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APPOINTMENTS

Class of 1942 Professor, 2024–present
Professor, 2022–present
Associate Professor With Tenure, 2019–2022
Associate Professor Without Tenure, 2017–2019
Assistant Professor, 2012–2017

Department of Chemistry, Massachusetts Institute of Technology, Cambridge, MA

Extramural Member, Koch Institute for Integrative Cancer Research, 2024–present

Massachusetts Institute of Technology, Cambridge, MA

Associate Member, 2015–present

Broad Institute of MIT and Harvard, Cambridge, MA

Investigator, Center for Musculoskeletal Research, 2015–present

Massachusetts General Hospital, Boston, MA

Member, Center for Environmental Health Sciences, 2015–2024

Massachusetts Institute of Technology, Cambridge, MA

American Cancer Society Postdoctoral Fellow, 2010–2012

Postdoctoral Research Associate, 2009–2010

Advisors: Professors Jeffery W. Kelly and R. Luke Wiseman
Departments of Chemistry and Molecular and Experimental Medicine
The Scripps Research Institute, La Jolla, CA

EDUCATION

Ph.D., Chemistry, 2009

Advisor: Professor Ronald T. Raines
Thesis: Understanding Collagen Structure and Stability
University of Wisconsin, Madison, WI

B.S., Chemistry, 2004

summa cum laude
Class Rank: 1 of 5995
Minor: Biochemistry
Research Advisors: Professors Felicia A. Etzkorn, David G. I. Kingston, and Harry C. Dorn
Virginia Tech, Blacksburg, VA

SELECTED HONORS AND AWARDS

- Genentech Lectureship, University of Illinois Urbana-Champaign, 2025
- Ralph Hirschmann Lectureship, Oberlin College, 2025
- Ono Pharma Foundation Breakthrough Science Award, 2024–2027
- MacVicar Faculty Fellow (for outstanding and sustained contributions to undergraduate education at MIT, including exceptional teaching and mentoring), 2022–2032
- Camille Dreyfus Teacher-Scholar, 2018–2023
- American Cancer Society Research Scholar, 2018–2023
- MIT Committed to Caring Award for Outstanding Graduate Student Mentoring, 2018
- National Science Foundation CAREER Award, 2017–2022

- Whitehead Career Development Chaired Professorship, 2016–2019
- d'Arbeloff Fund for Excellence in Education Awardee, 2016
- Journal of Molecular Biology Young Investigator Award, 2016
- National Institutes of Health Director's New Innovator Award, 2015–2020
- Smith Family Award for Excellence in Biomedical Research, 2014–2016
- 56th Edward Mallinckrodt Jr. Foundation Faculty Scholar, 2013–2017
- Outstanding Recent Alumnus, Virginia Tech College of Science, 2012
- American Cancer Society Postdoctoral Fellowship, 2010–2012
- Ralph Hirschmann and Daniel Rich Graduate Award in Bioorganic Chemistry Research, 2008
- American Chemical Society Division of Medicinal Chemistry Predoctoral Fellowship, 2007–2008
- United States Department of Homeland Security Graduate Fellowship, 2004–2007
- National Institutes of Health Chemistry-Biology Interface Traineeship, 2004–2007 (funding declined / training program completed)
- University of Wisconsin–Madison McElvain Fellowship, 2004–2005
- James Lewis Howe Award for Outstanding Achievement in Chemistry, Blue Ridge Division of the American Chemical Society, 2004
- Phi Kappa Phi Medallion for highest-ranking senior in the Virginia Tech College of Science, 2004
- Virginia Tech Excellence in Undergraduate Research Award, 2004
- Phi Beta Kappa, 2004
- United States Department of Homeland Security Undergraduate Scholarship, 2003–2004
- Virginia Tech Chemistry Merit Scholar, 2003

PUBLICATIONS

Halim, S.; Sebastian, R.M.; Liivak, K.E.; Patrick, J.E.; Hui, T.; Amici, D.R.; Giacomelli, A.O.; Butty, V.L.; Hahn, W.C.; Sánchez-Rivera, F.J.; Mendillo, M.L.; Lin, Y.-S.; **Shoulders, M.D.*** “Dominant-Negative *TP53* Mutations Potentiated by the Heat Shock Factor I-Regulated Proteostasis Network” *bioRxiv*, in review (2025). DOI: 10.1101/2024.11.01.621414.

- Cellular chaperones regulated by HSF1, a proteostasis transcription factor widely overexpressed in cancers, can dramatically expand the mutational landscape accessible to key oncoproteins.

Read, S.A.*; Ramezani-Moghadam, M.; Gloss, B.; Nguyen, R.; Woodham, B.; Ho, V.; Yuen, L.; Yoon, J.; Qiao, L.; Tu, T.; George, J.; **Shoulders, M.D.**; Ahlenstiel, G. “Hepatic Zinc Deficiency Dampens the Acute Phase Response in Patients with Alcohol-Associated Hepatitis” in review (2025).

- Loss of zinc stores in the liver result in failed acute phase responses to infection in patients with alcohol-associated hepatitis, suggesting zinc supplementation as a potentially useful adjuvant.

McDonald, J.L.; Shapiro, N.P.; Mengiste, A.A.; Kaines, S.; Whitney, S.M.; Wilson, R.H.*; **Shoulders, M.D.*** “*In Vivo* Directed Evolution of an Ultrafast Rubisco from a Semianaerobic Environment Imparts Oxygen Resistance” *Proceedings of the National Academy of Sciences, USA* **122**, e2505083122 (2025).

- Discovery of remarkably fast RuBisCO variants with high resistance to oxygenation, via the development of a fully integrated mutagenesis and selection platform for *in vivo* evolution.

Yamine, K.M.; Mirza Abularach, S.; Xiong, M.; Kim, S.; Bikovtseva, A.A.; Butty, V.L.; Schiavoni, R.P.; Bateman, J.F.; Lamandé, S.R.; **Shoulders, M.D.*** “Failed Cellular Surveillance Enables Pathogenic Matrix Deposition in a *COL2A1*-Related Osteoarthritis” *Journal of Biological Chemistry* **301**, 110436 (2025).

- Organoid models show that an inability of the cell to recognize folding defects caused by the Arg719Cys substitution in collagen-II leads to an ER storage defect and early onset osteoarthritis.

Yoon, J.; Zhang, Y.M.; Her, C.; Grant, R.A.; Ponomarenko, A.I.; Ackermann, B.E.; Hui, T.; Lin, Y.-S.; Debelouchina, G.T.; **Shoulders, M.D.*** “The Immune-Evasive Proline-283 Substitution in Influenza Nucleoprotein Increases Aggregation Propensity Without Altering the Native Structure” *Science Advances* **10**, ead6144 (2024).

- Comprehensive structural and biophysical studies explain why a key immune-evasive variant from the 1918 flu that is conserved in modern strains requires host chaperones to exist.

Mengiste, A.A.; McDonald, J.L.; Tran, M.N.T.; Plank, A.V.; Wilson, R.H.; Butty, V.L.; **Shoulders, M.D.*** “MutaT7^{GDE}: A Single Chimera for the Targeted, Balanced, Efficient, and Processive Installation of All Possible Transition Mutations *In Vivo*” *ACS Synthetic Biology* **13**, 2693–2701 (2024).

- Development and characterization of a new MutaT7-based technology for *in vivo* targeted mutagenesis that vastly simplifies the system while improving mutagenic properties on all axes.

Yamine, K.M.; Li, R.C.; Borgula, I.M.; DiChiara, A.S.; Mirda Abularach, S.; Raines, R.T.; **Shoulders, M.D.*** “An Outcome-Defining Role for the Triple-Helical Domain in Regulating Collagen-I Assembly” *Proceedings of the National Academy of Sciences, USA* **121**, e2412948121 (2024).

- Procollagen heterotrimerization was thought to be regulated entirely by the C-propeptide domain. This work overturns that paradigm, revealing key features in the triple helix that control assembly.

Chen, K.; **Shoulders, M.D.*** “Protein Glycosylation Patterns Shaped by the IRE1-XBP1s Arm of the Unfolded Protein Response” *Israel Journal of Chemistry* e202300162 (2024). Invited article in issue recognizing Prof. Jeffery W. Kelly’s Wolf Prize in Chemistry.

- Discussion of the discovery that the unfolded protein response plays unexpected roles in regulating *N*-glycosylation, and evidence for key biological consequences of this role.

Guerrero, R.F.; Harris, R.M.; **Shoulders, M.D.**; Ogbunugafor, C.B.* “Evolutionary Druggability: Leveraging Low-Dimensional Fitness Landscapes Towards New Metrics for Antimicrobial Interactions” *eLife* **12**, e88480 (2024).

- This study offers new perspectives on the concept of druggability that consider both how target variants are impacted by a drug and the generalizability of a drug against variants.

Yamine, K.M.; Mirda Abularach, S.; Kim, S.; Bikovtseva, A.A.; Lilianty, J.; Butty, V.L.; Schiavoni, R.P.; Bateman, J.F.; Lamandé, S.R.; **Shoulders, M.D.*** “ER Procollagen Storage Defect Without Coupled Unfolded Protein Response Drives Precocious Arthritis” *Life Science Alliance* **7**, e202402842 (2024).

- The first humanized, three-dimensional model of a genetic collagenopathy reveals an ER storage defect driving pathology, highlighting the cell’s poor ability to respond to misfolding triple helices.

Druso, J.E.; MacPherson, M.B.; Chia, S.B.; Elko, E.; Aboushousha, R.; Seward, D.J.; Abdelhamid, H.; Erickson, C.; Corteselli, E.; Tarte, M.; Peng, Z.; Bernier, D.; Zito, E.; **Shoulders, M.D.**; Thannickal, V.J.; Huang, S.; van der Vliet, A.; Anathy, V.; Janssen-Heininger, Y.M.W.* “ER Oxidative Stress Promotes Glutathione-Dependent Oxidation of Collagen-1A1 and Promotes Lung Fibroblast Activation” *American Journal of Respiratory Cell and Molecular Biology* **71**, 589–602 (2024).

- Glutathionylation of collagen type-I is a novel post-translational modification that promotes fibrogenesis, in association with enhanced ER oxidative stress.

Ogbunugafor, C.B.*; Guerrero, R.F.; Miller-Dickson, M.D.; Shakhnovich, E.I.; **Shoulders, M.D.** “Epistasis and Pleiotropy Shape Biophysical Protein Subspaces Associated with Drug Resistance” *Physical Review E* **108**, e054408 (2023).

- Deconstruction of bacterial enzyme protein space into biophysical subspaces based on catalytic parameters unveils new principles for how epistasis sculpts evolution.

Yoon, J.; Patrick, J.E.; Ogbunugafor, C.B.; **Shoulders, M.D.*** “Viral Evolution Shaped by Host Proteostasis Networks” *Annual Review of Virology* **10**, 77–98 (2023).

- Comprehensive review of key intellectual and experimental advances underpinning a new paradigm for viral evolution focused on the roles of host chaperone and quality control systems.

Yamine, K.M.; Mirda Abularach, S.; Sampurno, L.; Bateman, J.F.; Lamandé, S.R.; **Shoulders, M.D.*** “Using CRISPR/Cas9 to Generate a Heterozygous COL2A1 p.R719C iPSC Line (MCRli019-A-6) Model of Human Precocious Osteoarthritis” *Stem Cell Research* **51**, e103020 (2023).

- Development of a novel cell-based system to model the genetics of precocious osteoarthritis, an understudied but important collagenopathy.

Mengiste, A.A.; Wilson, R.H.; Weissman, R.F.; Papa, L.J. III; Hendel, S.J.; Moore, C.L.; Butty, V.L.; **Shoulders, M.D.*** “Expanded MutaT7 Toolkit Efficiently and Simultaneously Accesses All Possible Transition Mutations in Bacteria” *Nucleic Acids Research* **51**, e31 (2023).

- Development, optimization, and application of highly efficient MutaT7^{A→G} constructs, working in tandem with the original MutaT7^{C→T} to enable targeted hypermutagenesis *in vivo*.

Yoon, J.; Nekongo, E.E.; Patrick, J.E.; Hui, T.; Phillips, A.M.; Ponomarenko, A.I.; Hendel, S.J.; Sebastian, R.M.; Zhang, Y.M.; Butty, V.L.; Ogbunugafor, C.B.; Lin, Y.-S.; **Shoulders, M.D.*** “The Endoplasmic Reticulum Proteostasis Network Profoundly Shapes the Protein Sequence Space Accessible to HIV Envelope” *PLoS Biology* **20**, e3001569 (2022).

- Chemical regulation of the XBP1s and ATF6 arms of the unfolded protein response reveals that the ER proteostasis network broadly restricts HIV-1 envelope mutational tolerance.

King, D.T.; Serrano-Negrón, J.E.; Zhu, Y.; Moon, K.-M.; Moore, C.L.; **Shoulders, M.D.**; Foster, L.J.; Vocadlo, D.J.* “Thermal Proteome Profiling Reveals the O-GlcNAc-Dependent Meltome” *Journal of the American Chemical Society* **144**, 3833–3842 (2022).

- O-GlcNAc modifications destabilize a major subset of the modified proteome, serving as a bi-directional regulator of proteome stability. The work relies on techniques for HSF1 inhibition.

Choudhury, A.; Ratna, A.; Lim, A.; Sebastian, R.M.; Moore, C.L.; Filliol, A.A.; Bledsoe, J.; Dai, C.; Schwabe, R.F.; **Shoulders, M.D.**; Mandrekar, P.* “Loss of Heat Shock Factor 1 Promotes Hepatic Stellate Cell Activation and Drives Liver Fibrosis” *Hepatology Communications* **6**, 2781–2797 (2022).

- Inhibiting HSF1 exacerbates hepatic stellate cell activation in response to injury and leads to fibrosis, whereas inducing HSF1 activity prevents profibrogenic hepatic stellate cell activation.

Bateman, J.F.*; **Shoulders, M.D.**; Lamandé, S.R. “Collagen Misfolding Mutations: The Contributions of the Unfolded Protein Response to the Molecular Pathology” *Connective Tissue Research* **63**, e2036735 (2022).

