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Animal Reservoirs and Hosts for Emerging Alphaand Betacoronaviruses

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Running Title: Animal hosts for emerging alpha and betacoronaviruses

Article Summary: A review of coronaviruses in wildlife, livestock, and companion animals, and comprehensive data on receptor usage, hosts, and clinical presentation of 15 previously or currently emerging alpha-or beta-coronaviruses in people and animals.

Abstract: The ongoing global pandemic caused by coronavirus disease 2019 (COVID-19) has once again demonstrated the significance of the *Coronaviridae* family in causing human disease outbreaks. As SARS-CoV-2 was first detected in December 2019, information on its tropism, host range, and clinical presentation in animals is limited. Given the limited information, data from other coronaviruses may be useful to inform scientific inquiry, risk assessment and decision-making. We review the endemic and emerging alpha- and betacoronavirus infections of wildlife, livestock, and companion animals, and provide information on the receptor usage, known hosts, and clinical signs associated with each host for 15 coronaviruses discovered in people and animals. This information can be used to guide implementation of a One Health approach that involves human health, animal health, environmental, and other relevant partners in developing strategies for preparedness, response, and control to current and future coronavirus disease threats.

Keywords: Emerging infectious diseases; coronaviruses; COVID-19; SARS-CoV; SARS-CoV-2; MERS-CoV; zoonotic diseases

Background

Coronaviruses (CoVs) are a family of RNA viruses whose large genomes, propensity for mutation, and frequent recombination events have resulted in a diversity of strains and species that are capable of rapid adaptation to new hosts and ecological environments (1). This viral plasticity has garnered widespread concern over their zoonotic potential and the consequences of new emergence events in both human and animal populations. The emergence of a new strain of severe acute respiratory syndrome (SARS) coronavirus, SARS-CoV-2, which causes coronavirus disease 2019 (COVID-19) has once again demonstrated the significance of the *Coronaviridae* family in causing human disease outbreaks. SARS-CoV-2, a novel betacoronavirus, was first identified in human patients from Wuhan, China in December 2019 and has resulted in a global pandemic, an unprecedented public health emergency, and untold economic and societal repercussions worldwide. Like the 2002-03 SARS epidemic, the first cluster of COVID-19 cases were suspected to be associated with a live animal market where hundreds of animal species were sold, including wildlife, livestock, companion animals, and seafood (2). Zoonotic transmission of SARS-CoV-2 from

horseshoe bats (genus *Rhinolophus*) to humans is likely, perhaps through a yet unidentified intermediate host species (3).

While COVID-19 is novel in the breadth of the human outbreak, a number of pathogenic alphaand betacoronaviruses have shown similar patterns of emergence previously. As early as the 1930s, coronaviruses pathogenic to livestock, companion animals, and laboratory animals were identified (4). During the 1960s, two human coronaviruses, HCoV-229E and -OC43, were discovered in patients with common colds (5, 6). While there is speculation that HCoV-OC43 may also have emerged through a global pandemic in the late 1800s (7), the 2002-03 SARS outbreak is the first accepted global epidemic caused by a coronavirus. The SARS epidemic triggered research within this viral family (4). This research led to the discovery of two new human coronaviruses, HCoV-NL63 and -HKU1 (8, 9). HCoV-229E, -OC43, -NL63 and -HKU1 are now accepted as globally endemic "common cold" species that are typically associated with mild-to-moderate respiratory illness. In 2012, the most deadly human coronavirus to date was discovered in the Arabian peninsula: Middle East respiratory syndrome coronavirus (MERS-CoV) (10). A cumulative body of research on these and other coronaviruses has shown that most alpha and betacoronaviruses infecting humans have come from animal hosts, and that both historic patterns and coronavirus biology establish an urgent ongoing threat to human and animal health (11). While coronaviruses are divided into four viral genera, namely alpha-, beta-, gamma-, and deltacoronaviruses, here we focus on alpha- and betacoronaviruses since all known human coronaviruses are from these genera, and they may therefore pose an increased risk of causing future human pandemics.

This review is intended to compile data to inform a One Health approach to combatting emerging alpha- and betacoronaviruses. One Health is a collaborative, multisectoral, and transdisciplinary approach — working at the local, regional, national, and global levels — with the goal of achieving optimal health outcomes recognizing the interconnection between people, animals, plants, and their shared environment (12). For example, in Qatar, a One Health approach for MERS-CoV prevention and control has been implemented since early in the outbreak, and is associated with improvements in coordination, joint outbreak response rates, and diagnostic capacity (13). Similarly, in the United States, establishment of the One Health Federal Interagency COVID-19 Coordination Group has been instrumental in ensuring an efficient and coordinated all-of-government response by creating a mechanism to communicate, share timely updates, and align messaging (14). More generally, the One Health approach is endorsed as an effective means of combatting zoonotic diseases internationally by the Tripartite international health organizations, consisting of the Food and Agriculture Organization of the United Nations (FAO), the World Health Organization (WHO), and the World Organisation for Animal Health (OIE) (15).

