

**University of Pittsburgh
School of Medicine**

BIOGRAPHY

Name:	Bokai Zhu, PhD	Business Address:	Bridgeside Point 1;100 Technology Dr.; Room 565; Pittsburgh, PA 15219
E-Mail:	BZHU@pitt.edu	Business Phone:	412-383-0447

EDUCATION and TRAINING

List entries in each section chronologically

<i>Dates Attended</i>	<i>Name and Location of Institution</i>	<i>Degree Received and Year</i>	<i>Major Subject</i>
2002	Peking University China	B.S. 2006	Life Science
<i>Dates Attended</i>	<i>Name and Location of Institution</i>	<i>Degree Received and Year</i>	<i>Major Subject</i>
2006	Pennsylvania State University State College, PA	PhD 2012	Molecular Medicine Mentor: Dr. Jeffrey Peters
<i>Dates Attended</i>	<i>Name and Location of Institution</i>	<i>Degree Received and Year</i>	<i>Major Subject</i>
2012	Baylor College of Medicine Houston, Tx	Post-doc 2017	Circadian Rhythm Mentor: Dr. Bert O'Malley

APPOINTMENTS AND POSITIONS

ACADEMIC:

<i>Years Inclusive</i>	<i>Name and Location of Institution or Organization</i>	<i>Rank/Title</i>
2017 - 2018	Baylor College of Medicine Houston, TX	Instructor
2018 – 2026	University of Pittsburgh Pittsburgh, PA	Assistant Professor of Medicine
2026-present	University of Pittsburgh Pittsburgh, PA	Associate Professor of Medicine with tenure

**MEMBERSHIP in PROFESSIONAL and SCIENTIFIC
SOCIETIES**

<i>Organization</i>	<i>Year</i>
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American Diabetes Association
 Society for Research on Biological Rhythms
 American Society of Cell Biology

2018 – Present
 2020 – Present
 2022 - Present

HONORS

<i>Title of Award</i>	<i>Year</i>
The Eweson Lecture Series on Advances in Aging Research Travel Award	2026
Maximizing Investigators' Research Award (MIRA) R35	2025-2030
Hevolution/AFAR New Investigator Award in Aging Biology and Geroscience	2024
Pitt selection for Eastern Alliance of Digestive Disease Research Core Center Junior Faculty Exchange Program	2022
NIH Director's New Innovator Award	10/2020 – 09/2025
Pittsburgh Liver Research Center Pilot Research Award	04/2020 – 04/2021
W.M. Keck Foundation: Research Program 2019 Phase I Finalist/Pitt Nominee	11/2019
UPMC Competitive Medical Research Fund (CMRF) Research Award	07/2019 – 07/2021

CURRENT RESEARCH INTERESTS

Proteins are the building blocks of life, but keeping them healthy is a constant challenge for cells. The system that manages protein folding, repair, and clearance—called proteostasis—breaks down as we age, and this decline is a major driver of neurodegenerative diseases like Alzheimer's. Understanding why this protective system deteriorates with age, and whether it can be restored, is therefore a major focus of our research.

In our lab, we recently discovered something surprising: proteostasis doesn't run at a constant level, but instead follows a 12-hour rhythm, controlled by a unique biological clock that is separate from the circadian (24-hour) clock. This mammalian 12-hour oscillator helps cells anticipate stress and maintain balance in their protein environment. Our studies suggest that this rhythm serves as a built-in stress-management system, allowing cells to periodically coordinate protein production, folding, processing, and clearance before damage accumulates. We are now investigating how this protective rhythm changes during aging and whether strengthening or restoring it can improve cellular resilience. Even more exciting, our newest research shows that nuclear speckles—liquid-like compartments inside the nucleus—play a central role in this process. We've found that nuclear speckles act as sensors of protein stress and can even be rejuvenated to restore protein health. By "resetting" these structures, we've been able to improve proteostasis and reduce toxic protein buildup in models of tauopathy, a devastating neurodegenerative disease. These findings suggest that nuclear speckles are not simply passive storage sites inside the nucleus, but dynamic regulatory centers that help cells sense stress and coordinate protective gene programs. Our work reveals a previously unrecognized connection between biological timing, nuclear organization, and cellular resilience. By understanding how cells naturally coordinate stress responses across the day and how nuclear speckles regulate the genes that maintain protein quality control, we hope to uncover entirely new therapeutic strategies for aging and age-related neurodegenerative disorders. We are particularly interested in identifying ways to harness these natural protective mechanisms rather than targeting individual toxic proteins only after they have accumulated. Ultimately, our goal is not simply to treat the symptoms of diseases such as Alzheimer's and related dementias, but to target one of their root causes: the age-associated collapse of the cellular systems that keep proteins healthy. By restoring these fundamental protective mechanisms, we aim to promote healthier aging and develop interventions that preserve brain function.

For a detailed description of the research performed in the Zhu lab, please visit <http://www.bzhulab.com>.