- This critical perspective analyzes the collagenopathy literature, with a particular focus on the roles of ER stress in disease and opportunities for therapeutic targeting of stress pathways.

Molina, R.; Rix, G.; Mengiste, A.A.; Alvarez, B.; Seo, D.; Chen, H.; Hurtado, J.; Zhang, Q.; Garcia-Garcia, J.D.; Heins, Z.; Almhjell, P.J.; Arnold, F.H.; Kahlil, A.S.; Hanson, A.; Dueber, J.; Schaffer, D.; Chen, F.; Kim, S.; Fernandez, L.; **Shoulders, M.D.**; Liu, C.* “*In Vivo* Hypermutation and Continuous Evolution” *Nature Reviews Methods Primers* **2**, e36 (2022).

- Comprehensive discussion of state-of-the-art techniques for *in vivo* targeted mutagenesis, including MutaT7, EVOLVR, and Ortho-Rep, alongside detailed protocols for implementation.

Li, R.C.; Wong, M.Y.; DiChiara, A.S.; Hosseini, A.S.; **Shoulders, M.D.*** “Collagen’s Enigmatic, Highly Conserved *N*-Glycan Has an Essential Proteostatic Function” *Proceedings of the National Academy of Sciences, USA* **118**, e2026608118 (2021).

- Proper folding under stressful conditions of the most abundant protein in animals, collagen, relies on the presence of a C-terminal, highly conserved *N*-glycan, solving a decades-old mystery.

Hendel, S.J.; **Shoulders, M.D.*** “Directed Evolution in Mammalian Cells” *Nature Methods* **18**, 346–357 (2021).

- Comprehensive discussion of the emerging field of mammalian cell-based directed evolution, providing a framework for the future of this potentially transformative research field.

Dickinson, B.C.*; **Shoulders, M.D.*** “Molecular Synthetic Biology: From Understanding Life to Creating Smart Therapeutics” *Current Opinion in Chemical Biology* **64**, A1–A2 (2021).

- Editorial overview for co-edited journal issue, framing current issues and accomplishments in the field of molecular synthetic biology.

DiChiara, A.S.; Doan, N.-D.; Bikovtseva, A.A.; Butty, V.L.; Weiss, M.E.; Eyre, D.R.; Lamandé, S.R.; Bateman, J.F.; **Shoulders, M.D.*** “XBP1s-Mediated Endoplasmic Reticulum Proteostasis Network Enhancement Can Selectively Improve Folding and Secretion of an Osteogenesis Imperfecta-Causing Collagen-I Variant” *BioRxiv* (2021). doi: 10.1101/2021.04.15.439909.

- A conceptually distinctive potential approach for treating collagenopathies – leveraging the unfolded protein response to enhance folding and trafficking of disease-causing collagen variants.

Doan, N.-D.; Hosseini, A.S.; Bikovtseva, A.A.; Huang, M.S.; DiChiara, A.S.; Papa, L.J. III; Koller, A.; **Shoulders, M.D.*** “Elucidation of Proteostasis Defects Caused by Osteogenesis Imperfecta Mutations in the Collagen- $\alpha 2(I)$ C-Propeptide Domain” *Journal of Biological Chemistry* **295**, 9959–9973 (2020).

- Osteogenesis imperfecta-causing mutant collagens are retained by quality control and directed to ER-associated degradation, independent of the presence or absence of a triple-helical domain.

Nekongo, E.E.; Ponomarenko, A.I.; Dewal, M.B.; Butty, V.L.; Browne, E.P.; **Shoulders, M.D.*** “HSF1 Activation Can Restrict HIV Replication” *ACS Infectious Diseases* **6**, 1659–1666 (2020).

- Chemical control of heat shock factor-1 reveals that the host’s heat shock response inhibits production of infectious HIV virions and that the virus cannot easily escape such restriction.

Kung, L.H.W.; Sampurno, L.; Yammine, K.M.; Graham, A.; McDonald, P.; Bateman, J.F.*; **Shoulders, M.D.***; Lamandé, S.R. “CRISPR/Cas9 Editing to Generate a Heterozygous COL2A1 p.G1170S Human Chondrodysplasia iPSC Line, MCRli019-A-2, in a Control iPSC Line, MCRli019-A” *Stem Cell Research* **48**, e101962 (2020). * = **Co-Corresponding Authors**.

- Development of the first cell-based system to model the genetics of precocious osteoarthritis, an understudied but important collagenopathy.

Sebastian, R.M.; **Shoulders, M.D.*** “Chemical Biology Framework to Illuminate Proteostasis” *Annual Review of Biochemistry* **89**, 529–555 (2020).

- This review presents a comprehensive experimental framework for applying the methods of chemical biology to the problem of how cells solve protein folding challenges.

Liebelt, F.; Sebastian, R.M.; Moore, C.L.; Mulders, M.P.C.; Ovaa, H.; **Shoulders, M.D.***; Vertegaal, A.C.O.* “SUMOylation and Proteostasis Networks Converge to Minimize Aggregation and Promote Degradation in Response to Heat Shock” *Cell Reports* **26**, 236–249 (2019). * = **Co-Corresponding Authors**.

- Stress-induced enhancements in SUMOylation inhibit toxic protein aggregation and increase misfolded protein clearance until chaperones can be upregulated to restore proteostasis.

Wong, M.Y.; **Shoulders, M.D.*** “Targeting Defective Proteostasis in the Collagenopathies” *Current Opinion in Chemical Biology* **50**, 80–88 (2019).

- Review of the latest advances in collagen biochemistry argues for resculpting the ER proteostasis network as a viable strategy for next-generation therapies for the collagenopathies.

Doan, N.-D.; DiChiara, A.S.; Del Rosario, A.M.; Schiavoni, R.P.; **Shoulders, M.D.*** “Mass Spectrometry-Based Proteomics to Define Intracellular Collagen Interactomes” *Methods in Molecular Biology* **1944**, 95–114 (2019).

- Design, optimization, and application of strategies for collagen cloning/modification, collagen-producing cell line engineering, and immunoprecipitation-based interactome determination.

Papa, L.J. III; **Shoulders, M.D.*** “Genetic Engineering by DNA Recombineering” *Current Protocols in Chemical Biology* **11**, e70 (2019).

- Methodology for the rapid, straightforward, and robust genetic engineering of very large DNA sequences using advanced molecular biology strategies.

Wong, M.Y.; Chen, K.; Antonopoulos, A.; Kasper, B.T.; Dewal, M.B.; Taylor, R.J.; Whittaker, C.A.; Hein, P.P.; Dell, A.; Genereux, J.C.; Haslam, S.M.*; Mahal, L.K.*; **Shoulders, M.D.*** “XBP1s Activation Can Globally Remodel N-Glycan Structure Distribution Patterns” *Proceedings of the National Academy of Sciences, USA* **115**, E10089–E10098 (2018).

- Discovery that the IRE1-XBP1s axis of the unfolded protein response not only regulates proteostasis but also defines the molecular architecture of the cellular N-glycome.

Phillips, A.M.; Doud, M.B.; Gonzalez, L.O.; Butty, V.L.; Lin, Y.-S.; Bloom, J.D.; **Shoulders, M.D.*** “Enhanced ER Proteostasis and Temperature Differentially Impact the Mutational Tolerance of Influenza Hemagglutinin” *eLife* **7**, e38795 (2018).

- Demonstration that ER chaperones critically define the mutational pathways accessible to an evolving membrane protein, remarkably in precisely the opposite direction of higher temperature.

Phillips, A.M.; Ponomarenko, A.I.; Chen, K.; Ashenberg, O.; Miao, J.; McHugh, S.M.; Butty, V.L.; Whittaker, C.A.; Moore, C.L.; Bloom, J.D.; Lin, Y.-S.; **Shoulders, M.D.*** “Destabilized Influenza Variants Critical for Innate Immune System Escape are Potentiated by Host Chaperones” *PLoS Biology* **16**, e3000008 (2018).

- Destabilizing variants in influenza nucleoprotein required to escape the human host’s innate immune system are made possible by hijacking host chaperones to assist nucleoprotein folding.

DiChiara, A.S.; Li, R.C.; Suen, P.H.; Weickhardt, A.F.; Taylor, R.J.; Malhotra, D.; McCaslin, D.R.; **Shoulders, M.D.*** “A Cysteine-Based Molecular Code Informs Collagen C-Propeptide Assembly” *Nature Communications* **9**, e4206 (2018).

- The presence or absence of a single sulfur atom in the 30 kDa collagen C-propeptide domain controls the ability (or lack of ability) of fibrillar collagens to stably homotrimerize.

Richardson, C.E.R.; Nolan, E.M.; **Shoulders, M.D.***; Lippard, S.J.* “A Sensitive, Non-Radioactive Assay for Zn(II) Uptake into Metazoan Cells” *Biochemistry* **57**, 6807–6815 (2018). * = **Co-Corresponding Authors.**

- Application of the A12-resin for highly selective Zn(II) depletion from biological media, which was invented by us, to enable an efficient new strategy for quantifying cellular Zn(II) trafficking.

Wong, M.Y.; DiChiara, A.S.; Papa, L.J. III; Cheah, J.H.; Soule, C.K.; Hulleman, J.D.; **Shoulders, M.D.*** “A High-Throughput Assay for Collagen Secretion Reveals an Unanticipated Role for Hsp90 in Collagen Production” *Biochemistry* **57**, 2814–2827 (2018).

- The first high-throughput screen for small molecules that modulate collagen secretion leads to discovery of a surprising and highly selective function for cytosolic Hsp90 in collagen production.

Cole, K.S.; Grandjean, J.M.D.; Chen, K.; Witt, C.H.; O’Day, J.; **Shoulders, M.D.**; Wiseman, R.L.; Weerapana, E.* “Characterization of an A-Site Selective Protein Disulfide Isomerase A1 Inhibitor” *Biochemistry* **57**, 2035–2043 (2018).

- An A-site selective protein disulfide isomerase inhibitor selectively activates the IRE1 arm of the unfolded protein response and reduces secretion of amyloidogenic antibody light chains.

Berman, C.M.; Papa, L.J. III; Hendel, S.J.; Moore, C.L.; Suen, P.H.; Weickhardt, A.F.; Doan, N.-D.; Kumar, C.S.; Uil, T.G.; Butty, V.L.; Hoeben, R.C.; **Shoulders, M.D.*** “An Adaptable Platform for Directed Evolution in Human Cells” *Journal of the American Chemical Society* **140**, 18093–18103 (2018).

- Development of the first human cell-based platform for continuous directed evolution, opening doors to new types of human evolutionary biology and biotechnology experiments.

Moore, C.L.; Papa, L.J. III; **Shoulders, M.D.*** “A Processive Protein Chimera Introduces Mutations across Defined DNA Regions *In Vivo*” *Journal of the American Chemical Society* **140**, 2413–2416 (2018).

- Introduction of the MutaT7 chimera, a protein capable of delivering mutations to precisely controlled DNA stretches of any desired length to enable rapid evolution in living systems.

Richardson, C.E.R.; Cunden, L.S.; Butty, V.L.; Nolan, E.M.; Lippard, S.J.*; **Shoulders, M.D.*** “A Method for Selective Depletion of Zn(II) Ions from Complex Biological Media and Evaluation of Cellular Consequences of Zn(II) Deficiency” *Journal of the American Chemical Society* **140**, 2413–2416 (2018).

- Development of the A12-resin for highly specific removal of Zn(II) from diverse and complex biological fluids opens the door to precision studies of biological roles of Zn(II).

Wong, M.Y.; DiChiara, A.S.; Suen, P.H.; Chen, K.; Doan, N.-D.; **Shoulders, M.D.*** “Adapting Secretory Proteostasis and Function Through the Unfolded Protein Response” *Current Topics in Microbiology and Immunology* **414**, 1–25 (2018).

- This review highlights advances in our understanding of the unfolded protein response (UPR), with a focus on potential therapeutic opportunities associated with UPR modulation.

Phillips, A.M.; Gonzalez, L.O.; Nekongo, E.E.; Ponomarenko, A.I.; McHugh, S.M.; Butty, V.L.; Levine, S.S.; Lin, Y.-S.; Mirny, L.A.; **Shoulders, M.D.*** “Host Proteostasis Modulates Influenza Evolution” *eLife* **6**, e28652 (2017).

- Discovery that chaperone and quality control mechanisms in the host cell’s cytosolic proteostasis network are critical determinants of the mutational landscape accessible to influenza.

Maji, B.; Moore, C.L.; Zetsche, B.; Zhang, F.; **Shoulders, M.D.***; Choudhary, A.* “Multidimensional Chemical Control of CRISPR-Cas9” *Nature Chemical Biology* **13**, 9–11 (2017). * = **Co-
Corresponding Authors.**

- Development of the first method for small molecule-mediated control of Cas9 to confer doseable and rapidly reversible control of orthogonal genome targeting and editing specificity.

DiChiara, A.S.; Taylor, R.J.; Wong, M.Y.; Doan, N.-D.; Del Rosario, A.; **Shoulders, M.D.*** “Mapping and Exploring the Collagen-I Proteostasis Network” *ACS Chemical Biology* **11**, 1408–1421 (2016).

- Platform for biochemical studies of collagen-I production by human cells enables elucidation of the collagen-I interactome with key implications for the biochemistry of collagen-I production.

Moore, C.L.; Dewal, M.B.; Nekongo, E.E.; Santiago, S.; Lu, N.B.; Levine, S.S.; **Shoulders, M.D.*** “Transportable, Chemical Genetic Methodology for the Small Molecule-Mediated Inhibition of Heat Shock Factor 1” *ACS Chemical Biology* **11**, 200–210 (2016).

- Development and application of methodology to inducibly and selectively repress the cytosolic proteostasis network reveals mechanistic roles of heat shock factor 1 in protein (mis) folding.

Phillips, A.M.; **Shoulders, M.D.*** “The Path of Least Resistance: Mechanisms to Reduce Influenza’s Sensitivity to Oseltamivir” *Journal of Molecular Biology* **428**, 533–537 (2016).

- Commentary on evolutionary biology and structural approaches to delineate mechanisms of influenza drug resistance, including discussion of key insights and perspective on future goals.

