Curriculum Vitae: Scott Neal Keeney

Born: December 3, 1965, 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
Advisor: Prof. Stuart Linn

Postdoctoral Training

1993-1997 Department of Molecular and Cellular Biology
Harvard University, Cambridge, MA
Advisor: 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 Graduate Programs (2007–2010).

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
2008	Investigator, Howard Hughes Medical Institute
2012	Clayton S. White Endowed Lecture, Oklahoma Medical Research Foundation
2013	Keynote Speaker, University of Iowa Genetics PhD Program Retreat
2014	Keynote Speaker, Abcam Recombination Meeting celebrating the 50th anniversary of the Holliday model
2014	Elected, Fellow of the American Academy of Microbiology

Scientific Societies

Genetics Society of America, American Academy of Microbiology, American Society for Biochemistry and Molecular Biology, American Society for Microbiology, Harvey Society, NY Academy of Sciences, Faculty of 1000

Mentorship

PhD Students:

Completed dissertations in my laboratory (current position indicated) **(9 total)**:

Kehkooi Kee (Assistant Prof., Tsinghua University, Beijing);
Charanjit Arora (Attorney, UCLA);
Kiersten Henderson (postdoc, Fred Hutchinson Cancer Research Center);
James Dowdle (postdoc, Ohio State Univ);
Mariko Sasaki (postdoc, National Inst. Of Genetics, Mishima Japan);
Drew Thacker (postdoc, UCSF);
Ryan Kniewel (postdoc, Univ. of Madrid, Spain),
Sam Globus (Director of Scientific Operations, Celmatix)
Xuan Zhu (in transition)

Current **(5 total)**: Isabel Lam, Erman Karasu, Sam Tischfield, Xiaojing Mu

Postdoctoral Fellows:

Past (current position indicated) **(12 total)**:

Shohreh Maleki PhD (Research Asst. Prof., Karolinska Instit., Stockholm, Sweden);
Emmanuelle Martini PhD (Permanent position, CEA, France);
Monica DiGiacomo PhD (Postdoc, EMBL Rome);
Takashi Okada MD PhD (Asst. Prof., Dept of Urology, Ijinkai-Takeda General Hospital, Kyoto, Japan);
Matthew Neale PhD (Royal Society Fellow, Genome Stability Centre, Univ Sussex, UK);
Jing Pan PhD (Lecturer, University of Texas, Dallas);

Ignasi Roig PhD (Assistant Prof., Univ. Auton. Barcelona, Spain);
Viji Subramanian PhD (postdoc, NYU);
Esther de Boer PhD (Senior Research Scientist, Inst. Of Life Science, Univ. of Amsterdam);
Liisa Kauppi PhD (Group Leader, Univ. Helsinki);
Megan van Overbeek PhD (Staff Researcher, Caribou Biosciences, Berkeley CA);
Monika Mehta PhD (unemployed)

Current (graduate institution and postdoctoral fellowship information indicated) **(10 total)**:
Laurent Acquaviva PhD (Aix-Marseille University, France; Lalor Foundation Fellowship);
Corentin Claeys Bouuaert PhD (Univ. of Nottingham, UK);
Devanshi Jain PhD (London Res. Inst. CRUK; Human Frontiers Science Program Fellowship);
Sarah Seoyoung Kim PhD (Univ. of Oklahoma Health Sciences Center; Leukemia and Lymphoma Society Fellowship);
Julian Lange PhD (MIT; American Cancer Society Fellowship);
Elena Mimitou PhD (Columbia University; Helen Hay Whitney Fellowship);
Neeman Mohibullah PhD (University of Washington, Seattle);
Hajime Murakami PhD (Saitama University, Japan);
David Ontoso Picon PhD (Univ. of Salamanca, Spain);
Shintaro Yamada PhD (University of Tokyo)

Undergraduates (11 total):
Via the MSKCC Summer Undergraduate Research Program or HHMI EXROP
(Subsequent training and current position indicated)
Marc Waase, Cornell University, 1999 (MD PhD, Cornell/Rockefeller; Residency: Internal Medicine, NY Presbyterian Hospital; currently a Cardiology Fellow, NYPH)
Steven Quatela, Haverford College, 1999 (MD PhD, NYU; currently Clinical Fellow in Pediatric Hematology/Oncology, MSKCC)
Zareen Gauhar, Mount Holyoke College, Springfield MA, 2000 (PhD, Yale Med; currently Senior Scientific Director at Discovery USA)
Jennie Hann, Stanford University, 2002 (currently a PhD candidate in English, Johns Hopkins University)
Tara Berman, University of Pennsylvania, 2004, 2005 (MD Tel Aviv Univ; currently an Internal Medicine Resident, St Luke's-Roosevelt Hospital)
Alanna Li, Cornell University, 2007 (DDS 2014, Columbia Dental School; in private practice)
Meredith Spadaccia, University of Maryland, 2008 (currently a Research Technician, Mt Sinai)
Adolfo Cuesta, Haverford College, 2009 (currently a Research Technician, NYU)
Leslie Higuita-Montoya, Furman University, 2011 (currently in MPH program, Mt Sinai)
Danté Johnson, Louisiana State University, 2013 (RD&E Intern, SC Johnson)
Tomás Rodriguez, UC Davis, 2014 (entering MD PhD program, UMass Worcester)

