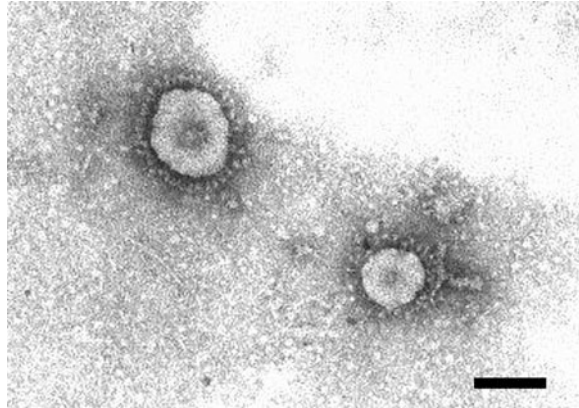


Gammacoronavirus[‡]

Coronaviridae

Nicola Decaro



■ Avian coronavirus (IBV). Fig. 1

Transmission electron micrograph, negative staining of purified virus. Length of bar (nm): 100 (Courtesy of Dr. A. Lavazza, Istituto Zooprofilattico di Lombardia ed Emilia Romagna, Italy)

Virion

Morphology:	Spherical
Envelope:	Yes
Diameter (nm):	120–160
Length (nm):	
Structural components:	Nucleocapsid, core, envelope
Buoyant density (g/mL):	1.23–1.24
Buoyant density method:	CsCl
Lipid composition:	Envelope lipids are derived from cytoplasmic membrane of host cell
Additional information:	Surface projections made by the spike (S) protein

Genome

Nucleic acid:	RNA
Strandedness:	

[‡]This chapter was reprinted from the first edition of the Springer Index of Viruses. Taxonomy and classification of the virus species described in this chapter may have changed.

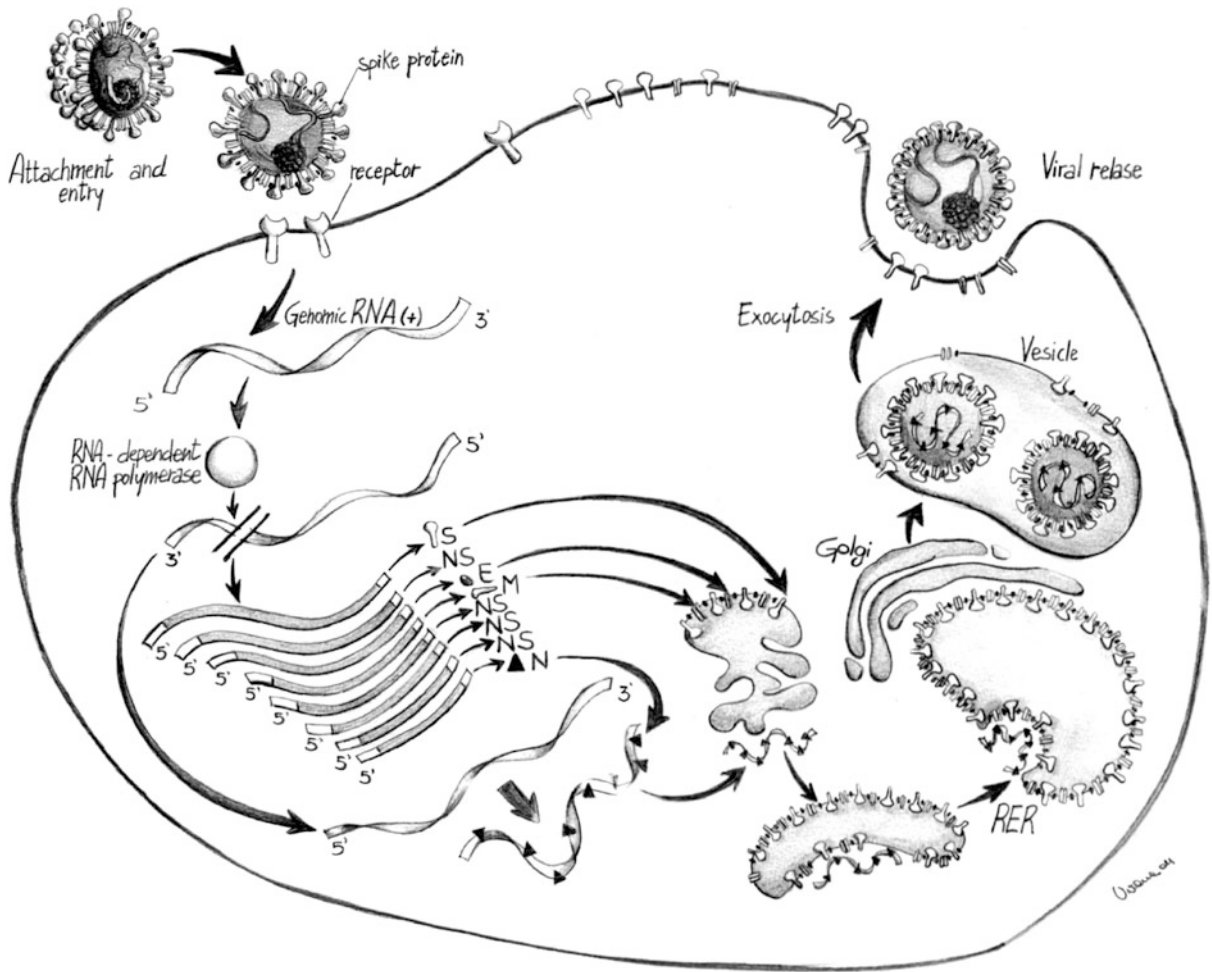
Polarity:		
Configuration:		
Segment organization:	Segment no. 1 (kb):	26.4–31.7
	One segment(s):	26.4–31.7 (kb) total (calculated)
G + C content (%):	37.6–41.8	
mRNA transcripts:	7–10	
Open reading frames:	7–10	
Additional information:	The genome contains a leader at the 5' end and a poly(A) tail; genes are arranged in the order 5'-replicase-S-E-M-N-3', with a variable number of other genes that are believed to be non-structural	

