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Chromatin Immunoprecipitation (ChIP) on Chip Experiments Uncover a Widespread Distribution of NF-Y Binding CCAAT Sites Outside of Core Promoters*[S]

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The CCAAT box is a prototypical promoter element, almost invariably found between −60 and −100 upstream of the major transcription start site. It is bound and activated by the histone fold trimer NF-Y. We performed chromatin immunoprecipitation (ChIP) on chip experiments on two different CpG islands arrays using chromatin from hepatic HepG2 and pre-B cell leukemia NALM-6 cell lines, with different protocols of probe preparation and labeling. We analyzed and classified 239 known or predicted targets; we validated several by conventional ChIPs with anti-YB and anti-YC antibodies, *in vitro* EMSAs, and ChIP scanning. The importance of NF-Y binding for gene expression was verified by the use of a dominant negative NF-YA mutant. All but four genes are new NF-Y targets, falling into different functional categories. This analysis reinforces the notion that NF-Y is an important regulator of cell growth, and novel unexpected findings emerged from this unbiased approach. (i) A remarkable proportion of NF-Y targets, 40%, are complex transcriptional units composed of divergent, convergent, and tandem promoters. (ii) 40–50% of NF-Y sites are not in core promoters but are in introns or at distant 3′ or 5′ locations. The abundance of "unorthodox" CCAAT positions highlights an unexpected complexity of the NF-Y-mediated transcriptional network.

The CCAAT box is a DNA element that controls transcriptional initiation in eukaryotic promoters; recent bioinformatic studies unambiguously identify it as one of the most widespread. The analysis on 1031 human promoters isolated through unbiased determination of mRNA start sites suggested that the CCAAT box or its reverse ATTGG is present in as many as 67% of promoters (1). A statistical, unbiased analysis of random octanucleotides on a large 13,000-promoter data set confirmed that the CCAAT is second only to the Sp1-binding GC box in terms of abundance, despite the fact that the percentage of CCAAT promoters was inferior, 7.5% (2). Furthermore, analysis of cell cycle-regulated genes identified the CCAAT box as specifically present in promoters of G_2/M genes (3). Most importantly, specific flanking nucleotides emerging from these studies matched specifically the consensus of the NF-Y transcription factor. A combination of EMSAs and transfections with highly diagnostic dominant negative vectors implicated NF-Y as the CCAAT activator (4). It is composed of three subunits, NF-YA, NF-YB, and NF-YC, all necessary for sequence-specific binding to a G/A, G/A, C, C, A, A, T, C/G, A/G, G/C consensus. NF-YB and NF-YC contain evolutionarily conserved histone fold motifs common to all core histones, mediating dimerization, a feature strictly required for NF-YA association and sequence-specific DNA binding (5, 6). In essentially all cases described so far, the binding of the trimer is important or essential for transcriptional regulation (7).

NF-Y is considered as a general promoter organizer: thanks to its histone-like nature, it presets chromatin structure locally (8), interfacing well with nucleosomes (9), it helps the binding of neighboring factors (reviewed in Refs. 4 and 5) and attracts coactivators, such as p300/CREB-binding protein (8, 10). The location of the CCAAT box is far from random, being positioned between −60 and −100 in the vast majority of the promoters analyzed. In general, our knowledge of the anatomy of NF-Y-binding sites in terms of flanking sequences, position with respect to transcriptional start sites, and promoter context (6, 11, 12) enables us to make predictions as to whether a gene will be regulated by NF-Y.

Chromatin Immunoprecipitation (ChIP)[1] experiments determined that NF-Y is bound *in vivo* before gene activation (10–13); NF-Y is bound to a transcribing cyclin B1 promoter during mitosis in HeLa cells (14). Indeed, binding to cell cycle-regulated promoters is not constitutive but is time-regulated, being found before activation and displaced when promoters are repressed (10). Furthermore, conditional knock-out experiments of CBF-B (NF-YA) unambiguously determined that the protein is required for cell proliferation of mouse embryo fibroblasts and mouse development (15).

The analysis of 130 mammalian CCAAT-containing promoters suggests a prevalence in genes that are active in a tissue- or

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[S] The on-line version of this article (available at http://www.jbc.org) contains three additional tables.

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[1] The abbreviations used are: ChIP, chromatin immunoprecipitation; Pipes, 1,4-piperazinediethanesulfonic acid; PMSF, phenylmethylsulfonyl fluoride; IP, immunoprecipitation; CTU, complex transcriptional unit; EMSA, electrophoretic mobility shift assay; CREB, cAMP-response element-binding protein.

development-specific way and in inducible genes, either by external stimuli or during the cell cycle (7). Whereas this is certainly informative, very little information exists as to the binding to other regions. Finding all genes targeted by a particular transcription factor is crucial to reconstruct its transcriptional network. To expand our knowledge of NF-Y binding *in vivo*, a valuable approach is to use DNA derived from ChIPs to probe microarrays. DNA arrays have been developed in which clones derived from a CpG island library have been spotted (16); CpG islands have long been known to be associated to regulatory elements in promoters (17) and also elsewhere in the genome. They are believed to be mainly associated to "housekeeping" genes (*i.e.* genes active in all cells), albeit at different levels (reviewed in Ref. 18). To gain a wider understanding of the NF-Y transcriptional circuitry, we took a high throughput genomic approach by screening with anti-YB chromatin-immunoprecipitated DNA two CpG island arrays.

EXPERIMENTAL PROCEDURES

Chromatin Immunoprecipitation Assay

The procedure for ChIP was essentially as described previously (10) with some modifications. Rabbit polyclonal anti-YB and anti-YC antibodies were derived by purification of the corresponding sera on affinity columns containing purified recombinant NF-YB or NF-YC linked to CnBr-Sepharose (Sigma). Nalm-6 and HepG2 cells, grown in RPMI, supplemented with 10% fetal calf serum, 2 mM L-glutamine, 50 μM β-mercaptoethanol, were treated by adding formaldehyde directly to tissue culture medium to a final concentration of 1% and incubated for 10 min at room temperature. Approximately 5×10^6 cells were used for each immunoprecipitation. Cross-linking reactions were stopped by the addition of phosphate-buffered saline-glycine to a final concentration of 0.125 M. Cells were washed twice with ice-cold phosphate-buffered saline, scraped, and centrifuged at 2000 rpm for 2 min. Cells were then resuspended in cell lysis buffer (5 mM Pipes, pH 8.0, 85 mM KCl, and 0.5% Nonidet P-40) containing protease inhibitors (100 ng/ml aprotinin and 100 ng/ml leupeptin) and 0.5 mM PMSF and kept on ice for 15 min. Cells were homogenized using a Dounce homogenizer (B pestel) several times, and the resultant homogenates were centrifuged at 5000 rpm for 5 min at 4 °C to pellet the nuclei. The pellets were resuspended in nuclei lysis buffer (50 mM Tris-HCl, pH 8.1, 10 mM EDTA, 0.1% SDS, and 0.5% deoxycholic acid) containing protease inhibitors and PMSF and kept on ice for 20 min. The nuclear lysates were sonicated on ice to an average chromatin length of 2–2.5 kb and then centrifuged at 12,000 rpm for 10 min at 4 °C. The supernatants were incubated in IP buffer (50 mM Tris-HCl, pH 8.1, 10 mM EDTA, 0.1% SDS, 0.5% deoxycholic acid, and 500 mM LiCl) containing protease inhibitors and PMSF, with Protein G-agarose (KPL) for 2 h at 4 °C in rotation. After removal of Protein G-agarose, the precleared lysates were used as soluble chromatin for ChIP. Chromatin was incubated at 4 °C overnight with 4 μg of anti-NF-YB or anti-NF-YC antibodies. No antibody and anti-FLAG (Sigma) control samples were included. Immunoprecipitates were recovered by incubation for 2 h at 4 °C with Protein G-agarose previously precleared in IP buffer (1 μg/μl bovine serum albumin, 1 μg/μl salmon testis DNA, protease inhibitors, and PMSF). To perform a second immunoprecipitation, 30 μl of elution buffer (50 mM $NaHCO_3$, 1% SDS) were added, and the recovered material was diluted with 270 μl of IP buffer. 2 μg of the second antibody were added and incubated at 4 °C overnight. The recovery proceeded as in the first IP reaction. Reversal of formaldehyde cross-linking, RNase A, and Proteinase K treatments were performed as previously described (19).

Data validation was performed with conventional ChIPs (10), with chromatin of 0.8 kb and with anti-YB as well as anti-YC purified polyclonal antibodies. The sequence of PCR primers used to analyze the genes reported in Fig. 2 are shown in Supplemental Table I.

Generation of ChIP Probes

DNAs from 20–30 individual ChIPs were used to generate a probe for array screening. Immunoprecipitated chromatin was used as template for random priming reactions in the presence of 10 mM amino allyl-UTP (Sigma catalog no. A-0410) using the BioPrime DNA labeling system (Invitrogen). The DNAs were desalted and concentrated with a Microcon YM30 filter column (Millipore Corp.) and then lyophilized. After resuspension in water, amino allyl-dUTP-labeled chromatin was coupled with Cy5 dye (Amersham Biosciences) solubilized in 0.1 M sodium bicarbonate, pH 9.0, for 1 h in the dark. After the addition of 0.1 M sodium acetate, pH 5.2, DNAs were purified with QIAquick columns (Qiagen) and lyophilized.

Amplicon Generation and Labeling

The generation of amplicons from individual ChIPs was performed following the protocols of LM-PCR described in Refs. 20 and 21. Briefly, two unidirectional linkers (oligonucleotide JW102, 5′-GCGGTGACCCGGGAGATCTGAATTC-3′; oligonucleotide JW103, 5′-GAATTCAGATC-3′) were annealed and ligated to the chromatin IPs, previously blunted by T4 DNA polymerase. The first amplicons were generated by PCR (one cycle at 55 °C for 2 min, 72 °C for 5 min, 95 °C for 2 min, followed by 15 cycles at 95 °C for 30 min, 55 °C for min, 72 °C for 1 min, and a final extension of 4 min at 72 °C). The reaction was purified using the Qiaquick PCR purification kit (Qiagen) or the GFX PCR purification kit (Amersham Biosciences) according to the manufacturer's instructions. One-tenth of these initial reactions were used to generate more amplicons, using the same PCR program for a subsequent 30 cycles. After purification of these last rounds of amplification, the DNA was quantified and examined by gene-specific PCR to ensure that the initial enrichment was maintained. 5 μg of amplicons for α-NF-YB, α-FLAG, and input DNA (subjected to the same number of PCR manipulations as the IPs) were labeled using the LabelIT Cy5/Cy3 nucleic acid labeling kit (Mirus), following the manufacturer's instructions, with a reagent/DNA ratio of 2.5 for Cy5 (IPs) and 1.5 for Cy3 (input).

CpG Microarray Hybridization

7776 CpG Array—The development of the 7776 CpG island array was described previously (21–23). Prior to hybridization, spotted CpG island slides were incubated with a solution of 3× SSC, 0.25% SDS, and 1.5 μg/μl salmon testis DNA under a glass coverslip at 37 °C for 30 min to block nonspecific binding. Slides were washed twice with water and dried for 5 min at 600 rpm in a centrifuge. Labeled DNAs were added to hybridization buffer (0.25 M $NaPO_4$, 4.5% SDS, 1 mM EDTA, and 1× SSC), denatured at 95 °C for 2 min, cooled to 60 °C, and dropped onto slides placed in prewarmed hybridization chambers. Incubation was performed at 60 °C overnight. After hybridization, the slides were washed successively at 50 °C with 1× SSC, 0.1% SDS at room temperature with 1× SSC (0.1%) and at room temperature with 0.2 SSC for 5 min each and then dried. Hybridized slides were scanned with the GenePix 4000A scanner (Axon), and the acquired images were analyzed with the software GenePix Pro, Version 3.0. A global normalization factor was determined for each replica, evaluating the anti-NF-YB ChIP Cy5/control ChIP Cy5 ratio relative to control repetitive elements. Data were normalized prior to comparison. After normalization, positive loci were defined by hybridization intensities at least 2 times greater than that of control.

