

## **CONCLUSIONS**

## CONCLUSIONS

- Almenys els primers 6 residus de la histona H1<sup>o</sup> constitueixen una regió no carregada que sembla no tenir capacitat d'adquirir estructura secundària definida.
- El domini N-terminal de la H1<sup>o</sup> té la capacitat d'estructurar-se en una hèlix  $\alpha$  que comprèn del residu 11, potser fins i tot des del 7, al 23.
- L'hèlix del domini N-terminal de la H1<sup>o</sup> comprèn els residus 21, 22 i 23, propis del domini globular. Per tant, el límit entre els dominis N-terminal i globular, definits tradicionalment per digestió tríptica, no coincideixen exactament amb els dominis estructurals. Proposem que el domini estructural N-terminal de la H1<sup>o</sup> comprèn del residu 1 al 23 i que el domini globular comença al residu 24.
- L'hèlix del domini N-terminal de la H1<sup>o</sup> presenta dues agrupacions de tres cadenes laterals bàsiques cadascuna, situades en cares oposades de l'hèlix i que probablement constitueixen llocs d'unió a segments de DNA no consecutius.
- El domini N-terminal de la H1<sup>o</sup> unit al DNA s'estructura en part en hèlix, molt probablement en la mateixa regió que s'estructura en presència de TFE.
- El domini N-terminal de la histona H1e s'estructura en dues hèlixs consecutives que avarquen del residu 17 al 27 i del 29 al 34, i probablement fins el 35.
- La segona hèlix del domini N-terminal de la H1e comprèn residus del domini globular definit per digestió tríptica. A nivell estructural, proposem que els dominis N-terminal i globular de la histona H1e es troben separats pel motiu Pro37-Pro38.
- Les dues hèlixs del domini N-terminal de la H1e es troben separades per un doblet de glicines que actua com a frontissa, donant una gran llibertat en la orientació relativa de les dues hèlixs.

- Les hèlixs del domini N-terminal de la H1e són amfipàtiques, amb les cadenes laterals dels residus bàsics situades en una cara de l'hèlix i dels residus apolars en l'altra cara. Constitueixen, probablement, un motiu d'unió al solc ample del DNA.
- La regió del domini C-terminal de la histona H1<sup>o</sup> que segueix al domini globular, s'estructura en una hèlix (residus 99 a 117) seguida d'un gir  $\beta$  o/i  $\sigma$  tipus I (residus 118 a 121).
- L'hèlix del domini C-terminal de la histona H1<sup>o</sup> és amfipàtica, amb les cadenes laterals dels 8 residus bàsics situades en una cara de l'hèlix i els 6 residus apolars en l'altra cara. Constitueix, probablement, un motiu d'unió al solc ample del DNA.
- El gir  $\beta$  o/i  $\sigma$  del domini C-terminal de la H1<sup>o</sup> és un motiu del tipus (S/T)-P-(K/R)-(K/R), descrit com a un lloc d'unió al solc estret del DNA.
- La regió del domini C-terminal de la histona H1<sup>o</sup> que segueix al domini globular s'estructura en hèlix  $\alpha$ , hèlix 3<sub>10</sub> i girs a l'unir-se al DNA, probablement en una estructura molt similar a la induïda pel TFE.

Per tant, les conclusions generals més importants que es poden extreure d'aquest treball són:

- El DNA induceix estructura secundària en regions dels dominis N- i C-terminals de les H1, concretament hèlixs  $\alpha$ , hèlix 3<sub>10</sub> i girs.**
- El TFE revela l'estructura secundària que adopten els pèptids un cop units al DNA i permet el seu estudi a alta resolució.**

## **BIBLIOGRAFIA**

## BIBLIOGRAFIA:

- Adachi, Y., Kas, E. i Laemmli, U.K. (1989). Preferential, cooperative binding of DNA topoisomerase II to scaffold-associated regions. *EMBO J.* **8**, 3997-4006.
- Affolter, M., Côté, J., Renaud, J. i Ruiz-Carrillo, A. (1987). Regulation of histone and BA globin gene expression during differentiation of chicken erythroid cells. *Mol. Cell. Biol.* **7**, 3663-3672.
- Ajiro, K., Borun, T.W. i Cohen, L.H. (1981). Phosphorylation states of different histone H1 subtypes and their relationship to chromatin functions during the HeLa S-3 cell cycle. *Biochemistry* **20**, 1445-1454.
- Ajiro, K., Nishimoto, T. i Takahashi, T. (1983). Histone H1 and H3 phosphorylation during premature chromosome condensation in a temperature-sensitive mutant (tsBN2) of baby hamster kidney cells. *J. Biol. Chem.* **258**, 4534-4538.
- Albig, W., Drabent, B., Kunz, J., Kalff-Suske, M., Grzeschik, K.H. i Doenecke, D. (1993). All known human H1 histone genes except H1<sup>o</sup> gene are clustered on chromosome 6. *Genomics* **16**, 649-654.
- Allan, J., Hartman, P.G., Crane-Robinson, C. i Aviles, F.X. (1980). The structure of histone H1 and its location in chromatin. *Nature* **288**, 675-679.
- Allan, J., Cowling, G.J., Harborne, N., Cattani, P., Craigie, R. i Gould, H. (1981). Regulation of the higher-order structure of chromatin by histones H1 and H5. *J. Cell Biol.* **90**, 279-288.
- Allan, J., Mitchell, T., Harborne, N., Bohm, L. i Crane-Robinson, C. (1986). Roles of H1 domains in determining higher order chromatin structure and H1 location. *J. Mol. Biol.* **187**, 591-601.
- Alland, L., Muhle, R., Hou Jr., H., Potes, J., Chin, L., Schreiber-Agus, N. i De Pinho, R.A. (1997). Role of NCoR and histone deacetylase in Sin3-mediated transcriptional and oncogenic repression. *Nature* **387**, 49-55.
- Allfrey, V., Faulkner, R.M. i Mirsky, A.E. (1964). Acetylation and methylation of histones and their possible role in the regulation of RNA synthesis. *Proc. Natl Acad. Sci. USA* **51**, 786-794.
- Almouzni, G., Khochbin, S., Dimitrov, S. i Wolffe, A.P. (1994). Histone acetylation influences both gene expression and development of *Xenopus laevis*. *Dev. Biol.* **165**, 654-669.
- Alvarez, J., Haris, P.I., Lee, D.C., i Chapman, D. (1987). Conformational changes in concanavalin A associated with demetallization and alpha-methylmannose binding studied by Fourier transform infrared spectroscopy. *Biochim. Biophys. Acta* **916**, 5-12.

- An, W., Leuba, S.H., van Holde, K.E. i Zlatanova, J. (1998). Linker histone protects linker DNA on only one side of the core particle and in a sequence-dependent manner. *Proc. Natl Acad. Sci. USA* **95**, 3396-3401.
- Annunziato, A.T., Frado, L.L., Seale, R.L. i Woodcock, C.L. (1988). Treatment with sodium butyrate inhibits the complete condensation of interphase chromatin. *Chromosoma* **96**, 132-138.
- Annunziato, A.T., Eason, M.B. i Perry, C.A. (1995). Relationship between methylation and acetylation of arginine-rich histones in cycling and arrested HeLa cells. *Biochemistry* **34**, 2916-2924.
- Arents, G., Burlingame, R.W., Wang, B.W., Love, W.E. i Moudrianakis, E.N. (1991). The nucleosomal core histone octamer at 3.1Å resolution: a tripartite protein assembly and a left-handed superhelix. *Proc. Natl Acad. Sci. USA* **88**, 10148-10152.
- Arents, G. i Moudrianakis, E.N. (1993). Topography of the histone octamer surface: repeating structural motifs utilized in the docking of nucleosomal DNA. *Proc. Natl Acad. Sci. USA* **90**, 10489-10493.
- Arrondo, J.L.R. i Goñi, F.M. (1999) Structure and dynamics of membrane proteins as studied by infrared Spectroscopy. *Prog. Biophys. Mol. Biol.* **72**, 367-405.
- Athey, B.D., Smith, M.F., Rankert, D.A., Williams, S.P. i Langmore, J.P. (1990). The diameters of frozen-hydrated chromatin fibres increase with DNA linker length: evidence in support of variable diameter models for chromatin. *J. Cell Biol.* **111**, 795-806.
- Aubert, D., Garcia, M., Benchaibi, M., Poncet, D., Chebloune, Y., Verdier, G., Nigon, V., Samarut, J. i Mura, C.V. (1991). Inhibition of proliferation of primary avian fibroblasts through expression of histone H5 depends on the degree of phosphorylation of the protein. *J. Cell Biol.* **111**, 497-506.
- Aue, W.P., Bertholdi, E. i Ernst, R.R. (1976). Two-dimensional spectroscopy. Applications to magnetic resonance. *J. Chem. Phys.* **64**, 2229-2246.
- Ausio, J., Dong, F. i van Holde, K.E. (1989). Use of selectively trypsinized nucleosome core particles to analyze the role of the histone tails in the stabilization of the nucleosome. *J. Mol. Biol.* **206**, 451-463.
- Azorín, F., Vives, J., Campos, J.L., Jordan, A., Lloveras, J., Puigjaner, L., Subirana, J.A., Mayer, R. i Brack, A. (1985). Interaction of DNA with lysine-rich polypeptides and proteins. The influence of polypeptide composition and secondary structure. *J. Mol. Biol.* **185**, 371-387.
- Bates, D.L. i Thomas, J.O. (1981). Histones H1 and H5: one or two molecules per nucleosome. *Nucleic Acids Res.* **9**, 5883-5894.

- Bax, A. i Davis, D.G. (1985). Practical aspects of two-dimensional spectroscopy. *J. Magn. Reson.* **65**, 355-360.
- Baxevanis, A.D., Bryant, S.H. i Landsman, D. (1995). Homology model building of the HMG-1 box structural domain. *Nucleic Acids Res.* **23**, 1604-1613.
- Bednar, J., Horowitz, R.A., Dubochet, J. i Woodcock, C.L. (1995). Chromatin conformation and salt induced compaction: three dimensional structural information from cryoelectron microscopy. *J. Cell Biol.* **131**, 1365-1376.
- Benyajati, C. i Worcel, A. (1976). Isolation, characterization and structure of the folded interphase genome of *Drosophila melanogaster*. *Cell* **9**, 393-407.
- Bode, J., Gomez-Lira, M.J. i Schroter, H. (1983). Nucleosomal particles open as the histone core becomes hyperacetylated. *Eur. J. Biochem.* **130**, 437-445.
- Böhm, L. i Creemers, P.C. (1993). Folding of terminal histone-H1 peptides in the presence of the oligonucleotide 5'-(AT)<sub>6</sub>-3'. *Biochimica et Biophysica Acta* **1202**, 230-234.
- Böhm, L. i Mitchell, T.C. (1985). Sequence conservation in the N-terminal domain of histone H1. *FEBS Letters* **193**, 1-4.
- Bone, J.R., Lavender, J., Richman, R., Palmer, M.J., Turner, M.B. i Kuroda, M.L. (1994). Acetylated histone H4 on the male X chromosome is associated with dosage compensation in *Drosophila*. *Genes Dev.* **8**, 96-104.
- Boulikas, T., Wiseman, J.M. i Garrard, W.T. (1980). Points of contact between histone H1 and the histone octamer. *Proc. Natl Acad. Sci. USA* **77**, 127-131.
- Bouvet, P., Dimitrov, S. i Wolffe, A.P. (1994). Specific regulation of chromosomal 5S rRNA gene transcription *in vivo* by histone H1. *Genes Dev.* **8**, 1147-1159.
- Boy de la Tour, E. i Laemmli, U.K. (1988). The metaphase scaffold is helically folded: sister chromatids have predominantly opposite helical handedness. *Cell* **55**, 937-944.
- Boyes, J. i Bird, A. (1992). Repression of genes by DNA methylation depends on CpG density and promoter strength: evidence for involvement of a methyl-CpG binding protein. *EMBO J.* **11**, 327-333.
- Bradbury, E.M., Cary, P.D., Chapman, G.E., Crane-Robinson, C., Danby, S.E., Rattle, H.W., Boublík, M., Palau, J. i Avilés, F.J. (1975). Studies on the role and mode of operation of the very-lysine-rich histone H1 (F1) in eukaryote chromatin. The conformation of histone H1. *Eur. J. Biochem.* **52**, 605-613.
- Bradbury, E.M., Danby, S.E., Rattle, H.W. i Giancotti, V. (1975). Studies on the role and mode of operation of the very-lysine-rich histone H1 (F1) in eukaryote chromatin. Histone H1 in chromatin and in H1 - DNA complexes. *Eur. J. Biochem.* **57**, 97-105.