As with other zoonotic diseases, effective implementation of a One Health approach for emerging coronaviruses requires an understanding of the transmission dynamics and human and animal hosts associated with the pathogen. This review therefore summarizes information from other coronavirus emergence events, which may be useful in identifying trends, establishing baselines, and informing decision-making using a One Health approach around the current COVID-19 pandemic and future emerging coronavirus threats. Specifically, we provide information on the receptor used by each current or previously emerging coronavirus since tropism can help predict host susceptibility (Table 1), all known hosts of each coronavirus and their host category (i.e., reservoir, intermediate, spillover, susceptible through experimental infection, or non-susceptible through experimental infection; Table 2), and clinical signs associated with coronavirus infection (Table 3).

Emerging Coronaviruses and Wildlife

More than 70% of zoonotic emerging infectious diseases in humans are caused by pathogens with a wildlife origin (16). A number of mammalian orders are now known to host coronaviruses, including carnivores, lagomorphs, non-human primates, ungulates and rodents (4). However, the attention has focused on Chiroptera (bats), which are hypothesized to be the origin host for all alphaand betacoronaviruses, and therefore all human coronaviruses (Table 2) (1, 4).

After rodents, bats are the second most diverse and abundant mammalian order, comprising 20% of all mammalian biodiversity worldwide (17). In the last two decades, research has intensified to determine why bats harbor more zoonotic diseases than other mammalian taxa, including pathogens that result in high-consequence human emerging infectious diseases like Ebola and Marburg filoviruses, Nipah and Hendra paramyxoviruses, and SARS-CoV, SARS-CoV-2, and MERS-CoV (18). Their gregariousness, sympatry with mixed species assemblages in roosts, long lifespan relative to size, absence of clinical illness due to viral infection, and increased metabolic rate likely all contribute to why bats are reservoirs to many viral pathogens (18).

Coronavirus richness and diversity detected from bats far exceeds those of other mammalian orders, with at least 11 of 18 chiropteran families across six continents testing positive for one or more coronavirus species (4). Recently, a study surveying the diversity of wildlife coronaviruses across global disease "hotspots" identified 100 distinct viruses, of which 91 were detected in bats (11). Interestingly, the study discovered that patterns of coronavirus diversity mirrored bat diversity and evolutionary history, reinforcing the idea that bats are the predominant reservoir of zoonotic and emerging coronaviruses (11). Based on extrapolations made in the same study, the authors predict that bats harbor ~3,204 coronaviruses, the majority of which remain undiscovered (11).

Despite the risks associated with bat-origin coronaviruses, bats play integral roles in ecosystems, including insect suppression through predation, prey for numerous predators, pollinators for economically and ecologically important plants, and seed dispersal for countless tropical trees and shrubs (19). Therefore, mitigating the risks of future emergence events from bats should focus on minimizing close interaction between people and bats and other wildlife, such as reductions to or cessation of wildlife sales at wet markets, wildlife hunting, and encroachment on wildlife habitat.

While further bat research may help us understand the origins of coronaviruses, other wildlife species are intermediate hosts for human emerging coronaviruses. Intermediate hosts may not only add complexity to coronavirus transmission dynamics, but may also amplify viral spillover to new hosts by closings gaps in interaction frequency between species, and by increasing transmissibility and/or infectiousness through viral adaptation (20). A canonical example is SARS-CoV, whose intermediate host is accepted to be palm civets (21). In this instance, close interaction between people and civets sold through wildlife markets likely facilitated transmission to humans, while passage and ongoing recombination in civet intermediate hosts is believed to have played a critical role in facilitating human receptor tropism (20, 22) (Table 1).

Some wildlife species are at risk of human coronavirus spillover. Wild great apes, all species of which are endangered, are one taxonomic group likely vulnerable to spillover from humans, at least in part because they are our closest living relatives. A number of documented respiratory outbreaks that resulted in clinical signs ranging from mild illness to death in chimpanzee and gorilla populations originate from a human source (23, 24). Perhaps most significantly, the human betacoronavirus HCoV OC43 was discovered as the causative agent of mild-to-moderate respiratory illness among wild chimpanzees in Côte D'Ivoire in late 2016 and early 2017 (Table 2) (25), suggesting their susceptibility to human coronaviruses. As the COVID-19 pandemic continues, there is concern that susceptible wildlife such as great apes may be exposed to the virus through human contact, resulting in establishment of a new host reservoir which could pose a risk of perpetuating enzootic transmission and zoonotic transmission into recovering human populations.

Wildlife infections of SARS-CoV-2 have already occurred – the first natural infection of SARS-CoV-2 in a wild animal, and the first confirmed animal cases in the United States, were in captive tigers (n=5) and lions (n=3) at a zoo in New York City (26). Unlike most other asymptomatic animal cases reported previously, the large cats demonstrated respiratory clinical signs that included coughing and wheezing, but ultimately made a full recovery (26) (Table 3). SARS-CoV-2 infection in captive wild felids highlights the complex interactions people may have with wildlife, including the potential for human-to-wildlife transmission. Given these interlinkages, framing risk using a One Health approach may more comprehensively address both the socio-economic and environmental drivers of disease emergence leading to potentially novel, mutually beneficial solutions. For example, risks could be reduced by regulation of wildlife trade and markets and development of sanitary

standards, which would not only protect public health and animal health, but also result in positive wildlife conservation outcomes.

