

Gene Section

Review

CTCF (CCCTC-binding factor (zinc finger protein))

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Identity

HGNC (Hugo): CTCF

Location: 16q22.1

Local order: AGRP, FAM65A, CTCF, RLTPR, ACD, PARD6A.

DNA/RNA

Description

76776 bp gene (Ensembl).

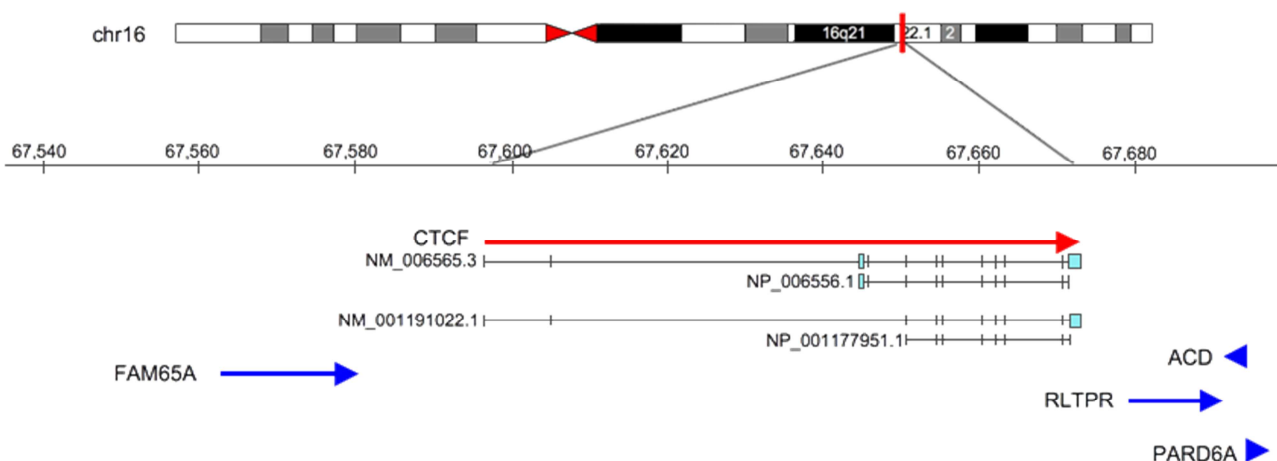


Figure 1. Schematic representation of CTCF location on chromosome 16, gene structure and transcripts. Chromosome 16 is represented with the characteristic banding pattern. The region surrounding the CTCF gene is enlarged. Genes are represented by arrows pointing in the direction of transcription. Transcripts are represented with exons as vertical bars and introns as lines. Distances are in kilo bases (NCBI Map Viewer).

