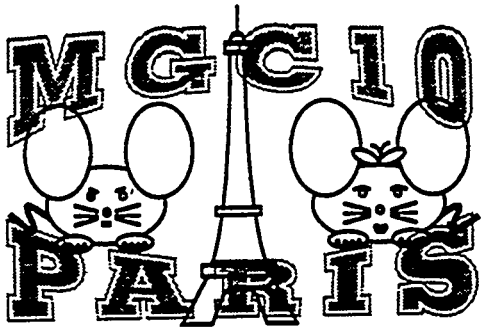
Cancer - 1
NO 107
Type 1 diabetes 137

10th International Mouse Genome Conference

October 7-10, 1996



10ème Conférence Internationale sur le Génome de la Souris

7-10 octobre 1996

Institut Pasteur - Paris, France

INSERM
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DISCLAIMER

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Program

Monday October 7

2:00 p.m.	Chromosome Committee Chairs and Co-Chairs
4:00	Nomenclature Committee
5:00	Registration at the Centre d'Information Scientifique
6:30	Welcome Party in the Main Lobby

Tuesday October 8

Morning Session: ***Mutation identification***

8:30 a.m.	Jean-Louis Guénet	*Welcome*
8:45	Jean Weissenbach	*The human genome project : from mapping to sequencing (KS1)*
9:30	David Beier	*Generation of a expressed sequence map of the mouse using Single-Strand Conformation Polymorphism (SSCP) mapping of cDNAs (69)*
9:45	Sally Camper	*Analysis of mutant mice reveals the hierarchy of transcription factors that control pituitary development (93)*
10:00	Kiran Chada	*The pygmy gene is an architectural factor involved in tumorigenesis (14)*
10:15	*Coffee*	
10:45	Maria Barbosa	*Positional cloning of the beige and Chediak-Higashi syndrome genes, homologous loci that regulate lysosomal protein trafficking (21)*
11:00	Karen Moore	*The beige gene is the murine orthologue of the human Chediak Higashi syndrome (37)*
11:15	Steve Brown	*Myosin VII mutations in the mouse: dissecting the function of a critical "hybrid" motor molecule in sensory hair cells (25)*
11:30	Nancy Jenkins	*Molecular genetic dissection of mouse unconventional myosin V (53)*
11:45	Eirikur Steingrimsson	*Molecular genetic analysis of b-HLH-Zip proteins related to* microphthalmia *(72)*
12:00 noon	*Lunch first service - Poster session - Computer Demonstrations*	
1:30 p.m.	*Lunch second service - Poster session - Computer Demonstrations*	

Afternoon Session: ***Genetic and Physical Mapping***

2:30	Margit Burmeister	*Comparative genetic and physical maps of mouse Chromosome 10 and human 19p13.3 (6)*
2:45	Roger Reeves	*From physical maps to sequence: Chr 16 Sequencing Consortium (7)*
3:00	Amir Zuberi	*Genetic and physical mapping of the H3 transplantation rejection locus on mouse Chromosome 2 (13)*
3:15	Kirsten Fischer Lindahl	*The end of H2: complete contig map and new class I gene subfamily (122)*
3:30	Christophe Chevillard	*Establishment of a physical map of the entire mouse* Igh *locus by the fragmentation of a complete YAC and partial BAC contig and the identification of a partial BAC contig (131)*
3:45	Robert Erickson	*A high resolution map and partial YAC of the Niemann-Pick C region of Chromosome 18 (57)*
4:00	Geneviève Gourdon	*CTG repeat changes in transgenic mice carrying the genomic DM region (202)*
4:15	*Coffee*	
4:45	Marie-Christine Simmler	*Analysis of a 94kb genomic sequence within the XIC region (17)*
5:00	Paul Denny	*Physical mapping of the mouse X chromosome (29)*
5:15	Yasushi Okazaki	*A genetic linkage map of the syrian hamster and localization of cardiomyopathy locus on chromosome 9qa2.1-b1 using RLGS spot-mapping (16)*
5:30	Jiri Forejt	*Toward positional cloning of the hybrid sterility 1* (Hst1) *gene on Chromosome 17 (88)*
5:45	Ryo Kominami	*Genetic analysis of T cell lymphoma induced by γ -ray irradiation (128)*

6:00	Michael Rhodes	*EUCIB: a high resolution microsatellite map of the mouse genome (35)*
6:15	Göran Levan	*Recent developments in the rat gene map and comparative mapping with the mouse (73)*
6:30	*Chromosome Committee meetings*	
7:30	*End of working sessions*	

Wednesday October 9

Morning Session: *Quantitative Inheritance and Multigenic Traits*

8:30 a.m.	Christos Ballas	*Quantitative genetics of cocaine induced stereotypy (30)*
8:45	Lorraine Flaherty	*QTLs and a possible mutation affecting contextual memory (109)*
9:30	Hiroshi Masuya	*Multigenic control of the anteroposterior axis formation in mouse limb development (65)*
9:45	Robert Williams	*QTLs controlling normal variation in neuron number and brain weight (15)*
10:00	Sharmila Basu	*Genetic basis of retinal phenotype modification in the ocular retardation mouse (4)*
10:15	*Coffee*	
10:45	Richard Mural	*Exon prediction, grail, and the challenge of automated annotation of DNA sequences (KS2)*
11:30	Anne Puel	*Mapping of the genes contributing to high and low antibody responsiveness in Biozzi mice (75)*
11:45	Rosemary Elliott	*At least two loci affect male sterility between* Mus macedonicus *and C57BL/6 (125)*
12:00 noon	*Lunch first service - Poster session - Computer Demonstrations*	
1:30 p.m.	*Lunch second service - Poster session - Computer Demonstrations*	

