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Nomenclature for factors of the SLA system, update 2008

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Abstract

This report summarizes the new swine leukocyte antigen (SLA) allele sequences and haplotypes designated by the SLA Nomenclature Committee of the International Society for Animal Genetics. There have been 74 new SLA alleles, comprising 18 SLA-1 alleles, 11 SLA-2 alleles, six SLA-3 alleles, two SLA-6 alleles, one SLA-DRA allele, 20 SLA-DRB1 alleles, three SLA-DQA alleles and 13 SLA-DQB1 alleles. Twelve new SLA class I and four new class II haplotypes have also been designated. This is the first official update since the 2005 reports on the nomenclature for factors of the SLA class I and II systems. This report also summarizes recent updates to the Immunopolymorphism Database–Major Histocompatibility Complex (IPD-MHC) website (http://www.ebi.ac.uk/ipd/mhc/sla/). All information has now been integrated to the SLA section of the IPD-MHC database, which serves as the repository for maintaining a list of all recognized *SLA* genes and their allelic sequences.

The International Society for Animal Genetics Nomenclature Committee for Factors of the Swine Leukocyte Antigen (SLA) System established the principles of a systematic nomenclature system for *SLA* genes and alleles that have been defined by means of DNA sequencing. Since the publication of the first nomenclature reports on the SLA class I (1) and class II (2) systems, there has been a considerable number of new and confirmatory sequences as well as SLA haplotype information accumulated. The SLA Nomenclature Committee has therefore decided to publish a report on recent updates to the Immunopolymorphism Database–Major Histocompatibility Complex (IPD-MHC) SLA sequence database that serves as the repository for maintaining a list of all recognized *SLA* genes and their allelic sequences.

The IPD-MHC SLA sequence database

The IPD-MHC SLA sequence database (http://www.ebi.ac.uk/ipd/mhc/sla/) has provided a repository for the sequences of the alleles designated by the SLA Nomenclature Committee for factors of the SLA system (3). This database is the primary source of information for the study of the polymorphic genes in the swine MHC system; it provides researchers a centralized platform to conveniently access the most recent nomenclature reports, maps of the SLA regions, lists of genes considered by the Committee as well as alleles recognized and their DNA and protein sequences. It also provides direct links to the alleles' associated publication abstracts and GenBank entries, phylogenetic analyses used for allele group assignment and lists of recognized SLA haplotypes. In addition, the IPD-MHC website offers

researchers convenient access to multiple nucleotide and amino acid sequence alignments of all the recognized SLA alleles with various display options, which allow for more direct and effective comparisons within and between species. These features have helped to facilitate the analysis and study of SLA class I and II genes.

Since its initial release, a considerable number of new and confirmatory sequences have been submitted to the Chairman of the SLA Nomenclature Committee for consideration of allele designations. The list of all recognized SLA alleles and haplotypes has rapidly grown in size in the past several years. As such, the SLA Nomenclature Committee has performed a major update to the database, which includes all the SLA genes, alleles and haplotypes recognized to date, revisions to several allele designations, DNA and protein sequence alignments and the most recent phylogenies. Moreover, recent updates on the whole IPD-MHC website structure included the integration of an online submission tool at http://www.ebi.ac.uk/ipd/mhc/submit.html. This now allows direct and convenient submission of new and confirmatory sequences to the SLA Nomenclature Committee for the consideration of allele designations.

Naming of genes within the SLA region

Sequencing and mapping of the entire SLA region based on the common Hp-1.1 (H01) haplotype have been completed (4). The genes in the SLA region considered by the SLA Nomenclature Committee are listed in Table 1. This list of genes remains essentially unchanged from the first nomenclature reports (1, 2), except that the putative SLA-wDYA pseudogene locus previously annotated between the class II DQ–DO interval will no longer be considered by the Committee because of insufficient evidence to support such annotation (4).