12K Array—The Cy5- and Cy3-labeled DNA were each resuspended in 10 μl of 1 μg/μl Cot-1 DNA (Invitrogen) and mixed together in order to have the same amount of input Cy3-labeled DNA for each IP Cy5-labeled DNA. The hybridization solution was then added to a final composition of 43% formamide, 4.3× SSPE, 0.42% SDS, 42 μg of salmon sperm DNA, 0.2 μg of tRNA, heated for 2 min at 95 °C and cooled down to 37 °C over 30 min. 95 μl of each mixture solution was applied to two human CpG 12K slides (University Health Network, The Microarray Center, Toronto, Canada) and hybridized at 37 °C for >18 h. The slides were prehybridized for 1 h at 42 °C with 25% formamide, 5× SSC, 0.1% SDS, and 10 μg/μl bovine serum albumin.

The slides were washed at room temperature for 5 min twice in 2× SSC, 0.1% SDS; once in 1× SSC, 0.1% SDS; and one final time in 0.1× SSC; dried; and immediately scanned using a ScanArray 4000 scanner (Packard). The hybridized microarrays were analyzed using the Quantarray microarray analysis software (Packard). Features of poor intensity (<500) and those that did not meet the quality control criteria (visual inspection, spot circularity, spot uniformity, and background uniformity for both channels) were discarded. After the background subtraction for each spot, the data were normalized to median (*i.e.* the ratio of the median value of all spots in the Cy5 channel (IP DNA) was normalized to the ratio of the median value of the control channel (Cy3 = input)). From a direct comparison of the arrays hybridized with the DNA of the α-NF-YB IP and the α-FLAG IP, only the spots that showed an enrichment >2-fold in the YB samples were further analyzed. Two independent experiments were performed, each consisting of one α-NF-YB IP and one control α-FLAG IP slide, normalized to the same input DNA, and the commonly enriched spots were considered.

Data Analysis

Positive clones were sequenced and mapped with BLAT. The presence of CCAAT sequences were searched for 2 kb on the flanking of the 7776 CpG island array and 500 bp on the 12K array, annotated in individual files corresponding to the genomic loci identified. The criteria for classifications are described below. Mouse orthologs were retrieved using BLAT. The annotated genes were classified according to functional categories, and the classification was compared with those performed on the MYC and E2F4 targets.

Expression Analysis of NF-Y-targeted Genes

HepG2 cells were infected with control green fluorescent protein, wild type NF-YA, or dominant negative YAm29 adenovirus.[2] Adenovirus vectors to express NF-YA or the YAm29 dominant negative mutant were generated using AdEasy, using HindIII and XbaI from the corresponding pcDNA3-based vectors, and introduced into the same sites of the shuttle vector pAdTrack-CMV. This plasmid was recombined with the vector pAdEasy1, followed by treatment with PacI and transfection into an E1-complementing cell line. We infected exponentially growing cells for 7 h in the absence of serum. Fetal calf serum was then added, and cells were incubated for 48 h. RNA was extracted using an RNA-Easy kit (Qiagen), according to the manufacturer's protocol. For cDNA synthesis, 4 μg of RNA were used with the M-MLV-RT kit (Invitrogen). Semiquantitative PCR analysis was performed with oligonucleotides detailed in Supplemental Table II.

Electrophoretic Mobility Shift Analysis of NF-Y Binding

EMSA analyses of Fig. 3 were performed under standard NF-Y conditions (6, 11, 22, 23), with anti-YB supershift antibodies and recombinant NF-Y and the indicated oligonucleotides. ^{32}P-Labeled oligonucleotides were incubated in 20 mM Tris-HCl, pH 7.8, 50 mM NaCl, 1 mM dithiothreitol, 3% glycerol, 5 mM $MgCl_2$ for 30 min at 20 °C with 5 ng of recombinant NF-Y trimer or with 5 μg of HepG2 nuclear extracts together with 200 ng of poly(dI-dC) (Sigma). The samples were loaded on a 4.5% polyacrylamide gel, run for 2 h, dried, and exposed. To produce recombinant NF-Y, *Escherichia coli* BL21 DE3LysS was induced at an A_{600} value of 0.6 by the addition of isopropyl-β-D-thiogalactopyranoside to a final concentration of 1 mM for 3 h. Bacterial pellets were resuspended and sonicated in sonication buffer (150 mM KCl, 20 mM Tris-HCl, pH 7.8, 0.05% Nonidet P-40, 0.1 mM EDTA, 5 mM 2-mercaptoethanol, 1 mM PMSF (Sigma), and protein inhibitors) and centrifuged at 23,000 $\times$ *g* in a Beckman SW 27Ti rotor for 30 min at 4 °C. The inclusion bodies pellet was resuspended in sonication buffer, sonicated, and centrifuged again. Inclusion bodies were finally resuspended in 6 M guanidium chloride, 20 mM sodium acetate (pH 5.2), 5 mM 2-mercaptoethanol, and 1 mM PMSF. The three subunits were mixed to a final concentration of 0.5 mg/ml and dialyzed against a 100-fold excess of BC300 (300 mM KCl, 20 mM Tris-HCl, pH 7.8, 0.05% Nonidet P-40, 5 mM 2-mercaptoethanol, 1 mM PMSF); glycerol concentration was adjusted to 20%, and proteins were loaded on a nickel-nitrilotriacetic acid-agarose column, washed with BC300, and eluted with 0.25 M imidazole. The proteins were finally dialyzed against BC100, the purity being routinely >80%.

RESULTS

Our goal was to identify novel targets of NF-Y in an unbiased way. The combination of chromatin immunoprecipitation with microarray analysis was performed in yeast (24–26) and humans (20, 27–30). In particular, DNA microarrays containing genomic fragments with CpG islands, often corresponding to regulatory regions, were probed with DNA recovered from chromatin immunoprecipitated using MYC, E2F4/6, and methyl CpG binding domain protein antibodies. We decided to take the same route and used two different reagents: a 7776 array and a 12K array from UHN (Toronto, Canada). We also tested two different ways of preparing probes for hybridization. For the 7776 array, we prepared several sequential ChIPs with chromatin from the liver HepG2 cell line, with a highly specific anti-NF-YB antibody, and, in parallel, control ChIPs with a commercially available anti-FLAG control. The chromatin used in this procedure was larger (~2–2.5 kb) than the one used in conventional ChIPs (0.5–1 kb). Because of the modifications of our routine ChIPs with extended chromatin, we first verified whether immunoprecipitated DNAs were indeed enriched in NF-Y-targeted fragments. We used oligonucleotides amplifying several CCAAT-containing promoters in semiquantitative PCRs. Fig. 1*A* shows that essentially all of the promoters tested were clearly positive in the anti-YB ChIP, compared with the FLAG and no antibody controls: the liver-specific genes *αGA*, *MVK*, *OAT*, and mATP synthase and the ubiquitous *HnRNPA1*, *NP95*, *PPP1R7*, *HMGB2*, *ABL*, *CDC25A*, β-actin, and *OGG1*. Note that only the last two genes were previously known to be regulated by NF-Y (31, 32), whereas all of the others were derived from a CCAAT-containing promoter data set.[3] In parallel ChIP analysis, CCAAT-less promoters, *p107*, α-tubulin, *RPS19*, and *YBL1*, were negative (Fig. 1*A*, *lower panel*).

For the 12K hybridization, we took a different approach, by PCR-amplifying chromatin from Nalm-6 cells after ligation of linker DNA. The advantage is that a very limited amount of ChIP material is required to yield enough DNA for hybridization. We also checked that the successive rounds of PCR amplifications would not decrease the enrichment of *bona fide*

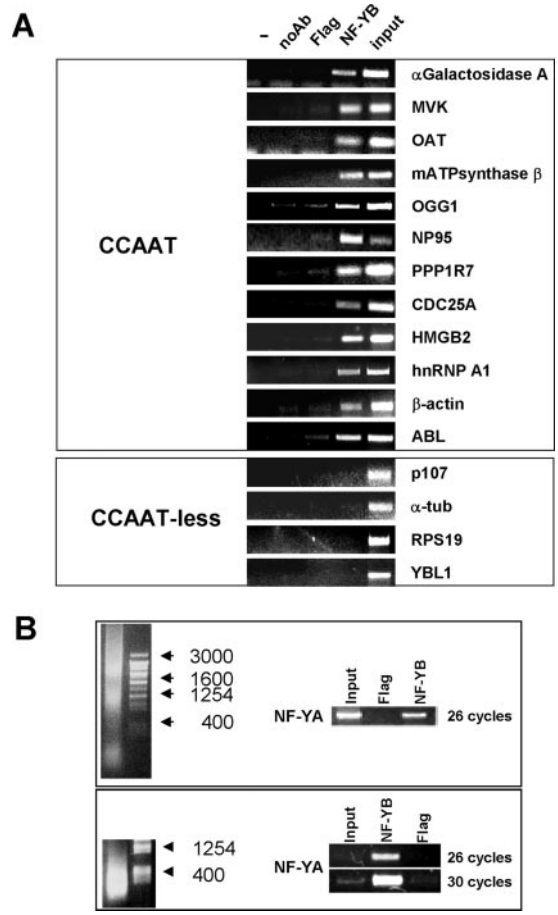

FIG. 1. **Validation of the NF-YB probes for the ChIP on chips.** *A*, analysis of NF-Y targets with DNA immunoprecipitated with the "extended chromatin" ChIP protocol from HepG2 chromatin. In the *upper panels*, genes predicted to be targeted, according to the CCAAT promoter data set (F. Romani and R. Mantovani, unpublished observations). In the *lower panel*, *bona fide* CCAAT-less promoters were assayed. *B*, the NF-YA gene promoter was PCR-amplified from NALM-6 chromatin ChIP (*upper panel*) and after the LM-PCR amplification procedure for probe preparation (see "Experimental Procedures").

[2] Imbriano, C., Gurtner, A., Cocchiarella, F., Di Agostino, S., Basile, V., Gostissa, M., Dobbelstein, M., Del Sal, G., Piaggio G., and Mantovani, R. (2005) *Mol Cell Biol.*, in press

[3] A. Testa and R. Mantovani, manuscript in preparation.

NF-Y targets in the amplicons. Indeed, Fig. 1*B* shows that the *NF-YA* promoter amplicon is no less, and in fact probably more, enriched in the final LM-PCR chromatin compared with the initial starting material. Therefore, we conclude that both of these procedures yield sufficiently enriched DNA for further genomic analysis.

Results of the 7776 Array—We used DNAs from 20–30 individual ChIPs to generate probes for the 7776 array screening. We identified at least 230 spots, in which the corrected signal obtained with the NF-YB chromatin was at least 2-fold higher than the anti-FLAG signal. We sequenced all positive clones and derived their chromosomal localizations. A positive clone will indicate that a bound NF-Y site lies somewhere within 2.5 kb of the CpG island. The genomic sequences surrounding the CpG island were therefore scrutinized for the presence of CCAAT sequences for a length of 2 kb on either sides. Table I shows a list of the positive clones. Several criteria helped us to classify them as follows.

