

Coronavirus disease 2019 and its potential animal reservoirs: A review

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Abstract

In the 21st century, the world has been plagued by coronavirus disease 2019 (COVID-19) caused by severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2), a virus of the family Coronaviridae epidemiologically suspected to be linked to a wet market in Wuhan, China. The involvement of wildlife and wet markets with the previous outbreaks simultaneously has been brought into sharp focus. Although scientists are yet to ascertain the host range and zoonotic potential of SARS-CoV-2 rigorously, information about its two ancestors, SARS-CoV and Middle East respiratory syndrome coronavirus (MERS-CoV), is a footprint for research on COVID-19. A 96% genetic similarity with bat coronaviruses and SARS-CoV-2 indicates that the bat might be a potential reservoir of SARS-CoV-2 just like SARS-CoV and MERS-CoV, where civets and dromedary camels are considered the potential intermediate host, respectively. Perceiving the genetic similarity between pangolin coronavirus and SARS-CoV-2, many scientists also have given the scheme that the pangolin might be the intermediate host. The involvement of SARS-CoV-2 with other animals, such as mink, snake, and turtle has also been highlighted in different research articles based on the interaction between the key amino acids of S protein in the receptor-binding domain and angiotensin-converting enzyme II (ACE2). This study highlights the potential animal reservoirs of SARS-CoV-2 and the role of wildlife in the COVID-19 pandemic. Although different causes, such as recurring viral genome recombination, wide genetic assortment, and irksome food habits, have been blamed for this emergence, basic research studies and literature reviews indicate an enormous consortium between humans and animals for the COVID-19 pandemic.

Keywords: ACE2 receptor, COVID-19, Intermediate host, SARS-CoV-2, wildlife.

Introduction

Coronaviruses are enveloped, spherical, or pleomorphic viruses belonging to the large Coronaviridae family of single-stranded RNA viruses under the Nidovirales order, with crown-like spikes on the outer surface [1], causing acute or persistent infection in a wide variety of mammals and birds [2]. The coronavirus family is subdivided into four genera: α , β , γ , and δ [3]. Six human coronavirus strains have been identified so far [4], comprising α -coronaviruses (HCoV-NL63 and HCoV-229E), β -coronaviruses (HCoV-OC43 and HCoV-HKU1), severe acute respiratory syndrome coronavirus (SARS-CoV) [5], and Middle East respiratory syndrome coronavirus (MERS-CoV) as well as SARS-CoV-2 [6]. Due to their widespread distribution, large genetic

diversity, frequent genome recombination, and growing human-animal interface, new coronaviruses have been emerging in humans periodically [7].

A novel coronavirus outbreak has occurred in Wuhan, China, at the end of December 2019, epidemiologically suspected to be linked to a wet market [8] and subsequently spreading worldwide. Scientific studies have reported that the virus is related to β -coronavirus; initially, Chinese researchers have named it Wuhan coronavirus or 2019 novel coronavirus. Later, it was named SARS-CoV-2, and the disease was named coronavirus disease 2019 (COVID-19) by the International Committee on Taxonomy of Viruses [7,9,10]. Unlike in many countries, from vegetable, poultry, and fish to illegal wild animals, including peacock, bear, deer, pangolin, civet, turtle, and bat, everything is sold in Chinese wet markets [11]. Among them, bats can host many mammalian detrimental viruses without showing any symptoms [12]. Scientific reports suggested that there is a 96% genetic similarity between bat coronaviruses and SARS-CoV-2 [13]; therefore, the bat might be a potential reservoir of SARS-CoV-2, just like SARS-CoV and MERS-CoV, where civets and dromedary camels are considered the potential intermediate hosts [14]. The