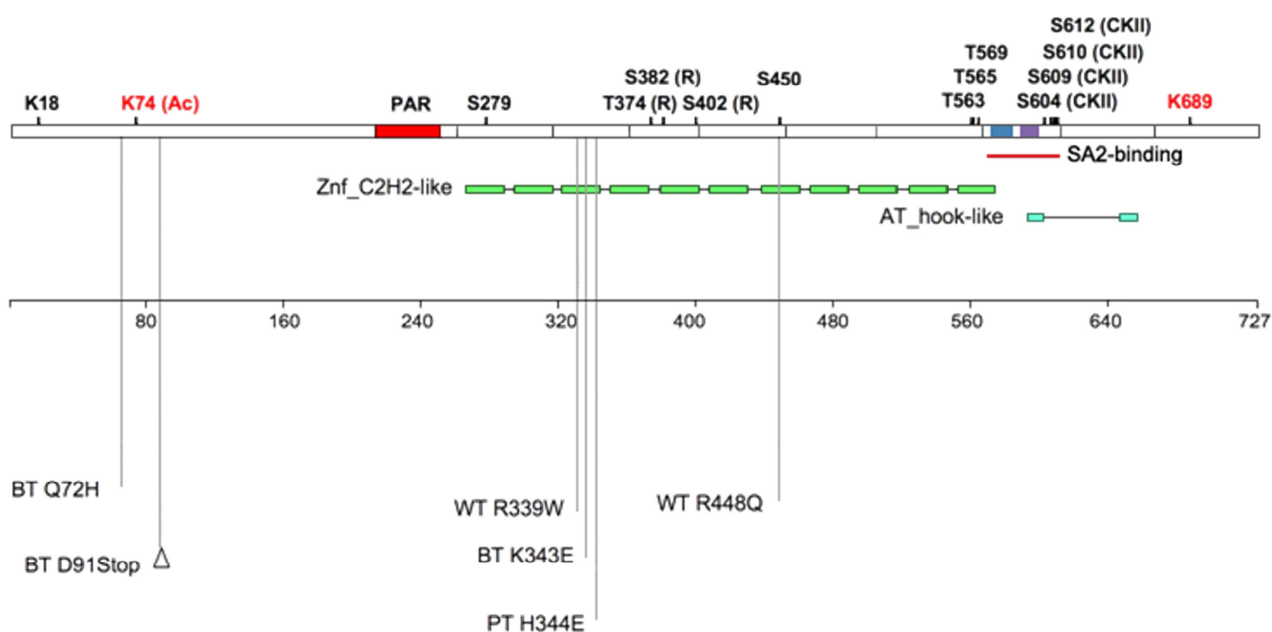


Figure 2. Schematic representation of the CTCF protein. Protein sequences encoded by exons are boxed. 11 ring fingers are indicated by green boxes as also putative AT-hooks by blue boxes (Ensembl). The interaction domain with the SA2 subunit of cohesin is underlined in red (Xiao et al., 2011). Phosphorylated residues are in black (PhosphoSitePlus), those sensitive to rapamycin are indicated by R (Chen et al., 2009) and those phosphorylated by CKII by CKII (El-Kady and Klenova, 2005; Klenova et al., 2001), sumoylated residues are in red (Kitchen and Schoenherr, 2010; MacPherson et al., 2009), acetylated residue is indicated by Ac (Choudhary et al., 2009). The domain containing poly(ADP-ribose)ylation sites (PAR) is boxed in red (Farrar et al., 2010), the NTP-binding site in blue and the NLS in purple. Residues mutated in tumors are indicated (see further), BT = breast tumor, PT = prostate tumor and WT = Wilms tumor.

Transcription

Ubiquitously highly expressed gene (GeneCards), 12 exons, 11 introns with at least 5 differentially spliced transcripts (Ensembl).

Pseudogene

No.

Protein

Description

CTCF was originally described as a c-myc activator (Klenova et al., 1993). It is a 727 aa protein with a MW of 82.8 kD, a charge of 8.5 and an iso electric point of 6.95 (Ensembl). The central domain with 11 zinc fingers of the C2H2 type is highly conserved.

Expression

CTCF is an abundant and ubiquitously expressed protein, yet absent in primary spermatocytes (Loukinov et al., 2002). It is downregulated during differentiation of human myeloid leukemia cells (Delgado et al., 1999; Torrano et al., 2005). Post-translational modifications include acetylation (Choudhary et al., 2009), sumoylation (Kitchen and Schoenherr, 2010; MacPherson et al., 2009), which is regulated by hypoxic stress (Wang et al., 2012a), phosphorylation, in particular ser604-612 by CKII (El-Kady and Klenova, 2005; Klenova et al., 2001), and poly(ADP-ribose)ylation (see figure 2). The latter modification is lost or decreased in proliferating cells

and in BT (Docquier et al., 2009) (for sites and role see Farrar et al., 2010; Yu et al., 2004; Guastafierro et al., 2013). CTCF is a downstream target protein of growth factor-induced pathways and is regulated by EGF and insulin through activation of ERK and AKT signaling cascades (Gao et al., 2007). It was recently shown to be regulated by NF- κ B (Lu et al., 2010).

Localisation

CTCF is localized in the nucleoplasm of proliferating cells with exclusion from the nucleolus. It was detected at the centrosomes and midbody during mitosis (Zhang et al., 2004). It is associated with the nuclear matrix (Dunn et al., 2003; Yusufzai and Felsenfeld, 2004) and the Lamina (Guelen et al., 2008; Ottaviani et al., 2009). Nucleolar translocation after growth arrest is accompanied by inhibition of nucleolar transcription (Torrano et al., 2006). Cytoplasmic expression was described in sporadic breast tumors (Rakha et al., 2004).

