

Cross-Species Transmission of Coronaviruses in Humans and Domestic Mammals, What Are the Ecological Mechanisms Driving Transmission, Spillover, and Disease Emergence?

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8 **Abstract**

9 Coronaviruses cause respiratory and digestive diseases in vertebrates. The recent pandemic, caused by
10 the novel severe acute respiratory syndrome coronavirus 2, is taking a heavy toll on society and
11 planetary health, and illustrates the threat emerging coronaviruses can pose to the wellbeing of humans
12 and other animals. Coronaviruses are constantly evolving, crossing host species barriers, and
13 expanding their host range. In the last few decades, several novel coronaviruses have emerged in
14 humans and domestic animals. Novel coronaviruses have also been discovered in captive wildlife or
15 wild populations, raising conservation concerns. The evolution and emergence of novel viruses is
16 enabled by frequent cross-species transmission. It is thus crucial to determine emerging coronaviruses'
17 potential for infecting different host species, and to identify the circumstances under which cross-
18 species transmission occurs in order to mitigate the rate of disease emergence. Here, I review (broadly
19 across several mammalian host species) up-to-date knowledge of host range and circumstances
20 concerning reported cross-species transmission events of emerging coronaviruses in humans and
21 common domestic mammals. All of these coronaviruses had similar host ranges, were closely related
22 (indicative of rapid diversification and spread), and their emergence was likely associated with high-
23 host-density environments facilitating multi-species interactions (e.g., shelters, farms, and markets)
24 and the health or wellbeing of animals as end- and/or intermediate spillover hosts. Further research is
25 needed to identify mechanisms of the cross-species transmission events that have ultimately led to a
26 surge of emerging coronaviruses in multiple species in a relatively short period of time in a world
27 undergoing rapid environmental change.

28 1 Introduction

29 Coronaviruses (CoVs) cause respiratory and digestive diseases in humans and other animals, and are
30 responsible for several emerging diseases. The severe acute respiratory syndrome (SARS) outbreak in
31 2002–2003 resulted in 8422 human cases and 916 deaths in 33 countries (1). In 2012, Middle East
32 respiratory syndrome (MERS) emerged, and over time has resulted in over 2,500 human cases and 866
33 deaths in 27 countries (2,3). As of mid-2021, the novel coronavirus disease 2019 (COVID-19)
34 pandemic has resulted in 4.2 million human deaths and 196.2 million cases in 221 countries and
35 territories (4). Other animals have also been affected by these and other emerging coronaviruses, all of
36 which resulted from cross-species transmission, and demonstrate the serious threat coronaviruses can
37 pose to humans and other animals globally.

38 Named after their crown-shaped spike surface proteins, coronaviruses are enveloped, positive-
39 sense single-stranded RNA viruses that belong to the family *Coronaviridae*, subfamily
40 *Orthocoronavirinae* (5,6). They split into four genera: *Alphacoronavirus*, *Betacoronavirus*,
41 *Deltacoronavirus*, and *Gammacoronavirus* (5). The first two genera infect mammals primarily,
42 whereas *Gammacoronaviruses* infect birds, and *Deltacoronaviruses* infect both mammals and birds
43 (7). Coronaviruses further split into species; however, they exist as quasispecies due to the rapid
44 evolution driven by their high mutation rates and homologous RNA recombination (8). Coronaviruses
45 have the largest genomes (26.4–31.7 kilobases) of all known RNA viruses; thus, their genomes are
46 especially prone to accumulation of mutations and recombined segments over time, which contributes
47 to their diverse host range and potential for disease emergence (9).

48 Bats are considered reservoirs for most *Alpha*- and *Betacoronaviruses*, while wild birds are
49 probable reservoirs for *Gamma*- and *Deltacoronaviruses* (10). Coronavirus spillover from reservoirs
50 to other species, and subsequent cross-species transmission, is primarily mediated by recombination in
51 the receptor-binding domain (RBD) of the spike protein (S) gene (11). RBD enables coronaviruses to
52 infect hosts by binding to a host receptor, e.g., angiotensin-converting enzyme 2 (ACE2) in the case of
53 SARS coronaviruses, for cell entry (7,12,13). Although research has revealed reservoirs and molecular
54 mechanisms enabling cross-species transmission, and that viral evolution is facilitated by frequent
55 cross-species transmission events (14), less is known about the environments favoring emerging
56 coronavirus evolution in non-reservoir hosts.

