Identification of a new, abundant superfamily of mammalian LTR-transposons

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ABSTRACT

A new superfamily of mammalian transposable genetic elements is described with an estimated 40,000 to 100,000 members in both primate and rodent genomes. Sequences known before as MT, ORR-1, Mstll, MER15 and MER18 are shown to represent (part of) the long terminal repeats of retrotransposon-like elements related to THE1 in humans. These transposons have structural similarities to retroviruses. However, the putative product of a 1350 base pair open reading frame detected in the consensus internal sequence of THE1 does not resemble retroviral proteins. The elements are named 'Mammalian apparent LTR-retrotransposons' (MaLRs). The internal sequence is usually found to be excised. Their presence in rodents, artiodactyls, lagomorphs, and primates, the divergence of the individual elements from their consensus, and the existence of a probably orthologous element in mouse and man suggest that the first MaLRs were distributed before the radiation of eutherian mammals 80-100 million years ago. MaLRs may prove to be very helpful in determining the evolutionary branching pattern of mammalian orders and suborders.

INTRODUCTION

The most numerous transposable genetic elements in mammals are the short and long interspersed nucleotide elements (SINEs and LINEs) represented in the human genome by Alu with an estimated 500-900,000 copies and L1 with 100,000 copies, respectively (1, 2). New copies of both types of elements find their way into the genome via reverse transcription of an RNA intermediate, a process called retrotransposition. SINEs are less than 500 base pairs (bp) long, are transcribed from an internal RNA polymerase III promoter, have an A rich 3' end, and are derived from structural RNA (1, 3). Full length L1 sequences are 6-7 kilobases (kb) long and may contain two open reading frames (ORFs) that code for products related to retroviral proteins such as reverse transcriptase (4, 5). Neither SINEs nor LINEs have long terminal repeats (LTRs).

The mammalian genome also harbors a variety of relatively low copy number endogenous proretroviruses, which may have entered the germlines of their animal hosts through retroviral

infection of germ cells, and are now stably integrated, vertically transmitted, and more or less incapable of infection (6, 7). Retroviruses may have evolved from an (LTR-)retrotransposon similar to gypsy in Drosophila or Ty3 in budding yeast, which acquired an envelope protein gene around the time of the emergence of mammals (8-11). Characteristic of (LTR-)retrotransposons and proretroviruses are two directly repeated sequences of several 100 bp (the LTRs) flanking a central region with more or less preserved ORFs related to the retroviral gag, pol-int, and sometimes env genes (Figure 1). Another hallmark of these transposons is a 4 to 6 bp target site duplication upon integration (of specific length for each type of element). The LTRs are essential and sufficient for normal integration into the host genome; their terminal sequences are recognized by a typespecific integrase, resulting in the exclusive utilization of viral DNA termini for integration (12). Furthermore, the LTRs control all aspects of transcription. LTRs of even closely-related retrovirus families show no overall sequence homology, but all retrotransposon LTRs share short elements functional in integration and transcription: (i) a terminal 5' TG and 3' CA dinucleotide, often extended to a short inverted repeat, (ii) RNA polymerase II promoter elements and transcription start site, and (iii) a polyadenylation signal and site. The transcription start- and polyadenylation sites define the borders between the so-called U3, R and U5 regions in the LTR. Solitary LTRs of endogenous retroviruses in the genome are thought to be excision products of homologous recombination between both LTRs. There are an estimated total of 1100-1600 and 3000-4000 copies of endogenous proviruses and their solitary LTRs in the human and mouse genome, respectively (6,7).

The estimated 40,000 copies of THE1s and their solitary LTRs formed the most widespread interspersed elements known in the primate genome apart from Alu and L1. A considerable number of other repeat families exists in mammals, exemplified by the 21 recently described medium reiterated sequences (MERs) in the human genome (17, 18). The most abundant of these MERs, as determined with a plaque hybridization assay of a genomic human library, is MER18 with 5000-10,000 copies, closely followed by MER10 with 4000-8000 copies (18). The MER10 sequence had already been known to be repetitive (19, 20) and had been named MstII repeat by Mermer *et al.* (21). These authors also had recognized the similarity of these elements to

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THE1-LTRs. An alignment of some members of these two (sub)families has been published recently (22). Members of the THE1/MstII family have also been called 'low-repeat sequence' (LRS) (23, 24). It will be shown here that the MER18 sequence, previously described as a human sex-chromosome-specific repeat (25), forms part of the LTR of a retrotransposon related to THE1 and MstII.

The most common interspersed repetitive element described in the mouse genome is L1 followed by the Alu-equivalent B1 SINE, the B2 SINE, and the 'Mouse Transposon' (MT, 26, 27). The latter three have been estimated to occur in similar numbers (1,26). It is shown in this paper that MT is related to the recently partly-described 'Origin-Region Repeat' (ORR-1) in rodents (28) and that both are more distantly related to the primate elements mentioned above. Indeed, several ORR-1 and MT repeats flank sequences that resemble the internal sequence of THE1.

The above mentioned elements, which comprise all of the most common unclassified interspersed repeats in primates and rodents, are identified here as members of a superfamily of Mammalian apparent LTR-retrotransposons (MaLRs). They form a class of mobile genetic elements distinct from SINEs, LINEs, and retroviruses. It is estimated that there are 40,000 to 100,000 copies, including solitary LTRs, in both primate and rodent genomes. I have derived novel consensus sequences for the LTRs of 20 MaLR subfamilies, based on the alignment of over 300 sequences found in GenBank[®] release 71. These sequences and their putative evolutionary relationship are presented in this paper.

METHODS

Databank searches were performed on a Sun computer using the IFind (29) program in the IntelliGeneticsTM Suite. Multiple alignments were initially made with the Genalign program (30) and significantly adjusted manually. Improved versions of consensus sequences were successively used for new databank searches. Subfamilies were detected when members of a family showed more similarity to each other than to their preliminary consensus sequence or after grouping sequences that share an insertion or deletion. Subfamily status was accepted when a subdivision of a family was accompanied by grouping of consensus sequences with multiple 'diagnostic' deletions, insertions or mutations. Some new subfamilies were detected by searching the databases with sequences that showed an overall (full length) but faint similarity to a previously determined consensus sequence.

For calculation of nucleotide substitution rates, each insertion or gap has been counted as a single substitution. Hypermutable CpG sites were excluded. All sequence divergence or similarity values mentioned in this article are corrected for superimposed substitutions using the algorithm of Jukes and Cantor (31).

RESULTS AND DISCUSSION

Identification of a superfamily of LTR-transposons

Initial computer searches were performed to determine the extent of the ORR-1 sequence in the origin of replication region near the Chinese hamster dihydrofolate reductase gene (28). Similarities were detected with MT repeats, and comparison with these elements allowed determination of the exact ends of ORR-1, deleting 30 bp of the 5' end and adding 200 bp to the 3' end of the published consensus (28). Surprisingly, searches with the new full-length ORR-1 consensus showed similarities to several primate sequences, most of which turned out to be THE1-LTRs or MstII repeats. Similarities were subsequently discovered between MstII and both the MER15 and MER18 sequences (18). Through comparison with the MstII consensus, I found that MER15 and MER18 actually represent part of the 5' and 3' arm, respectively, of one element. Consensus sequences of all the elements mentioned could be extended to include 5'-TG and 3'-CA terminal dinucleotides typical for retrotransposon LTRs.

The databanks were also screened with a consensus of the internal sequence of THE1 (adjusted from ref. 32) excluding any LTR sequence. Sequences similar to it were found to be flanked by MstII and MER15/18 elements, and, more surprising, by ORR-1 elements in the Syrian hamster μ class glutathione Stransferase gene (HAMMGLUTRA, 33) (Figure 2). For all locations of MaLRs, indicated by their GenBank® locus name in parentheses, refer to Table 1. This is strong evidence for a relationship between the rodent and primate repeat families such as was predicted by the LTR-sequence similarities. Searches with the 500 bp available of the HAMMGLUTRA internal sequence revealed six more internal sequences flanked by an ORR-1 and one by an MT (RATCYPOXG, 34). An element with two ORR1-LTRs present in the rat cytochrome P450 4A1 gene intron 4 (RATCYP4A1, 35) has a total length of 1912 bp (excluding an integrated B1 repeat) comparable to that of THE1 (2.3 kb).

A third line of evidence for their kinship is that solitary LTRs and complete members of each family are almost always flanked by a 5 bp direct (often imperfect) insertion repeat (see Table 1, column c), as has been observed for THE1 (15). Moreover, the published target site sequence specificity of THE1 (GYNAC) (15) is also obvious for all the other elements (unpublished data).

A picture has emerged of a large superfamily of THE1-like transposons that unites at least six very abundant mammalian repetitive elements: ORR-1 and MT elements in rodents, and THE1, MstII, and MER15 and MER18 in primates. For clarity



Figure 1. Comparison of the structure of a typical retrotransposon and MaLR. Noteworthy differences are the short internal sequence and the integration specificity of MaLRs, and the absence of homology to a conventional transcription initiation site, reverse transcriptase, or primer binding site (PBS). See text for details.

of reference, these names will still be used in this article to specify (members of) each family, except that the family of repeats comprising MER15 and MER18 is named MLT1 (Mammalian LTR-Transposon 1). In the future, it may be better to rename the other families MLT2, MLT3, and so on. Alignment of over 300 LTR sequences allowed subdivision of each family, based on the presence or absence of gaps or inserts and multiple diagnostic point mutations (alignment data to obtain subgroup consensus sequences are not shown). 17 of the derived subfamily consensus sequences are presented and compared in Figure 3. The subfamilies are indicated by a small case letter after the family name (e.g. THE1a), with subfamily 'a' being the most recently amplified (see below). Consensus sequences of three ancient MLT1 subfamilies (MLT1e-g), most similar to MLT1d, were too indefinite to be integrated in the Figure 3 alignments.

