

A rat genetic linkage map and comparative maps for mouse or human homologous rat genes

J. Yamada, T. Kuramoto, T. Serikawa

Institute of Laboratory Animals, Faculty of Medicine, Kyoto University, Sakyo-ku, Kyoto 606-01, Japan

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The rat (*Rattus norvegicus*) is used in a broad field of biomedical research, and numerous animal models for human diseases have been developed. The rat genetic map, however, remains poorly documented. Hedrich (1990) described a rat linkage map consisting of 13 groups, of which only 6 were assigned to chromosomes. Levan and coworkers (1991, 1992) collected mapping information from the literature, including their own works. Their tables and figures contain gene chromosomal assignments, cytogenetical localizations, and comparisons of the rat G-banding pattern with those of mice and humans, but do not include any information about gene orders or distances.

Recently, an informative rat genetic linkage map has been reported by Serikawa and colleagues (1992b). It is based on the segregation of 125 polymorphic markers in seven rat backcrosses and two F₂ crosses, and all of the linkage groups are assigned to particular chromosomes. The linkage map and the information on microsatellite markers became a great help for genetic studies with rat models for human diseases. Since then, a considerable amount of new data for the rat linkage map has appeared in several publications. We, therefore, have collected mapping data published up to the middle of 1993, including our recent reports, and have summarized it here in a list of mapped loci. This genetic map, constructed by combining several linkage data, and two comparative maps for mouse or human homologous rat genes should be very informative to many researchers working on genetic studies in rats, mice, or humans.

Rat genetic linkage map

Table 1 lists in alphabetical order 539 rat loci assigned to a particular chromosome and 8 loci that were not yet as-

signed to any chromosomes and remained in linkage groups (LG III, XI, XII, and XIII of Hedrich's map). There are now 547 entries; a substantial increases from the 214 of Levan's 1991 and 370 of their 1992 list.

A rat genetic linkage map is shown in Fig. 1. Out of 539 loci assigned to particular chromosomes, 276 are located on each linkage map. The loci assigned to chromosomes by methods other than linkage analysis are listed separately and alphabetically under each chromosome. The numbers of loci on each chromosome are as follows: (no. loci located on the linkage map/no. loci assigned to the chromosome in total), Chr 1, 40/69; Chr 2, 18/33; Chr 3, 21/40; Chr 4, 19/35; Chr 5, 16/38; Chr 6, 10/23; Chr 7, 6/23; Chr 8, 11/26; Chr 9, 2/17; Chr 10, 20/32; Chr 11, 4/10; Chr 12, 7/11; Chr 13, 8/19; Chr 14, 20/28; Chr 15, 0/9; Chr 16, 3/5; Chr 17, 5/16; Chr 18, 14/17; Chr 19, 27/31; Chr 20, 15/34; Chr X, 10/22; Chr Y, 0/1. On Chrs 6, 8, 11, 12, and 14, respectively, two, three, two, two, and two linkage groups are seen. As for Chrs 4, 8, 14, 19, 20, and X, two linkage groups aligned in parallel because of discord in the locus order, distance in the references, or absence of anchor loci by which the orientations of maps are determined.

Comparative mouse map

For the discussion of comparative mapping, we have applied the chromosome terminology of ISCN (1978); that is, rat chromosomes are designed by the prefix RNO (*Rattus norvegicus*), mouse chromosomes by MMU (*Mus musculus*), and human chromosomes by HSA (*Homo sapiens*). As shown in Fig. 2, we assigned mouse homologous rat genes on the mouse chromosomes, and they are shown by the mouse symbols. Location of the mouse loci have been referred from the mouse locus map of Hillyard and associates (1993). With a few exceptions MMU2, 3, 4, 6, 7, 8, 9, 11, 12, 14, 15, 16, 18, and X were homologous with

Table 1. A list of mapped loci in the rat.

Locus symbol	Locus name	Chr.	Mode	References
<i>A</i>	agouti	3	L	Castle, King (1949); Moutier et al. (1973a)
<i>A2M</i>	alpha-2-macroglobulin, liver	4	L, S	Yasue et al. (1992); Hilbert et al. (1991); Serikawa et al. (1992b)
<i>A2UG</i>	alpha 2U globulin	5	L, S	Serikawa et al. (1992b)
<i>A39</i>	hepatocyte antigen	13	S	Perrotte et al. (1989)
<i>ABL</i>	Abelson viral oncogene	3	A	Takahashi et al. (1986)
<i>ACADM</i>	medium-chain acyl-CoA dehydrogenase	2	S	Szpirer et al. (1989a)
<i>ACE</i>	angiotensin I converting enzyme, (RD31)	10	L, S	Hilbert et al. (1991); Jacob et al. (1991); Serikawa et al. (1992b); Cash et al. (1993); Kuramoto et al. (1993a); Kondo et al. (1993)
<i>ACO1</i>	aconitase 1	5	L	Adams et al. (1984); Cramer et al. (1986); Kondo, Yamada (1983)
<i>ACP1</i>	acid phosphatase 1	6	S	Yasue et al. (1991)
<i>ACP2</i>	acid phosphatase 2	3	L, S	Bender et al. (1986); Yasue et al. (1991)
<i>ACR</i>	proacrasin, spermatid-specific	7	S	Adhami et al. (1991)
<i>ACRM</i>	acetylcholine receptor, m3 muscarinic	17	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>ADA</i>	adenosine deaminase	3	S	Yasue et al. (1991)
<i>ADH</i>	alcohol dehydrogenase	2	S	Fulchignoni-Lataud et al. (1992)
<i>ADRA1B</i>	adrenergic receptor, alpha-1B	10	S	Serikawa et al. (1992b)
<i>ADRB2</i>	adrenergic receptor, beta-2	18	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Remmers et al. (1993b)
<i>AEP</i>	anion exchange protein (kidney band 3)	10	L, S	Serikawa et al. (1992b); Kondo et al. (1993); Kuramoto et al. (1993a)
<i>AFP</i>	alpha-fetoprotein	14	L, S	Szpirer et al. (1984); Gal et al. (1984); Hilbert et al. (1991); Serikawa et al. (1992b); Remmers et al. (1993a)
<i>AGL</i>	antigen L	20	L	Lynch, DeWitt (1978, 1980)
<i>AGT</i>	angiotensinogen	19	A	Mori et al. (1989)
<i>AHD2</i>	aldehyde dehydrogenase 2	5	L	Cramer et al. (1986); Serikawa et al. (1992b); Kuramoto et al. (1993b)
<i>AHDC</i>	aldehyde dehydrogenase C	13	L	Cramer et al. (1986)
<i>AK1</i>	adenylate kinase 1	3	S	Levan et al. (1986)
<i>AK2</i>	adenylate kinase 2	5	S	Yoshida (1979, 1982)
<i>AKT</i>	thymoma viral proto-oncogene (v-akt)	6	A	Bellacosa et al. (1993)
<i>AKP1</i>	kidney alkaline phosphatase 1	(XI)*	L	Adams et al. (1984); Cramer et al. (1986)
<i>ALB</i>	serum albumin	14	L, S	Shumiya, Nagase (1982, 1988); Szpirer et al. (1984); Hilbert et al. (1991); Remmers et al. (1993a)
<i>ALDOA</i>	aldolase A	1	L	Goldmuntz et al. (1993)
<i>ALDOB</i>	aldolase B	5	S	Szpirer et al. (1990)
<i>ALR</i>	aldose reductase (ALR-P-I)	4	S	Graham et al. (1991)
<i>ALRP1</i>	aldose reductase, pseudogene 1 (ALR-P1)	3	S	Graham et al. (1991)
<i>ALRP2</i>	aldose reductase, pseudogene 2 (ALR-P2)	4	S	Graham et al. (1991)
<i>ALRP3</i>	aldose reductase, pseudogene 3 (ALR-H)	6	S	Graham et al. (1991)
<i>AMDIA</i>	S-adenosylmethionine decarboxylase A	20	S	Pulkka et al. (1993)
<i>AMDIB</i>	S-adenosylmethionine decarboxylase B	20	S	Pulkka et al. (1993)
<i>AMDP</i>	S-adenosylmethionine decarboxylase, pseudogene	X	S	Pulkka et al. (1993)
<i>AMD3</i>	S-adenosylmethionine decarboxylase, related	3	S	Pulkka et al. (1993)
<i>AMPP</i>	amplicon, Py-induced	4	L, S	Serikawa et al. (1992b)
<i>AMY1</i>	amylase, pancreatic	2	L, S	Mizuno, Suzuki (1978); Serikawa et al. (1992b)
<i>AN</i>	lethal anemia	5	L	Castle, King (1941, 1944, 1947)
<i>APEH</i>	acyl-peptide hydrolase (RIK)	8	L, S	Erlandsson et al. (1991); Serikawa et al. (1992b)
<i>APOC3</i>	apolipoprotein C-III, (apo a02)	8	L, S	Serikawa et al. (1992b); Kobayashi et al. (1992b)
<i>AR</i>	androgen receptor	X	L, S	Gumbreck (1964); Serikawa et al. (1992b)
<i>ASGR</i>	asialoglycoprotein receptor, (ASGR1)	10	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Remmers et al. (1992)
<i>ATP1A1</i>	ATPase alpha-1, (nk2a1b)	2	L, S	Yasue et al. (1992); Kunieda et al. (1992a); Zha et al. (1993)
<i>ATP1A2</i>	ATPase alpha-2, (atpa2s)	13	S	Yasue et al. (1992); Kunieda et al. (1992a)
<i>ATP1A3</i>	ATPase alpha-3	1	S	Yasue et al. (1992)
<i>B</i>	brown	5	L	Nikaido et al. (1982); Cramer et al. (1986)
<i>B1</i>	hepatocyte antigen	11	S	Perrotte et al. (1989)
<i>B2M</i>	beta-2-microglobulin	3	L, S	Yasue et al. (1992); Kondo et al. (1993)
<i>BSIS</i>	brain specific identifier sequence	1	L, S	Serikawa et al. (1992b)
<i>BSP</i>	bone sialoprotein	14	L	Remmers et al. (1993a)
<i>C</i>	albino	1	L	Castle, King (1944)
<i>C3</i>	complement 3	9	S	Szpirer et al. (1987, 1988b)
<i>C4</i>	complement 4	20	L, S	Watters et al. (1987); Locker et al. (1990)
<i>C4BPA</i>	C4 binding protein, alpha	13	S	Anderson et al. (1990)
<i>C4BPB</i>	C4 binding protein, beta	13	S	Anderson et al. (1990)
<i>C6</i>	complement 6	(XI)*	L	Granados et al. (1984); Cramer et al. (1986)
<i>CALC</i>	calcitonin	1	S	Levan et al. (1986)
<i>CALM3</i>	calmodulin III	1	S	Serikawa et al. (1992b)
<i>CAMKI</i>	calmodulin-dependent protein kinase II	2	L	Zha et al. (1993)
<i>CAT</i>	catalase, liver	3	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>CBPI</i>	calcium-binding protein, intestinal, vitamin D dependent	X	L, S	Serikawa et al. (1992b)
<i>CBS</i>	cystathione beta synthase	20	S	Locker et al. (1990)
<i>CEAR</i>	carcinoembryonic antigen-related protein (CGM4)	1	L, S	Serikawa et al. (1992b)
<i>CEBPA</i>	CCAAT/enhancer binding protein (DBPCEP)	1	S	Szpirer et al. (1992a); Serikawa et al. (1992b)
<i>CEPB</i>	liver-activating protein (TCF5)	3	S	Szpirer et al. (1991b)

