C, et al.** A pneumonia outbreak associated with a new coronavirus of probable bat origin. *Nature* 579, 270–3, 2020. <https://doi.org/10.1038/s41586-020-2012-7>
- Zhu N, Zhang D, Wang W, Li X, Yang B, Song J, Zhao X, Huang B, Shi W, Lu R, et al.** A novel coronavirus from patients with pneumonia in China, 2019. *New England Journal of Medicine* 382, 727–33, 2020. <https://doi.org/10.1056/NEJMoa2001017>