

Education

- Ph.D. 1996 University of California, San Francisco. Thesis Title: "Biochemical Analysis of Wnt Signal Transduction." Thesis Adviser: Harold Varmus, M.D.
- B.A. 1989 University of California, San Diego. Major: Biochemistry

Postdoctoral Fellowship

- Postdoctoral Fellow in laboratory of Professor Roeland Nusse, August 1996-June 2003
Stanford University School of Medicine, Stanford, CA
- Visiting Scientist at The Scripps Research Institute, collaboration June 2002-June 2003
with Professor John Yates III, La Jolla, CA

Employment and Academic Appointments

- Scientist, Cellerant Therapeutics, Inc., Palo Alto, CA July 2003-July 2004
- Scientist, Targeted Molecules Corporation, San Diego, CA August 2004-March 2005
- Assistant Adjunct Professor, Cellular & Molecular Medicine, UCSD April 2005-September 2008
- Director, Human Embryonic Stem Cell Core Facility, UCSD April 2005-present
- Assistant Professor, Cellular & Molecular Medicine, UCSD October 2008-June 2015
- Associate Professor, Cellular & Molecular Medicine, UCSD July 2015-June 2019
- Professor, Cellular & Molecular Medicine, UCSD July 2019-present

Affiliations/Memberships

- Member, UCSD Moores Cancer Center 2005-present
- Member, International Society for Stem Cell Research 2005-present
- Investigator, Beta Cell Biology Consortium 2010-2014
- Member, UCSD Clinical & Translational Research Institute 2012-present
- Member, American Society for Cell Biology 2018-present
- Member, American Association for Cancer Research 2019-present

Honors and Award

- Caledonian Society, UCSD 1987
- Phi-Beta Kappa, UCSD 1989
- Summa Cum Laude, UCSD 1989

- National Center of Leadership in Academic Medicine 2014
- Vice-Chair, Gordon Research Conference, WNT Signaling, VT, USA 2017
- Maximizing Investigators' Research Award, NIGMS 2019
- Chair, Gordon Research Conference, WNT Signaling, VT, USA 2019
- The Mary Kay Foundation 202 Innovative Cancer Research Grant 2020
- Sanford Stem Cell Institute Pilot Award 2025
- Chair, Scientific Symposium, Wnt and Stem Cells, Stanford U., CA 2025

Academic Activities

Departmental (CMM)

- Organizer, CMM In-House Seminar Series 2005-2011
- Organizer, CMM Faculty Chalk Talk Series 2009-present
- Co-Organizer, CMM Symposium 2012
- Member, Junior Faculty Search Committee 2015-2016

Programmatic (Stem Cell Program)

- Director of Education, Sanford Discovery Center 2024-present
- Director, UCSD Human Embryonic Stem Cell Core Facility 2005-present
- Chair, UCSD HESCCF Oversight Committee 2007-present
- Member, SCRM Genomics Core Facility Oversight Committee 2014-2017
- Organizer, SCRM Stem Cell Seminar Series 2012-2013
- Co-Chair, SCRM Stem Cell Culture & Cell Analysis Core committee 2011
- Chair, SCRM Viral Vector Core committee 2011
- Member, Cell & Gene Meeting on the Mesa Committee 2016

University

- Member, CIRM Training Grant Review Committee 2007-2014
- Member, Executive Committee, NIH T32 CBIO Training Grant 2020-present
- Organizer, CMM Faculty Chalk Talk Series 2009-present
- Member, BMS Admissions Committee 2015-2022
- Moderator, Undergraduate Research Conference 2014-2017
- Panelist, BMS Program Review 2018
- Co-Chair, BMS Admissions Committee 2023, 2025

External

- Chair, 2019 Gordon Conference on WNT Signaling, Vermont August 2019
- Co-Chair, Gordon Conference on WNT Signaling, Vermont August 2017
- Member, Advisory Committee Cal Poly CIRM Bridges Program 2012-present
- Member, Advisory Committee SDSU CIRM Bridges Program 2018-present
- Chair, Organizing Committee, Wnt and Stem Cells, Stanford University, CA 2025
- Reviewer/Manuscripts: ACS Pharmacology & Translational Science, Biochemical Journal, Bioscience Reports, Blood, BMC Biology, Cancers, Cell Death & Differentiation, Cell Reports, Cell Stem Cell, Cells, CSH Protocols, Development, Developmental Biology, Developmental Neurobiology, ELife, EMBO, EMBO Reports, Experimental Hematology, Faseb, Genes, Genes & Development, International Journal of Molecular Sciences, iScience, Journal of Biological Chemistry, Journal of Clinical Investigation, Leukemia Research, Molecular Cancer Research, Molecular & Cellular Biology, Nature Biotechnology, Nature Communications, Oncogene, Oncotarget, PLoS, PNAS, Science Advances, Science Signaling, Scientific Reports, Stem Cells, Stem Cells and Development, Stem Cell Reports
- Guest Associate Editor: PLoS Genetics, ELife
- Reviewer/Grants **National:** Department of Defense, NIH, NSF, NYSTEM, Ohio Cancer Research, The Mary Kay Foundation, UC Irvine Dean's Triumvirate, UCSD ACS Institutional Research Grant; **International:** Czech Science Foundation, Deutsche Forschungsgemeinschaft (DFG), Deutsches Krebsforschungszentrum/Israel Ministry of Science and Technology, Dutch Cancer Society, European Research Council, Hungary OKTA, National Research Foundation of Korea, Netherlands Organisation for Scientific Research, Ontario Research Fund, Prostate Cancer Research Centre, Swiss Cancer Research, Swiss National Science Foundation, UK Medical Research Council), Cancer Research UK