Afternoon Session I: *Quantitative Inheritance and Multigenic Traits*

2:30	Hélène Courvoiser	*A major quantitative trait locus influences hyperactivity in the WKHA rat (102)*
2:45	Marie Damon	*Inter-strain differences in the phenobarbital responsiveness of detoxication functions in mouse liver (135)*
3:00	George Carlson	*Modifiers of the phenotypes induced by Alzheimer amyloid precursor protein (APP) overexpression in transgenic mice (5)*
3:15	Edward Wakeland	*Functional dissection of SLE pathogenesis with congenic strains (80)*
3:30	Alan Attie	*Synergism between BTBR and B57BL/6 alleles produces an insulin resistance syndrome in (BTBR x B57BL/6) F1 mice (146)*
3:45	Evie Melanitou	*Construction of congenic lines segregating a Type 1 Diabetes resistance allele of mouse chromosome 6 in a NOD background (90)*
4:00	Benjamin A. Taylor	*Analysis of multigenic obesity in strain crosses (163)*
4:15	*Coffee*	

Afternoon Session II: *Informatics and Databases*

4:45	Mark Strivens	*Integrated Data Resources for Mouse Genetics (28)*
5:00	Janan Eppig	*Mouse Informatics: Future developments (47)*
5:15	Judith Blake	*The Mouse Genome Database - MGD (49)*
5:30	Greg Lennon	*The I.M.A.G.E. consortium mouse gene project (112)*
5:45	Michael Seldin	*On-line Mouse/Human homology database (147)*
6:00	*Chromosome Committee meetings*	
7:30	*End of working sessions*	

Thursday October 10

Morning Session: *Gene identification and New Technologies*

8:30 a.m.	Jun-ichi Asakawa	*A pilot study for the assessment of detectability of germ cell mutations in mice by computer assisted two-dimensional DNA analysis (103)*
8:45	Piero Carninci	*High-efficiency full-length cDNA cloning by biotinylated CAP trapper (18)*
9:30	John Schimenti	*Chromosomal Deletion Complexes in Mice by Radiation of Embryonic Stem Cells (201)*
9:45	Martine Cohen Salmon	*Molecular basis of deafness: Identification of cochlear-specific transcripts in a mouse cochlear substracted cDNA library: Understanding of the pathogeny of the Usher type IB syndrome (205)*
10:00	Christine Disteche	*Altered transcriptional regulation of Clnc4 associated with the different chromosomal location in* Mus spretus *and laboratory strains of mice (32)*
10:15	*Coffee*	
10:45	J. E. Martin	*SHIRPA - A standardised protocol for phenotypic assessment (140)*
11:00	Maja Bucan	*Phenotype- and genotype-based screen for novel ENU-induced mutations in the mouse (66)*
11:15	Monica Justice	*The* albino *(c) and* pink-eyed dilution *(p) regions of mouse Chr 7: models for mammalian functional genomics (74)*
11:30	Corine Vernet	*The* quaking *STAR gene family (145)*
11:45	Miriam Meisler	*Two models of inherited neuromuscular disease in the mouse (1)*
12:00 noon	*Lunch first service - Poster session - Computer Demonstrations*	
1:30 p.m.	*Lunch second service - Poster session - Computer Demonstrations*	

Afternoon Session: *Imprinting and Mutation Identification*

2:30	Josephine Peters	*A new imprinting region in distal mouse Chromosome 2 (203)*
2:45	Luisa Dandolo	*Imprinting and the* H19-Igf2 *locus (51)*
3:00	Bruce Cattanach	*A model for Angelman syndrome in the mouse (108)*
3:15	Neal Copeland	*Position effect mutations: the* W *and* Sl *loci (76)*
3:30	Hee-Sup Shin	*Combined requirement of Phospholipase C isozymes, beta1 and beta4, for postnatal growth and development of the mouse (94)*
3:45	Colin Fletcher	*Positional cloning of mouse* tottering*: a model for human epilepsy/ataxia (77)*
4:00	Johannah Doyle	*Comparative mapping of human chromosome 19 region and identification of a candidate gene for the mouse* tottering *mutation (116)*
4:15	*Coffee*	
4:45	Bernard Dujon	*The Yeast Genome Program: from the sequence to the functional analysis and beyond (KS3)*
5:00	Lisa Stubbs	*Mouse translocation mutants as tools for anchoring disease-related phenotypes to the mouse and human genetic and physical maps (114)*
5:15	Duska J. Sidjanin	*The major intrinsic protein* (Mip) *gene is a mutated gene in the* HFI *mouse (206)*
5:30	Stephen Hardies	Mus spretus*-specific LINE-1 hybridization probes detect introgression of* Mus spretus *alleles into* Mus musculus domesticus *(40)*
6:00	*General discussion: future meetings*	
7:30	*BANQUET*	

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Reviews

Mammalian Genome

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Meeting report: 10th International Mouse Genome Conference

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Ten years after hosting the First International Mammalian Genome Conference in Paris in 1986, Dr. Jean-Louis Guénet presided over the Tenth Conference at the Pasteur Institute, October 7–10, 1996. The 1986 conference was a satellite to the Human Gene Mapping Workshop and had approximately 50 attendees. The 1996 meeting was attended by 300 scientists from around the world. In the interim, the number of mapped loci in the mouse increased from 1,000 to over 20,000. The contributions of Dr. Guénet to this decade of progress include more than 60 published gene mapping reports, the development of interspecific backcrosses for high-resolution genetic mapping [1], and ongoing investigations of mouse models of human neuromuscular disorders.

This Conference was dedicated to the memory of Dr. George D. Snell (1903–1996). Dr. Snell received the Nobel Prize in 1980 for fundamental contributions to the field of immunogenetics. His pioneering work at The Jackson Laboratory provided the basis for understanding the graft rejection process and the development of human organ transplantation. Identification of individual genes contributing to the multifactorial inheritance of transplant tolerance was a formidable challenge in 1942, when only 8 linkage groups and 23 mouse loci had been identified [2]. Dr. Snell established the first localization of a histocompatibility gene, on what is now known as Chromosome (Chr) 17 [3]. The subsequent mapping of more than 40 histocompatibility loci has contributed significantly to the development of the mouse genetic map.

This brief review highlights a few of the more than 200 papers presented in Paris.

