

Bovine-like coronaviruses in domestic and wild ruminants

Haitham Mohamed Amer

Department of Virology, Faculty of Veterinary Medicine, Cairo University, 11221 Giza, Egypt

Review

Cite this article: Amer HM (2018). Bovine-like coronaviruses in domestic and wild ruminants. *Animal Health Research Reviews* **19**, 113–124. <https://doi.org/10.1017/S1466252318000117>

Received: 30 April 2018
Revised: 27 July 2018
Accepted: 28 July 2018

Key words:

Bovine-like coronavirus; host-range variant; interspecies transmission; ruminant species; wildlife

Author for correspondence:

Haitham Mohamed Amer, Department of Virology, Faculty of Veterinary Medicine, Cairo University, 11221 Giza, Egypt.
E-mail: hamoamer@cu.edu.eg

Abstract

Coronaviruses (CoVs) produce a wide spectrum of disease syndromes in different mammalian and avian host species. These viruses are well-recognized for their ability to change tissue tropism, to hurdle the interspecies barriers and to adapt ecological variations. It is predicted that the inherent genetic diversity of CoVs caused by accumulation of point mutations and high frequency of homologous recombination is the principal determinant of these competences. Several CoVs (e.g. Severe acute respiratory syndrome-CoV, Middle East respiratory syndrome-CoV) have been recorded to cross the interspecies barrier, inducing different disease conditions in variable animal hosts. Bovine CoV (BCoV) is a primary cause of gastroenteritis and respiratory disease in cattle calves, winter dysentery in lactating cows and shipping fever pneumonia in feedlot cattle. Although it has long been known as a restrictive cattle pathogen, CoVs that are closely related to BCoV have been recognized in dogs, humans and in other ruminant species. Biologic, antigenic and genetic analyses of the so-called 'bovine-like CoVs' proposed classification of these viruses as host-range variants rather than distinct virus species. In this review, the different bovine-like CoVs that have been identified in domesticated ruminants (water buffalo, sheep, goat, dromedary camel, llama and alpaca) and wild ruminants (deer, wild cattle, antelopes, giraffes and wild goats) are discussed in terms of epidemiology, transmission and virus characteristics. The presented data denote the importance of these viruses in the persistence of BCoV in nature, spread to new geographical zones, and continuous emergence of disease epidemics in cattle farms.

Introduction

Coronaviruses (CoVs) form a large group of enveloped viruses that harbour the largest genome among all RNA viruses (26.4–31.7 kb in length). CoVs occupy the entire subfamily of *Coronavirinae* within the family *Coronaviridae*, order *Nidovirales*. Traditionally, CoVs were classified into three groups depending on their antigenic and genetic properties (Brian and Baric, 2005). However, these groups have been recently replaced with four genera: *Alphacoronavirus*, *Betacoronavirus*, *Gammacoronavirus* and *Deltacoronavirus*. The first two genera include only mammalian CoVs, while all avian CoVs are members of the other two genera (de Groot *et al.*, 2012).

CoVs infect a wide diversity of animal and bird species causing respiratory, enteric, neurologic and hepatic disorders. Since SARS-CoV was identified in 2003, a significant increase in the number of emerging CoVs has been shown in people and animals as a result of the growing interest in CoV research and the development of improved diagnostic tools (Woo *et al.*, 2009; Peck *et al.*, 2015). The accumulated information has confirmed the ability of CoVs to adapt new tissue tropisms, to jump host-species barriers and to acclimatize variable ecological niches (Decaro *et al.*, 2010b). These abilities were believed to be attributed to: (1) the high mutation rate (a single mutation/genome/round of replication) caused by low fidelity of the viral RNA polymerase (Drake and Holland, 1999), and (2) the exceptional tendency for homologous recombination mediated by random template switching during RNA replication (Woo *et al.*, 2006; Decaro and Buonavoglia, 2008). Cross-species transmission of CoVs was previously recorded for many CoVs [e.g. SARS-CoV in palm civet and human beings (Song *et al.*, 2005); Middle East respiratory syndrome CoV (MERS-CoV) in camels and people (Drosten *et al.*, 2014)]. Bovine CoV (BCoV) represents an excellent example of a CoV that extensively crosses the interspecies barrier. Several bovine-like CoVs were identified as aetiologic pathogens of enteric and/or respiratory diseases in a diverse spectrum of ruminant species (Saif, 2010), dogs (Decaro *et al.*, 2007; Erles *et al.*, 2007; Lorusso *et al.*, 2009) and even human beings (Zhang *et al.*, 1994).

Bovine CoV

BCoVs are commonly identified in the respiratory and intestinal tracts of healthy cattle, and contribute to different disease syndromes (Fulton *et al.*, 2015). The virus is involved as a major cause of calf diarrhoea (CD) during the first 3 weeks of life in both dairy and beef cattle herds

(Boileau and Kapil, 2010). High mortalities are mostly attributed to BCoV infections because they affect both small and large intestines, destroying villi and leading to severe, often bloody, diarrhoea (Torres-Medina *et al.*, 1985). Enteric BCoV infection is also associated with winter dysentery (WD) in adult dairy cattle, causing dramatic decrease in milk production and significant economic losses (Natsuaki *et al.*, 2007). Respiratory tract infection in growing (2–16 weeks of age) and feedlot calves has been frequently attributed to BCoV (Storz *et al.*, 2000; Decaro *et al.*, 2008b; Saif, 2010). The widespread distribution of BCoV could be explained by two main factors: (1) rapid transmission of the virus via faecal–oral and respiratory routes (Heckert *et al.*, 1990; Decaro *et al.*, 2008a), and (2) existence of carrier animals within infected herds. These carriers shed the virus in faeces, particularly during the stress of winter season and parturition, and serve as a source of infection to their neonates and reservoirs for reinfection on the farm (Carman and Hazlett, 1992).

Bovine-like CoVs

In 2008, the Coronavirus Study Group of the International Committee of Taxonomy of Viruses has proposed taxonomic grouping of six CoVs of people, cattle, pigs, horses and dogs [human CoV OC43 (HCoV-OC43), human enteric CoV, BCoV, porcine haemagglutinating encephalomyelitis virus, equine CoV and canine respiratory CoV] in a new virus species named Betacoronavirus 1 (de Groot *et al.*, 2008). Due to their close antigenic and genetic relatedness, members of Betacoronavirus 1 appear as host-range variants rather than separate viruses. It has been concluded that they may originate as a result of genetic recombination and interspecies transmission events (Zhang *et al.*, 1994; Lau *et al.*, 2011; Lau *et al.*, 2012). For instance, HCoV-OC43 likely evolved from ancestral BCoV strains that crossed the interspecies barrier and established an infection in human beings around 1890 (Vijgen *et al.*, 2005; Vijgen *et al.*, 2006).

Several CoV strains have been identified in the faeces, intestinal contents and sometimes in the respiratory secretions of a diverse group of domestic and wild (captive and free-range) ruminant species (Tables 1 and 2). Most of these viruses have demonstrated extensive biologic, antigenic and genetic similarities with BCoV and consequently they were termed as bovine-like CoVs (Tsunemitsu *et al.*, 1995). Experimental transmission of bovine-like CoVs to gnotobiotic and colostrum-deprived cattle calves suggest that cattle may be reservoirs for CoV strains to infect other domestic and wild ruminants and *vice versa*, in a process that helps maintenance and evolution of CoVs in these species (Tsunemitsu *et al.*, 1995; Hasoksuz *et al.*, 2007). It has been proposed that the broad host range of BCoV may be attributed to the presence of haemagglutinin-esterase protein that enables the virus to bind to different cell types (Saif, 2010).

Bovine-like CoVs in domestic ruminants

Water buffalo (*Bubalus bubalis*)

The domestic Asian buffalo (commonly named as water buffalo) is a large bovid originated from Southeastern Asia and tamed approximately 5000 years ago. It is used in many countries as a source of good quality meat, milk and leather, and as a labour animal in agriculture farms. The population of water buffalo in the world was estimated to be 172 million head with 95% living in Asia (mostly in India, China and Pakistan), 2.4% in South

America (principally in Brazil), 2.3% in Africa (only in Egypt), 0.3% in Europe and 0.02% in Australia (Borghese, 2011).

The first description of bovine-like CoVs in water buffalo dated back to 1985, when BCoV antibodies were detected using virus neutralization (VN) and haemagglutination inhibition (HI) assays in 52.9% of sera collected from water buffaloes of different age groups in Bulgaria. Seven faecal samples of diarrhoeic buffalo calves showed haemagglutinating activity that was suppressed by BCoV-specific antiserum (Muniappa *et al.*, 1985). In the early 1990s, bovine-like CoVs were detected in the faeces of suckling buffalo calves with profuse diarrhoea in Egypt using monoclonal antibody (MAB)-based enzyme-linked immunosorbent assay (ELISA) and immunoperoxidase assays (Abd El-Karim *et al.*, 1990). The CoV particles were identified in two further studies in Egypt using negative-contrast transmission electron microscopy (EM) in 20 and 55.2% of the faecal samples collected from diarrhoeic buffalo calves, and 8.3 and 19.1% of the faecal samples collected from apparently healthy buffalo calves, respectively (Byomi *et al.*, 1996; Abd El-Rahim, 1997). The epidemiological data presented by the Tri-national Health Research Project, USAID, indicated that CoV is the second most-common pathogen causing diarrhoea in buffalo calves in Egypt with a prevalence rate of 37.7% (Saleh, 1994; Garbe *et al.*, 1995).