Table 1 Names for genes in the SLA region considered by the International Society for Animal Genetics SLA Nomenclature Committee

Name[a,b]	Previous equivalent[c]	Molecular characteristics
SLA-1	PD1	Classical MHC class I α-chain
SLA-2	PD14	Classical MHC class I α-chain
SLA-3	PD7	Classical MHC class I α-chain
SLA-4		Classical MHC class I α-chain pseudogene
SLA-5		Classical MHC class I α-chain (possible pseudogene)
SLA-6	PD6	Nonclassical MHC class I α-chain
SLA-7		Nonclassical MHC class I α-chain
SLA-8		Nonclassical MHC class I α-chain
SLA-9		Classical MHC class I α-chain pseudogene
SLA-11		Nonclassical/classical MHC class I α-chain pseudogene
MIC-1		MHC class I chain-related pseudogene
MIC-2		MHC class I chain-related gene
SLA-DRA		MHC class II DR α-chain
SLA-DRB1		MHC class II DR β-chain
SLA-DRB2		MHC class II DR β-like pseudogene
SLA-DRB3		MHC class II DR β-like pseudogene
SLA-DRB4		MHC class II DR β-like pseudogene
SLA-DRB5		MHC class II DR β-like pseudogene
SLA-DQA		MHC class II DQ α-chain
SLA-DQB1		MHC class II DQ β-chain
SLA-DQB2		MHC class II DQ β-like pseudogene
SLA-wDYB		MHC class II DY β-like pseudogene
SLA-DMA		MHC class II DM α-chain
SLA-DMB		MHC class II DM β-chain
SLA-DOA		MHC class II DO α-chain
SLA-DOB1		MHC class II DO β-chain
SLA-DOB2		MHC class II DO β-like pseudogene

SLA, swine leukocyte antigen; MHC, major histocompatibility complex.
[a] Gene names were derived from the SLA haplotype Hp-1.1 (H01) (4).
[b] SLA-wDYA is excluded because of insufficient evidence to support the annotation of this locus (4).
[c] Refers to the cloned SLA class I genes defined by Singer et al. (16).

Naming of SLA alleles

The SLA Nomenclature Committee designates SLA alleles in parallel to the World Health Organization Human Leukocyte Antigen (HLA) Nomenclature System (1, 2). The naming conventions for SLA alleles are summarized in Table 2. The first two digits are used to designate groups of alleles that have similar DNA sequences. Group designations are based on phylogenetic analysis and the identification of DNA sequence motifs that can be used for differentiation of alleles with the help of molecular methods (28). The third and fourth digits are used to designate alleles with different protein sequences. The fifth and sixth digits are used to designate alleles that differ by synonymous nucleotide substitutions. The seventh and eighth digit would potentially be used to designate alleles with nucleotide substitutions outside the coding region that alter the protein expression. No such SLA alleles have been described to date.

In addition to the proposed use of 'N' or 'L' suffix to designate alleles that have no or a low protein expression, a 'Q' suffix is now used to designate alleles with profound sequence variations, which may significantly modify the expression as protein. This is demonstrated by the HLA-B*3565Q allele in which a nucleotide substitution is thought to affect its protein expression by disrupting the formation of a disulfide linkage (5). Three SLA alleles to date have adopted these suffixes in their designations: SLA-DRB1*0603Q (formerly designated SLA-DRB1*060202) because of the characteristic absence of exon 5 that encodes an intracytoplasmic domain and SLA-DRB1*kb03N and SLA-DRB1*kb04N because of the presence of premature stop signals at codon 52.

As delineated in the previous SLA reports (1, 2), alleles that have been confirmed by more than one laboratory, in more than one pig breed or by a second DNA typing method

are given official designations (conditions for acceptance of new allele sequences are also available at the IPD-MHC SLA website). Sequences that do not meet the requirements may be accepted but will be given a provisional alphanumeric allele name following the group designation (e.g. SLA-1*02we02) (Table 2). If the allele cannot be assigned to an existing group because of distinctive sequence motifs and/or insufficient sequence data, only a provisional alphanumeric allele name will be assigned (e.g. SLA-1*an01). A 'w' prefix is used to indicate a tentative allele group that does not contain any confirmed allele with official allele designation.

