

JOURNAL OF VIROLOGY

VOLUME 82 • APRIL 2008 • NUMBER 7

Lynn W. Enquist, *Editor in Chief* (2012)
Princeton University

Karen L. Beemon, *Editor* (2012)
Johns Hopkins University

Terence S. Dermody, *Editor* (2009)
Vanderbilt University School of Medicine

Daniel C. DiMaio, *Cover Editor* (2011)
Yale University School of Medicine

Robert W. Doms, *Editor* (2010)
University of Pennsylvania School of Medicine

Donald E. Ganem, *Minireview Editor* (2012)
University of California, San Francisco

Harry B. Greenberg, *Editor* (2008)
Stanford University School of Medicine

Beatrice H. Hahn, *Editor* (2009)
University of Alabama

Michael J. Imperiale, *Editor* (2011)
University of Michigan Medical School

Richard A. Koup, *Editor* (2008)
National Institute of Allergy and Infectious Diseases

Douglas S. Lyles, *Editor* (2012)
Wake Forest University

Grant McFadden, *Editor* (2012)
University of Florida

Jay A. Nelson, *Editor* (2012)
Oregon Health & Science University

Peter M. Palese, *Editor* (2010)
Mount Sinai School of Medicine

Stanley Perlman, *Editor* (2012)
University of Iowa

Nancy Raab-Traub, *Editor* (2011)
University of North Carolina

Charles M. Rice, *Editor* (2008)
The Rockefeller University

Susan R. Ross, *Editor* (2012)
University of Pennsylvania

Rozanne M. Sandri-Goldin, *Editor* (2010)
University of California, Irvine

Bert L. Semler, *Editor* (2012)
University of California, Irvine

Ganes C. Sen, *Editor* (2008)
The Cleveland Clinic Foundation

Anne Simon, *Editor* (2012)
University of Maryland

Ronald Swanstrom, *Editor* (2009)
University of North Carolina School of Medicine

EDITORIAL BOARD

Paul Ahlquist ('08)
Chris Aiken ('09)
Gillian Air ('09)
Lorraine Albritton ('10)
Antonio Alcami ('10)
David Anders ('08)
Raul Andino ('08)
Elliot J. Androphy ('08)
Carlos F. Arias ('09)
Eric Arts ('09)
Ann Arvin ('09)
Walter J. Atwood ('10)
Steve Bachenheimer ('09)
Joel Baines ('09)
Susan C. Baker ('08)
Dennis H. Bamford ('08)
Bruce W. Banfield ('10)
Lawrence Banks ('08)
Ralph Baric ('09)
Eric Barklis ('08)
Dan Barouch ('09)
Ralf Bartenschlager ('08)
David J. Barton ('08)
Chris Basler ('09)
Jeffrey M. Bergelson ('08)
Ben Berkhout ('09)
Ken Berns ('09)
Michael R. Betts ('10)
Paul D. Bieniasz ('08)
John A. Blaho ('10)
Keril Blight ('09)
Gary W. Blissard ('10)
David C. Bloom ('10)
James Borowicz ('08)
Michele Bouloy ('09)
Michel Brahic ('09)
Wade Bresnahan ('08)
David Brian ('09)
Margo A. Brinton ('08)
William Britt ('09)
Chris Broder ('09)
Jay Brown ('08)
Michael Buchmeier ('09)
Dennis R. Burton ('10)
Frederic D. Bushman ('09)
Andrew Byrnes ('10)
Ellen D. Cahir-McFarland ('10)
Craig Cameron ('09)
Gabriella Campadelli-Fiume ('10)
Ann Campbell ('09)
Michael J. Carter ('08)
Roberto Cattaneo ('09)
Bruce W. Chesebro ('09)
Paul Clapham ('10)
John M. Coffin ('09)
Jeffrey I. Cohen ('10)
Anamaris Colberg-Poley ('09)
Marc S. Collett ('10)
Peter Collins ('09)
Teresa Compton ('09)

