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Hypothesis

A HLA-DRB supertype chart with potential overlapping peptide binding function

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Abstract
HLA-DRB alleles are class II alleles that are associated with CD4+ T-cell immune response. DRB alleles are polymorphic and currently there are about 622 named in the IMGT/HLA sequence database. Each allele binds short peptides with high sensitivity and specificity. However, it has been suggested that majority of HLA alleles can be covered within few HLA supertypes, where different members of a supertype bind similar peptides showing distinct repertoires. Definition of DRB supertypes using binding data is limited to few (about 29) known alleles (< 5% of all known DRB alleles). Hence, we describe a strategy using structurally defined virtual pockets to group all known DRB alleles with regard to their overlapping peptide binding specificity.

Keywords: HLA, supertype, class II, peptide binding, overlapping function

Background:
Class II human leukocyte antigen molecules (HLA II) are glycoproteins that binds to various antigenic peptides processed by endocytic pathway and present them to CD4+ T cells for immune response [**1**]. The antigen binding groove is made up of 2 domains (α 1 and β 1) from α chain and β chain [**2**]. The amino acid residues lining these domains interact with antigenic peptide residues and form a stable HLA-II p complex which is recognized by the CD4+ T cells. Several autoimmune diseases (good pasture's syndrome, type 1 diabetes etc.) and parasitic diseases (malaria, filariasis etc.) are associated with CD4+ T cells involving HLA II molecules [**3**]. Class II HLA molecules are highly polymorphic and 622 DRB alleles are listed in IMGT/HLA database (release 2.22) [**4**]. The observed sequence polymorphism in class II is a challenge in the design of peptide based vaccines directed against CD4+ T cell associated diseases. An ideal peptide based vaccine is a cocktail of peptides with broad specificity to different ethnic groups. Thus, it is important to identify peptides with overlapping specificity to multiple alleles covering a wide range of ethnic diversity. It has been suggested that majority of alleles can be covered within few HLA supertypes, where different members of a supertype bind similar peptides, yet exhibiting distinct repertoires [**5**].

Sette and colleagues (1998) analysed DRB1*0101, DRB1*0401 and DRB1*0701 using a collection of 384 synthetic peptides with competitive binding assay data (IC50). Peptide binding data for these three alleles and nine other DRB alleles (DRB1*1501, DRB1*0405, DRB1*0802, DRB1*0901, DRB1*1101, DRB1*1201, DRB1*1302, DRB5*0101, DRB4*0101) were used to show overlapping peptide binding repertoires [**6**]. Maillere and colleagues (2002) described a new supertype for HLA DP4 alleles using DPA1*0103/DPB1*0401 (DP401) and DPA1*0103/DPB1*0402 (DP402) binding assay data (considering IC_{50} values for binding affinity) of various peptides derived from allergens, viruses, or tumor antigens [**7**]. Sette and colleagues (2002) showed that HLA-DQA1*0501/B*0201 (DQ2.3) and DQA1*0301/B*0302 (DQ3.2) share large overlapping peptide binding functions (using IC_{50} values for binding affinity) [**8**]. They also showed the cross reactivity of DR restricted epitopes with DQ alleles. Thus, a significant amount of functional overlap is observed using peptide binding assay data between different class II alleles in multiple layers. The number of class II alleles known and defined till is more than 1000. Therefore, it is important to establish theoretical methods to group alleles exhibiting peptide binding functional overlap.

Lund and colleagues (2004) developed specificity weight matrices using Gibbs sampling algorithm to define nine DRB supertypes [**9**]. Flower and Doytchinova (2005) clustered Class II HLA alleles into twelve supertypes (five DR, three DQ and four DP) based on hierarchical (using similarity field generated by CoMSIA) and non hierarchical (k-means) clustering [**10**]. Clustering of MHC peptide-binding repertoires was utilized elsewhere for supertype definition by Reche & Reinherz (2007) **[11].** These results provide frameworks for understanding class II supertypes. The current update for class II alleles is 1000 at IMGT/HLA. Therefore, it is important to develop novel methods to group class II alleles with overlapping peptide binding function. Here, we describe a method based on virtual pockets defined from structural data to group HLA DRB alleles with overlapping peptide binding repertoires. We chose DRB alleles which constituted 62% of the class II HLA alleles known till date for this study.

Methodology:

DRB specific peptides from MHCBN database:
We retrieved 1580 DRB specific immunogenic (CD4+ cytotoxicity) peptides from MHCBN, a database of MHC binders and non-binders [**12**]. We then created a subset data of 1064 DRB specific peptides that are documented to bind DRB alleles defined using sequence based nomenclature. This corresponds to 37 DRB alleles. It should be noted that this subset of DRB specific peptides have both binding specificity and CD4+ cytotoxicity. The remaining 516 DRB specific peptides are documented to bind DRB alleles defined using serological methods without sequence level specificity. Hence, this subset is neglected in further analysis.

DRB supertypes in MHCBN dataset:
The dataset consisting of 1064 DRB specific peptides were further analyzed to identify functional peptide binding overlap between alleles. This exercise identified 145 peptides binding to two or more DRB alleles, thus exhibiting peptide binding functional overlap (**Table 1** in supplementary material). The 145 peptides cover 29 DRB alleles. The grouping of DRB supertypes in MHCBN is illustrated in **Figure 1**.

DRB allele specific sequences from IMGT/HLA database:
We downloaded 622 DRB alleles (62% of known class II alleles) from IMGT/HLA for further analysis.

Peptide binding domain:
The peptide binding groove is formed by two domains each from alpha and beta chains (**Figure 2**). The β1 domain (first 90 residues in the N terminal) from beta chain that constitutes the peptide binding groove is considered for further analysis.

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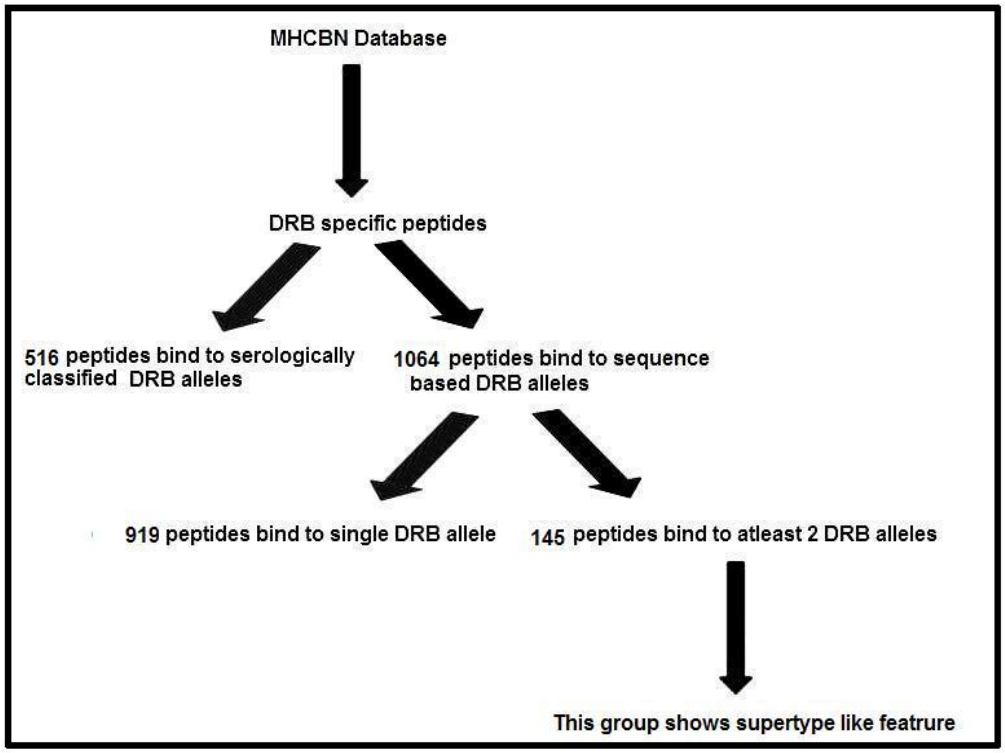

Figure 1: The grouping of DRB supertypes in MHCBN is illustrated.

