

# Stanford

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## Greg Barsh

Professor of Genetics and of Pediatrics, Emeritus

### CONTACT INFORMATION

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### Bio

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#### ACADEMIC APPOINTMENTS

- Professor Emeritus-Hourly, Genetics
- Member, Bio-X

#### PROFESSIONAL EDUCATION

- MD, University of Washington , Medicine (1984)
- BS, University of California, Irvine , Biology (1977)
- PhD, University of Washington , Genetics of Human Disease (1984)

### Research & Scholarship

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#### CURRENT RESEARCH AND SCHOLARLY INTERESTS

Color variation is one of the most readily apparent differences among closely related animals, and has been studied extensively as a model for Mendelian genetics over the last 100 years. Our laboratory is interested in the mechanisms that give rise to eye, hair, and skin coloration, both as a tool for studying gene action and interaction, and because many signaling pathways used by the pigmentary system play important roles in human development and disease.

All mammals use the same genetic toolbox, and several mouse coat color mutations have human counterparts such as oculocutaneous albinism or Chediak-Higashi syndrome. Applying the genetics of mouse hair color as a model, however, is relevant not only to rare inborn errors but also to common diseases including diabetes and obesity, neurodegeneration, and skin cancer. Production of normal hair and skin color depends on a series of processes--cell migration, stem cell renewal, paracrine regulation of cell physiology--used in many different contexts throughout the body; pigmentation phenotypes are especially well-suited for studying these processes because mutations are efficiently recognized, subtle effects on gene expression are easily detected, and the cell types and tissues involved are amenable to experimental manipulation.

Our original interest in mouse coat color genetics stems from mutations that cause a back-and-forth switch between pigment granules characteristic of red hair, to those characteristic of black, brown, or blond hair. Studies of these pigment type-switching mutations have identified one set of pathways important for body weight regulation, and another set of pathways implicated in neurodegeneration. Several current projects in the laboratory are directed at specific aspects of these pathways.

## Teaching

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### GRADUATE AND FELLOWSHIP PROGRAM AFFILIATIONS

- Genetics (Phd Program)

## Publications

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### PUBLICATIONS

- **Digital gene expression for non-model organisms** *GENOME RESEARCH*  
Hong, L. Z., Li, J., Schmidt-Kuentzel, A., Warren, W. C., Barsh, G. S.  
2011; 21 (11): 1905-1915
- **Ribosomal mutations cause p53-mediated dark skin and pleiotropic effects** *NATURE GENETICS*  
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2008; 40 (8): 963-970
- **A -defensin mutation causes black coat color in domestic dogs.** *Science*  
Candille, S. I., Kaelin, C. B., Cattanaach, B. M., Yu, B., Thompson, D. A., Nix, M. A., Kerns, J. A., Schmutz, S. M., Millhauser, G. L., Barsh, G. S.  
2007; 318 (5855): 1418-1423
- **Linkage and segregation analysis of black and brindle coat color in domestic dogs** *GENETICS*  
Kerns, J. A., Cargill, E. J., Clark, L. A., Candille, S. I., Berryere, T. G., Olivier, M., Lust, G., Todhunter, R. J., Schmutz, S. M., Murphy, K. E., Barsh, G. S.  
2007; 176 (3): 1679-1689
- **A healthy tan?** *New England journal of medicine*  
Barsh, G., Attardi, L. D.  
2007; 356 (21): 2208-2210
- **Effects of hypothalamic neurodegeneration on energy balance** *PLOS BIOLOGY*  
Xu, A. W., Kaelin, C. B., Morton, G. J., Ogimoto, K., Stanhope, K., Graham, J., Baskin, D. G., Havel, P., Schwartz, M. W., Barsh, G. S.  
2005; 3 (12): 2168-2176
- **PI3K integrates the action of insulin and leptin on hypothalamic neurons** *JOURNAL OF CLINICAL INVESTIGATION*  
Xu, A. W., Kaelin, C. B., Takeda, K., Akira, S., Schwartz, M. W., Barsh, G. S.  
2005; 115 (4): 951-958
- **Effects of G-protein mutations on skin color** *NATURE GENETICS*  
Van Raamsdonk, C. D., Fitch, K. R., Fuchs, H., de Angelis, M. H., Barsh, G. S.  
2004; 36 (9): 961-968
- **Dorsoventral patterning of the mouse coat by Tbx15.** *PLoS biology*  
Candille, S. I., Van Raamsdonk, C. D., Chen, C., Kuijper, S., Chen-Tsai, Y., Russ, A., Meijlink, F., Barsh, G. S.  
2004; 2 (1): E3-?
- **What controls variation in human skin color?** *PLoS biology*  
Barsh, G. S.  
2003; 1 (1): E27-?
- **Spongiform degeneration in mahoganoid mutant mice** *SCIENCE*  
He, L., Lu, X. Y., Jolly, A. F., Eldridge, A. G., Watson, S. J., Jackson, P. K., Barsh, G. S., Gunn, T. M.  
2003; 299 (5607): 710-712
- **Genetics of dark skin in mice** *GENES & DEVELOPMENT*