An outbreak of CD and neonatal mortality was later described in a herd of water buffaloes in Campania (Southern Italy) between October 2006 and April 2007. Bovine-like CoVs were identified in the intestinal contents of buffalo calves with severe diarrhoea (two dead and 17 alive) by conventional and real-time reverse transcription polymerase chain reaction (RT-PCR) assays. A virus strain (designated as 179/07-11) was isolated with HRT-18 cells, producing the typical cytopathic effects of BCoV. This strain shared many similarities with BCoVs including: (1) haemagglutination of mouse erythrocytes, (2) receptor-destroying enzymatic activity, (3) cross-reactivity with BCoV antisera in immunofluorescence (IF) assay, and (4) genomic organization. However, the inability of strain 179/07-11 to replicate in MDBK cells and to agglutinate chicken erythrocytes, along with the existence of considerable genetic distance between both bovine and buffalo strains, suggested the assignment of strain 179/07-11 as a prototype of a novel host-range variant of BCoV (named as bubaline CoV) (Decaro *et al.*, 2008c). Four further bubaline CoV strains were isolated afterwards and all showed similar biologic and antigenic characteristics to the prototype strain 179/07-11. Nevertheless, the genetic analysis showed that three of these strains were closely related to the prototype strain whereas the fourth shared higher genetic similarity to recent BCoV reference strains (Decaro *et al.*, 2010a). It is proposed that the bubaline CoV may be originated from interspecies transmission of a BCoV strain; however, no cattle, sheep or goat contact to the water buffalo herd was demonstrated at the time of the outbreak.

The first complete genome sequence of a bubaline CoV was retrieved from two strains identified in Bangladesh in 2014 (BufCoV HKU26 strains B1-24F and B1-28F). The overall nucleotide homology with BCoVs was ranged from 98 to 99%, which supports the taxonomic relevance of both types of CoVs. Nevertheless, the nature of the three accessory proteins that located between spike (S) and envelop (E) varies distinctively. The 4.9 kDa protein of BCoV was replaced with 2.9 kDa protein in BufCoV HKU26, a result of premature stop codon, and the 4.8 kDa protein was replaced with 3.2 and 5.1 kDa proteins in strains B1-24F and B1-28F, respectively, a result of frameshift deletion mutation (Lau *et al.*, 2016).

Table 1. A collective summary of bovine-like CoVs in domestic ruminants

Animal species	Country (state)	Samples		Test(s) of choice	Positive samples		Reference
		Type	No.		No.	%	
Water buffalo	Bulgaria	Serum	293	VNT, HI	155	52.9	Munniappa <i>et al.</i> (1985)
Water buffalo	Egypt	Faeces	ND	ELISA, IP	ND	ND	Abd El-Karim <i>et al.</i> (1990)
Water buffalo	Egypt	Faeces	54	NC-EM, HA	8	14.7	Byomi <i>et al.</i> (1996)
Water buffalo	Egypt	Faeces	132	NC-EM	39	29.6	Abd El-Rahim (1997)
Water buffalo	Italy	Faeces – intestinal contents	19	Conventional and real-time RT-PCR	19	100	Decaro <i>et al.</i> (2008c, 2010a)
Water buffalo	Bangladesh	Faeces	ND	RT-PCR	2	ND	Lau <i>et al.</i> (2016)
Sheep	USA (Idaho, Montana)	Faeces	28	EM	1	3.6	Harp <i>et al.</i> (1981)
Sheep	Chile	Intestinal contents	98	ELISA, EM	6	6.1	Reinhardt <i>et al.</i> (1995)
Sheep, goat	Spain	Faeces	226	Blocking ELISA	0	0	Muñoz <i>et al.</i> (1996)
Sheep, goat	Turkey	Intestinal contents	30	IHC	1	3.3	Ozmen <i>et al.</i> (2006)
Sheep	Sweden	Serum	218	ND	41	18.8	Tråvén <i>et al.</i> (1999)
Goat	South Korea	Serum	804	HI	8	1	Yang <i>et al.</i> (2008)
Dromedary camel	USA (Wisconsin)	Faeces	1	EM, IHC	1	100	Wünschmann <i>et al.</i> (2002)
Dromedary camel	UAE (Dubai)	Faeces Serum	293 59	RT-PCR VNT, IFA	14 59	4.8 100	Woo <i>et al.</i> (2014, 2016)
Dromedary camel	Saudi Arabia	Nasal/rectal swab	1309	RT-PCR	331	25.3	Sabir <i>et al.</i> (2016)
Llama, alpaca	USA (Oregon)	Faeces	45	ND	19	42	Cebra <i>et al.</i> (2003); Jin <i>et al.</i> (2007)
Alpaca	Peru	Faeces	14	IC	3	23	López <i>et al.</i> (2011)
Alpaca	Peru	Intestinal lavage	50	RT-PCR	20	40	Rojas <i>et al.</i> (2016)
Alpaca	USA (Oklahoma)	Faeces	1	RT-PCR	1	100	Genova <i>et al.</i> (2008)
Alpaca	USA (California)	Lung tissue	11	Isolation, EM, sequencing	1	9.1	Crossley <i>et al.</i> (2010, 2012)

VNT, virus neutralization test; HI, haemagglutination inhibition; HEHA, haemadsorption–elution–haemagglutination assays; ND, not defined; ELISA, enzyme-linked immunosorbent assay; IP, immunoperoxidase; NC-EM, negative contrast electron microscopy; HA, haemagglutination; RT-PCR, reverse transcription polymerase chain reaction; EM, electron microscopy; IHC, immunohistochemistry; IFA, immunofluorescent assay; UAE, United Arab of Emirates; IC, immunochromatography.

Sheep (*Ovis aries*)

Bovine-like CoVs have been identified as a cause of enteritis and neonatal mortality in domestic sheep in several countries worldwide (Tzipori *et al.*, 1978; Harp *et al.*, 1981; Pass *et al.*, 1982; Reinhardt *et al.*, 1995). However, the prevalence of infection was mostly low and of minor importance. Among 545 diarrhoeic lambs originated from 12 sheep flocks in southern Idaho and western Montana, USA, bovine-like CoVs were detected in lambs of only one flock (Harp *et al.*, 1981). As well, CoVs were detected in six (out of 98; 6.1%) dead lambs but not in healthy lambs and ewes in Chile (Reinhardt *et al.*, 1995). Two reports from Spain and Turkey demonstrated that *Cryptosporidium parvum*, *Giardia intestinalis*, *Escherichia coli* and rotavirus – but not CoV – were the leading causes of neonatal diarrhoea and mortalities in domestic sheep (Muñoz *et al.*, 1996; Ozmen *et al.*, 2006). A nationwide screening of BCoV-specific antibodies in Swedish sheep has demonstrated that 19% of all sera samples were positive. However, it was expected that these antibodies originated from contact with infected cattle faeces rather than a natural infection with bovine-like CoV (Tråvén *et al.*, 1999).

Goat (*Capra aegagrus hircus*)

Few studies have investigated the role of bovine-like CoV in goat kids with neonatal diarrhoea. Examination of faecal samples from diarrhoeic and non-diarrhoeic kids (1–45 days old) in Spain has demonstrated complete absence of CoVs (Muñoz *et al.*, 1996). While CoVs were detected in the faeces of one (out of 19; 3.3%) kid with neonatal enteritis in Turkey by immunohistochemistry (IHC). The positive reaction was obvious at the crypt epithelium of small intestine and in the submucosal macrophages (Ozmen *et al.*, 2006). A large-scale serosurveillance for viral diseases has been conducted in 144 native goat farms in South Korea between 2005 and 2006. Among 804 sera samples collected from five provinces of South Korea, CoV HI antibodies were only detected in eight samples (1%), as the least prevalent viral infection in two provinces, while it was entirely absent in the other districts (Yang *et al.*, 2008).

Camelids

Nowadays, six species of camelids exist. They are grouped into two tribes: Camelini that includes old world camels, and

Table 2. A collective summary of bovine-like CoVs in wild ruminants

Animal species	Country	Sample		Test(s) of choice	Positive sample		Reference
		Type	No.		No.	%	
Caribou/Reindeer	Canada	Serum	58	VNT, HI	4	6.9	Elazhary <i>et al.</i> (1981)
Elk/Wapiti	Canada	Faeces	11	Isolation	5	45.5	Smits, (1991)
Elk/Wapiti	USA (Kansas)	Faeces	2	EM, HA, Isolation	2	100	Majhdi <i>et al.</i> (1997)
Samber deer	USA (Ohio)	Faeces	3	Immune-EM, ELISA	3	100	Tsunemitsu <i>et al.</i> (1995)
White-tailed deer	USA (Ohio)	Faeces	3	Immune-EM, ELISA	1	100	Tsunemitsu <i>et al.</i> (1995)
Sika deer	Japan	Serum	179	VNT	2	1.1	Yokoi <i>et al.</i> (2009)
Water deer	South Korea	Nasal swabs	77	RT-PCR	3	3.9	Kim <i>et al.</i> (2018)
Musk oxen	UK	Faeces	ND	EM	ND	ND	Chasey <i>et al.</i> (1984)
Wisent	South Korea	Faeces	4	EM, RT-PCR	1	25	Chung <i>et al.</i> (2011)
Wood bison	Canada	Serum	31	Serology	2	7	Harms <i>et al.</i> (2019)
Water buck	UK	Faeces	9	EM, ELISA	9	100	Chasey <i>et al.</i> (1984)
Water buck	USA (Ohio)	Faeces	1	Immune-EM, ELISA	1	100	Tsunemitsu <i>et al.</i> (1995)
Sitatunga	UK	Faeces	ND	EM, ELISA	ND	ND	Chasey <i>et al.</i> (1984)
Sitatunga	South Korea	Faeces	3	EM, RT-PCR	1	33.3	Chung <i>et al.</i> (2011)
Stable antelope	USA (Ohio)	Faeces	1	Immune EM	1	100	Hasoksuz <i>et al.</i> (2007)
Nyala	South Korea	Faeces	2	EM, RT-PCR	1	50	Chung <i>et al.</i> (2011)
Giraffe	USA (Ohio)	Faeces	3	Immune EM	3	100	Hasoksuz <i>et al.</i> (2007)
Himalayan tahr	South Korea	Faeces	3	EM, RT-PCR	2	66.7	Chung <i>et al.</i> (2011)

VNT, virus neutralization test; HI, haemagglutination inhibition; EM, electron microscopy; HA, haemagglutination; ELISA, enzyme-linked immunosorbent assay; ND, not defined; RT-PCR, reverse transcription polymerase chain reaction.