Teaching Experience

Classroom

- Instructor, BGGN 231 Concepts in Stem Cell Biology Fall 2015-2021
- Lecturer, BIOM 200A Molecules to Organisms Fall 2008-2010
- Moderator, BIOM201 Seminars in Biomedical Research Fall 2009-2017
- Lecturer, FMPH191 Public Health Research Ethics Fall 2020-2021
- Lecturer, BIOM254 Molecular and Cell Biology Winter 2016
- Lecturer, BICD112 Stem Cells and Regeneration Spring 2018-2021
- Lecturer, CHEM239 CT2 Lecture Series Spring 2017
- Instructor, CMM250 Core Course in Stem Cell Biology 2016-2026
- Lecturer, CMM250 Core Course in Stem Cell Biology Winter 2011-2015
- Instructor, CMM251 Lab Course for hESC Research 2007-2014
- Instructor, CMM252 Current Literature in Stem Cell Biology 2009-2014
- Instructor, SOM204 Cell Biology Reading Workshop Fall 2006-2009

Surrozen 2011

Merck v. Surrozen PGR2026-00027

- Instructor, SOM C 220 Foundations of Human Biology Fall 2014–2017
- Guest Lecturer SDSU, MB 610 Graduate Bioethics Fall 2010–2022

Individual Instruction and Mentorship

- 9 Post-doctoral fellows
- 7 PhD students
- 16 PhD rotation students
- 1 MD student
- 29 Masters students
- 50 Undergraduates students

Invited Seminars

- SoCal Stem Cell Consortium, Burnham Institute, La Jolla, CA 2005
- Basic & Translational Research Rounds, Moores Cancer Center, La Jolla, CA 2005
- Stem Cell Meeting on the Mesa, Salk Institute, La Jolla, CA 2006
- Vanderbilt University, Nashville, TN 2006
- New Investigator/Junior PI Stem Cell Meeting, Salk Institute, La Jolla, CA 2006
- Universität Bonn, Germany 2007
- BD, San Jose, CA 2007
- Harvard Stem Cell Institute/California Junior Faculty Symposium, Boston, MA 2007
- UCSD Stem Cell Program, La Jolla, CA 2008
- Dartmouth School of Medicine, Hanover, NH 2008
- University of Southern California, Los Angeles, CA 2008
- University of California, Merced, CA 2008
- University of California, Santa Barbara, CA 2008
- Department of Bioengineering, UCSD, La Jolla, CA 2008
- Joint Symposium between National Yang Ming University, La Jolla, CA 2008
- Buffalo University, NY 2008
- 5th International Stem Cell School in Regenerative Medicine, Berlin, Germany 2008
- The Association of Biomolecular Resource Facilities Annual Meeting, Memphis, TN 2009
- WNT Meeting, Georgetown, Washington DC 2009
- UCSD Seminar Rheumatology, Allergy and Immunology, La Jolla, CA 2009
- Annual Meeting of the American Thoracic Society, San Diego, CA 2009
- Institut Gustave Roussy, Paris, France 2010
- Department of Bioengineering, UCSD, La Jolla, CA 2010
- Beta Cell Biology Consortium Meeting, Georgetown, Washington DC 2010
- Cal State Fullerton, CA 2011
- San Diego State University, CA 2011
- University of Pecs, Hungary 2011
- University of Debrecen, Hungary 2011
- National Yanming University, Taipei, Taiwan 2012
- National Foundation for Ectodermal Dysplasias, Orlando, Florida 2012

