GENOMICS 28, 179–183 (1995)

Murine Chromosomal Location of Five bHLH-Zip Transcription Factor Genes

EIRÍKUR STEINGRÍMSSON,* MICHÈLE SAWADOGO,† DEBRA J. GILBERT,* ANTONIS S. ZERVOS,‡ ROGER BRENT,‡ MICHAEL A. BLANAR,§ DAVID E. FISHER,¶ NEAL G. COPELAND,* AND NANCY A. JENKINS*,[1]

*Mammalian Genetics Laboratory, ABL-Basic Research Program, NCI-Frederick Cancer Research and Development Center, Frederick, Maryland 21702; †Department of Molecular Genetics, The University of Texas M. D. Anderson Cancer Center, 1515 Holcombe Boulevard, Houston, Texas 77030; ‡Department of Genetics, Harvard Medical School and Department of Molecular Biology, Massachusetts General Hospital, Boston, Massachusetts 02114; §Department of Cardiovascular Molecular and Cellular Biology, Mail Code K14-01, Bristol-Myers Squibb Pharmaceutical Research Institute, P.O. Box 4000, Princeton, New Jersey 08543-4000; and ¶Dana Farber Cancer Institute, 44 Binney Street, Boston, Massachusetts 02115

Received February 23, 1995; accepted May 12, 1995

The genes for the bHLH-Zip transcription factors *Tfap4, Mxi1, Tcfeb, Usf1,* and *Usf2* have been mapped in mouse by interspecific backcross analysis. *Mxi1, Usf1,* and *Usf2* have been mapped previously by *in situ* hybridization, but their positions on the meiotic linkage map had not been determined. The other two genes have not previously been mapped in mouse. These transcription factors belong to a growing family of transcriptional regulators, some of which are known to form a complex network of interacting proteins that control cell proliferation and apoptosis. As expected, based on mapping studies of other bHLH-Zip genes, these loci were well distributed among mouse chromosomes. In addition, some of the probes used in this study detected multiple, independently segregating loci, suggesting the possible existence of additional family members or species-specific pseudogenes.

INTRODUCTION

Transcription factors of the basic–helix–loop–helix–zipper (bHLH-Zip) family have been isolated in many different studies of cell-specific transcriptional control in eukaryotes. Proteins of this family contain a basic domain, used for DNA binding, and HLH and Zip domains, both used for oligomerization. Although several of the family members have been shown to contain transcriptional regulatory domains and nuclear localization signals, sequence similarity usually does not extend outside the bHLH-Zip domains.

As part of our effort to understand better the physiological functions of bHLH-Zip proteins, we have determined the murine chromosomal location of five family members, *Tfap4, Mxi1, Tcfeb, Usf1,* and *Usf2*. AP4 was identified as a human cellular protein that binds to a CAGCTG binding sequence in the SV40 enhancer and activates viral late gene transcription (Mermod *et al.,* 1988; Hu *et al.,* 1990). AP4 can also act synergistically with AP1 to activate both hMTIIA and SV40 late gene transcription (Mermod *et al.,* 1988). TFEB was isolated from a human B-cell cDNA library using a binding sequence from the adenovirus major late promoter (Carr and Sharp, 1990). USF was initially identified as a human cellular factor that binds to the upstream element CACGTG of the adenovirus major late promoter and stimulates transcription (Sawadogo and Roeder, 1985; Carthew *et al.,* 1985, 1987; Gregor *et al.,* 1990). It has been implicated in the expression of tissue-specific genes such as human growth hormone (Peritz *et al.,* 1988), mouse metallothionein I (Carthew *et al.,* 1987), rat γ-fibrinogen (Chodosh *et al.,* 1987), and Xenopus TFIIIA (Scotto *et al.,* 1989). Later, USF was shown to consist of two factors, USF1 and USF2 (Sawadogo *et al.,* 1988), both of which are present in many different cell types (Carthew *et al.,* 1987; Sirito *et al.,* 1994). USF2 was also isolated from a HeLa-cell expression library as a protein (referred to as FIP) that interacts with the bZip protein FOS (Blanar and Rutter, 1992). *In vitro* experiments showed that this protein binds to the CACGTG sequence of the adenovirus major late promoter and forms stable dimers with FOS only when the zipper domain of USF2 is present. MXI1 was isolated from a HeLa cell library, using a yeast interactive cloning system, as a protein that interacts specifically with MAX (Zervos *et al.,* 1993). This protein binds the

[1] To whom correspondence should be addressed at the Mammalian Genetics Laboratory, ABL-Basic Research Program, NCI-Frederick Cancer Research and Development Center, P.O. Box B, Bldg. 539, Frederick, MD 21702. Telephone: (301) 846-1260. Fax: (301) 846-6666.