Lamini that contains new world camels. Two species of old world camels include dromedary or one-humped camel (*Camelus dromedarius*) and Bactrian or two-humped camel (*Camelus bactrianus*). The majority of old world camels (90%) are dromedaries, which inhabit the African horn, North Africa, Middle East and Southwestern Asia. The Bactrian camel has an estimated worldwide population of 1.4 million animals living in central Asia (mostly in China and Mongolia) (Frankin, 2011). Few wild dromedary and Bactrian camels are still living in Australia and Gobi Desert, respectively (Saalfeld and Edwards, 2008; Animal Information Organization, 2018).

On the other hand, the new world camels include two wild species: guanaco (*Lama guanicoe*) and vicuña (*Vicugna vicugna*), and two domesticated species: llama (*Lama glama*) and alpaca (*Vicugna pacos*). All of these species are living in South America (mostly in the Andean highlands) and are used for food, textile and transport (Hirst, 2017). About 2.5–3.0 million llamas are currently distributing in Bolivia (70%), Chile, Peru, and Argentina. Similarly, a world population of 3.88 million alpacas are mostly concentrated in Peru (77%), Bolivia (13%), Chile and Argentina. Breeding of llama and alpaca for commercial uses is expanding outside South America, particularly in the USA, Australia and many European countries (Crossley *et al.*, 2010; Thomas and Morgan, 2013; La Vigna Alpacas, 2018).

Old world camelids

The role of dromedary camels (DCs) as the most likely source of human infection with MERS-CoVs is gradually establishing with continuous appearance of new evidence (Alagaili *et al.*, 2014;

Muhairi *et al.*, 2016; Sabir *et al.*, 2016; Miguel *et al.*, 2017). Because MERS-CoV has never been identified in cattle (Hemida *et al.*, 2013; Reusken *et al.*, 2013a, 2013b) and has many unique antigenic and genetic characteristics that make it distinct from BCoVs (Hemida *et al.*, 2013), it will not be discussed further in this review.

Although DCs are normal inhabitants of Northern and Eastern Africa and Southwestern Asia, the first report of bovine-like CoV infections in DCs came from the USA (Wünschmann *et al.*, 2002). A case of severe lethal gastroenteritis was recorded in a 6-week-old female camel calf in Wisconsin. CoV particles with typical club-shaped projections were identified in the faeces of the diarrhoeic camel calf by EM. The virus showed specific reactivity with two MAbs, prepared against BCoV S and nucleocapsid (N) proteins, in the epithelial cells of colonic crypts by IHC. The nature and origin of the CoV were not elucidated; however, the role of interspecies transmission was proposed because individuals of other animals like horses, zebras and reindeer were kept with the camel calf in the same barn at the time of infection.

In 2013, a novel CoV, designated as DcCoV UAE-HKU23, was identified in 14 (4.8%) leftover DC faecal samples (four with diarrhoea) in the Central Veterinary Research Laboratory, Dubai, UAE. Complete genome analysis of DcCoV UAE-HKU23 in three faecal samples has classified the virus as a member of lineage A1 of Betacoronaviruses (Woo *et al.*, 2014). However, genetic distance analysis and codon usage bias of polymerase, S and N genes of DcCoV UAE-HKU23 strains have demonstrated that it is distantly separated from other members of Betacoronavirus 1 and may form a unique cluster within the group (Woo *et al.*,

Table 3. Betacoronavirus 1 strains used in the phylogenetic analysis

Virus strain	Animal species	Year	Country	GenBank Accession	Clinical form	Reference
Bubaline 179/07/11	Water buffalo	2007	Italy	EU019216	Calf diarrhoea	Decaro <i>et al.</i> (2008c)
BuCoV HKU26 B1-24F	Water buffalo	2014	Bangladesh	KU558922	Winter dysentery	Lau <i>et al.</i> (2016)
BuCoV HKU26 B1-28F	Water buffalo	2014	Bangladesh	KU558923	Winter dysentery	Lau <i>et al.</i> (2016)
DcCoV UAE-HKU23-265F	Dromedary camel	2013	UAE	KF906249	Sporadic diarrhoea	Woo <i>et al.</i> (2014)
DcCoV UAE-HKU23-265F	Dromedary camel	2013	UAE	KF906250	Sporadic diarrhoea	Woo <i>et al.</i> (2014)
DcCoV UAE-HKU23-262F	Dromedary camel	2013	UAE	KF906250	Sporadic diarrhoea	Woo <i>et al.</i> (2014)
DcCoV UAE-HKU23-268F	Dromedary camel	2013	UAE	KF906251	Sporadic diarrhoea	Woo <i>et al.</i> (2014)
ACoV-00-1381	Alpaca	1998	USA	DQ915164	Neonatal diarrhoea	Jin <i>et al.</i> (2007)
CA08-1/2008	Alpaca	2008	USA	JQ410000	Respiratory disease	Crossley <i>et al.</i> (2012)
US/OH-WD470/1994	White-tailed deer	1994	USA	FJ425187	Sporadic diarrhoea	Alekseev <i>et al.</i> (2008)
US/OH-WD388/1994	Samber deer	1994	USA	FJ425189	Winter dysentery	Alekseev <i>et al.</i> (2008)
US/OH-WD388-TC/1994	Samber deer	1994	USA	FJ425188	TC adapted	Alekseev <i>et al.</i> (2008)
US/OH-WD388-Gnc/1994	Samber deer	1994	USA	FJ425190	Calf passaged	Alekseev <i>et al.</i> (2008)
Wisent/2010	Wisent	2010	South Korea	HM573326	Winter dysentery	Chung <i>et al.</i> (2011)
US/OH/2003	Giraffe	2003	USA	EF424623	Sporadic diarrhoea	Hasoksuz <i>et al.</i> (2007)
US/OH/2006	Giraffe	2006	USA	EF424624	Calf passaged	Hasoksuz <i>et al.</i> (2007)
US/OH-TC/2006	Giraffe	2006	USA	EF424622	TC adapted	Hasoksuz <i>et al.</i> (2007)
Himalyan Tahr1-10/01	Himalyan tahr	2010	South Korea	HM573327	Winter dysentery	Chung <i>et al.</i> (2011)
Himalyan Tahr2-10/01	Himalyan tahr	2010	South Korea	HM573328	Winter dysentery	Chung <i>et al.</i> (2011)
Nyala 10/01	Nyala	2010	South Korea	HM573330	Winter dysentery	Chung <i>et al.</i> (2011)
Sitatunga 10/01	Sitatunga	2010	South Korea	HM573329	Winter dysentery	Chung <i>et al.</i> (2011)
US/OH1/2003	Water buck	2003	USA	EF424621	Winter dysentery	Alekseev <i>et al.</i> (2008)
US/WD358/1994	Water buck	1994	USA	FJ425186	Winter dysentery	Alekseev <i>et al.</i> (2008)
BCoV Mebus	Cattle	1972	USA	U00735	Calf diarrhoea	Stair <i>et al.</i> (1972)
BCoV ENT	Cattle	1998	USA	NC_003045	Shipping fever	Storz <i>et al.</i> (2000)
BCoV LUN	Cattle	1998	USA	AF391542	Shipping fever	Storz <i>et al.</i> (2000)
BCoV DB2	Cattle	1983	USA	DQ811784	Calf diarrhoea	Tsunemitsu <i>et al.</i> (1991)
BCoV LY-381	Cattle	1965	USA	AF058942	Calf diarrhoea	Doughri <i>et al.</i> (1976)
BCoV Quebec	Cattle	1972	Canada	AF220295	Calf diarrhoea	Dea <i>et al.</i> (1980)
BCoV LSU-94LSS-051-2	Cattle	1994	USA	AF058943	Respiratory disease	Chouljenko <i>et al.</i> (1998)
BCoV 0501/2005	Cattle	2005	South Korea	EU686689	Winter dysentery	Park <i>et al.</i> (2006)
BCoV 0502/2005	Cattle	2005	South Korea	EU401986	Winter dysentery	Park <i>et al.</i> (2006)
BCoV Kakegawa	Cattle	1979	Japan	AB354579	Winter dysentery	Akashi <i>et al.</i> (1981)
BCoV OK-0514-03	Cattle	2003	USA	AF058944	Respiratory disease	Chouljenko <i>et al.</i> (1998)
HCoV 229E	Human	NA	Germany	AF304460	Respiratory disease	-

2016; Fig. 1). Recombinant N protein of DcCoV UAE-HKU23 has been generated and utilized for the detection of the virus-specific antibodies in sera of 59 camels originated from Sudan, Saudi Arabia, Oman and Pakistan (Woo *et al.*, 2014). Antibodies to the recombinant protein were identified in 98.3 and 100% of the tested sera samples using IF and VN assays. Immunization of mice with the recombinant N proteins of

DcCoV UAE-HKU23 and MERS-CoV has confirmed minimal cross-antigenicity between both viruses in Western blot (WB) and VN assays (Woo *et al.*, 2016). These results demonstrate that a Betacoronavirus, other than MERS-CoV, is circulating among DCs in different countries of Middle East and may contribute to pathological conditions of diarrhoea, particularly in camel calves.

