

Name: Walter F. Boron

Citizenship: United States

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 – present: 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.

2003 – 2007: **Principal Investigator** of Program Project Grant DK17433.

2007 – present: **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 (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 (London), 2008.

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.

Physiological Society (London)

American Society of Nephrology

International Society of Nephrology

Biophysical Society

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 Elect**, 8/1/2009-12/31/2009.

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-in-Chief**, 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. **Editor-in-Chief** 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.

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: R01 DK081567. 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.

Publications:

Original Papers

Peterson PE & WF Boron. 1,3-halogen shifts occurring via four-membered ring halonium ion intermediates in the solvolyses of 3-halo-1-butyl trifluoromethanesulfonates. *J Am Chem Soc* 93:4076–4077, 1971.

Boron WF & P De Weer. Intracellular pH transients in squid giant axons caused by CO₂, NH₃, and metabolic inhibitors. *J Gen Physiol* 67:91–112, 1976.

- Boron WF & P De Weer. Active proton transport stimulated by $\text{CO}_2/\text{HCO}_3^-$, blocked by cyanide. *Nature* 259:240–241, 1976.
- Boron WF & A Roos. Comparison of microelectrode, DMO, and methylamine methods for measuring intracellular pH. *Am J Physiol* 231:799–809, 1976.
- Russell JM & WF Boron. Role of chloride transport in regulation of intracellular pH. *Nature* 264:73–74, 1976.
- Boron WF. Intracellular pH transients in giant barnacle muscle fibers. *Am J Physiol* 233:C61–C73, 1977.
- 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.
- Roos A & WF Boron. Intracellular pH transients in rat diaphragm muscle measured with DMO. *Am J Physiol* 235:C49–C54, 1978.
- Boron WF, WC McCormick & A Roos. pH regulation in barnacle muscle fibers: dependence on intracellular and extracellular pH. *Am J Physiol* 237:C185–C193, 1979.
- Boron WF, WC McCormick & A Roos. pH regulation in barnacle muscle fibers: dependence on extracellular sodium and bicarbonate. *Am J Physiol* 240:C80–C89, 1981.
- Boron WF & EL Boulpaep. Intracellular pH regulation in the renal proximal tubule of the salamander: Na-H exchange. *J Gen Physiol* 81:29–52, 1983.
- 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.
- 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.
- Russell JM, WF Boron & MS Brodwick. Intracellular pH and Na fluxes in barnacle muscle with evidence for reversal of the ionic mechanism of intracellular pH regulation. *J Gen Physiol* 82:47–78, 1983.
- Boron WF. Intracellular-pH-regulating mechanism of the squid axon: relation between the external Na^+ and HCO_3^- dependences. *J Gen Physiol* 85:325–345, 1985.
- Knakal RC, WC Summers, EJ Cragoe Jr & WF Boron. Expression of a mammalian Na-H exchanger in muscle fibers of the giant barnacle. *Nature* 315:756–758, 1985.
- Chaillet JR & WF Boron. Intracellular calibration of a pH-sensitive dye in isolated, perfused salamander proximal tubules. *J Gen Physiol* 86:765–794, 1985.
- Chaillet JR, AG Lopes & WF Boron. Basolateral Na-H exchange in the rabbit cortical collecting tubule. *J Gen Physiol* 86:795–812, 1985.