Function

CTCF is an essential protein, since KO mice die before ED 9.5 (Heath et al., 2008) (reviewed in Filippova, 2008; Phillips and Corces, 2009). It interacts with numerous ubiquitous and cell-type specific genomic sites (Chen et al., 2008; Bao et al., 2008; Barski et al., 2007; Kim et al., 2007; Chen et al., 2012). The 11 Zn fingers would provide flexibility in DNA recognition (Filippova et al., 1996), the central 4 bind to a consensus DNA sequence (Filippova et al., 1998;

Renda et al., 2007). Multiple interacting proteins were described including RNA polymerase II (Chernukhin et al., 2007), cohesin (Parelho et al., 2008; Rubio et al., 2008; Wendt et al., 2008; Xiao et al., 2011), Suz12 (Li et al., 2008), CHD8 (Ishihara et al., 2006), YY1 (Donohoe et al., 2007), nucleophosmin (Yusufzai et al., 2004), Kaiso (Defossez et al., 2005) and Sin3A (Lutz et al., 2000). XPG endonuclease promotes DNA breaks and DNA demethylation at promoters allowing the recruitment of CTCF and gene looping, which is further stabilized by XPF (Le May et al., 2012). By mediating intra and interchromosomal contacts through its interaction with cohesin, CTCF plays a central role in organization of topological domains inside the nucleus. Cell-type specific binding sites lead to specific interactomes and transcriptional programs (Hou et al., 2010; Handoko et al., 2011; Dixon et al., 2012; Botta et al., 2010; reviewed by Merckenschlager and Odom, 2013). The plasticity in binding sites occupancy is linked to DNA methylation (Wang et al., 2012b) and could depend also on CTCF interaction with other factors (see concept of modular insulators in Weth et al., 2010). One thoroughly studied factor is the thyroid receptor (Awad et al., 1999; Lutz et al., 2003). Its peculiar chromosomal environment could explain the multiple (not necessarily exclusive) functions that were described for CTCF, including chromatin barrier (Cuddapah et al., 2009; Witcher and Emerson, 2009), promoter insulation from enhancer (Bell et al., 1999) or silencer (Hou et al., 2008), transcriptional activation (Gombert and Krumm, 2009) (for instance of the tumour suppressor genes INK4A/ARF (Rodriguez et al., 2010) and p53 (Soto-Reyes and Recillas-Targa, 2010)), repression (for instance hTERT (Renaud et al., 2005)), nucleosome positioning (Fu et al., 2008b), protection from DNA methylation (Mukhopadhyay et al., 2004; Schoenherr et al., 2003; Guastafierro et al., 2008), preservation of triplet-repeat stability (Cho et al., 2005; Filippova et al., 2001; Libby et al., 2008), imprinting (Fedoriw et al., 2004; Fitzpatrick et al., 2007), X chromosome inactivation (Chao et al., 2002), chromosome "kissing" (Ling et al., 2006), transvection (Liu et al., 2008), death signaling (Docquier et al., 2005; Gomes and Espinosa, 2010; Li and Lu, 2007), replication timing (Bergstrom et al., 2007), mitotic bookmarking (Burke et al., 2005), MHC class II gene expression (Majumder et al., 2008), V(D)J recombination (Guo et al., 2011; reviewed by Chaumeil and Skok, 2012), miRNA expression (Saito and Saito, 2012), telomere end protection (Deng et al., 2012), neuronal diversity (Monahan et al., 2012), myogenesis (Delgado-Olguin et al., 2011), splicing (Shukla et al., 2011) and angiogenesis (Tang et al., 2011). Considering the central role of CTCF in transcriptional regulation, it is likely to play a role in adaptive evolution in *Drosophila* (Ni et al., 2012), and in the evolutionary success of bilateria (Heger et al., 2012). Remodeling of CTCF binding sites and the accompanying interactome during evolution could be

driven by retrotransposon expansion (Schmidt et al., 2012).

Homology

49 orthologues were described including *D. melanogaster* (Smith et al., 2009) and *C. elegans* proteins (Moon et al., 2005), 3 paralogues: CTCFL or BORIS, originating from a gene duplication in reptiles (Hore et al., 2008; Loukinov et al., 2002), and possibly ZFP64 (Mack et al., 1997) and the Histone H4 transcription factor HINF-P (van Wijnen et al., 1991).

