

**PRESIDENT OF
THE ACADEMY**
Ralph J. Cicerone

EDITOR-IN-CHIEF
Randy Schekman

ASSOCIATE EDITORS
David Chandler
Alan Fersht
Jack Halpern
Dolores R. Piperno
Solomon H. Snyder
B. L. Turner II
Peter K. Vogt
Susan R. Wessler

EDITORIAL BOARD

**Animal, Nutritional, and
Applied Microbial Sciences**
David L. Denlinger
R. Michael Roberts
Linda J. Saif
Ryuzo Yanagimachi

Anthropology
Richard G. Klein
C. Owen Lovejoy
James F. O'Connell

Applied Mathematical Sciences
Peter J. Bickel
David L. Donoho

Applied Physical Sciences
Noel A. Clark
Francisco de la Cruz
Jerry P. Gollub
Harry L. Swinney

Astronomy
Neta A. Bahcall

Biochemistry
Michael R. Botchan
Jennifer A. Doudna
Edward D. Korn
Stephen C. Kowalczykowski
John Kuriyan
Michael A. Marletta
Kiyoshi Mizuuchi
Charles M. Radding
Venkatraman Ramakrishnan
Tom A. Rapoport
James A. Wells
William T. Wickner

**Biophysics and
Computational Biology**
David Baker
Adriaan Bax
William A. Eaton
Angela M. Gronenborn
Barry H. Honig
Robert Langer
Michael Levitt
Gregory A. Petsko

**Cellular and Developmental
Biology**
C. David Allis
Donald D. Brown
Eric H. Davidson
Brigid L. M. Hogan
Eric N. Olson
Michael Rosbash
David D. Sabatini
Gertrud M. Schüpbach

**Cellular and Molecular
Neuroscience**
Pietro V. De Camilli
Richard L. Huganir
L. L. Iversen
Yuh-Nung Jan
Eve Marder
Jeremy Nathans
Charles F. Stevens
Thomas C. Südhof
Joseph S. Takahashi
Richard W. Tsien

Chemistry
Stephen J. Benkovic
Harry B. Gray
Michael L. Klein
Raphael D. Levine
Jerrold Meinwald
Nicholas J. Turro

**Computer and
Information Sciences**
William H. Press

Economic Sciences
Roy Radner
Jose A. Scheinkman

Engineering Sciences
Mark E. Davis
Evelyn L. Hu
Katepalli R. Sreenivasan

**Environmental Sciences
and Ecology**
Robert E. Dickinson
David M. Karl
Robert May
David W. Schindler

Evolutionary Biology
Francisco J. Ayala
May R. Berenbaum
Sean B. Carroll
W. Ford Doolittle
Douglas J. Futuyma
Daniel L. Hartl
Masatoshi Nei
Gene E. Robinson

Genetics
Kathryn V. Anderson
Thomas W. Cline
Stanley N. Cohen
Barry Ganetzky
Iva S. Greenwald
Jeffrey C. Hall
Philip C. Hanawalt
Rudolf Jaenisch

Mary-Claire King
Jasper Rine
Reed B. Wickner

Geology
W. G. Ernst
James P. Kennett

Geophysics
Mark H. Thiemens

**Human Environmental
Sciences**
Ruth S. DeFries
Susan Hanson

Immunology
Peter Cresswell
Douglas T. Fearon
Tak Wah Mak
Philippa Marrack
William E. Paul
Ralph M. Steinman
Tadatsugu Taniguchi
Arthur Weiss

Mathematics
Richard V. Kadison
Robion C. Kirby

**Medical Genetics,
Hematology, and
Oncology**
C. Thomas Caskey
Joseph L. Goldstein
Mark T. Groudine
Tony Hunter
Philip W. Majerus
Inder M. Verma

**Medical Physiology
and Metabolism**
Charles A. Dinarello
Robert J. Lefkowitz
Salvador Moncada
David W. Russell

Microbial Biology
John M. Coffin
R. John Collier
Emil C. Gotschlich
E. Peter Greenberg
Diane E. Griffin
Peter M. Howley
Ralph R. Isberg
Elliott D. Kieff
Robert A. Lamb
Peter Palese
Thomas E. Shenk
Thomas J. Silhavy
Thomas E. Wellems

Physics
Anthony Leggett
Paul C. Martin
José N. Onuchic

**Physiology and
Pharmacology**
Richard W. Aldrich
Susan G. Amara
David Julius
Arthur Karlin
Ramón Latorre

Plant Biology
David Baulcombe
Anthony R. Cashmore
Maarten J. Chrispeels
Enrico Coen
Joseph R. Ecker
Robert Haselkorn
June B. Nasrallah

**Plant, Soil, and
Microbial Sciences**
Roger N. Beachy
James C. Carrington
Brian J. Staskawicz

**Psychological and Cognitive
Sciences**
J. Anthony Movshon
Dale Purves
Edward E. Smith

Social and Political Sciences
Alejandro Portes
Brian Skyrms
Kenneth W. Wachter

Sustainability Science
Barry R. Bloom
William C. Clark
Partha Sarathi Dasgupta
Robert W. Kates
Pamela A. Matson
Elinor Ostrom
Hans Joachim Schellnhuber

Systems Biology
Marc W. Kirschner

Systems Neuroscience
Thomas D. Albright
Robert Desimone
Fred H. Gage
Charles D. Gilbert
Marcus E. Raichle
Leslie G. Ungerleider

Submission to PNAS

Authors (members and nonmembers) may submit their manuscripts directly to PNAS at www.pnascentral.org. Authors must recommend three appropriate Editorial Board members, three NAS members who are expert in the paper's scientific area, and five qualified referees. No Academy member sponsor is required.

PNAS (ISSN-0027-8424) is published weekly in print by the National Academy of Sciences.

