

# APPLIED AND ENVIRONMENTAL MICROBIOLOGY

VOLUME 75 • MARCH 2009 • NUMBER 5

**L. Nicholas Ornston**, *Editor in Chief* (2011)  
*Yale University*

**Daniel J. Arp**, *Minireview Editor* (2009)  
*Oregon State University*

**Axel A. Brakhage**, *Editor* (2011)  
*HKI and University of Jena*

**Daniel Cullen**, *Editor* (2012)  
*USDA Forest Products Laboratory*

**Harold L. Drake**, *Editor* (2012)  
*University of Bayreuth*

**Katharine J. Gibson**, *Editor* (2011)  
*DuPont Experimental Station*

**Lone Gram**, *Editor* (2011)  
*Technical University of Denmark*

**Mansel W. Griffiths**, *Editor* (2010)  
*University of Guelph*

**Sophia Kathariou**, *Editor* (2012)  
*North Carolina State University*

**Michael J. Larkin**, *Editor* (2012)  
*The Queen's University of Belfast*

**Laura G. Leff**, *Editor* (2011)  
*Kent State University*

**Frank E. Löffler**, *Editor* (2013)  
*Georgia Institute of Technology*

**Charles R. Lovell**, *Editor* (2010)  
*University of South Carolina*

**Ellen L. Neidle**, *Editor* (2012)  
*University of Georgia*

**Douglas H. Ohlendorf**, *Editor* (2011)  
*University of Minnesota*

**Matthew R. Parsek**, *Cover Editor* (2009)  
*University of Washington*

**Donald W. Schaffner**, *Editor* (2010)  
*Rutgers, The State University of  
New Jersey*

**Janet L. Schottel**, *Editor* (2013)  
*University of Minnesota*

**Alfred M. Spormann**, *Editor* (2011)  
*Stanford University*

**Marylynn V. Yates**, *Editor* (2009)  
*University of California—Riverside*

**Jizhong Zhou**, *Editor* (2013)  
*University of Oklahoma*

## EDITORIAL BOARD

**Yousef Abu Kwaik** (2011)

**Luis A. Actis** (2011)

**Eric Altermann** (2009)

**Gary Andersen** (2010)

**Thomas Andlid** (2010)

**Adam Arkin** (2009)

**Beate Averhoff** (2010)

**Andrea Azcarate-Peril** (2009)

**Felix J. Baerlocher** (2009)

**Michael Bagdasarian** (2009)

**Bert Bago** (2010)

**Christopher E. Bagwell** (2011)

**Alan Bakalinsky** (2009)

**Katherine H. Baker** (2009)

**József Baranyi** (2010)

**Tamar Barkay** (2011)

**Florian Bauer** (2009)

**Gwyn A. Beattie** (2011)

**Harry Beller** (2009)

**Andrew K. Benson** (2009)

**Peter L. Bergquist** (2009)

**Tom Besser** (2010)

**Arvind A. Bhagwat** (2009)

**K. Johanna Bjorkroth** (2010)

**Rafael Blasco** (2010)

**Eckhard Boles** (2009)

**Paola Bonfante** (2009)

**Violaine Bonnefoy** (2010)

**Kathryn J. Boor** (2010)

**Katherine A. Borkovich**  
(2009)