International Mouse Chromosome Committee meetings. Issues related to the generation of consensus genetic maps from multiple independent crosses and the development of new formats for presentation of genetic and physical data were discussed at this year's committee meetings. Software for on-line editing of the maps was introduced by The Jackson Laboratory informatics group. Henceforth, the Committee Maps will be continuously updated by committee members. The committee-generated consensus maps can be accessed electronically at (http://www.informatics.jax.org/mgd.html). *Mammalian Genome* will continue to publish a printed version on an annual basis, with the next issue scheduled for publication in August 1997.

Mutant generation and identification. The discovery of the lysosomal trafficking regulator gene *Lyst* responsible for the mouse beige mutation and the human Chediak Higashi syndrome was described by Maria Barbosa (University of Florida) and Karen Moore (Millenium). The two groups initially identified nonoverlapping cDNAs that were later shown to be 5′ and 3′ portions of the large *Lyst* transcript [4,5]. Identification of the calcium channel alpha subunit gene responsible for the allelic neurological mutations tottering and leaner was reported by Colin Fletcher (Frederick Cancer Center, Md.). This work was facilitated by a congenic strain that narrowed the nonrecombinant interval and the availability of two independent alleles. From comparative mapping, Johannah Doyle (Oak Ridge National Laboratory) predicted that the same gene would be mutated in the human disorders Familial Hemiplegic Migraine and Episodic Ataxia 2, a prediction that was recently confirmed [6]. A defect in the major intrinsic protein gene *Mip* was shown to be associated with cataract development in the *Hfi* mouse by Duska Sidjamin (Univ. Pennsylvania). Jonathan Stoye (Mill Hill) described the cloning of the *Fv1* gene responsible for resistance to the murine leukemia virus (MLV). This locus encodes a product with homology to retroviral *gag* genes, suggesting that endogenous mammalian retroviruses may serve unsuspected biological functions.

A screening program for identification of mutations affecting vision and hearing was described by Muriel Davisson (Jackson Laboratory). Seventeen new vision and 15 new vestibular variants have already been identified. A Mutagenesis Handbook Database with protocols, screening techniques, and updates on projects in progress is under development at the MRC, Harwell (http://www.mgu.har.mrc.ac.uk/MGU-welcome.html). Maya Bucan (Univ. Pennsylvania) described the screening of 1000 offspring of ENU mutagenized males, using a protocol that combines a whole genome screen for dominant behavioral traits with a hemizygous screen for novel mutations within the W^{19H} deletion on Chr 5.

Physical and genetic maps. A genetically anchored YAC framework map of the mouse X Chr was described by Paul Denny (MRC, Harwell) and represents the first step towards a complete physical map of this 160-Mb chromosome. Results of a large-scale sequence spanning 94 kb around the *Xist* locus were presented by Marie-Christine Simmler (Pasteur Institute), including identification of a unique transcript expressed in testis, and comparison of methods for sequence analysis. Substantial progress on the physical map and DNA sequencing of mouse Chr 16 was reported by Roger Reeves (Johns Hopkins, Baltimore, Md.). Sequence comparison with human Chr 21 led to the identification of genes not recognized by computer software. Analysis of a 2-Mb contig of the H2 major histocompatibility region revealed an ancient family of eight MHC class I genes (Kirsten Fischer Lindahl, University of Texas Southwestern, Dallas).

Genetic mapping of expressed sequence tags in the mouse complements DNA sequence analysis and provides access to cDNA libraries from early developmental time points and diverse tissues. The chromosomal mapping of >1000 brain cDNAs using SSCP to detect interstrain variation was reported by David Beier (Harvard Medical School, Boston). Greg Lennon (Lawrence Livermore, California) described the mouse EST project of the I.M.A.G.E. consortium. Forty thousand cDNAs from 22 cDNA libraries, including normalized libraries prepared by Bento Soares, have been sequenced at Washington University, St. Louis and deposited into dbEST (http://www-bio.llnl.gov/bbrp/image/image.html). The goal is to complete 400,000 sequences in 2 years, and the donation of additional mouse cDNA libraries for this project was requested. Systematic mapping of the mouse ESTs is not yet planned. The fact that 80% of the positionally cloned human disease genes are represented in the human EST database (51/62)

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indicates that completion of the mouse EST project will have a major impact on positional cloning.

New technology and resources. A novel two-step method for generating nested deletions around a locus was described by John Schimenti (Jackson Laboratory). After targeted integration of a negatively selectable marker in ES cells, cells are irradiated to generate random chromosomal deletions and grown in selective medium to isolate clones that have lost the marker. The length and extent of the resulting set of nested deletions can be determined by PCR assay for loss of heterozygosity, with ES cells derived from an F_1 hybrid between two inbred strains. The SHIRPA protocol for standardized evaluation of new mutants was described by J. E. Martin (Royal London Hospital). One person can evaluate 100 mice per day with 5-step protocol that includes assessment of body posture, spontaneous activity, transfer arousal, piloerection, startle response, gait, mobility, grip strength, pinna and corneal reflex, and response to toe pinch and handling. Adoption of a standardized protocol would provide objective, reproducible data and would facilitate comparison of mutant phenotypes described in different laboratories. CAP trapper, an efficient method for constructing full-length cDNA libraries on the basis of chemical introduction of a biotin group into the diol residue of the cap site followed by selection for full-length cDNA with streptavidin-coated magnetic beads, was described by P. Carninci (RIKEN, Japan).

Chromatin structure and gene regulation. On the basis of analysis of mild alleles at the Steel locus that are located at distances up to 180 kb from the MCGF structural gene, Neal Copeland (Frederick Cancer Center, Md.) proposed that long-distance position effects may be more common in the mammalian genome than has been recognized [7]. Bruce Cattanach (Harwell, UK) presented a mouse model for the Angelman and Prader Willi syndromes that affect imprinted loci; the relationship is supported by expression studies, comparative mapping, and phenotypic analysis. A new imprinted region of mouse Chr 2 was described by Jo Peters (Harwell, UK). Analysis of targeted mutations of *Pax1* by Rudi Balling (Munich) demonstrated that the severe spontaneous alleles of undulated that involve sizable deletions are likely to disrupt additional genes.

