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## **spFRET studies of nucleosome dynamics modulated by histone modifications, histone variants and neighboring nucleosomes**

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# References

- [1] H. Schiessel, "The physics of chromatin," *Journal of Physics: Condensed Matter*, vol. 15, pp. R699–R774, May 2003.
- [2] W. Flemming, *Zellsubstanz, Kern und Zelltheilung*. F.C.W. Vogel, 1882.
- [3] D. E. Olins and A. L. Olins, "Chromatin history: our view from the bridge," *Nature Reviews Molecular Cell Biology*, vol. 4, no. 10, pp. 809–814, 2003.
- [4] A. L. Olins and D. E. Olins, "Spheroid chromatin units (nu bodies)," *Science*, vol. 183, no. 4122, pp. 330–332, 1974.
- [5] C. L. Woodcock, J. Safer, and J. Stanchfield, "Structural repeating units in chromatin. Evidence for their general occurrence," *Experimental Cell Research*, vol. 97, no. 1, pp. 101–110, 1976.
- [6] T. J. Richmond, J. Finch, B. Rushton, D. Rhodes, and A. Klug, "Structure of the nucleosome core particle at 7 Å resolution," *Nature*, vol. 311, no. 5986, pp. 532–537, 1984.
- [7] K. Luger, A. W. Mäder, R. K. Richmond, D. F. Sargent, and T. J. Richmond, "Crystal structure of the nucleosome core particle at 2.8 Å resolution.," *Nature*, vol. 389, no. 6648, pp. 251–260, 1997.
- [8] D. Lleres, J. James, S. Swift, D. G. Norman, and A. I. Lamond, "Quantitative analysis of chromatin compaction in living cells using FLIM-FRET," *Journal Of Cell Biology*, vol. 187, no. 4, pp. 481–496, 2009.
- [9] A. L. Olins, "Nu-bodies are close-packed in chromatin," *Cold Spring Harbor Symposium on Quantitative Biology XLII*, pp. 325–329, 1978.
- [10] D. E. Olins and A. L. Olins, "Nucleosomes: The structural quantum in chromosomes," *American Scientist*, vol. 66, no. 6, pp. 704–711, 1978.
- [11] A. L. Olins, J. P. Breillatt, R. D. Carlson, M. B. Senior, E. B. Wright, and D. E. Olins, "On nu models for chromatin structure," in *The Molecular Biology of the Mammalian Genetic Apparatus, Part A* (P. O. P. Tso, ed.), pp. 211–237, Elsevier/North Holland Biomedical Press, 1977.
- [12] C. A. Davey, D. F. Sargent, K. Luger, A. W. Maeder, and T. J. Richmond, "Solvent mediated interactions in the structure of the nucleosome core particle at 1.9 Å resolution.," *Journal Of Molecular Biology*, vol. 319, no. 5, pp. 1097–1113, 2002.
- [13] K. Luger and T. J. Richmond, "DNA binding within the nucleosome core," *Current opinion in structural biology*, vol. 8, no. 1, pp. 33–40, 1998.
- [14] H. Schiessel, "The nucleosome: a transparent, slippery, sticky and yet stable DNA-protein complex," *The European physical journal E, Soft matter*, vol. 19, no. 3, pp. 251–262, 2006.
- [15] P. Prinsen and H. Schiessel, "Nucleosome stability and accessibility of its DNA to proteins.," *Biochimie*, vol. 92, no. 12, pp. 1722–1728, 2010.

