Recent Advances in HIV-1 CTL Epitope Characterization

Christian Brander and Philip J. R. Goulder

AIDS Research Center, Massachusetts General Hospital,
149 13th Street, Room 5234,
Charlestown, MA 02129, USA,
and Harvard Medical School Boston, MA USA

Updated November 1999

Since the last update of the Los Alamos HIV Immunology Database in 1998, the role of CTL in HIV and SIV infection has been further recognized as a beneficial and essential part of the host immune response against these viruses [Schmitz (1999), Brander & Walker(1999)]. As the full picture of the precise role of HIV specific CTL is still emerging, it becomes clear that under certain circumstances these cells are able to contribute significantly to the control of viral replication in infected individuals [Ogg (1998)]. Along with more sophisticated techniques to detect and quantify CTL responses, including ELISPOT and Tetramer methodologies [McMichael & O'Callaghan(1998), Goulder (2000b)], more detailed analyses of the genetic background of infected individuals may provide new insights into HIV pathogenesis [Tang (1999), Carrington (1999)].

The identification of HLA alleles which are associated with more rapid or slower disease progression, may now be linked to the importance and dominance of certain CTL epitopes. It is intriguing that thus far, only HLA-B alleles have been consistently associated with HIV-1 disease progression, which may be due to the relative distance of HLA-A genes to the central part of the MHC region containing HLA class III genes involved in the antigen processing. It is interesting that for some alleles (e.g. HLA-A1) no optimal epitopes have been defined, despite relative high frequencies in diverse populations. The mechanisms for HLA association and disease progression and the pattern of class I alleles that present HIV-derived CTL epitopes, including HLA alleles that are frequent in non-Caucasoid populations, require further investigation and these results will also need to be considered for the design of (epitope based) vaccines.

The current update of the list of optimal CTL epitope has undergone a few improvements:

There are an increased number of epitopes listed and the nomenclature for the HLA alleles has been updated. Accordingly, the order of the epitopes may have changed slightly: e.g. the 'HLA-B62' allele is now listed as HLA-B*1501. The data for the HLA class I binding motifs have been added for as many HLA alleles as possible and are mainly based on the database by Rammensee and co-workers [Rammensee (1999)].

This year's update has also been modified as more attention was given to epitopes that were contributed by personal communication. The individuals who kindly submitted their unpublished epitopes over the last few years were asked for more detailed titration/truncation data. We have now highlighted with an asterisk (*) those epitopes contributed as personal communications for which we had a chance to review the titration data. As a consequence of this enhanced scrutiny, a number of epitopes (mainly from our own laboratories) had to be removed from the list of optimal epitopes since the characterization did not fulfill all the stricter inclusion criteria. We would like to define these inclusion criteria still further as: a) detailed HLA restriction, possibly including subtype analysis; and b) titration curves with single amino acid truncated, longer and shorter versions of the epitope. In this regard, we found that titration curves with truncated peptides can easily be performed by ELISPOT, even at low numbers of CTL clones added per well (M. Altfeld, unpublished). In addition, an HLA-B35 restricted epitope in gp120 reported by Shiga *et al*., [Shiga (1996)], was included without peptide titrations being performed, since it has been used successfully in tetramer staining procedure in later studies [Ogg (1999)].

Some of the newly added epitopes deserve special attention as these are the first ones of a series of epitopes that have been identified in individuals with acute HIV-1 infection (M. Altfeld, unpublished data). These preliminary studies suggest that responses which are immunodominant in acute infection may differ from those seen in chronic infection. These findings will need more confirmation, but may also help to explain the immunodominance of certain epitopes in chronic infection. One possible explanation for these different responses could be that the responses elicited during acute infection are diminished over time (for various reasons, [Brander & Walker(1999)]) and that a new generation of epitopes that may be more resistant to CTL escape remain detectable in chronic infection. In this regard, the clustering of CTL epitopes to certain regions of the HIV genome may need to be revisited and more studies in acute infected individuals may help to complete the picture of the role CTL play in HIV infection.

We would like to express our gratitude to the large number of researchers in the field who continuously contribute to this database. We very much welcome any criticism, comments and additions to this list since we are sure that some epitopes will unintentionally escape our attention, despite close monitoring of the literature. Please write or call us with any comments at:

Christian Brander
phone: (617) 724-5789
FAX: (617) 726-5411
brander@helix.mgh.harvard.edu

Bruce D. Walker
phone: (617) 724-8332
FAX: (617) 726-4691
bwalker@helix.mgh.harvard.edu

Philip J.R. Goulder
phone: (617) 726-5787
FAX: (617) 726-5411
goulder@helix.mgh.harvard.edu

Bette Korber
phone: (505) 665-4453
FAX: (505) 665-3493
btk@t10.lanl.gov

Table 1 Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
A*0201 (A2)				2 6 C	[Falk (1991), Barouch (1995)]
			1° anchor	**L** **L**	
				M **V**	
			2° anchor	V	
	p17	77–85	LAI	SLYNTVATL	[Johnson (1991), Parker (1992), Parker (1994)]
	RT	33–41	LAI	ALVEICTEM	[Haas (1998)], and G. Haas pers. comm.
	RT	346–354	LAI	VIYQYMDDL	[Harrer (1996a)]
	RT	476–484	LAI	ILKEPVHGV	[Walker (1989), Tsomides (1991)]
	gp41	818–827	LAI	SLLNATDIAV	[Dupuis (1995)]
	gp120	311–320	IIIB	RGPGRAFVTI	[Alexander-Miller (1996)]
	nef	136–145	LAI	PLTFGWCYKL	[Haas (1996)], and B. Maier, B. Autran pers. comm.
	nef	180–189	LAI	VLEWRFDSRL	[Haas (1996)], and B. Maier, B. Autran pers. comm.
A*0202 (A2)				2 C	[Barouch (1995)]
				L **L**	
				V	
	p17	77–85	LAI	SLYNTVATL	P. Goulder, submitted
A*0301 (A3)				2 C	[DiBrino (1993), Rammensee (1995)]
				L **K**	
				V **Y**	
				M **F**	
	p17	18–26	LAI	KIRLRPGGK	[Harrer (1996b)]
	p17	20–28	LAI	RLRPGGKKK	B. Culmann, D.Lewinsohn, S. Riddell pers. comm., B. Wilkes, D. Ruhl pers. comm. and [Goulder (1997a)]
	p17	20–29	LAI	RLRPGGKKKY	[Goulder (2000c)]
	RT	33–43	LAI	ALVEICTEMEK	[Haas (1998)], and G. Haas pers. comm.
	RT	325–333	LAI	AIFQSSMTK	[Threlkeld (1997)]
	gp120	37–46	LAI	TVYYGVPVWK	[Johnson (1994)]
	gp41	775–785	LAI	RLRDLLLIVTR	[Takahashi (1991)]
	nef	73–82	LAI	QVPLRPMTYK	[Koenig (1990), Culmann (1991)]