Flanking sequences are essential for high affinity NF-Y binding both at the 5′ and 3′ of the pentanucleotide, with a variation of 2 logs in K_d *in vitro*, between high and low affinity sites (for details, see Refs. 6, 7, 11, and 23). In essence, functional low affinity CCAAT boxes are rare and mostly found in proximity of high affinity ones. We classified as high affinity those NF-Y sites having optimal sequences both at the 5′ and at the 3′ of the pentanucleotide (+++ in Table I); medium affinity those with optimal nucleotides at the 5′ or 3′ end (++ in Table I); low affinity those only harboring the CCAAT pentanucleotide (+ in Table I). In most clones, multiple CCAAT boxes were identified, with various degrees of consensus match; in these cases, we referred only to the highest affinity ones.

We singled out the clones with a location appropriate for a "promoter" definition (*i.e.* whenever a mapped known gene or multiple clustered expressed sequence tags generated from a localized area were nearby). This is because the CCAAT position is quite constant, 60–100 bp from the transcriptional start site within the promoters analyzed (7), and exceptions to this rule are sporadic (32–34). In all cases in which multiple CCAAT boxes were detected throughout the locus, the clone was classified as "canonical" if one of them was present in the promoter, within 200 bp from the transcriptional start sites.

We further separated the promoters into two categories, based upon the type of transcriptional unit. CpG islands are abundant not only in simple promoters but also in divergent, convergent, and tandemly linked promoters as well (18, 35); we collectively classified them as complex transcriptional units (CTUs).

Species conservation of TF target sites or regulatory regions in general (and of CCAAT boxes in particular) is a hallmark of functional importance, as detailed in transfection experiments and phylogenetic footprints. We thus retrieved information of the mouse orthologous genes and analyzed them for the presence of a CCAAT sequence at the corresponding position. This could only be possible, with a good degree of confidence, for the promoter (canonical and CTUs) data set, by taking the transcriptional start site as the pivotal point. The sequences of all of the loci are individually provided as Supplemental Table III.

In all clones retrieved, at least one CCAAT pentanucleotide could be found. This is well expected, given the 4–5 kb of DNA analyzed on both sides of the CpG clones and the average frequency of the core CCAAT (or ATTGG) pentanucleotide, one every 0.5 kb. However, a consensus high affinity NF-Y site (+++ in Table I) is theoretically present every 16 kb (7). Given the overall length of DNA analyzed in all of the loci (750 kb), the total number of CCAAT boxes expected would be 1500, with 46 high affinity ones. Indeed, 1135 CCAAT were scored, with 252 of these matching the NF-Y consensus; thus, although there is a slight negative skewing for the pentanucleotide around the CpG island regions analyzed, the NF-Y optimal sites were 6-fold overrepresented.

To validate our analysis, we performed conventional ChIPs, with 1 kb of chromatin. Selections of the identified targets in each of the different classes were probed with anti-NF-YB and NF-YC antibodies. Furthermore, we also performed sequential immunoprecipitations of chromatin with both antibodies (re-ChIP). The results of these experiments are shown in Fig. 2. All targets tested scored positive, further confirming that clones emerging from the ChIP on chip analysis are indeed positive for NF-Y binding *in vivo*.

Results of the 12K Array—Table II contains the genes that emerged from the 12K array screenings with the anti-YB probes. The criteria mentioned above for the classification were also applied here, except that the flanking DNA considered was shorter (1 kb) due to the restricted length of the probe. Clones showing >2-fold higher signals with respect to the FLAG control were 1205 and 783 on 5121 and 4371 spots analyzed, respectively, corresponding to 23 and 18% of positivity. 119 clones were in common; of these, 65 clones were mappable based on the sequences retrievable from the Sanger Centre. Core promoters were 10%, and noncanonical CCAAT were nearly 50%. Several CTUs were also present. Overall, the distribution was highly reminiscent of the 7776 array. Here, again, we validated selected clones by conventional ChIP; all showed a substantial enrichment with respect to the FLAG control (Fig. 2*A*, *right panels*).

Analysis of NF-Y Targets—To pinpoint specifically the sites of interactions, we performed *in vitro* EMSAs with HepG2 nuclear extracts and oligonucleotides corresponding to selected CCAAT boxes found in the CpG island regions of the HepG2 targets. Fig. 3 shows that essentially all CCAAT boxes are able to interact with a binding activity in nuclear extracts. This is identified as NF-Y by (i) supershift with the diagnostic anti-YB antibody and (ii) association with recombinant NF-Y. Therefore, we conclude that the identified targeted genes do contain NF-Y binding CCAAT boxes.

To further check whether the predicted CCAAT boxes were correctly evaluated, we performed ChIP scanning experiments on three loci. We immunoprecipitated chromatin from HepG2 with anti-YB and anti-YC antibodies and amplified three different regions of the CDKN2A-MTAP and EMX2-EMX2OS CTUs and the canonical PMSC6 gene. Results shown in Fig. 4 indicate that only one amplicon of the CDKN2A-MTAP loci was positive with both NF-Y antibodies, corresponding to the +++ CCAAT box indicated in Table I, despite the presence of other CCAAT elements in the proximity of the negative amplicons. In the case of the EMX2-EMX2OS locus, amplicons 2 and 3 were positive, corresponding to the core promoter regions of both genes, whereas an amplicon in the proximity of two high affinity sites in an intronic region of EMX2OS was not enriched compared with the control. In the PSMC6 locus, only the high affinity core promoter CCAAT was bound *in vivo*. Collectively, these experiments support the classification of Tables I and II and suggest that the genes are indeed under NF-Y control.

Function of NF-Y on Selected Targets—To verify the role of NF-Y binding in the expression of the newly discovered genes, we used adenoviral vectors expressing wild type NF-YA and the well characterized dominant negative YAm29 mutant, capable of associating to the histone fold motif dimer but crippled in the DNA-binding subdomain and hence incapable of binding to the CCAAT box. HepG2 cells were used for the infections, and mRNA analysis of a number of target genes retrieved from the 7776 array was performed by semiquantitative reverse

TABLE I

Classification of NF-Y-targeted genes

NF-Y-targeted genes are classified according to three categories (canonical, noncanonical, and complex transcriptional units) and to the relative match to a consensus NF-Y-binding site (+++, perfect match; ++, mismatch at the 5′ or 3′ + mismatches at the 5′ and 3′ −, no match). The presence of a CCAAT sequence in the mouse orthologs is indicated, as well as the locus link or accession numbers. In the noncanonical CCAAT cohort, we indicated whether a CCAAT was present in introns (in), or at the far 5′ (up) or 3′ (do) ends of the gene.

+++ CCAAT CANONICAL POSITION

Gene	Description	LocusLink/Acc.N.	Mouse cons.
HOXB13	Homeobox protein Hox-B13	10481	yes
USP13	ubiquitin specific protease 13	8975	yes
CDC10	cell division cycle 10 homolog (S. cerevisiae)	989	yes
TIMP3	tissue inhibitor of metalloproteinase 3	7078	yes
BET1	Golgi vesicular membrane trafficking protein p18	10282	no
RPL41	ribosomal protein L41	6171	no
ELAVL1	embryonic lethal, abnormal vision, Drosophila-like 1	1994	yes
SLIT3	slit homolog 3 (Drosophila)	6586	yes
SURB7	suppressor of RNA polymerase B homolog (yeast)	9412	yes
EPAS1	endothelial PAS domain protein 1	2034	yes
SALL4	Zn-finger, C2H2 type motif	57167	yes
CLDN15	claudin 15 (Moderately similar to murine Cldn7)	24146	yes
ZF6	zinc finger protein zfp6 (ubiquitin UBF-fl) KRAB box	84914	n.a.
dfp	DNA/pantothenate metabolism flavoprotein, C terminal motif	79717	yes
TTL.4	(LOC164395) tubulin-tyrosine ligase family member	BC036213	yes
PIP5K1A	phosphatidylinositol-4-phosphate 5-kinase, type I,alpha	8394	yes
GRIA4	glutamate receptor, ionotrophic, AMPA 4	2893	yes
RUN.1	(FLJ30780) pleckstrin-like, transporter activity	BC034693	yes
LOC340319		BM126499	yes
cDNA	Mus musculus adult male liver tumor cDNA	AK050417	yes
LOC340784	homeobox protein hmx2 like	BF590391	yes
LOC221576		AK055503	n.a.

++ CCAAT CANONICAL POSITION

Gene	Description	LocusLink/Acc.N.	Mouse cons.
GAPD	glyceraldehyde-3-phosphate dehydrogenase	2597	no
ACTR6	actin-related protein 6	64431	yes
BA526D8.4	KRAB box	BE244356	no

+ CCAAT CANONICAL POSITION

Gene	Description	LocusLink/Acc.N.	Mouse cons.
swajar		AL120625	no
LOC348225		AI192520	no

+++ CTU

Gene	Description	LocusLink/Acc.N.	Mouse cons.
CSDA	cold shock domain protein A	8531	no
HIST1H3F	histone 1, H3f	8968	yes
HIST1H2BH	histone 1, H2bh	8345	yes
GGPS1	geranylgeranyl diphosphate synthase 1	9453	yes
BCAA	retinoblastoma binding protein 1-like 1	51742	yes
TSNAX	translin-associated factor X	7257	no
SIAT8D	sialyltransferase 8D (alpha-2, 8-polysialyltransferase)	7903	yes
DGKI	diacylglycerol kinase, iota	9162	yes
DREV1	DORA reverse strand protein 1(methyltransferase motif)	51108	yes
CDKN2A	cyclin-dependent kinase inhibitor 2A	1029	yes
MTAP	methylthioadenosine phosphorylase	4507	yes
TA-KRP	T-cell activation kelch repeat protein	84541	yes
KHDRBS3	Sam68-like phosphotyrosine protein	10656	yes
TYMS	thymidylate synthetase	7298	yes
H2AFJ	H2A histone family, member J	55766	yes
HIST4H4	histone 4, H4	121504	no
LALP1	lysosomal apyrase-like protein 1	57089	yes
ARHGAP11A	GTPase-activator protein for Rho-like (KIAA0013)	9824	yes
MRS3/4	putative mitochondrial solute carrier	81894	n.a.
MGC13523		112611	yes
UNG2	uracil-DNA glycosylase 2	10309	no
PGM3	phosphoglucomutase 3	5238	yes
RORB	nuclear orphan receptor ROR-beta	6096	no
MLR2	MLR2,ligand-dependent corepressor (KIAA1795)	84458	yes
TIP-1	Tax interaction protein 1	30851	yes
zf-C3HC4.67	Zn-finger, RING motif (FLJ20445)	54708	yes
EMX2	empty spiracles homolog 2 (Drosophila)	2018	yes
EMX2OS	Antisense transcripts at the EMX2	AY117034	yes
FLT3LG	fms-related tyrosine kinase 3 ligand	126133	yes
FLJ20643	coiled coil-4 domain	55011	no
C6orf182		285753	yes
SESN1	sestrin 1	27244	yes
LOC286286	Interleukin 1/heparin-binding growth factor motif	286286	n.a.
Zf-C2H2.157	MGC23143	BI756946	yes
Zf-C2H2.156	FLJ14768	AK027674	yes
MGC2963		83460	yes
goywu	similar to LOC147447	BC028301	n.a.
LOC283701		BF175200	n.a.
LOC219854		BM042915	n.a.
deeley		BC015151	n.a.
chawmy		R56808	n.a.
korly		AW628837	yes
chular		BI520627	n.a.
teyzu		BC036249	n.a.
skalaw		AA889736	n.a.
woner		BE141244	n.a.