- Chaillet JR, K Amsler & WF Boron. Optical measurement of intracellular pH in single LLC-PK₁ cells: demonstration of Cl-HCO₃ exchange. *Proc Natl Acad Sci, USA* 83:522–526, 1986.
- Lopes AG, AW Siebens, G Giebisch & WF Boron. Electrogenic Na/HCO₃ cotransport across the basolateral membrane of the isolated perfused *Necturus* proximal tubule. *Am J Physiol* 253:F340–F350, 1987.
- Siebens AW & WF Boron. Effect of electroneutral luminal and basolateral lactate transport on intracellular pH in salamander proximal tubules. *J Gen Physiol* 90:799–831, 1987.
- Boron WF, E Hogan & JM Russell. pH-sensitive activation of the intracellular-pH regulation system in squid axons by ATP γ S. *Nature* 332:262–265, 1988.
- Ganz MB, G Boyarsky, WF Boron & RB Sterzel. Effects of angiotensin II and vasopressin on intracellular pH of glomerular mesangial cells. *Am J Physiol* 254:F787–F794, 1988.
- Nakhoul NL, AG Lopes, JR Chaillet & WF Boron. Intracellular pH regulation in the S3 segment of the rabbit proximal tubule in HCO₃⁻-free solutions. *J Gen Physiol* 92:369–393, 1988.
- Nakhoul NL & WF Boron. Acetate transport in the S3 segment of the rabbit proximal tubule and its effect on intracellular pH. *J Gen Physiol* 92:395–412, 1988.
- Boyarsky G, MB Ganz, RB Sterzel & WF Boron. pH regulation in single glomerular mesangial cells. I. Acid extrusion in the absence and presence of HCO₃⁻. *Am J Physiol* 24:C844–C856, 1988.
- Boyarsky G, MB Ganz, RB Sterzel & WF Boron. pH regulation in single glomerular mesangial cells. II. Na⁺-dependent and -independent Cl-HCO₃ exchangers. *Am J Physiol* 24:C859–C896, 1988.
- Boron WF & RC Knakal. Intracellular pH-regulating mechanism of the squid axon: interaction between DNDS and extracellular Na⁺ and HCO₃⁻. *J Gen Physiol* 93:123–150, 1989.
- Siebens AW & WF Boron. Depolarization-induced alkalization in proximal tubules. I. Characteristics and dependence on Na⁺. *Am. J. Physiol* 256:F342–F353, 1989.
- Siebens AW & WF Boron. Depolarization-induced alkalization in proximal tubules. II. Effects of lactate and SITS. *Am J Physiol* 256:F354–F365, 1989.
- Ganz MB, G Boyarsky, RB Sterzel & WF Boron. Arginine vasopressin enhances pHi regulation in the presence of HCO₃⁻ by stimulating three acid-base transport systems. *Nature* 337:648–651, 1989.
- Geibel JP, G Giebisch & WF Boron. Effects of acetate on luminal acidification processes in the S3 segment of the rabbit proximal tubule. *Am J Physiol* 257:F586–F594, 1989.
- Geibel JP, G Giebisch & WF Boron. Basolateral sodium-coupled acid-base transport mechanisms of the rabbit proximal tubule. *Am J Physiol* 257:F790–F797, 1989.

- Boyarsky G, MB Ganz, EJ Cragoe & WF Boron. Intracellular pH dependence of Na-H exchange and acid loading in quiescent and arginine vasopressin-activated mesangial cells. *Proc Natl Acad Sci, USA* 87:5921–5924, 1990.
- Geibel J, G Giebisch & WF Boron. Angiotensin II stimulates both Na-H exchange and Na/HCO₃ co-transport in the rabbit proximal tubule. *Proc Natl Acad Sci, USA* 87:7917–7920, 1990.
- Nakhoul NL, L Chen & WF Boron. Intracellular pH regulation in the rabbit S3 proximal tubule. Basolateral Cl-HCO₃ exchange and Na/HCO₃ cotransport. *Am J Physiol* 258:F371–F381, 1990.
- Ganz MB, MC Perfetto & WF Boron. Effects of mitogens and other agents on mesangial cell proliferation, pH and Ca²⁺. *Am J Physiol* 259:F269–F278, 1990.
- Boyarsky G, N Rosenthal, E Barrett & WF Boron. Effect of diabetes on Na-H exchange by single isolated hepatocytes. *Am J Physiol* 260:C167–C175, 1991.
- Davis BA, E Hogan & WF Boron. Role of G proteins in stimulation of Na-H exchange by cell shrinkage. *Am J Physiol* 262:C533–C536, 1992.
- Davis BA, E Hogan & WF Boron. Activation of Na-H exchange by intracellular lithium in barnacle muscle fibers. *Am J Physiol: Cell* 263:C246–C256, 1992.
- Boron WF & RC Knakal. Intracellular pH-regulating mechanism of the squid axon. Dependence on extracellular pH. *J Gen Physiol* 99:817–837, 1992.
- Tardieux I, P Webster, J Ravesloot, WF Boron, JA Lunn, JE Heuser & NW Andrews. Lysosome recruitment and fusion are early events required for trypanosome invasion of mammalian cells. *Cell* 71:1117–1130, 1992.
- Boyarsky G, W-R Schlue, MBE Davis, B Ransom & WF Boron. Intracellular pH regulation in single cultured astrocytes from rat forebrain. *Glia* 8:241–248, 1993.
- Nakhoul NL, LK Chen & WF Boron. Effect of basolateral CO₂/HCO₃ on intracellular pH regulation in the rabbit S3 proximal tubule. *J Gen Physiol*. 102:1171–1205, 1993.
- Gupta A, CJ Schwiening & WF Boron. Effects of CGRP, forskolin, PMA and ionomycin on pH_i dependence of Na-H exchange in UMR-106 cells. *Am J Physiol* 266:C1083–C1092, 1994.
- Schwiening CJ & WF Boron. Regulation of intracellular pH in pyramidal neurones from the rat hippocampus by Na⁺-dependent Cl⁻-HCO₃⁻ exchange. *J Physiol* 475:59–67, 1994.
- Kaplan DL & WF Boron. Long-term expression of c-H-ras stimulates Na-H and Na⁺-dependent Cl-HCO₃ exchange in NIH-3T3 fibroblasts. *J Biol Chem* 269:4116–4124, 1994.
- Ganz MB & WF Boron. Long-term effects of growth factors on pH and acid-base transport in rat glomerular mesangial cells. *Am J Physiol* 266:F576–F585, 1994.