A total of 311 THE1-related sequences were discovered in the GenBank DNA sequence database (release 71) and are listed in Table 1. Only 30 of these show similarities to an internal sequence, out of which 4 had been isolated by screening with an internal sequence-containing probe. Hence, most MaLRs seem to remain in the genome as solitary LTRs, probably as a result of internal recombination. The LTRs range in length from 327 (ORR1a) to 568 bp (MLT1e). Their terminal 100 nucleotides are relatively well-conserved between families, while the central region is highly divergent in sequence and length. No obvious and conserved potential transcription start site could be located, although a possible TATA-box is indicated in the THE1 and MLT1 sequences in Figure 3. A transcription start site is tentatively positioned 23 bp downstream, supported by sequence information of a processed pseudogene (HUMIGLAB, 36) that apparently had been transcribed from this position (unpublished data). Deka et al. (15) suggested a transcription start 40 bp more downstream based on the truncation of a THE1 element at this

a	
	λ-1 ORR-1 μ class glutathione S-transferase gene
	TR internal sequence St I TR
b	THE1
HANNGLUTRA 3657	CASAGTTTOGAGTCTGOCCAGCTOGCTTTCAGGTTTGATCCCGTATTTCCTG-ACTTATGTCCCTT
THE1-int. 1267	TAAGATTTGACTGCCCCGCTGGATTTCGGACTTGCATGGACCCCGTTARCCCCTTTGTTTTTGGCCAAT
RAMMILUTRA 3593	CCCCGGTGTTTTTGGAATGGTAATATATATCCTGTGGTTTACTTTCT-G
THE1-int. 1336	TTCTCCCATTTGGAATGGCTGTATTTACCCAATACCTGTACCCKCATTGTATCTAGGAAGTAACTAGCTTG
ENGLISTRA 3547	ATTTTGATTTTTACAGGTGATTACAGTTAAGAGATTGTATGAATCTCAGAAGAGACTTTGAAATTTAAACC
THE1-int. 1408	CTTTTGA-TTTTACAGGCTCATAGGCGGAAGGGACTTGCCTTGTCTCAGATGAGACTTTGGACTGTGGACT
ENGGLUTRA 3476	TTTAAGT-AAGTTTGAGACTGTGAT-AGACTATGGAG-ACT-TTGAAGTTGGACTGAATGCATTTGTGCAT
THE1-int. 1477	TTTGGGTTAATGCTGAAA-TGAGTTAAGACTTTGGGGRACTGTTGG-GAAGGCATRATG-GTTT-TGAAA
ORRID-LTR 1	TGTGGTGGTTTGAATRAAAATGGCC
ENMALUTRA 3407	TATGTATGACTACTAGCCTTTGGAGGTCCAGGGAGTGAAA-GTGGTGGTTTGAAAAAAAAAA
THE1-int. 1545	TGTG-AGGAC-ATGAGA-TTT GGARGGGGCCAGGG-TRGAA end

Figure 2. Evidence for a relationship between the rodent ORR1 and primate THE1 repeat families. A region in intron 7 of the Syrian hamster μ class glutathione S-transferase gene (HAMMGLUTRA, 33) shows homology to the consensus THE1-internal sequence bordered by two ORR-1s. a) Schematic comparison of the intron 7 sequence with the primate THE1. An internal deletion apparently has taken place in the hamster element. The remainder is flanked by identical 5 bp repeats, as is observed for all THE1 elements. b) Sequence alignment of the intron 7 sequence, in inverse orientation, with the THE1a internal and the ORR1b-LTR consensus sequences. Note that the ORR1b similarity is at exactly the same position as the THE1-3' LTR would be.

point. Notably conserved between all families is the 3' terminal region that contains the polyadenylation signal $\{AA(T)TAAA\}$ and site. This site is usually at a C/TA dinucleotide followed by GT clusters (37), which are both present in each MaLR consensus sequence.

The orientation of the sequences is opposite to the previously published, partial consensus sequences of MstII (21, 22), MER15 and MER18 (18), ORR-1 (28) and MT (26, 27), but conforms to that of the published THE1 sequence (13). It is supported by the presence of a 1353 bp ORF in this orientation in the 1576 bp consensus internal sequence of THE1 elements (unpublished results). Preliminary analysis has not yet revealed significant similarities of the putative product of this ORF to any protein present in the databanks. The present orientation is also supported by 12 cases of transcriptional 3' processing at the proposed site in LTRs of each family (Table 1 and ref. 14). A survey of the orientation of MaLRs within transcription units reveals a very marked (7:1) bias against fixation of positively oriented elements in introns, while no bias in orientation is observed in flanking regions of genes (Table 2). This can be explained by the potential for 3' processing by the LTRs of integrating MaLRs. Integration in the positive orientation inside a gene must have usually led to a premature transcription termination. Selection against alleles with such a mutation is obviously strong.

Reverse transcription of the minus strand of most (LTR-)retrotransposons is primed from a tRNA annealed to a primer-binding site, a short region of complementarity immediately downstream of the 5'-LTR-internal domain junction. There is no complementarity to any tRNA in the consensus internal sequence of the THE1/MstII family, but conventional primer-binding sites are, for example, also absent in the yeast retrotransposon Tf1 (38) and the hepatitis B virus genome (39). The retrotransposon plus-strand is primed at a short polypurine tract just upstream of the internal-domain-3'LTR junction. Consistent with this, 17 of the 20 3' terminal nucleotides in the consensus primate as well as rodent internal sequences are purines (*italicized* in Figure 2).

The structure of the LTRs, the presence of the functional polyadenylation site, the long ORF, the purine-rich stretch, and the 5 bp target site duplication suggest a classification of these elements among (LTR-)retrotransposons and proretroviruses (Figure 1). However, the term retrotransposon has been reserved for elements with a reverse transcriptase-encoding region, which is seemingly absent in these elements. The name Mammalian *apparent* LTR-Retrotransposon or otherwise Mammalian LTR-Retrosequence (both MaLR) is therefore proposed for this superfamily. Its evidently successful strategy of distribution, apparently without a self-encoded reverse transcriptase, forms an intriguing unknown.

Evolutionary relationship of the MaLR families

The consensus sequences of MstII and THE1-LTRs show a gradual transformation from THE1a to MLT1a (see Figure 3) that coincides with a gradual increase in average sequence divergence of the copies from their subfamily consensus sequence. A similar correlation can be observed for the MLT1, ORR-1 and MT families. The older (more diverged) subgroups' consensus sequences actually form intermediates between the 'younger' subgroups of different families; for the rodent families MT and ORR-1 highest similarity is seen between MTd and ORR1d, and among the rodent-specific subfamilies the oldest (ORR1d) shows the highest similarity to the MLT1 and

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Table 1. Location of all MaLR sequences detected in GenBank release 71, ordered by their locus name