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possible origin of SARS-CoV-2 from Malayan pangolin (*Manis javanica*) has been reported as well [15]. However, the exact potential reservoir and intermediate host of the virus have not yet been identified. For several reasons, this pandemic is given the greatest attention by the World Health Organization (WHO) and nearly all countries worldwide. As reported by the WHO, 8093 people from 26 countries were infected with SARS-CoV with a mortality rate of 9% in 2003. Besides other coronaviruses, SARS-CoV-2 shows a fast transmissibility rate and a higher mortality rate due to comorbidity [16]. According to a WHO report, a much higher degree of transmission is observed in SARS-CoV-2, where more than 138.68 million people became infected across 223 countries, with a mortality rate 2.15% so far until the preparation of this manuscript. SARS-CoV-2 has shown a median basic case reproduction number (R_0) of 5.7 [17], which indicate its remarkable contagiousness. Altogether, the estimated R_0 , case morbidity, and case mortality rate of SARS-CoV-2 are noticeably higher than SARS-CoV, and the genetic recombination event observed at the S protein in the receptor-binding domain (RBD) region of SARS-CoV-2 might have enhanced its transmission ability [18]. However, after phylogenetic and recombination analyses with the sarbecovirus subgenus, the novel virus demonstrated a dissimilar clustering with a SARS-like coronavirus sequence, rejecting the chance of recent recombination [19]. Full genome analysis of SARS-CoV-2 showed that it is different from SARS-CoV and MERS-CoV, but it forms a unique lineage with the sarbecovirus [8]. It was observed previously that MERS-CoV expresses cell receptors after continuous passaging, leading to a mutation in the S protein gene that enhances viral entry in animal species causing cross-species transmission [20].

To reveal the cause of the unique high contagiousness, zoonotic association, and animal-to-human transmission dynamics of SARS-CoV-2, further molecular and epidemiological studies are needed. More studies might facilitate the prevention and control of the current pandemic and the preparation for future similar outbreaks. This review discusses the different coronavirus diseases along with their possible animal reservoirs and the potential intermediate host of COVID-19.

Primary Reservoirs and Hosts of Coronaviruses

Although it is challenging to ascertain the natural animal reservoir and host range of coronaviruses and determine their zoonotic potential, it has paramount importance, as the recent SARS-CoV-2 and two other near-past serious outbreaks SARS and MERS have caused thousands of deaths [5,6,21,22]. Studies have found zoonotic connections with all three coronaviruses, and the bat is the suspected host; however, they seem to use a range of intermediate hosts. Several novel coronavirus strains have emerged in the last two

decades in animals, such as pigs, horses, monkeys, camels, and civets, with potential for zoonotic transmission. Coronavirus infections have been reported in children caused by bovine coronaviruses [23,24] and laboratory animals, such as mice, rats, guinea pigs, rabbits, and poultry, manifested as respiratory infections and reproductive disorders [25]. Different gastrointestinal (GI) disorders, respiratory illnesses, and nervous symptoms have been reported in coronavirus infections in bovine, canine, feline, and swine species [23,24,26-28]. Initially, scientists have predicted raccoon dogs and palm civets as the key reservoirs of SARS-CoV, later viral RNA detection confirmed palm civets as the secondary host [29], although the details linking bat and farmed palm civets are unclear [30-32]. After detecting the anti-SARS antibody in *Rhinolophus* bats, it was considered a potential source of virus replication [33]. In 2012, MERS-CoV belonged to the β -coronavirus in Saudi Arabia, where dromedary camels were identified as the primary host [34]. Further, the virus was detected from *Pipistrellus* and *Perimyotis* bats [35]; therefore, the bat was confirmed as the potential reservoir of MERS-CoV infections.

What is COVID-19?

COVID-19 is a highly transmittable and pathogenic viral infection affecting mainly the respiratory system and executes symptoms closely similar to that of pneumonia [8]. Before its worldwide spread, the virus was first identified in Wuhan, China. The disease is caused by SARS-CoV-2, a virus of the family Coronaviridae [36]. Coronaviridae is a large family of RNA viruses that infect mammals (including humans) and birds. "Corona" means "crown" and they are so named because of their appearance. These viruses are responsible for diseases, such as MERS [21] and SARS. It has been found through genomic analysis that SARS-CoV-2 is phylogenetically related to SARS-like bat viruses [17]. Therefore, it is assumed with great certainty that the primary reservoir of this virus could be bats, although the intermediate source of origin and pathways of human transmission are still obscure [1]. However, it has been confirmed widely that the human-to-human transmission of the virus occurs exceptionally rapidly than any other from the family.

