

## **Paul Bennett Savage**

C100 BNSN

Department of Chemistry and Biochemistry  
Brigham Young University, Provo, UT 84602

Phone: (801) 422-4020

Fax: (801) 422-0153

Email: paul\_savage@byu.edu

### **Education**

#### **University of Wisconsin**

Madison, Wisconsin

Doctor of Philosophy, Organic Chemistry, Biotechnology Minor, **1993**

#### **Brigham Young University**

Provo, Utah

Bachelor of Science, Chemistry, **1988**

### **Experience**

#### **University of Wisconsin**

Madison, Wisconsin

Research Assistant, **1988 - 1993**

Advisor - Dr. Samuel H. Gellman

#### **The Ohio State University**

Columbus, Ohio

NIH Postdoctoral Fellow, **1993 - 1995**

Advisor - Dr. Leo A. Paquette

#### **Brigham Young University**

Provo, Utah

Assistant Professor, **1995 - 2000**

Associate Professor, **2000 - 2004**

Professor, **2004 - 2005**

Associate Chair, **2004 - 2010**

Reed M. Izatt Professor of Chemistry and Biochemistry, **2005 - present**

*Research Emphases* - Discovery of the structural requirements of glycolipids for stimulation of natural killer T cells. Development of non-peptide mimics of antimicrobial peptides. Control of TLR2-mediated responses through lipopeptide structure.

### **Awards and Service**

- Reed M. Izatt and James J. Christensen Faculty Excellence in Research Award, **2010**
- Temporary Reviewer, NIH (various study sections) **2000 - 2010**
- Brigham Young University Sponsored Research Award, **2008**
- Brigham Young University Karl G. Maeser Research and Creative Arts Award, **2006**
- Stoel Rives Utah Innovation Award, Biotechnology, **2006**
- Brigham Young University Technology Transfer Award, **2005**
- Brigham Young University Karl G. Maeser Excellence in Teaching Award, **2004**
- Chair, NIH F04 Study Section, **2004**
- Advisory Committee, NIH COBRE Program, Kansas University Medical Center, **2002 - 2006**
- Brigham Young University Creative Works Award, **2001**
- Brigham Young University Young Scholar Award, **2000**
- College of Physical and Mathematical Sciences Award for Excellence in Teaching, **1999**
- National Science Foundation CAREER Award, **1998 - 2002**
- Student Award for Excellence in Teaching-Department of Chemistry, **1997, 1998**
- National Institutes of Health Postdoctoral Fellowship, **1994 - 1995**
- National Research Service Award (Biotechnology Trainee), **1990 - 1993**

