

SEQUENCE REGISTER

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Conservation of *Tcr-gV5* and limited allelic sequence polymorphism of the other *Tcr-gV* genes used by mouse tissue-specific gd-T lymphocytes

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The mouse *Tcr-g* locus comprises seven *Tcr-gV*, four *Tcr-gJ*, and four *Tcr-gC* segments which generate only six major types of functional g chains, Vg7-, Vg4-, Vg6-, or Vg5-Jg1-Cg1, Vg2-Jg2-Cg2, and Vg1-Jg4-Cg4 (Brenner et al. 1988). A complete analysis of restriction fragment length polymorphism (RFLP) of the *Tcr-g* locus in wild and inbred mice suggested its relative conservation compared to other loci of the immunoglobulin (*Ig*) gene family (Roger et al. 1993a). Three haplotypes have been characterized in laboratory mice: *gA*, *gB*, and *gC*, represented by BALB/c, DBA/2, and AKR prototypes. *Tcr-gA* and *-gC* haplotypes are highly related. By contrast, *Tcr-gB*, likely inherited from Asian mouse subspecies, appeared very different by RFLP analysis. Yet only partial sequence data have been reported on *gA* and *gB Tcr-gV* genes (Roger and Seman 1992; Roger et al. 1993c; Kalataradi et al. 1994). Here, the complete sequence of all *Tcr-gV* genes of the two haplotypes is described.

Tcr-gV1, *-V2*, and *-V3* genes from *Tcr-gB* L₁ mice were co-amplified by polymerase chain reaction PCR from T lymphocytes cDNA using leader and pan *Tcr-gC* primers, cloned in M13, and subsequently sequenced (Fig. 1). When compared with BALB/c, *Tcr-gB-V1* sequence exhibits 16 nucleotide differences leading to 10 amino acid changes (n° 3, 7, 12, 23, 27, 29, 32, 42, 50, and 62). *Tcr-gB-V2* diverges from that of BALB/c by 7 nucleotides and 6 amino acid substitutions (n° 16, 24, 60, 63, 74, and 80). Finally, *Tcr-gV3* genes exhibit 6 nucleotide changes leading to 6 amino acid replacements (n° 12, 27, 31, 32, 73, and 74). As expected from RFLP analysis, the above results indicate that *Tcr-gV1*, *-V2*, and *-V3* genes present a high allelic variation superior to that found among *Tcr-gV* alleles (Smith et al. 1986; Roger et al. 1993c). *Tcr-gV1*, *-V2*, and *-V3* sequences characterized in L₁ mice are identical to AKR sequences for the corresponding regions described by Kalataradi and co-workers (1994).

Tcr-gB-V4, *-V5*, *-V6*, and *-V7* from L₁ display fewer variations from their *Tcr-gA* counterparts. Both *Tcr-gV4* and *-V6* exhibit 4 nucleotide substitutions leading to 3 amino acid changes (n° 12, 57, and 78 for *Tcr-gV4* and n° 26, 44, and 56 for *Tcr-gV6*). The L₁ *Tcr-gV7* sequence is identical to that isolated from the BW 51-47 cell line of AKR (*Tcr-gB*) origin (Pelkonen et al. 1987) and reveals two adjacent nucleotide permutations leading to a single amino acid change (n° 62) compared with *Tcr-gA*. Of interest, *Tcr-gV5* is entirely conserved between *Tcr-gA* and *-gB* haplotypes. This gene is the first rearranged during ontogeny and is expressed on epidermal dendritic T cells in association with Vd1. Moreover, this Vg5/Vd1 Tcr exhibits no junctional diversity, suggesting a specificity for a monomorphic ligand directly depending on the V sequence. The conserved structure of *Tcr-gV5* might reflect a selective pressure necessary to preserve recognition of this monomorphic ligand likely present on keratinocytes (Havran et al. 1991).