Replication

Entry mechanism:	Receptor-mediated endocytosis
Site of transcription:	Cytoplasm
Transcriptase:	Virus-encoded RNA-dependent RNA polymerase
Site of genome replication:	Cytoplasm
Replicase:	Virus-encoded RNA-dependent RNA polymerase
Replication intermediate:	Negative-strand RNA intermediate
Site of virion assembly:	Cytoplasm, the intermediate compartment
Egress mechanism:	Budding through the pre-Golgi and Golgi
Additional information:	Only the membrane (M) and envelope (E) proteins are required for the production of virus-like particles (VLPs)

History

Year of event	Event	References
1930	First report of infectious bronchitis in poultry in North Dakota	Schalk AE, Hawn MC (1931) J Am Vet Med Assoc 78:413–422
1936	First demonstration of a coronavirus disease, infectious bronchitis (IB), in domestic fowl	Beach JR, Schalm OW (1936) Poult Sci 15:199–206
1937	First cultivation of infectious bronchitis virus in chick embryos	Beaudette ER, Hudson CB (1937) J Am Vet Med Assoc 90:51–58
1949	“Stunting and curling” in chick embryos is an IB pathognomonic lesion	Fabricant J (1951) Cornell Vet 39:414–431
1973	Coronavirus-like (turkey coronavirus, TuCoV) particles identified by electron microscopy in turkeys with bluecomb disease	Ritchie JM et al (1973)
1975	ICTV approves Coronaviridae family with one genus, Coronavirus	Tyrrell DAJ et al (1975)
1977	Coronavirus (IBV) RNA shown to be infectious	Lomnicz B (1977)
1980	Coronavirus (IBV) subgenomic mRNAs form a 3' coterminal nested set	Stern DI, Kennedy SI (1980)
1987	First report on a coronavirus genome (IBV) complete sequence.	Bournnell MEG et al (1987)
1987	Frameshift in translation of replicase gene experimentally demonstrated in vitro	Brierley AS et al (2000)



■ Alpha-, Beta-, and Gammacoronavirus replication cycle. Fig. 2
 HE protein is present only in some Betacoronaviruses (Courtesy of Dr Viviana Tarallo, Department of Veterinary Public Health, Valenzano, Italy)