57 Agriculture and industrialization expanded the global abundance of humans and domestic
58 mammals (i.e., livestock and pets). Today, their combined biomass makes up 96% of all mammalian
59 biomass on Earth (15). This may be the primary reason for disease emergence in humans and other
60 animals (16). To help curb coronavirus disease emergence, it is important to identify current host
61 ranges of existing coronaviruses in humans and domestic animals, and the circumstances associated
62 with their cross-species transmission.

63 This review provides an updated succinct summary of known host ranges and cross-species
64 transmissions of recently emerged coronaviruses in humans and domestic mammals. Moreover, I
65 discuss commonalities among the ecological circumstances related to spillover and emergence of
66 several coronaviruses in various mammalian hosts, and how these may inform One Health
67 interventions for preventing disease emergence.

68 2 Emerging human coronaviruses

69 There are seven known human coronaviruses: the *Betacoronaviruses* SARS-CoV-1, MERS-CoV, and
70 SARS-CoV-2, which caused SARS, MERS, and COVID-19, respectively, and the *Alphacoronaviruses*

71 NL63 and 229E and *Betacoronaviruses* OC43 and HKU1, which cause the common cold in humans
72 (17). The latter four may not be labeled as recently emerging coronaviruses, although they have spilled
73 over at some point in the past. Bats are considered reservoirs for NL63 and 229E, whereas rodents are
74 putative reservoirs for OC43 and HKU1 (17–19). NL63 possibly emerged several hundred years ago
75 from recombination between ancestors to 229E in hipposiderid bats and coronaviruses circulating in
76 African trident bats (19,20). Based on phylogenetic analyses, cattle and camelids have been identified
77 as probable intermediate spillover hosts for OC43 and 229E emergence one and two centuries ago,
78 respectively (17,18,20). The bovine-to-human spillover that led to OC43 emergence likely coincided
79 with a pandemic in 1890 (17,21,22). Indeed, OC43 and bovine coronavirus share 96% global
80 nucleotide identity (23). Finally, extant lineages of HKU1 trace their most recent common ancestor to
81 the 1950s, when it possibly spilled over from rodents (20).

82 Next, this section covers plausible spillover events—from reservoirs to humans via potential
83 intermediate host species—that generated the recent SARS-CoV-1, MERS-CoV, and SARS-CoV-2,
84 and their cross-species transmission potential.

85 **2.1 SARS-CoV-1**

86 SARS emerged in Guangdong, China, and caused the devastating 2000–2003 outbreak in several
87 countries (1). Successful efforts curbed the epidemic: only a few cases occurred in late 2003 and early
88 2004 (24). There have been no known SARS-CoV-1-related cases since.

89 Based on genetic and epidemiologic investigations, the first SARS-CoV-1-infected individuals
90 likely contracted the virus from masked palm civets or other wildlife in wet markets (24–27). Civet
91 isolates revealed ongoing adaptation, suggesting that they were not reservoir hosts, but intermediate
92 spillover hosts that contracted the virus from horseshoe bats (26–30). Substantial evidence confirms
93 bats as SARS reservoirs (26,28,29,31,32).

94 Wildlife samples from a market in Shenzhen revealed that SARS-CoV-1 shared 99.8%
95 nucleotide identity with isolates from civets and a raccoon dog, and that a ferret badger had
96 seroconverted against SARS-CoV-1 (24,26). Initial human cases reported direct or indirect contact
97 with these animals via handling, killing, meat serving, or residing near wet markets (33). Surveys
98 showed that animal (especially civet) traders, although asymptomatic, had disproportionately high
99 seroconversion against SARS-CoV-1, suggesting they have been exposed to SARS-CoV-related
100 viruses for several years before the SARS epidemic (24,26). Intermediate spillover hosts were not
101 necessarily required for the evolution of SARS-CoV-1, since a bat SARS-like coronavirus is able to
102 bind to ACE2 in humans and civets for cell entry (34). Nonetheless, civets may have amplified the
103 virus and brought it closer to humans (35).