Institutional Service

MSKCC:
1998–2006 Molecular Biology Seminar Committee

2008–2013	MSKCC Committee on Appointments and Promotions
2008–2014	Sloan Kettering Institute Committee on Appointments and Promotions
2009–present	Postdoc/Faculty Forum, "Chalk Talk Tips"
2010–present	Oversight Committee, Genomics Core Laboratory,
2011	Chair, MSKCC Task Force on Genomics and Proteomics
2013–present	Chair, Oversight Committee, Proteomics Core Facility

Graduate Education:

2007–2010 Co-Director, Biochemistry and Cell & Molecular Biology (BCMB) Allied Programs
2003–2007 BCMB First Year Advisor
GSK First Year Mentor: Eric Alonso, Elizabeth Wasmuth, Yvonne Gruber, Chong Luo

Teaching:

2005–2008	Weill BCMB, Molecular Genetics Course Director
1998–present	Weill BCMB, Molecular Genetics Course, 2–3 lectures per year
1998–2005	Weill BCMB, Gene Structure and Function (2 lectures per year)
1998, 2000, 2002	Weill BCMB, Nucleic acids enzymology (3–6 lectures per year)
2006	Weill BCMB Focus Group, "Meiosis"
2006–present	GSK Core Course, 2-6 lectures per year

Committees:

1997–2007	Weill BCMB Retreat Committee
1999–2003, 2006	Weill BCMB ACE Committee
2004–2010	Weill BCMB Curriculum Committee
2007–2012	Weill BCMB Admissions Committee
2013	Search Committee, Weill Graduate School Dean

Thesis and thesis-defense committees:

Weill/Cornell: (partial listing from **> 30 total**) Pearl Chang, Liwei Xu, Karen Lee, Jale Refik-Rogers, Ligeng Tian, Chonghui Chen, Chunling Gong, Rob Gillespie, Ryan Heller, Yun Jiang, Hilary Gerber, Claudio Alarcon, Kelly Yule George, Carrie Adelman, Jan Theunissen, Borko Amulic, Ram Madabhushi, Jennifer Lee, Jaclyn Gareau, Sohini Sanyal, Yu-Hung (Jeff) Chen, Cristina Ghenoiu, Ryo Hayama, Zhenjian Cai, Emily Bauer, Ying Liu, Min Hsu, Zhicheng (Ray) Qiu, Sujan Devbhandari, James Bellush

GSK **(5 total)**: Muge Akpinar, Sadia Rahman, Elizabeth Wasmuth, Lei Wei, Weiran Feng

MD/PhD Program **(4 total)**: Tom Nguyen, Josh Silverman, Isaac Klein, Xiao Peng

External (**3 total**): Angelique Girard (Greg Hannon lab, Cold Spring Harbor); Tracy Callender (Nancy Hollingsworth lab, Stonybrook University); Huei-Mei Chen (Janet Leatherwood lab, Stonybrook University)

Extramural Service

Editorial Review:

Genetics (Associate Editor 2007–2011)
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, Genome Research, 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

Conference organization:

Meiosis Gordon Conference (vice-Chair 2006; Chair 2008)
FASEB Yeast Chromosomes Conference (co-Organizer 2012)
3R Meeting, Japan (Member of foreign advisory board, 2012, 2014)
NY Academy of Sciences Genome Integrity Discussion Group (co-Organizer, 2014–present)
Keystone Symposium on Replication and Recombination (co-Organizer, 2017)
FASEB Conference on Genetic Recombination and Genome Rearrangements (vice-Chair 2017; Chair 2019)

Grant Reviews:

Genetic Mechanisms of Cancer 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 10/2015)
NIGMS Council, Ad Hoc Consultant, 5/2013
NIH ZRG1 GGG F(80) (R15 study section), 3/2015
Ad hoc reviewer (partial listing): European Research Council; Cancer Research UK (Review Panel Member, 9/2014); NIH Nuclear Dynamics and Transport study section (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.