Peer Reviewed Research Articles

1. Kubra, S[#], Sun, M.[#], Dion, W., Bian, Y., Catak, A., Luong, H., Wang, H., Pan, Y., Liu, J-J., Ponna, A., Liu, L., Sipula, I., Luo, J-H., Jurczak, M.J., Liu, S., and **Zhu, B.** The histone methyltransferase complex subunit RBBP5 serves as a central epigenetic regulator of proteostasis dynamics. *PLoS Biology* (2026). DOI: 10.1371/journal.pbio.3004048.
2. Doshi, NK, Pesaresi, T., Pagadala, T., Dion, W., Zhang, Y., David, NL., Amorim, N., Wang, W., Kumar NGV., **Zhu, B.**, Liu, S., Patwari P., Fazeli, PK., Steinhauser, ML. Branched chain amino acids prime metabolic inflammation. *Molecular Metabolism* (2025). DOI: <https://doi.org/10.1016/j.molmet.2025.102308>
3. Anaya, E.S., Dion, W., Saha, P.K., Cox, A.R., de Groot, E., Ahmed A., Felix, J.B., **Zhu, B.**, Pangas, S.A., Hartig, S.M. A mouse model of lipodystrophy reveals relationships between beige fat appearance and female fertility. *Endocrinology* (2025). DOI: 10.1210/endo/bqaf164
4. Dion, W[#], Tao, Y[#], Chambers, M., Zhao, S., Arbuckle, R., Sun, M., Kubra, S., Schaich, M., Nie, Y., Ye, M., Jamal, I., Larsen, M.B., Camarco, D., Dupont, C., Wang, H., Wang, B., Liu, S., Pi, S., Van Houten, B., Chen, B.B., Chen, Y.^{*}, Chen, X.^{*}, and **Zhu, B^{*}**. SON-dependent nuclear speckle rehabilitation alleviates proteinopathies. *Nature Communications* (2025). DOI: <https://doi.org/10.1038/s41467-025-62242-7>.
[Featured in UPMC News Blog: <https://inside.upmc.com/nuclear-speckle-rejuvenation-next-frontier-for-treating-neurodegeneration/>].
[Featured in UC San Diego Today: <https://today.ucsd.edu/story/antiparasitic-drug-shows-power-against-alzheimers-and-dementia>].
5. Lv B, Dion, W, Yang, H, Xun, J, Kim D, **Zhu, B**, and Tan JX. A TBK-independent primordial function of STING in lysosome biogenesis. *Molecular Cell* (2024). DOI: 10.1016/j.molcel.2024.08.026
6. **Zhu B***, Liu S, David NL, Dion W, Doshi NK, Siegel LB, Amorim T, Andrews RE, Kumar GVN, Li, H, Irfan S, Pesaresi T, Sharma AX, Sun M, Fazeli PK, and Steinhauser ML *. (* co-corresponding authors). Evidence for ~12-h ultradian gene program in humans. *npj Biological Timing and Sleep* (2024). DOI: 10.1038/s44323-024-00005-1.
7. Amorim, T., Kumar, N.GV., David, N.L., Dion, W., Pagadala, T., Doshi, N.K., **Zhu, B.**, Parkhitko, A., Steinhauser, M.L., and Fazeli, P.K. Methionine and one carbon metabolism as a regulator of bone remodeling with fasting. *JCI insight* (2024). DOI: 10.1172/jci.insight.177997
8. **Zhu, B.**, Zhu X., Borland M.G., Ralph, D.H., Chiaro C.R., Krausz, K.W., Ntambi, J.M., Glick, A.B., Patterson A.D., Perdew, G.H., Gonzalez F.J., and Peters, J.M. Activation of Peroxisome Proliferator-Activated Receptor- β/δ (PPAR β/δ) in keratinocytes by endogenous fatty acids. *Biomolecules* (2024). DOI: <https://doi.org/10.3390/biom14060606>
9. Mooli, R., **Zhu, B.**, Khan, S., Jurczak, M., and Ramakrishnan, S., Epigenetically active chromatin in neonatal iWAT reveals GABPa as a potential regulator of beige adipogenesis. *Frontiers in Endocrinology* (2024). DOI: 10.3389/fendo.2024.1385811
10. Jia M, Sayed K, Kapetanaki MG, Dion W, Rosas L, Irfan S, Valenzi E, Mora AL, Lafyatis RA, Rojas M, **Zhu B**, and Benos PV. LEF1 isoforms regulate cellular senescence and aging. *Aging Cell* (2023). DOI: <https://doi.org/10.1111/accel.14024>
11. **Zhu B*** and Liu S (*corresponding author). Preservation of ~12-hour ultradian rhythms of gene expression of mRNA and protein metabolism in the absence of canonical circadian clock. *Frontiers in Physiology* (2023). DOI: <https://doi.org/10.3389/fphys.2023.1195001>
12. Singh R, Meng H, Shen T, Lumahan LEV, Nguyen S, Shen H, Dasgupta S, Qin L, Karri D, **Zhu B**, Yang F, Coarfa C, O'Malley BW, and Yi P. TRAF4- mediated nonproteolytic ubiquitination of androgen receptor promotes castration-resistant prostate cancer. *Proceedings of the National Academy of Sciences* (2023) May 8. DOI: 10.1073/pnas.2218229120.
13. Scott, MR, Zong W, Ketchesin KD, Seney ML, Tseng, GC, **Zhu, B***, McClung CA*. (* co-corresponding authors). Twelve-hour rhythms in transcript expression within the human dorsolateral prefrontal cortex are altered in schizophrenia. *PLoS Biology* (2023). DOI: <https://doi.org/10.1371/journal.pbio.3001688>