• International Symposium on Stem Cells and Cancer. Kaoshunig, Taiwan	2012
• Joint Symposium between National Yang Ming University, La Jolla, CA	2012
• Cancer Stem Cell Symposium, UCSD, La Jolla, CA	2012
• Beta Cell Biology Consortium Meeting, Washington DC	2013
• Karlsruhe Institute of Technology, Germany	2013
• Universität Heidelberg, Germany	2013
• 14th Annual UC Systemwide Bioengineering Symposium, UCSD, La Jolla, CA	2013
• Tanabe Research Laboratories, La Jolla, CA	2013
• National Foundation for Ectodermal Dysplasia, Houston, TX	2013
• Therapeutics Discovery Symposia, Boston, MA	2014
• Beta Cell Biology Consortium Meeting, Washington DC	2014
• National University of Singapore	2014
• EMBO Workshop on WNT signaling, Broome, Australia	2014
• 1 st Kyoto University – UC San Diego Joint Symposium, Kyoto, Japan	2015
• Stem Cell Science Symposium, SCRM, La Jolla, CA	2015
• Biopath – Professional Pathways in Biological Sciences, UCSD	2016
• WNT Conference, Brno, Czech Republic	2016
• CT2 Lecture – UCSD Moores Cancer Center	2017
• JW Pharmaceuticals, Seoul Korea	2019
• Organoids Are Us – Doherty Institute, Melbourne, Australia	2018
• European Wnt Meeting, Heidelberg, Germany	2018
• American Society for Cell Biology, San Diego, CA	2018
• The Third Leo and Anne Albert Charitable Trust Workshop: Reducing the Burden of Bone Metastatic Prostate Cancer, San Diego, CA	2019
• JW Pharmaceuticals, Seoul, Korea	2019
• Boehringer Ingelheim Pharma, Germany	2020
• University of Illinois Chicago	2021
• Immuno-oncology Interest Group, UC San Diego, CA	2021
• Cell Bio Virtual 2021-An Online ASCB/EMBO Meeting	2021
• Prostate Cancer Foundation, San Diego, CA	2021
• UT Health Houston, TX	2022
• EMBO Workshop WNT 2020, Japan	2022
• Immune Oncology Symposium, UC San Diego, CA	2023
• Gordon Research Seminar, WNT Signaling, Spain	2023
• Gordon Research Conference, WNT Signaling, Spain	2023
• University of Heidelberg, Germany	2023
• UC BIC Systemwide Symposium	2024
• European Wnt Meeting, Heidelberg, Germany	2024
• Uniklinik Köln, Molekulare Zellbiologie, Köln, Germany	2024
• Uni-Klinikum, Molekulare Zellbiologie, Frankfurt, Germany	2024
• Karlsruhe Institute of Technology (KIT), Karlsruhe, Germany	2024
• MD Anderson UT Health Houston, TX	2025

- Gordon Research Conference, WNT Signaling, Lewiston, ME 2025
- Stanford University, Wnt and Stem Cells 2025
- San Diego State University, CA 2025
- Innovations in Countermeasures and Toxicology Research Conference, Chicago, IL 2026

Publications (peer reviewed)

- De Jaime-Soguero, A., Romitti, M., Costagliola, S., Jauch, A., **Willert, K.**, Fojer, F., Acebrón, S.P. Long-term prevention of aneuploidy in human pluripotent stem cells by fine-tuning GSK3 activity. *bioRxiv* (2025). doi.org/10.1101/2025.10.27.684724.
- Wu, C.N.C., De Luna, N., Hairston, E., Jeffs, E.D., Keys, A., Adams, S.R., Advani, S.J. Gaasterland, T., Carson, D.A., **Willert, K.** FZD7 expression marks mammary tumor initiating cells. *Proc Natl Acad Sci U S A*, 122 (46) e2522465122 (2025). Doi.org/10.1073/pnas.2522465122.
- Lopes, A.L., Paulino, A.C., Thaumaturgo, M.A.S., Araujo, W.M., Caloba, P., Kawanishi, K., **Willert, K.**, De Oliveira, R.P., Machado, J.C., Lemos, F., *et al.* Dietary intake of the red meat-derived glycan Neu5Gc fuels colorectal cancer through up-regulation of Wnt signaling pathway. *Cancer Lett* 616, 217598 (2025). PMID: 40023392.
- Trieger, G. W., Pessentheiner, A. R., Purcell, S. C., Green, C. R., DeForest, N., **Willert, K.**, Majithia, A. R., Metallo, C. M., Godula, K., Gordts, P. L. S. M. Glycocalyx engineering with heparan sulfate mimetics attenuates Wnt activity during adipogenesis to promote glucose uptake and metabolism. *J Biol Chem*. 2023 Mar 15;:104611. doi: 10.1016/j.jbc.2023.104611. PMID: 36931394
- Do, M., Wu, C. N. C., Sonavane, P. R., Juarez, E. F., Adams, S. R., Ross, J., Rodriguez y Baena, A., Patel, C., Mesirov, J. P., Carson, D. A., Advani, S. J., **Willert, K.** A FZD7-specific antibody-drug conjugate induces ovarian tumor regression in preclinical models. *Molecular Cancer Therapeutics*, DOI: 10.1158/1535-7163.MCT-21-0548 (2022). PMID: 34667113.
- Chai, G., Szenker-Ravi, E., Chung, C., Li, Z., Wang, L., Khato, M., Marshall, T., Jiang, N., Yang, X., McEvoy-Venneri, J., Stanley, V., Anzenberg, P., Lang, N., Wazny, V., Yu, J., Virshup, D., Nygaard, R., Mancina, F., Merdzanic, R., Pereira Toralles, M., Leite Pitanga, P., Puri, R., Hernan, R., Chung, W., Bertoli-Avella, A., Al-Sanna, N., Zaki, M., **Willert, K.**, Reversade, B., Gleeson, J. A human pleiotropic multiorgan condition caused by deficient Wnt secretion. *New England Journal of Medicine*, DOI: 10.1056/NEJMoa2033911 (2021). PMID: 34587386
- Gumber, D., Do, M., Suresh Kumar, N., Sonavane, P.R., Wu, C.N.C., Cruz, L.S., Grainger, S., Carson, D., Gaasterland, T., **Willert, K.** Selective activation of FZD7 promotes mesendodermal differentiation of human pluripotent stem cells. *eLife* 2020;9:e63060 DOI: 10.7554/eLife.63060 (2020). PMID: 33331818