**James Borneman** (2011)

**Dulal Borthakur** (2009)

**Thomas L. Bott** (2009)

**Kostas Bourtzis** (2009)

**Gesche Braker** (2011)

**Michael G. Bramucci** (2011)

**Byron Brehm-Stecher** (2010)

**Frederick Breidt, Jr.** (2010)

**Neil C. Bruce** (2010)

**Alison Buchan** (2011)

**George Bullerjahn** (2010)

**William Burkhardt III** (2010)

**H. J. Busscher** (2010)

**Mark P. Buttner** (2009)

**Murulee Byappanahalli** (2009)

**Douglas R. Call** (2010)

**Terri A. Camesano** (2009)

**Russell W. Carlson** (2010)

**Michael J. Carter** (2010)

**Jinru Chen** (2011)

**Shicheng Chen** (2011)

**Wilfred Chen** (2009)

**Yi Chen** (2011)

**Michael L. Chikindas** (2010)

**Luca Cocolin** (2010)

**James Cole** (2010)

**Michael T. Collins** (2010)

**James M. Cregg** (2009)

**Patricia Cruz** (2010)

**Tom Curtis** (2010)

**Rolf Daniel** (2009)

**Steven L. Daniel** (2011)

**Michelle Danyluk** (2010)

**Atin R. Datta** (2010)

**Frank B. Dazzo** (2010)

**Angelo DePaola, Jr.** (2009)

**Ronald P. de Vries** (2011)

**Alan DiSpirito** (2011)

**Jan Dolfig** (2010)

**Daniel P. Dougherty** (2009)

**Irina S. Druzhinina** (2011)

**Doris d'Souza** (2011)

**Nicole Dubilier** (2010)

**Siobain Duffy** (2010)

**Nancy DuTeau** (2011)

**Richard Eaton** (2010)

**Leo Eberl** (2011)

**T. S. Edrington** (2010)

**Henry L. Ehrlich** (2010)

**Christopher Elkins** (2011)

**Marie Elliot** (2011)

**David Emerson** (2009)

**K.-D. Entian** (2010)

**Slava Epstein** (2010)

**Danilo Ercolini** (2009)

**David Faguy** (2011)

**Joseph O. Falkinham III** (2010)

**Brian Federici** (2009)

**Juan Ferré** (2009)

**Matthew W. Fields** (2011)

**Turlough Finan** (2010)

**Steven E. Finkel** (2010)

**Madilyn Fletcher** (2011)

**Steven Foley** (2011)

**Christopher Francis** (2010)

**James A. Fraser** (2009)

**Herbert L. Fredrickson**  
(2010)

**Masao Fukuda** (2009)

**Rebecca Gast** (2011)

**Manuela Giovannetti** (2009)

**Mark Gomelsky** (2011)

**Heidi Goodrich-Blair** (2009)

**Lawrence Goodridge** (2009)

**Joerg Graf** (2011)

**Irene R. Grant** (2010)

**Leslie Gregg-Jolly** (2011)

**Jean Guard-Bouldin** (2010)

**Mary Lou Guerinot** (2011)

**Martin W. Hahn** (2010)

**Theo A. Hansen** (2010)

**Hauke Harms** (2010)

**Steven Harris** (2011)

**Valerie J. (Jody) Harwood** (2009)

**Terry C. Hazen** (2010)

**Qiang He** (2010)

**Zhili He** (2010)

**Brian Hedlund** (2011)

**Hermann Heipieper** (2011)

**Alfredo Herrera-Estrella** (2011)

**David Hibbett** (2011)

**Russell T. Hill** (2011)

**Dallas G. Hoover** (2009)

**David J. Hopper** (2010)

**Hor-Gil Hur** (2009)

**Fumio Inagaki** (2010)

**Douglas Inglis** (2009)

**Janet K. Jansson** (2010)

**Lee-Ann Jaykus** (2009)

**Tom Jeffries** (2011)

**Paul R. Jensen** (2011)

**Carlos A. Jerez** (2011)

**Mike Jetten** (2010)

**D. Barrie Johnson** (2011)

**Yves Jouanneau** (2009)

**Ari Jumpponen** (2009)

**Juan Luis Jurat-Fuentes**

(2009)