Invited Talks

Conferences (partial listing, 2011–present):

FASEB Recombination Meeting (Colorado, 7/2011)
EMBO Meiosis Meeting (Italy, 9/2011)
Meiosis Gordon Conference (New London, NH, 6/2012)
EMBO Workshop on Recombination (Spain 5/2012)
FASEB Yeast Chromosomes (Colorado 7/2012 (Co-Organizer))
Nucleic Acids Gordon Conference (Maine, 6/2011)
TOPO2011, Topoisomerase Meeting (Taipei, Taiwan 10/2011)
German Society for Cell Biology (Dresden, Germany 3/2012)
Royal Society International Meeting on Recombination (Chichely UK 11/2012)
3R Meeting (Member of foreign advisory board; Awaji Island Japan 11/2012)
Symposium in honor of Paul Burgoyne (NIMR, London 1/2013)
North American Testis Workshop (San Antonio TX 4/2013)
Symposium in honor of Jim Haber (Brandeis Univ, Waltham MA, 6/2013)
FASEB Recombination Meeting (Colorado, 7/2013)
Wenner-Gren Foundation Symposium on Mammalian Meiosis (Stockholm 8/2013)
EMBO Meiosis Meeting (Dresden, Germany 9/2013)
Chromosome Dynamics Gordon Conference; Keynote speaker, Gordon Research Seminar (Il Ciocco Italy, 5/2013)

Abcam Recombination Meeting, Alicante Spain, 5/2014 (keynote speaker)
Meiosis Gordon Conference (New London, NH, 6/2014)
FASEB Yeast Chromosomes (Colorado, 7/2014)
3R Meeting (Member of foreign advisory board; Hakone Japan 11/2014)
Joint Keystone Symposia on DNA Replication and Recominbation/Genomic Instability and DNA Repair (Whistler, Canada, 3/2015)
80th Cold Spring Harbor Laboratory Symposium on Quantitative Biology (CSHL, 5/2015)
Ramon Areces Foundation Symposium on Meiosis (Salamanca, Spain, 6/2015)
Gordon Research Conference on Chromosome Dynamics (New Hampshire 6/2015)
FASEB Recombination Meeting (Steamboat Springs, CO, 7/2015)

Future: EMBO Meiosis Meeting (Oxford UK, 9/2015); 10th Quinquennial Conf. on Responses to DNA Damage (Egmond aan Zee, Netherlands, 4/17/2016); Abcam Recombination Meeting (Alicante Spain, 5/16/2016)

Seminars (partial listing, 2011–present): UC Santa Cruz, Dept of MC&DB, 1/24/11; McGill University, 3/14/11; Univ. Rome Tor Vergata, 9/16/11; National Inst. of Health, 10/5/11; Stanford University, 2/15/12; Oklahoma Medical Research Foundation, 3/8/12; University of Salamanca, Spain, 5/14/12; London Research Institute, Cancer Research UK, 11/7/12; Genome Stability Center, Univ. Sussex UK, 11/8/12; Hunter College, 11/12/12; National Inst. Of Genetics, Mishima Japan, 11/22/12; UC San Diego, 2/14/13; Cornell Univ., Mol Bio & Genetics, 3/29/13; MD Anderson Smithville TX, 4/8/13; Harvard Med. School Dept. of Genetics, 6/12/13; University of Helsinki, 9/3/13; University of Iowa Graduate Student Retreat (Keynote speaker), 10/11/13; Virginia Tech, 11/8/13; University of Vienna, 5/15/14; University of Colorado Medical School, Denver, 9/17/14; University of Colorado Boulder, 9/18/14; Columbia Univ Biological Sciences, 9/29/14; Columbia Physicians and Surgeons, Dept of Genetics, 11/11/14; Osaka University, Japan, 11/14/14; Rockefeller Univ., 12/17/14; Cold Spring Harbor Laboratory, 12/18/14; ETH Zurich, 11/9/15; Univ. Basel, 11/10/15; Johns Hopkins Biochem and Mol Bio, 1/25/16.

Research Support

Howard Hughes Medical Institute, 8/1/2008–present
R01 GM058673 (Keeney, PI), 1/1/1999–3/31/2016, “Mechanism of meiotic recombination initiation in yeast.”
R01 GM105421 (formerly HD40916; M. Jasin, mPI; Keeney, mPI), 8/15/2001–12/31/2016, “Role of Spo11 and recombination in mouse meiosis.”

Publications

1. Nishida C, Choi SY, Kim J, Keeney S, and Linn S. (1988) DNA polymerase δ 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. Juan JY, Keeney SN, and Gregory EM. (1991) Reconstitution of the *Deinococcus radiodurans* aposuperoxide dismutase. *Arch. Biochem. Biophys*. **286**:257-263.

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

5. 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.

6. 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.

7. 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.

8. 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.

9. 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.

10. 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.

11. 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.

12. 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.