Fitch, K. R., McGowan, K. A., Van Raamsdonk, C. D., Fuchs, H., Lee, D., Puech, A., Heralut, Y., Threadgill, D. W., de Angelis, M. H., Barsh, G. S.  
2003; 17 (2): 214-228

- **Genetic approaches to studying energy balance: Perception and integration** *NATURE REVIEWS GENETICS*  
Barsh, G. S., Schwartz, M. W.  
2002; 3 (8): 589-600
- **A biochemical function for attractin in agouti-induced pigmentation and obesity** *NATURE GENETICS*  
He, L., Gunn, T. M., Bouley, D. M., Lu, X. Y., Watson, S. J., Schlossman, S. F., Duke-Cohan, J. S., Barsh, G. S.  
2001; 27 (1): 40-47
- **Genetics of body-weight regulation** *NATURE*  
Barsh, G. S., Farooqi, I. S., O'Rahilly, S.  
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- **Melanocortin 1 receptor variation in the domestic dog** *MAMMALIAN GENOME*  
Newton, J. M., Wilkie, A. L., He, L., Jordan, S. A., Metallinos, D. L., Holmes, N. G., Jackson, I. J., Barsh, G. S.  
2000; 11 (1): 24-30
- **Antagonism of central melanocortin receptors in vitro and in vivo by Agouti-related protein** *SCIENCE*  
Ollmann, M. M., Wilson, B. D., Yang, Y. K., Kerns, J. A., Chen, Y. R., Gantz, I., Barsh, G. S.  
1997; 278 (5335): 135-138
- **Regulatory mutations in TBX3 disrupt asymmetric hair pigmentation that underlies Dun camouflage color in horses** *NATURE GENETICS*  
Imsland, F., McGowan, K., Rubin, C., Henegar, C., Sundstrom, E., Berglund, J., Schwochow, D., Gustafson, U., Imsland, P., Lindblad-Toh, K., Lindgren, G., Mikko, S., Millon, et al  
2016; 48 (2): 152-158
- **Recurrent Evolution of Melanism in South American Felids** *PLOS GENETICS*  
Schneider, A., Henegar, C., Day, K., Absher, D., Napolitano, C., Silveira, L., David, V. A., O'Brien, S. J., Menotti-Raymond, M., Barsh, G. S., Eizirik, E.  
2015; 11 (2)
- **Coordinated Regulation of Hepatic Energy Stores by Leptin and Hypothalamic Agouti-Related Protein (Retracted article. See vol. 34, pg. 13865, 2014)** *JOURNAL OF NEUROSCIENCE*  
Warne, J. P., Varonin, J. M., Nielsen, S. S., Olofsson, L. E., Kaelin, C. B., Chua, S., Barsh, G. S., Koliwad, S. K., Xu, A. W.  
2013; 33 (29): 11972-11985
- **Molecular and Functional Analysis of Human beta-Defensin 3 Action at Melanocortin Receptors** *CHEMISTRY & BIOLOGY*  
Nix, M. A., Kaelin, C. B., Ta, T., Weis, A., Morton, G. J., Barsh, G. S., Millhauser, G. L.  
2013; 20 (6): 784-795
- **Genetic Architecture of Skin and Eye Color in an African-European Admixed Population** *PLOS GENETICS*  
Beleza, S., Johnson, N. A., Candille, S. I., Absher, D. M., Coram, M. A., Lopes, J., Campos, J., Araujo, I. I., Anderson, T. M., Vilhjalmsson, B. J., Nordborg, M., Correia e Silva, A., Shriver, et al  
2013; 9 (3)
- **Levels of the Mahogunin Ring Finger 1 E3 Ubiquitin Ligase Do Not Influence Prion Disease** *PLOS ONE*  
Silvius, D., Pitstick, R., Ahn, M., Meishery, D., Oehler, A., Barsh, G. S., DeArmond, S. J., Carlson, G. A., Gunn, T. M.  
2013; 8 (1)
- **Coordinated regulation of hepatic energy stores by leptin and hypothalamic agouti-related protein.** *The Journal of neuroscience : the official journal of the Society for Neuroscience*  
Warne, J. P., Varonin, J. M., Nielsen, S. S., Olofsson, L. E., Kaelin, C. B., Chua, S., Barsh, G. S., Koliwad, S. K., Xu, A. W.  
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Kaelin, C. B., Barsh, G. S.  
