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Nucleotide sequence of a dog class I cDNA clone

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The major histocompatibility complex (MHC) of the dog, termed DLA, can be divided into three serologically defined loci, designated *DLA-A*, *DLA-B*, and *DLA-C* (Bull et al. 1987), and a fourth region (termed *DLA-D*) defined by mixed leucocyte culture reactivity (Deeg et al. 1986). The DLA-A antigens are characterized as class I molecules by their association with β_2-microglobulin (Krumbacher et al. 1986) and by the correlation of serologic DLA-A specificities with protein polymorphisms (van der Feltz and Ploegh 1984; Neefjes et al. 1986). The *DLA-B* locus codes for class II antigens which are constitutively expressed on almost all circulating lymphocytes in the dog (Doxiadis et al. 1989). The DLA-C antigens are thought to be weakly expressed class I antigens (van der Feltz and Ploegh 1984). Recently, allelic polymorphism within the class I and class II regions of the *DLA* complex has been studied by restriction fragment length polymorphism (RFLP) analysis (Sarmiento and Storb 1988a, b, 1989). Based on the RFLP studies, the *DLA* class I region has been presumed to have at least eight class I genes, including the canine homologues of *HLA-A, -B* and *HLA-E* genes (Sarmiento and Storb 1989). Moreover, the DNA polymorphism detected by the human *HLA-B7* probe corresponded to the serologically defined *DLA-A* allelic series (Sarmiento and Storb 1989). In this report, we describe the nucleotide sequence of a cDNA clone which encodes a class I gene in the dog.

To isolate DLA class I cDNA clones, a lambda ZAP phage cDNA library (Stratagene, La Jolla, California) constructed from the spleen of a dog (serotyped as *DLA-A9, B6, C11*) was screened by plaque hybridization (Benton and Davis 1977) using a ^{32}P-labeled human HLA-B7 cDNA clone (Sood et al. 1981) as a probe. The hybridization was performed in a buffer containing 50% (v/v) formamide, 0.1% Denhardt's solution, 5× saline-sodium phosphate-EDTA (SSPE; 0.9 *M* NaCl, 0.05 *M* NaH_2PO_4, 5 m*M* ethylenediaminetetraacetate), 5% dextran sulfate, 1% sodium dodecyl sulfate (SDS), and 200 μg/ml salmon sperm DNA overnight at 42 °C. The filters were washed twice at room temperature in 2×SSPE, once in 2×SSPE, 0.5% SDS, and once in 0.5×SSPE. Twenty clones were isolated and plaque-purified after screening over 600 000 plaques. The cDNA inserts were contained within a phagemid, pBluescript SK(⁻), which was excised from the lambda ZAP phage in vivo by helper virus (Short et al. 1988). Single- and double-stranded DNA preparations were made for sequencing. The sequencing primers included T3 and T7 promoters flanking the pBluescript polylinker and three synthetic oligonucleotides termed A1 (spanning codons 1–9 in the sense strand, 5′-CGAATTCCACTCCCTG-AGGTATTTCTAC-3′), A2 (spanning codons 279–284 in the complementary strand, 5′-GACAATGGTGGACA-GAGG-3′), and A3 (spanning codons 201–209 in the complementary strand, 5′-AGAATTCCAGCGCCCAG-CACCTCAGGGT-3′). Four additional synthetic oligonucleotides (kindly provided by Y. Choo) based on the human *HLA-B27* gene sequence were used for sequencing and were termed SP83–88 (spanning codons 83–88 in the sense strand), SP171–176 (spanning codons 171–176 in the sense strand), SP246–251 (spanning codons 246–251 in the sense strand), and SPC221–226 (spanning codons 221–226 in the complementary strand). The complete sequences of six full-length clones were determined on both strands using the dideoxy chain termination procedure (Sanger et al. 1977) and Sequenase (US Biochemicals, Cleveland, Ohio).