- Bradbury, E.M. (1992). Reversible histone modifications and the chromosome cell cycle. *BioEssays* **14**, 6-16.
- Braunstein, M., Rose, A.B., Holmes, S.G., Allis, C.D. i Broach, J.R. (1993). Transcriptional silencing in yeast is associated with reduced histone acetylation. *Genes Dev.* **7**, 592-604.
- Braunstein, M., Sobel, R.E., Allis, C.D., Turner, B.M. i Broach, J.R. (1996). Efficient transcriptional silencing in *Saccharomyces cerevisiae* requires a heterochromatin acetylation pattern. *Mol. Cell. Biol.* **16**, 4349-4356.
- Breneman, J.W., Yau, P., Teplitz, R.L. i Bradbury, E.M. (1993). A light microscope study of linker histone distribution in rat metaphase chromosomes and interphase nuclei. *Experimental Cell Research* **206**, 16-26.
- Brownell, J.E., Zhou, J., Ranalli, T., Kobayashi, R., Edmondson, D.G., Roth, S.Y. i Allis, C.D. (1996). *Tetrahymena* histone acetyltransferase A: a homolog to yeast Gcn5p linking histone acetylation to gene activation. *Cell* **84**, 843-851.
- Buck, M. (1998). Trifluoroethanol and colleagues: Cosolvents come of age. Recent studies with peptides and proteins. *Q. Rev. Biophys.* **31**, 297-355.
- Buckle, R.S., Maman, J.D. i Allan, J. (1992). Site-directed mutagenesis studies on the binding of the globular domain of linker histone H5 to the nucleosome. *J. Mol. Biol.* **223**, 651-659.
- Bustin, M. i Reeves, R. (1996). High-mobility-group chromosomal proteins: architectural components that facilitate chromatin function. *Prog. Nucleic Acid Res. Mol. Biol.* **54**, 35-100.
- Butler, P.J.G. (1984). A defined structure of the 30 nm chromatin fibre which accommodates different nucleosomal repeat lengths. *EMBO J.* **3**, 2599-2604.
- Byler, O.M. i Susi, H. (1986) Examination of the secondary structure of proteins by deconvoluted FTIR spectra. *Biopolymers* **25**, 469-487.
- Cerf, C., Lippens, G., Muyldemans, S., Segers, A., Ramakrishnan, V., Wodak, S.J., Hallenga, K. i Wyns, L. (1993). Homo- and heteronuclear two-dimensional NMR studies of the globular domain of histone H1: Sequential assignment and secondary structure. *Biochemistry* **32**, 11345-11351.
- Cerf, C., Lippens, G., Ramakrishnan, V., Muyldemans, S., Segers, A., Wyns, L., Wodak, S.J. i Hallenga, K. (1994). Homo- and heteronuclear two-dimensional NMR studies of the globular domain of histone H1: Full assignment, tertiary structure, and comparison with the globular domain of histone H5. *Biochemistry* **33**, 11079-11086.
- Chang, L., Loranger, S.S., Mizzen, C., Ernst, S.G., Allis, C.D. i Annunziato, A.T. (1997). Histones in transit: cytosolic histone complexes and diacetylation of H4 during nucleosome assembly in human cells. *Biochemistry* **36**, 469-480.

- Chen, H., Lin, R.J., Schiltz, R.L., Chakravarti, D., Nash, A., Nagy, L., Privalsky, M.L., Nakatani, Y. i Evans, R.M. (1997). Nuclear receptor coactivator ACTR is a novel histone acetyltransferase and forms a multimeric activation complex with PCAF and CBP /p300. *Cell* **90**, 569-580.
- Chen, Y.H., Yang, J.T. i Chau, K.H. (1974). Determination of the helix and β-form proteins in aqueous solution by circular dichroism. *Biochemistry* **13**, 3350-3359.
- Chihev, C.C. i Wolffe, A.P. (1992). The chromosomal organization of *Xenopus laevis* 5S ribosomal RNA genes *in vivo*. *Mol. Cell. Biol.* **12**, 45-55.
- Chou, P.Y. i Fasman, G.D. (1974). Prediction of protein conformation. *Biochemistry* **13**, 222-245.
- Churchill, M.E.A. i Suzuki, M. (1989). ‘SPKK’ motifs prefer to bind to DNA at A/T-rich sites. *EMBO J.* **8**, 4189-4195.
- Churchill, M.E.A. i Travers, A.A. (1991). Protein motifs that recognize structural features of DNA. *Trends Biochem. Sci.* **16**, 92-97.
- Cirillo, L.A., McPherson, C.E., Bossard, P., Stevens, K., Cherian, S., Shim E.Y., Clark, K.L., Burley, S.K. i Zaret, K.S. (1998). Binding of the winged helix transcription factor HNF3 to a linker histone site on the nucleosome. *EMBO J.* **17**, 244-254.
- Clark, D.J. i Thomas, J.O. (1986). Salt-dependent co-operative interaction of histone H1 with linker DNA. *J. Mol. Biol.* **187**, 569-580.
- Clark, D.J., Hill, C.S., Martin, S.R. i Thomas, J.O. (1988). α-Helix in the carboxi-terminal domain of histones H1 and H5. *EMBO J.* **7**, 69-75.
- Clark, D.J. i Kimura, T. (1990). Electrostatic mechanism of chromatin folding. *J. Mol. Biol.* **211**, 883-896.
- Clark, D.J., O'Neill, L.P. i Turner, B.M. (1993). Selective use of H4 acetylation sites in the yeast *Saccharomyces cerevisiae*. *Biochem. J.* **294**, 557-561.
- Clark, K.L., Halay, E.D., Lai, E. i Burley, S.K. (1993). Co-crystal structure of the HNF-3/fork head DNA recognition motif resembles histone H5. *Nature* **364**, 412-420.
- Clore, G.M., Gronenborn, A.M., Nilges, M., Sukumaran, D.K. i Zarbock, J. (1987). The polypeptide fold of the globular domain of histone H5 in solution. A study using nuclear magnetic resonance, distance geometry and restrained molecular dynamics. *EMBO J.* **6**, 1833-1842.
- Cockerill, P.N. i Garrard, W.T. (1986). Chromosomal loop anchorage of the kappa immunoglobulin gene occurs next to the enhancer in a region containing topoisomerase II sites. *Cell* **44**, 273-282.
- Cole, R.D. (1984). A mini review of microheterogeneity in H1 histone and its possible significance. *Anal. Biochem.* **136**, 24-30.

- Collas, P., Courvalin, J.C. i Poccia, D. (1996). Targeting of membranes to sea urchin sperm chromatin is mediated by a Lamin B receptor-like integral membrane protein. *J. Cell Biol.* **135**, 1715-1725.
- Cook, P.R. i Brazell, I.A. (1975). Supercoils in human DNA. *J. Cell Sci.* **19**, 261-279.
- Cook, P.R. (1988). The nucleoskeleton: artefact, passive framework or active site? *J. Cell Sci.* **90**, 1-6.
- Craig, J.M., Boyle, S., Perry, P. i Bickmore, W.A. (1997). Scaffold attachments within the human genome. *J. Cell Sci.* **110** 2673-2682.
- Crane-Robinson, C. i Ptitsyn, O.B. (1989). Binding of the globular domain of linker histones H5/H1 to the nucleosome: a hypothesis. *Protein Eng.* **2**, 577-582.
- Creemers, P., Monestier, M. i Böhm, L. (1992). Epitope recognition in histone H1 by SLE autoantibodies in the presence of a DNA-ligand. *Autoimmunity* **12**, 167-174.
- Crippa, M.P., Alfonso, P.J. i Bustin, M. (1992). Nucleosome core binding region of chromosomal protein HMG-17 acts as an independent functional domain. *J. Mol. Biol.* **228**, 442-449.
- Crippa, M.P., Trieschmann, L., Alfonso, P.J., Wolffe, A.P. i Bustin, M. (1993). Deposition of chromosomal protein HMG-17 during replication affects the nucleosomal ladder and transcriptional potential of nascent chromatin. *EMBO J.* **12**, 3855-3864.
- Csordas, A. (1990). On the biological role of histone acetylation. *Biochem. J.* **265**, 23-38.
- Daban, J.-R. i Bermúdez, A. (1998). Interdigitated solenoid model for compact chromatin fibers. *Biochemistry* **37**, 4299-4304.
- Dargupta, S. i Bell, J. (1993). Design of helix ends. *Int. J. Pept. Res.* **41**, 499-511.
- Dasso, M., Dimitrov, S. i Wolffe, A.P. (1994). Nuclear assembly is independent of linker histones. *Proc. Natl Acad. Sci. USA* **91**, 12477-12481.
- Davey, C., Pennings, S., Meersseman, G., Wess, T.J. i Allan, J. (1995). Periodicity of strong nucleosome positioning sites around the chicken adult  $\beta$ -globin gene may encode regularly spaced chromatin. *Proc. Natl Acad. Sci. USA* **92**, 11210-11214.
- De Capoa, A., Febbo, F.R., Giovannelli, F., Niveleau, A., Zardo, G., Marenzi, S. i Caiafa, P. (1999). Reduced levels of poly(ADP-ribosylation) result in chromatin compaction and hypermethylation as shown by cell-by-cell computer-assisted quantitative analysis. *FASEB J.* **13**, 89-93.
- De Lange, R.J., Farnbrough, D.M., Smith, E.L. i Bonner, J. (1969a). Calf and pea histone IV: the complete amino acid sequence of calf thymus histone IV; presence of N-acetyllysine. *J. Biol. Chem.* **244**, 319-334.