0888-7543/95 $12.00

TABLE 1

Loci Mapped in Interspecific Backcross Mice

Locus	Probe	Enzyme	Fragment sizes[a] C57BL/6	Fragment sizes[a] *M. spretus*
Tfap4	pT7β/AP-4; 1.5-kb *Hin*dIII–*Bam*HI fragment of human cDNA	*Hin*cII	4.7, 2.7, 0.96	3.4, 2.4,[b] 0.96
		*Bgl*I	15.5, 9.4, 5.2, 1.3	15.5, 11.5, 1.3
Mxi1	pMXI.1; 2.4-kb *Eco*RI fragment of human cDNA	*Eco*RI	8.6, 5.4, 3.0, 2.4	4.6, 3.5
Tcfeb	pBS-TFEB; human cDNA fragment	*Bgl*I	4.9, 2.6	5.2, 2.4[b]
	T12; 188-bp genomic mouse PCR fragment	*Sac*I	6.7	5.8
Usf1	p43MO12; 650-bp mouse cDNA fragment	*Eco*RI	9.4, 6.3, 3.3	9.4, 6.3, 3.6
	pW11ΔX; ~1-kb *Pvu*II fragment of a mouse cDNA, 3′ untranslated region	*Xba*I	8.0, 6.8, 4.8, 3.1	7.8, 5.3, 4, 3.2
Usf2	pBAT9-FIP; 0.9-kb *Eco*RI fragment of human cDNA	*Xba*I	5.3, 4.6, 2.3	9.4, 5.3, 3.8[b]
	pM2; 1.7-kb mouse cDNA fragment	*Hin*dIII	23.0, 16.0, 9.4	9.4, 4.4

[a] The underlined restriction fragment sizes indicate the restriction fragments typed in the backcross analysis.
[b] The two underlined fragments cosegregated.

MYC–MAX consensus site as a dimer with MAX; however, it does not seem to contain a transcriptional activation domain and may therefore be involved in sequestering MAX proteins in the cell to limit the number of functional MYC–MAX heterodimers (Zervos *et al.*, 1993).

MATERIALS AND METHODS

Mice. C57BL/6J and *Mus spretus* mice were maintained at the NCI-Frederick Cancer Research and Development Center. The *M. spretus* mice used for the interspecific backcrosses were a gift from E. M. Eicher (The Jackson Laboratory, Bar Harbor, ME). The ((C57BL/6J × *M. spretus*)F_1 × C57BL/6J) interspecific backcross was performed at the NCI-FCRDC. Various subsets from 205 N_2 progeny were used for mapping.

Probes. The probes used to map these transcription factors are listed in Table 1. All probes were human cDNA probes, except the *Usf1* probes and the *Usf2* probe pM2 which are mouse cDNA probes, and the PCR generated *Tcfeb* probe, which was made from a mouse genomic λ clone containing the gene (E.S., N.G.C., and N.A.J., unpublished results). The primers used for generating the *Tcfeb* probe are 5′TGAACATGGCTGAGCTGGCCCAG3′ and 5′GTGGCTGAAGTCCAGGTGATGGAA3′, corresponding to nucleotides 1320 through 1342 and 1507 through 1474, respectively, of the human *Tfeb* cDNA (Carr and Sharp, 1990).

The map locations in our interspecific backcross of marker loci used to position *Usf1-rs1* on chromosome 8 and *Mxi1* on chromosome 19 are reported for the first time in this paper. These loci and their corresponding probes are as follows: A 1.43-kb mouse *Lpl* cDNA probe (Kirchgessner *et al.*, 1989) detected 5.0-, 4.4-, 3.6-, 0.7-, and 0.5-kb *Taq*I fragments in C57BL/6J DNA and 10.5-, 5.0-, 2.8-, 0.8-, 0.6-, and 0.5-kb *Taq*I fragments in *M. spretus* DNA. The 10.5-, 2.8-, 0.8-, and 0.6-kb *M. spretus*-specific fragments all cosegregated and were used to follow the segregation of the *Lpl* locus in backcross mice. A 5.8-kb genomic clone containing the human *Adra2a* gene (Kobilka *et al.*, 1987) detected 6.9-, 5.8-, and 2.3-kb *Hin*dIII fragments in C57BL/6J DNA and 8.2-, 6.9-, 5.8-, and 2.3-kb *Hin*dIII fragments in *M. spretus* DNA. The 8.2-kb fragment was used to follow the segregation of the *Adra2a* locus.