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- **Genome-Wide Association Studies of Quantitatively Measured Skin, Hair, and Eye Pigmentation in Four European Populations** *PLOS ONE*  
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- **Unraveling the thread of nature's tapestry: the genetics of diversity and convergence in animal pigmentation** *PIGMENT CELL & MELANOMA RESEARCH*  
Kronforst, M. R., Barsh, G. S., Kopp, A., Mallet, J., Monteiro, A., Mullen, S. P., Protas, M., Rosenblum, E. B., Schneider, C. J., Hoekstra, H. E.  
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- **Guidelines for Genome-Wide Association Studies** *PLOS GENETICS*  
Barsh, G. S., Copenhaver, G. P., Gibson, G., Williams, S. M.  
2012; 8 (7)
- **A Candidate Mechanism Underlying the Variance of Interictal Spike Propagation** *JOURNAL OF NEUROSCIENCE*  
Sabolek, H. R., Swiercz, W. B., Lillis, K. P., Cash, S. S., Huberfeld, G., Zhao, G., Ste Marie, L., Clemenceau, S., Barsh, G., Miles, R., Staley, K. J.  
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- **Ancestral Components of Admixed Genomes in a Mexican Cohort** *PLOS GENETICS*  
Johnson, N. A., Coram, M. A., Shriver, M. D., Romieu, I., Barsh, G. S., London, S. J., Tang, H.  
2011; 7 (12)
- **Reduced ribosomal protein gene dosage and p53 activation in low-risk myelodysplastic syndrome** *BLOOD*  
McGowan, K. A., Pang, W. W., Bhardwaj, R., Perez, M. G., Pluvinage, J. V., Glader, B. E., Malek, R., Mendrysa, S. M., Weissman, I. L., Park, C. Y., Barsh, G. S.  
2011; 118 (13): 3622-3633
- **Coat pattern genetics in cats**  
Kaelin, C. B., Xu, X., Hong, L. Z., David, V. A., McGowan, K. A., Barsh, G. S., Menotti-Raymond, M.  
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- **A Nervous Origin for Fish Stripes** *PLOS GENETICS*  
Kelsh, R. N., Barsh, G. S.  
2011; 7 (5)
- **PDK1-Foxo1 in Agouti-Related Peptide Neurons Regulates Energy Homeostasis by Modulating Food Intake and Energy Expenditure** *PLOS ONE*  
Cao, Y., Nakata, M., Okamoto, S., Takano, E., Yada, T., Minokoshi, Y., Hirata, Y., Nakajima, K., Iskandar, K., Hayashi, Y., Ogawa, W., Barsh, G. S., Hosoda, et al  
2011; 6 (4)
- **Loop-Swapped Chimeras of the Agouti-Related Protein and the Agouti Signaling Protein Identify Contacts Required for Melanocortin 1 Receptor Selectivity and Antagonism** *JOURNAL OF MOLECULAR BIOLOGY*  
Patel, M. P., Fabersunne, C. S., Yang, Y., Kaelin, C. B., Barsh, G. S., Millhauser, G. L.  
2010; 404 (1): 45-55
- **Haploinsufficiency of Ribosomal Protein S6 In Mice Mimics Bone Marrow Failure Syndromes In Humans** *52nd Annual Meeting and Exposition of the American-Society-of-Hematology (ASH)*  
Park, C. Y., McGowan, K. A., Glader, B., Barsh, G. S., Weissman, I. L.  
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- **Tabby pattern genetics - a whole new breed of cat** *PIGMENT CELL & MELANOMA RESEARCH*  
Kaelin, C., Barsh, G.  
2010; 23 (4): 514-516
- **Independent regulation of hair and skin color by two G protein-coupled pathways** *PIGMENT CELL & MELANOMA RESEARCH*  
Van Raamsdonk, C. D., Barsh, G. S., Wakamatsu, K., Ito, S.  
2009; 22 (6): 819-826
- **Dominant Role of the p110 beta Isoform of PI3K over p110 alpha in Energy Homeostasis Regulation by POMC and AgRP Neurons** *CELL METABOLISM*  
Al-Qassab, H., Smith, M. A., Irvine, E. E., Guillermet-Guibert, J., Claret, M., Choudhury, A. I., Selman, C., Piipari, K., Clements, M., Lingard, S., Chandarana, K., Bell, J. D., Barsh, et al  
2009; 10 (5): 343-354