## References

---

- [16] K. Luger, "Dynamic nucleosomes," *Chromosome Research*, vol. 14, no. 1, pp. 5–16, 2006.
- [17] A. Flaus and T. Owen-Hughes, "Mechanisms for nucleosome mobilization," *Biopolymers*, vol. 68, no. 4, pp. 563–578, 2003.
- [18] T. Fletcher and J. Hansen, "Core histone tail domains mediate oligonucleosome folding and nucleosomal DNA organization through distinct molecular mechanisms," *The Journal of biological chemistry*, vol. 270, no. 43, pp. 25359–25362, 1995.
- [19] W. Krajewski and J. Ausio, "Modulation of the higher-order folding of chromatin by deletion of histone H3 and H4 terminal domains," *Biochemical Journal*, vol. 316, pp. 395–400, 1996.
- [20] V. Allfrey, R. Faulkner, and A. Mirsky, "Acetylation and methylation of histones and their possible role in regulation of RNA synthesis," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 51, no. 5, pp. 786–794, 1964.
- [21] M. S. Cosgrove, "Histone proteomics and the epigenetic regulation of nucleosome mobility.," *Expert review of proteomics*, vol. 4, no. 4, pp. 465–478, 2007.
- [22] M. Shogren-Knaak, H. Ishii, J. Sun, M. Pazin, J. Davie, and C. Peterson, "Histone H4-K16 acetylation controls chromatin structure and protein interactions," *Science*, vol. 311, no. 5762, pp. 844–847, 2006.
- [23] P. J. J. Robinson, W. An, A. Routh, F. Martino, L. Chapman, R. G. Roeder, and D. Rhodes, "30 nm chromatin fibre decompaction requires both H4-K16 acetylation and linker histone eviction.," *Journal Of Molecular Biology*, vol. 381, no. 4, pp. 816–825, 2008.
- [24] T. Jenuwein and C. Allis, "Translating the histone code," *Science*, vol. 293, no. 5532, pp. 1074–1080, 2001.
- [25] K. Polach and J. Widom, "Mechanism of Protein Access to Specific DNA Sequences in Chromatin: A Dynamic Equilibrium Model for Gene Regulation," *Journal Of Molecular Biology*, vol. 254, no. 2, pp. 130–149, 1995.
- [26] F.-T. Chien and J. van Noort, "10 Years of Tension on Chromatin: Results from Single Molecule Force Spectroscopy," *Current Pharmaceutical Biotechnology*, vol. 10, no. 5, pp. 474–485, 2009.
- [27] L. Stryer and R. Haugland, "Energy transfer - a spectroscopic ruler," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 58, no. 2, pp. 719–726, 1967.
- [28] R. M. Clegg, "Fluorescence resonance energy transfer and nucleic acids," *Methods in enzymology*, vol. 211, pp. 353–388, 1992.
- [29] T. Ha, "Single-molecule fluorescence resonance energy transfer," *Methods (San Diego, Calif)*, vol. 25, no. 1, pp. 78–86, 2001.
- [30] R. Roy, S. Hohng, and T. Ha, "A practical guide to single-molecule FRET," *Nature Methods*, vol. 5, no. 6, pp. 507–516, 2008.
- [31] N. K. Lee, A. N. Kapanidis, Y. Wang, X. Michalet, J. Mukhopadhyay, R. H. Ebright, and S. Weiss, "Accurate FRET measurements within single diffusing biomolecules using alternating-laser excitation.," *Biophysical Journal*, vol. 88, no. 4, pp. 2939–2953, 2005.
- [32] A. Gansen, K. Tóth, N. Schwarz, and J. Langowski, "Structural variability of nucleosomes detected by single-pair Förster resonance energy transfer: histone acetylation, sequence variation, and salt effects.," *The Journal of Physical Chemistry B*, vol. 113, no. 9, pp. 2604–2613, 2009.
- [33] P. T. Lowary and J. Widom, "New DNA sequence rules for high affinity binding to histone octamer and sequence-directed nucleosome positioning," *Journal Of Molecular Biology*, vol. 276, no. 1, pp. 19–42, 1998.
- [34] W. J. A. Koopmans, R. Buning, and J. van Noort, "Engineering mononucleosomes for single-pair FRET experiments.," in *Methods in Molecular Biology: Protocols in DNA Nanotechnology* (G. Zuccheri and B. Samori, eds.), pp. 291–303, Humana Press, 2011.