Dewal, M.B.; DiChiara, A.S.; Antonopoulos, A.; Taylor, R.J.; Harmon, C.J.; Haslam, S.M.; Dell, A.; **Shoulders, M.D.*** “XBP1s Links the Unfolded Protein Response to the Molecular Architecture of Mature *N*-Glycans” *Chemistry and Biology* **22**, 1301–1312 (2015).

- Discovery that stress signaling via the unfolded protein response is a fundamental mechanism employed by cells to regulate protein *N*-glycosylation.

Choudhary, A. §; Kamer, K.J. §; **Shoulders, M.D.** §; Raines, R.T.* “4-Ketoproline: An Electrophilic Proline Analog for Bioconjugation” *Biopolymers: Peptide Science* **104**, 110–115 (2015). §**Co-First Authors.**

- In an approach readily extended to a variety of other proteins and peptides, incorporation of 4-ketoproline in collagen permits non-destabilizing, covalent functionalization by nucleophiles.

Genereux, J.C.; Qu, S.; Zhou, M.; Ryno, L.M.; Wang, S.; **Shoulders, M.D.**; Kaufman, R.J.; Lasmézas, C.I.; Kelly, J.W.; Wiseman, R.L.* “Unfolded Protein Response-Induced ERdj3 Secretion Links Endoplasmic Reticulum Stress to Extracellular Proteostasis” *EMBO Journal* **34**, 4–19 (2015).

- Identification of the first stress-induced secreted chaperone, revealing a direct link between unfolded protein response activation and the adaptation of extracellular proteostasis.

Chen, J.J.; Genereux, J.C.; Hulleman, J.D.; **Shoulders, M.D.**; Wiseman, R.L.* “ATF6 Activation Reduces the Secretion and Extracellular Aggregation of Destabilized Variants of an Amyloidogenic Protein” *Chemistry and Biology* **21**, 1564–1574 (2014).

- ATF6 activation enhances quality control stringency and shuttles destabilized transthyretin variants to degradation, thereby preventing secretion and subsequent amyloidogenesis.

Ryno, L.M.; Genereux, J.C.; Naito, T.; Morimoto, R.I.; Powers, E.T.; **Shoulders, M.D.**; Wiseman, R.L.* “Characterizing the Altered Cellular Proteome Induced by the Stress-Independent Activation of Heat Shock Factor I” *ACS Chemical Biology* **9**, 1273–1283 (2014).

- Application of RNA-seq and quantitative proteomics to establish how the cytosolic protein folding environment is modified by heat shock factor I activation.

Shoulders, M.D.[§]; Ryno, L.M.[§]; Cooley, C.B.; Kelly, J.W.; Wiseman, R.L.* "Broadly Applicable Methodology for the Doseable, Rapid, and Small Molecule-Mediated Regulation of Transcription Factors in Human Cells" *Journal of the American Chemical Society* **135**, 8129–8132 (2013). [§]Co-First Authors.

- Development of chemical biology methodology to potentially control the activity of any transcription factor of interest within the physiologically relevant regime in any cell model system.

Shoulders, M.D.; Ryno, L.M.; Genereux, J.C.; Moresco, J.J.; Tu, P.G.; Wu, C.; Yates, J.R. III; Su, A.I.; Kelly, J.W.; Wiseman, R.L.* "Stress-Independent Activation of XBP1s and/or ATF6 Reveals Three Functionally Diverse ER Proteostasis Environments" *Cell Reports* **3**, 1279–1292 (2013).

- Proof-of-principle for a general approach to treat diverse protein misfolding-related diseases by adapting the cell's proteostasis network via selective activation of stress responses.

Krow, G.R.*; **Shoulders, M.D.**; Edupuganti, R.; Gandla, D.; Yu, F.; Sonnet, P.E.; Sender, M.; Choudhary, A.; DeBrosse, C.; Ross, C.W. III; Carroll, P.; Raines, R.T.* "Synthesis of 5-Fluoro- and 5-Hydroxymethanopyrrolines via Lithiation of *N*-BOC-Methanopyrrolidines. Constrained C^γ-Exo and C^γ-Endo Flp and Hyp Conformer Mimics" *Journal of Organic Chemistry* **77**, 5331–5344 (2012).

- Detailed physical organic analyses reveal that proline ring pucker must not be assigned based solely on cis:trans amide preferences.

Krow, G.R.*; Edupuganti, R.; Gandla, D.; Yu, F.; Sender, M.; Sonnet, P.E.; Zdilla, M.J.; DeBrosse, C.; Cannon, K.C.; Ross, C.W. III; Choudhary, A.; **Shoulders, M.D.**; Raines, R.T.* "Synthesis of Conformationally Constrained 5-Fluoro- and 5-Hydroxymethanopyrrolidines. Ring Puckered Mimics of *Gauche* and *Anti*-3-Fluoro- and 3-Hydroxypyrrrolidines" *Journal of Organic Chemistry* **76**, 3626–3634 (2011).

- Establishment of baseline amide preferences to enable determination of the contributions of α -ester substituents to cis:trans amide ratios in the methanopyrrolines.

Shoulders, M.D.; Raines, R.T.* "Interstrand Dipole–Dipole Interactions Can Stabilize the Collagen Triple Helix" *Journal of Biological Chemistry* **286**, 22905–22912 (2011).

- Electrostatic interactions rescue the stability of triple helices with amino acid sequences expected to be destabilizing, providing a new framework to understand collagen stability.

Shoulders, M.D.; Kotch F.W.; Choudhary, A.; Guzei, I.A.; Raines, R.T.* "The Aberrance of the 4S Diastereomer of 4-Hydroxyproline" *Journal of the American Chemical Society*, **132**, 10857–10865 (2010).

- Hydrogen bonding can compromise the benefits of an underlying stereoelectronic effect for protein conformational stability.

Shoulders, M.D.; Satyshur, K.A.; Forest, K.T.; Raines, R.T.* "Stereoelectronic and Steric Effects in Side Chains Preorganize a Protein Main Chain" *Proceedings of the National Academy of Sciences, USA* **107**, 559–564 (2010).

- Peptide backbone conformational preorganization via subtle modifications to amino acid side chains can confer extraordinary stability upon proteins without perturbing their structure.

Krow, G.R.*; Liu, N.; Sender, M.; Lin, G.; Centafont, R.; Sonnet, P.E.; DeBrosse, C.; Ross, C.W. III; Carroll, P.J.; **Shoulders, M.D.**; Raines, R.T.* "Oligomers of a 5-Carboxymethanopyrrolidine β -Amino Acid—A Search for Order" *Organic Letters* **12**, 5438–5441 (2010).

- The highly constrained β -amino acid (1*S*,4*R*,5*R*)-5-syn-carboxy-2-azabicyclo[2.1.1]hexane enables the preparation of well-defined peptide foldamers in the absence of hydrogen bonds.

Shoulders, M.D.; Kamer, K.J.; Raines, R.T.* "Origin of the Stability Conferred upon Collagen by Fluorination" *Bioorganic and Medicinal Chemistry Letters* **19**, 3859–3862 (2009).

- (2*S*,4*R*)-4-Fluoroproline stabilizes collagen triple helices by a mechanism distinct from the hydrophobic effect.

Shoulders, M.D.; Raines, R.T.* "Collagen Structure and Stability" *Annual Review of Biochemistry* **78**, 929–958 (2009).

- Comprehensive and highly cited review of current knowledge regarding the physicochemical basis of collagen structure and stability and the preparation of synthetic collagen mimetics.

Shoulders, M.D.; Raines, R.T.* “Modulating Collagen Triple-Helix Stability with 4-Chloro, 4-Fluoro, and 4-Methylprolines” *Advances in Experimental Medicine and Biology* **611**, 251–252 (2009).

- Rational application of steric and stereoelectronic effects enables the preparation of synthetic collagen mimetics with predictable thermal stability over a >50 °C range.

Shoulders, M.D.; Guzei, I.A.; Raines, R.T.* “4-Chloroproline: Synthesis, Conformational Analysis, and Effect on the Collagen Triple Helix” *Biopolymers* **89**, 443–454 (2008).

- Conclusive demonstration that deleterious steric interactions can overwhelm favorable stereoelectronic effects on triple-helix stability.

Shoulders, M.D.; Hodges, J.A.; Raines, R.T.* “Reciprocity of Steric and Stereoelectronic Effects in the Collagen Triple Helix” *Journal of the American Chemical Society* **128**, 8112–8113 (2006).

- Fundamental interplay between steric and stereoelectronic effects in proteins provides a new means to modulate the conformational stability of both natural and synthetic proteins.

PATENTS AND PATENT APPLICATIONS

Shoulders, M.D.; Wilson, R.H.; Zhao, Y. “Efficient Purification of Ribulose-1,5-Bisphosphate Carboxylase/Oxygenase (RuBisCO) from Complex Cellular Material Using Liquid-Liquid Phase Separation” **November 1, 2024**, US Patent Application No. 63/715,169.

Shoulders, M.D.; Berman, C.; Papa, L.J. III; Hendel, S.J.; Moore, C.L. “Methods and Compositions for Performing Continuous Directed Evolution” **Aug. 16, 2022**, U.S. Patent No. 11,414,677.

Shoulders, M.D.; Lippard, S.J.; Nolan, E.M.; Richardson, C.E.R.; Cunden, L.S. “Compositions and Methods for Selectively Sequestering Metal Ions” **March 16, 2021**, U.S. Patent No. 10,946,361.

Raines, R.T.; **Shoulders, M.D.;** Hodges, J.A. “Collagen Mimics” **June 25, 2019**, U.S. Patent No. 10,329,341.

Raines, R.T.; **Shoulders, M.D.;** Hodges, J.A. “Collagen Mimics” **Sept. 12, 2017**, U.S. Patent No. 9,758,569.

SELECTED PRESENTATIONS

“Protein Folding and Evolution” Hirschmann Lecturer at the Oberlin College Department of Chemistry and Biochemistry, Oberlin, OH, 2025.

“Mechanisms of Procollagen Folding and Assembly” Invited Talk at the Collagen Gordon Research Conference, New London, New Hampshire, 2025.

“Directed Evolution in Mammalian Cells” Invited Seminar at the Evolution by Nature and by Design Symposium at the École Polytechnique Fédérale de Lausanne Institute of Chemical Sciences and Engineering, Lausanne, Switzerland, 2025.

“Illuminating and Leveraging Protein Evolution” Invited Talk at the Ono Pharma Foundation Symposium, Cambridge, MA, 2025.

Convocation Address at the Virginia Tech Department of Chemistry Commencement Ceremony, Blacksburg, VA, 2025.

“EPIc: Enhanced Photosynthesis in Crops” Invited Lecture at the Abdul Latif Jameel Water & Food Systems Laboratory 10th Anniversary Event, Massachusetts Institute of Technology, Cambridge, MA, 2025.

“Proteostasis, Evolution, and Viruses” Genentech Lecturer at the University of Illinois–Urbana-Champaign Department of Chemistry, Urbana-Champaign, IL, 2025.

“Chaperonin Compatibility, RuBisCO Biogenesis and Novel Carboxylation Catalysis” at the 42nd Eastern Regional Photosynthesis Conference, Woods Hole, MA, 2025.

“Factors that Define the Molecular Architecture of the *N*-Glycome” Invited Talk at the MIT-Imperial Seed Fund 10th Anniversary Event, Massachusetts Institute of Technology, Cambridge, MA (Webinar).

“Proteostasis and Evolution” Invited Seminar at the Institute of Physico-Chemical Biology, Paris, France, 2025.

“Enabling Directed Evolution in Complex Living Systems” Invited Seminar at Academia Sinica Institute of Chemistry, Taipei, Taiwan, 2025.

“Collagen Folding and Assembly in the Secretory Pathway” Invited Seminar at the University of Wisconsin–Milwaukee Department of Biological Sciences, Milwaukee, WI, 2025.

“Proteostasis and Evolution” Invited Seminar at the Australian National University School of Biology, Canberra, Australia, 2025.

“Collagen Proteostasis” Invited Seminar at Simon Fraser University Department of Molecular Biology and Biochemistry, Burnaby, British Columbia, CA, 2024.

“EpiC: Towards Enhanced Photosynthesis in Crops” Invited Seminar at the Annual Meeting of the MIT Corporation Development Committee, Cambridge, MA, 2024.

“Collagen Proteostasis in Health and Disease” Invited Seminar at the University of New Mexico Department of Chemistry and Chemical Biology, Albuquerque, NM, 2024.

“Enabling Directed Evolution in Complex Living Systems” Invited Seminar at the University of Rochester Department of Chemistry, Rochester, NY, 2024.

“EpiC: Towards Enhanced Photosynthesis in Crops” Invited Seminar at the MIT J-WAFS MIT Alumni Association Meeting, Cambridge, MA, 2024.

“Collagen Proteostasis in Health and Disease” Invited Seminar at the University of Wyoming Department of Molecular Biology, Laramie, WY, 2024.

“Continuous Directed Evolution in Living Systems” Invited Seminar at the École Polytechnique Fédérale de Lausanne Institute of Chemical Sciences and Engineering, Lausanne, Switzerland, 2023.

“Collagen Glycoproteostasis” Keynote Lecture at the Annual Meeting of the Society for Glycobiology, Waikoloa Village, HI, 2023.

“Collagen Proteostasis in Health and Disease” Invited Seminar at the University of Geneva Department of Molecular and Cellular Biology, Geneva, Switzerland, 2023.

“Viral Evolution, Protein Folding, and Host Chaperones” Invited Seminar at the National Taiwan University Department of Chemistry, Taipei, Taiwan, 2023.

“Collagen Proteostasis in Health and Disease” Invited Seminar at the Proteostasis Consortium Seminar Series (Virtual), 2023.

“Chaperones and Protein Evolution” Enhancing Photosynthesis in Crops Workshop, Massachusetts Institute of Technology, Cambridge, MA, 2023.

“Do We Help Viruses Evolve?” Invited Seminar at the Indian Institute for Science Education and Research, Bhopal, India, 2023.

“Folding and Evolving Disulfide-Containing ER Client Proteins” Keynote Lecture at the University of Vermont Redox Biology Retreat, Burlington, VT, 2023.