- De Lange, R.J., Farnbrough, D.M., Smith, E.L. i Bonner, J. (1969b). Calf and pea histone IV: complete amino acid sequence of pea seedling histone IV; comparison with the homologous calf thymus histone. *J. Biol. Chem.* **244**, 5669-5679.
- De Lange, T. (1992). Human telomeres are attached to the nuclear matrix. *EMBO J.* **11**, 717-724.
- D'Erme, M., Zardo, G., Reale, A. i Caiafa, P. (1996). Cooperative interactions of oligonucleosomal DNA with the H1e histone variant and its poly(ADP-ribosyl)ated isoform. *Biochem. J.* **316**, 475-480.
- Dimitrov, S.I., Russanova, V.R. i Pashev, I.G. (1987). The globular domain of histone H5 is internally located in the 30nm fibre: an immunochemical study. *EMBO J.* **6**, 2387-2392.
- Dimitrov, S., Almouzni, G., Dasso, M., i Wolffe, A.P. (1993). Chromatin transitions during early *Xenopus* embryogenesis: changes in histone H4 acetylation and in linker histone type. *Dev. Biol.* **160**, 214-227.
- Dimitrov, S., Dasso, M.C. i Wolffe, A.P. (1994). Remodeling sperm chromatin in *Xenopus laevis* egg extracts: the role of core histone phosphorylation and linker histone B4 in chromatin assembly. *J. Cell Biol.* **126**, 591-601.
- DiNardo, S., Voelkel, K. i Sternglanz, R. (1984). DNA topoisomerase II is required for segregation of daughter molecules at the termination of DNA replication. *Proc. Natl Acad. Sci. USA* **81**, 2616-2620.
- Ding, H.-F., Rimsky, S., Batson, S.C., Bustin, M. i Hansen, U. (1994). Stimulation of RNA polymerase II elongation by chromosomal protein HMG-4. *Science* **265**, 796-799.
- Doenecke, D. i Tönjes, R. (1986) Differential distribution of lysine and arginine residues in the closely related histones H1° and H5. Analysis of a human H1° gene. *J. Mol. Biol.* **187**, 461-464.
- Domínguez, V., Piña, B., Suau, P. (1992). Histone H1 synthesis in neurons and neuroblasts. *Development* **115**, 181-185.
- Dou, Y., Mizzen, C.A., Abrams, M., Allis, C.D. i Gorovsky, M.A. (1999). Phosphorylation of linker histone H1 regulates gene expression in vivo by mimicking H1 removal. *Mol. Cell* **4**, 641-647.
- Draves, P.H., Lowary, P.T. i Widom, J. (1992). Co-operative binding of the globular domain of histone H5 to DNA. *J. Mol. Biol.* **225**, 1105-1121.
- Drew, H.R. i Travers, A.A. (1985). DNA bending and its relation to nucleosome positioning. *J. Mol. Biol.* **186**, 773-790.
- Dunphy, W.G. i Newport, J.W. (1988). Unraveling of mitotic control mechanisms. *Cell* **55**, 925-928.

- Dwivedi, A. i Krimm, S. (1984). Vibrational analysis of peptides, polypeptides, and proteins. XVIII. Conformational sensitivity of the alpha-helix spectrum: alpha I- and alpha II-poly(L-alanine). *Biopolymers* **23**, 923-943.
- Dyson, J., Rance, M., Houghten, R.A., Wright, P.E. i Lerner, R.A. (1988). Folding of immunogenic peptide fragments of proteins in water solution. II. The nascent helix. *J. Mol. Biol.* **201**, 201-217.
- Earnshaw, W.C. (1988). Mitotic chromosome structure. *Bioessays* **9**, 147-150.
- Earnshaw, W.C. (1991). Large scale chromosome structure and organization. *Curr. Opin. Struct. Biol.* **1**, 237-244.
- Ebralidse, K.K., Hebbes, T.R., Clayton, A.L., Thorne, A.W. i Crane-Robinson, C. (1993). Nucleosomal structure at hyperacetylated loci probed in nuclei by DNA-histone crosslinking. *Nucleic Acids Res.* **21**, 4734-4738.
- Edmondson, D.G., Smith, M.M. i Roth, S.Y. (1996). Repression domain of the yeast global repressor Tup1 interacts directly with histones H3 and H4. *Genes Dev.* **10**, 1247-1259.
- Eickbusch, T.H. i Moudrianakis, E.N. (1978). The histone core complex: an octamer assembled by two sets of protein-protein interactions. *Biochemistry* **17**, 4955.
- Einck, L. i Bustin, M. (1985). The intracellular distribution and function of the high mobility group chromosomal proteins. *Exp. Cell Res.* **156**, 295-310.
- Erard, M., Lakhdar-Ghazal, F. i Amalric, F. (1990). Repeat peptide motifs which contain  $\beta$ -turns and modulate DNA condensation in chromatin. *Eur. J. Biochem.* **191**, 19-26.
- Ernst, S.G., Miller, H., Brenner, G.A., Nocenta-McGrath, C., Francis, C. i McIsaac, R. (1987). Characterization of a cDNA clone coding for a sea urchin histone H2A variant related to the H2A.F/Z histone protein of vertebrates. *Nucleic Acids Res.* **15**, 4629-4644.
- Fedoseeva, G., Srebreva, L., Zlatanova, J. i Tsanev, R. (1983). Dynamic of H1° contents in rat liver after partial hepatectomy. *Int. J. Biochem.* **15**, 1489-1491.
- Felsenfeld, G. i McGhee, J.D. (1986). Structure of the 30nm fibre. *Cell* **44**, 375-377.
- Felsenfeld, G. (1992). *Nature* **355**, 219-224.
- Finch, J.T., Lutter, L.C., Rhodes, D., Brown, A.S., Rushton, B., Levitt, M. i Klug, A. (1977). Structure of nucleosome core particles of chromatin. *Nature (London)* **269**, 29-36.
- Flaus, A., Luger, K., Tan, S. i Richmond, T.J. (1996). Mapping nucleosome position at single base-pair resolution by using site-directed hydroxyl radicals. *Proc. Natl Acad. Sci. USA* **93**, 1370-1375.

- Fletcher, T.M. i Hansen, J.C. (1995). Core histone tail domains mediate oligonucleome folding and nucleosomal DNA organization through distinct molecular mechanisms. *J. Biol. Chem.* **270**, 25359-25362.
- Fletcher, T.M. and Hansen, J.C. (1996). The nucleosomal array: structure/function relationships. *Crit. Rev. in Euk. Gene Expression* **6**, 149-188.
- Foisner, R. i Gerace, L. (1993). Integral membrane proteins of the nuclear envelope interact with lamins and chromosomes, and binding is modulated by mitotic phosphorylation. *Cell* **73**, 1267-1279.
- Franke, W.W. (1987). Nuclear lamins and cytoplasmic intermediate filament proteins: a growing multigene family. *Cell* **48**, 3-4.
- Galán, A., Sot, B., Llorca, O., Carrascosa, J.L., Valpuesta, J.M. i Muga, A. (2001). Excluded volume effects on the refolding and assembly of an oligomeric protein. *J. Biol. Chem.* **276**, 957-964.
- Garcia-Ramirez, M., Dong, F. i Ausio, J. (1992). Role of the histone 'tails' in the folding of oligonucleosomes depleted of histone H1. *J. Biol. Chem.* **267**, 19587-19595.
- Garcia-Ramirez, M., Rocchini, C. i Ausio, J. (1995). Modulation of chromatin folding by histone acetylation. *J. Biol. Chem.* **270**, 17923-17928.
- García-Segura, L.M., Luquin, S., Martínez, P., Casas, M.T. i Suau, P. (1993). Differential expression and gonadal hormone regulation of histone H1° in developing and adult rat brain. *Dev. Brain Res.* **73**, 63-70.
- Gasser, S.M. i Laemmli, U.K. (1986a). Cohabitation of scaffold binding regions with upstream enhancer elements of three developmentally regulated genes of *D. melanogaster*. *Cell* **46**, 521-530.
- Gasser, S.M. i Laemmli, U.K. (1986b). The organization of chromatin loops: characterization of a scaffold attachment site. *EMBO J.* **5**, 511-518.
- Gasser, S.M., Amati, B.B., Cardenas, M.E. i Hofmann, J.F. (1989). Studies on scaffold attachment sites and their relationship to genome function. *Int. Rev. Cytol.* **119**, 57-96.
- Gjerset, R., Gorka, C., Hasthorpe, S., Lawrence, J.J. i Eisen, H. (1982). Developmental and hormonal regulation of protein H1° in rodents. *Proc. Natl. Acad. Sci. USA* **70**, 2333-2337.
- Glass, J.R. i Gerace, L. (1990). Lamins A and C bind and assemble at the surface of mitotic chromosomes. *J. Cell. Biol.* **111**, 1047-1057.
- Godde, J.S. i Wolffe, A.P. (1996). Nucleosome assembly of CTG triplet repeats. *J. Biol. Chem.* **271**, 15272-15279.

- Goormaghtigh, E., De Meutter, J., Vanloo, B., Brasseur, R., Rosseneu, M., i Ruysschaert, J.M. (1989). Evaluation of the secondary structure of apo B-100 in low-density lipoprotein (LDL) by infrared spectroscopy. *Biochim. Biophys. Acta* **1006**, 147-150.
- Gorka, C., Fakan, S. i Lawrence, J.J. (1993). Light and electron immunocytochemical analysis of histone H1° distribution in the nucleus of Friend erythroleukemia cells. *Exp. Cell Res.* **205**, 152-158.
- Gorovsky, M.A., Pleger, G.L., Keevert, J.B. i Johmann, C.A. (1973). Studies on histone fraction F2A1 in macro and micronuclei of *Tetrahymena pyriformis*. *J. Cell. Biol.* **57**, 773-781.
- Goytisolo, F.A., Gerchman, S.E., Yu, X., Rees, C., Graziano, V., Ramakrishnan, V. i Thomas, J.O. (1996). Identification of two DNA-binding sites on the globular domain of histone H5. *EMBO J.* **15**, 3421-3429.
- Graziano, V., Gerchman, S.E., Schneider, D.K. i Ramakrishnan, V. (1994). Histone H1 is located in the interior of the chromatin 30 nm filament. *Nature* **368**, 351-354.
- Green, G.R. i Poccia, D.L. (1985). Phosphorylation of sea urchin sperm H1 and H2B histones precedes chromatin decondensation and H1 exchange during pronuclear formation. *Dev. Biol.* **108**, 235-245.
- Güntert, P. i Wüthrich, K. (1991). Improved efficiency of protein structure calculations from NMR using the program DIANA with redundant dihedral angle constraints. *J. Biomol. NMR* **1**, 447-556.
- Güntert, P., Mumenthaler, C. i Wuthrich, K. (1997). Torsion angle dynamics for NMR structure calculation with the new program DYANA. *J Mol Biol.* **273**, 283-298.
- Gurley, L.R., Walters, R.A. i Tobey, R.A. (1975). Sequential phosphorylation of histone subfractions in the Chinese hamster cell cycle. *J. Biol. Chem.* **250**, 3936-3944.
- Gurley, L.R., D'Anna, J.A., Barham, S.S., Deavan, L.L. i Tobey, R.A. (1978). Histone phosphorylation and chromatin structure during mitosis in Chinese hamster cells. *Eur. J. Biochem.* **84**, 1-15.
- Guschin, D., Chandler, S. i Wolffe, A.P. (1998). Asymmetric linker histone association directs the asymmetric rearrangement of core histone interactions in a positioned nucleosome containing a thyroid hormone response element. *Biochemistry* **37**, 8629-8636.
- Halmer, L. i Gruss, C. (1996). Effects of cell cycle dependent histone H1 phosphorylation on chromatin structure and chromatin replication. *Nucl. Acids Res.* **24**, 1420-1427.