Altogether, *Tcr-gV* genes located at the 5' end of the *Tcr-g* locus (*Tcr-gV7*, *-V4*, *-V6*, and *-V5*) are more conserved than those genes

located at the 3' end (*Tcr-gV1* and *-V2*). Interestingly, gd T cells expressing these 5' end genes are mostly found in epithelia. Their *Tcr* usually display limited diversity (Tonegawa et al. 1989). They may also react to some ligands independently of the *Ig*-equivalent CDR3 region (Ohmen et al. 1991; Kalataradi et al. 1994). Allelic variations of *Tcr-gV* sequences might thus have consequences on the gd T cell repertoire as recently suggested (Kalataradi et al. 1994; Roger et al. 1993b; Sperling et al. 1992).

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Terg-V1
Tcr-gB
Tcr-gA
 1
 Gln Leu Lys Gln Thr Glu Val Ser Val Thr Arg Ala Thr Asp Glu Ser Ala Gln Ile Ser
 CAG CTA AAG CAA ACT GAA ATA TCC GTC ACC AGA GCG ACA GAT GAG AGT GCG CAA ATA TCC
 CAG CTG GAG CAA ACT GAA TTA TCG GTC ACC AGA GAG ACA GAT GAG AGT GCG CAA ATA TCC
 Glu
 21
 Cys Ile Ala Ser Leu Pro Asp Phe Gly Asn Thr Glu Ile His Trp Tyr Arg Gln Lys Ala
 TGT ATA GCT TCT CTT CCA GAC TTC GCG AAC CAA GAA ATA CAC TGG TAC CGG CAA AAA GCA
 TGT ATA GTT TCT CTT CCA TAT TTC TCC AAC ACA GAT ATA CAT TGG TAC CGG CAA AAA GCA
 Val Tyr Ser Ala
 41
 Lys Gln Phe Glu Tyr Leu Ile Tyr Val Gln Thr Asn Tyr Asn Gln Arg Pro Leu Gly Gly
 AAA CAG TTT GAG TAT CTA ATA TAT GTC CAA ACA AAC TAC AAT CAA CGA CCC TTA GGA GGG
 AAA AAG TTT GAG TAT CTA ATA TAT GTC TCA ACA AAC TAC AAT CAA CGA CCC TTA GGA GGG
 Lys Ser
 61
 Lys His Lys Lys Ile Glu Ala Ser Lys Asp Phe Gln Thr Ser Thr Ser Thr Leu Lys Ile
 AAG CAC AAA AAA ATT GAA GCA AGT AAA GAT TTT CAA ACT TCT ACC TCA ACC TTG AAA ATA
 AAG AAC AAA AAA ATT GAA GCA AGT AAA GAT TTT CAA ACT TCT ACC TCA ACC TTG AAA ATA
 Asn
 81
 Asn Tyr Leu Lys Lys Glu Asp Glu Ala Thr Tyr Tyr Cys Ala Val Trp Met
 AAT TAC TTG AAG AAA GAA GAT GAA GCC ACC TAC TGT GCA GTC TGG AT
 AAT TAC TTG AAG AAA GAA GAT GAA GCC ACC TAC TGT GCA GTC TGG ATA