Rat and hamster genetic maps. A complete genetic map of the hamster genome was generated with the RLGS two-dimensional DNA technology by Yasushi Okazaki with Yoshihide Hayashizaki (RIKEN, Japan). The map was used to localize a cardiomyopathy locus and will facilitate genetic analysis of other hamster mutants [8]. Recent progress on the genetic map of the rat includes establishment of the database RATMAP (http://ratmap.gen.gu.se) and organization of a Rat Genetic Nomenclature Committee. Goran Levan (Goteborg University, Sweden) reported that 1600 genes have been mapped to rat chromosomes by linkage analysis and FISH, providing 85% coverage of the genome.

Informatics and databases. MRC Harwell's new web site (http://www.mgu.har.mrc.ac.uk/MGU-welcome.html) will provide genetic imprinting maps, chromosomal aberrations, searchable lists of mouse frozen embryo and mutant stocks, and a mutagenesis handbook (Mark Strivens, MRC Harwell). Judith Blake and Janan Eppig (The Jackson Laboratory) described the evolving status of the Mouse Genome Database, a comprehensive database for genetic and biological data (http://www/informatics.jax.org), and the Gene Expression Database for Mouse Development (GXD) (http://www.informatics.jax.org/gxd.html), a database containing images of embryonic expression data.

Quantitative trait analysis. Several groups reported progress in identification and refined localization of quantitative trait loci (QTLs). Phenotypes currently under investigation include obesity, diabetes, insulin resistance, hyperactivity in the rat, Alzheimer disease, brain and retinal development, antibody responsiveness, and psychomotor response to cocaine. Lorraine Flaherty (Albany, NY) identified loci affecting contextual memory in crosses between inbred strains and also in progeny of a mutagenesis experiment. Miroshi Masuya (Mishima, Japan) described two loci that modify the preaxial polydactyly phenotype of *Rim4* mutant mice as well as several classic limb mutants, suggesting an important role in formation of the anterioposterior axis of the limb. Ed Wakeland (U. Florida, Gainesville) described the phenotypes of four congenic lines generated by marker-assisted selection to separate the components of susceptibility to systemic lupus erythematosus (SLE) in the NZM2410 mouse strain.

Guest lectures. Jean Weissenbach (Pasteur Institute) reported on the current status of the human genome project, including the mapping of more than 15,000 ESTs by a consortium of American and European laboratories [9]. The genetic length of the CEPH-based human genetic map is 3700 cM. Mutations in microsatellite markers were found to be responsible for some apparent double recombinants. The future role of silicon chip-based mutation detection for genetic disorders was also discussed. Bernard Dujon (Pasteur Institute) described the challenge of deriving functional information from the complete sequence of the yeast genome [10]. This genome contains approximately 6000 protein coding genes, only ⅓ of which were recognized prior to the sequence analysis. The EUROFAN project, with 138 participating laboratories, will focus on functional analysis of the 2000 yeast genes whose function is currently unpredictable. Since a significant fraction of yeast genes have sequence similarity to mammalian genes, the functional genomics of the yeast will have profound implications for mammalian genetics. Richard Mural (Oak Ridge National Laboratory) described improvements in the GRAIL software for exon prediction, and demonstrated the powerful analytical and graphical programs now available for genomic sequence (11). He emphasized the importance of developing new methods of annotation that would enable investigators to contribute data from experimental analysis of gene function as additions to sequence entries in the databases.

Future meetings: The Eleventh Mouse Genome Conference, organized by Edward Wakeland (U. Florida, Gainesville), will be held from October 12 to 16 in St. Petersburg, Florida. Registration information is available electronically at the website (http://mcbio.med.buffalo.edu/11imgc/) and by email (dmiller@mcbio.med.buffalo.edu). Membership in the International Mammalian Genome Society (IMGS), which sponsors these Conferences, is open to all interested investigators. Special membership rates are available for conference registration and subscriptions to *Mammalian Genome*. To become a member of the IMGS, contact Darla Miller, IMGS Administrative Manager, Department of Molecular Biology, Roswell Park Cancer Institute, Buffalo, New York 14263, USA.

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REVIEW ARTICLE
The Role of the Laboratory Mouse in the Human Genome Project

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Introduction

The long-term goal of the human genome project is to identify and establish the function of each of the estimated 100,000 genes in the genome. The gene-discovery phase of the project is proceeding rapidly, via large-scale sequencing of genomic and cDNA clones. Establishing the functional roles for these genes is the challenge for the future. New methods have improved the power of the laboratory mouse to address questions of gene function and have attracted many investigators to the field. There has been dramatic progress in the efficiency of positional cloning of mutant mouse genes, induction of new mutants by chemical mutagenesis, targeted mutation of cloned genes by homologous recombination, strategies for analysis of polygenic traits, and comparative mapping of the human and mouse chromosomes. The contents of recent issues of the journals *Human Molecular Genetics, Nature Genetics,* and *Genomics* demonstrate the striking extent to which mouse genes and mouse mutants now occupy the attention of human geneticists. This paper provides a brief survey of recent developments with particular relevance to human genetics and the analysis of gene function.

Two useful reference books have recently been published. The excellent textbook by Silver (1995) provides historical background and an up-to-date account of current methods in mouse genetics. The third edition of *Genetic Variants and Strains of the Laboratory Mouse* (Lyon et al. 1996) provides comprehensive information, including descriptions of mouse strains, mutants, polymorphisms, and chromosome variants.

The Human Mouse Comparative Map

The key to establishing relationships between human and mouse genes is the comparative map. The human and mouse genomes contain ~150 conserved segments with nearly identical gene content. The identified conserved linkage groups now span almost 90% of the genome, and new mapping data are rapidly filling the gaps (Dietrich et al. 1995; Nadeau et al. 1995; Debry and Seldin 1996). Conserved linkage relationships make it possible to use gene identification and map position in one species to predict location in the other and to recognize true homologies between mouse mutants and human disease. A small portion of the Debry/Seldin comparative map, showing the short arm of human chromosome 2, is reproduced in figure 1. The 27 genes that have been mapped in both species fall into four conserved linkage groups that are located on mouse chromosomes 6, 11, 12, and 17. The indicated gene order is derived from meiotic mapping of the mouse genes, since most human genes are mapped cytogenetically and are not ordered within chromosome bands.