- Grainger, S., Nguyen, N., Richter, J., Setayesh, J., Lonquich, B., Oon, C.H., Wozniak, J.M., Barahona, R., Kamei, C., Houston, J., Carillo-Terrazas, M., Drummond, I., Gonzalez, D., **Willert, K.***, Traver, D.* EGFR is required for Wnt9a/Fzd9b signalling specificity. *Nature Cell Biology*, DOI: 10.1038/s41556-019-0330-5 (2019). PMID: 31110287 (*co-corresponding authors).
- Richter, J., Stanley, E.G., Ng, E.S., Elefanty, A.G., Traver, D.*, **Willert, K.*** WNT9A is a conserved regulator of hematopoietic stem and progenitor cell development. *Genes*, doi: 10.3390/genes9020066 (2018). PMID: 29382179 (*co-corresponding authors).
- Huggins, I.J., Bos, T., Gaylord, O., Lonquich, B., Jessen, C., Puranen, A., Richter, J., Rossdam, C., Brafman, D., Gaasterland, T., **Willert, K.** The WNT target SP5 negatively regulates WNT transcriptional programs in human pluripotent stem cells. *Nature Communications*, DOI: 10.1038/s41467-017-01203-1 (2017).
- Rodvold, J.J., Chiu, K.T., Hiramatsu, N., Nussbacher, J.K., Galimberti, V., Mahadevan, N.R., **Willert, K.**, Lin, J., Zanetti, M. Intercellular transmission of the unfolded protein response promotes survival and drug resistance in cancer cells. *Sci Signal*, doi: 10.1126/scisignal.aah7177 (2017). PMID: 28588081
- Richter J., Traver, D., **Willert, K.** The role of Wnt signaling in hematopoietic stem cell development. *Crit Rev Biochem Mol Biol*, 52:414-424 (2017). PMID: 28508727
- Minegishi, K., Hashimoto, M., Ajima, R., Takaoka, K., Shinohara, K., Ikawa, Y., Nishimura, H., McMahon, A., **Willert, K.**, Okada, Y., Sasaki, H., Shi, D., Fujimori, T., Ohtsuka, T., Igarashi, Y., Yamaguchi, T., Shimono, A., Shiratori, H. Hamada, H. A Wnt5 activity asymmetry and intercellular signaling via PCP proteins polarize node cells for left-right symmetry breaking. *Developmental Cell*, 40: 439-452 (2017).
- Grainger, S., Lonquich, B., Oon, C.H., Nguyen, N., **Willert, K.**, Traver, D. CRISPR guide RNA validation in vitro. Zebrafish, PMID: 27829120 (2016).
- Grainger, S., Richter, J., Espín Palazón, R., Pouget, C., Lonquich, B., Wirth, S., Grassme, K.S., Herzog, W., Swift, M.R., Weinstein, B.M., Traver, D., **Willert, K.** Wnt9a is required for the aortic amplification of nascent hematopoietic stem cells. *Cell Reports*, 17: 1595-1606 (2016).
- Wang, Z., Li B., Zhou, L., Yu, S., Su, Z., Song, J., Sun, Q., Sha, O., Wang, X., Jiang, W., **Willert K.**, Wei, L., Carson, D.A., Lu, D. Prodigiosin inhibits Wnt/b-catenin signaling and exerts anticancer activity in breast cancer cells. *Proc Natl Acad Sci U S A*, pii: 201616336 (2016). PMID: 27799526.
- Belinson, H., Nakaatani, J., Babineau, B., Birnbaum, R., Ellegood, J., Bershteyn, M., McEvelly, R., Long, J., **Willert, K.**, Klein, O., Ahituv, N., Lerch, J., Rosenfeld, M., Wynshaw-Boris, A. Prenatal β -catenin/Brn2/Tbr2 transcriptional cascade regulates adult social and stereotypic behaviors. *Molecular Psychiatry*, DOI: 10.1038/mp.2015.207 (2016). PMID: 26830142.

