

Mouse Chromosome 3

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Introduction

Mouse Chromosome (Chr) 3 is marked by more than 50 molecular markers and several interesting mutant genes. Conserved regions with homology to human chrs 1p, 4q, and 8 have been defined. The conserved regions include two multigene families, amylase and carbonic anhydrase. Physical mapping on pulse-field gels has demonstrated conservation of certain intergenic distances on mouse Chr 3 and human chr 1. This report presents a new composite map of Chr 3. In addition, we have recommended for inclusion in future crosses five reference loci which span the linkage map and which can be typed by restriction fragment length variation (RFLV) and polymerase chain reaction (PCR). Widespread utilization of these reference loci would contribute to the generation of reliable composite maps in the future.

The mouse Chr 3 map

The map of mouse Chr 3 was generated by M.F. Seldin using data from crosses between inbred laboratory strains, interspecific crosses and recombinant inbred (RI) strains. A locus list including citations to the linkage data on which the map is based is presented in Table 1. The composite map is represented in Fig. 1. Map distances are measured from the centromere, based on the estimated distance from the centromere to *Car-1*, which was determined with a Robertsonian translocation chromosome (Davisson et al. 1976). The framework of the map was based on recombination data for the loci *Car-1*, *Evi-1*, *Amy-2* and *Egf*, obtained from four backcrosses. The major source of deviation between this map and the map generated by The Jackson Laboratory is due to the current estimate that the *Evi-1* to *Amy-1* distance is 39 cM, in contrast to the previous value of 54 cM. (Measurements of this dis-

tance vary from 27–53 cM in the four backcrosses cited in Table 1). The positions of *Gba*, *Es26* and *Es27* have been corrected, and small changes in the positions of several other loci are indicated. It should be emphasized that map positions are approximate, and that the order of closely linked genes which have not been typed in the same cross is uncertain.

Since recombination frequencies vary in different crosses, the composite map may distort the order of loci which were not mapped in the same backcross. In deriving the composite map, data from RI strains was used to determine gene position as a supplement to backcross data. For a fuller discussion of the method used to generate the map, the reader is referred to the discussion in the Mouse Chromosome 1 Committee Report.

Three linkage groups on mouse Chr 3 are conserved in the human genome

All of the genes mapped to the region between *Gba* and *Amy-2* are conserved on human chr 1, with the exception of *Csfm*, which is on human chr 5q (Mosely and Seldin 1989; Buchberg et al. 1989). Physical mapping of five loci from this linkage group demonstrated conservation of gene order and intergenic distance in the two species (Kingsmore et al. 1990). The 10 cM region between *Fabpi* and *Egf* is conserved on human chr 4q. The carbonic anhydrase genes, *Car-1*, *Car-2* and *Car-3*, are linked on human chr 8; no other loci have yet been mapped to this conserved group.

The structures of the amylase gene clusters in human and mouse are quite different. In mouse, the salivary amylase gene is located 21 kb upstream of a pancreatic amylase gene (Wiebauer et al. 1985). In the 230 kb human gene cluster, the two pancreatic amylase genes are located upstream of the three salivary amylase genes, and several copies of an endogenous retrovirus and an actin pseudogene are interspersed with the amylase genes (Samuelson et al. 1990). The human genes were derived from a single pancreatic amylase gene during primate evolution. The adjacent retrovirus is required for tissue-specific expression of human salivary amylase (Ting and Meisler, unpublished data).

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Table 1. Mouse Chr 3 loci.