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14. Dai T, Rosario SR, Katsuta E, Sawant Dessai A, Paterson EJ, Novickis AT, Cortes Gomez E, **Zhu B**, Liu S, Wang H, Abrams SI, Seshadri M, Bshara W, Dasgupta S. Hypoxic activation of PFKFB4 in breast tumor microenvironment shapes metabolic and cellular plasticity to accentuate metastatic competence. *Cell Reports* (2022); Dec 6;41(10):111756. doi: 10.1016/j.celrep.2022.111756. PubMed PMID: 36476868.
15. Rinsky, M., Weizman, E., Ben-Asher, HB. Eyal G., **Zhu, B.** and Levy, O. Temporal gene expression patterns in the coral *Euphyllia paradivisa* reveal the complexity of biological clocks in the cnidarian-algal symbiosis. *Science Advances* (2022). DOI: 10.1126/sciadv.abo6467
16. Meng, H, Gonzalez, N, Jung, SY, Lu Y, Putluri N, **Zhu, B**, Dacso, CC, Lonard, D and O'Malley BW. Defining the mammalian coactivation of hepatic 12-h clock and lipid metabolism. *Cell Reports* (2022); DOI: <https://doi.org/10.1016/j.celrep.2022.110491>
17. Dion, W., Ballance, H., Lee J., Pan Y., Irfan S., Edwards, C., Sun., M., Zhang J., Zhang X., Liu S. and **Zhu, B.** Four-dimensional nuclear speckle phase separation dynamics regulate proteostasis. *Science Advances* (2022); DOI: 10.1126/sciadv.abl4150
[Featured in UPMC News Blog: <https://inside.upmc.com/cellular-tides-influence-repair-of-faulty-proteins-involved-in-age-related-diseases/>].
18. Moreno-Smith, M., Milazzo, G., Tao, L., Fekry B., **Zhu, B.**, Mohammad M., Giacomo S., Borkar R., Reddy K., Capasso M., Vasudevan S., Sumazin P., Hicks, J., Putluri N., Perini G., Eckel-Mahan K., Burris T., and Barbieri E. Restoration of the molecular clock is tumor suppressive in neuroblastoma. *Nature Communications* (2021); DOI: <https://doi.org/10.1038/s41467-021-24196-4>
19. Meng, H, Gonzalez, N, Lonard, D, Putluri N, **Zhu, B**, Dacso, CC, York, B and O'Malley BW. XBP1 links the 12-hour clock to NAFLD and regulation of membrane fluidity and lipid homeostasis. *Nature Communications* (2020); DOI: <https://doi.org/10.1038/s41467-020-20028-z>
20. Sawant Dessai A, Palestino Dominguez M, Chen UI, Hasper J, Prechtel C, Yu C, Katsuta E, Dai T, **Zhu B**, Jung SY, Putluri N, Takabe K, Zhang XH, O'Malley BW, and Dasgupta S. Transcriptional repression of SIRT3 potentiates mitochondria aconitase activation to drive aggressive prostate cancer to bone. *Cancer Research* (2020); DOI: 10.1158/0008-5472.CAN-20-1708
21. **Zhu, B.** Decoding the function and regulation of the mammalian 12h-clock. *Journal of Molecular Cell Biology* (2020); doi: 10.1093/jmcb/mjaa021
22. Gao, Y., Chen, L., Han, Y., Wu F., Yang, W., Zhang, Z., Huo, T., Zhu, Y., Yu, C., Kim H., Lee M., Tang, Z., Philips, K., He, B., Jung, S.Y., Song, Y., **Zhu, B.**, Xu, R. and Feng Q. Acetylation of histone H3K27 signals the transcriptional elongation for estrogen receptor alpha. *Communications Biology* (2020); <https://doi.org/10.1038/s42003-020-0898-0>
23. Pan, Y, Ballance, H, Meng, H, Gonzalez, N, Kim, SM, Abdurehman, L, York, B, Chen, X, Schnytzer, Y, Levy, O, Dacso, CC, McClung, CA, O'Malley BW, Liu S, **Zhu, B.** 12-h clock regulation of genetic information flow by XBP1s. *PLoS Biology* (2020); DOI: 10.1371/journal.pbio.3000580
[Featured in UPMC News Blog: <https://inside.upmc.com/what-do-a-mouse-an-ocean-snail-and-a-sea-anemone-have-in-common/>].
24. Antoulas, A.C., **Zhu, B.**, Zhang, Q., York, B., O'Malley, B.W. and Dacso, C.C. A novel mathematical method for disclosing oscillations in gene transcription: a comparative study. *PLoS One* (2018); 13(9): e0198503
25. Koh, E., Chernis, N., Saha, P., Xiao, L., Bader, D.A., **Zhu, B.**, Rajapakshe, K., Hamilton, M.P., Liu, X., Perera D., Chen X., York, B., Trauner M., Coarfa, C., Bajaj M., Moore, D.D., Deng T., McGuire, S.E. and Hartig, S.M. miR-30a remodels subcutaneous adipose tissue inflammation to improve insulin sensitivity in obesity. *Diabetes* (2018). DOI: 10.2337/db17-1378
26. Borland, M.G., Kehres, E.M., Lee, C., Wagner, A.L., Shannon, B.E., Albrecht, P.P., **Zhu, B.**, Gonzalez, F.J., Peters, J.M. Inhibition of tumorigenesis by peroxisome proliferator-activated receptor (PPAR)-dependent cell cycle blocks in human skin carcinoma cells. *Toxicology* (2018). DOI: 10.1016/j.tox.2018.05.003

