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Nomenclature for factors of the dog major histocompatibility system (DLA), 1998. First report of the ISAG DLA Nomenclature Committee

Key words:
dog; MHC; DLA; nomenclature; genetics

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Abstract: A Nomenclature Committee for factors of the dog major histocompatibility system or dog leukocyte antigen (DLA) has been convened under the auspices of the International Society for Animal Genetics (ISAG) to define a sequence-based nomenclature for the genes of the DLA system. The remit of this committee includes: i) assignment of gene names; ii) rules for naming alleles; iii) assignment of names to published alleles; iv) assignment of names to new alleles; and v) rules for acceptance of new alleles.

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This first International Society for Animal Genetics (ISAG) dog major histocompatibility system (MHC) Nomenclature Report considers the rules for acceptance of dog leukocyte antigen (DLA) genes and alleles, together with an appropriate sequence based nomenclature. Names have been assigned to existing sequences, where appropriate. The report also includes sequence alignments (both nucleotide and amino acid) for DLA class II alleles, including data which has not been previously published.

There is a table for each class II locus, which lists all published and unpublished sequence data, with accession numbers and references, plus equivalents for new and previously used allele names.

The Committee would like to acknowledge the contribution of the IUIS Committee on Nomenclature of DLA Determinants (1) (a subcommittee of the Nomenclature Committee of the International Union of Immunological Societies), which started this work over 20 years ago.

In 1990, Klein (2) proposed the use of the term Cafa (from *Canis familiaris*) to describe the class I and II genes in the dog MHC region. However, many publications before and since have continued to use the term DLA. The Nomenclature Committee has affirmed the use of the term DLA. This proposal has the approval of Dr. Ronald Bontrop, the Editor of *Immunogenetics*, who maintains the register of MHC symbols for all species.

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Genes in the DLA complex

Official name	Locally assigned name	Molecular characteristics	References
–	DLA-A	?	23
–	DLA-79	Non-classical class I gene associated with 7.9-kb Hind III fragment	11–13
–	DLA-88	Class I gene associated with 8.8-kb Hind III fragment	11, 13
–	DLA-12	Non-classical class I gene associated with 12-kb Hind III fragment	11, 13
–	DLA-12a	Class I pseudogene associated with 12-kb Hind III fragment	11
–	C1pg-26	Not in DLA region. Class I processed gene associated with 2.6-kb Hind III fragment	11
–	DLA-53	Class I pseudogene associated with 5.3-kb Hind III fragment	11
–	DLA-64	Non-classical class I gene associated with 6.4-kb Hind III fragment	11, 13
–			
DLA-DRA1	DRA	DR alpha chain	24, 25
DLA-DRB1	DRB1	DR beta chain	23, 24
DLA-DRB1	DRBB1		17, 26
DLA-DRB2	DRB2	DRB pseudogene	24, 27
DLA-DRB2	DRBB2		17, 26
DLA-DQA1	DQA1	DQ alpha chain	24, 26
DLA-DQB1	DQB1	DQ beta chain	22, 24
–	DQB2	?pseudogene	22, 24
–	DPA	DP alpha chain	24
–	DPB1	DP beta chain	24
–	DPB2		24
–	DOB	DO beta chain	24
LMP2	LMP2		J.A. Gerlach, personal communication

Table 1

Assignment of DLA gene names

Class I

The assignment of official names for the class I genes has been considered by the committee. Studies suggest that four class I genes can be transcribed, and Table 1 lists those that have been identified to date.

Evidence from other species (cattle, horse, mouse, rat) suggests that there are different numbers of class I genes on different haplotypes. In cattle, there are no clear locus specific characteristics so that it is not possible to assign alleles to particular loci just from the sequence data (S. Ellis, personal communication).

Although there appear to be locus-specific characteristics which distinguish the different dog class I genes, the committee considers it premature to assign official DLA names to these genes and needs to examine more data before naming the genes. Evidence from family studies may be needed in the dog to confirm that particular alleles belong to the same allelic series, and more data on the mapping of genes in the dog MHC is necessary.