New allele sequences and groups

A total of 74 new SLA alleles have been named since the previous reports (Table 3). These comprised 18 SLA-1 alleles, 11 SLA-2 alleles, six SLA-3 alleles, two SLA-6 alleles, one DRA allele, 20 DRB1 alleles, three DQA alleles and 13 DQB1 alleles. Of the new alleles, 19 were confirmed either by more than one laboratory or by unique polymerase chain reaction–sequence-specific primer (PCR-SSP) patterns; thus, those 19 received official allele designations (four-digit allele name). Additionally, 22 previously published tentative alleles (with provisional alphanumeric names) were confirmed either by sequences identified in other breeds or laboratories; therefore, 21 of those 22 received official allele designations (the exception was SLA-1*an02 because of insufficient sequence data for a group assignment; Table 4). Based on the identification of the new sequences, three new allele groups have been designated: SLA-6*w04, SLA-DRB1*13 and SLA-DRB1*14.

Table 2 Assignment of names and numbers for SLA alleles

Nomenclature	Indication
SLA	The SLA region and prefix for a SLA gene
SLA-1	A particular SLA locus
SLA-1*01	A group of SLA alleles (based on DNA sequence similarity)
SLA-1*0101	A specific confirmed SLA allele
SLA-1*0101L	A low-expression SLA allele
SLA-1*0101N	A null SLA allele
SLA-1*0101Q	An SLA allele with profound sequence variations that may significantly modify the encoded protein expression
SLA-1*010101	An SLA allele that differs by synonymous nucleotide substitution
SLA-1*01010101	An SLA allele that contains synonymous nucleotide substitution outside the coding region that may modify the encoded protein expression
SLA-1*w10	A provisional allele group that does not contain any confirmed allele
SLA-1*01ab01	A tentative SLA allele with a provisional alphanumeric designation
SLA-1*ab01	A tentative SLA allele without a group designation because of distinctive sequence motif and/or insufficient sequence data

SLA, swine leukocyte antigen.

Renaming of SLA alleles and groups

Because of the confirmation of alleles, several allele groups now have the provisional 'w' prefix omitted in the group designations, i.e., SLA-1*08, SLA-1*11–13, SLA-2*07, SLA-2*10–12 and SLA-DRB1*11. In addition, three SLA class II alleles have been renamed. SLA-DQB1*0401 now becomes SLA-DQB1*040101 because of the designation of SLA-DQB1*040102 in the Meishan pig breed, which differs synonymously at nucleotide (nt) +270; this has been confirmed by PCR-SSP reactions (6). SLA-DRB1*060201 was renamed SLA-DRB1*0602 after SLA-DRB1*060202 was renamed SLA-DRB1*0603Q because of its characteristic absence of the exon 5 coding region, which may significantly affect its protein expression.

On the other hand, the SLA-2*07rh12 that was derived from SLA class I haplotype Hp-14.0 (serotype H12) contains only partial exon 2 sequence (190 bp; nt +149 to 338) and it matches SLA-2*0101, SLA-2*0102 and SLA-2*07we01. It was decided that this allele designation should remain in the database until further characterization is performed.

Polymorphism of the SLA genes

In the first SLA nomenclature reports (1, 2), there were 81 classical class I alleles (SLA-1, SLA-2 and SLA-3), seven nonclassical class I alleles (SLA-6) and 127 class II alleles (SLA-DRA, -DRB1, -DQA, -DQB1 and -DMA) with allele designations. As a result of this update, there are now a total of 125 class I alleles (44 SLA-1, 46 SLA-2, 26 SLA-3 and nine SLA-6) and 164 class II alleles (13 DRA, 82 DRB1, 20 DQA, 44 DQB1 and five DMA) with allele designations.

Classical SLA class I system

The SLA-1, SLA-2 and SLA-3 genes are highly polymorphic. There are 12 SLA-1 allele groups with a total of 44 alleles (including eight tentative alleles without group designation); 14 SLA-2 allele groups with a total of 46 alleles (including four tentative alleles without group designation) and seven SLA-3 allele groups with a total of 26 alleles (including one tentative allele without group designation).