Richard C. Condit ('10)
Karl-Klaus Conzelmann ('10)
Susan F. Cotmore ('10)
James Crowe ('09)
Bryan Cullen ('10)
James N. Culver ('10)
James Cunningham ('08)
Blossom Damania ('10)
Nancy Davis ('09)
Andrew J. Davison ('10)
William O. Dawson ('10)
Juan Carlos de la Torre ('08)
Mark R. Denison ('08)
Cynthia A. Derdeyn ('10)
Prashant Desai ('09)
Ronald Desrosiers ('09)
Ulrich Desselberger ('09)
Michael S. Diamond ('08)
Dimitar Dimitrov ('09)
Dirk Dittmer ('10)
Valerian Dolja ('08)
Esteban Domingo ('09)
Philip R. Dormitzer ('10)
Tanya Dragic ('08)
Theo Dreher ('08)
Jean D. Dubuisson ('08)
Jackie Dudley ('09)
Rebecca E. Dutch ('09)
Ellie Ehrenfeld ('10)
Maribeth Eiden ('09)
Roselyn J. Eisenberg ('09)
John H. Elder ('08)
Richard M. Elliott ('10)
Michael Emler ('09)
Alan Engelman ('09)
Francis Ennis ('08)
Mariano Esteban ('10)
Roger Everett ('10)
Erik Falck-Pedersen ('10)
Paul J. Farrell ('10)
Michael Farzan ('09)
Heinz Feldmann ('08)
Ana Fernandez-Sesma ('09)
Jane Flint ('08)
Ron Fouchier ('10)
Genoveffa Franchini ('09)
Manuel Franco ('09)
Nigel Fraser ('09)
Eric O. Freed ('08)
Daved H. Fremont ('10)
Teryl Frey ('09)
Ilya Frolov ('10)
Klaus Frueh ('10)
Robert S. Fujinami ('08)
Dana H. Gabuzda ('08)
Michael Gale ('10)
Thomas Gallagher ('08)
Robert Garcea ('09)
J. Victor Garcia-Martinez ('10)
Adolfo Garcia-Sastre ('10)
Richard Gaynor ('09)

Adam P. Geballe ('10)
Chou-Zen Giam ('09)
Donald Gilden ('08)
Stephen P. Goff ('09)
Francisco Gonzalez-Scarano ('08)
Felicia Goodrum ('10)
Heinrich Gottlinger ('08)
Patrick Green ('10)
Charles Grose ('09)
Linda Guarino ('09)
Nancy Haigwood ('09)
Otto A. Haller ('08)
Linda Hanley-Bowdoin ('10)
J. Marie Hardwick ('08)
Reuben Harris ('10)
Ronald Hartig ('09)
Kim Hasenkrug ('09)
S. Diane Hayward ('10)
Patrick Hearing ('09)
Franz Heinz ('09)
Mark Heise ('08)
Ann B. Hill ('08)
Vanessa Hirsch ('09)
James M. Hogle ('09)
Brenda Hogue ('09)
Thomas Hohn ('08)
Eddie Holmes ('09)
Fred Homa ('09)
Edward A. Hoover ('09)
Thomas Hope ('09)
Curt M. Horvath ('10)
Jim Hoxie ('09)
Jianming Hu ('10)
Stephen Hughes ('09)
Lindsey Hutt-Fletcher ('08)
Bertram Jacobs ('08)
Michael A. Jarvis ('10)
Ronald T. Javier ('10)
Kuan-Teh Jeang ('09)
David C. Johnson ('08)
R. Paul Johnson ('10)
Welkin Johnson ('09)
Paul Jolicœur ('08)
Jae Jung ('09)
David Kabat ('08)
Cheng Kao ('09)
Michael Katze ('08)
Yoshihiro Kawaoka ('10)
Kenneth Kaye ('09)
Vineet N. KewalRamani ('09)
Alexander Khromykh ('10)
Elliott Kieff ('08)
Margaret Kielian ('10)
Paul R. Kinchington ('08)
Frank Kirchhoff ('10)
Karla Kirkegaard ('08)
David Knipe ('08)
Georg Kochs ('10)
Dan Kolakofsky ('08)
Sarah Kopecky-Bromberg ('10)

