

PRESIDENT OF THE ACADEMY

Marcia K. McNutt

EDITOR-IN-CHIEF

May R. Berenbaum

ASSOCIATE EDITORS

Huda Akil
Richard Eisenberg
Angela M. Gronenborn
Philippa Marrack
Dolores R. Piperno
Natasha V. Raikhel
Christine E. Seidman
Neil H. Shubin
B. L. Turner II
Stephen T. Warren
Mary C. Waters
David A. Weitz

ARTHUR M. SACKLER COLLOQUIUM EDITORS

Baruch Fischhoff
Dietram A. Scheufele

EDITORIAL BOARD

Animal, Nutritional, and Applied Microbial Sciences

Stephen M. Beverley
David L. Denlinger
John J. Eppig
Caroline S. Harwood
R. Michael Roberts
Linda J. Saif

Anthropology

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

Applied Mathematical Sciences

Peter J. Bickel
David L. Donoho
Donald B. Rubin
James A. Sethian
Bin Yu

Applied Physical Sciences

Gabriel Aeppli
Zachary Fisk
Angel Rubio
John D. Weeks

Astronomy

Neta A. Bahcall

Biochemistry

Michael R. Botchan
F. Ulrich Hartl
Stephen C. Kowalczykowski
Kiyoshi Mizuuchi
Brenda A. Schulman
James A. Wells

Biophysics and

Computational Biology

David Baker
Adriaan Bax
Axel T. Brunger
William F. DeGrado
Alan Fersht
Yale E. Goldman
Barry H. Honig
Robert Langer
Michael Levitt
Susan Marqusee
J. Andrew McCammon
Peter B. Moore
Joseph D. Puglisi
John W. Sedat
Michael F. Summers

Cellular and Developmental Biology

Denis Duboule
Brigid L. M. Hogan
Satyajit Mayor
Roeland Nusse
Michael Rosbash
Janet Rossant
Gertrud M. Schüpbach

Cellular and Molecular Neuroscience

David E. Clapham
Nancy Y. Ip
Yuh-Nung Jan
Jeremy Nathans
Solomon H. Snyder
Charles F. Stevens
Joseph S. Takahashi
Gina Turrigiano

Chemistry

Lia Addadi
Stephen J. Benkovic
Marcetta Y. Darensbourg
Michael L. Klein
Tobin J. Marks
Chad A. Mirkin
Catherine J. Murphy
Amy C. Rosenzweig
Peter J. Rossky

Computer and Information Sciences

William H. Press

Earth, Atmospheric, and Planetary Sciences

Donald E. Canfield
Thure E. Cerling
W. G. Ernst
Jean Jouzel
A. R. Ravishankara
Lisa Tauxe
Mark H. Thiemens

Economic Sciences

Paul R. Milgrom
Jose A. Scheinkman

Engineering Sciences

Alexis T. Bell
James J. Collins
Pablo G. Debenedetti
Evelyn L. Hu
Rakesh K. Jain
John A. Rogers
John H. Seinfeld

Environmental Sciences and Ecology

Edward F. DeLong
Robert E. Dickinson
James A. Estes
Alan Hastings
David M. Karl
Nancy Knowlton
Simon A. Levin
François M. M. Morel
Mary Power
Andrea Rinaldo
David W. Schindler

Evolutionary Biology

W. Ford Doolittle
Scott V. Edwards
Douglas J. Futuyma
Daniel L. Hartl
David M. Hillis
Hopi E. Hoekstra
David Jablonski
Richard E. Lenski
Gene E. Robinson
Nils C. Stenseth
Joan E. Strassmann

Genetics

Kathryn V. Anderson
John Carlson
Iva S. Greenwald
Philip C. Hanawalt
Mary-Claire King
Douglas E. Koshland
Jasper Rine
Allan C. Spradling
Anne M. Villeneuve

Human Environmental Sciences

Arun Agrawal
Anthony J. Bebbington
Ruth S. DeFries
Susan Hanson
Emilio F. Moran
Robert J. Scholes
B. L. Turner II
Arild Underdal

Immunology and Inflammation

Robert L. Coffman
Peter Cresswell
K. Christopher Garcia
Tak Wah Mak
Ruslan Medzhitov
Carl F. Nathan
Lawrence Steinman
Tadatsugu Taniguchi
Arthur Weiss

Mathematics

Robion C. Kirby
Kenneth A. Ribet
Srinivasa S. R. Varadhan

Medical Genetics, Hematology, and Oncology

Anton J. Berns
Dennis A. Carson
C. Thomas Caskey
James E. Cleaver
Joseph L. Goldstein
Tony Hunter
Carol L. Prives
Owen N. Witte

Medical Physiology and Metabolism

Christopher K. Glass
Barbara B. Kahn
Robert J. Lefkowitz
David J. Mangelsdorf
Andrew R. Marks