Year of event	Event	References
1996	An IBV-related coronavirus is isolated from pheasants	Gough AE et al (1996)
1996	ICTV recognises Coronaviridae as containing two genera: Coronavirus and Torovirus	Cavanagh JG et al (1997)
1996	ICTV recognises the order Nidovirales containing families Coronaviridae and Arteriviridae	Cavanagh JG et al (1997)
2005	Design of wide-spectrum inhibitors of coronavirus main protease	Yang Y et al (2005)
2008	Identification of a novel coronavirus (beluga whale coronavirus, BWCoV) from a beluga whale	Mihindukulasuriya KA et al (2008)
2009	ICTV recognises the family Coronaviridae as containing two subfamilies, Coronavirinae and Torovirinae, with the former including three genera	Carstens K et al (2010)

Year of event	Event	References
2009	According to the new taxonomy, genus Coronavirus is replaced by genera Alpha-, Beta- and Gammacoronavirus, corresponding to the old antigenic groups	Carstens K (2010)
2009	IBV, TuCoV, PhCoV, BWCoV and related viruses are recognised as host variants of a unique species, Avian coronavirus, of the genus Betacoronavirus	Carstens K (2010)
2009	Identification in wild birds of new putative members of the genus Gammacoronavirus	Woo J et al (2009)