The nucleotide and predicted amino acid sequence of the longest [1511 base pairs (bp)] DLA class I cDNA clone (pBT-I16, available to interested investigators) is illus-

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The nucleotide sequence data reported in this paper have been submitted to the GenBank nucleotide sequence database and have been assigned the accession number M32283.

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Met Glu Val Val Met Pro Arg Ala Leu Leu Val Leu Leu Ser Ala Ala Leu Ala Leu Thr    -5
ATG GAG GTG GTG ATG CCG CGA GCC CTC CTC GTG CTG CTG TCG GCG GCC CTG GCC CTG ACC    60

Pro Thr Arg Ala|Gly Ser His Ser Leu Arg Tyr Phe Tyr Thr Ser Val Ser Arg Pro Gly    16
CCG ACC CGG GCG|GGC TCC CAC TCC CTG AGG TAT TTC TAC ACC TCC GTG TCC CGG CCC GGC   120

Ala Gly Asp Pro Arg Phe Ile Ala Val Gly Tyr Val Asp Asp Thr Gln Phe Val Arg Phe    36
GCG GGG GAC CCC CGC TTC ATC GCC GTC GGC TAC GTG GAC GAC ACG CAG TTC GTG CGG TTC   180

Asp Ser Asp Ala Ala Thr Gly Arg Met Glu Pro Arg Ala Pro Trp Val Glu Gln Glu Gly    56
GAC AGC GAC GCG GCC ACT GGG AGG ATG GAG CCG CGG GCG CCG TGG GTG GAG CAG GAG GGG   240

Pro Glu Tyr Trp Asp Arg Gln Thr Arg Thr Ile Lys Glu Thr Ala Arg Thr Phe Arg Val    76
CCG GAG TAT TGG GAC CGG CAG ACG CGG ACC ATC AAG GAG ACC GCA CGG ACT TTC CGA GTG   300

Asp Leu Asp Thr Leu Arg Gly Tyr Tyr Asn Gln Ser Glu Ala|Gly Ser His Thr Arg Gln    96
GAC CTG GAC ACC CTG CGC GGC TAC TAC AAC CAG AGC GAG GCC|GGG TCT CAC ACC CGC CAG   360

Thr Met Tyr Gly Cys Asp Leu Gly Pro Asp Gly Arg Leu Leu Arg Gly Tyr Ser Gln Asp   116
ACC ATG TAC GGC TGT GAC CTG GGG CCC GAC GGG CGC CTT CTC CGC GGG TAC AGT CAG GAC   420

Ala Tyr Asp Gly Ala Asp Tyr Ile Ala Leu Asn Glu Asp Leu Arg Ser Trp Thr Ala Ala   136
GCC TAC GAC GGC GCC GAT TAC ATC GCC CTG AAC GAG GAC CTG CGC TCC TGG ACC GCG GCG   480

Asp Thr Ala Ala Gln Ile Thr Gln Arg Lys Trp Glu Ala Ala Gly Val Ala Glu Leu Gln   156
GAC ACG GCG GCG CAG ATC ACC CAG CGC AAG TGG GAA GCG GCA GGT GTA GCA GAG CTA CAA   540

Trp Arg Asn Tyr Leu Glu Thr Thr Cys Val Glu Trp Leu Arg Arg Tyr Leu Glu Met Gly   176
TGG AGG AAC TAC CTG GAG ACG ACG TGC GTG GAG TGG CTG CGG AGG TAC CTG GAG ATG GGG   600

Lys Glu Thr Leu Leu Arg Ala|Asp Pro Pro Ser Thr Arg Val Thr His His Pro Val Ser   196
AAG GAG ACG CTG CTG CGC GCA|GAC CCC CCA AGC ACA CGT GTG ACC CAC CAC CCC GTC TCT   660

Asp His Glu Val Thr Leu Arg Cys Trp Ala Leu Gly Phe Tyr Pro Ala Glu Ile Thr Leu   216
GAC CAT GAG GTC ACC CTG AGG TGC TGG GCG CTG GGC TTC TAC CCT GCG GAG ATC ACC CTG   720

