Zoonotic and anthroponotic potential of COVID-19 and its implications for public health

Amr El-Sayed¹ · Mohamed M. Abdel-Daim^{2,3} · Mohamed Kamel¹

Received: 16 November 2020 / Accepted: 5 September 2021 / Published online: 14 September 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Introduction

Coronaviruses belonging to the *Coronaviridae* family are enveloped, single-stranded, positive-sense RNA viruses. Several members of coronaviruses can infect man and animals to induce respiratory and enteric diseases. To date, seven coronaviruses (-CoV) are known to be human pathogens, namely HCoV-NL63, HCoV-229E, HCoV-OC43, HKU1, SARS-CoV, MERS-CoV, and SARS-CoV-2 (Contini et al. 2020). While SARS-CoV, MERS-CoV, and SARS-CoV-2 (*betacoronaviruses*) are responsible for serious and even fatal respiratory diseases, the remaining four viruses (HCoV-NL63 and HCoV-229E (*alpha* CoVs), and both HCoV-OC43 and HKU1 (*beta* CoVs)) are linked to 10–30% of the common cold and mild respiratory infections which can be accidentally fatal. Five out of these seven viruses (with the exception of HCoV-OC43 and HCoV-HKU1) seem more likely to have speciated from ancestor bat-associated viruses (El-Sayed and Kamel 2021). Both HCoV-OC43 and HCoV-HKU1 are likely to have direct ancestral links with rodents representing as their primordial hosts. Their human transmissions may occur via domestic animals such as pigs or cattle (Corman et al. 2018, Lau et al. 2015). Whether the viral

spillover required an intermediate host or was transmitted directly from bats to humans is not always known (Table 1) (Wu et al. 2020, Singla et al. 2020, El-Sayed and Kamel 2021). Over the past 20 years, in 2002, 2012, and 2019, serious new coronaviruses emerged for the first time, namely, SARS-CoV, MERS-CoV, and SARS-CoV-2. All of the three viruses had a zoonotic potential and represented a great public health threat (Tables 2, 3, and 4 and Figure 1) (Sharun et al. 2021, El-Sayed and Kamel 2021).

Since the emergence of SARS-CoV-2 in Wuhan, the virus carried out continuous mutation and progressive evolution. Among the main initiators for continuous mutations is the ability of SARS-CoV-2 to easily cross the interspecies barrier. Such mutations aim to adapt the viral genome to its new host species. For instance, in 2002, SARS-CoV required only two mutations (K479N and S487T) to spill over from palm civet to humans. Understanding the adaptation process can help in the control of possible epizootics (Garry 2021).

Moreover, in a recent work, mapping of 2034 different SARS-CoV-2 mutations could detect five antibody neutralization escape mutations of the virus (Starr et al. 2021). Out of these, three mutations raised extra worry: the UK (VOC 202012/01 (B.1.1.7 lineage)), the South African (VOC 202012/02 (B.1.351 lineage)), and the Brazilian Amazon (VOC 202101/02 (P.1)) variants (Burki 2021). This concern is based on the alarming data about higher fatalities among patients infected with the B.1.1.7 lineage when compared with other patients. In addition, this mutation is characterized by its higher spread rate and ability to escape from vaccinal protection (Iacobucci 2021, Muik et al. 2021, Supasa et al. 2021). SARS-CoV-2 continuous mutation represents a serious challenge for the international public health and the intensive efforts to control the pandemic through mass vaccination. The present work focuses on the zoonotic and reverse zoonotic aspects of SARS-CoV-2 and the most serious mutations of the virus.

Amr El-Sayed and Mohamed Kamel contributed equally to this work.

Responsible Editor: Philippe Garrigues

✉ Mohamed Kamel
m_salah@cu.edu.eg

¹ Department of Medicine and Infectious Diseases, Faculty of Veterinary Medicine, Cairo University, Giza 12211, Egypt

² Department of Pharmaceutical Sciences, Pharmacy Program, Batterjee Medical College, P.O. Box 6231, Jeddah 21442, Saudi Arabia

³ Pharmacology Department, Faculty of Veterinary Medicine, Suez Canal University, Ismailia 41522, Egypt

Table 1 The table lists the seven human pathogenic coronaviruses and provides an overview of their reservoir and intermediate hosts, year of discovery, and the needed receptors for a successful invasion

Zoonotic coronaviruses	Genus and subgenus	Natural reservoir	Intermediate host	Year of discovery	Receptors	Reference
SARS-CoV	β -CoV / <i>Sarbecovirus</i>	Bats	Civets Raccoon	2002	ACE2	(Wu et al. 2005) (Freuling et al. 2020)
MERS-CoV	β -CoV / <i>Merbecovirus</i>		Dromedary camels	2012	DPP4	(Azhar et al. 2019)
SARS-CoV-2	β -CoV / <i>Sarbecovirus</i>		? (Table 2)	2019	ACE2	(Zhu et al. 2020)
HCoV-NL63	α -CoV / <i>Setracovirus</i>		?	2004	ACE2	(Hofmann et al. 2005)
HCoV-229E	α -CoV / <i>Duvinacovirus</i>		Dromedary camels	1966	Aminopeptidase N (CD13)	(Gagneur et al. 2002, Corman et al. 2018, Lim et al. 2016)
HCoV-OC43	β -CoV / <i>Embecovirus</i>	Rats	Cattle and swine	1967	Glycan-based receptors carrying 9-O-acetylated sialic acid and major histocompatibility complex class I (HLA class I)	(Gagneur et al. 2002, Corman et al. 2018, Lim et al. 2016, Collins 1994)
HCoV-HKU1	β -CoV / <i>Embecovirus</i>		?	2005	Glycan-based receptors carrying 9-O-acetylated sialic acid and the major histocompatibility complex class I C molecule (HLA-C)	(Abdel-Moneim and Abdelwhab 2020, Lim et al. 2016, Chan et al. 2008)
Possibly zoonotic coronaviruses (in experimental studies)						
SADS-CoV	α -CoV / <i>Rhinacovirus</i>		Swine	2017	Not identified	(Edwards et al. 2020, Yang et al. 2020b)

Ongoing potential for SARS-CoV-2 transmission

The ongoing potential for zoonotic and anthroponotic SARS-CoV-2 transmission was highlighted following reports of viral spillover from animal to man transmission (mink to human) (Salajegheh Tazerji et al. 2020, Jo et al. 2020, Singla et al. 2020, Oude Munnink et al. 2020), and reverse spillover from human to animal transmission (man to dog and man to cat) (Salajegheh Tazerji et al. 2020, Mallapaty 2020, CDC 2020a, OIE 2020c). Since then, several studies were carried out to investigate the ability of SARS-CoV-2 to infect different animal species (Tables 2 and 4).