Table 1. *Continued.*

Locus symbol	Locus name	Chr.	Mode	References
<i>CHGA</i>	chromogranin A	6	S	Simon-Chazottes et al. (1993)
<i>CK2B</i>	Ca-calmodulin-dependent protein kinase, beta	14	S	Levan et al. (1991); Brom et al.
<i>CKB</i>	creatine kinase, brain	6	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>CLATP</i>	ATP citrate lyase	10	L	Remmers et al. (1992); Cash et al. (1993)
<i>CPA1</i>	carboxypeptidase A1, (D4MIT3)	4	L, S	Serikawa et al. (1992b); Jacob et al. (1992); Dissen et al. (1993)
<i>CPB</i>	carboxypeptidase B	2	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>CPBR</i>	carboxypeptidase B related	1	L	Goldmuntz et al. (1993)
<i>CRYA1</i>	alpha crystallin 1	20	L	Skow et al. (1985)
<i>CRYG1</i>	gamma crystallin 1	9	L, S	Donner et al. (1985); DenDunnen et al. (1987); Hilbert et al. (1991); Serikawa et al. (1992b)
<i>CRYG2</i>	gamma crystallin 2	9	S	Donner et al. (1985); DenDunnen et al. (1987)
<i>CRYG3</i>	gamma crystallin 3	9	S	Donner et al. (1985); DenDunnen et al. (1987)
<i>CRYG4</i>	gamma crystallin 4	9	S	Donner et al. (1985); DenDunnen et al. (1987)
<i>CRYG5</i>	gamma crystallin 5	9	S	Donner et al. (1985); DenDunnen et al. (1987)
<i>CRYG6</i>	gamma crystallin 6	9	S	Donner et al. (1985); DenDunnen et al. (1987)
<i>CS1</i>	catalase, erythrocyte	(XIII)*	L	Yamada et al. (1981); Kendall (1985)
<i>CSF1R</i>	colony stimulating factor-1 receptor	18	L	Remmers et al. (1993b)
<i>CSNA</i>	alpha-casein	14	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>CT</i>	cell surface alloantigen	20	L	Marshak et al. (1977)
<i>CSPMO2</i>	cell surface protein (MRC OX-2)	11	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>CTR</i>	chymotrypsin B	19	L, S	Serikawa et al. (1992b)
<i>CU1</i>	curly 1	5	L	Castle, King (1944, 1947)
<i>CYP1A1</i>	cytochrome P450 C6	8	S	Levan et al. (1991)
<i>CYP1A2</i>	cytochrome P450 Q42	8	S	Levan et al. (1991)
<i>CYP2B1</i>	cytochrome P450 b	1	L	Rampersaud, Waltz (1987)
<i>CYP2B2</i>	cytochrome P450 e	1	L	Rampersaud, Waltz (1987)
<i>CYP1IB1</i>	cytochrome P-450, subfamily (steroid 11-beta hydroxylase)	7	L, S	Cicila et al. (1993)
<i>CYP1IB2</i>	cytochrome P-450, subfamily (aldosterone synthase)	7	L, S	Cicila et al. (1993)
<i>CYPBE</i>	cytochrome P450b/e	1	S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>CYPE</i>	cytochrome P450e	1	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>D1CEP1</i>	DNA segment, pASC-Ha-2	1	L	Hilbert et al. (1991)
<i>D1CEP2</i>	DNA segment, YNH24-Ha-6	1	L	Hilbert et al. (1991)
<i>D1CEP3</i>	DNA segment, YNH24-Hi-3	1	L	Hilbert et al. (1991)
<i>D1CEP4</i>	DNA segment, STMS (2B1)	1	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Goldmuntz et al. (1993)
<i>D1KYO1</i>	DNA segment, (mouse Ckmm)	1	S	Kondo et al. (1993)
<i>D1N40</i>	DNA segment, STMS	1	L	Goldmuntz et al. (1993)
<i>D1N64</i>	DNA segment, STMS	1	L	Goldmuntz et al. (1993)
<i>D2CEP1</i>	DNA segment, pASC-Hi-3	2	L	Hilbert et al. (1991)
<i>D2KYO1</i>	DNA segment, RAPD	2	S	Serikawa et al. (1992a)
<i>D2NIR</i>	DNA segment, RAPD	2	L	Zha et al. (1993)
<i>D2N2R</i>	DNA segment, RAPD	2	L	Zha et al. (1993)
<i>D2N28</i>	DNA segment, STMS	2	L	Zha et al. (1993)
<i>D2N35</i>	DNA segment, STMS	2	L	Zha et al. (1993)
<i>D2N91</i>	DNA segment, STMS	2	L	Zha et al. (1993)
<i>D3KYO1</i>	DNA segment, STMS	3	L, S	Kuramoto et al. (1993b)
<i>D3KYO2</i>	DNA segment, STMS	3	L, S	Kuramoto et al. (1993b)
<i>D3KYO3</i>	DNA segment, (mouse D0Nds33)	3	L	Kondo et al. (1993)
<i>D3KYO4</i>	DNA segment, (mouse II-1a)	3	L	Kondo et al. (1993)
<i>D3KYO5</i>	DNA segment, (mouse II-1b)	3	L	Kondo et al. (1993)
<i>D4CEP1</i>	DNA segment, YNZ22-Hi-1	4	L	Hilbert et al. (1991)
<i>D4CEP2</i>	DNA segment, YNZ22-Hi-21	4	L	Hilbert et al. (1991)
<i>D4KYO1</i>	DNA segment, (mouse D6Nds6)	4	S	Kondo et al. (1993)
<i>D4MIT2</i>	DNA segment, STMS	4	L	Jacob et al. (1992)
<i>D4MIT5</i>	DNA segment, STMS	4	L	Jacob et al. (1992)
<i>D4MIT6</i>	DNA segment, STMS	4	L	Jacob et al. (1992)
<i>D4RP1</i>	DNA segment, MMU4 homolog	5	S	Szpirer et al. (1989b, 1990)
<i>D5CEP1</i>	DNA segment, STMS (A8)	5	L, S	Hilbert et al. (1991)
<i>D5GOT1</i>	DNA segment	5	A	Klinga et al. (1990)
<i>D5KYO1</i>	DNA segment, STMS	5	A, L, S	Kuramoto et al. (1993b)
<i>D6CEP1</i>	DNA segment, INS310-Hi-11	6	L	Hilbert et al. (1991)
<i>D6CEP2</i>	DNA segment, pMV10.2-Ha-10	6	L	Hilbert et al. (1991)
<i>D6CEP3</i>	DNA segment, pMV10.2-Ha-11	6	L	Hilbert et al. (1991)
<i>D6CEP4</i>	DNA segment, pMV10.2-Hi-4	6	L	Hilbert et al. (1991)
<i>D6CEP5</i>	DNA segment, pMV10.2-Hi-6	6	L	Hilbert et al. (1991)
<i>D6CEP6</i>	DNA segment, pMV10.2-Hi-7	6	L	Hilbert et al. (1991)
<i>D6CEP7</i>	DNA segment, pMV10.2-Hi-8	6	L	Hilbert et al. (1991)
<i>D6CEP8</i>	DNA segment, STMS (D3)	6	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>D7CEP1</i>	DNA segment, STMS (E5)	7	L, S	Serikawa et al. (1992b); Kondo et al. (1993)
<i>D7KYO1</i>	DNA segment, (mouse Myc)	7	L, S	Kondo et al. (1993)
<i>D7KYO2</i>	DNA segment, (mouse Wnt-1)	7	S	Kondo et al. (1993)
<i>D8CEP1</i>	DNA segment, pMV10.2-Ha-8	8	L	Hilbert et al. (1991)
<i>D8GOT1</i>	DNA segment	8	S	Levan et al. (1991)
<i>D9CEP1</i>	DNA segment, AW-Hi-10	9	L	Hilbert et al. (1991)
<i>D9KYO1</i>	DNA segment, RAPD	9	S	Serikawa et al. (1992a)
<i>D9KYO2</i>	DNA segment, STMS	9	S	Kuramoto et al. (1993b)
<i>D9S7h</i>	DNA segment	3	L	Kuramoto et al. (1993b)
<i>D10CEP1</i>	DNA segment, pASC-Hi-8	10	L	Hilbert et al. (1991)

Table 1. *Continued.*

Locus symbol	Locus name	Chr.	Mode	References
D10KYO1	DNA segment, (mouse Gfap)	10	L	Kondo et al. (1993)
D10KYO2	DNA segment, (mouse Sigie)	10	S	Kondo et al. (1993)
D10MIT1	DNA segment, STMS (RR24)	10	L	Jacob et al. (1991); Cash et al. (1993); Kuramoto et al. (1993a)
D10MIT2	DNA segment, STMS (RR92)	10	L	Jacob et al. (1991); Kuramoto et al. (1993a)
D10MIT3	DNA segment, STMS (RR1023)	10	L	Jacob et al. (1991); Cash et al. (1993)
D10N1	DNA segment, RAPD (F10F1)	10	L	Remmers et al. (1992); Cash et al. (1993)
D10N2	DNA segment, RAPD (F16F2)	10	L	Remmers et al. (1992)
D11CEP1	DNA segment, EFD-Ha-1	11	L	Hilbert et al. (1991)
D12CEP1	DNA segment, pMV10.2-Ha-3	12	L	Hilbert et al. (1991)
D12CEP2	DNA segment, YNZ2-Ha-4	12	L	Hilbert et al. (1991)
D12CEP3	DNA segment, YNZ2-Ha-2	12	L	Hilbert et al. (1991)
D12CEP4	DNA segment, STMS (H4)	12	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
D13KYO1	DNA segment, RAPD	13	S	Serikawa et al. (1992a)
D13KYO2	DNA segment, RAPD	13	S	Serikawa et al. (1992a)
D13KYO3	DNA segment, STMS	13	L, S	Kuramoto et al. (1993b)
D13KYO4	DNA segment, (mouse Bcl-2)	13	L, S	Kondo et al. (1993)
D14CEP1	DNA segment, PER-Hi-1(4)	14	L	Hilbert et al. (1991)
D14CEP2	DNA segment, PER-Hi-4	14	L	Hilbert et al. (1991)
D14CEP3	DNA segment, YNZ2-Ha-7	14	L	Hilbert et al. (1991)
D14CEP4	DNA segment, YNZ2-Ha-14	14	L	Hilbert et al. (1991)
D14CEP5	DNA segment, YNZ2-Hi-1	14	L	Hilbert et al. (1991)
D14CEP6	DNA segment, YNZ2-Hi-5	14	L	Hilbert et al. (1991)
D14CEP7	DNA segment, YNZ2-Hi-13(5)	14	L	Hilbert et al. (1991)
D14KYO1	DNA segment, RAPD	14	S	Serikawa et al. (1992a)
D14N52	DNA segment, STMS	14	L	Remmers et al. (1993a)
D15KYO1	DNA segment, STMS	15	S	Kuramoto et al. (1993b)
D16CEP1	DNA segment, pASC-Ha-6	16	L	Hilbert et al. (1991)
D16FC1	DNA segment	16	A	Yeung et al. (1993)
D16KYO1	DNA segment, STMS	16	L, S	Kuramoto et al. (1993b)
D17CEP1	DNA segment, YNH24-Ha-4	17	L	Hilbert et al. (1991)
D17CEP2	DNA segment, YNH24-Hi-7	17	L	Hilbert et al. (1991)
D17CEP3	DNA segment, STMS (F4)	17	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
D17TPL2	DNA segment (Tpl2)	17	A	Yeung et al. (1993)
D18CEP1	DNA segment, AW-Ha-13	18	L	Hilbert et al. (1991)
D18CEP2	DNA segment, PER-Hi-5	18	L	Hilbert et al. (1991)
D18CEP3	DNA segment, pUCJ-Hi-6	18	L	Hilbert et al. (1991)
D18CEP4	DNA segment, YNZ2-Hi-14	18	L	Hilbert et al. (1991)
D18CEP5	DNA segment, YNZ2-Hi-19	18	L	Hilbert et al. (1991)
D18MIT1	DNA segment, STMS (RR1094)	18	S	Jacob et al. (1991)
D18NIR	DNA segment, STMS	18	L	Remmers et al. (1993b)
D19CEP1	DNA segment, AW-Ha-1	19	L	Hilbert et al. (1991)
D19CEP2	DNA segment, AW-Ha-3	19	L	Hilbert et al. (1991)
D19CEP3	DNA segment, AW-Hi-2	19	L	Hilbert et al. (1991)
D19CEP4	DNA segment, pASC-Hi-1	19	L	Hilbert et al. (1991)
D19CEP5	DNA segment, pASC-Hi-5(3)	19	L	Hilbert et al. (1991)
D19CEP6	DNA segment, pUCJ-Ha-5	19	L	Hilbert et al. (1991)
D19SF1	DNA segment, CAC5-1	19	L	Pravenc et al. (1992)
D19SF2	DNA segment, MS15-2	19	L	Pravenc et al. (1992)
D20CEP1	DNA segment, AW-Hi-6	20	L	Hilbert et al. (1991)
D20CEP2	DNA segment, AW-Hi-11	20	L	Hilbert et al. (1991)
D20CEP3	DNA segment, pASC-Ha-7	20	L	Hilbert et al. (1991)
D20CEP4	DNA segment, pASC-Hi-9	20	L	Hilbert et al. (1991)
D20CEP5	DNA segment, PER-Hi-13	20	L	Hilbert et al. (1991)
D20CEP6	DNA segment, pMV10.2-Hi-2	20	L	Hilbert et al. (1991)
D20KYO1	DNA segment, (mouse Tnfa)	20	L, S	Kondo et al. (1993)
DBP	D site of albumin promoter binding protein	1	S	Szpirer et al. (1992a)
DDC	DOPA-decarboxylase	14	S	Vassort et al. (1993)
DHFRI	dihydrofolate reductase 1	2	S	Hanson et al. (1990)
DHFR2	dihydrofolate reductase 2	4	S	Hanson et al. (1990)
DI	diabetes insipidus	3	L	Stoli (1984a)
DIA4	diaphorase 4 (NADA/NADPH)	19	S	Yasue et al. (1991)
DPRP	decidual prolactin-related protein	17	S	Roby et al. (1993)
DRD1L	dopamine receptor, D1-like-2	14	L	Remmers et al. (1993a)
DSII	a region of proviral insertions in Moloney MuLV-induced rat thymomas	5	S	Szpirer et al. (1989b, 1990)
DW3	dwarf-3	20	L	Gill, Kunz (1979)
DXCEP1	DNA segment, INS310-Hi-3(11)	X	L	Hilbert et al. (1991)
DXCEP2	DNA segment, INS310-Hi-9(4)	X	L	Hilbert et al. (1991)
DXCEP3	DNA segment, pASC-Hi-6(2)	X	L	Hilbert et al. (1991)
DXCEP4	DNA segment, PER-Ha-2(2)	X	L	Hilbert et al. (1991)
DXCEP5	DNA segment, PER-Ha-7	X	L	Hilbert et al. (1991)
DXCEP6	DNA segment, PER-Hi-12	X	L	Hilbert et al. (1991)
EAG1	endothelial antigen 1	13	L	Cramer et al. (1985)
EGFR	epidermal growth factor receptor, (ERBB1)	14	S	Szpirer et al. (1991b)
ELA1	elastase I, (elail)	7	L, S	Serikawa et al. (1992b); Kunieda et al. (1992a)
ENO1	enolase 1	5	S	Yoshida (1978, 1982)
ENO2	enolase 2	4	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
EPO	erythropoietin	4	S	Levan et al. (1991)