- [35] G. Li and J. Widom, "Nucleosomes facilitate their own invasion," *Nature Structural & Molecular Biology*, vol. 11, no. 8, pp. 763–769, 2004.
- [36] G. Li, M. Levitus, C. Bustamante, and J. Widom, "Rapid spontaneous accessibility of nucleosomal DNA.," *Nature Structural & Molecular Biology*, vol. 12, no. 1, pp. 46–53, 2005.
- [37] A. Gansen, F. Hauger, K. Tóth, and J. Langowski, "Single-pair fluorescence resonance energy transfer of nucleosomes in free diffusion: optimizing stability and resolution of subpopulations," *Analytical biochemistry*, vol. 368, no. 2, pp. 193–204, 2007.
- [38] A. Gansen, A. Valeri, F. Hauger, S. Felekyan, S. Kalinin, K. Tóth, J. Langowski, and C. A. M. Seidel, "Nucleosome disassembly intermediates characterized by single-molecule FRET," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 106, no. 36, pp. 15308–15313, 2009.
- [39] M. Tomschik, H. Zheng, K. van Holde, J. Zlatanova, and S. H. Leuba, "Fast, long-range, reversible conformational fluctuations in nucleosomes revealed by single-pair fluorescence resonance energy transfer," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 102, no. 9, pp. 3278–3283, 2005.
- [40] W. J. A. Koopmans, A. Brehm, C. Logie, T. Schmidt, and J. van Noort, "Single-pair FRET microscopy reveals mononucleosome dynamics," *Journal of Fluorescence*, vol. 17, no. 6, pp. 785–795, 2007.
- [41] W. J. A. Koopmans, T. Schmidt, and J. van Noort, "Nucleosome Immobilization Strategies for Single-Pair FRET Microscopy," *Chemphyschem: a European journal of chemical physics and physical chemistry*, vol. 9, no. 14, pp. 2002–2009, 2008.
- [42] W. J. A. Koopmans, R. Buning, T. Schmidt, and J. van Noort, "spFRET using alternating excitation and FCS reveals progressive DNA unwrapping in nucleosomes," *Biophysical Journal*, vol. 97, no. 1, pp. 195–204, 2009.
- [43] A. N. Kapanidis, N. K. Lee, T. A. Laurence, S. Doose, E. Margeat, and S. Weiss, "Fluorescence-aided molecule sorting: analysis of structure and interactions by alternating-laser excitation of single molecules.," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 101, no. 24, pp. 8936–8941, 2004.
- [44] J. Widengren, V. Kudryavtsev, M. Antonik, S. Berger, M. Gerken, and C. A. M. Seidel, "Single-molecule detection and identification of multiple species by multiparameter fluorescence detection," *Analytical Chemistry*, vol. 78, no. 6, pp. 2039–2050, 2006.
- [45] T. Torres and M. Levitus, "Measuring conformational dynamics: a new FCS-FRET approach.," *The Journal of Physical Chemistry B*, vol. 111, no. 25, pp. 7392–7400, 2007.
- [46] M. Tomschik, K. van Holde, and J. Zlatanova, "Nucleosome dynamics as studied by single-pair fluorescence resonance energy transfer: a reevaluation," *Journal of Fluorescence*, vol. 19, no. 1, pp. 53–62, 2009.
- [47] I. Rasnik, S. A. McKinney, and T. Ha, "Nonblinking and long-lasting single-molecule fluorescence imaging," *Nature Methods*, vol. 3, no. 11, pp. 891–893, 2006.
- [48] L. Kelbauskas, N. Chan, R. Bash, P. DeBartolo, J. Sun, N. Woodbury, and D. Lohr, "Sequence-dependent variations associated with H(2)A/H2B depletion of nucleosomes," *Biophysical Journal*, vol. 94, no. 1, pp. 147–158, 2008.
- [49] L. Kelbauskas, N. Woodbury, and D. Lohr, "DNA sequence-dependent variation in nucleosome structure, stability, and dynamics detected by a FRET-based analysis," *Biochemistry And Cell Biology-Biochimie Et Biologie Cellulaire*, vol. 87, no. 1, pp. 323–335, 2009.
- [50] H. Neumann, S. M. Hancock, R. Buning, A. Routh, L. Chapman, J. Somers, T. Owen-Hughes, J. van Noort, D. Rhodes, and J. W. Chin, "A method for genetically installing site-specific acetylation in recombinant histones defines the effects of H3 K56 acetylation," *Molecular Cell*, vol. 36, no. 1, pp. 153–163, 2009.