Microbial Biology

Yuan Chang
John M. Coffin
R. John Collier
Jorge E. Galan
Stephen P. Goff
E. Peter Greenberg
Diane E. Griffin
Ralph R. Isberg
Michael B. A. Oldstone
Peter Palese
Lalita Ramakrishnan

Thomas E. Shenk
Thomas J. Silhavy
Peter K. Vogt

Physics

Curtis G. Callan Jr.
Anthony Leggett
Herbert Levine

Physiology and Pharmacology

Richard W. Aldrich
Susan G. Amara
Francisco Bezanilla
Gail Mandel

Plant Biology

David Baulcombe
Philip N. Benfey
Joseph R. Ecker
June B. Nasrallah
Krishna K. Niyogi
Julian I. Schroeder

Plant, Soil, and Microbial Sciences

Julia Bailey-Serres
Vicki L. Chandler
Sheng Yang He
Donald R. Ort
Craig S. Pikaard
Brian J. Staskawicz

Psychological and Cognitive Sciences

Renee Baillargeon
Susan T. Fiske
Michael S. Gazzaniga
Susan Gelman
Dale Purves
Jennifer Richeson

Social and Political Sciences

Adrian Raftery
Stephen W. Raudenbush
Kenneth W. Wachter

Sustainability Science

Arun Agrawal
Gregory P. Asner
Anthony J. Bebbington
William C. Clark
Ruth S. DeFries
Carl Folke
Susan Hanson
Bonnie J. McCay
Emilio F. Moran
Hans Joachim Schellnhuber
B. L. Turner II
Arild Underdal

Systems Neuroscience

Thomas D. Albright
Emery N. Brown
Robert Desimone
Fred H. Gage
Charles D. Gilbert
Tony Movshon
Marcus E. Raichle
Peter L. Strick
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 is published weekly by the National Academy of Sciences, 500 Fifth Street, NW, NAS 338, Washington, DC 20001.

ISSN 1091-6490 (Online)

ISSN 0027-8424 (Print)

Correspondence: PNAS, 500 Fifth Street, NW, NAS 338, Washington, DC 20001 USA. Email: 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 106–116, copyright as a collective work only; author(s) retains copyright to individual articles. **Requests for Permission:** See www.pnas.org/page/about/rights-permissions for details. Address requests to reproduce material published in Volumes 1–89 to the original author(s); email other requests to PNASpermissions@nas.edu, fax 202-334-2739, or PNAS Permissions Editor, 500 Fifth Street, NW, NAS 338, 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 PNAS, P.O. Box 936110, Atlanta, GA 31193-6110 USA. For subscription help, email pnas.subs@sheridan.com, phone 717-632-3535, or visit www.pnas.org/page/subscriptions/subscribers.

2019 Rates: Individual online only, \$235; institutional online only, \$535–9,060. Subscriptions are entered on a calendar-year basis. **International Subscribers:**

Sales agent information can be found online at www.pnas.org/page/subscriptions/subs-faq#contact.

Change of Address: PNAS, Subscriber Services, PO Box 465, Hanover, PA 17331 USA. Phone 717-632-3535, email pnas.subs@sheridan.com. Please send notification 6 weeks in advance and list the old and new addresses.

PNAS is published online at www.pnas.org.

PNAS STAFF

Publisher

Kenneth R. Fulton

Executive Editor

Diane M. Sullenberger

Deputy Executive Editor

Daniel H. Salsbury

Senior Recruiting Editor

David Stopak

Recruiting Editor

Jennifer Robinson

Front Matter Editor

Gene Russo

Editorial Manager

Etta Kavanagh

Assistant Editorial Managers

Josiah W. Armour

Kathryn Murphy DeTura

Editorial Staff

James B. Allison

Daniela Torres Checo

Pablo Luis Clemente

Brianna Costache

Abigail Fox

Samantha Fuller

Jenny Geyer

Julia Glueck

Jeffrey King

Rachel Laney

Matt Longabaugh

Amy McDermott

Kiefer McDowell

Melanie Michel

Tom Myers

Andrew Schroeder

Megan E. Shuler

Jacob D. Svobodny

Rocio Vidal-Ronchas

Director of Publication

Midori Baer

Editorial Production

Manager

Sharon Jane Chua

Production Staff

Delaney Cruickshank

Elizabeth Griffith

Jennifer H. Nguyen

Danielle Robbins

Kat Rodenhizer

Audrey Springer

Subscription Specialist

Kay McLaughlin

Marketing Associate

Kirsten Ronald

Media and Communications

Manager

Prashant Nair

Media Staff

Brian M. Doctrow

Taylor Gedeon

Melissa Suran

Senior Financial and

Administrative Officer

Anton L. Bandy

Business Staff

Kim Mann

Vilija B. Teel

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/site/authors/coi.xhtml 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 main text 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 at www.pnas.org in PNAS Latest Articles.

The articles in PNAS report original research by independent authors and have not been endorsed by the National Academies.