Compared with the SLA-1 and SLA-3 alleles, the SLA-2 alleles have extra 9 bp in the leader sequence. In addition, several polymorphic sites appear to be locus specific for SLA-2 alleles. These are G at nt +11, C at nt +15, A at nt +20, A at nt +25, C at nt +28, A at nt +31 and T at nt +33. The only site that appears to be locus specific for SLA-3 alleles is the G at nt +550. Locus-specific PCR primers have

Table 3 Designation of new SLA alleles

Group	Allele	Previous designation	Breeds or cell lines from which the sequence was derived	Confirmatory method	Accession number	Submitting authors
SLA-1*02	0202		SK-RST	PCR-SSP	EU440334	Ho et al.
SLA-1*06	06an04	04	Duroc		AB211035	Ando et al. (17)
SLA-1*08[a]	08an03	03	Duroc		AB211034	Ando et al. (17)
	08pt13		PT-K75		EU440337	Ho et al.
	08sk11		SK-RST		EU440332	Ho et al.
SLA-1*w10	w10cs01		Meishan		DQ303230	Ho et al. (6)
SLA-1*11[a]	1101		LLC-PK1 (Hampshire)	PCR-SSP	EU440341	Ho et al.
	11jh01		Korean native pig		DQ883208	Lee et al. (8)
	11jh02		Korean native pig		DQ883209	Lee et al. (8)
	11mp11		MPK		EU440338	Ho et al.
SLA-1*12[a]	1201		PT-K75	PCR-SSP	EU440335	Ho et al.
	12hy01		KNP1012		DQ992492	Kim et al.
SLA-1*13[a]	1301		PT-K75		EU440336	Ho et al.
			SPL010035D12		AK237395	Uenishi et al. (18)
SLA-1*	cs02		Meishan		DQ303229	Ho et al. (6)
	es11		ESK-4		EU440342	Ho et al.
	es12		ESK-4		EU440343	Ho et al.
	sk13		SK-RST		EU440333	Ho et al.
	st11		ST		EU440331	Ho et al.
SLA-2*04	040202		MPK	PCR-SSP	EU432087	Ho et al.
SLA-2*09	w09pt22		PT-K75		EU432085	Ho et al.
SLA-2*10[a]	1001		SPL010037G02		AK237409	Uenishi et al. (18)
			PT-K75		EU432084	Ho et al.
	10es21		ESK-4		EU432090	Ho et al.
	10sk21		SK-RST		EU432083	Ho et al.
SLA-2*11[a]	110101		SK-RST	PCR-SSP	EU432082	Ho et al.
	110102	w11cs01	Meishan	PCR-SSP	DQ303222	Ho et al. (6)
SLA-2*12[a]	1201		ST	PCR-SSP	EU432080	Ho et al.
SLA-2*	es22		ESK-4		EU432089	Ho et al.
	jh01		Korean native pig		DQ883210	Lee et al. (8)
	jh02		Korean native pig		DQ883211	Lee et al. (8)
SLA-3*03	0303		Korean native pig		EF589961	Lee et al. (8)
			KNP3002		DQ992512	Kim et al.
			KNP3008		DQ992517	Kim et al.
	0304	03cs01	Meishan	PCR-SSP	DQ303226	Ho et al. (6)
	03pt31		PT-K75		EU432095	Ho et al.
SLA-3*05	0503	05jh01	Korean native pig		DQ883213	Lee et al. (8)
			KNP3009		DQ992518	Kim et al.
SLA-3*04	04es32		ESK-4		EU432098	Ho et al.
SLA-3*	hm22	m22	Sinclair		DQ104340	Ho et al.
SLA-6*01	0105		Meishan	PCR-SSP	EU432057	Ho et al.
SLA-6*w04[b]	w04jh01		Korean native pig		DQ883214	Lee et al. (8)
DRA*02	0201jh01		Korean native pig		DQ883222	Lee et al. (8)
DRB1*02	0201du02	02du02	Duroc		EU039935	Luetkemeier et al. (27)
	02du01		Duroc		EU039934	Luetkemeier et al. (27)
	02du03		Duroc		EU039936	Luetkemeier et al. (27)
DRB1*04	0404	04ns01	Canadian Yorkshire		EU087426	Nino-Soto et al. (19)
			UTR010019G11		BP173021	Uenishi et al. (18)
			OVR010045B03		AK234340	Uenishi et al. (18)
DRB1*07	07yo02		Yorkshire		EU039952	Luetkemeier et al. (27)
DRB1*10	10jh01		Korean native pig		DQ883226	Lee et al. (8)
	10Lu03		Lanyu		EU039958	Luetkemeier et al. (27)
DRB1*11[a]	1102		SK-RST	PCR-SSP	EU432075	Ho et al.
DRB1*14[b]	1401	cs01	Meishan		DQ303220	Ho et al. (6)
		La01	Landrace		EU431322	Luetkemeier et al. (27)