locus name	location	a)	b)	c)	d)		
PRIMATES							
AGMORS 3A	177-542	+	THE15	TCATG	African green monkey origin-enriched DNA		
AGMORS 4A	1-242	-	MSTa		African green monkey origin-enriched DNA		
CEBGLOBIN	11088-11433	+	MLTIA	GATGR	Chimpanzee A and G gamma globin genes, 3' FR Colors single conv concerts sequence boxologous to THE-1		
GAL6 '	1-309 (5' LTR)	1	MSTh		Galago single copy genomic sequence homologous to THE-1. Galago single copy genomic sequence homologous to THE-1.	•	
GAL /	14430-14825	+	MLT1a	GATRM	Galago gamma globin gene. 3' FR	•	
GIBHBGGL	9454-9778	+	MLT1a	GATGR	Gibbon A and G gamma globin genes, 3' FR		
HUM7SKP17	499-end	-	MLT1a		Human 75K pseudogene integration site		
HUMA1MBG1	269-686	-	MLT1c	AACAC	Human α_1 -microglobulin-bikunin , 5' FR (-1285 to -870)		
HUMACTG3PS	1-75	+	MSTa		Human gamma-actin like pseudogene insertion site.		
HUMACTSA	534-901	-	THELC	CCAGG	Human vascular smooth muscle α -actin, 5'FR (-1213 to -84	(46)	
HUMACT SG2	1590-1929	-	MLTID		Human enteric smooth muscle 7-actin, intron 1 Human adenceine deaminase gene 51 FP		
HUMADAG	1025 - 1 Alu 1 - 1717	+	THEID	GCCAC	Human adenosine deaminase gene, 5' FR. (-2911 to -2219)		
HUMADAG	14448-1 Alu 1-15469	_	MLTIC	GTYAG	Human adenosine deaminase gene, intron 1		
HUMAIGRA	1-end	-	MSTa		Human interspersed repetitive DNA detected with H-ras VI	TR/	
HUMAIGRB	1-end	-	MSTa		Human interspersed repetitive DNA detected with HUMSATMP	IA	
HUMAIGRC	1-end	-	MSTa		Human interspersed repetitive DNA detected with HUMSATMA	iA C	
HUMAIGRD	Alu (50-end	-	MSTa		Human interspersed repetitive DNA detected with HUMSATMA	1A 43	
HUMAIGRE	1-end 686-1098	Ţ.,	MLT1b	VATTC	Human genomic clone containing Alu repeat	'n	
HUMALURC	Alu 191-255	_	MLT1c	INITO	Human clone containing Alu repeat		
HUMAMD01	14098-4305	-	MTc		Human S-adenosylmethionine decarboxylase gene, intron 1.		
HUMAMINONA	1-163	+	MLT1d		Human aminopeptidase gene, 5' FR (-1071 to -908)		
HUMAPBO3	1418-1779	-	THE1b	CYRTC	Human apolipoprotein B gene, intron 4.		
HUMAPOAIA	<441-899	-	MLT1d		Human apolipoprotein A-I gene, 5' FR (<-2030 to -1586)		
HUMBCR221	1-80 Alu 370-523	-	MLT15		Human BCR gene, bcr2 region in intron 1		
HUMBCR221	2979-end 12-ond	-	MLTI MITIa		Human BCR gene, bcr2 region in intron 1		
HUMBEXIT	11340-11829	+	MLT1d	TCAGT	Human factor XIII & subunit gene, intron 5.		
HUMBEXIII	12011-ca.12585	-	MLT1e		Human factor XIII B subunit gene, intron 5.		
HUMBFXIII	16512-16873	-	THE1b	GCYAC	Human factor XIII β subunit gene, intron 5.		
HUMBKVHO1	1-84	+	MSTb		Human BK virus enhancer like sequence, 5' adjacent regio	on	
HUMBLASTIA	261-577 Alu 894-963	+	THELC	GAC (T) A	Human EBV inducible BLAST-1 gene, 5' FR (-1317 to -615)	•	
HUMC21DLA	1340-1831	-	MUTIC	YAWGC	Human ring chromosome 21 DNA.		
HUMCALPUS	1-278	_	MLTIC	GCMIG	Human calpastatin gene, intron 1.		
HUMCAM3X01	1-86 Alu	_	MSTD		Human calmodulin III gene, 5' FR (<-1370)		
HUMCAPG	3050-3364 Alu	-	MLT1a		Human cathepsin G gene, 3'FR		
HUMCCG1	5109-end	+	ORR1b		Human X-linked CCG1 cDNA, 3' UTR		
HUMCCND3PS	54-407	-	THE15		Human pseudo-D3-type cyclin gene, 5' flanking site		
HUMCETP2	1-348	-	MLTId		Human cholesteryl transfer protein gene, intron 2.		
HUMCEXIII	1-65 2745-cs 3055	+	MLTIC MLTIS		Human coagulation factor All gene, 5 rk (<-356 to -292) Human cCMP phosphodiesterase gene B-subunit, intron 3		
HUMCHR10F	1-end	_	MLT1c		Human chromosome 10 polymorphic microsatellite site.		
HUMCLGNA	1974-end	+	MLT1c		Human neutrophil collagenase cDNA, 3' UTR		
HUMCOL2C2	<500-end	-	MLT1c		Human type VI alpha-2 collagen gene, 3' UTR		
HUMCR2CD21	1-ca.232	+	MLT1f		Human complement receptor 2 gene, 5' FR (to ca1100)		
HUMCYP450	2710-2978	-	MSTD		Human cytochrome p450 CYPIAI gene, intron 1		
HUMDNAPOLA	1-275	-	MLTIA TUPIN	CATTO	Human DNA polymerase & gene, 5' FR (to -1296).		
HUMDYSKW	ca.515-868	_	MLT1b	GATIC	Human muscular dystrophy gene, intron 44.		
HUMDYSTRO	12241-12588	-	MLT1a	RTYAC	Human muscular dystrophy gene, intron 44.		
HUMDYSTRO	ca.14779-end	+	MSTb		Human muscular dystrophy gene, intron 44.		
HUMDYSTROP	22772- L1 -23666	-	MLT1b	GGGRR	Human muscular dystrophy gene, intron 44		
HUMDYSTX60	170-536	-	MLT1a	STCTM	Human muscular dystrophy gene, intron 59		
HUME HS 2A	1052- L1 -2180	-	MLTIe	ATTCT	Human DNA with some similarity to HIV-1 DNA		
HUMERCISK	1502-end (311TP)	Ŧ	10610		Hela cell uniform extrachromosomal circular DNA		
HUMFOLP12	w 1112-end	_	MLT1b		Human DHFR pseudogene psi-1 integration site.		
HUMG 6PDGEN	ca.18500-18833	-	MLT1		Human glucose-6-phosphate dehydrogenase, 3' FR		
HUMGPP3A01	474-end	-	MLT1a		Human platelet glycoprotein IIIa, intron 1.		
HUMGUSBA	735-76 2xAlu 1543-63	+	MSTD		Human β -D-glucuronidase gene, 5' FR (ca -3000)		
HUMGYPA09	1-310	-	MSTa	DOVIC	Human glycophorin A gene, 3' UTR.		
NUMBER	119-290 A1U 384-850	+	MITID	CHECT	Human Na'/H' exchanger gene, 5' FR (-1260 to -528)		
HUMMALGGR	//04-030/ 36999-37336	-	MLT1e	CATCP	numan 196 receptor gène, intron 3 Human à gamma globin gene 31 FP		
HUMHBB	41777-42114	+	MJ.T1>	GATGR	Human G gamma globin gene, 3' FR		
HUMHBVINT	1259-end	-	MLT1a	onron	Human hepatocarcinoma insertion site of hepatitis B vir	rus	
HUMHLAEHCM	1015->1172 (5'LTR)	+	MSTC		Human MHC class I HLA-E/HLA-6.2 gene, 3' FR		
	<1218-end (int.)						
HUMHLASBA	8613-9027	-	MSTD	TGGAY	Human MHC class II HLA-SB- α gene, intron 4		
HUMHPDIAC	367-end	+	THPIC		numan manu Class II ALA-SB-C gene, intron 4 Human nanilloma virus tune 160 integration site		
HUMHPRTB	7326- Alu -8006	+	MLT1a	GTKCT	Human HPRT gene, intron 1		
HUMHPRTB	<33866-34315	-	MLTIe	•	Human HPRT gene, intron 5		
HUMHPRTB	54766-55142	+	MLT1b	YTCAC	Human HPRT gene, 3' FR		
HUMIFNAR	22644- Alu -23293	-	MLT1e	YCYAW	Human interferon alpha/beta receptor gene, intron 6		
HUMIGCC5	1-57 (int) 58-552 (LTR)	-	MSTD		Human inactive IgH Cg2 gene, 5' FR		
HUMICOD3	1-3/(1nt) 38-304 (LTR)	-			numan igh Cei gene, 5' FK		
HUMTCHPC	1-end (5! (TP)	+	MOTH		numan Ign Cg1 gene, 5. FK Human Ign Cg1-Cg1 intergenic region		
HUMIGHHSG3	1-665) (internal)	-	<u>10110</u>		numan iyn cyb-cyr incergenic region.		
HUMIGHHSG4	1-665 (internal)	-	MSTD		Human IgH Cv4- Cg intergenic region.		
HUMIGHVHA	1470-end	+	MLT1b		Human IgH variable region, hv4005 gene, 3'FR		
HUMIGHVV2	979-end	+	MLT1b		Human IgH variable region, V71-2 gene 3' FR		
HUMIGKV18B	<388-517	-	MSTC		Human IgH 5VDJ-CG region recombination site		
HUMIGLAB	29-00 32935-33303	+	THELC	CORCO	numan igL J-C region processed pseudogene, 5' UTR.		
NUMIGLAMB	2622-3232	-	int LTG	GORGU	numan iy lambua conscant region /, 5' FK		