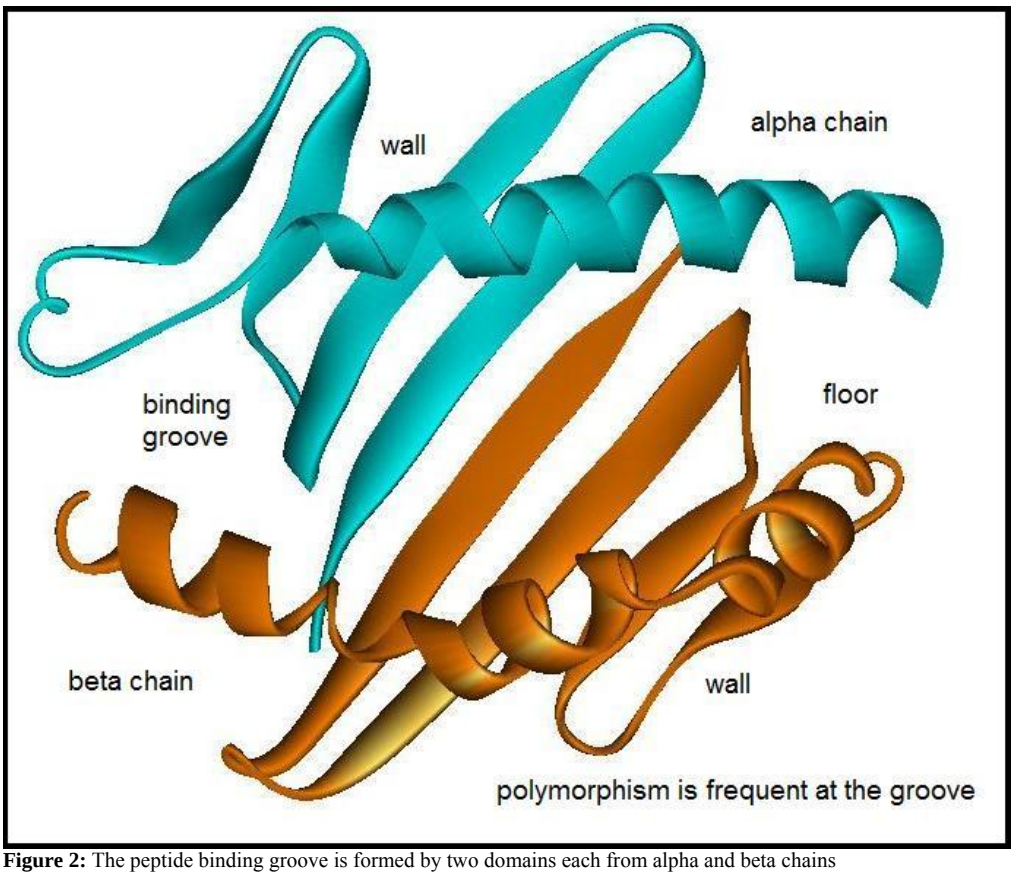

Figure 2: The peptide binding groove is formed by two domains each from alpha and beta chains

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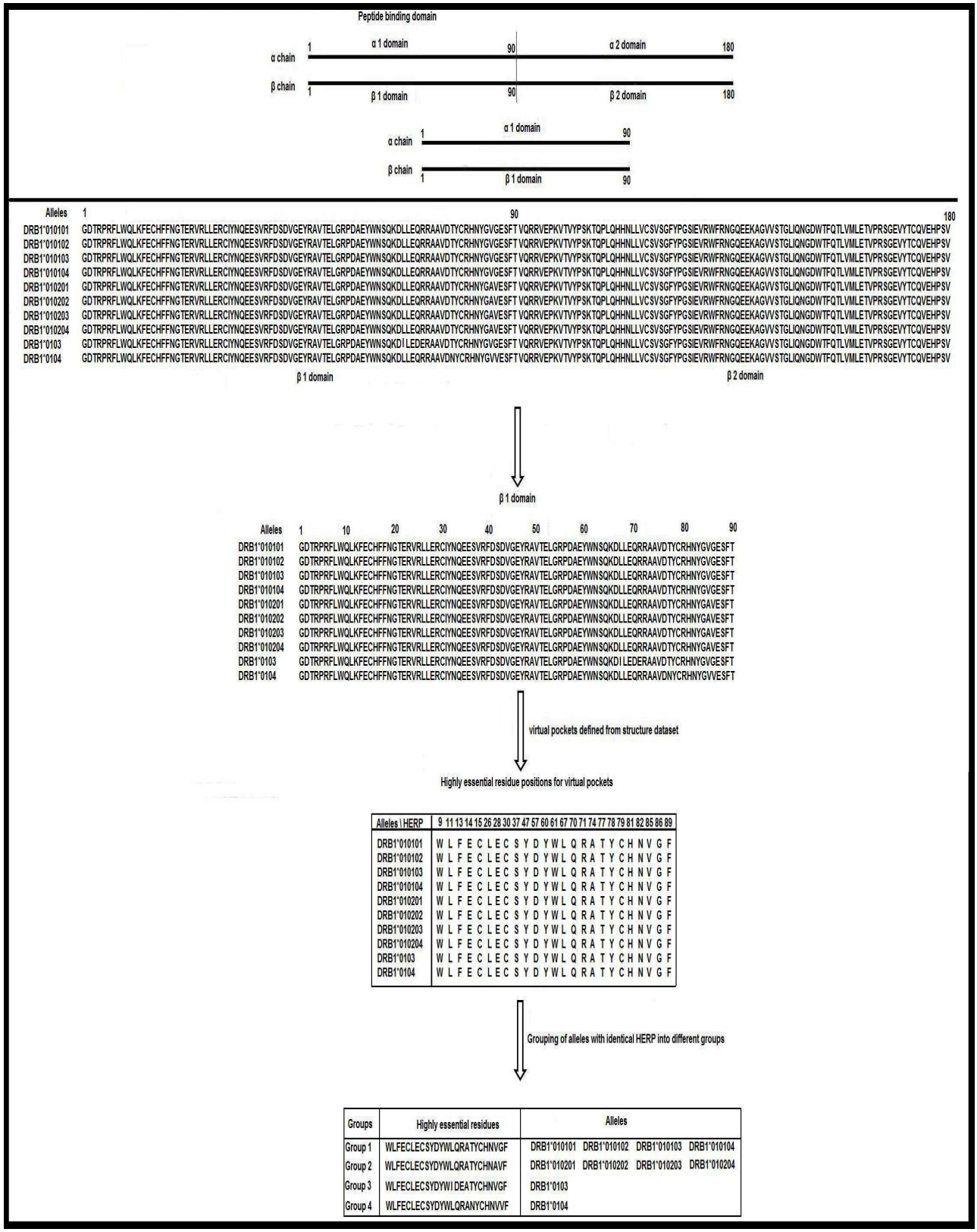

Figure 3: The workflow for the identification of DRB alleles in IMGT/HLA with overlapping function is given.