“Enabling Continuous Directed Evolution in Complex Systems” Invited Seminar at the ETH Zürich Department of Biosystems Science and Engineering, Basel, Switzerland, 2023.

“Proteostasis and Mutational Change” Invited Seminar at the Northwestern University Department of Biochemistry and Molecular Genetics, Chicago, IL, 2023.

“*N*-Glycosylation: The Fulcrum of Collagen Proteostasis” Invited Seminar at the GlycoMIT Symposium, Cambridge, MA 2023.

“Proteostasis, Biotechnology, and Cancer” Invited Seminar at the Koch Institute for Integrative Cancer Research, Cambridge, MA 2023.

“Host Proteostasis and Viral Evolution” Invited Seminar at the 2022 National Science Foundation Molecular and Cellular Biosciences CAREER Awardee Conference, Alexandria, VA, 2022.

“Host Proteostasis and Viral Evolution” Invited Seminar at the University of Rhode Island Department of Chemistry, Providence, RI, 2022.

“Viral Evolution and Proteostasis” Moses Gomberg Seminar at the University of Michigan Department of Chemistry, Ann Arbor, MI, 2022.

“Viral Evolution and Proteostasis” Invited MORE seminar at California State–Los Angeles (Virtual), 2022.

“Integrating Chemical Genetics and Evolution to Illuminate Proteostasis” Invited seminar at PacifiChem, 2021.

“Cysteines and Disulfide Bonds in Collagen Folding and Misfolding” Invited Seminar at the Functional Disulfides in Health and Disease Conference, Weizmann Institute of Science, 2021.

“Host Chaperones and Viral Evolution” Student-Invited Seminar at the University of Georgia Department of Biochemistry and Molecular Biology, Athens, Georgia, 2020.

“Continuous Directed Evolution in Mammalian Cells” Invited Seminar at the 259th National Meeting of the American Chemical Society, 2020.

“Understanding and Sculpting Collagen Proteostasis” Invited Seminar at Ardelyx, Inc. Fremont, CA, 2020.

“Proteostasis, Evolution, and Pathogens” Invited Seminar at the Case Western Reserve University Department of Physiology and Biophysics, Cleveland, OH, 2020.

“Roads to Academia” Invited Talk at the Massachusetts Institute of Technology Graduate Student Council, Cambridge, MA, 2020.

“Chaperoning Evolution” Invited Seminar at the Boston College Department of Chemistry, Chestnut Hill, MA, 2019.

“The Unfolded Protein Response, XBP1s, and the Molecular Architecture of the *N*-Glycome” Invited Seminar at the Boston Glycobiology Discussion Group, Cambridge, MA, 2019.

“Viruses, Proteostasis, and Immune System Escape” Invited Seminar at the Broad Institute Infectious Disease & Microbiome Program Meeting, Cambridge, MA, 2019.

“Molecular Code for Intracellular Collagen Assembly” Invited Seminar ANYL-24 at the 257th National Meeting of the American Chemical Society, San Diego, CA, 2019.

“Cysteine Code for Collagen Assembly” Invited Seminar at the RTR-60 Symposium, Broad Institute, Cambridge, MA, 2019.

“XBP1s and the Molecular Architecture of the *N*-Glycome” Invited Seminar at the FASEB Endoplasmic Reticulum (ER) Conference: From Unfolded Proteins to Disease, Snowmass Village, CO, 2019.

“Surviving Extreme Mutation Rates to Enable Rapid Adaptation” Invited Keynote Lecture at the 19th Annual PROTEO Symposium, Quebec City, Quebec, Canada, 2019.

“Modulating Host Proteostasis to Restrict Viral Adaptation” Invited Seminar MEDI-236 at the 257th National Meeting of the American Chemical Society, Orlando, FL, 2019.

“Viruses, Proteostasis, and Evolution” Invited Seminar at the Tenure-Track Faculty Lunch, MIT School of Science, Cambridge, MA, 2019.

“Viruses, Proteostasis, and Evolution” Invited Seminar in Molecular and Genomic Medicine at the Harvard University Department of Medicine’s Division of Genetics, Boston, MA 2019.

“Protein Folding, Assembly, and Evolution in Cells” Invited Seminar at Tufts University Department of Chemistry, Medford, MA, 2018.

“Chaperone Hijacking and Viral Evolution” Invited Seminar at The Scripps Research Institute Department of Chemistry, La Jolla, CA, 2018.

“Elucidating Mechanisms of Complex Protein Assembly and Evolution” Invited Seminar at the University of California–Berkeley College of Chemistry, Berkeley, CA, 2018.

“New Strategies to Explore the Interplay Between Proteostasis and Evolution” Invited Seminar BIOL-113 at the 256th National Meeting of the American Chemical Society, Boston, MA, 2018.

“Protein Assembly and Evolution in Cells” Invited Seminar at the National Tsing Hua University Department of Chemistry, Hsinchu City, TW, 2018.

“Proteostasis, Chaperones, and Evolution” Invited Seminar at the Caltech Division of Chemistry and Chemical Engineering, Pasadena, CA, 2018.

“Proteostasis, Chaperones, and Evolution” Invited Seminar at the Northwestern University Department of Molecular Biosciences, Evanston, IL, 2018.

“Solving Complex Problems in Protein Assembly and Evolution” Invited Seminar at the University of California–San Francisco Department of Pharmaceutical Chemistry, San Francisco, CA, 2018.

“Elucidating Mechanisms of Complex Protein Assembly and Evolution” Invited Seminar at the University of California–Santa Barbara Department of Chemistry, Santa Barbara, CA, 2018.

“Elucidating Mechanisms of Complex Protein Assembly and Evolution” Invited Seminar at the University of California–San Diego Department of Chemistry, San Diego, CA, 2018.

“Folding and Evolving Complex Proteins” Invited Seminar at the University of California–Los Angeles Department of Chemistry and Biochemistry, Los Angeles, CA, 2018.

“Proteostasis, Biomolecular Assembly, and Evolution” Invited Seminar at the University of California–Irvine Department of Chemistry, Irvine, CA, 2018.

“Protein Folding, Assembly, and Evolution” Invited Seminar at the Stanford University Department of Chemical and Systems Biology, Palo Alto, CA, 2018.

“Proteostasis, Protein Assembly, and Flu Evolution” Invited Seminar at the Cornell University Department of Chemistry and Chemical Biology, Ithaca, NY, 2018.

“Immune Escape by the 1918 Flu Relies on Host Chaperones and the Heat Shock Response” Seminar at the CSHL Protein Homeostasis in Health and Disease Meeting, Cold Spring Harbor, NY, 2018.

“Protein Folding Challenges in Biomolecule Assembly and Evolution” Invited Seminar at the New York University Department of Chemistry, New York, NY, 2018.

“Proteostasis, Biomolecule Assembly, and Evolution” Invited Seminar at the University of Pennsylvania Department of Chemistry, Philadelphia, PA, 2018.

“Host Proteostasis Modulates RNA Virus Evolution” Invited Seminar BIOL-174 at the 255th National Meeting of the American Chemical Society, New Orleans, LA, 2018.

“Protein Folding Challenges in Biomolecule Assembly and Evolution” Invited Seminar at the Princeton University Department of Chemistry, Princeton, NJ, 2018.

“Modulating Proteostasis, Illuminating Evolution” Invited Seminar at the University of Wisconsin Department of Chemistry, Madison, WI, 2018.

“Protein Folding Challenges in Biomolecule Assembly and Evolution” Invited Seminar at the University of Washington Department of Chemistry, Seattle, WA, 2018.

“Protein Folding Challenges in Biomolecule Assembly and Evolution” Invited Seminar at the University of Massachusetts Institute for Applied Life Sciences, Amherst, MA, 2018.

“Understanding Proteostasis, Illuminating Evolution” Invited Seminar at the Yale University Chemical Biology Institute, New Haven, CT, 2018.

“Viral Evolution, the 1918 Spanish Flu, and the Chemical Biology of Proteostasis” Invited Seminar at the University of Southern California Department of Chemistry, Los Angeles, CA, 2018.

“Manipulating Proteostasis, Illuminating Evolution” Invited Seminar at Simon Fraser University Department of Molecular Biology and Biochemistry, Burnaby, British Columbia, CA, 2018

“Host Proteostasis, Viral Evolution, and the 1918 Spanish Flu” Invited Seminar at The Scripps Research Institute Department of Chemistry, Jupiter, FL, 2018.

“Host Proteostasis Modulates Influenza Evolution” Invited Seminar at the Indiana University Department of Chemistry, Bloomington, IN, 2017.

“Proteostasis and the Collagenous Extracellular Matrix” Invited Seminar at the University of Nebraska Department of Chemistry, Lincoln, NE, 2017.

“Protein Folding in Health and Disease” Invited Seminar at the Creighton University Department of Chemistry, Omaha, NE, 2017.

“Host Proteostasis Modulates Influenza Evolution” Invited Seminar at the University of Vermont Department of Biology, Burlington, VT, 2017.

“Host Proteostasis Modulates RNA Virus Evolution” Invited Seminar at the Oxford University Ludwig Center for Cancer Research, Oxford, United Kingdom, 2017.

“Proteostasis and RNA Virus Evolution” Invited Seminar at the Imperial College–London Department of Life Sciences, London, United Kingdom, 2017.

“Proteostasis and Viral Evolution” Invited Seminar at Cambridge University Institute for Medical Research, Cambridge, United Kingdom, 2017.

“Stress, Glycomics, and Disease – A Combined Perspective” Invited Seminar at the Society for Glycobiology Meeting, Portland, OR, 2017.

“ER Proteostasis Network Remodeling Synergizes with Enhanced Quality Control to Resolve Disease-Causing Collagen Secretion Defects” Seminar at the FASEB From Unfolded Proteins in the ER to Disease Conference, Saxton’s River, VT, 2017.

“Manipulating and Probing Proteostasis in Health and Disease” Invited Seminar at the University of Melbourne Murdoch Childrens Research Institute, Melbourne, Australia, 2017.

“Folding and Quality Control Mechanisms of Collagen” Invited Seminar at the 3rd Annual Meeting of the Biophysical Society of Canada, Montreal, Quebec, Canada, 2017.

“Multidimensional Chemical Control of CRISPR-Cas9” Invited Seminar at CPhI North America, Philadelphia, PA, 2017.

“Identifying and Ameliorating Collagen Misfolding Defects” Seminar 6227 at the National Meeting of the American Society of Biochemistry and Molecular Biology, Chicago, IL, 2017.

“Manipulating and Probing Proteostasis in Complex Biological Systems” Invited Seminar at the Penn State University Department of Chemistry, State College, PA, 2017.

“Chemical Biology Strategies Illuminating How the Proteostasis Network Modulates Evolutionary Excursions in Sequence Space by RNA Viruses” Seminar BIOL-174 at the 253rd National Meeting of the American Chemical Society, San Francisco, CA, 2017.

“Modulating and Elucidating Metazoan Proteostasis in Health and Disease” Invited Seminar at the Virginia Tech Department of Chemistry, Blacksburg, VA, 2017.

“Development and Application of Small Molecule Methods for Precision Control of Cellular Proteostasis” Invited Seminar at the MIT Center for Environmental Health Sciences External Advisory Board Meeting, Cambridge, MA, 2017.

“Making Better Bone” Seminar at the FASEB Protein Folding in the Cell Conference, Saxton’s River, VT, 2016.

“Folding and Quality Controlling Nascent Collagen” Invited seminar at Harvard University School of Dental Medicine, Boston, MA, 2016.

“Making Bone: Solving Complex Protein Folding Problems in the Endoplasmic Reticulum” Invited seminar at the University of Massachusetts Medical School, Worcester, MA, 2016.

“Protein Folding, Quality Control, and Modification in the Secretory Pathway” Invited seminar at The Scripps Research Institute, La Jolla, CA, 2016.

“Application of Chemical Biology Strategies to Probe and Manipulate Proteostasis” Invited seminar BIOL-158 at the 251st National Meeting of the American Chemical Society, San Diego, CA, 2016.

“Molecular Strategies to Delineate Complex Cellular Protein Folding Pathways – The Collagen-I Example” Invited Keynote Lecture at the Quebec & Ontario Mini-Symposium on Bioorganic and Organic Chemistry, Montreal, Quebec, Canada, 2015.

“Viruses, Evolution, and the Proteostasis Network” Invited seminar at Leiden University Medical Center, Leiden, Netherlands, 2015.

“Collagen-I Misfolding-Related Diseases and the Unfolded Protein Response” Invited seminar at the Gordon Research Conference on Collagen, New London, NH, 2015.

“XBP1s Links the Unfolded Protein Response to the Molecular Architecture of the Mature N-Glycome” Poster at the Carbohydrates Gordon Research Conference, Mount Snow, VT, 2015.

“Proteostasis and RNA Viruses” Invited seminar at the Genome Institute of Singapore, Singapore, 2015.

“Hijacking the Host Cell Proteostasis Network to Potentiate RNA Virus Evolution” Invited seminar at Duke-National University of Singapore Graduate Medical School, Singapore, 2015.

“Viral Evolutionary Trajectories Regulated by the Host’s Proteostasis Network” Invited seminar at Harvard Medical School, Boston, MA, 2015.

“Protein Evolution in Eukaryotic Cells” Invited seminar at the Campus for Research Excellence and Technological Enterprise, Singapore, 2014.

“Hijacking Host Chaperones to Potentiate Viral Evolution” Invited seminar at the Broad Institute, Cambridge, MA, 2014.

“Protein Misfolding in the Collagenopathies” Invited seminar at Proteostasis Therapeutics, Cambridge, MA, 2014.

“Hijacking Host Chaperones to Potentiate Influenza Adaptation” Seminar at the Protein Folding and Viral Evolution Meeting, Cambridge, MA, 2014.

“Heavy Metals, Protein Misfolding, and the Human Proteostasis Network” Invited seminar at the NIH/MIT Center for Environmental Health Sciences, Cambridge, MA, 2014.

“Protein Folding and Misfolding in Health and Disease” Invited seminar at the MIT Chemistry Visiting Committee Meeting, Cambridge, MA, 2014.