- Kumar, N., Richter, J., Cutts, J., Bush, K.T., Trujillo, C., Nigam, S.K., Gaasterland, T., Brafman, D., **Willert, K.** Generation of an expandable intermediate mesoderm restricted progenitor cell line from human pluripotent stem cells. *ELife*, 4:e08413. DOI: 10.7554/eLife.08413 (2015). PMID: 26554899.
- Aznar, N., Midde, K., Dunkel, Y., Lopez-Sanchez, I., Pavlova, Y., Marivin, A., Barbazán, J., Murray, F., Nitsche, U., Janssen, K.-P., **Willert, K.**, Goel, A., Abal, M., Garcia-Marcos, M., Ghosh, P. Daple is a Novel Non-Receptor GEF Required for Trimeric G protein Activation in Wnt Signaling. *ELife*, 4:e07091 (2015). PMID: 26126266
- Ross, J., Busch, J., Mintz, E., Ng, D., Stanley, A., Brafman, D., Sutton, V.R., Van den Veyver, I., **Willert, K.** A rare human syndrome provides genetic evidence that WNT signaling is required for reprogramming of fibroblasts into induced pluripotent stem cells. *Cell Reports*, 9:1770-80 (2014). PMID: 25464842.
- Moya, N., Gaasterland, T., **Willert, K.***, Brafman, D.* Endogenous WNT signaling regulates hESC-derived neural progenitor cell heterogeneity and specifies their regional identity. *Stem Cell Reports*, 3:1015-28 (2014). PMID: 25458891 (*co-corresponding authors).
- Fernandez, A., Huggins, I. J., Perna, L., Brafman, D., Lu, D., Yao, S., Gaasterland, T., Carson, D., **Willert K.** The WNT receptor FZD7 is required for maintenance of the pluripotent state in human embryonic stem cells. *Proc Natl Acad Sci U S A*, 111:1409-14 (2014). PMID: 24474766.
- Bauer, M., Bénard, J., Gaasterland, T., **Willert, K.***, Cappellen, D.*. WNT5A encodes two isoforms with distinct functions in cancers. *PLoS ONE*, 8:e80526 (2013). PMID: 242460510 (*co-corresponding authors).
- Brafman, D., Moya, N., Soltero, S., Fellner, T., Robinson, M., Vomberg-McMillen, Z., Gaasterland, T., **Willert, K.** Analysis of SOX2 expressing cell populations derived from human pluripotent stem cells. *Stem Cell Reports*, 1: 464-78 (2013). PMID: 24286033.
- Green, J.L., Bauer, M., Yum, K.W., Li, Y.C., Cox, M.L., **Willert, K.**, Wahl, G.M. Use of a molecular genetic platform technology to produce human Wnt proteins reveals distinct local and distal signaling activities. *PLoS One*, 8:e58395 (2013). PMID: 23516471.
- Brafman, D., Phung, C., Kumar, N., **Willert, K.** Regulation of endodermal differentiation of human embryonic stem cells through integrin-ECM interactions. *Cell Death and Differentiation*, 20:369-81 (2013). PMID: 23154389.
- Brafman, D., Chien, S., **Willert, K.** Arrayed cellular microenvironments for identifying culture and differentiation conditions for stem, primary and rare cell populations. *Nature Protocols* 7, 703-17 (2012). PMID: 22422316.
- Gallegos, T.F., Kouznetsova, V., Kudlicka, K., Sweeney, D.E., Bush, K.T., **Willert, K.**, Farquhar, M.G., Nigam, S.K. A Protein Kinase A and Wnt-dependent network regulating an intermediate

stage in epithelial tubulogenesis during kidney development. *Developmental Biology*, 364, 11-21 (2012). PMID: 22290330.