## Publications (Authored and Coauthored)

152. Pollard, J. E.; Snarr, J.; Chaudhary, V.; Jennings, J. D.; Shaw, H.; Geiss, B.; Wright, J.; Jia, W.; Bishop, R. E.; Savage, P. B. *J. Antimicrob. Chemother.* submitted. *In vitro* evaluation of the potential for resistance development to ceragenin CSA-13.
151. Freigang, S.; Landais, E.; Zadorozhny, V.; Yoshida, K.; Liu, Y.; Deng, S.; Palinksi, W.; Savage, P. B.; Bendelac, A.; Teyton, L. *J. Immunol.* submitted. Scavenger receptor-mediated uptake controls the bioactivity of the prototypic NKT cell agonist  $\alpha$ -galactosylceramide *in vivo*.
150. Albacker, L. A.; Chaudary, V.; Chang, Y.-J.; Kim H. Y.; Chuang Y.-T.; Pichuvant, M.; DeKruyff, R. H.; Savage, P. B.; Umetsu, D. T. *Nature Medicine* submitted. A fungal glycosphingolipid directly activates natural killer T cells and rapidly induces airway disease.
149. Bai, L.; Picard, D.; Anderson, B.; Chaudhary, V.; Luoma, A.; Jabri, B.; Adams, E. J.; Savage, P. B.; Bendelac, A. *Eur. J. Immunol.* **2012**, in press. The majority of CD1d-sulfatide specific T cells in human blood use a semi-invariant V $\delta$ 1 TCR.
148. Nagant, C.; Savage, P. B.; Dehaye, J. P. *J. Appl. Microbiol.* **2012**, in press. Effect of pluronic acid F-127 on the toxicity towards eukaryotic cells of CSA-13, a cationic steroid analogue of antimicrobial peptides.
147. Kim, H. Y.; Chang, Y.-J.; Subramanian, S.; Lee, H.-H.; Albacker, L. A.; Matangkasombut, P.; Savage, P. B.; McKenzie, A. N. J.; Smith, D. E.; Rottman, J. B.; DeDruff, R. H.; Umetsu, D. T. *J. Allergy Clin. Immunol.* **2012**, *129*, 216-U319. Innate lymphoid cells responding to IL-33 mediate airway-hyperreactivity independent of adaptive immunity.
146. Pereira, R. L.; Reis, V. O.; Semedo, P.; Buscariollo, B. N.; Donizzeti-Oliveira, C.; Cenedeze, M. A.; Pacheco-Silva, A.; Savage, P. B.; Camara, N. O. S.; Keller, A. C. *PLoS One* **2012**, *7*, 10.1371. Invariant natural killer T cell agonist modulates experimental focal and segmental glomerulosclerosis.