“Developing a Chemical Biology Toolbox to Regulate Protein Folding in Cells” Invited seminar at the University of Massachusetts Department of Chemistry, Lowell, MA, 2013.

“Defining the Endoplasmic Reticulum Protein Folding Environment to Dictate Trafficking of Amyloidogenic Proteins” Invited seminar at the Mount Holyoke College Department of Chemistry, South Hadley, MA, 2013.

“Small Molecule-Mediated, Rapid and Dosable Control of Transcription Factor Function in Human Cells” Seminar BIOL-0002 at the 243rd National Meeting of the American Chemical Society, San Diego, CA, 2012.

“Deciphering and Dictating Endoplasmic Reticulum Protein Homeostasis” Seminar at the Mesa-Wide ER Stress Association Meeting, Sanford-Burnham Medical Research Institute, La Jolla, CA, 2012.

“Forces that Stabilize the Collagen Triple Helix” Invited seminar MEDI-0006 at the 236th National Meeting of the American Chemical Society, Philadelphia, PA, 2008.

TEACHING AND EDUCATION AT MIT

Course Leadership (Undergraduate and Graduate)

- **Chemistry 5.08 Fundamentals of Chemical Biology:** Capstone course for the joint Chemistry and Biology Major at MIT; SP25.
- **Chemistry 5.111 Principles of Chemical Science:** MIT General Institute Requirement; up to 500 students taught per semester; SP13–15, FA15 & 16, FA18 & 19, SP21, and FA24.
- **Chemistry 5.48 Protein Folding in Health and Disease:** PhD-level course in fundamental and advanced topics related to protein folding, especially in biological settings. Developed the course content and structure; SP23 & 24.
- **Chemistry 5.54 Advances in Chemical Biology:** PhD-level course taught each autumn from 2013–16, 2018–19, and 2021–23; co-developed course content and structure; this class has often been the highest-rated full-term lecture course in the MIT Chemistry Department.
- **Chemistry 5.921 Seminar in Biological Chemistry:** PhD student seminar course associated with departmental chemical biology seminars; FA13–19, SP16–19, FA22–24, SP23, and SP25.
- **Chemistry 5.302 Introduction to Experimental Chemistry:** Laboratory course providing MIT undergraduates a stimulating, hands-on experience with chemical phenomena. Developed the course content and lab manual; Independent Activities Period (IAP)19 & IAP20.

edX MOOC (Massive Online Open Course) Development – an MITx Initiative

- **Chemistry 5.02x General Chemistry-II:** Led the development and implementation of a publicly available, second-semester General Chemistry course for the edX platform (2020–2022).
- **Chemistry 5.01x General Chemistry-I:** Co-led (with Prof. Sylvia Ceyer) the development, roll-out (11/2020), and implementation of a publicly available, first-semester General Chemistry course for the edX platform (2019–2021).

Course Content Creation and Improvement for MIT Residential and edX Courses

- Conceived and led the development and testing, in 2020–2021, of a set of nine **General Chemistry Guided Learning Demonstrations (GLDs)** for use both residentially on the MITx platform and globally on the edX platform. These GLDs bring the lab to the classroom via high-quality video-based experiments integrated with a suite of associated problems. The modules teach key concepts of general chemistry using an active learning-based, online approach. They help to fill the gap in education created by the absence of laboratory experiences linked to MIT’s required first-year chemistry courses.
- Completely revamped the introductory laboratory course **Chemistry 5.302** in 2019–2020, implementing a modernized curriculum providing intentional exposure to the major sub-disciplines of chemistry.
- Conceived and co-led (with Prof. Troy Van Voorhis) the creation of a **Fundamental Chemistry Knowledge Module** delivered on the MITx platform that serves to fill gaps in student understanding of background material required for success in fulfilling MIT’s Chemistry General Institute Requirement. This module, developed in 2016–2017, is now made available each semester to MIT undergraduates taking first-year chemistry courses on-campus. In 2021, led an extensive update and modernization of the module.
- Co-led (with Prof. Troy Van Voorhis) the development of a suite of **MITx problems** and other content to support a publicly available General Chemistry course to be delivered by MIT on the edX platform (2013–2016).

ACTIVE RESEARCH GRANTS

Grantham Foundation for the Protection of the Environment Research Grant “EPIc: Enhanced Photosynthesis in Crops” 2025–2028, \$3,200,000; Role: **Co-Principal Investigator** with Dr. Robert Wilson (Research Scientist at MIT Department of Chemistry)

MIT International Science and Technology Initiatives Global Seed Fund for Collaborative Research “Peptide Inhibitors of TANGO1 as Anti-Fibrotic Therapeutics” 2025–2027, \$28,600 Role: **Co-Principal Investigator** with Prof. Bradley Pentelute (MIT Department of Chemistry)

MIT HEALS Innovator Grant “Elucidating How Proteostasis Networks Enable Oncogene Mutagenesis and Tumor Evolution” 2025–2026, \$300,000 Role: **Co-Principal Investigator** with Profs. Joseph Davis and Francisco Sánchez-Rivera (MIT Department of Biology)

National Institutes of Health / National Institute of Arthritis, Musculoskeletal, and Skin Diseases 1R01AR082995 “Collagen Proteostasis in Health and Disease” 2024–2029, \$3,342,625 Role: **Principal Investigator**

National Science Foundation / Division of Chemistry: Molecular Foundations of Biotechnology Research Grant 2330699 “Continuous Evolution of RNAs with Novel Functions in Mammalian Cells” 2024–2027, \$1,650,000, Role: **Co-Principal Investigator** with Prof. Samie Jaffrey (Weill Medical College of Cornell University)

Ono Pharma Foundation Breakthrough Science Initiatives Award Program “Expanding the PROTACs Paradigm” 2024–2027, \$1,035,000 Role: **Principal Investigator**

MIT Abdul Latif Jameel Water and Food Systems (J-WAFS) Lab Water and Food Grand Challenge Grant “EPIc: Enhanced Photosynthesis in Crops” 2023–2026, \$1,500,000 Role: **Lead Principal Investigator**

National Science Foundation / Division of Molecular and Cellular Biosciences: Systems and Synthetic Biology Cluster EAGER Grant 2244770 “Leveraging Chaperones to Escape the Plant RuBisCO Catalytic Catch-22” 2023–2025, \$300,000 Role: **Principal Investigator**

National Institutes of Health / National Institute of Allergy and Infectious Diseases 1R01AI168166 “Defining the Interplay Between Viral Adaptation and Host Proteostasis” 2022–2027, \$3,030,728 Role: **Principal Investigator**

National Institutes of Health / National Institute of General Medical Sciences’ Maximizing Investigator’s Research Award 1R35GM136354 “Leveraging Next-Generation Directed Evolution Platforms and Chemical Control of Proteostasis to Deliver Robust Biotechnologies and Illuminate Roles of Chaperone Networks in Protein Evolution” 2020–2026, \$1,865,495 Role: **Principal Investigator**

National Science Foundation / Division of Molecular and Cellular Biosciences: Molecular Biophysics Cluster Research Grant 2236194 “Procollagen Assembly” 2022–2025, \$994,050 Role: **Principal Investigator**

COMPLETED RESEARCH AND EDUCATION GRANTS

MIT International Science and Technology Initiatives Global Seed Fund for Collaborative Research “Continuous Directed Evolution of RuBisCO to Improve Photosynthesis” 2023–2025, \$26,300 Role: **Principal Investigator**

Merkin Institute of Transformative Technologies in Healthcare Grant “Directed Evolution of CRISPR-Based Systems in Mammalian Cells” 2022–2025, \$800,000 Role: **Co-Principal Investigator** with Prof. Amit Choudhary (co-PI at Harvard Medical School)

Gift Award “Directed Evolution of Biological Carbon Fixation” 2022–2025, \$1,000,000 Role: **Principal Investigator**

MIT Research Support Committee Grant “The Charles E. Reed Faculty Initiatives Fund” 2022–2025, \$75,000 Role: **Principal Investigator**

MIT International Science and Technology Initiatives MIT-France Seed Fund for Collaborative Research “Unveiling a Central Regulatory Mechanism of Nature’s Most Abundant Enzyme” 2022–2025, \$25,000 Role: **Principal Investigator**

National Institutes of Health / National Institute of Arthritis, Musculoskeletal, and Skin Diseases 1R56AR082995 “Collagen Proteostasis in Health and Disease” 2023–2024, \$225,623 Role: **Principal Investigator**

National Institutes of Health / National Institute of General Medical Sciences’ Maximizing Investigator’s Research Award 1R35GM136354-03S1 “Diversity Supplement” 2022–2024, \$134,564 Role: **Principal Investigator**

John W. Jarve Seed Fund for Science Innovation Grant “New Strategies for *In Vivo* Directed Evolution” 2019–2024, \$200,000 Role: **Principal Investigator**

MIT Deshpande Center Innovation Grant “Continuous Directed Evolution in Mammalian Cells” 2022–2023, \$100,000 Role: **Principal Investigator**

MIT International Science and Technology Initiatives Global Seed Funds for Collaborative Research “The Unfolded Protein Response, Lipid Biology, and Disease” 2020–2023, \$26,000 Role: **Principal Investigator**

American Cancer Society – Ellison Foundation Research Scholar Grant RSG-18-122-01-CSM “New Connections: Stress, Proteostasis, Sugars, and Cancer” 2018–2023, \$792,000 Role: **Principal Investigator**

Camille Dreyfus Teacher-Scholar Award “Molecular Mechanisms of Protein Folding and Evolution in Living Cells” 2018–2023, \$75,000 Role: **Principal Investigator**

National Institutes of Health / National Institute of General Medical Sciences’ Maximizing Investigator’s Research Award 1R35GM136354-02S1 “Equipment Supplement” 2021–2022, \$85,263 Role: **Principal Investigator**

MIT Deshpande Center Ignition Grant “Continuous Directed Evolution in Mammalian Cells” 2021–2022, \$50,000 Role: **Principal Investigator**

National Institutes of Health / National Institute of Arthritis, Musculoskeletal, and Skin Diseases 1R01AR071443 “Defining and Modulating Mechanisms of Collagen Proteostasis” 2017–2022, \$1,701,000 Role: **Principal Investigator**

National Science Foundation / Division of Molecular and Cellular Biosciences Genetic Mechanisms Cluster Grant 1652390 “CAREER: Integrating Chemical Biology Methods and RNA Virus Models to Elucidate How the Metazoan Proteostasis Network Modulates Protein Evolutionary Landscapes” 2017–2022, \$1,034,621 Role: **Principal Investigator**

MIT Alumni Class Funds Grant “Bringing the Lab to the Chemistry GIRs via Guided Learning Demonstrations” 2020–2021, \$50,000 Role: **Principal Investigator**

G. Harold and Leila Y. Mathers Foundation Research Grant “Aging, Proteostasis Collapse, and Osteoarthritis: A New Perspective on an Old Disease” 2018–2021, \$750,000 Role: **Principal Investigator**

National Institutes of Health / Office of the Director’s New Innovator Award 1DP2GM119162 “Continuous Directed Evolution of Biomolecules in Human Cells for Medical Research” 2015–2020, \$2,340,000 Role: **Principal Investigator**

MIT International Science and Technology Initiatives-Imperial College London Seed Funds for Collaborative Research “Factors that Define the Molecular Architecture of the *N*-Glycome” 2017–2020, \$45,000 Role: **Principal Investigator**

National Institutes of Health / National Institute on Alcohol Abuse and Alcoholism 1R01AA025289 “Targeting Proteotoxic Responses in Liver Fibrosis” 2017–2019, \$61,880 (to Shoulders) Role: **Co-Investigator** (PI: Mandrekar, University of Massachusetts Medical School)

MIT Center for Environmental Health Sciences Pilot Grant “Mechanisms of Zinc-Mediated Sensitivity to Cadmium Exposure” 2017–2018, \$34,000 Role: **Principal Investigator**

MIT International Science and Technology Initiatives Global Seed Funds for Collaborative Research “Induced Pluripotent Stem Cells, Proteomics, and the Collagen Misfolding-Related Diseases” 2016–2018, \$26,000 Role: **Principal Investigator**

National Institutes of Health / National Institute on Aging 1R21AG054961 “Aggregate Proximity-Induced, Proteostasis Network-Modulated Destabilization of the Proteome” 2016–2018, \$420,000 Role: **Principal Investigator**

National Institutes of Health / National Institute of Arthritis, Musculoskeletal, and Skin Diseases 1R03AR067503 “Unveiling the Proteostasis Network of Normal and Disease-Causing Collagen-I” 2015–2018, \$234,000 Role: **Principal Investigator**

56th Edward Mallinckrodt Jr. Foundation Faculty Scholar Award “Peering Beyond the Elements of the Central Dogma for the Disease Therapies of Tomorrow” 2013–2017, \$400,000 Role: **Principal Investigator**

d’Arbeloff Fund for Excellence in Education Grant “Leveraging MITx to Deliver Foundational Knowledge Essential for Success in MIT’s Chemistry General Institute Requirement” 2016–2017, \$63,000 Role: **Principal Investigator** (co-PI: Van Voorhis, MIT)

Jeptha H. and Emily V. Wade Award for Creative Research “Irreversible Proteome Dysfunction Triggered by Protein Aggregates” 2016–2017, \$75,000 Role: **Principal Investigator**

Smith Family Foundation Excellence in Biomedical Research Award “Hijacking the Host Cell’s Protein Homeostasis Network to Potentiate Viral Evolution” 2014–2016, \$300,000 Role: **Principal Investigator**

Singapore-MIT Alliance for Research and Technology Phase 2 Grant “Chemical Biology Strategies to Improve the Efficacy, Enhance the Stability, and Reduce the Immunogenicity of Dengue Virus-Targeting Therapeutic Monoclonal Antibodies” 2014–2015, \$230,000 Role: **Principal Investigator**

Mizutani Foundation for Glycoscience Innovation Grant “Protein Homeostasis Network-Mediated Remodeling of the N-Glycoproteome” 2014–2015, \$50,000 Role: **Principal Investigator**

