



Review

Conserved tegument protein complexes: Essential components in the assembly of herpesviruses



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ABSTRACT

One of the structural components of herpesviruses is a protein layer called the tegument. Several of the tegument proteins are highly conserved across the herpesvirus family and serve as a logical focus for defining critical interactions required for viral assembly. A number of studies have helped to elucidate a role for conserved tegument proteins in the process of secondary envelopment during the course of herpesviral assembly. This review highlights how these tegument proteins directly contribute to bridging the nucleocapsid and envelope of virions during secondary envelopment.

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1. Introduction

The *Herpesviridae* family of viruses contains three subfamilies *Alpha*, *Beta* and *Gammaherpesvirinae* whose natural hosts include mammals, birds and reptiles (Davison et al., 2009; Pellett and Roizman, 2013). Members of the *Herpesviridae* family are associated with a range of significant diseases that occur during either primary productive infection and/or during reactivation from latency

(Arvin and Gilden, 2013; Damania and Cesarman, 2013; Longnecker et al., 2013; Mocarski et al., 2013; Roizman et al., 2013; Yamanishi et al., 2013). This review will highlight the role viral structural tegument proteins play in the assembly of members from across the *Herpesviridae* family including: herpes simplex virus type 1 and type 2 (HSV-1 and HSV-2); varicella zoster virus (VZV; chickenpox virus); human cytomegalovirus (HCMV); Kaposi's sarcoma-associated herpesvirus (KSHV); Epstein-Barr virus (EBV); mouse cytomegalovirus (MCMV); mouse herpesvirus 68 (MHV68); and pseudorabies virus (PrV). A particular focus will be on the most characterised tegument protein families which include pUL11, pUL16, pUL36 and pUL37 (Table 1). These tegument proteins are

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Table 1
Key conserved *Herpesviridae* tegument proteins.

Protein family	<i>Herpesviridae</i> gene	Subfamily	Virion component	Role in assembly
pUL11	HSV-1 ^a <i>UL11</i>	Alpha	Yes (Loret et al., 2008; MacLean et al., 1989)	Yes (Baines and Roizman, 1992; Fulmer et al., 2007; Leege et al., 2009a)
	PrV <i>UL11</i>	Alpha	Yes (Kopp et al., 2003; Kramer et al., 2011)	Yes (Kopp et al., 2003)
	VZV <i>ORF49</i>	Alpha	Yes (Sadaoka et al., 2007)	Yes (Sadaoka et al., 2014; Sadaoka et al., 2007)
	HCMV <i>UL99</i>	Beta	Yes (Baldick and Shen, 1996; Varnum et al., 2004)	Yes (Seo and Britt, 2007; Silva et al., 2003)
	MCMV <i>M99</i>	Beta	Yes (Kattenhorn et al., 2004)	Not determined
	EBV <i>BBLF1</i>	Gamma	Yes (Johannsen et al., 2004)	Yes (Chiu et al., 2012)
	MHV68 <i>ORF38</i>	Gamma	Yes (Shen et al., 2014; Vidick et al., 2013)	Possibly (Shen et al., 2014)
pUL16	HSV-1 <i>UL16</i>	Alpha	Yes (Loret et al., 2008; Nalwanga et al., 1996)	Yes (Starkey et al., 2014)
	PrV <i>UL16</i>	Alpha	Yes (Klupp et al., 2005; Kramer et al., 2011)	Minor? (Klupp et al., 2005)
	VZV <i>ORF44</i>	Alpha	Yes (Sadaoka et al., 2014)	Yes (Sadaoka et al., 2014; Zhang et al., 2010)
	HCMV <i>UL94</i>	Beta	Yes (Varnum et al., 2004; Wing et al., 1996)	Yes (Phillips and Bresnahan, 2012)
	MCMV <i>M94</i>	Beta	Yes (Kattenhorn et al., 2004)	Yes (Maninger et al., 2011; Mohr et al., 2010)
	EBV <i>BGLF2</i>	Gamma	Yes (Johannsen et al., 2004)	Not determined
	MHV68 <i>ORF33</i>	Gamma	Yes (Guo et al., 2009; Vidick et al., 2013)	Yes (Guo et al., 2009; Shen et al., 2015)
pUL36	HSV-1 <i>UL36</i>	Alpha	Yes (Heine et al., 1974; Loret et al., 2008)	Yes (Desai et al., 2008; Desai, 2000; Roberts et al., 2009; Sandbaumhuter et al., 2013)
	PrV <i>UL36</i>	Alpha	Yes (Klupp et al., 2002; Kramer et al., 2011)	Yes (Fuchs et al., 2004; Luxton et al., 2006)
	VZV <i>ORF22</i>	Alpha	Not determined	Possibly (Zhang et al., 2010)
	HCMV <i>UL48</i>	Beta	Yes (Baldick and Shen, 1996; Varnum et al., 2004; Yu et al., 2011)	Yes (Das et al., 2014)
	EBV <i>BPFL1</i>	Gamma	Yes (Johannsen et al., 2004)	Not determined
	KSHV <i>ORF64</i>	Gamma	Yes (Zhu et al., 2005)	Not determined
pUL37	HSV-1 <i>UL37</i>	Alpha	Yes (Loret et al., 2008; McLauchlan et al., 1994; Schmitz et al., 1995)	Yes (Desai et al., 2001; Leege et al., 2009b; Pasdeloup et al., 2010; Roberts et al., 2009; Sandbaumhuter et al., 2013)
	PrV <i>UL37</i>	Alpha	Yes (Kramer et al., 2011)	Yes (Klupp et al., 2001; Leege et al., 2009b)
	VZV <i>ORF21</i>	Alpha	Not determined	Possibly (Xia et al., 2003; Zhang et al., 2010)
	HCMV <i>UL47</i>	Beta	Yes (Baldick and Shen, 1996; Varnum et al., 2004; Yu et al., 2011)	Yes (Cappadona et al., 2015)
	EBV <i>BOFL1</i>	Gamma	Yes (Johannsen et al., 2004)	Not determined
	KSHV <i>ORF63</i>	Gamma	Yes (Zhu et al., 2005)	Not determined

