Curriculum Vitae

Name: Scott Neal Keeney

Date of Birth: December 3, 1965

Place of Birth: Baltimore, Maryland

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Education:

1987 Virginia Polytechnic Institute and State University
B.S. Biochemistry, Blacksburg, VA

1993 University of California
Ph.D. Biochemistry, Berkeley, CA
Mentor: Prof. Stuart Linn

Postdoctoral Training:

1993-1997 Department of Molecular and Cellular Biology
Harvard University, Cambridge, MA
Mentor: Prof. Nancy Kleckner

Positions and Appointments:

Sept. 1997–present Molecular Biology Program, Memorial Sloan-Kettering Cancer Center.
Assistant Member (1997–2004), Associate Member (2004–2006), Member (2006–present).

Jan. 1998–present Molecular Biology Program and Biochemistry and Structural Biology Program, Weill Graduate School of Medical Sciences, Cornell University.
Assistant Professor (1998–2005), Associate Professor (2005–2007), Professor (2007–present), Co-Director, BCMB Allied Programs (2007–present).

Sept. 2006–present Gerstner Sloan-Kettering Graduate School of Biomedical Sciences.
Associate Professor (9/2006–11/2006), Professor (11/2006–present).

Aug. 2008–present Investigator, Howard Hughes Medical Institute

Honors and Awards:

1983 Marshall Hahn Scholarship
1983-1987 National Merit Award Scholarship
1986 Phi Beta Kappa
1987 James Lewis Howe Undergraduate Research Award, Blue Ridge Section of the American Chemical Society

1987	B.S., *summa cum laude*, in honors, Virginia Tech
1987-1988	University of California Regents Fellowship
1988-1991	National Science Foundation Graduate Fellowship
1994-1997	Fellow, Damon Runyon-Walter Winchell Foundation
1998-2001	Awardee, NY City Council Speaker's Fund for Biomedical Research
2004	Louise and Allston Boyer Young Investigator Award, MSKCC
2005-2010	Leukemia and Lymphoma Society Scholar
2007	Finalist, Blavatnik Young Scientist Award, NY Academy of Sciences

Scientific Societies:

American Society for Biochemistry and Molecular Biology, American Society for Microbiology, Genetics Society of America, Harvey Society

Editorial Review:

Genetics (Associate Editor 2007–)
Genes to Cells (Associate Editor 2003–)
Chromosoma (Associate Editor 2006–)
Ad hoc reviewer (partial listing): Cell, Chromosoma, Current Biology, Developmental Cell, EMBO Journal, Genetics, Genes & Development, International Journal of Andrology, Journal of Biological Chemistry, Journal of Cell Biology, Journal of Cell Science, Molecular Cell, Molecular and Cellular Biology, Nature, Nature Genetics, Nature Structural and Molecular Biology, Nucleic Acids Research, Proceedings of the National Academy of Science USA, Science, PLoS Biology, PLoS Genetics, Trends in Genetics

Grant Reviews:

Genetic Mechanisms of Cancer peer review committee, American Cancer Society (6/2003–6/2007)
NIH Molecular Genetics A (MGA) study section (ad hoc 10/2007, regular member 10/2008–6/2012)
Ad hoc reviewer: NIH study sections: Nuclear Dynamics and Transport (NDT, 6/2006, 2/2008). NSF, Israel Science Foundation, Marathon (Italy), Austrian Science Fund, Council for Chemical Sciences of the Netherlands Organisation for Scientific Research, Wellcome Trust (U.K.), Swiss National Science Foundation, New Jersey Commission on Cancer Research.

Peer-Reviewed Publications:

1. Juan JY, Keeney SN, and Gregory EM. (1991) Reconstitution of the *Deinococcus radiodurans* aposuperoxide dismutase. *Arch. Biochem. Biophys*. **286**:257-263.

2. Keeney S, Wein H, and Linn S. (1992) Biochemical heterogeneity in xeroderma pigmentosum complementation group E. *Mutat. Res.* **273**:49-56.

3. Keeney S., Chang GJ, and Linn S. (1993) Characterization of a human DNA damage binding protein implicated in xeroderma pigmentosum E. *J. Biol. Chem*. **268**:21293-21300.

