Name: Walter F. Boron

Education:
A.B. *Summa cum laude*, 1971, Saint Louis University, Chemistry
M.D., 1977, Washington University (St. Louis)
Ph.D., 1977, Washington University, Physiology and Biophysics

Academic Positions:
1977 – 1978: Postdoctoral Fellow, Dept. of Physiology and Biophysics, Washington University School of Medicine, St. Louis, MO.
1978 – 1980: Postdoctoral Fellow, Dept. of Physiology, Yale University School of Medicine, New Haven, CT.
1980 – 1984: Assistant Professor, Dept. of Physiology, Yale University School of Medicine, New Haven, CT.
1984 – 1987: Associate Professor, Dept. of Physiology, Yale University School of Medicine, New Haven, CT.
1987 – 2007: Professor, Dept. of Cellular & Molecular Physiology, Yale University School of Medicine, New Haven, CT.
2007 – Professor, Dept. of Physiology & Biophysics, Case Western Reserve University, Cleveland, OH.

Administrative Positions:
1987 – 1989: Director of Medical Studies, Dept. of Cellular & Molecular Physiology, Yale University School of Medicine, New Haven, CT.
1989 – 1998: Chairman, Dept. of Cellular & Molecular Physiology, Yale University School of Medicine, New Haven, CT.
December 1, 2003 – Principal Investigator of Program Project Grant DK17433.
September 1, 2007 – : David N. & Inez Myers/Antonio Scarpa, MD, PhD Chairman, Dept. of Physiology & Biophysics, Case Western Reserve University, Cleveland, OH.

Honors and Awards:
Marcus Award (undergraduate research in chemistry), 1971.
Phi Beta Kappa, Alpha Sigma Nu, Pi Mu Epsilon, Beta Beta Beta
Grass Foundation MBL Fellow, 1975.
Sigma Xi
NIH Research Service Award (postdoctoral fellowship), 1977 – 1980.
Searle Scholar, 1981 – 1984.
NIH Research Career Development Award, 1983 – 1988.
Young Investigator Award of the **American Society of Nephrology** and the American Heart Association, 1986.
Charles W. Bohmfalk Teaching Award (for excellence in teaching), Yale University School of Medicine, 1993.
Robert F. Pitts Lecture and Award, Renal Commission of the International Union of Physiological Sciences, 1993.
Carl W. Gottschalk Lecture and Award, Renal Section of the American Physiological Society, 1998.
Elected Fellow, American Academy for the Advancement of Science, 1998.

NIH "MERIT" Award (NIDDK), 2002 – 2112.
Homer Smith Award, **American Society of Nephrology**, 2005.
Sharpey-Schafer Award, Physiological Society, 2008.
Palade Gold Medal, Wayne State University, 2010.
Ray G. Daggs Award, American Physiological Society, 2011

Memberships:

American Physiological Society: Program Representative, Renal Section, 1984-1987; Chairman, Renal Section, 1990-1993; Council, 1995-1998; President-elect/President/Past-President, 1998-2001.
American Society of Nephrology
Biophysical Society
Salt and Water Club
Society of General Physiologists: Treasurer, 1988-1991.
Society for Neuroscience
International union of Physiological Societies: **Member**, National Organizing Committee for IUPS 2005; **Chair**, US Scientific Programming Committee; **Chair**, International Scientific Programming Committee, **Secretary-General**, 1/1/2010-12/31/2013.

Editorial Positions:

American Journal of Physiology: *Renal, Fluid and Electrolyte Physiology*: Editorial Board, 1984 – 1988.
Annual Review of Physiology: Special Section Editor, volume 48, 1986.
Journal of Physiology (London): an Editor, 1985 – 1992.
Physiological Reviews: Associate Editor, Jan. 1, 1985 – Dec. 31, 1990; Editor, Jan. 1, 1994 – Dec. 31, 1999.
Medical Physiology. A Cellular and Molecular Approach. (A textbook for medical students) Philadelphia: WB Saunders, 1319 pages, 2003: Co-editor (with EL Boulpaep)
Physiology (formerly, News in Physiological Sciences). Editor July 1, 2003 – Present

Meetings Organized:

Na^+ -H^+ Exchange, Intracellular pH, and Cell Function. Yale Univ., Dept. of Physiology: Tenth Conference on Membrane Transport Processes. Dec. 11-13, 1984: Co-organizer (with PS Aronson).
pH. Multi-symposium "Theme" for Spring 1986 FASEB meeting, St. Louis. Organizer.
Intracellular pH. American Physiological Society Conference. July 1996. Snowmass, Colorado: Co-organizer (with R Gillies).
Frontiers of Cellular and Molecular Physiology. Yale Univ., Dept. of Physiology Conference, Jan. 22-23, 1998: Co-organizer.
From Genomes to Functions. 2005 Meeting of the International Union of Physiological Sciences (IUPS), San Diego, CA: Member, National Organizing Committee; Chair, US Scientific Programming Committee; Chair, International Scientific Programming Committee.

Visiting or Special Lectureships:

Visiting Lecturer, Cardiovascular Research Institute, University of California at San Francisco, April 7 – 8, 1986.

Beckman Lecturer, Department of Physiology, University of Cork, Ireland, April 1997.
Plenary Lecturer, Gordon Conference on Membrane Transporters, July 1998.
Major Lecturer, Annual Meeting of the German Physiological Society, March 1999.
Keynote Lecturer, Second Annual Membrane Biology Conference, University of Missouri, Columbia, November 1999.
After-Dinner Lecturer, Cell & Molecular Physiology Section of the American Physiological Society, New Orleans, April 22, 2002.
Dunaway-Burnham Visiting Scientist, Dartmouth University School of Medicine, Hanover, NH, January 20 – 22, 2003.
Dr. John J. Spitzer Distinguished Lecturer, Louisiana State University Health Sciences Center, New Orleans, LA, October 4, 2004.
Suk-Ki Hong Memorial Lectures, SUNY Buffalo, May 24, 2006.
Keynote speaker, Medical Student Research Forum, New York Medical College, February 5, 2007.
Frontiers of Science Lecture, Wayne State University, Detroit, MI, 2008.
Gottschalk Lecture, University of North Carolina, Chapel Hill, NC, 2009.
F.C. MacIntosh Lectureship, McGill University, Montreal, Canada, 2009.
Visiting Scientist, Perinatal Biology Seminar, Loma Linda University, Loma Linda, California, 2010
Plenary Lecture. Joint Meeting of the Scandinavian and German Physiological Societies, Univeristy of Copenhagen, Denmark, 2010
Guest speaker. 3rd Annual Graduate Student Research Day, Department of Physiology and Biophysics, Dalhousie University, Nova Scotia, Canada, 2010.
Keynote address, Center for Membrane Protein Research, Texas Tech University Health Science Center, 2010

Current Grant Support:

NIH: R37 DK30344. PI: WF Boron. Title: Physiology of electrogenic Na/HCO3 cotransporters. Period: December 1, 2007 – November 30, 2011. Direct costs: $222,639 for current year.
NIH: P01 HD32573. PI: GH Haddad. Title of Project #2: Bicarbonate Transport in Neurons & Astrocytes in Hypoxia. Period: August 1, 2007 – July 31, 2010. Direct costs: $156,000 for current year.
NIH: R01DK081567. WF Boron. Title: Regulation of proximal tubule transport. Period: May 4, 2009 – March 31, 2014. Direct costs $394,392.
Office of Naval Research: N00014-01-10608. PI: WF Boron. Instrumentation for studying Biology and Cellular Biology of Gas Channels. Period: April 15, 2009 – April 14, 2010. Direct costs: $359,000.
Ohio Board of Regents: PI: WF Boron. Case Program in Structural Biology. Period: April 15, 2009 – April 14, 2010. Direct Costs: $359,000.
Office of Naval Research: N00014-08-10532. PI: WF Boron. Title: Gas Transport through Channels. Period: June 1, 2008 – July 31, 2010. Direct costs: $181,230 for current year.
NIH: R01 NS18400. PI: WF Boron. Title: The Molecular Physiology of Bicarbonate Transport in the Brain. Period: September 30, 2008 – August 31, 2013. Direct Costs: $336,706 for current year.