SARS-CoV-2 is believed to originate from horseshoe bats. However, the intermediate host of SARS-CoV-2 remains unknown (Swelum et al. 2020, El-Sayed and Kamel 2021). For the detection of the intermediate host of SARS-CoV-2, the serological approach was used by Zhang and his team (2020) who investigated sera from 35 different animal species (Zhang et al. 2020c). In parallel, the molecular approach for the determination of possible intermediate hosts was carried out by Dames and his team. To achieve this goal, the team determined first the susceptible (potential target) animal species which own the required receptors for SARS-CoV-2 binding. The team studied the angiotensin-converting enzyme 2 (ACE2) sequences of 410 vertebrate species, including 252

Table 2 Although the intermediate host of SARS-CoV-2 between bats and man is not definitely known, the table lists the animal species suggested to play an epidemiological role as SARS-CoV-2 intermediate hosts

Possible SARS-CoV-2 intermediate host	Reference
Pangolin	(Tang et al. 2020, Wong et al. 2020, Lam et al. 2020, Zhang et al. 2020e, Singla et al. 2020)
Bamboo rats	(Kumar O.R. et al. 2020)
Civets	(Kumar O.R. et al. 2020)
Turtle	(Liu et al. 2020, Hobbs and Reid 2020)
Frogs	(Zhang et al. 2020a)
Bovidae	(Luan et al. 2020)
Mink	(Oude Munnink et al. 2021).
Snakes (were excluded later from the list of possible intermediate hosts)	(Ji et al. 2020, Gautam et al. 2020)

Table 3 The zoonotic potential of SARS-CoV, MERS-CoV, and SARS-CoV-2 viruses is presented. The three viruses are bat-borne viruses and spread later to infect humans and other animal species

Coronavirus	Susceptible species	References
SARS-CoV	Bats, human, primates, raccoon dog, red fox, ferret, chicken, mink, civet cat, field rat, pigs	(Gautam et al. 2020, Chen et al. 2005, Wang et al. 2005)
MERS-CoV	Bats, human, primates, dromedary camels, alpaca, cattle, sheep, goat, buffaloes, donkey, horse, llama	(Gautam et al. 2020, Vergara-Alert et al. 2017, Wit et al. 2013)
SARS-CoV-2	Bats, human, dog, snake, pangolin, cats, ferrets, and other species (Table 4)	Table 4

mammals for their binding affinity to SARS-CoV-2 (Damas et al. 2020). This step was followed by focussing on animal species that might play a role as intermediate hosts for SARS-CoV-2 according to the ACE2 analysis profiles (Damas et al. 2020) (Table 2).

The study of Dames and his team (2020) and similar designed studies provided valuable data not only about possible intermediate hosts but also about animal species that might maintain the virus in circulation by acting as reservoir hosts. Out of the 103 investigated species, receptor analysis referred to the possible role of 21 species of primates, including Angola colobus and rhesus macaques, in addition to various species of cervid deer and cetacean species as SARS-CoV-2 potential reservoir. Two-thirds of the involved artiodactyl mammals (e.g., domesticated large and small ruminants, wild ruminants, as well as giraffe, gazelle, okapi, hippopotamus, and scimitar-horned oryx) showed a medium score for ACE2-

SARS-CoV-2 binding. Rodents varied in their susceptibility according to their species. Meanwhile, camels are unlikely to play a role in disease spread, although they are susceptible to other coronaviruses (Damas et al. 2020).

Among the susceptible farm animal species, the small and large ruminants could be infected with SARS-CoV-2 (Praharaj et al. 2020, Deng et al. 2020), water buffaloes (Praharaj et al. 2020), rabbits (Santini and Edwards 2020, Praharaj et al. 2020), horses (Santini and Edwards 2020, Praharaj et al. 2020), and pigeons (Frutos et al. 2020). Meanwhile, the poultry and farmed birds (except pigeons) are resistant to infection (Suarez et al. 2020). On the other hand, the role of pigs in the spread of SARS-CoV-2 is debated. While some reports confirm their epidemiological role (Wu et al. 2020), other reports list pigs among the animals of no epidemiological importance for COVID-19 transmission (Schlottau et al. 2020). The severity of clinical signs in

Table 4 The table enumerates the known animal species to be either susceptible or resistant to infection by SARS-CoV-2

SARS-CoV-2 susceptible species (besides human and bats)	Serology	Virus isolation	Reference
Dog	Yes	No	(Sit et al. 2020, OIE 2020c)
Cat	Yes	Yes	(OIE 2020b, 2020a, CDC 2020a)
Tigers	Yes	Yes	(APHIS 2020)
Lions	Yes	Yes	(APHIS 2020, USDA 2020, OIE 2020b, Jo et al. 2020)
Fox	Yes	Yes	(Praharaj et al. 2020)
Mink	Yes	Yes	(Oreshkova et al. 2020)
Ferrets	Yes	Yes	(Shi et al. 2020, Kim et al. 2020)
Monkey	Yes	Yes	(Munster et al. 2020, Lu et al. 2020)
Rhesus macaques, tree shrews, cynomolgus macaques, and African green monkeys	Yes	Yes	(Oude Munnink et al. 2021)
Mice	Yes	Yes	(Bao et al. 2020)
Hamsters	Yes	Yes	(Sia et al. 2020, Chan et al. 2020, Bao et al. 2020)
Tree shrew	Yes	?	(Zhao et al. 2020)
Raccoon	Yes	Yes	(Jo et al. 2020)
Rabbits	Yes	Yes	(Santini and Edwards 2020, Praharaj et al. 2020)
Horses	Yes	Yes	(Santini and Edwards 2020, Praharaj et al. 2020)
Large and small ruminants	Yes	Yes	(Praharaj et al. 2020, Deng et al. 2020)
Water buffaloes	Yes	Yes	(Praharaj et al. 2020)

Non-susceptible animal species including guinea pig, mouse, pigs, European hedgehog, lesser hedgehog tenrec, chicken, and ducks were found referent to vulnerability (Ruiz-Arrondo et al. 2020)(Shi et al. 2020; Schlottau et al. 2020)(Wu et al. 2020, Suarez et al. 2020)

Figure 1 Zoonotic potential of SARS-CoV, MERS-CoV, and SARS-CoV-2 viruses

animals varies in relation to the species susceptibility to the virus being almost asymptomatic in dogs, associated with moderate respiratory and/or gastrointestinal disorders in cats, and severe and almost fatal in minks (Hobbs and Reid 2020).

Although the high susceptibility of mink to SARS-CoV-2 infection is known since summer 2020, the decision of culling all farmed minks in Denmark was taken in the 5th of November after it was clear that the virus can spill back from mink to humans, and that the virus can mutate in the infected minks. The new mutations arose widespread public health concern as they occurred in the viral spike (S) glycoprotein, responsible for receptor binding. Such mutations may develop different invasion strategies to human cells and may not respond to already developed vaccines and therapies which may have catastrophic consequences on the international public health (Koopmans 2021, Frutos and Devaux 2020, Hammer et al. 2021). A third reason explaining the panic and public health concern in relation to mink infections is the high evolutionary rate of the virus in mink population when compared to its evolutionary rate in human or other animal species. The high density of animals in the cages allows not only the rapid uncontrolled spread of the virus in the population but also the subjection of human workers to higher viral load due to the high mink density in farms, which can potentially shorten the

generation interval for SARS-CoV-2 in humans (normally ranges around 4 to 5 days) (Oude Munnink et al. 2021).

The international concern was calmed down through the culling of the entire farmed mink population (15 million farmed minks) in Denmark, Spain, and the Netherlands. Later on, SARS-CoV-2 could be isolated from wild free-ranging American mink (*Neovison vison*) in Utah, USA (OIE 2021). In addition to wild free-ranging minks, the virus could also hit several mink farms in Utah, leading to severe economic losses. Mink to human viral transmission was reported where there were several staffers on Utah farms who attracted the infection after coming in contact with infected animals (Stout et al. 2021, Shriner et al. 2021, Cahan 2020). In addition to the USA, mink to human viral transmission could be confirmed in the Netherlands, Spain, Italy, Sweden, and Greece (Koopmans 2021).

