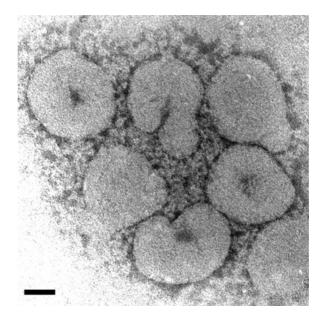
# Torovirus<sup>‡</sup>

#### Coronaviridae

Eric J. Snijder · Raoul J. de Groot



Berne virus. Fig. 1

Negative staining of extracellular virions, showing the pleiomorphism of toroviruses. Length of bar [nm]: 40.[courtesy of M. Weiss, University of Berne, Switzerland; reprinted with permission from Snijder EJ, Horzinek MC (1993) J Gen Virol 74:2305–2316]

#### Virion

Morphology:	pleiomorphic
Envelope:	yes
Diameter [nm]:	120–140
Length [nm]:	-
Structural components:	helical nucleocapsid, envelope
Buoyant density [g/mL]:	1.14–1.18
Additional information:	nucleocapsid is tubular, either straight or bent into doughnut-like structure (torus) resulting in oval, elongated, or kidney-shaped virions; envelope is densely studded with two types of surface projections, 17–20 nm and 6 nm in length

<sup>&</sup>lt;sup>‡</sup>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.

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#### Genome

Nucleic acid:	RNA
Strandedness:	single-stranded
Polarity:	positive-sense
Configuration:	linear
Segments:	1
Size [kb]:	25–30
G + C content [%]:	35–40
Transcription units:	5
Additional information:	3'-polyadenylated

## **Replication Strategy**

Entry mechanism:	unknown
Site of transcription:	cytoplasm
Transcriptase:	viral RNA-dependent RNA polymerase
Site of genome replication:	cytoplasm
Replicase:	viral RNA-dependent RNA polymerase
Replication intermediate:	genomic minus strand RNA
Site of virion assembly:	cytoplasm and intracellular membranes
Egress mechanism:	budding of nucleocapsid through intracellular membranes, transport to cell membrane, exocytosis
Additional information:	gene expression through a 3' co-terminal nested set of subgenomic mRNAs

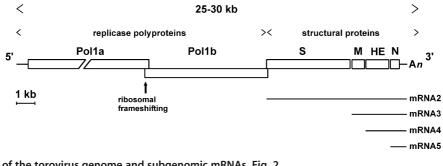
## History

Year	Event/Discovery	Reference
1972	Isolation of Berne virus (BEV; equine torovirus) from a diarrhoeal horse during routine diagnostic work	Weiss M, et al. (1983) J Gen Virol 64:1849–1858
1979	Isolation of Breda virus (BRV; bovine torovirus) from diarrhoeal calves	Woode GN, et al. (1985) Vet Microbiol 7:221–240
1984	First reports on possible human toroviruses	Beards GM, et al. (1984) Lancet ii:1050–1052
1989	Publication of the first (partial) torovirus genome sequence (3' end of Berne virus genome)	Snijder EJ, et al. (1989) J Gen Virol 70:3363–3370
1990	Description of a 3'-coterminal nested set of viral mRNAs in Berne virus-infected cells	Snijder EJ, et al. (1990) J Virol 64:331–338
1990	Sequence analysis of the Berne virus replicase gene reveals an evolutionary relationship with coronaviruses	Snijder EJ, et al. (1990) Nucleic Acids Res 18:4535–4542

Year	Event/Discovery	Reference
1992	Genus Torovirus assigned to the family Coronaviridae	Cavanagh D, et al. (1993) Arch Virol 128:395–396
1996	Classification of the families Coronaviridae (incl. Toroviruses) and Arteriviridae in novel order Nidovirales	Cavanagh D, et al. (1997) Arch Virol 142:629–633
1997	Genetic characterization of Breda virus; identification of the hemagglutinin-esterase as a structural protein	Cornelissen LAHM, et al. (1997) J Virol 71:5277–5286
1998	Identification and characterization of a porcine torovirus (PoTV)	Kroneman A, et al. (1998) J Virol 72:3507–3511