Outbreak Scenario

Several recent epidemics of viral respiratory infections have mostly emerged and spread worldwide from China. Several reasons behind it are speculated, including lots of livestock farming with limited sanitation and lax oversight; dense human population mixing with all sorts of domestic and exotic animals in wet markets; and huge trade due to the production of a wide range of commodities, tourism, and military transactions with most countries worldwide [37]. At the very end of 2019, an outbreak of the serious pneumonic disease in humans

was reported in Wuhan, China. A novel coronavirus was identified from the patients [38] and named SARS-CoV-2. Soon after identifying the primary case, human-to-human transmission occurred very rapidly and spread globally within 1 month. Because of this, on January 30, 2020, the WHO declared a global public health emergency. It was speculated that the virus might have originated from Huanan Seafood Market in Wuhan City, Hubei Province, China, as contact tracing showed that many of the early cases had a connection to the market [36]. The identification of SARS-CoV-2 from environmental samples of the market provided further evidence of the role of this market in the emergence of this novel virus [39]. The total confirmed cases worldwide and in Bangladesh are illustrated in Figure-1.

Transmission Dynamics of SARS-CoV-2

The transmission dynamics of SARS-CoV-2 are illustrated in Figure-2 [8,13,15,36,40-43].

Malayan Pangolin and SARS-CoV-2

The role of wild animal and wet markets seems important in the emergence of SARS-CoV-2, as previous outbreaks of SARS from 2002 to 2003 involved similar types of wet markets [44]. Moreover, it was observed that a number of mammalian species were brought to the Huanan Seafood Market (predicted to be linked with the COVID-19 outbreak) before the outbreak [39], which made the basis for the speculation of zoonotic transmission. Therefore, several research studies have been conducted in different parts of the world to gather scientific evidence of the SARS-CoV-2-related virus in

wild animals. However, a coronavirus closely related to SARS-CoV-2 was detected from a *Rhinolophus affinis* bat in Yunnan in 2013. Studies on pangolins smuggled into southern China succeeded in identifying the related virus [15]. Similar viruses have not yet been detected in other wildlife species.

Malayan pangolin, also named Sunda pangolin or Javan pangolin (*M. javanica*), is a carnivore habituated in Southeast Asia [45]. Interests grew to identify SARS-CoV-2-related viruses in pangolins due to its close contact with humans as a food source and the use of its scales in traditional Chinese medicine [46]. As the current pandemic of COVID-19 is the worst in a century, many research studies are ongoing to understand the viral evolution. A link between COVID-19 and pangolin coronavirus (pangolin-CoV) was proven in some recent studies, although evidence is not enough to prove if pangolins are the host; rather, they more certainly might be the intermediate host [15]. Recently published data showed that pangolin-CoV has approximately 85.5-92.4% genomic similarity with SARS-CoV-2 and is also closely related to bat coronavirus [47]. The study revealed structural similarity between pangolin-CoV and human coronavirus that allowed the transmission into human cells and proposed an exceptional bat-to-pangolin-to-human transmission [48]. Although the coronavirus was detected years ago as a potential human pathogen as well as a respiratory and GI tract infectious agent in domestic and wild animals (cattle, buffalo, rabbit, camel, dog, cat, civet, rat, mouse, bat, etc.), its genetic diversity and zoonotic transmission are yet to be proven with enough certainty [2].

Viral Sequence Analysis from Malayan Pangolin

The previous findings have suggested that β -coronavirus might naturally live in pangolin and potentially can infect humans. The pangolin is also one of the major suspects for the zoonotic transmission of the ongoing COVID-19 outbreak [49]. However, the pathogenesis of this pangolin-CoV remains to be studied. Recent molecular-level investigations have shown that pangolin-CoV is 91% and 90% related to the novel SARS-CoV-2 (causing COVID-19) and bat coronavirus, respectively [50]. Another recent study has suggested about 85-92% genetic similarity of pangolin-CoV and SARS-CoV-2, where pangolin-associated coronaviruses belong to two sublineages of SARS-CoV-2-related coronaviruses [15]. These findings showed an identical cleavage site in the spike protein (S protein) between the viruses [51]. The S protein of coronaviruses binds to host receptors through RBDs and plays an essential role in initiating virus infection and determining host tropism [4]. A previous study has suggested that SARS-CoV-2, SARS-CoV, and Bat-CoV-RaTG13 have similar RBDs, suggesting that they use the same receptor angiotensin-converting enzyme II (ACE2) [51]. Scientific analysis showed that pangolin-CoV-2020 had a much conserved