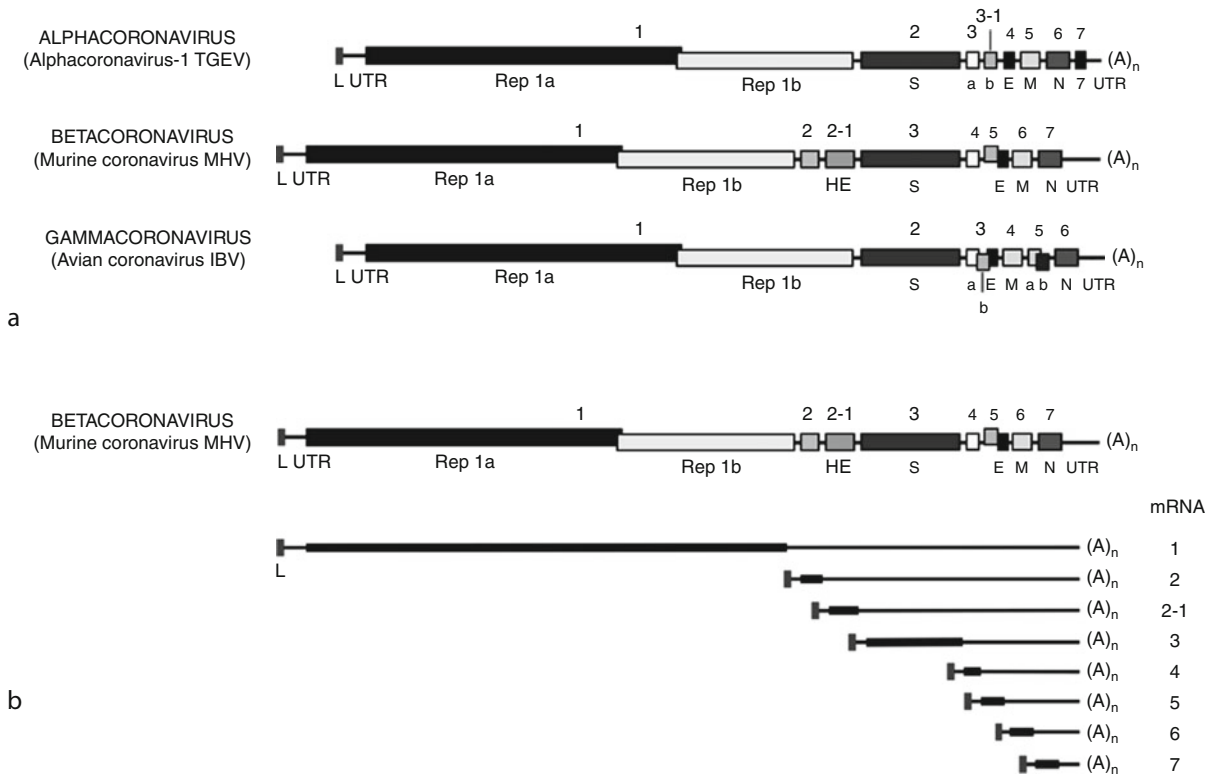
Genus Members

Species name	Synonyms	Wild-type strains/ isolates	Natural host range	Experimental host range	Membership status
Avian coronavirus	Avian infectious bronchitis virus (IBV); Turkey coronavirus (TuCoV); Pheasant coronavirus (PhCoV); Duck coronavirus (DuCoV); Goose coronavirus (GoCoV); Pigeon coronavirus (PgCoV); Quail coronavirus (QCoV)	IBV:Massachusetts M41;4/91;H; TuCoV: Minnesota; PhCoV:ph/UK/6/99; PgCoV:03/653; QCoV:Italy/Elvia/2005	Domestic fowl, turkeys, other domestic birds	Quail, gulls, suckling mice (IBV); chicken (TuCoV)	Type species
Beluga Whale coronavirus SW1 (BWCoV-SW1)		SW1	Beluga whales (<i>Delphinapterus leucas</i>)		Approved member
Asian leopard cat coronavirus (ALCCoV)		Guangxi/F230/2006	Asian leopard cats (<i>Prionailurus bengalensis</i>)		Tentative member
Black-headed gull coronavirus		CIR-66152; CIR-66146; CIR-66187; CIR-66185	Black-headed gull (<i>Chroicocephalus ridibundus</i>)		Tentative member
Brent goose coronavirus		KR-70	Russian Brent goose (<i>Branta bernicla</i>)		Tentative member
Bulbul coronavirus HKU11 (BuCoV-HKU11)		796; 934	Bulbuls (<i>Pycnonotus jocosus</i>)		Tentative member
Chinese ferret badger coronavirus Guanxi/2006 (CFBCoV-Guanxi/2006)		Guangxi/F247/2006; Guangxi/F250/2006	Chinese ferret badgers (<i>Melogale moschata</i>)		Tentative member

Species name	Synonyms	Wild-type strains/ isolates	Natural host range	Experimental host range	Membership status
Glaucous gull coronavirus		PBA-173	Glaucous gull (<i>Larus hyperboreus</i>)		Tentative member
Glaucous- winged gull coronavirus		CIR-66002	Glaucous-winged gull (<i>Larus glaucescens</i>)		Tentative member
Munia coronavirus HKU13 (Munia coronavirus HKU13)		3514	3,514		Tentative member
Pintail coronavirus PBA-124		10; 15; 25; PBA-124	Pintail (<i>Anas acuta</i>)		Tentative member
Rock sandpiper coronavirus		CIR-65885; CIR-65828; CIR-65824; CIR-665821	Rock sandpiper (<i>Calidris ptilocnemis</i>)		Tentative member
Snow goose coronavirus		WIR-159	Snow goose coronavirus (<i>Anser caerulescens</i>)		Tentative member
Thrush coronavirus HKU12 (ThCoV- HKU12)		600	Thrushes (<i>Turdus hortulorum</i> , <i>Turdus merula</i>)		Tentative member
Western sandpiper coronavirus		KR-28	Western sandpiper (<i>Calidris mauri</i>)		Tentative member

Nucleotide Sequences

Genomic region	Species	Strain	Nucleotides	Access number	References
Complete genome	Avian coronavirus (IBV)	Beaudette	27,608	M95169	Bournnell ME et al (1987)
Complete genome	Avian coronavirus (TuCoV)	TuCoV-540	27,771	EU022525	Cao R et al (2008)
Complete genome	BuCoV-HKU11	796	26,476	FJ376620	Woo J et al (2009)
Complete genome	ThCoV-HKU12	600	26,396	NC_011549	Woo J et al (2009)
Complete genome	MuCoV-HKU13	3514	26,552	NC_011550	Woo J et al (2009)
Complete genome	BWCoV-SW1	SW1	31,686	NC_010646	Mihindukulasuriya KA et al (2008)
Genomic very 3' end	Avian coronavirus (PhCoV)	ph/UK/602/95	443	AJ619604	Cavanagh PR et al (2002)
Replicase (partial)	Avian coronavirus (QCoV)	Italy/Elvia/2005	429	EF446156	Circella M et al (2007)
Replicase (partial)	Avian coronavirus (PgCoV)	03/428-1	208	AJ854131	Jonassen CM et al (2005)
Replicase (partial)	Avian coronavirus (GCoV)	03/586-1	208	AJ854114	Jonassen CM et al (2005)