4. Reardon JT, Nichols AF, Keeney S, Smith CA, Taylor JS, Linn S, and Sancar A. (1993) Comparative analysis of binding of human damaged DNA-binding protein (XP-E) and Escherichia coli damage recognition protein (UvrA) to the major ultraviolet photoproducts: T[c,s]T, T[t,s]T, T[6,4]T, and T[Dewar]T. *J. Biol. Chem*. **268**:21301-21308.

5. Keeney S, Eker APM, Vermeulen W, Brody T, Hoeijmakers, JHJ, Bootsma D, and Linn S. (1994) Correction of the DNA repair defect in xeroderma pigmentosum E by injection of a DNA damage binding protein. *Proc. Natl. Acad. Sci. USA* **91**:4053-4056.

6. Dualan, R, Brody T, Keeney S, Nichols AF, Admon A, and Linn S. (1995) Chromosomal localization and cDNA cloning of the genes (*DDB1* and *DDB2*) for the p127 and p48 subunits of a human damage-specific DNA binding protein. *Genomics* **29**:62-69.

7. Keeney S, and Kleckner N. (1995) Covalent protein-DNA complexes at the 5′ strand termini of meiosis-specific double-strand breaks in yeast. *Proc. Natl. Acad. Sci. USA* **92**:11274-11278.

8. Vaisman A, Keeney S, Nichols AF, Linn S, and Chaney SG. (1996) Cisplatin-induced alterations in the expression of the mRNAs for UV-damage recognition protein. *Oncol. Res*. **8**:7-12.

9. Keeney S, and Kleckner N. (1996) Communication between homologous chromosomes: genetic alterations at a nuclease-hypersensitive site can alter mitotic chromatin structure at that site both in cis and in trans. *Genes Cells* **1**:475-489.

10. Keeney S, Giroux CN, and Kleckner N. (1997) Meiosis-specific DNA double-strand breaks are catalyzed by Spo11, a member of a widely conserved protein family. *Cell* **88**:375-384.

11. Keeney S, Baudat F, Angeles M, Zhou Z-H, Copeland NG, Jenkins NA, Manova K, and Jasin M. (1999) A mouse homolog of the *Saccharomyces cerevisiae* meiotic recombination DNA transesterase Spo11p. *Genomics* **61**, 170-182.

12. Cha RS, Weiner BM, Keeney S, Dekker J, and Kleckner N. (2000) Progression of meiotic DNA replication is modulated by interchromosomal interaction proteins, negatively by Spo11p and positively by Rec8p. *Genes Dev*. **14**, 493-503.

13. Baudat F, Manova K, Yuen JP, Jasin M, and Keeney S. (2000) Chromosome synapsis defects and sexually dimorphic meiotic progression in mice lacking Spo11. *Mol. Cell* **6**, 989-998.

14. Keeney S (2001) Mechanism and control of meiotic recombination initiation. (Review) *Curr. Top. Dev. Biol.* **52**, 1-53.

15. Mahadevaiah SK, Turner JMA, Baudat F, Rogakou EP, de Boer P, Blanco-Rodriguez J, Jasin M, Keeney S, Bonner WM, and Burgoyne PS. (2001) Recombinational DNA double strand breaks in mice precede synapsis. *Nat. Genet.* **27**, 271-276.

16. Klein U, Esposito G, Baudat F, Keeney S, and Jasin M. (2002) Mice deficient for the type II topoisomerase-like DNA transesterase Spo11 show normal immunoglobulin somatic hypermutation and class switching. *Eur. J. Immunol*. **32**, 316-321.

17. Kee K, and Keeney S. (2002) Functional interactions between *SPO11* and *REC102* during initiation of meiotic recombination in *Saccharomyces cerevisiae*. *Genetics* **160**, 111-122.

18. Diaz RL, Alcid AD, Berger JM, and Keeney S. (2002) Identification of residues critical for meiotic DNA double-strand break formation by yeast Spo11. *Mol. Cell. Biol*. **22**, 1106-1115.

19. Martini E, Keeney S, and Osley MA. (2002) A role for histone H2B during UV-induced DNA repair in Saccharomyces cerevisiae. *Genetics* **160**, 1375-1387.