**David Kaplan** (2010)

**Levente Karaffa** (2009)

**Boran Kartal** (2011)

**Charles W. Kaspar** (2010)

**James E. Keen** (2010)

**Martin Keller** (2009)

**John J. Kelly** (2009)

**Robert M. Kelly** (2011)

**Angela Kent** (2010)

**Lee Kerkhof** (2009)

**Philip J. Kersten** (2010)

**Mary Jo Kirisits** (2010)

**Maia Kivisaar** (2010)

**Staffan Kjelleberg** (2011)

**Martin G. Klotz** (2011)

**Allan Konopka** (2011)

**Joel E. Kostka** (2010)

**George Kowalchuk** (2009)

**Lee Krumholz** (2009)

**Indira Kudva** (2010)

**Kirsten Kuesel** (2010)

**Timothy M. LaPara** (2009)

**Laurie LaPat-Polasko** (2009)

**Gisèle LaPointe** (2010)

**Luis Larrondo** (2011)

**Jared Leadbetter** (2010)

**Yin-Won Lee** (2010)

**Mary Beth Leigh** (2010)

**Jeffrey T. LeJeune** (2009)

**Michael Lemke** (2011)

**Tine Rask Licht** (2011)

**Celeste Linde** (2011)

**Markus Linder** (2011)

**Nic D. Lindley** (2010)

**John T. Lisle** (2009)

**Shuang-Jiang Liu** (2011)

**Wen-Tso Liu** (2010)

**Jon Lloyd** (2010)

**G. T. Macfarlane** (2011)

**Sandra Macfarlane** (2011)

**Robert Mach** (2009)

**Walter F. Mahaffee** (2011)

**Antonio Maldonado** (2011)

**Mike Manefield** (2011)

**Helene Marquis** (2009)

**Terence L. Marsh** (2011)

**Andrew P. Martin** (2011)

**Maria Esperanza Martínez-  
Romero** (2010)

Jan Martinussen (2011)	Jakob Pernthaler (2009)	Randall S. Singer (2009)	Paul van der Wielen (2011)
Juergen Marxsen (2011)	M. Julia Pettinari (2011)	Brajesh Singh (2010)	Kumar Venkitanarayanan (2011)
Harold D. May (2010)	Gregg Pettis (2011)	Kaarina Sivonen (2011)	Alain Vertes (2010)
J. Vaun McArthur (2011)	Laurent Philippot (2011)	Joan L. Slonczewski (2011)	Anne K. Vidaver (2011)
Katherine McMahon (2009)	Flynn Picardal (2010)	Kornelia Smalla (2009)	Adrián A. Vojnov (2010)
Brian McSpadden-Gardener (2010)	Roger W. Pickup (2010)	Hauke Smidt (2011)	Gerrit Voordouw (2011)
Rick Meinersmann (2009)	James L. Pinckney (2011)	Patricia A. Sobczyk (2010)	Carmen Wachter (2010)
Jiangong Meng (2009)	Anton F. Post (2010)	John Spear (2010)	Michael Wagner (2010)
William Metcalf (2011)	Rolf Prade (2009)	Andrew Spiers (2010)	Irene Wagner-Döbler (2011)
Patricia D. Millner (2009)	Jim I. Prosser (2011)	Dirk Springael (2009)	Suzanne Walker (2009)
Donald K. Milton (2009)	Cheryl L. Quinn (2009)	Eric Stabb (2010)	Judy D. Wall (2009)
Kiwamu Minamisawa (2011)	John P. Quinn (2009)	Lucas J. Stal (2009)	Peng G. Wang (2009)
William W. Mohn (2011)	Jos M. Raaijmakers (2011)	Alberts J. M. Stams (2010)	Todd Ward (2010)
Sylvain Moineau (2011)	Gerald R. Reeck (2010)	Robert J. Steffan (2010)	Bart Weimer (2010)
Istvan Molnar (2011)	Bernd Rehm (2009)	Alexander Steinbüchel (2011)	Alan Welman (2009)
Melanie Mormile (2010)	Gregor Reid (2009)	Craig Stephens (2009)	Marvin Whiteley (2010)
Volker Müller (2010)	Walter Reineke (2010)	John Stolz (2010)	Martin Wiedmann (2011)
Peter Muriana (2011)	Geoffrey D. Robson (2011)	Wolfgang Streit (2009)	Steve Wilhelm (2009)
Yuji Nagata (2009)	Margie Romine (2011)	Marc Strous (2011)	Rolf-M. Wittich (2011)
István Nagy (2010)	Neil Rowan (2011)	Joseph Sturino (2010)	Mark J. Wolcott (2010)
Cindy H. Nakatsu (2010)	Edward G. Ruby (2010)	Marcelino Suzuki (2010)	K. Eric Wommack (2009)
Diane G. Newell (2010)	Michael J. Sadowsky (2010)	Zuzana Sýkorová (2011)	Thomas K. Wood (2011)
Walter G. Niehaus, Jr. (2010)	Daâd A. Saffarini (2011)	Ken Takai (2010)	Randy Worobo (2010)
Brendan A. Niemira (2009)	Badal C. Saha (2010)	Ralph Tanner (2011)	Michael Wyman (2009)
Hideaki Nojiri (2009)	Andrew D. Sails (2010)	Gerald W. Tannock (2011)	Dong Xu (2011)
Kenneth M. Noll (2011)	Sima Sariaslani (2009)	Ron Teather (2010)	Jian Xu (2010)
Norbert Nowotny (2009)	Brian Sauders (2010)	Andreas Teske (2009)	Jagjit Yadav (2011)
George-John Nychas (2009)	Patrick D. Schloss (2009)	Chris M. Thomas (2009)	Ching-Hong Yang (2011)
Mark R. O'Brian (2009)	Andreas Schmid (2011)	Michael G. Thomas (2009)	Suleyman Yildirim (2011)
Kevin P. O'Connell (2011)	Andreas Schramm (2010)	Ian P. Thompson (2011)	Jill Zeilstra-Ryalls (2011)
Ronald S. Oremland (2009)	Bernhard Seiboth (2011)	Tim Tolker-Nielsen (2009)	Chuanlun Zhang (2009)
Mark Osborn (2010)	Verena Seidl (2009)	Eva M. Top (2009)	Qijing Zhang (2011)
Joerg Overmann (2010)	Verena Seidl (2009)	Effie Tsakalidou (2010)	Erwin G. Zoetendal (2009)
Hans Paerl (2011)	Gordon Shephard (2010)	Masataka Tsuda (2009)	Angeles Zorreguieta (2010)
Rebecca Ehrlich Parales (2011)	Simon D. Silver (2011)	Jos Vanderleyden (2010)	
	Pascal Simonet (2009)	Wouter van der Star (2011)	
	Mitch Singer (2011)		