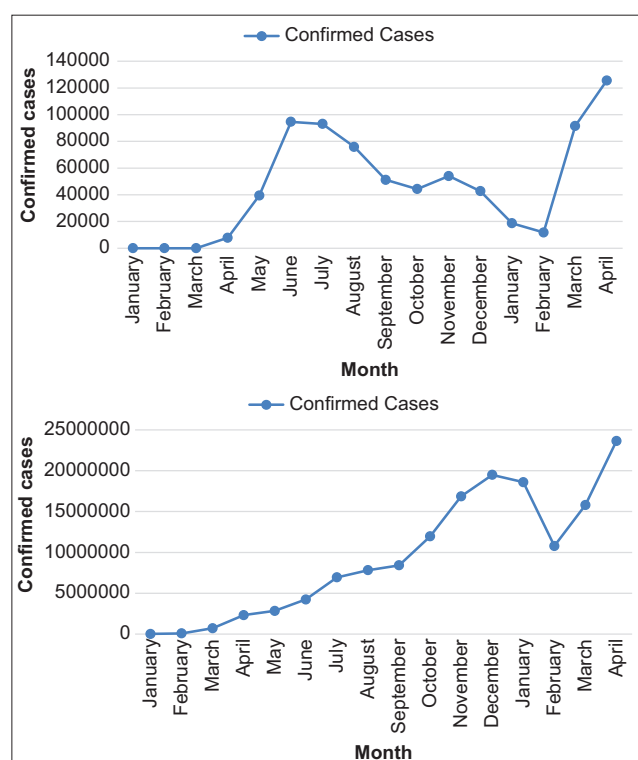


Figure-1: Monthly COVID-19 confirmed cases from January' 2020 to April' 2021 (a) World data (b) Bangladesh data.