145. Leszczynska, K.; Namoit, D.; Byfield, F.; Cruz, K.; Zendzian-Piotrowska, M.; Fein, Savage, P. B.; Diamond, S.; McCulloch, C.; Bucki, R.; Janmey, P. *J. Immunol.* **2012**, in press. Cathelicidin LL-37 increases lung epithelial cell stiffness, decreases trans-epithelial permeability, and prevents epithelium invasion by *Pseudomonas aeruginosa*.
144. Bozkurt-Güzel, Ç.; Savage, P. B.; Gerçeker, A. A. *Chemotherapy* **2012**, *57*, 505-510. *In vitro* activities of the novel ceragenin CSA-13, alone or in combination with colistin, tobramycin and ciprofloxacin against *Pseudomonas aeruginosa* strains isolated from cystic fibrosis patients.
143. Bai, L.; Constantinides, M. G.; Thomas, S. Y.; Reboulet, R.; Meng, F.; Krentgen, F.; Teyton, L.; Savage, P. B.; Bendelac, A. *J. Immunol.* **2012**, *188*, 3053-3061. Distinct antigen-presenting cells explain the cytokine bias of  $\alpha$ -galactosylceramide variant *in vivo*.
142. Scanlon, S.; Thomas, S.; Ferreira, C. M.; Bai, L.; Krausz, T.; Savage, P. B.; Bendelac, A. *J. Exp. Med.* **2011**, *208*, 2113-2124. Airborne lipid antigens mobilize resident intravascular NKT cells to induce allergic airway inflammation.
141. Smith, P. A.; Jackson-Lepage, C. R.; Savage, P. B.; Bowerbank, C. R.; Lee, E. D.; Lukacs, M. *J. Anal. Chim. Acta* **2011**, *690*, 215-220. Use of a hand-portable gas chromatograph-toroidal ion trap mass spectrometer for self-chemical ionization identification of degradation products related to O-ethyl S-2-diisopropylaminoethyl methyl phosphonothiolate (VX).
140. Deng, S.; Mattner, J.; Zang, Z.; Bai, L.; Teyton, L.; Bendelac, A.; Savage, P. B. *Org. Biomol. Chem.* **2011**, *9*, 7659-7662. Impact of sugar stereochemistry on natural killer T Cell stimulation by bacterial glycolipids.
139. Nagant, C.; Feng, Y.; Lucas, B.; Braeckmans, K.; Savage, P. B.; Dehaye, J.-P. *J. Appl. Microbiol.* **2011**, *111*, 763-772. Effect of a low concentration of a cationic steroid antibiotic (CSA-13) on the formation of a biofilm by *Pseudomonas aeruginosa*.
138. Mohammed, J. P.; Fusakio, M. E.; Rainbow, D. B.; Moule, C.; Fraser, H. I.; Clark, J.; Todd, J.