- Hansen, J.C., Ausio, J., Stanik, V.H. i van Holde, K.E. (1989). Homogenous reconstituted oligonucleosomes, evidence for salt-dependent folding in the absence of histone H1. *Biochemistry* **28**, 9129-9136.
- Hansen, J.C. i Wolffe, A.P. (1992). The influence of chromatin folding on transcription initiation and elongation by RNA polymerase III. *Biochemistry* **31**, 7977-7988.
- Haris, P.I., i Chapman, D. (1995). The conformational analysis of peptides using Fourier transform IR spectroscopy. *Biopolymers* **37**, 251-263.
- Harper, E.T. i Rose, G.D. (1993). Helix stop signals in proteins and peptides: The capping box. *Biochemistry* **32**, 7605-7609.
- Hartman, P.G., Chapman, G.E., Moss, T. i Bradbury, E.M. (1977). Studies on the role and mode of operation of the very-lysine-rich histone H1 in eukaryotic chromatin: the three structural regions of the histone H1 molecule. *Eur. J. Biochem.* **77**, 45-51.
- Harvey, R.P., Whiting, J.A., Coles, L.S., Krieg, P.A. i Wells, J.R.E. (1983). H2A.F: an extremely variant histone H2A sequence expressed in the chicken embryo. *Proc. Natl Acad. Sci. USA* **80**, 2819-2823.
- Hatch, C.L. i Bonner, W.M. (1988). Sequence of cDNAs for marmalalian H2A.Z, an evolutionarily diverged but highly conserved basal histone H2A isoprotein species. *Nucleic Acids Res.* **16**, 1113-1124.
- Hayes, J.J., Tullius, T.D. i Wolffe, A.P. (1990). The structure of DNA in a nucleosome. *Proc. Natl Acad. Sci. USA* **87**, 7405-7409.
- Hayes, J.J., Clark, D.J. i Wolffe, A.P. (1991). Histone contribution to the structure of DNA in a nucleosome. *Proc. Natl Acad. Sci. USA* **88**, 6829-6833.
- Hayes, J.J. i Wolffe, A.P. (1993). Preferential and asymmetric interaction of linker histones with 5S DNA in the nucleosome. *Proc. Natl Acad. Sci. USA* **90**, 6415-6419.
- Hayes, J.J., Pruss, D. i Wolffe, A.P. (1994). Histone domains required to assemble a chromatosome including the *Xenopus borealis* somatic 5S rRNA gene. *Proc. Natl Acad. Sci. USA* **91**, 7817-7821.
- Hayes, J.J., Kaplan, R., Ura, K., Pruss, D. i Wolffe, A.P. (1996). A putative DNA binding surface in the globular domain of a linker histone is not essential for specific binding to the nucleosome. *J. Biol. Chem.* **271**, 25817-25822.
- Hebbes, T.R., Thorne, A.W., Clayton, A.L. i Crane-Robinson, C. (1992). Histone acetylation and globin gene switching. *Nucleic Acids Res.* **20**, 1017-1022.
- Hebbes, T.R., Clayton, A.L., Thorne, A.W. i Crane-Robinson, C. (1994). Core histone hyperacetylation co-maps with generalized DNase I sensitivity in the chicken  $\beta$ -globin chromosomal domain. *EMBO J.* **13**, 1823-1830.

- Heinzel, T., Laviusky, R.M., Mullen, T.M., Soderstrom, M., Laherty, C.D., Torchia, J.T., Yang, W.-M., Brard, C., Ngo, S.G., Davie, J.R., Seto, E., Eisenman, R.M., Rose, D.W., Glass, C.K. i Rosenfeld, M.G. (1997). N-CoR, mSIN3, and histone deacetylase in a complex required for repression by nuclear receptors and Mad. *Nature* **387**, 43-48.
- Herzyk, E., Lee, D.C., Dunn, R.C., Bruckdorfer, K.R., i Chapman, D. (1987). Changes in the secondary structure of apolipoprotein B-100 after Cu<sup>2+</sup>-catalysed oxidation of human low-density lipoproteins monitored by Fourier transform infrared spectroscopy. *Biochim. Biophys. Acta* **922**, 145-154.
- Hill, C.S., Martin, S.R. i Thomas, J.O. (1989). A stable  $\alpha$ -helical element in the carboxi-terminal domain of free and chromatin-bound histone H1 from sea urchin sperm. *EMBO J.* **8**, 2591-2599.
- Hill, C.S., Rimmer, J.M., Green, B.N., Finch, J.T. i Thomas, J.O. (1991). Histone-DNA interactions and their modulation by phosphorylation of Ser-Pro-X-Lys/ Arg-motifs. *EMBO J.* **10**, 1939-1948.
- Hink, A.P., Eberhardt, E.S. i Markley, J.L. (1993). NMR strategy for determining Xaa-Pro peptide bond configurations in proteins: mutants of Staphylococcal Nuclease with altered configuration at proline-117. *Biochemistry* **32**, 11810-11818.
- Hirano, T. i Mitchison, T.J. (1993). Topoisomerase II does not play a scaffolding role in the organization of mitotic chromosomes assembled in *Xenopus* egg extracts. *J. Cell Biol.* **120**, 601-612.
- Hirano, T. i Mitchison, T.J. (1994). A heterodimeric coiled-coil protein required for mitotic chromosome condensation *in vitro*. *Cell* **79**, 449-458.
- Hogan, M.E., Rooney, T.F. i Austin, R.H. (1987). Evidence for kinks in DNA folding in the nucleosome. *Nature (London)* **328**, 554-557.
- Holloway, P.W., i Mantsch, H.H. (1989). Structure of cytochrome b5 in solution by Fourier-transform infrared spectroscopy. *Biochemistry* **28**, 931-935.
- Horlein, A.J., Naar, A.M., Heinzel, T., Torchia, J., Gloss, B., Kurokawa, R., Ryan, A., Kamei, Y., Soderstrom, M., Glass, C.K. i Rosenfeld, M.G. (1995). Ligand-independent repression by the thyroid hormone receptor mediated by a nuclear receptor co-repressor. *Nature* **377**, 397-404.
- Horowitz, R.A., Agard, D.A., Sedat, J.W. i Woodcock, C.L. (1994). The three dimensional architecture of chromatin *in situ*: electron tomography reveals fibers composed of a continuously variable zig-zag nucleosomal ribbon. *J. Cell Biol.* **125**, 1-10.

- Hsieh, C.-L. (1994). Dependence of transcriptional repression on CpG methylation density. *Mol. Cell. Biol.* **14**, 5487-5494.
- Ichimura, S., Mita, K. i Zama, M. (1982). Essential role of arginine residues in the folding of deoxyribonucleic acid into nucleosome cores. *Biochemistry* **21**, 5329-5334.
- Isenberg, I. (1979). Histones. *Annu. Rev. Biochem.* **48**, 159-191.
- Izaurrealde, E. Kas, E. i Laemmli, U.K. (1989). Highly preferential nucleation of histone H1 assembly on scaffold-associated regions. *J. Mol. Biol.* **210**, 573-585.
- Jackson, D.A., Yuan, J. i Cook, P.R. (1988). A gentle method for preparing cyto- and nucleoskeletons and associated chromatin. *J. Cell Sci.* **90**, 365-378.
- Jackson, D.A., Dickinson, P. i Cook, P.R. (1990). The size of chromatin loops in HeLa cells. *EMBO J.* **9**, 567-571.
- Jackson, J.B., Pollock Jr, J.M. i Rill, R.L. (1979). Chromatin fractionation procedure that yields nucleosomes containing near-stoichiometric amounts of high mobility group non histone chromosomal proteins. *Biochemistry* **18**, 3739.
- Jackson, M., Haris, P.I., i Chapman, D. (1991). Fourier transform infrared spectroscopic studies of Ca(2+)-binding proteins. *Biochemistry* **30**, 9681-9686.
- Jackson, M., Mantsch, H.H., i Spencer, J.H. (1992). Conformation of magainin-2 and related peptides in aqueous solution and membrane environments probed by Fourier transform infrared spectroscopy. *Biochemistry* **31**, 7289-7293.
- Jackson, V., Shires, A., Tanphaichitr, N. i Chalkley, R. (1976). Modification to histones immediately after synthesis. *J. Mol. Biol.* **104**, 471-483.
- Jeanteur, D., Lakey, J.H. i Pattus, F. (1991). The bacterial porin superfamily: sequence alignment and structure prediction. *Mol. Microbiol.* **5**, 2153-2164.
- Jeppesen, P. i Turner, B.M. (1993). The inactive X chromosome in female mammals is distinguished by a lack of histone H4 acetylation, a cytogenetic marker for gene expression. *Cell* **74**, 281-291.
- Jiménez, M.A., Bruix, M., González, C., Blanco, F.J., Nieto, J.L., Herranz, J. i Rico, M. (1993). CD and <sup>1</sup>H-NMR studies on the conformational properties of peptide fragments from the C-terminal domain of thermolysin. *Eur. J. Biochem.* **211**, 569-581.
- Jiménez, M.A., Muñoz, V., Rico, M. i Serrano, L. (1994). Helix stop and start signals in peptides and proteins. The capping box does not necessarily prevent helix elongation. *J. Mol. Biol.* **242**, 487-496.
- Johns, E.W. (1982). *The HMG Chromosomal Proteins*. Academic Press, New York.

- Johnson, N.P., Lindstrom, J., Baase, W.A. i von Hippel, P.H. (1994). Double-stranded DNA templates can induce  $\alpha$ -helical conformation in peptides containing lysine and alanine: Functional implication for leucine zipper and helix-loop-helix transcription factors. *Proc. Natl. Acad. Sci. USA* **91**, 4840-4844.
- Jost, J.-P. i Hofsteenge, J. (1992). The repressor MDBP-2 is a member of the histone H1 family that binds preferentially *in vitro* and *in vivo* to methylated non specific DNA sequences. *Proc. Natl. Acad. Sci. USA* **89**, 9499-9503.
- Kadosh, D. i Struhl, K. (1997). Repression by Ume6 involves recruitment of a complex containing Sin3 corepressor and Rpd3 histone deacetylase to target promoters. *Cell* **89**, 365-371.
- Kandolf H. (1994). The H1A histone variant is the *in vivo* repressor of oocyte-type 55 gene transcription in *Xenopus laevis* embryos. *Proc. Natl Acad. Sci. USA* **91**, 7257-7260.
- Karantza, V., Freire, E. i Moudrianakis, E.N. (1996). Thermodynamic studies of the core histones: pH and ionic strength effects on the stability of the (H3-H4)/(H3-H4)<sub>2</sub> system. *Biochemistry* **35**, 2037-2046.
- Käs, E., Izaurrealde, E. i Laemmli, U.K. (1989). Specific inhibition of DNA binding to nuclear scaffolds and histone H1 by distamycin: The role of oligo(dA)·oligo(dT) tracks. *J. Mol. Biol.* **210**, 587-599.
- Kass, K.U., Goddard, J.P. i Adams, R.L.P. (1993). Inactive chromatin spreads from a focus of methylation. *Mol. Cell Biol.* **13**, 7372-7379.
- Kaufman, P.D. i Botchan, M.R. (1994). Assembly of nucleosomes: do multiple assembly factors mean multiple mechanisms? *Curr. Opin. Genet. Dev.* **4**, 229-235.
- Kermekchiev, M., Workman, J.L. i Pikaard, C.S. (1999). Nucleosome binding by the polymerase I transactivator upstream binding factor displaces linker histone H1. *Mol. Cell. Biol.* **17**, 5833-5842.
- Khadake, J.R. i Rao, M.R.S. (1997a). Condensation of DNA and chromatin by an SPKK-containing octapeptide repeat motif present in the C-terminus of histone H1. *Biochemistry* **36**, 1041-1051.
- Khadake, J.R. i Rao, M.R.S. (1997b). Preferential condensation of SAR-DNA by histone H1 and its SPKK containing octapeptide repeat motif. *FEBS Letters* **400**, 193-196.
- Khan, A.R., Johnson, K.A., Braam, J. i James, M.N.G. (1997). Comparative modeling of the three-dimensional structure of the calmodulin-related TCH2 protein from *Arabidopsis*. *Prot. Struc. Func. Genet.* **27**, 144-153.
- Khochbin, S. i Wolffe, A.P. (1994). Developmentally regulated expression of linker-histone variants in vertebrates. *Eur J. Biochem.* **225**, 501-510.