20. Arora C, Kee K, Maleki S, and Keeney S. (2004) Antiviral protein Ski8 is a direct partner of Spo11 in meiotic DNA break formation, independent of its role in cytoplasmic RNA metabolism. *Mol. Cell* **13**, 549-559.

21. Henderson KA, and Keeney S. (2004) Tying synaptonemal complex initiation to the formation and programmed repair of DNA double-strand breaks. *Proc. Natl. Acad. Sci. USA* **101**, 4519-4524.

22. Kee K, Protacio RU, Arora C, and Keeney S. (2004) Spatial organization and dynamics of the association of Rec102 and Rec104 with meiotic chromosomes. *EMBO J.* **23**, 1815-1824.

23. Kauppi L, Jeffreys AJ, and Keeney S. (2004) Where the crossovers are: Recombination distributions in mammals. *Nature Rev. Genet.* **5**, 413-424.

24. Di Giacomo M, Barchi M, Baudat F, Edelmann W, Keeney S, and Jasin M (2005) Distinct DNA damage-dependent and independent responses drive the loss of oocytes in recombination-defective mouse mutants. *Proc. Natl. Acad. Sci. USA* **102**, 737-742.

25. Ahn S-H, Henderson KA, Keeney S, and Allis CD (2005) H2B (Ser10) phosphorylation is induced during apoptosis and meiosis in S. cerevisiae. *Cell Cycle* **4**, 780-783.

26. Barchi M, Mahadevaiah S, Di Giacomo M, Baudat F, de Rooij DG, Burgoyne PS, Jasin M, and Keeney S (2005). Surveillance of different recombination defects in mouse spermatocytes yields distinct responses despite elimination at an identical developmental stage. *Mol. Cell. Biol.* **25**, 7203-7215.

27. Neale M, Pan J, and Keeney S (2005) Endonucleolytic processing of covalent protein-linked DNA double-strand breaks. *Nature* **436**, 1053-1057.

28. Henderson K, Kee K, Maleki S, Santini P, and Keeney S (2006) Cyclin-dependent kinase directly regulates initiation of meiotic recombination. *Cell* **125**, 1321-1332.

29. Neale M and Keeney S (2006) Clarifying the mechanics of DNA strand exchange in meiotic recombination (invited review). *Nature* **442**, 153-158.

30. Martini E, Diaz RL, Hunter N, and Keeney S (2006). Crossover homeostasis in yeast meiosis. *Cell* **126**, 285-295.

31. Liebe B, Pethukhova G, Barchi M, Bellani M, Braselmann H, Nakano T, Pandita MTK, Jasin M, Fornace A, Meistrich ML, Baarends WM, Schimenti J, de Lange T, Keeney S, Camerini-Otero RD, and Scherthan H (2006). Mutations that affect meiosis in male mice influence the dynamics of the mid-preleptotene and bouquet stages. *Exp. Cell Res.* **312**, 3768-3781.

32. Keeney S (2007) Spo11 and the formation of DNA double-strand breaks in meiosis. In *Genome Dynamics and Stability*, vol. 2, "Recombination and Meiosis." D. Lankenau, Ed., Springer. Published online May 2007.

33. Maleki S, Neale MJ, Arora C, Henderson KA, and Keeney S (2007) Interactions between Mei4, Rec114, and other proteins required for meiotic DNA double-strand break formation in *Saccharomyces cerevisiae*. *Chromosoma* **116**, 471-486.

34. Kauppi L, Jasin M, and Keeney S (2007) Meiotic crossover hotspots contained in haplotype block boundaries of the mouse genome. *Proc. Natl. Acad. Sci. USA* **104**, 13396-13401.

35. Barchi M, Roig I, Di Giacomo M, de Rooij DG, Keeney S, and Jasin M (2008) ATM promotes the obligate XY crossover and both crossover control and chromosome axis integrity on autosomes. *PLoS Genet*. **4**, e1000076.

36. Kidane D, Jonason AS, Gorton TS, Mihaylov I, Pan J, Keeney S, Ashley T, Keh A, Liu Y, Banerjee U, Zelterman D, and Sweasy JB (2009) DNA polymerase beta is critical for mouse meiotic synapsis. Submitted.