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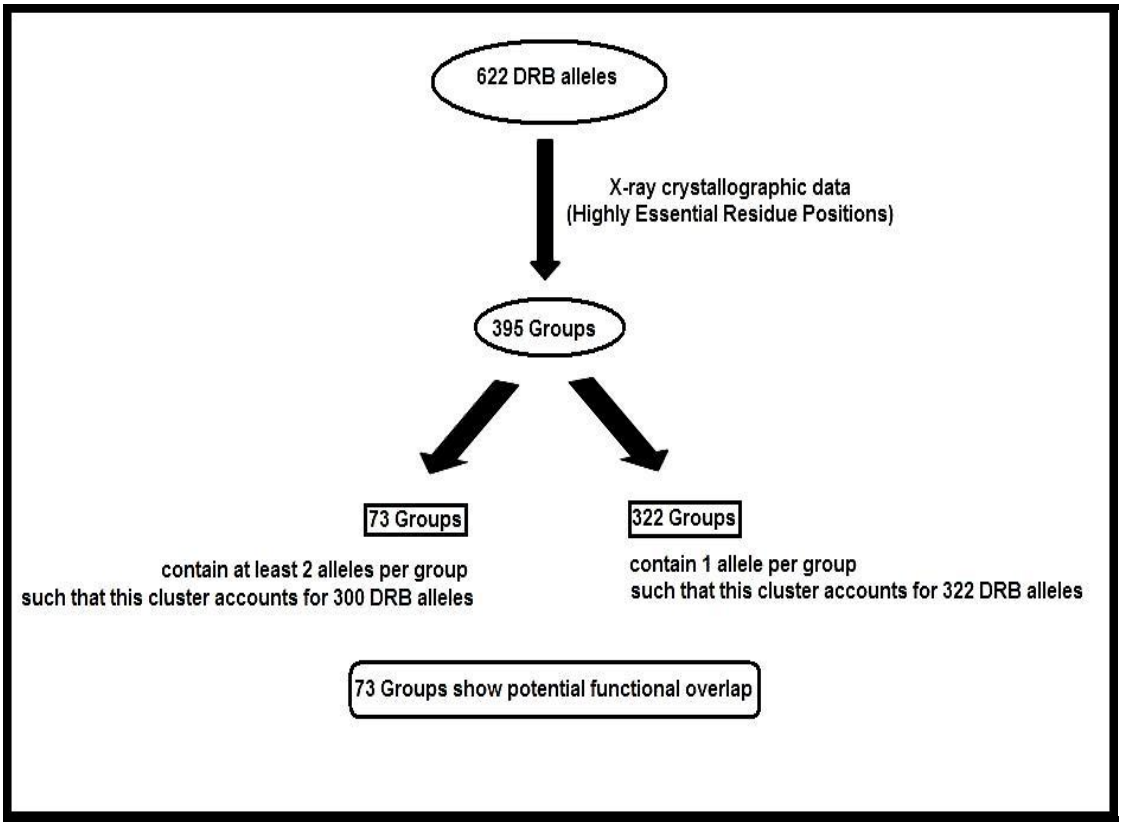

Figure 4: The workflow for the grouping DRB alleles is shown.

Virtual pockets in DRB molecules:
The peptide binds with the DRB molecules through peptide residue position specific interactions with the pockets in the groove. These virtual binding pockets accommodate the side chains of amino acid residues of antigenic peptides. Mohanapriya and colleagues (2009) defined nine virtual pockets using 15 non-redundant class II HLA-peptide crystal structures **[13]**. The HLA amino acid residues lying in these virtual binding pockets show polymorphism which determines the specificity and sensitivity. These residue positions forming the virtual pockets are called highly essential residue positions (HERP) as defined elsewhere by Mohanapriya and colleagues (2009) **[13]**. The number of HERP defined for the beta chain of class II molecules is twenty-five.

Grouping of HLA DRB alleles for overlapping peptide binding:
We extracted the residues corresponding to the 25 HERP in 622 DRB alleles in IMGT/HLA. The sequence stretch formed by the discontinuous HERP in 622 DRB alleles was compared among themselves to cluster those having similar sequence stretch. Thus, we obtained 395 groups by this procedure such that alleles within the same group share the HERP sequence stretch. This procedure generated 73 groups (**Table 2** in supplementary material) containing two or more alleles and 322 groups with only one allele. The hypothesis is that alleles within the group show functional overlap thereby exhibiting potential supertypes. It should be noted that alleles in 322 groups do not share HERP sequence stretch among them. The workflow for the identification of DRB alleles in IMGT/HLA with overlapping function is given in **Figure 3** and the grouping is shown in **Figure 4**.

Validation of grouping for HLA DRB alleles:
Table 3 shows 32 peptides (retrieved from MHCBN) binding to DRB1*1101 and DRB1 *1104 with CD4+ cyto-toxicity. **Table 2** (see supplementary material) shows that these two alleles (DRB1*1101 and DRB1 *1104) fall under the same category. **Table 3** (see supplementary material) also shows 6 peptides (retrieved from MHCBN) binding to DRB1*1301 and DRB1*1302 with CD4+ cyto-toxicity. **Table 2** (see supplementary material) shows that these two alleles (DRB1*1301 and DRB1*1302) fall under the same category. Thus, peptide data in **Table 3** (see supplementary material) validates the theoretical supertype like grouping in **Table 2** (see supplementary material).

Discussion:
HLA-DRB alleles are associated with CD4+ T-cell immune response. DRB alleles are polymorphic (sequence level variation) in the population and about 622 DRB alleles are named in IMGT/HLA sequence database till date. Each of these alleles bind short peptide antigens with high sensitivity and specificity for CD4+ T-cell immune response. However, it has been suggested that majority of alleles can be covered within few HLA supertypes, where different members of a supertype bind similar peptides, yet exhibiting distinct repertoires **[6].** The binding of peptides to HLA alleles is usually assessed using competitive binding assay in IC_{50} values. Thus, supertypes are defined using peptide binding IC_{50} values known for two or more alleles. Sette and colleagues (1998) analysed DRB1*0101, DRB1*0401 and DRB1*0701 using a collection of 384 synthetic peptides with competitive binding assay data (IC_{50}). Peptide binding data for these three alleles and nine other DRB alleles (DRB1*1501, DRB1*0405, DRB1*0802, DRB1*0901, DRB1*1101, DRB1*1201, DRB1*1302, DRB5*0101, DRB4*0101) were used to show overlapping peptide binding repertoires [**6**]. However, this study accounts for just 12 alleles, which is far less than the number of known 622 alleles. Flower and Doytchinova (2005) clustered 347 DRB alleles into five DR supertypes based on hierarchical (using similarity field generated by CoMSIA) and non hierarchical (k-means) clustering [**10**]. We use the

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IC_{50} values known for two or more alleles that are made available at the MHCBN database (database of allele specific binders and non-binders). We extracted 1064 HLA-DRB (sequence based definition) specific peptides from MHCBN. 145 peptides in the dataset are found to bind more than one allele covering 29 alleles. These alleles exhibit supertype like function. This accounts for only 4.6% of known 622 DRB alleles till date. Therefore, it is important to develop framework charts to group defined DRB alleles into potential supertypes with overlapping peptide binding function. Here, we define a methodology for grouping DRB alleles from sequence data using virtual pockets.