Table 1. *Continued.*

Locus symbol	Locus name	Chr.	Mode	References
<i>ERBB2</i>	avian erythroblastosis viral oncogene homolog B2, (neu)	10	L, S	Szpirer et al. (1991b); Remmers et al. (1992)
<i>ES1</i>	esterase 1	19	L	Augustinsson, Henricson (1966); Womack (1973); Osten et al. (1993)
<i>ES2</i>	esterase 2	19	L	Womack, Sharp (1976); Serikawa et al. (1992b); Pravenec et al. (1992); Osten et al. (1993)
<i>ES3</i>	esterase 3	19	L	Pravenec et al. (1992); Womack (1972); Pravenec et al. (1992)
<i>ES4</i>	esterase 4	19	L	Womack, Sharp (1976)
<i>ES6</i>	esterase 6	8	L	Pravenec et al. (1987); Serikawa et al. (1992b); Kobayashi et al. (1992b)
<i>ES7</i>	esterase 7	19	L	Matsumoto (1980)
<i>ES8</i>	esterase 8	19	L	Matsumoto (1980)
<i>ES9</i>	esterase 9	19	L	Hedrich, Deimling (1987a)
<i>ES10</i>	esterase 10	19	L, S	Hedrich, Deimling (1987a); Pravenec et al. (1992)
<i>ES14(SI)</i>	esterase 14	19	L	Yamada et al. (1980); Hedrich et al. (1987b); Pravenec et al. (1992)
<i>ES15</i>	esterase 15	19	L	Hedrich et al. (1987b)
<i>ES16</i>	esterase 16	19	L	Hedrich et al. (1987b)
<i>ES18</i>	esterase 18	19	L	Hedrich et al. (1987b)
<i>ESD</i>	esterase D	15	S	Yasue et al. (1991)
<i>F</i>	fawn	3	L	Robinson (1982)
<i>F5</i>	coagulation factor 5	13	S	Dahlbäck et al. (1988)
<i>FA</i>	fatty	5	L	Truett et al. (1991)
<i>FABP1</i>	fatty acid binding protein, liver, (fabplg)	4	L, S	Serikawa et al. (1992b); Kunieda et al. (1992a)
<i>FDP</i>	fructose-1,6-bisphosphatase	17	S	Fulchignoni-Lataud et al. (1992)
<i>FGA</i>	fibrinogen, alpha	2	A, S, L	Marino et al. (1986); Serikawa et al. (1992b)
<i>FGB</i>	fibrinogen, beta	2	A, S	Marino et al. (1986); Szpirer et al. (1987, 1988b)
<i>FGG</i>	fibrinogen, gamma, (fibg2)	2	A, S, L	Marino et al. (1986); Serikawa et al. (1992b); Kunieda et al. (1992a); Zha et al. (1993)
<i>FH</i>	fumarate hydratase	13	L	Carleer, Ansay (1975); Cramer et al. (1985); Kuramoto et al. (1993b)
<i>FOS</i>	murine FBJ viral oncogene homolog	6	A	Li et al. (1989)
<i>FPGS</i>	folypolyglutamate synthetase	3	S	Levan et al. (1986)
<i>FST</i>	follistatin	2	L, S	Serikawa et al. (1992b)
<i>FT</i>	fertility	20	L	Skow et al. (1985); Gill et al. (1979, 1982)
<i>FUCA</i>	alpha-L-fucosidase	5	S	Yoshida (1978)
<i>FZ</i>	fuzzy	1	L	Palm, Ferguson (1976)
<i>G6PD</i>	glucose-6-phosphate dehydrogenase	X	S	Yoshida (1978)
<i>GAD1</i>	glutamic acid decarboxylase 1	3	S	Vassort et al. (1993)
<i>GAD2</i>	glutamic acid decarboxylase 2	17	S	Vassort et al. (1993)
<i>GALK</i>	galactokinase	10	S	Levan et al. (1986)
<i>GANC</i>	alpha-glucosidase, neutral C	3	S	Yasue et al. (1991)
<i>GC</i>	group-specific component (GL1, VDBG)	14	L, S	Moutier et al. (1973b); Cooke et al. (1987)
<i>GCK</i>	glucokinase (GLUKA)	14	L, S	Serikawa et al. (1992b); Remmers et al. (1993a)
<i>GDC1</i>	alpha-glycerophosphate dehydrogenase	8	L	Eriksson et al. (1976); Serikawa et al. (1992b)
<i>GDH</i>	glucose dehydrogenase	5	S	Yoshida (1984b)
<i>GGTB2</i>	glycoprotein 3-beta-galactosyl transferase 2	5	S	Szpirer et al. (1989b)
<i>GH</i>	growth hormone (RD17)	10	L, S	Cooke et al. (1986); Hilbert et al. (1991); Jacob et al. (1991); Serikawa et al. (1992b); Remmers et al. (1992); Kuramoto et al. (1993a)
<i>GJA1</i>	gap junction protein, heart (connexin 43)	18	L, S	Serikawa et al. (1992b); Remmers et al. (1993b)
<i>GLA</i>	alpha-galactosidase	X	S	Levan et al. (1986)
<i>GLB1</i>	beta-galactosidase	8	S	Yasue et al. (1991)
<i>GLO1</i>	glyoxalase	20	L, S	Stolc et al. (1980); Gill et al. (1982); Yasue et al. (1991)
<i>GLS</i>	glutaminase (glut)	9	S	Mock et al. (1989); Kunieda et al. (1992a)
<i>GLUT1</i>	glucose transporter, brain, (GLUTB, gtg3)	5	L, S	Szpirer et al. (1990); Serikawa et al. (1992b); Kunieda et al. (1992a); Kuramoto et al. (1993b)
<i>GOT1</i>	glutamic oxaloacetic transaminase 1	1	S	Levan et al. (1986)
<i>GPD1</i>	glucose-6-phosphate dehydrogenase	(XIII)*	L	Kendall (1985)
<i>GPI</i>	glucosidase isomerase	1	S	Yoshida (1984a)
<i>GRL</i>	glucocorticoid receptor	18	L, S	Hilbert et al. (1991); Goldner-Sauvé et al. (1991); Serikawa et al. (1992b)
<i>GST</i>	glutathione-S-transferase, placental	1	A, S	Masuda et al. (1986); Yasue et al. (1992)
<i>GSTA1</i>	glutathione-S-transferase Ya	8	S	Yamada et al. (1992)
<i>GSTA2</i>	glutathione-S-transferase Yc	9	S	Yamada et al. (1992)
<i>GSTA3</i>	glutathione-S-transferase Yb1	2	S	Muramatsu et al. (1993)
<i>GSTA4</i>	glutathione-S-transferase Yb2	2	S	Muramatsu et al. (1993)
<i>GSTPL1</i>	glutathione-S-transferase like 1	3	S	Yasue et al. (1992)
<i>GSTPL2</i>	glutathione-S-transferase like 2	5	S	Yasue et al. (1992)
<i>GSTPL3</i>	glutathione-S-transferase like 3	8	S	Yasue et al. (1992)
<i>GSTPL4</i>	glutathione-S-transferase like 4	10	S	Yasue et al. (1992)
<i>GSTPL5</i>	glutathione-S-transferase like 5	16	S	Yasue et al. (1992)
<i>GSTPL6</i>	glutathione-S-transferase like 6	X	S	Yasue et al. (1992)
<i>GUSB</i>	beta-glucuronidase	12	S	Yasue et al. (1991)
<i>H</i>	hooded	14	L	Moutier et al. (1973b)
<i>HAGH</i>	hydroxyacyl glutatione hydrolase	2	S	Yasue et al. (1991)
<i>HAO1</i>	hydroxiacid oxidase, (GOX1)	3	L, S	Yamada et al. (1989); Serikawa et al. (1992b); Kondo et al. (1993); Kuramoto et al. (1993b)