Table 1 (cont.) Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
A*1101 (A11)				2 C **K** V I F Y	[Zhang (1993), Rammensee (1995)]
	p17	84–92	LAI	TLYCVHQRI	[Harrer (1998)]
	p24	349–359	III B	ACQGVGGPGHK	[Sipsas (1997)]
	RT	325–333	LAI	AIFQSSMTK	[Johnson & Walker(1994), Zhang (1993), Threlkeld (1997)]
	RT	508–517	LAI	IYQEPFKNLK	B. Culmann pers. comm.
	nef	75–82	LAI	PLRPMTYK	[Culmann (1991)]
	nef	84–92	LAI	AVDLSHFLK	[Culmann (1991)]
A*2402 (A24)				2 C **Y** **I** **L** **F**	[Maier (1994)]
	p17	28–36	LAI	KYKLKHIVW	[Ikeda-Moore (1998)] and D. Lewinsohn pers. comm.
	p24	296–306	HIV-1 clade A	RDYVDRFFKTL	[Dorrell (1999)] and S. Rowland-Jones pers. comm.
	gp120	53–62	LAI	LFCASDAKAY	[Lieberman (1992), Shankar (1996)]
	gp41	591–598	LAI	RYLKDQQLL	[Dai (1992)]
	Nef	138–147	LAI	RYPLTFGW	[Goulder (1997b), Ikeda-Moore (1998)]
A*2501 (A25)					
	p24	145–155	LAI	QAISPRTLNAW	I. Kurane, K. West, pers. comm.
	p24	203–212	LAI	ETINEEAAEW	[Klenerman (1996), van Baalen (1996)]

Table 1 (cont.) Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
A*2601 (A26)				12 6 C **V** **Y** **T** **F** **I** **L** **F** D I E L V	[Dumrese (1998)]
	p24	167–175	LAI	EVIPMFSAL	[Goulder (1996a)]
A*3002 (A30)				12 C **Y** **Y** **F** **L** **V** R	[Rammensee (1999)]
	p17	74–86	LAI	RSLYNTVATLY	P. Goulder et al, submitted
A*3101 (A31)				2 C **R** L V Y F	[Falk (1994), Rammensee (1999)]
	gp41	775–785	LAI	RLRDLLLIVTR	[Safrit (1994a), Safrit (1994b)]
A*3201 (A32)					
	RT	559–568	LAI	PIQKETWETW	[Harrer (1996b)]
	gp120	419–427	HXB2	RIKQIINMW	[Harrer (1996b)]

Table 1 (cont.) Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
A*6802 (A68)					
	gp41	782–790	LAI	IVTRIVELL	B. Wilkes pers. comm.*
	RT	71–79	A/B/D	ITLWQRPLV	S. Rowland-Jones, pers. comm.
	RT	85–93	Clade D	DTVLEEMNL	S. Rowland-Jones, pers. comm.
A*7401(A19)					
	RT	71–79	A/B/D	ITLWQRPLV	S. Rowland-Jones, pers. comm.
B*0702 (B7)				123 C **P** **L** A R R K	[Englehard (1993), Rammensee (1999)]
	p24	148–156	LAI	SPRTLNAWV	D. Lewinsohn pers. comm.
	p24	179–187	LAI	TPQDLNTML	[Wilson (1999)],B. Wilkes, D. Ruhl, P. Goulder pers. comm.*
	gp120	303–312	LAI	RPNNNTRKSI	[Safrit (1994b)]
	gp41	843–851	LAI	IPRRIRQGL	B. Wilkes, D. Ruhl pers. comm.*
	nef	68–77	LAI	FPVTPQVPLR	[Haas (1996)], and B. Maier, B. Autran pers. comm.
	nef	71–79	LAI	TPQVPLRPM	P. Goulder, pers. comm.*
	nef	77–85	LAI	RPMTYKAAL	[Bauer (1997)]
	nef	128–137	LAI	TPGPGVRYPL	[Culmann-Penciolelli (1994), Haas (1996)]
B*0801 (B8)				23 5 C **K** **K** **L** **R** PR L	[Hill (1992), Sutton (1993), DiBrino (1994a)]
	p17	24–31	LAI	GGKKKYKL	[Rowland-Jones (1993), Goulder (1997d)]
	p17	74–82	LAI	ELRSLYNTV	[Goulder (1997d)]
	p24	260–267	LAI	EIYKRWII	[Sutton (1993), Goulder (1997d)]
	p24	329–337	LAI	DCKTILKAL	[Sutton (1993)]
	gp120	2–10	III B	RVKEKYQHL	[Sipsas (1997)]
	gp41	591–598	LAI	YLKDQQLL	[Johnson (1992), Shankar (1996)]
	RT	185–193	LAI	GPKVKQWPL	[Walker (1989), Sutton (1993)]
	nef	13–20	LAI	WPTVRERM	[Goulder (1997d)]
	nef	90–97	LAI	FLKEKGGL	[Culmann-Penciolelli (1994), Price (1997)]

Table 1 (cont.) Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
B*1402 (B14)				23 5 C **R R L** **K H** L Y F	[DiBrino (1994b)]
	p24	298–306	LAI	DRFYKTLRA	[Harrer (1996b)]
	gp41	589–597	LAI	ERYLKDQQL	[Johnson (1992)]
B*1501 (B62)				2 C **Q Y** **L F** **M**	[Barber (1997)] [Barber (1997)] [Barber (1997)]
	p24	267–277	LAI	GLNKIVRMY	[Johnson (1991)], P. Goulder pers. comm.*
	RT	415–426	III B	LVGKLNWASQIY	P. Johnson pers. comm.
	RT	476–485	LAI	ILKEPVHGVY	[Johnson (1991)], and P. Johnson pers. comm.
	nef	117–127	LAI	TQGYFPDWQNY	B. Culmann pers. comm.
B*1516 (B63)				2 9 **T Y** **S I** **V** **F**	[Barber (1997), Seeger (1998)]
	gp120	379–387	LAI	SFNCGGEFF	[Wilson (1997)], and C. Wilson pers. comm.
B*1801 (B18)					
	p24	293–302	HIV-1 clade B/D	FRDYVDRFYK	[Ogg (1998)]
	nef	135–143	LAI	YPLTFGWCY	[Culmann (1991), Culmann-Penciolelli (1994)]
B*2703 (B27)					
	p24	260–269	HIV-2	RRWIQLGLQK	[Rowland-Jones (1998)], and S. Rowland-Jones, pers. comm.