The binding groove in DRB molecules is formed by alpha and beta chains (**Figure 2**). It accommodates peptides of length 12-35 **[13].** The peptides bound to the groove have an extended conformation in class II unlike class I. The sequence similarity between defined class II alleles is more than 70% and hence their structural similarity is high (**Figure 5**). The receptor backbone is highly similar and only their side-chain orientations vary. Therefore, the peptide binding specificity is determined by the side chains influenced by polymorphism of the MHC alleles. Mohanapriya and colleagues (2009) defined virtual pockets using HERP extracted from HLA-peptide structural complexes **[13].** The hypothesis is that the 25 residues at the HERP forming the virtual pockets are deterministic of peptide binding and its specificity. The high degree of sequence homology between known DRB alleles and hence their structural similarity suggests the influence of polymorphic residues at the virtual pockets to determine peptide specificity **(Figure 6).** We thus theoretically grouped the known 622 DRB alleles using virtual pockets defined from structural datasets. The grouping (**Figure 4**) using the procedure illustrated in **Figure 3** produced 73 groups consisting of at least 2 alleles covering about 300 alleles. Thus, the 73 groups exhibit overlapping peptide binding function. This grouping is validated using known peptides (32 peptides bind to DRB1*1101 and DRB1 *1104 and 6 peptides bind to DRB1*1301 and DRB1*1302) that are clustered within the same groups in this study. The data presented here serves in general as a framework for understanding peptide binding overlap in particular for HLA-DRB supertype definition and groupings. Each DRB allele contains nine virtual pockets by definition. Thus, the 622 DRB alleles theoretically contain a pool of 5598 virtual pockets made of HERP residues in the dataset. The current analysis shows that the 622 DRB alleles accounts for only 569 unique pockets (**Figure 7**). This constitutes only about 10% of theoretically possible virtual pockets suggesting overlap of virtual pockets among 90% of the remaining pocket combinations. Thus, the study demonstrates the possible degree of overlap within virtual pockets for potential functional overlap among DRB alleles. The described framework finds application in the design of epitopes with cross reactivity across DRB specific ethnic population towards peptide vaccine development.

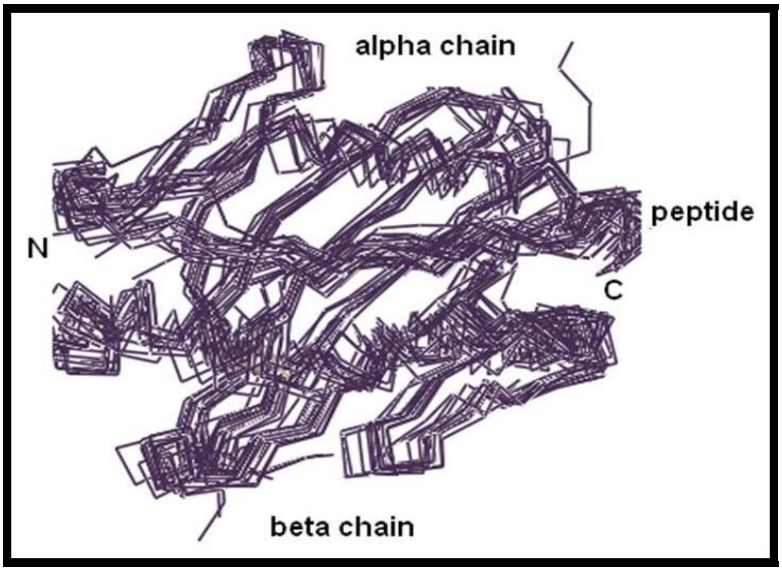

Figure 5: The sequence similarity between defined class II alleles is more than 70% and hence their structural similarity is high.

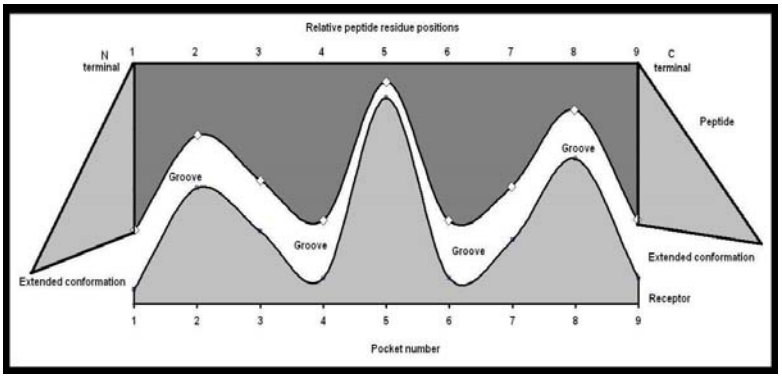

Figure 6: The high degree of sequence homology between known DRB alleles and hence their structural similarity suggests the influence of polymorphic residues at the virtual pockets to determine peptide specificity. The average virtual pockets are generated using a dataset of 15 structures described elsewhere **[13].**

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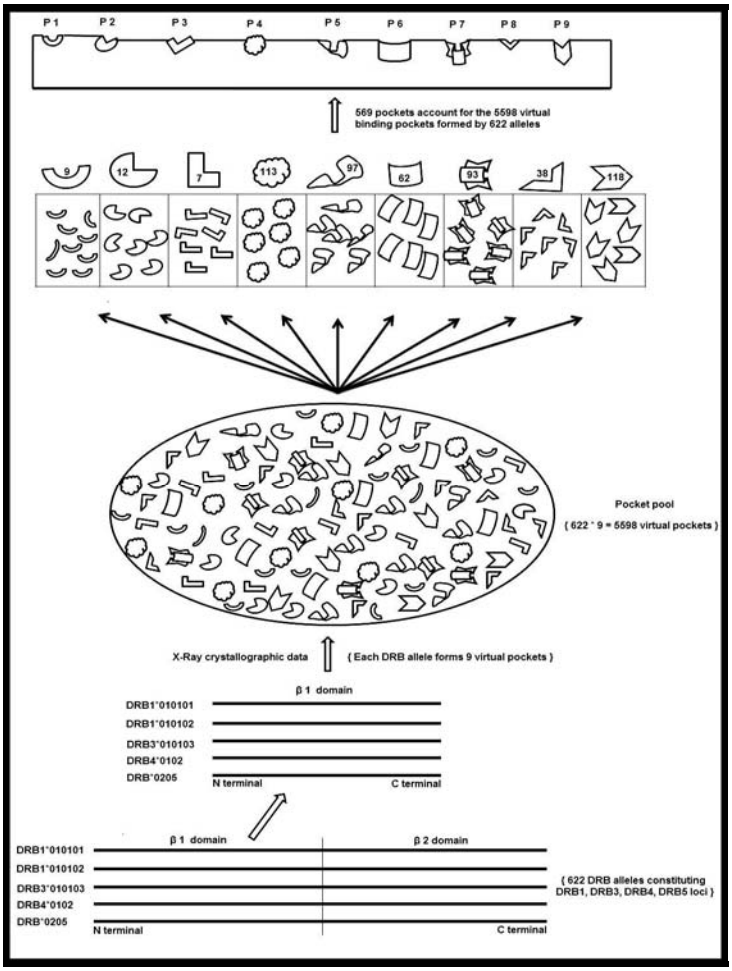

Figure 7: Grouping showing that the 622 DRB alleles accounts for 569 unique pockets

Conclusion:

HLA DRB alleles are associated with CD4+ T-cell immune response and relevant diseases. Design of vaccine candidates with cross reactivity across DRB specific ethnic population requires a consideration of peptide binding functional overlap among DRB alleles. We grouped the known 622 DRB alleles using virtual pockets defined from structural datasets. The grouping produced 73 groups consisting of at least 2 alleles covering about 300 alleles. Thus, the 73 groups exhibit overlapping peptide binding function. This grouping is validated using known peptides (32 peptides bind to DRB1*1101 and DRB1 *1104 and 6 peptides bind to DRB1*1301 and DRB1*1302) that are clustered within the same groups. The data presented here serves as a framework for understanding peptide binding overlap for HLA-DRB supertype definition and groupings.