Table 1. *Continued.*

Locus symbol	Locus name	Chr.	Mode	References
<i>HBB</i>	hemoglobin beta chain	1	L	Brdicka (1968); French et al. (1971); Lindpaintner et al. (1992); Goldmuntz et al. (1993)
<i>HC</i>	hemagglutinin capacity	20	L	Heslop, Jolly (1979)
<i>HD</i>	hypodactyly	5	L	Moutier et al. (1973c); Moutier (1980)
<i>HDC</i>	histidine carboxylase	3	S	Sullivan et al. (1991)
<i>HE</i>	hematoma	1	L	Dunning, Curtis (1939)
<i>HEOXG</i>	heme oxygenase	19	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>HEXA</i>	hexosaminidase A	8	S	Yasue et al. (1991)
<i>HGF</i>	hepatic growth factor	4	S	Szpirer et al. (1992a)
<i>HHITTS</i>	testis-specific histone, H1t and H4t	17	S	Serikawa et al. (1992b)
<i>HM</i>	hooded modifier	14	L	Stolc (1984b)
<i>HNF1A</i>	hepatic nuclear factor 1, (TCF1)	12	S	Szpirer et al. (1992a)
<i>HP</i>	haptoglobin, (hpab)	19	L, S	Serikawa et al. (1992b); Kunieda et al. (1992a)
<i>HPRT</i>	hypoxanthine phosphoribosyl transferase	X	S	Yoshida (1978); Szpirer et al. (1984)
<i>HRAS</i>	Harvey rat sarcoma viral oncogene homolog	1	S	Szpirer et al. (1985); Fang et al. (1985)
<i>HRASP</i>	Harvey sarcoma proto-oncogene	X	S	Szpirer et al. (1985)
<i>HSD3B</i>	hydroxy-delta-5-steroid dehydrogenase	2	L	Zha et al. (1993)
<i>HSP70</i>	heat shock protein 70	20	L	Wurst et al. (1989)
<i>HTR1A</i>	5-hydroxytryptamine-1a receptor	2	S	Serikawa et al. (1992b)
<i>HX</i>	histocompatibility X	X	—	Mullen, Hilderman (1972)
<i>HY</i>	histocompatibility Y	Y	—	Mullen, Hilderman (1972)
<i>HYD</i>	hydrocephalus	X	—	Koto et al. (1987)
<i>IC</i>	ichthyosis	1	L	Knox, Lister-Rosenoer (1978)
<i>IA</i>	incisor absence	5	L	Greep (1941); Moutier (1980)
<i>IDH1</i>	isocitrate dehydrogenase 1	9	S	Yasue et al. (1991)
<i>IFNA</i>	interferon, alpha	5	S	Islam et al. (1989)
<i>IFNB1</i>	interferon, beta	5	S	Szpirer et al. (1989b, 1990)
<i>IGF1</i>	insulin-like growth factor I	7	L, S	Serikawa et al. (1992b)
<i>IGF2</i>	insulin-like growth factor II	1	L, S	Serikawa et al. (1992b); Lindpaintner et al. (1992); Goldmuntz et al. (1993)
<i>IGFBP</i>	insulin-like growth factor binding protein (IGF-BP3)	14	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>IGH1</i>	Ig heavy chain 1	6	L	Bazin et al. (1974)
<i>IGH2</i>	Ig heavy chain 2	6	CH, S	Schröder et al. (1980); Pear et al. (1986)
<i>IGH3</i>	Ig heavy chain 3	6	L	Beckers, Bazin (1975)
<i>IGHε</i>	Ig heavy chain, epsilon	6	L, S	Pear et al. (1986); Hilbert et al. (1991); Serikawa et al. (1992b)
<i>IGK</i>	immunoglobulin kappa chain 1, (D4MIT8)	4	L, S, W	Collard et al. (1982); Perlmann et al. (1985); Jacob et al. (1992)
<i>IGL</i>	immunoglobulin lambda chain	11	S	Szpirer et al. (1988a)
<i>IL3</i>	interleukin 3	10	L	Kunieda et al. (1992b)
<i>IL6</i>	interleukin 6, (il6g)	4	S	Szpirer et al. (1991b); Serikawa et al. (1992b); Kunieda et al. (1992a)
<i>IL6R1</i>	interleukin 6 receptor	2	S	Szpirer et al. (1991c)
<i>INHA</i>	inhibin, alpha-subunit, (inhbab1)	9	S	Serikawa et al. (1992b); Kunieda et al. (1992a)
<i>INS1</i>	insulin 1	1	A, L	Soares et al. (1985); Mori et al. (1992a)
<i>INS2</i>	insulin 2	1	A	Soares et al. (1985)
<i>IRJHM</i>	immune response to JHM	14	L	Watanabe et al. (1987); Hedrich et al. (1989)
<i>ITGA4</i>	integrin alpha-4	3	S	Szpirer et al. (1992b)
<i>ITGA5</i>	integrin alpha-5	7	S	Szpirer et al. (1992b)
<i>ITGB1</i>	integrin beta-1	19	S	Szpirer et al. (1992b)
<i>ITPA</i>	inosine triphosphatase 1	3	S	Yasue et al. (1991)
<i>IVD</i>	isovaleryl-CoA dehydrogenase	3	S	Szpirer et al. (1989a); Serikawa et al. (1992b)
<i>K</i>	kinky	(III)*	L	Castle, King (1944)
<i>KAL</i>	kallikrein, renal	1	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>KCPVD</i>	K ⁺ channel protein, voltage dependent	4	S	Serikawa et al. (1992b)
<i>KRAS2</i>	Kirsten rat viral oncogene homolog (v-Ki-ras 2)	4	S	Szpirer et al. (1985)
<i>LALBA</i>	alpha-lactalbumin	7	S	Serikawa et al. (1992b)
<i>LAPI</i>	leucin arylaminopeptidase	1	L	van Zutphen et al. (1981, 1985); Serikawa et al. (1992b)
<i>LCA</i>	leucocyte common antigen, (CD45)	13	S	Goldner-Sauvé et al. (1991); Serikawa et al. (1992b)
<i>LCK1</i>	lymphocyte tyrosine kinase 1	5	S	Szpirer et al. (1989b, 1990)
<i>LCK2</i>	lymphocyte tyrosine kinase 2	7	S	Szpirer et al. (1989b, 1990)
<i>LDHA</i>	lactate dehydrogenase A	1	S	Yoshida (1984a)
<i>LDHB</i>	lactate dehydrogenase B	4	S	Yasue et al. (1991)
<i>LDR1</i>	LDHA regulator 1	1	L	Stolc, Gill (1983)
<i>LG</i>	Grüneberg lethal	1	L	Grünberg (1939)
<i>LSN</i>	leukosianin	1	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Lindpaintner et al. (1992)
<i>LSNR</i>	leukosianin-related	12	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>LX</i>	polydactyly-luxate	8	L	Kren (1975)
<i>LY2</i>	peripheral T-cell antigen	1	L	DeWitt, McCullough (1975); Butcher et al. (1979)
<i>LYP</i>	T-cell lymphopenia	4	L	Jacob et al. (1992)
<i>MANB</i>	mannosidase, alpha B, lysosomal	20	L	van de Berg et al. (1981)
<i>MBP</i>	myelin basic protein	18	L, S	Yasue et al. (1991); Goldner-Sauvé et al. (1991); Serikawa et al. (1992b)
<i>MBPA</i>	mannose-binding protein (serum) A	16	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Kuramoto et al. (1993b)
<i>MDH2</i>	malate dehydrogenase, mitochondrial	12	L, S	Serikawa et al. (1992b)
<i>MDHL</i>	malate dehydrogenase like enzyme	3	L	Matsumoto et al. (1982)
<i>MEI</i>	malic enzyme 1 (solubule)	8	S	Levan et al. (1986)

Table 1. *Continued.*

Locus symbol	Locus name	Chr.	Mode	References
<i>MLV12</i>	Moloney MuLV integration site 2, (<i>mlvi2e</i>)	2	S	Tsichlis et al. (1985); Kunieda et al. (1992a)
<i>MLV13</i>	Moloney MuLV integration site 3	15	S	Tsichlis et al. (1985)
<i>MLV14</i>	Moloney MuLV integration site 4	7	S	Hanson et al. (1988); Tsichlis et al. (1989)
<i>MOS</i>	Moloney sarcoma oncogene (<i>v-mos</i>)	5	S	Szpirer et al. (1989b, 1990)
<i>MPI</i>	mannose phosphate isomerase	8	S	Yoshida (1978)
<i>MT1PA</i>	metallothionein-1 pseudogene a	1	L, S	Serikawa et al. (1992b)
<i>MT1PB</i>	metallothionein-1 pseudogene b	2	L, S	Serikawa et al. (1992b)
<i>MUPI</i>	major urinary protein 1	5	L	van Zutphen et al. (1981); Nikaido et al. (1982)
<i>MX1</i>	interferon-inducible protein 78KDa, homolog of murine myxovirus resistance 1	11	S	Levan et al. (1991), Haller et al. (1992)
<i>MYB</i>	avian myeloblastosis viral oncogene homolog (<i>v-myb</i>)	1	S	Yasue et al. (1992)
<i>MYC</i>	c-myc oncogene	7	A, CH, L, S	Wiener et al. (1982); Sümegi et al. (1983); Tsichlis et al. (1985); Serikawa et al. (1992b); Kunieda et al. (1992a); Kondo et al. (1993)
<i>MYCB</i>	MYC-like oncogene	3	S	Ingvarsson et al. (1988b)
<i>MYCL1</i>	MYC-like oncogene	5	S	Ingvarsson et al. (1987, 1988b)
<i>MYCN</i>	MYC-like oncogene	6	S	Ingvarsson et al. (1987, 1988b)
<i>MYCS</i>	s-myc protein	X	L, S	Serikawa et al. (1992b)
<i>MYHSE</i>	myosin heavy chain, embryonic skeletal muscle, (RD9), (MYH3)	10	L, S	Hilbert et al. (1991); Jacob et al. (1991); Serikawa et al. (1992b); Remmers et al. (1992); Cash et al. (1993); Kuramoto et al. (1993a)
<i>MYL2</i>	myosin light chain, muscle 2	1	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Lindpaintner et al. (1992); Goldmuntz et al. (1993)
<i>MYLCIV</i>	myosin light chain, alkali, cardiac ventricles	8	L, S	Serikawa et al. (1992b)
<i>NCAM</i>	neural cell adhesion molecule	8	L, S	Yasue et al. (1992); Kobayashi et al. (1992b)
<i>NEFM</i>	neurofilament protein middle polypeptide	15	S	Yasue et al. (1992)
<i>NEFML</i>	neurofilament protein-like	14	S	Yasue et al. (1992)
<i>NEU1</i>	neuraminidase-1	20	L	van de Berg et al. (1981)
<i>NGFB</i>	nerve growth factor, beta	2	S	Levan et al. (1991)
<i>NGFG</i>	nerve growth factor, gamma	1	S	Yasue et al. (1992)
<i>NGFI</i>	nerve growth factor-induced gene	18	S	Serikawa et al. (1992b)
<i>NGFR</i>	nerve growth factor receptor, fast	10	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Kondo et al. (1993)
<i>NP</i>	nucleoside phosphorylase 1	15	S	Yasue et al. (1991)
<i>NPY</i>	neuropeptide Y, (D4MIT7)	4	L, S	Serikawa et al. (1992b); Jacob et al. (1992)
<i>NRAS2</i>	neuroblastoma homolog 2 (<i>v-ras</i>)	1	L	Kunieda et al. (1990)
<i>OLF</i>	olf-alpha (olfactory specific G) protein	18	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Remmers et al. (1993b)
<i>ORM</i>	orosomucoid	5	S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>P</i>	pink eyed dilution	1	L	Brdicka (1968)
<i>P9KA</i>	protein 9Ka	2	L, S	Serikawa et al. (1992b)
<i>PA</i>	placental antigen	20	L	Misra et al. (1989a, 1989b)
<i>PAH</i>	phenylalanine hydroxylase	7	S	Fulchignoni-Lataud et al. (1990)
<i>PBPC1</i>	prostatic binding protein 1	5	A	Zhang et al. (1988)
<i>PBPC2</i>	prostatic binding protein 2, C2	1	A, L, S	Serikawa et al. (1992b)
<i>PBPC3</i>	prostatic binding protein 3	5	A	Zhang et al. (1988)
<i>PCCB</i>	propionyl-CoA carboxylase, beta	8	S	Szpirer et al. (1989a)
<i>PCK</i>	phosphoenolpyruvate carboxykinase	3	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>PDGFB</i>	platelet-derived growth factor beta oncogene homolog (<i>v-sis</i>)	7	S	Fang et al. (1985)
<i>PEPB</i>	peptidase 2	7	S	Yasue et al. (1991)
<i>PEPC</i>	peptidase 3	13	L	Womack, Cramer (1980); Cramer et al. (1986); Serikawa et al. (1992b); Kondo et al. (1993)
<i>PEPD</i>	peptidase 4	1	S	Yoshida (1984a)
<i>PEPS</i>	peptidase 7	14	S	Yasue et al. (1991)
<i>PERF</i>	peripherin	7	L, S	Serikawa et al. (1992b); Kondo et al. (1993)
<i>PF4</i>	platelet factor 4	14	L	Remmers et al. (1993a)
<i>PK2</i>	phosphofructokinase 2	X	S	Darville et al. (1989)
<i>PKFB1</i>	6-phosphofructo-2-kinase/fructose-2,6-bisphosphatase, liver and muscle	X	A, L, S	Hilliker et al. (1991); Hilbert et al. (1991); Serikawa et al. (1992b)
<i>PKFB2</i>	6-phosphofructo-2-kinase/fructose-2,6-bisphosphatase, heart	13	S	Hilliker et al. (1991)
<i>PFLG</i>	profilagrin	2	S	Serikawa et al. (1992b)
<i>PG1</i>	pepsinogen 1	(XII)*	L	Cramer (1981); Hamada et al. (1987)
<i>PG2</i>	pepsinogen 2	(XII)*	L	Hamada et al. (1987)
<i>PGD</i>	phosphogluconate dehydrogenase	5	L, S	Koga et al. (1972); Carter, Parr (1969); Serikawa et al. (1992b)
<i>PGK</i>	phosphoglycerate kinase	X	S	Levan et al. (1986); Serikawa et al. (1992b)
<i>PGM1</i>	phosphoglucomutase 1	5	S	Koga et al. (1972); Yoshida (1979, 1982)
<i>PGY1</i>	P-glycoprotein 1/multi drug resistance 1	4	S	Hanson et al. (1988)
<i>PJ</i>	alpha 1-antitrypsin	6	S	Fulchignoni-Lataud et al. (1992)
<i>PIM1</i>	proviral integration, MCF	20	S	Yasue et al. (1992)
<i>PKATA</i>	peroxisomal 3-ketoacyl-CoA thiolase	8	L, S	Serikawa et al. (1992b)
<i>PKC</i>	protein kinase C type I	1	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>PKCS</i>	protein F1 (substrate of protein kinase C)	11	S	Serikawa et al. (1992b)
<i>PKL</i>	pyruvate kinase, L-type	2	L, S	Fulchignoni-Lataud et al. (1990); Serikawa et al. (1992b); Zha et al. (1993)
<i>PL2</i>	placental antigen 2	17	S	Levan et al. (1991)
<i>PLCD1</i>	phospholipase C-delta 1	8	S	Katsuya et al. (1992)