HUMI GMUD	3400->3635	-	MLT1a		Human IgH Cu-CS intron/intergenic region.
HUMI GMUD	4638-7324	-	MLT1c	GRTKT	Human IgH Cu-C5 intron/intergenic region.
HUMINSRC/D	1180- 2xAlu -2395	-	MSTa	GGKYC	Human insulin receptor, intron 14
HUMINT2	11442-end	+	MLT1c		Human int-2 proto-oncogene, 3' FR.
HUMLACI02	<53-end	+	MLT1b		Human lipoprotein associated coagulation inhibitor, exon 2
HUMLDHBB/C	1507-1574 y 1-end	-	MSTa		Human lactate dehydrogenase B pseudogene integration site
HUMLTR	224-2531	-	THE1c	GACTG	Human muscular dystrophin gene, intron 43.
HUMMER15A	1-154	-	MLT1b		Human repetitive DNA fragment sequenced from Alu-primers
HUMMER15B	1-141	-	MLT1c		Human repetitive DNA fragment sequenced from Alu-primers
HUMMER18A	78-end	-	MLT1b		Human repetitive DNA fragment sequenced from Alu-primers
HUMMETIPG	195-299 W	+	MLT1b		Huamn methalothionein I pseudogene integration site.
HUMNK25	437-866	+	MSTC	GGTKY	Human neurokinin A receptor gene, exon 5 and 3' FR
HUMNKG2D	<1489-end (int.)	+	MLT1		Natural killer cell membrane protein NKG2D cDNA, 3' UTR
HUMP450SCC	1-214	+	MLT1f		Human CYP11A1 gene, 5' FR (to -2117)
HUMPADP	1-ca 250	+	MLT1b		Human amyloid A4 precursor gene, 5' FR (-3700 to -3450)
HUMPCI	1-281	-	MLT1d		Human protein C inhibitor gene, 5' FR (-2200 to -1919)
HUMPCI	6854-7246	-	MLT1b	TCTYY	Human protein C inhibitor gene, intron 1
HUMPCI	9254-9603	-	MLTIa	CTCAY	Human protein C inhibitor gene, intron 2
HUMPECORIA	1-ca.220	-	MLTIe		Human polymorphic site near THRB gene.
HUMPPPB1A2	1->169	-	MSTD		Human protein phosphotyrosyl phosphatase 1B gene, intron x.
HUMPROSA	1-202	-	THEID		Human vitamin K dependent protein S, 5' UTR
HUMPSCIZ	1991- >2191	+	MSTA		Human clone ps12 DNA (from artificial chromosome?)
NUMPER D2	1-0/	+	MLTID		Human prostatic secretory protein PSP94; 5' FR (to -740).
HUMRELPS	1-111	+	MLTID		RFLP site in human genome linked to Huntington's disease.
HUMRSO4C	20-322	-	THELA	TCATT	Uriginal o-repeat, genomic clone found to be repetitive
HUMPSOLTP	21-2286	-	THELS	CATAC	Ruman genomic clone isolated with homesout clone
HUME A A 1 A	1054-2274	Ξ	Mena	GAIAC	Ruman genomic THEI Isolated with o-repeat clone
HIMSARIA	1934-2374	-	MUR1-	GAAGI	numan serum amylold A, intron 1
HIMSEDC	4104-4492	Ξ	MIMIN	KTCAC	Target site of numan cnr. 6 duplication unit on chr.16
HIMSFYPPDB	351-579/580-816/817-end	-	MITIL	RIGAC	Tandem reports on human V neeudooutocore) resien
HUMSEXRPA	351-580/581-818/819-end	_	MLT1b		Tandem repeats on human i pseudoautosomai region
HUMSTOMC	1646-2001 (int)	÷	MT.TT		Human Talk constant region C-3 gene 51 PB
101210120	2002-2441 (3'LTP)		<u>Entrance</u>		numan igh constant region ovo gene, 5° rk
HUMS TOMOA	2137-2290 (int)	+	MT T1 C		Human Tall constant region C.4 gans 51 FD
101010101	2291-2732 (3'LTR)		CHATTC.		numan ign constant region ow gene, 5° rk
HUMSMAAA	1-251	-	MSTD		Human aortic-type smooth muscle alpha-actin, intron 8
HUMTHEP2	1-136	-	MLTId		Human genomic integration site of a THEL.
HUMTHEP2	158-493 Alu 783-824	+	THE1b	CCTTG	Human genomic clone isolated with probe for o-repeat
HUMTNFZ	5249-56021	-	MLT1d		Human tumor necrosis factor receptor, 3' FR
HUMTPO01	697->1076	-	MLT1d		Human thyroid peroxidase gene, 5' FR (-1903 to ca1500)
HUMT PO04	1-448 (int) 449-866 (LTR)	+	MSTb		Human thyroid peroxidase gene, intron 3
HUMT PO06	1790-2231 (3'LTR)	-	MLT1d		Human thyroid peroxidase gene, intron 6
	2232- >2610 (int.)				······································
HUMTRANSC	498-2699				
		-	<u>THEla</u>	GATGC	Human calmodulin family member gene, 3'-UTR
HUMUBIBP	1-106 ¥ 595-779	-	<u>THEla</u> MLT1e	GATGC	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site.
HUMUBIBP HUMUDPCNA	1-106 ¥ 595-779 L1 315-519	-	<u>THEla</u> MLT1e MSTc	GATGC	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1
HUMUBIBP HUMUDPCNA HUMUG2PC	1-106 ¥ 595-779 L1 315-519 261-end		<u>THEla</u> MLTle MSTc MSTb	GATGC	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site.
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB	1-106 \ \ 595-779 L1 315-519 261-end 1-162 \ \		<u>THEla</u> MLT1e MSTc MSTb THE1b	GATGC	Human calmodulin family member gene, 3'-UTR Human ublquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA	1-106 \ \ 595-779 L1 315-519 261-end 1-162 \ 1-52		<u>THE1a</u> MLT1e MSTC MSTb THE1b THE1a	GATGC	Human calmodulin family member gene, 3'-UTR Human ublquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948)
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVCAMA	1-106 \vee 595-779 L1 315-519 261-end 1-162 \vee 1-52 1-113 \vee		THE1a MLT1e MSTC MSTD THE1b THE1a MLT1d	GATGC	Human calmodulin family member gene, 3'-UTR Human ubiquitin UB pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVCAMA HUMVWFAB HUMXT0	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥	+	THELA MLTLe MSTC MSTD THELD THELA MLTLd	GATGC Sequence	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain CDNAs. There are similarities to
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVWFAB HUMXT0	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥	+	THE1A MLT1e MSTC MSTb THE1b THE1A MLT1d	GATGC Sequence 11 THE1-	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain CDNAs. There are similarities to -, 9 MstII-, and 27 MLT1-LTRs and 3 internal sequences.
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVWFAB HUMXT0	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥		THE1A MLT1e MSTC MSTb THE1b THE1a MLT1d MLT1b	GATGC Sequence 11 THE1-	Human calmodulin family member gene, 3'-UTR Human Ubquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site d tags of human brain CDNAs. There are similarities to , 9 MstII-, and 27 MLT1-LTRS and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVWFAB HUMXT0 M24686 MACCLINE	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722	+ - +	THE1a MLT1e MSTC MSTb THE1b THE1a MLT1d MLT1b MLT1a	GATGC Sequence 11 THE1- GATGR	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain cDNAs. There are similarities to , 9 MstII-, and 27 MLT1-LTRs and 3 internal sequences. Human majotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globin genes, 3' FR
HUMUBIBP HUMDDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVWFAB HUMXT0 M24686 MACGLINE MACFSP94 WACFSP94	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122	+ + + + +	THELA MLTLE MSTC MSTD THELD THELA MLTLA MLTLD MLTLA	GATGC Sequence 11 THE1- GATGR	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain cDNAs. There are similarities to -, 9 MstII-, and 27 MLT1-LTRS and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globbin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740)
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVWFAB HUMXT0 M24686 MACGLINE MACPSP94 MACRHPV1 MACKHPV1	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end	+	THE1A MLT1e MSTC MSTb THE1b THE1a MLT1d MLT1b MLT1a MLT1b MLT1a	GATGC Sequence 11 THE1- GATGR	Human calmodulin family member gene, 3'-UTR Human Ubracetylglucosaminyltransferase I gene, intron 1 Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site d tags of human brain cDNAs. There are similarities to , 9 MstII-, and 27 MLTI-LTRS and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740) Integration site for Rhesus monkey papilloma virus
HUMUBIBP HUMUGPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVWFAB HUMXT0 M24686 MACGLINE MACPSP94 MACRHPV1 MNKGLINE TADBECDC	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end 5370-5721 1000	+ -++++	THELA MLTIE MSTC MSTD THELA MLTIA MLTID MLTIA MLTIA MLTIA	GATGC Sequence 11 THE1- GATGR GATGR	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain cDNAs. There are similarities to , 9 MstII-, and 27 MLT1-LTRS and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR(to -740) Integration site for Rhesus monkey papilloma virus Spider monkey A and G gamma globin genes, 3' FR
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVTAB HUMXT0 M24686 MACGLINE MACPSP94 MACRHPV1 MNKGLINE TARHBEGPS	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end 5370-5721 10694-11048	+ - + + + + + + +	THELA MLTLE MSTC MSTb THELD THELA MLTLA MLTLA MLTLA MLTLA	GATGC Sequence 11 THE1- GATGR GATGR GATGR	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain cDNAs. There are similarities to , 9 MstII-, and 27 MLT1-LTRs and 3 internal sequences. Human mgiotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740) Integration site for Rhesus monkey papilloma virus Spider monkey A and G gamma globin genes, 3' FR Tarsier gamma globin gene, 3' FR
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVWFAB HUMXT0 M24686 MACGLINE MACPSP94 MACRHPV1 MNKCLINE TARHBEGPS RODE:	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end 5370-5721 10694-11048 ****	+ - + + + + +	THELA MLTLe MSTb THELD THELA MLTLA MLTLA MLTLA MLTLA	GATGC Sequence 11 THE1- GATGR GATGR GATGR	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain cDNAs. There are similarities to ., 9 MstII-, and 27 MLTI-LTRs and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740) Integration site for Rhesus monkey papilloma virus Spider monkey A and G gamma globin genes, 3' FR
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HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVWFAB HUMXT0 M24686 MACGLINE MACPSP94 MACRHPV1 MNKGLINE TARHBEGPS CRUDHFRORI CRUDHFRORI CRUDHFRORI	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end 5370-5721 10694-11048 WTS 3112-3364 5357-5396 1-30 Åu 226-205	+ - + + + + +	THELA MLTIE MSTC MSTD THELD THELA MLTIA MLTIA MLTIA MLTIA ORRID MLTIA	GATGC Sequence 11 THEI- GATGR GATGR GATGR GTAGY	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain cDNAs. There are similarities to -, 9 MstII-, and 27 MLT1-LTRS and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740) Integration site for Rhesus monkey papilloma virus Spider monkey A and G gamma globin genes, 3' FR Tarsier gamma globin gene, 3' FR Chinese hamster DHFR gene origin region of replication Chinese hamster DHFR gene origin region of replication
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HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVTAAB HUMXT0 M24686 MACGLINE MACPSP94 MACRHPV1 MNKGLINE TARHBEGPS RODEJ CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end 5370-5721 10694-11048 *76 3112-3364 5357-5396 1-30 Alu 216-end <980->1200 (1nt.) 1335-end (31/TP)	+ + + + + + + + +	THELA MLTIe MSTC THELD THELD THELA MLTIA MLTIA MLTIA MLTIA MLTIA ORRID MLTIA	GATGC Sequence 11 THE1- GATGR GATGR GATGR GTAGY	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site d tags of human brain cDNAs. There are similarities to , 9 MstII-, and 27 MLTI-LTRS and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740) Integration site for Rhesus monkey papilloma virus Spider monkey A and G gamma globin genes, 3' FR Tarsier gamma globin gene, 3' FR Chinese hamster DHFR gene origin region of replication chinese hamster Alu type 2 integration site. Syrian hamster androgen-dependent expressed protein cDNA,