- Waisbren SJ, JP Geibel, WF Boron & IM Modlin. Luminal perfusion of isolated gastric glands. *Am J Physiol* 266:C1013–C1027, 1994.
- Waisbren SJ, JP Geibel, IM Modlin & WF Boron. Unusual permeability properties of gastric gland cells. *Nature* 368:332–335, 1994.
- Davis BA, EM Hogan & WF Boron. Shrinkage-induced activation of $\text{Na}^+\text{-H}^+$ exchange in barnacle muscle fibers. *Am J Physiol* 266:C1744–C1753, 1994.
- 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.
- Chen LK & WF Boron. Acid extrusion in the S3 segment of the rabbit proximal tubule: I. Effect of bilateral $\text{CO}_2/\text{HCO}_3^-$. *Am J Physiol* 268:F179–F192, 1995.
- Chen LK & WF Boron. Acid extrusion in the S3 segment of the rabbit proximal tubule: II. Effect of basolateral $\text{CO}_2/\text{HCO}_3^-$. *Am J Physiol* 268: F193–F203, 1995.
- Ravesloot JH, T Eisen, R Baron & WF Boron. Role of Na-H exchangers and vacuolar H^+ pumps in intracellular pH regulation in neonatal rat osteoclasts. *J Gen Physiol* 105:177–208, 1995.
- Zhao J, EM Hogan, MO Bevensee & WF Boron. Out-of-equilibrium $\text{CO}_2/\text{HCO}_3^-$ solutions and their use in characterizing a novel K/HCO_3^- cotransporter. *Nature* 374:636–639, 1995.
- Bevensee MO, CJ Schwiening & WF Boron. Use of BCECF and propidium iodide to assess membrane integrity of acutely isolated CA1 neurons from rat hippocampus. *J Neurosci Meth* 58:61–75, 1995.
- Apkon M & WF Boron. Extracellular but not intracellular alkalinization constricts rat cerebral arterioles. *J Physiol* 484:743–753, 1995.
- Kanai Y, S Nussberger, MF Romero, WF Boron, SC Hebert & MA Hediger. Electrogenic properties of the epithelial and neuronal high affinity glutamate transporter. *J Biol Chem* 270:16561–16568, 1995.
- Hogan EM, MA Cohen & WF Boron. K^+ - and HCO_3^- -dependent acid-base transport in squid giant axons: Base efflux. *J Gen Physiol* 106:821–844, 1995.
- Hogan EM, MA Cohen & WF Boron. K^+ - and HCO_3^- -dependent acid-base transport in squid giant axons: Base influx. *J Gen Physiol* 106:845–862, 1995.
- Singh SK, HJ Binder, WF Boron, JP Geibel. Fluid absorption in isolated perfused colonic crypts. *J Clin Invest* 96:2373–2379, 1995.
- Singh SK, HJ Binder, JP Geibel & WF Boron. An apical permeability barrier to NH_3/NH_4 in isolated, perfused colonic crypts. *Proc Natl Acad Sci, USA* 92:11573–11577, 1995.