The high susceptibility of minks to SARS-CoV-2 associated with virus exposure in high density populations in the farms favor sustained and rapid virus transmission. In the USA, not only mink with respiratory signs tested positively to SARS-CoV-2 but also other apparently healthy animals in the farm. The virus could spread from infected mink to infect healthy mink, and even dogs and cats in the farm (CDC 2020b). Phylogenetic analysis of SARS-CoV-2 isolates

detected in mink farms in the Netherlands revealed the presence of at least five different SARS-CoV-2 clusters (A, B, C, D, and E) which clustered with human isolates. Epidemiological data analysis indicated the zoonotic transmission of the virus from the farmed mink to the farm workers; however, the source of new human infections among the workers was not only limited to infected minks (Oude Munnink et al. 2020, Oude Munnink et al. 2021). In spite of their clustering in different clusters, and although several mutations were detected upon blasting the sequence of Wuhan strain with the Danish mink isolates, no amino acid substitutions occurred in all investigated mink samples. However, the high sequence diversity of mink isolates indicates the infection's persistence for several generations and its circulation in the mink population for a long time before being discovered (Oude Munnink et al. 2021).

The evolved minks' SARS-CoV-2 mutations in Denmark and the Netherlands circulated faster in mink and human population than the original wild strains. A mink-associated S protein mutation (Y453F mutation) was detected in all mink isolates from Denmark and several farms in the Netherlands. In this mutation, tyrosine substitution with phenylalanine at amino acid 453 occurs in the RBD region (receptor binding domain). The substitution in position 453 in viral S protein contacts the ACE2 receptors at position 34, which differs between human (Histidine) and mink (Tyrosine), which indicates the adaptation of the virus to mink cellular receptors (Larsen et al. 2021, Lassaunière et al. 2020).

However, the lack of the Y453F in mink isolates indicates its minor role in the disease pathogenesis in minks. The Y453F mutation was also isolated from human patients in Russia, the USA, and South Africa without known history of mink contact. Meanwhile, the S protein (S1 subunit) of about half of the mink isolates from Denmark poses an additional deletion of histidine and valine amino acids (positions 69 and 70). The same mutation was also reported in human patients in the UK, France, Germany, Norway, Sweden, Malaysia, New Zealand, Australia, Canada, and Côte d'Ivoire (Oude Munnink et al. 2021, Welkers et al. 2021).

Although the cluster-five SARS-CoV-2 mutation Y453F did not provide an additional advantage to the virus such as reduction of antibody neutralization capacity or escape from vaccinal protection, it enhanced the viral transmission process the providing fourfold higher ACE2 receptor binding affinity in comparison to the wild-type RBD-spike binding potential (Rafael Bayarri-Olmos et al. 2021).

In mink isolates, additional mutations were also reported in S protein sequence, including the I692V and M1229I mutations (Oude Munnink et al. 2021, Welkers et al. 2021) or L452M, F486L, and N501T mutations which were observed

in the receptor binding motif (RBM) of mink SARS-CoV-2 isolates (Elaswad et al. 2020). Notably, the N501T mutation improved the efficiency of SARS-CoV-2 binding to mink and ferret ACE2 receptors which indicate viral adaptation to the mustelid members. Similarly, infection of felines or canines with SARS-CoV-2 resulted in new mutations to adapt to its new host species (Garry 2021).

Different combinations of the previously listed mutations can occur which result in the presence of the different variants such as (453F), (69-70delHV, 453F), (69-70delHV, 453F, 1147L), and (69-70delHV, 453F, 692V, 1229I) isolates (Lassaunière et al. 2020).

However, the transmissibility potential of mink-related SARS-CoV-2 mutations remained as the original isolates. Even humans infected with cluster 5 did not show additional clinical signs. The prevalence of detection of mink related isolates in the population potentially dropped following culling of farmed minks (ECDC 2020).

Among the reported SARS-CoV-2 mutations are the D614G isolates characterized by the presence of a point mutation in the viral S protein which led to the substitution of an aspartic acid-to-glycine at amino acid position 614. Mutated isolates were not reported in original Wuhan isolates as they were first identified in late January 2020, and began emerging in March (Zhang et al. 2020b, Daniloski et al. 2021). At that time (March 2020), analysis of SARS-CoV-2 genomes revealed the emergence of four new genetic clusters characterized by being super-spreaders (SSs) (Yang et al. 2020a). The mutated isolates significantly shorter infection doubling time from more than 6 days in original Wuhan isolates to 3 days (Jackson et al. 2021).

This mutation provided a clear phenotypic advantage as it enabled better binding to human ACE2 receptors. The better binding affinity is not only reflected on the speed of spread (up to 8-fold more effective spread than wild-type S-Virus) but also enhanced the infectivity of the virus (3-fold higher viral load in the patients). Therefore, they could rapidly surpass other isolates in prevalence so that most of the circulating strains at present and supplanted S(D614) globally as the predominant form of the virus (Jackson et al. 2021).

The enhancement of the viral binding and ability to enter the cells through the substitution of aspartic acid-to-glycine amino acid is not fully understood. However, several hypotheses were suggested such as this substitution: (1) improves the cleavage efficiency of spike protein, (2) reform the shape of the S protein to favour better RBD-ACE2 interaction, (3) increase the density of the S proteins on the outer surface of the virus, (4) increases the stability of spike trimers, or possibly (5) the mutated viruses are more resistant to be neutralized by the antibodies (Jackson et al. 2021).

Documented cases of direct zoonotic and reverse zoonotic COVID-19

The zoonotic and reverse zoonotic SARS-CoV-2 transmission was reported between human and (1) domestic cats (man to cat) (Hosie et al. 2021) and cat to man (Zhang et al. 2020d, Patterson et al. 2020); (2) man to mink (Oreshkova et al. 2020, Oude Munnink et al. 2020) and mink to man (Oude Munnink et al. 2020); man to ferrets, mice, hamsters, and captive gorillas (Hedman et al. 2021). To the present time, the dogs, lions, and tigers are considered to be dead-end of the infection where man to dog (Sit et al. 2020, Patterson et al. 2020), lion (McAloose et al. 2020), and tiger (McAloose et al. 2020) transmission could be reported but not the reverse one (Figure 2).

One Health approach to control the disease

SARS-CoV-2 is a serious problem for the international community at present. The virus can invade various body systems and lead to organ dysfunction (El-Sayed et al. 2021a, El-Sayed et al. 2021b). The wide host range of SARS-CoV-2 and its geographical distributions raised the alarms of a panzootic accompanying the actual pandemic situation (Enserink 2020, Manes et al. 2020, WHO report 2020, James Gorman 2020). For the pandemic control, several COVID-19 vaccines are now commercially available to prevent further spread of the disease among humans (CDC 2019, Creech et al. 2021) (Table 5). However, despite the present restricted biosecurity measures and early warning surveillance, immunization of human population alone is not enough as the virus started to endemize in all susceptible species to

prevent viral spillover back to humans. It is well confirmed that SARS-CoV-2 can infect several domestic and wild animal species and circulate in wild animals. It cannot be excluded that the virus will continue to mutate. Further evolution towards higher fatality or potential to spread, or the occurrence of new mutations is the ongoing present threat. The change in viral antigenicity may lead to failure of coverage by the already available vaccines, increase risk of re-infection, and failure of therapeutic benefits by the administration of monoclonal antibodies or convalescent patients' plasma, which would have catastrophic effects on global public health and economy. Therefore, it is important to apply a robust (One Health approach/Human-Animal-ecosystem) concept to combat the ongoing pandemic and future similar emerging zoonotic disease events (Sharun et al. 2021, Hobbs and Reid 2020). One of the urgent responses among the required measures is developing vaccines for veterinary uses in parallel to those adopted for human use. Pioneer trials to develop COVID-19 animal vaccines were carried out by Zoetis which developed a SARS-CoV-2 vaccine for domestic and zoo animals. The vaccine was primarily designed for and test in pet animals and could provide high protection and safety levels. Following the emergency culling of millions of farmed minks, the vaccine was shifted and adapted to minks (Zoetis 2021). However, in the San Diego Zoo, where at least three gorillas at the Safari Park were naturally infected with the disease, the remaining great apes were subjected to infection risk. Therefore, other non-human primates, including orangutans ($n=4$) and bonobos ($n=5$), were emergency vaccinated with Zoetis experimental vaccine (Petersen 2021, Jennewein 2021).