Table 1. *Continued.*

Locus symbol	Locus name	Chr.	Mode	References
<i>PLANH</i>	plasminogen activator inhibitor	12	L, S	Serikawa et al. (1992b)
<i>PLP</i>	parathyroid-like peptide	2 or 4	S	Hendy et al. (1988); Levan et al. (1990)
<i>PLPA</i>	prolactin-like protein A	17	S	Levan et al. (1991)
<i>PLPB</i>	prolactin-like protein B	17	S	Levan et al. (1991)
<i>PLPC</i>	prolactin-like protein C	17	S	Deb et al. (1991)
<i>PMCH</i>	pro-melanin-concentrating hormone	7	S	Nahon et al. (1992)
<i>PND</i>	pronatriodilatin (atrial natriuretic factor), (anf)	5	L, S	Szpirer et al. (1989b, 1990); Serikawa et al. (1992b); Kunieda et al. (1992a); Kuramoto et al. (1993b)
<i>PP</i>	pyrophosphatase, inorganic	20	S	Yasue et al. (1991)
<i>PP63</i>	insulin receptor tyrosine kinase inhibitor	11	S	Falquierho et al. (1991)
<i>PPY</i>	pancreatic polypeptide	10	L, S	Serikawa et al. (1992b); Remmers et al. (1992); Cash et al. (1993); Kuramoto et al. (1993a); Kondo et al. (1993)
<i>PRL</i>	prolactin	17	A, L, S	Cooke et al. (1986); Hilbert et al. (1991); Serikawa et al. (1992b)
<i>PRLR</i>	prolactin receptor	2	L, S	Serikawa et al. (1992b)
<i>PRM1</i>	protamine-1, spermatic specific	10	S	Adham et al. (1991)
<i>PRPS2</i>	phosphoribosylpyrophosphate synthetase subunit II	X	L, S	Serikawa et al. (1992b)
<i>PRRI</i>	ventral prostatic proline rich polypeptide	10	A	Zhang et al. (1989)
<i>PRT1</i>	protenase-1, submandibular gland	1	L	von Deimling, Günther (1982)
<i>PRT2</i>	protenase-2, submandibular gland	1	L	von Deimling, Günther (1982)
<i>PTH</i>	parathyroid hormone	1	S	Levan et al. (1986)
<i>PTHR</i>	parathyroid hormone related	1	L	Goldmuntz et al. (1993)
<i>PTHLH</i>	parathyroid hormone-like peptide	4	L, S	Hendy et al. (1988); Szpirer et al. (1991a); Serikawa et al. (1992b)
<i>PTP</i>	protein-tyrosine-phosphatase	3	L, S	Serikawa et al. (1992b)
<i>PTV1</i>	MYC activator, Moloney murine leukemia virus integration site 1, (MLV11, MIS1)	7	S	Tsichlis et al. (1985); Koehne et al. (1989)
<i>R</i>	red-eyed dilution	1	L	Castle, King (1949)
<i>RAF1</i>	3611-MSL viral oncogene	4	S	Ingvarsson et al. (1988a)
<i>RAFAS</i>	breakage region for RAF-rearrangement	13	S	Ingvarsson et al. (1988a)
<i>RARA</i>	retinoic acid receptor, alpha chain	10	S	Levan et al. (1991)
<i>RARB</i>	retinoic acid receptor, beta chain	15	S	Levan et al. (1991)
<i>RARG</i>	retinoic acid receptor, gamma chain	7	S	Mattei et al. (1991)
<i>RB1</i>	retinoblastoma protein	15	S	Szpirer et al. (1991b)
<i>RBP2</i>	retinol binding protein II, cellular	8	L, S	Serikawa et al. (1992b)
<i>RDY</i>	retinal dystrophy	3	L	La Vail (1981)
<i>REN</i>	renin	13	A, L, S	Pravence et al. (1991); Mori et al. (1992b); Serikawa et al. (1992b); Kuramoto et al. (1993b)
<i>RN5S1</i>	ribosomal 5s RNA 1	12	A	Szabo et al. (1978)
<i>RN5S2</i>	ribosomal 5s RNA 2	19	A	Szabo et al. (1978)
<i>RNR1</i>	ribosomal 18s and 28s RNA	3	A, CH	Kano et al. (1976); Szabo et al. (1978); Sasaki et al. (1986)
<i>RNR2</i>	ribosomal 18s and 28s RNA	11	A, CH	Kano et al. (1976); Szabo et al. (1978); Sasaki et al. (1986)
<i>RNR3</i>	ribosomal 18s and 28s RNA	12	A, CH	Kano et al. (1976); Szabo et al. (1978); Sasaki et al. (1986)
<i>RNU1</i>	small nuclear RNA Ulb 3	2	A	Levan et al. (1991)
<i>RONU</i>	Rowett nude (RNU)	10	L	Cash et al. (1993); Kuramoto et al. (1993a)
<i>RPL35P</i>	ribosomal protein L35a related pseudogene	17	S	Serikawa et al. (1992b)
<i>RTIA</i>	MHC-A (class I)	20	L	Bogden, Aptekman (1960); Frenzl et al. (1960); Palm (1962, 1971)
<i>RTJB</i>	MHC-B (class II), D20RW1	20	L, S	Stark et al. (1977); Lobel, Cramer (1981); Locker et al. (1990); Jacob et al. (1992)
<i>RTIC</i>	MHC-C	20	L	Kohoutova et al. (1980)
<i>RTID</i>	MHC-D	20	L	Lobel, Cramer (1981)
<i>RTIE</i>	MHC-E	20	L	Kunz et al. (1982)
<i>RT2</i>	cell surface alloantigen	19	L	Owen (1962); Palm (1962); Pravenec et al. (1992)
<i>RT3</i>	cell surface alloantigen	13	L	Brdicka, Frenzl (1978)
<i>RT4</i>	cell surface alloantigen	1	L	Kren et al. (1973)
<i>RT5</i>	cell surface alloantigen	8	L	Kren et al. (1973); Kren (1975)
<i>RT6</i>	cell surface alloantigen	1	L	DeWitt, McCullough (1975)
<i>RT9</i>	cell surface alloantigen	19	L	Kunz et al. (1985)
<i>RT11</i>	cell surface alloantigen	20	L	Kunz et al. (1989)
<i>RTLH1</i>	cell surface alloantigen	20	L	Wonigeit (1979)
<i>RTP1</i>	rat tear protein 1	5	L	Kondo et al. (1987, 1988)
<i>RTP2</i>	rat tear protein 2	1	L	Kondo et al. (1987, 1989)
<i>RW</i>	warfarin resistance	1	L	Greaves, Ayres (1969, 1976, 1977)
<i>S</i>	silver	5	L	Castle (1953)
<i>SA</i>	SA gene	1	L	Lindpaintner et al. (1992)
<i>SAII</i>	transformation suppressor	5	CH	Islam et al. (1989)
<i>SCN2A</i>	sodium channel II, alpha	3	L, S	Hilbert et al. (1991); Yasue et al. (1992); Serikawa et al. (1992b); Kuramoto et al. (1993b)
<i>SECR</i>	secretin	1	S	Serikawa et al. (1992b)
<i>SH</i>	shaggy	5	L	Castle, King (1947)
<i>SHBG</i>	sex hormone-binding globulin (ABP)	10	L, S	Sullivan et al. (1991); Hilbert et al. (1991); Serikawa et al. (1992b); Remmers et al. (1992); Cash et al. (1993); Kuramoto et al. (1993a)