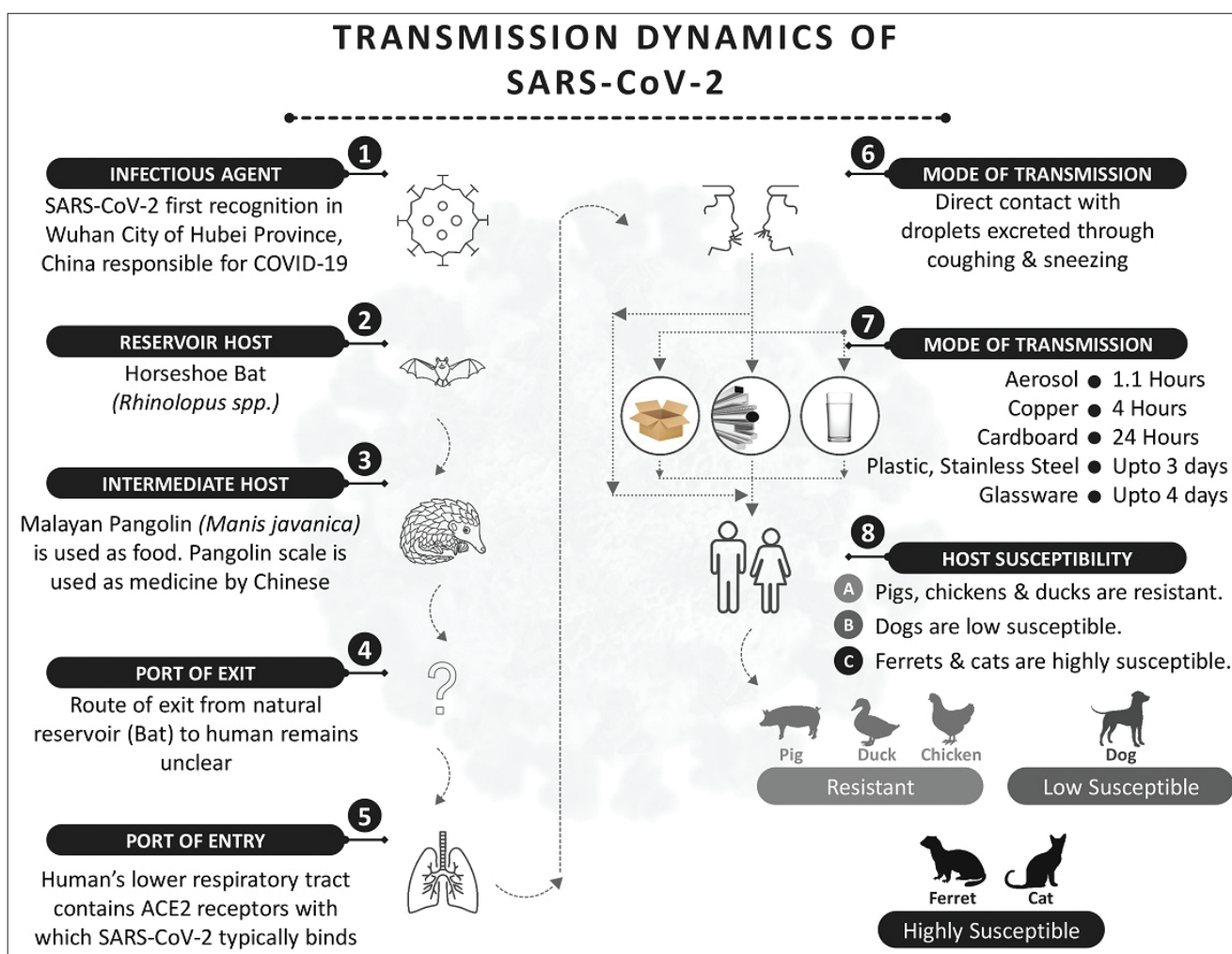


Figure-2: Transmission dynamics of SARS-Cov-2; source modifiers: (1) [41], (2) [13], (3) [15], (4) [40], (5) [8], (6) [36], (7) [42], (8) [43].

RBD to these three viruses rather than MERS-CoV, suggesting that pangolin-CoV is very likely to use ACE2 as its receptor. In contrast, the ACE2 receptor is present in pangolins with high sequence conservation with those in the gene homolog in humans. However, these findings do not prove a zoonotic link of pangolin-CoV-2020.

By reviewing the available genetic data, it can be concluded that the determination of several lineages of pangolin-CoV and their similarity with SARS-CoV-2 might indicate that pangolin could be a potential intermediate host of the human novel virus with an unknown potential to infect humans. Results from different studies did not discard the chance of having other coronaviruses in pangolins. Moreover, available data do not support with certainty that SARS-CoV-2 emerged directly from pangolin-CoV. Thus, extended surveillance of coronaviruses in pangolins is necessary to improve the understanding of the range of coronaviruses in pangolins. Although the transmission link between pangolins and humans is not yet clear from published data, preventive actions such as wildlife conservation and limiting human exposure to wildlife could effectively reduce the spillover risks of coronaviruses from wild animals to humans.

Evolutionary Perspectives

The evolutionary history was inferred using the neighbor-joining method. The optimal tree with the sum of branch length of 2.98423808 is shown. The evolutionary distances were computed using the maximum composite likelihood method and are in the units of the number of base substitutions per site. The proportion of sites where at least an unambiguous base is present in at least one sequence for each descendent clade is shown next to each internal node in the tree. The analysis involved 26 nucleotide sequences (Table-1). All positions containing gaps and missing data were eliminated. There were a total of 21,197 positions in the final dataset. Evolutionary analyses were conducted in MEGA7 and are illustrated in Figure-3.

Bats and SARS-CoV-2

Bats are the natural host of many coronaviruses and may cause diseases in many other animals through evolution [7,40]. It is hypothesized that most human coronaviruses might have emerged from the bat reservoir [30,71]. Based on the assumption after the COVID-19 pandemic, interest

Table-1: Comparison between SARS-CoV and SARS-CoV-2.

Features	SARS-CoV	SARS-CoV-2	References
Emergence date	November-2002	December-2019	[76-79]
Area of emergence	Guangdong, China	Wuhan, China	
Date of fully controlled	July-2003	Not controlled yet	
Key hosts	Bat, palm civets, and Raccon dogs	Bat and Malayan pangolin	[15,36,80,81]
Number of countries infected	26	220	[82]
Entry receptor in humans	ACE2 receptor	ACE2 receptor	[36,83,84]
Sign and symptoms	Fever, malaise, myalgia, headache, diarrhea, shivering, cough, and shortness of breath	Cough, fever, and shortness of breath	[84-86]
Disease caused	SARS, ARDS	SARS, COVID-19	[41,87]
Total infected patients	8,098	66422058 (till December 7, 2020)	[1,88]
Total died patients	776 (9.6% mortality rate)	1532418 (2.31% mortality rate) (till December 7, 2020)	[82]