Royal G. and Mae H. Westaway Family Memorial Fund Grant “A Humanized Directed Evolution Platform to Unveil Oncogenic Subversion of the Proteostasis Network” 2014–2015, \$75,000 Role: **Principal Investigator**

MIT Center for Environmental Health Sciences Pilot Grant “Understanding and Ameliorating Arsenic-Induced Protein Misfolding” 2014–2015, \$41,000 Role: **Principal Investigator**

MIT International Science and Technology Initiatives Global Seed Funds for Collaborative Research “Elucidating How Adenoviral Evolution is Enabled by the Host Cell’s Protein Folding Machinery” 2013–2015, \$15,000 Role: **Principal Investigator**

Singapore-MIT Alliance for Research and Technology Phase 1 Grant “Chaperone Hijacking: Influenza Adaptation, Drug Resistance, and the Host’s Proteostasis Network” 2014, \$24,000 Role: **Principal Investigator**

American Cancer Society Postdoctoral Fellowship “Novel Cancer Therapies: Selective Inhibition of Pro-Survival Unfolded Protein Response Signaling” 2010–2012, \$150,000 Role: **Principal Investigator**

MAJOR MENTEE FELLOWSHIPS AWARDED DURING/FOR TENURE IN SHOULDERS LAB

14 National Science Foundation Graduate Research Fellowships (Agata Bikovtseva; Jessica Bonnar; Ra’Mal Harris; Samuel Hendel; Michelle Huang; Rasia Li; Jingting Lin; Christopher Moore; Louis Papa; Angela Phillips; Andrew Sabol; Sorin Srinivasa; Rebecca Taylor; Madeline Wong)

EMBO Postdoctoral Fellowship “Procollagen Folding and Assembly” 2023–2025, \$130,000 Role: **Primary Mentor** to Postdoctoral Fellow Chiara Giannone

National Institutes of Health/NIAMS Ruth L. Kirschstein National Research Service Award Individual Predoctoral Fellowship 1F31AR079263 “Chondronoids for Studying Collagen-II Homeostasis and Diseases” 2021–2024, \$165,700 Role: **Primary Mentor** to PhD Student Kathryn Yammine

Ford Foundation Dissertation Fellowship (Christopher Moore, declined)

Canadian Institutes of Health Research Postdoctoral Fellowship “Understanding and Resolving Dysregulated Collagen-I Proteostasis Linked to Osteogenesis Imperfecta” 2016–2018, \$125,000 Role: **Primary Mentor** to Postdoctoral Fellow Ngoc-Duc Doan

National Institutes of Health/NIAMS Ruth L. Kirschstein National Research Service Award Individual Predoctoral Fellowship 1F31AR067615 “A Novel Approach to Osteogenesis Imperfecta: The Collagen Protein Folding Problem” 2015–2018, \$165,700 Role: **Primary Mentor** to PhD Student Andrew DiChiara

UNCF-Merck Postdoctoral Science Research Fellowship “Elucidating the Influences of the Host’s Proteostasis Network on HIV-1 Evolution and Adaptation” 2015–2017, \$92,000 Role: **Primary Mentor** to Postdoctoral Fellow Emmanuel Nekongo

Prof. Amar G. Bose Research Grant “Novel Self-Healing Biomaterials from the Fibronectin–Collagen Interaction” 2014–2016, \$75,000 Role: **Primary Mentor** to PhD Student Madeline Wong

Fonds de Recherche Santé Québec Postdoctoral Fellowship “Elucidating the Etiologies of Osteogenesis Imperfecta: An Avenue to Mechanism-Based Therapy” 2014–2016, \$90,000 Role: **Primary Mentor** to Postdoctoral Fellow Ngoc-Duc Doan

COMMITTEES, SERVICE, AND AFFILIATIONS

MIT Institute-Wide Service (Selected)

- *Ad hoc* Working Group on the Bioeconomy, Member 2025–present
- Standing Faculty Committee on **Graduate Programs**, Member 2024–present
- Koch Institute for Integrative Cancer Research **Community Council**, Member 2024–present
- Committed to Caring Program **Junior Faculty Mentor**, 2019–2021 & 2024–present
- Standing Institute Committee on the **Assessment of Biohazards & Embryonic Stem Cell Research** Oversight, Member 2013–present
- MIT **HEALS** Innovator and Breakthrough **Grant Review** Committee, Member 2025
- **Provost’s Task Force** on Faculty and Staff **Sexual Misconduct Survey**, Co-Chair 2024–2025
- MIT Abdul Latif Jameel Water and Food Systems Lab **Research Grant Review**, 2023 & 2025
- Standing Institute Committee on **Sexual Misconduct Prevention and Response**, Member 2021–2025
- **Regeneron Prize** Internal Selection Committee, Member 2020–2021 & 2023–2025
- **Founder and Co-Director**, MIT Homeschool Internship Program in Science and Technology, 2015–2025
- MIT International Science and Technology Initiatives **Internal Grant Review**, 2014 & 2018–2025
- **Breakout Session Chair** for MIT **HEALS** Launch, 2024
- Program Planning Committee for **MIT HEALS Launch**, Member 2024
- Koch Institute for Integrative Cancer Research **Graduate Fellowships Program**, Reviewer 2024
- **Faculty Advisor** for the MIT Chapter of the Society for the Advancement of Chicanos/Hispanics and Native Americans in Science (SACNAS), 2023–2024
- **Japan Global Start-Up Campus**: Life Sciences Working Group, Member 2023
- **Japan-MIT Study**, Faculty Participant (Tokyo), 2023
- **MacVicar Faculty Fellows Selection** Committee, Member 2022–2023
- **Faculty Leadership Program**, Participant 2022–2023
- MIT-Netherlands **Seed Funds Selection Board**, Member 2022
- MIT Summer Undergraduate Research Programs **Applications Review**, 2020–2022
- **First-Year Undergraduate Student Advisor**, 2019–2022
- **MIT Undergraduate Admissions**, Reader 2021
- Faculty Mentor, **MIT Postdoctoral Association Mentoring Program**, 2019–2021

- MIT International Science and Technology Initiatives **Global Classroom Fund Selection Board**, Member 2018
- Standing Institute Committee on **Community Giving**, Member 2014–2017
- **HHMI Graduate Fellowship** Internal Selection Committee, Member 2014 & 2015

MIT Chemistry Department Service (Selected)

- **Laboratory Space** Committee, Member 2024–present
- **Faculty Mentor** for Assistant Professor Oleta Johnson, 2023–present
- **FacultyREF** for MIT ChemREFS (Resources for Easing Friction and Stress), a confidential resource for students that is committed to improving the PhD experience in the MIT Chemistry Department, 2021–present
- Chemistry **Graduate Admissions**, Reader 2019–present
- **Quality of Life** Committee, Member 2015–2019 and Chair 2019–present:
- Chemical Biology **Seminar Series Coordinator**, 2013–2020, 2022–present
- **Environmental Health and Safety** Committee, Member 2012–present
- Chair or Member on >50 **PhD student thesis committees** (not including Shoulders Lab PhD students), 2012–present
- MIT HEALS Graduate **Fellowship Nominations** Review, 2025
- **Appointments** Committee, Member 2024–2025
- **Faculty Search** Committee (Chemical Biology Chair), 2019–2025
- Departmental Diversity, Equity, and Inclusion Program Administrator **Search Committee**, Member 2024
- **Future Faculty Symposium** Panel on Academic Careers, 2024
- Development and implementation of sustainable **Scientific Ethics Training Program**, 2023–2024
- Faculty Leader for required **NIH Ethics Training**, 2022–2024
- Faculty **Mentorship Evaluation and Accountability** Working Group, Chair 2022–2024
- Member of the faculty group responsible for **mentorship evaluations of chemistry department faculty** being considered for promotion, 2022–2024
- Ad hoc Committee for the **Development of Biophysical Chemistry Curricula**, Member 2022–2024
- Department of Chemistry **Instrumentation Facility** Committee, Member 2014–2024
- Chemistry and Chemistry & Biology Major **Undergraduate Advisor**, 2013–2024
- PhD Student **Registration Officer** for Chemical Biology, 2020–2021
- Lead Coordinator, “**Introducing the MIT General Institute Requirement for Chemistry**” Video Project, 2019–2020
- **Graduate Admissions** Committee, Member 2012–2019
- DOW-MIT ACCESS Program Applications Review, 2017
- **Committee on Joint and Flex Chemistry Majors**, Member 2015–2017: Development and implementation of both a joint “Chemistry and Biology” major with the MIT Biology Department and the “Flexible” Chemistry degree path, resulting in a significant expansion of the department’s undergraduate degree program.

External Service and Affiliations (Selected)

- **Grant Reviewer** for the Alberta Alzheimer’s Research Program, American Cancer Society, Army Research Office Core Programs, Austrian Science Fund, Center for the Advancement of Science in Space, Chan Zuckerberg Biohub, Department of Energy, Dutch Research Council, Dystonia Medical Research Foundation, European Research Council, French National Research Agency, National Institutes of Health, National Science Foundation (NSF), NSF Graduate Research Fellowship Program, Natural Sciences and Engineering Research Council of Canada, Swiss National Science Foundation, United Kingdom Biotechnology and Biological Sciences Research Council, United Kingdom Medical Research Council, Wellcome Trust/DBT India Alliance
- **Peer Reviewer** for assorted professional journals, including: *ACS Central Science*; *ACS Chemical Biology*; *ACS Sensors*; *ACS Synthetic Biology*; *Advanced Science*; *Ageing Research Reviews*; *Aggregate*; *American Journal of Physiology-Cell Physiology*; *Analytical Biochemistry*;

Analytical Chemistry; Angewandte Chemie; Biochemistry; Bioconjugate Chemistry; Biomacromolecules; Bioorganic and Medicinal Chemistry Letters; Biophysical Journal; Biotechnology Journal; Cell Chemical Biology; Cell Reports; Cellular and Molecular Life Sciences; ChemBioChem; Chemical Communications; Chemical Research in Toxicology; Chemical Science; Chemistry – A European Journal; Current Opinion in Chemical Biology; eLife; Essays in Biochemistry; Experimental Cell Research; Gut Microbes; Industrial and Engineering Chemistry Research; International Journal of Biological Macromolecules; iScience; Israel Journal of Chemistry; Journal of Biological Chemistry; Journal of Materials Science; Journal of Molecular Biology; Journal of Organic Chemistry; Journal of Physical Chemistry; Journal of Proteome Research; Journal of Structural Biology; Journal of the American Chemical Society; Journal of the Mechanical Behavior of Biomedical Materials; Langmuir; Life Science Alliance; Matrix Biology; Molecular and Cellular Proteomics; Molecular Biology of the Cell; Molecular Neurobiology; Molecular Systems Biology; Molecular Therapy; Nature; Nature Biotechnology; Nature Chemical Biology; Nature Communications; Nature Communications Biology; Nature Methods; Nature Nanotechnology; Nature Protocols; Nucleic Acids Research; Organic and Biomolecular Chemistry; Pharmacological Research; PLoS Biology; Proceedings of the National Academy of Sciences, USA; Protein Science; Review Commons; Science; Science Advances; Scientific Reports; Synthetic and Systems Biotechnology; Trends in Biochemical Sciences; Trends in Pharmacological Sciences

- **Faculty Mentor** for the Smith Family Foundation, 2023–present
- **Co-Editor**, *Current Opinion in Chemical Biology* Synthetic Biology Issue, 2021
- **Guest Editor**, *eLife*
- **Session Organizer/President**, 255th and 256th National Meetings of the American Chemical Society, 2014 International Chemical Biology Society Meeting
- **Member**, American Association for the Advancement of Science, American Chemical Society, American Society for Biochemistry and Molecular Biology, Protein Society

CONSULTING

Spinnaker Biosciences, 2019–2020

MENTORING, ADVISING, AND GROUP AFFILIATES

Research Scientist

- Robert Wilson (2022–present; Ph.D., Australian National University, Advisor: Spencer Whitney): Robbie is leading our lab's efforts to improve the capabilities of the photosynthetic enzyme RuBisCO using a comprehensive slate of next-generation technologies.

PhD Students

- Anton Barybin (2022–present; NSF Fellow): Anton is a chemical biology student using mammalian cell-based directed evolution to develop novel biotechnologies.
- Tierani Green (2024–present; MIT Dean of Science Fellow): Tierani is studying the biochemistry of collagen proteostasis using organoid- and mouse-based model systems.
- Stephanie Halim (2022–present; Croucher Scholar, MathWorks Science Fellow): Stephanie is a biochemistry student studying how viral evolution is influenced by host proteostasis.
- Cale Locicero (2023–present; NSF Fellow): Cale is developing and applying methods for *in vivo* directed evolution.
- Edward Lee (2024–present; NSF Fellow): Edward is studying how proteostasis shapes viral host switching.
- Kristi Liivak (2024–present; John A. Lyons Fellow): Kristi is developing and applying strategies for *in vivo* directed evolution of biomolecules.
- Katelyn Meister (2025–present): Katelyn is a chemical engineering student interested in defining molecular and structural mechanisms of procollagen assembly.
- Andrew Sabol (2021–present; NSF Fellow): Andrew is a chemical biology student developing and applying methods for *in vivo* directed evolution.

- Michael Xiong (2023–present): Michael is synthesizing megaproteins and discovering small molecules that can correct collagen proteostasis defects.
- Yunlong Zhao (2023–present): Yunlong is a chemical biology student using *in vivo* directed evolution to create enhanced RuBisCO variants for agricultural applications

Postdoctoral Associates

- Aditi Dixit (2024–present; Ph.D., Indian Institute for Science and Engineering Research–Bhopal, Advisor: Prof. Jeet Kalia): Aditi is developing a new class of small molecule-based protein degraders.
- Chiara Giannone (2023–present; EMBO Postdoctoral Fellow; Ph.D., San Raffaele University, Advisor: Prof. Roberto Sitia): Chiara is studying how cells fold and quality control nascent procollagen molecules.
- Jiacheng Lin (2023–present; Ph.D., Cambridge University, Advisor: Michele Vendruscolo): Jiacheng is using combined machine learning and synthetic biology approaches to address practical, climate-relevant challenges in agriculture.
- Minh Thuan Nguyen (Peter) Tran (2023–present; Ph.D., University of Tasmania, Advisor: Alex Hewitt): Peter aims to develop new strategies for continuous directed evolution.