Table 1. *Continued.*

Locus symbol	Locus name	Chr.	Mode	References
<i>SHDL</i>	steroid hydroxylase, hepatic	1	S	Serikawa et al. (1992b)
<i>SMST</i>	somatostatin	11	L, S	Yasue et al. (1992); Serikawa et al. (1992b)
<i>SORD</i>	sorbitol dehydrogenase	3	S	Yasue et al. (1991)
<i>SP</i>	serum protein	20	L	Cramer (1983)
<i>SPI</i>	Sp-1 transcription factor	7	S	Szpirer et al. (1991c)
<i>SPAT</i>	serine, pyruvate aminotransferase, (AGXT)	9	A, S	Mori et al. (1992d)
<i>SPIN1</i>	serine protease inhibitor 1	6	S	Pagés et al. (1990)
<i>SPIN2</i>	serine protease inhibitor 2	6	S	Pagés et al. (1990)
<i>SPIN3</i>	serine protease inhibitor 3	6	S	Pagés et al. (1990)
<i>ST</i>	stub	(III)*	L	Castle, King (1944)
<i>SVP1</i>	seminal vesicle protein 1	3	L	Gasser (1972); Moutier et al. (1973a)
<i>SVS2P</i>	seminal vesicle secretion II protein	3	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Kondo et al. (1993); Kuramoto et al. (1993b)
<i>SVS4</i>	seminal vesicle secretion IV	3	L	Kobayashi et al. (1992a)
<i>SYB2</i>	synaptobrevin 2 (vesicle associated membrane protein, VAMP-2)	10	L, S	Archer III et al. (1990); Hilbert et al. (1991); Serikawa et al. (1992b); Kuramoto et al. (1993a)
<i>TAC</i>	tachykinin (D4MIT1)	4	L	Jacob et al. (1992)
<i>TAC1R</i>	tachykinin 1 (substance P) receptor	4	S, A, L	Mori et al. (1992c); Hilbert et al. (1991); Serikawa et al. (1992b)
<i>TAC2R</i>	tachykinin 2 (substance K) receptor	20	S	Mori et al. (1992c)
<i>TAC3R</i>	tachykinin 3 (neuromedine K) receptor	2	S	Mori et al. (1992c)
<i>TAL2</i>	tail anomaly lethal 2	1	L	Morriss-Kay, Hunt (1986)
<i>TAMI</i>	tamase (submaxillary gland)	1	L	Matsumoto et al. (1984)
<i>TAT</i>	tyrosine aminotransferase	19	L, S	Fulchignoni-Lataud et al. (1990); Serikawa et al. (1992b)
<i>TBM1</i>	tubular basement membrane 1	1	L	Matsumoto et al. (1984)
<i>TBM2</i>	tubular basement membrane 2	3	L	Matsumoto et al. (1984)
<i>TCP1</i>	t-complex protein 1	1	L, S	Yasue et al. (1992); Serikawa et al. (1992b); Goldmuntz et al. (1993)
<i>TCP1L</i>	t-complex protein 1-like	4	S	Yasue et al. (1992)
<i>TCRB</i>	T-lymphocyte receptor, beta chain, (D4MIT4)	4	L, S	Levan et al. (1991); Jacob et al. (1992); Dissen et al. (1993)
<i>TCRG</i>	T-lymphocyte receptor, gamma chain	17	S	Yasue et al. (1992)
<i>TF</i>	transferrin	8	S	Szpirer et al. (1987, 1988b)
<i>TG</i>	thyroglobulin	7	S	Brocas et al. (1985)
<i>TGFA</i>	transforming growth factor, alpha	4	L, S	Serikawa et al. (1992b)
<i>THRA1</i>	thyroid hormone receptor, alpha 1 (ERBA1)	10	S	Szpirer et al. (1991b)
<i>THRΒ</i>	thyroid hormone receptor, beta (ERBA2)	15	S	Szpirer et al. (1991b)
<i>THY1</i>	thymus cell antigen-1	8	L, S	Serikawa et al. (1992b); Kunieda et al. (1992a)
<i>TILP</i>	trypsin inhibitor-like protein, pancreatic	18	L, S	Serikawa et al. (1992b); Remmers et al. (1993b)
<i>TK</i>	thymidine kinase (soluble)	10	S	Yoshida (Levan et al. 1986)
<i>TKG</i>	T-kininogen	11	L, S	Serikawa et al. (1992b)
<i>TLS1</i>	thymic lymphoma susceptible 1	1	L	Shisa, Hiai (1985)
<i>TNF</i>	tumor necrosis factor	20	L, S	Serikawa et al. (1992b); Kondo et al. (1993)
<i>TNP1</i>	transition protein-1, spermatid specific	9	S	Adham et al. (1991)
<i>TNP2</i>	transition protein-2, spermatid specific	10	S	Adham et al. (1991)
<i>TNT</i>	troponin T, fast skeletal	1	L	Goldmuntz et al. (1993)
<i>TON</i>	tonin	1	L, S	Hilbert et al. (1991); Serikawa et al. (1992b)
<i>TPII</i>	triosephosphate isomerase 1	4	S	Levan et al. (1986)
<i>TPL1</i>	tumor progression	8	S	Bear et al. (1989)
<i>TPM</i>	alpha-tropomyosin	8	L, S	Serikawa et al. (1992b)
<i>TRAGGL</i>	Asp-, Gly-, Glu- and Leu-tRNAs cluster	13	S	Serikawa et al. (1992b)
<i>TRP53</i>	transformation related protein 53	10	S	Yasue et al. (1992)
<i>TRP53L1</i>	transformation related protein 53-like 1	9	S	Yasue et al. (1992)
<i>TRP53L2</i>	transformation related protein 53-like 2	14	S	Yasue et al. (1992)
<i>TRP53L3</i>	transformation related protein 53-like 3	18	S	Yasue et al. (1992)
<i>TRPM2</i>	testosterone-repressed prostate message 2	15	S	Goldner-Sauvé et al. (1991)
<i>TRY1</i>	trypsin I, pancreatic	4	L, S	Serikawa et al. (1992b)
<i>TTR</i>	transthyretin	18	L, S	Serikawa et al. (1992b); Remmers et al. (1993b)
<i>UCP</i>	uncoupling protein	19	L, S	Hilbert et al. (1991); Serikawa et al. (1992b); Osten et al. (1993)
<i>UGT2B2</i>	androsterone UDP-glucuronosyl-transferase	14	A	Satoh et al. (1993)
<i>UMPH2</i>	uridine monophosphatase	10	S	Yasue et al. (1991)
<i>VDR</i>	1,25-dehydroxy vitamin-D3 receptor	7	S	Szpirer et al. (1991d)
<i>VET</i>	vestigial testes	X	—	Bardin et al. (1973)
<i>W</i>	waltzing	1	L	King (1936); Castle, King (1949)
<i>YES1</i>	avian Y73 sarcoma virus	1	S	Levan et al. (1986)
<i>ZI</i>	zitter	3	L	Rehm et al. (1982); Yamada et al. (1989); Serikawa et al. (1992b)

An asterisk notes the linkage group in Hedrick's map (1990).

For method of gene localization (Mode), the following codes have been used: A, in situ hybridization; CH, cytogenetic rearrangement; L, linkage studies; S, somatic cell hybrids; W, flow-sorted chromosomes.

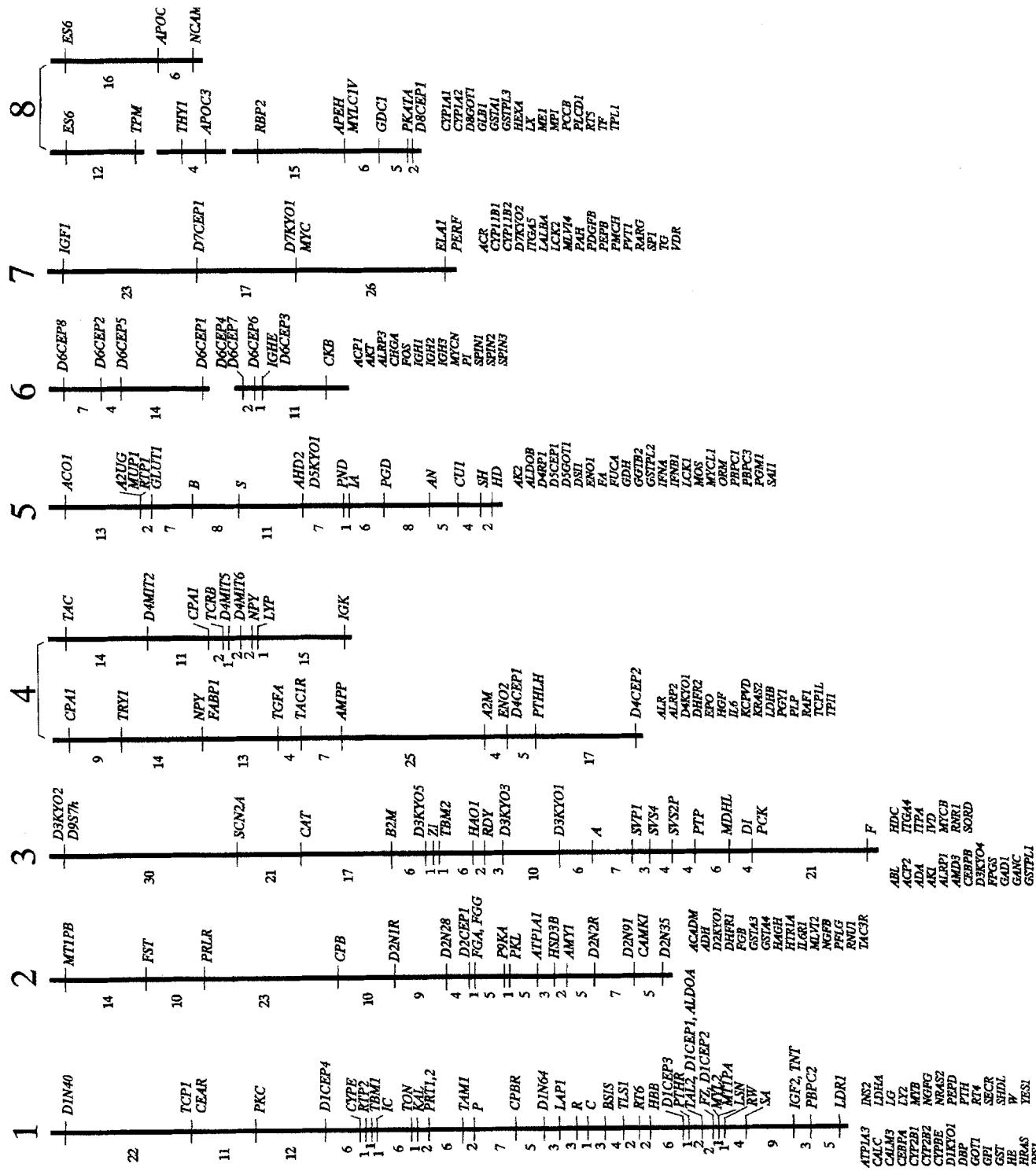


Fig. 1. A rat genetic linkage map. The genes assigned only to each chromosome are alphabetically listed under each chromosome. Numbers to the left of the chromosomes are estimated distances between the two loci in cM.