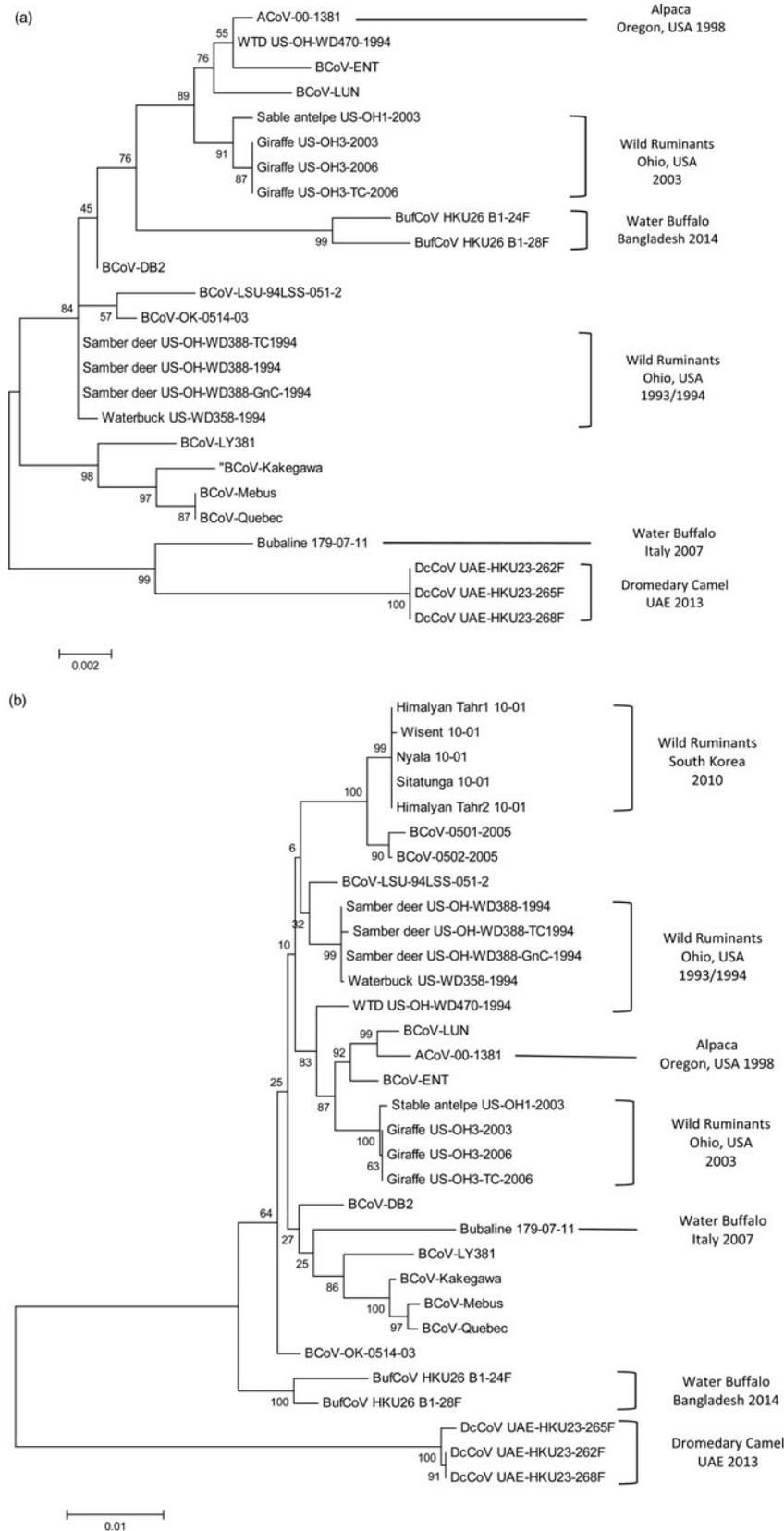


Fig. 1. Phylogenetic analysis of bovine-like coronaviruses based on the sequence of (a) nucleocapsid gene and (b) spike gene. Reference bovine coronaviruses were included for comparison purposes. Sequences were downloaded from GenBank (Table 3) and aligned together using Clustal W algorithm of MegAlign program, Lasergene software, version 3.18 (DNASar, Madison, WI). Phylograms were constructed by MEGA 7.0 software using the maximum likelihood method. The strength of the tree was evaluated by bootstrapping of 1000 replicates. Bootstrap values are shown at the branch nodes of the tree. Bovine-like coronaviruses are grouped according to the type of animal(s), state or country of origin, and year of identification as indicated in the brackets at the right side. The scale bar at the bottom indicates the number of nucleotide changes per site.

Recently, three species of CoVs were identified in DCs in Saudi Arabia during a surveillance study that included 1309 nasal and rectal swab samples collected between May 2014 and April 2015 (Sabir *et al.*, 2016). These CoVs included two Betacoronaviruses:

MERS-CoV (group C) and camel HKU23-CoVs (group A), and one Alphacoronavirus (similar to human CoV 229E). All CoV-positive samples except three were nasal swabs, which indicates that the respiratory tract is the major shedding portal for

CoV in DCs. Regardless of MERS-CoV that has been detected in DCs in many countries worldwide, the HKU-23-CoV was detected in DCs in Dubai short time earlier (Woo *et al.*, 2014) and a closely related camelid Alphacoronavirus was isolated from alpacas in the USA in 2007 (Crossley *et al.*, 2010; Crossley *et al.*, 2012). The high prevalence of CoVs in the collected samples, the frequent co-infections and the lack of symptoms in most CoV-positive cases propose that these CoVs are enzootic in DCs, at least in Saudi Arabia, and that they may play an important role in CoV ecology.

New world camelids

CoV infection of llamas and alpacas was first recognized during an outbreak of severe diarrhoea in Oregon, USA in 1998. Among 39 pathogens detected, CoV was identified as the primary cause of the diarrhoeal complex in juvenile animals (crias) with a prevalence rate of 42%. Sick crias developed clinical symptoms similar to BCoV-infected cattle calves with variable degrees of severity and frequent deaths (Cebra *et al.*, 2003; Cebra, 2007). A single alpaca CoV (designated ACoV-00-1381) was isolated from the diarrhoeic samples by propagation in HRT-18 G cells. Sequence and phylogenetic analysis of the complete ACoV-00-1381 genome revealed close homology (>99.5%) with two BCoV strains involved in shipping fever pneumonia and enteritis in feedlot calves: LUN and ENT, respectively (Storz *et al.*, 1996; Chouljenko *et al.*, 2001; Fig. 1). A common ancestral origin of alpaca CoV and both strains of BCoV was proposed (Jin *et al.*, 2007).

Bovine-like CoV was also acknowledged as a potential cause of neonatal diarrhoea in alpacas in two separate studies conducted in Cusco in southern Peruvian highlands. In the first, CoVs have been detected in three out of 14 (23%) of the alpaca crias using immunochromatography (López *et al.*, 2011). While in the second, the virus was detected in 20 out of 50 (40%) of the crias during an episode of diarrhoea in January and February 2010 using RT-PCR (Rojas *et al.*, 2016). All the cases in the second study showed co-infection with other (up to three) enteric pathogens including *Eimeria* spp., *Cryptosporidium* spp., *E. coli* and rotavirus. However, the exact role of CoV in disease development and progression was unclear.

CoV-associated diarrhoea in adult alpacas is generally a rare event and is supported mostly by anecdotal evidence. A single report has documented the identification of a CoV in faecal specimen collected from 4-year-old hembra (female alpaca) in Stillwater, Oklahoma (Genova *et al.*, 2008). The virus was classified as a member of antigenic group 2 CoVs (later termed as Betacoronaviruses) as a result of its cross-reactivity with MAB specific for N protein of antigenic group 2 CoVs in IHC.

In contrast to all previous reports that correlate CoVs in alpaca with gastroenteritis, a novel CoV was retrieved from the lung tissue of a clinical case with alpaca respiratory syndrome (ARS) in California on October 2007. The CoV was isolated with the CRFK cell line and its identity was confirmed by transmission EM, sequence analysis of a short conserved fragment within the polymerase gene (Crossley *et al.*, 2010), and later by full-genome sequencing (Crossley *et al.*, 2012). The widespread nature of respiratory CoV in alpacas was verified through testing 40 sera samples taken from animals with a history of ARS and 167 sera samples randomly selected from alpacas with unknown disease history. The majority of samples with ARS history (60%) has shown antibody titres $\geq 1:16$ in VN assay using the plaque-purified respiratory alpaca CoV. However, only 3% of the samples

collected from animals with unknown history showed similar titres (Crossley *et al.*, 2010).

No consequent outbreaks of the respiratory alpaca CoV was recorded in the USA or elsewhere, which raised questions about the origin and circulation of the virus in the alpaca population. Genome sequencing of the respiratory alpaca CoV revealed close homology with the Alphacoronaviruses (particularly with HCoV-229E; 92.2%), unlike the enteric alpaca CoVs that were routinely identified as Betacoronaviruses. Comparison of S gene sequences from the respiratory alpaca CoV and a range of HCoV-229 isolates recovered from 1962 to 2003 showed close genetic homology with HCoV-229 strains isolated from the 1960s until the early 1980s. It was concluded that a common ancestor of HCoV-229E and respiratory alpaca CoV may have existed either in people or alpacas before 1960, and crossed the interspecies barrier to establish infection in the other species thereafter (Crossley *et al.*, 2012). The virus may have circulated among alpacas at low levels for decades before suddenly appearing during the 2007 outbreak. Explanation of the absence of further disease outbreaks in the subsequent years needs further investigation.

Bovine-like CoVs in captive and free-range wild ruminants

Deer (Cervidae)

Deer are one of the most widely distributed ruminant animals on the Earth. They constitute a natural component of the biological communities in all continents except Australia and Antarctica. All deer species are included in the family Cervidae with two subclasses: (1) old world deer (subfamily *Cervinae*), which contains 33 deer species including elk (wapiti), muntjac, chital, sika deer and sambar deer, (2) new world deer (subfamily *Capreolinae*), which comprises 21 deer species including reindeer (caribou), pudu and European elk (moose) (Bertin, 2017). Breeding of deer (particularly in game farms) is currently a growing interest for venison production, which is characterized by high-protein content and low-cholesterol level (Smits, 1991). To date, bovine-like CoVs were demonstrated in only six deer species, which are caribou/reindeer (*Rangifer tarandus caribou*) (Elazhary *et al.*, 1981), elk/wapiti (*Cervus elephus*) (Smits, 1992; Majhdi *et al.*, 1997; Dagainakatte *et al.*, 1999), sambar deer (*Cervus unicolor*), white-tailed deer (*Odocoileus virginianus*) (Tsunemitsu *et al.*, 1995; Alekseev *et al.*, 2008), sika deer (*Cervus nippon yesoensis*) (Yokoi *et al.*, 2009) and water deer (Kim *et al.*, 2018).