Physical mapping has provided high-resolution comparisons for a few regions of the human and mouse genomes. For example, the relative positions of six known genes in the 600-kb interval between LDHC and MYOD1 are clearly conserved (fig. 2). Large-scale comparative genomic sequencing of intervals like this one could result in gene discovery based on conservation of functional sequences. At an average spacing of 30 kb per gene, comparative sequencing might identify an additional 15–20 genes located between LDHC and MYOD1.

Mouse mapping has been facilitated by the development of cumulative mapping panels whose shared use is similar to that of the human CEPH pedigrees, except that linkage phase is known and every meiosis is informative. The widely used BSB and BSS backcrosses from the Jackson Laboratory, with 94 meioses each, have been typed for >1,500 genes and markers (Rowe et al. 1994). The European Community Interspecific Backcross contains 1,000 meioses (European Backcross Collaborative Group 1994). A large number of genes have been mapped on other backcrosses in the laboratories of Nancy Jenkins and Neal Copeland, and Michael Seldin and Christine Kozak. Consensus maps are compiled by the International Mouse Chromosome Committees and published as an annual supplement to the journal *Mammalian Genome*. On line

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0002-9297/96/5904-0005$02.00

IN SITU	HUMAN	Mouse	Map	Chr
2p25	ACP1	Acp1	S	12
2p25-p24	TPO	Tpo	15.0	12
2p25-p24	RRM2	Rrm2	7.0	12
2p25	ODC1	Odc	6.0	12
2p23	POMC	Pomc1	4.0	12
2p24.1	MYCN	Nmyc1	4.0	12
2p24-p22	ADCY3	Adcy3	S	12
2p24-p23	APOB	Apob	2.0	12
2p	SDC	Synd1	1.0	12
2p12	REG1A	Reg1a	S	12
2p22-p21	hSos1	Sos1	44.0	17
2p22-p21	PRKR	Prkr	S	17
2p22-p21	MSH2	Msh2	45.9	17
2p21	LHCGR	Lhcgr	46.5	17
2p22	XDH	Xdh	49.0	17
2p21	SPTBN1	Spnb2	12.0	11
2p13-p12	REL	Rel	13.0	11
2p13	ANX4	Anx4	39.0	6
2p13	TGFA	Tgfa	39.0	6
2p13	EGR4	Egr4	38.5	6
2p13-p12	MAD	Mad	35.0	6
2p12-p11.1	CTNNA2	Catna2	33.4	6
2p	SFTP3	Sftp3	32.0	6
2p12	CD8A	Cd8a	31.5	6
2p12	CD8B1	Cd8b	31.5	6
2p11	FABP1	Fabp1	30.0	6
2p12	IGK	Igk	30.0	6

Figure 1 Comparative gene map of the short arm of human chromosome 2 with four conserved linkage groups on mouse chromosomes 6, 11, 12, and 17. Mouse map positions are given in centimorgans from the centromere. The complete comparative map can be accessed electronically at http://www3.ncbi.nlm.nih.gov//Homology/. Adapted from Debry and Seldin (1996) with permission. S = syntenic, subchromosomal location not known.

sources of updated information for crosses, comparative human/mouse maps, and related data are listed in table 1.

Conserved Linkage and Isolation of the Usher *1B* Gene

An example of the practical value of the comparative chromosome map is provided by the isolation of the gene responsible for Usher syndrome1B, the most frequent cause of deaf-blindness in humans. Usher *1B* and the mouse deafness mutant *shaker1* had previously been mapped to a conserved linkage group on mouse chromosome 7 and human chromosome 11q13, suggesting that they might be caused by mutations in orthologous genes. The *shaker1* gene was isolated in 1995 by positional cloning. The mutated gene, *Myosin 7a,* encodes an unconventional myosin expressed in the hair cells of the inner ear (Gibson et al. 1995). Within a short time, mutations were also identified in the *MYO7A* gene of Usher patients (Weil et al. 1995), and the papers describing the mouse and human mutations were published back to back. This paradigm motivates much of the current effort in positional cloning of mouse mutants.

Positional Cloning of Spontaneous Mouse Mutants

The array of abnormal phenotypes associated with single-gene mutations in the mouse have fascinated biologists for decades and are now proving to be a valuable resource for identification of the underlying molecular disorders. Of the 600 spontaneous mouse mutants described in the new edition of the *Mouse Locus Catalog* (Doolittle et al. 1996), 70 have been cloned within the past few years, and >50 additional cloning projects are in progress. Several mouse mutants have led to the identification of homologous human disease genes (table 2).

The current success in positional cloning of mouse mutants can be attributed to the efficiency of high-resolution genetic mapping, the density of genetic markers, and the availability of physical mapping resources. Crosses segregating the mutant of interest and containing several thousand informative meioses can be readily generated, localizing the mutant genes to intervals of <500 kb. The 6,600 microsatellites developed by the Whitehead/MIT Genome Center have provided essential polymorphic markers for high-resolution genetic mapping of mutants (Dietrich et al. 1996). Many of these microsatellites are polymorphic between inbred strains, as well as in the more distantly related *Mus musculus castaneus* and *M. spretus.* Independent mapping of candidate genes contributed to many of the successful positional cloning projects, and knowledge of the human/mouse conserved linkage groups has been important for recognition of candidate genes. Physical resources for positional cloning in the mouse include >10 genome equivalents of YAC clones, as well as P1 and bacterial artificial chromosome libraries that can be screened commercially. The mouse expressed sequence tag (EST) project at Washington University plans to generate 5′ end sequences from 200,000 to 400,000 cDNAs from embryonic and adult tissues. By focusing on coding sequence and on tissues and embryonic stages not readily available from human sources, it is anticipated that many novel genes will be identified. Mapping these ESTs in mouse and man would enhance their value for positional cloning efforts in both species.