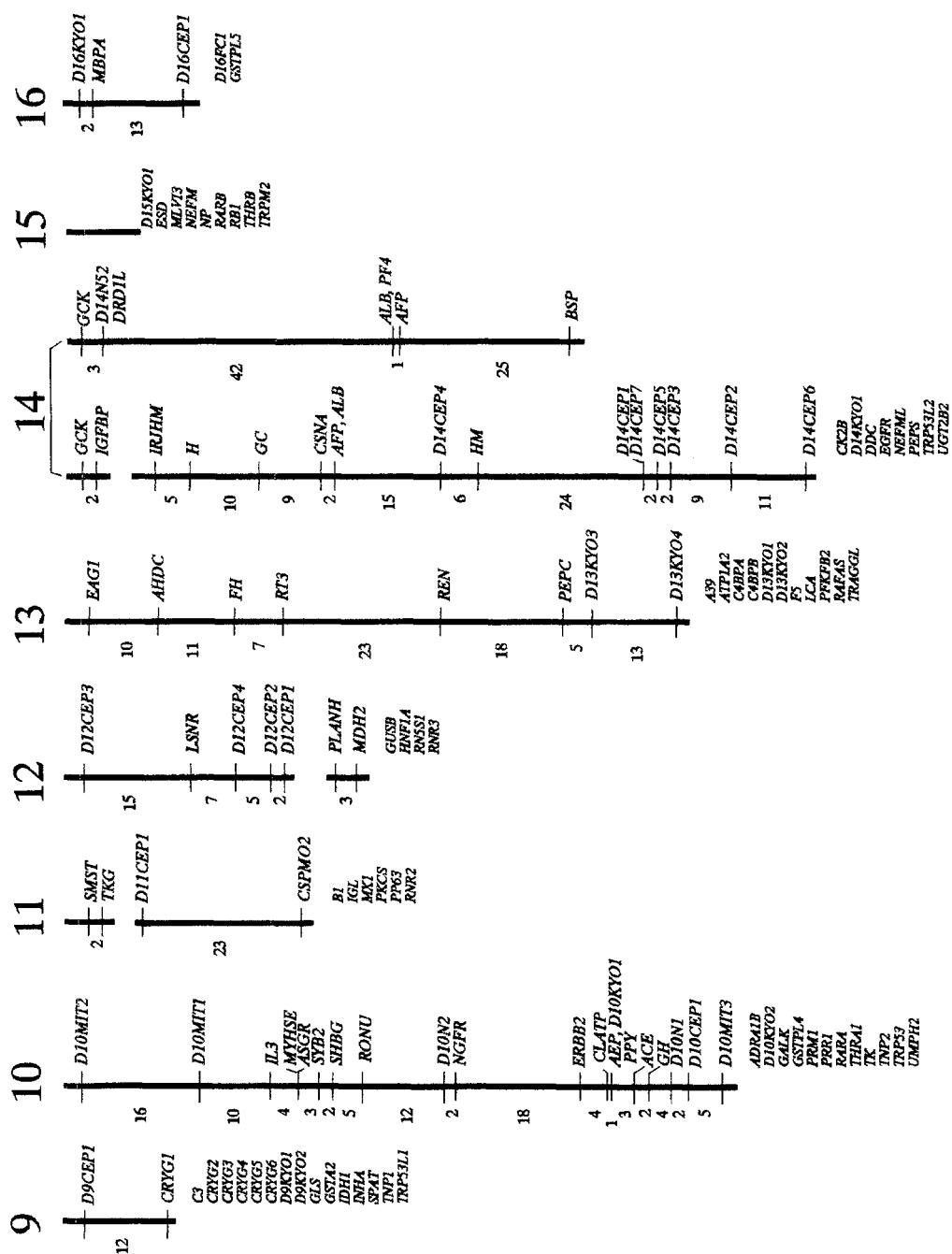


Fig. 1. Continued.

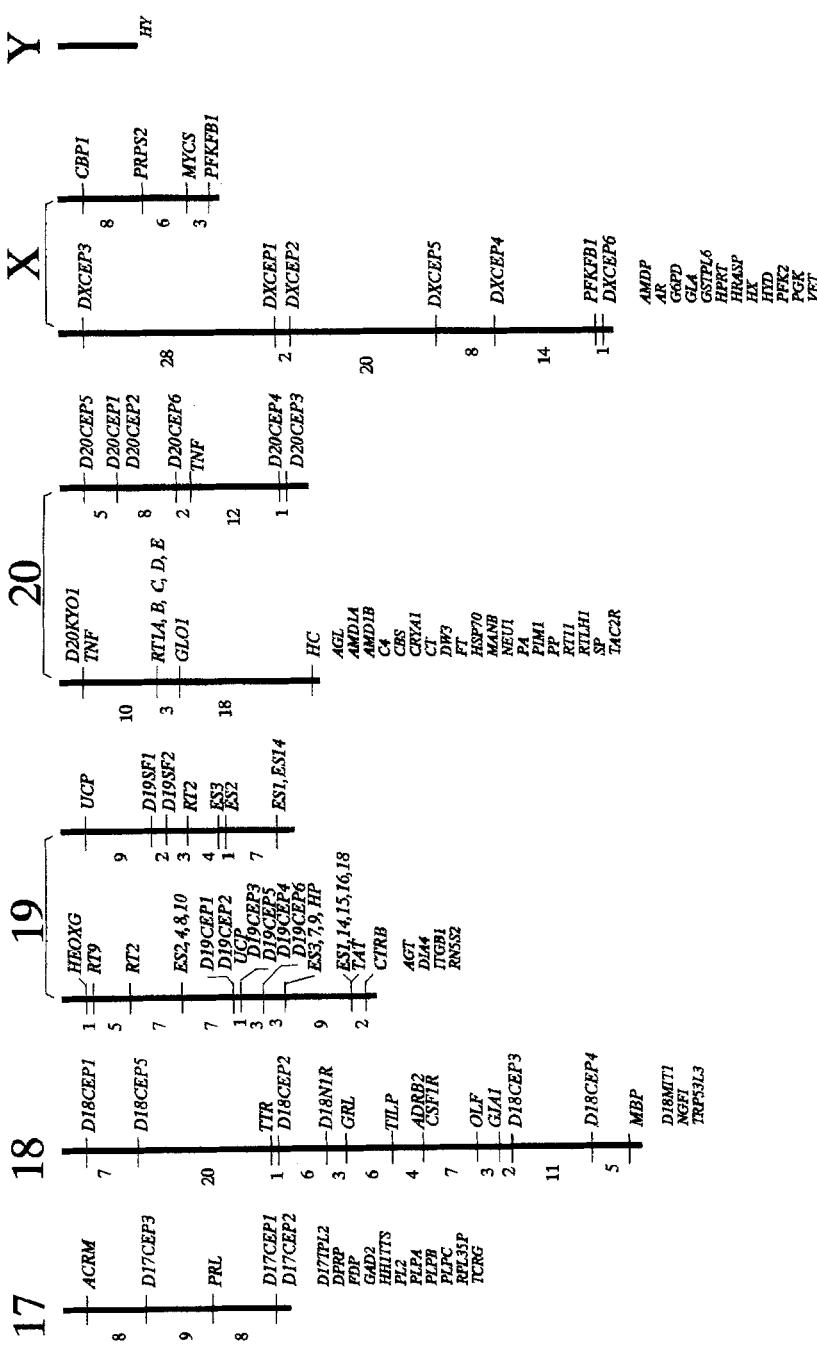


Fig. 1. *Continued.*

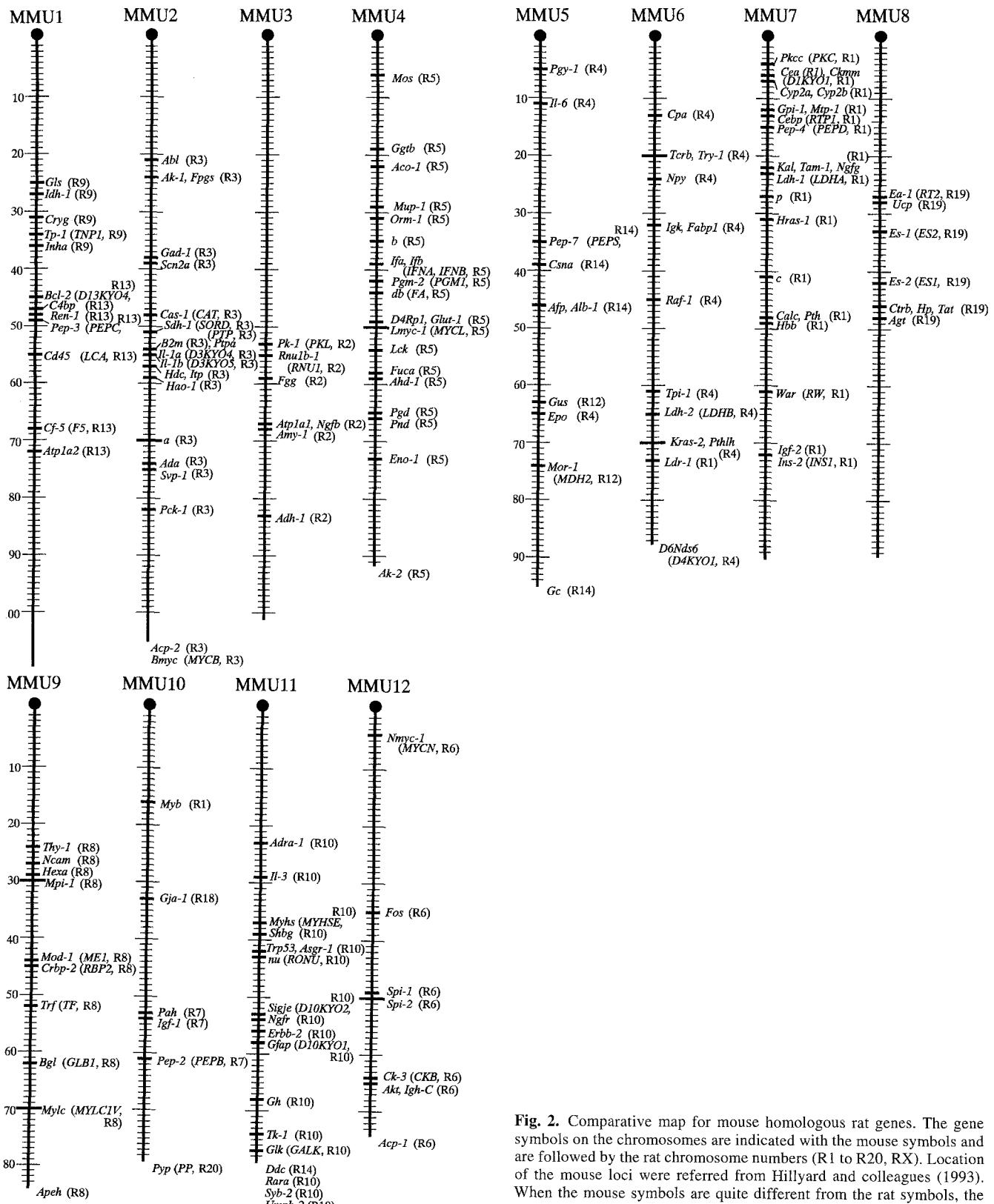


Fig. 2. Comparative map for mouse homologous rat genes. The gene symbols on the chromosomes are indicated with the mouse symbols and are followed by the rat chromosome numbers (R1 to R20, RX). Location of the mouse loci were referred from Hillyard and colleagues (1993). When the mouse symbols are quite different from the rat symbols, the rat symbols are shown in parentheses.