Locus ^a	Name	Map ^b	Method of Analysis ^{c,d}	Reference
<i>Acrb-2</i>	acetylcholine receptor β -2 neural	39.6	C:3	Bessis et al. 1990
<i>Acts</i>	skeletal α actin; the mouse skeletal α actin clone detects sequences that map to mouse Chr 18 (Howard et al. 1990)	X	C: somatic cell	Czosnek et al. 1982
<i>Adh-1</i>	alcohol dehydrogenase-1	72.1	B:3,8,13; C:9	Chapman et al. 1979; Bonhomme et al. 1979; Holmes et al. 1981; Ceci et al. 1987; Gisselbrecht et al. 1989
<i>Adh-1ps</i>	alcohol dehydrogenase-1 pseudogene	56.0	C:9	Ceci et al. 1987
<i>Adh-1t</i>	alcohol dehydrogenase-temporal	72.1	B:14	Balek et al. 1982; Holmes et al. 1983
<i>Adh-3</i>	alcohol dehydrogenase-3	72.1	B:7,8,9,10,13	Holmes et al. 1981a, 1981b and 1981c; Duley and Holmes 1982; Prochazka et al. 1985; Holmes et al. 1985; Mucenski et al. 1988
<i>Adh-3t</i>	alcohol dehydrogenase-3-temporal	72.1	B:13	Holmes et al. 1979, 1981c
<i>Adh-5</i>	alcohol dehydrogenase-5	X	somatic cell	Giri et al. 1989
<i>Ahr-1</i>	aldehyde reductase-1	72.1	B:7,13	Duley and Holmes 1982
<i>Ampd-1</i>	AMP deaminase-1 (muscle form)	51.4	C:1	Kingsmore et al. 1989
<i>Ampd-2</i>	AMP deaminase-2 (nonmuscle form)	54.2	C:1	Moseley et al. 1990
<i>Amy-1</i>	amylase-1, salivary	53.6	B:3,5,8,9;13 C:7,9,10,11	Lane and Eicher 1979; Bonhomme et al. 1979; Eicher and Lane 1980; von Diemling et al. 1984; Paul and Elliott 1987; Blatt et al. 1988
<i>Amy-2</i>	amylase-2 pancreatic	53.6	B:9; C:1,2,7,9,10,11	Bloor and Meisler 1980; Paul and Elliott 1987; Blatt et al. 1987; Moseley and Seldin 1989
<i>Ap2</i>	adipocyte protein aP2	4.6	B:9,12	Heuckeroth et al. 1987
<i>Arnt</i>	aryl hydrocarbon receptor nuclear translator	X	somatic cell	Brooks et al. 1989
<i>Atp1a1</i>	Na,K ATPase α -1	51.3	C:1,14	Kent et al. 1987; Moseley and Seldin 1989; Kingsmore et al. 1990
(<i>Atpa-1</i>)	see <i>Atp1a1</i>			
<i>Bmn</i>	β -mannosidase activity (liver, kidney)	72.1	B:9	Lundin 1987
<i>Cacy</i>	calcyclin	46.9	C:1	Moseley and Seldin 1989; Kingsmore et al. 1990
<i>Call1</i>	calpactin I light chain	46.9	C:9,10,12	Saris et al. 1987; van Heynegen et al. 1989
<i>Cap1</i>	calcium binding protein, placental	46.9	C:9,10	van Heynegen et al. 1989
<i>Car-1</i>	carbonic anhydrase-1	4.6	B:14	Eicher et al. 1976
<i>Car-2</i>	carbonic anhydrase-2	4.6	B:3,7,8,9,10,12,14 C:1	Eicher et al. 1976; Bonhomme et al. 1979; Elliot 1979; von Diemling et al. 1984; Paul and Elliott 1987; Novak et al. 1988; Moseley and Seldin 1989; Copeland and Jenkins 1990
<i>Car-3</i>	carbonic anhydrase-3	7.0	C:14	Beachey et al. 1990
<i>Cd1</i>	cluster designation 1	46.6	C:1	Moseley et al. 1990
<i>Cd2</i>	cluster designation 2	50.4	C:1	Moseley and Seldin 1989; Kingsmore et al. 1990
<i>cdm</i>	cadmium resistance	65.6	A:9	Taylor et al. 1973; Taylor et al. 1976
<i>Cnp-2</i>	cyclic nucleotide phosphodiesterase-2	42.8	C:9,11	Bernier et al. 1988
<i>coa</i>	cocoa	8.5	A:14	Sweet and Prochazka 1985; Novak et al. 1988
<i>Csfm</i>	colony stimulating factor, macrophage	52.4	C:2,3	Gisselbrecht et al. 1989; Buchberg et al. 1989
<i>D3Nds1</i>	DNA segment, Chr 3	33.3	C:4	Unpublished data
<i>D3Tu33</i>	DNA segment, Chr 3 Tubingen-33 (previously <i>D17Tu33</i>)	61.9	C:12	Vincek et al. 1989 (originally designated <i>D17Tu33</i> , but data more consistent with Chr 3 localization)
<i>D3Tu51</i>	DNA segment, Chr 3 Tubingen-51	46.9	C:1,9,10,12	Vincek et al. 1989 (originally designated <i>D17Tu51</i> , but subsequent data has established localization to Chr 3)

Table 1. Continued.