27. Dasgupta, S., Rajapakshe, K., **Zhu, B.**, Nikolai B.C., Yi, P., Putluri, N., Choi, J.M., Jung, S.Y., Coarfa, C., Westbrook, T.F., Zhang, X.H., Foulds, C.E., Tsai, S.Y., Tsai, M.J. and O'Malley, B.W. Glycolytic enzyme PFKFB4 activates oncogenic coactivator SRC-3 to drive breast tumorigenesis and metastasis. *Nature* (2018). DOI: 10.1038/s41586-018-0018-1
28. Borland, M.G., Yao, P., Kehres, E.M., Lee, C., Pritzlaff, A.M., Ola, E., Wagner, A.L., Shannon, B.E., Albrecht, P.P., **Zhu, B.**, Kang, B., Robertson, G.P., Gonzalez, F.J. and Peters, J.M. Inhibition of melanoma tumorigenicity by PPAR β/δ and PPAR γ . *Toxicological Sciences* (2017). DOI: 10.1093/toxsci/kfx147
29. Gates, L.A., Shi, J., Rohira, A.D., Feng, Q., **Zhu, B.**, Bedford, M.T., Sagum, C.A., Jung, S.Y., Qin, J., Tsai, M., Tsai, S.Y., Li, W., Foulds, C.E. and O'Malley, B.W. Acetylation on histone H3 lysine 9 mediates a switch from transcription initiation to elongation. *Journal of Biological Chemistry* (2017). DOI: 10.1074/jbc.M117.802074
30. **Zhu, B.**, Zhang, Q., Pan, Y., Mace, E.M., York, B., Antoulas, A.C., Dasco, C.C. and O'Malley, B.W. A cell-autonomous mammalian 12 hr clock coordinates metabolic and stress rhythms. *Cell Metabolism* (2017). 25(6):1305-1319.e9. DOI: 10.1016/j.cmet.2017.05.004
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<http://science.sciencemag.org/content/356/6345/twil>]
 [Featured in "editors' choice" highlight in the issue of *Science Translational Medicine* :28 Jun 2017:
<http://stm.sciencemag.org/content/9/396/eaan6728.full>]
 [Featured in the *Scientist* magazine: <http://www.the-scientist.com/?articles.view/articleNo/49603/title/Mammals-May-Have-a-12-hour-Clock/>].
31. Suresh, S., Durakoglugil, D., Zhou X., **Zhu, B.**, Sarah, C., Xing C., Xie X.J., York, B. and O'Donnell, K. SRC-2-mediated coactivation of anti-tumorigenic target genes suppresses MYC-induced liver cancer. *PLoS Genetics* (2017). DOI: 10.1371/journal.pgen.1006650
32. Yao, P.L., Chen, L., Dobrzański, T.P., **Zhu, B.**, Kang, B., Muller, R., Gonzalez, F.J. and Peters, J.M. Peroxisome proliferator-activated receptor- β/δ (PPAR β/δ) inhibits human neuroblastoma cell tumorigenesis by p53- and SOX2-mediated cell differentiation. *Molecular Carcinogenesis* (2016). DOI: 10.1002/mc.22607
33. Fleet, T., Stashi, E., **Zhu, B.**, Rajapakshe, K., Marcelo, K.L., Kettner, N., Gorman, B.K., Coarfa, C., Loning, F., O'Malley, B.W. and York, B. Genetic and environmental models of circadian disruption link SRC-2 function to hepatic pathology. *Journal of Biological Rhythms* (2016). DOI: 10.1177/0748730416657921
34. Romere, C., Duerrschmid, C., Bournat, J., Constable, P., Jain, M., Xia, F., Saha, P.K., Del Solar, M., **Zhu, B.**, York, B., Sarkar, P., Rendon, D.A., Gaber, M.W., LeMaire, S.A., Coselli, J.S., Milewicz, D.M., Sutton, R., Butte, N.F., Moore, D.D. and Chopra, A.R. Asprosin, a fasting-induced glucogenic protein hormone. *Cell* (2016). DOI: 10.1016/j.cell.2016.02.063
35. **Zhu, B.**, Gates, L.A., Stashi, E., Dasgupta, S., Gonzalez, N., Dean, A., Dasco, C.C., York, B. and O'Malley, B.W. Co-activator-dependent oscillation of chromatin accessibility dictates circadian gene amplitude via REV-ERB loading. *Molecular Cell* (2015) Nov 20. DOI: 10.1016/j.molcel.2015.10.024
36. Fleet, T., Zheng, B., Lin, F., **Zhu, B.**, Dasgupta, S., Stashi, E., Tackett, B., Thevananther, S., Rajapakshe, K., Gonzalez, N., Dean, A., Mao, J., Malonvannaya, A., Qin, J., Coarfa, C., Demayo, F., Dasco, C.C., Foulds, C.E., O'Malley, B.W. and York, B. SRC-2 orchestrates polygenic inputs for fine-tuning glucose homeostasis. *Proceedings of the National Academy of Sciences* (2015) Oct 20. DOI: 10.1073/pnas.1519073112
37. Yao, P.L., Chen, L., Dobrzański, T.P., Philips, D.A., **Zhu, B.**, Kang, B.H., Gonzalez, F.J. and Peters, J.M. Inhibition of human testicular embryonic carcinoma cell tumorigenicity by peroxisome proliferator-activated receptor- β/δ and retinoid acid receptor-dependent mechanisms. *Oncotarget* (2015) DOI: 10.18632/oncotarget.5415
38. **Zhu, B.**, Ferry, C.H., Markell, L.M., Blazanin, N., Glick, A.B., Gonzalez, F.J. and Peters, J.M. The nuclear receptor PPAR β/δ promotes oncogene-induced cellular senescence through repression of endoplasmic reticulum stress. *Journal of Biological Chemistry* (2014) Jul 18;289(29):20102-19
39. Stashi, E., Lanz, R.B., Mao, J., Michailidis, G., **Zhu, B.**, Kettner, N., Putluri, N., Reineke, E.L., Reineke, L.C., Dasgupta, S., Dean, A., Stevenson, C.R., Sivasubramanian, N., Sreekumar, A., DeMayo, F., York, B., Loning, F. and

- O'Malley, B.W. SRC-2 is an essential co-activator for orchestrating metabolism and circadian rhythm. *Cell Reports* (2014) 6 (4): 633-645
40. Yao, P.L., Morales, J.L., **Zhu, B.**, Kang, B.H., Gonzalez, F.J. and Peters, J.M. Activation of peroxisome proliferator-activated receptor- β/δ (PPAR β/δ) inhibits human breast cancer cell line tumorigenicity. *Molecular Cancer Therapeutics* (2014) 13(4):1008-17
 41. Lahoti, J., Hughes, J.M., Kusnadi, A., John, K., **Zhu, B.**, Murray, I., Gowda, K., Peters, J.M., Amin, S. and Perdew, G.H. Ah receptor antagonism attenuates growth factor expression, proliferation and migration in fibroblast-like synoviocytes from rheumatoid arthritis patients. *Journal of Pharmacology and Experimental Therapeutics* (2014) 348 (2):236-245
 42. **Zhu, B.**, Ferry, C.H., Bility, M.T., Blazanin, N., Khozoie, C., Glick, A.B., Gonzalez, F.J. and Peters, J.M. PPAR β/δ promotes HRAS-induced senescence and tumor suppression by potentiating p-ERK and repressing p-AKT activity. *Oncogene* (2013) doi:10.1038/onc.2013.477
 43. Khozoie, C., Borland, M.B., **Zhu, B.**, Baek, S., John, S., Hager, G.L., Shan, Y.M., Gonzalez, F.J. and Peters, J.M. Analysis of the peroxisome proliferator-activated receptor-beta/delta (PPARbeta/delta) cistrome reveals novel co-regulatory role of ATF4. *BMC Genomics* (2012) 13(1): 665
 44. **Zhu B.**, Khozoie C, Bility, M.T., Ferry, H.C., Blazanin, N., Glick, A., Gonzalez F.J, Peters JM. PPAR β/δ crosstalks with E2F and attenuates mitosis in HRAS-expressing cells. *Molecular and Cellular Biology* (2012) 32:2065-2082
 45. Borland MG., Khozoie C., Albrecht PP., **Zhu B.**, Lee C., Lahoti TS., Gonzalez FJ., Peters JM. Stable over-expression of PPAR β/δ and PPAR γ to examine receptor signaling in human HaCaT keratinocytes. *Cellular Signaling* (2011) 23: 2039-50
 46. Foreman JE., Chang WC., Palkar PS., **Zhu B.**, Borland MG., Williams JL., Kramer LR., Clapper ML., Gonzalez FJ., Peters JM. Functional characterization of peroxisome proliferator-activated receptor- β/δ expression in colon cancer. *Molecular Carcinogenesis* (2011) 50 :884-900
 47. **Zhu, B.**, Bai, R., Kennet, M.J., Kang, B., Gonzalez, F.J. and Peters, J.M. Chemoprevention of chemically-induced skin tumorigenesis by ligand activation of peroxisome proliferator-activated receptor- β/δ (PPAR β/δ) and inhibition of cyclooxygenase 2 (COX2). *Molecular Cancer Therapeutics* (2010) 9: 3267-77
 48. Bility, M.T., **Zhu, B.**, Blazanin, N., Glick, A.B., Kang, B.H., Gonzalez, F.J. and Peters, J.M. Ligand activation of peroxisome proliferator-activated receptor β/δ and inhibition of cyclooxygenase 2 (COX2) enhances inhibition of skin tumorigenesis. *Toxicological Sciences* (2010) 113: 27-36.
 49. He, P., Borland, M.G., **Zhu, B.**, Sharman, A.K., Amin, S., El-Bayoumy, K., Gonzalez, F.J. and Peters, J.M. Effect of ligand activation of peroxisome proliferator-activated receptor beta/delta in human lung cancer cell lines. *Toxicology* (2008) 29: 2406-2414.
 50. Girror, E.E., Hollingshead, H.E., He, P., **Zhu, B.**, Perdew, G.H. and Peters, J.M. Quantitative expression patterns of peroxisome proliferator-activated receptor beta/delta protein in mice. *Biochemical and Biophysical Research Communications* (2008) 371: 456-461.