Mutations

Note

SNP at AA 630 /K /E 90 /D /G 447 fR (NCBI).

Germinal

Non-coding mutations only.

Somatic

Mutations are rare and include point mutations of Zn-fingers in breast (BT) (Aulmann et al., 2003), prostate (PT) and Wilms tumor (WT) (Filippova et al., 2002; Tiffen et al., 2013), insertion in BT (Aulmann et al., 2003) (see figure 2), and indels in AML (Dolnik et al., 2012).

Implicated in

Various cancers

Note

There is evidence for a tumor-suppressor role of CTCF (reviewed in Fiorentino and Giordano, 2012). LOH of CTCF was described in many cancers together with potential tumor suppressor genes (TSG), including E-Cad, since it is part of a larger deletion (Cancer Chromosomes; Sanger institute). In addition to WT (Yeh et al., 2002; Mummert et al., 2005), BT (Rakha et al., 2004), PT (Filippova et al., 1998), LOH was found in laryngeal squamous cell carcinoma (Grbesa et al., 2008), however, there is no evidence that CTCF is the TSG at 16q22.1 (Rakha et al., 2005), except possibly in lobular carcinoma in situ of the breast (Green et al., 2009). CTCF was also described to be overexpressed in BT (Docquier et al., 2005). An indirect role of CTCF in tumor progression is mainly suggested by mutation or aberrant methylation of its binding sites (reviewed by Recillas-Targa et al., 2006). Interestingly, a causal link between LOH of CTCF and hypermethylation was proposed by Mummert et al. in 2005, although no real correlation was found by Yeh et al. in 2002. Methylation of CTCF sites was first described in the IGF2 imprinting control region in WT (Cui et al., 2001). Aberrant methylation of this region was also found in PT (Fu et al., 2008a; Paradowska et al., 2009), HNSCC (De Castro Valente Esteves et al., 2006; Esteves et al., 2005), colorectal cancer (Nakagawa et al., 2001), osteosarcoma (Ulaner et al., 2003), ovarian carcinoma (Dammann et al., 2010) and laryngeal

squamous cell carcinoma (Grbesa et al., 2008). Hypomethylation was described in bladder cancer (Takai et al., 2001). YY1 binds with CTCF to a hypomethylated form of the macrosatellite DXZ4 on the inactive X chromosome in some male carcinomas (Moseley et al., 2012). Microdeletions were described in Beckwith-Wiedemann syndrome and WT (Prawitt et al., 2005; Sparago et al., 2007; Beygo et al., 2013). Other methylated CTCF targets were found in the genes AWT1 or WT1-AS in WT (Hancock et al., 2007), Bcl6 in B cell lymphomas (Lai et al., 2010), the miR125b locus in breast cancer (Soto-Reyes et al., 2012), p53, pRb (De La Rosa-Velazquez et al., 2007; Davalos-Salas et al., 2011), ARF (Tam et al., 2003; Rodriguez et al., 2010), INK4B, BRCA1 (Butcher et al., 2004; Butcher and Rodenhiser, 2007; Xu et al., 2010) and Rasgrf1 (Yoon et al., 2005). CTCF and its paralogue BORIS regulate pRb in lung cancer (Fiorentino et al., 2011), and CTCF could regulate the response to oestrogen in breast cancer (Zhang et al., 2010).

We describe below the rare cases of point mutations affecting the CTCF protein.

Invasive ductal breast carcinoma, grade 2

Note

G2 grade tumor, no protein detected (Aulmann et al., 2003).

Cytogenetics

14 bp insertion at AA D91, see figure 2.

Invasive ductal breast carcinoma, grade 3

Note

G3 grade tumor (Aulmann et al., 2003).

Cytogenetics

LOH and Q72H, figure 2.

Breast cancer

Note

Zinc finger mutation (Filippova et al., 2002).

Cytogenetics

LOH and K343E, figure 2.

Prostate cancer

Note

Zinc finger mutation (Filippova et al., 2002).

Cytogenetics

LOH and H344E, figure 2.

Wilms tumor

Note

Zinc finger mutation (Filippova et al., 2002).

Cytogenetics

LOH and R339W or R448Q, figure 2.

Acute myeloid leukemia (AML)

Note

(Dolnik et al., 2012).

Cytogenetics

indels.

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