

PRESIDENT OF THE ACADEMY

Marcia K. McNutt

EDITOR-IN-CHIEF

May R. Berenbaum

ASSOCIATE EDITORS

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

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

Stephen M. Beverley
 David L. Denlinger
 Caroline S. Harwood
 Xiang-Jin Meng
 R. Michael Roberts

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
 Christopher Jarzynski
 Mehran Kardar
 Angel Rubio

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
 Yale E. Goldman
 Barry H. Honig
 Robert Langer
 Michael Levitt
 Karolin Luger
 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
 Roeland Nusse
 Michael Rosbash
 Janet Rossant
 Gertrud M. Schüpbach

Cellular and Molecular Neuroscience

Nancy Y. Ip
 Liqun Luo
 Jeremy Nathans
 Joseph S. Takahashi

Chemistry

Lia Addadi
 Joanna Aizenberg
 Stephen J. Benkovic
 Marcetta Y. Darensbourg
 Tobin J. Marks
 Chad A. Mirkin
 Amy C. Rosenzweig

Computer and Information Sciences

William H. Press

Earth, Atmospheric, and Planetary Sciences

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

Economic Sciences

Matthew O. Jackson
 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
 Hopi E. Hoekstra
 David Jablonski

Richard E. Lenski
 Nancy A. Moran
 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
 Catherine L. Kling
 Robert J. Scholes
 B. L. Turner II
 Arild Underdal

Immunology and Inflammation

Robert L. Coffman
 Peter Cresswell
 K. Christopher Garcia
 Tak Wah Mak
 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
 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

Physics

Curtis G. Callan Jr.
 J. C. Seamus Davis

Anthony Leggett
 Herbert Levine
 Bernard F. Schutz

Physiology and Pharmacology

Richard W. Aldrich
 Susan G. Amara
 Francisco Bezanilla

Plant Biology

David Baulcombe
 Philip N. Benfey
 Dominique Bergmann
 Gloria M. Coruzzi
 Joseph R. Ecker
 June B. Nasrallah
 Krishna K. Niyogi
 Julian I. Schroeder

Plant, Soil, and Microbial Sciences

Julia Bailey-Serres
 Vicki L. Chandler
 Sean Cutler
 Sheng Yang He
 Donald R. Ort
 Craig S. Pikaard
 Pamela C. Ronald

Psychological and Cognitive Sciences

Renee Baillargeon
 Martin S. Banks
 Randall Engle
 Susan T. Fiske
 Michael S. Gazzaniga
 Susan Gelman
 David J. Heeger
 Jennifer Richeson
 Henry L. Roediger
 Elke U. Weber
 Timothy D. Wilson

Social and Political Sciences

Dalton Conley
 Mark Granovetter
 Margaret Levi
 Douglas S. Massey
 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
 Catherine L. Kling
 Bonnie J. McCay
 Hans Joachim Schellnhuber
 B. L. Turner II
 Arild Underdal

Systems Neuroscience

Thomas D. Albright
 Emery N. Brown
 Charles D. Gilbert
 David J. Heeger
 Tony Movshon
 Marcus E. Raichle
 Peter L. Strick
 Leslie G. Ungerleider

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. 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 106–117, copyright as a collective work only; author(s) retains copyright to individual articles. **Requests for Permission:** See <https://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. 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, fax 978-750-4470, or <http://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. For subscription help, email pnas.subs@sheridan.com, phone 717-632-3535, or visit <https://www.pnas.org/page/subscriptions/subscribers>.

2020 Rates: Individual online only, \$235; institutional online only, \$535–9,060. Subscriptions are on a calendar-year basis. **International Subscribers:** Sales agent information can be found at <https://www.pnas.org/page/subscriptions/subs-faq#contact>. **Change of Address:** PNAS, Subscriber Services, PO Box 465, Hanover, PA 17331. 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 <https://www.pnas.org>.

PNAS STAFF

Publisher

Kenneth R. Fulton

Executive Editor

Diane M. Sullenberger

Deputy Executive Editor

Daniel H. Salsbury

Managing Editor

Emma P. Shumeyko

Associate Managing Editor,

Editorial Board Services

Etta Kavanagh

Assistant Managing Editors

Josiah W. Armour

Andrew Schroeder

Senior Recruiting Editor

David Stopak

Front Matter Editor

Gene Russo

Senior Editorial

Coordinators

James B. Allison

Daniela Torres Checo

Pablo Luis Clemente

Jeffrey King

Jacob D. Svobodny

Editorial Staff

Emille Beller

Michael Casini

Adriahna Conway

Emily A. Densmore

Alvin Deskins

Abigail Fox

Abi Franklin

Amy McDermott

Kiefer McDowell

Meghan Ramil

Becca Saltzman

Linda Sjostrom

Lilli Sutton

Evelyn Waugh

Digital Product Manager

Michael S. Hardesty

Product Staff

Danielle Robbins

Kat Rodenhizer

Production Manager

Sharon Jane Chua

Production Staff

Delaney Cruickshank

Chloe Fells

Jennifer H. Nguyen

Audrey Springer

Subscription Specialist

Kay McLaughlin

Marketing/Data Analytics

Manager

Kirsten Ronald

Marketing Assistant

Gerald Allen

Media and Communications

Manager

Prashant Nair

Media Staff

Brian M. Doctrow

Hannah Jordan

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.

Competing Interest

All authors, members, referees, and editors must disclose any association that poses a competing interest in connection with the manuscript. Authors must acknowledge all funding sources supporting the work. See <https://www.pnas.org/page/authors/competing-interest> for details.

Information for Authors

Please see the complete Information for Authors at <https://www.pnas.org>.

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