

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

EDITOR-IN-CHIEF
Inder M. Verma

ASSOCIATE EDITORS

Richard Eisenberg
Alan Fersht
Dolores R. Piperno
Solomon H. Snyder
B. L. Turner II
Peter K. Vogt
Stephen T. Warren
David A. Weitz
Susan R. Wessler

EDITORIAL BOARD

**Animal, Nutritional, and
Applied Microbial Sciences**

David L. Denlinger
John J. Eppig
R. Michael Roberts
Linda J. Saif

Anthropology

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

Applied Mathematical Sciences

Peter J. Bickel
David L. Donoho

Applied Physical Sciences

Francisco de la Cruz
John D. Weeks

Astronomy

Neta A. Bahcall

Biochemistry

Michael R. Botchan
F. Ulrich Hartl
Edward D. Korn
Stephen C. Kowalczykowski
John Kuriyan
Michael A. Marletta
Kiyoshi Mizuuchi
Charles M. Radding
Venkatraman Ramakrishnan
James A. Wells

**Biophysics and
Computational Biology**

David Baker
Adriaan Bax
Axel T. Brunger
William A. Eaton
Angela M. Gronenborn
Barry H. Honig
Robert Langer
Michael Levitt
Gregory A. Petsko
John W. Sedat

**Cellular and Developmental
Biology**

Eric H. Davidson
Brigid L. M. Hogan
Eric N. Olson
Michael Rosbash

David D. Sabatini
Gertrud M. Schüpbach
Richard A. Young

**Cellular and Molecular
Neuroscience**

David E. Clapham
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

Chemistry

Stephen J. Benkovic
Harry B. Gray
Jack Halpern
Michael L. Klein
Raphael D. Levine
Tobin J. Marks
Jerrold Meinwald
Peter J. Rossky
David A. Tirrell

**Computer and
Information Sciences**

Butler W. Lampson
William H. Press

**Earth, Atmospheric, and
Planetary Sciences**

Thure E. Cerling
W. G. Ernst
Mark H. Thieme

Economic Sciences

Roy Radner
Jose A. Scheinkman

Engineering Sciences

Alexis T. Bell
Mark E. Davis
Pablo G. Debenedetti
Mildred S. Dresselhaus
Evelyn L. Hu

**Environmental Sciences
and Ecology**

Robert E. Dickinson
Paul G. Falkowski
David M. Karl
Simon A. Levin
Robert May
William W. Murdoch
David W. Schindler

Evolutionary Biology

May R. Berenbaum
W. Ford Doolittle
Douglas J. Futuyma
Daniel L. Hartl
David M. Hillis
Richard E. Lenski
Masatoshi Nei
Gene E. Robinson
Neil H. Shubin

Genetics

Kathryn V. Anderson
Stanley N. Cohen

Barry Ganetzky
Iva S. Greenwald
Jeffrey C. Hall
Philip C. Hanawalt
Mary-Claire King
Douglas E. Koshland
Jasper Rine
Allan C. Spradling
Reed B. Wickner

Human Environmental Sciences

Ruth S. DeFries
Susan Hanson

Immunology

Peter Cresswell
Douglas T. Fearon
Tak Wah Mak
Philippa Marrack
Ruslan Medzhitov
William E. Paul
Tadatsugu Taniguchi
Arthur Weiss

Mathematics

Richard V. Kadison
Robion C. Kirby
Kenneth A. Ribet

**Medical Genetics, Hematology,
and Oncology**

Dennis A. Carson
C. Thomas Caskey
Joseph L. Goldstein
Mark T. Groudine
Tony Hunter
Philip W. Majerus
Gregg L. Semenza
Owen N. Witte

**Medical Physiology
and Metabolism**

Robert J. Lefkowitz
David J. Mangelsdorf
David W. Russell

Microbial Biology

John M. Coffin
R. John Collier
Stephen P. Goff
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

Curtis G. Callan, Jr.
Anthony Leggett
Herbert Levine
Boris I. Shraiman

**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**

James C. Carrington
Vicki L. Chandler
Brian J. Staskawicz

**Psychological and Cognitive
Sciences**

Michael S. Gazzaniga
Wilson S. Geisler
Dale Purves

Social and Political Sciences

Adrian Raftery
Kenneth W. Wachter
Mary C. Waters

Sustainability Science

Anthony J. Bebbington
Barry R. Bloom
F. Stuart Chapin III
William C. Clark
Ruth S. DeFries
Susan Hanson
Emilio F. Moran
Stephen Polasky
Hans Joachim Schellnhuber
B. L. Turner II

Systems Biology

Wing Hung Wong

Systems Neuroscience

Thomas D. Albright
Robert Desimone
Fred H. Gage
Charles D. Gilbert
J. Anthony Movshon
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, 500 Fifth Street, NW, NAS 340, 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 106–110, 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 202-334-2739, or PNAS Permissions Editor, 500 Fifth Street, NW, NAS 340, 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 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.

Subscriptions: Send payments to National Academy of Sciences, P.O. Box 417404, Boston, MA 02241-7404 USA. For subscription help, e-mail pnas.subs@sheridan.com, phone 717-632-3535, or visit www.pnas.org/subscriptions. **2014**

Rates: Individual online only—\$230; US/non-US, institutional online only, \$475–\$8040. Subscriptions are entered on a calendar-year basis.

International Subscribers: Sales agent information can be found online at www.pnas.org/site/subscriptions/orders.shtml. **Change of Address:** PNAS, Subscriber Services, PO Box 465, Hanover, PA 17331 USA. Phone 717-632-3535, e-mail pnas.subs@sheridan.com. 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 pnas.subs@sheridan.com or call 717-632-3535.

Single Copies: \$40 per issue in the US, \$50 non-US. To order, e-mail pnas.subs@sheridan.com or call 717-632-3535. **Canadian GST:** Registration Number R-133130880.

Postmaster: Send address changes to PNAS, Subscriber Services, PO Box 465, Hanover, PA 17331 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

Deputy Executive Editor

Daniel H. Salsbury

Recruiting Staff

David J. Harris

David Stopak

Editorial Staff

James B. Allison

Josiah W. Armour

Teresa V. Callahan

Ryan Conley

Samantha Fuller

Allyson Heisler

Elizabeth Huhn

Meredith C. Jones

Etta Kavanagh

Jacob Kendall-Taylor

Jeffrey King

Jay Leamy

Kathryn Murphy

Tom Myers

Greg Pelkofski

May B. Piotrowski

Emilie Raymer

Andrew Schroeder

Dane Secor

Jared Stevenson

Publication Director

Dana M. Compton

Production Staff

Katherine Brown

Benjamin Jipson

Kay McLaughlin

Kelly Newton

Kat Rodenhizer

Audrey Springer

Marketing Staff

Brittany Campbell

Media Staff

Prashant Nair

Sandeep Ravindran

Luwam A. Yeibio

Nicholette Zeliadt

Senior Finance Officer

Janice Guzman

Business Staff

Rachel Howard

Shenine Shelton

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.