In conclusion, the clear interaction between humans and animal hosts susceptible to SARS-CoV-2 and their capability

Figure 2 Direct zoonotic and reverse zoonotic COVID-19 between humans and animals

Table 5 The commercially available vaccine for humans and protection against COVID-19. Source: CDC (2019), Creech et al. (2021) in addition to the homepages of the manufacturers

Producer	Types	Efficiency	Efficiency against South African isolate	Doses	Storage conditions
Human vaccines					
Oxford Astrazeneca	Viral vector vaccine (dsDNA encoding virus S protein protected in a virus carrier)	82%	10%	2 doses (12-week interval)	2–8 °C
J & J		72%	57%	1 dose	2–8 °C
Sputnik V	Encapsulated mRNA vaccine (mRNA encoding S protein protected in a lipid nanoparticle)	91%	?	2 doses (28-day apart)	2–8 °C
BioNTech/ Pfizer		95%	?	2 doses (3-week interval)	–70 °C
Moderna		94.1%	?	2 doses (28-day interval)	–20 °C
Novavax		Virus-like particle vaccine (coated nanoparticles with synthetic S protein and adjuvant)	89%	49%	2 doses (3 weeks apart)
Sinopharm	Inactivated vaccine	79%	?	2 doses (3 weeks apart)	2–8 °C
Animal vaccine					
Zoetis	Prepared for protection of dogs, cats, and minks Emergency use for orangutans and bonobos				

to host new mutations of the virus underlines the importance of developing One Health response strategy for emerging zoonotic disease events and the parallel implementation of disease control strategies in man and animals. The developed vaccines or antiviral preparations used for the control of COVID-19 should be adapted for human and domestic animals susceptible to SARS-CoV-2 to overcome the serious public health threat.

Author contribution AE and MK manuscript writing and revision. MMA conducted manuscript moderation and revision. All the authors had contributed, critically reviewed, revised, and approved the final manuscript.

Data availability Not applicable.

Declarations

Ethical approval Not applicable.

Consent to participate Not applicable

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

References

- Abdel-Moneim AS, Abdelwhab EM (2020) Evidence for SARS-CoV-2 infection of animal hosts. *Pathogens* 9(7):529. <https://doi.org/10.3390/pathogens9070529>
- APHIS (2020) APHIS. USDA statement on the confirmation of COVID-19 in a tiger in New York. Available online: https://www.aphis.usda.gov/aphis/newsroom/news/sa_by_date/sa-2020/NY-zoo-covid-19
- Azhar EI, Hui DSC, Memish ZA, Drosten C, Zumla A (2019) The Middle East respiratory syndrome (MERS). *Infect Dis Clin North Am* 33(4):891–905. <https://doi.org/10.1016/j.idc.2019.08.001>
- Bao L, Deng W, Huang B, Gao H, Liu J, Ren L, Wei Q, Yu P, Xu Y, Qi F, Qu Y, Li F, Lv Q, Wang W, Xue J, Gong S, Liu M, Wang G, Wang S et al (2020) The pathogenicity of SARS-CoV-2 in hACE2 transgenic mice. *Nature* 583(7818):830–833. <https://doi.org/10.1038/s41586-020-2312-y>
- Burki T (2021) Understanding variants of SARS-CoV-2. *Lancet* 397(10273):462. [https://doi.org/10.1016/S0140-6736\(21\)00298-1](https://doi.org/10.1016/S0140-6736(21)00298-1)
- Cahan E (2020) COVID-19 hits U.S. mink farms after ripping through Europe. *Science*. <https://doi.org/10.1126/science.abe3870>
- CDC (2019) CDC reports at <https://www.cdc.gov/coronavirus/2019-ncov/vaccines/different-vaccines.html>
- CDC (2020a) Confirmation of COVID-19 in two pet cats in New York. Available online: <https://www.cdc.gov/media/releases/2020/s0422-covid-19-cats-NYC.html>
- CDC (2020b) COVID-19 and animals. https://files.ssi.dk/Mink-cluster-5-short-report_AFO2. Accessed 13 Mar 2021
- Chan CM, Lau SKP, Woo PCY, Tse H, Zheng B-J, Chen L, Huang J-D, Yuen K-Y (2008) Identification of major histocompatibility complex class I c molecule as an attachment factor that facilitates coronavirus HKU1 spike-mediated infection. *J Virol* 83(2):1026–1035. <https://doi.org/10.1128/jvi.01387-08>
- Chan JF-W, Zhang AJ, Yuan S, Poon VK-M, Chan CC-S, Lee AC-Y, Chan W-M, Fan Z, Tsoi H-W, Wen L, Liang R, Cao J, Chen Y, Tang K, Luo C, Cai J-P, Kok K-H, Chu H, Chan K-H, Sridhar S, Chen Z, Chen H, To KK-W, Yuen K-Y (2020) 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:ciaa325*. <https://doi.org/10.1093/cid/ciaa325>
- Chen W, Yan M, Yang L, Ding B, He B, Wang Y, Liu X, Liu C, Zhu H, You B, Huang S, Zhang J, Mu F, Xiang Z, Feng X, Wen J, Fang J, Yu J, Yang H, Wang J (2005) SARS-associated coronavirus transmitted from human to pig. *Emerg Infect Dis* 11(3):446–448. <https://doi.org/10.3201/eid1103.040824>
- Collins AR (1994) Human coronavirus OC43 interacts with major histocompatibility complex class I molecules at the cell surface to establish infection. *Immunological Investigations* 23(4-5):313–321. <https://doi.org/10.3109/08820139409066826>
- Contini C, Caselli E, Martini F, Maritati M, Torreggiani E, Seraceni S, Vesce F, Perri P, Rizzo L, Tognon M (2020) COVID-19 is a