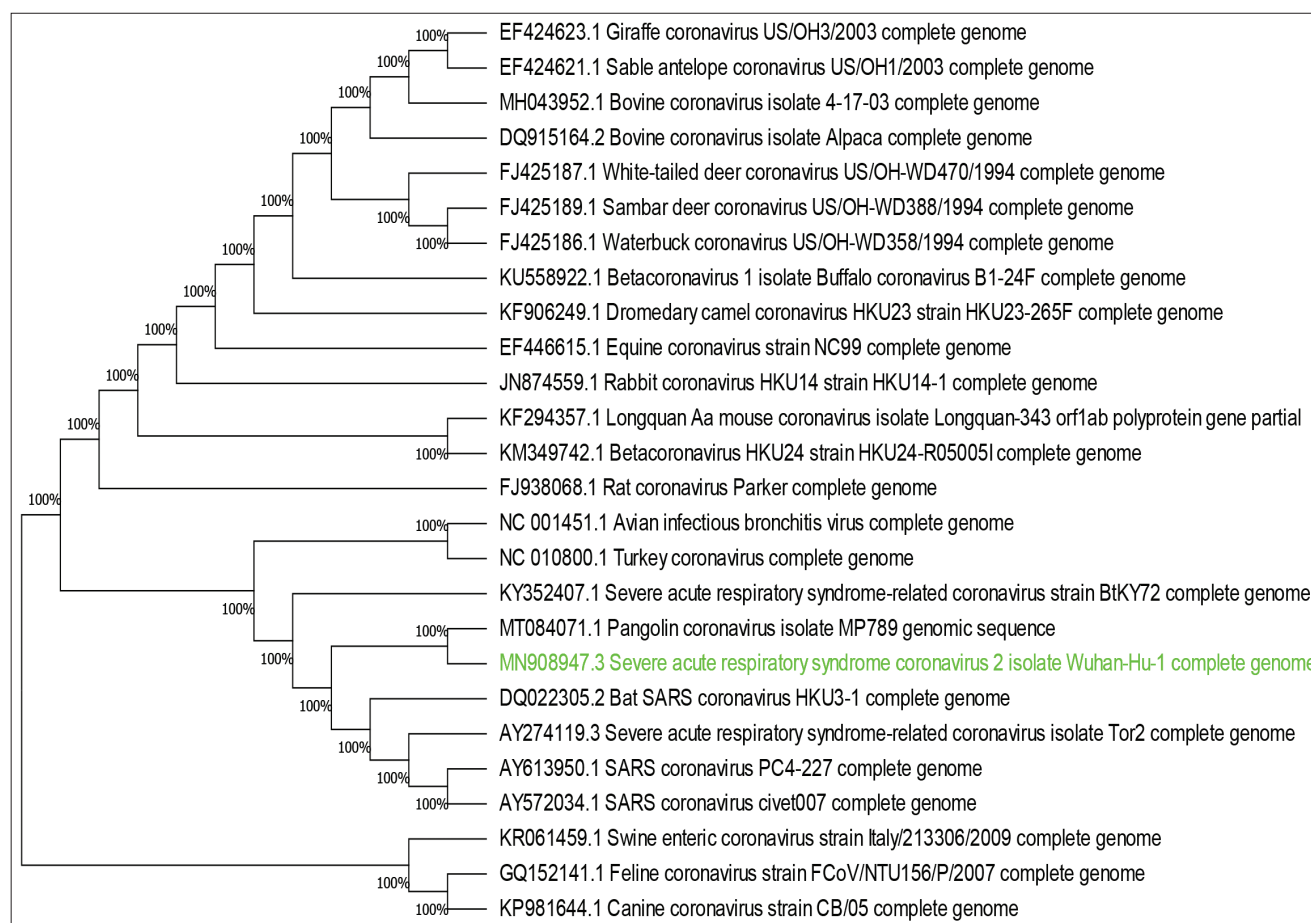


Figure-3: Evolutionary relationships of taxa.

grew among several researchers to determine the genetic connection between SARS-CoV-2 and bat coronaviruses and was successfully confirmed by several studies [4,19,72,73]. SARS-related coronavirus (RaTG13) showed 96.2% similarity with SARS-CoV-2 [19] but was not very closely linked to the genomes of SARS-CoV (~79%) or MERS-CoV (~50%) [74]. Further, the ACE2 receptor was used by both SARS-CoV and SARS-CoV-2 [51]. Although the overall genomic nucleotides differ by ~4% between SARS-CoV-2 and Bat-CoV-RaTG13, the genomic average dS was 0.17, which means that the divergence at the neutral sites is 17% between these two viruses [75]. SARS-CoV-2 is classified as

a novel β -coronavirus belonging to the sarbecovirus subgenus of the Coronaviridae family. The genome sequence of SARS-CoV-2 is about 89% identical to bat SARS-like CoVZXC21 and 82% identical to human SARS-CoV [41]. It has been reported that SARS-CoV-2 uses the same cell entry receptor (ACE2) to infect humans, as SARS-CoV [13], so a clinical similarity between the two viruses could be expected.