Table 1 (cont.) Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
B*2705 (B27)				12 C **R** **L** **F** K K R R G I A	[Jardetzky (1991), Rammensee (1995)]
	p17	19–27	LAI	IRLRPGGKK	[McKinney (1999)], and D. Lewinsohn pers. comm.
	p24	265–274	LAI	KRWIILGLNK	[Nixon (1988), Buseyne (1993), Goulder (1997c)]
	gp41	791–799	LAI	GRRGWEALKY	[Lieberman (1992)], and J. Lieberman pers. comm.
	nef	105–114	LAI	RRQDILDLWI	[Goulder (1997a)]
B*3501 (B35)				2 C **P** **Y** A F V M S L I	[Hill (1992), Rammensee (1999)]
	p17	36–44	LAI	WASRELERF	[Goulder (1997b)]
	p17	124–132	JH31	NSSKVSQNY	[Rowland-Jones (1995)]
	p24	245–253	HIV-2	NPVPVGNIY	[Rowland-Jones (1995)]
	p24	254–262	U455	PPIPVGDIY	[Rowland-Jones (1995)]
	RT	262–270	LAI	TVLDVGDAY	B. Wilkes, D. Ruhl pers. comm.*
	RT	273–282	III B	VPLDEDFRKY	[Sipsas (1997), Shiga (1996)]
	RT	328–336	III B	NPDIVIYQY	[Sipsas (1997), Shiga (1996)]
	RT	342–350	LAI	HPDIVIYQY	[Rowland-Jones (1995)]
	gp120	42–52	LAI	VPVWKEATTTL	B. Wilkes, D. Ruhl pers. comm.*
	gp120	77–85	LAI	DPNPQEVVL	[Shiga (1996)]
	gp41	611–619	LAI	TAVPWNASW	[Johnson (1994)]
	nef	74–81	LAI	VPLRPMTY	[Culmann (1991), Culmann-Penciolelli (1994)]

Table 1 (cont.) Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
B*3701 (B37)				2 C **D F** **E M** **L** **I**	[Falk (1993)]
	nef	120–128	LAI	YFPDWQNYT	[Culmann (1991)], and B. Culmann, pers. comm.
B*3901 (B39)				2 C **R L** **H**	[Falk (1995a)]
	p24	193–201	LAI	GHQAAMQML	I. Kurane, K. West, pers. comm.
B*4001 (B60)				2 C **E L**	[Falk (1995b)]
	p17	92–101	LAI	IEIKDTKEAL	A. Trocha and S. Kalams pers. comm.*
	p24	176–184	LAI	SEGATPQDL	A. Trocha and S. Kalams pers. comm.*
	RT	369–377	LAI	IEELRQHLL	P. Goulder, M. Altfeld, pers. comm.*
	gp41	810–819	LAI	QELKNSAVSL	P. Goulder, M. Altfeld, pers. comm.*
	nef	92–101	LAI	KEKGGLEGL	P. Goulder, M. Altfeld, pers. comm.*
B*4201 (B42)					
	p24	179–187	LAI	TPQDLNTML	P. Goulder et al, submitted
	RT	438–446	LAI	YPGIKVRQL	B. Wilkes, D. Ruhl, pers. comm.*
	nef	128–137	LAI	TPGPGVRYPL	P. Goulder, pers. comm.*
B*4402 (B44)				2 C **E F** **Y**	[Rammensee (1999)]
	p24	294–304	HIV-1 clade B	RDYVDRFYKTL	[Ogg (1998)]
	p24	306–316	SF2	AEQASQDVKNW	D. Lewinsohn pers. comm.
	gp120	30–38	SF33	AENLWVTVY	[Borrow (1997)]

Table 1 (cont.) Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
B*5101 (B51)					
				2 C	[Falk (1995a)]
				A F	
				P I	
				G	
	RT	42–50	LAI	EKEGKISKI	[Haas (1998)], and G. Haas pers. comm.
	RT	295–302	III B	TAFTIPSI	[Sipsas (1997)]
	gp41	557–565	III B	RAIEAQQHL	[Sipsas (1997)]
B*5201 (B52)					
				2 C	[Rammensee (1999)]
				I	
				V	
				Q	
	p24	275–282	LAI	RMYSPTSI	B. Wilkes, D. Ruhl, pers. comm.*
B*5301 (B53)				2 C	
				P L	[Hill (1992)]
	HIV-2 gag	173–181	HIV-2	TPYDINQML	[Gotch (1993)]
	p24	308–316	LAI	QASQEVKNW	[Buseyne (1997)], and F. Buseyne pers. comm.
B*5501 (B55)					
				2 C	[Barber (1995)]
				P	
				A	
	gp120	42–51	LAI	VPVWKEATTT	[Shankar (1996)], and J. Lieberman pers. comm.

Table 1 (cont.) Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
B*5701 (B57)				12 C **A F** **T W** **S** K Y	[Barber (1997)]
	p24	147–155	III B	ISPRTLNAW	[Johnson (1991), Goulder (1996b)]
	p24	162–172	LAI	KAFSPEVIPMF	[Goulder (1996b)]
	p24	240–249	LAI	TSTLQEQIGW	[Goulder (1996b)]
	p24	311–319	LAI	QASQEVKNW	[Goulder (1996b)]
	Pol	888–896	LAI	KTAVQMAVF†	C. Hay pers. comm.
	RT	399–407	LAI	IVLPEKDSW†	[van der Burg (1997)],C. Hay pers. comm.
	nef	116–125	LAI	HTQGYFPDWQ†	[Culmann (1991)]
	nef	120–128	LAI	YFPDWQNYT†	[Culmann (1991)]
B*5703 (B57)					
	p24	162–172	LAI	KAFSPEVIPMF	Goulder et al, submitted
	p24	162–169	LAI	KAFSPEVI	Goulder et al, submitted
B*5801 (B58)				12 C **A F** **T W** **S** K V I	[Barber (1997), Falk (1995b)]
	p24	240–249	LAI	TSTLQEQIGW	[Goulder (1996b)]
	p24	241–250	LAI	TSTVEEQIQW	[Bertoletti (1998)]
B*8101 (B81)					
	p24	179–187	LAI	TPQDLNTML	P. Goulder et al, submitted