- Mulligan, K., Fuerer, C., Ching, W., Fish, M., **Willert, K.**, Nusse, R. Secreted Wingless-interacting molecule (SWIM) promotes long-range signaling by maintaining Wingless solubility. *Proc Natl Acad Sci U S A*, 109: 370-7 (2011). PMID: 22203956.
- Brafman, D., Chang, C.-W., Fernandez, A., **Willert, K.**, Varghese, S., Chien, S. Long-term human pluripotent stem cell self-renewal on synthetic polymer surfaces. *Biomaterials*, 31, 9135-9144 (2010), PMID: 20817292.
- Hu, T., Li, C., Cao, Z., Van Raay, T.J., Smith, J.G., **Willert, K.**, Solnica-Krezel, L., Coffey, R.J. Myristoylated naked2 antagonizes WNT- β -catenin activity by degrading dishevelled-1 at the plasma membrane. *J. Biol. Chem.*, 285(18):13561-8 (2010). PMID: 20177058.
- Lu, D., Liu, J.X., Endo, T., Zhou, H., Yao, S., **Willert, K.**, Schmidt-Wolf, I.G., Kipps, T.J., Carson, D.A. Ethacrynic acid exhibits selective toxicity to chronic lymphocytic leukemia cells by inhibition of the Wnt/ β -catenin pathway. *PLoS One*, 4(12):e8294 (2009). PMID: 200115388.
- Brafman, D., de Minicis, S., Seki, E., Shah, K.D., Teng, D., Brenner, D.*, **Willert, K.***, Chien, S.* Investigating the Role of the Extracellular Environment in Modulating Hepatic Stellate Cell Biology with Arrayed Combinatorial. *Integrative Biology*, 1, 513 – 524 (2009) (*co-corresponding authors). PMID: 20023766.
- Lancaster, M.A., Louie, C.M., Silhavy, J.L., Sintasath, L., DeCambre, M., Nigam, S.K., **Willert, K.**, Gleeson, J.G. Impaired Wnt/ β -catenin signaling disrupts adult renal homeostasis and leads to cystic kidney ciliopathy. *Nat Med.* 15:1046-54 (2009). PMID: 19718039.
- Eguchi, A., Meade, B.R., Chang, Y.-C., Fredrickson, C.T., **Willert, K.**, Puri, N., Dowdy, S.F. Efficient siRNA Delivery into Primary Cells by Peptide Transduction-dsRNA Binding Domain (PTD-DRBD) Fusion Protein. *Nat. Biotechnology*, 27:567-71 (2009). PMID: 19448630.
- Brafman, D.A., Shah, K.D., Fellner, T., Chien, S., **Willert, K.** Defining long-term maintenance conditions of human embryonic stem cells with arrayed cellular microenvironment technology. *Stem Cells Dev.* 18:1141-54. (2009). PMID: 19327010.
- Soda M., **Willert K.**, Kaushansky K., Geddis, A. Inhibition of GSK-3 α promotes survival and proliferation of megakaryocytic cells through β -catenin-independent signaling. *Cellular Signaling*. 20:2317-23 (2008). PMID: 18804163.
- Galli L.M., Barnes T., Cheng T., Acosta L., Anglade A., **Willert K.**, Nusse R., Burrus L.W. Differential Inhibition of Wnt-3a by Sfrp-1, Sfrp-2, and Sfrp-3. *Developmental Dynamics* 235, 681-90 (2006). PMID: 16425220.