The map locations in our interspecific backcross of several additional marker loci used to position the bHLH-Zip loci have been previously reported as follows: chromosome 1, *At3*, *Spna1*, and *Tgfb2* (Dickinson *et al.*, 1990); chromosome 2, *Acra* and *Cas1* (Siracusa *et al.*, 1990); chromosome 7, *Tgfb1* (Dickinson *et al.*, 1990), *Gpi1* (Siracusa *et al.*, 1991), and *Rras* (Law *et al.*, 1993); chromosome 8, *Scvr* (Freeman *et al.*, 1990); chromosome 16, *Prm1*, *Igl*, and *Smst* (Bressan *et al.*, 1991); chromosome 17, *Cak*, *Tic1/Pim2*, and *Vav* (Perez *et al.*, 1994); chromosome 19, *Bpag2* (Copeland *et al.*, 1993a); and chromosome X, *Pgk1* and *Btk* (Rawlings *et al.*, 1993).

DNA isolation and Southern blot analysis. High-molecular-weight genomic DNAs were prepared from frozen mouse tissues as described (Jenkins *et al.*, 1982). Restriction endonuclease digestions, agarose gel electrophoresis, and Southern blot transfers and hybridizations were performed as described (Jenkins *et al.*, 1982). All blots were prepared with Zetabind nylon membrane (Cuno).

Probes for the *Tfap4*, *Mxi1*, *Tcfeb*, *Usf1*, and *Usf2* loci were labeled with [α-^{32}P]dCTP using a Prime-It II random priming kit (Stratagene). Washing was carried out to a final stringency of 0.5×–1.0× SSCP, 0.1% SDS at 65°C.

Statistical analysis. Statistical analysis of the recombination frequencies from the results of the interspecific backcross was performed as described (Green, 1981) using the computer program SPRETUS MADNESS. Gene order was determined by minimizing the number of recombination events required to explain the allele distribution patterns ("pedigree analysis") (Avner *et al.*, 1988).

RESULTS AND DISCUSSION

The murine chromosomal locations of the bHLH-Zip transcription factor genes *Tfap4*, *Mxi1*, *Tcfeb*, *Usf1*, and *Usf2* were determined by interspecific backcross (IB) analysis using progeny derived from matings of ((C57BL/6J × *M. spretus*)F_1 × C57BL/6J) mice. This IB mapping panel has been typed for over 1800 loci that are well distributed among all of the mouse autosomes and the X chromosome (Copeland *et al.*, 1993b). DNA from C57BL/6J and *M. spretus* mice was digested with several restriction enzymes and analyzed by Southern blot hybridization for informative restriction fragment length polymorphisms (RFLPs), using each of the bHLH-Zip probes listed in Table 1. Only *M. spretus*-specific RFLPs were followed in the backcross mice since all backcrosses were to C57BL/6J and C57BL/6J-specific RFLPs could be followed only by hybridization intensity. The strain distribu-