<i>de</i>	droopy ear	52.4	A:5,13,14	Curry 1959; Lane 1980; Lane and Eicher 1979; Holmes et al. 1981
<i>Egf</i>	epidermal growth factor	66.1	C:1,8,9,10,11	Zabel et al. 1985; Mucenski et al. 1988; Moseley and Seldin 1989
<i>Emv-27</i>	endogenous ecotropic MuLV-27	53.6	C:14	Taylor and Rowe 1989
<i>Es-16</i>	esterase-16	12.1	B:13	von Diemling et al. 1981, 1984, 1986
<i>Es-26</i>	esterase-26	37.3	B:13	von Diemling et al. 1981, 1984, 1986; Novak et al. 1988
<i>Es-27</i>	esterase-27, serum cholinesterase	27.3	B:13	von Diemling et al. 1985, 1986
<i>Evi-1</i>	ecotropic viral integration site-1	14.2	C:1,2,8,9,10,12	Copeland et al. 1988; Mucenski et al. 1988; Moseley and Seldin 1989; Gisselbrecht et al. 1989; Copeland and Jenkins 1990
<i>Fabpi</i>	fatty acid binding protein intestinal	56.6	C:9	Sweetser et al. 1987
<i>Fcgr1</i>	high affinity Fc γ receptor	46.9	C:1	Unpublished data
<i>Fgfb*</i>	fibroblast growth factor basic	19.7	C:1	Unpublished data
<i>Fgg</i>	γ fibrinogen	46.3	C:8,9	Blatt et al. 1988
<i>Fim-3</i>	Friend MuLV integration site-3	14.2	C:3	Sola et al. 1988; Copeland et al. 1989; Gisselbrecht et al. 1989
<i>ft</i>	flaky tail	46.4	A:5	Lane 1972; Lane and Eicher 1979
<i>Gba</i>	β glucocerebrosidase	46.6	C:1	O'Neill et al. 1989; Moseley and Seldin 1989 (some of the <i>Gba</i> assignments were in error; this position includes the corrected data)
<i>Gbp-1</i>	guanine nucleotide-binding protein-1	68.3	C:7,13	Prochazka et al. 1985
<i>H-23</i>	histocompatibility-23	63.6	B:7,13	Bailey 1975; Mobraaten et al. 1984
<i>H-28</i>	histocompatibility-28	83.3	B:7,13	Bailey 1975; Mobraaten et al. 1984
<i>H-37</i>	histocompatibility-37	(X)	B:7	Bailey 1975
<i>Hao-2</i>	hydroxyacid oxidase-2 (kidney)	44.0	B:3,13	Holmes 1977 and 1978; Gisselbrecht et al. 1989
<i>Hist2</i>	histone gene (2)	X	C: somatic cell	Graves et al. 1985
<i>Hnl</i>	hypothalamic norepinephrine level	63.6	A: congenics	Eleftheriou et al. 1974
<i>Hsp86-3</i>	heat shock protein 86 kilodalton-3	X	C: somatic cell	Moore et al. 1989
<i>If-1</i>	interferon inducibility locus	88.6	A:7,13	De Maeyer et al. 1975; Mobraaten et al. 1984
<i>Il-2</i>	interleukin 2	8.3	C:4, somatic cell	Fiorentino et al. 1989
<i>(Ly-37)</i>	see <i>Cd2</i>			
<i>(Ly-38)</i>	see <i>Cdl</i>			
<i>ma</i>	matted	44.4	A:5,13	Lane 1972; Lane and Eicher 1979; Lane 1980; Mobraaten et al. 1984
<i>Mmv-2</i>	MCF endogenous virus-2	X	somatic cell	Hoggan et al. 1986
<i>Mmv-12</i>	MCF endogenous virus-12	X	somatic cell	Hoggan et al. 1986
<i>Mov-10</i>	Moloney leukemia virus-10	X	somatic cell	Jaenisch et al. 1981; Munke et al. 1986
<i>Mpmv-9</i>	modified polytropic murine leukemia virus-9	92.2	C:6,7,10	Frankel et al. 1990
<i>Mpmv-20</i>	modified polytropic murine leukemia virus-20	11.3	C:11,12	Frankel et al. 1990
<i>my</i>	blebs	34.4	A:5	Carter 1956; Davisson et al. 1976; Eicher and Lane 1980
<i>Ngfb</i>	nerve growth factor β	51.4	C:1,2	Zabel et al. 1984; Dracopoli et al. 1988; Buchberg et al. 1989; Kingsmore et al. 1990
<i>Nras</i>	<i>Nras</i> oncogene	51.4	C:1,2	Ryan et al. 1984; Buchberg et al. 1989
<i>Odc-3</i>	ornithine decarboxylase-3	X	C:10; proximal mouse Chr 3	Richards-Smith and Elliott 1984
<i>op</i>	osteopetrosis	52.4	A:5 and see <i>Csfm</i>	Lane and Eicher 1979; Yoshida et al. 1990
<i>Oua-1</i>	ouabain resistance-1	X	A: somatic cell	Kozak et al. 1979
<i>Pgk-1ps3</i>	phosphoglycerate kinase-1 pseudogene 3	9.4	C:10, somatic cell	Adra et al. 1988

