

PROMOTION RECOMMENDATION
THE UNIVERSITY OF MICHIGAN
MEDICAL SCHOOL
DEPARTMENT OF CELL AND DEVELOPMENTAL BIOLOGY

Benjamin L. Allen, Ph.D., assistant professor of cell and developmental biology, Department of Cell and Developmental Biology, Medical School, is recommended for promotion to associate professor of cell and developmental biology, with tenure, Department of Cell and Developmental Biology, Medical School.

Academic Degrees:

Ph.D.	2004	University of Wisconsin-Madison
B.S.	1998	Cornell University

Professional Record:

2009-present	Assistant Professor of Cell and Developmental Biology, University of Michigan
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Summary of Evaluation:

Teaching: Dr. Allen is an outstanding didactic instructor. He has been a lecturer and a laboratory instructor for the M1 medical histology course, where he consistently received positive reviews. He has also taught histology to first year dental students (DENT 510), graduate Developmental Genetics (CDB 581) and Organogenesis (CDB 582/583). Dr. Allen currently serves as the course director for CDB 581, the flagship Developmental Biology course for the Department. Dr. Allen is also the associate director for the Michigan Post-Baccalaureate Research Education Program (PREP), an NIH-funded program designed to prepare underrepresented minority students for the pursuit of advanced degrees (Ph.D. and M.D.) in the biomedical sciences. In addition to his efforts in classroom instruction, Dr. Allen is an exceptional laboratory-based mentor. Dr. Allen has mentored 10 undergraduates and 19 graduate rotation students and has served or continues to serve as thesis advisor for six graduate students and a post-doctoral fellow; three of his students have successfully defended their Ph.D. thesis. Dr. Allen has served or continues to serve on twenty-five Ph.D. thesis committees. His graduate students have been appointed to four different NIH-funded training grants, and have won numerous individual fellowships, including three NRSA F31 individual pre-doctoral and one NSF graduate research fellowship. As further evidence of his strong devotion to the teaching mission, Dr. Allen has performed significant teaching outside of the University of Michigan. He is a founding faculty member of Developing Future Biologists, an outreach program designed to encourage underrepresented students in Puerto Rico to pursue graduate studies in developmental biology. Dr. Allen is also an instructor in the prestigious Cold Spring Harbor Laboratory Course on "Mouse Development, Stem Cells and Cancer." This three week NIH-funded course provides students from around the globe the opportunity to receive hands-on instruction in all aspects of mouse embryology.

Research: The major goal of Dr. Allen's research is to elucidate the mechanisms that control Hedgehog signaling, one of the seven critical embryonic morphogenetic signaling pathways, during embryonic and postnatal development, as well as adult tissue homeostasis, repair and regeneration. Further, Dr. Allen is pursuing the deregulation of Hedgehog signaling in the initiation and progression of developmental diseases and childhood and adult cancers. Dr. Allen has been very productive, publishing 25 papers, 16 since his arrival at Michigan. Importantly, his work has been published in highly visible journals, including *Cell Reports*, *Development*, *Developmental Cell* and *Journal of Cell Biology*. Dr. Allen's scientific contributions include: 1) the identification of novel components of the Hedgehog signaling pathway, 2) the elucidation of novel mechanisms controlling Hedgehog activity during embryogenesis, and 3) the discovery of a novel, dose-dependent role for Hedgehog signaling in pancreatic cancer. As a consequence, Dr. Allen has also been very successful in securing research funding, receiving an AHA Scientist Development Grant and two current NIH R01 awards. Further evidence of his research impact is reflected by his many national/international invitations to present extramural lectures.

Recent and Significant Publications:

Holtz AM, Peterson KA, Nishi Y, Morin S, Song JY, Charron F, McMahon AP, Allen, BL, Essential role for ligand-dependent feedback antagonism of vertebrate Hedgehog signaling by PTCH1, PTCH2, and HHIP1 during neural patterning. *Development* 140:3423-3434, 2013. (Cover Article)

Mathew E, Zhang Y, Holtz AM, Kane KT, Song JY, Allen BL, Pasca di Magliano M: Dosage-dependent regulation of pancreatic cancer growth and angiogenesis by Hedgehog signaling. *Cell Rep* 9:484-494, 2014. (Recommended by Faculty of 1000)

Carpenter BS, Barry RL, Verhey KJ, Allen BL: The heterotrimeric kinesin-2 complex interacts with and regulates GLI protein function. *J Cell Sci* 128:1034-1050, 2015. (Featured Article; Cover Article)

Holtz AM, Griffiths SC, Davis SJ, Bishop B, Siebold C, Allen BL: HHIP1 is a secreted, heparan sulfate-binding Hedgehog pathway antagonist, *J Cell Biol* 209:739-758, 2015. (Featured Article; Cover Article)

Song JY, Holtz AM, Pinsky JM, Allen BL: Distinct structural requirements for CDON and BOC in the promotion of Hedgehog signaling. *Dev Biol* 402:239-252, 2015.