Cariboo/reindeer

The evidence of bovine-like CoVs in Cariboo was demonstrated through a surveillance study that investigated the prevalence of antibodies to five bovine respiratory and enteric viruses in two caribou herds in Northern Quebec, Canada. While bovine viral diarrhoea virus was the most prevalent in both years, bovine-like CoV was the least prevalent (bovine parainfluenza 3 virus was absent from all samples). Among 30 samples collected in 1978 and 28 samples in 1979, CoV-specific antibodies were detected in four (13.3%) and zero (0%) samples in both years, respectively. The source of bovine-like CoV infection was unclear because both caribou herds had no direct contact with domestic ruminants for at least 25 years (Elazhary *et al.*, 1981).

Elk/wapiti

CoVs have been frequently linked to enteritis and scouring in neonatal elk. The virus was isolated as the only pathogen in five

out of 11 calves with diarrhoea (45.5%) in western North America (Smits, 1991; Smits, 1992). In a subsequent study, two CoV isolates were retrieved from faecal samples collected from 10-month-old captive elk calves with diarrhoea in the USA (Majhdi *et al.*, 1997). The virus isolates in the latter study (designated WY-28 and WY-29) showed a high degree of antigenic and genetic relation to BCoV, based on several observations: (1) comparable protein profiles as determined by SDS-PAGE, (2) similar transcriptional patterns in Northern blot analysis, (3) significant sequence homology (99%) between N gene sequence of both viruses, (4) cross-reactivity with MAb specific for S protein of BCoV in WB, and (5) ability of four MAbs specific for N protein of elk CoV, to detect BCoV in intestinal tissues by IHC (Majhdi *et al.*, 1997; Dagainakatte *et al.*, 1999).

Samber and white-tailed deer

Infection of samber deer with bovine-like CoVs was only recorded during an outbreak of diarrhoea that occurred in a wild animal park in southern Ohio, USA in the winter season of 1993/1994. Affected animals showed severe symptoms of bloody diarrhoea, which resemble WD in adult cattle, with a mortality rate of 30%. In another wild animal park in north central Ohio, episodes of watery diarrhoea in white-tailed deer were also monitored throughout 1994. CoV particles were identified in faecal samples collected from three samber deer and one white-tailed deer using immunocytochemistry and antigen detection ELISA. Two CoV isolates (KI-D2 from samber deer and WTD from white-tailed deer) were recovered in the Cariboo HRT-18 cell line. Both isolates demonstrated close relationship with several BCoV strains causing CD and WD based on similar biologic (haemagglutination and receptor-destroying activities) and antigenic reactivity in HI, VN, IF and WB tests (Tsunemitsu *et al.*, 1995). Analysis of the full genome sequence of both isolates (either cell culture-adapted or gnotobiotic calf-passaged) confirmed the marked similarity with BCoVs, particularly LUN and ENT strains isolated in 1998 (Fig. 1b), with no specific genetic markers that can discriminate KI-D2 and WTD from BCoV strains (Aleksiev *et al.*, 2008). Additionally, 30 sera samples were acquired from free-range healthy white-tailed deer located in a third wild animal park in Ohio. Two samples (6.6%) were seropositive against both isolates and several BCoV strains in IF assay (Tsunemitsu *et al.*, 1995).

Sika deer

This type of deer is a native species in Hokkaido, Japan. A single observation of potential infection with bovine-like CoV was reported in a serosurveillance study that evaluated the prevalence of antibodies to eight bovine viruses in sika deer. Serum samples were collected from a farm of sika deer in eastern Hokkaido between June 2006 and September 2007 and from wild animals during the hunting season of 2000. Among 179 farmed deer, only two (1.1%) samples were reactive to BCoV in VN assay. Unfortunately, not all samples collected from wild sika deer (no = 97) were tested for BCoV (Yokoi *et al.*, 2009).

Water deer

The evidence of water deer (*Hydropotes inermis*) infection with bovine-like CoVs was not demonstrated in captive animals during a study that extended between 2010 and 2012 in South Korea (Kim *et al.*, 2014). However, in a recent study that involved 77 nasal swab samples, collected during 2016 and 2017 from non-captive water deer living in Chungnam Wild Animal Rescue Center, South Korea, three positive samples (3.9%) were obtained.

The phylogenetic analysis, based on a partial sequence of the polymerase gene, indicated close relationship of the three water deer CoVs with BCoV (99.2%). Complete genome sequencing of a single water deer CoV strain (designated W17-18) revealed close relationship to BCoV and other bovine-like CoVs (homology >98%) with minor unique genetic characteristics of the non-structural protein 4.8 kDa. This report is the only one that proposes the implication of bovine-like CoVs in respiratory diseases of wild ruminants (Kim *et al.*, 2018).

Wild cattle

Similar to domestic cattle, wild bovidae have also been associated with CoV-induced scours in calves and WD in adults. During the winter season of 1979–1980, an outbreak of diarrhoea occurred among a group of musk oxen (*Ovibos moschatus*) in Whipsnade zoological park in Bedfordshire, UK. CoVs were identified in the faecal samples collected from diseased animals using EM. Unfortunately, virus strains were not isolated or characterized due to technical limitations (Chasey *et al.*, 1984). CoVs are also among the common pathogens isolated from bison (*Bison bison*) calves with diarrhoea (Haigh *et al.*, 2002). However, the actual prevalence of CoVs in bison is underestimated because bison mask the clinical signs of the disease syndrome (Berezowski, 2001). CoVs were also demonstrated in the faeces of adult wisent – European bison (*Bison bonasus*) suffering from severe diarrhoea in the National Zoo of South Korea. The outbreak started in a wisent, albeit no cattle were housed in the zoo and no cattle farms existed in the vicinity, and spread to other wild ruminants in the park. All identified CoVs were quite similar in terms of nucleotide and deduced amino acid sequence. They also showed high level of genetic relationship (99.4–99.5%) to BCoVs isolated in South Korea after 2004, particularly BCoV-0501 and BCoV-0502 strains (Fig. 1b). It was concluded that all bovine-like CoVs characterized in this study were replicates of a single strain that has no restricted host specificity. This strain may originate, via an unclear pathway, from the same ancestor of BCoV-0501 and BCoV-0502 strains of cattle (Chung *et al.*, 2011). More recently, a serological study was conducted in a population of wood bison (*B. bison athabasca*) that were reintroduced in the wild in southwestern Yukon, Canada since 1988. Antibodies to BCoV were demonstrated in only two out of 31 (7%) of the animals tested (Harms *et al.*, 2019).

Antelopes

The antelope is a deer-like mammal that belongs to the family Bovidae but is not cattle, buffalo, sheep or goat. Antelope is not a taxonomic name rather than a common term that collects a variety of grazing ruminants characterized by long legs and permanent horns. These old world animals are indigenous to Africa and Euroasia and may be found in parts of the Americas (Estes, 2017). To date, the role of bovine-like CoVs in CD and WD was only described in four species of antelopes including waterbuck (*Kobus ellipsiprymnus*) (Chasey *et al.*, 1984; Tsunemitsu *et al.*, 1995), sitatunga (*Tragelaphus spekei*) (Chasey *et al.*, 1984; Chung *et al.*, 2011), nyala (*Tragelaphus angasii*) (Chung *et al.*, 2011) and sable antelope (*Hippotragus niger*) (Hasoksuz *et al.*, 2007).

Waterbuck

In the beginning of 1982, an outbreak of watery diarrhoea was suddenly erupted in a herd of nine waterbucks in the Cotswold wildlife

park in Oxfordshire, England. Four animals (two adults and two calves) were lost and bovine-like CoVs were identified in the faeces of affected animals using EM and ELISA. Attempts to propagate these viruses in HRT-18 cell culture were unsuccessful. Additionally, experimental infection of gnotobiotic cattle calves with the faecal materials of dead waterbucks did not reveal clinical reproduction of the disease. The inoculated calves did not shed the virus in their faeces, did not develop antibody responses and were not immune against experimental challenge with BCoV field strain (Chasey *et al.*, 1984). Infection of waterbuck with bovine-like CoVs was further confirmed in another epizootic outbreak of diarrhoea that occurred in Ohio wild animal park in 1993 and 1994. The aetiologic virus (designated KI-WB) has been isolated in cell culture and has close biologic and antigenic relation to BCoVs (Tsunemitsu *et al.*, 1995). Unlike the virus detected in the UK in 1982, the gnotobiotic and colostrum-deprived calves experimentally infected with KI-WB strain developed signs of acute diarrhoea and excreted the virus in their faeces and nasal secretions.

Sitatunga

CoVs were identified in faecal samples collected from sitatunga on two different occasions. The first was during an outbreak of diarrhoea in Whipsnade Zoological Park in the winter season of 1979/1980 (and again in February 1984) using EM and ELISA (Chasey *et al.*, 1984). The second occurred during an outbreak that affected four animal species, including sitatunga, in the National Zoo of South Korea in 2010. Sitatunga was the only animal that showed both enteric and respiratory symptoms. Among 16 affected animals in the park, rectal swabs were taken from three adult sitatunga (older than 2 years) and all of these samples showed the characteristic CoV particles by EM (Chung *et al.*, 2011).

Nayla

Two nayla animals were affected during the diarrhoea epidemic that occurred in the National Zoo of South Korea in 2010. The CoV particles detected in the faeces of affected animals were quite similar to those identified in wisent, sitatunga and Himalayan tahr, suggesting all of these are host-range variants of the same strain (Chung *et al.*, 2011).

Sable antelope

An outbreak of diarrhoea occurred in several ruminant species in an Ohio wild animal park in 2003. The outbreak started in a sable antelope and spread 1–2 weeks later to giraffes that were housed in a separate barn 0.5 miles away. A single faecal sample was obtained from the sable antelope and was tested by immunocytochemistry using BCoV-specific antisera. CoV particles were detected in the faecal sample, but, unlike the giraffe isolates, the virus strain could not be adapted to cell culture or to induce productive infection in gnotobiotic calves (Hasoksuz *et al.*, 2007). Genetic analysis revealed close relatedness with the giraffe isolates, several BCoVs, and to a lesser extent with KI-D2, WTD and KI-WB strains isolated from sambar deer, white-tailed deer and waterbuck, respectively (Alekseev *et al.*, 2008; Fig. 1).