Emerging Coronaviruses and Livestock

Some coronaviruses naturally infect livestock and can have devastating economic consequences, such as swine acute diarrhea syndrome (SADS) coronavirus, porcine epidemic diarrhea virus (PEDV), and Betacoronavirus 1. While recent studies suggest that pigs are not susceptible hosts for SARS-CoV-2 infection (27, 28), pigs are a common host for alpha- and betacoronaviruses, with six different viral species causing disease (29) (Table 2). Of these, the enteric alphacoronaviruses PEDV and SADS-CoV (a strain of the *Rhinolophus* bat coronavirus HKU2), are considered re-emerging and emerging, respectively (29). While PEDV was first detected in China in the 1970s, a highly pathogenic variant caused considerable losses to the United States pork industry in 2013-14 (30). SADS-CoV is highly pathogenic in swine and was first detected in Guangdong province in 2016-17, causing the death of nearly 25,000 piglets (31) (Table 3). SADS-CoV emerged within 100km of the accepted locale of the SARS index case, and like SARS-CoV and SARS-CoV-2, SADS-CoV is suspected to originate in horseshoe bats (*Rhinolophus* spp.) (31) (Table 2). Unlike SARS-CoV and SARS-CoV-2, however, SADS-CoV has not been detected outside of China (29).

Among betacoronaviruses, a strain of Betacoronavirus 1also infects pigs (29). Porcine hemagglutinating encephalomyelitis virus (PHEV) has been circulating for decades and causes rapid death in piglets (29) (Table 3). Unlike other coronaviruses, Betacoronavirus 1 is a unique species complex, in that its distinct strains are host-specific to a range of different species, including wild and domestic ungulate, rabbits, and canines (20, 32). Perhaps the most well-studied strain of Betacoronavirus 1is bovine coronavirus (BCoV), which is of economic significance as it can be associated with a suite of clinical disease in calves and cattle, including calf diarrhea, winter dysentery, and respiratory infection (32) (Table 3). BCoV also infects a number of other livestock species including horses, sheep, and camels (20, 32) (Table 2).

Livestock have also been intermediate hosts in the emergence of three human coronaviruses. First, an unknown ungulate species, speculated to be cattle, is accepted as the intermediate host of human coronavirus OC43 (HCoV-OC43) (7, 33), a strain of Betacoronavirus 1 (Table 2). Based on molecular clock calculations, HCoV-OC43 is predicted to have jumped from livestock to humans around 1890, a timeframe coincident with pandemics of respiratory disease in both cattle (which resulted in widespread culling) and people (although this outbreak is historically attributed to influenza) (7). Dromedary camels are accepted as established hosts of MERS-CoV and are thought to be associated with the emergence of HCoV-229E in people based on closely related viruses found in camelids (34) (Table 2). Dromedary camels inhabit the Middle East and Northern Africa and comprise 90% of extant camels on earth. In much of their range, dromedaries are an important livestock species that are used as racing animals, working animals, and for their milk, meat, and hides.

Livestock can also be spillover hosts of human coronavirus infection. Following the 2002-03 SARS outbreak, a study conducted on farms in Xiqing County, China, tested livestock (pigs, cattle, chickens, and ducks) and companion animals (dogs and cats), leading to discovery of one pig that was positive for SARS-CoV by antibody test and RT-PCR (35) (Table 2). A larger and more complex series of livestock outbreaks of SARS-CoV-2 has been ongoing since April 2020, as 40 mink farms in the Netherlands, four in Denmark, one in Spain, and two in the United States have identified mink positive for SARS-CoV-2. In all outbreaks, mink were suspected to be initially infected by COVID-19-positive farm workers (36). In the Netherlands, unpublished reports have identified plausible instances of spillback from mink to humans in ongoing investigations (26). National surveillance and control efforts have been implemented in each country, which have identified other SARS-CoV-2 positive species living on mink farms, including 7 barn cats in the Netherlands (out of 24 sampled), and 1 dog in Denmark. Both countries have implemented mandatory reporting of any positive animals, and depopulation of affected farms. In the Netherlands to-date, more than 1.5 million mink have been culled and a moratorium has been placed on the mink industry, which highlights the

necessity of early and coordinated One Health action to prevent bi-directional transmission of zoonotic diseases (26).

Emerging Coronaviruses and Companion Animals

Companion animals are an important part of many households and can improve both the physical and mental well-being of their owners (37). In the United States, approximately 71.5 million households (57%) own at least one companion animal (38). Among households with companion animals, dogs (67%) and cats (44%) are the most commonly owned (38). Despite the many benefits of pet ownership, close interactions with pets pose risks for zoonotic disease transmission. Zoonotic diseases that are spread between people and companion animals include rabies, salmonellosis, campylobacteriosis, and hookworms, among others (37, 39, 40). Companion animals are estimated to be a source of more than 70 human diseases (41), and the burden of zoonotic diseases attributed to interactions with companion animal is substantial. For example, rabies kills an estimated 59,000 people per year globally, and 99% of human rabies cases originate from rabid dogs (40).