104 Additional mammals are susceptible to SARS-CoV-1 infection. Cats, ferrets, guinea pigs,
105 golden hamsters, common marmosets, grivets, and cynomolgus and rhesus macaques can be infected
106 under experimental inoculation, seroconvert, and display similar pathological signs as humans, and the
107 monkeys and guinea pigs usually display mild clinical signs, while cats and golden hamsters show no
108 clinical signs (36–44). In two studies, inoculated ferrets only exhibited signs of lethargy (36,37).
109 Furthermore, cats and ferrets can shed SARS-CoV-1 and transmit the virus within each species (36).
110 Cats have also been naturally infected by SARS-CoV-1 in an apartment block where residents had
111 SARS, suggesting possible human-to-cat transmission (36). Although swine are susceptible to SARS-
112 CoV-1 both experimentally and naturally, viral replication in (and shedding from) swine is poor (45–
113 47). Mice and poultry are not susceptible to SARS-CoV-1 infection (45,48,49). Thus, SARS-CoV-1
114 was not uniquely adapted to humans, yet likely restricted to mammals.

115 **2.2 MERS-CoV**

116 MERS cases are still being reported since it became endemic in the Arabian peninsula. MERS does
 117 sporadically spread to other parts of the world, although with limited human-to-human transmission
 118 (50,51). Most outbreaks originate from independent spillover events.

119 Bats are putative reservoirs for MERS, while dromedary camels and other camelids are
 120 intermediate spillover hosts (52–54). Although rare, camel-to-human transmission does occur (51,55).
 121 Infected camels shed MERS-CoV via bodily fluids, especially nasal secretions, and exhibit sneezing,
 122 coughing, fever, and loss of appetite (56,57). Camel care-takers or consumers of camel products are at
 123 risk of contracting MERS-CoV (51). People in direct or indirect contact with camels have
 124 disproportionately high seroconversion against MERS-CoV (58). Surveys from 2010–2013 in Saudi
 125 Arabia show that 90% of 310 and 74% of 203 camels were MERS-CoV seropositive (59,60). Historical
 126 seropositive samples and phylogenetic analyses suggest that MERS-like coronaviruses have been
 127 circulating in camels for at least a few decades before MERS recently emerged in humans (52,60–63).
 128 Camel markets with both live and dead animals are believed to serve as hotspots for MERS-CoV
 129 transmission (64).

130 MERS-CoV may infect additional species. Rhesus macaques, common marmosets, swine,
 131 llamas, rabbits, and alpacas have been infected experimentally, and the monkeys developed mild-to-
 132 moderate and moderate-to-severe disease, respectively, swine and llamas displayed rhinorrhea, while
 133 rabbits and alpacas showed no clinical signs, although alpacas shed MERS-CoV and transmitted it
 134 within its species (65–68). A virological survey found MERS-CoV in sheep, goats, donkeys, and a
 135 cow, but not in buffaloes, mules, or horses (69). A serological study confirms that equids might not be
 136 susceptible to MERS-CoV infection, although *in vitro* inoculation suggests otherwise (70). However,
 137 in an experimental inoculation study, sheep and horses did not show evidence of viral replication or
 138 seroconversion (68). Mice, golden hamsters, ferrets, and poultry are not considered susceptible to
 139 MERS-CoV infection, mainly because of their low host receptor homology with that of the MERS-
 140 CoV-susceptible species (67,71).

141 **2.3 SARS-CoV-2**

142 The current COVID-19 pandemic was initially reported in Wuhan, China in 2019 (72,73), although the
 143 origin of its pathogen, SARS-CoV-2, is still unclear. Its ancestor probably originated in bats, since
 144 SARS-CoV-2 is most closely related to the 2013 and 2019 isolates from horseshoe bats in Yunnan,
 145 China at the genome level, although not at the RBD level, suggesting neither might bind to human
 146 ACE2, and are thus not immediate ancestors of SARS-CoV-2 (72,74,75).