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMYCAMA HUMYWFAB HUMXT0 M24686 MACGLINE MACGLINE TARHBEGPS RODEJ CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDA49C	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end 5370-5721 10694-11048 W28 3112-3364 5357-5396 1-30 Alu 216-end <980->1200 (int.) 1335-end (3'LTR) Was 586-634	+	THELA MLT1e MSTC MSTC THELA MLT1A MLT1A MLT1A MLT1A MLT1A MLT1A MLT1A MLT1A MTC	GATGC Sequence 11 THE1- GATGR GATGR GATGR GTAGY	Human calmodulin family member gene, 3'-UTR Human UDPacetylglucosaminyltransferase I gene, intron 1 Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vacular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site d tags of human brain cDNAs. There are similarities to , 9 MstII-, and 27 MLTI-LTRs and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740) Integration site for Rhesus monkey papiloma virus Spider monkey A and G gamma globin genes, 3' FR Tarsier gamma globin gene, 3' FR Chinese hamster DHFR gene origin region of replication Chinese hamster DHFR gene origin region of replication Chinese hamster Alu type 2 integration site. Syrian hamster androgen-dependent expressed protein cDNA, 3' UTR. DNA recombined with CAP gene 3'FP uppe CDP applification
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HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVTAB HUMXT0 M24686 MACGLINE MACR5P94 MACRPV1 MIXGLINE TARHBEGPS RODE: CRUDHFORI CRUDHFORI CRUDHFORI CRUDHFORI CRUDHFORI CRUDHFORI CRUDHFORI CRUDHFORI CRUDHFORI CRUDHFORI CRUDHFORI CRUBAS321 MUSAB321 MUSACHRA MUSACHRA MUSACHRA MUSATRVL2 MUSANTRVL2 MUSATRVL2 MUSAPP9 MUSCR2A MUSCR2A MUSCYTCC MUSD1H2K MUSD1H2K MUSD1H2K MUSD1H2K MUSD1H2K MUSD1H2K MUSD1H2K MUSECDD MUSECDD MUSECDD MUSECDD	1-106 ¥ [595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end 5370-5721 10694-11048 TF 3112-3364 [5357-5336 1-30 Alu 216-end (980->1200 (int.) 1335-end (3'LTR) Mys [586-634 3003-3369 (3'LTR) 3687-3754 (5'LTR) 2453(LTR) 54-end(int) 2544-2850 (5'LTR) 2851-2992 B1 (int) 1-110 724-1073 524->918 4449-4775 B2 526-700 5638-5954 1-16 IAP IAP 403-454 3520-end 1239-21442 9749-10085 34929- L1 -36733 2281-2601 2219-2314 (5'LTR) 2480-end (3'LTR) 2480-end (3'LTR)		THELA MLTLe MSTC MSTC MSTC MSTD THELA MLTLA MLTLA MLTLA MLTLA MLTLA MLTLA MITLA ORRID MTC ORRID ORRID ORRID ORRID ORRIC MTC ORRIC MTC ORRIC MTC ORRIA	GATGC Sequence 11 THE1- GATGR GATGR GATGR GTAGY CCTTT AGTAC GRCCC CCTTT AGYTC CTKAS ACART GGCTG	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain cDNAs. There are similarities to , 9 MstIr-, and 27 MLT1-TTRs and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey A and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740) Integration site for Rhesus monkey papilloma virus Spider monkey A and G gamma globin genes, 3' FR Tarsier gamma globin gene, 3' FR Chinese hamster DHFR gene origin region of replication Chinese hamster DHFR gene origin region of replication Chinese hamster DHFR gene origin region of replication Chinese hamster Alu type 2 integration site. Syrian hamster androgen-dependent expressed protein cDNA, 3' UTR. DNA recombined with CAD gene 3'FR upon CAD amplification Syrian hamster μ class glutathione S-transferase gene, intron 7. Adenovirus integration site in hamster kidney cell line. Mouse α -subunit gene of thyrotropin, intron 3 Rat bone gla protein (BGP) gene, 5. FR (to -500) Recombination hotspot in mouse MHC Pb/Ob intergenic region Mouse acetylcholine receptor γ subunit,5'FR(-2519 to-2127) Mouse acetylcholine receptor γ subunit,5'FR(-250) Ruse angin gene, 3' UTR Mouse transplantation antigen P91A, intron 5 Integration site of IAP DNA 9 kb upstream of the angiotensinogen gene in Swiss mice Mouse alkaline phosphatase pseudogene, 3' FR Mouse blymphocyte activation antigen B7 mRNA, 3'UTR Mouse complement receptor CDNA, 3' UTR Mouse complement receptor CDNA, 3' UTR Mouse SI and MT repeat DNA region Mouse B1 and MT repeat DNA region Mouse B1 and MT repeat DNA region Mouse elongation factor 2 processed pseudogene, 5' FR Mouse elongation fa
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVG4PB HUMVCAMA HUMVWFAB HUMXT0 M24686 MACGLINE MACRSP94 MACRHPV1 MNKGLINE TARHBEGPS RODEI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI MISA49C HAMAGLUTRA HAMGLUTRA HAMGLUTRA HAMGLUTRA HAMGLUTRA HAMGLUTRA MUSAB321 MUSACHRB MUSACHRB MUSACHRB MUSACHRB MUSACHRA MUSACHRA MUSATRVL1 MUSATRVL1 MUSATRVL1 MUSATRVL1 MUSATRVL1 MUSATRVL1 MUSAFCR1 MUSBCCD MUSCR2A MUSCYTCC MUSDA1H2K MUSCT2N MUSCP2PS MUSEF2PS MUSEF2PS MUSEF2PS	1-106 ¥ 595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end 5370-5721 10694-11048 *78 3112-3364 15357-53361 1-30 Alu 216-end <980->1200 (int.) 1335-end (3'LTR) Mys 586-634 3003-3369 (3'LTR) 264-53(1rR) 54-end(int) 2544-2850 (5'LTR) 244-53(1rR) 54-end(int) 2544-2850 (5'LTR) 2542-918 24459-175 B2 526-700 5638-5954 1-16 IAP IAP 403-454 3520-end 1239->142 9749-10085 34929- L1 -36733 2281-2601 12219-2314 (5'LTR) 2480-end (3'LTR) 2480-end (3'LTR) 1486-1856 795-967 B2 1106->1265 12926-3266 1-53 L1 372-end 64-459 1-58 237-end (-PU)		THELA MLT1e MSTC MSTC MSTC MSTD THELA MLT1A MLT1A MLT1A MLT1A MLT1A MLT1A MLT1A ORR1b MTC ORR1b ORR1b ORR1b ORR1b ORR1b ORR1c MTC MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC ORR1b MTC	GATGC Sequence 11 THE1- GATGR GATGR GATGR GTAGY CCTTT AGTAC GRCCC CCTTT AGYTC CTKAS ACART GGCTG	Human calmodulin family member gene, 3'-UTR Human ubiquitin Ub B pseudogene integration site. Human UDPacetylglucosaminyltransferase I gene, intron 1 Human U2 small nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site ed tags of human brain cDNAs. There are similarities to , 9 MstII-, and 27 MLT1-LTRs and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740) Integration site for Rhesus monkey papilloma virus Spider mokey A and G gamma globin genes, 3' FR Tarsier gamma globin gene, 3' FR Chinese hamster DHFR gene origin region of replication Chinese hamster DHFR gene origin region of replication Chinese hamster DHFR gene origin region of replication Syrian hamster adrogen-dependent expressed protein cDNA, 3' UTR. DNA recombined with CAD gene 3'FR upon CAD amplification Syrian hamster μ class glutathione S-transferase gene, intron 7. Adenovirus integration site in hamster kidney cell line. Mouse α -subunit gene of thyrotropin, intron 3 Rat bone gla protein (BGP) gene, 5. FR (to -500) Recombination hotspot in mouse MHC Pb/Ob intergenic region Mouse acetylcholine receptor β subunit,5'FR(-2519 to-2127) Mouse acetylcholine receptor β subunit gene, intron 7 Mouse agrin gene, 3' UTR Mouse dranplantation antigen P1A, intron 5 Integration site of IAP DNA 9k bu patream of the angiotensinogen gene in Swiss mice Mouse alkaline phosphatase pseudogene, 3' FR Mouse ba-Fc-gamma-RII gene intron 4 Mouse β -globin bh3-bl intergenic region. Mouse alkaline phosphatase pseudogene, 3' FR Mouse complement receptor cDNA, 3' UTR Mouse Class II E β gene, intron 2. Mouse thing extraction circular DNA Mouse el and MT repeat DNA region Mouse bit and MT repeat DNA region Mouse MiC class II E β gene, intron 2. Mouse
HUMUBIBP HUMUDPCNA HUMUG2PC HUMUG4PB HUMVCAMA HUMVWFAB HUMXT0 M24686 MACGLINE MACRPSP94 MACRHPV1 MNKGLINE TARHBEGPS RODE CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDHFRORI CRUDAFRORI CRUDHFRORI CRUDAFRORI MARADA HAMMGLUTRA HAMVI1 M22992 M25490 MUSACHRA MUSACHRA MUSACHRA MUSACHRA MUSACHRA MUSACHRA MUSACHRA MUSACHRA MUSACHRA MUSATRVL1 MUSACHRA MUSATRVL1 MUSACHRA MUSATRVL2 MUSAFIAA MUSBFCGR1 MUSBFCGR1 MUSBFCGR1 MUSBFCGR1 MUSBFCGR1 MUSBCC2 MUSCYTCC M	1-106 ¥ [595-779 L1 315-519 261-end 1-162 ¥ 1-52 1-113 ¥ 1-200 9380-9722 1-122 371-end 5370-5721 10694-11048 X78 3112-3364 5357-5396 1-30 Alu 216-end (3570-5396) 1-30 Alu 216-end (3570-5396) 1-30 Alu 216-end (3570-5396) 1-30 Alu 216-end (3570-5396) 1-30 Alu 216-end (3570-5396) (3570-5396) (3570-5396) (3570-534) (3570-534) (3570-534) 2651-2992 Bl (110) 1-110 724-1073 524-9918 4449-4775 B2 526-700 5638-5954 1-16 IAP IAP 403-454 3520-end 1239-31442 9749-10085 34929-1 L1 -36733 2281-2601 (2219-2314 (5*LTR) 2480-end (3*LTR) 1486-1856 795-967 B2 106-31265 [2926-3266 1-53 L1 372-end 64-459 1-58 237-end (-Py) 1-101	++++++++ ++ ++ +++++++++++++	THELA MLTLE MSTC MSTC MSTC MSTC MLTLA MLTLA MLTLA MLTLA MLTLA MLTLA MLTLA MSTC MSTC ORRID MTC ORRID ORRID ORRID ORRID ORRID ORRID MTC ORRID ORRID ORRID ORRID ORRID ORRID ORRID ORRID ORRID MTC ORRID MTC ORRID MTC ORRID MTC ORRID MTC ORRID MTC ORRID MTC ORRID MTC ORRID OR ORD ORD ORD ORD ORD ORD ORD ORD ORD	GATGC Sequence 11 THEI- GATGR GATGR GATGR GTAGY CCTTT AGTAC GRCCC CCTTT AGYTC CTKAS ACART GGCTG	Human calmodulin family member gene, 3'-UTR Human UDPacetylglucosaminyltransferase I gene, intron 1 Human UDPacetylglucosaminyltransferase I gene, intron 1 Human UDP amall nuclear RNA pseudogene insertion site. U4 pseudogene integration site, 140 bp 5' of coding region Human vascular cell adhesion molecule-1 gene, 5'FR(<-2948) Human von Willebrand factor pseudogene recombination site dt ags of human brain cDNAs. There are similarities to ', 9 MstII-, and 27 MLT1-LTRs and 3 internal sequences. Human angiotensinogen (serpin) gene, intron 1 Rhesus monkey and G gamma globin genes, 3' FR Rhesus monkey prostatic secretory p94, 5'FR (to -740) Integration site for Rhesus monkey papiloma virus Spider monkey A and G gamma globin genes, 3' FR Tarsier gamma globin gene, 3' FR Chinese hamster DHFR gene origin region of replication Chinese hamster DHFR gene origin region of replication Chinese hamster Alu type 2 integration site. Syrian hamster androgen-dependent expressed protein cDNA, 3' UTR. DNA recombined with <i>CAD</i> gene 3'FR upon CAD amplification Syrian hamster μ class glutathione S-transferase gene, intron 7. Adenovirus integration site in hamster kidney cell line. Mouse G-subunit gene of thyrotropin, intron 3 Rat bone gla protein (BGP) gene, 5. FR (to -500) Recombination hotspot in mouse MHC <i>Pb/Ob</i> intergenic region Mouse acetylcholine receptor β subunit, 5'FR(-2519 to -2127) Mouse argin gene, 3' UTR Mouse agrin gene, 3' UTR Mouse distingene fixe fixe marks mice Mouse alkaline phosphatase pseudogene, 3' FR Mouse b lymphocyte activation antigen B7 mRNA, 3'UTR Mouse Single stranded-DNA binding protein cDNA, 3' UTR Mouse Cyp2d-11 gene, intron 1 Mouse B1 and MT repeat DNA region Mouse Cyp2d-11 gene, intron 1 Mouse B1 and MT repeat DNA region Mouse B1 and MT repeat DNA region Mouse B1 and MT repeat DNA region Mouse B1 and MT repeat D