Other Peer Reviewed Review Articles and Book Chapters

1. **Zhu, B.** in Biological Time Control: Autonomous Clocks in Cellular Organization, Dynamics, and Function (ed Mustafa G. Aydogan) 73-86 (Springer Nature Switzerland, 2026). DOI 10.1007/978-3-032-36189-9_5.
2. Chen X., and **Zhu, B.** Decoding the functions of nuclear speckles in neurodegeneration. *Trends in Neurosciences* 2026 Mar 6;. doi: 10.1016/j.tins.2026.01.010.
3. Dion, W and **Zhu, B.** Basic research and opportunities for translational advancement in the field of mammalian ~12-hour ultradian chronobiology. *Frontiers in Physiology* (2024); <https://doi.org/10.3389/fphys.2024.1497836>
4. **Zhu, B.** Logic of the temporal compartmentalization of the hepatic metabolic cycle. *Physiology* (2022); <https://doi.org/10.1152/physiol.00003.2022>
5. Asher, G and **Zhu, B.** Beyond circadian rhythms: Emerging roles of ultradian rhythms in control of liver functions.

Hepatology (2022); <https://doi.org/10.1002/hep.32580>

6. Ballance, H and **Zhu, B.** Revealing the hidden reality of the mammalian 12-h ultradian rhythms. *Cellular and Molecular Life Sciences* (2021); <https://doi.org/10.1007/s00018-020-03730-5>
7. **Zhu, B.**, Dacso, C.C. and O'Malley, B.W. Unveiling “Musica Universalis” of the Cell: A brief history of biological 12h rhythms. *Journal of Endocrine Society* (2018); 2(7):727-752. DOI: 10.1210/js.2018-00113
8. Peters, J.M., Kim, D.J., Bility, M.T., Borland, M.G., **Zhu, B.** and Gonzalez, F.J. Regulatory mechanisms mediated by peroxisome proliferator-activated receptor- β/δ in skin cancer. *Molecular Carcinogenesis* (2019); <https://doi.org/10.1002/mc.23033>

Articles published on preprint servers

1. Yadav, N., Pelcher, O., Mooli, R.G.R., Cameron, R.B., Delaidelli, A., Rao, K.B.N., Manikandan, B., Visser, S., Cobos, A.C.T., Parmar, V., Kayola, Y., Natarajan, S.K., Patel, Y., Zhang, J., Shah, H., Vallabhapurapu, S.D., Khan, S.R., Mochizuki, A.Y., Abdullah, K.G., Hu, B., Lucas, C.G., Sievers, P., Sahm, F., Donson, A.M., Foreman, N.K., Roussel, M.F., Pearce, T.M., Dirks, P., Pajtler, K.W., Mack, S.C., Rich, J., Gilbertson, R.J., Holland, E.C., Ramakrishnan, S.K., Abel, T.J., Ramachandran, S., Agnihotri, S., **Zhu, B.**, Venneti, S., Faubert, B., Taylor, M.D., Hulleman, E., Pollack, I.F., Phoenix, T., Michealraj, K.A. Adenosylhomocysteinase drives epigenetic and metabolic reprogramming in ZFTA-RELA ependymoma. *BioRxiv* (2026). doi: <https://doi.org/10.64898/2026.10.06.757085>
2. Munoz-Mayorga, D., Lyu, X., Jati, S., Zhang, J., Rossitto, L-A., Tao, Y., Zhao, S., Hui, E., Kauffman, A., Zhu, B., and Xu, C. A non-canonical androgen signaling pathway drives microglial activation and tau pathology in females. *Research Square* (2026). <https://doi.org/10.21203/rs.3.rs-10286730/v1>.
3. Anaya, E.S., Masschelin, P., Dion, W., Saha, P.K., Sharp, R.M., Patel, P., Lieu, E.L., de Groot, E., Guan, D., Kim, K.H., Cox, A.R., **Zhu, B.**, and Hartig, S.M. GABPA Expression in Adipocytes Governs Thermal Regulation and Systemic Metabolism. Available at *SSRN* (2026): <https://ssrn.com/abstract=6815054>
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5. Kubra, S., Sun, M., Dion, W., Catak, A., Luong, H., Wang, H., Pan, Y., Liu, J-J., Ponna, A., Liu, L., Sipula, I., Luo, J-H., Jurczak, M.J., Liu, S., and **Zhu, B.** The SET1/COMPASS subunit RBBP5 orchestrates epigenetic control of global proteostasis and the 12h oscillator to safeguard metabolic and cellular homeostasis. *BioRxiv* (2025). doi: <https://doi.org/10.1101/2024.09.13.612812>.