Comparison between SARS-CoV and SARS-CoV-2

The key features comparing the viruses are shown in Table-1 [1,15,36,41,77-88].

Table-1: GenBank accession numbers of coronavirus sequences used in this study.

SL	Accession no.	Organism	Location	References
01	MN908947	Severe acute respiratory syndrome coronavirus 2	China	[38]
02	FJ425187	White-tailed deer coronavirus US/OH-WD470/1994	USA	[52]
03	FJ425186	Waterbuck coronavirus US/OH-WD358/1994	USA	[52]
04	NC_010800	Turkey coronavirus	Canada	[53]
05	GQ152141	Feline coronavirus	Taiwan	[54]
06	EF424623	Giraffe coronavirus US/OH3/2003	USA	[55]
07	KF294357	Longquan Aa mouse coronavirus	China	[56]
08	MT084071	Pangolin coronavirus	China	[57]
09	JN874559.1	Rabbit coronavirus HKU14	China	[58]
10	FJ938068	Rat coronavirus Parker	USA	[59]
11	FJ425189	Sambar deer coronavirus US/OH-WD388/1994	USA	[54]
12	AY274119.3	Severe acute respiratory syndrome-related coronavirus	Canada	[60]
13	KY352407.1	Severe acute respiratory syndrome-related coronavirus	Kenya	[61]
14	AY613950.1	SARS coronavirus PC4-227	China	[62]
15	KR061459.1	Swine enteric coronavirus	Italy	[63]
16	EF446615.1	Equine coronavirus	USA	[64]
17	AY572034.1	Civet SARS CoV 007/2004	China	[44]
18	KM349742.1	China Rattus coronavirus HKU24	China	[58]
19	KP981644.1	Canine coronavirus	Italy	[65]
20	KU558922.1	Buffalo coronavirus B1-24F	Bangladesh	[66]
21	MH043952.1	Bovine coronavirus	USA	[67]
22	DQ022305.2	Bat SARS coronavirus HKU3-1	China	[58]
23	NC_001451.1	Infectious bronchitis virus	Canada	[68]
24	EF424621.1	Sable antelope coronavirus US/OH1/2003	USA	[64]
25	DQ915164.2	Bovine coronavirus isolate Alpaca	USA	[69]
26	KF906249.1	Dromedary camel coronavirus HKU23	UAE	[70]

Are there Other Animal Reservoirs of SARS-CoV-2?

The transmission of pathogens from animals to humans and vice versa is called zoonotic spillovers [88], which are speculated to be responsible for about 70-75% of the emerging epidemics in recent decades [89]. Wild animals, especially bats, are widely suspected as a reservoir host of many viruses and might play an important role in transmitting etiological agents of Nipah, Hendra, Ebola, SARS, MERS, 229E, NL63, and recently COVID-19 [7,90]. Domestic animals are suspected as intermediate and amplifying hosts of coronaviruses, where the ancestor of HCoV-OC43 was found in domestic cattle and swine, and this host switching caused the pandemic of human respiratory diseases in 1890 [91]. Some scientists have indicated snakes as the possible reservoir and intermediate host of SARS-CoV-2 [92]. Further, the turtle (*Chrysemys picta bellii*, *Chelonia mydas*, and *Pelodiscus sinensis*) was speculated as a potential intermediate host of SARS-CoV-2 besides snake and pangolin based on the interaction between the key amino acid of the S protein in RBD and ACE2 [47]. It is still obscure which animal species served as the intermediate host, but some scientists indicated that two potential hosts of SARS-CoV-2 might be bats (*R. affinis*) and mink, where mink are considered intermediate host [93].