Table 1 (cont.) Best Defined HIV CTL Epitopes

HLA	Protein	AA	Isolate	Sequence	Reference
C*0102 (Cw1)				23 C **A** **L** **L** P	[Barber (1997)]
	p24	168–175	LAI	VIPMFSAL	[Goulder (1997b)]
C*0401 (Cw4)				2 6 C **Y** **L** **P** **F** **F** **M** V I L	[Falk (1994)]
	gp120	379–387	LAI	SFNCGGEFF	[Johnson (1993)], Wilson 97
C*0802 (Cw8)					
	p24	180–188	LAI	TPQDLNTML	[Goulder (2000a)]
	p24	183–191	LAI	DLNTMLNTV	P. Goulder pers. comm.*
	nef	82–91	LAI	KAAVDLSHFL	[Nixon (1999)]

* indicates personal communications in which truncation/titration data was provided

† subtype of B57 not determined

Primary anchors are bold faced, secondary anchors are not.

The amino acid position numbers were assigned by the authors, and are not always compatible with the HXB2R numbering system used in other parts of this database.

REFERENCES

[Alexander-Miller (1996)] M. A. Alexander-Miller, K. C. Parker, T. Tsukui, C. D. Pendleton, J. E. Coligan, & J. A. Berzofsky. Molecular analysis of presentation by HLA-A2.1 of a promiscuously binding V3 loop peptide from the HIV-1 Envelope protein to human cytotoxic T lymphocytes. *Int Immunol* **8**:641–649, 1996.

[Barber (1995)] L. D. Barber, B. Gillece-Castro, L. Percival, X. Li, C. Clayberger, & P. Parham. Overlap in the repertoires of peptides bound in vivo by a group of related class I HLA-B allotypes. *Curr Biol* **5**:179–90, 1995.

[Barber (1997)] L. D. Barber, L. Percival, K. L. Arnett, J. E. Gumperz, L. Chen, & P. Parham. Polymorphism in the α1 Helix of the HLA-B Heavy Chain Can Have an Overriding Influence on Peptide-Binding Specificity. *J Immunol* **158**:1660–1669, 1997.

[Barouch (1995)] D. Barouch, T. Friede, S. Stevanovic, L. Tussey, K. Smith, S. Rowland-Jones, V. Braud, A. McMichael, & H. G. Rammensee. HLA-A2 subtypes are functionally distinct in peptide binding and presentation. *J Exp Med* **182**:1847–56, 1995.

[Bauer (1997)] M. Bauer, M. Lucchiari-Hartz, R. Maier, G. Haas, B. Autran, K. Eichmann, R. Frank, B. Maier, & A. Meyerhans. Structural constraints of HIV-1 Nef may curtail escape from HLA-B7-restricted CTL recognition. *Immunol Lett* **55**:119–22, 1997.

[Bertoletti (1998)] A. Bertoletti, F. Cham, S. McAdam, T. Rostron, S. Rowland-Jones, S. Sabally, T. Corrah, K. Ariyoshi, & H. Whittle. Cytotoxic T cells from human immunodeficiency virus type 2-infected patients frequently cross-react with different human immunodeficiency virus type 1 Clades. *J Virol* **72**:2439–2448, 1998.

[Borrow (1997)] P. Borrow, H. Lewicki, X. Wei, M. S. Horwitz, N. Peffer, H. Meyers, J. A. Nelson, J. E. Gairin, B. H. Hahn, M. B. Oldstone, & G. M. Shaw. Anti-viral pressure exerted by HIV-1-specific cytotoxic T lymphocytes (CTLs) during primary infection demonstrated by rapid selection of CTL escape virus. *Nat Med* **3**:205–11, 1997.

[Brander & Walker(1999)] C. Brander & B. D. Walker. T lymphocyte responses in HIV-1 infection: implications for vaccine development. *Curr Opin Immunol* **11**:451–9, 1999.

[Buseyne (1993)] F. Buseyne, M. McChesney, F. Porrot, S. Kovarik, B. Guy, & Y. Riviere. Gag-specific cytotoxic T lymphocytes from human immunodeficiency virus type 1 infected individuals: gag epitopes are clustered in three regions of the p24 gag protein. *J Virol* **67**:694–702, 1993.

[Buseyne (1997)] F. Buseyne, S. Stevanovic, H. Rammensee, & Y. Riviere. Characterization of an HIV-1 p24 gag epitope recognized by a CD8+ cytotoxic T-cell clone. *Immunol Lett* **55(3)**:145–149, 1997.

[Carrington (1999)] M. Carrington, G. W. Nelson, M. P. Martin, T. Kissner, D. Vlahov, J. J. Goedert, R. Kaslow, S. Buchbinder, K. Hoots, & S. J. O'Brien. HLA and HIV-1: heterozygote advantage and B*35-Cw*04 disadvantage [see comments]. *Science* **283**:1748–52, 1999.

[Culmann (1991)] B. Culmann, E. Gomard, M.-P. Kieny, B. Guy, F. Dreyfus, A.-D. Saimot, D. Sereni, D. Sicard, & J.-P. Levy. Six epitopes with human cytotoxic CD8+ cells in the central region of the HIV-1 Nef protein. *J Immunol* **146**:1560–1565, 1991.

[Culmann-Penciolelli (1994)] B. Culmann-Penciolelli, S. Lamhamedi-Cherradi, I. Couillin, N. Guegan, J. P. Levy, J. G. Guillet, & E. Gomard. Identification of multirestricted immunodominant regions recognized by cytolytic T lymphocytes in the human immunodeficiency virus type 1 Nef protein (See comments in J Virol 1995 Jan;69(1):618). *J Virol* **68**:7336–43, 1994.

[Dai (1992)] L. C. Dai, K. West, R. Littaua, K. Takahashi, & F. A. Ennis. Mutation of human immunodeficiency virus type 1 at amino acid 585 on gp41 results in loss of killing by CD8+ A24-restricted cytotoxic T lymphocytes. *J Virol* **66**:3151–3154, 1992.

[DiBrino (1993)] M. DiBrino, K. C. Parker, & J. S. et al. Endogenous peptides bound to HLA-A3 possess a specific combination of anchor residues that permit identification of potential antigenic peptides. *Proc Natl Acad Sci USA* **90**:1508–1512, 1993.