Terg-V3
Tcr-gB
Tcr-gA
 1
 Gln Leu Glu Gln Thr Glu Leu Ser Val Thr Arg Ala Thr Asp Glu Ser Ala Gln Ile Ser
 CAG CTG GAG CAA ACT GAA TTA TCG GTC ACC AGA GAG ACA GAT GAG AGT GCG CAA ATA TCC
 CAG CTG GAG CAA ACT GAA TTA TCG GTC ACC AGA GAG ACA GAT GAG AGT GCG CAA ATA TCC
 Glu
 21
 Cys Ile Val Phe Leu Pro Tyr Phe Ser Asn Ser Val Ile His Trp Tyr Arg Gln Lys Thr
 TGT ATA GTT TCT CTT CCA TAI TTC TCC ACC ICA GII ATA CAT TGG TAC CGG CAA AAA CCA
 TGT ATA GTT TCT CTT CCA TGT TTC TCC AAC ACA GCT ATA CAT TGG TAC CGG CAA AAA CCA
 Cys Thr Ala
 41
 Asn Gln Gln Phe Glu Tyr Leu Ile Tyr Val Ala Thr Asn Tyr Asn Gln Gln Pro Leu Glu
 AAT CAA CAG TTT GAG TAT CTA ATA TAT GTC GAG ACA AAC TAC AAT CAA CAA CCC TTA GGA
 AAT CAA CAG TTT GAG TAT CTA ATA TAT GTC GAG ACA AAC TAC AAT CAA CAA CCC TTA GGA
 61
 Gly Lys Asn Lys Lys Ile Glu Ala Ser Lys Asp Phe Lys Ser Ser Thr Ser Thr Leu Lys
 GGG AAG AAC AAG AAA ATT GAA GCA AGT AAA GAT TTT AAA AGI TCT ACC TCA ACC TTG AAA
 GGG AAG AAC AAG AAA ATT GAA GCA AGT AAA GAT TTT CAA ACT TCT ACC TCA ACC TTG AAA
 Gln Thr
 81
 Ile Asn Tyr Leu Lys Lys Glu Asp Glu Ala Thr Tyr Tyr Cys Ala Val Trp Met
 ATA AAT TAC TTG AAG AAA GAA GAT GAA GCC ACC TAC TAC TGT GCA GTC TGG ATG AG
 ATA AAT TAC TTG AAG AAA GAA GAT GAA GCC ACC TAC TAC TGT GCA GTC TGG ATG AG

Terg-V5
Tcr-gB
Tcr-gA
 1
 Gly Asp Ser Trp Ile Ser Gln Asp Gln Leu Ser Phe Thr Arg Arg Pro Asn Lys Thr Val
 GGA CAG TCC TGG ATA TCT CAG GAT CAG CTC TCC TTT ACC CGA AGA CCA AAC AAG ACG GTG
 GGA CAG TCC TGG ATA TCT CAG GAT CAG CTC TCC TTT ACC CGA AGA CCA AAC AAG ACG GTG
 21
 His Ile Ser Cys Lys Leu Ser Gly Val Pro Leu His Asn Thr Ile Val His Trp Tyr Gln
 CAC ATA AGT TGC AMG CTC TCT GGG GTT CCC CTT CAT AAC ACC ATT GTG CAC TGG TAC CAA
 CAC ATA AGT TGC AMG CTC TCT GGG GTT CCC CTT CAT AAC ACC ATT GTG CAC TGG TAC CAA
 41
 Leu Lys Glu Gly Glu Pro Cys Leu Arg Arg Ile Phe Tyr Gly Ser Val Lys Thr Tyr Lys Gln
 CTG AAA GAA GGG GAG CCC CTG AGA CGA ATC TTC TAT GGC TCA GTC AAA ACT TAC AAA CAA
 CTG AAA GAA GGG GAG CCC CTG AGA CGA ATC TTC TAT GGC TCA GTC AAA ACT TAC AAA CAA
 61
 Asp Lys Ser His Ser Arg Leu Glu Ile Asp Glu Lys Asp Asp Gly Thr Phe Tyr Leu Ile
 GAC AAG TCC CAC TCC CGC TTG GAA ATT GAT GAG AAG GAT GAT GGT ACC TTT TAC CTG ATA
 GAC AAG TCC CAC TCC CGC TTG GAA ATT GAT GAG AAG GAT GAT GGT ACC TTT TAC CTG ATA
 81
 Ile Asn Asn Val Val Thr Ser Asp Glu Ala Thr Tyr Tyr Cys Ala Cys Trp Asp
 ATC AAC AAT GTT GTC ACA TCG GAT GAA GCC ACG TAC TAC TGT GCC TGC TGG GAT CT
 ATC AAC AAT GTT GTC ACA TCG GAT GAA GCC ACG TAC TAC TGT GCC TGC TGG GAT CT