A number of common coronaviruses have been discovered in companion animals, although none of the coronaviruses that are endemic in companion animal populations are zoonotic. One of the most common respiratory diseases in dogs is canine infectious respiratory disease (CIRD), or kennel cough, which typically causes cough and nasal discharge in puppies and dogs (42, 43). While kennel cough can be caused by a number of pathogens, most frequently the bacterium *Bordetella bronchiseptica*, canine respiratory coronavirus (CRCoV) is a contributing pathogen to this syndrome (42, 44) (Table 1). CRCoV is believed to originate from BCoV, either through a common ancestor, host variant, or a host species shift, and is therefore considered a strain of Betacoronavirus-1 (42, 44). Regardless of how CRCoV and BCoV are genetically related, experimental studies shown that dogs challenged with BCoV can become infected and transmit the virus to other dogs, though they do not exhibit clinical signs of disease (45) (Table 2 and 3).

Canine enteric coronavirus (CCoV) is an alphacoronavirus often associated with mild enteritis in puppies and dogs, especially in group housing situations (46). In 2005, however, a novel, highly pathogenic variant strain of CCoV-II, CB/05, was first identified (47) (Table 2). This new variant is now pantropic, and has a mortality rate of up to 100% in isolated outbreaks in puppies (47) (Table 3). Due to its increased pathogenicity and changes in tissue tropism, CCoV is considered an emerging pathogen (46).

While CCoV is generally considered to be specific to dogs, cats experimentally challenged with the virus can be infected with CCoV and mount an anamnestic response to further exposure, although they do not develop clinical signs of illness (48) (Table 3). Indeed, while there exist two serotypes of feline coronavirus (FCoV), FCoV type I and FCoV type II, type II is hypothesized to have originated from a recombination event between FCoV type I and CCoV, which suggests co-infections of coronaviruses among companion animals may yield opportunity for the emergence of new disease (49).

Companion animals may also act as spillover hosts for human coronaviruses. A study following the 2002-03 SARS outbreak discovered that pet cats living in a Hong Kong apartment complex were naturally infected with SARS during the epidemic (50). Following the epidemic, challenge experiments in cats and ferrets found that both species could be experimentally infected and transmit the infection to naive animals of the same species they were housed with (50) (Table 2). In this experiment, cats did not demonstrate clinical signs of illness, although ferrets became lethargic, developed conjunctivitis, and died on days 16 and 21 post-infection. However, unlike human cases, there was no evidence that SARS-CoV-associated pneumonia was a cause of death (Table 3). Rather, the main findings in deceased ferrets were marked hepatic lipidosis and emaciation (50).

Companion animals, specifically dogs and cats, are among the most commonly infected groups of animals in the ongoing COVID-19 pandemic. Natural cases of suspected human-to-animal transmission have been confirmed in dogs from Hong Kong and the United States (51), and in cats in China, Hong Kong, the United States, and several European countries (26). Experimental challenge studies additionally suggest that like SARS-CoV, a number of companion animals, including cats,

ferrets, and golden hamsters and are all susceptible to SARS-CoV-2 infection under laboratory conditions (27, 28, 52-54) (Table 2). Furthermore, studies in cats, hamsters and ferrets show they are capable of both direct and indirect transmission to healthy conspecifics in experimental settings (27, 28, 53, 54), which underscores the need for infection prevention and control practices between people to companion animals.

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

Conclusions

A considerable number of mammalian species, including wildlife, livestock, and companion animals, are susceptible to infection with alpha- and betacoronaviruses. The propensity of alpha- and betacoronaviruses to jump to new hosts, coupled with their relatively large host ranges, suggests that a One Health approach should be used to develop strategies to mitigate the effects of current and future coronavirus emergence events. During the COVID-19 pandemic, One Health collaboration between public health and veterinary sectors has already bolstered critical healthcare resources and infrastructure, leading to improvements in diagnostic testing capacity and human resource availability (55). In the United States, the One Health Federal Interagency COVID-19 Coordination Group has developed risk communication and messaging for companion animals, livestock, and wildlife and has been instrumental in coordinating joint outbreak response and diagnostic testing in animals. As these examples highlight, integration of the One Health approach into preparedness planning, joint epidemiological investigations, surveillance, laboratory diagnostics, risk assessment and field research is not only warranted, but necessary to safeguard the health, welfare and safety of people, animals, and their shared environment.

Table 1. - Current or previously emerging coronaviruses.