- A.; Peterson, L. B.; Savage, P. B.; Wills-Karp, M.; Ridgway, W. M.; Wicker, L. S.; Mattner, J. *J. Immunol.* **2011**, *187*, 337-349. Identification of Cd101 as a susceptibility gene for *novosphingobium aromaticivorans*-induced liver autoimmunity.
137. Blumenfeld, H. J.; Tohn, R.; Haeryfar, S. M. M.; Liu, Y.; Savage, P. B.; Delovitch, T. L. *Clin. Exp. Immunol.* **2011**, *166*, 121-133. Structure-guided design of an iNKT cell agonist for optimum protection from type 1 diabetes in NOD mice.
136. Chang, Y. J.; Kim, H. Y.; Albacker, L. A.; Lee, H. H.; Baumgarth, N.; Akira, S.; Savage, P. B.; Endo, S.; Yamamura, T.; Maaskant, J.; Kitano, N.; Singh, A.; Bhatt, A.; Besra, G. S.; van den Elzen, P.; Appelmelk, B.; Franck, R. W.; Chen, G. W.; DeKruyff, R. H.; Shimamura, M.; Illarionov, P.; Umetsu, D. T. *J. Clin. Invest.* **2011**, *121*, 57-69. Influenza infection in suckling mice expands an NKT cell subset that protects against airway hyperreactivity.
135. Polat, Z. A.; Savage, P. B.; Genberg, C. G. *J. Ocular Pharmacol. Therapeutics* **2011**, *21*, 1-5. *In vitro* amoebicidal activity of a ceragenin, CSA-13, against *Acanthamoeba castellanii* and its cytotoxic potential.
134. Trainor, E. A.; Horton, K. E.; Savage, P. B.; Testerman, T. L.; McGee, D. J. *Infect. Immun.* **2011**, *79*, 88-97. The role of the HefC efflux pump in *Helicobacter pylori* cholesterol-dependent resistance to ceragenins and bile salts.
133. Leszczynska, K.; Namiot, A.; Cruz, K.; Byfield, F. J.; Won, E.; Mendez, G. Wojciech, S.; Savage, P. B.; Bucki, R.; Janmey, P. A. *J. Appl. Microbiol.* **2011**, *110*, 229-238. Potential of ceragenin CSA-13 and its mixture with pluronic F-127 as treatment for topical bacterial infections.
132. Byfield, F. J.; Kowalski, M.; Cruz, K.; Leszczynska, K.; Namiot, A.; Savage, P. B.; Bucki, R.; Janmey, P. A. *J. Immunol.* **2011**, *187*, 6402-6409. Cathelicidin LL-37 increases lung epithelial cell stiffness, decreases transepithelial permeability, and prevents epithelial invasion by *Pseudomonas aeruginosa*.
131. Braun, N. A.; Mendez-Fernandez, Y. V.; Covarrubias, R.; Porcelli, S. A.; Savage, P. B.; Yagita, H.; Van Kaer, L.; Major, A. S. *Arteriosclerosis Thrombosis Vasc. Biol.* **2010**, *30*, 1758-U178. Development of spontaneous anergy in invariant natural killer T cells in a mouse model of dyslipidemia.
130. Epand, R. F.; Pollard, J. E.; Wright, J. O.; Savage, P. B.; Epand, R. M. *Antimicrob. Agents Chemother.* **2010**, *54*, 3708-3717. Depolarization, bacterial membrane composition and the antimicrobial action of ceragenins.
129. Smith, P. A.; Lepage, C. J.; Lukacs, M.; Martin, N.; Shufutinsky, A.; Savage, P. B. *Int. J. Mass Spectrosc.* **2010**, *295*, 113-118. Field-portable gas chromatography with transmission quadrupole and cylindrical ion trap mass spectrometric detection: chromatographic retention index data and ion/molecule interactions for chemical warfare agent identification.
128. Semmling, V.; Lukacs-Kornek, V.; Thaiss, C. A.; Quast, T.; Hochheiser, K.; Panzer, U.; Rossjohn, J.; Perlmutter, P.; Cao, J.; Godfrey, D. I.; Savage, P. B.; Knolle, P. A.; Kolanus, W.; Förster, I.; Kurts, C. *Nature Immunol.* **2010**, *11*, 313-U57. Alternative cross-priming through CCL17/CCR4-mediated CTL attraction towards NKT cell-licensed dendritic cells.
127. Bucki, R.; Leszczynska, K.; Byfield, F. J.; Fein, D. E.; Won, E.; Cruz, K.; Namiot, A.; Kulakowska, A.; Namiot, Z.; Savage, P. B.; Diamond, S.; Janmey, P. A. *Antimicrob. Agents Chemother.* **2010**, *54*, 2525-2533. Combined antibacterial and anti-inflammatory activity in a cationic disubstituted dexamethasone spermine conjugate (D2S).
126. Lee, H.-H.; Meyer, E. H.; Goya, S.; Pichavant, M.; Kim, H. Y.; Umetsu, S. E.; Jones, J. C.; Savage, P. B.; Casasnovas, J. M.; Kaplan, G.; Freeman, G. J.; DeKruyff, R. H.; Umetsu, D. T. *J. Immunology* **2010**, *185*, 522-5235. Apoptotic cells activate NKT cells through Ig-like mucin-like-1 resulting in airway hyperreactivity.
125. Lara, D.; Feng, Y.; Bader, J.; Savage, P. B.; Maldonado, R. A. *J. Parasitol.* **2010**, *96*, 638-642.