- multifaceted challenging pandemic which needs urgent public health interventions. *Microorganisms* 8(8). <https://doi.org/10.3390/microorganisms8081228>
- Corman VM, Muth D, Niemeyer D, Drosten C (2018) Hosts and sources of endemic human coronaviruses. *Adv Virus Res* 100:163–188. <https://doi.org/10.1016/bs.aivir.2018.01.001>
- Creech CB, Walker SC, Samuels RJ (2021) SARS-CoV-2 vaccines. *JAMA*. 325:1318–1320. <https://doi.org/10.1001/jama.2021.3199>
- Damas J, Hughes GM, Keough KC, Painter CA, Persky NS, Corbo M, Hiller M, Koepfli K-P, Pfenning AR, Zhao H, Genereux DP, Swofford R, Pollard KS, Ryder OA, Nweeia MT, Lindblad-Toh K, Teeling EC, Karlsson EK, Lewin HA (2020) Broad host range of SARS-CoV-2 predicted by comparative and structural analysis of ACE2 in vertebrates. *Proc Natl Acad Sci U S A* 117(36):22311–22322. <https://doi.org/10.1073/pnas.2010146117>
- Daniloski Z, Jordan TX, Ilmain JK, Guo X, Bhabha G, tenOever BR, Sanjana NE (2021) The Spike D614G mutation increases SARS-CoV-2 infection of multiple human cell types. *Elife* 10:e65365. <https://doi.org/10.7554/eLife.65365>
- Deng J, Jin Y, Liu Y, Sun J, Hao L, Bai J, Huang T, Lin D, Jin Y, Tian K (2020) Serological survey of SARS-CoV-2 for experimental, domestic, companion and wild animals excludes intermediate hosts of 35 different species of animals. *Transbound Emerg Dis* 67(4): 1745–1749. <https://doi.org/10.1111/tbed.13577>
- ECDC (2020) Detection of new SARS-CoV-2 variants related to mink – 12 November 2020. ECDC: Stockholm; 2020. available at <https://psnews.ro/wp-content/uploads/2020/11/document.pdf>
- Edwards CE, Yount BL, Graham RL, Leist SR, Hou YJ, Dinno KH, Sims AC, Swanson J, Gully K, Scobey TD, Cooley MR, Currie CG, Randell SH, Baric RS (2020) Swine acute diarrhea syndrome coronavirus replication in primary human cells reveals potential susceptibility to infection. *Proc Natl Acad Sci U S A* 117(43):26915–26925. <https://doi.org/10.1073/pnas.2001046117>
- Elaswad A, Fawzy M, Basiouni S, Shehata AA (2020) Mutational spectra of SARS-CoV-2 isolated from animals. *PeerJ* 8:e10609–e10609. <https://doi.org/10.7717/peerj.10609>
- El-Sayed A, Abdel-Daim MM, Kamel M (2021a) Causes of respiratory failure in COVID-19 patients. *Environ Sci Pollut Res* 28:1–6. <https://doi.org/10.1007/s11356-021-14200-1>
- El-Sayed A, Aleya L, Kamel M (2021b) COVID-19: a new emerging respiratory disease from the neurological perspective. *Environ Sci Pollut Res* 28:1–15. <https://doi.org/10.1007/s11356-021-12969-9>
- El-Sayed A, Kamel M (2021) Coronaviruses in humans and animals: the role of bats in viral evolution. *Environ Sci Pollut Res* 28:1–12. <https://doi.org/10.1007/s11356-021-12553-1>
- Enserink M (2020) Coronavirus rips through Dutch mink farms, triggering culls
- Freuling CM, Breithaupt A, Müller T, Sehl J, Balkema-Buschmann A, Rissmann M, Klein A, Wylezich C, Höper D, Wernike K, Aebischer A, Hoffmann D, Friedrichs V, Dorhoi A, Groschup MH, Beer M, Mettenleiter TC (2020) Susceptibility of raccoon dogs for experimental SARS-CoV-2 infection. *Emerg Infect Dis* 26(12):2982–2985. <https://doi.org/10.3201/eid2612.203733>
- Frutos R, Devaux CA (2020) Mass culling of minks to protect the COVID-19 vaccines: is it rational? *New Microbes New Infect* 38: 100816. <https://doi.org/10.1016/j.nmni.2020.100816>
- Frutos R, Serra-Cobo J, Chen T, Devaux CA (2020) COVID-19: time to exonerate the pangolin from the transmission of SARS-CoV-2 to humans. *Infect Genet Evol* 84:104493. <https://doi.org/10.1016/j.meegid.2020.104493>
- Gagneur A, Sizun J, Vallet S, Leger MC, Picard B, Talbot PJ (2002) Coronavirus-related nosocomial viral respiratory infections in a neonatal and paediatric intensive care unit: a prospective study. *J Hosp Infect* 51(1):59–64. <https://doi.org/10.1053/jhin.2002.1179>
- Garry RF (2021) Mutations arising in SARS-CoV-2 spike on sustained human-to-human transmission and human-to-animal passage. *Image* 908(1148):292
- Gautam A, Kaphle K, Shrestha B, Phuyal S (2020) Susceptibility to SARS, MERS, and COVID-19 from animal health perspective. *Open Vet J* 10(2):164–177. <https://doi.org/10.4314/ovj.v10i2.6>
- Hammer AS, Quaade ML, Rasmussen TB, Fonager J, Rasmussen M, Mundbjerg K, Lohse L, Strandbygaard B, Jørgensen CS, Alfaro-Núñez A, Rosenstjerne MW, Boklund A, Halasa T, Fomsgaard A, Belsham GJ, Bøtner A (2021) SARS-CoV-2 transmission between mink (Neovison vison) and Humans, Denmark. *Emerg Infect Dis* 27(2):547–551. <https://doi.org/10.3201/eid2702.203794>
- Hedman HD, Krawczyk E, Helmy YA, Zhang L, Varga C (2021) Host diversity and potential transmission pathways of SARS-CoV-2 at the human-animal interface. *Pathogens* 10(2):180. <https://doi.org/10.3390/pathogens10020180>
- Hobbs EC, Reid TJ (2020) Animals and SARS-CoV-2: species susceptibility and viral transmission in experimental and natural conditions, and the potential implications for community transmission. *Transbound Emerg Dis*. 68:1850–1867. <https://doi.org/10.1111/tbed.13885>
- Hofmann H, Pyrc K, van der Hoek L, Geier M, Berkhout B, Pöhlmann S (2005) Human coronavirus NL63 employs the severe acute respiratory syndrome coronavirus receptor for cellular entry. *Proc Natl Acad Sci U S A* 102(22):7988–7993. <https://doi.org/10.1073/pnas.0409465102>
- Hosie MJ, Hofmann-Lehmann R, Hartmann K, Egberink H, Truyen U, Addie DD, Belák S, Boucraut-Baralon C, Frymus T, Lloret A, Lutz H, Marsilio F, Pennisi MG, Tasker S, Thiry E, Möstl K (2021) Anthropogenic infection of cats during the 2020 COVID-19 pandemic. *Viruses* 13(2):185. <https://doi.org/10.3390/v13020185>
- Iacobucci G (2021) Covid-19: New UK variant may be linked to increased death rate, early data indicate. *BMJ*:n230. <https://doi.org/10.1136/bmj.n230>
- Jackson CB, Zhang L, Farzan M, Choe H (2021) Functional importance of the D614G mutation in the SARS-CoV-2 spike protein. *Biochem Biophys Res Commun* 538:108–115. <https://doi.org/10.1016/j.bbrc.2020.11.026>
- James Gorman (2020) NCBI news available at <https://bit.ly/38A9LjB>
- Jennwein C (2021) Orangutans and bonobos at zoo get experimental animal COVID vaccine. *Times of San Diego*
- Ji W, Wang W, Zhao X, Zai J, Li X (2020) Cross-species transmission of the newly identified coronavirus 2019-nCoV. *J Med Virol* 92(4): 433–440. <https://doi.org/10.1002/jmv.25682>
- Jo WK, Oliveira-Filho EF, Rasche A, Greenwood AD, Osterrieder K, Drexler JF (2020) Potential zoonotic sources of SARS-CoV-2 infections. *Transbound Emerg Dis*. 68:1824–1834. <https://doi.org/10.1111/tbed.13872>
- Kim Y-I, Kim S-G, Kim S-M, Kim E-H, Park S-J, Yu K-M, Chang J-H, Kim EJ, Lee S, Casel MAB, Um J, Song M-S, Jeong HW, van Lai D, Kim Y, Chin BS, Park J-S, Chung K-H, Foo S-S et al (2020) Infection and rapid transmission of SARS-CoV-2 in ferrets. *Cell Host Microbe* 27(5):704–709.e2. <https://doi.org/10.1016/j.chom.2020.03.023>
- Koopmans M (2021) SARS-CoV-2 and the human-animal interface: outbreaks on mink farms. *Lancet Infect Dis* 21(1):18–19. [https://doi.org/10.1016/S1473-3099\(20\)30912-9](https://doi.org/10.1016/S1473-3099(20)30912-9)
- Kumar O.R., V. Ramkumar, Pruthivishree BS, Pande T, Sinha DK, Singh BR, Dhama K, Malik YS (2020) SARS-CoV-2 (COVID-19): zoonotic origin and susceptibility of domestic and wild animals. *Journal of Pure and Applied Microbiology* 14(suppl 1):741–747. 10.22207/jpam.14.spl1.11
- Lam TT-Y, Jia N, Zhang Y-W, Shum MH-H, Jiang J-F, Zhu H-C, Tong Y-G, Shi Y-X, Ni X-B, Liao Y-S, Li W-J, Jiang B-G, Wei W, Yuan T-T, Zheng K, Cui X-M, Li J, Pei G-Q, Qiang X et al (2020) Identifying SARS-CoV-2-related coronaviruses in Malaysian