PATHOGEN (Abbreviation)	DISEASE (Abbreviation)	VIRAL GENUS	RECEPTOR (Abbreviation) [Suspected]
Alphacoronavirus 1 (ACoV1); Strain Canine Enteric Coronavirus (CCoV)	Canine Coronavirus Infection (CCoV)	Alphacoronavirus	Aminopeptidase N (APN, CD13) (46)
Alphacoronavirus 1 (ACoV1); Strain Feline Infectious Peritonitis Virus (FIPV)	Feline Infectious Peritonitis Virus (FIP)	Alphacoronavirus	Aminopeptidase N (APN, CD13) (56)
Bat Coronavirus HKU10	NA	Alphacoronavirus	Unknown (57)
Ferret Systemic Coronavirus (FRSCV)	Ferret Systemic Coronavirus (FRSCV)-associated disease	Alphacoronavirus	Unknown (58)
Human Coronavirus NL63	Common cold	Alphacoronavirus	Angiotensin-converting enzyme 2 (ACE2) (59)
Human Coronavirus 229E	Common cold	Alphacoronavirus	Human aminopeptidase N (hAPN, CD13) (60)
Porcine Epidemic Diarrhea Virus (PEDV)	Porcine Epidemic Diarrhea (PED)	Alphacoronavirus	[Aminopeptidase N (APN, CD13)] (61, 62)
Rhinolophus Bat Coronavirus HKU2; strain Swine Acute Diarrhea Syndrome Coronavirus (SADS-CoV)	Swine Acute Diarrhea Syndrome (SADS)	Alphacoronavirus	Unknown (31)
Betacoronavirus 1; strain Bovine Coronavirus	NA	Betacoronavirus	Human leukocyte antigen class I (HLA-1) (63)
Betacoronavirus 1; strain Canine Respiratory Coronavirus	Canine Infectious Respiratory Disease (CIRD)	Betacoronavirus	Human leukocyte antigen class I (HLA-1) (63)
Betacoronavirus1; strain Human Coronavirus OC43	Common cold	Betacoronavirus	Human leukocyte antigen class I (HLA-1) (64)
Human coronavirus HKU1	Common cold	Betacoronavirus	Human leukocyte antigen class I (HLA-1) (63, 65)
Middle East Respiratory Syndrome-Related Coronavirus (MERS-CoV)	Middle East respiratory syndrome (MERS)	Betacoronavirus	Dipeptidyl peptidase 4 (DPP4, CD26) (66)
Severe Acute Respiratory Syndrome – Related Coronavirus (SARS-CoV)	Severe acute respiratory syndrome (SARS)	Betacoronavirus	Angiotensin-converting enzyme 2 (ACE2) (67)
Severe Acute Respiratory Syndrome – Related Coronavirus 2 (SARS-CoV-2)	Coronavirus Disease 2019 (COVID-19)	Betacoronavirus	Angiotensin-converting enzyme 2 (ACE2) (68)

Note: A list of all coronaviruses that are described in Table 2 and 3 (below), including the receptor used for viral entry.

Table 2. - Hosts and reservoirs of current or previously emerging coronaviruses.

PATHOGEN	RESERVOIR HOST(S) [Suspected]		INTERMEDIATE / AMPLIFYING HOST(S) [Suspected]	SPILLOVER HO	ST(S)	SUSCEPTIBLE HOST(S) [Suspected]	NON- SUSCEPTIBLE HOST(S)	
Alphacoronavirus1 (ACoV1); Strain Canine	Domestic dog (Canis lupus familiaris)	(69)	Unknown/None identified	Carnivores; (70- family Canidae 72)		Unknown/None identified	Unknown/None identified	
Enteric Coronavirus (CCoV)	James 15)			Carnivores; family Felidae Carnivores; family Mustelidae	(73) (71)			
				Carnivores; family Viverridae	(71)			
Alphacoronavirus1 (ACoV1); Strain Feline Infectious Peritonitis Virus (FIPV)	Domestic cat (Felis catus)	(74, 75)	Unknown/None identified	Carnivores: family Felidae	(76- 78)	Mouse (79) (Mus musculus)		
Bat Coronavirus HKU10	Leschenault's rousettes bat (Rousettus leschenaulti)	(80)	Unknown/None identified	Pomona leaf- nosed bats (Hipposideros pomona)	(81)	Unknown/None identified	Unknown/None identified	
Ferret Systemic Coronavirus (FRSCV)	Ferret (Mustela putorius)	(82)	Unknown/None identified	Ferret (Mustela putorius)	(83, 84)	Unknown/None identified	Unknown/None identified	
Human coronavirus NL63	Bats; family Hipposideridae	(85)	Unknown/None identified	Human	(8, 86)	Unknown/None identified	Cattle (Bos taurus) Domestic pig (Sus scrofa) Donkey (Equus africanus) Goat (Capra aegagrus) Sheep (Ovis aries)	
Human Coronavirus 229E	Bats; family Hipposideridae	(85, 88, 89)	Dromedary camels (34) (Camelus dromedarius)	Alpaca (Vicugna pacos)	(90)	Domestic cat (91) (Felis catus)		