[DiBrino (1994a)] M. DiBrino, K. C. Parker, D. H. Margulies, J. Shiloach, R. V. Turner, M. Garfield, W. E. Biddison WE, & J. E. Coligan. The HLA-B14 peptide binding site can accommodate peptides with different combinations of anchor residues. *J Biol Chem* **269**, 1994a.

[DiBrino (1994b)] M. DiBrino, K. C. Parker, J. Shiloach, R. V. Turner, T. Tsuchida, M. Garfield, W. E. Biddison, & J. E. Coligan. Endogenous peptides with distinct amino acid anchor residue motifs bind to HLA-A1 and HLA-B8. *J Immunol* **152**:620–31, 1994b.

[Dorrell (1999)] L. Dorrell, T. Dong, G. S. Ogg, S. Lister, S. McAdam, T. Rostron, C. Conlon, A. J. McMichael, & S. L. Rowland-Jones. Distinct recognition of non-clade B human immunodeficiency virus type 1 epitopes by cytotoxic T lymphocytes generated from donors infected in Africa. *J Virol* **73**:1708–14, 1999.

[Dumrese (1998)] T. Dumrese, S. Stevanovic, F. H. Seeger, N. Yamada, Y. Ishikawa, K. Tokunaga, M. Takiguchi, & H. Rammensee. HLA-A26 subtype A pockets accommodate acidic N-termini of ligands. *Immunogenetics* **48**:350–3, 1998.

[Dupuis (1995)] M. Dupuis, S. K. Kundu, & T. C. Merigan. Characterization of HLA-A*0201-restricted cytotoxic T-cell epitopes in conserved regions of the HIV type 1 gp160 protein. *J Immunol* **155**:2232–2239, 1995.

[Englehard (1993)] V. H. Englehard, E. L. Huczko, & W. Bodner et al. Peptides bound to HLA-B7 determined by mass spectrometry. *J Cell Biochem Suppl 1993* **17C**:56, 1993.

[Falk (1991)] K. Falk, O. Rotzschke, S. Stevanovic, G. Jung, & H.-G. Rammensee. Allele-specific motifs revealed by sequencing of self-peptides eluted from MHC molecules. *Nature* **351**:290–296, 1991.

[Falk (1993)] K. Falk, O. Rotzschke, B. Grahovac, D. Schendel, S. Stevanovic, G. Jung, & H. G. Rammensee. Peptide motifs of HLA-B35 and -B37 molecules [published erratum appears in Immunogenetics 1994;39(5):379]. *Immunogenetics* **38**:161–2, 1993.

[Falk (1994)] K. Falk, O. Rotzschke, & B. Grahavac. Allele-specific peptide motifs of HLA-C molecules. *Proc Natl Acad Sci USA* **90**:12005–12009, 1994.

[Falk (1995a)] K. Falk, O. Rotzschke, M. Takiguchi, V. Gnau, S. Stevanovic, G. Jung, & H. Rammensee. Peptide motifs of HLA-B38 and B39 molecules. *Immunogenetics* **41**:162–164, 1995a.

[Falk (1995b)] K. Falk, O. Rotzschke, M. Takiguchi, V. Gnau, S. Stevanovic, G. Jung, & H. Rammensee. Peptide motifs of HLA-B58, B60, B61, and B62 molecules. *Immunogenetics* **41**:165–168, 1995b.

[Gotch (1993)] F. Gotch, S. N. McAdam, & C. E. Allsopp et al. Cytotoxic T-cells in HIV-2 seropositive Gambians. Identification of a virus specific MHC-restricted peptide epitope. *J Immunol* **151**:3361–3369, 1993.

[Goulder (1996a)] P. Goulder, C. Conlon, K. McIntyre, & A. McMichael. Identification of a novel human leukogen antigen A26-restricted epitope in a conserved region of Gag. *AIDS* **10(12)**:1441–1443, 1996a.

[Goulder (1996b)] P. J. R. Goulder, M. Bunce, P. Krausa, K. McIntyre, S. Crowley, B. Morgan, A. Edwards, P. Giangrande, R. E. Phillips, & A. J. McMichael. Novel, cross-restricted, conserved and immunodominant cytotoxic T lymphocyte epitopes in slow HIV Type 1 infection. *AIDS Res and Hum Retroviruses* **12**:1691–1698, 1996b.

[Goulder (1997a)] P. Goulder, A. Sewell, D. Lalloo, D. Price, J. Whelan, J. Evans, G. Taylor, G. Luzzi, P. Giangrande, R. Phillips, & A. J. McMichael. Patterns of immunodominance in HIV-1-specific cytotoxic T lymphocyte responses in two human histocompatibility leukocyte antigens (HLA)-identical siblings with HLA-A*0201 are influenced by epitope mutation. *J Exp Med* **8**:1423–33, 1997a.

[Goulder (1997b)] P. J. Goulder, M. Bunce, G. Luzzi, R. E. Phillips, & A. J. McMichael. Potential underestimation of HLA-C-restricted cytotoxic T-lymphocyte responses. *AIDS* **11(15)**:1884–1886, 1997b.

[Goulder (1997c)] P. J. R. Goulder, R. E. Phillips, R. A. Colbert, S. McAdam, G. Ogg, M. A. Nowak, P. Giangrande, G. Luzzi, B. Morgan, A. Edwards, A. McMichael, & S. Rowland-Jones. Late Escape from an immunodominant cytotoxic T-lymphocyte response associated with progression to AIDS. *Nature Med* **3**:212–216, 1997c.

[Goulder (1997d)] P. J. R. Goulder, S. W. Reid, D. A. Price, C. A. O'Callaghan, A. J. McMichael, R. E. Phillips, & E. Y. Jones. Combined structural and immunological refinement of HIV-1 HLA-B8 restricted cytotoxic T lymphocyte epitopes. *Eur J Immunol* **27**:1515–1521, 1997d.

[Goulder (2000a)] P. J. R. Goulder, C. Brander, K. Annamalai, N. Mngqundaniso, U. Govender, Y. Tang, S. He, K. E. Hartman, C. A. O'Callaghan, G. S. Ogg, M. A. Altfeld, E. S. Rosenberg, H. Cao, S. A. Kalams, M. Hammond, M. Bunce, S. I. Pelton, S. A. Burchett, K. McIntosh, H. M. Coovadia, & B. D. Walker. Differential narrow focusing of immunodominant HIV gag-specific CTL responses in infected African and Caucasoid adults and children. *submitted* 2000a.