++ CTU

Gene	Description	LocusLink/Acc.N.	Mouse cons.
PRRG2	proline-rich Gla(G-carboxyglutamic acid)polypeptide 2	5639	no
NOSIP	nitric oxide synthase interacting protein	51070	no
SDF2	stromal cell-derived factor 2	6388	yes
ZMPSTE24	zinc metalloproteinase (STE24 homolog, yeast)	10269	yes
ZNF345	zinc finger 345	25850	yes
VPS39	Vam6/Vps39-like (KIAA0770)	AB018313	no
KRAB.94	KRAB box and Zn-finger, C2H2 type	CA773758	n.a.
DZIP3	zinc finger DAZ interacting protein 3	9666	yes
SUPT6H	suppressor of Ty 6 homolog (S. cerevisiae)	6830	yes
FLJ33696		AK091015	no
CAPN3	calpain 3, (p94)	825	no
DPP4	dipeptidylpeptidase 4	1803	yes
CPEB3	cytoplasmic polyadenylation element binding protein 3	22849	yes
DCC	deleted in colorectal (and gastric) cancers	1630	no
DKFZP564G2022		25963	yes
KIAA1524		57650	yes
wydey		AL602942	n.a.
karo		W88511	n.a.
smarwo		BI917433	n.a.
peyjor		BG181173	n.a.

+ CTU

Gene	Description	LocusLink/Acc.N.	Mouse cons.
FLRT2	fibronectin leucine rich transmembrane protein 2	AA330057	n.a.
HCCS	holocytochrome c synthase (cytochrome c heme-lyase)	3052	no
RAD51	RAD51 homolog (RecA homolog, E. coli) (S. cerevisiae)	5888	no
LOC90408		CA867896	n.a.
perva		BG329674	n.a.

+++ CCAAT NON CANONICAL POSITION

FUNCTIONAL LOCALIZATION		LocusLink/Acc.N.	up\in\do
PSMC6	proteasome 26S subunit, ATPase, 6	5706	up
SNAPC1	small nuclear RNA activating complex, polypeptide1	6617	up
BCL11B	B-cell CLL/lymphoma 11B	64919	up
MARK2	MAP/microtubule affinity-regulating kinase 2	2011	up
SHOX2	short stature homeobox 2	6474	do
ZNF323	zinc finger protein 323	64288	up
METTL2	methyltransferase like 2	55798	up\in
ITM2C	integral membrane protein 2C	81618	up\in
PITPNM3	retinal degeneration B alpha 3	83394	in
BRF1	subunit of RNA polymerase III transcription initiation factor IIIB	2972	in
MPRG	membrane progestin receptor gamma	54852	in
FLJ10900	flavodoxin activity	55253	in
USP10	ubiquitin specific protease 10	9100	in
PSCDBP	pleckstrin homology, Sec7 and coiled-coil domains	9595	up
SLC8A2	Sodium/calcium exchanger protein	6543	do
DPP10	dipeptidylpeptidase 10	57628	in
PGRMC1	progesterone receptor membrane component 1	10857	up\in
TLP19	endoplasmic reticulum thioredoxin superfamily member	51060	in
KLHL3	kelch-like 3 (Drosophila)	26249	in
RUNX2	runt-related transcription factor 2	860	up
LRP2	LDL receptor family member glycoprotein 330	4036	up\in
CAV1	caveolin 1, caveolae protein, 22kDa	857	in
MSX2	msh homeo box homolog 2 (Drosophila)	4488	do
C22orf4	RabGAP/TBC domain, putative GTPase activator	25771	up\in
GNA12	guanine nucleotide binding protein (G protein) alpha 12	2768	in
BIGM103	BCG-induced gene in monocytes	64116	up\in
CHRNB1	cholinergic receptor, nicotinic, beta polypeptide 1	1140	in
snRNA U1		-	-
pkinase.19	doublecortin CaM kinase-like 1 family member (KIAA1765)	BG207160	in
SNX6	sorting nexin 6	58533	up
HATPase_c	ATP-binding region, ATPase-like	BF701789	in
Tropomyosin.1	KRAB box and Zn-finger (LOC126017)	AI023896	up
M.13	M protein repeat motif (KIAA1276)	AB033102	up
LOC126731		126731	in
KIAA0318 **(X2)**	RIM binding protein 2	23504	in
KRAB.147	FLJ36040	BC039903	up
F-box.23	Cyclin-like F-box motif (FLJ11467)	80028	in
LOC91661		BC001610	up\in
LOC285527		BF509863	in

++ CCAAT NON CANONICAL POSITION

FUNCTIONAL LOCALIZATION		LocusLink/Acc.N.	up\in\do
RFC3	replication factor C (activator 1) 3	5983	up
GTF2H2	basic transcription factor 2	2966	up
HCMOGT-1	sperm antigen HCMOGT-1	92521	in
GABRA4	gamma-aminobutyric acid (GABA) A receptor, alpha 4	2557	in
D1S155E	NRAS-related gene	7812	up
ADRBK2	adrenergic, beta, receptor kinase 2	157	up\in
NOPE	likely ortholog of mouse neighbor of Punc E11	57722	up\in
PAX2	paired box gene 2	5076	up
NKX6-1	NK6 transcription factor related, locus 1 (Drosophila)	4825	last in
RHCE	Rhesus blood group, CcEe antigens	6006	up
MTPN	myotrophin	136319	up
FEZL	likely ortholog of zebrafish too few (tof)	55079	up\in
EIF3S8	eukaryotic translation initiation factor 3, subunit 8	8663	up
BRD2	bromodomain containing 2	6046	up\in
RAB3C	member RAS oncogene family	115827	up\in
LOC161527	coiled coil-4 domains	161527	do
zf-C2H2.32	(LOC1524859)	AK091130	up
KRAB.149	MGC5384	BG721665	up\in
KRAB.155	LOC91661	91661	up
F-box.28	(KIAA1332)	AK055598	up
SCAN.25	zinc finger protein 42 (LOC284312)	AK091098	do
CNTN4	contactin 4	152330	in
HOM-TES-103	intermediate filament-like	25900	in
FLJ22170		80169	up\in
LOC338811		AL834160	up\in
torgar	similar to p18,inhibits CDK4	BC025350	in
DUF105.17	(KIAA0930)	BC038414	up
zf-C2H2.150	(LOC90333)	AA354849	in
FLJ13798		79831	up\in
LOC151658		BI459706	in
LOC351624		BU734267	in
seybey		BQ011841	in
sopu		BF514827	do
joma		T78282	in

+ CCAAT NON CANONICAL POSITION

FUNCTIONAL LOCALIZATION		LocusLink/Acc.N.	up\in\do
PAI-RBP1	PAI-1 mRNA-binding protein	26135	up\in
SCARB1	scavenger receptor class B, member 1	949	in
TM7SF3	transmembrane 7 superfamily member 3	51768	up\in

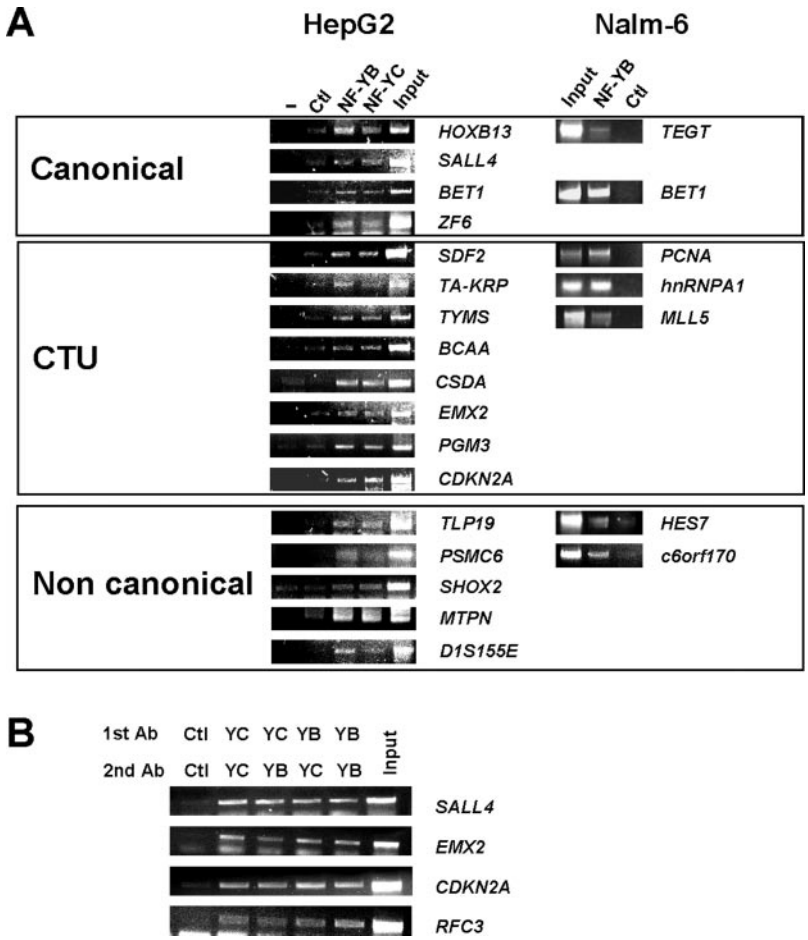

FIG. 2. **Validation of the positive clones.** *A*, conventional ChIP analysis (*upper panels*) of several NF-Y targets from the HepG2 screening with the anti-YB, anti-YC, and control antibodies. In the *right panels*, positives from the Nalm-6 screening were validated with the anti-YB antibody. *B*, sequential ChIPs were performed with the indicated anti-NF-Y antibodies or with the controls. Details on the oligonucleotides used are shown in Supplemental Table I.

transcription-PCR. The results are shown in Fig. 5. The control YBL1 transcript generated by a CCAAT-less promoter was unchanged (Fig. 5, *bottom panel*). All other loci were variously affected; in some cases (CDC10, BET1, and EMX2), the effect of the YAm29 was relatively modest with respect to the controls. For other genes, reduction was quite severe; expression of TIMP3, MTAP, TIP-1, and SHOX2 was nearly abolished. We also analyzed two complex loci. In the TYMS-s.FLJ147447 divergent units, both mRNA were affected, albeit modestly; in the TLP19 locus, in which the CpG island is located between exons 2 and 3, we analyzed three transcripts: in addition to TLP19, the convergent SBBI18, generated just upstream from the CpG island, and the divergent FLJ14844, which starts far upstream. Interestingly, the TLP19 and SBBI18 were severely affected by YAm29, whereas FLJ14844 was not. Taken collectively, these data confirm that the targeted genes are indeed affected by inhibition of NF-Y activity and that CTUs can be regulated simultaneously.

DISCUSSION

The results of the ChIP on chips analysis presented here represent a major and unexpected advance in our understanding of NF-Y genomic strategy in two specific directions: the identification of a high proportion of CTUs and of NF-Y sites away from promoters found in introns or at distant 3′ or 5′ locations.

The number of NF-Y-regulated genes found in our analysis is more in line with the 7.6% figure recently obtained by Fitzgerald *et al.* (2); in fact, were NF-Y indeed involved in the majority (67%) of promoters, as suggested by Suzuki *et al.* (1), we would expect a much larger number of positive clones. However, several considerations can be put forward to explain the relative paucity of isolated targets. (i) In the 7776 CpG experiments, we applied a stringent cut-off by normalizing for the higher signals observed with anti-YB DNA in clones containing repetitive sequences; recent reports, however, suggested that CCAAT boxes are present and conserved in some families of repetitive DNA of retroviral origin (36). This finding matches the well known importance of NF-Y sites in many (actually most) retroviral long terminal repeats (reviewed in Ref. 7).[4] Thus, our normalization is likely to have obscured a larger set of targets. (ii) It is likely that only a minority of genes are expressed at high levels in all cells and hence activated by NF-Y at all times. Many of the ubiquitous genes, in fact, are only active under specific circumstances (stress, apoptotic signals, a specific cell cycle phase, or environmental stimulus). Cell cycle promoters, for example, to which NF-Y association fluctuates considerably (10), are potentially underrepresented; indeed, other anti-YB positives, such as cyclin B1, that scored between 1.5 and 2 in fluorescence intensity above the FLAG control in the 7776 array are bona fide NF-Y targets.[5] (iii) In similar ChIP on chip experiments, an equivalent number of clones were retrieved for MYC (28) and fewer for E2F4, E2F6, and methyl CpG binding domain proteins (20, 27, 30). Alternative approaches indicate that MYC high affinity sites are only a part of the overall binding strategy (37). Thus, it is likely that our data constitute a fraction of all of the potential NF-Y targets. (iv) Most importantly, only clones that showed positivity for multiple hybridizations were considered. In the case of the 12K array, positivity was scored in 15–20% of clones of the individual

[4] G. Donati and R. Mantovani, unpublished results.
[5] A. Testa and R. Mantovani, unpublished results.