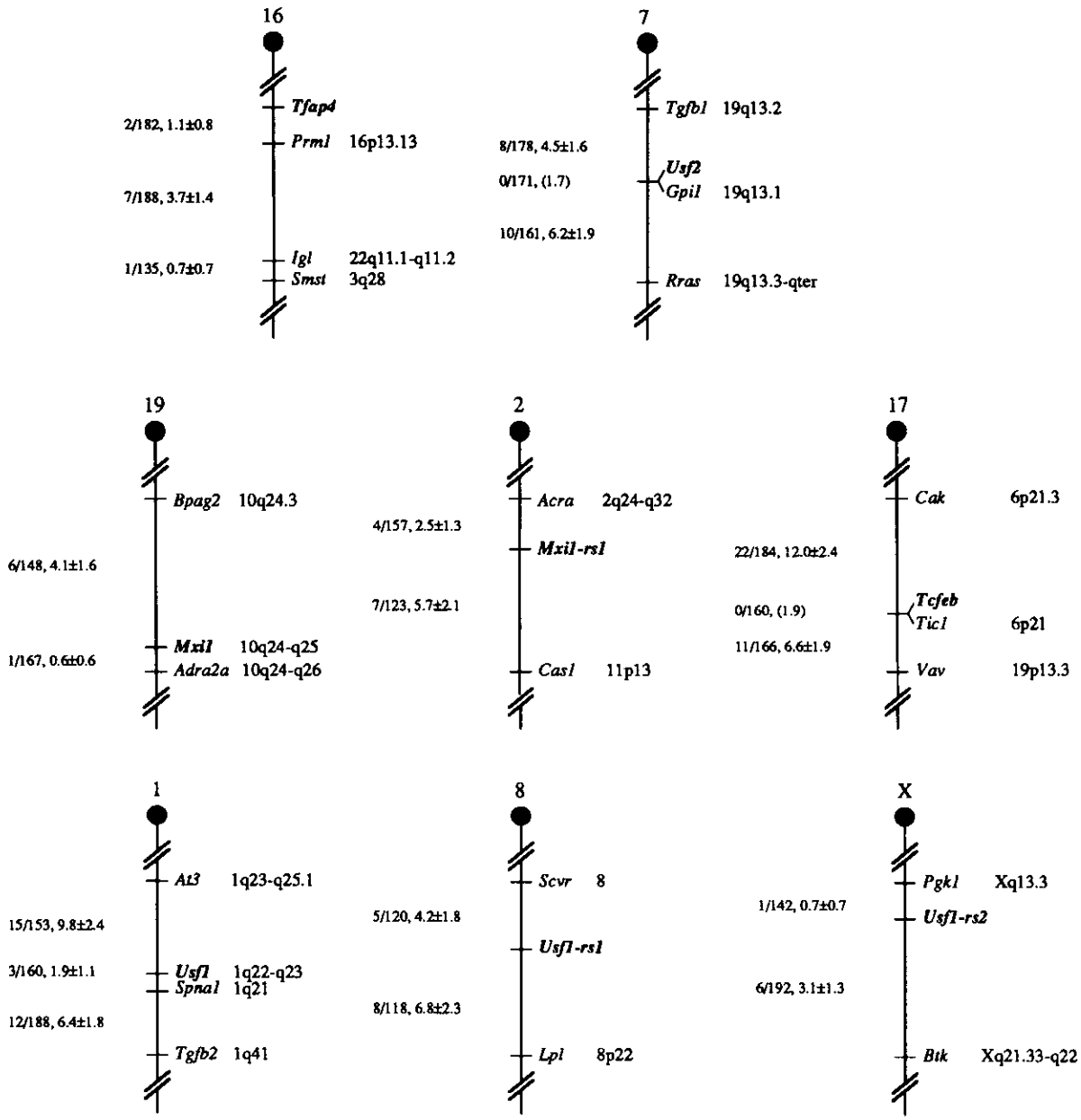

FIG. 1. Partial mouse chromosome linkage maps showing the map locations of *Tfap4, Mxi1, Tcfeb, Usf1,* and *Usf2.* The number of recombinant N_2 animals over the total number of N_2 animals typed plus the recombination frequencies expressed as genetic distances in centimorgans (±1 standard error) is shown for each pair of loci to the left of the chromosome maps. Where no recombinants were found between loci, the upper 95% confidence limit of the recombination distance is given in parentheses. No double crossover events were observed for the markers analyzed. The positions of loci mapped in human chromosomes are shown to the right of the chromosome maps. References for the map positions of most human loci can be obtained from GDB (Genome Data Base), a computerized database of human linkage information maintained by the William H. Welch Medical Library of The Johns Hopkins University (Baltimore, MD).

tion pattern of each RFLP in the IB mice was then determined and used to position the bHLH-Zip loci on the interspecific map.

The mapping results showed that these bHLH-Zip transcription factors are well dispersed throughout the mouse genome as each locus mapped to a different mouse chromosome (Fig. 1). The human MXI1 probe detected two independently segregating *M. spretus*-specific fragments (Table 1). One of these fragments mapped to chromosome 19 and the other to chromosome 2 (Fig. 1). The human MXI1 gene has been mapped to chromosome 10q24–q25, which shows a region of linkage homology to mouse chromosome 19 (Edelhoff *et al.,* 1994; Wechsler *et al.,* 1994; Shapiro *et al.,* 1994). We therefore assume that the chromosome 19 locus represents the authentic mouse *Mxi1* locus. These interspecific mapping results are consistent with *in situ* mapping data, which assigned the murine *Mxi1* locus to chromosome 19D and a related *Mxi1* locus to chromosome 2C (Edelhoff *et al.,* 1994).