MUSIGCD17	2962-3347	+	ORR1c RG	GAM	Mouse IgH constant region Co gene, 3' UTR
MUSIGCR	<1925-2174	-	MLT1		Mouse IgH constant region Cy2a gene, 3' FR
MUSIGMUD3	3554-39071	-	MLTIC		Mouse IgH constant region, Cµ-Co intergenic region.
MUSIGMUD3	13908-4063	+	MLT1C		Mouse IgH constant region, Cµ-Cō intergenic region.
MUSILZR	B1 000-002 250-657	-	MIC DC	300	Mouse interleukine receptor, 5' FR (-800 to -650)
MUSIDE	13022-40331	-	MID RG.	AIC	Polyoma virus integration site in mouse genome
MUSLDHAG	19923-09 10266	_	OPPId		Mouse locate debudrogenese. introp 5
MUSLDHAG	<12704-end	_	OPPIN		Mouse lactate dehydrogenese-A, Intron 5.
MUSLDHADS	12460-2703	_	OPPIC		Mouse lactate dehydrogenese-A, 5' FR
MUSLEP	1351-490	-	MTC		Mouse lactoferrin gene 5' FP (-2310 to-2170)
MUSMCKA	3219-3551	-	ORBIA GG	STC	Mouse muscle creating kinase gene intron 1
MUSMHC4H2S	7869-8265	-	MTa CA	CAC	Mouse MHC complement component C4 gene, intron 15
MUSMHCAB1	(TG) n-90-498	+	MTd		Mouse MHC class II Ob gene cDNA, 5' FR (-1180 to -760)
MUSMHCT2A	<4820-5425 (int.)	+	ORR1c		Mouse MHC class I thymus leukemia antigen (Tla)-T2a-a
	5426-end (3'LTR)				chain (H-2a) gene, 3' FR
MUSMHH2CAS	2028-2425	-	MTC GT	(T)AG	Mouse maternally transmitted MHC class I gene, intron 3
MUSMHKBA	1-323	+	ORR1b		Mouse MHC class I gene H-2Kb, 5' FR (to - 1697)
MUSMHTLAC	5157-end (int.)	+	int.		Mouse MHC class I Tla gene 17.3.A, 3' FR
MUSMKR2	2257-end	+	MTC		Mouse multifinger gene mKr2 cDNA, 3' UTR
MUSMS 6 HM	37-511	-	MTa GT	YAG	Mouse HyperMutable minisatellite locus
MUSMTREPA	1-end	-	MTa		Mouse genomic clone selected with MT repeat in MUSINS
MUSMTREPB	1-end	-	MTb		Mouse genomic clone selected with MT repeat in MUSINS
MUSMTREPC	1-end	+	MTb		Mouse genomic clone selected with MT repeat in MUSINS
MUSNLAM23	1-end	-	MTC		Mouse DNA fragment contacting the nuclear lamina
MUSPCPA2	1084-1140 B2	-	ORR1a		Mouse mastocytoma proteoglycan core protein gene, intron 2
MUSPERIOE	475-end	-	ORR1a		Mouse hexamer repeat sequence genomic clone
MUSPERSP5	1-157	+	ORR1b		Mouse spleen mRNA containing period repeat, 5' UTR.
MUSPOLRSB2	73-413-polyA	+	MTa		SV40 transformation induced polIII transcribed B2 RNA
MUSPRPC2	6992-end	-	MTb		Mouse proline rich protein (M14) gene, 3' FR
MUSQ2K1	1-31/	+	MIC		Mouse MHC class I (Qa) Q2-k gene, 5' FR (<-552 to -236)
MUSQAQ1K	1-282	+	MIC		Mouse MHC class I (Qa) Q1-k gene, 5' FR (<-540 to -158)
MUSRENZIA	1-9/ IAP 3101-3289	+	MIC		Mouse renin gene, 3' FR
MUSREPMT1	1/J-eng	-	MTa		mouse genomic clone detected with MUSREPMT2a
MUSREPMT2	263-end	-	MTa		Mouse genomic clone detected with MUSREPMT2a
MUSREPHIS		-	MTa		Mouse cerebellum mkNA repetitive portion
MUSREPHI4	100-eng 2710-3049	Ť	OPP1 - CT	C	Mouse genomic clone detected with MUSREPMIZa
MUSREDIZA	548-end	I	MIT1a GI	GAC	Mouse ribosomal protein L52, processed pseudogene, rk
MUSSAAIB	3675-37401	-	MTC		Mouse serum amuloid A=1 gene 3' FP
MUSSAA2B	3624-39191	-	MTC		Mouse serum amyloid λ -2 gene, 3' FR
MUSSNU3P	74-173<	+	ORRIA		Mouse US processed pseudogene, 5' FR
MUSTCP1X	1600-1680-polyA	+	MTC		Mouse t-complex gene Tcp-1x cDNA, 3' UTR
MUSTHROMBO	ca.171-569	+	MTC		Mouse thrombomodulin gene, 5' FR (-2600 to -2100)
MUSTSG 64 X	1-end	-	MLT1d		Mouse expressed sequence tag.
MUSTSPCO2	1675-2029	-	ORR1d GR	RAT	Mouse T cell receptor α chain variable region, Va 8 3' FR
MUSU7PS23	1-124	-	MTa		Mouse 117 programed preudogene 51 PD
					nouse of processed pseudogene, 5° rk
MUSUG1PB	1-110 ¥	+	ORR1a		Mouse U1 processed pseudogene integration site.
MUSUG1PB MUSYPT13	1-110¦ ₩ 1-172	+ -	ORR1a ORR1a		Mouse Ul processed pseudogene, 5° rK Mouse Ul processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2
MUSUG1PB MUSYPT13 RAT55REP	1-110 ¥ 1-172 B2 120-348	+ - +	ORR1a ORR1a MLT1		Mouse U1 processed pseudogene, 5 rk Mouse U1 processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements
MUSUG1PB MUSYPT13 RAT55REP RATAPI	1-110 ₩ 1-172 B2 120-348 8684-8985	+ - + -	ORR1a ORR1a MLT1 ORR1b KC	AYC	Mouse Ul processed pseudogene, 5 TK Mouse Ul processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat acyl-peptide hydrolase gene, intron 14
MUSUG1PB MUSYPT13 RAT55REP RATAPI RATB5RG	1-110¦ ♥ 1-172 B2 120-348 8684-8985 1-278	+ -+ +	ORR1a ORR1a MLT1 ORR1b KC ORR1d	AYC	Mouse U processed pseudogene, 5 rk Mouse U processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat acyl-peptide hydrolase gene, intron 14 Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100)
MUSUG1PB MUSYPT13 RAT55REP RATAPI RATB5RG RATCATO1	1-110; ♥ 1-172 B2;120-348 8684-8985 1-278 634-ca.1045	+ - + - + +	ORR1a ORR1a MLT1 ORR1b KC ORR1d ORR1d	AYC	Mouse UI processed pseudogene, 5° FR Mouse UI processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100) Rat catalase gene, 5' FR (-4040 to -3630)
MUSUG1PB MUSYPT13 RAT55REP RATAPI RATB5RG RATCATO1 RATCGM1AC6	1-1101 ♥ 1-172 B2 1120-348 8684-8985 1-278 634-ca.1045 1262-501 14005	+ - + - + + -	ORR1a ORR1a MLT1 ORR1b KC ORR1d ORR1d MTc	AYC	Mouse U1 processed pseudogene, 5' FR Mouse U1 processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat acyl-peptide hydrolase gene, intron 14 Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100) Rat catalase gene, 5' FR (-4040 to -3530) Rat CEA related protein 1 gene, intron 4
MUSUGIPB MUSYPT13 RAT55REP RATAPI RATB5RG RATCAT01 RATCGM1AC6 RATCGM4AA DATCGM4AA	1-1101 ♥ 1-172 B2 1120-348 8684-8985 1-278 634-ca.1045 1262-501 14096-4333 14293 15322	+ - + - + +	ORR1a ORR1a MLT1 ORR1b KC ORR1d ORR1d MTc MTc	AYC	Mouse UI processed pseudogene integration site. Mouse UI processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat acyl-peptide hydrolase gene, intron 14 Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100) Rat CEA related protein 1 gene, intron 4 Rat CEA related protein 4 gene, intron 4
MUSUGIPB MUSYPT13 RAT55REP RATAPI RATB5RG RATCATO1 RATCGM1AC6 RATCGM4AA RATCRYG RATCRYG	$1-1101 \forall $ $1-172 \\ B2 120-348 \\ 8684-8985 \\ 1-278 \\ 634-ca.1045 \\ 262-501 \\ 4096-4333 \\ 14783-15373 \\ -14010 \\ 15105 \\ $	+ - + - + + +	ORR1a ORR1a MLT1 ORR1b KC ORR1d MTc MTc ORR1a MS ORR1a	AYC	Mouse UI processed pseudogene integration site. Mouse UI processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat acyl-peptide hydrolase gene, intron 14 Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100) Rat catalase gene, 5' FR (-4040 to -3630) Rat CEA related protein 1 gene, intron 4 Rat CEA related protein 4 gene, intron 4 Rat gamma A-B crystallin genes, intergenic region
MUSUGIPB MUSYPT13 RAT55REP RATAPI RATB5RG RATCATO1 RATCGM1AC6 RATCGM4AA RATCRYG RATCRYG RATCRYG RATCRYG	1-1101 ♥ 1-172 B2 120-348 8684-8985 1-278 634-ca.1045 262-501 4096-4333 14783-15373 ca.14910-15195 92216-22567	+ - + - + + +	ORR1a ORR1a MLT1 ORR1b KC ORR1d MTc ORR1a MS ORR1a MS ORR1a CC	AYC	Mouse UI processed pseudogene, 5' regration site. Mouse UI processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100) Rat catalase gene, 5' FR (-4040 to -3630) Rat CEA related protein 1 gene, intron 4 Rat Gamma A-B crystallin genes, intergenic region Rat gamma A-B crystallin genes, intergenic region
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MUSUGIPB MUSYPT13 RAT55REP RATAPI RATB5RG RATCATO1 RATCGM1AC6 RATCGM4AA RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG	1-1101 ♥ 1-172 B2 1120-348 8684-8985 1-278 634-ca.1045 1262-501 14096-4333 14783-15373 ca.14910-15195 22216-22567 ca.29694-29990 41224-41627	+ - + - + + +	ORRIA ORRIA MLTI ORRID KC ORRID MTC MTC ORRIA ORRIA ORRIA ORRIA ORRIA ORRIA	AYC ACC AAY	Mouse U processed pseudogene integration site. Mouse U processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat acyl-peptide hydrolase gene, intron 14 Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100) Rat cEA related protein 1 gene, intron 4 Rat CEA related protein 1 gene, intron 4 Rat gamma A-B crystallin genes, intergenic region Rat gamma B-C crystallin genes, intergenic region Rat gamma C-D crystallin genes, intergenic region Rat gamma D-D crystallin genes, intergenic region
MUSUGIPB MUSYPT13 RAT55REP RATAPI RATB5RG RATCATO1 RATCGM1AC6 RATCGM4AA RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG	$1-1101 \psi$ $1-172$ $B2 120-348$ $8684-8985$ $1-278$ $634-ca.1045$ $ 262-501$ $ 4096-4333$ $14783-15373$ $ca.14910-15195$ $22216-22567$ $ca.29694-29990$ $41224-41627$ $264-63$	+ - + - + + +	ORRIA ORRIA MLTI ORRIA ORRIA MTC ORRIA ORRIA ORRIA ORRIA ORRIA ORRIA ORRIA ORRIA ORRIA ORRIA ORRIA ORRIA	AYC ACC AAY	Mouse UI processed pseudogene integration site. Mouse UI processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat acyl-peptide hydrolase gene, intron 14 Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100) Rat catalase gene, 5' FR (-4040 to -3630) Rat CEA related protein 1 gene, intron 4 Rat CEA related protein 4 gene, intron 4 Rat gamma A-B crystallin genes, intergenic region Rat gamma B-C crystallin genes, intergenic region Rat gamma D-C crystallin genes, intergenic region
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MUSUGIPB MUSYPT13 RAT55REP RATAPI RAT65RG RATCGM1AC6 RATCGM1AC6 RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG RATCYG RATCYP5E1 RATCYPE17 RATCYPE41	$1-1101 \psi$ $1-172$ $B2 120-348$ $8684-8985$ $1-278$ $634-ca.1045$ $ 262-501$ $ 4096-4333$ $14783-15373$ $ca.14910-15195$ $22216-22567$ $ca.29694-29990$ $41224-41627$ $264-663$ $1-77$ $<1487-1861$ $4275-6343$	+ $+$ $+$ $+$ $+$ $+$ $+$ $+$ $+$ $+$	ORR1A ORR1A MLT1 ORR1b ORR1d MTC MTC ORR1A ORR1A ORR1A ORR1A ORR1A CORR1A TA MTC RY MTC MTC ORR1B RTC	AYC ACC AAY RRG YTY YAT	Mouse U1 processed pseudogene, 5' regration site. Mouse U1 processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat acyl-peptide hydrolase gene, intron 14 Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100) Rat catalase gene, 5' FR (-4040 to -3630) Rat CEA related protein 4 gene, intron 4 Rat CEA related protein 4 gene, intron 4 Rat gamma A-B crystallin genes, intergenic region Rat gamma B-C crystallin genes, intergenic region Rat gamma D-E crystallin genes, intergenic region Rat gamma D-E crystallin genes, intergenic region Rat G2B1 gene, 5' FR (to -743) Rat CYP2B2 gene, 5' FR (to -1685) Rat CYP17 gene, 5' FR (to -1685)
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MUSUGIPB MUSYPT13 RAT55REP RATAPI RATB5RG RATCATO1 RATCGM1AC6 RATCGM1AC6 RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG RATCRYG RATCY17G RATCYPEA1 RATCYPA11 RATCYPA1 RATCYPA1 RATCYPA3 RATCYPOXG RATDBP02 RATDBP02 RATGFIL4 RATIID3G	$1-1101 \psi$ $1-172$ $B2 120-348$ $8684-8985$ $1-278$ $634-ca.1045$ $ 262-501$ $ 4096-4333$ $14783-15373$ $ca.14910-15195$ $22216-22567$ $ca.29694-29990$ $41224-41627$ $264-663$ $1-77$ $c1487-1861$ $4275-6343$ $c14580-15019$ $1-238 (5'LTR) 239-465$ $ ID 577-647 B1 (int)$ $882-ca.1210$ $1136-end$ $8747-9107$	+ $+$ $+$ $+$ $+$ $+$ $+$ $+$ $+$ $+$	ORR1A ORR1A MLT1 ORR1b ORR1d ORR1d ORR1A ORR1A ORR1A ORR1A ORR1A ORR1A TA MTC ORR1A MTC ORR1B MTC ORR1B MTC	AYC ACC ARY YTY YAT	Mouse U1 processed pseudogene, 5' FR fatton site. Mouse U1 processed pseudogene integration site. Mouse ypt1 gene for ras-related protein, intron 2 Rat genomic DNA containing multiple repetitive elements Rat acyl-peptide hydrolase gene, intron 14 Rat NADH-cytochrome b5 reductase gene, 5' FR(to -1100) Rat catalase gene, 5' FR (-4040 to -3630) Rat Cat related protein 1 gene, intron 4 Rat CEA related protein 1 gene, intron 4 Rat CEA related protein 4 gene, intron 4 Rat CEA related protein 1 genes, intergenic region Rat gamma A-B crystallin genes, intergenic region Rat gamma D-C crystallin genes, intergenic region Rat gamma D-C crystallin genes, intergenic region Rat gamma D-C crystallin genes, intergenic region Rat GYZB2 gene, 5' FR (-1242 to -743) Rat CYZB2 gene, 5' FR (to -743) Rat CYZB2 gene, 5' FR (to -743) Rat clofibrate-inducible CYP4AI gene, intron 4 Rat genomic clone, ca. 4 kb upstream of NADPH-cytochrome P-450 oxidoreductase gene Rat vitamin D binding protein (Gc-globulin) gene, intron 2 Rat insuline-like growth factor IA gene, 3 FR Rat CYZ2D3 gene, 3' FR
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THE/MstII families (highest to MLT1a). These observations and the distribution of the (sub)families over mammalian species suggested an evolutionary relationship of MaLRs as depicted in Figure 4.