TABLE II

NF-Y-targeted genes in Nalm-6 cells are classified according to same criteria used in Table I

+++ CCAAT CANONICAL POSITION

Gene	Description	LocusLink/Acc.N.	mouse cons.
TEGT	testis enhanced gene transcript (BAX inhibitor 1)	7009	yes
PXMP4	peroxisomal membrane protein	11264	yes
BET1	Golgi vescicular membrane trafficking protein p18	10282	no
CENPF	centromere protein F	1063	yes

++ CCAAT CANONICAL POSITION

Gene	Description	LocusLink/Acc.N.	mouse cons.
STX16	Syntaxin 16	8675	yes
BCL2L11	BCL2 like 12	10018	yes

+++ CTU

Gene	Description	LocusLink/Acc.N.	mouse cons.
RPNS1	splicing related factor	10921	yes
BM766743		BM766743	yes
RAMP	RA-regulated nuclear matricx-associated protein	51514	yes
DKFZP434B16	hypothetical protein	25896	yes
CBX5	chromobox homolog 5	23468	yes
hnRNPA1	heterogeneous nuclear pribonucleoprotein A1	3168	yes
MLL5	myeloid/lymphoid or mixed-lineage leukemia 5	55904	n.a.
BC017007		BC017007	n.a.
ZNF261	zinc finger protein 261	9203	n.a.
AI791676			n.a.
NUDT2	nudix-type motif 2	318	n.a.
BU660279		BU660279	n.a.
HMGN3	high mobility group nucleosomal binding domain 3	9324	n.a.
AL525401		AL525401	n.a.
GART	phosphoribosylglicinamide formyltransferase	2618	yes
SON	SON DNA binding protein	6651	yes
PCNA	proliferating cell nuclear antigen	5111	yes
CDS2	CDP-diacyl glycerolsynthetase 2	8760	yes

++ CTU

Gene	Description	LocusLink/Acc.N.	mouse cons.
KCTD1	potassium channel tertramerization domain containing 10	83892	no
UBE3B	ubiquitin protein ligase E3B	89910	no
LYAR	hypothetical protein(Znfinger domain)	55646	no
ZNF509	Zinc finger protein 509	166793	no
TNFRSF6	tumor necrosis factor receptor superfamily member 6	355	yes
ACTA2	actin alpha smooth muscle aortic	59	n.a.

+ CTU

Gene	Description	LocusLink/Acc.N.	mouse cons.
AP4B1	adaptor-related protein complex 4beta1	10717	no
DCLRE1B	DNA cross-link repair 1B	64858	no
LIG3	ligaseIII,DNA,ATP dependent	3980	no
CCT6B	chaperonin containing TCP1 subunit 6B (zeta 2)	10693	no

+++ CCAAT NON CANONICAL POSITION

FUNCTIONAL LOCALIZATION		LocusLink/Acc.N.	up/in/do
AMD1	Adenosylmethionine decarboxylase 1	262	in
ABCG2	ATP-binding cassette subfamily G, member 2	9429	up
HES7	hairy and enhancer of split 7	84667	up
AK056941	hypotetical protein		up
KIAA1539	KIAA1539	80256	up
LOC51244	hypothetical protein	51244	up
FLCN	folliculin	201163	up/in
VPS52	vacuolar protein sorting 52	6293	do
BG619122		BG619122	in

++ CCAAT NON CANONICAL POSITION

FUNCTIONAL LOCALIZATION		LocusLink/Acc.N.	up/in/do
CACNA2D3	calcium channel voltage dependent alpha2delta3 subynit	55799	in
GALNT2	GalNAc-T2	2590	in
DXYS155E	DNA sement on chromosom X and Y 155 expressed sequence	8227	in
ASMT	Acetylserotonin o-methyltransferase	438	in
GPR160	G proteincoupled receptor 160	26996	in/up
CR626017	hypothetical protein	CR626017	up
UBE2D3	ubiquitin conjugating enzymeE2D 3	7323	up
GAS2L1	growth arrest -specific 2 like 1	10634	up
CHPT1	choline phosphotransferasi 1	56994	up
CPN12	Calpain 12	1047968	in
DNAJB6	DNAJ(HSP40) homolog B6	10049	in
GDF6	growth differentiation factor 6	382255	in
KIAA0101	unknown	9768	in/do
MGC4093	hypothetical protein	80776	up

+ CCAAT NON CANONICAL POSITION

FUNCTIONAL LOCALIZATION		LocusLink/Acc.N.	up/in/do
BX104541		BX104541	in
SH3GL1	SH3-domain grb2-like 1	6455	up
SYNJ2	synaptojanon 2	8871	up
C6ORF170	chromosome 6 open reading frame 170	221322	up
PSMB7	proteosome subunit beta type,7	5695	up
CR608644	cDNA clone	CR608644	in
c9orf52	chromosom9 open reading frame 52	158219	in
MSRA	methionin sulfoxide reductase A	4482	in
NAALADL2	N-acetylated alpha-linked acidic peptidase 2	254827	in
SPAG16	sper associated antigen 16	79582	in

PROMOTER no CCAAT

Gene	Description	LocusLink/Acc.N.
ICK	intestinal cell (MAK-like) kinase	22858

INTRON no CCAAT

Gene	Description	LocusLink/Acc.N.
FAM49B	family with sequence similarity 49B	51571

experiments, yet only 119 of them overlapped. We believe that suboptimal hybridization conditions prevent the successive and reproducible identification of the same set of targets, precluding the possibility of calculating the exact number of NF-Y-targeted loci. These shortcomings notwithstanding, our data lead to several interesting considerations.

Conservation of NF-Y Sites—Among the identified genes, only four were previously established through mutagenesis of CCAAT, but not by ChIP analysis: (i) the *UNG2-UNG1* tandemly linked genes were functionally dissected, and CCAAT boxes were found to be of importance for both genes (38); (ii) *TIMP2* (and the related *TIMP1/3*) are clearly under NF-Y control (39–42); (iii) proliferating cell nuclear antigen, a CTU in which the CCAAT box is found in the first intron (43); and (iv) *MTAP*, a gene in which two separated suboptimal CCAAT boxes are important (44). For others, NF-Y-binding was more than suspected. (i) The divergent promoters of the H2B-H3 and of H2A-H4 loci belong to the wide family of histone genes; detailed mutational analysis of other histone promoters clearly evidenced the importance of NF-Y (45, 46). (ii) Functional analysis of the *NKX6.1* promoter pointed to a double CCAAT region as essential (47). (iii) *PAX2* and *TLP19* belong to gene families for which formal proof of NF-Y involvement was obtained with other members: *PAX3/7/8* (48–50) and other endoplasmic reticulum stress-inducible genes, respectively (51–53). The analysis of the conservation between human and mouse promoters represents a good example of phylogenetic footprint, since 52 of 72 (74%) mouse orthologous promoters do contain CCAAT at the expected position; this percentage increases to 86% if we consider the optimal NF-Y sites (Tables I and II). Thus, the notion that conservation of the CCAAT is an integral part of the expression strategy within gene families and across species is reinstated.

The CCAAT Box and Complex Transcriptional Units—It is somewhat surprising to find a high frequency of CTUs in our analysis; 24% of the loci analyzed contained bidirectional promoters, and 15–17% contained tandem promoters. Most bidirectional promoters are divergent (60%), and the rest are convergent, generating partially overlapping transcripts. This result was not anticipated; previous data identified only a minute number (essentially histones, UNG1-UNG2, and AIRC-GPAT) actually containing such units (7).[6] An unexpected abundance of bidirectional promoters in the human genome has recently been documented; as many as 11% of the total are divergent, either with overlapping or nonoverlapping transcripts (35, 54). Furthermore, the bidirectional arrangement is often conserved among mouse orthologs and important for expression of both transcripts. We analyzed the ChIP on chip experiments previously performed on the 7776 array, obtaining figures of 15% for E2F4 and 23% for MYC targets as bidirectional promoters (27, 29). This suggests that (i) MYC and NF-Y sites are enriched in bidirectional promoters and/or (ii) that CpG islands are indeed specifically abundant in such units. CCAAT-less bidirectional promoters, do exist (*e.g.* the YBL1 promoter analyzed in Figs. 1 and 5); NF-Y, therefore, cannot be considered as a hallmark for such units. Nevertheless, in all systems tested so far, centrally located CCAAT boxes are important for the expression of divergent genes (45); the data obtained with the dominant negative NF-Yam29 presented in Fig. 5 on the TYMS and TLP19 loci confirm this assumption. The biological significance of the higher frequency of complex CTUs regulated by NF-Y as well as the molecular details of divergent co-regulation require further dissection.

CCAAT at Distant Locations—A second unanticipated result is the abundance (40–50%) of sites away from promoters, with almost half of them located in introns. This clearly means that NF-Y is not a promoter-specific factor. It is im-

[6] R. Mantovani, unpublished results.

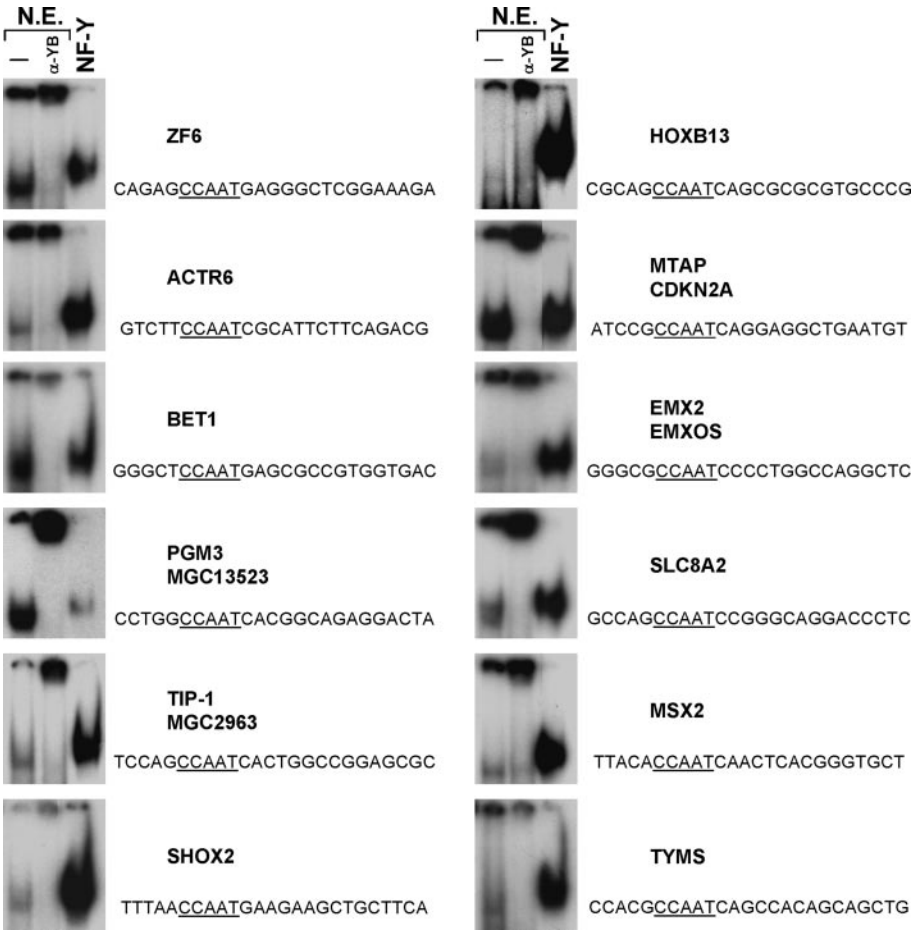

FIG. 3. **Identification of NF-Y-binding CCAAT boxes.** Shown is an EMSA analysis of CCAAT boxes of genes regulated by NF-Y, as in Fig. 4. Labeled oligonucleotides, depicted for each target, were labeled and incubated with 5 μg of HepG2 nuclear extract alone or in the presence of anti-YB supershifting antibody. Recombinant NF-Y (1 ng) was incubated in parallel. The different electrophoretic mobility of the latter is due to the presence of a thioredoxin moiety in the NF-YC subunit.