Master's Degree Students

- Joseph Ye (2025–present): Joseph is a computer science student developing and applying machine learning-based approaches to engineer agriculturally relevant enzymes.

Undergraduate Students

- Lillian Beliveau (2025–present; currently sophomore at MIT): Lily is studying molecular mechanisms of procollagen folding and assembly.
- Kieran Obiozo (2025–present; currently sophomore at MIT): Kieran is developing methods for recombinant production of procollagens.
- Nathan Shapiro (2023–present; currently junior at MIT): Nathan aims to develop plant RuBisCO variants with improved activities.

Technical Associates

- Berenice Chavez (2024–present; joint with Prof. Oleta Johnson): Berenice manages the laboratory and provides technical assistance with experiments.
- Yixin Hu (2024–present): Yixin is studying roles of procollagen *N*-glycosylation *in vivo* and developing screens for small molecule modulators of collagen proteostasis.
- April Wu (2025–present): April is developing new variants of plant RuBisCO with improved kinetic properties.

Visiting Professor Alumni

- Madhusudan Dey, Ph.D. (Visiting Professor, 2017; currently Professor of Biological Sciences at the University of Wisconsin–Milwaukee): Madhu participated in all aspects of the Shoulders Lab research program.
- C. Brandon Ogbunugafor, Ph.D. (Martin Luther King, Jr. Visiting Professor and Visiting Professor at MIT, 2022–2024; currently Associate Professor of Ecology and Evolution at Yale University): Brandon participated in evolution-related aspects of the Shoulders Lab research program, and in numerous pan-MIT initiatives.

Graduate Alumni

- Chet Berman, Ph.D. (2013–2018; NIH/NIGMS Biotechnology Program Trainee; MIT Presidential Fellow; currently Scientist-II at Adimab): Chet devised and applied the first platform for continuous directed evolution of biomolecule function in human cells.
- Jessica Bonnar (2023–2025; NSF Fellow; currently MIT Biology PhD student in Prof. Thomas Schwartz's laboratory): Jess studied mechanisms of collagen proteostasis.
- Kenny Chen, Ph.D. (2015–2020; currently Senior Scientist at Sanofi): Kenny studied the roles of the unfolded protein response in *N*-glycosylation and how cancer cells attain neoplastic *N*-glycosylation patterns.

- Andrew DiChiara, Ph.D. (2012–2017; NIH/NIAMS Ruth L. Kirschstein F31 Predoctoral Fellow; currently Principal Research Scientist-I at AbbVie): Andrew devised strategies to treat diseases caused by dysregulated collagen homeostasis and elucidated fundamental collagen assembly mechanisms.
- Samuel Hendel, Ph.D. (2016–2022; NSF Fellow; currently Associate at Scion Life Sciences): Sam invented new strategies and technologies to enable continuous directed evolution in mammalian cells.
- Seo-yeon Kim, Ph.D. (2019–2025; Kwanjeong Scholar): Seo-yeon developed novel mouse models to illuminate collagen glycoproteostasis, and used mass spectrometry to elucidate the basis of collagen quality control.
- Rasia “Chichi” Li, Ph.D. (2016–2022; NSF Fellow; currently Scientist-I at NGM Biopharmaceuticals): Chichi studied the roles of *N*-glycosylation in procollagen proteostasis and the molecular mechanism of collagen heterotrimerization.
- Julie McDonald, Ph.D. (2022–2025; Fellow of the Martin Family Society of Fellows for Sustainability): Julie applied next-generation directed evolution technologies and the principles of proteostasis to enhance carbon capture by photosynthetic organisms.
- Amanuella Mengiste, Ph.D. (2018–2025; Robert J. Silbey and Future of Science Graduate Fellow, BroadIgnite Awardee; currently Postdoctoral Fellow at the Ragon Institute and Harvard Medical School with Prof. Brandon DeKosky): Mani developed and applied next-generation directed evolution methods to address challenges in biotechnology.
- Christopher Moore, Ph.D. (2012–2018; NSF Fellow, Broadnext10 Awardee; currently Director at GentiBio): Chris developed a series of chemical biology methods crucial for enabling studies of the structure and function of the cellular proteostasis network.
- Louis Papa, Ph.D. (2014–2019; NSF Fellow, MIT Presidential Fellow; currently Research Scientist at Stylus Medicine): Louis developed several new *in vivo* directed evolution platforms and recombineering techniques.
- Jessica Patrick, Ph.D. (2019–2024; currently AMC Trail Crew in White Mountains, NH): Jess studied how cellular proteostasis networks influence the mutational trajectories accessible to influenza hemagglutinin and to oncoproteins.
- Angela Phillips, Ph.D. (2013–2018; NSF Fellow, MIT Presidential Fellow; received HHMI Hanna H. Gray Fellowship; currently Assistant Professor and HHMI Freeman-Hrabowski Investigator in the Department of Microbiology and Immunology at the University of California–San Francisco): Angela discovered that host cell proteostasis network mechanisms shape the evolution of RNA viruses, including influenza, thereby defining the fitness of adaptive viral variants.
- Anna Ponomarenko, Ph.D. (2015–2020; currently Scientist-II at Ultragenyx Pharmaceuticals): Anna used deep mutational scanning to understand how chaperones modulate influenza evolution and to discover the unexpected function of HSF1 as an anti-HIV restriction factor.
- Christopher Richardson, Ph.D. (2014–2019; joint with Prof. Stephen Lippard; NIH/NIBIB Neurobiological Engineering Program Trainee; currently Senior Director at Bausch + Lomb): Chris developed and applied new methods to understand the roles of zinc in metazoan cell biology.
- Rebecca Sebastian, Ph.D. (2016–2022; currently Senior Scientist-I at Abbvie): Rebecca discovered the proteostatic function of SUMO2/3 modifications during stress and characterized how chaperones influence the mutational trajectories accessible to the p53 oncoprotein.
- Sorin Asha Srinivasa, Ph.D. (2020–2025; joint with Prof. Catherine Drennan; NSF Fellow): Sorin used a combination of biochemical and structural approaches to illuminate molecular mechanisms of procollagen assembly.
- Madeline Wong, Ph.D. (2013–2018; NSF Fellow, Bose Research Grant Awardee; currently Educator in Seattle, WA): Madeline discovered a surprising role for cytosolic Hsp90 in collagen secretion, worked to define the function of collagen’s conserved *N*-glycan, and demonstrated that the unfolded protein response controls the architecture of the *N*-glycome.
- Kathryn Yamine, Ph.D. (2018–2024; MIT Presidential Fellow and NIH/NIAMS Ruth L. Kirschstein F31 Predoctoral Fellow; currently Postdoctoral Fellow at Boston Children’s Hospital

with Prof. Alan Beggs): Kathryn developed new technologies to model collagenopathies *in vitro* and elucidated fundamental mechanisms of procollagen assembly.

- Jimin Yoon, Ph.D. (2018–2024; Kwanjeong Scholar and Mathworks Fellow; currently Postdoctoral Fellow at Stanford University with Prof. Dan Herschlag): Jimin studied how host chaperones help viruses develop resistance to antiviral drugs and host immunity.

Postdoctoral Alumni

- Ngoc-Duc Doan, Ph.D. (2014–2019; CIHR and FRSQ Postdoctoral Fellow; currently Scientist-III at MacroGenics): Duc used quantitative proteomics to compare and contrast the interactomes of normal and misfolding collagen-I variants.
- Mahender Dewal, Ph.D. (2012–2015; currently Chief Scientific Officer at Expansion Technologies): Mahender discovered that the XBP1s arm of the unfolded protein response regulates the molecular architecture of *N*-glycans on secreted proteins.
- Pyae Hein, Ph.D. (2014–2015; currently Director at Dragonfly Therapeutics): Pyae studied how unfolded protein response activation influences protein *N*-glycosylation patterns.
- Azade Hosseini, Ph.D. (2016–2018; currently Venture Associate at NYU Innovation Fund): Azade studied mechanisms of collagen type-I assembly and quality control.
- Emmanuel Nekongo, Ph.D. (2012–2017; UNCF-Merck Postdoctoral Fellow; currently Senior Manager at Veroem Solutions): Emmanuel studied how the cellular protein folding environment affects HIV evolutionary trajectories.
- Robert Wilson (2020–2022; Ph.D., Australian National University, Advisor: Spencer Whitney; currently Research Scientist-III at Massachusetts Institute of Technology): Robbie developed new strategies for continuous *in vivo* directed evolution of plant RuBisCO.

Undergraduate Alumni

- Huda Abdelghani (MIT Undergraduate, 2024; currently junior at MIT): Huda explored the molecular mechanism of collagen C-propeptide assembly.
- Sophia Mirda Abularach (MIT Undergraduate, 2021–2023; currently PhD student and NSF Fellow in Developmental Biology at Stanford University): Sophia studied roles of dysregulated collagen proteostasis in osteoarthritis.
- Lucas Akin (MIT-Amgen Scholar from the University of Texas–Austin, 2015): Luke worked toward development of a microwave-based cellular thermal shift assay to assess protein stability in cells.
- Agata Bikovtseva (2017–2021; awarded NSF Graduate Research Fellowship senior year; currently Ph.D. student in Chemistry and Chemical Biology at Harvard University): Agata used biochemical and proteomic techniques to study how cells handle misfolding collagen molecules.
- Abigail Caron (MIT Undergraduate, 2012; currently Ph.D. student in evolutionary biology at the University of Chicago): Abby developed chemical biology methods to inhibit multiple myeloma-related transcription factors.
- Gina Choi (MIT Undergraduate, 2019; currently Associate Consultant at HelloAdvisor): Gina used glycomic and chemical biology methods to understand how stress responses regulate *N*-glycome composition.
- Erika Ding, Ph.D. (MIT Undergraduate, 2015–2016; Chemical and biomolecular engineering at the University of California–Berkeley): Erika worked on a microwave-based cellular thermal shift assay to measure protein stability in intact cells.
- Nora Enright (MIT Undergraduate, 2016; currently Ph.D. student in bioengineering at Stanford University): Nora studied how the unfolded protein response modulates protein *N*-glycosylation patterns in cancer.
- Xavier Bonilla Garcia (2022 MIT Summer Research Program Scholar-Bio; currently B.S. student in chemistry at the University of Puerto Rico): Xavier studied how cells quality control misfolded procollagen.
- Apolonia Gardner (MIT Undergraduate, 2017; currently Ph.D. student in Health Sciences and Technology at Harvard-MIT): Apolonia studied how host chaperones modulate viral evolution.
- Luna Gonzalez (MIT Undergraduate, 2015–2017; currently Ph.D. student in Mathematics at University of California–Los Angeles): Luna developed algorithms to model how the human proteostasis network influences RNA virus evolution.

- Nicholas Guiliano (MIT Undergraduate, 2017–2018): Nicholas explored how dysregulated zinc homeostasis promotes cadmium toxicity.
- Chyleigh Harmon, M.D. (MIT Undergraduate, 2012–2014; currently Family Physician in St. Louis, MO): Chyleigh employed activity-based protein profiling methods to uncover compounds that can protect the proteome from stress.
- Ra'Mal Harris (2022 MIT Summer Research Program-Bio Scholar; awarded NSF Fellowship during later Research Technician appointment in the Shoulders Lab; currently Ph.D. student in Chemistry and Chemical Biology at Harvard University): Ra'Mal devised new selection couples for protein evolution in mammalian cells.
- Helen Hobbs, Ph.D. (MIT-Amgen Undergraduate Scholar from Oregon State University, 2013; currently Helen Hay Whitney Postdoctoral Fellow at University of California–Irvine with Prof. Chang Liu): Helen explored new therapeutic strategies for the collagenopathies.
- Grayden Holliday (2025 MIT Summer Research Program-Bio Scholar; currently senior in Biochemistry at Washington & Lee University): Grayden is studying small molecule-based approaches to modulate glycoprotein degradation.
- Michelle Huang, Ph.D. (MIT Undergraduate, 2016–2019; awarded NSF Graduate Research Fellowship senior year; currently Postdoctoral Fellow in chemical engineering at Stanford University): Michelle studied mechanisms of collagen-I folding and quality control.
- Emma Jakubicka (2025; currently sophomore at MIT): Emma explored the use of machine learning-informed approaches to enhance RuBisCO activity.
- Karun Kaushik (2022–2023; currently co-founder and CEO at Delve): Karun studied how mutations impact the biophysical properties of viral proteins.
- Abigail Kolyer (2020; currently senior in biological engineering at MIT): Abigail studied roles of collagen proteostasis in osteoarthritis.
- Jingting Lin (2021–2024; awarded NSF Graduate Research Fellowship senior year; Ph.D. student in Biological and Biomedical Sciences at Harvard University): Jingting used mass spectrometry and biochemical assays to study mechanisms of collagen quality control.
- Nancy Lu, Ph.D. (MIT Undergraduate, 2013–2014; Ph.D. student in chemical and biological engineering at Princeton University; currently Management Consultant at Qral Group): Nancy devised chemical biology methods to regulate the heat shock response in human cells.
- Diya Malhotra (Visiting Summer Student from the University of Michigan, 2015 & 2016; currently Associate at Oliver Wyman): Diya studied the molecular mechanism of collagen heterotrimer assembly.
- Meryl Mendoza (2021 MIT Summer Research Program Scholar-Bio; currently Ph.D. student in Cell and Molecular Biology at the University of Pennsylvania): Meryl developed techniques for directed evolution in mammalian cells.
- Daniel Mirny, Ph.D. (MIT Undergraduate, 2015; currently Assistant Professor in the IESE School of Business at the University of Navarra): Daniel piloted microwave-based methodologies for determining protein stability in cells via thermal shift assays.
- Angelina O'Brien (2024; MIT Summer Research Program Scholar; currently Ph.D. student in Biological and Biomedical Sciences at Harvard University): Angelina applied machine learning methods to enhance RuBisCO function.
- Anna Plank (2021–2024; Ph.D. student in Microbiology at Columbia University): Anna developed T7 RNA polymerase-chimeras for *in vivo* directed evolution.
- Sebastian Santiago, Ph.D. (MIT Undergraduate, 2014–2015; awarded NSF Graduate Research Fellowship; currently Postdoctoral Fellow at Amgen): Sebastian piloted bioluminescent resonant energy transfer sensors of protein misfolding in live cells.
- Vansh Sethi (2024; visiting undergraduate from University of Waterloo): Vansh developed methods to rapidly purify RuBisCO from complex leaf lysates.
- Pateece Suen, Ph.D. (2012–2015 MIT Chemistry UROP in Shoulders Lab; 2015–2017 Research Technician; currently Postdoctoral Fellow in Cellular and Molecular Medicine at University of California–San Diego with Prof. Samara Reck-Peterson): Pateece worked on understanding mechanisms of collagen assembly and on the development of a human cell-based continuous directed evolution platform.