Ulrich Koszinowski ('09)
Mark Krystal ('08)
Richard Kuhn ('10)
Laimonis Laimins ('09)
Michael Lairmore ('09)
Robert A. Lamb ('09)
Paul F. Lambert ('10)
Nathaniel Landau ('09)
Benhur Lee ('09)
David A. Leib ('08)
Andrew Leigh Brown ('09)
Stanley M. Lemon ('10)
Laura Levy ('10)
Jeffrey Lifson ('10)
Brett Lindenbach ('10)
Maxine L. Linial ('10)
Howard Lipton ('09)
Richard Lloyd ('09)
Dan Loeb ('10)
Volker Lohmann ('10)
Richard Longnecker ('10)
Susana López Charretón ('09)
Anice Lowen ('10)
Jeremy Luban ('08)
Guangxiang G. Luo ('10)
Margaret MacDonald ('10)
Erich Mackow ('09)
Shinji Makino ('10)
Malcolm A. Martin ('08)
John Mascola ('10)
William S. Mason ('09)
Paul S. Masters ('10)
Thomas Mettenleiter ('08)
A. Dusty Miller ('09)
Chris Miller ('09)
Edward S. Mocarski ('08)
David Montefiori ('09)
Ronald C. Montelaro ('08)
Darius Moradpour ('09)
Elizabeth Moran ('08)
Thomas Moran ('10)
Trudy Morrison ('09)
Casey Morrow ('09)
Anne Moscona ('08)
Ashlee V. Moses ('08)
Don Mosier ('09)
Bernard Moss ('10)
Karen L. Mossman ('08)
Karl Mürner ('09)
Brian R. Murphy ('08)
Nicholas A. Muzyczka ('08)
Peter Nagy ('10)
Glen R. Nemerov ('09)
Max L. Nibert ('08)
Stuart T. Nichol ('10)
Janko Nikolich-Zugich ('10)
Edward G. Niles ('10)
Douglas Nixon ('09)
Isabel Suarez Novella ('10)
Don Nuss ('09)
Jennifer Nyborg ('09)
Peter O'Hare ('09)

David A. Ornelles ('08)
Klaus Osterrieder ('10)
James Ou ('09)
Leslie Parent ('10)
Greg Pari ('09)
Griffith D. Parks ('10)
Colin R. Parrish ('10)
John Patton ('09)
Mark E. Peeples ('10)
Andrew Pekosz ('09)
Philip E. Pellett ('10)
Michael Perdue ('09)
Lenore Pereira ('09)
Daniel Perez ('09)
B. Matija Peterlin ('08)
Louis Picker ('09)
Theodore C. Pierson ('10)
David J. Pintel ('10)
James M. Pipas ('08)
Paula Pitha-Rowe ('10)
B. V. Venkataram Prasad ('10)
Vinayaka R. Prasad ('10)
Chris Preston ('09)
Vincent R. Racaniello ('08)
Kathryn L. Radke ('08)
Gerrit Hall ('10)
Robert F. Ramig ('10)
Lee Ratner ('09)
Stuart C. Ray ('10)
Matthias Reddehase ('09)
Barbara Rehmann ('10)
Alan R. Rein ('08)
Rolf Renne ('10)
Marilyn Resh ('10)
Felix A. Rey ('10)
Andrew Rice ('09)
Alan Rickinson ('08)
Bert K. Rima ('10)
Charles R. Rinaldo ('08)
Erle S. Robertson ('10)
Harriet L. Robinson ('09)
George Rohrmann ('10)
Bernard Roizman ('09)
Raymond P. Roos ('10)
John K. Rose ('10)
Monica Roth ('10)
Rob Ruigrok ('09)
Bill Ruyechan ('09)
Charles E. Samuel ('08)
Peter Sarnow ('08)
Quentin Sattentau ('09)
Dorothea L. Sawicki ('09)
Priscilla A. Schaffer ('08)
Brian Schaffhausen ('10)
John Schiller ('10)
Connie S. Schmaljohn ('10)
Matthias S. Schnell ('08)
Paul Sharp ('09)
Megan L. Shaw ('10)
Kunitada Shimotohno ('10)
Stuart Siddell ('09)

Aleem Siddiqui ('09)
Robert Siliciano ('09)
Robert Silverman ('09)
Guido Silvestri ('09)
Tony Simmons ('09)
John Sinclair ('10)
John Sixbey ('10)
Mark Slifka ('10)
James Smiley ('09)
Greg Smith ('09)
Eric Snijder ('09)
Joseph Sodroski ('09)
Richard R. Spaete ('10)
Patricia G. Spear ('08)

Paul Spearman ('09)
Samuel Speck ('09)
Deborah Spector ('09)
Katherine R. Spindler ('08)
Arun Srivastava ('09)
Leonidas Stamatatos ('09)
Mario Stevenson ('08)
Mark F. Stinski ('10)
Victor Stollar ('09)
Jonathan P. Stoye ('08)
Klaus Strebel ('09)
Daniel Strelow ('10)
William Sugden ('08)
Ren Sun ('08)