- pangolins. *Nature* 583(7815):282–285. <https://doi.org/10.1038/s41586-020-2169-0>
- Larsen HD, Fonager J, Lomholt FK, Dalby T, Benedetti G, Kristensen B, Urth TR, Rasmussen M, Lassaunière R, Rasmussen TB, Strandbygaard B, Lohse L, Chaine M, Møller KL, Berthelsen A-SN, Nørgaard SK, Sönksen UW, Boklund AE, Hammer AS et al (2021) Preliminary report of an outbreak of SARS-CoV-2 in mink and mink farmers associated with community spread, Denmark, June to November 2020. *Euro Surveill* 26(5):2100009. <https://doi.org/10.2807/1560-7917.ES.2021.26.5.210009>
- Lassaunière R, Fonager J, Rasmussen M, et al (2020) Working paper on SARS-CoV-2 spike mutations arising in Danish mink, their spread to humans and neutralization data
- Lau SKP, Woo PCY, Li KSM, Tsang AKL, Fan RYY, Luk HKH, Cai J-P, Chan K-H, Zheng B-J, Wang M, Yuen K-Y (2015) 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* 89(6):3076–3092. <https://doi.org/10.1128/JVI.02420-14>
- Lim YX, Ng YL, Tam JP, Liu DX (2016) Human coronaviruses: a review of virus-host interactions. *Diseases* 4(3):26. <https://doi.org/10.3390/diseases4030026>
- Liu Z, Xiao X, Wei X, Li J, Yang J, Tan H, Zhu J, Zhang Q, Wu J, Liu L (2020) Composition and divergence of coronavirus spike proteins and host ACE2 receptors predict potential intermediate hosts of SARS-CoV-2. *J Med Virol* 92(6):595–601. <https://doi.org/10.1002/jmv.25726>
- Lu S, Zhao Y, Yu W, Yang Y, Gao J, Wang J, Kuang D, Yang M, Yang J, Ma C, Xu J, Qian X, Li H, Zhao S, Li J, Wang H, Long H, Zhou J, Luo F, Ding K, Wu D, Zhang Y, Dong Y, Liu Y, Zheng Y, Lin X, Jiao L, Zheng H, Dai Q, Sun Q, Hu Y, Ke C, Liu H, Peng X (2020) Comparison of SARS-CoV-2 infections among 3 species of non-human primates. <https://doi.org/10.1101/2020.04.08.031807>
- Luan J, Jin X, Lu Y, Zhang L (2020) SARS-CoV-2 spike protein favors ACE2 from Bovidae and Cricetidae. *J Med Virol*:10.1002/jmv.25817 <https://doi.org/10.1002/jmv.25817>
- Mallapaty S (2020) Coronavirus can infect cats — dogs, not so much. *Nature*. <https://doi.org/10.1038/d41586-020-00984-8>
- Manes C, Gollakner R, Capua I (2020) Could Mustelids spur COVID-19 into a panzootic? *Veterinaria italiana*
- McAlouse D, Laverack M, Wang L, Killian ML, Caserta LC, Yuan F, Mitchell PK, Queen K, Mauldin MR, Cronk BD, Bartlett SL, Sykes JM, Zec S, Stokol T, Ingeman K, Delaney MA, Fredrickson R, Ivančić M, Jenkins-Moore M, Mozingo K, Franzen K, Bergeson NH, Goodman L, Wang H, Fang Y, Olmstead C, McCann C, Thomas P, Goodrich E, Elvinger F, Smith DC, Tong S, Slavinski S, Calle PP, Terio K, Torchetti MK, Diel DG (2020) From people to Panthera: natural SARS-CoV-2 infection in tigers and lions at the Bronx Zoo. <https://doi.org/10.1101/2020.07.22.213959>
- Muik A, Wallisch A-K, Sängner B, Swanson KA, Mühl J, Chen W, Cai H, Maurus D, Sarkar R, Türeci Ö, Dormitzer PR, Şahin U (2021) Neutralization of SARS-CoV-2 lineage B.1.1.7 pseudovirus by BNT162b2 vaccine-elicited human sera. *Science* 371(6534):1152–1153. <https://doi.org/10.1126/science.abg6105>
- Munster VJ, Feldmann F, Williamson BN, van Doremalen N, Pérez-Pérez L, Schulz J, Meade-White K, Okumura A, Callison J, Brumbaugh B, Avanzato VA, Rosenke R, Hanley PW, Saturday G, Scott D, Fischer ER, de Wit E (2020) Respiratory disease and virus shedding in rhesus macaques inoculated with SARS-CoV-2. *bioRxiv*:2020.03.21.001628. <https://doi.org/10.1101/2020.03.21.001628>
- OIE (2020a) A case of a Belgian cat positive for Covid-19. Available online: https://www.oie.int/fileadmin/Home/eng/Our_scientific_expertise/docs/pdf/COV-19/Belgium_28.03.20.pdf
- OIE (2020b) COVID-19 (SARS-COV-2), available under https://www.oie.int/wahis_2/public/wahid.php/Reviewreport/Review?reportid=34054
- OIE (2020c) COVID-19 (SARS-COV-2), Hong Kong (SAR - PRC) 2020. Available online: https://www.oie.int/wahis_2/public/wahid.php/Reviewreport/Review?page_refer=MapFullEventReport&reportid=33546. Accessed on 22 June 2020
- OIE (2021) Events in animals: OIE - World Organisation for Animal Health. <https://www.oie.int/en/scientific-expertise/specific-information-and-recommendations/questions-and-answers-on-2019-novel-coronavirus/events-in-animals>. Accessed 13 Mar 2021. 113Z
- Oreshkova N, Molenaar RJ, Vreman S, Harders F, Oude Munnink BB, der Honing H-v, Renate W, Gerhards N, Tolsma P, Bouwstra R, Sikkema RS, Tacken MG, de Rooij MM, Weesendorp E, Engelsma MY, Bruschke CJ, Am Smit L, Koopmans M, van der Poel WH, Stegeman A (2020) SARS-CoV-2 infection in farmed minks, the Netherlands, April and May 2020. *Euro Surveill* 25(23):2001005. <https://doi.org/10.2807/1560-7917.ES.2020.25.23.2001005>
- Oude Munnink BB, Sikkema RS, Nieuwenhuijse DF, Molenaar RJ, Munger E, Molenkamp R, van der Spek A, Tolsma P, Rietveld A, Brouwer M, Bouwmeester-Vincken N, Harders F, der Honing RH, Wegdam-Blans MC, Bouwstra RJ, GeurtsvanKessel C, van der Eijk, Annemiek A., Velkers FC, Smit LA, Stegeman A, van der Poel, Wim H.M., Koopmans MP (2020) Jumping back and forth: anthroponotic and zoonotic transmission of SARS-CoV-2 on mink farms. <https://doi.org/10.1101/2020.09.01.277152>
- Oude Munnink BB, Sikkema RS, Nieuwenhuijse DF, Molenaar RJ, Munger E, Molenkamp R, van der Spek A, Tolsma P, Rietveld A, Brouwer M, Bouwmeester-Vincken N, Harders F, Hakze-van der Honing R, Wegdam-Blans MCA, Bouwstra RJ, GeurtsvanKessel C, van der Eijk AA, Velkers FC, Smit LAM et al (2021) Transmission of SARS-CoV-2 on mink farms between humans and mink and back to humans. *Science* 371(6525):172–177. <https://doi.org/10.1126/science.abe5901>
- Patterson EI, Elia G, Grassi A, Giordano A, Desario C, Medardo M, Smith SL, Anderson ER, Prince T, Patterson GT, Lorusso E, Lucente MS, Lanave G, Lauzi S, Bonfanti U, Stranieri A, Martella V, Solari Basano F, Barrs VR et al (2020) Evidence of exposure to SARS-CoV-2 in cats and dogs from households in Italy. *Nat Commun* 11(1):6231. <https://doi.org/10.1038/s41467-020-20097-0>
- Petersen J (2021) In what's believed to be a first among great apes, several gorillas at San Diego Zoo in the US have been infected with COVID-19. | World News Australia. <https://search.informit.org/doi/10.3316/TVNEWS.TSM202101120060>. Accessed 13 Mar 2021.452Z
- Praharaj MR, Garg P, Khan RIN, Sharma S, Panigrahi M, Mishra BP, Mishra B, Gandham RK, Singh RK, Majumdar S (2020) Prediction analysis of SARS-COV-2 entry in Livestock and Wild animals. *bioRxiv*
- Rafael Bayarri-Olmos, Anne Rosbjerg, Laust Bruun Johnsen, Charlotte Helgstrand, Theresa Bak-Thomsen, Peter Garred, Mikkel-Ole Skjoedt (2021) The SARS-CoV-2 Y453F mink variant displays a striking increase in ACE-2 affinity but does not challenge antibody neutralization. *bioRxiv*:2021.01.29.428834. <https://doi.org/10.1101/2021.01.29.428834>
- Ruiz-Arrondo I, Portillo A, Palomar AM, Santibanez S, Santibanez P, Cervera C, Oteo JA (2020) Detection of SARS-CoV-2 in pets living with COVID-19 owners diagnosed during the COVID-19 lockdown in Spain: a case of an asymptomatic cat with SARS-CoV-2 in Europe. <https://doi.org/10.1101/2020.05.14.20101444>
- Salajegheh Tazerji S, Magalhães Duarte P, Rahimi P, Shahabinejad F, Dhakal S, Singh Malik Y, Shehata AA, Lama J, Klein J, Safdar M, Rahman MT, Filipiak KJ, Rodríguez-Morales AJ, Sobur MA, Kabir F, Vazir B, Mboera L, Caporale M, Islam MS et al (2020) Transmission of severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) to animals: an updated review. *J Transl Med* 18(1):358. <https://doi.org/10.1186/s12967-020-02534-2>