Role of Wildlife in COVID-19

Wildlife is extensively responsible for zoonotic epidemics, including 75% of the emerging infectious

human diseases [94]. From 2000 to 2013, 25 emerging or reemerging infectious diseases were identified as great perils for mankind, closely linked to wildlife [95]. Human infections with SARS-CoV, HIV, Nipah virus, and H5N1 influenza originated clearly from wildlife [96]. As the pandemic feature of SARS-CoV-2 shares common attributes with major outbreaks in recent years, such as SARS-CoV, avian influenza, MERS, and Ebola, the origin and spread of these viruses are often thought to be intimately linked to wildlife. The risk of zoonotic disease transmission is largely exacerbated by the breach of barrier between humans and wildlife [97]. Change in the ecosystem elevates the epidemiological interactions between wildlife and livestock, contributing to the zoonotic transfer [97]. Loss of wildlife biodiversity affects the correlation between the host and the vector, accelerating the spread of infectious diseases [98]. Wildlife habitat destruction leads to expanded wildlife trade [99]. According to Beirne [100], wildlife trade is one of the preponderant risk factors causing pathogen spillover. Furthermore, for COVID-19, there is a suspicion that SARS-CoV-2 is interlinked with intermediate animal host, as the initial COVID-19 cases were identified from a wet market in Wuhan where wild animals are bought and sold [101]. Wet markets massively promote wildlife trade, and this practice has led to the mushrooming of zoonotic diseases among the animals and to purchasers at markets [102].

SARS-CoV-2 has been isolated from a wide range of animal species and captive wildlife in close contact with human COVID-19 cases. This virus has

also been shown to infect wild species under experimental conditions. At present, coronavirus has been found in cattle, horses, ferrets, bats, dogs, and others [103]. The evidence of SARS-CoV-2-positive confirmation with respiratory symptoms in several tigers in Bronx Zoo (New York City, United States) indicates the occasional spillover from humans to domestic or captive animals [104]. Other than New York City, COVID-19-positive Malayan tigers were enlisted in a zoo in Tennessee, where the caretaker was also SARS-CoV-2-infected [105]. Furthermore, minks on two farms in the Netherlands were reported with SARS-CoV-2 infection associated with clinical signs and pathological and virological findings [106]. In addition, the virus has also been exhibited to infect an immense number of wild species under experimental conditions, such as rhesus and cynomolgus macaques, ferrets, cats, and golden Syrian hamsters [107-111].

In contrast, wildlife is being implicitly blamed for the pandemic, but researchers relentlessly try to find a way out of this catastrophic disaster. For example, ACE2 receptors in cats and ferrets are close to human ACE2 [112]. ACE2 receptors of rhesus macaques, Syrian hamsters, and common marmosets have been reported to be profoundly similar to that of humans; among them, hamster ACE2 showed the maximum binding affinity to both SARS-CoV-2 and SARS-CoV spike proteins, indicating an effective animal model for vaccines and drugs against SARS-CoV-2 [112].

Conclusion and Perspectives

COVID-19, a devastating respiratory disease, is evolving as a potential threat to mankind, challenging science and technology. Zoonotic transmission has become the burning question because this new virus is analogous to the same family of viruses as SARS-CoV linked with civets and MERS-CoV connected with dromedary camels. Furthermore, the SARS-CoV-2 genomic sequence in humans and pangolins is noteworthy. These animals are suspected to be the reservoir for this infection. Because findings have suggested that this disease might be from any wild animals, there is a need for more extensive research on exotic animals, environmental change, pollution, wildlife conservation, food habit, and others to ascertain the role of the animals in the spread of the virus. This study reviewed the transmission potential of SARS-CoV-2 cases identified in different wild and domestic animals. Although there is no independent corroboration that humans can transmit COVID-19 to their pets or other animals, it is recommended to follow preventive measures. However, to ameliorate the pandemic, constructive public health strategies, regular monitoring and surveillance, efficacious medication, and a mass vaccination program are needed. In addition, the ecofriendly Wild Animal Conservation Law executing the concept of One Health is anticipated to make an extensive and systematic revision to control the wildlife trade and breach the zoonotic transmission chain.

Authors' Contributions

MSI: Conceptualization, data curation, formal analysis, and drafted and edited the manuscript. FMYH: Conceptualization, phylogenetic analysis and drafted the manuscript. CN: Formal analysis visualization, and drafted and revised the manuscript. JA: Data curation, formal analysis, and reviewed and edited the manuscript. MSN: Data curation and visualization. MAF: Data curation and reviewed and edited the manuscript. SC: Supervision, validation, and reviewed and edited the manuscript. All authors read and approved the final manuscript.

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Competing Interests

The authors declare that they have no competing interests.

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