Kleinschmidt, A.M. i Martison, H.G. (1981). Structure of nucleosome core particles containing uH2A. *Nucleic Acids Res.* **27**, 565-574.

Kleinschmidt, J.A. i Steinbeisser, H. (1991). DNA dependent phosphorylation of histone H2A.X during nucleosome assembly in *Xenopus laevis* oocytes: involvement of protein phosphorylation in nucleosome spacing. *EMBO J.* **10**, 3043-3050.

Kokubo, T., Gong, D.-W., Wootton, J.C., Horikoshi, M. i Roeder, R.G. (1993). Molecular cloning, structural relationships and interactions of *Drosophila* TFIID subunits. *Nature* **367**, 484-487.

Kornberg, R. (1974). Chromatin structure: a repeating unit of histones and DNA. *Science* **184**, 868-871.

Kornberg, R. i Thomas, J.O. (1974). Chromatin structure: oligomers of histones. *Science* **184**, 865-88.

Koshland, D. i Strunnikov, A. (1996). Mitotic chromosome segregation. *Annu. Rev. Cell Dev. Biol.* **12**, 305-333.

Kress, H., Tonjes, R. i Doenecke, D. (1986). Butyrate induced accumulation of a 2.3 kb polyadenylated histone H1° mRNA in HeLa cells. *Nucleic Acids Res.* **14**, 7189-7197.

Kumar, A., Ernst, R.R. i Wüthrich, K. (1980). A two-dimensional nuclear overhauser enhancement (2D-NOE) experimental for the elucidation of complete proton-proton cross-relaxation networks in biological macromolecules. *Biochem. Biophys. Res. Commun.* **95**, 1-6.

Kumar, N.M. i Walker, I.O. (1980). The binding of histones H1 and H5 to chromatin in chicken erythrocyte nuclei. *Nucleic Acids Res.* **8**, 3535-3551.

Kuo, M.-H., Brownell, J.E., Sobal, R.E., Ranalli, T.A., Cook, R.G., Edmondson, D.G., Roth, S.Y. i Allis, C.D. (1996). Transcription-linked acetylation by Gcn5p of histones H3 and H4 at specific lysines. *Nature* **383**, 269-272.

Laemmli, U.K., Kas, E., Poljak, L. i Adachi, Y. (1992). Scaffold-associated regions: cis-acting determinants of chromatin structural loops and functional domains. *Current Opinion in Genetics and Development* **2**, 275-285.

Lafarga, M., García-Segura, L.M., Rodríguez, J.R. i Suau, P. (1995). Expression of histone H1° in transcriptionally activated supraoptic neurons. *Mol. Brain Res.* **29**, 317-324.

Laherty, C.D., Yang, W.M., Sun, J.M., Davie, J.R., Seto, E. i Eisenman, R.M. (1997). Histone deacetylase associated with the mSin3 corepressor mediate Mad transcriptional repression. *Cell* **89**, 349-356.

- Lambert, S., Muyldermans, S., Baldwin, J., Kilner, J., Ibel, K. i Wijns, L. (1991). Neutron scattering studies of chromatosomes. *Biochem. Biophys. Res. Commun.* **179**, 810-816.
- Langan, T.A. (1982). Characterization of highly phosphorylated subcomponents of rat thymus H1 histone. *J. Biol. Chem.* **257**, 14835-14846.
- Langan, T.A., Gautier, J., Lohka, M., Hollingsworth, R., Moreno, S., Nurse, P., Maller, J. i Sclafani, R.A. (1989). Mammalian growth-associated H1 histone kinase: a homolog of *cdc<sup>2+</sup>*/CDC28 protein kinases controlling mitotic entry in yeast and frog cells. *Mol. Cell. Biol.* **9**, 3860-3868.
- Lavender, J.S., Birley, A.J., Palmer, M.J., Kuroda, M.I. i Turner, B.M. (1994). Histone H4 acetylated at lysine 16 and other components of the *Drosophila* dosage compensation pathway colocalize on the male X chromosome through mitosis. *Chromosome Res.* **2**, 398-404.
- Laybourn, P.J. i Kadonaga, J.T. (1992). Threshold phenomena and long distance activation of transcription by RNA polymerase II. *Science* **257**, 1682-1685.
- Lee, D.Y., Hayes, J.J., Pruss, D. i Wolffe, A.P. (1993). A positive role for histone acetylation in transcription factor binding to nucleosomal DNA. *Cell* **72**, 73-84.
- Lee, H.L. i Archer, T.K. (1998). Prolonged glucocorticoid exposure dephosphorylates histone H1 and inactivates the MMTV promoter. *EMBO J.* **17**, 1454-1466.
- Lee, K.-M. i Hayes, J.J. (1997). The N-terminal tail of histone H2A binds to two distinct sites within the nucleosome core. *Proc. Natl Acad. Sci. USA* **94**, 8959-8964.
- Lee, K.-M. i Hayes, J.J. (1998). Linker DNA and H1-dependent reorganization of histone-DNA interactions within the nucleosome. *Biochemistry* **37**, 8622-8628.
- Lennox, R.W. i Cohen, L.H. (1983). The H1 complements of dividing and nondividing cells of the mouse. *J. Biol. Chem.* **258**, 262-268.
- Lennox, R.W. (1984). Differences in evolutionary stability among mammalian H1 subtypes. *J. Biol. Chem.* **259**, 669-672.
- Leuba, S.H., Yang, G., Robert, C., Samori, B., van Holde, K., Zlatanova, J. i Bustamante, C. (1994). Three-dimensional structure of extended chromatin fibers as revealed by tapping-mode scanning force microscopy. *Proc. Natl Acad. Sci. USA* **91**, 11621-11625.
- Levinger, L. i Varshavsky, A. (1980). High-resolution fractionation of nucleosomes: minor particles 'whiskers' and separation of nucleosomes containing and lacking A24 semihistone. *Proc. Natl Sci. USA* **77**, 3244-3248.
- Lewis, C.D. i Laemmli, U.K. (1982). Higher order metaphase chromosome structure: evidence for metalloprotein interactions. *Cell* **29**, 171-181.

- Lewis, J.D., Meehan, R.R., Henzel, W.J., Maurer-Fogy, I., Jeppesen, P., Klein, G. i Bird, A. (1992). Purification, sequence and cellular localization of a novel chromosomal protein that binds to methylated DNA. *Cell* **69**, 905-914.
- Lin, R., Leone, J.W., Cook, R.G. i Allis, C.D. (1989). Antibodies specific to acetylated histones document the existence of deposition- and transcription-related histone acetylation in *Tetrahymena*. *J. Cell. Biol.* **108**, 1577-1588.
- Lin, R., Cook, R.G. i Allis, C.D. (1991). Proteolytic removal of core histone amino termini and dephosphorylation of histone H1 correlate with the formation of condensed chromatin and transcriptional silencing during *Tetrahymena* macronuclear development. *Genes Dev.* **5**, 1601-1610.
- Lindsey, G.G., Orgeig, S., Thompson, P., Davies, N. i Maeder, D.L. (1991). Extended C-terminal tail of wheat histone H2A interacts with DNA of the linker region. *J. Mol. Biol.* **218**, 805-813.
- Liu, K., Lauderdale, J.D. i Stein, A. (1993). Signals in chicken  $\beta$  globin DNA influence chromatin assembly *in vitro*. *Mol. Cell Biol.* **13**, 7596-7603.
- Losa, R., Thoma, F. i Koller, T. (1984). Involvement of the globular domain of histone H1 in the higher order structures of chromatin. *J. Mol. Biol.* **175**, 529-551.
- Lowary, P.T. i Widom, J. (1989). Higher-order structure of *Saccharomyces cerevisiae* chromatin. *Proc. Natl Acad. Sci. USA* **86**, 8266-8270.
- Luger, K., Mader, A.W., Richmond, R.K., Sargent, D.F. i Richmond, T.J. (1997). Crystal structure of the nucleosome core particle at 2.8 Å resolution. *Nature* **389**, 251-260.
- Mahadevan, L.C., Willis, A.C. i Barrah, M.J. (1991). Rapid histone H3 phosphorylation in response to growth factors, phorbol esters, okadaic acid and protein synthesis inhibitors. *Cell* **65**, 775-783.
- Mannironi, C., Bonner, W.M. i Hatch, C.L. (1989). H2A.X a histone isoprotein with a conserved C-terminal sequence is encoded by a novel mRNA with both DNA replication type and poly A 3' processing signals. *Nucleic Acids Res.* **17**, 9113-9126.
- Mardian, J.K.W., Paton, A.E., Bunick, G.J. i Olins, D.E. (1980). Nucleosome cores have two specific binding sites for nonhistone chromosomal proteins HMG14 and HMG17. *Science* **209**, 1534-1536.
- Marion, D. i Wüthrich, K. (1983). Application of phase-sensitive two-dimensional correlated spectroscopy (COSY) for measurement of proton-proton spin-spin coupling constants. *Biochem. Biophys. Res. Commun.* **113**, 967-974.
- Marsh, W.H. i Fitzgerald, P.J. (1973). Pancreas acinar regeneration-XIII. Histone synthesis and modification. *Fed. Proc. Fed. Am. Soc. Exp. Biol.* **32**, 886-889.

Mathis, G. i Althaus, F.R. (1990). Uncoupling of DNA excision repair and nucleosomal unfolding in poly (ADP-ribose) depleted mammalian cells. *Carcinogenesis* **11**, 1237-1239.

Mathis, D.J., Oudet, P., Waslyk, B. i Chambon, P. (1978). Effect of histone acetylation on structure and *in vitro* transcription of chromatin. *Nucleic Acids Res.* **5**, 3523-3547.

Matsumoto, Y., Yasuda, H., Mita, S., Marunouchi, T. i Yamada, M. (1980). Evidence for the involvement of H1 histone phosphorylation in chromosome condensation. *Nature* **284**, 181-183.

McGhee, J.D. i Felsenfeld, G. (1979). Reaction of nucleosome DNA with dimethyl sulfate. *Proc. Natl Acad. Sci. USA* **76**, 2133-2137.

McGhee, J.D. i Felsenfeld, G. (1982). Reconstitution of nucleosorne core particles containing glucosylated DNA. *J. Mol. Biol.* **158**, 685-698.

McKeon, F., Kirschner, M. i Caput, D. (1986). Homologies in both prirary and secondary structure between nuclear envelope and intermediate filament proteins. *Nature (London)* **319**, 463-468.

Meehan, R.R., Lewis, J.D., McKay, S., Kleiner, E.L. i Bird, A.P. (1989). Identification of a mammalian protein that binds specifically to DNA containing methylated CpGs. *Cell* **58**, 499-507.

Meehan, R.R., Lewis, J.D. i Bird, A.P. (1992). Characterization of MeCP2, a vertebrate DNA binding protein with affinity for methylated DNA. *Nucleic. Acids Res.* **20**, 5085-5092.

Meersseman, G., Pennings, S. i Bradbury, E.M. (1991). Chromatosome positioning on assembled long chromatin. Linker histones affect nucleosome placement on 5S DNA. *J. Mol. Biol.* **220**, 89-100.

Megee, P.C., Morgan, B.A. i Smith, M.M. (1995). Histone H4 and the maintenance of genome integrity. *Genes Dev.* **9**, 1716-1727.

Mielke, C., Kohwi, Y., Kohwi-Shigematsu, T. i Bode, J. (1990). Hierarchical binding of DNA fragments derived from scaffold-attached regions: Correlation of properties *in vitro* and function *in vivo*. *Biochemistry* **29**, 7475-7485.