■ Genome organization of Alpha-, Beta-, and Gammacoronavirus prototypes (a) and transcription map of Murine coronavirus MHV (b). Fig. 3
Numbers above bars = ORFs; L leader; UTR untranslated region; Rep replicase; (A)_n poly A (Modified from Springer Index of Viruses, 1st edition, with permission)

Genomic region	Species	Strain	Nucleotides	Access number	References
replicase (partial)	Avian coronavirus (DCoV)	03/1094	208	AJ8541	Jonassen CM et al (2005)
Genomic 3' end	ALCCoV	Guangxi/F230/2006	12,801	EF584908	Dong PD et al (2007)
Replicase (partial)	CBFCoV-Guanxi/2006	Guangxi/F247/2006	1,179	EF584909	Dong PD et al (2007)
Replicase (partial)	Snow goose coronavirus	WIR-159	561	GU396690	Muradrasoli S et al (2010)
Replicase (partial)	Rock sandpiper coronavirus	CIR-65885	562	GU396689	Muradrasoli, et al (2010)
Replicase (partial)	Black-headed gull coronavirus	CIR-66152	562	GU396686	Muradrasoli S et al (2010)
Replicase (partial)	Glaucous-winged gull coronavirus	CIR-66002	562	GU396682	Muradrasoli S et al (2010)
Replicase (partial)	Glaucous gull coronavirus	PBA-173	541	GU396674	Muradrasoli, et al (2010)
Replicase (partial)	Brent goose coronavirus	KR-70	531	GU396676	Muradrasoli S et al (2010)
Replicase (partial)	Western sandpiper coronavirus	KR-28	535	GU396675	Muradrasoli S et al (2010)
Replicase (partial)	Pintail coronavirus	PBA-124	542	GU396673	Muradrasoli S et al (2010)

Proteins

Protein name	Protein name abbreviation	Number of amino acids	Molecular weight (kDa)	Time of expression	Accession numbers	Additional information
Polyprotein 1ab (replicase complex)	pp1ab	6262–6663	740–800	Throughout	NP_066134; ACH72792; YP_001941164; ACJ12052; ACJ12043; ACJ12061; YP_001876435	Encoded by two ORFs, 1a and 1b; pseudoknot involved in frameshifting; cleaved to several products, including an RNA-dependent RNA polymerase
Spike glycoprotein	S	1156–1472	150–220	Throughout	ADC79651; ABF61518; YP_001941166; YP_001876437; ACJ12044; YP_002308506; YP_002308497	Highly glycosylated; forms homotrimers; cleaved to S1 and S2 subunits in some members
Membrane protein	M	217–260	217–264	Throughout	ACD93207; ACZ17397; AAF35863; YP_001941170; YP_002308508; YP_002308499; ACJ12046; YP_001876439	N-linked or O-linked glycans; triple-spanning
Envelope protein	E	82–110	9–12	Throughout	CAZ86711; CAZ86702; ADQ57408; ABW81430; YP_002308498; ACJ12045; YP_002308507; ABQ39959; YP_001876438	Essential for virion assembly; E plus M forms virus-like particles
Nucleocapsid protein	N	343–417	50–60	Throughout	AAB24054; AAB48157; AAV88459; AAF23873; CAI40312; ACJ12057; ACJ12048; ACJ12066; ABW87831	Highly basic phosphoprotein; forms a helical nucleocapsid
IBV non-structural protein 3a	IBVns3a	57–61	6.7	Throughout	AAT70773; CAA42115; ABW81428; ACC60267	Unique to Avian coronavirus; absent in some strains; not essential for replication
IBV non-structural protein 3b	IBVns3b	62–72	7.4	Throughout	AAT70774; CAA42488; CAA43123; ABQ84824; ACV87274; ACV87252	Unique to Avian coronavirus; not essential for replication
IBV non-structural protein 5a	IBVns5a	65	7.4	Throughout	AAA70240; NP_040836; ABW75145; ACV87248; CAF22050	Unique to Avian coronavirus; not essential for replication
IBV non-structural protein 5b	IBVns5b	80–90	9.5	Throughout	ABG36793; ABQ84764; ABQ84859; ACC60264; ACV87269	Unique to Avian coronavirus; not essential for replication
MuCoV/ BuCoV/ ThCoV non-structural protein 6	MuCoV/ BuCoV/ ThCoV ns6	91–108	10.3–12.2		YP_002308500; ACJ12047; YP_002308509	Putative accessory protein unique to MuCoV/BuCoV/ThCoV; gene located between M and N genes