- **Agouti protein, mahogunin, and attractin in pheomelanogenesis and melanoblast-like alteration of melanocytes: a cAMP-independent pathway** *PIGMENT CELL & MELANOMA RESEARCH*  
Hida, T., Wakamatsu, K., Sviderskaya, E. V., Donkin, A. J., Montoliu, L., Lamoreux, M. L., Yu, B., Millhauser, G. L., Ito, S., Barsh, G. S., Jimbow, K., Bennett, D. C.  
2009; 22 (5): 623-634
- **Scientists <- Editors <- Scientists: The Past, Present, and Future of PLoS Genetics** *PLOS GENETICS*  
Barsh, G. S., Copenhaver, G. P.  
2009; 5 (7)
- **Signals of recent positive selection in a worldwide sample of human populations** *GENOME RESEARCH*  
Pickrell, J. K., Coop, G., Novembre, J., Kudaravalli, S., Li, J. Z., Absher, D., Srinivasan, B. S., Barsh, G. S., Myers, R. M., Feldman, M. W., Pritchard, J. K.  
2009; 19 (5): 826-837
- **Genetics of Sex-linked yellow in the Syrian Hamster** *GENETICS*  
Alizadeh, A., Hong, L. Z., Kaelin, C. B., Raudsepp, T., Manuel, H., Barsh, G. S.  
2009; 181 (4): 1427-1436
- **Molecular and Evolutionary History of Melanism in North American Gray Wolves** *SCIENCE*  
Anderson, T. M., vonHoldt, B. M., Candille, S. I., Musiani, M., Greco, C., Stahler, D. R., Smith, D. W., Padhukasahasram, B., Randi, E., Leonard, J. A., Bustamante, C. D., Ostrander, E. A., Tang, et al  
2009; 323 (5919): 1339-1343
- **Frequent somatic mutations of GNAQ in uveal melanoma and blue naevi** *NATURE*  
Van Raamsdonk, C. D., Bezrookove, V., Green, G., Bauer, J., Gaugler, L., O'Brien, J. M., Simpson, E. M., Barsh, G. S., Bastian, B. C.  
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- **New ligands for melanocortin receptors** *20th Conference of the Pennington-Biomedical-Research-Center*  
Kaelin, C. B., Candille, S. I., Yu, B., Jackson, P., Thompson, D. A., Nix, M. A., Binkley, J., Millhauser, G. L., Barsh, G. S.  
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- **PLoS Genetics Turns Three: Looking Back, Looking Ahead** *PLOS GENETICS*  
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- **Mutations in ribosomal proteins cause p53-mediated dark skin** *International Investigative Dermatology Meeting*  
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NATURE PUBLISHING GROUP.2008: S110-S110
- **Genetics of dark skin: new genes, new pathways**  
Barsh, G., McGowan, K., van Raamsdonk, C., Attardi, L., Bastian, B.  
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- **Hypothalamic neurodegeneration and adult-onset obesity in mice lacking the Ubb polyubiquitin gene** *PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES OF THE UNITED STATES OF AMERICA*  
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- **Activation of stat3 signaling in AgRP neurons promotes locomotor activity** *CELL METABOLISM*  
Mesaros, A., Koralov, S. B., Rother, E., Wunderlich, F. T., Ernst, M. B., Barsh, G. S., Rajewsky, K., Bruening, J. C.  