Giraffe (*Giraffa camelopardalis*)

Giraffes are the tallest animals and the largest ruminants on the Earth. They mostly inhabit Africa and are considered vulnerable to extinction, with an overall worldwide population of 97,000 animals (Milman, 2017). A single report described isolation and characterization of bovine-like CoVs from giraffes during the

outbreak of diarrhoea in an Ohio wild animal park in 2003 (Hasoksuz *et al.*, 2007). Bovine-like CoVs were identified in the faeces of three (two males and one female) giraffes by immunocytochemistry. The virus was successfully adapted and isolated from the faecal extract of a 24-year-old male giraffe with HRT-18 cell culture. The virus isolate (designated as GiCoV-OH3) revealed close biologic, antigenic and genetic relationship with different strains of BCoV, principally with the enteric strains ENT and DB2.

Although infection in giraffes was conclusive from the outbreak progression in the wild animal park, the definite source of this outbreak remains uncertain. The infection may have originated from wild animals in the park, which harbour the virus without clinical signs, or from a nearby cattle farm. The latter possibility was supported by the ability of GiCoV-OH3 strain to induce severe diarrhoea when orally administered into a gnotobiotic cattle calf, with virus shedding that lasts for 2–3 days. The risk of virus transmission between cattle and giraffes seems important, particularly in Africa where grazing regions of both animals overlap. This may allow virus evolution and potential spread of new CoV strains to remote regions upon change in pastures, game farming and transfer of wild animals to zoological parks.

Himalayan tahr (*Hemitragus jemlahicus*)

Tahr is a wild species of goat native to the Himalayan mountains in Central Asia. They are specially adapted to life on the mountain slopes and are now considered a near-threatened species (Bhatnagar and Lovari, 2008). During the epizootic outbreak of WD that affected several ruminant species in the National Zoo of South Korea in 2010, three Himalayan tahrs presented signs of weakness, depression, anorexia, bloody diarrhoea and dehydration. Bovine-like CoVs were demonstrated in the faeces of affected animals using EM and their genetic characteristics were analysed (Chung *et al.*, 2011).

Conclusion

Bovine-like CoVs are widely distributed in domestic ruminants other than cattle and in captive and free-range wild ruminant species. The majority of bovine-like CoVs have confirmed close relationship with different BCoV strains that produce gastroenteritis in neonatal calves and lactating cows, and respiratory disease complex in growing and steer calves. It is generally accepted today that bovine-like CoVs are host-range variants of BCoV, which is crossing the interspecies barriers on a regular basis. Transmission of BCoV variants from cattle to other ruminants and *vice versa* allows persistence of the infection in nature, recurrent emergence of epidemics and continuous evolution of the virus. Wild ruminants, in particular, are not confined to discrete geographic regions and are always moving to seek new pastures, to escape from predators, and to find mates. Human activities, including – but not restricted to – deforestation, over-hunting and game farming, also force wild animals to change habitats. Continuous movement of wild animals promotes virus transmission to new terrestrial areas, and, importantly, provides a window for the virus to adapt to new hosts and to develop into novel strains.

References

- Abd El-Karim IA, El-Sanousi AA, Aly NM and Reda IM (1990) Detection of coronavirus antigen in fecal samples obtained from newborn buffalo calves. *Veterinary Medical Journal Giza* 38, 77–85.

- Abd El-Rahim IHA (1997) Rota and/or coronavirus infections in newborn buffalo calves in Upper Egypt. *Proceedings of the 4th Scientific Congress, Egyptian Society for Cattle Diseases*. Assuit, Egypt, pp. 210–220.
- Akashi H, Inaba Y, Miura Y, Sato K, Tokuhisa S, Asagi M and Hayashi Y (1981) Propagation of the Kakegawa strain of bovine coronavirus in suckling mice, rats and hamsters. *Archives of Virology* **67**, 367–370.
- Alagaili AN, Briese T, Mishra N, Kapoor V, Sameroff SC, Burbelo PD, De Wit E, Munster VJ, Hensley LE, Zalmout IS, Kapoor A, Epstein JH, Karesh WB, Daszak P, Mohammed OB and Lipkin WI (2014) Middle East respiratory syndrome coronavirus infection in dromedary camels in Saudi Arabia. *MBio* **5**, e00884–14.
- Alekseev KP, Vlasova AN, Jung K, Hasoksuz M, Zhang X, Halpin R, Wang S, Ghedin E, Spiro D and Saif LJ (2008) Bovine-like coronaviruses isolated from four species of captive wild ruminants are homologous to bovine coronaviruses, based on complete genomic sequences. *Journal of Virology* **82**, 12422–12431.
- Animal Information Organization (2018) Wild Bactrian camel. Endangered animals. Available at <http://www.animalinfo.org/species/artiperi/camebact.htm>.
- Berezowski J (2001) Diseases of Bison. Available at <http://www.usask.ca/wcvm/herdmed/specialstock/bison/bisondis.html>.
- Bertin J (2017) Types of deer around the world. Available at <http://www.animalwisdom.com/types-of-deer-around-the-world-1345.html>.
- Bhatnagar YV and Lovari S (2008) “*Hemitragus jemtalicus*”. The IUCN Red List of Threatened Species. Available at <http://www.iucnredlist.org/details/9919/0>.
- Boileau MJ and Kapil S (2010) Bovine coronavirus associated syndromes. *Veterinary Clinics of North America: Food Animal Practice* **26**, 123–146.
- Borghese A (2011) Situation and perspectives of buffalo in the world, Europe and Macedonia. *Macedonian Journal of Animal Science* **1**, 281–296.
- Brian DA and Baric RS (2005) Coronavirus genome structure and replication. *Current Topics in Microbiology and Immunology* **287**, 1–30.
- Byomi A, Herbst W and Baljer G (1996) Some viral agents associated with neonatal calf diarrhoea. *Assuit Veterinary Medical Journal* **35**, 1–9.
- Carman PS and Hazlett MJ (1992) Bovine coronavirus infection in Ontario 1990–1991. *Canadian Veterinary Journal* **33**, 812–814.
- Cebra CK (2007) Diarrhoea in llama and alpaca crias. *The AABP Proceedings* **40**, 170–173.
- Cebra CK, Mattson DE, Baker RJ, Sonn RJ and Dearing PL (2003) Potential pathogens in feces from unweaned llamas and alpacas with diarrhoea. *Journal of American Veterinary Medical Association* **223**, 1806–1808.
- Chasey D, Reynolds DJ, Bridger JC, Debney TG and Scott AC (1984) Identification of coronaviruses in exotic species of Bovidae. *Veterinary Record* **115**, 602–603.
- Chouljenko VN, Kousoulas KG, Lin X and Storz J (1998) Nucleotide and predicted amino acid sequences of all genes encoded by the 3' genomic portion (9.5 kb) of respiratory bovine coronaviruses and comparisons among respiratory and enteric coronaviruses. *Virus Genes* **17**, 33–42.
- Chouljenko VN, Lin XQ, Storz J, Kousoulas KG and Gorbalenya AE (2001) Comparison of genomic and predicted amino acid sequences of respiratory and enteric bovine coronaviruses isolated from the same animal with fatal shipping pneumonia. *Journal of General Virology* **82**, 2927–2933.
- Chung JE, Kim HR, Bae YC, Lee OS and Oem JK (2011) Detection and characterization of bovine-like coronaviruses from four species of zoo ruminants. *Veterinary Microbiology* **148**, 396–401.
- Crossley B, Barr B, Magdesian KG, Ing M, Mora D, Jensen D, Loretta A, McConnell T and Mock R (2010) Identification of a novel coronavirus possibly associated with acute respiratory syndrome in alpacas (*Vicugna pacos*) in California, 2007. *Journal of Veterinary Diagnostic Investigation* **22**, 94–97.
- Crossley BM, Mock RE, Callison SA and Hietala SK (2012) Identification and characterization of a novel alpaca respiratory coronavirus most closely related to the human coronavirus 229E. *Viruses* **4**, 3689–3700.
- Daginakatte GC, Chard-Bergstrom C, Andrews GA and Kapil S (1999) Production, characterization, and uses of monoclonal antibodies against recombinant nucleoprotein of elk coronavirus. *Clinical Diagnostic Laboratory Immunology* **6**, 341–344.
- Dea S, Roy RS and Begin ME (1980) Bovine coronavirus isolation and cultivation in continuous cell lines. *American Journal of Veterinary Research* **41**, 30–38.
- Decaro N and Buonavoglia C (2008) An update on canine coronaviruses: viral evolution and pathobiology. *Veterinary Microbiology* **132**, 221–234.
- Decaro N, Desario C, Elia G, Mari V, Lucente MS, Cordioli P, Colaianni ML, Martella V and Buonavoglia C (2007) Serological and molecular evidence that canine respiratory coronavirus is circulating in Italy. *Veterinary Microbiology* **121**, 225–230.
- Decaro N, Campolo M, Desario C, Cirone F, D'Abramo M, Lorusso E, Greco G, Mari V, Colaianni ML, Elia G, Martella V and Buonavoglia C (2008a) Respiratory disease associated with bovine coronavirus infection in cattle herds in Southern Italy. *Journal of Veterinary Diagnostic Investigation* **20**, 28–32.
- Decaro N, Mari V, Desario C, Campolo M, Elia G, Martella V, Greco G, Cirone F, Colaianni ML, Cordioli P and Buonavoglia C (2008b) Severe outbreak of bovine coronavirus infection in dairy cattle during the warmer season. *Veterinary Microbiology* **126**, 30–39.
- Decaro N, Martella V, Elia G, Campolo M, Mari V, Desario C, Lucente M, Lorusso A, Greco G, Corrente M, Tempesta M, and Buonavoglia C (2008c) Biological and genetic analysis of a bovine-like coronavirus isolated from water buffalo (*Bubalus bubalis*) calves. *Virology* **370**, 213–222.
- Decaro N, Cirone F, Mari V, Nava D, Tinelli A, Elia G, Sarno A, Martella V, Colaianni M, Aprea G, Tempesta M and Buonavoglia C (2010a) Characterisation of bubaline coronavirus strains associated with gastroenteritis in water buffalo (*Bubalus bubalis*) calves. *Veterinary Microbiology* **145**, 245–251.
- Decaro N, Mari V, Elia G, Addie DD, Camero M, Lucente MS, Martella V and Buonavoglia C (2010b) Recombinant canine coronaviruses in dogs, Europe. *Emerging Infectious Diseases* **16**, 41–47.
- de Groot RJ, Ziebuhr J, Poon LL, Woo PC, Talbot P, Rottier PJM, Holmes KV, Baric R, Perlman S and Enjuanes L (2008) Revision of the Family Coronaviridae. Taxonomic Proposal of the Coronavirus Study Group to the ICTV Executive Committee. Available at <https://data.ictvonline.org/proposals/2008.085-122V.v4.Coronaviridae.pdf>.
- de Groot RJ, Baker SC, Baric R, Enjuanes L, Gorbalenya AE, Holmes KV, Perlman S, Poon L, Rottier PJM, Talbot PJ, Woo PCY and Ziebuhr J (2012) Family Coronaviridae. In King AMQ, Adams M, Carstens E and Lefkowitz E (eds), *Virus Taxonomy: Ninth Report of the International Committee on Taxonomy of Viruses*. San Diego: Elsevier Science Publishing Co., Inc, pp. 8.6–828.
- Doughri AM, Storz J, Hajer I and Fernando HS (1976) Morphology and morphogenesis of a coronavirus infecting intestinal epithelial cells of newborn calves. *Experimental and Molecular Pathology* **25**, 355–370.
- Drake JW and Holland JJ (1999) Mutation rates among RNA viruses. *Proceedings of the National Academy of Science USA* **96**, 13910–13913.
- Drosten C, Kellam P and Memish ZA (2014) Evidence for camel-to-human transmission of MERS coronavirus. *New England Journal of Medicine* **371**, 1359–1360.
- Elazhary MA, Frechette JL, Silim A and Roy RS (1981) Serological evidence of some bovine viruses in the caribou (*Rangifer tarandus caribou*) in Quebec. *Journal of Wildlife Diseases* **17**, 609–612.
- Erles K, Shiu KB and Brownlie J (2007) Isolation and sequence analysis of canine respiratory coronavirus. *Virus Research* **124**, 78–87.
- Estes R (2017) Antelope. Available at <https://www.britannica.com/animal/antelope-mammal>.
- Frankin WL (2011) Family Camelidae (Camels). In Wilson DE and Mittermeier RA (eds), *Handbook of the Mammals of the World*. Barcelona, Spain: Lynx Ediciones, pp. 206–246.
- Fulton RW, Herd HR, Sorensen NJ, Confer AW, Ritchey JW, Ridpath JF and Burge LJ (2015) Enteric disease in postweaned beef calves associated with Bovine coronavirus clade 2. *Journal of Veterinary Diagnostic Investigation* **27**, 97–101.
- Garbe JA, Amarín M and Hicheri K (1995) The Tri-national Animal Health Research Project (TAHRP) – Project No. 398-0158.21. Final Evaluation Report. United States Agency for International Development. 110 pp.
- Genova SG, Streeter RN, Simpson KM and Kapil S (2008) Detection of an antigenic group 2 coronavirus in an adult alpaca with enteritis. *Clinical and Vaccine Immunology* **15**, 1629–1632.
- Haigh JC, Mackintosh C and Griffin F (2002) Viral, parasitic and prion diseases of farmed deer and bison. *Revue Scientifique Et Technique* **21**, 219–248.