The original serological data in the dog may have to be ignored, as it was assumed that there were 3 expressed class I alleles, whereas later evidence (3, 4) showed that the originally defined

Definition of the hypervariable region boundaries for DLA class I and class II loci

	Inclusive codon boundaries for the hypervariable regions		
DLA locus	HVR 1	HVR 2	HVR 3
Class I: DLA-88	62–77	91–116	152–158
DRB1	8–16	26–38	56–74
DQA1	25	55	68–82
DQB1	9–13	26–37	57–75

Table 2

DLA-B locus codes for a class II molecule, thus making the serology difficult to interpret. An attempt will be made to correlate the original serological data with the current molecular data, by DNA sequencing some of the class II alleles from dogs used in the serology studies of the First, Second and Third Canine Immunology workshops (5–8).

Class II

Within the dog class II region, clear homologues have been identified for human HLA-DRA, -DRB, -DQA and -DQB genes. These will be named similarly, but the numbering of genes will be sequential, based on those numbers already in common use, and with no attempt to co-ordinate numbers between dog and human homologues. Thus DLA-DRB1 may or may not be a homologue of HLA-DRB1, as the identification of exact gene homologues may require considerably more sequence data than is currently available.

Table 1 also lists the DLA class II genes that have been identified to date. Where sufficient cloning and sequencing data have confirmed homology between the human and dog genes, official names have been assigned. Where such data are not yet available, such as for the putative DPA and DPB genes, no official names have been assigned.

Rules for naming alleles

The nomenclature described in this report is largely based on the human leukocyte antigen (HLA) nomenclature system (9), and the bovine leukocyte antigen (BoLA) system (10). However, we have decided to name alleles sequentially within a locus if they exhibit any polymorphism within defined hypervariable regions. This decision was