- Santini JM, Edwards SJL (2020) Host range of SARS-CoV-2 and implications for public health. *Lancet Microbe* 1(4):e141–e142. [https://doi.org/10.1016/S2666-5247\(20\)30069-0](https://doi.org/10.1016/S2666-5247(20)30069-0)
- Schlottau K, Rissmann M, Graaf A, Schön J, Sehl J, Wylezich C, Höper D, Mettenleiter TC, Balkema-Buschmann A, Harder T, Grund C, Hoffmann D, Breithaupt A, Beer M (2020) SARS-CoV-2 in fruit bats, ferrets, pigs, and chickens: an experimental transmission study. *Lancet Microbe* 1(5):e218–e225. [https://doi.org/10.1016/S2666-5247\(20\)30089-6](https://doi.org/10.1016/S2666-5247(20)30089-6)
- Sharun K, Tiwari R, Natesan S, Dhama K (2021) SARS-CoV-2 infection in farmed minks, associated zoonotic concerns, and importance of the One Health approach during the ongoing COVID-19 pandemic. *Vet Q* 41(1):50–60. <https://doi.org/10.1080/01652176.2020.1867776>
- Shi J, Wen Z, Zhong G, Yang H, Wang C, Huang B, Liu R, He X, Shuai L, Sun Z, Zhao Y, Liu P, Liang L, Cui P, Wang J, Zhang X, Guan Y, Tan W, Wu G et al (2020) Susceptibility of ferrets, cats, dogs, and other domesticated animals to SARS-coronavirus 2. *Science* 368(6494):1016–1020. <https://doi.org/10.1126/science.abb7015>
- Shriner SA, Ellis JW, Root JJ, Roug A, Stopak SR, Wiscomb GW, Zierenberg JR, Ip HS, Torchetti MK, DeLiberto TJ (2021) SARS-CoV-2 exposure in escaped mink, Utah, USA. *Emerg Infect Dis* 27(3):988–990. <https://doi.org/10.3201/eid2703.204444>
- Sia SF, Yan L-M, Chin AWH, Fung K, Choy K-T, Wong AYL, Kaewpreedee P, Perera RAPM, Poon LLM, Nicholls JM, Peiris M, Yen H-L (2020) Pathogenesis and transmission of SARS-CoV-2 in golden hamsters. *Nature* 583(7818):834–838. <https://doi.org/10.1038/s41586-020-2342-5>
- Singla R, Mishra A, Joshi R, Jha S, Sharma AR, Upadhyay S, Sarma P, Prakash A, Medhi B (2020) Human animal interface of SARS-CoV-2 (COVID-19) transmission: a critical appraisal of scientific evidence. *Vet Res Commun* 44(3–4):119–130. <https://doi.org/10.1007/s11259-020-09781-0>
- Sit THC, Brackman CJ, Ip SM, Tam KWS, Law PYT, To EMW, Yu VYT, Sims LD, Tsang DNC, Chu DKW (2020) Infection of dogs with SARS-CoV-2. *Nature*:1–6
- Starr TN, Greaney AJ, Addetia A, Hannon WW, Choudhary MC, Dingsen AS, Li JZ, Bloom JD (2021) Prospective mapping of viral mutations that escape antibodies used to treat COVID-19. *Science* 371(6531):850–854. <https://doi.org/10.1126/science.abb9302>
- Stout AE, Guo Q, Millet JK, de Matos R, Whittaker GR (2021) Coronaviruses associated with the superfamily Musteloidea. *mBio* 12(1):e02873–20. <https://doi.org/10.1128/mBio.02873-20>
- Suarez DL, Pantin-Jackwood MJ, Swayne DE, Lee SA, DeBlois SM, Spackman E (2020) Lack of susceptibility of poultry to SARS-CoV-2 and MERS-CoV. <https://doi.org/10.1101/2020.06.16.154658>
- Supasa P, Zhou D, Dejnirattisai W, Liu C, Mentzer AJ, Ginn HM, Zhao Y, Duyvesteyn HM, Nutalai R, Tuekprakhon A, Wang B, Paesen GC, Slon-Campos J, López-Camacho C, Hallis B, Coombes N, Bewley K, Charlton S, Walter TS, Barnes E, Dunachie SJ, Skelly D, Lumley SF, Baker N, Shaik I, Humphries H, Godwin K, Gent N, Sienkiewicz A, Dold C, Levin R, Dong T, Pollard AJ, Knight JC, Klennerman P, Crook D, Lambe T, Clutterbuck E, Bibi S, Flaxman A, Bittaye M, Belij-Rammerstorfer S, Gilbert S, Hall DR, Williams MA, Paterson NG, James W, Carroll MW, Fry EE, Mongkolsapaya J, Ren J, Stuart DI, Screaton GR (2021) Reduced neutralization of SARS-CoV-2 B.1.1.7 variant by convalescent and vaccine sera. *Cell*. <https://doi.org/10.1016/j.cell.2021.02.033>
- Swelum AA, Shafi ME, Albaqami NM, El-Saadony MT, Elsify A, Abdo M, Taha AE, Abdel-Moneim A-ME, Al-Gabri NA, Almainan AA, Saleh Al-Wajeeh A, Tufarelli V, Staffa VN, Abd El-Hack ME (2020) COVID-19 in human, animal, and environment: a review. *Front Vet Sci* 7:578. <https://doi.org/10.3389/fvets.2020.00578>
- Tang X, Wu C, Li X, Song Y, Yao X, Wu X, Duan Y, Zhang H, Wang Y, Qian Z, Cui J, Lu J (2020) On the origin and continuing evolution of SARS-CoV-2. *National Science Review* 7(6):1012–1023. <https://doi.org/10.1093/nsr/nwaa036>
- USDA (2020) Confirmed cases of SARS-CoV-2 in animals in the United States. Available at https://www.aphis.usda.gov/aphis/ourfocus/animalhealth/sa_one_health/sars-cov-2-animals-us
- Vergara-Alert J, van den Brand JMA, Widagdo W, Muñoz M, Raj S, Schipper D, Solanes D, Cerdón I, Bensaid A, Haagmans BL, Segalés J (2017) Livestock susceptibility to infection with Middle East respiratory syndrome coronavirus. *Emerg Infect Dis* 23(2):232–240. <https://doi.org/10.3201/eid2302.161239>
- Wang M, Jing HQ, Xu HF, Jiang XG, Kan B, Liu QY, Wan KL, Cui BY, Zheng H, Cui ZG (2005) Surveillance on severe acute respiratory syndrome associated coronavirus in animals at a live animal market of Guangzhou in 2004. *Zhonghua liu xing bing xue za zhi = Zhonghua liuxingbingxue zazhi* 26(2):84–87
- Welkers MRA, Han AX, Reusken, Chantal B E M, Eggink D (2021) Possible host-adaptation of SARS-CoV-2 due to improved ACE2 receptor binding in mink. *Virus Evol* 7(1). <https://doi.org/10.1093/ve/veaa094>
- WHO report (2020) SARS-CoV-2 mink-associated variant strain – Denmark available at: <https://bit.ly/3kd5IB4>
- de Wit E, Rasmussen AL, Falzarano D, Bushmaker T, Feldmann F, Brining DL, Fischer ER, Martellaro C, Okumura A, Chang J, Scott D, Benecke AG, Katze MG, Feldmann H, Munster VJ (2013) Middle East respiratory syndrome coronavirus (MERS-CoV) causes transient lower respiratory tract infection in rhesus macaques. *Proc Natl Acad Sci U S A* 110(41):16598–16603. <https://doi.org/10.1073/pnas.1310744110>
- Wong MC, Javornik Cregeen SJ, Ajami NJ, Petrosino JF (2020) Evidence of recombination in coronaviruses implicating pangolin origins of nCoV-2019. *bioRxiv*:2020.02.07.939207. <https://doi.org/10.1101/2020.02.07.939207>
- Wu D, Tu C, Xin C, Xuan H, Meng Q, Liu Y, Yu Y, Guan Y, Jiang Y, Yin X, Cramer G, Wang M, Li C, Liu S, Liao M, Feng L, Xiang H, Sun J, Chen J et al (2005) Civets are equally susceptible to experimental infection by two different severe acute respiratory syndrome coronavirus isolates. *J Virol* 79(4):2620–2625. <https://doi.org/10.1128/JVI.79.4.2620-2625.2005>
- Wu L, Chen Q, Liu K, Wang J, Han P, Zhang Y, Hu Y, Meng Y, Pan X, Qiao C, Tian S, Du P, Song H, Shi W, Qi J, Wang H-W, Yan J, Gao GF, Wang Q (2020) Broad host range of SARS-CoV-2 and the molecular basis for SARS-CoV-2 binding to cat ACE2. *Cell Discov* 6:68. <https://doi.org/10.1038/s41421-020-00210-9>
- Yang X, Dong N, Chan EW-C, Chen S (2020a) Genetic cluster analysis of SARS-CoV-2 and the identification of those responsible for the major outbreaks in various countries. *Emerg Microbes Infect* 9(1):1287–1299. <https://doi.org/10.1080/22221751.2020.1773745>
- Yang Y-L, Yu J-Q, Huang Y-W (2020b) Swine enteric alphacoronavirus (swine acute diarrhea syndrome coronavirus): an update three years after its discovery. *Virus Res* 285:198024. <https://doi.org/10.1016/j.virusres.2020.198024>
- Zhang C, Zheng W, Huang X, Bell EW, Zhou X, Zhang Y (2020a) Protein structure and sequence reanalysis of 2019-nCoV genome refutes snakes as its intermediate host and the unique similarity between its spike protein insertions and HIV-1. *J Proteome Res* 19(4):1351–1360. <https://doi.org/10.1021/acs.jproteome.0c00129>
- Zhang L, Jackson CB, Mou H, Ojha A, Rangarajan ES, Izard T, Farzan M, Choe H (2020b) The D614G mutation in the SARS-CoV-2 spike protein reduces S1 shedding and increases infectivity. *bioRxiv*:2020.06.12.148726. <https://doi.org/10.1101/2020.06.12.148726>
- Zhang N, Xu Q, Zhang R, Zhao J (2020c) A comment on “Serological survey of SARS-CoV-2 for experimental, domestic, companion and wild animals excludes intermediate hosts of 35 different species of animals”.
- Zhang Q, Zhang H, Gao J, Huang K, Yang Y, Hui X, He X, Li C, Gong W, Zhang Y, Zhao Y, Peng C, Gao X, Chen H, Zou Z, Shi Z-L, Jin