- [51] T. R. Blosser, J. G. Yang, M. D. Stone, G. J. Narlikar, and X. Zhuang, "Dynamics of nucleosome remodeling by individual ACF complexes.," *Nature*, vol. 462, no. 7276, pp. 1022–1027, 2009.
- [52] J. G. Yang and G. J. Narlikar, "FRET-based methods to study ATP-dependent changes in chromatin structure.," *Methods (San Diego, Calif)*, vol. 41, no. 3, pp. 291–295, 2007.
- [53] M. G. Poirier, M. Bussiek, J. Langowski, and J. Widom, "Spontaneous access to DNA target sites in folded chromatin fibers.," *Journal Of Molecular Biology*, vol. 379, no. 4, pp. 772–786, 2008.
- [54] M. G. Poirier, E. Oh, H. S. Tims, and J. Widom, "Dynamics and function of compact nucleosome arrays.," *Nature Structural & Molecular Biology*, vol. 16, no. 9, pp. 938–944, 2009.
- [55] A. Thåström, J. M. Gottesfeld, K. Luger, and J. Widom, "Histone-DNA binding free energy cannot be measured in dilution-driven dissociation experiments," *Biochemistry*, vol. 43, no. 3, pp. 736–741, 2004.
- [56] C. Claudet, D. Angelov, P. Bouvet, S. Dimitrov, and J. Bednar, "Histone octamer instability under single molecule experiment conditions," *The Journal of biological chemistry*, vol. 280, no. 20, pp. 19958–19965, 2005.
- [57] B. Treutlein, J. Exler, G. Ängst, and J. Michaelis, "Single-pair Fluorescence Resonance Energy Transfer study of mononucleosomes dynamics," in *Biophysical Journal*, p. 292, 2009.
- [58] H. S. Tims, K. Gurunathan, M. Levitus, and J. Widom, "Dynamics of nucleosome invasion by DNA binding proteins.," *Journal Of Molecular Biology*, vol. 411, no. 2, pp. 430–448, 2011.
- [59] V. Böhm, A. R. Hieb, A. J. Andrews, A. Gansen, A. Rocker, K. Tóth, K. Luger, and J. Langowski, "Nucleosome accessibility governed by the dimer/tetramer interface.," *Nucleic Acids Research*, vol. 39, no. 8, pp. 3093–3102, 2011.
- [60] P. Becker, "Chromatin Protocols," pp. 1–17, 2003.
- [61] I. Duband-Goulet, K. Ouararhni, and A. Hamiche, "Methods for chromatin assembly and remodeling," *Methods (San Diego, Calif)*, vol. 33, no. 1, pp. 12–17, 2004.
- [62] Y. Santoso and A. N. Kapanidis, "Probing biomolecular structures and dynamics of single molecules using in-gel alternating-laser excitation.," *Analytical Chemistry*, vol. 81, no. 23, pp. 9561–9570, 2009.
- [63] A. Gansen, A. R. Hieb, V. Böhm, K. Tóth, and J. Langowski, "Closing the Gap between Single Molecule and Bulk FRET Analysis of Nucleosomes," *Plos One*, vol. 8, no. 4, p. e57018, 2013.
- [64] E. V. Amirgoulova, J. Groll, C. D. Heyes, T. Ameringer, C. Röcker, M. Möller, and G. U. Nienhaus, "Biofunctionalized polymer surfaces exhibiting minimal interaction towards immobilized proteins.," *Chemphyschem: a European journal of chemical physics and physical chemistry*, vol. 5, no. 4, pp. 552–555, 2004.
- [65] J. Groll, T. Ameringer, J. P. Spatz, and M. Moeller, "Ultrathin coatings from isocyanate-terminated star PEG prepolymers: layer formation and characterization.," *Langmuir : the ACS journal of surfaces and colloids*, vol. 21, no. 5, pp. 1991–1999, 2005.
- [66] C. Eggeling, S. Berger, L. Brand, J. Fries, J. Schaffer, A. Volkmer, and C. A. M. Seidel, "Data registration and selective single-molecule analysis using multi-parameter fluorescence detection," *Journal of Biotechnology*, vol. 86, no. 3, pp. 163–180, 2001.
- [67] A. Hoffmann, D. Nettels, J. Clark, A. Borgia, S. E. Radford, J. Clarke, and B. Schuler, "Quantifying heterogeneity and conformational dynamics from single molecule FRET of diffusing molecules: recurrence analysis of single particles (RASP)," *Physical Chemistry Chemical Physics*, vol. 13, no. 5, p. 1857, 2011.
- [68] T. E. Tomov, R. Tsukanov, R. Masoud, M. Liber, N. Plavner, and E. Nir, "Disentangling Subpopulations in Single-Molecule FRET and ALEX Experiments with Photon Distribution Analysis," *Biophysical Journal*, vol. 102, no. 5, pp. 1163–1173, 2012.