Terg-V7
Tcr-gB
Tcr-gA
 1
 Asn Leu Glu Glu Arg Ile Met Ser Ile Thr Lys Leu Glu Gly Ser Ser Ala Ile Met Thr
 AAC TTG GAA GAA AGA ATA ATG TCA ATC ACC AAG CTA GAG GGG TCC TCT GCT ATA ATG ACT
 AAC TTG GAA GAA AGA ATA ATG TCA ATC ACC AAG CTA GAG GGG TCC TCT GCT ATA ATG ACT
 21
 Cys Asp Thr His Arg Thr Gly Thr Tyr Ile His Trp Tyr Arg Phe Gln Lys Gly Arg Ala
 TGT GAT ACT CAC AGA ACA GGC ACT TAC ATC CAG TGG TAC CBA TTC CAG AAA GGG AGS GCC
 TGT GAT ACT CAC AGA ACA GGC ACT TAC ATC CAG TGG TAC CBA TTC CAG AAA GGG AGS GCC
 41
 Pro Glu His Leu Leu Tyr Tyr Asn Phe Val Ser Ser Thr Thr Val Val Asp Ser Arg Phe
 CCA GAG CAC CTT CTC TAC TAT AAC TTC GTC AGT TOC ACA ACT GTG GTG GAT TCC AGA TTC
 CCA GAG CAC CTT CTC TAC TAT AAC TTC GTC AGT TOC ACA ACT GTG GTG GAT TCC AGA TTC
 61
 Asn Ser Glu Lys Tyr His Val Tyr Glu Gly Pro Asp Lys Arg Tyr Lys Phe Val Leu Arg
 AAT ICA GAG AAA TAT CAT GTT TAT GAA GGC CCG GAC AAG AGG TAT AAA TTT GTG CTT CGS
 AAT TTG GAG AAA TAT CAT GTT TAT GAA GGC CCG GAC AAG AGG TAT AAA TTT GTG CTT CGS
 Leu
 81
 Asn Val Glu Glu Ser Asp Ser Ala Leu Tyr Tyr Cys Ala Ser Trp Ala
 AAT GTG GAG GAG TCC GAT TCT GCT CTG TAC TAC TGT GCC TCC TGG GCT
 AAT GTG GAG GAG TCC GAT TCT GCT CTG TAC TAC TGT GCC TCC TGG GCT

Terg-V2
Tcr-gB
Tcr-gA
 1
 Gln Leu Glu Gln Thr Glu Leu Ser Val Thr Arg Glu Thr Asp Glu Ser Val Gln Ile Ser
 CAG CTG GAG CAA ACT GAA TTA TCG GTC ACC AGA GAG ACA GAT GAG AGI GTG CAA ATA TCC
 CAG CTG GAG CAA ACT GAA TTA TCG GTC ACC AGA GAG ACA GAT GAG AAT GTG CAA ATA TCC
 Asn
 21
 Cys Ile Val Phe Leu Pro Tyr Phe Ser Asn Thr Ala Ile His Trp Tyr Arg Gln Lys Thr
 TGT ATA GTT III CTT CCA TAT TTC TCC AAC ACA GCT ATA CAT TGG TAC CGG CAA AAA ACA
 TGT ATA GTT YAT CTT CCA TAT TTC TCC AAC ACA GCT ATA CAT TGG TAC CGG CAA AAA ACA
 Tyr
 41
 Asn Gln Gln Phe Glu Tyr Leu Ile Tyr Val Ala Thr Asn Tyr Asn Gln Arg Pro Leu Glu
 AAT CAA CAG TTT GAG TAT CTA ATA TAT GTC GCA ACA AAC TAC AAT CAA CGA CCC TTA GGA
 AAT CAA CAG TTT GAG TAT CTA ATA TAT GTC GCA ACA AAC TAC AAT CAA CGA CCC TTA GGA
 Gly
 61
 Gly Lys Asn Lys Lys Ile Glu Ala Ser Lys Asp Phe Lys Thr Ser Thr Ser Thr Leu Lys
 GGG AAG AAC AMS AAA ATT GAA GCA AGT AAA GAT TTT AAA ACT TCT ACC TCA ACC TTG AAA
 GGG AAG CAC AAA AAA ATT GAA GCA AGT AAA GAT TTT AAA AGT TCT ACC TCA ACC TTG GAA
 His Ser
 81
 Ile Asn Tyr Leu Lys Lys Glu Asp Glu Ala Thr Tyr Tyr Cys Ala Val Trp Met
 ATA AAT TAC TTG AAG AAA GAA GAT GAA GCC ACC TAC TAC TGT GCA GTC TGG ATG AG
 ATA AAT TAC TTG AAG AAA GAA GAT GAA GCC ACC TAC TAC TGT GCA GTC TGG ATG AG