The significant difference between subfamilies in average sequence divergence of copies to their consensus (Figure 4) is consistent with a punctuated nature of subfamily formation. Similar observations have been made for Alu and L1 (reviewed in 40). The consensus sequence of each subgroup may represent the approximate sequence of one or a few transpositionally competent 'source elements' or 'master genes' at the various periods during evolution when they gave rise to a much larger number of defective elements than in intermittent periods. There is no indication of a contemporary distribution of elements in human, mouse, or rat, although the existence of small groups of recently distributed MaLRs, with too few representatives in the databanks to be recognized, cannot be ruled out. It is interesting to note that the length of the LTRs generally seems to have declined in evolution; the youngest member of each family always has the shortest consensus sequence (see Figure 3).

ORR-1 and MT MaLRs form two families confined to rodents. They are more similar to each other than to the other families and may share a common ancestor in an early rodent. Their occurrence in presumably human sequences can actually be an omen for a cloning artifact. Indeed, the 3' end of a human CCG1 cDNA (HUMCCG1), which contains an ORR1-LTR, was found to be of hamster origin (41). This may also be the case for the sequence including the MT in intron 1 of the human Sadenosylmethionine decarboxylase gene (HUMAMD01, 42), further evidenced by a drop from 12% to 1% in CpG content of the DNA before and after the MT homology. MTa, the most recently amplified MaLR subfamily, has, so far, only been found in mouse sequence entries. This is consistent with its average sequence divergence from the consensus of 6.5%, which is less than half the synonymous divergence between rat and mouse (18-23%) (43,44), indicating that it amplified after the mouserat split.

MstII and THE1-MaLRs form a primate branch of the superfamily. The only sequences hybridizing to a human THE1a clone in genomic DNA of the prosimian galago, GAL6 and G-AL7 (45), are members of the MSTb subgroup. Comparison of this subgroup's sequence divergence in the human genome (21%) to the estimated divergence of noncoding human DNA since the diversion from prosimians 50-60 million years (Myr) ago (13-19%) (46, 47) supports an amplification prior to this event. Accordingly, the MSTa and THE1 subfamilies have substitution levels supporting a later distribution in simians only.

In contrast, members of the MLT1 family, predominantly found in primate databank entries, are also present in rodent, rabbit, and artiodactyl (cow and sheep) genomes (see Table 1). This family is presumably the oldest group in the MaLR superfamily. The divergence percentage of most MLT1 subfamilies agree with a distribution before primate evolution. Indeed, Kaplan *et al.* (18) found that their MER18 probe (= MLT1b), but not their MER10 probe (= MSTb, HUMHLASBA) hybridized to bovine chromosomal DNA. However, hybridization to mouse or hamster DNA was not observed. The apparently much higher neutral nucleotide substitution rate in rodents than in higher primates and other mammals (48) may obscure detection of 80-100 Myr old MLT1 elements in rodent genomes both by hybridization or databank searches. This could be an explanation for the relatively low number of MLT1-MaLRs found in the rodent databases and the failure of the MER18 probe to hybridize with rodent DNA, although it is also possible that the major amplification of MLT1 elements occurred after the rodent-primate split.

An MLT1a element is present in the gamma globin region of all studied simians and prosimians (HUMHBB, CEBGLOBIN, GIBHBGGL, MACGLINE, MNKGLINE, GCRGEBEB, TARBGPS) (47) implying that this transposon has integrated over 55 Myr ago in the DNA of a common ancestor of at least all primates. In fact, an orthologous MLT1c-MaLR seems present in the immunoglobulin heavy chain C_{μ} - C_{δ} intergenic region of both human and mouse (HUMIGMUD, HUMIGCMUDE, MUSIGMUD3) (49-51) (Figure 5a). It is present in the human genome with a full-length internal sequence and two LTRs (the 366 bp repeats in ref. 50). Akahori et al. (52) noted that one of two 63 bp repeats (the 'sigma-gamma core sequences'), which are part of the R-U5 region of the MaLR's LTRs, is conserved in the mouse C_{μ} - C_{δ} intron, leading them to suggest a function for this sequence in immunoglobulin expression or construction. Actually, a 150 bp region in mouse that is inverse duplicated (comprising the 'unique sequence inverted repeats' in ref. 51) is 69% similar to both the MLT1c consensus and the 5' LTR of the human MLT1c (Figure 5b). Several lines of evidence (see legend to Figure 5) suggest that this MaLR has integrated before the diversion of rodents and primates.

The above observations imply that the MaLR class of transposons has originated before the radiation of eutherian mammals 80-100 Myr ago. A much more recent origin had previously been suggested based on ϕ -tests indicating that THE1 like repeats are present as single or oligo loci copies in prosimians and in high copy number in higher primates (53) and on sequence data from the prosimian galago, suggesting that the internal sequence had become flanked by LTRs during simian evolution (45).