A number of interesting mouse genes have been isolated from insertional mutants caused by random integration of microinjected transgenes (table 3). The transgene provides a probe for isolation of the disrupted gene (Meisler 1992; Meisler et al. 1996). Approximately 3% of transgene insertion sites are associated with visible, viable mutations, and another 10% result in prenatal lethality. Although some transgene insertion sites have deletions that may span several centimorgans (Keller et al. 1994), insertions have already facilitated the cloning of several novel genes.

Chemical Mutagenesis and Genetic Dissection of Complex Pathways: The Clock Mutation

Most of the classical mouse mutants arose spontaneously or were induced by radiation. The success of posi-

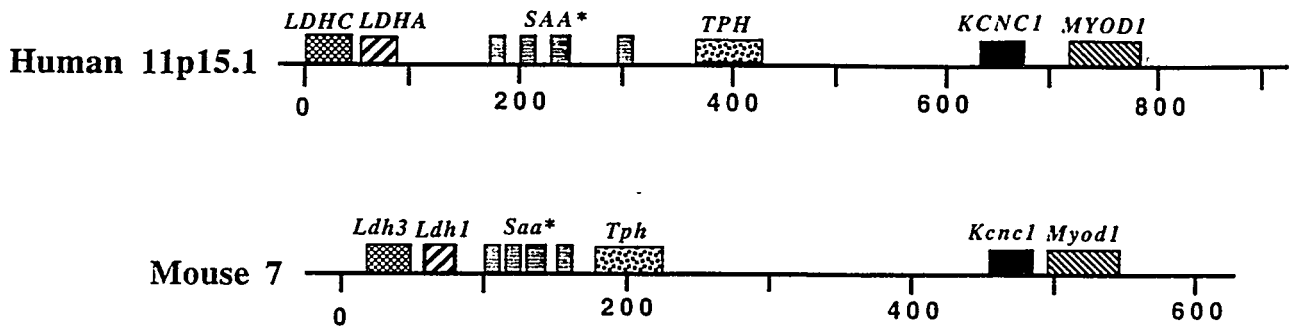

Figure 2 Comparative physical map of genes in the interval between *LDHC* and *MYOD1* on human chromosome 11p15.1 and proximal mouse chromosome 7. The human map was derived by partial digest mapping of overlapping YAC clones (Sellar et al. 1994). The mouse map was determined by long-range restriction mapping of genomic DNA (Stubbs et al. 1994). Box width represents the interval to which the gene was mapped, not the size of the gene. Distances are given in kilobases. The clustering of human SAA1, SAA2, SAA3, and SAA4 (indicated by asterisks [*]) was recently shown to be conserved in the mouse (de Beer et al. 1996)

tional cloning has regenerated interest in mutagenesis to provide genetic access to novel pathways. An exciting indicator of future possibilities was the recent identification of the *clock* mutation affecting circadian rhythm. Vitaterna et al (1994) monitored the wheel-running behavior of 304 offspring of males mutagenized with N-ethyl, N-nitrosourea (ENU). One animal had an extended periodicity that was 6 SD units above the mean. Homozygotes for this mutation demonstrate a complete loss of periodicity when maintained in constant darkness. This is the first mammalian gene controlling diurnal rhythms to be identified, and it paves the way for genetic identification of novel mammalian genes affecting other behavioral and regulatory processes. Positional cloning of the *clock* gene is in progress.

Application of chemical mutagenesis to the mammalian genome required the development of mutagenesis protocols with high mutation rates (on the order of 10^{-3} per locus per generation), to permit identification of mutants in any locus by analysis of a few thousand animals. ENU has one of the highest in vivo mutation rates (Russell et al. 1979). Use of ENU was pioneered by Bill Dove and colleagues to generate models of phenylketonuria (McDonald et al. 1990). It has also been applied to the generation of new alleles of existing mutants such as the circling mutant kreisler (Cordes and Barsh 1994). High mutation rates are also obtained with the mutagen chlorambucil (Flaherty et al. 1992), which produces small deletions that may be amenable to cloning by representational difference analysis (Baldocchi et al. 1996). Translocations induced by alkylating agents provide physical markers that facilitate cloning (Rutledge et al. 1986; Woychik et al. 1990). Preliminary studies indicate that as many as 15% of induced translocations are accompanied by easily detectable phenotypes (W. Generoso and L. Stubbs, personal communication).

The variety of chemical mutagens now at our disposal is likely to initiate a renaissance of interest in induced mutations that will enrich our knowledge of basic biology and human genetic disease. Potential targets for mutagenesis screening include the visual, immune, and neurological systems. A pilot project for the production and distribution of ENU mutagenized male mice or their offspring to interested investigators is under discussion (M. Bucan, personal communication). The combination of chemical mutagenesis with positional cloning should permit the isolation of

Table 1

On-Line Information Sources

Source	Uniform Resource Locator
Mouse Genome Database	http://www.informatics.jax.org/mgd.html
Mouse Locus Catalog	
Chromosome Committee reports	
Debry/Seldin Human/mouse homology map	http://www3.ncbi.nlm.nih.gov//Homology/
Jackson Laboratory Backcross	http://www.informatics.jax.org/crossdata.html
EUCIB Backcross	http://www.hgmp.mrc.ac.uk/MBx/MBxHomepage.html
Mouse genetic nomenclature	http://www.informatics.jax.org/nomen/
Mouse genetic and physical maps	http://www.genome.wi.mit.edu/cgi-bin/mouse/index