- Duncan, A.W., Rattis, F.M., DiMascio, L.N., Congdon, K.L., Paxianos, G, Zhao, C., Yoon, K., Cook, J. M., **Willert, K.**, Gaiano, N., Reya, T. Integration of Notch and Wnt signaling in hematopoietic stem cell maintenance. *Nature Immunology*. **6**, 448-52 (2005). PMID: 15665828.
- Galli L.M., **Willert K.**, Nusse R., Yablonka-Reuveni Z., Nohno T., Denetclaw W., Burrus L.W. A proliferative role for Wnt-3a in chick somites. *Dev Biol*. **269**, 489-504 (2004). PMID: 15110715.
- **Willert, K.**, Brown J., Danenberg E., Duncan A., Weissman I.L., Reya T., Yates III J.R., and Nusse R. Wnt proteins are lipid-modified and can act as stem cell factors. *Nature* **423**, 448-452 (2003). PMID: 12717451.
- Reya, T., Duncan A., Ailles L., Domen J., Scherer D., **Willert K.**, Hintz L., Nusse R., and Weissman I.L. A role for Wnt signalling in self-renewal of haematopoietic stem cells. *Nature* **423**, 409-414 (2003). PMID: 12717450.
- Wilson, S., Rydström, A., Trimborn, T., **Willert, K.**, Nusse, R., Jessel, T., and Edlund, T. The status of Wnt signalling regulates neural and epidermal fates in the chick embryo. *Nature* **411**, 325-330 (2001). PMID: 11357137.
- Reya, T., O'Riordan, M., Okamura, R., Devaney, E., **Willert, K.**, Nusse, R., and Grosschedl, R. Wnt signaling regulates B lymphocyte proliferation through a LEF-1 dependent mechanism. *Immunity* **13**, 15-24, (2000). PMID: 10933391.
- **Willert, K.**, Logan, C.Y., Arora, A., Fish, M., and Nusse, R. A *Drosophila* Axin homolog, Daxin, inhibits Wnt signaling. *Development* **126**, 4165-4173 (1999). PMID: 10457025.
- **Willert, K.**, Shibamoto, S., and Nusse, R. Wnt-induced dephosphorylation of Axin releases β -catenin from the Axin complex. *Genes and Development* **13**, 1768-1773 (1999). PMID: 10421629.
- Millar, S. E., **Willert, K.**, Salinas, P. C., Roelink, H., Nusse, R., Sussman, D. J. and Barsh, G. S. WNT signaling in the control of hair growth and structure. *Dev Biol* **207**, 133-149 (1999). PMID: 10049570.
- Korinek, V., Barker, N., **Willert, K.**, Molenaar, M., Roose, J., Wagenaar, G., Markman, M., Lamers, W., Destree, O. and Clevers, H. Two members of the Tcf family implicated in Wnt/b-catenin signaling during embryogenesis in the mouse. *Mol Cell Biol* **18**, 1248-1256 (1998). PMID: 9488439.
- Nusse, R., Samos, C. H., Brink, M., **Willert, K.**, Cadigan, K. M., Wodarz, A., Fish, M. and Rulifson, E. Cell culture and whole animal approaches to understanding signaling by Wnt proteins in *Drosophila*. *Cold Spring Harb Symp Quant Biol* **62**, 185-190 (1997). PMID: 9598351.
- **Willert, K.**, Brink, M., Wodarz, A., Varmus, H. and Nusse, R. Casein kinase 2 associates with and phosphorylates dishevelled. *Embo J* **16**, 3089-3096 (1997). PMID: 9214626.

- Shackleford, G. M., **Willert, K.**, Wang, J. and Varmus, H. E. The *Wnt-1* proto-oncogene induces changes in morphology, gene expression, and growth factor responsiveness in PC12 cells. *Neuron* **11**, 865-875 (1993). PMID: 8240810.
- Young, J. A., Bates, P., **Willert, K.** and Varmus, H. E. Efficient incorporation of human CD4 protein into avian leukosis virus particles. *Science* **250**, 1421-1423 (1990). PMID: 2175047.

Publications (invited reviews and book chapters)

- Hodson, K., Arredondo, H.M., Humphrey, W.E., Flanagan, D.J., Vincan, E., **Willert, K.**, Pearson, H.B., and Pheesse, T.J. (2025). Targeting Cancer with Paris' Arrow: An Updated Perspective on Targeting Wnt Receptor Frizzled7. Doi.org/10.3390/sci7020061.
- Sonavane, P., and **Willert, K.** (2023). Wnt signaling and the regulation of pluripotency. *Curr Top Dev Biol* **153**, 95-119. PMID: 36967203
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Publications (submitted and in preparation)

- None

Patents

- Compositions of active WNT protein. US Patent 7,153,832. Issued on Dec. 26, 2007.
- Compositions of active WNT protein. US Patent 7,335,643. Issued on Feb. 26, 2008.
- Compositions of active WNT protein. US Patent 8,642,335. Issued on Feb. 4, 2014.
- Compositions of Active WNT Protein. US Patent 9,139,636. Issued on Sep. 22, 2015.
- FZD7 specific antibodies and vaccines to treat cancer and control stem cell function. International Publication Number WO 2016/205551 A2 and WO 2016/205566 A1. Issued on Dec. 22, 2016.
- Compositions of Active Wnt Protein. US Patent 9,725,696. Issued on Aug. 8, 2017
- FZD7 specific antibodies and vaccines to treat cancer and control stem cell function. US Patent 10,766,962. Issued Sep. 8, 2020.

Funding

Current

- Sanford Stem Cell Institute Pilot Grant, Role: PI 05/01/25-04/30/26
- NIH/University of Alabama Subaward R01 AR081646 “Mechanisms of Wnt5a signaling in skeletal development and disease.” Role: Subaward PI 09/01/21-08/31/26
- NIH/NINDS R01NS131151 “Developing a Synthetic Adeno-Associated Virus (AAV) for Engineering Safer Gene Therapies.” Role: Co-I 02/01/23-01/31/28
- CIRM EDUC4-12804 “Interdisciplinary Stem Cell Training Grant.” Role: Co-I 12/01/21-11/30/26