- Bevensee MO, TR Cummins, GG Haddad, WF Boron & G Boyarsky. pH regulation in single CA1 neurons acutely isolated from the hippocampi of immature and mature rats. *J Physiol* 494:315–328, 1996.
- Grishin AV, MO Bevensee, NN Modyanov, V Rajendran, WF Boron & MJ Caplan. Functional expression of the cDNA encoded by the human ATP1AL1 Gene. *Am J Physiol* 271:F539–F551, 1996.
- Steel A, S Nussberger, MF Romero, WF Boron, CAR Boyd & M. Hediger. Stoichiometry and pH dependence of the rabbit proton-dependent oligopeptide transporter PepT1. *J Physiol* 493: 563–569, 1997.
- Romero MF, MA Hediger, EL Boulpaep & WF Boron. Expression cloning of the renal electrogenic Na/HCO₃ cotransporter. *Nature* 387:409–413, 1997.
- Nussberger S, A Steel, D Trotti, MF Romero, WF Boron & MA Hediger. Symmetry of H⁺ binding to the intra- and extracellular side of the H⁺-coupled oligopeptide cotransporter PepT1: *J Biol Chem* 272:7777–7785, 1997.
- Apkon M, RA Weed & WF Boron. Motor responses of cultured rat cerebral vascular smooth muscle cells to intra- and extracellular pH changes. *Am J Physiol* 273:H434–H445, 1997.
- Gunshin H, B Mackenzie, UV Berger, Y Gunshin, MF Romero, WF Boron, S Nussberger, JL Gollan, MA Hediger. Cloning and characterization of a proton-coupled mammalian metal ion transporter. *Nature* 388: 482–488, 1997.
- Zahler R, ZT Zhang, M Manor & WF Boron. Sodium kinetics of Na, K-ATPase α isoforms in intact transfected HeLa cells. *J Gen Physiol* 110: 201–213, 1997.
- Bevensee MO, RA Weed & WF Boron. Intracellular pH regulation in cultured astrocytes from rat hippocampus. I. Role of HCO₃⁻. *J Gen Physiol* 110:453–465, 1997.
- Bevensee MO, M Apkon & WF Boron. Intracellular pH regulation in cultured astrocytes from rat hippocampus. II. Electrogenic Na/HCO₃ cotransport. *J Gen Physiol* 110:467–483, 1997.
- Hogan EM, BA Davis & WF Boron. Intracellular Cl⁻ dependence of Na-H Exchange in barnacle muscle fibers under normotonic and hypertonic conditions. *J Gen Physiol* 110:629–639, 1997.
- Nakhoul NL, BA Davis, MF Romero & WF Boron. Effect of expressing the water channel aquaporin-1 on the CO₂ permeability of *Xenopus* oocytes. *Am J Physiol* 274:C543–C548, 1998.
- Romero MF, P Fong, UV Berger, MA Hediger & WF Boron. Cloning and functional expression of rNBC, an electrogenic Na⁺-HCO₃⁻ cotransporter from rat kidney. *Am J Physiol* 274:F425–F432, 1998.
- Cooper GJ & WF Boron. Effect of pCMBS on the CO₂ permeability of *Xenopus* oocytes expressing Aquaporin 1 or its C189S mutant. *Am J Physiol* 275: C1481–C1486, 1998.