Anti-trypanosomatid activity of ceragenins.

124. Monine, M. I.; Posner, R. G.; Savage, P. B.; Faeder, J. R.; Hlavacek, W. S. *Biophys. J.* **2010**, *95*, 48-56. Modeling multivalent ligand-receptor interactions with steric constraints on configurations of cell-surface receptor aggregates.
123. Freigang, S.; Zadorozhny, V.; McKinney, M.; Krebs, P.; Schrantz, N.; Masuda, K.; Liu, Y.; Savage, P. B.; Bendelac, A.; Cravatt, B. F.; Teyton, L. *J. Clin. Invest.* **2010**, *120*, 1873-1884. Fatty acid amide hydrolyase shapes NKT cell responses by regulating the serum transport of lipid antigen.
122. Pollard, J.; Wright, J.; Feng, Y.; Geng, D.; Genberg, C.; Savage, P. B. *Anti-Infectives in Medicinal Chemistry* **2009**, *8*, 290-294. Activities of ceragenin CSA-13 against established biofilms in an *in vitro* model of catheter decolonization.
121. Leszczynska, K.; Namiot, A.; Fein, D. E.; Wen, Q.; Namiot, Z.; Savage, P. B.; Diamond, S.; Janmey, P. A.; Bucki, R. Bactericidal activities of the cationic steroid CSA-13 and the cathelicidin peptide LL-37 against *Helicobacter pylori* in simulated gastric juice. *BMC Microbiol.* **2009**, *9*, 187.
120. Morshed, S. R.; Takahashi, T.; Savage, P. B.; Kambham, N.; Strober, S. *Clin. Immunol.* **2009**, *132*, 321-333.  $\beta$ -galactosylceramide alters invariant natural killer T cell function and is effective treatment for lupus.
119. Howell, M. D.; Streib, J. E.; Kim B. E.; Lesley, L.; Dunlap, A.; Geng, D.; Savage, P. B.; Leung, D. Y. M. *J. Invest. Dermatol.* **2009**, *129*, 2668-2675. Ceragenins: a new class of anti-viral compounds to treat orthopox infections.
118. Yin, N.; Long, X.; Goff, R. D.; Zhou, D.; Cantu, C.; Mattner, J.; Saint Mezdard, P.; Teyton, L.; Bendelac, L.; Savage, P. B. *ACS Chem. Biol.* **2009**, *4*, 191-197. Alpha anomers of iGb3 and Gb3 stimulate cytokine production by natural killer T cells. PMID: PMC2843501
117. Kim, H. Y.; Pichavant, M.; Matangkasombut, P.; Koh, Y. I., Savage, P. B.; DeKruyff R. H.; Umetsu, D. T. *J. Immunol.* **2009**, *182*, 3252-3261. The development of airway hyperreactivity in T-bet-deficient mice requires CD1d-restricted NKT cells.
116. Bai, L.; Sagiv, Y.; Liu Y.; Freigang, S.; Yu, K. A. O.; Teyton, L.; Porcelli, S. A.; Savage, P. B.; Bendelac, A. *Proc. Natl Acad. Sci.* **2009**, *106*, 10254-10259. Lysosomal recycling terminates CD1d-mediated presentation of short and polyunsaturated variants of the NKT cell lipid antigen  $\alpha$ GalCer.
115. Roohi, S.; Amir, N.; Ahmed, M.; Savage, P. B.; Saluhiddin, S. M.; Jehangir, M. *J. Radioanal. Nuclear Chem.* **2009**, *97*, 57-62. Synthesis, quality control and biological evaluation of  $^{99m}$ Tc labeled CSA-13.
114. Farruggia, G.; Iotti, S.; Prodi, L.; Zaccheroni, N.; Montalti, M.; Savage, P. B.; Andreani, G.; Trapani, V.; Wolf, F. I. *J. Fluorescence* **2009**, *19*, 11-19. A simple spectrofluorometric assay to measure total intracellular magnesium by a hydroxyquinoline derivative.
113. Isogai, E.; Isogai, H.; Takahashi, K.; Okumura, K.; Savage, P. B. *Oral Microbiol. Immunol.* **2009**, *24*, 170-172. Ceragenin CSA13 exhibits antimicrobial activity against cariogenic and periodontopathic bacteria.
112. Epand, R. M.; Epand, R. F.; Savage, P. B. *Drug News Perspect.* **2008**, *21*, 307-311. Ceragenins (cationic steroid compounds), a novel class of antimicrobial agents.
111. Saha, S.; Savage, P. B.; Bal M. *J. Appl. Microbiol.* **2008**, *105*, 822-828. Enhancement of the efficacy of erythromycin in multiple antibiotic-resistant gram-negative bacterial pathogens.
110. Koh, Y. I.; Kim, H. Y.; Meyer, E. H.; Pichavant, M.; Akabri, O.; Yasumi, T.; Savage, P. B.; DeKruyff, R. H.; Umetsu, D. T. *J. Immunol.* **2008**, *181*, 4560-4569. Activation of nonclassical CD1d restricted natural killer T cells induces airway hyperreactivity in  $\beta$ 2-microglobulin deficient mice.