Pending

- NIH/NCI 1R01CA297085 “WNT receptor FZD7 in tumor initiating cells.” Role: PI 01/01/25-12/31/29
- NIH/NIGMS 1R01GM164587 “Extracellular regulation of genome stability.” Role: PI 07/01/26-06/30/31
- NIH 1R21AR087646 “Targeted FZD activation in skin wound repair.” Role: PI 03/01/25-02/28/26
- Department of Defense, Peer Reviewed Cancer Research Program “Determining the Therapeutic Benefit of Targeting WNT/FZD7 in Metastasis” Role: Co-PI (Partnering PI: Toby Phesse, Cardiff University, UK) 07/01/26-06/30/29

Completed

- NIH/NIHOD S10 OD038286 “Full Spectrum Flow Cytometer” Role: PI 01/02/24-01/31/25
- NIH 1R01 HL135205-01 (MPI) “Wnt signaling in hematopoietic development.” Role: PI 01/01/17-06/30/25
- NIH R35 GM134961 “Exploring Wnt-Fzd signaling specificities.” Role: PI 01/01/20-12/31/24
- Pfizer “Targeting FZD7 in cancer.” Role: PI 07/01/18-01/31/23
- Supplement to NIH R35 GM 134961-02S1 “Exploring Wnt-Fzd signaling specificities.” Role: PI 01/01/21-12/31/21
- The Mary Kay Foundation “Targeted Killing of FZD7-Positive Ovarian Tumors.” Role: PI 07/01/20-06/30/22
- University of California Academic Senate San Diego Division “Detection of WNT-induced aneuploidy by single cell CNV analysis.” Role: PI 03/01/20-02/28/21
- Pedal the Cause “Targeting FZD7 in human cancers.” Role: PI 11/01/18-10/31/19

- NIH R13 HD097874-01 “Gordon Research Conference on Wnt Signaling.” Role: PI 05/11/19-11/30/19
- CIRM DISC2-09615 “Targeted off-the-shelf immunotherapy to treat refractory cancers.” Role: Co-I (PI: Dr. Kaufman, UCSD) 05/01/17-10/31/19
- NIH Subaward “Elucidating the transcriptional regulation of Wnt/beta-catenin signaling.” Role: Co-I (PI: Dr. Brafman, Arizona State) 04/01/17-03/31/22
- NIH 2R01 GM110304-06 “Analyzing the role of Wnt signaling in pluripotency.” Role: PI 03/01/19-02/01/20
- NIH R21 CA210227-02 “MyD88-dependent mechanisms of Helicobacter pylori-induced gastric cancer progression.” Role: Co-I (PI: Dr. Obonyo, UCSD) 07/01/16-06/30/18
- NIH 1R01 GM110304-03 “Analyzing the role of Wnt signaling during reprogramming.” Role: PI 04/10/14-02/28/19
- Takeda-Sanford Alliance “New materials and methods to instruct hematopoietic stem cell fate from human pluripotent precursors.” Role: Co-PI 07/01/16-06/30/18
- Sanford Consortium for Regenerative Medicine “Imaging FZD7-positive cancer stem cells in mice.” Role: PI 09/01/16-08/31/17
- University of California Cancer Research Coordinating Committee “Targeting FZD7 in human cancers.” Role PI 07/01/15-06/30/16
- UCSD HS Research Grant “Visualizing Wnt-induced chromosomal instability in cells.” Role: PI 04/01/15-03/31/16
- NIH U01 DK089567 “Epigenetic strategies for the in vitro generation of replacement beta cells.” Role: Co-PI 10/01/10-09/30/14
- NIH U01 DK072473 “Generating pluripotent stem cell marker lines with AAV-mediated homologous recombination.” Role: Co-PI 01/01/11-12/31/11
- NIH 1R13 CA128448-01 “Wnt signaling in development and disease.” Role: PI 06/01/07-05/31/08
- CIRM RT2-02604 “Homologous recombination in human pluripotent stem cells using adeno-associated virus.” Role: PI 04/01/11-09/30/14
- CIRM RT2-01889 “Development of Synthetic Microenvironments for Stem Cell Growth and Differentiation.” Role: Co-PI 07/01/11-06/30/14
- CIRM CL1-00522-1 “Enhancing Facilities for Genetic Manipulation and Engineering of Human Embryonic Stem Cells at UCSD.” Role: PI 08/01/07-10/31/14
- CIRM RB1-01406 “WNT signaling and the control of cell fate decisions in human pluripotent stem cells.” Role: PI 12/01/09-03/31/13

Karl Willert, Ph.D.

Page 15

- CIRM RS1-00173-1 “Combinatorial platform for optimizing microenvironments to control hESC fate.” Role: Co-PI 03/01/07-12/31/09
- National Foundation for Ectodermal Dysplasias “A model for focal dermal hypoplasia using human induced pluripotent stem cell.” Role: PI 04/01/12-03/31/13