				Human	(5)				
Porcine Epidemic Diarrhea Virus (PEDV)	Bats; family Vespertillionidae	(92, 93)	Unknown/None identified	Domestic pig (Sus scrofa)			entified	Unknown/None identified	
Rhinolophus Bat Coronavirus HKU2; Strain Swine Acute Diarrhea Syndrome Coronavirus (SADS-CoV)	Bats; family Rhinolophidae	(31)	Unknown/None identified	Domestic pig (Sus scrofa)	(31)	Mouse (Mus musculus)	(94)	Unknown/Non identified	e
Betacoronavirus 1; strain Bovine Coronavirus	Rodent; family Muridae	(95)	Unknown/None identified	Cattle (Bos taurus)	(96)	Turkey (Meleagris gallopavo)	(97)	Chicken (Gallus gallus)	(97)
Betacoronavirus 1; strain Canine Respiratory coronavirus	Rodent; family Muridae	(95)	[Cattle] (44) (Bos taurus)	Domestic dog (Canis lupus familiaris)	(42)	Unknown/None ide	entified	Unknown/Non identified	e
Betacoronavirus1; strain Human coronavirus OC43	Rodent; family Muridae	(95)	Artiodactyl; family (7) Bovidae	Chimpanzees (Pan troglodytes)	(98)	Mouse (Mus musculus)	(99)	Unknown/Non identified	e
				Human	(6)				
Human coronavirus HKU1	Rodent; family Muridae	(20, 100)	Unknown/None identified	Human	(9)	Unknown/None ide	Unknown/None identified		e
Middle East Respiratory Syndrome-Related	Bats; family Vespertillionidae	(100, 101)	Dromedary camels (102) (Camelus dromedarius)	Human	(10)	Alpaca (Vicugna pacos)	(103)	Ferret (Mustela putorius furo)	(104)
Coronavirus (MERS-CoV)						Common marmoset (Callithrix jacchus)	(105, 106)	Golden hamster (Mesocricetus auratus)	(107)
						Domestic pig (Sus scrofa)	(108)	Horse (Equus ferus caballus)	(108)
						Llama (Lama glama)	(108)	Mouse (Mus musculus)	(109)
						Rhesus macaque (Macaca mulatta)	(110, 111)	Sheep (Ovis aries)	(108)
						New Zealand White rabbit	(112)		

(Oryctolagus cunuculus)

							cunucuius)			
Severe Acute Respiratory Syndrome – Related Coronavirus (SARS-CoV)	Bats; family Rhinolophidae	(57, 113- 115)	Masked palm civet (Paguma larvata)	(21, 116)	Chinese ferret badger (Melogale moschata)	(21, 114)	African green monkey (Chlorocebus aethiops)	(114)	Chickens (Gallus gallus)	(117)
					Domestic cat (Felis catus)	(50, 114, 118)	Cynomolgus macaque (Macaca fascicularis)	(114, 119)		
					Domestic dog (Canis lupus familiaris)	(118)	Domestic cat (Felis catus)	(50, 114)		
					Domestic pig (Sus scrofa)	(35, 114)	Domestic pig (Sus scrofa)	(114, 117)		
					Human	(120, 121)	Ferret (Mustela putorius)	(50, 114)		
					Racoon dog (Nyctereutes procyonoides)	(21, 114)	Golden hamster (Mesocricetus auratus)	(114, 122)		
					procyonoraes)		Guinea pig (Cavia porcellus)	(114)		
							Masked palm civet (Paguma larvata)	(114, 123)		
							Mouse (Mus musculus)	(114, 124)		
							Rat (Rattus sp)	(114)		
							Rhesus macaque (Macaca mulatta)	(114, 125)		
Severe Acute Respiratory Syndrome – Related Coronavirus 2 (SARS-	[Bats: family Rhinolophidae]	(3)	Unknown/None ident	tified	Domestic cat (Felis catus)	(14, 26)	Cynomolgus macaque (Macaca fascicularis)	(126)	Chickens (Gallus gallus)	(27, 28)
CoV-2)					Domestic dog (Canis lupus familiaris)	(51)	Domestic cat (Felis catus)	(27, 54)	Domestic pig (Sus scrofa)	(27, 28)
					Human	(127)	Domestic dog (Canis lupus familiaris)	(27)	Japanese Quail	(pers. comm)

Mink	(26, 36)	Egyptian fruit bat (Rousettus aegyptiacus)	(28)	(Coturnix japonica) Mouse (Mus musculus)	(128)
Lion (Panthera leo)	(26)	Ferret (Mustela putorius)	(27, 28, 53)	Pekin duck (Anas platyrhinchos)	(pers. comm)
Puma (Puma concolor)	(26)	Golden hamster (Mesocricetus auratus	(52)	Turkey (Meleagris gallopavo)	(pers. comm)
Tiger (Panthera tigris)	(26)	Rhesus macaque (Macaca mulatta)	(129)	White Chinese geese (Anser cygnoides)	(pers. comm)

Note: All hosts discovered for each coronavirus are presented below. For the purposes of this table: Reservoir host - a species in which the pathogen endemically circulates, and is considered to have co-evolved with; Intermediate host - species that harbor a recent common ancestor of the coronavirus and/or played a role in the natural selection/adaptation of the virus before its spillover. Spillover host – non-endemically infected species where one or more individuals are considered to have acquired the virus through natural infection (e.g., exposure an infected conspecific or inter-species transmission). Susceptible hosts – species where one or more individuals can become infected with the virus through experimental challenges or otherwise laboratory-controlled infection studies. *In vitro* studies, or studies using transgenic animal models to induce susceptibility were not included in this table. Non-susceptible hosts – species where experimental challenge or otherwise laboratory-controlled infection studies have occurred that did not result in viral infection. For all categories, infection is considered detection of viral RNA from host samples and/or the host mounting a detectable antibody response. Therefore, infection as it is used here does not necessarily imply hosts naturally or experimentally infected with a virus are capable of transmitting the infection to others.