147 Conversely, isolates (pangolin-CoVs) from smuggled and diseased pangolins in Guangdong
 148 (2018–2019) are closely related to SARS-CoV-2 in the RBD region (76–80). Molecular binding
 149 simulations show that S proteins of SARS-CoV-2 and pangolin-CoVs can potentially recognize ACE2
 150 in both humans and pangolins, suggesting possible pangolin-to-human spillover (76,77). However,
 151 because pangolin-CoVs (including strains from Guangxi) are not the closest relatives to SARS-CoV-2
 152 at the genome level, they are likely not direct ancestors of SARS-CoV-2 (76,78,79). Nevertheless, a
 153 2019 pangolin-CoV isolate from Guangdong displayed high genome-wide similarity with both SARS-
 154 CoV-2 and SARS-CoV-2’s closest relative (from bats), suggesting SARS-CoV-2 may have originated
 155 from recombination among coronaviruses present in bats and other wildlife (76,77,79,81).

156 Like SARS-CoV-1, SARS-CoV-2 infects species with high ACE2 homology. Cats, ferrets,
 157 golden hamsters, tree shrews, common marmosets, grivets, and cynomolgus and rhesus macaques have

158 been infected with SARS-CoV-2 experimentally, shed the virus, and displayed similar or milder
159 clinical and pathological signs as humans, although cats may not show signs of disease (82–91).
160 Conversely, dogs have low susceptibility to SARS-CoV-2, and show lack of clinical signs or dog-to-
161 dog transmission, possibly due to their low levels of ACE2 in the respiratory tract (82,91–93). Yet, cat-
162 to-cat, ferret-to-ferret, hamster-to-hamster, and bat-to-bat transmission of SARS-CoV-2 have been
163 confirmed experimentally (82,90,91,94). However, mice, swine and poultry are not susceptible to
164 SARS-CoV-2 infection (49,71,82).

165 Accumulating evidence supports naturally occurring human-to-cat SARS-CoV-2 transmission,
166 such as multiple reports worldwide of SARS-CoV-2-positive cats from confirmed or suspected SARS-
167 CoV-2-positive owners (95). Natural human-to-dog transmission may be possible, as was confirmed
168 by seroconversion and SARS-CoV-2 presence in two out of 15 dogs in close contact with COVID-19
169 patients, where the viral sequences from each dog-and-owner pair were identical (92). Serological and
170 virological surveys, conducted several months after the pandemic started, indicate that SARS-CoV-2
171 prevalence is much lower in pet and street cats and dogs than in humans, even if pet owners had
172 suspected or confirmed SARS-CoV-2 infection (96–100). Thus, cats and dogs can get infected under
173 natural conditions, but rarely. However, certain environments might amplify natural infections and
174 cross-species transmission. Human-to-mink, mink-to-mink, and mink-to-human transmission of
175 SARS-CoV-2 have occurred on fur farms in several countries (95,101–104). SARS-CoV-2 has also
176 been transmitted to tigers, lions, and gorillas in zoos, raising concern for wildlife conservation (105).

177 Apart from the mink farm outbreaks, evidence so far suggests limited SARS-CoV-2
178 maintenance in domestic mammals or risk for secondary zoonoses (104). However, the panzootic
179 potential of SARS-CoV-2 necessitates expanding veterinary surveillance (104,106), especially if
180 domestic and/or wild animals were to maintain SARS-CoV-2 as the human population undergoes
181 vaccination, making COVID-19 control more difficult.

182 **3 Emerging coronaviruses in domestic mammals**

183 Since the advent of agriculture (~8,000 BC), several spillover events have led to the emergence of
184 novel pathogens in humans and domesticated animals (16). Genetic analyses place the common
185 ancestor to all known coronaviruses at around 8,000 BC, and those of each genus at around 2,400–
186 3,300BC (10). Like humans, domestic mammals have been experiencing an increasing rate of novel
187 coronavirus emergence, especially within the last century.

188 Bovine coronavirus (BCoV) likely emerged from rodent-CoVs around 1400 AD (17,107).
189 BCoV is transmitted via the fecal–oral route, causing bloody diarrhea and respiratory infections in
190 cattle (108–110). BCoV-like viruses have also been detected in other domestic and wild ruminants
191 (108). BCoV can infect dogs experimentally, although subclinically (111). Turkeys show clinical signs
192 of enteritis when infected with BCoV experimentally, but chickens are not susceptible (112). Equine-
193 CoV, discovered in 1999, plausibly also descended from BCoV and causes enteritis in horses (113–
194 115).