Protein name	Protein name abbreviation	Number of amino acids	Molecular weight (kDa)	Time of expression	Accession numbers	Additional information
MuCoV/ BuCoV/ ThCoV non- structural protein 7a	MuCoV/ BuCoV/ ThCoV ns7a	123	13.8		ACJ12040; YP_002308502; YP_002308511	putative accessory protein unique to MuCoV/BuCoV/ ThCoV; gene located downstream of N gene
MuCoV/ BuCoV/ ThCoV non- structural protein 7b	MuCoV/ BuCoV/ ThCoV ns7b	83–85	9.1–9.3		ACJ12041; YP_002308503; YP_002308512	Putative accessory protein unique to MuCoV/BuCoV/ ThCoV; gene located downstream of N gene
MuCoV/ BuCoV/ ThCoV non- structural protein 7c	MuCoV/ BuCoV/ ThCoV ns7C	77–94	9.1–11.2		ACJ12042; YP_002308513; YP_002308504	Putative accessory protein unique to MuCoV/BuCoV/ ThCoV; gene located downstream of N gene
BWCoV-SW1 non- structural protein 5a	BWCoV-SW1 ns5a	138	15.6		YP_001876440	Putative accessory protein unique to BWCoV-SW1; gene located between M and N genes
BWCoV-SW1 non- structural protein 5b	BWCoV-SW1 ns5b	172	19.4		YP_001876441	Putative accessory protein unique to BWCoV-SW1; gene located between M and N genes
BWCoV-SW1 non- structural protein 5c	BWCoV-SW1 ns5c	175	20.1		YP_001876442	Putative accessory protein unique to BWCoV-SW1; gene located between M and N genes
BWCoV-SW1 non- structural protein 6	BWCoV-SW1 ns6	228	25.3		YP_001876443	Putative accessory protein unique to BWCoV-SW1; gene located between M and N genes
BWCoV-SW1 non- structural protein 7	BWCoV-SW1 ns7	161	18.4		YP_001876444	putative accessory protein unique to BWCoV-SW1; gene located between M and N genes
BWCoV-SW1 non- structural protein 8	BWCoV-SW1 ns8	59	6.8		YP_001876445	Putative accessory protein unique to BWCoV-SW1; gene located between M and N genes
BWCoV-SW1 non- structural protein 9	BWCoV-SW1 ns9	152	17.3		YP_001876446	Putative accessory protein unique to BWCoV-SW1; gene located between M and N genes
BWCoV-SW1 non- structural protein 10	BWCoV-SW1 ns10	210	23.7		YP_001876447	Putative accessory protein unique to BWCoV-SW1; gene located between M and N genes

Biology

Species	Permissive cell lines	Tissue tropism	Cytopathic effects	Additional information
Avian coronavirus (IBV)	Chicken eggs and kidney cells; Vero (Beaudette strain)	Respiratory epithelium; also kidney, oviduct, gut	Embryonic stunting/ curling (egg); syncytia (cells)	Can cause viral persistence; some strains highly nephropathogenic; some strains haemagglutinating
Avian coronavirus (TuCoV)	Embryonated turkey and chicken eggs	Intestinal epithelium, bursa of Fabricius	Embryonic stunting/ curling	Amniotic inoculation is required
Avian coronavirus (PhCoV)	Embryonated chicken eggs	Respiratory tissues and kidneys	Embryonic stunting/ curling	Allantoic route inoculation

Diseases

Disease	Causative agent	Affected organisms	Disease CHARACTERISTICS	Transmission route/vector	Treatment	Geographic distribution
Infectious bronchitis of poultry	Avian coronavirus (IBV)	Chickens	Sneezing, coughing; nephritis; declined egg production	Aerosol	No specific treatment	World-wide
Bluecomb disease, mud fever	Avian coronavirus (TuCoV)	Turkeys	Enteritis, wet droppings, depression	Faecal-oral	No specific treatment	World-wide
Pheasant respiratory and kidney disease	Avian coronavirus (PhCoV)	Pheasants	Rapid death, sneezing, poor hatchability, small size, variable color-pale buff to greenish brown	Aerosol	No specific treatment	World-wide