Miick, S.M., Martínez, G.V., Fiori, W.R., Todd, A.P., i Milhauser, G.L. (1992). Short alanine-based peptides may form 3(10)-helices and not alpha-helices in aqueous solution. *Nature* **359**, 653-655.

Mirzabekov, A.D., Pruss, D.V. i Elbralidse, K.K. (1990). Chromatin superstructure-dependent cross-linking with DNA of the histone H5 residues Thr1, His25 and His62. *J. Mol. Biol.* **211**, 479-491.

Mizzen, C.A., Yang, X.J., Kobuko, T., Brownell, J.E., Bannister, A.J., Owen-Hughes, T., Workman, J., Berger, S.L., Kouzavides, T., Nakatani, Y., i Allis, C.D. (1996). The TAF<sub>II</sub>250 subunit of TFIID has histone acetyltransferase activity. *Cell* **87**, 1261-1270.

Morán, F., Montero, F., Azorín, F. i Suau, P. (1985). Condensation of DNA by the C-terminal domain of histone H1. A circular dichroism study. *Biophysical Chemistry* **22**, 125-129.

Morán, F., Rodríguez, A.T., Suau, P i Montero, F. (1989). *Biophys. Chem.* **33**, 133.

Mueller, R.D., Yasuda, H., Bradbury, E.M. (1985). Phosphorylation of histone H1 through the cell cycle of *Physarum polycephalum*. 24 sites of phosphorylation at metaphase. *J. Biol. Chem.* **260**, 5081-5086.

Muñoz, V. i Serrano, L. (1994). Elucidating the folding problem of helical peptides using empirical parameters. *Nat. Struct. Biol.* **1**, 399-409.

Muñoz, V., Serrano, L., Jiménez, M.A. i Rico, M. (1995). Structural analysis of peptides encompassing all  $\alpha$ -helices of three  $\alpha/\beta$  parallel proteins: Che-Y, Flavodoxin and P21-Ras: implications for  $\alpha$ -helix stability and the folding of  $\alpha/\beta$  parallel proteins. *J. Mol. Biol.* **247**, 648-669.

Nan, X., Meehan, R.R. i Bird, A.P. (1993). Dissection of the methyl-CpG binding domain from the chromosomal protein MeCP2. *Nucleic. Acids Res.* **21**, 4886-4892.

Nan, X., Tate, P., Li, E. i Bird, A.P. (1996). MeCP2 is a transcriptional repressor with abundant binding sites in genomic chromatin. *Mol. Cell. Biol.* **16**, 414-421.

Nan, X., Campoy, J. i Bird, A. (1997). MeCP2 is a transcriptional repressor with abundant binding sites in genomic chromatin. *Cell* **88**, 1-11.

Nelson, P.P., Albright, S.C., Wiseman, J.M. i Garrard, W.T. (1979). Reassociation of histone H1 with nucleosomes. *J. Biol. Chem.* **254**, 11751-11760.

Newport, J. i Spann, T. (1987). Disassembly of the nucleus in mitotic extracts: membrane vesicularization, lamin disassembly, and chromosome condensation are independent processes. *Cell* **48**, 219-230.

Newport, J., Wilson, K.L. i Dunphy, W.G. (1990). A lamin-independent pathway for nuclear envelope assembly. *J. Cell Biol.* **111**, 2247-2259.

Nightingale, K., Dimitrov, S., Reeves, R. i Wolffe, A.P. (1996). Evidence for a shared structural role for HMG1 and linker histones B4 and H1 in organizing chromatin. *EMBO J.* **15**, 548-561.

Ogryzko, V.V., Schiltz, R.L., Russanova, V., Howard, B.H. i Nakatani, Y. (1996). The transcriptional coactivators p300 and CBP are histone acetyltransferases. *Cell* **87**, 953-959.

- Ohaviano, Y. i Gerace, L. (1985). Phosphorylation of the nuclear lamin during interphase and mitosis. *J. Biol. Chem.* **260**, 624-632.
- Oliva, R., Bazett-Jones, D.P., Locklear, L. i Dixon, G.H. (1990). Histone hyperacetylation can induce unfolding of the nucleosome core particle. *Nucleic Acids Res.* **18**, 2739-2747.
- Padmanabhan, S., Zhang, W., Capp, M.W., Anderson, C.F. i Record, M.T. (1997). Binding of cationic (+4) alanine- and glycine-containing oligopeptides to double-stranded DNA: Thermodynamic analysis of effects of coulombic interactions and  $\alpha$ -helix induction. *Biochemistry* **36**, 5193-5206.
- Panyim, S. i Chalkley, R. (1969). A new histone found only in mammalian tissues with little cell division. *Biochem. Biophys. Res. Commun.* **37**, 1042-1049.
- Panzeter, P.L., Realini, C.A. i Althaus, F.R. (1992). Noncovalent interactions of poly(adenosine diphosphate ribose) with histones. *Biochemistry* **31**, 1379-1385.
- Parthun, M.R., Widom, J. i Gottschling, D.E. (1996). The major cytoplasmic acetyltransferase in yeast: links to chromatin replication and histone metabolism. *Cell* **87**, 85-94.
- Paulson, J.R. i Laemmli, U.K. (1977). The structure of histone-depleted metaphase chromosomes. *Cell* **12**, 817-828.
- Pherson, J.R. i Cole, R.D. (1982) Histone H1 subfractions and H1° turnover at different rates in nondividing cells. *Biochemistry* **21**, 456-460.
- Pherson, J.R. (1989). Thymine dimer formation as a probe of the path of DNA in and between nucleosomes in intact chromatin. *Proc. Natl Acad. Sci. USA* **86**, 9149-9153.
- Pherson, J.R. i Cohen, L.H. (1992). Effects of DNA looping on pyrimidine dimer formation. *Nucleic Acids Res.* **20**, 1321-1324.
- Pherson, J.R. i Fried, V.A. (1992). Macro H2A, a core histone containing a large nonhistone region. *Science* **257**, 1396-1400.
- Pennings, S., Meersseman, G. i Bradbury, E.M. (1994). Linker histones H1 and H5 prevent the mobility of positioned nucleosomes. *Proc. Natl Acad. Sci. USA* **91**, 10275-10279.
- Perry, C.A., Allis, C.D. i Annunziato, A.T. (1993). Parental nucleosomes segregated to newly replicated chromatin are underacetylated relative to those assembled *de novo*. *Biochemistry* **32**, 13615-13623.
- Peterson, C.L. i Tamkun, J.W. (1995). The SWI/SNF complex: a chromatin remodeling machine? *TIBS* **20**, 143-146.
- Piña, B., Martínez, P., Simon, L. i Suau, P. (1984). Differential kinetics of histone H1°

accumulation in neuronal and glial cells from rat cerebral cortex neurons during postnatal development. *Biochem. Biophys. Res. Commun.* **123**, 697-702.

Piña, B., Martínez, P. i Suau, P. (1987). Changes in H1 complement in differentiating rat-brain cortical neurons. *Eur. J. Biochem.* **164**, 71-76.

Pluta, A.F.; Cooke, C.A. i Earnshaw, W.C. (1990). Structure of the human centromere at metaphase. *Trends Biochem. Sci.* **15**, 181-185.

Poccia, D. (1986). Remodeling of nucleoproteins during gametogenesis, fertilization, and early development. *Int. Rev. Cytol.* **105**, 1-65.

Poirier, G.G. i Savard, P. (1980). ADP-ribosylation of pancreatic histone H1 and of other histones. *Can. J. Biochem.* **58**, 509-515.

Poirier, G.G., de Murcia, G., Jongstra-Bilen, J., Niedergang, C. i Mandel, P. (1982). Poly(ADP-ribosyl)ation of polynucleosomes causes relaxation of chromatin structure. *Proc. Natl. Acad. Sci. USA* **79**, 3423-3427.

Ponte, I., Martínez, P., Ramírez, A., Jorcano, J.L., Monzó, M. i Suau, P. (1994). Transcriptional activation of histone H1° during neuronal terminal differentiation. *Dev. Brain Res.* **80**, 35-44.

Ponte, I., Vidal-Taboada, J.M. i Suau, P. (1998). Evolution of the vertebrate H1 histone class: evidence for the functional differentiation of the subtypes. *Mol. Biol. Evol.* **15**, 702-708.

Prestrelski, S.J., Byler, D.M., i Thompson, M.P. (1991). Infrared spectroscopic discrimination between alpha- and 3(10)-helices in globular proteins. Reexamination of Amide I infrared bands of alpha-lactalbumin and their assignment to secondary structures. *Int. J. Peptide Protein Res.* **37**, 508-512.

Prevelige, P.E., Jr. i Fasman, G.D. (1987). Structural studies of acetylated and control inner core histones. *Biochemistry* **26**, 2944-2955.

Pruss, D., Bushman, F.D. i Wolffe, A.P. (1994). HIV integrase directs integration to sites of severe DNA distortion within the nucleosome core. *Proc. Natl Acad. Sci. USA* **91**, 5913-5917.

Pruss, D., Hayes, J.J. i Wolffe, A.P. (1995). Nucleosomal anatomy – where are the histones? *BioEssays* **17**, 161-170.

Pruss, D., Bartholomew, B., Persinger, J., Hayes, J., Arents, G., Moudrianakis, E.N. i Wolffe, A.P. (1996). An asymmetric model for the nucleosome: a binding site for linker histones inside the DNA gyres. *Science* **274**, 614-617.

Puhl, H.L. i Behe, M.J. (1993). Structure of nucleosomal DNA at high salt concentration as probed by hydroxyl radical. *J. Mol. Biol.* **229**, 827-832.

- Ramakrishnan, V., Finch, J.T., Graziano, V., Lee, P.L. i Sweet, R.M. (1993). Crystal structure of globular domain of histone H5 and its implications for nucleosome binding. *Nature* **362**, 219-223.
- Rattner, J.B. i Lin, C.C. (1985). Radical loops and helical coils coexist in metaphase chromosomes. *Cell* **42**, 291-296.
- Reeves, R. i Nissen, M.S. (1990). The A-T-DNA binding domain of mammalian high mobility group I chromosomal proteins. *J. Biol. Chem.* **265**, 8573-8582.
- Reik, W. i Surani, M.A. (1989). Cancer genetics. Genomic imprinting and embryonal tumours. *Nature* **338**, 112-13.
- Renz, M., Nehls, P. i Hozier, J. (1977). Involvement of histone H1 in the organization of the chromosome fiber. *Proc. Natl. Acad. Sci. USA* **74**, 1879-1883.
- Richardson, J.S. i Richardson, D.C. (1988). Amino acid preferences for specific locations of the ends of  $\alpha$  helices. *Science* **240**, 1648-1652.
- Richmond, T.J., Finch, J.T., Rushton, B., Rhodes, D. i Klug, A. (1984). Structure of the nucleosome core particle at 7 Å resolution. *Nature (London)* **311**, 532-537.
- Rodríguez, A.T., Pérez, L., Morán, F., Montero, F. i Suau, P. (1991). Cooperative interaction of the C-terminal domain of histone H1 with DNA. *Biophysical Chemistry* **39**, 145-152.
- Roth, S.Y. i Allis, C.D. (1992). H1 phosphorylation and chromatin condensation: exceptions which define the rule? *Trends Biochem. Sci.* **17**, 93-98.
- Ruiz-Carrillo, A., Wangh, L.J. i Allfrey, V.G. (1975). Processing of newly synthesized histone molecules. *Science* **190**, 117-128.
- Saitoh, N., Goldberg, I. i Earnshaw, W.C. (1995). The SMC proteins and the coming of age of the chromosome scaffold hypothesis. *BioEssays* **17**, 759-766.
- Sandeen, G., Wood, W.I. i Felsenfeld, G. (1980). The interaction of high mobility proteins HMG14 and 17 with nucleosomes. *Nucleic Acids Res.* **8**, 3757-3778.
- Sandman, K., Krzycki, J.A., Dobrinski, B., Lurz, R. i Reeve, J.N. (1990). HMf, a DNA-binding protein isolated from the hyperthermophilic archaeon *Methanofervidus fervidus*, is most closely related to histones. *Proc. Natl. Acad. Sci. USA* **92**, 1624-1628.
- Santisteban, M.S., Arents, G., Moudrianakis, E.N. i Smith, M.M. (1997). Histone octamer function *in vivo*: mutations in the dimer-tetramer interfaces disrupt both gene activation and repression. *EMBO J.* **16**, 2493-2506.
- Satchwell, S.C. i Travers, A.A. (1989). Asymmetry and polarity of nucleosomes in chicken erythrocyte chromatin. *EMBO J.* **8**, 229-238.