195 There are two dog coronaviruses: an *Alphacoronavirus* called canine enteric coronavirus
196 (CCoV), transmitted fecal-orally, with serotypes CCoV-I and CCoV-II, and a *Betacoronavirus* called
197 canine respiratory coronavirus (CRCoV), which causes kennel cough (116). CRCoV was discovered
198 in 2003 from a kennel outbreak (117). It was later also detected in samples from 1996 (118). It is
199 closely related to BCoV and OC43, and genetic analyses suggest that CRCoV arose from a recent host-
200 species shift of BCoV from bovine to canine hosts (117,119).

201 CCoV was first isolated from an outbreak in military dogs in 1971 (116). Initially, CCoV
202 infections were believed to be restricted to the enteric tract causing mild diarrheal disease (120), but
203 an increasing number of lethal pantropic infections suggests that CCoV is responsible for an emerging
204 infectious disease in canines (116). There are three proposed subtypes of CCoV-II: original CCoV-IIa,
205 recombinant CCoV-IIb, and CCoV-IIc (116). The two biotypes of CCoV-IIa have different tissue
206 tropism and pathogenicity: “classical” CCoV-IIa is restricted to the small intestine causing enteritis,
207 but the emerging “pantropic” CCoV-IIa causes leukopenia and is often fatal (116,121). In 2019, an
208 Asian pantropic CCoV-IIa strain was also isolated from a wolf in Italy (122), suggesting spillover to
209 wildlife of imported strains (123). Cats and swine are also susceptible to CCoV (124–126).

210 There are six porcine coronaviruses: four *Alphacoronaviruses*, transmissible gastroenteritis
211 virus (TGEV), porcine respiratory coronavirus (PRCoV), porcine epidemic diarrhoea virus (PEDV),
212 and swine acute diarrhea syndrome coronavirus (SADS-CoV), one *Betacoronavirus*, porcine
213 haemagglutinating encephalomyelitis virus (PHEV), and one *Deltacoronavirus*, porcine
214 deltacoronavirus (PDCoV) (127). TGEV, PEDV, SADS-CoV and PDCoV cause severe enteritis that
215 are fatal in piglets, PHEV causes digestive and/or neurological disease, and PRCoV causes mild
216 respiratory disease (127).

217 TGEV, discovered in 1946 (128), likely emerged from CCoV-II (129), and its less virulent
218 descendent PRCoV was identified in 1984 (130). PHEV, first described in 1957, likely descended from
219 BCoV (127). PEDV emerged in the 1970s in Europe and Asia, likely from bat-CoVs, and was
220 introduced in North America in 2013 after a new PEDV strain emerged in China in 2010 (131–134).
221 A serological study indicates that PEDV subsequently spilled over from domestic to feral swine
222 populations in the US (135). PDCoV was first detected in swine samples from 2009 in Hong Kong
223 (10,132). In 2014, PDCoV caused the first-reported outbreaks in USA and South Korea (136,137). It
224 was proposed that the virus’ ancestor originated from recombination between sparrow-CoV and
225 bulbul-CoV (138). PDCoV is most closely related to *Deltacoronaviruses* sampled from Asian leopard
226 cats and ferret badgers in Guangdong and Guangxi markets (the first documented cases of
227 *Deltacoronaviruses* in mammals) (139), suggesting that these species could have acted as intermediates
228 for interspecies PDCoV spillover (140). In 2016, SADS outbreaks emerged in Guangdong with
229 evidence strongly suggesting bat-to-swine spillover origin (141).