Diagnosis

Method	Species	Sample material	Detection target	References
Electron microscopy	Avian coronavirus (IBV, TuCoV, PhCoV)	Respiratory and/or cloacal specimens, kidneys	Particle morphology	Reagan RL et al (1948)
Cultivation in embryonated chicken eggs	Avian coronavirus (IBV, TuCoV, PhCoV)	Respiratory and/or cloacal specimens, kidneys	Embryonic alterations (stunting and curling)	Cunningham CH, Stuart HO (1947)
Agar gel precipitin test	Avian coronavirus (IBV, TuCoV, PhCoV)	Respiratory and/or cloacal specimens, kidneys	Viral antigens	Lohr M (1981)
Immunofluorescence assay	Avian coronavirus (IBV, TuCoV, PhCoV)	Tracheal, intestinal, renal sections	Viral antigens	Yagyu K, Ohta S (1990)

Method	Species	Sample material	Detection target	References
Immunoperoxidase assay	Avian coronavirus (IBV, TuCoV, PhCoV)	Tracheal, intestinal, renal sections	Viral antigens	Naqi S (1990)
Enzyme-linked immunosorbent assay with monoclonal antibodies	Avian coronavirus (IBV, TuCoV, PhCoV)	Respiratory and/or cloacal specimens, kidneys	Viral antigens	Naqi S et al (1993)
RT-PCR amplification of the spike-protein gene	Avian coronavirus (IBV, TuCoV, PhCoV)	Respiratory and/or cloacal specimens, kidneys	Viral rna	Lin J et al (1991)
Nested RT-PCR amplification of the nucleocapsid-protein gene	Avian coronavirus (IBV, TuCoV, PhCoV)	Respiratory and/or cloacal specimens, kidneys	Viral rna	Falcone DJ et al (1997)
Real-time RT-PCR amplification of the 5'-UTR	Avian coronavirus (IBV, TuCoV, PhCoV)	Respiratory and/or cloacal specimens, kidneys	Viral rna	Callison B et al (2006)
Real-time polymerase chain reaction/high-resolution melt curve analysis for IBV strain differentiation	Avian coronavirus (IBV)	Respiratory and/or cloacal specimens, kidneys	Viral rna	Hewson I et al (2010)

Vaccine Strains

Strain	Attenuation process	Additional information	References
Avian coronavirus IBV many strains	Inactivated vacciness	Poor effective	Cavanagh D (2007)
Avian coronavirus IBV many strains	Passage in embryonated domestic fowl eggs	Highly effective; may induce sterilising immunisation	Cavanagh D (2007)

Vector Constructs

Vector name	Backbone strain	Application	Insertion capacity (kb)	Additional information	References
IBV CD-61	Avian coronavirus (IBV Beaudette)	Expression	1	Transcription regulated by ibv control sequences	Penzes et al (1996)
vNotI/IBV(FL)	Avian coronavirus (IBV Beaudette)	Reverse genetics	27.6	Recombinant vaccinia virus containing the full-length genome of mhv	Casais R et al (2001)
IBV c-DNA	Avian coronavirus (IBV Beaudette)	Reverse genetics	27.6	Full-length genome infectious clone constructed through ligation of five inserts	Youn JG et al (2005)

References

- Carstens (2010)
- Cavanagh (1997)
- Enjuanes L, Siddell SG, Spaan WJ (1998) Coronaviruses and arteriviruses. Plenum, New York
- Enjuanes L, Brian D, Cavanagh D, Holmes K, Lai MMC, Laude H, Masters P et al (1999a) Coronaviridae. In: Murphy FA et al (eds) Virus taxonomy. Academic, New York
- Enjuanes L, Spaan SE, Cavanagh D (1999b) Nidovirales. In: Murphy FA et al (eds) Virus taxonomy. Academic, New York
- Holmes KV, Lai MMC (1996) Coronaviridae: the viruses and their replication. In: Fields BN, Knipe DM, Howley PM (eds) Fundamental virology. Academic, New York
- Lai and Cavanagh (1997)
- Perlman S, Gallagher T, Snijder EJ (2008) Nidovirales. ASM Press, Washington, DC
- Siddell SG (1995) In: Fraenkel-Conrat H, Wagner RR (eds) The coronaviridae. Plenum, New York
- Sturman and Holmes (1983)