Selected peer-reviewed publications (in chronological order)

1. Boron WF & P De Weer. Intracellular pH transients in squid giant axons caused by CO_2, NH_3, and metabolic inhibitors. *J Gen Physiol* 67:91–112, 1976. *[First demonstration of pH_i regulation, NH_4^+ prepulse]*
2. Boron WF & P De Weer. Active proton transport stimulated by CO_2/HCO_3^-, blocked by cyanide. *Nature* 259:240–241, 1976.

3. Russell JM & WF Boron. Role of chloride transport in regulation of intracellular pH. *Nature* 264:73–74, 1976.
4. Boron WF, JM Russell, MS Brodwick, DW Keifer & A Roos. Influence of cyclic AMP on intracellular pH regulation and chloride fluxes in barnacle muscle fibers. *Nature* 276:511–513, 1978.
5. Boron WF & EL Boulpaep. Intracellular pH regulation in the renal proximal tubule of the salamander: basolateral HCO_3^- transport. *J Gen Physiol* 81:53–94, 1983. *[Discovery of NBC]*
6. Boron WF & JM Russell. Stoichiometry and ion dependencies of the intracellular-pH-regulating mechanism in squid giant axons. *J Gen Physiol* 81:373–399, 1983.
7. Knakal RC, WC Summers, EJ Cragoe Jr & WF Boron. Expression of a mammalian Na-H exchanger in muscle fibers of the giant barnacle. *Nature* 316:756–758, 1985.
8. Boron WF, E Hogan & JM Russell. pH-sensitive activation of the intracellular-pH regulation system in squid axons by ATPγS. *Nature* 332:262–265, 1988.
9. Ganz MB, G Boyarsky, RB Sterzel & WF Boron. Arginine vasopressin enhances pH_i regulation in the presence of HCO_3^- by stimulating three acid-base transport systems. *Nature* 337:648–651, 1989.
10. Waisbren SJ, JP Geibel, IM Modlin & WF Boron. Unusual permeability properties of gastric gland cells. *Nature* 368:332–335, 1994. *[Discovery of first gas-impermeable membrane]*
11. Fei YJ, Y Kanai, S Nussberger, V Ganapathy, FH Leibach, MF Romero, SK Singh, WF Boron & MA Hediger. Expression cloning of a mammalian proton-coupled oligopeptide transporter. *Nature* 368:563–566, 1994.
12. Romero, MF, MA Hediger, EL Boulpaep & WF Boron. Expression cloning of the renal electrogenic Na/HCO_3 cotransporter. *Nature* 387:409–413, 1997. *[Cloning of NBC]*
13. Nakhoul, NL, MF Romero, BA Davis & WF Boron. Effect of expressing the water channel aquaporin-1 on the CO_2 permeability of *Xenopus* oocytes. *Am J Physiol* 43:C543–548, 1998. *[Discovery of first gas channel]*
14. Cooper GJ & WF Boron. Effect of pCMBS on the CO_2 permeability of *Xenopus* oocytes expressing Aquaporin 1 or its C189S mutant. *Am J Physiol* 275:C1481–C1486, 1998.
15. Bevensee, MO, BM Schmitt, I Choi, MF Romero and WF Boron. An electrogenic Na^+-HCO_3^- cotransporter (NBC) with a novel COOH-terminus, cloned from rat brain. *Am J Physiol* 278:C1200–C1211, 2000.
16. Grichtchenko II, MF Romero & WF Boron. External bicarbonate dependence of the rat electrogenic Na/HCO_3 cotransporter (rNBC) expressed in oocytes. *J Gen Physiol* 115:533–545, 2000.
17. Choi I, C Aalkjær, EL Boulpaep & WF Boron. An electroneutral sodium/bicarbonate cotransporter NBCn1 and associated sodium channel. *Nature* 405:571–575, 2000.
18. Schmitt BM, UV Berger, RM Douglas, MO Bevensee, MA Hediger, GG Haddad & WF Boron. Na/HCO_3 co-transporters in rat brain: expression in glia, neurons and choroid plexus. *J Neurosci* 20:6839–6848, 2000.
19. Grichtchenko II, I Choi, X Zhong, P Bray-Ward, JM Russell & WF Boron. Cloning, characterization and chromosomal mapping of a human electroneutral Na^+-driven Cl-HCO_3 exchanger. *J Biol Chem* 276:8358-8363, 2001. *[Cloning of NDCBE]*
20. Virkki LV, GJ Cooper & WF Boron. Cloning and functional expression of MIPfun, a Major Intrinsic Protein homologue from the lens of killifish (*Fundulus heteroclitus*). *Am J Physiol*: *Regulatory, Integrative and Comparative* 281:R1994–R2003, 2001.
21. Virkki LV, D Wilson, RD Vaughan-Jones & WF Boron. Functional characterization of NBC4 as an electrogenic Na^+-HCO_3^- cotransporter (NBCe2). *Am J Physiol Cell Physiol* 282:C1278–C1289, 2002.
22. Virkki LV, C Franke, P Somieski & WF Boron. Cloning and functional characterization of a novel AQP from *Xenopus laevis* oocytes. *J Biol Chem* 277:40610–40616, 2002.
23. Choi I, L Hu, JD Rojas, BM Schmitt & WF Boron. Role of glycosylation in the renal electrogenic Na^+-HCO_3^- cotransporter (NBCe1). *Am J Physiol Renal Physiology* 284: F1199-F1206, 2003.
24. Zhao J, Y Zhou & WF Boron. Effect of the isolated removal of either basolateral CO_2 or Basolateral HCO_3^- on HCO_3^- Reabsorption by the Rabbit S2 Proximal Tubule. *Am J Physiol Renal Physiol* 285: F359–F369, 2003.