- Harms NJ, Jung TS, Andrew CL, Surujballi OP, VanderKop M, Savic M and Powell T (2019) Health status of reintroduced wood bison (*Bison bison athabascae*): assessing the conservation value of an isolated population in Northwestern Canada. *Journal of Wildlife Diseases* 55, 1–12. doi: 10.7589/2017-09-235.
- Harp JA, Myers LL, Rich JE and Gates NL (1981) Role of *Salmonella arizonae* and other infective agents in enteric disease of lambs. *American Journal of Veterinary Research* 42, 596–599.
- Hasoksuz M, Alekseev K, Vlasova A, Zhang X, Spiro D, Halpin R, Wang S, Ghedin E and Saif LJ (2007) Biologic, antigenic, and full-length genomic characterization of a bovine-like coronavirus isolated from a giraffe. *Journal of Virology* 81, 4981–4990.
- Heckert RA, Saif LJ and Agnes AG (1990) A longitudinal study of bovine coronavirus enteric and respiratory infections in dairy calves in two herds in Ohio. *Veterinary Microbiology* 22, 187–201.
- Hemida MG, Perera RA, Wang P, Alhammedi MA, Siu LY, Li M, Poon LL, Saif L, Alnaeem A and Peiris M (2013) Middle East respiratory syndrome (MERS) coronavirus seroprevalence in domestic livestock in Saudi Arabia, 2010 to 2013. *Euro Surveillance* 18, 20659.
- Hirst K (2017) What connects llamas and alpacas, vicunas, and guanacos? Available at www.thoughtco.com/llama-and-alpaca-domestication-history-170646.
- Jin L, Cebra CK, Baker RJ, Mattson DE, Cohen SA, Alvarado DE and Rohrmann GF (2007) Analysis of the genome sequence of an alpaca coronavirus. *Virology* 365, 198–203.
- Kim SH, Choi H, Yoon J, Woo C, Chung HM, Kim JT and Shin JH (2014) Pathogens in water deer (*Hydropotes inermis*) in South Korea, 2010–12. *Journal of Wildlife Diseases* 50, 478–483.
- Kim JH, Jang JH, Yoon SW, Noh JY, Ahn MJ, Kim Y, Jeong DG and Kim HK (2018) Detection of bovine coronavirus in nasal swab of non-captive wild water deer, Korea. *Transboundary and Emerging Diseases* 65, 627–631.
- La Vigna Alpacas (2018) World distribution of alpacas. Available at <http://www.lavignaalpacas.com/alpaca-facts/world-distribution-of-alpacas>.
- Lau SK, Lee P, Tsang AK, Yip CC, Tse H, Lee RA, So LY, Lau YL, Chan KH, Woo PC and Yuen KY (2011) Molecular epidemiology of human coronavirus OC43 reveals evolution of different genotypes over time and recent emergence of a novel genotype due to natural recombination. *Journal of Virology* 85, 11325–11337.
- Lau SK, Woo PC, Yip CC, Fan RY, Huang Y, Wang M, Guo R, Lam CS, Tsang AK, Lai KK, Chan KH, Che XY, Zheng BJ and Yuen KY (2012) Isolation and characterization of a novel Betacoronavirus subgroup A coronavirus, rabbit coronavirus HKU14, from domestic rabbits. *Journal of Virology* 86, 5481–5496.
- Lau SK, Tsang AK, Ahmed SS, Alam MM, Ahmed Z, Wong PC, Yuen KY and Woo PC (2016) First genome sequences of buffalo coronavirus from water buffaloes in Bangladesh. *New Microbes and New Infections* 11, 54–56.
- López WP, Chamorro ML and Garmendia AEB (2011) [Rapid detection of rotavirus and coronavirus in alpaca crias (*Vicugna pacos*) with diarrhea in the Cusco region, Peru]. *Revista de Investigaciones Veterinarias del Perú* 22, 407–411.
- Lorusso A, Desario C, Mari V, Campolo M, Lorusso E, Elia G, Martella V, Buonavoglia C and Decaro N (2009) Molecular characterization of a canine respiratory coronavirus strain detected in Italy. *Virus Research* 141, 96–100.
- Majhdi F, Minocha HC and Kapil S (1997) Isolation and characterization of a coronavirus from elk calves with diarrhea. *Journal of Clinical Microbiology* 35, 2937–2942.
- Miguel E, Chevalier V, Ayelet G, Ben Bencheikh MN, Boussini H, Chu DK, El Berbri I, Fassi-Fihri O, Faye B, Fekadu G, Grosbois V, Ng BC, Perera RA, So TY, Traore A, Roger F and Peiris M (2017) Risk factors for MERS coronavirus infection in dromedary camels in Burkina Faso, Ethiopia, and Morocco, 2015. *Euro Surveillance* 22, 30498.
- Milman O (2017) Giraffes must be listed as endangered, conservationists formally tell US. Guardian News and Media. Available at www.theguardian.com/environment/2017/apr/19/giraffes-endangered-species-conservation-hunting.
- Muhairi SA, Hosani FA, Eltahir YM, Mulla MA, Yusof MF, Serhan WS, Hashem FM, Elsayed EA, Marzoug BA and Abdelazim AS (2016) Epidemiological investigation of Middle East respiratory syndrome coronavirus in dromedary camel farms linked with human infection in Abu Dhabi Emirate, United Arab Emirates. *Virus Genes* 52, 848–854.
- Muniappa L, Mitov BK and Kharalambiev KE (1985) [Demonstration of coronavirus infection in buffaloes]. *Veterinarno-meditsinski Nauki* 22, 27–32.
- Muñoz M, Alvarez M, Lanza I and Cármenes P (1996) Role of enteric pathogens in the aetiology of neonatal diarrhoea in lambs and goat kids in Spain. *Epidemiology and Infection* 117, 203–211.
- Natsuaki S, Goto K, Nakamura K, Yamada M, Ueo H, Komori T, Shirakawa H and Uchinuno Y (2007) Fatal winter dysentery with severe anemia in an adult cow. *Journal of Veterinary Medical Sciences* 69, 957–960.
- Ozmen O, Yukari B, Haligur M and Sahinduran S (2006) Observations and immunohistochemical detection of Coronavirus, *Cryptosporidium parvum* and *Giardia intestinalis* in neonatal diarrhoea in lambs and kids. *Schweizer Archiv Fur Tierheilkunde* 148, 357–364.
- Park SJ, Kim GY, Choy HE, Hong YJ, Saif LJ, Jeong JH, Park SI, Kim HH, Lee BJ, Cho HS, Kim SK, Kang MI and Cho KO (2006) Detection and characterization of bovine coronaviruses in fecal specimens of adult cattle with diarrhea during the warmer seasons. *Journal of Clinical Microbiology* 44, 3178–3188.
- Pass DA, Penhale WJ, Wilcox GE and Batey RG (1982) Intestinal coronavirus-like particles in sheep with diarrhoea. *Veterinary Record* 111, 106–107.
- Peck KM, Burch CL, Heise MT and Baric RS (2015) Coronavirus host range expansion and Middle East respiratory syndrome coronavirus emergence: biochemical mechanisms and evolutionary perspectives. *Annual Review of Virology* 2, 95–117.
- Reinhardt G, Zamora J, Tadich N, Polette M, Aguilar M, Riedemann S and Palisson J (1995) Diagnosis of coronavirus in sheep in Valdivia province, Xth Region, Chile. *Archivos de Medicina Veterinaria* 27, 129–132.
- Reusken CB, Ababneh M, Raj VS, Meyer B, Eljarah A, Abutarbush S, Godeke GJ, Bestebroer TM, Zutt I, Muller MA, Bosch BJ, Rottier PJ, Osterhaus AD, Drosten C, Haagmans BL and Koopmans MP (2013a) Middle East respiratory syndrome coronavirus (MERS-CoV) serology in major livestock species in an affected region in Jordan, June to September 2013. *Euro Surveillance* 18, 20662.
- Reusken CB, Haagmans BL, Müller MA, Gutierrez C, Godeke GJ, Meyer B, Muth D, Raj VS, Smits-De Vries L, Corman VM, Drexler JF, Smits SL, El Tahir YE, De Sousa R, van Beek J, Nowotny N, van Maanen K, Hidalgo-Hermoso E, Bosch BJ, Rottier P, Osterhaus A, Gortázar-Schmidt C, Drosten C and Koopmans MP (2013b) Middle East respiratory syndrome coronavirus neutralising serum antibodies in dromedary camels: a comparative serological study. *The Lancet Infectious Diseases* 13, 859–866.
- Rojas M, Mancho A, Rocha A, Fornells L, Silva R, Mendes G, Dias H, Sandoval N, Pezo D and Santos N (2016) Outbreak of diarrhea among preweaning alpacas (*Vicugna pacos*) in the southern Peruvian highland. *The Journal of Infection in Developing Countries* 10, 269–274.
- Saalfeld WK and Edwards GP (2008) Ecology of feral camels in Australia. Managing the impacts of feral camels in Australia: a new way of doing business (DKCRC Report 47). Alice Springs: Desert Knowledge Cooperative Research Centre. ISBN 1-74158-094-3.
- Sabir JS, Lam TT, Ahmed MM, Li L, Shen Y, Abo-Aba SE, Qureshi MI, Abu-Zeid M, Zhang Y, Khiyami MA, Alharbi NS, Hajrah NH, Sabir MJ, Mutwakil MH, Kabli SA, Alsulaimany FA, Obaid AY, Zhou B, Smith DK, Holmes EC, Zhu H and Guan Y (2016) Co-circulation of three camel coronavirus species and recombination of MERS-CoVs in Saudi Arabia. *Science* 351, 81–84.
- Saif LJ (2010) Bovine respiratory coronavirus. *Veterinary Clinics of North America: Food Animal Practice* 26, 349–364.
- Saleh SM (1994) Epidemiological studies on diarrhea in cattle newborn calves fed on colostrum from vaccinated and control-pregnant cows. *Trinational Animal Health Research Project (TAHRP), 2nd Annual Workshop*. Sharm El-Sheikh, Egypt.
- Smits JE (1991) A brief review of infectious and parasitic diseases of wapiti, with emphasis on western Canada and the northwestern United States. *Canadian Veterinary Journal* 32, 471–479.