Two different probes were used to map *Usf1* (Table 1). The p43MO12 probe, which contains *Usf1* coding

sequences, detected a 3.6-kb *M. spretus*-specific *Eco*RI fragment that mapped to the X chromosome. A 12.5-kb *M. spretus*-specific *Hin*cII fragment also mapped to the X chromosome (data not shown). The pW11ΔX probe, which contains *Usf1* 3′ untranslated sequences, detected two *M. spretus*-specific fragments, 4.0 and 5.3 kb in size, that mapped to chromosome 8 and chromosome 1, respectively. The *Usf1* locus on chromosome 1 likely represents the authentic *Usf1* locus, since *in situ* hybridization has been used to map this gene to mouse chromosomes 1 and 11 (Henrion *et al.,* 1995). While the position on chromosome 1 is consistent with our mapping data, the positions on chromosomes 8, 11, and X may reflect strain-specific differences between *Mus spretus,* used in our study, and the WMP strain used by Henrion *et al.* (1995). In addition, the human USF1 locus has been mapped to human chromosome 1q22–q23 (Shieh *et al.,* 1993), which shows a region of linkage homology to mouse chromosome 1. A USF1 pseudogene has been reported to reside on human chromosome 21 (M. Sawadogo and M. J. Siciliano, unpublished results), a region that is not homologous to any of the mouse *Usf1* loci.

The identification of one *Mxi1*- and two *Usf1*-related loci in mouse raises the interesting question of whether these loci represent previously unidentified bHLH-Zip genes. While this may be the case, no human MXI1-related loci have been identified. One human USF1-related locus has been identified, but it does not map to a region conserved with any of the mouse *Usf1*-related genes. It is possible that additional studies may identify such loci; however, it is also possible that these loci represent species-specific pseudogenes.

The human chromosomal locations of *Tcfeb* and *Usf2* can be predicted on the basis of known human and mouse linkage homologies (Fig. 1). *Tcfeb* maps to mouse chromosome 17 in a region of linkage homology with human chromosome 6p21, suggesting that the human TCFEB locus will map to chromosome 6p21. Likewise, *Usf2* is flanked by loci that map to human chromosome 19q13, suggesting that the human USF2 locus will map to chromosome 19q13. *Tfap4* maps 1.1 cM proximal of *Prm1*, which maps to human chromosome 16p13.13, suggesting that the human homologue of TFAP4 will map to chromosome 16p13. However, as *Tfap4* is the most proximal gene mapped so far to mouse chromosome 16 and the proximal extent of the human chromosome 16 homology has not been defined, it is not possible to predict with certainty the human chromosomal location of TFAP4.

Finally, several of the genes mapped in this study are located in the vicinity of known mouse mutations. However, more details about the function and expression patterns of these genes are needed before any relationship between these genes and mutations can be established.

ACKNOWLEDGMENTS

We thank Mary Barnstead and Debbie Barnhardt for expert technical assistance, Robert Tjian for the Ap4 cDNA, and Michael C. Schotz for the Lpl cDNA. This research was supported, in part, by the National Cancer Institute, DHHS, under Contract NO1-CO-46000 with ABL.

REFERENCES

Avner, P., Amar, L., Dandolo, L., and Guenet, J.-L. (1988). Genetic analysis of the mouse using interspecific crosses. *Trends Genet.* **4:** 18–23.

Blanar, M. A., and Rutter, W. J. (1992). Interaction cloning: Identification of a helix–loop–helix zipper protein that interacts with *c-Fos. Science* **256:** 1014–1018.

Bressan, A., Somma, M. P., Lewis, J., Santolamazza, C., Copeland, N. G., Gilbert, D. J., Jenkins, N. A., and Lavia, P. (1991). Characterization of the opposite-strand genes from the mouse *Htf9* locus. *Gene* **103:** 201–209.

Carr, C. S., and Sharp, P. A. (1990). A helix–loop–helix protein related to the immunoglobulin E box-binding proteins. *Mol. Cell. Biol.* **10:** 4384–4388.