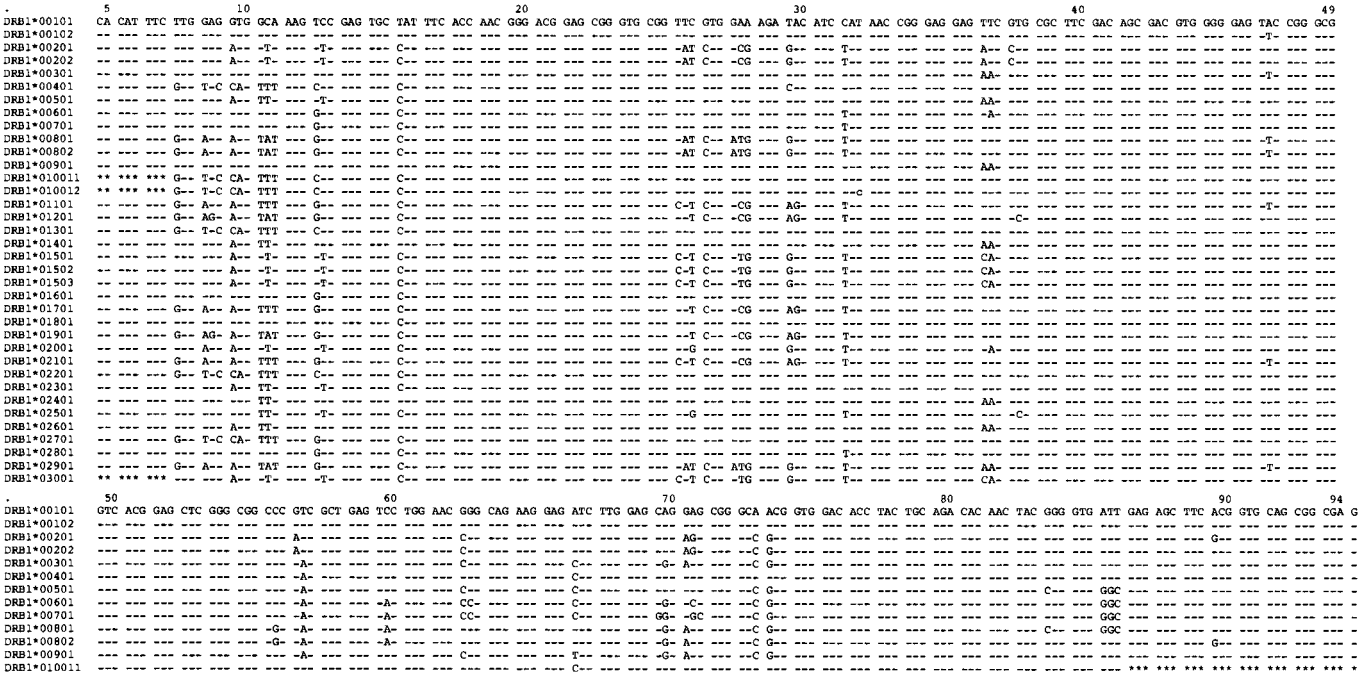

Fig. 1. **DLA-DRB1 nucleotide sequence alignment.**

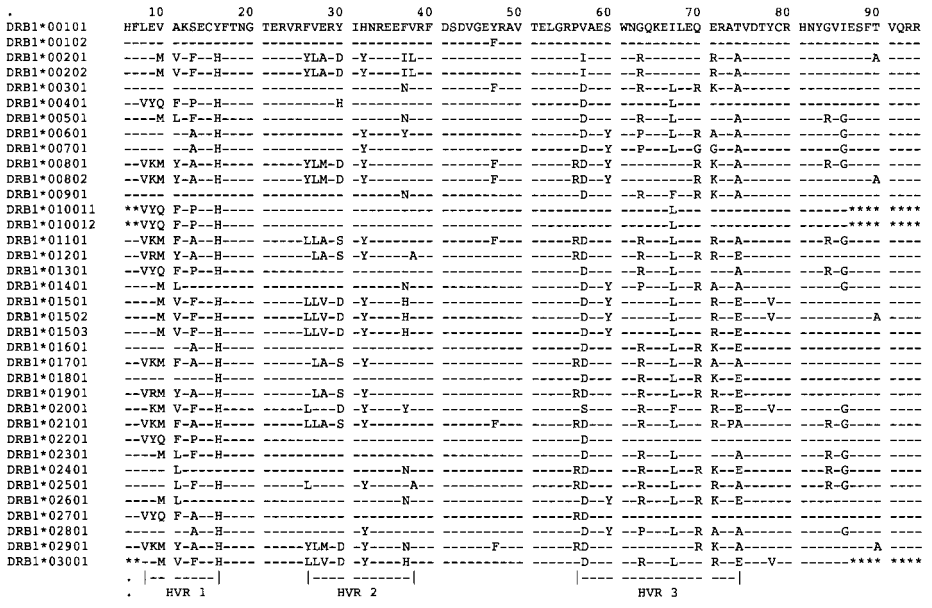

Fig. 2. **DLA-DRB1 amino acid sequence alignment.**

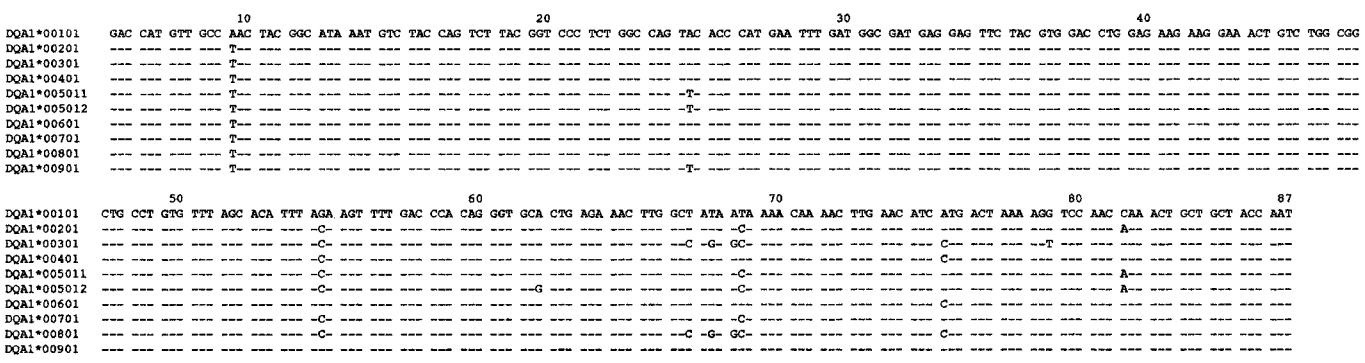

Fig. 3. **DLA-DQA1 nucleotide sequence alignment.**

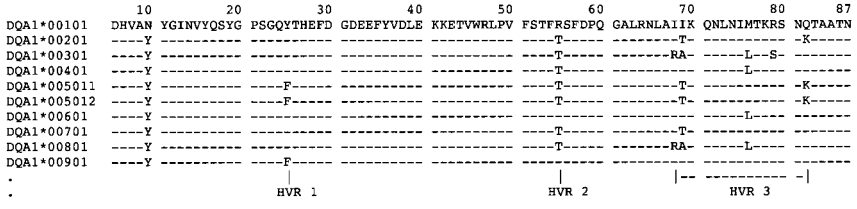

Fig. 4. **DLA-DQA1 amino acid sequence alignment.**

taken for several reasons. Firstly, data from other species suggest that alleles which share hypervariable regions (HVRs) also share antigen binding specificity and thus have functional similarity. Although there are no functional data nor crystalline structures yet available for the MHC loci of the dog, it seems reasonable to assume that these data will prove similar to those in other species, if, and when, such data

does become available. Secondly, it was felt that since any coding change in any of the HVR might cause the binding of a different peptide, then any such coding difference should result in a different major type allele name. Thirdly, the human HLA nomenclature system, (and also to some extent the BoLA nomenclature system), were originally based on serological data, which has resulted in the naming of class II major types to be mainly based on the first HVR. Also, the assignment of a new HLA-DRB allele, for example, may often take into consideration the serological data for that allele. There are no such serological data currently available for any of the dog MHC loci. Fourthly, although the concept of naming related alleles in some sort of hierarchical system is very attractive, there is no clear way in which this can be meaningfully done for the dog MHC at the current time. We have considered the use of dendograms to aid such a naming system for major types, but found that this tended to base the assignment of major types on the first HVR only. Since we wanted a system based on all three HVR, this was not acceptable to the committee. Fifthly, a precedent for such a system for naming alleles already exists in the human HLA nomenclature, for HLA-DPB, where a system based on six variable regions is used.

The extent of the HVR is well known for HLA-DRB1, but has not been defined for other HLA loci. We defined the HVR in DLA-