Thr Trp Gln Arg Asp Gly Glu Asp Gln Thr Gln Asp Thr Glu Val Val Asp Thr Arg Pro   236
ACC TGG CAG CGG GAT GGG GAG GAC CAG ACC CAG GAC ACA GAG GTT GTG GAC ACA AGG CCT   780

Ala Gly Asp Gly Thr Phe Gln Lys Trp Ala Ala Val Val Val Pro Ser Gly Gln Glu Gln   256
GCA GGA GAT GGG ACC TTC CAG AAG TGG GCG GCC GTG GTG GTG CCT TCT GGA CAG GAG CAG   840

Arg Tyr Thr Cys His Val Gln His Glu Gly Leu Pro Glu Pro Ile Thr Arg Arg Trp|Glu   276
AGA TAC ACG TGC CAC GTC CAG CAT GAG GGG CTG CCG GAG CCT ATC ACG CGG AGA TGG|GAG   900

Pro Ser Pro Leu Ser Thr Ile Val Ile Val Ser Ile Ala Ala Leu Val Leu Leu Val Val   296
CCT TCC CCT CTG TCC ACC ATT GTC ATC GTC AGC ATT GCT GCT CTG GTT CTC CTC GTG GTC   960

Ala Gly Val Ile Gly Ala Val Ile Trp Arg Lys Gln Arg Ser|Gly Gly Lys Gly Pro Gly   316
GCT GGG GTG ATT GGA GCT GTG ATC TGG AGG AAG CAG CGC TCA|GGA GGA AAA GGA CCA GGC  1020

Tyr Ser His Ala Ala|Arg Asp Asp Ser Ala Gln Gly Ser Asp Val Ser Leu Thr Ala Pro   336
TAC TCT CAT GCT GCA|CGT GAT GAC AGT GCC CAG GGC TCT GAT GTG TCT CTG ACA GCT CCT  1080

Arg|Val ***                                                                      338
AGA|GTG TGA GACCAGCTGCCTGTGGGACTGACGGATGCAAGATGTGTTCACATCTCACGTGATGACATCAACAACC  1156
CTGGCTTGTCTCTGCAAACAGTGTCAGGATGTGCCTGTGTCCCTAGGAGCATAATGTGAGGAGGTGGGGAGATTGGCCC  1235
ACCCTGCCCACCATGACCTGTCCCTAATCTGATGTGCGCTCTCCTCTCTGATGTGCTTTCCTGTCCAGGAGAGGCAGGG  1314
CTGGACCATCTCCATCCCTGTCTTTGTTTCATGTTGAGTACTAATCTCTTACTATCCGATTGAAAATAAGAATCCAGAT  1393
ATGAGTTTGTGTTTCCTGAGTCTTGGGATGTGGGGCTGATGAGGTAATAAAAGGAGATTTGTGAAGTTGAGAGAGCAAA  1472
TAAATGGAAGCCCTGAGAACCTTCCAGAAAAAAAAAAAA                                          1511
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Fig. 1. Nucleotide sequence and predicted amino acid sequence of a DLA class I cDNA clone. The exon borders are indicated by *vertical lines*. The two putative polyadenylation signals in the 3′ untranslated region are *underlined*. The *numbers* indicate the amino acid (*top line*) and nucleotide (*bottom line*) sequence positions. The *asterisks* represent the stop codon (TGA).

trated in Figure 1. The longest open-reading frame contains 362 codons flanked by 425 bp of the 3′ untranslated region. The first of the two putative polyadenylation signals (5′-AATAAA-3′) is located 349 nucleotides downstream from the termination codon (TGA) and the second polyadenylation signal is found 22 bp upstream from the poly(A) tail (Fig. 1). The signal peptide, which contains two in-frame methionine (ATG) codons at positions −24 and −20, is composed of 24 N-terminal residues. The remaining 338 amino acids represent the extracellular portion of the alpha chain (α1 domain, 90 residues; α2 domain, 93 residues; α3 domain, 92 residues), the transmembrane region (35 residues), and the cytoplasmic tail (28 residues). The dog sequence is characterized by an insertion of 3 bp in exon 3 (at the position designated Leu-155) and by a deletion of four codons from exon 5. Four cysteines involved in disulfide bonds are present in the extracellular portion at positions 101, 165, 204, and 260. The conserved site for N-linked glycosylation, Asn-Gln-Ser, is found at positions 86–88 and the serine phosphorylation site (SD/EXSL) is present between residues 329 and 333 of the cytoplasmic domains of the dog clone. The *DLA* class I sequence also contains the Arg-Phe-Asp-Ser sequence at positions 35–38 which is found in other class I antigen α1 domains and in MHC class II antigen β1 domains (Young et al. 1987).