Service: Dr. Allen has dedicated an extraordinarily large fraction of his time to service at the institutional, national, and international levels. He is currently the director of the Microscopy and Image Analysis Laboratory at UM, a key core facility in the Medical School that serves users throughout the university. Dr. Allen is also the associate director for the UM PREP program. He has served on numerous committees in the Department of Cell and Developmental Biology (Development, Executive, Graduate Recruitment, Graduate Admissions, Seminar, Social, Outreach, and Website). He also served as the chair of the Cellular and Molecular Biology Retreat committee, and is a current member of the Medical Scientist Training Program operating committee. Dr. Allen has served on 10 graduate student candidacy examination

committees, chairing three of them, and also serves on mentoring committees for fellows in three sister clinical departments, as well as on seven different advisory committees for graduate students in the Medical Scientist and the Cellular and Molecular Biology Training programs. He was/is co-organizer of the 2015 and 2016 Midwest Society for Developmental Biology regional meetings hosted on the University of Michigan campus, attracting more than 150 scientists from the Midwest each year. In 2014, Dr. Allen organized the 2014 International Hedgehog meeting, also hosted at UM, drawing 165 scientists from around the world. He has served as an ad hoc reviewer for multiple international funding agencies, including the Medical Research Council (GBR), National Research Agency (FRA), and Netherlands Organization for Scientific Research (NLD). Dr. Allen has also served as an ad hoc reviewer for 26 different scientific periodicals, including *Cancer Cell*, *Cell Reports*, *Development*, *Developmental Biology*, *eLife*, *Nature Cell Biology*, *PloS Biology* and *Science*.

External Reviewers:

Reviewer A: “He has made important contributions to the field and has worked to bring investigators with common interests together, at Michigan, in the country, and internationally... It is clear that Ben is a team builder and a precious member of this community... I had the opportunity to see Ben interact with his faculty colleagues and with the leaders in the field, and to watch as he promoted the work of his graduate students. From this (and other) interactions, it is clear that Ben is a team builder and a precious member of this community... Ben is certainly intellectually independent and, even more obviously, he is a strong collaborator....Ben has made a series of important contributions to the understanding of the regulation of Hedgehog signaling, which is a fundamental importance for human health. He appears to be a stellar member of the Michigan academic community, who certainly merits promotion.”

Reviewer B: “Ben has made several key contributions to understanding the molecular mechanism by which mammalian cells receive and transduce Hh signals. Indeed, several of these studies represent important milestones in the field. Ben’s work combines the best developmental neurobiology with the latest approaches from cell and molecular biology. His work is offering new insight into long-standing questions about the development of the mammalian nervous system... His ability to integrate detailed molecular and cellular experiments with a deep knowledge of the biology and an eye for interesting and important problems has led him to develop a world leading research programme. His recent research provides evidence of a continuing upward trajectory and he is well placed to continue to capitalized on his output... He has established productive and long standing collaborations with several groups that complement his expertise.”

Reviewer C: “Dr. Allen has identified outstanding questions in the literature and designed experiments that effectively address them. The result has been original findings that have significantly advanced our knowledge...”

Reviewer D: “Ben’s defining signature is that he publishes papers that challenge the dogma, and uses unusual rigor and depth to support his novel conclusions... His studies are having profound effects on the field ... He uses a powerful combination of mouse genetics, *in vitro* assays and

biochemistry, and identifies effective collaborators. He also contributes to the research of many of his colleagues, and is dedicated to graduate education.”

Reviewer E: “...Dr. Allen has provided extensive service to the community. For example, he has organized the international Hh meeting, which I attended and was excellent... I am impressed by the large number of students that Dr. Allen has mentored or co-mentored. It seems apparent that he is sought out for his guidance, and is valued by your students.”

Summary of Recommendation:

Dr. Allen is a world-recognized expert in the study of Hedgehog signaling in development and disease. Further, he has distinguished himself as an exceptional teacher and mentor, displaying a dedication to both student education at the University of Michigan and to student outreach throughout the world. Additionally, Dr. Allen has displayed a strong commitment to service across the university. Therefore, I enthusiastically recommend Benjamin Allen, Ph.D. for promotion to associate professor of cell and developmental biology, with tenure, Department of Cell and Developmental Biology, Medical School.



Marschall S. Runge, M.D., Ph.D.
Executive Vice President for Medical Affairs
Dean, Medical School

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