Table 1. Continued.

<i>Pk-1</i>	pyruvate kinase (may be the same as <i>Pklr</i>)	37.6	B:3	Sola et al. 1988; Gisselbrecht et al. 1989
<i>Pklr</i>	pyruvate kinase liver, red blood cells (see <i>Pk-1</i>)	46.6	C:1	Unpublished data
<i>Pmv-26</i>	polytropic murine virus-26	75.8	C:9,12	Frankel et al. 1989
<i>Pmv-28</i>	polytropic murine virus-28	46.9	C:11,12	Frankel et al. 1989
<i>Pmv-38</i>	polytropic murine virus-38	47.1	C:9,11	Frankel et al. 1989
<i>Pmv-39</i>	polytropic murine virus-39	57.8	C:9,12	Frankel et al. 1989
<i>rcm</i>	rostral cerebellar malformation	69.4	A:13	Lane et al. 1990
<i>Rnu1b-1</i>	U1b1 small nuclear RNA	46.7	C:8	Lund et al. 1988
<i>Rnu1b-3</i>	U1b3 small nuclear RNA	46.9	C:8,10	Blatt et al. 1988; Lund et al. 1988
<i>soc</i>	soft coat	47.4	A:5	Southard 1971; Eicher and Lane 1980
<i>spa</i>	spastic	41.4	A:5	Lane 1972; Lane and Eicher 1979
<i>sut</i>	subtle gray	16.2	A:13	Lane 1988
<i>Tmevd-2</i>	TMEV induced demyelinating disease susceptibility	8.8	A:9	Melvoid et al. 1990
<i>Tshb</i>	thyrotropin stimulating hormone β subunit	51.4	C:1	Kourides et al. 1984; Naylor et al. 1986; Dracopoli et al. 1988; Moseley and Seldin 1989; Kingsmore et al. 1990
<i>Va</i>	varitint-waddler	75.6	A:5,13	Curry 1959; Lane 1972; Lane 1980; Lane and Eicher 1979; Eicher and Lane 1980; Holmes et al. 1981a and 1981b; Duley and Holmes 1982; Mobraaten et al. 1984
<i>Xmmv-22</i>	xenotropic-MCF leukemia virus-22	46.3	C:9	Blatt et al. 1988
<i>Xmmv-47</i>	xenotropic-MCF leukemia virus-47	35.0	C:12	Wejman et al. 1985
<i>Xmmv-65</i>	xenotropic-MCF leukemia virus-65	46.3	C:9,12,13	Wejman et al. 1985

Map positions are based at the centromere (Davisson et al. 1976), and were calculated using data from inbred laboratory strains, interspecific crosses and recombinant inbred strains. Loci which have been assigned to Chr 3 but not regionally mapped are included. Since recombination frequencies may vary depending on the specific cross examined, the composite map positions may distort gene order when loci have not been mapped with respect to each other in an individual backcross. In deriving the composite map, RI strain data was only used to determine gene position as a supplement to backcross data. For a fuller discussion of the considerations applied to generating map positions, the reader is referred to the Mouse Chromosome 1 Committee Report.

^a Loci in parenthesis indicate loci whose names have been changed. Asterisk indicates provisional designation.

^b The map positions are measured in cM from the centromere. For those loci in which no position can be reasonably assigned, an X is shown. Parenthesis indicate uncertainty of linkage to mouse Chr 3.