[Goulder (2000b)] P. J. R. Goulder, Y. Tang, C. Brander, M. R. Betts, A. Trocha, S. He, E. S. Rosenberg, C. A. O. Graham Ogg, S. A. Kalams, R. E. McKinney, K. Mayer, R. A. Koup, S. I. Pelton, S. K. Burchett, K. McIntosh, & B. D.

Walker. Functionally inert HIV-specific cytotoxic T lymphocytes do not play a major role in chronically infected adults and children. *submitted* 2000b.

[Goulder (2000c)] P. J. R. Goulder, Y. Tang, S. I. Pelton, & B. D. Walker. HLA-B57-restricted CTL activity in a single infected subject towards two optimal HIV epitopes, one of which is entirely contained within the other. *J Virol* 2000c.

[Haas (1996)] G. Haas, U. Plikat, P. Debre, M. Lucchiari, C. Katlama, Y. Dudoit, O. Bonduelle, M. Bauer, H. Ihlenfeldt, G. Jung, B. Maier, A. Meyerhans, & B. Autran. Dynamics of viral variants in HIV-1 Nef and specific cytotoxic T lymphocytes in vivo. *J Immunol* **157**:4212–4221, 1996.

[Haas (1998)] G. Haas, A. Samri, E. Gomard, A. Hosmalin, J. Duntze, J. M. Bouley, H. G. Ihlenfeldt, C. Katlama, & B. Autran. Cytotoxic T-cell responses to HIV-1 reverse transcriptase, integrase and protease. *AIDS* **12(12)**:1427–36, 1998.

[Harrer (1996a)] E. Harrer, T. Harrer, P. Barbosa, M. Feinberg, R. P. Johnson, S. Buchbinder, & B. D. Walker. Recognition of the highly conserved YMDD region in the human immunodeficiency virus type 1 reverse transcriptase by HLA-A2-restricted cytotoxic T lymphocytes from an asymptomatic long-term nonprogresser. *J Inf Dis* **173**:476–479, 1996a.

[Harrer (1996b)] T. Harrer, E. Harrer, S. A. Kalams, P. Barbosa, A. Trocha, R. P. Johnson, T. Elbeik, M. B. Feinberg, S. P. Buchbinder, & B. D. Walker. Cytotoxic T lymphocytes in asymptomatic long-term nonprogressing HIV-1 infection. Breadth and specificity of the response and relation to in vivo viral quasispecies in a person with prolonged infection and low viral load. *J Immunol* **156**:2616–2623, 1996b.

[Harrer (1998)] T. Harrer, E. Harrer, P. Barbosa, F. Kaufmann, R. Wagner, S. Bruggemann, J. R. Kalden, M. Feinberg, R. P. Johnson, S. Buchbinder, & B. D. Walker. Recognition of two overlapping CTL epitopes in HIV-1 p17 by CTL from a long-term nonprogressing HIV-1-infected individual. *J Immunol* **161**:4875–81, 1998.

[Hill (1992)] A. V. Hill, J. Elvin, A. C. Willis, M. Aidoo, C. E. Allsopp, F. M. Gotch, X. M. Gao, M. Takiguchi, B. M. Greenwood, & A. R. Townsend et al. Molecular analysis of the association of HLA-B53 and resistance to severe malaria (see comments). *Nature* **360**:434–9, 1992.

[Ikeda-Moore (1998)] Y. Ikeda-Moore, H. Tomiyama, M. Ibe, S. Oka, K. Miwa, Y. Kaneko, & M. Takiguchi. Identification of a novel HLA-A24-restricted cytotoxic T-lymphocyte epitope derived from HIV-1 Gag protein. *AIDS* **12**:2073–4, 1998.

[Jardetzky (1991)] T. S. Jardetzky, W. S. Lane, R. A. Robinson, D. R. Madden, & D. C. Wiley. Identification of self peptides bound to purified HLA-B27. *Nature* **353**:326–9, 1991.

[Johnson (1991)] R. P. Johnson, A. Trocha, L. Yang, G. P. Mazzara, D. L. Panicali, T. M. Buchanan, & B. D. Walker. HIV-1 gag-specific cytotoxic T lymphocytes recognize multiple highly conserved epitopes. Fine specificity of the gag-specific response defined by using unstimulated peripheral blood mononuclear cells and cloned effector cells. *J Immunol* **147**:1512–1521, 1991.

[Johnson (1992)] R. P. Johnson, A. Trocha, T. M. Buchanan, & B. D. Walker. Identification of overlapping HLA class I-restricted cytotoxic T-cell epitopes in a conserved region of the human immunodeficiency virus type 1 envelope glycoprotein: definition of minimum epitopes and analysis of the effects of sequence variation. *J Exp Med* **175**:961–971, 1992.

[Johnson (1993)] R. P. Johnson, A. Trocha, T. M. Buchanan, & B. D. Walker. Recognition of a highly conserved region of human immunodeficiency virus type 1 gp120 by an HLA-Cw4-restricted cytotoxic T-lymphocyte clone. *J Virol* **67**:438–445, 1993.

[Johnson (1994)] R. P. Johnson, S. A. Hammond, A. Trocha, R. F. Siliciano, & B. D. Walker. Induction of a major histocompatibility complex class I-restricted cytotoxic T-lymphocyte response to a highly conserved region of human immunodeficiency virus type 1 (HIV-1) gp120 in seronegative humans immunized with a candidate HIV-1 vaccine. *J Virol* **68**:3145–3153, 1994.

[Johnson & Walker(1994)] R. P. Johnson & B. D. Walker. CTL in HIV-1 infection: Responses to structural proteins. *Curr Topics Microbiol Immunol* **189**:35–63, 1994.

[Klenerman (1996)] P. Klenerman, G. Luzzi, K. McIntyre, R. Phillips, & A. McMichael. Identification of a novel HLA-A25 restricted epitope in a conserved region of p24 gag (positions 71-80). *AIDS* **10**:348–350, 1996.

[Koenig (1990)] S. Koenig, T. R. Fuerst, L. V. Wood, R. M. Woods, J. A. Suzich, G. M. Jones, V. F. de la Cruz, R. T. D. Jr., S. Venkatesan, B. Moss, W. E. Biddison, & A. S. Fauci. Mapping the fine specificity of a cytotoxic T-cell response to HIV-1 Nef protein. *J Immunol* **145**:127–135, 1990.