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- **Melanocyte-lineage expression of Cre recombinase using Mitf regulatory elements** *PIGMENT CELL & MELANOMA RESEARCH*  
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- **The PIAS-like protein Zimp10 is essential for embryonic viability and proper vascular development** *MOLECULAR AND CELLULAR BIOLOGY*  
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- **Frequent Somatic Mutations of GNAQ in Uveal Melanoma and Intradermal Melanocytic Proliferations** *20th International Pigment Cell Conference/5th International Melanoma Research Congress*  
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2007; 45 (12): 744-756
- **How the dog got its spots** *NATURE GENETICS*  
Barsh, G. S.  
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- **How hair gets its pigment** *CELL*  
Barsh, G., Cotsarelis, G.  
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- **Mammalian Comparative Sequence Analysis of the Agrp Locus** *PLOS ONE*  
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Claret, M., Smith, M. A., Batterham, R. L., Selman, C., Choudhury, A. I., Fryer, L. G., Clements, M., Al-Qassab, H., Heffron, H., Xu, A. W., Speakman, J. R., Barsh, G. S., Viollet, et al  
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- **Insulin action in AgRP-expressing neurons is required for suppression of hepatic glucose production** *CELL METABOLISM*  
Koenner, A. C., Janoschek, R., Plum, L., Jordan, S. D., Rother, E., Ma, X., Xu, C., Enriori, P., Hampel, B., Barsh, G. S., Kahn, C. R., Cowley, M. A., Ashcroft, et al  
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- **Spongiform neurodegeneration-associated E3 ligase mahogunin ubiquitylates TSG101 and regulates endosomal trafficking** *MOLECULAR BIOLOGY OF THE CELL*  
Kim, B. Y., Olzmann, J. A., Barsh, G. S., Chin, L., Li, L.  
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Jackson, P. J., Douglas, N. R., Chai, B., Binkley, J., Sidow, A., Barsh, G. S., Millhauser, G. L.  
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- **Signal transducer and activator of transcription (Stat) binding sites but not Stat3 are required for fasting-induced transcription of Agouti-related protein messenger ribonucleic acid** *MOLECULAR ENDOCRINOLOGY*  
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- **Skin layer-specific transcriptional profiles in normal and recessive yellow (Mc1r(e)/Mc1r(e)) mice** *PIGMENT CELL RESEARCH*  
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Xu, A. W., Barsh, G. S.  
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Kuijper, S., Beverdam, A., Kroon, C., Brouwer, A., Candille, S., Barsh, G., Meijlink, F.  
2005; 132 (7): 1601-1610
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