^c The letters indicate how "alleles" were determined: A, phenotype or biologic property; B, gene product (cell surface antigen, protein electrophoresis etc.); C, RFLVs. For clones used to identify RFLVs the reader should refer to the specific references and/or "List of Mouse DNA Clones and Probes," J.T. Eppig, The Jackson Laboratory.

^d The numbers refer to the data that were used in addition to specific references to derive the map position (see following). This informa-

tion is included to supplement the information provided by the references. Numbers are underlined in the table to indicate that unpublished data submitted to the Committee was included in the analysis. 1: complete haplotypes in 114 and incomplete haplotypes in 338 interspecific backcross mice (see specific references and R.J. Oakey and M.F. Seldin, unpublished data); 2: complete haplotypes in 83-198 interspecific backcross mice (see specific references); 3: incomplete haplotypes in 38-74 interspecific backcross mice (see specific references); 4: complete haplotype data in 92-299 intraspecific backcross (unpublished data kindly provided by J. Todd); 5: included in nine overlapping three- or four-point crosses that derive from analysis of 125-500 meiotic events in each of multiple individual crosses (specific references); 6: haplotype data in 75 intraspecific backcrosses, W.N. Frankel, unpublished data; 7: CXB strains, see specific references and compiled by D.W. Bailey and currently maintained by B.A. Taylor; 8: AXB and BXA RI strains, see specific references and compiled formerly by M. Nesbitt and currently by B. Paigen; 9: BXD RI strains, see specific references and compiled by B.A. Taylor; 10: BXH RI strains, see specific references and compiled by B.A. Taylor; 11: AKXD RI strains, see specific references and compiled by B.A. Taylor; 12: AKXL, see specific references and compiled by B.A. Taylor; 13: three-point mapping data, see specific reference in table for data; 14: two-point mapping data, see specific reference in table for data.

Table 2. Mutant genes on Chr 3. Mapping data for these loci are available in Table 1. Descriptions and additional references can be found in Green (1989).

Symbol	Name	Phenotype
<i>cdm</i>	cadmium resistance	resistance to cadmium induced necrosis of testis
<i>coa</i>	cocoa	pigmentation of coat and eye
<i>de</i>	droopy ear	immature skeleton, disturbed mesenchyme
<i>ft</i>	flaky tail	stretched skin, small ears
<i>ma</i>	matted	defect of hair cuticle
<i>my</i>	blebs	multiple developmental defects
<i>op, csfm</i>	osteopetrosis	skeletal defects due to defect of macrophage growth factor
<i>rcm</i>	rostral cerebellar malformation	Purkinje and granule cells in anterior lobe of cerebellum are disorganized; balance defect
<i>soc</i>	soft coat	abnormal morphology of hair and epidermis
<i>spa</i>	spastic	tremor, stiffness, possible glycine receptor deficiency
<i>sut</i>	subtle grey	reduction in yellow pigment
<i>va</i>	varitint waddler	complex phenotype with behavioral, hearing, and pigmentation abnormalities

Table 3. Reference loci for Chr 3.

Locus	Map Position	RFLV Probe	PCR Product	PCR Variant	°C, Mg ⁺⁺ cycles	PCR Primer Sequences	
GBASE Fig.1							
<i>Car-1</i>	4	5	Venta et al. 1985	220 bp	<i>Hha</i> I site	59°, 1.5 40 cyc	1 - CAT TTC CGT ACGT CTG AAC TT 2 - GAG TCG GGA TCC AAA TCA CC
<i>Il-2</i>	—	8	Fiorentino et al. 1989	130 bp	(CAG) _n	55°, 1	1 - GTG CTC CTT GTC AAC AGC GCA 2 - CTC CTG TAG GTC CAT CAA CAG C
<i>Gba</i>	52	46	O'Neill et al. 1989	—	—	—	—
<i>Amy-1</i>	68	49	Wiebauer et al. 1985	190 bp	(CA) _n	50°, 2	1 - GAA CAT ATG TGT AAG TAA AAT GTA C 2 - GAT TTT AAT TCA TTA ATT AAG GGT TAG
<i>Adh-1</i>	83	67.5	Ceci et al. 1987	330 bp	—	55°, 2 40 cyc	1 - CTT ACT GGG TGA CAT AGA CG 2 - CCT TTC ATC CAT GTA CAT ATA C