Please also see [Google Scholar](#) and <https://www.ncbi.nlm.nih.gov/myncbi/bokai.zhu.3/bibliography/public/>

RESEARCH

Current Grant Support:

Grant Number (funded)	Grant Title	Role in Project %Effort Calendar Months	Years Inclusive	Source \$ Amount (include direct and indirect if PI) (If Co-I list sub-award)
R35 GM157978	Decoding the Functions of Nuclear Speckle in Protein Quality Control	PI 5.4 CM	06/01/2025- 04/31/2030	NIGMS \$2,305,500 total

N/A	Rejuvenation of Nuclear speckles to Delay Aging	PI 1.68 CM	12/31/2023 – 12/30/2026	Hevolution/AFAR New Investigator Award in Aging Biology and Geroscience \$375,000 total
N/A	SON-Dependent Nuclear Speckle Rejuvenation: A Novel Proteostasis-Based Therapeutic Strategy for Alzheimer's Disease	Co-PI 1.2CM	02/2026-02/2028	Cure Alzheimer's fund \$75,000/year (subaward)
R01 DK114356-06A1	Metabolic Impacts of Type II Interferon signals in Obesity	Co-I 1.2 CM	07/01/2022 – 06/30/2026	NIDDK \$36,240/year (subaward)
R01 DK 134851-01A1	Deciphering the Physiology of Neonatal Beige Adipocytes	Co-I 0.36 CM	03/13/2024 – 02/28/2028	NIDDK \$9,056/year (subaward)
N/A	Nuclear speckle Rejuvenation to Treat Retinitis Pigmentosa	Co-I 2.0 Cm	09/01/2024 – 08/31/2027	Foundation Fighting Blindness \$150,000/year (subaward)

Pending Grant Support

Grant Number	Grant Title	Role in Project %Effort (must not exceed 100%) Calendar Months (must not exceed 12 months)	Years Inclusive	Source \$ Amount (include direct and indirect if PI) (If Co-I list sub-award)
R01	Deciphering the tug of war between tauopathy and nuclear speckles	Co-PI 4.8 CM	07/01/2027 – 06/31/2032	NIA \$5,320,610
R01	Repositioning Pyrvinium Pamoate for disease modification in	Co-PI 4.8 CM	07/01/2027 – 06/31/2032	NIA \$4,703,140

	AD and related tauopathy			
R21	Developing Functional Genomic Tools to Define Causality between Nuclear Speckle Biophysics and Genome Function	PI 1.2 CM	07/01/2027-06/31/2029	NHGRI \$418,518.00
2640269	Tools4cell: Developing an integrated toolkit for interrogating nuclear speckle function	PI 3.0 CM	04/01/2027-03/31/2031	NSF \$1,119,428

Prior Grant Support:

Grant Number (funded)	Grant Title	Role in Project %Effort (must not exceed 100%) Calendar Months (must not exceed 12 months)	Years Inclusive	Source \$ Amount (include direct and indirect if PI) (If Co-I list sub-award)
11855	Nuclear Speckle Rejuvenation Delays Aging	PI 1.2 CM	06/01/2023 – 11/30/2025	Richard King Mellon Foundation \$220,056
DP2GM140924	Decoding the Regulation and Functions of mammalian 12h-clock	PI 3.3 CM	09/30/2020 – 05/31/2025	National Institute of General Medical Science \$2,371,875
R21 AG071893	Ultradian to circadian transcriptome re-wiring underlies liver aging	PI 0.12 CM	09/15/2022 – 05/31/2025	NIA \$437,250
1703170	EAGER: Collaborative Research Data Science Applications in Cyberphysical Systems for Health	Co-PI	09/07/2017 – 08/31/2018	NSF

N/A	Boosting the Hepatic 12h Clock to Prevent Non-alcoholic Fatty Liver Diseases	PI	01/01/2018 – 12/31/2021	American Diabetes Association \$138,000/year
N/A	Uncovering Novel Mechanisms of Epigenetic and Metabolic Regulation of Mammalian 12h-clock	PI	07/01/2019 – 06/30/2021	UPMC Competitive Medical Research Fund Research Award \$20,000/year
N/A	12h-24h Reprogramming Drives NAFLD	PI	09/1/2020 – 09/01/2021	Pittsburgh Liver Research Center Pilot & Feasibility Research Award \$25,000/year

Other Research Related Activities

Patents

Repurposing Pyrvinium as an Effective Therapeutic Drug to Reduce Tauopathy
Bokai Zhu, William Dion, Yuren Tao, Xu Chen. Filed on 08/01/2024: WO2025038296A2

Repurposing Pyrvinium as an effective therapeutic drug to treat Retinitis Pigmentosa
Bokai Zhu, William Dion, Yuanyuan Chen. Filed on 08/01/2025: WO2026033412

Grant Review Committee

Research Grant Review Committee of the American Diabetes Association's
Core Research Program

2019 – 2024

Ad hoc grant reviewer for UK Wellcome Trust foundation

Editorial Positions

Ad hoc peer reviewer for *Advanced Science*, *Trends in Endocrinology and Metabolism*, *Nucleic Acids Research*, *eLife*, *Science Translational Medicine*, *Cell Reports*, *Hepatology*, *JCI Insight*, *Communications Biology*, *Communications Medicine*, *Scientific Report*, *Cell Death & Disease*, *Molecular and Cellular Biology*, *Journal of Molecular Cell Biology*, *Journal of Neuroendocrinology*, *Journal of Steroid Biochemistry and Molecular Biology*, *Experimental Eye Research*, *Toxicological Sciences*, *Molecular Pharmacology*, *Cell Biochemistry and Function*, *Experimental Gerontology* and *Molecular Cancer*.