Table 3 *Continued*

Group	Allele	Previous designation	Breeds or cell lines from which the sequence was derived	Confirmatory method	Accession number	Submitting authors
DRB1*	be01		Berkshire		EU039962	Luetkemeier et al. (27)
	du05		Duroc		EU039938	Luetkemeier et al. (27)
	er01		Erhualian		EU039954	Luetkemeier et al. (27)
	ha01		Hampshire		EU039948	Luetkemeier et al. (27)
	ha04		Hampshire		EU039950	Luetkemeier et al. (27)
	La02		Landrace		EU039939	Luetkemeier et al. (27)
	La03		Landrace		EU039940	Luetkemeier et al. (27)
	La04		Landrace		Eu039941	Luetkemeier et al. (27)
	La05		Landrace		EU039942	Luetkemeier et al. (27)
	Lu02		Lanyu		EU039957	Luetkemeier et al. (27)
	me02		Meishan		EU039961	Luetkemeier et al. (27)
DQA*02	0204	0902	Landrace		DQ159901	Peng et al.
			OVRM10206E09		AK236590	Uenishi et al. (18)
	02cs01		Meishan		EU432059	Ho et al.
	02jh01		Korean native pig		DQ883217	Lee et al. (8)
DQB1*01	01be01		Berkshire		EU039932	Luetkemeier et al. (27)
	01ha02		Hampshire		EU039919	Luetkemeier et al. (27)
	01Lu01		Lanyu		EU039924	Luetkemeier et al. (27)
	01me03		Meishan		EU039931	Luetkemeier et al. (27)
DQB1*02	02du01		Duroc		EU039909	Luetkemeier et al. (27)
	02La03		Landrace		EU039912	Luetkemeier et al. (27)
	02me01		Meishan		EU039929	Luetkemeier et al. (27)
DQB1*04	040102		Meishan	PCR-SSP	DQ303218	Ho et al. (6)
	04sk51		SK-RST		EU432068	Ho et al.
DQB1*06	0602	fn01	Duroc		EU193303	Woo et al.
		409	Duroc		EU431321	Luetkemeier et al. (27)
DQB1*08	08Lu03		Lanyu		EU039926	Luetkemeier et al. (27)
DQB1*	es51		ESK-4		EU432061	Ho et al.
	Lu02		Lanyu		EU039925	Luetkemeier et al. (27)

SLA, swine leukocyte antigen; PCR-SSP, polymerase chain reaction–sequence-specific primer.
[a] Allele group confirmed; tentative designation 'w' omitted.
[b] New allele group.

recently been developed to distinguish most SLA-1 and SLA-3 alleles based on polymorphisms in the 3′ untranslated region (6–9).

Nonclassical SLA class I system

The nonclassical SLA-6 gene appears to be largely monomorphic. There are only nine SLA-6 alleles representing four allele groups with very minor nucleotide substitutions between alleles. The extent of polymorphism of the SLA-7 and SLA-8 genes, on the other hand, has not been well characterized. There are only two reported alleles for each locus (10, 25). Sequence comparisons showed that the SLA-7 alleles differ from each other at eight nucleotide positions, while the SLA-8 alleles differ from each other at seven positions.