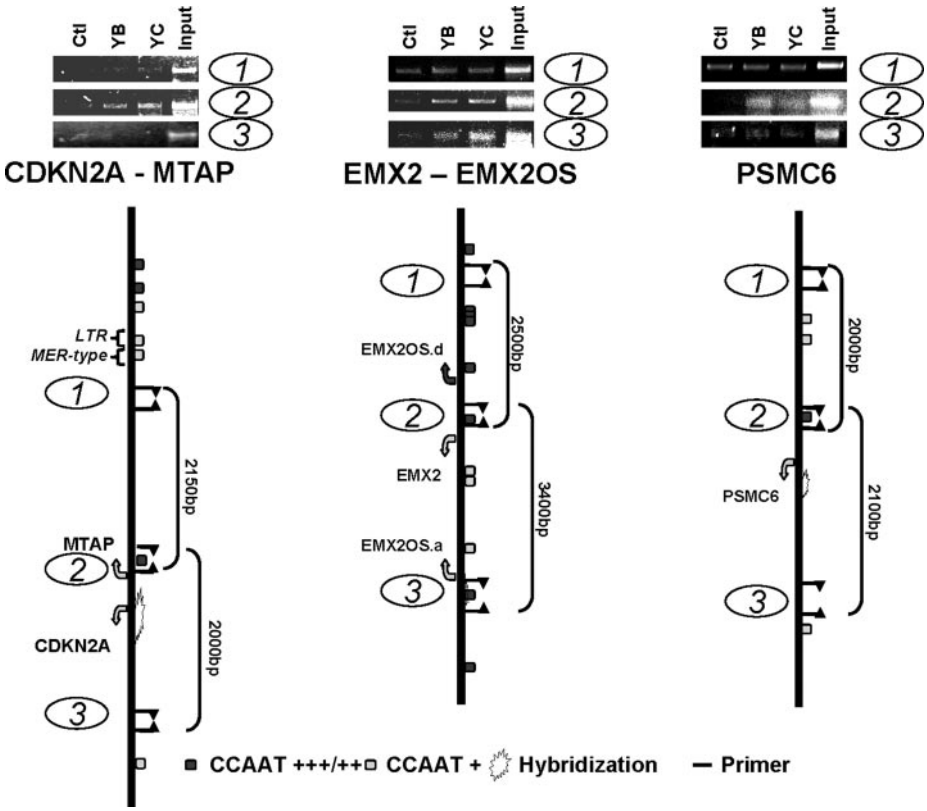

FIG. 4. **ChIP scanning of NF-Y binding to CCAAT boxes.** ChIP analysis of HepG2 chromatin with the indicated antibodies was performed on three different loci. Different amplicons, as indicated in the schemes, were amplified and shown in the *upper panels*.

portant to emphasize that this finding would have been completely obscured had we used a promoter array chip, as available information on CCAAT locations would have suggested. Of course, the assumption that the CCAAT box was almost exclusively a promoter element was based upon standard promoter-driven analysis, thus merely reflecting the fact that

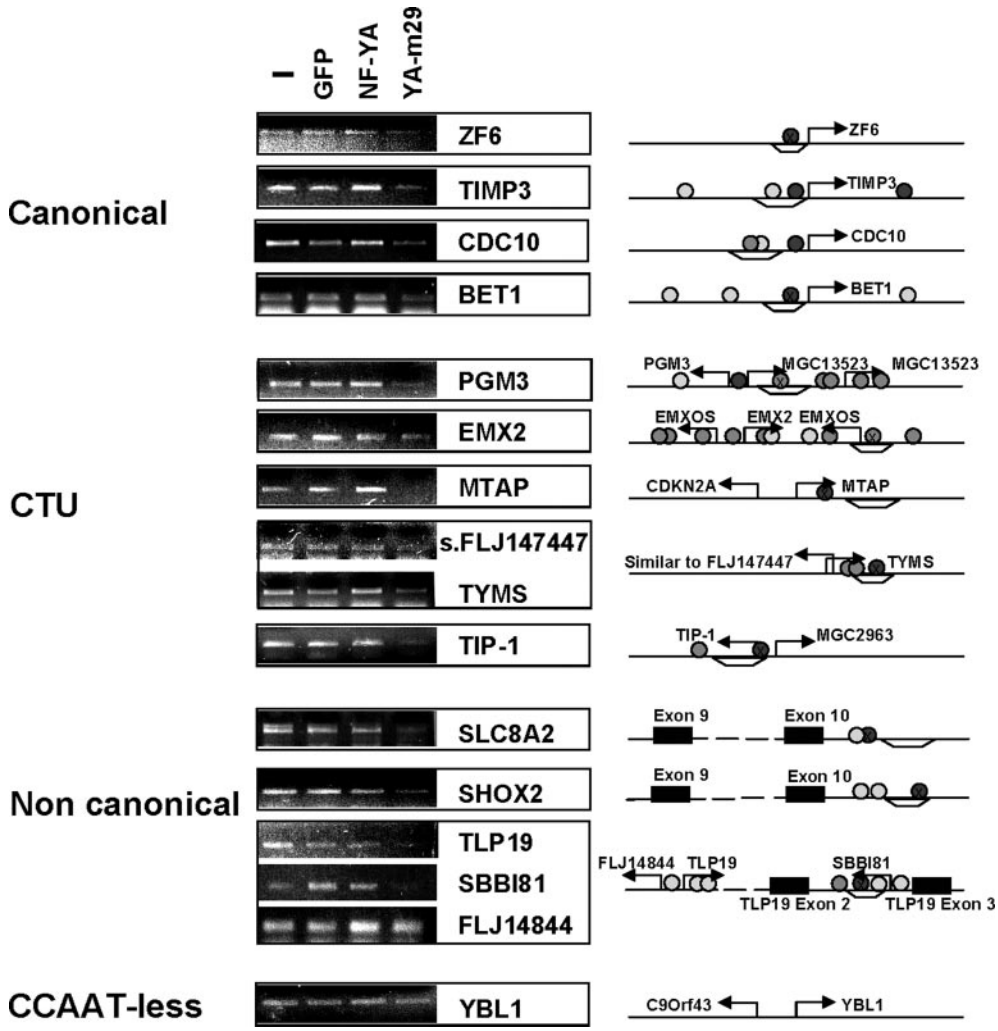

FIG. 5. **Functional importance of NF-Y binding for target genes expression.** Shown is semiquantitative reverse transcription-PCR analysis of mRNAs extracted from HepG2 cells uninfected or infected with control green fluorescent protein (*GFP*) adenovirus or with adenovirus producing wild type or the DN YAm29 mutant, respectively. The unaffected CCAAT-less YBL1 transcript was used for mRNA normalization. Details on the oligonucleotides used are shown in Supplemental Table II. The positions of the CCAAT boxes are marked by *circles* (+ (*light gray*), ++ (*gray*), and +++ (*dark gray*)), positions of exons are marked by *black boxes*, positions of the hybridizing CpG island clones are marked by *white boxes*, and positions of transcripts are marked by *arrows*.

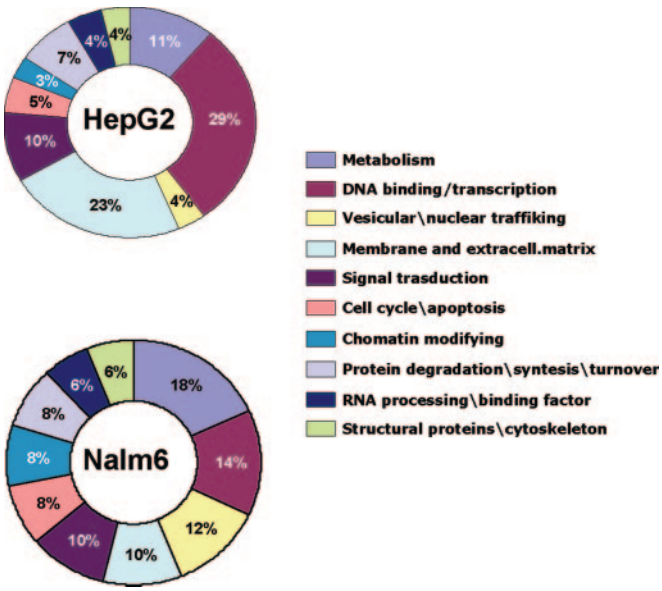

FIG. 6. **Functional classification of NF-Y target genes.** The genes targeted by NF-Y whose function is known or inferred were classified according to the function of the encoded protein.

far greater information had been gathered from such sequences. Only a handful of cases of distant locations were previously described. (i) In the major histocompatibility complex class II genes, upstream enhancers were shown to be dependent upon Y-boxes and neighboring RFX-binding sites (34). (ii) Sequences were found in the *HOXB4* gene, that contain a highly conserved NF-Y site in a crucial intronic enhancer (in fact, it is not even a perfect pentanucleotide, CCATT or GCAAT), and similar deviant sequences were noticed at corresponding locations in other introns of *HOX* gene clusters (33). Interestingly, CCAAT boxes exist in *HOX* gene promoters as well (55–57), one of which (*HOXB13*) was identified here; they are perfect CCAAT, whereas the intronic ones are modified, most likely to accommodate the binding of additional cooperating factors, as shown for YY1 in the case of *HOXB4* (33). This suggests that there might be a plethora of specialized CCAAT versions, slightly deviating from optimal sites. It is even possible that we are largely underestimating the number of binding sites by focusing on the perfect pentanucleotide. NF-Y binding has been so far invariably associated with regulatory regions, which is confirmed by the expression analysis with the dominant negative NF-Yam29 shown here. An important implication of our data, therefore, is that new enhancers or regulatory regions could be uncov-

ered via this strategy. *In vivo* functional dissection of the distant regions isolated here with enhancer-based assays is necessary to establish this point.

Functional Classification of NF-Y Targets—Fig. 6 shows the functional classification of the annotated genes. In both HepG2 and Nalm-6, prominent classes are (i) DNA-binding and transcription factors in general, which represent >25% of the total, and (ii) membrane/extracellular matrix proteins coding genes and signal transduction genes. Far fewer genes code for structural proteins, proteins involved in mRNA processing and in vescicular and nuclear trafficking. This could be due to particular skewing of the CpG library (16), but we note that many of the genes identified in both HepG2 and Nalm-6 are indeed important for cell growth.