230 There is one coronavirus that primarily infects cats: feline coronavirus (FCoV). This
231 *Alphacoronavirus* exists in two serotypes: FCoV-I and FCoV-II (142). Both cause digestive diseases
232 and are transmitted fecal-orally. FCoV-I is the most common type, but less virulent than FCoV-II
233 (143,144). Comparative sequence studies indicate FCoV-I is genetically similar to CCoV-I, and FCoV-
234 II emerged from recombination between FCoV-I and CCoV-II (121,142,145,146). Conceivably,
235 FCoV-I and CCoV-I evolved from a common ancestor, while CCoV-II and FCoV-II arose as more
236 virulent recombinants (129). For each serotype, there are two biotypes with different pathogenicity:
237 feline enteric coronavirus (FECV) and feline infectious peritonitis virus (FIPV). FECV usually causes
238 mild diarrhea, whereas FIP is lethal. FIPV evolves from FECV via within-host mutations in the S gene
239 that alter cell tropism, and emerges during persistent infection of FECV (142,147). However, a novel
240 FIPV strain may have been transmitted horizontally (144). In 2004, a disease resembling FIP was also
241 discovered in ferrets caused by an emerging ferret systemic coronavirus, a decade after the first and
242 less virulent ferret coronavirus (enteric) was discovered (148). FIP likely emerged in the late 1950s,
243 within a decade after the first TGE cases in swine in USA (128,149). Thus, FCoV is closely related to
244 TGEV and CCoV, and recombinants among all three have emerged (150–152), probably because all
245 three can cross-infect cats, swine, and dogs (125,151,153–155).

246 **4 Discussion**

247 Coronaviruses in humans and domestic animals are closely related (Figure 1), and have emerged
248 recently and at an increasing rate. The circumstances associated with their emergence are high-animal-
249 density environments that favor interspecies interactions, such as kennels, shelters, farms, and markets
250 (Table 1), which increase disease prevalence and promote cross-species transmission. Indeed, studies
251 show that seroprevalence of CCoV is higher in kennels compared to the rest of the dog population, and
252 shelters co-housing dogs with cats harbor recombinant canine-feline coronaviruses (116,151,153,156).
253 Further, commercial agriculture has led to large numbers of domestic animals living in close proximity
254 to humans, possibly driving the emergence of OC43 from cattle, and 229E and MERS from camelids.

255 Additionally, animals kept under poor conditions or exposed to stress (e.g., during transport)
256 suffer from poor health and suppressed immune systems, rendering them more susceptible to infections
257 (64,157). For example, mink fur farms, where animals are usually kept in small, unhygienic enclosures,
258 generated new strains of SARS-CoV-2 causing secondary zoonoses (95,101–103). The wildlife trade
259 and wet markets are conducive to disease emergence as well, since animals are transported and kept in
260 small, unhygienic cages next to many different animal species (157). Indeed, a study showed that civets
261 in markets were disproportionately positive for SARS-CoV-1 compared to civets on the supplying
262 farms (30). Further, SARS-CoV-1 isolates from a civet and a racoon dog at the same market, but from
263 different regions of China, had an identical S-gene sequence, which differed from that of the other civet
264 isolates, indicating the occurrence of cross-species transmission at the market (26). Accordingly, the
265 concept of One Health is important for suppressing coronavirus emergence.

266 Little is still known about host ranges and cross-species transmissions of coronaviruses. Most
267 studies on this topic have been motivated by finding appropriate animal models for vaccine
268 development, or identifying potential host species enabling viral persistence. However, future studies
269 should expand their surveys beyond domestic, captive or common laboratory animals for a fuller
270 comprehension of coronavirus emergence and the extent of its radiation (Figure 1a). Surveillance
271 efforts of coronaviruses in the wild are underway (e.g., PREDICT, Global Virome Genome) (158,159),
272 which are important for identifying new coronaviruses with zoonotic potential (reviewed in (160)),
273 tracking spillover pathways, and potentially filling in the host range gaps of known coronaviruses in
274 humans and domestic mammals.

275 Concurrently with the global expansion of humans and domestic mammals, various
276 coronaviruses have emerged as a result of cross-species transmission among humans, and domestic
277 and wild animals. Conceivably, the human and domestic mammal population increase yielded a large
278 enough susceptible population to maintain coronavirus circulation, provided more opportunities for
279 novel coronavirus emergence via spillover among different species, and brought humans and domestic
280 animals in closer contact with wild reservoirs (161–163). The mechanisms governing the surge and
281 radiation of these recently emerged coronaviruses require further investigation. Actions reducing
282 people's dependency on domestic animals and demand for animal products, while improving the health
283 of the animals remaining in captivity, may mitigate coronavirus emergence.