Terg-V4
Tcr-gB
Tcr-gA
 1
 Lys Leu Glu Gln Pro Glu Ile Ser Ile Ser Arg Ala Arg Asp Glu Thr Ala Gln Ile Ser
 CAA CCT GAA ATA TCA ATT TCC AGA GCA AGA GAT GAG ACT ACC CAT ATI TTC TTA GAT
 AAG TTG GAG CAA CCT GAA ATA TCA ATT TCC AGA CCA ASA GAT GAG ACT GCA CAA ATA TCC
 Pro
 21
 Cys Lys Val Phe Ile Glu Ser Phe Arg Ser Val Thr Ile His Trp Tyr Arg Gln Lys Pro
 TGT AAA GTT TTC ATC GAA AGC TTT AGG AGT GTA ACC ATA CAC TGG TAC CGG CAG AAA CCA
 TGT AAA GTT TTC ATC GAA AGC TTT AGG AGT GTA ACC ATA CAC TGG TAC CGG CAG AAA CCA
 41
 Asn Gln Gly Leu Glu Phe Leu Leu Tyr Val Leu Ala Thr Pro Thr His Ile Phe Leu Asp
 AAC CAA GGT TTA GAG TTT CTA TTA TAT GTC CTT GCA ACC CCT ACC CAT ATI TTC TTA GAT
 AAC CAA GGT TTA GAG TTT CTA TTA TAT GTC CTT GCA ACC CCT ACC CAT GTT TTC TTA GAT
 Val
 61
 Gln Gly Tyr Lys Lys Met Glu Ala Ser Lys Asn Pro Ser Ala Ser Thr Ser Thr Leu Thr
 AAG GAG TAC AAG AAA ATG GAG GCA AGT AAA AAT CCT AGT GCT TCT ACA TCG ACA TTG ACA
 AAG GAG TAC AAG AAA ATG GAG GCA AGT AAA AAT CCT AGT GCT TCT ACA TCG ATA TTG ACA
 Ile
 81
 Ile Tyr Ser Leu Glu Glu Glu Asp Glu Ala Thr Tyr Tyr Cys Ser Tyr Gly TER
 ATA TAT TCC TTG GAG GAA GAA GAC GAA GCT ATC TAC TAC TGT TCC TAC GGC TAA AG
 ATA TAT TCC TTG GAG GAA GAA GAC GAA GCT ATC TAC TAC TGT TCC TAC GGC TAA AG