An important corollary to this analysis is the identification of genes that are targeted by NF-Y and MYC/E2F4. *LALP1*, *MRS3/4*, *GTF2H2*, and *EIF3S8* are shared with MYC; *CSDA*, *RAD51*, *TYMS*, and *D1S155E* are shared with MYC and E2F4. Thus, new transcriptional networks can be constructed; this is particularly relevant, since NF-Y is known to be cooperating with E2Fs in many systems (58) and to be controlled by MYC through direct protein-protein interactions (59). A precise mapping of the E2F and MYC regulatory areas, possibly adjacent to CCAAT boxes, as well as functional co-expression experiments, should provide a clue for their coregulation.

In conclusion, although we are still far from having a complete map of NF-Y targets on hand, the criteria employed here reveal new twists in the genomic strategy, mainly concerning its role in complex units and at nonpromoter locations. To build a complete understanding of the transcriptional networks in which the trimer takes part, it will be important to widen the analysis to lower affinity sites, in different cell types, under various growth conditions and with various partner activators.

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Supplementary 1

List of Chip oligonucleotides.

HOXB13	5'cttgcgagctgggagcgattta3'
	5'cccagcaagccttcgatatcct3'
CDKN2A	5'ggctagacacaaaggactcggt3'
	5'caggaacagccgcgctcc3'
PGM3	5'ggcccgcatccccctctc3'
	5'ggctccggacgtttacgattcact3'
SALL4	5'cttctcggctggtggacatc3'
	5'ctccgccacaaattcctggag3'
D1S155E	5'gttccttgaggacaagtctatatccg3'
	5'gagatgattcatccaatgggggaag3'
CSDA	5'ccttgtcagctgcgggtgtc3'
	5'agggcgggcgaggggaga3'
BET1	5'agcgggaacgttggatcagagac3'
	5'agggcccagcgaaacaccaactt3'
EMX2	5'ccctcactccaggatccctc3'
	5'ggcttgatgattggtcgctattactc3'
PSMC6	5'cccgggaggtggaggttgc3'
	5'gggtgggggttgtgggtagaaa3'
BCAA	5'gaggccatccgggaaagaggta3'
	5'ggggaggggacgacgaaaaat3'
ZF6	5'ctcagggcgcgcttttaagg3'
	5'cgagccctcattggctctga3'
TLP19	5'gatgagggaagccaatggtcaa3'
	5'ccaggccttgggtttacagcat3'
SHOX2	5'gggaggattccccatctgacac3'
	5'aactatccccacacaggcagca3'
SDF2	5'atggtaattggagagggatgtgaa3'
	5'taccgtctggagaggcttagt3'
MTPN	5'caggcatgagccactgcac3'
	5'agtcagttctgttcttcctagggt3'
TA-KRP	5'cgacggccacaggctgg3'
	5'caccacacgacccacctgc3'
TYMS	5'ccgacaggagcaccccag3'
	5'ggtccgtgggccggag3'
RFC3	5'agaccttgcaatcaaatggcagga3'
	5'gcgtcgatgccctctagttc3'
α Galactosidase A	5'actcgggatcactaaggtgccg3'
	5'ccggacagcataaatttccgcg3'
MVK	5'cacagctggccgcgccacc3'

	5'cagagcgcccgtgcctcaag3'
OAT	5'gctcaggaggcgcgaggcg3'
	5'ggtacctgacagcgcctgag3'
mATPsynthase β	5'acaggaactcggccccttcct3'
	5'gcgtagtccgggtggagactg3'
OGG1	5'cggagtgcagacaatcccgg3'
	5'ctccttgcgacttatcttctcc3'
NP95	5'ccgcgattcaattgtcgcgcc3'
	5'ccctggaccctcggcgtcc3'
PPP1R7	5'gcggcctcatgacggaactac3'
	5'actgttgctgccccgcgccg3'
CDC25A	5'cttctgctctgggctccgcc3'
	5'caagccgacctacacctcttac3'
HMGB2	5'cagccccaaccagtcagcgtg3'
	5'cccaacggagacgcttccctc3'
hnRNP A1	5'catgctttgccaagcgacttgac3'
	5'ggagcaagctgacgaacgtatc3'
β actin	5'caccccaaggcggccaacgc3'
	5'cgcgtcgcgccgctgggttt3'
ABL	5'cacacgccacacaacgtgag3'
	5'ccaatgagttgcgcaggcgc3'
p107	5'tacacctcccagcaggctctg3'
	5'ctcccaggcgcgctacccac3'
α tub	5'gccgttgggtggagtcagcg3'
	5'cagaaagtggcccctcagcat3'
HMGB1	5'tcagcctctttgcccggcatac3'
	5'gtgagagcgggagccagacg3'
RPS19	5'ccaggcctccacgcgcgac3'
	5'cagctcggagcccccgcttac3'
YBL1	5'gcctgcctcgggtcctaaaggg3'
	5'ggtctgaccctgcgaggtttccgtt3'
TEGT	5'agccaatggaaaggcaggagt3'
	5'catctgtccgcagaaggaagc3'
MLL5	5'tttgcaacagcctccccctac3'
	5'cgagggagggacagacagtga3'
HES7	5'atctttaagccgcgcattggt3'
	5'ctggggctgcaaactctgcta3'
c6orf170 up	5'gatatgccaagtcggtgctgtg3'
	5'cgaatcccttaacgtgccaaaa3'
PCNA	5'aaccggttacctccagaaccag3'
	5'ggggtcagccttccctagcc3'

Supplementary 2

List of RT-PCR oligonucleotides.

CDC10F	GAG GAG AGG AGC GTC AAC AGC
CDC10R	GAT ACT GCC TTC CTC TGA CCC T
TIMP3F	TCG GGC TCA TCG TGC TCC TGG G
TIMP3R	GAT ACC GAT AGT TCA GCC CCT TGC G
BET1F	CTG GCA ACT ATG GGA ACT ATG GC
BET1R	GCT TTG TTT GGC TCC CTC TGG
Znf6F	CCT GGG TTG TTG GTG TGG AGT G
Znf6R	TGC TGA TGT TGA ATG AGG CTG CTC
MTAPF	ATT GAC AGG ACC ACT ATG AGA CC
MTAPR	TCT TCA GGT TAT GGA GGG TTT CT
PGM3F	CCT GGT GGA GAT TGG AGA AAG TTT G
PGM3R	CCT GGG GGT GTA ACT GCT TGT C
TIP1F	GAA GAC AAG ACG GAC AAG GGT ATT TAT G
TIP1R	CAG ACG CAC CAC CTC CTC CGA
EMX2F	GCC CCA TAA ATC CGT TCC TCA ACG
EMX2R	CAT ACT TTT ACC TGA GTT TCC GTG AGG
SHOx2F	CCG AGT GCA GGT TTG GTT TCA
SHOx2R	ATG CTG GAG TTC TTG CTG GTG
SLC8A2F	TCA AGG GGA TGG GGA CAG GAA
SLC8A2R	GGC GAA GAG GAT GTA CAG GAG
TPL19(ERp19)F	TCG TCT CGG GGC CAC CTG TTT G
TPL19(ERp19)R	CAT CCC CTG AAC AAC TTG CTC GG
SBBI80(TPL19locus)F	CCG CTC TGC CTG GTC TAC TGC
SBBI80(TPL19locus)R	GCG TAG ACT GAT GGG GTG GTG G
FLJ14844(TPL19loc)F	GGG GCA AGG GTA CAG CTC GC
FLJ14844(TPL19loc)R	GCA TTT CTG TGA TTG GTT TGG CTT CTG C
TYMSF	CAA GGG ATC CAC AAA TGC TAA AGA G
TYMSR	TGT GCA TCT CCC AAA GTG TGT ATA AAG
sLOC147447(TYMloc)F	GCT GGG ACG CGG CTT ACC TCC
sLOC147447(TYMloc)R	TCA GGA AGG ACG ACC GCA CGG G

FIGURE LEGEND.

+++ CCAAT boxes are indicated in Red.

++ CCAAT boxes are indicated in Orange.

+ CCAAT boxes are indicated in Yellow.

Primers used for CHIP validations are in Blue.

Arrows indicate the Start Site(s) of the gene(s) and direction of transcription.