109. Lai, X.-Z.; Feng, Y.; Pollard, J.; Chin, J. N.; Rybak, M. J.; Bucki, R.; Epand, R. F.; Epand, R. M.; Savage, P. B. *Acc. Chem. Res.* **2008**, *41*, 1233-1240. Ceragenins: cholic acid-based mimics of antimicrobial peptides.
108. Pichavant, M.; Goya, S.; Meyer, E. H.; Johnston, R. A.; Kim, H. Y.; Matagkasombut, P.; Zhu, M.; Iwakura, Y.; Savage, P. B.; DeKruyff, R. H.; Shore, S. A.; Umetsu, D. T. *J. Exp. Med.* **2008**, *205*, 385-393. Ozone exposure in a mouse model induces airway hyperreactivity that requires the presence of natural killer T cells and IL-17.
107. Mattner, J.; Savage, P. B.; Leung, P.; Oertelt, S. S.; Wang, V.; Trivedi, O.; Scanlon, S. T.; Teyton, L.; Hart, J.; Ridgway, W. M.; Wicker, L. S.; Gershwin, E. M.; Bendelac, A. *Cell Host Microbe* **2008**, *3*, 304-315. Liver autoimmunity triggered by microbial activation of NKT cells.
106. Matangkasombut, P.; Pichavant, M.; Yasumi, T.; Hendricks, C.; Savage, P. B.; DeKruyff, R. H.; Umetsu, D. T. *J. Allergy Clin. Immunol.* **2008**, *121*, 1287-1289. Direct activation of natural killer T cells induces airway hyperreactivity in nonhuman primates.
105. Fuangswasdi, S.; Kaveevivitchai, N.; Tuntulani, T.; Savage, P. B. *J. Solution Chem.* **2008**, *37*, 45-58. Complexing properties of phenolic diazacrown ethers with transition and heavy metal ions.
104. Zajonc, D.; Savage, P. B.; Bendelac, A.; Wilson, I.; Teyton, L. *J. Mol. Biol.* **2008**, *377*, 1104-1116. Crystal structures of mouse CD1d-iGb3 complex and its cognate V $\alpha$ 14 T cell receptor suggest a model for dual recognition of foreign and self glycolipids.
103. Bucki, R.; Namiot, D. B.; Namiot, Z.; Savage, P. B.; Janmey, P. A. *J. Antimicrob. Chemother.* **2008**, *62*, 329-335. Salivary mucins inhibit antibacterial activity of cathelicidin-derived LL-37 peptide but not the cationic steroid CSA-13.
102. Savage, P. B.; Nielsen, J.; Lai, X.-Z.; Feng, Y.; Li, Y.; Nelson, G.; Linford, M. R.; Genberg, C. Antibacterial activities of thin films containing ceragenins. In Camesano, T.A. and Mello, C. (Eds.). *Microbial Surfaces: Structure, Interactions and Reactivity*. ACS Symposium Series 984, Washington, D.C.: American Chemical Society, **2008**, 65-78.
101. Liu, Y.; Deng, S.; Bai, L.; Freigang, S.; Mattner, J.; Teyton, L.; Bendelac, A.; Savage, P. B. *Bioorg. Med. Chem. Lett.* **2008**, *18*, 3052-3055. Synthesis of diglycosylceramides and evaluation of their iNKT cell stimulatory properties. PMID: PMC2846726
100. Chin, J. N.; Jones, R. N.; Sader, H. S.; Savage, P. B.; Rybak, M. J. *J. Antimicrob. Chemother.* **2008**, *61*, 365-370. Potential synergy activity of the novel ceragenin, CSA-13 against clinical isolates of *Pseudomonas aeruginosa*, including multi-drug resistant *P. aeruginosa*.
99. Posner, R. G.; Geng, D.; Haymore, S.; Bogert, J.; Pecht, I.; Licht, A.; Savage, P. B. *Org. Lett.* **2007**, *9*, 3551-3554. Trivalent antigens for degranulation of mast cells.
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96. Sagiv, Y.; Bai, L.; Wei, D. G.; Agami, R.; Savage, P. B.; Teyton, L.; Bendelac, A. *J. Exp. Med.* **2007**, *204*, 921-928. A distal effect of microsomal triglyceride transfer protein deficiency on the lysosomal recycling of CD1d.
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94. Meyer, E. H.; Wurbel, M. A.; Staton, T. L.; Pichavant, M.; Savage, P. B.; Kan, M. J.; DeKruyff, R.; Butcher, E. C.; Campbell, J. J.; Umetsu, D. *Immunity* **2007**, *179*, 4661-4671. iNKT cells require CCR4 to localize to the airways and to induce airway-hyperreactivity.

93. Chin, J. N.; Rybak, M. J.; Cheung, C. M.; Savage, P. B. *Antimicrob. Agents Chemother.* **2007**, *51*, 1268-1273. Antimicrobial activity of novel ceragenins against clinical isolates of resistant *Staphylococcus aureus*.
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89. Savage, P. B.; Bendelac, A.; Teyton, L. *Chem. Soc. Rev.* **2006**, *35*, 771-779. Glycolipids for natural killer T cells.
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and a one-step preparation of an acid chloride terminated monolayers on scribed silicon.

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