SLA class II system

The SLA-DRB1 and -DQB1 loci display a very high degree of polymorphism. There are 14 SLA-DRB1 allele groups and a total of 82 alleles (including 21 tentative alleles without group designation) and nine SLA-DQB1 allele groups with a total of 44 alleles (including six tentative alleles without group designation). The SLA-DQA locus also exhibits a moderate degree of polymorphism with five allele groups and a total of 20 alleles (including one tentative allele without group designation). The SLA-DRA locus, on the other hand, exhibits a very limited polymorphism with 13 alleles representing three allele groups. This limited polymorphism is homologous to the HLA system; only three HLA-DRA alleles have been identified to date. Only one study has been published regarding the polymorphisms of the SLA-DMA locus (11). This study characterized five SLA-DMA alleles that showed only a few nucleotide substitutions in exons 3 and 4. They were all designated as a single group. There are 16 alleles designated in the SLA-DRB pseudogene system (DRB2–DRB5). This number remains unchanged since the previous nomenclature report (2). The extent of polymorphism of other SLA class II genes

Table 4 Confirmatory SLA sequences

Group	Allele	Previous designation	Breed or cell line from which the sequence was derived	Accession number	Submitting authors
SLA-1*07	0702	07ce08	ST	EU440330	Ho et al.
SLA-1*08[a]	0801	w08sz01	Korean native pig	EF589959	Lee et al. (8)
SLA-1*	an02[b]		Duroc	AB428519	Ando et al. (17)
SLA-2*01	0102	01an06	Duroc	AB429063	Ando et al. (17)
SLA-2*02	0202	02Lw02	ST	EU432081	Ho et al.
SLA-2*03	0302	03sp01	Sinclair	DQ104338	Ho et al.
SLA-2*04	040201	04sx01	PK13, PK15	EU170458	Ho et al.
SLA-2*05	0502	05sz01	Korean native pig	EF589960	Lee et al. (8)
SLA-2*07[a]	0701	w07ss01	LLC-PK1 (Hampshire)	EU432088	Ho et al.
SLA-2*10[a]	1002	10an01	Duroc	AB429064	Ando et al. (17)
SLA-3*04	0402	04sc19	ST	EU432092	Ho et al.
SLA-3*05	0502	05sm14	SK-RST, PT-K75, ESK-4	EU432094	Ho et al.
			Duroc	AB428520	Ando et al. (17)
SLA-3*06	0602	06an03	Meishan	DQ303227	Ho et al. (6)
SLA-6*01	0103	01sc01	Meishan	EU432055	Ho et al.
	0104	01sx01	Meishan	EU432056	Ho et al.
DRA*01	010103	0101ta01	Meishan	EU432070	Ho et al.
DRA*02	020202	0202mm16	Korean native pig	DQ883223	Lee et al. (8)
	020203	0202mw01	Hunan Shaziling	EF143987	Tang et al. (26)
DRB1*11[a]	1101	w11an01	Korean native pig	DQ883225	Lee et al. (8)
DRB1*13[c]	1301	ss08	Hampshire and Berkshire	EU039949	Luetkemeier et al. (27)
			LLC-PK1 (Hampshire)	EU432079	Ho et al.
DQB1*02	0204	02sh02	Large white Yorkshire	EU039916	Luetkemeier et al. (27)
DQB1*05	0503	05an01	Korean native pig	DQ883223	Lee et al. (8)

SLA, swine leukocyte antigen.

[a] Allele group confirmed; tentative designation 'w' omitted.

[b] Permanent allele name not assigned because of insufficient sequence data.

[c] New allele group.

(DMB, DOA and DOB1) and pseudogenes (DQB2, wDYB and DOB2) also remains uncharacterized. There is only one sequence for each of these loci, which was derived from the only completely sequenced SLA haplotype Hp-1.1 (4).