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Supplementary material

Table 1: Class II HLA specific peptides from MHCBN with overlapping peptide binding

Peptide	alleles	DRB alleles
DGVNYATGNLPGCSA	19	DRB1*0102, DRB1*0301, DRB1*0302, DRB1*0401, DRB1*0402, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*1101, DRB1*1102, DRB1*1103, DRB1*1104, DRB1*1301, DRB1*1302, DRB1*1402, DRB1*1502, DRB1*1601, DRB1*1501, DRB1*0101
IDTLTCGFADLMGYA	18	DRB1*0102, DRB1*0301, DRB1*0302, DRB1*0401, DRB1*0402, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*1101, DRB1*1102, DRB1*1103, DRB1*1104, DRB1*1301, DRB1*1302, DRB1*1402, DRB1*1502, DRB1*1501, DRB1*0101
NLGKVIDTLTCGFA	17	DRB1*0102, DRB1*0301, DRB1*0401, DRB1*0402, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*1101, DRB1*1102, DRB1*1103, DRB1*1104, DRB1*1301, DRB1*1302, DRB1*1402, DRB1*1502, DRB1*1501, DRB1*0101
TCGFADLMGYIPLVA	17	DRB1*0102, DRB1*0301, DRB1*0401, DRB1*0402, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*1101, DRB1*1102, DRB1*1103, DRB1*1104, DRB1*1301, DRB1*1302, DRB1*1502, DRB1*1601, DRB1*1501, DRB1*0101
DLMGYIPLVGAPLGA	14	DRB1*0102, DRB1*0402, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*1101, DRB1*1102, DRB1*1103, DRB1*1104, DRB1*1402, DRB1*1502, DRB1*1601, DRB1*1501, DRB1*0101
VYLLPRRGPRLGVRA	13	DRB1*0102, DRB1*0402, DRB1*0802, DRB1*0901, DRB1*1101, DRB1*1102, DRB1*1103, DRB1*1301, DRB1*1302, DRB1*1502, DRB1*1601, DRB1*1501, DRB1*0101
RHNWVNHAVPLAMKLI	12	DRB1*0301, DRB1*0401, DRB1*0405, DRB1*1101, DRB1*1201, DRB4*0101, DRB1*1302, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*0101, DRB5*0101
GLAYKFVVPGAATPY	11	DRB1*0401, DRB1*0405, DRB1*1101, DRB1*1201, DRB4*0101, DRB1*1302, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*0101, DRB5*0101
HNWVNHAVPLAMKLI	11	DRB1*0301, DRB1*0401, DRB1*0405, DRB1*1101, DRB1*1201, DRB4*0101, DRB1*1302, DRB1*0701, DRB1*0802, DRB1*0901, DRB5*0101
KSKYKLATSVLAGLL	11	DRB1*0401, DRB1*0405, DRB1*1101, DRB3*0101, DRB4*0101, DRB1*1302, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*0101, DRB5*0101
LVNLLIFHINGKIIKNS	11	DRB1*0301, DRB1*0405, DRB1*1101, DRB1*1201, DRB4*0101, DRB1*1302, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*0101, DRB5*0101
QIVGGVYLLPRRGPA	11	DRB1*0102, DRB1*0401, DRB1*0402, DRB1*1101, DRB1*1102, DRB1*1104, DRB1*1301, DRB1*1302, DRB1*1601, DRB1*1501, DRB1*0101
GAARALAHGVRVLEA	10	DRB1*0102, DRB1*0402, DRB1*0701, DRB1*0901, DRB1*1101, DRB1*1103, DRB1*1302, DRB1*1402, DRB1*1502, DRB1*1501
GWLLSPRGSRPSWGA	10	DRB1*0102, DRB1*0302, DRB1*0401, DRB1*0402, DRB1*0802, DRB1*1101, DRB1*1104, DRB1*1302, DRB1*1402, DRB1*1501
KYKIAGGIAGGLALL	10	DRB1*0401, DRB1*0405, DRB1*1101, DRB1*1201, DRB1*1302, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*0101, DRB5*0101
SSVFNVVNSSIGLIM	10	DRB1*0401, DRB1*0405, DRB1*1101, DRB1*1302, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*1501, DRB1*0101, DRB5*0101
GAPLGGAARALAHGA	9	DRB1*0102, DRB1*0402, DRB1*0802, DRB1*1101, DRB1*1104, DRB1*1302, DRB1*1402, DRB1*1501, DRB1*1502
MNYYGKQEENWYSLKK	9	DRB1*0401, DRB1*0405, DRB1*1101, DRB1*1302, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*0101, DRB5*0101
VKNVIGPMKAVCVE	9	DRB1*1101, DRB1*1201, DRB4*0101, DRB1*1302, DRB1*0701, DRB1*0802, DRB1*0901, DRB1*0101, DRB5*0101
MRKLAILSVSSFLFV	8	DRB1*0401, DRB1*0405, DRB1*1101, DRB1*1302, DRB1*0701, DRB1*0901, DRB1*0101, DRB5*0101
AGLLLGNVSTVLLGGV	7	DRB1*0401, DRB1*0405, DRB1*1302, DRB1*0701, DRB1*0901, DRB1*0101, DRB5*0101
RDRIGDNELEERIIYPGT	7	DRB1*1101, DRB1*1301, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
TASHTRLSCDCDDKFYDC	7	DRB1*1101, DRB1*1301, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
TRLSCDCDDKFYD	7	DRB1*1101, DRB1*1301, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
TRLSCDCDDKFYDCLKNS	7	DRB1*1101, DRB1*1301, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
CDCDDKFYDCLKNSADTI	6	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
CPDVMSAGESKHGLTNTA	6	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
DCDDKFYDCLKNS	6	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
DVMSAGESKHGLTNTASH	6	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
GDNELEERIIYPGTLWCG	6	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
GLTNTASHTRLSCDCDDK	6	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
IPLVGAPLGGAARA	6	DRB1*0102, DRB1*0402, DRB1*0802, DRB1*1104, DRB1*1502, DRB1*0101
LSCDCDDKFYDCL	6	DRB1*1101, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0301, DRB1*0101
RLSCDCDDKFYDC	6	DRB1*1101, DRB1*1301, DRB1*0301, DRB1*0701, DRB1*1501, DRB1*0101
RRGPRLGVRATRKTA	6	DRB1*0402, DRB1*0802, DRB1*1101, DRB1*1301, DRB1*1402, DRB1*1601
THDMCPDVMSAGESKHGL	6	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
YFVGKMYFNLIDTKCYKL	6	DRB1*1101, DRB1*1301, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501
ACCRTHDMCPDVMSAGES	5	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501
CDCDDKFYDCLKN	5	DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
DKFYDCLKNSADTISSYF	5	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*0101
GPNELGRFKHTDACCRTH	5	DRB1*1301, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501
GWQIRDRIGDNELEERII	5	DRB1*1101, DRB1*1301, DRB1*0401, DRB1*0701, DRB1*0101
HTRLSCDCDDKFY	5	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*0101
KMYFNLIDTKCYKLEHPV	5	DRB1*1101, DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501
NLIDTKCYKLEHPVTGCG	5	DRB1*1101, DRB1*1301, DRB1*0401, DRB1*0701, DRB1*1501
PGGGQIVGGVYLLPA	5	DRB1*0102, DRB1*0701, DRB1*0901, DRB1*1103, DRB1*1501
SCDCDDKFYDCLK	5	DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
SHTRLSCDCDDKF	5	DRB1*1101, DRB1*0401, DRB1*0701, DRB1*0301, DRB1*0101
ASHTRLSCDCDDK	4	DRB1*1101, DRB1*0401, DRB1*1501, DRB1*0101
CDDKFYDCLKNSA	4	DRB1*1101, DRB1*0401, DRB1*0701, DRB1*0101
DKFYDCLKNSADT	4	DRB1*1101, DRB1*0401, DRB1*0701, DRB1*0101
GSLFLLLLSTSHGWQIRD	4	DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
GTLWCGHGNKSSGPNELG	4	DRB1*0301, DRB1*0401, DRB1*0701, DRB1*1501
GYKVLVLNPSVAAT	4	DRB1*0401, DRB1*1101, DRB1*1201, DRB1*1302
LGRFKHTDACCRTHDMCP	4	DRB1*1301, DRB1*0301, DRB1*0701, DRB1*1501
LLLLSTSHGWQIRDRIGD	4	DRB1*0401, DRB1*0701, DRB1*1501, DRB1*0101
LTNTASHTRLSCD	4	DRB1*1101, DRB1*0401, DRB1*0701, DRB1*1501
QYIKANSKFIGITE	4	DRB3*0101, DRB1*1101, DRB1*1104, DRB1*1302
RLGVRATRKTSERSA	4	DRB1*0402, DRB1*0802, DRB1*1101, DRB1*1104
RRRSRNLGKVIDTLA	4	DRB1*0402, DRB1*0802, DRB1*1101, DRB1*1104
TASHTRLSCDCDD	4	DRB1*1101, DRB1*0401, DRB1*0701, DRB1*1501
TISSYFVGKMYFNLIDTK	4	DRB1*1101, DRB1*0401, DRB1*0701, DRB1*1501
TNTASHTRLSCDC	4	DRB1*1101, DRB1*0401, DRB1*0701, DRB1*1501
VHFFKNIVTARTP	4	DRB1*1501, DRB1*1302, DRB1*0401, DRB1*0402
VHFFKNIVTPATP	4	DRB1*1501, DRB1*1302, DRB1*0401, DRB1*0402
VHFFKNIVTPRAP	4	DRB1*1501, DRB1*1302, DRB1*0401, DRB1*0402
VHFFKNIVTPRTP	4	DRB1*1501, DRB1*1302, DRB1*0402, DRB5*0101