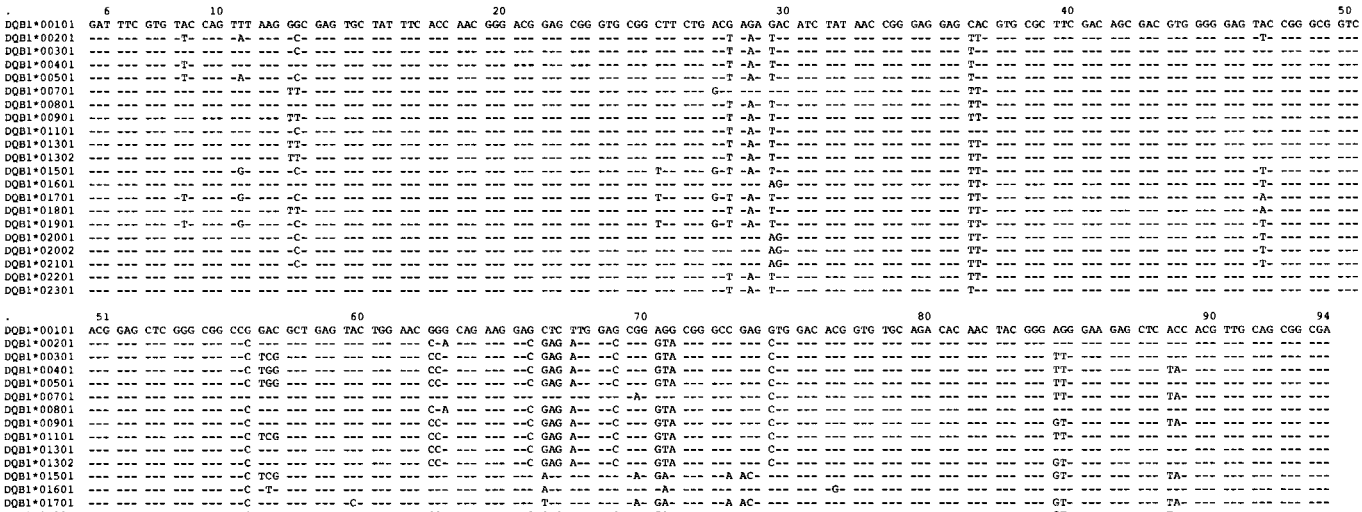

Fig. 5. **DLA-DQB1 nucleotide sequence alignment.**

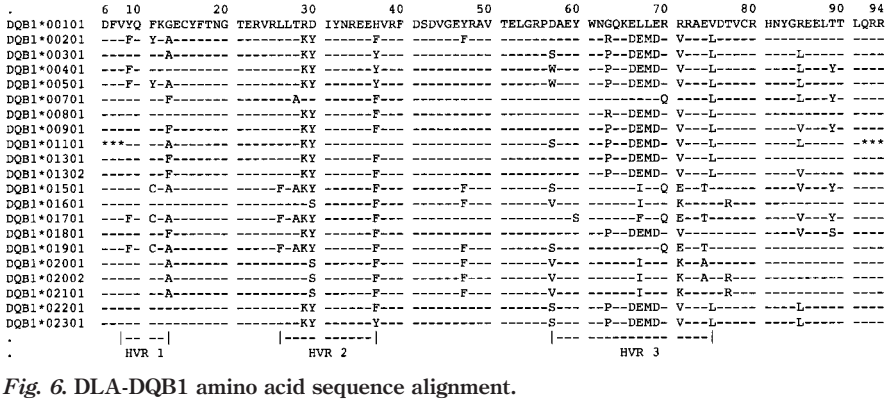

Fig. 6. **DLA-DQB1 amino acid sequence alignment.**

Accession numbers and references for DRB1 sequences

Official allele name	Previous allele names					Accession number	Reference
	Sarmiento et al. (16)	Wagner et al. (17)	Francino et al. (14)	Kennedy et al. (15)	Other		
DRB1*00101	Dw4	D1	–	–	–	M57529	16
DRB1*00102	Dw3	D3	–	–	–	M57528	16
DRB1*00102	–	–	–	–	Dw3	S76138	28
DRB1*00201	Dw1	D2	–	–	–	M57537	16
DRB1*00202	–	D2a	–	–	–	U44777	17
DRB1*00301	–	–	–	0902	–	AJ003012	15
DRB1*00401	D4	D4m[2]	–	–	–	M57532	16, 17
DRB1*00501	–	–	–	2302	–	AJ003017	15
DRB1*00501	–	D24[1]	–	–	–	AF098496	a
DRB1*00601	D6	D6m[2]	–	–	–	M57534	16, 17
DRB1*00701	D7	–	–	–	–	M57533	16
DRB1*00801	D8	D8m[2]	–	–	–	M57535	16, 17
DRB1*00802	–	–	–	08var2[1]	–	AJ012456	b
DRB1*00901	–	D9	–	–	–	M57531	16
DRB1*010011	–	–	D25[1]	–	–	AF016910	c
DRB1*010012	–	–	Cafa-10	–	1102[1]	X93572	14
DRB1*01101	–	–	Cafa-11	–	1112[1]	X93573	14
DRB1*01201	–	–	–	1902	–	AJ003015	15
DRB1*01301	–	D13	–	–	–	U44778	17
DRB1*01401	–	D14	–	–	–	U44779	17
DRB1*01501	D15/Dw8	D15m[2]	–	–	–	M57536	16, 17
DRB1*01502	–	–	–	1502	–	AJ003013	15
DRB1*01503	–	–	–	1503	–	AJ003014	15
DRB1*01601	–	–	–	18var1[1]	–	AJ012454	b
DRB1*01701	–	D17	–	–	–	U44780	17
DRB1*01801	–	D18	–	–	–	U44781	17
DRB1*01901	–	D19	–	–	–	U44782	17
DRB1*02001	–	D20	–	–	–	U58684	17
DRB1*02101	–	D21	–	–	–	U44783	17
DRB1*02201	–	D22	–	–	–	U58685	17
DRB1*02301	–	–	–	2301	–	AJ003016	15
DRB1*02401	–	–	–	2401	–	AJ003018	15
DRB1*02501	–	–	–	2501	–	AJ003019	15
DRB1*02601	–	–	–	2601	–	AJ003020	15
DRB1*02701	–	drb 26	–	–	–	AF061039	29
DRB1*02801	–	drb 25	–	–	–	AF061038	29
DRB1*02901	–	–	–	08var1[1]	–	AJ012455	b
DRB1*03001	–	–	D23[1]	–	–	AF016911	c
partial sequence	–	–	D24[1]	–	–	AF016912	c
partial sequence	–	–	–	–	1-Dob-A[1]	M30129	d
partial sequence	–	–	–	–	1-Dob-B[1]	M30130	d
partial sequence	–	–	–	–	2-Dob[1]	M30131	d
partial sequence	–	–	–	–	3-Lab[1]	M30132	d