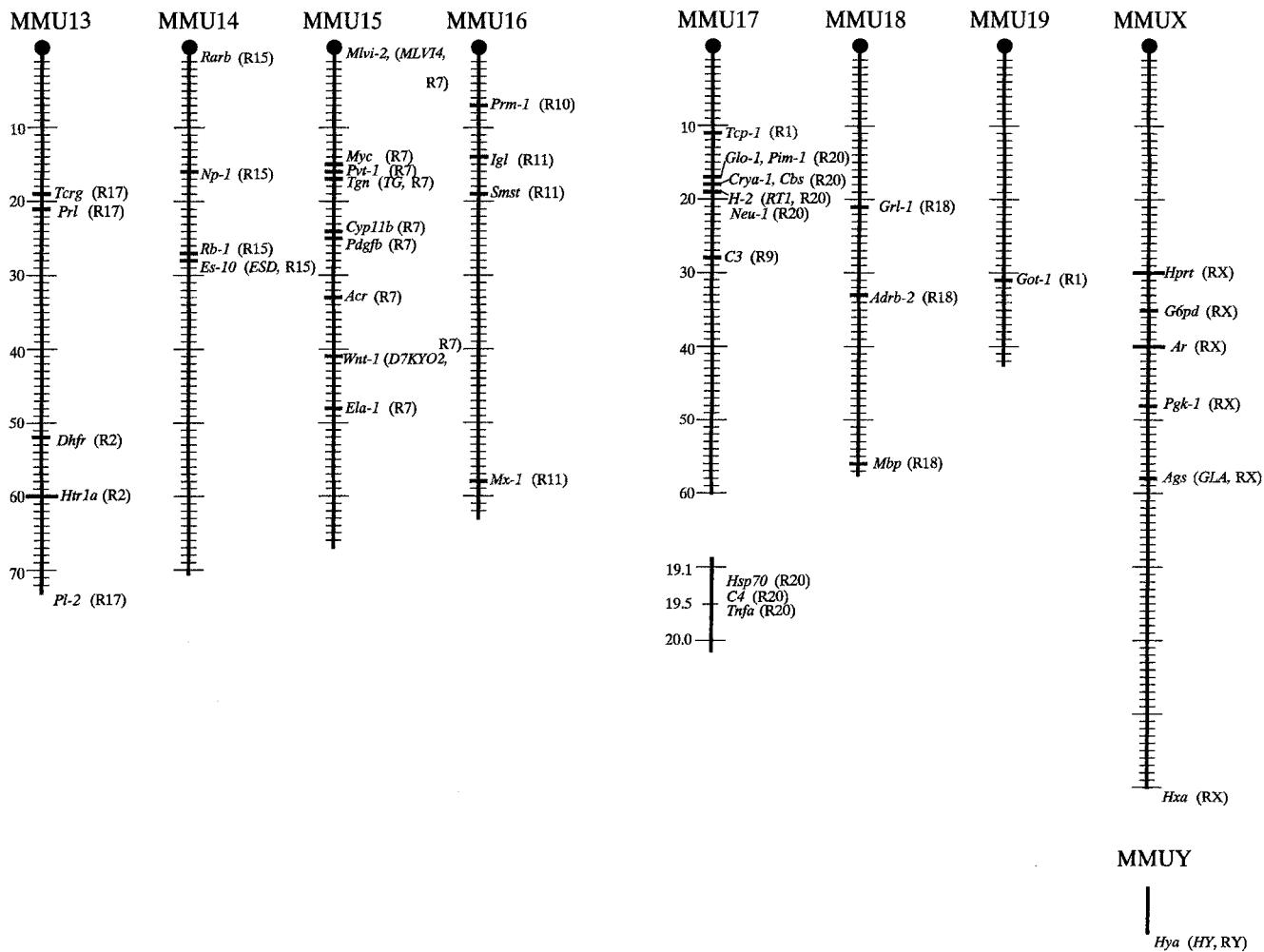


Fig. 2. Continued.

RNO3, 2, 5, 4, 1, 19, 8, 10, 6, 15, 7, 11, 18, and X, respectively. It seems that MMU1 consists of a homologous RNO9 (centromeric half) and RNO13 (telomeric half); this has already been deduced from the G-banding patterns by Levan and coworkers (1991). Conserved linkage of homologous genes between MMU7 and RNO1, and between MMU11 and RNO10, were confirmed. On MMU5, 10, 13, 16, and 17, the rat homologs belong to two or three different chromosomes.

Although the gene orders on homologous chromosomes or chromosomal segments between the two species are fairly well preserved, a few genes are ordered in the opposite direction in the two species, and only one rat homolog was assigned on MMU19 and MMUY. In order to compare more precisely the gene orders among the different species, we have to wait to obtain a more complete rat gene map. Resemblance between mouse and rat maps is considered to reflect the phylogenetically close relationships between the two species.

Comparative human map

In Fig. 3, we assigned human homologous rat genes to the human chromosomes, shown by the human symbols. Lo-

cation of the human loci have been referred from the 1991 catalog of human mapped genes of McAlpine and associates (1991). All of the human homologous rat genes shown on HSA17 and HSAX locate on RNO10 and RNOX, respectively. In the other human chromosomes, human homologous rat genes are divided into two or more rat chromosomes. Out of 218 human homologous rat genes in this map, 169 genes (77.5%) are known also in the mouse. The remaining 49 human homologous rat genes (22.5%) have not been reported yet in the mouse. This suggests that the rat makes considerable contributions in the area of biomedical research, as well as the mouse. In fact, the rat provides a variety of models for human disease, including hypertension, diabetes, various cancers, and so on.

In order to make comparisons of the rat genes with those of mouse and human homologs, we have performed searches that were as precise as possible. There is a possibility, however, that there may be some misunderstandings or misreading of the homologs. If this is the case, we hope that they will be quickly corrected by new studies.

We can now use chromosome numbers instead of linkage groups in rat gene mapping, as in the mouse or human. We have no doubt that the rat genetic linkage map will be furnished with more newly assigned genes within the next couple of years, by currently available techniques and

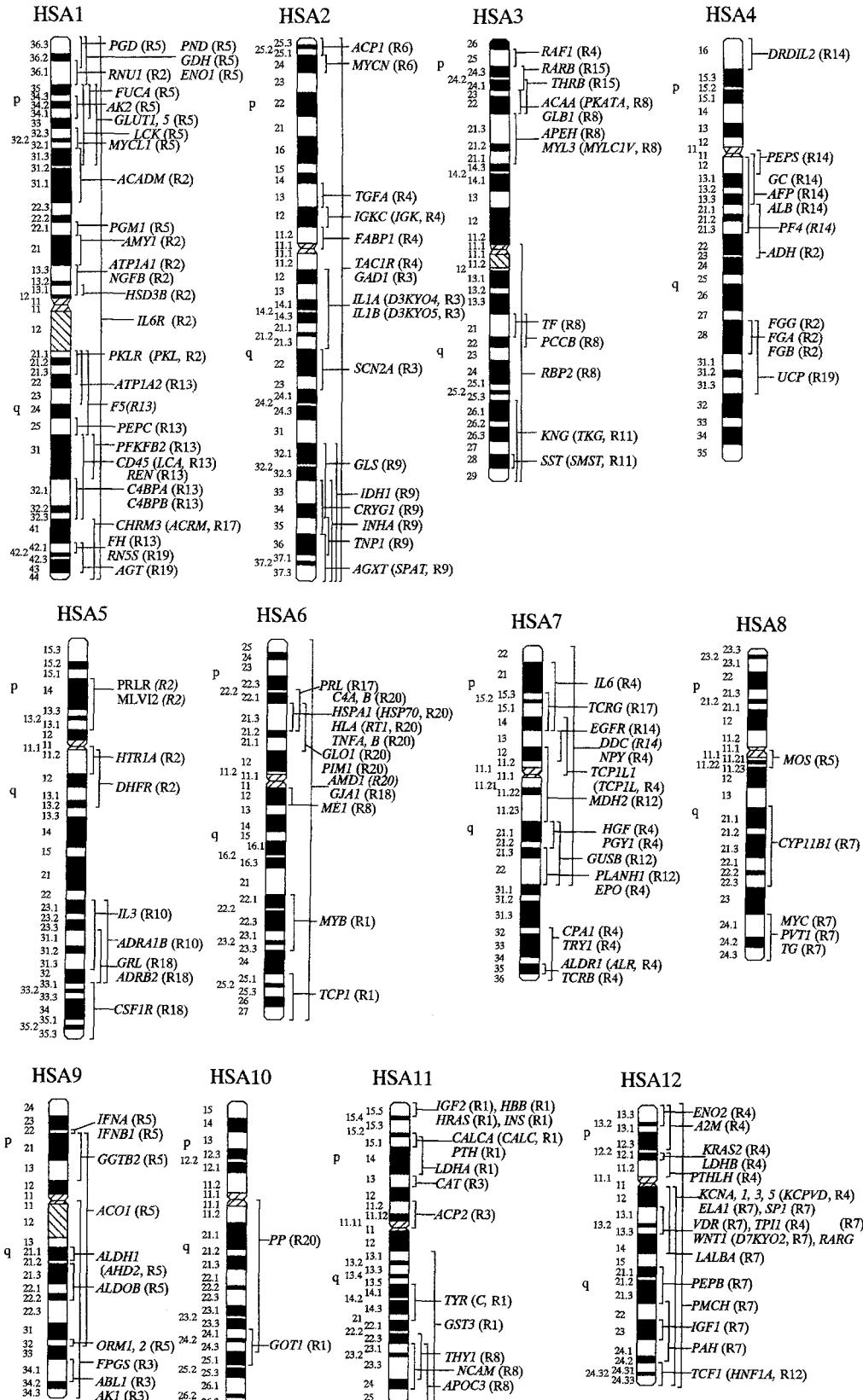
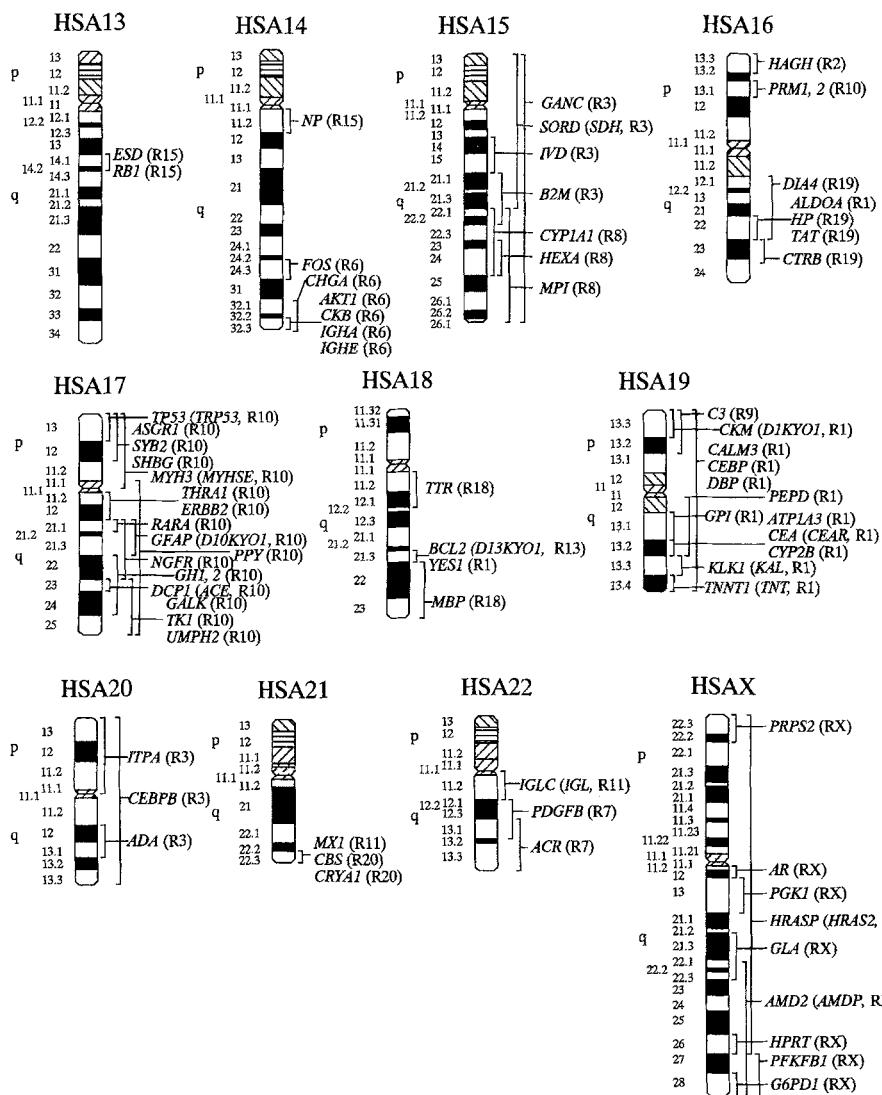


Fig. 3. Comparative map for human homologous rat genes. The gene symbols on the chromosomes are indicated with the human symbols and are followed by the rat chromosome numbers (R1 to R20, RX). Location of the human loci were referred from McAlpine and coworkers (1991). When the human symbols are quite different from the rat symbols, the rat symbols are shown in parentheses.

**Fig. 3. Continued.**

newly developed DNA technologies. In this way, comparisons of genes among rat-mouse-human will become easier and also more precise.

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