ISSN 0973-2063 (online) 0973-8894 (print)
Bioinformation 4(7): 300-309 (2010)

AYIKANSKFIGITE	3	DRB1*1101, DRB1*1104, DRB1*1302
CPKYVKQNTLKLATG	3	DRB1*1101, DRB1*1301, DRB1*0402
CPKYVKQNTLKLATGMRNVPEKQT	3	DRB3*1101, DRB3*1103, DRB3*1104
DDKFYDCLKNSAD	3	DRB1*1101, DRB1*0401, DRB1*0101
GLTNTASHTRLSC	3	DRB1*1101, DRB1*0701, DRB1*1501
IIYPGTLWCGHGNKSSGP	3	DRB1*0301, DRB1*0401, DRB1*0701
KFYDCLKNSADTI	3	DRB1*1101, DRB1*0401, DRB1*0101
MSAGESKHGLTNTASHTR	3	DRB1*0401, DRB1*0701, DRB1*1501
NTASHTRLSCDCD	3	DRB1*1101, DRB1*0701, DRB1*1501
QAIKANSKFIGITE	3	DRB1*1101, DRB1*1104, DRB1*1302
QPRGRRQPIPKARQA	3	DRB1*0102, DRB1*0402, DRB1*0802
QYIKANSKFAGITE	3	DRB1*1101, DRB1*1104, DRB1*1302
QYIKANSKFIAITE	3	DRB1*1104, DRB1*1101, DRB1*1302
QYIKANSKFIGATE	3	DRB1*1101, DRB1*1104, DRB1*1302
QYIKANSKFIGIAE	3	DRB1*1101, DRB1*1104, DRB1*1302
QYIKANSKFIGITA	3	DRB1*1101, DRB1*1104, DRB1*1302
VHAFKNIVTPRTP	3	DRB1*1501, DRB1*0401, DRB1*0402
VHFAKNIVTPRTP	3	DRB1*0401, DRB1*0402, DRB1*1501
VHFFANIVTPRTP	3	DRB1*1302, DRB1*0401, DRB1*0402
VHFFKNAVTPRTP	3	DRB1*1302, DRB1*0401, DRB1*0402
VHFFKNIATPRTP	3	DRB1*1302, DRB1*0401, DRB1*0402
AADHRQLQLSISSCLQQL	2	DRB4*0103, DRB4*0101
ALFNRLLDDLGF	2	DRB1*0401, DRB1*0404
ASDYKSAHKGFKGVD	2	DRB1*1501, DRB5*0101
AVSFWLRVPKVSSHLE	2	DRB1*1101, DRB1*1104
CGHGNKSSGPNELGRFKH	2	DRB1*0401, DRB1*0701
CPKAVKQNTLKLATG	2	DRB1*0402, DRB1*1301
CPKYVKQNALKLATG	2	DRB1*1101, DRB1*1301
CPKYVKQNTLKAATG	2	DRB1*1301, DRB1*0402
DCLKNSADTISSYFVGKM	2	DRB1*0301, DRB1*0701
DFEFEQMFTDAMG	2	DRB1*0401, DRB1*0404
ENPVVHFFKNIVTPR	2	DRB1*1501, DRB5*0101
ESKHGLTNTASHT	2	DRB1*0701, DRB1*1501
ESKHGLTNTASHTRLSCD	2	DRB1*0701, DRB1*1501
FDLEMLGDVESPS	2	DRB1*0401, DRB1*0404
FNNFTVSFWLRVPKVSASHLE	2	DRB1*1101, DRB1*1104
FPSKTSASIGSLCADARMYG	2	DRB1*0402, DRB1*0401
FYDCLKNSADTIS	2	DRB1*0401, DRB1*0101
GDYKTTICGKGLSATVTGGQ	2	DRB1*0402, DRB1*0401
GRHLIFCHSKRKCDELATKL	2	DRB1*1501, DRB5*0101
GSDTITLPCRIKQFINMWQE	2	DRB1*0402, DRB1*0401
GTEKLIETYFSKNYQDYEYL	2	DRB1*0402, DRB1*0401
HGLTNTASHTRLS	2	DRB1*0701, DRB1*1501
HTNVCFWYIPPSLRTLEDNE	2	DRB1*0301, DRB1*0101
KGFKGVDAQGTLSKI	2	DRB1*1501, DRB5*0101
KHGLTNTASHTRL	2	DRB1*0701, DRB1*1501
KHTDACCRTHDMCPDVMS	2	DRB1*0301, DRB1*0701
KNCSFNISTSIRGKV	2	DRB1*1101, DRB1*0401
LYGNEGMGWAGWLLA	2	DRB1*0401, DRB1*1302
NTWTTCQSIAFPSKTSASIG	2	DRB1*0402, DRB1*0401
PTDPRRRSRNLGKVA	2	DRB1*1101, DRB1*1104
QDVRFPGGGQIVGGA	2	DRB1*0102, DRB1*0901
QYIKANSAFIGITE	2	DRB1*1101, DRB1*1302
QYIKANSKFIGITEL	2	DRB1*0401, DRB3*0101
QYIKANSKFIGITELKKLE	2	DRB1*1101, DRB1*1104
RQPIPKARQPEGRA	2	DRB1*0701, DRB1*1104
SKHGLTNTASHTR	2	DRB1*0701, DRB1*1501
SLKPCVKLTPLCVSL	2	DRB1*1101, DRB1*0401
TASFWLRVPKVSSHLE	2	DRB1*1101, DRB1*1104
TKRNTLRRPQDVKFA	2	DRB1*0102, DRB1*0402
TVAFWLRVPKVSSHLE	2	DRB1*1101, DRB1*1104
TVSAWLRVPKVSSHLE	2	DRB1*1101, DRB1*1104
TVSFALRVPKVSSHLE	2	DRB1*1101, DRB1*1104
TVSFWLRVPKVASHLE	2	DRB1*1101, DRB1*1104
TVSFWLRVPKVSAHLE	2	DRB1*1101, DRB1*1104
TVSFWLRVPKVSASHLE	2	DRB1*1101, DRB1*1104
TVSFWLRVPKVSSALE	2	DRB1*1101, DRB1*1104
TVSFWLRVPKVSSHAE	2	DRB1*1101, DRB1*1104
TVSFWLRVPKVSSHLA	2	DRB1*1101, DRB1*1104
VAKVKIKPLEDKILV	2	DRB5*0101, DRB1*1501
VHFFKAIVTPRTP	2	DRB1*1302, DRB1*0402
VHFFKNIVAPRTP	2	DRB1*1501, DRB1*1302
VITQACPKVSFEPIP	2	DRB1*1101, DRB1*0401
VLLKEFTVSGNILTIRLT	2	DRB4*0101, DRB4*0101
VLPWNAFPGKVCGSNLLSIC	2	DRB1*0402, DRB1*0401
YDCLKNSADTISS	2	DRB1*0401, DRB1*0101
YPWPLYGNEGMGWA	2	DRB1*1302, DRB1*1501
YTTGAVRQIFGDYKTTICGK	2	DRB1*0402, DRB1*0401