- Schild, C., Claret, F-X., Wahli, W. i Wolffe, A.P. (1993). A nucleosome-dependent static loop potentiates estrogen-regulated transcription from the *Xenopus* vitellogenin B1 promoter *in vitro*. *EMBO J.* **12**, 423-433.
- Schwarz, P.M. i Hansen, J.C. (1994). Formation and stability of higher order chromatin structures. *J. Biochem.* **269**, 16284-16298.
- Schwarz, P.M., Felthauser, A., Fletcher, T.M. i Hansen, J.C. (1996). Reversible oligonucleosome self-association: dependence on divalent cations and core histone tail domains. *Biochemistry* **35**, 4009-4015.
- Sedat, J. i Manuelidis, L. (1978). A direct approach to the structure of mitotic chromosomes. *Cold Spring Harb. Symp. Quant. Biol.* **42**, 331-350.
- Sera, T. i Wolffe, A.P. (1998). The role of histone H1 as an architectural determinant of chromatin structure and as a specific repressor of transcription on the *Xenopus* oocyte 5S rRNA gene. *Mol. Cell Biol.* **18**, 3668-3680.
- Shelby, R.D., Vafa, O. i Sullivan, K.F. (1997). Assembly of CENP-A into centromeric chromatin requires a cooperative array of nucleosomal DNA contact sites. *J. Cell Biol.* **136**, 501-513.
- Shen, X., Yu, L., Weir, J.W. i Gorovsky, M.A. (1995). Linker histones are not essential and affect chromatin condensation *in vivo*. *Cell* **82**, 47-56.
- Shen, X. i Gorovsky, M.A. (1996). Linker histone H1 regulates specific gene expression but not global transcription *in vivo*. *Cell* **86**, 475-483.
- Shim, E.Y., Woodcock, C. i Zaret, K.S. (1998). Nucleosome positioning by the winged helix transcription factor HNF3. *Genes Dev.* **12**, 5-10.
- Shrader, T.E. i Crothers, D.M. (1989). Artificial nucleosome positioning sequences. *Proc. Natl Acad. Sci. USA* **86**, 7418-7422.
- Siegfried, Z. i Cedar, H. (1997). DNA methylation: a molecular lock. *Curr. Biol.* **7**, R305-R307.
- Simpson, R. T. (1978). Structure of the chromatosome, a chromatin core particle containing 160 base pairs of DNA and all the histones. *Biochemistry* **17**, 5524-5531.
- Singer, D.S. i Singer, M.F. (1976). Studies on the interaction of histone H1 with superhelical DNA: characterization of the recognition and binding regions of H1 histone. *Nucleic Acids Res.* **3**, 2531-2547.
- Sinha, S., Maity, S.N., Lu, J. i de Crombrugghe, B. (1995). Recombinant rate CBF-C, the third subunit of CBF/NFY, allows formation of a protein-DNA complex with CBF-A and CBF-B and with yeast HAP2 and HAP3. *Proc. Natl Acad. Sci. USA* **92**, 1624-1628.

- Sivolob, A.V. i Khrapunov, S.N. (1995). Translational positioning of nucleosomes on DNA: the role of sequence-dependent isotropic DNA bending stiffness. *J. Mol. Biol.* **247**, 918-931.
- Stambolova, M., Simeonova, V., Srebreva, L., Zlatanova, J.S. i Tsanev, R.. (1984). Histone H1° in developing rat brain cells. *Differentiation* **28**, 1191-1194.
- Stargell, L.A., Bowen, J., Dadd, C.A., Dedon, P.A., Davis, M., Cook, R.G., Allis, C.D. i Gorovsky, M.A. (1993). Temporal and spatial association of histone H2A variant hv1 with transcriptionally competent chromatin during nuclear development in *Tetrahymena thermophila*. *Genes Dev.* **7**, 2641-2651.
- Staynov, D.Z. i Crane-Robinson, C. (1988). Footprinting of linker histones H5 and H1 on the nucleosome. *EMBO J.* **7**, 3685-3691.
- Stoler, S., Keith, K.C., Curnick, K.E. i Fitzgerald-Hayes, M. (1995). A mutation in CSE4, an essential gene encoding a novel chromatin associated protein in yeast, causes chromatin non disjunction and cell cycle arrest at mitosis. *Genes Dev.* **9**, 573-586.
- Strahl, B.D. i Allis, C.D. (2000). The language of covalent histone modifications. *Nature* **403**, 41-45.
- Strunnikov, A.V., Larionov, V.L. i Koshland, D. (1993). SMC1: an essential yeast gene encoding a putative head-rod-tail protein is required for nuclear division and defines a new ubiquitous protein farnily. *J. Cell Biol.* **123**, 1635-1648.
- Strunnikov, A.V., Hogan, E. i Koshland, D. (1995). SMC2, a *Saccharomyces cerevisiae* gene essential for chromosome segregation and condensation defines a subgroup within the SMC-farnily. *Genes Dev.* **9**, 587-599.
- Suau, P., Bradbury, E.M. I Baldwin, J.P. (1979). Higher-order structures of chromatin in solution. *Eur. J. Biochem.* **97**, 593-602.
- Subirana, J.A. (1990). Analysis of the charge distribution in the C-terminal region of histone H1 as related to its interaction with DNA. *Biopolymers* **29**, 1351-1357.
- Sugita, K., Koizumi, K. i Yoshida, M. (1992). Morphological reversion of sis-transformed NIH3T3 cells by trichostatin A. *Cancer Res.* **52**, 168-172.
- Sullivan, K.F., Hechenberger, M. i Masri, K. (1994). Human CENP-A contains a histone H3 related histone fold domain that is required for targeting to the centromer. *J. Cell Biol.* **127**, 581-592.
- Sullivan, S.A., Aravind, L., Makalowska, I., Baxevanis, A.D., Landsman, D. (2000). The Histone Database: a comprehensive WWW resource for histones and histone fold-containing proteins. *Nucleic Acids Res.* **28**, 320-322.

- Sun, J.-M., Wiaderkiewicz, R. i Ruiz-Carrillo, A. (1989). Histone H5 in the control of DNA synthesis and cell proliferation. *Science* **245**, 68-71.
- Sun, J.-M., Ali, Z., Lurz, R. i Ruiz-Carrillo, A. (1990). Replacement of histone H1 by H5 in vivo does not change the nucleosome repeat length of chromatin but increases its stability. *EMBO J.* **9**, 1651-1658.
- Sung, M.T. i Dixon, G.H. (1970). Modification of histones during spermiogenesis in trout: a molecular mechanism for altering histone binding to DNA. *Proc. Natl Acad. Sci. USA* **67**, 1616-1623.
- Surewicz, W.K., Leddy, J.J., i Mantsch, H.H. (1990). Structure, stability, and receptor interaction of cholera toxin as studied by Fourier-transform infrared spectroscopy. *Biochemistry* **29**, 8106-8111.
- Surewicz, W.K., Mantsch, H.H. i Chapman, D. (1993) Determination of protein secondary structure by Fourier transform infrared spectroscopy: A critical assessment. *Biochemistry* **32**, 389-394.
- Susi, H. (1969) in *Structure and Stability of Biological Macromolecules* (Timasheff, S.N., & Stevens, L., Eds.) pp 575-663, Dekker, New York.
- Suzuki, M. (1989). SPKK, a new nucleic acid-binding unit of protein found in histone. *EMBO J.* **8**, 797-804.
- Suzuki, M., Gerstein, M. i Johnson, T. (1993). An NMR study on the DNA-binding SPKK motif and a model for its interaction with DNA. *Protein Eng.* **6**, 565-574.
- Talasz, H., Helliger, W., Puschendorf, B. i Lindner, H. (1996). *In vivo* phosphorylation of histone H1 variants during the cell cycle. *Biochemistry* **35**, 1761-1767.
- Taniura, H., Glass, C. i Gerace, L. (1995). A chromatin binding site in the tail domain of nuclear lamins that interacts with the core histones. *J. Cell Biol.* **131**, 33-44.
- Taunton, J., Hassig, C.A. i Schreiber, S.L. (1996). A mammalian histone deacetylase related to a yeast transcriptional regulator Rpd3. *Science* **272**, 408-411.
- Taylor, W. R., Chadee, D. N., Allis, C. D., Wright, J. A. i Davie, J. R. (1995). Fibroblasts transformed by combinations of *ras*, *myc* and mutant p53 exhibit increased phosphorylation of histone H1 that is independent of metastatic potential. *FEBS Letters* **377**, 51-53.
- Thoma, F., Koller, T. i Klug, A. (1979). Involvement of histone H1 in the organization of the nucleosome and the salt-dependent superstructures of chromatin. *J. Cell Biol.* **83**, 402-427.

- Thoma, F., Losa, R. i Koller, T. (1983). Involvement of the domains of histones H1 and H5 in the structural organization of soluble chromatin. *J. Mol. Biol.* **167**, 619-640.
- Thomas, J.O. i Wilson, C.M. (1986). Selective radiolabelling and identification of a strong nucleosome binding site on the globular domain of histone H5. *EMBO J.* **5**, 3531-3537.
- Thomas, J.O. (1989). Chemical radiolabeling of lysines that interact strongly with DNA in chromatin. *Methods Enzymol.* **170**, 369-385.
- Thomas, J.O., Rees, C. i Finch, J.T. (1992). Cooperative binding of the globular domains of histones H1 and H5 to DNA. *Nucleic Acids Res.* **20**, 187-194.
- Tomaszewski, R. i Jerzmanowski, A. (1997). The AT-flanks of the oocyte-type 5S RNA gene of *Xenopus laevis* act as a strong signal for histone H1-mediated chromatin organization *in vitro*. *Nucleic Acids Res.* **25**, 458-465.
- Torii, H. i Tasumi, M. (1992) Model calculations of the amide-I infrared bands of globular proteins. *J. Chem. Phys.* **96**, 3379-3387.
- Travers, A.A. (1994). Chromatin structure and dynamics. *BioEssays* **16**, 657-662.
- Travers, A.A. (1999). The location of the linker histone on the nucleosome. *Trends Biochem Sci.* **24**, 4-7.
- Tremethick, D.J i Drew, H.R. (1993). High mobility group proteins 14 and 17 can space nucleosomes *in vitro*. *J. Biol. Chem.* **268**, 11389-11393.
- Truss, M., Bartsch, J., Schelbert, A., Haché, R.J.G. i Beato, M. (1995). Hormone induces binding of receptors and transcription factors to a rearranged nucleosome on the MMTV promoter *in vivo*. *EMBO J.* **14**, 1737-1751.
- Turner, B.M. (1991). Histone acetylation and control of gene expression. *J. Cell. Sci.* **99**, 13-20.
- Turner, B.M., Birley, A.J. i Lavender, J. (1992). Histone H4 isoforms acetylated at specific lysine residues define individual chromosomes and chromatin domains in *Drosophila* polytene nuclei. *Cell* **69**, 375-384.
- Ura, K., Wolffe, A.P. i Hayes, J.J. (1994). Core histone acetylation does not block linker histone binding to a nucleosome including a *Xenopus borealis* 5S rRNA gene. *J. Biol. Chem.* **269**, 27171-27174.
- Ura, K., Hayes, J.J. i Wolffe, A.P. (1995). A positive role for nucleosome mobility in the transcriptional activity of chromatin templates: restriction by linker histones. *EMBO J.* **14**, 3752-3765.
- Ura, K., Kurumizaka, H., Dimitrov, S., Almouzni, G., i Wolffe, A.P. (1997). Histone acetylation: influence on transcription by RNA polymerase, nucleosome mobility

and positioning, and linker histone dependent transcriptional repression. *EMBO J.* **16**, 2096-2107.