- [69] M. Dahan, A. A. Deniz, T. Ha, D. S. Chemla, P. G. Schultz, and S. Weiss, "Ratiometric measurement and identification of single diffusing molecules," *Chemical Physics*, vol. 247, no. 1, pp. 85–106, 1999.
- [70] A. A. Deniz, M. Dahan, J. R. Grunwell, T. Ha, A. E. Faulhaber, D. S. Chemla, S. Weiss, and P. G. Schultz, "Single-pair fluorescence resonance energy transfer on freely diffusing molecules: observation of Förster distance dependence and subpopulations," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 96, no. 7, pp. 3670–3675, 1999.
- [71] M. Grunstein, "Histone acetylation in chromatin structure and transcription.," *Nature*, vol. 389, no. 6649, pp. 349–352, 1997.
- [72] T. Kouzarides, "Chromatin modifications and their function.," *Cell*, vol. 128, no. 4, pp. 693–705, 2007.
- [73] C. L. Peterson and M.-A. Laniel, "Histones and histone modifications.," *Current biology : CB*, vol. 14, no. 14, pp. R546–51, 2004.
- [74] M. D. Shahbazian and M. Grunstein, "Functions of site-specific histone acetylation and deacetylation.," *Annual Review Of Biochemistry*, vol. 76, pp. 75–100, 2007.
- [75] D. E. Sterner and S. L. Berger, "Acetylation of histones and transcription-related factors.," *Microbiology and molecular biology reviews : MMBR*, vol. 64, no. 2, pp. 435–459, 2000.
- [76] X.-J. Yang, "Lysine acetylation and the bromodomain: a new partnership for signaling.," *BioEssays : news and reviews in molecular, cellular and developmental biology*, vol. 26, no. 10, pp. 1076–1087, 2004.
- [77] Q. Li, H. Zhou, H. Wurtele, B. Davies, B. Horzodovsky, A. Verreault, and Z. Zhang, "Acetylation of histone H3 lysine 56 regulates replication-coupled nucleosome assembly.," *Cell*, vol. 134, no. 2, pp. 244–255, 2008.
- [78] M. S. Cosgrove, J. D. Boeke, and C. Wolberger, "Regulated nucleosome mobility and the histone code.," *Nature Structural & Molecular Biology*, vol. 11, no. 11, pp. 1037–1043, 2004.
- [79] H. Masumoto, D. Hawke, R. Kobayashi, and A. Verreault, "A role for cell-cycle-regulated histone H3 lysine 56 acetylation in the DNA damage response.," *Nature*, vol. 436, no. 7048, pp. 294–298, 2005.
- [80] A. Ozdemir, S. Spicuglia, E. Lasonder, M. Vermeulen, C. Campsteijn, H. G. Stunnenberg, and C. Logie, "Characterization of lysine 56 of histone H3 as an acetylation site in *Saccharomyces cerevisiae*.," *The Journal of biological chemistry*, vol. 280, no. 28, pp. 25949–25952, 2005.
- [81] F. Xu, K. Zhang, and M. Grunstein, "Acetylation in histone H3 globular domain regulates gene expression in yeast.," *Cell*, vol. 121, no. 3, pp. 375–385, 2005.
- [82] B. A. Garcia, S. B. Hake, R. L. Diaz, M. Kauer, S. A. Morris, J. Recht, J. Shabanowitz, N. Mishra, B. D. Strahl, C. D. Allis, and D. F. Hunt, "Organismal differences in post-translational modifications in histones H3 and H4.," *The Journal of biological chemistry*, vol. 282, no. 10, pp. 7641–7655, 2007.
- [83] I. Celic, H. Masumoto, W. P. Griffith, P. Meluh, R. J. Cotter, J. D. Boeke, and A. Verreault, "The sirtuins hst3 and Hst4p preserve genome integrity by controlling histone h3 lysine 56 deacetylation.," *Current biology : CB*, vol. 16, no. 13, pp. 1280–1289, 2006.
- [84] I. Celic, A. Verreault, and J. D. Boeke, "Histone H3 K56 hyperacetylation perturbs replisomes and causes DNA damage.," *Genetics*, vol. 179, no. 4, pp. 1769–1784, 2008.
- [85] C.-C. Chen, J. J. Carson, J. Feser, B. Tamburini, S. Zabaronic, J. Linger, and J. K. Tyler, "Acetylated lysine 56 on histone H3 drives chromatin assembly after repair and signals for the completion of repair.," *Cell*, vol. 134, no. 2, pp. 231–243, 2008.
- [86] C. Das, M. S. Lucia, K. C. Hansen, and J. K. Tyler, "CBP/p300-mediated acetylation of histone H3 on lysine 56," *Nature*, vol. 459, no. 7243, pp. 113–117, 2009.