37. Wojtasz L, Daniel K, Roig I, Bolcun-Filas E, Xu H, Boonsanay V, Eckmann C, Cooke HJ, Jasin M, Keeney S, McKay MJ, and Toth A (2009) Mouse HORMAD1 and HORMAD2, two conserved meiotic chromosomal proteins, are depleted from synapsed chromosome axes with the help of TRIP13 AAA-ATPase. Submitted.

38. Roig I, de Rooij D, Jasin M, and Keeney S (2009) The mouse PCH2 ortholog, TRIP13, is required for completion of synapsis and efficient recombination leading to both crossovers and non-crossovers. In preparation.

Book Chapters and Other Non-Peer-Reviewed Publications:

1. Nishida C, Choi SY, Kim J, Keeney S, and Linn S. (1988) DNA polymerase d plus HeLa or human fibroblast cell-free extracts complement permeabilized xeroderma pigmentosum fibroblasts: Application for purification of repair factors, in: E.C. Friedberg and P.C. Hanawalt (Eds.), Mechanisms and Consequences of DNA Damage Processing, Liss, New York, pp. 337-341.

2. Keeney S, and Linn S. (1990) A critical review of permeabilized cell systems for studying mammalian DNA repair. Mutat. Res. 236, 239-252.

3. Baudat F, and Keeney S. (2001) Meiotic recombination: Making and breaking go hand in hand. (Minireview) *Curr. Biol.*, **11**, R45-R48.

4. Martini E, and Keeney S. (2002) Sex and the single (double-strand) break. (Minireview) *Mol. Cell* **9**, 700-702.

5. Maleki S, and Keeney S (2004) Modifying histones and initiating meiotic recombination: New answers to an old question. (Minireview) *Cell* **118**, 404-406.

6. Okada T, and Keeney S (2005) Homologous recombination: Needing to have my say. (Dispatch) *Curr. Biol.***15**, R200-R202.

7. Henderson KA and Keeney S (2005) Synaptonemal complex formation: Where does it start? (Minireview) *Bioessays* **27**, 995-998.

8. Keeney S and Neale MJ (2006) Initiation of meiotic recombination by formation of DNA double-strand breaks: Mechanism and regulation. (Meeting proceedings). *Biochem. Soc. Trans.* **34**, 523-525.

9. Pan J and Keeney S (2007) Molecular cartography: Mapping the landscape of meiotic recombination. (Invited primer.) *PLoS Biology* **5**, 2775-2777.

10. Murakami H and Keeney S (2008) Regulating the formation of DNA double-strand breaks in meiosis (Preview). *Genes Dev*. **22**, 286-292.

11. Roig, I and Keeney, S (2008) Probing meiotic recombination decisions (preview). *Dev. Cell* **15**, 331-332.

12. Kniewel, R and Keeney, S (2009) Histone methylation sets the stage for meiotic DNA breaks (Minireview). *EMBO J*. **28**, 81-83.
13. Murakami H, Borde V, Nicolas A, and Keeney S (2009) Gel electrophoresis assays for analyzing DNA double-strand breaks in *Saccharomyces cerevisiae* at various spatial resolutions. *Methods Mol. Biol*. 557, 117–142.
14. Neale MJ and Keeney S (2009) End-labeling and analysis of Spo11-oligonucleotide complexes in *Saccharomyces cerevisiae*. *Methods Mol. Biol*. 557, 183–195.
15. Pan J and Keeney S (2009) Detection of SPO11-oligonucleotide complexes from mouse testes. *Methods Mol. Biol*. 557, 197–207.
16. Thacker D and Keeney S (2009) PCH'ing together an understanding of crossover control (minireview). *PLoS Genet*., in press.

Books:

1. Keeney S (Editor) (2009) *Meiosis, Volume 1, Molecular and Genetic Methods.* Vol. 557 in the *Methods in Molecular Biology* series, Humana Press, New York.
2. Keeney S (Editor) (2009) *Meiosis, Volume 2, Cytological Methods.* Vol. 558 in the *Methods in Molecular Biology* series, Humana Press, New York.