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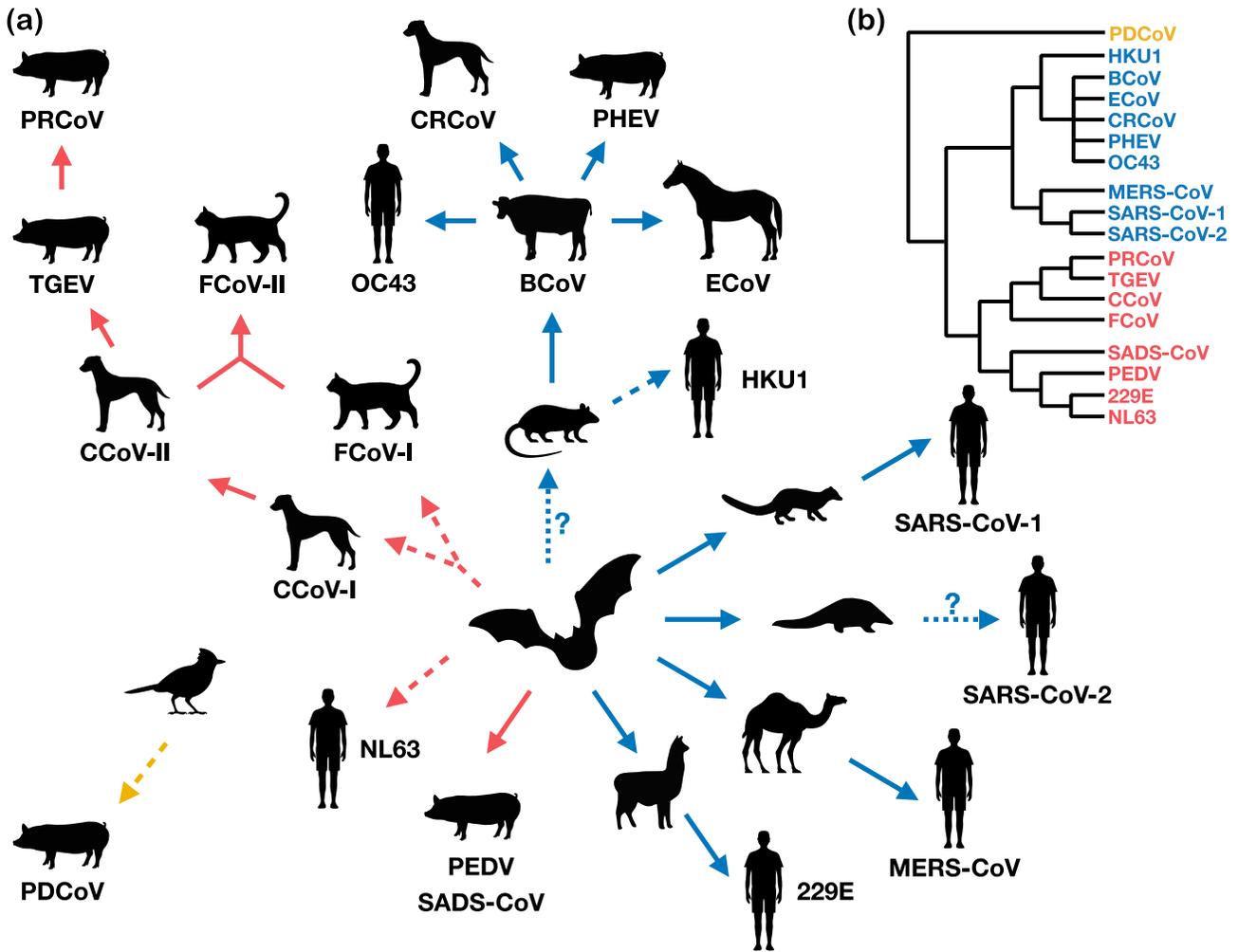
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773 **Figure 1.** (a) The evolution and radiation of coronaviruses in humans and domestic mammals (via
 774 potential wild intermediate spillover host species). The radiation suggests there could be a vicious
 775 cycle of coronavirus emergence, whereby newly emerged viruses in new hosts increase the likelihood
 776 of producing more new recombinants. Red, blue and yellow arrows indicate the direction of spillover
 777 of coronavirus emergence for *Alphacoronaviruses*, *Betacoronaviruses* and *Deltacoronaviruses*,
 778 respectively. Solid arrows represent direct (confirmed or suspected) coronavirus transmission
 779 between host species (although indirect transmission via an unidentified intermediate host is not
 780 excluded), and dashed arrows represent suspected indirect transmission via an unidentified
 781 intermediate host (although direct transmission is not excluded) (10,17,104,127,139,141,164). Dotted
 782 arrows with a question mark indicate uncertain spillover events. (b) A simplified phylogeny of the
 783 coronaviruses covered in this review, drawn from published findings (5,129,165).