Table 2

Recently Cloned Spontaneous Mouse Mutants and Homologous Human Disorders

Mouse Mutant (Symbol)	Human Disorder	Gene Product	Conserved Linkage Group	
			Human	Mouse
beige (*bg*)	Chediak Higashi syndrome	Vesicle protein, WD40 domain	1q44	13
diabetes (*db*)	...	Leptin hormone receptor		4
dominant white spotting (*W*)	Piebaldism	MCGF receptor	4q12	5
dwarf, Snell (*dw*)	Panhypopituitarism	Pit-1 transcription factor	3p11	16
extra toes (*Xt*)	Cephalopolysyndactyly	GLI3 transcription factor	7p13	13
Hypodactyly (*Hd*)	...	Hoxal3	7p14	6
kidney and retinal degeneration (*Krd*)	Renal coloboma syndrome	Pax2 haploinsufficiency	10q25	19
motor endplate disease (*med*)	...	Sodium channel Scn8a	12q13	15
mottled (*mo*)	Menkes disease	ATP7A	Xq13	X
multiple intestinal neoplasia (*min*)	Adenomatous polyposis coli	APC	5q21	18
obesity (*ob*)	...	Leptin, peptide hormone	7q32	6
ocular retardation (*or*)	...	Chx10 homeobox gene	(*14q24*)	12
osteopetrosis (*oc*)	...	Transporter, 12 TM type	11q13	19
reeler (*rl*)	...	Reelin, EGF motif protein	(*7q21-36*)	5
retinal degeneration slow (*rd2*)	Retinitis pigmentosa	Peripherin 2	6p21-cen	17
shaker1 (*sh1*)	Usher 1B	Myosin VIIA	11q13	7
small eye (*sey*)	Aniridia	Pax6	11p13	2
Snell's Waltzer (deafness) (*sv*)	...	Myosin VI	(*6p12-q12*)	9
spasmodic (*spd*)	Hyperekplexia	Glycine receptor alpha 1 subunit	5q32	11
spastic (*spa*)	...	Glycine receptor beta subunit	4q32	3
splotch (*sp*)	Waardenberg syndrome 1	Pax1	20p11	2
staggerer (*sg*)	...	RORa, retinoic acid receptor		9
testicular feminization (*tfm*)	Androgen insensitivity	Androgen receptor	Xq11-q12	X
tight skin (*tsk*)	Marfan	Fibrillin 1	15q21.1	2
trembler (*tr*)	Charcot-Marie-Tooth IA	Peripheral myelin protein	17p12-11.2	11
weaver (*wv*)	...	Potassium channel GIRK2	21q	16
X-linked immune deficiency (*xid*)	Agammaglobulinemia	Bruton tyrosine kinase	Xq21-q22	X

Note.—Predicted human locations that have not been confirmed experimentally are italicized in parentheses. Ellipses (...) indicate human disorder not identified.

novel genes affecting any phenotype of interest for which a robust assay can be developed. Analysis of chemically induced mutants may be as important in the future as spontaneous mutations have been in the past.

Targeted Mutation by Homologous Recombination: Disease Models and Gene Function

The ability to introduce specific alterations into the germ line of the mouse is one of the most dramatic developments in modern biology. This technique has been used to create precise molecular models for human single-gene disorders such as cystic fibrosis and Tay Sachs disease (table 4); twenty-six disease-related targeted mutations are included in the recent review by Majzoub and Muglia (1996). Although the physiological abnormalities in the mouse are frequently not identical to those in human patients, these mouse models can be extremely valuable for testing interventions (Searle et al. 1994), evaluating constructs for gene therapy (Cox et al. 1993; Phelps et al. 1995), and identifying modifier loci that influence disease severity (Rozmahel et al. 1996). Several hundred targeted knockouts of individual genes have also been generated to provide basic information about in vivo functions (Bronson and Smithies 1994). Some unanticipated results of knockout experiments include the discovery of the role of the *Src* oncogene in tooth formation (H. Varmus, personal communication) and the importance of the epithelial sodium transport gene for newborn lung function (Hummler et al. 1996).

Contiguous Gene Syndromes and "Designer Deletions"

Deletions are a common source of human inherited disorders. Deletions that were induced by radiation and chemicals have been used to identify regions of imprinting in the mouse genome (Cattanach and Jones 1994). In 1995, a general method for inducing deletions 3 or 4 cM in length with predetermined ends was described (Ramirez-Solis et al. 1995). The procedure in-

Table 3

Mouse Mutants Cloned from Transgene Insertion Sites

Mouse Mutant (Symbol)	Phenotype	Gene Product	Conserved Linkage Group	
			Human	Mouse
dystonia muscularis (*dt*)	Muscle weakness	Dystonin, BPAG1	6p12-p11	1
Fused (*Fu*)	Skeletal, neurological	Transcription factor	(*16p13-21*)	17
Hβ58	Early development	Yeast homolog		10
limb deformity (*ld*)	Fused radius/ulna	Formin, structural protein	15q13.3-q14	2
microopthalmia (*mi*)	Small eyes, deaf	Transcription factor MITF	3p14.1-p12.3	6
motor endplate disease (*med*)	Ataxia, paralysis	Sodium channel Scn8a	12q13	15
polycycstic kidney disease	Kidney disease	TPR repeat protein	(*14q11*)	14
Pygmy (*pg*)	Small size	HMGI-C	(*12q13-14*)	10
reeler (*rl*)	Ataxia	Reelin	(*7q21-36*)	5

Note.—Predicted human locations that have not been confirmed experimentally are italicized in parentheses.

volves four gene-targeting events by homologous recombination in embryonic stem cells. This method will make it possible to produce precise mouse models of contiguous gene syndromes. Induced deletions can also be used in combination with chemical mutagenesis to identify functional genetic elements within a specified deleted interval.

Combination of Deletions with Mutagenesis for Functional Analysis of Defined Chromosome Intervals

An efficient strategy for identification and localization of functional genetic elements is to cross chemically mutagenized mice with mice carrying induced deletions, so that recessive mutations located within the deletion are visible in the offspring. This approach was pioneered by Gene Rinchik at the Oak Ridge National Laboratory, using a radiation-induced deletion around the albino locus (Rinchik et al. 1990). Analysis of 3,000 offspring of ENU-treated males resulted in identification of many distinct functional elements within the deletion (Rinchik et al. 1993*a*, 1993*b*). This method eliminates the need for a genome scan to chromosomally map each new mutant and can generate multiple alleles of each locus that include gain of function as well as loss of function. Saturation mutagenesis with ENU could in principle identify all of the functional elements within a target region, although there is some evidence of differential gene sensitivity to mutagenesis. Several efforts to apply this approach are in progress; regions for which dense transcript maps are already available would be particularly productive targets.