Sequence length variations

Sequence length variations have been observed in several SLA alleles. Alleles assigned to the SLA-3*07 allele group have a distinctive 9-bp insertion in exon 2, which appears to result from a duplication of the preceding sequence (nt +230 to 238). SLA-3*0402 and SLA-3*04es32 both have an identical 3-bp deletion in exon 3 (codon 150; nt +510 to 512). SLA-3*04es32, in addition, has a unique 12-bp insertion in exon 4 (between nt +744 and +745). SLA-3*0501 has a distinctive 3-bp insertion in exon 5 (between nt +939 and +940). SLA-2*0302 and SLA-2*w09pt22 have an identical 6-bp deletion (codon 294–295; nt +943 to 948) in exon 5. In the SLA-DQA system, all but the SLA-DQA*01 group alleles have an identical 3-bp insertion in exon 3 (between nt +463 and +464). SLA-DRB1*0603Q (formerly designated SLA-DRB1*060202), as mentioned previously, is missing in the entire exon 5 (24 bp), which encodes an intracytoplasmic domain of the mature DR β-chain protein. Despite having such a profound sequence modification, this allele does not appear to be a sequence artifact as it has been detected independently in two porcine cDNA libraries constructed from the Landrace–Yorkshire commercial pigs (12, 13) and in a commercially available porcine embryonic kidney cell line (Ho CS, Franzo-Romain MH, Lee YJ, Lee JH, Smith DM, unpublished data). It is still not known which sequence length modifications may affect the structural integrity of the SLA proteins and thus modify their surface expression or function. It has been suggested that the three extra amino acids in the α1 domain of the SLA-3*07 group alleles should not significantly alter the structure of the peptide-binding groove; therefore, these alleles may still produce functional proteins (7).

SLA haplotypes

In the previous nomenclature reports, there were 15 unique SLA class I haplotypes (Hp-1.0–Hp-15.0) (with two subtypes) and 17 unique class II haplotypes (Hp-0.1–Hp-0.17) that have been defined by means of high-resolution DNA sequencing. Since then, there have been 12 new class I

Table 5 Designation of SLA class I haplotypes

Hp-	Breed[a]	Previous designations	SLA-1	SLA-3	SLA-2	SLA-6	References
1a.0	Large white	H01	0101	0101	0101	0101	(4)
1b.0	Large white	H28	01rh28	01rh28	0101	ND	
2.0	NIH, Sinclair, Hanford	a, b, H10	0201, 0701	Null	0201	w02sa01	(7, 20)
3.0	NIH	c, H59	Null	0301	0301	0103	(7, 20)
4a.0	NIH, Duroc	d, H04	0401	0401	0401	0102	(7, 20)
4b.0	Yucatan	x	0401	0401	040201	0104	(7)
4c.0	Meishan	K	0401	0401	0401	0104	(6)
5.0	Yucatan	w	0401	05sw01	w08sw01	Null	(7)
6.0	Yucatan	y	08sy01	0601	05sy01	03sy01	(7)
7.0	Yucatan	z	0801	0701	0502	0101	(7)
8.0	Westran	None	02we02, 04we01	0302	07we01	01we01	(9)
9.0	Sinclair, Hanford	a	0601	0501	0601	ND	
10.0	Sinclair	c	0501	hm22	0302	ND	
11.0	Sinclair	d	0101, w09sm09	0701sm19	0501	ND	
12.0	Hanford	e	08sm08, w09sm09	0502	10sm01	ND	
13.0	Hanford	f	w10sm21	0401	w13sm20	ND	
14.0	Large white	H12	0102	01rh12	07rh12	ND	
15.0	Large white	H34	0102	07rh34	05rh34	ND	
16.0	Clawn	c1	0401	0602	w09an02	ND	(21)
17.0	Clawn	c2	ND	03an02	06an03	ND	(21)
18.0	Meishan	M	0401	0304	06me01	0102	(6)
19.0	Meishan	N	08ms05, 13ms21	0602	w09sn01	0105	(6)
20.0	Meishan	L	w10cs01, cs02	0101	110102	0103	(6)
21.0	Commercial breeds	H03	rh03	0601	05rh03	ND	
25.0	Hampshire[b]	None	1101	0302	0701	ND	
27.0	Duroc	d1	06an04, 08an03	0101	0102	ND	(17)
56.0	Korean native pig	None	11jh01	0303	jh01	w04jh01	(8)
59.0	Korean native pig	None	11jh02	0503	jh02	0102	(8)
60.0	Duroc	d2	an02	0502	1002	ND	(17)

ND, not determined; Null, no expression of this locus detected; SLA, swine leukocyte antigen.

[a] Breed in which the haplotype was characterized; haplotype may be found in other breeds.

[b] Haplotype was observed in the LLC-PK1 porcine cell line that was derived from a Hampshire pig (22).

haplotypes (with one subtype Hp-4c.0 that differs from Hp-4a.0 at the SLA-6 locus) and four new class II haplotypes (with one subtype Hp-0.15b) designated. These resulted in a total of 26 unique class I haplotypes and 20 unique class II haplotypes (Tables 5 and 6).