Terg-V6
Tcr-gB
Tcr-gA
 1
 Leu Thr Ser Pro Leu Gly Ser Tyr Val Ile Lys Arg Lys Gly Asn Thr Ala Phe Leu Lys
 TCA CCT CTG GGG TCA TAT GTC ATC AAG AGG AAA GGA AAT ACG GCT TTT CTC AAA
 CTC ACG TCA CCT CTG GGG TCA TAT GTC ATC AAG AGS AAA GSA AAT ACG GCT TTT CTC AAA
 21
 Cys Gln Ile Lys Thr Gly Val Gln Lys Pro Asp Ala Tyr Ile His Trp Tyr Gln Glu Lys
 TGT CAA ATA AAA ACA GSI GTT CAG AMG CCC GAT GCA TAC ATA CAC TGG TAC CAA GAG AAG
 TGT CAA ATA AAA ACA AGT GTT CAG AMG CCC GAT GCA TAC ATA CAC TGG TAC CAA GAG AAG
 Ser
 41
 Pro Gly Gln His Leu Gln Arg Met Leu Cys Ser Ser Ser Lys Glu Asn Ile Val Tyr Glu
 CCA GGC CAG CGT CTC CAA AGA ATG CTG TGT AGT TCT TCA AAA GAA ACA ATT GTC TAT GAG
 CCA GGC CAG CGT CTC CAA AGA ATG CTG TGT AGT TCT TCA AAA GAA ACA ATT GTC TAT GAG
 Arg Thr
 61
 Lys Asp Phe Ser Asp Glu Arg Tyr Glu Ala Arg Thr Trp Gln Ser Asp Leu Ser Ser Val
 AAA GAT TTT AGT GAC GAA AGA TAT GAG GCA AGG ACA TGG CAG AGT GAT TTG TCT TCA GTC
 AAA GAT TTT AGT GAC GAA AGA TAT GAG GCA AGG ACA TGG CAG AGT GAT TTG TCT TCA GTC
 81
 Leu Thr Ile His Gln Val Thr Glu Glu Asp Thr Gly Thr Tyr Tyr Cys Ala Cys Trp Asp
 CTC ACC ATA CAC CAA GTG ACA GAA GAG GAC ACG GGA ACT TAT TAC TGT GCA TGC TGG GAT
 CTC ACC ATA CAC CAA GTG ACA GAA GAG GAC ACG GGA ACT TAT TAC TGT GCA TGC TGG GAT

Fig. 1 Nucleotide and deduced amino acid sequences of *Terg-V* genes. Codons presenting divergent nucleotide between *Tcr-gA* and *Tcr-gB* sequences are *underlined*. Only divergent amino acids are noticed under *Tcr-gA* genes. *Tcr-gB-V1*, *-V2*, *-V3*, *-V4*, *-V5*, *-V6* and *-V7* and *Tcr-gA-V7* sequences were determined in this work, whereas *Tcr-gA-V1*, *-V2*, *-V3*, *-V4*, *-V5* and *-V6* genes (M12832, M13337, M12831, X04397, M13336, X04315, M13338, M30171) were previously described (Hayday et al. 1985; Garman et al. 1986; Heilig and Tonegawa 1986; Kalataradi et al. 1994). *Numbering* corresponds to the coding region in BALB/c (Heilig and Tonegawa 1986). To determine sequences, cDNA preparations from thymus, spleen, or skin were amplified by PCR as previously described (Roger et al. 1993d) using leader or 5' *Terg-V* gene primers (*Terg-V1-V3*: 5'-TGCTGCCTCTGGGTTTTTGGGCT-3'; *Terg-V4*: 5'-CAACCT-GAAATATCAATTTC-3'; *Terg-V5* (5'*Terg-V5* intron): 5'-GATGTCTCTTCTTGGCTTC-3'; *Terg-V6*: 5'-TCACCTCTGGGGT-CATATGT-3'; *Terg-V7*: 5'-GCAGACAAACATCTCCAAC-3') and a pan-*Terg-C* primer (5'-GGAAAGAACTTTTCAAGGA-3'). Products of the appropriate size were purified by electroelution, then cloned in M13mp19. DNA from at least three different positive plates was sequenced using Sequenase® (US Biochemicals, Cleveland, OH)