Wesley I. Sundquist ('08)
Richard Sutton ('09)
Yuri Svitkin ('09)
Sankar Swaminathan ('10)
John M. Taylor ('10)
Alice Telesnitsky ('08)
Timothy Tellinghuisen ('10)
Mary J. Tevethia ('08)
Heinz-Juergen Thiel ('09)
David A. Thorley-Lawson ('10)
Steven Tracy ('09)
Paula Traktman ('10)
Didier Trono ('08)

Terrance Tumpey ('09)
Kenneth L. Tyler ('10)
Luis P. Villarreal ('09)
Herbert W. Virgin IV ('08)
Peter K. Vogt ('08)
Volker M. Vogt ('08)
Bruce Walker ('09)
Christopher Walker ('09)
Fred C. Wang ('09)
Richard Ward ('09)
David Watkins ('08)
Scott Weaver ('10)
Susan Weiss ('09)
Sandra Weller ('08)

Judith White ('09)
J. Lindsay Whitton ('10)
Reed B. Wickner ('09)
Luc L. Willems ('08)
Bryan Williams ('10)
Carolyn Williamson ('10)
Scott W. Wong ('10)
David L. Woodland ('10)
Richard Wyatt ('08)
Otto Yang ('09)
T. S. Benedict Yen ('10)
Jonathan Yewdell ('08)
Jerome Zack ('10)

Samuel Kaplan, *Chairman, Publications Board*

Barbara M. Goldman, *Director, Journals*

Julie Nachman, *Assistant Production Editor*

Judith Nedrow, *Production Editor*

Karen Esplin, *Assistant Production Editor*

The *Journal of Virology* (ISSN 0022-538X), a publication of the American Society for Microbiology (ASM), 1752 N St., N.W., Washington, DC 20036-2904, is devoted to the dissemination of fundamental knowledge concerning viruses of bacteria, plants, and animals. Investigators are invited to submit reports of original research in all areas of basic virology, including biochemistry, biophysics, genetics, immunology, morphology, physiology, and pathogenesis and immunity. Instructions to authors are published in the January issue each year; reprints are available online and from the Journals Department. The *Journal* is issued twice monthly, one volume per year. Nonmember print subscription prices (per year) are: \$1,800, U.S.; \$1,931, Canada (plus 6% GST, or 14% GST+HST where applicable); \$1,985, Europe; \$2,046, Latin America; \$2,053, rest of world. Member print subscription prices (per year) are: \$264, U.S.; \$413, Canada (plus 6% GST, or 14% GST+HST where applicable); \$449, Europe; \$510, Latin America; \$517, rest of world. Single copies are: \$100, nonmember; \$50, member (Canadians add 6% GST, or 14% GST+HST where applicable). For prices of electronic versions, contact the Subscriptions Unit, ASM. Correspondence relating to subscriptions, defective copies, missing issues, and availability of back issues should be directed to the Subscriptions Unit, ASM; correspondence relating to reprint orders should be directed to the Reprint Order Unit, ASM; and correspondence relating to disposition of submitted manuscripts, proofs, and general editorial matters should be directed to the Journals Department, American Society for Microbiology, 1752 N St., N.W., Washington, DC 20036-2904. Phone: (202) 737-3600.

Claims for missing issues from residents of the United States, Canada, and Mexico must be submitted within 3 months after publication of the issues; residents of all other countries must submit claims within 6 months of publication of the issues. Claims for issues missing because of failure to report an address change or for issues "missing from files" will not be allowed.

Periodicals postage paid at Washington, DC 20036, and at additional mailing offices.

POSTMASTER: Send address changes to *Journal of Virology*, ASM, 1752 N St., N.W., Washington, DC 20036-2904.

Made in the U.S.A. Printed on acid-free paper.

doi:10.1128/JVI.82.7.2008

CODEN: JOVIAM

Copyright © 2008, American Society for Microbiology. All Rights Reserved.

The code at the top of the first page of an article in this journal indicates the copyright owner's consent that copies of the article may be made for personal use or for personal use of specific clients. This consent is given on the condition, however, that the copier pay the stated per-copy fee through the Copyright Clearance Center, 222 Rosewood Drive, Danvers, MA 01923, for copying beyond that permitted by Sections 107 and 108 of the U.S. Copyright Law. This consent does not extend to other kinds of copying, such as copying for general distribution, for advertising or promotional purposes, for creating new collective works, or for resale.