^a EBV, Epstein-Barr virus; HCMV, human cytomegalovirus; HSV-1, herpes simplex virus type 1; KSHV, Kaposi's sarcoma-associated herpesvirus; MCMV, mouse cytomegalovirus; MHV68, mouse herpesvirus 68; PrV, pseudorabies virus; VZV, varicella zoster virus.

Table 2
Conserved tegument interactions.

Interaction	<i>Herpesviridae</i> member	Method of detection
pUL11–pUL16	HSV-1 ^a	Y2H (Fossum et al., 2009; Lee et al., 2008; Vittone et al., 2005); CoIP (Loomis et al., 2003); GST pulldown (Loomis et al., 2003; Yeh et al., 2008)
	PrV	GST pulldown (Harper et al., 2010)
	VZV	Y2H (Stellberger et al., 2010); CoIP (Sadaoka et al., 2014)
	HCMV	Y2H (Liu et al., 2009; Phillips and Bresnahan, 2011; Phillips et al., 2012; To et al., 2011); CoIP (Phillips et al., 2012; To et al., 2011); Colocalization (Liu et al., 2009)
	MCMV	Y2H (Fossum et al., 2009); CoIP (Maninger et al., 2011)
	EBV	Y2H (Fossum et al., 2009)
	MHV-68	Y2H (Lee et al., 2011); CoIP (Lee et al., 2011; Shen et al., 2014); Colocalization (Shen et al., 2014)
pUL36–pUL37	HSV-1	Y2H (Lee et al., 2008; Vittone et al., 2005); CoIP (Kelly et al., 2012; Vittone et al., 2005)
	PrV	Y2H (Klupp et al., 2002); CoIP (Klupp et al., 2002)
	VZV	Y2H (Stellberger et al., 2010)
	HCMV	Y2H (To et al., 2011); CoIP (Bechtel and Shen, 2002; Tullman et al., 2014); Colocalization (Cappadona et al., 2015)
	EBV	Y2H (Fossum et al., 2009)
	KSHV	Y2H (Rozen et al., 2008); CoIP (Rozen et al., 2008)

^a CoIP, coimmunoprecipitation; EBV, Epstein-Barr virus; GST, glutathione-S-transferase; HCMV, human cytomegalovirus; HSV-1, herpes simplex virus type 1; KSHV, Kaposi's sarcoma-associated herpesvirus; MCMV, mouse cytomegalovirus; MHV68, mouse herpesvirus 68; PrV, pseudorabies virus; VZV, varicella zoster virus; Y2H, yeast-two hybrid.

known to form conserved interactions important for viral assembly (Table 2). Further information on tegument interactions not emphasized in this review is available elsewhere (Maringer et al., 2012; Mettenleiter, 2006).

2. Herpesviral structure and replication

Herpesvirions consist of four morphologically distinct structures, the DNA core, capsid, tegument, and envelope (Pellett and

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