## References

---

- [87] R. Driscoll, A. Hudson, and S. P. Jackson, "Yeast Rtt109 promotes genome stability by acetylating histone H3 on lysine 56.," *Science*, vol. 315, no. 5812, pp. 649–652, 2007.
- [88] J. Han, H. Zhou, B. Horazdovsky, K. Zhang, R.-M. Xu, and Z. Zhang, "Rtt109 acetylates histone H3 lysine 56 and functions in DNA replication.," *Science*, vol. 315, no. 5812, pp. 653–655, 2007.
- [89] E. M. Hyland, M. S. Cosgrove, H. Molina, D. Wang, A. Pandey, R. J. Cottee, and J. D. Boeke, "Insights into the role of histone H3 and histone H4 core modifiable residues in *Saccharomyces cerevisiae*.," *Molecular and cellular biology*, vol. 25, no. 22, pp. 10060–10070, 2005.
- [90] A. Rufiange, P.-E. Jacques, W. Bhat, F. Robert, and A. Nourani, "Genome-wide replication-independent histone H3 exchange occurs predominantly at promoters and implicates H3 K56 acetylation and Asf1.," *Molecular Cell*, vol. 27, no. 3, pp. 393–405, 2007.
- [91] S. K. Williams, D. Truong, and J. K. Tyler, "Acetylation in the globular core of histone H3 on lysine-56 promotes chromatin disassembly during transcriptional activation.," *Proceedings of the National Academy of Sciences*, vol. 105, no. 26, pp. 9000–9005, 2008.
- [92] W. Xie, C. Song, N. L. Young, A. S. Sperling, F. Xu, R. Sridharan, A. E. Conway, B. A. Garcia, K. Plath, A. T. Clark, and M. Grunstein, "Histone h3 lysine 56 acetylation is linked to the core transcriptional network in human embryonic stem cells.," *Molecular Cell*, vol. 33, no. 4, pp. 417–427, 2009.
- [93] F. Xu, Q. Zhang, K. Zhang, W. Xie, and M. Grunstein, "Sir2 deacetylates histone H3 lysine 56 to regulate telomeric heterochromatin structure in yeast.," *Molecular Cell*, vol. 27, no. 6, pp. 890–900, 2007.
- [94] B. Yang, A. Miller, and A. L. Kirchmaier, "HST3/HST4-dependent deacetylation of lysine 56 of histone H3 in silent chromatin.," *Molecular biology of the cell*, vol. 19, no. 11, pp. 4993–5005, 2008.
- [95] R. K. McGinty, J. Kim, C. Chatterjee, R. G. Roeder, and T. W. Muir, "Chemically ubiquitylated histone H2B stimulates hDot1L-mediated intranucleosomal methylation.," *Nature*, vol. 453, no. 7196, pp. 812–816, 2008.
- [96] H. Neumann, S. Y. Peak-Chew, and J. W. Chin, "Genetically encoding N<sup>ε</sup>-acetyllysine in recombinant proteins.," *Nature chemical biology*, vol. 4, no. 4, pp. 232–234, 2008.
- [97] K. Luger, T. J. Rechsteiner, and T. J. Richmond, "Preparation of nucleosome core particle from recombinant histones.," *Methods in enzymology*, vol. 304, pp. 3–19, 1999.
- [98] V. A. T. Huynh, P. J. J. Robinson, and D. Rhodes, "A method for the in vitro reconstitution of a defined "30 nm" chromatin fibre containing stoichiometric amounts of the linker histone.," *Journal Of Molecular Biology*, vol. 345, no. 5, pp. 957–968, 2005.
- [99] A. Routh, S. Sandin, and D. Rhodes, "Nucleosome repeat length and linker histone stoichiometry determine chromatin fiber structure," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 105, no. 26, pp. 8872–8877, 2008.
- [100] J. Somers and T. Owen-Hughes, "Mutations to the histone H3 alpha N region selectively alter the outcome of ATP-dependent nucleosome-remodelling reactions.," *Nucleic Acids Research*, vol. 37, no. 8, pp. 2504–2513, 2009.
- [101] R. Bash, H. Wang, C. Anderson, J. Yodh, G. Hager, S. M. Lindsay, and D. Lohr, "AFM imaging of protein movements: histone H2A-H2B release during nucleosome remodeling.," *FEBS letters*, vol. 580, no. 19, pp. 4757–4761, 2006.
- [102] M. Bruno, A. Flaus, C. Stockdale, C. Rencurel, H. Ferreira, and T. Owen-Hughes, "Histone H2A/H2B dimer exchange by ATP-dependent chromatin remodeling activities.," *Molecular Cell*, vol. 12, no. 6, pp. 1599–1606, 2003.
- [103] A. J. Ruthenburg, H. Li, D. J. Patel, and C. D. Allis, "Multivalent engagement of chromatin modifications by linked binding modules.," *Nature Reviews Molecular Cell Biology*, vol. 8, no. 12, pp. 983–994, 2007.