Ad hoc Academic Editor for *PloS Biology*.

INVITED SEMINARS AND LECTURESHIPS

- Invited Speaker, Center for Translational Environmental Health Research annual symposium: Tick Tox:” Circadian Rhythms and the Environment”. Nov 30th, 2016. Texas A&M University.
- Invited Speaker, Post-doctoral Scientific Seminar. Sep 15th, 2017. Baylor College of Medicine.
- Invited Speaker, Department of Pharmacology and Toxicology at University of Utah, Oct 31st, 2017
- Invited Speaker, Department of Integrative Biology and Physiology at University of Minnesota Medical School, Nov

13th, 2017

- Invited Speaker, Aging Institute at University of Pittsburgh School of Medicine, Nov 20th, 2017
- Invited Speaker, College of Agriculture and Life Sciences at the North Carolina State University, Feb 19th, 2018
- Invited Speaker, CPCB seminar series. University of Pittsburgh. Sep 21st, 2018
- Invited Speaker, Bridgeside Point Research Forum, University of Pittsburgh, Nov 15th, 2018.
- Invited Speaker, Pittsburgh Institute for Neurodegenerative Diseases, University of Pittsburgh, Jan 16th, 2019
- Invited Speaker, 12/12 Senior Vice Chancellor Research Seminar Series, University of Pittsburgh, Feb 8th, 2019
- Invited Speaker, Keynote speaker at University of Pittsburgh Center for Sleep and Circadian Science Retreat, April 8th, 2019
- Invited Speaker, DOME Research Seminar Series, University of Pittsburgh, Sept 25th, 2019
- Invited Speaker, First Annual "Summer Sleep and Circadian Workshop in Indispensable Methods" Workshop at Center for Sleep and Circadian Science. Aug 11th, 2020.
- Invited Speaker, University of Pittsburgh Center for Sleep and Circadian Science Sleep Grand Rounds. Jan 7th, 2021.
- Invited Speaker, University of Pittsburgh Pittsburgh Liver Research Center Seminar Series. Jan 19th, 2021.
- Invited Speaker, 2nd International Conference on Cell and Experimental Biology (CEB-2021). July 14th, 2021. Virtual presentation.
- Invited Speaker, University of Pittsburgh Department of Developmental Biology. Dec 1st, 2021. Virtual presentation.
- Invited Speaker, University of Pittsburgh Department of Biological Sciences. Jan 31st, 2022. Hybrid presentation.
- Invited Speaker, University of Oklahoma Health Science Center/Oklahoma Medical Research Foundation/Oklahoma Nathan Shock Center on Aging. Feb 4th, 2022. Virtual presentation.
- Invited Speaker, University of Pennsylvania Center for Molecular Studies in Digestive & Liver Diseases. April 21st, 2022. Virtual presentation.
- Invited Speaker, University of Pittsburgh Magee-Women's Research Institute. April 27th, 2022.
- Invited Speaker, Chinese Society for Biological Rhythms Seminar Series 2022. Sep 11th, 2022. Virtual presentation.
- Invited Speaker, Joint meeting of American Society for Cell Biology (ASCB) and European Molecular Biology Organization (EMBO) at the Special Interest Subgroup session: "Biological time control: from the discovery of fundamental principles to the development of novel experimental and theoretical approaches". Dec 3rd, 2022.
- Invited Speaker, Vascular Medicine Institute, University of Pittsburgh, Jan 18th, 2023.
- Invited Speaker. ER stress Journal Club. Sep 12th, 2023. Virtual presentation.
- Invited Speaker. Bench-to-bedside Medical Grand Rounds. Oct 3rd, 2023. University of Pittsburgh, School of Medicine.
- Invited Speaker, 9th Annual Great Lake Nuclear Receptor Conference, Oct 19th-Oct 20th, 2023. Roswell Park Comprehensive Cancer Center.
- Invited Speaker, Latin American Symposium on Chronobiology, Oct 25th to Oct 28th, 2023. Riviera Maya, Mexico.
- Selected Speaker, EMBL symposium: Biological oscillators: rhythms and synchronization across scales. March 19-22, 2024. Heidelberg, Germany.
- Selected Speaker, CSHL meeting: Protein Homeostasis in Health and Disease, Apr 24th to Apr 28th, 2024. Cold Spring Harbor, NY, USA.
- Invited Speaker, Westlake University, Hangzhou, China, June 17th, 2024.
- Invited Speaker, Stomatology Hospital, Zhejiang University School of Medicine, Hangzhou, China, June 18th, 2024.
- Invited Speaker, Xiangya School of Medicine, Changsha, China, June 19th, 2024.
- Invited Speaker, Center for Quantitative Biology, Peking University, Beijing, China, June 24th, 2024.
- Invited Speaker. ER stress Journal Club. Sep 10th, 2024. Virtual presentation.
- Invited Speaker, University of California, Berkely, Oct 11th, 2024.
- Invited Speaker, 2024 PKU bioNET, Buck Institute for Research on Aging, Oct 12th, 2024.
- Invited Speaker, American Society for Cell Biology (ASCB) at the Special Interest Subgroup session: "Biological Time Control: From Fundamental Principles to the Development of Novel Approaches". Dec 10th, 2024.
- Invited Speaker, ADRC special seminar, University of California, San Diego, Dec 17th, 2024.