partial sequence	–	–	–	–	4-Pood[1]	M30133	d

[1] unpublished alleles; [2] modification of original Sarmiento sequence, corrected by Wagner, same accession number

References: a=Wagner, GenBank 1998; unpublished; b=Kennedy, submitted; c=Francino, GenBank 1997, unpublished; d=Motoyama, GenBank 1996, unpublished

Table 3

DRB1 to be the same as those in HLA-DRB1. The DLA-DQB1 gene is very like DLA-DRB1, and thus we defined very similar regions as the HVR. For DLA-DQA1, which is much less variable, we selected the most polymorphic areas as the HVR. The extent of these regions are given in Table 2.

This system for naming alleles will result in more major types than in the HLA or BoLA systems. Since the current HLA system may soon run out of new allele numbers for some loci (e.g. HLA-DPB), we have introduced the use of an extra digit in the allele names, as compared to HLA and BoLA.

The rules used for the establishment of allele names are:

1. Names will be based on the amino acid sequences.
2. Allele names will consist of 5 or 6 digits; the first three digits indicating the major type, the fourth and fifth digits indicating the subtype, and the sixth digit (if present) indicating non-expressed variation (silent substitutions). To aid recognition of DLA alleles, we recommend that alleles should be verbalised as in the following example: DRB1*01501 = "DRB1* zero-fifteen, zero-one".
3. Class I alleles within a single major type will be identical for the three HVR in exons 2 and 3. Differences outside the HVR will be indicated as subtypes of the major type.
4. Class II alleles within a single major type will be identical for the three HVR in exon 2. Differences outside the HVR will be indicated as subtypes of the major type.
5. If a name is given on the basis of a partial sequence, the first full-length sequence that includes the original partial sequence will assume the allele name.
6. If minor sequence errors are identified the sequence will be corrected.