- [104] S. D. Taverna, H. Li, A. J. Ruthenburg, C. D. Allis, and D. J. Patel, "How chromatin-binding modules interpret histone modifications: lessons from professional pocket pickers," *Nature Structural & Molecular Biology*, vol. 14, no. 11, pp. 1025–1040, 2007.
- [105] A. J. Bannister, P. Zegerman, J. F. Partridge, E. A. Miska, J. O. Thomas, R. C. Allshire, and T. Kouzarides, "Selective recognition of methylated lysine 9 on histone H3 by the HP1 chromo domain.," *Nature*, vol. 410, no. 6824, pp. 120–124, 2001.
- [106] C. Dhalluin, J. E. Carlson, L. Zeng, C. He, A. K. Aggarwal, and M. M. Zhou, "Structure and ligand of a histone acetyltransferase bromodomain.," *Nature*, vol. 399, no. 6735, pp. 491–496, 1999.
- [107] R. H. Jacobson, A. G. Ladurner, D. S. King, and R. Tjian, "Structure and function of a human TAFII250 double bromodomain module.," *Science*, vol. 288, no. 5470, pp. 1422–1425, 2000.
- [108] M. Kasten, H. Szerlong, H. Erdjument-Bromage, P. Tempst, M. Werner, and B. R. Cairns, "Tandem bromodomains in the chromatin remodeler RSC recognize acetylated histone H3 Lys14.," *The EMBO journal*, vol. 23, no. 6, pp. 1348–1359, 2004.
- [109] M. Lachner, D. O'Carroll, S. Rea, K. Mechtler, and T. Jenuwein, "Methylation of histone H3 lysine 9 creates a binding site for HP1 proteins.," *Nature*, vol. 410, no. 6824, pp. 116–120, 2001.
- [110] H. Li, S. Ilin, W. Wang, E. M. Duncan, J. Wysocka, C. D. Allis, and D. J. Patel, "Molecular basis for site-specific read-out of histone H3K4me3 by the BPTF PHD finger of NURF," *Nature*, vol. 442, no. 7098, pp. 91–95, 2006.
- [111] J. Wysocka, T. Swigut, H. Xiao, T. A. Milne, S. Y. Kwon, J. Landry, M. Kauer, A. J. Tackett, B. T. Chait, P. Badenhorst, C. Wu, and C. D. Allis, "A PHD finger of NURF couples histone H3 lysine 4 trimethylation with chromatin remodelling.," *Nature*, vol. 442, no. 7098, pp. 86–90, 2006.
- [112] K. Wang, H. Neumann, S. Y. Peak-Chew, and J. W. Chin, "Evolved orthogonal ribosomes enhance the efficiency of synthetic genetic code expansion.," *Nature Biotechnology*, vol. 25, no. 7, pp. 770–777, 2007.
- [113] P. E. Dawson, T. W. Muir, I. Clark-Lewis, and S. B. Kent, "Synthesis of proteins by native chemical ligation.," *Science*, vol. 266, no. 5186, pp. 776–779, 1994.
- [114] H. Ferreira, A. Flaus, and T. Owen-Hughes, "Histone modifications influence the action of Snf2 family remodelling enzymes by different mechanisms.," *Journal Of Molecular Biology*, vol. 374, no. 3, pp. 563–579, 2007.
- [115] M. D. Simon, F. Chu, L. R. Racki, C. C. de la Cruz, A. L. Burlingame, B. Panning, G. J. Narlikar, and K. M. Shokat, "The site-specific installation of methyl-lysine analogs into recombinant histones.," *Cell*, vol. 128, no. 5, pp. 1003–1012, 2007.
- [116] S. D. Taverna, B. M. Ueberheide, Y. Liu, A. J. Tackett, R. L. Diaz, J. Shabanowitz, B. T. Chait, D. F. Hunt, and C. D. Allis, "Long-distance combinatorial linkage between methylation and acetylation on histone H3 N termini.," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 104, no. 7, pp. 2086–2091, 2007.
- [117] J. Zlatanova and A. Thakar, "H2A.Z: View from the Top," *Structure*, vol. 16, no. 2, pp. 166–179, 2008.
- [118] A. A. Thambirajah, D. Dryhurst, T. Ishibashi, A. Li, A. H. Maffey, and J. Ausi , "H2A.Z stabilizes chromatin in a way that is dependent on core histone acetylation.," *The Journal of biological chemistry*, vol. 281, no. 29, pp. 20036–20044, 2006.
- [119] Y.-J. Park, P. N. Dyer, D. J. Tremethick, and K. Luger, "A new fluorescence resonance energy transfer approach demonstrates that the histone variant H2AZ stabilizes the histone octamer within the nucleosome," *The Journal of biological chemistry*, vol. 279, no. 23, pp. 24274–24282, 2004.
- [120] H. Zhang, D. N. Roberts, and B. R. Cairns, "Genome-wide dynamics of Htz1, a histone H2A variant that poises repressed/basal promoters for activation through histone loss.," *Cell*, vol. 123, no. 2, pp. 219–231, 2005.