Figure 2 summarizes the comparison of the predicted amino acid sequences of class I genes from the dog, cat, ox, and human. In the coding region, the DLA class I clone appears to be most similar to the cat class I gene with 84.5% overall nucleotide and 77.5% amino acid sequence similarity with the *pFLA24* sequence (Yuhki et al. 1989). The dog class I sequence also has 84.4% and 82.9% nucleotide similarity with the bovine BL3-7 clone (Ennis et al. 1988) and the human *HLA-A11* allele (Cowan et al. 1987), respectively (Fig. 2). Pairwise comparison of the individual domains reveals that the α1 and α3 domains of the dog class I clone have 81% and 88% amino acid similarity with those of the human *HLA-A11* allele, respectively (Fig. 2). The DLA α2 domain has 84.9% amino acid similarity with the BoLA BL3-7 clone, while the transmembrane and cytoplasmic domains of the DLA clone are most closely related to those of the cat class I clones with 60% and 75% protein sequence similarity,

α1	10	20	30	40	50	60	70	80	90
DLA-A	GSHSLRYPYT	SVSRPGAGDP	RFIAVGYVDD	TQFVRFDSDA	ATGRMEPRAP	WVEQEGPEYW	DRQTRTIKET	ARTFRVDLDT	LRGYYNQSEA
FLA	-------F--	A-----L-E-	---S------	----------	PNP-E-----	-M--------	--N--IYLD-	-QIS--N-N-	F-R------S
BoLA	-------F--	G-----L-E-	----------	----------	-PNPR---V-	-M--------	--N--IY-D-	-QI-----N-	---------T
HLA-A11	----M--F--	------R-E-	----------	----------	-SQ-------	-I--------	-QE--NV-AQ	SQ-D----G-	----------

α2	100	110	120	130	140	150	160	170	180	183
DLA-A	GSHTRQTMYG	CDLGPDGRLL	RGYSQDAYDG	ADYIALNEDL	RSWTAADTAA	QITQRKWEAA	GVAELQWRNY	LETTCVEWLR	RYLEMGKETL	LRA
FLA	---NI-R---	--VD--R-F-	------S---	K---------	----------	---R------	----/-E---	--G------A	K--D------	V--
BoLA	---NI-A---	--V-------	--FW-FG---	R-------E-	----------	---K------	-A--/T----	--GE------	----N--D--	---
HLA-A11	----I-I---	--V-S---F-	---R------	K---------	-------M--	---K------	HA--/-Q-A-	--GR--- --	----N-----	Q-T

α3	193	203	213	223	233	243	253	263	273	275
DLA-A	DPPSTRVTHH	PVSDHEVTLR	CWALGFYPAE	ITLTWQRDGE	DQTQDTEVVD	TRPAGDGTFQ	KWAAVVVPSG	QEQRYTCHVQ	HEGLPEPITR	RW
FLA	ES-N----R-	-I--R-----	----------	---------Q	-H-----L-E	----------	----------	E---------	-K------NL	--
BoLA	---KAH----	SI--R-----	--------E-	-S-----E--	-----M-L-E	---S------	----L-----	E------R--	----Q--L-L	--
HLA-A11	---K-HM---	-I----A---	----------	----------	-------L-E	----------	----------	E---------	-----K-L-L	--