ACTR6

GGAGGAGATAGGAACGAGGACGGGATGTGGAGAAGTGGGGAAAGGCAGGCCGACGTTGGCAGGGTGCGAGGAGGCCTTGGAGAAAGGAGGGTGGATGGGG

CAGGCCCCCAGGGGAGGCAAGGAGCGCCGACAGAAGGGCCCAGGCGCTTGCAGGGCGCGAGTTCCCACCTCAAGCACCGTGGCGGCTCCCGCGCTGCGCA

CCTGGAAGTGCGCAGGCTGCTCCGCCGCCTCGTCGGCGCGCTGGTAGCTGAAGCAGGCTTCTGCTATGTCCAGGTGGCCGAGGGGCAGCGGGTCGTGGGG

GTTCTTGAAGTAGCAGAGGCAGCAGCGGCGCCCGTCCAACACGAACCGACGGCTGCGGTAGCCACGCAGTCGCGCTGGTTCCCGCGCGGTACCCGCCCCG

GGCTCTGCAGCCTCCCCATCGCCGTCGCTGCCCTCCTCTGCCCGGGTTCCGGCCCCGGTATGGCTGCCTGCGCGCCAACCGTTTGTTCCCCGGCCCCCGC

GCCTTCGCGCTGCGGCTGCTGCGCTCCCTGCCCCCGCGGTGCCCCCTTCCCGCCGCCCCGCTCCTCTCTCAGGCGCTCAAAGTGGCCTGGAATTTGTAGA

ACGCCCCCCTCCAAGCCCGTTGGCAGTTGTCCTAGCCCGCTGGCCCTTGCCCCCGCCCGCTGGCCGTTGCCCCCGCGACGCCCCGGAAGCCAGGTCCTGC

CTCCCGCACCTGCCAAGTCCCCGCCCTGCCGGAGTCTCGCTCTGTCGCCCAGGCTGGAGTGTAGTGGAGCCATCTCGGCTCACTGCAACCTCCGCCTCCC

CGGTTCAAGCAATTCTCCCGCCTCAGCCTCCCGAGTACTTGGGATTACAGGCGCCCGCCACCTCGCCCGGCTACTTTTTGTATTTTTAATAGAGACGGGG

TTTCGCCGTGTTGGTCAGGCTGGTCTCAAGCTCCTGACCTCAAGTGATCTGCTTGCCTTGGTCTCCTAAAGTGCTGGGATTACAGGCGTGAGCCACCGCG

TCCGGCCCAAAAGCCTTTTTTGGATGAGAAAGACTCACTCAGCTTCGTCCTGAAGAGCAAGTGGGCTGGGGAAGAGGAGAGTATGAATGTGAGTCCAAGA

GCAAGTTTTGCACTTTTTTCTTCAAAGAATGTCACCGTCTGAAGAATGCGATTGGAAGACACACACACACACACACACACACACACACGCAGCCGGTT

CTCTACAGGATTAGAAAAAACTTGCGCGAATTAATCTGCGTAGTTAAAAACAAATACGAAATGAGCGAGAAAGCACATAGTAGTCAAATCTCGCCACCAC

ATAAACAGGTTAAGTTTGGAAGCACAGCCCCTAACATTCGGTGCTGCTTAGCATCTCCGACTTCCGGCGTCCTCCGTTGCTAAGGTGACCAGAGGCGCGT

ACTR6

CCTAACGCTCCGCCCAACAAACCATAGAGTACCGGAAAAAGCTCGAGCAGAGGGGTCGGAAAGGGAAAACAACTACGGCTGCGGTGTGGTTGGTGGTGAG

ATGACGACCTTAGTGCTGGATAATGGAGCTTACAACGCCAAAATCGGTTACAGCCATGAAAATGTGTCGTAAGTACTTTCTTTCTCCGAGGGACAAGATA

TATACGCCTAGTGGTTTCATGTGCTACGTTTCATCTCCGGACATCAATGAACTGCAGACACCCCCGCGCGGCCCTGACTTAGCCAGAGGGATTCCCTGGT

TGGAGCTGGGTGGGTGATTGTGATGCTTTGAATTGAAATTGATTTTGGTTTTAGTTTTGGGCTGCGAGGCCCCGGAAGTGGGATATATGTTTTATTTCGT

AACAGGAAATAGCCAAAGAAAATAGGCTTATAGAGATGCGTTCCTGACAGAAGGGTCCGTAAAGTTCATCAGCCTTTGGAAACTATGGGCACGGTGTTTG

GGTGTATGCGGATTTTCCTGGGTACAAGATTATAGGTTTCATTAGATTCTCAAAGGGTTCTATGACCCTCCAAAAGTCTAAAAATCACGGTCTTAGGATC

TAGAGGCTTTGAAGACTTTGGCCTACTGGCCGACCTAGTTGGTAAGGTCAATTAAACAGAAGTACTGTTAATACAATGGCATTCATAACATGTATAGTCA

TAAAATATATGTTTGAATAAATAAGCAAACCTAAAGACACGCCTTTCCTTTATCAAATTAACAGAGCATTAAAAAAAATTCTTTCCTTCCTCCCTCCTTT

CCTTCTTTTTCATTTCTTTTGAAACAGAAATGAAAGAGGGAAATCAAACTGAGTAGGAATGTAAATTGTTACAATCTTTCTGGAAAACGTTTTGGCAATG

TGTATCATTATCATTGTCACCGAGGCTGGAGTGCCGTGGTGCGATCTCAGCTCACTGCAGCCTGAATTCAAGTGATTCTCCCGCCTCAGCCTCCAGAGTA

GCTGGGATTATAGGCGTGCACCACCACTCCCAGCGAATTTTTTGTATTTTTGTTAGAGACGGGGTTTCATCATGTTGGCCAGGCCGGTCTCGAGCCCCTG

GCCTCAAGCAGTCTACCCGCGTTGGCCTCCCAAAGTGCTGGTATTAGGGGCGTGAGCCCTACACCCAGCTGACAAAGCAATTTTTTTTTTTTTTTTGGA

GAGGGAGTCTGGCTCTCTTGTCCAGGCTGGAGTGCAGTGGCACGATCTCGGCTCGCTGCAACCTCTGCCTCCCGGGTTCAAGCCATTCTCATGCCTCAGC

CTCCCAAGTAGCTGGGACTACAGTTGCGCACCACCACGCCTGGCTAAGTTTTGTATTTTTAGTAGAGACGGGGGTTTCACCATTTTGGCCATGCTGGTCT

GGAATTCCTGACCTCGTGATCTGCCTGCTTCAGCCTCCTAAAGTGCTGGGATTACAGGTGTGAGCCACCGCACCGGGCCATGACACAGCAATTCTGTTAT

TACCTAGAGAATTAATTAGAAGTGCTTTGTATTATTCATAGTCATCGTATACAGGCAGCCAAAAAATGGGAAGGAAGCTAAATAATCAGGAATAGCATAAT

TGGCTAAATACACCAAAATACAACCTGAGACTGATAACAAATTCAAGCTTCTTAAAATTATGTCTTCAAAGAACATTTAAACATGTAGAGAAAATGCTGA

CAGTATTATAAGTGAAATAAGCAGGTGTAAAACATTTTTTTACAGTATTATCCCAGTGTCATCTCGTATACACATACAGACACATTTGTATGCATACATG

TGTGTATAATTAATAATGGCTCTAGTTTGTCTTCCAAACCAGAT

ADRBK2

CCTGGGGAATTACAAAAAAGATAGCTGTTGAAATCTTACAGGCAGAAGACCATAGATAAATTAGTAATACTTTACTCACAGATCAAACTTTTTTTTTTTT

TGAGATGGAGTCTTGCTATGTTGCCCAGGCTGGAGTGCAGTGGTGTAGTCTGGGCTGATTGCCATCTCCGCCTCCTGGGTTCAAGCGATTCGCCCGCCTC

AGCCTCCCAAGTAGTTGGGATTACAGGCATGCGCCACCACGCCTGGCTAATAGTTTTGTATTTTTAGTAGAGACAGAGTTTCACCATGTTGGCCAGGCTG

GTCTCAAACTCCTGACCTCAGGTGATCTAGCTGCCTCAGCCTCCCAAAGTGCTGGAATTACAGGCATGAGCCACCACACCCAGCTCACAGATCAAACTTT

TGATCCAATTTTTACCACCTGCTTAGCACAGCCACCTGAATCAGAGAGTTAGTCCTTACAGAGAGATTTTTTTTTTTTGAGATGAGGTCTTGCTCTATTA

CCTAGGCAGCCGTGCAGTGGCATGCTCATGACTCACTGCAGCCTCGAACTCCAGGGCTCCAGTGATCCTCCCACCTCAGCCTCCCAGGTAGGTGGAACCA

CAGGCACACACAACCATATGGGGCTAATTTCTAAAAGTTTTTTGTAGAGGTGGGGTCTCCCTAAGTTGCCCAAGCTGGTCTTGAACTCCTACCCTCAAAC

TACCCTCTTGGTTTGGCCTCCCAAACTGTTGAGGGATTACAGGTGTGACCCACTGTGCCTGGTCCTCCTAGAAAGACCTTGCAGTGTGGGTAGCACTTAA

AATGGAACAGATGATGTAGGCAAATGCCTTTCTTTAGATGAGGCAATGTGGAAAGGAAGCAGAGCAGACTGACCAAGAGCATGGAGCCTGGTGCCTATGG

CCTGGGTTCAAATCCCACTGAGAAGCTGCACATACCTAGGAGTGTTATGTAAATCTCTCTGTGCTTCAGTCCCTGTTCTGAGATACACGAATGTTAGGCC

GAGCGTGGTGGCTCACACCTATATTCCCAGCACTTTGGGAGGCTGAGGCAGACGGATCACCTGAGGTCAGGAATTCGAGACCAGCCTCATCAACATGGTG

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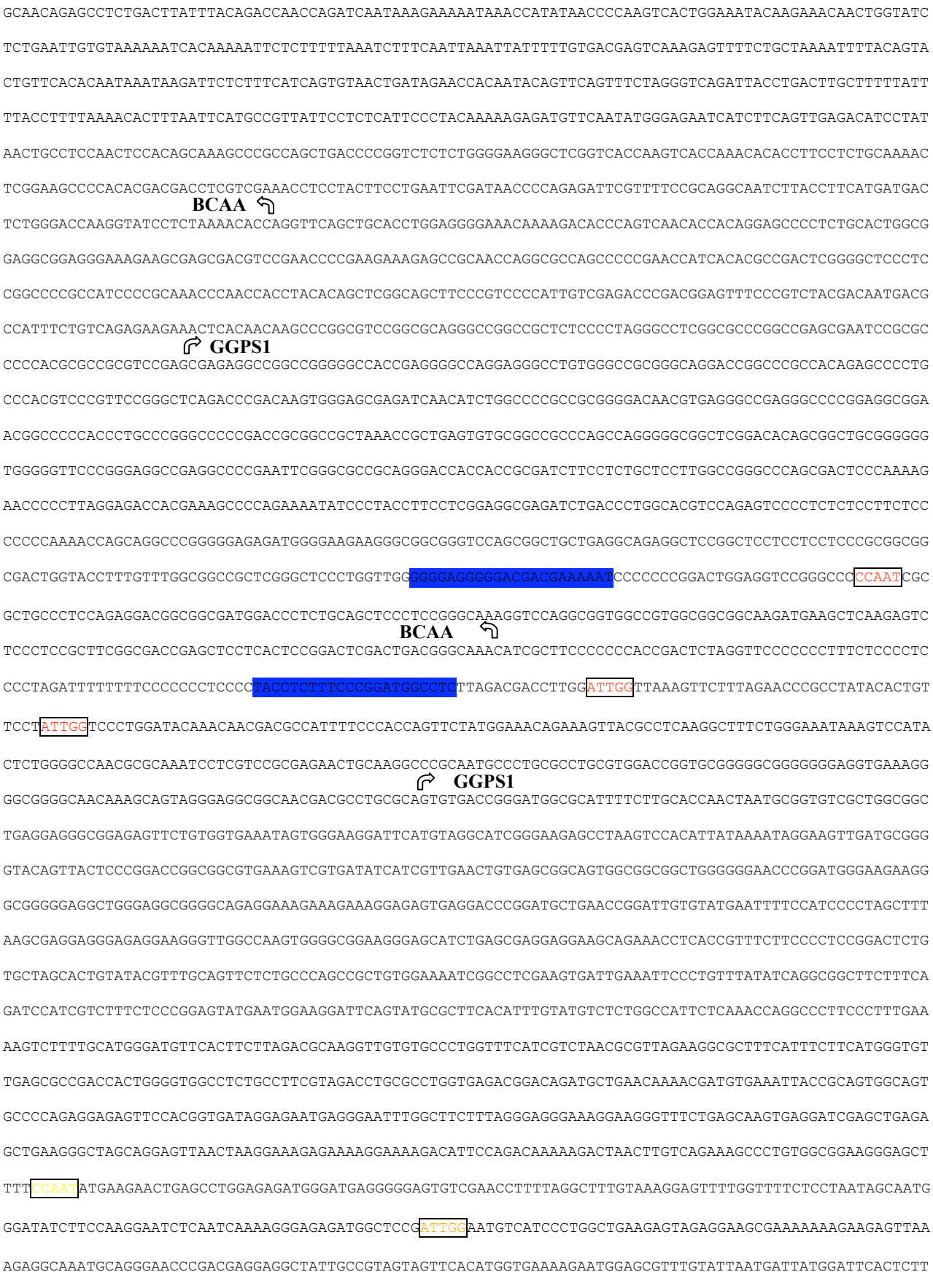

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BRF1 (exon 2)

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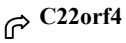

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CLDN15

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CNTN4 (INTRON 2)

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FLRT2

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GABRA4 (Exon 7)

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GAPD

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GNA12 (EXONS 3,4)

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GRIA4

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GRIA4

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GRIA4

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HCCS - perva

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perva

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Hypothetical protein LOC161527

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HIST1H3F - HIST1H2BH

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HOM-TES-103 (LAST EXON)

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HOXB13

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HOXB13

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hypothetical protein BC001610

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hypothetical protein BC001610

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hypothetical protein FLJ13798

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hypothetical protein FLJ13798

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Hypothetical protein FLJ20643 – FLT3LG

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FLJ20643

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FLT3LG

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Hypothetical protein FLJ22170(EXON 3,4,5,6,7)

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Hypothetical protein FLJ33696

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CTAG

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moyroy

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MPRG(Intron 5)

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MSX2

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MTPN

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MTPN

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NKX6-1(EXON 2,3)

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RUN.1

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SCAN.25 (EXON 5,6)

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SCARB1 (Intron 1)

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SDF2

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C6orf182

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Seybey(Exon 2,3,4)

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Shergy (intron 2)

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SHOX2 (last exon)

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shufee (Exon 4)

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Sopu (exon 2)

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swajar

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TIMP3

TIMP3

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TIP-1 – MGC2963

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TLP19 (INTRON 2)

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Torgar (similar to p18)

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Torgar

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Tropomyosin.1

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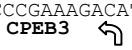

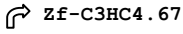

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Chromatin Immunoprecipitation (ChIP) on Chip Experiments Uncover a Widespread Distribution of NF-Y Binding CCAAT Sites Outside of Core Promoters

Anna Testa, Giacomo Donati, Pearlly Yan, Francesca Romani, Tim H.-M. Huang, M. Alessandra Viganò and Roberto Mantovani

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