Duplication of the SLA-1 locus has now been observed in seven class I haplotypes (Hp-2.0, -8.0, -11.0, -12.0, -19.0, -20.0 and -27.0) (Table 5). Phylogenetic analysis based on the exons 2 and 3 coding regions is still unable to differentiate alleles between these loci. Based on the observation of a crossover in the Sinclair and Hanford miniature pig crosses, SLA-1*0201 of Hp-2.0 and SLA-1*w09sm09 of Hp-11.0 have been assigned to the centromeric SLA-1 locus, whereas SLA-1*0701 and SLA-1*0101 have been assigned to the telomeric SLA-1 locus in their respective haplotypes (Ho et al., unpublished data).

Crossover regions in the recombinant SLA haplotypes of the National Institutes of Health (NIH) and Clawn miniature pigs have recently been studied using microsatellite markers (14). An identical crossover point was mapped to the class III region near the complement C2 locus of the recombinant haplotypes Hp-2.4 and Hp-3.4 (previously designated *h* and *g*, respectively) in the NIH miniature pigs. An additional crossover point was also observed in Hp-2.4 in the class I region telomeric to the MIC-2 locus. In the Clawn miniature pigs, a crossover point was mapped to a 208-kb fragment in the class I region of the recombinant Hp-16.17, while two different crossover points were observed in the recombinant Hp-17.16 in the class I region centromeric to the SLA-11 locus and near the nonclassical class I genes.

Conclusion

Overall, this systematic nomenclature for SLA class I and II alleles is critical for further development of research in swine immunology and diseases as well as the use of swine as transplantation models and xenotransplantation donors. It facilitates communication about SLA alleles and haplotypes, particularly in outbred pigs. MHC proteins play a central role in the presentation of antigenic peptides to T

Table 6 Designation of SLA class II haplotypes

Hp-	Breed[a]	Previous designation	SLA-DRA	SLA-DRB1	SLA-DQA	SLA-DQB1	References
0.1	Large white, Korean native pig	H01	010101	0101	0101	0101	(4, 8)
0.2	NIH, Sinclair, Hanford	a, b	010101	0201	0201	0201	(7, 20)
0.3	NIH	c	0201	0301	0102	0301	(7, 20)
0.4	NIH	d	010102	0201	020201	040101	(7, 20)
0.5	Yucatan	x	020301	0501	020202	0201	(7)
0.6	Yucatan	w	020203	0501	0103	0801	(7)
0.7	Yucatan	y	0203my01	0601	01my01	0601	(7)
0.8	Yucatan	z	010101	0801	0203	0202	(7)
0.9	Westran	None	0101we01	0201	03we01	0402we01	(9)
0.10	Sinclair, Hanford	a	ND	0401	ND	0801	
0.11	Sinclair	c	020202	0901	ND	0402	
0.12	Sinclair	d	020201	0602	0301	0701	
0.13	Hanford, Duroc	e, d2	ND	0403	ND	0303	(17)
0.14	Meishan	M, K	010103	0901	0301	0801	(6)
0.15a	Meishan	N	0201	0401	0203	0201	(6)
0.15b	Banna	None	020301	0402	020202	0202	(23, 24)
0.16	Clawn	c1	ND	11ac21	ND	0601	(21)
0.17	Clawn	c2	ND	0801	ND	0501	(21)
0.18	Meishan	L	010103	1401	02cs01	040102	(6)
0.25	Hampshire[b]	None	ND	1301	ND	0901	
0.30	Korean native pig, Duroc	d1	020202[c]	1101	02jh01[c]	0503	(8, 17)

ND, not determined; SLA, swine leukocyte antigen.

[a] Breed in which the haplotype was characterized; haplotype may be found in other breeds.

[b] Haplotype was observed in the LLC-PK1 porcine cell line that was derived from a Hampshire pig (22).

[c] Allele not determined in the Duroc pigs.

cells and updated nomenclature and knowledge of SLA alleles will be extremely useful in the study of cell-mediated immunity to pathogens and vaccine development (15).

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