784 **Table 1.** First reported outbreaks and probable host species involved in the cross-species transmission events of recently emerging
785 coronaviruses (or new virulent strains of re-emerging coronaviruses) in humans and domestic mammals covered in this review. The entry
786 “Unknown” may either suggest that an intermediate spillover host exists but it has not been identified, or that it may not exist. Question
787 marks represent uncertainty. FCoV-I × CCoV-II denotes recombination between FCoV-I and CCoV-II.

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Primary host	Emerging coronavirus (or new virulent strain)	Year & location of first reported cases	Intermediate spillover host or host of viral predecessor	Potential reservoir host	Environment associated with emergence	References
Human	SARS-CoV-1	2002 Guangdong, China	Masked palm civet (<i>Paguma larvata</i>)	Bat (<i>Rhinolophus</i> spp.)	Wet market	(1,24–30,164)
	MERS-CoV	2012 Saudi Arabia	Dromedary camel (<i>Camelus dromedarius</i>)	Bat (<i>Taphozous perforatus</i> , <i>Rhinopoma hardwickii</i> and <i>Pipistrellus kuhlii</i>)	Camel farm and market	(2,3,52–54,64,164)
	SARS-CoV-2	2019 Wuhan, China	Malayan pangolin (<i>Manis javanica</i>)?	Bat (<i>Rhinolophus</i> spp.)	Wildlife trade and/or wet market?	(72,73,75,79)
Pig	Porcine epidemic diarrhoea virus (PEDV)	1978 Belgium	Unknown	Bat (<i>Scotophilus kuhlii</i>)	Swine farm	(164)
	<i>New virulent PEDV strain</i>	2010 Southern China	Unknown	Bat (<i>Scotophilus kuhlii</i>)	Swine farm	(132)
	Porcine deltacoronavirus (PDCoV)	2009 Hong Kong	Asian leopard cat (<i>Prionailurus bengalensis</i>)? Ferret badger (<i>Melogale moschata</i>)?	Avian, sparrow and bulbul	Illegal live-animal market?	(132,138–140)
	Swine acute diarrhea syndrome coronavirus (SADS-CoV)	2016 Guangdong, China	Unknown	Bat (<i>Rhinolophus</i> spp.)	Swine farm	(141,164)

Cross-species transmission of coronaviruses

Dog	Canine respiratory coronavirus (CRCoV)	2003 United Kingdom	Cattle (BCoV)	Rodents? Bats?	Kennel	(10,17,106, 115,116,118)
	Canine enteric coronavirus (CCoV)	1971 Germany	Unknown	Bat (<i>Rhinolophus</i> spp.?)	Military dog kennel	(10,115,126, 164)
	<i>Pantropic CCoV-IIa</i>	2005 Italy	Unknown	Bat (<i>Rhinolophus</i> spp.?)	Pet shop	(10,115,120, 126)
Cat	Feline coronavirus (FCoV)	1963 United States	FCoV-I: Unknown FCoV-II: Cat and/or dog (FCoV-I × CCoV-II)	Bat (<i>Rhinolophus</i> spp.?)	Shelters and catteries	(10,127,149)
	<i>Horizontally-transmitted FIP FCoV-II</i>	2011 Taiwan	Cat and/or dog (FCoV-I × CCoV-II)	Bat (<i>Rhinolophus</i> spp.?)	Shelter	(10,127,144)