Table 2: Grouping of DRB alleles using HERP stretch

Group	HERP Stretch	Alleles number	Alleles
1	ESSECYDYNFDYWLQKRNYCHNVVF	17	DRB1*030101, DRB1*030102, DRB1*030104, DRB1*030105, DRB1*030106, DRB1*0308, DRB1*0316, DRB1*0318, DRB1*0322, DRB1*0323, DRB1*0328, DRB1*0332, DRB1*0333, DRB1*0334, DRB1*0336, DRB1*0337, DRB1*0339
2	ESSECFDYYFDYWFDRATYCHNVGF	16	DRB1*110102, DRB1*110103, DRB1*110104, DRB1*110105, DRB1*110106, DRB1*110107, DRB1*1133, DRB1*1139, DRB1*1149, DRB1*1151, DRB1*1161, DRB1*1162, DRB1*1166, DRB1*131401, DRB1*131402, DRB1*131403
3	WPRECFDYSFDYWIQAATYCHNVVF	12	DRB1*150102, DRB1*150103, DRB1*150104, DRB1*150105, DRB1*150106, DRB1*1506, DRB1*1509,

ISSN 0973-2063 (online) 0973-8894 (print)
Bioinformation 4(7): 300-309 (2010)

			DRB1*1513, DRB1*1516, DRB1*1520, DRB1*1522, DRB1*1524
4	ESSECFDYYFDYWFDRATYCHNVVF	10	DRB1*110101, DRB1*110401, DRB1*110402, DRB1*1135, DRB1*1138, DRB1*1143, DRB1*1144, DRB1*1146, DRB1*1160, DRB1*1311
5	EVHECFDYYYSYWLQRATYCHNVGF	9	DRB1*040501, DRB1*040502, DRB1*040503, DRB1*040504, DRB1*040505, DRB1*0429, DRB1*0430, DRB1*0445, DRB1*0448
6	ESSECFDYNFDYWIDEATYCHNVVF	9	DRB1*130101, DRB1*130102, DRB1*130103, DRB1*130201, DRB1*1335, DRB1*1351, DRB1*1359, DRB1*1369, DRB1*1380
7	WPRECFDYSFDYWIQAATYCHNVGF	9	DRB1*150201, DRB1*150202, DRB1*150203, DRB1*150204, DRB1*150205, DRB1*1508, DRB1*1514, DRB1*1519, DRB1*1526
8	WLFECLECSYDYWLQRATYCHNVGF	8	DRB1*010101, DRB1*010102, DRB1*010103, DRB1*010104, DRB1*0105, DRB1*0107, DRB1*0112, DRB1*0119
9	EVHECFDYYYDYWLQRETYCHNVVF	8	DRB1*040301, DRB1*040302, DRB1*040303, DRB1*040304, DRB1*0439, DRB1*0452, DRB1*0460, DRB1*0471
10	WGYKCFELFYVSWIDRQTVCHNVGF	8	DRB1*070101, DRB1*070102, DRB1*0703, DRB1*0705, DRB1*0707, DRB1*0713, DRB1*0714, DRB1*0715
11	ERSECYDYFYVSWLQKRNYCHNVGF	8	DRB3*01010201, DRB3*01010202, DRB3*010103, DRB3*010104, DRB3*0104, DRB3*0106, DRB3*0110, DRB3*0111
12	ELSECFEHYYDYWLQKQNYCHNVGF	8	DRB3*020201, DRB3*020202, DRB3*020203, DRB3*020204, DRB3*020205, DRB3*0210, DRB3*0218, DRB3*0223
13	EVHECFDYYYDYWLQKATYCHNVGF	7	DRB1*040101, DRB1*040102, DRB1*040103, DRB1*0416, DRB1*0426, DRB1*0433, DRB1*0463
14	ESSECFDYYFDYWIDEATYCHNVVF	7	DRB1*110201, DRB1*110202, DRB1*131403, DRB1*116501, DRB1*116502, DRB1*1322, DRB1*1352
15	EACECNIYYYDYWLRRETYCYNVVF	7	DRB4*0102, DRB4*01030101, DRB4*010302, DRB4*010303, DRB4*010304, DRB4*0106, DRB4*0107
16	ESGECFDYYYSYWIDRLTYCHNVGF	6	DRB1*080302, DRB1*0814, DRB1*0818, DRB1*0823, DRB1*0827, DRB1*0833
17	ESSECFDYFYDYWLRRETYCHNVVF	6	DRB1*1117, DRB1*140502, DRB1*140503, DRB1*142301, DRB1*142302, DRB1*1456
18	ESSECFDYNFDYWIDEATYCHNVGF	6	DRB1*1120, DRB1*130202, DRB1*130203, DRB1*1334, DRB1*1373, DRB1*1374
19	ESSECFDYNFDYWFDRATYCHNVGF	5	DRB1*1109, DRB1*1128, DRB1*130502, DRB1*135001, DRB1*135002
20	ESSECFDYFYAHWLRRETYCHNVVF	5	DRB1*140102, DRB1*140103, DRB1*1426, DRB1*1454, DRB1*1460
21	WLFECLECSYDYWLQRATYCHNAVF	4	DRB1*010201, DRB1*010202, DRB1*010203, DRB1*010204
22	EVHECFDYYYDYWLQRATYCHNVVF	4	DRB1*0404, DRB1*0423, DRB1*0432, DRB1*0440
23	ESGECFDYYYSYWFDRLTYCHNVGF	4	DRB1*080101, DRB1*080102, DRB1*080103, DRB1*0826
24	ESSECFDYFYDYWLRRETYCHNVGF	4	DRB1*1414, DRB1*1436, DRB1*144401, DRB1*144402
25	QDYECFHDDYDYWFDRATYCHNVGF	4	DRB5*010101, DRB5*010102, DRB5*0105, DRB5*0113
26	ESSECYDYNFDYWLQKRNYCHNVGF	3	DRB1*030501, DRB1*030502, DRB1*0309
27	EVHECFDYSYDYWLQRETYCHNVVF	3	DRB1*040601, DRB1*040602, DRB1*0446
28	EVHECFDYYYDYWLQRETYCHNVGF	3	DRB1*040701, DRB1*040702, DRB1*040703
29	ESGECFDYYYDYWFDRLTYCHNVGF	3	DRB1*080201, DRB1*080202, DRB1*080203
30	ESSECFDYYFDYWLDRATYCHNVGF	3	DRB1*110801, DRB1*110802, DRB1*1325
31	ESSECFDYFFDYWFDRATYCHNVGF	3	DRB1*1110, DRB1*111201, DRB1*111202
32	ESSECFDYYFDYWIDRATYCHNVGF	3	DRB1*111901, DRB1*111902, DRB1*1382
33	ESSECFDYYYDYWFDRATYCHNVGF	3	DRB1*1137, DRB1*130701, DRB1*130702
34	ESGECLEHLFVSWFDRATYCHNAVF	3	DRB1*120201, DRB1*120202, DRB1*1213
35	ESGECLEHLFVSWIDRATYCHNAVF	3	DRB1*1206, DRB1*1207, DRB1*1210
36	ESSECFDYFYAHWLRRATYCHNVVF	3	DRB1*140101, DRB1*143201, DRB1*143202
37	WPRECFDYSYDYWFDRATYCHNVGF	3	DRB1*160101, DRB1*160102, DRB1*1603
38	WPRECFDYSYDYWIDRATYCHNVGF	3	DRB1*160501, DRB1*160502, DRB1*1607
39	ESSECFEYNYDYWLQKRNYCHNVGF	2	DRB1*030201, DRB1*030202
40	ESSECYDYNYDYWLQKRNYCHNVVF	2	DRB1*0306, DRB1*0326
41	EVHECFDYYYDYWLQRATYCHNVGF	2	DRB1*0408, DRB1*0461
42	EVHECFDYYYDYWFDRATYCHNVVF	2	DRB1*0415, DRB1*0436
43	ESGECFDYYYDYWFDRLTYCHNVVF	2	DRB1*080401, DRB1*080402
44	YTECYLRFVRAWNLRRVYCRNYVET	2	DRB1*080403, DRB1*080404
45	ESGECFDYFYDYWFDRLTYCHNVGF	2	DRB1*0809, DRB1*0821
46	ESGECFDYYFDYWFDRLTYCHNVVF	2	DRB1*0828, DRB1*1167
47	ESSECFDYYFDYWFDEATYCHNVVF	2	DRB1*1103, DRB1*1324
48	YTECHLRFVREWNLRRVYCRNYVET	2	DRB1*110403, DRB1*110404
49	ESSECFDYYFDYWFDRATYCHNAVF	2	DRB1*110601, DRB1*110602
50	ESSECFDYYFDYWFDEATYCHNVGF	2	DRB1*111101, DRB1*111102
51	ESSECFDYYFDYWIDEATYCHNVGF	2	DRB1*111401, DRB1*1323
52	ESSECFDYDFDYWFDRATYCHNVGF	2	DRB1*1124, DRB1*1362
53	ESSECFDYYFDYWFDRANYCHNVGF	2	DRB1*112701, DRB1*112702
54	ESSECFDYYFDYWLQRATYCHNVVF	2	DRB1*1134, DRB1*1344
55	ESSECFDYYYDYWIDEATYCHNVVF	2	DRB1*1148, DRB1*1370
56	ESSECFDYYYDYWFDRATYCHNVVF	2	DRB1*1150, DRB1*1156
57	ESSECFDYFYDHWLRRETYCHNVVF	2	DRB1*1152, DRB1*1408
58	ESSECFDYYFDYWFDRETYCHNVVF	2	DRB1*115401, DRB1*115402
59	ESSECFDYNFDYWFDRATYCHNVVF	2	DRB1*1158, DRB1*1342
60	ESGECLEHLFVSWIDRATYCHNVGF	2	DRB1*120101, DRB1*120102
61	ESGECLEHLFDYWIDRATYCHNAVF	2	DRB1*1204, DRB1*1209
62	ESGECLEHFFVSWIDRATYCHNAVF	2	DRB1*1205, DRB1*1214
63	ESSECFDYYYSYWIDKATYCHNVGF	2	DRB1*130301, DRB1*130302
64	ESSECFDYFYDYWIDEATYCHNVVF	2	DRB1*1308, DRB1*1372
65	ESSECYDYNFDYWIDEATYCHNVGF	2	DRB1*1327, DRB1*1341
66	ESSECFDYFFDYWIDEATYCHNVVF	2	DRB1*1364, DRB1*1383
67	ESSECFDYFYAHWLRRETYCHNVGF	2	DRB1*140701, DRB1*140702
68	WPRECFDYSFDYWFQAATYCHNVGF	2	DRB1*1504, DRB1*1515
69	ESSECFEYFYDYWLDRLTYCHNVGF	2	DRB1*1440, DRB1*1477
70	WPRECFDYSYDYWLDRATYCHNVGF	2	DRB1*160201, DRB1*160202
71	ELSECFEHNYDYWLQKQNYCHNVGF	2	DRB3*0206, DRB3*0220
72	ELSECFEHYYVSWLQKQNYCHNVGF	2	DRB3*0209, DRB3*0221
73	ELSECFEYFYVSWLQKQNYCHNVVF	2	DRB3*030101, DRB3*030102