These loci can be typed by Southern blot or by PCR. Map positions from the new composite map in Fig. 1 and from GBASE, the on-line database of The Jackson Laboratory, are given. The order of these loci is the same on both maps, and any gene on Chr 3 is expected to be within 20 or 30 cM of one of these markers. For additional sources of these probes, see "List of Mouse DNA Clones and Probes," J.T. Eppig, The Jackson Laboratory. Primer sequences

were kindly made available prior to publication by P.J. Venta (*Car-2*), J. Todd, C. Hearne (*Adh-1* and *Il-2*), and M. Meisler (*Amy-1*). PCR conditions are: temperature of annealing, °C; Mg⁺⁺, mM; cyc, number of cycles. The *Car-2* PCR product must be digested with *Hha* I to detect genetic variation among strains. The *Amy-1* primers amplify a *spretus* fragment which differs from the inbred strains tested; there is no amplified product from C57BL/6J.

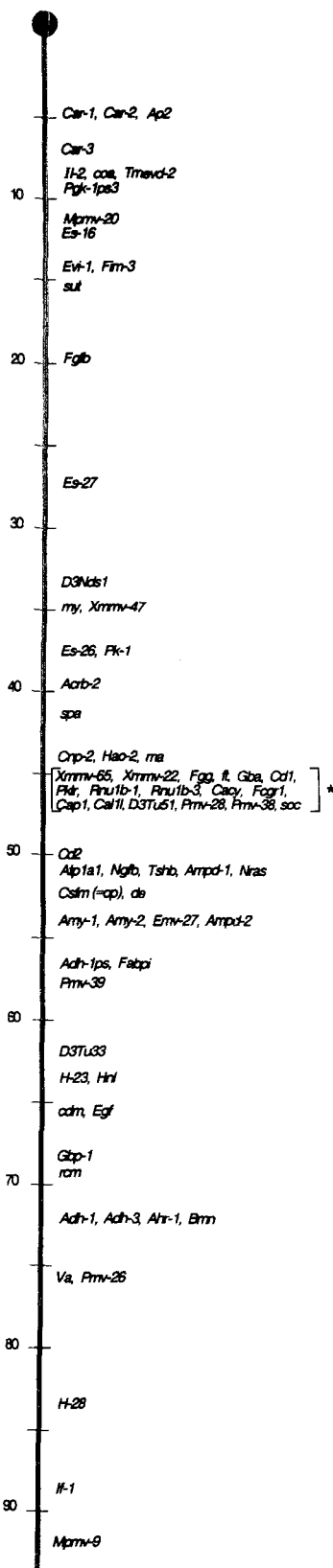


Fig. 1. Composite map of Chr 3. The map is based at the centromere (Davisson et al. 1976). Linkage data and locus names are provided in Table 1. Loci that have been assigned to Chr 3 but not regionally mapped can also be found in Table 1. *Loci within the bracket are located between 46–47 cM on the map; gene order not indicated.

The carbonic anhydrase gene cluster on proximal Chr 3 is also organized differently in human and mouse. The three human carbonic anhydrase genes are localized within 180 kb with the gene order *Car-1–Car-3–Car-2* (Tashian et al. 1990). In the mouse, *Car-3* is reported to be >1 cM distal to the other two genes (Beechey et al. 1990).

Mutant genes mapped to Chr 3

The spontaneous mutant *op*, osteopetrosis, has a recessive skeletal defect which includes a doomed skull and accumulation of bone which lacks marrow cavities (Green 1989). The close linkage of *op* and the *Csfm* gene encoding a macrophage colony stimulating factor led to the demonstration of a single base pair (bp) insertion in the coding region of *Csfm* in the *op* mutant (Yoshida et al. 1990). Other mutant genes which have been mapped to Chr 3 are listed in Table 2. With the exception of *op*, the molecular basis for these interesting phenotypes remains to be discovered.

Reference loci for Chr 3

Incorporation of a common set of reference loci into future crosses will greatly facilitate the growth of composite genetic maps by providing the basis for direct comparison among crosses. Towards this end, we recommend that the following five loci be included in future crosses: *Car-1*, *Il-2*, *Gba*, *Amy-1* and *Adh-1*. These loci span the chromosome, so that any gene on Chr 3 is expected to be within 20 or 30 cM of a marker. Cloned probes for these loci which detect RFLVs are available, and PCR primers which detect some genetic variation are available for four of these markers (Table 3). We are grateful to colleagues for providing unpublished primer sequences.

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