[Lieberman (1992)] J. Lieberman, J. A. Fabry, M.-C. Kuo, P. Earl, B. Moss, & P. R. Skolnik. Cytotoxic T lymphocytes from HIV-1 seropositive individuals recognize immunodominant epitopes in gp160 and reverse transcriptase. *J Immunol* **148**:2738–2747, 1992.

[Maier (1994)] R. Maier, K. Falk, O. Rotzschke, B. Maier, V. Gnau, S. Stevanovic, G. Jung, H. G. Rammensee, & A. Meyerhans. Peptide motifs of HLA-A3, -A24, and -B7 molecules as determined by pool sequencing. *Immunogenetics* **40**:306–8, 1994.

[McKinney (1999)] D. McKinney, D. Lewinson, S. Riddell, P. Greenberg, & D. Mosier. The Antiviral Activity of HIV-Specific CD8+ CTL clones is limited by elimination due to encounter with HIV-infected targets. *J. Immuno* **163**:861–7, 1999.

[McMichael & O'Callaghan(1998)] A. J. McMichael & C. A. O'Callaghan. A New Look at T Cells. *J Exp Med* **187(9)**:1367–1371, 1998.

[Nixon (1988)] D. Nixon, A. Townsend, J. Elvin, C. Rizza, J. Gallway, & A. McMichael. HIV-1 gag-specific cytotoxic T lymphocytes defined with recombinant vaccinia virus and synthetic peptides. *Nature* **336**:484–487, 1988.

[Nixon (1999)] D. F. Nixon, D. Douek, P. J. Kuebler, X. Jin, M. Vesanen, S. Bonhoeffer, Y. Cao, R. A. Koup, D. D. Ho, & M. Markowitz. Molecular tracking of an Human Immunodeficiency Virus nef specific cytotoxic T-cell clone shows persistence of clone-specific T-cell receptor DNA but not mRNA following early combination antiretroviral therapy. *Immunol Lett* **66**:219–28, 1999.

[Ogg (1998)] G. S. Ogg, X. Jin, S. Bonhoeffer, P. R. Dunbar, M. A. Nowak, S. Monard, J. P. Segal, Y. Cao, S. L. Rowland-Jones, V. Cerundolo, A. Hurley, M. Markowitz, D. D. Ho, D. F. Nixon, & A. J. McMichael. Quantitation of HIV-1-specific cytotoxic T lymphocytes and plasma load of viral RNA. *Science* **279**:2103–6, 1998.

[Ogg (1999)] G. S. Ogg, X. Jin, S. Bonhoeffer, P. Moss, M. A. Nowak, S. Monard, J. P. Segal, Y. Cao, S. L. Rowland-Jones, A. Hurley, M. Markowitz, D. D. Ho, A. J. McMichael, & D. F. Nixon. Decay kinetics of human immunodeficiency virus-specific effector cytotoxic T lymphocytes after combination antiretroviral therapy. *J Virol* **73**:797–800, 1999.

[Parker (1992)] K. C. Parker, M. A. Bednarek, L. K. Hull, U. Utz, B. C. H. J. Zweerink, W. E. Biddison, & J. E. Coligan. Sequence motifs important for peptide binding to the human MHC class I molecule, HLA-A2. *J Immunol* **149**, 1992.

[Parker (1994)] K. C. Parker, M. A. Bednarek, & J. E. Coligan. Scheme for ranking potential HLA-A2 binding peptides based on independent binding of individual peptide side-chains. *J Immunol* **152**, 1994.

[Price (1997)] D. A. Price, P. J. Goulder, P. Klenerman, A. K. Sewell, P. J. Easterbrook, M. Troop, C. R. Bangham, & R. E. Phillips. Positive selection of HIV-1 cytotoxic T lymphocyte escape variants during primary infection. *Proc Natl Acad Sci USA* **94**:1890–5, 1997.

[Rammensee (1995)] H.-G. Rammensee, T. Friede, & S. Stevanovic. MHC ligands and peptide motifs: first listing. *Immunogenetics* **41**:178–228, 1995.

[Rammensee (1999)] H. Rammensee, J. Bachmann, N. Emmerich, & S. Stevanovic. SYFPEITHI: An Internet Database for MHC Ligands and Peptide Motifs. 1999.

[Rowland-Jones (1993)] S. L. Rowland-Jones, S. H. Powis, J. Sutton, I. Mockridge, F. M. Gotch, N. Murray, A. B. Hill, W. M. Rosenberg, J. Trowsdale, & A. J. McMichael. An antigen processing polymorphism revealed by HLA-B8-restricted cytotoxic T lymphocytes which does not correlate with TAP gene polymorphism. *Eur J Immunol* **23**:1999–2004, 1993.

[Rowland-Jones (1995)] S. L. Rowland-Jones, J. Sutton, K. Ariyoshi, T. Dong and , F. Gotch, S. McAdam, D. Whitby, S. Sabally, A. Gallimore, T. Corrah, M. Takiguchi, T. Schultz, A. McMichael, & H. Whittle. HIV-specific cytotoxic T-cells in HIV-exposed but uninfected Gambian women. *Nature Medicine* **1**:59–64, 1995.

[Rowland-Jones (1998)] S. L. Rowland-Jones, T. Dong, K. R. Fowke, J. Kimani, P. Krausa, H. Newell, T. Blanchard, K. Ariyoshi, J. Oyugi, E. Ngugi, J. Bwayo, K. S. MacDonald, A. J. McMichael, & F. A. Plummer. Cytotoxic T cell responses to multiple conserved HIV epitopes in HIV- resistant prostitutes in Nairobi [see comments]. *J Clin Invest* **102**:1758–65, 1998.

[Safrit (1994a)] J. T. Safrit, C. A. Andrews, T. Zhu, D. D. Ho, & R. A. Koup. Characterization of human immunodeficiency virus type 1-specific cytotoxic T lymphocyte clones isolated during acute seroconversion: recognition of autologous virus sequences within a conserved immunodominant epitope. *J Exp Med* **179**:463–472, 1994a.

[Safrit (1994b)] J. T. Safrit, A. Y. Lee, C. A. Andrews, & R. A. Koup. A region of the Third Variable Loop of HIV-1 gp120 is recognized by HLA-

B7-Restricted CTLs from two acute seroconversion patients. *J Immunol* **153**:3822–3830, 1994b.