Table 3. – Clinical presentation of current or previously emerging coronaviruses.

PATHOGEN	HOST	HOST TYPE	BODY SYSTEM	CLINICAL PRESENTATION		VAC	CINE
Alphacoronavirus1 (ACoV1); Strain	Domestic dog	Reservoir	Gastrointestinal	Vomiting, diarrhea, and dehydration	(130) (49)	Yes	(130)
Canine Enteric Coronavirus (CCoV)	Carnivores; family Canidae	Spillover	Unknown	Unknown	(70) (72)	No	(131)
	Carnivores; family Felidae	Spillover	Gastrointestinal	Mild diarrhea	(73)	No	(131)
	Carnivores; family Mustelidae	Spillover	Unknown	Unknown	(71)	No	(131)
	Carnivores; family Viverridae	Susceptible	Unknown	Unknown	(71)	No	(131)
Alphacoronavirus1 (ACoV1); Strain Feline Infectious	Domestic cat	Reservoir	Multi-systemic	Varies: fever, weight loss, diarrhea, ascites, thoracic effusion, ocular signs, neurologic signs, and death	(130, 132)	Yes*	(130)
Peritonitis Virus (FIPV)	Carnivores: family Felidae	Spillover	Multi-systemic	Weight loss, fever, diarrhea, jaundice	(133)	No	(131)
Bat Coronavirus HKU10	Leschenault's rousettes bat	Reservoir	NA	Asymptomatic	(81)	No	(131)
	Pomona leaf-nosed bats	Spillover	Unknown	Lower body weight than non-infected bats	(81)	No	(131)
Ferret Systemic Coronavirus (FRSCV)	Ferret	Reservoir, Spillover	Multi-systemic	Anorexia, weight loss, diarrhea, lymphadenopathy, anemia, and neurologic signs	(134)	No	(131)
Human coronavirus NL63	Bats; family Hipposideridae	Reservoir	NA	Asymptomatic	(93)	No	(131)
	Human	Spillover	Respiratory	Fever, cough, rhinorrhea	(135)	No	(136)
Human Coronavirus 229E	Bats; family Hipposideridae	Reservoir	NA	Asymptomatic	(93)	No	(131)
	Dromedary camels	Intermediate	NA	Asymptomatic	(34)	No	(131)
	Alpaca	Spillover	Respiratory	Acute respiratory signs, death	(137)	No	(131)
	Human	Spillover	Respiratory	Nasal congestion, rhinorrhea. Can progress to pneumonia.	(138)	No	(136)
	Domestic cat	Susceptible	NA	Asymptomatic	(91)	No	(131)
Porcine Epidemic Diarrhea Virus	Bats; family Vespertillionidae	Reservoir	Unknown	Unknown	(93)	No	(131)
(PEDV)	Domestic pig	Spillover	Gastrointestinal	Vomiting, diarrhea, and death in piglets, diarrhea and agalactia in pregnant sows	(130, 139)	Yes+	(131)

Rhinolophus Bat Coronavirus HKU2;	Bats; family Rhinolophidae	Reservoir	NA	Asymptomatic	(93)	No	(131)
strain Swine Acute Diarrhea Syndrome	Domestic pig	Spillover	Gastrointestinal	Severe, acute diarrhea, rapid weight loss, death in piglets	(140)	No	(131)
Coronavirus (SADS-CoV)	Mouse	Susceptible	NA	Asymptomatic	(94)	NA	(94)
Betacoronavirus1;	Rodent; family Muridae	Reservoir	Unknown,	Unknown	(95)	No	(131)
strain Bovine Coronavirus	Cattle	Spillover	Respiratory, gastrointestinal	Respiratory signs, diarrhea, anorexia, lethargy	(130)	Yes	(130)
	Turkey	Susceptible	Gastrointestinal	Diarrhea, reduced weight gain, and enteritis	(97)	NA	
Betacoronavirus 1;	Rodent; family Muridae	Reservoir	Unknown	Unknown	(95)	No	(131)
strain Canine	[Cattle]	Intermediate	Unknown	Unknown	(43)	No	(130)
Respiratory coronavirus	Domestic dog	Spillover	Respiratory	Mild cough, nasal discharge, inappetence, bronchopneumonia	(43)	No	(42)
Betacoronavirus1;	Rodent; family Muridae	Reservoir	Unknown,	Unknown	(95)	No	(131)
strain Human coronavirus OC43	Artiodactyl; family Bovidae	Intermediate	Unknown, suspected host	Unknown	(43)	No	(131)
	Chimpanzees	Spillover	Respiratory	Coughing, sneezing	(25)	No	(131)
	Human	Spillover	Respiratory	Nasal congestion, rhinorrhea. Can progress to pneumonia	(6)	No	(136)
	Mouse	Susceptible	Neurological	Anorexia, weight loss, neurologic signs	(99)	No	(131)
Human coronavirus HKU1	Rodent; family Muridae	Reservoir	Unknown, suspected host	Unknown, suspected host	(20)	No	(131)
	Human	Spillover	Respiratory	Rhinorrhea, cough, fever	(141)	No	(136)
Middle East Respiratory	Bats; family Vespertillionidae	Reservoir	NA	Asymptomatic	(93)	No	(131)
Syndrome-Related Coronavirus (MERS-	Dromedary camels	Intermediate	Respiratory	Often asymptomatic, or can present with fever, nasal discharge	(142)	No	(131)
CoV)	Human	Spillover	Respiratory, multi- systemic	Variable: coughing, shortness of breath, fatigue, myalgia, arthralgia, fever, headaches, vomiting, and diarrhea, sore throat and rhinorrhea. Can progress to pneumonia, acute renal failure, multiorgan failure, and death	(142)	No	(143)
	Alpaca	Susceptible	NA	Asymptomatic	(103)	No	(131)
	Common marmoset	Susceptible	Respiratory	Pneumonia	(105)	No	(131)
	Domestic pig	Susceptible	Respiratory	Nasal discharge	(108)	No	(131)
	Llama	Susceptible	Respiratory	Nasal discharge	(108)	No	(131)
	Rhesus macaque	Susceptible	NA	Asymptomatic	(112)	No	(131)