Correspondence: PNAS, 700 11th Street, NW, Suite 450, Washington, DC 20001 USA. E-mail: PNAS@nas.edu.

Copyright: Volumes 90–105, copyright © 1993–2008 by the National Academy of Sciences of the United States of America, all rights reserved. Volumes 1–89 and 106–107, copyright as a collective work only; author(s) retains copyright to individual articles. **Requests for Permission:** See www.pnas.org/misc/rightperm.shtml for details.

Address requests to reproduce material published in Volumes 1–89 to the original author(s); e-mail other requests to PNASpermissions@nas.edu, fax 1-202-334-2739, or PNAS Permissions Editor, 700 11th Street, NW, Suite 450, Washington, DC 20001 USA. Please cite the exact material to be reprinted and state specifically where it will be used.

Photocopies: PNAS is registered with the Copyright Clearance Center (CCC), 222 Rosewood Drive, Danvers, MA 01923 USA, fax 1-978-750-4470, or www.copyright.com. Authorization to photocopy items for the internal or personal use of specific clients is granted by the National Academy of Sciences provided that the proper fee is paid directly to CCC. **Microforms:** Contact UMI at www.umi.com or P.O. Box 1346, Ann Arbor, MI 48106-1346 USA.

Advertising: Mark Chesnek, 700 11th Street, NW, Suite 450, Washington, DC 20001 USA. Phone 1-202-334-2696, fax 1-202-334-1346, e-mail mchesnek@nas.edu.

Subscriptions: Send payments to PNAS, c/o AIP, P.O. Box 503284, St. Louis, MO 63150-3284 USA. For subscription help, e-mail subs@aip.org, phone 1-516-576-2270, or visit www.pnas.org/subscriptions. **2010 Rates:** US, individual—\$375 (first class delivery available at a surcharge of \$315); non-US, individual—\$585; US/non-US, institutional online only, \$1,305–7,215. Subscriptions are entered on a calendar-year basis.

Exclusive Agent for Subscribers in Japan: USACO Corporation, 17-12 Higashi-Azabu, 2-Chome, Minato-ku, Tokyo 106-0044, Japan. Phone 81 3 3505 3256, fax 81 3 3505 6282, e-mail tokyo-sales@usaco.co.jp. **Change of Address:** PNAS, c/o AIP, Suite 1N01, 2 Huntington Quadrangle, Melville, NY 11747 USA. Phone 1-800-344-6902, fax 1-516-349-9704, e-mail subs@aip.org. Please send notification 6 weeks in advance and list the old and new addresses. **Claims:** Requests for replacement copies will not be honored more than 60 days after the issue date for domestic subscribers and not more than 90 days after the issue date for foreign subscribers. Claims will not be honored for more than two issues per calendar year for the same subscriber. To make a claim, e-mail subs@aip.org or call 1-800-344-6902. **Single Copies:** \$40 per issue in the US, \$50 non-US. To order, e-mail subs@aip.org or call 1-800-344-6902. **Canadian GST:** Registration Number R-133130880.

Postmaster: Send address changes to PNAS, c/o AIP, Suite 1N01, 2 Huntington Quadrangle, Melville, NY 11747 USA. Periodicals postage paid at Washington, DC, and additional mailing offices.

PNAS is available online at www.pnas.org.
PRINTED IN THE USA



Printed on acid-free paper effective Volume 84, Issue 1, and on 80% post-consumer recycled paper effective Volume 107, Issue 1. Printed with soy ink.

PNAS STAFF

Publisher
Kenneth R. Fulton

Executive Editor
Diane M. Sullenberger

Managing Editor
Daniel H. Salsbury

Recruiting Editor
David Stopak

Editorial Staff
James B. Allison
Josiah W. Armour
Teresa V. Callahan
Kirti Chadha
Victoria Chihos
Ryan Conley
Julia M. Diez d'Aux
Kathleen E. Dugan
Benjamin Jipson
Meredith C. Jones
Nicole Joy
Eitta Kavanagh
Jacob Kendall-Taylor
Kay McLaughlin
Kathryn Murphy
Tom Myers
Prashant Nair
Jennifer Nelson
Nhat-Thanh Ngo
Matthew Parks
May B. Piotrowski
Dane Secor
Megan Stevens

Production Manager
Dana M. Compton

Production Staff
Kelly A. Gerrity
Sophie Mohin
Kelly A. Newton
Kat Rodenhizer
Audrey Springer

Marketing Manager
Mark Chesnek

Marketing Staff
Jennifer Bradley

Media Staff
Sola Ayeni-Biu
Todd Johnston
Jenny Ruth Morber
Ashley Truxon

Finance Manager
Simone Marshall-Campbell

Business Staff
Metina Booze
Juanita Culler
Sara Spizzirri

Authorship

Authorship should be limited to those who have contributed substantially to the work. Authors must indicate their specific contributions to the published work; this information will be published as a footnote to the paper. The corresponding author must have obtained permission from all authors for the submission of each version of the paper and for any change in authorship.

Conflict of Interest

All authors, members, referees, and editors must disclose any association that poses a conflict of interest in connection with the manuscript. Authors must acknowledge all funding sources supporting the work. See www.pnas.org/misc/coi.shtml for details.

Supporting Information

Authors may use Supporting Information to enhance their papers in PNAS by providing additional substantive material for online posting, but the print version of the paper must stand on its own merits.

Cover Images

Authors are encouraged to submit scientifically interesting and visually arresting images for the cover.

Information for Authors

Please see the complete Information for Authors, available online at www.pnas.org.

PNAS Online

PNAS articles are published daily online before print at www.pnas.org in PNAS Early Edition.

The articles in PNAS report original research by independent authors and do not necessarily represent the views of the National Academies.