---

**Thomas E. Shenk**, *Chairman, Publications Board*      **Barbara M. Goldman**, *Director, Journals*  
**Barbara S. Slinker**, *Production Editor*  
**Ellie Ghatineh**, *Assistant Production Editor*      **Michael E. Lerman**, *Assistant Production Editor*

---

*Applied and Environmental Microbiology* (ISSN 0099-2240), a publication of the American Society for Microbiology (ASM), 1752 N St., N.W., Washington, DC 20036-2904, is devoted to the advancement and dissemination of applied knowledge as well as ecological knowledge, both applied and fundamental, concerning microorganisms. Instructions to authors are published in the January issue each year; reprints are available online and from the Journals Department. *Applied and Environmental Microbiology* is published twice monthly, one volume per year. Nonmember print subscription prices (per year) are: \$1,361, U.S.; \$1,455, Canada (plus 5% GST, or 13% HST where applicable); \$1,471, Europe; \$1,508, Latin America; \$1,512, rest of world. Member print subscription prices (per year) are: \$173, U.S.; \$288, Canada (plus 5% GST, or 13% HST where applicable); \$283, Europe; \$320, Latin America; \$324, rest of world. Single copies are: \$100, nonmember; \$50, member (Canadians add 5% GST, or 13% 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: (205) 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 *Applied and Environmental Microbiology*, ASM, 1752 N St., N.W., Washington, DC 20036-2904.

Made in the United States of America. Printed on acid-free paper. doi:10.1128/AEM.75.5.2009 CODEN: AEMIDF

Copyright © 2009, 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, Inc., 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.