	New Zealand White rabbit	Susceptible	Respiratory	Asymptomatic	(112)	No	(131)
Severe Acute	Bats; family	Reservoir	Unknown,	Unknown	(93)	No	(131)
Respiratory Syndrome	Rhinolophidae						
Related Coronavirus(SARS-CoV)	Masked palm civet	Intermediate, Susceptible	Respiratory	Fever, lethargy, pneumonia	(114, 123)	No	(131)
	Chinese ferret badger	Spillover	NA	Asymptomatic	(114)	No	(131)
	Domestic cat	Spillover, Susceptible	NA	Asymptomatic	(50, 114)	No	(131)
	Domestic dog	Spillover	Unknown	Unknown	(118)	No	(131)
	Domestic pig	Spillover, Susceptible	NA	Asymptomatic	(114, 117)	No	(131)
	Human	Spillover	Respiratory	Fever, cough, shortness of breath, difficulty breathing, pneumonia	(132)	No	(143)
	Racoon dog	Spillover	NA	Asymptomatic	(114, 123)	No	(131)
	African green monkey	Susceptible	NA	Asymptomatic	(114)	No	(131)
	Cynomolgus macaque	Susceptible	Respiratory	Lethargy, skin rash, and respiratory distress	(114, 119)	No	(131)
	Ferret	Susceptible	Respiratory	Lethargy, conjunctivitis, weight loss	(50, 114)	No	(131)
	Golden hamster	Susceptible	NA	Asymptomatic	(114, 122)	No	(131)
	Guinea pig	Susceptible	NA	Asymptomatic	(114)	No	(131)
	Mouse	Susceptible	Non-specific	Asymptomatic or weight loss and dehydration	(114, 124)	No	(131)
	Rat	Susceptible	NA	Asymptomatic	(114)	No	(131)
	Rhesus macaque	Susceptible	Non-specific	Transient fever	(114, 125)	No	(131)
Severe Acute Respiratory Syndrome	[Bats: family Rhinolophidae]	Reservoir	Unknown	Unknown	(3)	No	NA
Related Coronavirus2 (SARS-CoV-2)	Domestic cat	Spillover, Susceptible	Respiratory	Asymptomatic or ocular discharge and sneezing, or death in juvenile cats	(14, 26, 27)	No	NA
	Domestic dog	Spillover, Susceptible	NA	Asymptomatic	(51)	No	NA
	Human	Spillover	Respiratory	Fever, cough, shortness of breath or difficulty breathing		No	NA

Mink	Spillover	Gastrointestinal and Respiratory	Respiratory and gastrointestinal signs, increased mortality	(26, 36, 144)	No	NA
Lion	Spillover	Respiratory	Cough, inappetence, wheezing	(26)	No	NA
Puma	Spillover	Unknown	Unknown	(26)	No	NA
Tiger	Spillover	Respiratory	Cough, inappetence, wheezing	(26)	No	NA
Cynomolgus macaque	Susceptible	Respiratory	Asymptomatic, nasal discharge	(126)	No	NA
Egyptian fruit bat	Susceptible	1 7	Asymptomatic, mild rhinitis	(28)		NA
Ferret	Susceptible	Respiratory	Asymptomatic or fever, cough, inappetence	(27,	No	NA
	•			28,		
				53)		
Golden hamster	Susceptible	Respiratory	Weight loss, lethargy, ruffled fur, hunched posture, tachypnea	(52)	No	NA
Rhesus macaque	Susceptible	Respiratory	Changes in respiratory pattern, piloerection,	(129)	No	NA
-	-		reduced appetite, pale appearance, hunched			
			posture, dehydration, coughing			

Note: The clinical presentation of disease in all hosts described in Tables 1 and 2 (above) other than non-susceptible hosts. * = Not recommended by the AAFP

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for administration; *Conditional license for use.

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