- Eileen Tan-Aristy (MIT Undergraduate, 2019; currently Technical Program Manager at Google, Inc.): Eileen engineered cell lines to modulate the heat shock response with small molecules.
- Rebecca Taylor, Ph.D. (MIT Undergraduate, 2012–2015; awarded NSF Graduate Research Fellowship senior year; currently Postdoctoral Fellow in biochemistry at the Max Planck Institute for Biochemistry with Prof. John Briggs): Becca studied the folding and misfolding of collagen-I associated with osteogenesis imperfecta.
- Marissa Vera (2020 MIT Summer Research Program Scholar; currently Ph.D. student in chemistry at Massachusetts Institute of Technology): Marissa studied how chaperones influence the ability of influenza to escape host antibodies.
- Yiwen Wang (2023 Visiting Summer Student from Tsinghua University; currently Ph.D. student in Chemistry at Columbia University): Yiwen worked on the development of new MutaT7 modalities.
- Rachel Weissman (MIT Undergraduate, 2020–2021; currently Ph.D. student and NSF Fellow in molecular and cell biology at the University of California–Berkeley): Rachel developed strategies for *in vivo* directed evolution of new enzymes based on the MutaT7 system.
- April Wu (2023–2025; currently Research Technician at MIT): April developed a new, LC-MS-based assay for medium-throughput and complete RuBisCO kinetic characterization.
- Yu Meng Zhang (MIT Undergraduate, 2020–2023; currently PhD student in Virology at Harvard University): Yu Meng studied how viruses hijack their host's chaperones to potentiate their evolution.

Technical Associate Alumni

- Ra'Mal Harris (2022–2024; 2022 MIT Summer Research Program-Bio Scholar; awarded NSF Fellowship during final year of Technician appointment in the Shoulders Lab; currently Ph.D. student in Chemistry and Chemical Biology at Harvard University): Ra'Mal developed new selection couples for protein evolution in mammalian cells.
- Patreece Suen, Ph.D. (2012–2015 MIT Chemistry UROP in Shoulders Lab; 2015–2017 Research Technician; currently Postdoctoral Fellow at the University of California–San Diego): Patreece worked on understanding mechanisms of collagen assembly and on the development of a human cell-based continuous directed evolution platform.
- Alexander Weickhardt, M.D. (2016–2018; currently Resident at the University of California–San Francisco): Alex assisted with large-scale recombinant protein production to enable structural biology studies on collagen type-I.

High Schooler Alumni

- R. William Crouch (MIT HIP-SAT Intern, 2025; currently junior in high school): William studied the function of novel mini-Cas variants derived from directed evolution campaigns.
- Daniel Eaton (MIT HIP-SAT Intern, 2024; currently senior in high school): Daniel optimized methods for the production of ultra-long, sequence-defined megaproteins.
- Rose Evard (MIT HIP-SAT Intern, 2018; currently M.S. student in Molecular Life Sciences at the University of Lausanne): Rose studied how osteogenesis imperfecta-causing mutations disrupt assembly of collagen-I.
- Brittan Gallo (MIT HIP-SAT Intern, 2022): Brittan developed selection couples to enable directed evolution in mammalian cells.
- Ahmin Haider (MIT HIP-SAT Intern, 2025; currently junior in high school): Ahmin expressed, purified, and characterized disease-causing collagen C-propeptide variants.
- Anika Harris (High School Intern, 2024; currently senior in high school): Anika developed methodologies to enable the efficient translation of megaproteins from circular RNAs.
- Christopher Hillenbrand (Research Science Institute High School Scholar in the Shoulders Lab, 2014; MIT B.S. in 2019; currently Ph.D. student in chemistry at Yale University): Chris studied strategies for engineering the adenoviral genome for synthetic biology applications.
- Camden Holm (MIT HIP-SAT Intern, 2016; currently Ph.D. student in Biomedical Engineering at Worcester Polytechnic Institute): Camden studied how protein primary amino acid sequences influence *N*-glycan maturation.
- Karun Kaushik (MIT HIP-SAT Intern, 2021–2022; currently co-founder and CEO at Delve): Karun used computational approaches to assess deep mutational scanning data.

- Jocelyn Koelb (MIT HIP-SAT Intern, 2018; currently senior in biochemistry and political science at Northeastern University): Jocelyn designed and validated new selection circuits for application in a human cell-based directed evolution platform.
- Caiden Kumar (MIT HIP-SAT Intern, 2015): Caiden focused on the application of novel molecular biology techniques for the modification of the adenoviral genome.
- Joshua Miner (MIT HIP-SAT Intern, 2024; currently first-year at North Carolina State University): Joshua developed and applied new selection technologies for the *in vivo* evolution of RuBisCO catalytic activity.
- Kiera Murray (MIT HIP-SAT Intern, 2019): Kiera studied methods for the high-yielding recombinant expression of collagen's C-propeptide domain.
- Rebecca Schooler (MIT HIP-SAT Intern, 2017; currently Research Associate-I at Novo Nordisk): Rebecca worked on the development of a protocol for *in vitro* refolding of collagen type-I's C-propeptide domain.
- Ellie Strano (MIT HIP-SAT Intern, 2023; currently Senior in High School): Ellie studied how cells fold nascent procollagen.
- Eileen Tan-Aristy (MIT HIP-SAT Intern, 2017; MIT B.S. in 2022; currently Technical Program Manager at Google, Inc.): Eileen engineered cell lines to modulate the heat shock response with small molecules.

Chemical Education Sub-Group Alumni

- Nicholas Boekelheide, Ph.D. (2020–2021; currently Lecturer in the MIT Experimental Study Group): Nick was funded by an Alumni Class Funds grant to develop Guided Learning Demonstrations to support the residential general chemistry courses.
- Patricia Christie, Ph.D. (2016 and 2020–2021; currently Senior Lecturer in the MIT Experimental Study Group): Patti co-managed the development of a Fundamental Knowledge Module for 5.111 Principles of Chemical Science supported by a grant from the d'Arbelloff Fund for Excellence in Education. Later, Patti was funded by an Alumni Class Funds grant to develop Guided Learning Demonstrations to support the residential general chemistry courses.
- David Grimes, Ph.D. (2019–2021; currently MIT Digital Learning Fellow and Instructor): David helped lead the development of MOOC General Chemistry courses for the EdX platform.
- Alisa Krishtal, Ph.D. (2020–2022; currently Senior Software Engineer at FRiKINtech): Alisa was an Instructor funded by an MITx grant to develop MOOC General Chemistry courses for the EdX platform.
- Ilana Porter, Ph.D. (2016; currently postdoctoral fellow in energy sciences within the SLAC National Accelerator Laboratory at Stanford University with Prof. Matthias Kling): Ilana contributed at all levels from coding to designing content for the 5.111 Principles of Chemical Science Fundamental Knowledge Module.
- Dina Sharon (2020; currently Hertz Foundation Fellow and Ph.D. student in chemistry at Massachusetts Institute of Technology): Dina contributed to the development of MOOC General Chemistry courses for the EdX platform.

Current Thesis Committees (non-Shoulders Lab)

- Sunhee Bae (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Laura Kiessling)
- Lucas Bartel (MIT Dept. of Chemistry [Member]; Advisor: Prof. Gabriela Schlau-Cohen)
- Camryn Carter (MIT Dept. of Chemistry [Member]; Advisor: Prof. Bin Zhang)
- Cordiana Cozier (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Oleta Johnson)
- Christa Imrich (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Cathy Drennan)
- Debajit Kalita (Jawaharlal Nehru Centre for Advanced Scientific Research [External Examiner]; Advisor: Prof. Bani Kanta Sarma)
- Ghazal Kamyabi (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Elizabeth Nolan)
- Franklin Kostas (MIT Dept. of Chemistry [Member]; Advisor: Prof. Xiao Wang)
- Andrea Marcano-Delgado (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Cathy Drennan)
- Rachel Motz (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Elizabeth Nolan)
- Juliet Okorie (MIT Dept. of Chemical Engineering [Member]; Advisor: Prof. Kristala Prather)
- Aaron Petty (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Oleta Johnson)

- Paulina Rios (MIT Dept. of Biology [Member]; Advisor: Prof. Francisco Sánchez-Rivera)
- David Sarabia-Castillo (MIT Dept. of Chemistry [Member]; Advisor: Prof. Bradley Pentelute)
- Dina Sharon (MIT Dept. of Chemistry [Member]; Advisor: Prof. Adam Willard)
- Marissa Vera (MIT Dept. of Chemistry [Member]; Advisor: Prof. Laura Kiessling)
- Theodore Warner (MIT Dept. of Chemistry [Member]; Advisor: Prof. Laura Kiessling)

Past Thesis Committees (non-Shoulders Lab)

- Alaa Al-Shaer, Ph.D. (Simon Fraser University Dept. of Molecular Biology and Biochemistry [External Examiner]; Advisor: Prof. Nancy Forde)
- Gisele Andree, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Cathy Drennan)
- Lindsey Backman, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Cathy Drennan)
- Carolyn Barnes, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Laura Kiessling)
- Amir Bitran, Ph.D. (Harvard University Biophysics Program [External Examiner]; Advisor: Prof. Eugene Shakhnovich)
- Isabella Borgula, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Ronald Raines)
- Tess Branon, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Alice Ting)
- Aneth Canale, Ph.D. (University of Massachusetts Medical School–Worcester Dept. of Biochemistry and Molecular Pharmacology [External Examiner]; Advisor: Prof. Dan Bolon)
- Alan Carter (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Laura Kiessling)
- Wen Chyan, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Ronald Raines)
- Kurt Cox, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Alice Ting)
- Peng Dai, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Bradley Pentelute)
- Roger Diehl, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Laura Kiessling)
- Andrew Dorfeuille, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Cathy Drennan)
- Amanda Edwards, Ph.D. (Harvard University Medical School Program in Biological and Biomedical Sciences [External Examiner]; Advisor: Prof. Loren Walensky)
- Ethan Evans, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Bradley Pentelute)
- Alex Genshaft, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Alex Shalek)
- Yisu Han, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Alice Ting)
- Jordan Ho, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Laura Kiessling)
- Victoria Hung, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Alice Ting)
- Emily Johnson, Ph.D. (University of Liverpool Department of Musculoskeletal and Ageing Science [External Examiner]; Advisor: Dr. Elizabeth Laird)
- Pornchai Kaewsapsak, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Alice Ting)
- Gabriel Kline, Ph.D. (Scripps Research Institute Dept. of Chemistry [External Examiner]; Advisor: Prof. Jeffery Kelly)
- Kellie Kolb, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Alex Shalek)
- Michael Lee, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Bradley Pentelute)
- Wankyu Lee, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. JoAnne Stubbe)
- Qiao Li, M.S. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Laura Kiessling)
- Zeyu Lu, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Bradley Pentelute)
- Vinita Lukose, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Barbara Imperiali)
- Venkata Shiva Mandala, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Mei Hong)
- Eric Miller, Ph.D. (MIT Dept. of Chemical Engineering [Member]; Advisor: Prof. Hadley Sikes)
- Chloe Morgan, M.S. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Mei Hong)
- Rida Mourtada, Ph.D. (MIT Health Sciences and Technology [Chair]; Advisor: Prof. Loren Walensky)
- Janet Jie Ying Peet, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Elizabeth Nolan)
- Valerie Ressler, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Ronald Raines)
- Aezin Saebi, Ph.D. (MIT Dept. of Chemistry [Member]; Advisors: Profs. Stephen Buchwald and Bradley Pentelute)
- Deepsing Syangtan, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Laura Kiessling)

- Minh Thuan Nguyen Tran, Ph.D. (University of Tasmania [External Examiner]; Advisor: Prof. Alex Hewitt)
- Clair Travis (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Ronald Raines)
- Suan Tuang, M.D.-Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Bradley Pentelute)
- Marc Wadsworth, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Alex Shalek)
- Elizabeth Wittenborn, Ph.D. (MIT Dept. of Chemistry [Member]; Advisor: Prof. Cathy Drennan)
- Evans Wralstad, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Ronald Raines)
- Jinyi Yang, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Ronald Raines)
- Sezin Yigit, Ph.D. (Tufts University Dept. of Chemistry [External Examiner]; Advisor: Prof. David Kaplan)
- Kristin Zuromski, Ph.D. (MIT Dept. of Chemistry [Chair]; Advisor: Prof. Tania Baker)

Undergraduate Advising at MIT

- Academic advisor for MIT Chemistry or Chemistry and Biology majors Peyton Acoff, Alexander Alabugin, Luke Anderson, Shahul Alam, Balyn Brotheridge, Karen Camacho, Erica Flear, Annaliese Getz, Katherine Hobgood, Madeleine Kline, Jessica Mann, Emma Martin, Adebayo Ojute, Tanyaporn Pattarabanjird, Reuben Sanders, Rebecca Sloan, Michael Yan, and Chanwoo Yoon
- First-year faculty advisor for MIT undergraduates Maximilian Bolzan, Paige Cooksey, Hillel Dei, Neil Deshmukh, Abigail Dulski, Caleb Frieson, Reuben Fuchs, Jason Li, Hendrik Mayer, Matthew Nay, Christopher Rinard, Miles Roper, Alejandro Tanon, Jordan Tierney, and Mason Weinstock