- Schmitt BM, D Biemesderfer, EL Boulpaep, MF Romero & WF Boron. Immunolocalization of the electrogenic Na⁺-HCO₃⁻ cotransporter (NBC) in mammalian and amphibian kidney. *Am J Physiol* 276:F27–F38, 1999.
- Bevensee MO, E Bashi, W-R Schlue, G Boyarsky & WF Boron. Shrinkage-induced activation of Na⁺/H⁺ exchange in rat renal mesangial cells. *Am J Physiol* 276:C674–C683, 1999.
- Choi I, MF Romero, N Khandoudi, A Bril & WF Boron Cloning and characterization of a human electrogenic Na⁺-HCO₃⁻ cotransporter isoform (hhNBC). *Am J Physiol* 276:C576–C584, 1999.
- Marino CR, V Jeanes, WF Boron & BM Schmitt. Expression and distribution of the Na⁺-HCO₃⁻ cotransporter in human pancreas. *Am J Physiol* 277:G487–G494, 1999.
- Jensen LJ, BM Schmitt, UV Berger, NN Nsumu, WF Boron, MA Hediger, D Brown & S Breton. Localization of sodium bicarbonate co-transporter (NBC) protein and mRNA in rat epididymis. *Biol Reprod* 60:573–579, 1999.
- Bevensee MO, Ebashi & WF Boron. Effect of trace levels of nigericin on intracellular pH and acid-base transport in rat renal mesangial cells. *J Membrane Biol* 169:131–139, 1999.
- Heyer M, S Müller-Berger, MF Romero, WF Boron and Frömter E. Stoichiometry of the rat kidney Na⁺-HCO₃⁻ cotransporter expressed in *Xenopus laevis* oocytes. *Pflügers Arch* 438:322–329, 1999.
- Roussa E, MF Romero, BM Schmitt, WF Boron, SL Alper & F Thévenod. Immunolocalization of anion exchanger AE2 and Na⁺-HCO₃⁻ cotransporter in rat parotid and submandibular glands. *Am J Physiol* 277: G1288 – G1296, 1999.
- Bevensee, MO, BM Schmitt, J. Lopes, I Choi, MF Romero and WF Boron. An electrogenic Na⁺-HCO₃⁻ cotransporter (NBC) with a novel COOH-terminus, cloned from rat brain. *Am J Physiol* 278:C1200–C1211, 2000.
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- Choi I, C Aalkjær, EL Boulpaep & WF Boron. An electroneutral sodium/bicarbonate cotransporter NBCn1 and associated sodium channel. *Nature* 405:571–575, 2000. [doi:10.1038/35014615](https://doi.org/10.1038/35014615)
- Schmitt BM, UV Berger, RM Douglas, MO Bevensee, MA Hediger, GG Haddad & WF Boron. Na/HCO₃ cotransporters in rat brain: expression in glia, neurons and choroid plexus. *J Neurosci* 20:6839–6848, 2000. [doi:20/18/6839](https://doi.org/10.1523/JNEUROSCI.2018-00.2000)
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in rat and *Ambystoma* kidney. *J Am Soc Nephrol* 11:2179–2189, 2000. [doi:10.1046-6673/1112-2179](https://doi.org/10.1046-6673/1112-2179)

Douglas RM, BM Schmitt, Y Xia, MO Bevensee, D Biemesderfer, WF Boron & GG Haddad. Sodium-hydrogen exchangers and sodium-bicarbonate co-transporters: ontogeny of protein expression in the rat brain. *Neuroscience* 102:217–228, 2001. [doi:10.1016/S0306-4522\(00\)00473-5](https://doi.org/10.1016/S0306-4522(00)00473-5)

Grichtchenko II, I Choi, P Bray-Ward, JM Russell, I Choi & WF Boron. Cloning, characterization and chromosomal mapping of a human electroneutral Na⁺-driven Cl-HCO₃ exchanger. *J Biol Chem* 276:8358–8363, 2001. [doi:10.1074/jbc.C000716200](https://doi.org/10.1074/jbc.C000716200)

Davis BA, EM Hogan, GJ Cooper, E Bashi, J Zhao & WF Boron. Inhibition of K/HCO₃ cotransport in squid axons by quaternary ammonium ions. *J Membrane Biol* 183:25–32, 2001. [doi:10.1007/s00232-001-0050-0](https://doi.org/10.1007/s00232-001-0050-0)

Khandoudi N, J Albadine, P Robert, S Krief, I Berrebi-Bertrand, X Martin, MO Bevensee, WF Boron & A Brill. Inhibition of the cardiac electrogenic sodium bicarbonate cotransporter reduces ischaemic injury. *Cardiovasc Res* 52:387–396, 2001. [doi:10.1016/S0008-6363\(01\)00430-8](https://doi.org/10.1016/S0008-6363(01)00430-8)

Virkki LV, GJ Cooper & WF Boron. Cloning and functional expression of MIP (AQP0) homolog from killifish (*Fundulus heteroclitus*) lens. *Am J Physiol: Regulatory, Integrative and Comparative* 281:R1994–R2003, 2001. [doi:0363-6119/01](https://doi.org/10.0363-6119/01)

Virkki LV, D Wilson, RD Vaughan-Jones & WF Boron. Functional characterization of NBC4 as an electrogenic Na⁺-HCO₃⁻ cotransporter (NBCe2). *Am J Physiol Cell Physiol* 282:C1278–C1289, 2002. [doi:10.1152/ajpcell.00589.2001](https://doi.org/10.1152/ajpcell.00589.2001)

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(Updated 10-08-09)