25. Virkki LV, I Choi, BA Davis & WF Boron. Cloning of a Na^+-driven Cl-HCO_3 exchanger from squid giant fiber lobe. *Am J Physiol Cell Physiol* 285:C771-780, 2003.
26. Bouyer P, Y Zhou & WF Boron. An increase in intracellular calcium concentration that is induced by basolateral CO_2, in rabbit renal proximal tubule. *Am J Physiol Renal Physiol* 285:F674-687, 2003.
27. Bouyer P, Y Zhou & WF Boron. An increase in intracellular calcium concentration that is induced by basolateral CO_2, in rabbit renal proximal tubule. *Am J Physiol Renal Physiol* 285:F674-687, 2003.
28. Bouyer P, RS Bradley, J Zhao, W Wang, GB Richerson & WF Boron. Effect of extracellular acid-base disturbances on the intracellular pH of neurons cultured from rat medullary raphe or hippocampus. *J Physiol* 559:85-101, 2004.
29. Zhou Y, J Zhao, P Bouyer & WF Boron. Evidence from renal proximal tubules that HCO_3^- and solute reabsorption are acutely regulated not by pH but by basolateral HCO_3^- and CO_2. *Proc Natl Acad Sci USA* 102:3875-80, 2005.
30. Lu J, CM Daly, MD Parker, HS Gill, PM Piermarini, MF Pelletier & WF Boron. Effect of human carbonic anhydrase II on the activity of the human electrogenic $NaHCO_3$ cotransporter NBCe1-A in *Xenopus* oocytes. *J Biol Chem* 281:19241-19250, 2006.
31. Zhou Y, P Bouyer & WF Boron. Effects of angiotensin II on the CO_2 dependence of HCO_3^- reabsorption by the rabbit S2 renal proximal tubule. *Am J Physiol: Renal Physiol*, 290:F666-673, 2006.
32. Toye AM, MD Parker, CM Daly, J Lu; LV Virkki, MF Pelletier & WF Boron. The Human NBCe1-A mutant R881C, associated with proximal renal tubular acidosis, retains function but is mistargeted in polarized renal epithelia. *Am J Physiol Cell Physiol* 291: 788–801, 2006.
33. Gill HS & WF Boron. Expression and purification of the cytoplasmic N-terminal domain of the Na/HCO_3 co-transporter NBCe1-A: Structural insights from a generalized approach. *Protein Expr Purif* 49:228-234, 2006.
34. Gill HS & WF Boron. Preliminary X-ray diffraction analysis of the cytoplasmic N-terminal domain of the Na/HCO_3 cotransporter NBCe1-A. *Acta Crystallograph Sect F Struct Bio Cryst Comm*un 62:534-537, 2006.
35. Endeward V, R Musa-Aziz, GJ Cooper, LM Chen, MF Pelletier, LV Virkki, CT Supuran, LS King, WF Boron & G Gros. Evidence that Aquaporin 1 is the major pathway for CO_2 transport in the human erythrocyte membrane. *FASEB J* 20: 1974–1981, 2006.
36. Choi I, HS Yang & WF Boron. The electrogenicity of the rat sodium-bicarbonate cotransporter NBCe1 requires interactions among transmembrane segments of the transporter. *J Physiol* 578:131–142, 2007.
37. Piermarini PM & WF Boron. Evidence against a direct interaction between intracellular carbonic anhydrase II and pure C-terminal domains of SLC4 bicarbonate transporters. *J Biol Chem* 282:1409-1421, 2007.
38. Piermarini PM, I Choi & WF Boron. Cloning and characterization of an electrogenic Na/HCO_3 cotransporter from the quid giant fiber lobe. *Am J Physiol Cell Physiol* 292:C2032-45, 2007.
39. Bouyer P, H Sakai, T Itokawa, T Kawano, CM Fulton, WF Boron & KL Insogna. Colony-stimulating factor-1 increases osteoclast intracellular pH and promotes survival via the electroneutral Na/HCO_3 cotransporter NBCn1. *Endocrinology* 148: 831–840, 2007.
40. Lu J & WF Boron. Effects of mutations in the KKMIK motif at the extracellular end of TM5 on the DIDS-sensitivity of the electrogenic Na/HCO_3 cotransporter NBCe1-A. *AJP Cell Physiol* 292:C1787-98, 2007.
41. Parker MD, MT Young, CM Daly, RW Meech, WF Boron & MJ Tanner. A conductive pathway generated from fragments of the human red cell anion exchanger AEI. *J Physiol*, 581:33-50, 2007.
42. Zhou Y, P Bouyer, WF Boron. Role of the AT_{1A} receptor in the CO_2-induced stimulation of HCO_3^- reabsorption by renal proximal tubules. *Am J Physiol Renal Physiol*, 293:F110-20, 2007.
43. Chen LM, I Choi, GG Haddad & WF Boron. Chronic continuous hypoxia decreases the expression of SLC4A7 (NBCn1) and SLC4A10 (NCBE) in mouse brain. *Am J Physiol Regul Integr Comp Physiol* 293:R2412–R2420, 2007.