## References

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- [121] D. W. Abbott, V. S. Ivanova, X. Wang, W. M. Bonner, and J. Ausio, "Characterization of the stability and folding of H2A.Z chromatin particles: implications for transcriptional activation.," *The Journal of biological chemistry*, vol. 276, no. 45, pp. 41945–41949, 2001.
- [122] R. K. Suto, M. J. Clarkson, D. J. Tremethick, and K. Luger, "Crystal structure of a nucleosome core particle containing the variant histone H2A.Z.," *Nature structural biology*, vol. 7, no. 12, pp. 1121–1124, 2000.
- [123] C. M. Weber, J. G. Henikoff, and S. Henikoff, "H2A.Z nucleosomes enriched over active genes are homotypic," *Nature Structural & Molecular Biology*, vol. 17, no. 12, pp. 1500–1507, 2010.
- [124] S. V. Kumar and P. A. Wigge, "H2A.Z-Containing Nucleosomes Mediate the Thermosensory Response in Arabidopsis," *Cell*, vol. 140, no. 1, pp. 136–147, 2010.
- [125] National Human Genome Research Institute - Histone Database. <http://research.nhgri.nih.gov/histones/index.cgi>, checked may 2014.
- [126] Protein Calculator v3.4. <http://protcalc.sourceforge.net/>, checked may 2014.
- [127] R. Buning and J. van Noort, "Single-pair FRET experiments on nucleosome conformational dynamics.," *Biochimie*, vol. 92, no. 12, pp. 1729–1740, 2010.
- [128] T. T. M. Ngo, R. Zhou, J. Yodh, and T. Ha, "Asymmetric Unwrapping of Nucleosome Revealed by Single Molecule Fluorescence-Force Spectroscopy," *Biophysical Journal*, vol. 104, no. S1, p. 210a, 2013.
- [129] A. Prunell and R. D. Kornberg, "Variable center to center distance of nucleosomes in chromatin," *Journal Of Molecular Biology*, vol. 154, no. 3, pp. 515–523, 1982.
- [130] P. J. J. Robinson, L. Fairall, V. Huynh, and D. Rhodes, "EM measurements define the dimensions of the "30-nm" chromatin fiber: Evidence for a compact, interdigitated structure," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 103, no. 17, pp. 6506–6511, 2006.
- [131] T. Schalch, S. Duda, D. F. Sargent, and T. J. Richmond, "X-ray structure of a tetranucleosome and its implications for the chromatin fibre.," *Nature*, vol. 436, no. 7047, pp. 138–141, 2005.
- [132] F. Song, P. Chen, D. Sun, M. Wang, L. Dong, D. Liang, R.-M. Xu, P. Zhu, and G. Li, "Cryo-EM study of the chromatin fiber reveals a double helix twisted by tetranucleosomal units.," *Science*, vol. 344, no. 6182, pp. 376–380, 2014.
- [133] S. C. Howell, K. Andresen, I. Jimenez-Useche, C. Yuan, and X. Qiu, "Elucidating Internucleosome Interactions and the Roles of Histone Tails," *Biophysical Journal*, vol. 105, no. 1, pp. 194–199, 2013.
- [134] M. Kruithof, F.-T. Chien, A. Routh, C. Logie, D. Rhodes, and J. van Noort, "Single-molecule force spectroscopy reveals a highly compliant helical folding for the 30-nm chromatin fiber," *Nature Structural & Molecular Biology*, vol. 16, no. 5, pp. 534–540, 2009.
- [135] T. Ha, T. Enderle, D. F. Ogletree, D. S. Chemla, P. R. Selvin, and S. Weiss, "Probing the interaction between two single molecules: fluorescence resonance energy transfer between a single donor and a single acceptor," *Proceedings Of The National Academy Of Sciences Of The United States Of America*, vol. 93, no. 13, pp. 6264–6268, 1996.
- [136] J. Widom, "A relationship between the helical twist of DNA and the ordered positioning of nucleosomes in all eukaryotic cells.," *Proceedings of the National Academy of Sciences*, vol. 89, no. 3, pp. 1095–1099, 1992.
- [137] J.-P. Wang, Y. Fondufe-Mittendorf, L. Xi, G.-F. Tsai, E. Segal, and J. Widom, "Preferentially Quantized Linker DNA Lengths in *Saccharomyces cerevisiae*," *PLoS Computational Biology*, vol. 4, no. 9, p. e1000175, 2008.
- [138] K. Brogaard, L. Xi, J.-P. Wang, and J. Widom, "A map of nucleosome positions in yeast at base-pair resolution.," *Nature*, vol. 486, no. 7404, pp. 496–501, 2012.

- [139] G. Zheng, X.-J. Lu, and W. K. Olson, "Web 3DNA—a web server for the analysis, reconstruction, and visualization of three-dimensional nucleic-acid structures.," *Nucleic Acids Research*, vol. 37, no. Web Server issue, pp. W240–6, 2009.
- [140] K. Tóth, N. Brun, and J. Langowski, "Trajectory of nucleosomal linker DNA studied by fluorescence resonance energy transfer," *Biochemistry*, vol. 40, no. 23, pp. 6921–6928, 2001.
- [141] A. J. Andrews and K. Luger, "Nucleosome Structure(s) and Stability: Variations on a Theme," *Annual Review Of Biophysics, Vol 40*, vol. 40, pp. 99–117, 2011.
- [142] J. G. Yodh, Y. L. Lyubchenko, L. S. Shlyakhtenko, N. Woodbury, and D. Lohr, "Evidence for Nonrandom Behavior in 208-12 Subsaturated Nucleosomal Array Populations Analyzed by AFM," *Biochemistry*, vol. 38, no. 48, pp. 15756–15763, 1999.
- [143] T. H. Eickbush and E. N. Moudrianakis, "The histone core complex: an octamer assembled by two sets of protein-protein interactions.," *Biochemistry*, vol. 17, no. 23, pp. 4955–4964, 1978.
- [144] K. Rippe, J. Mazurkiewicz, and N. Kepper, "Interactions of Histones with DNA: Nucleosome Assembly, Stability, Dynamics, and Higher Order Structure," *DNA Interactions with Polymers and Surfactants*, p. 135, 2008.