Carthew, R. W., Chodosh, L. A., and Sharp, P. A. (1985). An RNA polymerase II transcription factor binds to an upstream element in the adenovirus major late promoter. *Cell* **43:** 439–448.

Carthew, R. W., Chodosh, L. A., and Sharp, P. A. (1987). The major late transcription factor binds to and activates the mouse metallothionein I promoter. *Genes Dev.* **1:** 973–980.

Chodosh, L. A., Carthew, R. W., Morgan, J. G., Crabtree, G. R., and Sharp, P. A. (1987). The adenovirus major late transcription factor activates the rat γ-fibrinogen promoter. *Science* **238:** 684–688.

Copeland, N. G., Gilbert, D. J., Li, K., Sawamura, D., Giudice, G. J., Chu, M.-L., Jenkins, N. A., and Uitto, J. (1993a). Chromosomal localization of mouse bullous pemphigoid antigens, BPAG1 and BPAG2: Identification of a new region of homology between mouse and human chromosomes. *Genomics* **15:** 180–181.

Copeland, N. G., Jenkins, N. A., Gilbert, D. J., Eppig, J. T., Maltais, L. J., Miller, J. C., Dietrich, W. F., Weaver, A., Lincoln, S. E., Steen, R. G., Stein, L. D., Nadeau, J. H., and Lander, E. S. (1993b). A genetic linkage map of the mouse: Current applications and future prospects. *Science* **262:** 57–66.

Dickinson, M. E., Kobrin, M. S., Silan, C. M., Kingsley, D. M., Justice, M. J., Miller, D. A., Ceci, J. D., Lock, L. F., Lee, A., Buchberg, A. M., Siracusa, L. D., Lyons, K. M., Derynck, R., Hogan, B. L. M., Copeland, N. G., and Jenkins, N. A. (1990). Chromosomal localization of seven members of the murine TGF-β superfamily suggests close linkages to several morphogenetic mutant loci. *Genomics* **6:** 505–520.

Edelhoff, S., Ayer, D. E., Zervos, A. S., Steingrímsson, E., Jenkins, N. A., Copeland, N. G., Eisenman, R. N., Brent, R., and Disteche, C. M. (1994). Mapping of two genes encoding members of a distinct subfamily of MAX interacting proteins: *MAD* to human chromosome 2 and mouse chromosome 6, and *MXI1* to human chromosome 10 and mouse chromosome 19. *Oncogene* **9:** 665–668.

Freeman, M., Ashkenas, J., Rees, D. J. G., Kingsley, D. M., Copeland, N. G., Jenkins, N. A., and Krieger, M. (1990). An ancient, highly conserved family of cysteine-rich protein domains revealed by cloning type I and type II murine macrophage scavenger receptors. *Proc. Natl. Acad. Sci. USA* **87:** 8810–8814.

Green, E. L. (1981). Linkage, recombination, and mapping. *In* "Genetics and Probability in Animal Breeding Experiments," pp. 77–113, Macmillan, New York.

Gregor, P. D., Sawadogo, M., and Roeder, R. G. (1990). The adenovirus major late transcription factor USF is a member of the helix–loop–helix group of regulatory proteins and binds to DNA as a dimer. *Genes Dev.* **4:** 1730–1740.

Henrion, A. A., Martinez, A., Mattei, M.-G., Kahn, A., and Raymondjean, M. (1995). Structure, sequence and chromosomal location of the gene for USF2 transcription factors in mouse. *Genomics* **25:** 36–43.

Hu, Y.-F., Lüscher, B., Admon, A., Mermod, N., and Tjian, R. (1990). Transcription factor Ap-4 contains multiple dimerization domains that regulate dimer specificity. *Genes Dev.* **4:** 1741–1752.

Jenkins, N. A., Copeland, N. G., Taylor, B. A., and Lee, B. K. (1982). Organization, distribution and stability of endogenous ecotropic murine leukemia virus DNA sequences in chromosomes of *Mus musculus*. *J. Virol.* **43:** 26–36.

Kirchgessner, T. G., LeBoeuf, R. C., Langner, C. A., Zollman, S., Chang, C. H., Taylor, B. A., Schotz, M. C., Gordon, J. I., and Lusis, A. J. (1989). Genetic and developmental regulation of the lipoprotein lipase gene: Loci both distal and proximal to the lipoprotein lipase structural gene control enzyme expression. *J. Biol. Chem.* **264:** 1473–1482.