13. *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. **Corresponding authors.*

14. 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.

15. Keeney S (2000) Meiotic machinations (News and Views). *Nat. Genet.* **25**, 248.

16. 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. **Corresponding authors.*

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

18. 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.

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

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

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

22. Diaz RL, Alcid AD, Berger JM, and Keeney S. (2002) Identification of residues in yeast Spo11p critical for meiotic DNA double-strand break formation. *Mol. Cell. Biol.* **22**, 1106-1115.

23. 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.

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

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

26. 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.

27. 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.

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

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

30. 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. **Corresponding authors.* PMC545532

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

32. 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.

33. 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. **Corresponding authors.* PMC1190256

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

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

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

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

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

39. 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.

40. 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.

41. Keeney S (2007) Spo11 and the formation of DNA double-strand breaks in meiosis. In *Genome Dynamics and Stability*, vol. 2, "Recombination and Meiosis: Crossing Over and Disjunction." R. Egel and D.-H. Lankenau, Eds., Springer, Berlin, pp. 81-123.

42. 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. PMC2084462

43. 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. PMC1948908

44. Pan J and Keeney S (2007) Molecular cartography: Mapping the landscape of meiotic recombination. (Invited primer.) *PLoS Biology* **5**, 2775-2777. PMC2140090

45. Murakami H and Keeney S (2008) Regulating the formation of DNA double-strand breaks in meiosis. (Perspective article.) *Genes Dev*. **22**, 286-292. PMC2731648

46. Barchi M, Roig I, Cole F, 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. **Corresponding authors.* PMC2374915

47. Roig I and Keeney S (2008) Probing meiotic recombination decisions (preview). *Dev. Cell* **15**, 331-332. PMID: 18804427

48. Kniewel R and Keeney S (2009) Histone methylation sets the stage for meiotic DNA breaks (Minireview). *EMBO J*. **28**, 81-83. PMC2634739

49. 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. PMC3157973

50. Neale MJ and Keeney S (2009) End-labeling and analysis of Spo11-oligonucleotide complexes in *Saccharomyces cerevisiae*. *Methods Mol. Biol*. **557**, 183–195. PMC3162315

51. Pan J and Keeney S (2009) Detection of SPO11-oligonucleotide complexes from mouse testes. *Methods Mol. Biol*. **557**, 197–207. PMC3157917

52. Keeney S (Editor) (2009) *Meiosis, Volume 1, Molecular and Genetic Methods.* Vol. 557 in the *Methods in Molecular Biology* series, Humana Press, New York. PMID: 19799171

53. Keeney S (Editor) (2009) *Meiosis, Volume 2, Cytological Methods.* Vol. 558 in the *Methods in Molecular Biology* series, Humana Press, New York. PMID: 19777686

54. Thacker D and Keeney S (2009) PCH'ing together an understanding of crossover control (minireview). *PLoS Genet.* **5**, e1000576. PMC2708908

55. Wojtasz L, Daniel K, Roig I, Bolcun-Filas E, Xu H, Boonsanay V, Eckmann CR, 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. *PLoS Genet*. **5**, e1000702. PMC2758600

56. Kidane D, Jonason AS, Gorton TS, Mihaylov I, Pan J, Keeney S, de Rooij DG, Ashley T, Keh A, Liu Y, Banerjee U, Zelterman D, and Sweasy JB (2010) DNA polymerase beta is critical for mouse meiotic synapsis. *EMBO J.* **29**, 410-3423. PMC2824467.

57. Sasaki M, Lange J, and Keeney S (2010) Genome destabilization by homologous recombination in the germline. *Nature Rev. Mol. Cell. Biol.* **11**, 192-195. PMC3073813

58. Cole F, Keeney S, and Jasin M (2010) Evolutionary conservation of meiotic DSB proteins: More than just Spo11. (Invited review) *Genes Dev*. **24**, 1201-1207. PMC2885656.

59. Roig I, Dowdle JA, Toth A, de Rooij DG, *Jasin M, and *Keeney S (2010) Mouse TRIP13/PCH2 is required for recombination and normal higher-order chromosome structure during meiosis. *PLoS Genet*. **6**, e1001062. **Corresponding authors.* PMC2920839

60. Cole F, *Keeney S, and *Jasin M (2010) Comprehensive, fine-scale dissection of homologous recombination outcomes at a hotspot in mouse meiosis. *Mol. Cell* **39**, 700-710. **Corresponding authors.* PMC3196603

61. Kauppi L, Barchi M, Baudat F, Romanienko PJ, *Keeney S, and *Jasin M (2011) Distinct properties of the XY pseudoautosomal region crucial for male meiosis. *Science* **331**, 916-920. **Corresponding authors.* PMC3151169

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