Table 3: Validation of DRB alleles grouping using peptides with known overlapping function from MHCBN database

Peptides	HLA DRB alleles
AVSFWLRVPKVSSHLE	DRB1*1101, DRB1*1104
AYIKANSKFIGITE	DRB1*1101, DRB1*1104, DRB1*1302
DGVNYATGNLPGCSA	DRB1*1101, DRB1*1104, DRB1*1301, DRB1*1302

ISSN 0973-2063 (online) 0973-8894 (print)
Bioinformation 4(7): 300-309 (2010)

DLMGYIPLVGAPLGA	DRB1*1101, DRB1*1104
FNNFTVSFWLRVPKVSASHLE	DRB1*1101, DRB1*1104
GAPLGGAARALAHGA	DRB1*1101, DRB1*1104, DRB1*1302
GWLLSPRGSRPSWGA	DRB1*1101, DRB1*1104, DRB1*1302
IDTLTCGFADLMGYA	DRB1*1101, DRB1*1104, DRB1*1301, DRB1*1302
NLGKVIDTLTCGFA	DRB1*1101, DRB1*1104, DRB1*1301, DRB1*1302
PTDPRRRSRNLGKVA	DRB1*1101, DRB1*1104
QAIKANSKFIGITE	DRB1*1101, DRB1*1104, DRB1*1302
QIVGGVYLLPRRGPA	DRB1*1101, DRB1*1104, DRB1*1301, DRB1*1302
QYIKANSKFAGITE	DRB1*1101, DRB1*1104, DRB1*1302
QYIKANSKFIAITE	DRB1*1101, DRB1*1104, DRB1*1302
QYIKANSKFIGATE	DRB1*1101, DRB1*1104, DRB1*1302
QYIKANSKFIGIAE	DRB1*1101, DRB1*1104, DRB1*1302
QYIKANSKFIGITA	DRB1*1101, DRB1*1104, DRB1*1302
QYIKANSKFIGITE	DRB1*1101, DRB1*1104, DRB1*1302
QYIKANSKFIGITELKKLE	DRB1*1101, DRB1*1104
RLGVRATRKTSERSA	DRB1*1101, DRB1*1104
RRRSRNLGKVIDTLA	DRB1*1101, DRB1*1104
TASFWLRVPKVSSHLE	DRB1*1101, DRB1*1104
TCGFADLMGYIPLVA	DRB1*1101, DRB1*1104, DRB1*1301, DRB1*1302
TVAFWLRVPKVSSHLE	DRB1*1101, DRB1*1104
TVSAWLRVPKVSSHLE	DRB1*1101, DRB1*1104
TVSFALRVPKVSSHLE	DRB1*1101, DRB1*1104
TVSFWLRVPKVASHLE	DRB1*1101, DRB1*1104
TVSFWLRVPKVSAHLE	DRB1*1101, DRB1*1104
TVSFWLRVPKVSASHLE	DRB1*1101, DRB1*1104
TVSFWLRVPKVSSALE	DRB1*1101, DRB1*1104
TVSFWLRVPKVSSHAE	DRB1*1101, DRB1*1104
TVSFWLRVPKVSSHLA	DRB1*1101, DRB1*1104
VYLLPRRGPRLGVRA	DRB1*1101, DRB1*1301, DRB1*1302

ISSN 0973-2063 (online) 0973-8894 (print)
Bioinformation 4(7): 300-309 (2010)