44. Zhou Y & WF Boron. Role of endogenously secreted angiotensin II in the CO_2-induced stimulation of HCO_3 reabsorption by renal proximal tubules. *Am J Physiol Renal Physiol* 294:F245–252, 2008.

45. Chen LM, ML Kelly, JD Rojas, MD Parker, HS Gill, BA Davis & WF Boron. Use of a new polyclonal antibody to study the distribution and glycosylation of the sodium-coupled bicarbonate transporter NCBE in rodent brain. *Neuroscience* 151:374–385, 2008.

46. Bevensee MO & WF Boron. Effects of acute hypoxia on intracellular-pH regulation in astrocytes cultured from rat hippocampus. *Brain Res* 1193:143-152, 2008.

47. Davis BA, EM Hogan, JM Russell & WF Boron. ATP dependence of Na^+-driven Cl-HCO_3 exchange in squid axons. *J Membrane Biol* 222:107-113, 2008.

48. Chen LM, ML Kelly, MD Parker, P Bouyer, HS Gill, JM Felie, BA Davis & WF Boron. Expression and localization of Na-driven Cl-HCO_3^- exchanger (SLC4A8) NDCBE in rodent CNS. *Neuroscience* 153:162–174.

Edited Books

Aronson PS and WF Boron (eds.). *Na^+-H^+ Exchange, Intracellular pH, and Cell Function. Current Topics in Membranes and Transport*. New York: Academic Press. 315 pp., 1986.

Boron WF & EL Boulpaep (eds.). *Medical Physiology: A Cellular and Molecular Approach.* Philadelphia: Saunders. 1391 pp., 2003.

Boron WF & EL Boulpaep (eds.). *Medical Physiology: A Cellular and Molecular Approach.* Updated Edition. Philadelphia: Saunders. 1391 pp., 2005.

Boron WF & EL Boulpaep (eds). *Medical Physiology. A Cellular and Molecular Approach, 2nd Edition.* Philadelphia: Elsevier. 1337 pp., 2008.