- M (2020d) A serological survey of SARS-CoV-2 in cat in Wuhan. *Emerg Microbes Infect* 9(1):2013–2019. <https://doi.org/10.1080/22221751.2020.1817796>
- Zhang T, Wu Q, Zhang Z (2020e) Probable pangolin origin of SARS-CoV-2 associated with the COVID-19 outbreak. *Curr Biol* 30(7):1346–1351.e2. <https://doi.org/10.1016/j.cub.2020.03.022>
- Zhao Y, Wang J, Kuang D, Xu J, Yang M, Ma C, Zhao S, Li J, Long H, Ding K (2020) Susceptibility of tree shrew to SARS-CoV-2 infection. *bioRxiv*
- Zhu N, Zhang D, Wang W, Li X, Yang B, Song J, Zhao X, Huang B, Shi W, Lu R, Niu P, Zhan F, Ma X, Wang D, Xu W, Wu G, Gao GF, Tan W, China Novel Coronavirus Investigating and Research Team (2020) A novel coronavirus from patients with pneumonia in China, 2019. *N Engl J Med* 382(8):727–733. <https://doi.org/10.1056/NEJMoa2001017>
- Zoetis (2021) COVID-19 animal vaccines | Zoetis. <https://www.zoetis.com/news-and-media/feature-stories/posts/zoetis-emerging-infectious-disease-capabilities-support-covid-19-solutions-for-great-apes-and-minks.aspx>. Accessed 13 Mar 2021.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.