[Schmitz (1999)] J. E. Schmitz, M. J. Kuroda, S. Santra, V. G. Sasseville, M. A. Simon, M. A. Lifton, P. Racz, K. Tenner-Racz, M. Dalesandro, B. J. Scallon, J. Ghrayeb, M. A. Forman, D. C. Montefiori, E. P. Rieber, N. L. Letvin, & K. A. Reimann. Control of viremia in simian immunodeficiency virus infection by CD8+ lymphocytes. *Science* **283**:857–60, 1999.

[Seeger (1998)] F. H. Seeger, D. Arnold, T. Dumrese, H. de la Salle, D. Fricker, H. Schild, H. G. Rammensee, & S. Stevanovic. The HLA-B* 1516 motif demonstrates HLA-B-specific P2 pocket characteristics. *Immunogenetics* **48**:156–60, 1998.

[Shankar (1996)] P. Shankar, J. A. Fabry, D. M. Fong, & J. Lieberman. Three regions of HIV-1 gp160 contain clusters of immunodominant CTL epitopes. *Immunol Lett* **52**:23–30, 1996.

[Shiga (1996)] H. Shiga, T. Shioda, H. Tomiyama, Y. Takamiya, S. Oka, S. Kimura, Y. Yamaguchi, T. Gojoubori, H. G. Rammensee, K. Miwa, & M. Takiguchi. Identification of multiple HIV-1 cytotoxic T-cell epitopes presented by human leukocyte antigen B35 molecule. *AIDS* **10**:1075–1083, 1996.

[Sipsas (1997)] N. V. Sipsas, S. A. Kalams, A. Trocha, S. He, W. A. Blattner, B. D. Walker, & R. P. Johnson. Identification of type-specific cytotoxic T lymphocyte responses to homologous viral proteins in laboratory workers accidentally infected with HIV-1. *J Clin Invest* **99**:752–62, 1997.

[Sutton (1993)] J. Sutton, S. Rowland-Jones, W. Rosenberg, D. Nixon, F. Gotch, X.-M. Gao, N. Murray, A. Spoonas, P. Driscoll, M. Smith, A. Willis, & A. McMichael. A sequence pattern for peptides presented to cytotoxic T lymphocytes by HLA B8 revealed by analysis of epitopes and eluted peptides. *Eur J Immunol* **23**:447–453, 1993.

[Takahashi (1991)] K. Takahashi, L.-C. Dai, T. R. Fuerst, W. E. Biddison, P. L. Earl, B. Moss, & F. A. Ennis. Specific lysis of human immunodeficiency virus type 1-infected cells by a HLA-A3.1-restricted CD8+ cytotoxic T-lymphocyte clone that recognizes a conserved peptide sequence within the gp41 subunit of the envelope protein. *Proc Natl Acad Sci USA* **88**:10277–10281, 1991.

[Tang (1999)] J. Tang, C. Costello, I. P. Keet, C. Rivers, S. Leblanc, E. Karita, S. Allen, & R. A. Kaslow. HLA class I homozygosity accelerates disease progression in human. *AIDS Res Hum Retroviruses* **15**:317–24, 1999.

[Threlkeld (1997)] S. C. Threlkeld, P. A. Wentworth, S. A. Kalams, B. M. Wilkes, D. J. Ruhl, E. Kepgh, J. Sidney, S. Southwood, B. D. Walker, & A. Sette. Degenerate and promiscuous recognition by CTL of peptides presented by the MHC class I A3-like superfamily. *J Immunol* **159 (4)**:1648–1657, 1997.

[Tsomides (1991)] T. J. Tsomides, B. D. Walker, & H. N. Eisen. An optimal viral peptide recognized by CD8+ T-cells binds very tightly to the restricting class I major histocompatibility complex protein on intact cells but not to the purified class I protein. *Proc Natl Acad Sci USA* **88**:11276–11280, 1991.

[van Baalen (1996)] C. A. van Baalen, M. R. Klein, R. C. Huisman, M. E. Dings, S. R. Kerkhof Garde, A. M. Geretti, R. Gruters, C. A. van Els, F. Miedema, & A. D. Osterhaus. Fine-specificity of cytotoxic T lymphocytes which recognize conserved epitopes of the Gag protein of human immunodeficiency virus type 1. *J Gen Virol* **77**:1659–1665, 1996.

[van der Burg (1997)] S. H. van der Burg, M. R. Klein, O. Pontesilli, A. M. Holwerda, J. Drijfhout, W. M. Kast, F. Miedema, & C. J. M. Melief. HIV-1 reverse transcriptase-specific CTL against conserved epitopes do not protect against progression to AIDS. *J Immunol* **159**:3648–3654, 1997.

[Walker (1989)] B. D. Walker, C. Flexner, K. Birch-Limberger, L. Fisher, T. J. Paradis, A. Aldovini, R. Young, B. Moss, & R. T. Schooley. Long-term culture and fine specificity of human cytotoxic T-lymphocyte clones reactive with human immunodeficiency virus type 1. *Proc Natl Acad Sci USA* **86**:9514–9518, 1989.

[Wilson (1997)] C. C. Wilson, S. A. Kalams, B. M. Wilkes, D. J. Ruhl, F. Gao, B. H. Hahn, I. C. Hanson, K. Luzuriaga, S. Wolinsky, R. Koup, S. P. Buchbinder, R. P. Johnson, & B. D. Walker. Overlapping epitopes in human immunodeficiency virus type 1 gp120 presented by HLA A, B, and C molecules: effects of viral variation on cytotoxic T-lymphocyte recognition. *J Virol* **71**:1256–64, 1997.

[Wilson (1999)] C. C. Wilson, R. C. Brown, B. T. Korber, B. M. Wilkes, D. J. Ruhl, D. Sakamoto, K. Kunstman, K. Luzuriaga, I. C. Hanson, S. M. Widmayer, A. Wiznia, S. Clapp, A. J. Ammann, R. A. Koup, S. M. Wolinsky, & B. D. Walker. Frequent detection of escape from cytotoxic T-lymphocyte recognition in perinatal human immunodeficiency virus (HIV) type 1 transmission: the ariel project for the prevention of transmission of HIV from mother to infant. *J Virol* **73**:3975–85, 1999.

[Zhang (1993)] Q.-I. Zhang, R. Gavioli, G. Klein, & M. G. Masucci. An HLA-All-specific motif in nonamer peptides derived from viral and cellular proteins. *Proc Natl Acad Sci USA* **90**:2217–2221, 1993.