Tumor-Suppressor Genes and Loss of Heterozygosity (LOH)

Detection of LOH during tumorigenesis is facilitated in the mouse because large numbers of independent tumors can be generated on a uniform heterozygous genetic background with readily distinguishable alleles. The wild mouse–derived inbred strains SPRET/Ei and CAST/Ei carry unique alleles that differ from other laboratory strains at most microsatellite markers (Dietrich et al. 1994). All heterozygous F1 mice produced from

Table 4

Molecular Models of Human Inherited Disorders Generated by Homologus Recombination

Human Disorder	Targeted Gene	Mouse Phenotype
Cystic fibrosis	Cystic fibrosis transmembrane receptor	Gastrointestinal and pancreatic abnormalities
Neurofibromatosis 1	NF1	Neural crest–derived and myeloid tumors
Hemophilia A	Factor VIII	Clotting defect
Tay Sachs Disease	β-hexosaminidase A	Neuronal storage defect
Niemann-Pick Type A	Acid sphyingomyelinase	Neurodegeneration
Gaucher's Disease	β-glucocerebrosidase	Glucocerebroside storage
Retinoblastoma	RB phosphoprotein	Pituitary tumors
Glycogen-storage disease	Glucose 6 phosphatase	Glycogen storage; hepatomegaly, enlarged kidney
Lipid-storage diseases	Sphingolipid activator protein (SA)	Sphingolipid storage disease, leukodystrophy

crosses between laboratory strains and CAST/Ei or SPRET/Ei are genetically identical. Multiple tumors can be generated in each mouse by treatment with carcinogens or crossing with transgenic mice with constitutive expression of an activated oncogene. This approach has been used to identify LOH in a variety of tumor types, including insulinomas (Dietrich et al. 1994; Parangi et al. 1995), hepatocarcinomas (Davis et al. 1994; Manenti et al. 1995), and lung tumors (Herzog et al. 1995). LOH can be detected using microsatellite markers spanning the genome or by the restriction landmark method (Ohsumi et al. 1995). Sets of microsatellite markers with resolution of 10 cM and 30 cM, as well as a genotyping service, are available from Research Genetics. Analysis of LOH in hybrid mice holds great promise for the identification of genes involved in the complex progression from hyperplasia to tumor.

Gene Interaction and Complex Traits

The same factors that facilitate detection of LOH in hybrid mice also make the mouse a powerful system for identification of quantitative trait loci (QTLs). John Todd pioneered the use of microsatellites and mapped four loci contributing to insulin dependent diabetes (Idd) (Todd et al. 1991). The mapping of QTLs associated with hypertension in the rat by Eric Lander and his colleagues was another early demonstration of this approach to an important human disease (Jacob et al. 1991). Polygenic interstrain differences in cancer susceptibility and aging have also been identified. Some of the mouse QTLs appear to correspond with independently mapped human QTLs (Debry and Seldin 1996).

Interstrain variation has been used to map quantitative modifiers of major disease genes such as cystic fibrosis (Rozmahel et al. 1996) and colon cancer (Dietrich et al. 1993); these modifiers may play a role in the variable course of the human diseases. Although efficient strategies for positional cloning of QTLs will require further development, several interesting candidate genes have been identified within QTL intervals, including the defective Fc receptor near the Idd3 locus affecting autoimmune diabetes (Prins et al. 1993) and the phospholipase gene as a potential modifier of colon cancer (MacPhee et al. 1995). Once identified, candidate genes can be rigorously evaluated by a variety of methods.

Crosses between mutant mice can be used to examine directly the combinatorial effects of mutations in individual genes. The effects of quantitive changes in expression of *ApoE, ApoA1,* and the LDL receptor on atherosclerosis have been examined in crosses between overexpressing transgenic mice and mice carrying targeted "knockout" mutations (Smithies and Maeda 1995). A direct correlation between blood pressure and plasma levels of angiotensinogen was demonstrated using combinations of mutants (Smithies and Maeda 1995). Combining mutations in *Pax1* and *Pdgfra* produced spina bifida, a novel phenotype found in neither single mutation (Helwig et al. 1995). Experimental manipulations of this type are likely to be important in the future investigation of complex physiological and developmental processes.

Comparative Sequencing and Gene Discovery

In the course of the 160 million years of separate evolution of the human and mouse genomes, functional sequences have been highly conserved, and nonfunctional sequences have diverged with a mutation rate of roughly 1% per million years. As a result, direct comparison of genomic sequence can distinguish exons and other functional elements from nonfunctional regions. The comparative maps are a guide to appropriate conserved regions for sequence comparison, such as that shown in figure 2. The largest published comparative DNA sequence is a 100-kb region of T-cell receptor gene family (Koop and Hood 1994); the unusually high level of conservation in intergenic regions of this gene family may be related to the history of gene duplications in the region. Comparative sequencing was used successfully to identify the intensively sought gene *DMAHP* (DM locus–associated homeodomain protein) that is located downstream of the expanded trinucleotide repeat in myotonic dystrophy (Boucher et al. 1995). Altered expression of *DMAHP* may be responsible for some of the clinical features of this disorder.

One unexpected result of comparative sequencing has been the discovery of conserved sequence blocks several kilobases in length that do not contain conserved protein-coding information (Hood et al. 1993; Griffith et al. 1996; R. Reeves, personal communication). Potential roles for these conserved, noncoding sequences include generating RNA products, contributing to chromosome function, or regulating gene expression as enhancers or locus control regions.

Conclusions

We are entering an exciting era of interaction between human and mouse genetics. Tens of thousands of novel human genes will be identified by large-scale genomic and cDNA sequencing during the next few years. Analysis of spontaneous and induced mouse mutations will play a major role in characterization of gene function, and experimental manipulation of the mouse will contribute to analysis of gene interaction and the inheritance of polygenic phenotypes. Comparative sequencing of human and mouse genomic DNA could play an important role in gene discovery. The mouse EST project will contribute to identification of genes expressed in

stages of development and in tissues not readily obtainable from human sources.

Acknowledgments

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