It has been suggested that the study of the taxonomic distribution of Alu elements (from 55 Myr ago on) can be used to solve the branching order in the higher primate evolution (3, 54) and the distribution of a rodent L1-subfamily (Lx) has been used to delineate the murine subfamily relationships (55). Since many (abundant) MaLR subfamilies seem to have amplified during the radiation of the eutherian (sub)orders, the detection of the presence of orthologous elements or the general distribution patterns of these elements may be used to untangle this higher order branching pattern. For example, the ORR1b-MaLR in the

Position numbers refer to those in the database entry. | denotes an abrupt end to the homology with the consensus. If this is caused by recombination with or integration of a known element, this is indicated (ψ = pseudogene, Mys = Mys endogenous proretroviral LTR, ID = rat identifier element, IAP = rodent intracisternal A particle DNA, AS = artiodactyl SINE, C = rabbit C-repeat). < and > indicate possible extension of the element. (int.) = internal sequence ^a) Orientation of the element in the sequence entry. ^b) Type of LTR as presented in Figure 3. Elements with internal sequences are underlined. ^{c)} Target site duplication sequence in the orientation of the element. The same symbols for degenerate bases are used as in figure 3. ^d) Description of site. UTR = untranslated terminal region of mRNA. FR = flanking region. ⁺ No databank entries exist for GAL6 and GAL7 (45). * The left and right arm of the THE1b-LTR in HUMDYSIN7 (60) are separated and face opposite directions.



Figure 3. Alignment of MaLR-LTR consensus sequences. Each sequence shown is a consensus sequence and defines a subfamily. It is derived by alignment of at least 6 members found in the databases. Grouped consensus sequences represent families. Families could only be aligned in the regions denoted with a gray bar between the grouped consensus sequences. Conserved sites are shown at the top line, with capitals indicating (virtually) invariable sites. The MSTc consensus is partial, since homology extended only between two members beyond the sequence presented. The consensus sequences of three more, highly diverged MLT1 subfamilies are still too indefinite to be integrated in this figure. The underlined region in the U3 part of the ORR1a and ORR1b consensus sequences is often found to be tandemly duplicated. The consensus (and functional) polyadenylation signal and site (the R/U5 boundary) are indicated. Similarly, a tentative TATA-box and transcription initiation site (the U3/R boundary) are marked. The length of the consensus sequences represent inserts of that length. M = A/C, K = G/T, S = G/C, N = A/G/C/T. Underlined numbers in the consensus sequences represent inserts of that length.

Syrian hamster μ -class glutathione S-transferase gene (HAMMGLUTRA) that is absent in the same gene in rat. This is due to a MaLR insertion in the hamster lineage rather than to a deletion in the murid lineage, since the apparent deletion in rat DNA (33) comprises exactly the above MaLR sequence plus one of the 5 bp insertion repeats. Since members of the ORR1b subfamily are present in both murids and hamsters, they must have been distributed around the time of the hamster-murid split. Their average sequence divergence is consistent with this. Most rodents more closely related to hamsters than murids could therefore be expected to be 'labeled' with this MaLR insert.

Estimate of the number of MaLRs in the genome

Over time, most MaLRs have diverged considerably from their consensus sequence. This, and the existence of multiple subfamilies, complicates estimates of their frequency in the genome by hybridization experiments. For instance, Kaplan *et al.* (18) estimated the number of MER15 and MER18 elements in humans to be 700 to 1,500 and 5000 to 10,000, respectively, although they represent the 5' and 3' arm of the same MaLR-LTR subgroup (MLT1b). The 3' arm is better conserved between MLT1 subgroups, possibly accounting for this discrepancy. Related difficulties are also evident in the original estimates of



Figure 4. Schematic representation of the putative relationship of the MaLR families and subfamilies, in part based on their distribution among mammalian species and the sequence alignments in Figure 3. The tip of each branch corresponds to the approximate period of amplification for each subfamily as calculated from the average (corrected) sequence divergence of the copies from their consensus sequence. These divergence values, presented with standard deviation underneath the subfamily names, are for copies found in human DNA, or, for ORR1 and MT, in murine DNA. The time scale functions only as a general guideline, since the correlation of sequence divergence and age depends on disputed assumptions regarding neutral nucleotide substitution rates (52, 58, 59). Values used are $6.5 \cdot 10^{-9}$ substitutions/site/Myr for rodents (48), and the over evolution gradually diminishing rates for the human branch as calculated by Bailey *et al.* (46).

the THE1-LTR reiteration frequency (16). Based on S1 nuclease protection of their THE1a-LTR (o-repeat) clone by genomic DNA fragments, a frequency of 2,000 and 37,000 elements per human haploid genome was estimated when using stringent or less

Table 2. Orientation of MaLR sequences in comparison with the transcriptional unit in or near which they are located

orientation	5' flanking	introns	3' UTR and 3' flanking	intergenic	total
similar	21	8	18	5	52
inverse	18	56	20	7	101

Orthologous elements and elements multiplied through gene duplications have been counted only once. The bias within introns against fixation of elements in the same orientation as the gene is probably due to the presence of the potent polyadenylation site in MaLR-LTRs.

Table 3. The number of copies of each family found in GenBank release 71, and estimates of the reiteration frequencies of each family in the human and mouse genomes.

	human databases	genome	mouse databases	genome	rat databases	cow/sheep databases	rabbit databases	
THE1	31 (26)	9-16,000				<u></u>		
MstII	40 (36)	12 - 21,000						
MLT1	101 (101)	34 - 60,000	4 (4)	$22 - 6.000^{+}$	4 (4)	4 (4)	2 (2)	
ORR1	1*		25 (25)	10 - 38.000	18 (18)	. (.)	- (-)	
MT	1*		39 (33)	13-50,000	16 (16)			
total	172 (163)	55-97,000	68 (62)	25-94,000	39 (39)			

The numbers between parentheses indicate the number of elements sequenced by chance, i.e. not by searching with a MaLR-probe. These numbers have been used to estimate the relative frequency of each family in the genomes. For the estimations of the absolute numbers I have used a conservative estimate of 500,000 Alus in the human and 80,000 B1 and B2 elements in the mouse genome (1). * Probably of artificial origin. [†] Possibly an underestimate since most copies may have diverged too much to be detected.

stringent digestion conditions. The lower number may reflect the frequency of the small THE1a subgroup, of which only three copies not isolated with an o-repeat clone are found in the databanks. The higher number, which has generally been adopted as the number of THE1s in the human genome, may include most or all of the closely related MstII elements. Frequency of the latter group has been estimated to be only 4-8,000 (18, 21) using probes that lack the (best conserved) terminal bases.

The only frequency information available for the rodent elements comes from the observation that hybridization of nick-translated total mouse genomic DNA was as strong to a 200 bp MT-fragment as to clones carrying the 130-150 bp B1 and B2 SINEs (26). B1 and B2 each have an estimated frequency of 80,000 elements in the mouse genome (1). Correcting for the difference in length, this result predicted about 55,000 MT elements in the mouse genome.

Table 3 lists the recurrence of each family in sequences present in GenBank 71 and an estimate of their frequency in the genomes. The estimates are based on the recurrence of the families relative to each other and to the roughly 1,500 Alu (Jerzy Jurka, pers. commun.), 270 B1 and 160 B2 elements present in the human and mouse entries in this release. The numbers obtained in this way may form an underestimation, since MaLRs are-probably unlike SINEs-underrepresented in introns (Table 2), which form a major part of the available non-coding sequence information. The higher limit of reiteration frequencies in human shown in Table 3 is based on the assumption that 37,000 is the total number of THE1- and MstII-LTRs in the human genome and that maximally 10% of the elements are complete retrotransposons with two LTRs. An even higher estimate (>200,000) would follow from the presence of 25 MaLR-LTR sequences that can be detected in 271 randomly obtained chromosome 4 sequence tags with an average length of 440 bp (data not shown, 56). The random nature with which these sequences were acquired could make this last method of estimation actually the most accurate (especially when more sequence tags become available), unless



b



Figure 5. A putatively orthologous MaLR sequence in mouse and human. a) Comparison of the mouse and human immunoglobulin heavy chain $C_{\mu}-C_{\delta}$ intergenic region aligned relative to the putatively orthologous MLT1. In the mouse this MaLR has largely been deleted and the remainder has been inverse duplicated. MaLR-LTRs are indicated with open arrows, C_{μ} and C_{δ} exons are indicated with boxes, μ_m = membrane carboxyl-terminal exons for C_{μ} . b) Alignment of the human (HUMIGMUD, 49) and mouse (MUSIGMUD3, 51) orthologous sequences and the MLT1c-LTR consensus sequence. Bars indicate identical nucleotides between the MLT1c-consensus or the human element and either one of the mouse copies. Flanking the LTR, the 5' end of the consensus MST internal sequence (a consensus MLT1 internal sequence can not yet be derived) is shown in lowercase. Evidence for a common origin of the human and mouse elements is threefold. (i) They have the same location. (ii) The mouse element is more similar to the human 5' LTR than to any other (MLT1c-) sequence in the databases or even the MLT1c-consensus. Several bases shared between human and mouse are different from the consensus sequence, possibly reflecting mutations that took place after integration but before the rodent-primate split. (iii) Sequence similarity extends into the internal sequence, while 90-95% of the MaLRs occur as solitary LTRs with the internal sequence cleanly deleted.

chromosome 4 has an unrepresentative number of MaLRs. The higher limit of the rodent elements' reiteration frequencies is based on the aforementioned hybridization experiments.

Heinlein et al. (26) published hybridization results indicating that MTs are much more commonly cotranscribed in mouse brain than B1, B2 or LINEs. However, MaLRs seem not significantly overrepresented in human brain transcripts compared to other repetitive elements; among the 2723 published 'expressed sequence tags' (57) from human brain cDNA libraries are 313 with Alu, 58 with L1, and 48 with MaLR sequences (HUMXT0... in Table 1). These numbers are comparable to the estimated relative numbers of these repeats in the genome. Data on the MaLR sequences present in these expressed sequence tags will be added to the EST database (57).

It should be noted that the newly discovered MLT1-family has almost twice as many representatives in the human genome as the combined THE1/MstII-family. It could very well be that more distantly related MaLR families exist in both the human and mouse genome, and that the total number of MaLRs is significantly higher than is calculated here. The present estimate of 40,000 to 100,000 MaLRs implies that they occur on average each 30 to 100 kb and comprise 0.5% to 2% of both the human and mouse genome. Furthermore, the presence of transcription termination sites and probably other transcriptional regulatory elements in the MaLR-LTRs would suggest that the distribution of MaLRs has had a considerable influence on the evolution of the mammalian genome.

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