#### **Genus Members**

Species	Abbr.	Synonym(s)	Wild-type isolates	Host range	Membership status
Equine torovirus	EqTV	Berne virus (BEV)	P138/72	horses	type species
Bovine torovirus	BoTV	Breda virus (BRV)	I, II	cattle	approved member
Porcine torovirus	PoTV			pigs	approved member
Human torovirus	HuTV			humans	approved member



• Organization of the torovirus genome and subgenomic mRNAs. Fig. 2 Genes are represented by boxes.

#### **Nucleotide Sequences**

Genomic region	Virus species	Strain	Nucleotides	Accession number	Reference
nucleocapsid protein gene and genomic 3' end	BEV	P138/72	730	D00563	Snijder EJ, et al. (1989) J Gen Virol 70:3363–3370
hemagglutinin-esterase protein gene (pseudogene)	BEV	P138/72	534	X52375	Snijder EJ, et al. (1991) Virology 180:448–452
membrane protein gene	BEV	P138/72	760	X52505	den Boon JA, et al. (1991) Virology 182:655–663
spike protein gene	BEV	P138/72	4858	X52506	Snijder EJ, et al. (1990) Virology 178:355–363
replicase gene (3' end of ORF1a + ORF1b)	BEV	P138/72	7920	X52374	Snijder EJ, et al. (1990) Nucl Ac Res 18:4535–4542

Genomic region	Virus species	Strain	Nucleotides	Accession number	Reference
replicase gene (5' end ORF1a) and genomic 5' end	BEV	P138/72	1580	X56016	Snijder EJ, et al. (1991) J Gen Virol 72:1635–1643
nucleocapsid protein gene and genomic 3' end	BRV	2			Kroneman A, et al. (1998) J Virol 72:3507–3511
hemagglutinin-esterase protein gene	BRV	2	1260	Y10866	Cornelissen L, et al. (1997) J Virol 71:5277–5286
3'-terminal region of genome (S-HE-M-N genes)	BRV	1	7550	AF076621	Duckmanton L, et al. (1998) Virus Res 58:83–96
nucleocapsid protein gene and genomic 3' end	PoTV	Markelo			Kroneman A, et al. (1998) J Virol 72:3507–3511

## Proteins

Protein	Abbr.	MW [kDa]	Time of expression	Accession numbers	Additional information
replicase polyprotein		600-800	early	P18458, Q65826, Q65827	C-terminal part; protein is assumed to be cleaved
spike protein	S	175–200	late	P23052, O90304	highly glycosylated; cleaved post- translationally
membrane protein	М	26	late	P27904, O90305	triple-spanning, unglycosylated envelope protein
hemagglutinin- esterase	HE	65	late	P31964, CAA71819, O39517	envelope protein, acetyl-esterase, glycosylated
nucleocapsid protein	N	19–20	late	P23051, O90306	highly basic, phosphorylated

## Biology

Virus species	Permissive cell lines	Tissue tropism	Cytopathic effects	Additional information
BEV	embryonic mule skin, equine dermis	unknown	rounding of cells, detachment from surface	no syncytia, in contrast to most coronaviruses
BRV		intestinal epithelium	villous atrophy, necrosis of epithelium	thus far, BRV cannot be grown in vitro
PoTV		probably: intestinal epithelium	unknown	thus far, PoTV cannot be grown in vitro
HuTV		probably: intestinal epithelium	unknown	thus far, HuTV cannot be grown in vitro

## Diseases

Disease		Affected organism			Geographic distribution
gastroenteritis	BRV	cattle	(watery) diarrhoea with virus excretion	presumably faecal- oral	world-wide

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