Usachenko, S.I., Gavin, I.M. i Bavykin, S.G. (1996). Alterations in nucleosome core structure in linker histone-depleted chromatin. *J. Biol. Chem.* **271** 3831-3836.

van Daal, A., White, E.M., Gorovsky, M.A. i Elgin, S.C.R. (1988). *Drosophila* has a single copy of the gene encoding a highly conserved histone H2A variant of the H2A.F/Z type. *Nucleic Acids Res.* **16**, 7487-7497.

van Daal, A. i Elgin, S.C.R. (1992). A histone variant, H2AvD, is essential in *Drosophila melanogaster*. *Mol. Biol. Cell.* **3**, 593-602.

van Gelder, P., Saint, N., van Boxtel, R., Rosenbusch, J.P. i Tommassen, J. (1997). Pore functioning of outer membrane protein PhoE of *Escherichia coli*: mutagenesis of the constriction loop L3. *Prot. Eng.* **10**, 699-706.

van Holde, K.E. (1988). *Chromatin*. Springer-Verlag, New York.

van Holde, K.E. i Zlatanova, J. (1995). Chromatin higher order structure: chasing a mirage? *J. Biol. Chem.* **270**, 8373-8376.

van Holde, K. i Zlatanova, J. (1996). What determines the folding of the chromatin fiber. *Proc. Natl Acad. Sci. USA* **93**, 10548-10555.

Varga-Weisz, P., Zlatanova, J., Leuba, S.H., Schroth, G.P. i van Holde, K. (1994). Binding of histones H1 and H5 and their globular domains to four way junction DNA. *Proc. Natl Acad. Sci. USA* **91**, 3525-3529.

Verdaguer, N., Perelló, M., Palau, J. i Subirana, J.A. (1993). Helical structure of basic proteins from spermatozoa. Comparison with model peptides. *Eur. J. Biochem.* **214**, 879-887.

Vermaak, D., Steinbach, O.C., Dimitrov, S., Rupp, R.A.W. i Wolffe, A.P. (1998). The globular domain of histone H1 is sufficient to direct specific gene repression in early *Xenopus* embryos. *Current Biology* **8**, 533-536.

Vernet, G., Sala-Rovira, M., Maeder, M., Jacques, F. i Herzog, M. (1990). Basic nuclear proteins of the histone less eukaryote *Gypthecodinium cohnii* (Pyrrhophyta): two dimensional electrophoresis and DNA binding properties. *Biochim. Biophys. Acta* **1048**, 281-289.

Vettesse-Dadey, M., Grant, P.A., Hebbes, R.T., Crane-Robinson, C., Allis, C.D., i Workman, J.L. (1996). Acetylation of histone H4 plays a primary role in enhancing transcription factor binding to nucleosomal DNA *in vitro*. *EMBO J.* **15**, 2508-2518.

Vila, R., Ponte, I., Jiménez, M.A., Rico, M. i Suau, P. (2000). A helix-turn motif in the C-terminal domain of histone H1. *Protein Science* **9**, 627-636.

- Wade, P.A., Pruss, D. i Wolffe, A.P. (1997). Histone acetylation: chromatin in action. *Trends Biochem. Sci.* **22**, 128-132.
- Walters, L. i Kaiser, E.T. (1985). Design of DNA-binding peptides: Stabilization of  $\alpha$ -helical structure by DNA. *J. Am. Chem. Soc.* **107**, 6422-6424.
- Wang, X., Moore, S.C., Laszczak, M. i Ausió, J. (2000). Acetylation increases the alpha-helical content of the histone tails of the nucleosome. *J Biol. Chem.* **275**, 35013-35020.
- Wang, Y.H., Amirhaeri, S., Kang, S., Wells, R.D. i Griffith, J.D. (1994). Preferential nucleosome assembly at DNA triplet repeats from the myotonic dystrophy gene. *Science* **265**, 1709-1712.
- Warburton, P.E. i Earnshaw, W.C. (1997). Untangling the role of DNA topoisomerase II in mitotic chromosome structure and function. *BioEssays* **19**, 97-99.
- Wellman, S.E. (1996). Carboxyl-terminal peptides from histone H1 variants: DNA binding characteristics and solution conformation. *Biopolymers* **39**, 491-501.
- Welsh, S.L. i Cole, R.D. (1979). Differences between subfractions of H1 histone in their interactions with DNA. *J. Biol. Chem.* **254**, 662-665.
- Welsh, S.L. i Cole, R.D. (1980). Differences among subfractions of H1 histone in retention of linear and superhelical DNA on filters. *J. Biol. Chem.* **255**, 4516-4518.
- West, M.H.P. i Bonner, W.M. (1980). Histone H2B can be modified by the attachment of ubiquitin. *Nucleic Acids Res.* **8**, 4671-4680.
- White, E., Shapiro, D.L., Allis, C.D. i Gorovsky, M.A. (1988). Sequence and properties of the message encoding *Tetrahymena* hv1, a highly conserved histone H2A variant that is associated with active genes. *Nucleic. Acids Res.* **16**, 179-198.
- Williams, S.P. i Langmore, J.P. (1991). Small angle x-ray scattering of chromatin. *Biophys. J.* **69**, 606-618.
- Wishart, D.S., Sykes, B.D. i Richards, F.M. (1991). Relationship between nuclear magnetic resonance chemical shift and secondary structure. *J. Mol. Biol.* **222**, 311-333.
- Wishart, D.S., Brigam, C.G., Holm, A., Hodges, R.S. i Sykes, B.D. (1995).  $^1\text{H}$ ,  $^{13}\text{C}$  and  $^{15}\text{N}$  random coil NMR chemical shifts of the common amino acids. I. Investigations of the nearest-neighbor effects. *J. Biomol. NMR* **5**, 67-81.
- Wolffe, A.P. i Pruss, D. (1996). Deviant nucleosomes: the functional specialization of chromatin. *Trends Genet.* **12**, 58-62.
- Wolffe, A.P., Wong, J. i Pruss, D. (1997a). Activators and repressors: making use of chromatin to regulate transcription. *Genes to Cells* **2**, 291-302.

Wolffe, A.P., Khochbin, P.S. i Dimitrov, S. (1997b). What do linker histones do in chromatin? *BioEssays* **19**, 249-255.

Wolffe, A.P. (1998). *Chromatin, Structure and function*. Academic Press, L.A. California, USA.

Wong, J., Shi, Y.-B. i Wolffe, A.P. (1995). A role for nucleosome assembly in both silencing and activation of the *Xenopus* TRbA gene by the thyroid hormone receptor. *Genes Dev.* **9**, 2696-2711.

Wong, J., Shi, Y.-B. i Wolffe, A.P. (1997). Determinants of chromatin disruption and transcriptional regulation instigated by the thyroid hormone receptor: hormone regulated chromatin disruption is not sufficient for transcriptional activation. *EMBO J.* **16**, 3158-3171.

Woodcock, C.L., Frado, L.L. i Rattner, J.B. (1984). The higher-order structure of chromatin: evidence for a helical ribbon arrangement. *J. Cell Biol.* **99**, 42-52.

Woodcock, C.L., Grigoryer, S.A., Horowitz, R.A. i Whitaker, N. (1993). A folding model for chromatin that incorporates linker DNA variability produces fibers that mimic the native structures. *Proc. Natl Acad. Sci. USA* **90**, 9021-9025.

Woodcock, C.L. (1994). Chromatin fibers observed *in situ* in frozen hydrated sections. Native fiber diameter is not correlated with nucleosome repeat length. *J. Cell Biol.* **125**, 11-19.

Wüthrich, K., Billeter, M. i Braun, W. (1984). Polypeptide secondary structure determination by nuclear magnetic resonance observation of short proton-proton distances. *J. Mol. Biol.* **180**, 715-740.

Wüthrich, K. (1986). *NMR of Protein and Nucleic Acids*. New York: John Wiley and Sons.

Yang, G., Leuba, S.H., Bustamente, C., Zlatanova, J. i van Holde, K. (1994). Role of linker histones in extended fibre structure. *Nature Struct. Biol.* **1**, 761-763.

Yang, X.-J., Ogryzko, V.V., Nishikawa, J.-I., Howard, B. i Nakatani, Y. (1996). A p300/CBP-associated factor that competes with the adenoviral E1A oncoprotein. *Nature* **382**, 319-324.

Yasuda, H., Matsumoto, Y., Mita, S., Marunouchi, T. i Yamada, M. (1981). A mouse temperature-sensitive mutant defective in H1 histone phosphorylation is defective in deoxyribonucleic acid synthesis and chromosome condensation. *Biochemistry* **20**, 4414-4419.

Yoshida, M., Nomura, S. i Beppu, T. (1987). Effects of trichostatins on differentiation of murine erythroleukemia cells. *Cancer Res.* **47**, 3688-3691.

- Zarbock, J., Clore, G.M. i Gronenborn, A.M. (1986). Nuclear magnetic resonance study of the globular domain of chicken histone H5: resonance assignment and secondary structure. *Proc. Natl Acad. Sci. USA* **83**, 7628-7632.
- Zardo, G., Marenzi, S. i Caiafa, P. (1998). H1 histone as a trans-acting factor involved in protecting genomic DNA from full methylation. *Biol. Chem.* **379**, 647-654.
- Zardo, G. i Caiafa, P. (1998). The unmethylated state of CpG islands in mouse fibroblasts depends on the poly(ADP-ribosyl)ation process. *J. Biol. Chem.* **273**, 16517-16520.
- Zentgraf, H. i Franke, W.W. (1984). Differences of supra nucleosomal organization in different kinds of chromatin: cell type-specific globular subunits containing different numbers of nucleosomes. *J. Cell Biol.* **99**, 272-286.
- Zhou, Y.B., Gerchman, S.E., Ramakrishnan, V., Travers, A. i Muyldermans, S. (1998). Position and orientation of the globular domain of linker histone H5 on the nucleosome. *Nature* **395**, 402-405.
- Zlatanova, J. i Van Holde, K. (1992). Histone H1 and transcription: still an enigma? *J. Cell Sci.* **103**, 889-895.
- Zlatanova, J. i van Holde, K. (1996). The linker histones and chromatin structure: new twists. *Prog. Nucleic Acids Res. Mol. Biol.* **52**, 217-259.
- Zweidler, A. (1992). Role of individual histone tyrosines in the formation of the nucleosome complex. *Biochemistry* **31**, 9205-9211.