Assignment of names to be published and new alleles

Using the above guidelines, and the HVR definitions, each locus was considered in turn, and allele names were assigned.

Class I

No official names for the class I alleles will be given until it has been clarified that they all belong to the allelic series as published (11–13)

Accession numbers and references for DQA1 sequences

	Previous Allele names				
Official Allele name	Sarmiento et al. (19) (partial sequences)	Polvi et al. (18) (partial sequences)	Wagner et al. (20)	Accession number	Reference
DQA1*00101	0101	–	–	M74907	19
DQA1*00101	–	–	Dqa2	U44786	20
DQA1*00201	0201	–	–	M74909	19
DQA1*00201	–	–	Dqa9[1]	U75455	a
DQA1*00301	–	0301	–	Y07944	18
DQA1*00401	–	0203	–	Y07943	18
DQA1*00401	–	–	Dqa4	U44788	20
DQA1*005011	0202	–	–	M74910	19
DQA1*005011	–	–	Dqa3	U44787	20
DQA1*005012	–	–	Dqa5	U44789	20
DQA1*00601	–	0103	–	Y07942	18
DQA1*00601	–	–	Dqa6	U44790	20
DQA1*00701	–	–	Dqa7	U44842	20
DQA1*00801	–	–	Dqa8[1]	U61400	a
DQA1*00901	0102	–	–	M74908	19
DQA1*00901	–	–	Dqa1	U44785	20

[1] unpublished sequences
References: a=Wagner, GenBank 1996, unpublished

Table 4

Accession numbers and references for DQB1 sequences

Official allele name	Previous allele names			Francino[a]	Accession number	Reference
	Sarmiento et al. (21) (partial sequences)	Polvi et al. (18) (partial sequences)	Wagner et al. (22)[2]			
DQB1*00101	0101[2]	–	–	–	M90802	21
DQB1*00101	–	–	dqb2[2]	–	AF043147	22
DQB1*00101	–	–	–	dqb0102[1]	AF016905	a
DQB1*00201	0201[2]	–	–	–	M90803	21
DQB1*00201	–	–	dqb3[2]	–	AF043148	22
DQB1*00201	–	–	–	dqb0203[1]	AF016908	a
DQB1*00301	0301[2]	–	–	–	M90804	21
DQB1*00301	–	–	dqb6[2]	–	AF043151	22
DQB1*00401	0401[2]	–	–	–	M90805	21
DQB1*00401	–	–	dqb5[2]	–	AF043150	22
DQB1*00501	–	0501[2]	–	–	Y07947	18
DQB1*00501	–	–	dqb12[2]	–	AF043157	22
DQB1*00701	–	0701[2]	–	–	Y07949	18
DQB1*00701	–	–	dqb4[2]	–	AF043149	22
DQB1*00701	–	–	–	dqb1001[1]	AF016907	a
DQB1*00801	–	0801[1, 2]	–	–	AF043492	b
DQB1*00801	–	–	dqb1[2]	–	AF043167	22
DQB1*01101	–	–	–	dqb1101[1]	AF016904	a
DQB1*01301	–	–	dqb13	–	AF043158	22
DQB1*01302	–	–	dqb14	–	AF043159	22
DQB1*01303	–	–	dqb7	–	AF043152	22
DQB1*01303	–	–	–	dqb0901[1]	AF016906	a
DQB1*01501	–	–	dqb15	–	AF043160	22
DQB1*01601	–	–	dqb16	–	AF043161	22
DQB1*01701	–	–	dqb17	–	AF043162	22
DQB1*01801	–	–	dqb18	–	AF043163	22
DQB1*01901	–	–	dqb9	–	AF043154	22
DQB1*02001	–	–	dqb20	–	AF043165	22
DQB1*02002	–	–	dqb19	–	AF043164	22
DQB1*02101	–	–	dqb11	–	AF043156	22
DQB1*02201	–	–	dqb10	–	AF043155	22
DQB1*02301	–	–	dqb8	–	AF043153	22
DQB1*02301	–	–	–	dqb0303[1]	AF016909	a
partial sequence	–	0302	–	–	Y07946	18
partial sequence	–	0601	–	–	Y07948	18
partial sequence	–	0202	–	–	Y07945	18