Kobilka, B. K., Matsui, H., Kobilka, T. S., Yang-Feng, T. L., Francke, U., Caron, M. G., Lefkowitz, R. J., and Regan, J. W. (1987). Cloning, sequencing and expression of the gene coding for the human platelet α_2-adrenergic receptor. *Science* **238:** 650–656.

Law, C.-L., Torres, R. M., Sundberg, H. A., Parkhouse, R. M. E., Brannan, C. I., Copeland, N. G., Jenkins, N. A., and Clark, E. A. (1993). Organization of the murine *Cd22* locus: Mapping to chromosome 7 and characterization of two alleles. *J. Immunol.* **151:** 175–187.

Mermod, N., Williams, T. J., and Tjian, R. (1988). Enhancer binding factors AP-4 and AP-1 act in concert to activate SV40 late transcription in vitro. *Nature* **332:** 557–561.

Perez, J. L., Shen, X., Finkernagel, S., Sciorra, L., Jenkins, N. A., Gilbert, D. J., Copeland, N. G., and Wong, T. W. (1994). Identification and chromosomal mapping of a receptor tyrosine kinase with a putative phospholipid binding sequence in its ectodomain. *Oncogene* **9:** 211–219.

Peritz, L. N., Fodor, E. J., Silversides, D. W., Cattini, P. A., Baxter, J. D., and Eberhardt, N. L. (1988). The human growth hormone gene contains both positive and negative control elements. *J. Biol. Chem.* **263:** 5005–5007.

Rawlings, D. J., Saffran, D. C., Tsukada, S., Largaespada, D. A., Grimaldi, J. C., Cohen, L., Mohr, R. N., Bazan, J. F., Howard, M., Copeland, N. G., Jenkins, N. A., and Witte, O. N. (1993). Mutation of unique region of Bruton's tyrosine kinase in murine X-linked immunodeficiency. *Science* **261:** 358–361.

Sawadogo, M., and Roeder, R. G. (1985). Interaction of a gene-specific transcription factor with the adenovirus major late promoter upstream of the TATA box region. *Cell* **43:** 165–175.

Sawadogo, M., Van Dyke, M. W., Gregor, P. D., and Roeder, R. G. (1988). Multiple forms of the human gene-specific transcription factor USF. I. Complete purification and identification of USF from HeLa cell nuclei. *J. Biol. Chem.* **263:** 11985–11993.

Scotto, K. W., Kaulen, H., and Roeder, R. G. (1989). Positive and negative regulation of the gene for transcription factor IIIA in *Xenopus laevis* oocytes. *Genes Dev.* **3:** 651–662.

Shapiro, D. N., Valentine, V., Eagle, L., Yin, X., Morris, S. W., and Prochownik, E. V. (1994). Assignment of the human MAD and MXI1 genes to chromosomes 2p12–p13 and 10q24–q25. *Genomics* **23:** 282–285.

Shieh, B.-H., Sparkes, R. S., Gaynor, R. B., and Lusis, A. J. (1993). Localization of the gene-encoding upstream stimulatory factor (USF) to human chromosome 1q22–q23. *Genomics* **16:** 266–268.

Siracusa, L. D., Silan, C. M., Justice, M. J., Mercer, J. A., Bauskin, A. R., Ben-Neriah, Y., Duboule, D., Hastie, N. D., Copeland, N. G., and Jenkins, N. A. (1990). A molecular genetic linkage map of mouse chromosome 2. *Genomics* **6:** 491–504.

Siracusa, L. D., Jenkins, N. A., and Copeland, N. G. (1991). Identification and applications of repetitive probes for gene mapping in the mouse. *Genetics* **127:** 169–179.

Sirito, M., Lin, Q., Maity, T., and Sawadogo, M. (1994). Ubiquitous expression of the 43- and 44-kDa forms of transcription factor USF in mammalian cells. *Nucleic Acids Res.* **22:** 427–433.

Wechsler, D. S., Hawkins, A. L., Li, X., Jabs, E. W., Griffin, C. A., and Dang, C. V. (1994). Localization of the human Mxi1 transcription factor gene (MXI1) to chromosome 10q24–q25. *Genomics* **21:** 669–672.

Zervos, A. S., Gyuris, J., and Brent, R. (1993). Mxi1, a protein that specifically interacts with Max to bind Myc–Max recognition sites. *Cell* **72:** 223–232.