- Smits JE** (1992) Elk diseases survey in western Canada and northwestern United States. In Brown RD (ed.) *The Biology of Deer*. New York, NY: Springer-Verlag, pp. 101–106.
- Song HD, Tu CC, Zhang GW, Wang SY, Zheng K, Lei LC, Chen QX, Gao YW, Zhou HQ, Xiang H, Zheng HJ, Chern SW, Cheng F, Pan CM, Xuan H, Chen SJ, Luo HM, Zhou DH, Liu YF, He JF, Qin PZ, Li LH, Ren YQ, Liang WJ, Yu YD, Anderson L, Wang M, Xu RH, Wu XW, Zheng HY, Chen JD, Liang G, Gao Y, Liao M, Fang L, Jiang LY, Li H, Chen F, Di B, He LJ, Lin JY, Tong S, Kong X, Du L, Hao P, Tang H, Bernini A, Yu XJ, Spiga O, Guo ZM, Pan HY, He WZ, Manuguerra JC, Fontanet A, Danchin A, Niccolai N, Li YX, Wu CI and Zhao GP** (2005) Cross-host evolution of severe acute respiratory syndrome coronavirus in palm civet and human. *Proceeding of the National Academy of Sciences of the USA* **102**, 2430–2435.
- Stair EL, Rhodes MB, White RG and Mebus CA** (1972) Neonatal calf diarrhea: purification and electron microscopy of a coronavirus-like agent. *American Journal of Veterinary Research* **33**, 1147–1156.
- Storz J, Stine L, Liem A and Anderson GA** (1996) Coronavirus isolation from nasal swab samples in cattle with signs of respiratory tract disease after shipping. *Journal of American Veterinary Medical Association* **208**, 1452–1455.
- Storz J, Purdy CW, Lin X, Burrell M, Truax RE, Briggs RE, Frank GH and Loan RW** (2000) Isolation of respiratory bovine coronavirus, other cytodid viruses, and *Pasteurella* spp from cattle involved in two natural outbreaks of shipping fever. *Journal of American Veterinary Medical Association* **216**, 1599–1604.
- Thomas SM and Morgan ER** (2013) Effect on performance of weanling alpacas following treatments against gastro-intestinal parasites. *Veterinary Parasitology* **198**, 244–249.
- Torres-Medina A, Schlafer DH and Mebus CA** (1985) Rotaviral and coronavirus diarrhea. *Veterinary Clinics of North America: Food Animal Practice* **1**, 471–493.
- Trávén M, Carlsson U, Lundén A and Larsson B** (1999) Serum antibodies to bovine coronavirus in Swedish sheep. *Acta Veterinaria Scandinavica* **40**, 69–74.
- Tsunemitsu H, Yonemichi H, Hirai T, Kudo T, Onoe S, Mori K and Shimizu M** (1991) Isolation of bovine coronavirus from feces and nasal swabs of calves with diarrhea. *Journal of Veterinary Medical Sciences* **53**, 433–437.
- Tsunemitsu H, El-Kanawati ZR, Smith DR, Reed HH and Saif LJ** (1995) Isolation of coronaviruses antigenically indistinguishable from bovine coronavirus from wild ruminants with diarrhea. *Journal of Clinical Microbiology* **33**, 3264–3269.
- Tzipori S, Smith M, Makin T and McCaughan C** (1978) Enteric coronavirus-like particles in sheep. *Australian Veterinary Journal* **54**, 320–321.
- Vijgen L, Keyaerts E, Moes E, Thoelen I, Wollants E, Lemey P, Vandamme AM and Van Ranst M** (2005) Complete genomic sequence of human coronavirus OC43: molecular clock analysis suggests a relatively recent zoonotic coronavirus transmission event. *Journal of Virology* **79**, 1595–1604.
- Vijgen L, Keyaerts E, Lemey P, Maes P, Van Reeth K, Nauwynck H, Pensaert M and Van Ranst M** (2006) Evolutionary history of the closely related group 2 coronaviruses: porcine hemagglutinating encephalomyelitis virus, bovine coronavirus, and human coronavirus OC43. *Journal of Virology* **80**, 7270–7274.
- Woo PC, Lau SK, Yip CC, Huang Y, Tsoi HW, Chan KH and Yuen KY** (2006) Comparative analysis of 22 coronavirus HKU1 genomes reveals a novel genotype and evidence of natural recombination in coronavirus HKU1. *Journal of Virology* **80**, 7136–7145.
- Woo PC, Lau SK, Huang Y and Yuen KY** (2009) Coronavirus diversity, phylogeny and, jumping. *Experimental Biology and Medicine* **234**, 1117–1127.
- Woo PC, Lau SK, Wernery U, Wong EY, Tsang AK, Johnson B, Yip CC, Lau CC, Sivakumar S, Cai JP, Fan RY, Chan KH, Mareena R and Yuen KY** (2014) Novel betacoronavirus in dromedaries of the Middle East, 2013. *Emerging Infectious Diseases* **20**, 560–572.
- Woo PC, Lau SK, Fan RY, Lau CC, Wong EY, Joseph S, Tsang AK, Wernery R, Yip CC, Tsang CC, Wernery U and Yuen KY** (2016) Isolation and characterization of dromedary camel coronavirus UAE-HKU23 from dromedaries of the Middle East: minimal serological cross-reactivity between MERS coronavirus and dromedary camel coronavirus UAE-HKU23. *International Journal of Molecular Sciences* **17**, E691.
- Wünschmann A, Frank R, Pomeroy K and Kapil S** (2002) Enteric coronavirus infection in a juvenile dromedary (*Camelus dromedarius*). *Journal of Veterinary Diagnostic Investigation* **14**, 441–444.
- Yang DK, Hwang IJ, Kim BH, Kweon CH, Lee KW, Kang MI, Lee CS and Cho KO** (2008) Serosurveillance of viral diseases in Korean native goats (*Capra hircus*). *Journal of Veterinary Medical Sciences* **70**, 977–979.
- Yokoi K, Okazaki H, Inahara K and Hatama S** (2009) Prevalence of eight bovine viruses in sika deer (*Cervus nippon yesoensis*) in Japan. *Veterinary Record* **165**, 754–755.
- Zhang XM, Herbst W, Kousoulas KG and Storz J** (1994) Biological and genetic characterization of a hemagglutinating coronavirus isolated from a diarrhoeic child. *Journal of Medical Virology* **44**, 152–161.