[1] unpublished sequences. [2] sequence identities confirmed by J.L. Wagner, October 1998
References: a=Francino, GenBank 1997, unpublished, b=Polvi, GenBank 1998, unpublished

Table 5

Class II

Nucleotide and amino acid alignments are given for DLA-DRB1, -DQA1 and -DQB1, in Figs. 1–6.

References and accession numbers for each sequence for DLA-DRB1, -DQA1 and -DQB1, are given in Tables 3, 4 and 5, respectively. The equivalents for all previous names are also indicated. Due to some partial sequences, some of the equivalents for DQB are probable rather than definite.

DRB1: references 14–17, J. M. Angles confirmatory sequence for DRB1*02401 (personal communication).

DQA1: references 18–20.

DQB1: references 18, 21, 22.

Conditions for acceptance of new sequences

1. For class I genes full-length exon 2 and exon 3 sequences are required.
2. For class II genes the sequence for the first domain (exon 2) must be included.
3. Sequencing should be performed on both strands of the template DNA.
4. Where a sequence is obtained from cDNA or where polymerase chain reaction (PCR) products are subcloned prior to sequencing, a minimum of three clones must be sequenced. Alternatively, identical sequences from two different dogs are acceptable.
5. If direct sequencing of PCR amplified material is performed from a homozygous animal, products from at least two separate PCR reactions should be sequenced.
6. If direct sequencing of PCR amplified material is performed from a heterozygous animal, products from at least two separate PCR reactions should be sequenced, and the sequence should also be confirmed by cloning and sequencing.
7. Where possible sequences should be confirmed by another laboratory.
8. An accession number in a nucleotide sequence database should be obtained.
9. Submission of a sequence to the Nomenclature Committee should include a computer-readable copy of the sequence.
10. DNA, if possible from an animal homozygous for the allele, should be made available for a central repository maintained by the Nomenclature Committee. This DNA will be amplified and made available as reference material for other researchers.

Submission of new sequences

Sequences of new DLA genes or alleles should be submitted to the chairman of the DLA Nomenclature Committee, Lorna Kennedy, to receive official names. The sequence data or accession number(s) should be sent by e-mail to the address given. Electronic submissions of sequence data are preferred. All sequence information will remain confidential until published or available on sequence databases. The Committee encourages the use of DLA as a keyword to ensure sequences may be found in database searches.

The use of numbers or names for alleles, genes or specificities which pre-empt formal designations such as "DLA-E", "DQA1*00401" or "DLA-DM" before consideration by the Nomenclature Committee is strongly discouraged.

Sequence database

The committee plans to establish a database of DLA allele sequences which would also include other data, such as how the sequence was obtained, and how many clones were sequenced, etc. We will also record the breed of dog in which the sequence was found. This data will not be made public at this time, however, as such information may cause assumptions to be made about the restriction of particular alleles to certain breeds. (This is in keeping with the policy of the human HLA nomenclature committee, which also records the ethnic origin of all sequences submitted, but does not release that information.) Most of the DLA alleles listed in this report have been found in more than one breed, and many have been found in most breeds tested ($n=60$). To date, only one allele (DLA-DRB1*02401) has been found to be limited to a single breed (Japanese Akita). However, as there are over 250 known breeds, there are still many breeds that have not been sampled, so DRB1*02401 may yet be found in another breed.

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