- Invited Speaker, PKUBIO100 Academic Forum, Peking University, Beijing, China. May 3rd to May 4th, 2025
- Invited Speaker, Steel City Condensates 2025 Symposium, Carnegie Mellon University, May 22nd, 2025.
- Invited Speaker, Hevolution/AFAR New Investigator Grantee Conference and The Paul F. Glenn/AFAR Conference on the Biology of Aging, Ritz-Carlton Bacara, Santa Barbara, California, May 27-30, 2025.
- Invited Speaker, 2025 SCBA Hepatology Division & CALS Scientific Symposium, Geneva, NY, July 20-25, 2025.
- Invited Speaker, University-Wide Conference (Endocrine Grand Rounds), University of Pittsburgh, Oct 10th, 2025
- Invited Speaker, IDP seminar series (biweekly virtual seminars on intrinsically disordered proteins), virtual, Jan 8th, 2026.
- Invited Speaker, 31st annual Midwest stress response and molecular chaperone meeting, Northwestern University, Jan 16th, 2026
- Invited Speaker, Biomedical Pioneering Innovation Centre (*BIOPIC*), Peking University, April 14, 2026
- Invited Speaker, The 12th International Symposium on 3D Genomics, Xi'an, China, April 16-19, 2026.
- Invited Speaker, Cold Spring Harbor Laboratory Symposium on Genome Organization & Nuclear Function, Cold Spring Harbor, NY, April 28 - May 2, 2026.
- Invited Speaker, 3rd annual Pittsburgh Cell Biology conference, Pittsburgh, PA, May 5th, 2026.
- Invited Speaker, Society for Research on Biological Rhythms 2026 biennial meeting, Omni Amelia Island Resort & Spa, FL, May 9–13, 2026.
- Invited Speaker, 2nd ZTTK community conference, Boston, MA, July 17-19, 2026
- Invited Speaker, 17th Annual Research Day on Aging, University of Pittsburgh, Pittsburgh, PA, Nov 2nd, 2026.
- Invited Speaker, the 3rd symposium of the Pittsburgh Center for Biomolecular Condensates, Pittsburgh, PA, Oct 19th, 2026.
- Invited Speaker, Department of genetics and development seminar series, Colombia University, New York City, NY, Nov 4th, 2026.

MENTORING

Post-doctoral:

Dates	Mentor Role	Name of Mentee	Position of Student	Mentee Achievements
2018-2022	Supervisor	Heather Ballance	Post-Doctoral Associate	T32 Awardee - Geriatrics
2020	Supervisor	Baby Anjum	Post-Doc	
2022-2025	Supervisor	Syeda Kubra	Post-Doctoral Associate	
2023 –2025	Supervisor	Ahmet Alperen Catak, MD	Visiting Scholar	
2024 – 2026	Supervisor	Imran Jamal	Post-Doc	
2026- Present	Supervisor	Guoqiang Ma	Post-Doc	
2026- Present	Supervisor	Yeuran Oh	Post-Doc	

Graduate students:

Dates	Mentor Role	Name of Mentee	Position of Student	Mentee Achievements
2020 – April, 2025	Supervisor	William Dion	Graduate Student, Integrative system Biology Graduate Program	Was Supported by T32 and an NIA F32 Fellowship Award. Currently pursuing post-doctoral training

				at Scripps Research Institute
2022 – 2024	Supervisor	Michelle Sun	Master of Science in Biostatistics Graduate Program	Currently enrolled at University of Chicago Genetics, Genomics and Systems Biology Ph.D. program.
2023 – Present	Supervisor	Haokun Wang	Cell Biology and Molecular Physiology Program	
2024 – Present	Supervisor	Yu Bian	Cell and Molecular Pathology Program	
2025 – Present	Supervisor	Maci Chambers	Cell Biology and Molecular Physiology Program	

Undergraduate Students:

Dates	Mentor Role	Name of Mentee	Mentee Achievements
2020 – Present	Supervisor	Jane Lee	05/2020 – 08/2020; 06/2021 – 08/2021; Awarded Summer Undergraduate Research Fellowship Award (SURP)
2020-2021	Supervisor	Claire Cheng	
2020	Supervisor	Saad Irfan	MD Class of 2026 at Lewis Katz School of Medicine
2021 – 2023	Supervisor	Daniella Santucci	
2022 – 2023	Supervisor	Claire Dupont	Currently Lab Technician in the Zhu Lab
2022	Supervisor	Nathan Ritchey	2022 SURP Student, currently a medical student enrolled at Ohio State University
2022 – 2024	Supervisor	Aishwarya Ponna	
2023	Supervisor	Maci Chambers	2023 SURP Student, currently a Ph.D. graduate

			student in Dr. Bokai Zhu's lab in IBGP program
2023	Supervisor	Aryan Bangalore	2023 SURP Student
2023 – 2024	Supervisor	Eleanor Ickes	
2023 – Present	Supervisor	Evan Lan	2025 SURP student
2022 – 2025	Supervisor	Hannah Luong	2024 SURP Student; currently a Genentech Web-lab/Dry-lab intern
2025 – Present	Supervisor	Brooke Hudec	2024 SSoE Summer Undergraduate Research Internship (SURI)

Comprehensive examination committee- Graduate Students:

2026	Joseph Schinderle	MGDB Program	University of Pittsburgh.
2026	Jason Yeung	ISB Program	University of Pittsburgh

Thesis committee - Graduate Students:

2021 – 2025	Kaitlyn Peterson, Neuroscience Graduate Program, University of Pittsburgh.
2021 – 2024	Tianyi Zhou, Biology Graduate Program, University of Houston: 2021 to 2024.
2023 – 2025	Ankit Sharma, Integrative system Biology Program/MSTP, University of Pittsburgh.
2026-present	Jason Yeung, Integrative system Biology Program, University of Pittsburgh.

Lab Rotations – Graduate Students

2020	Jiwon Lee	CPCB Program	University of Pittsburgh
2020	William Dion	ISB Program	University of Pittsburgh
2020	Margaret Champion	ISB Program	University of Pittsburgh
2021	Jing Zhang	IBGP Program	University of Pittsburgh
2021	Ramya Donepudi	ISB Program	University of Pittsburgh
2022	Haokun Wang	IBGP Program	University of Pittsburgh
2024	Maci Chambers	IBGP Program	University of Pittsburgh
2024	Yu Bian	CMP Program	University of Pittsburgh
2025	Sam Vasquez	IBGP Program	University of Pittsburgh
2025	Hassan Mustafa	IBGP Program	University of Pittsburgh
2026	Rachel Hvasta	IBGP Program	University of Pittsburgh
2026	JJ Ammerall	IBGP Program	University of Pittsburgh

SERVICE

University and Medical School:

2019 – 2021	Joint CMU-Pitt Program in Computational Biology (CPCB) graduate students' admission committee
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2020 – 2024 Interdisciplinary Biomedical Graduate Program (IBGP) graduate students' admission committee