TM	285	294	304	310	CYT 320	330	338	% IDENTITY WITH DLA-A	
DLA-A	EPSPLSTIVI	VSIAA/LVLL	VVAGVIGAVI	////WRKQRS	GGKGPGYSHA	ARDDSAQGSD	VSLTAPRV	NUCLEOTIDE	AMINO ACID
FLA	---S-PF-T-	LG-I-GVAV-	--TV-V----	////---KC-	-----I--QP	-----T----	S--M--K-	84.5	78.1
BoLA	--P/QTSFL-	MG-IVG----	---L-A----	////---K--	-E--RI-TQ-	-SS-------	----V-K-	84.4	77.8
HLA-A11	-L-SQP--P-	-G-I-G----	/G-VIT---V	AAVM--RKS-	DR--GS-TQ-	-GS-------	-----CK-	82.9	76.9

Fig. 2. Alignment of predicted amino acid sequences and domain structures of class I molecules from dog, cat, ox, and human. The standard one-letter amino acid code is used. The *numbers* indicate the DLA class I cDNA amino acid sequence which is given in full (*top line*). *Dashes* indicate sequence identity with the top line. *Slashes* indicate gaps introduced to maximize alignment. The sequences have been published elsewhere as follows: *pFLA24* (Yuhki et al. 1989), *BoLA-BL3-7* (Ennis et al. 1988), and *HLA-A11* (Cowan et al. 1987).

respectively. Thus, the dog class I clone appears to be closely related to particular class I alleles of other species, supporting the hypothesis of trans-species evolution of MHC genes (Klein 1987). Most of the amino acid differences are found at positions reported to have high variability in other species (Fig. 2; Parham et al. 1988). The *DLA* class I sequence contains 13 dog-specific residues at Asp-19, Thr-66, Ile-67, Glu-69, Arg-72, Leu-155 (3 bp insert), Thr-163, Asp-233, Val-284, Ala-289, Gly-298, Gln-308, and Arg-337. The dog sequence shares eight residues with one or both of the *FLA* class I alleles (Yuhki et al. 1989) at Ser-114, Met-175, Arg-189, Ile-271, Leu-280, Pro-315, His-319, and Pro-336. Some of the latter substitutions may be unique to the carnivore lineage.

Further comparison of the dog and human class I sequences (Parham et al. 1989) demonstrates that the dog class I cDNA clone shares a total of 31, 25, and 22 locus-specific nucleotides with the human *HLA-A*, *-B*, and *-C* loci, respectively (data not shown). The latter finding, the percent nucleotide and amino acid similarity, and the length of the peptide encoded by the dog cDNA suggest that the *DLA* class I gene reported in this paper represents a canine homologue of the *HLA-A* locus. Based on linked polymorphisms at eight positions in exon 4, the *HLA-A* sequences have been divided into two groups: *HLA-A2/A28* family and *HLA-A1/A3/A11* family (Parham et al. 1989). The dog sequence shares six out of eight characteristic nucleotide substitutions in exon 4 with members of the *HLA-A1/A3/A11* family, in contrast to sharing only two out of eight positions with the *HLA-A2/A28* family (data not shown). This is in agreement with our previous finding of cross-reactivity between dog lymphocytes and human alloantisera to the *HLA-A1/A3/A11* family of molecules (unpublished observations). Moreover, all chimpanzee *ChLA-A* alleles described thus far have been related to alleles of the *HLA-A1/A3/A11* family (Parham et al. 1989).

In conclusion, it is worth noting that the sequence data presented here are representative of all the class I clones isolated from the dog spleen cDNA library. This finding is consistent with the expression of a single class I gene in the dog. It also suggests that the DLA class I clone reported here is functional despite the insertion of a codon in exon 3. The other class I genes detected by RFLP studies of dog genomic DNA may represent pseudogenes or genes that are transcribed at very low levels in the adult spleen. We propose that the dog class I gene reported in this paper be termed the *DLA-A* gene and that the sequence be designated the *DLA-A9* allele. Further sequence analysis of other *DLA-A* types will elucidate the degree of allelic variation in the class I region of the canine MHC.

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