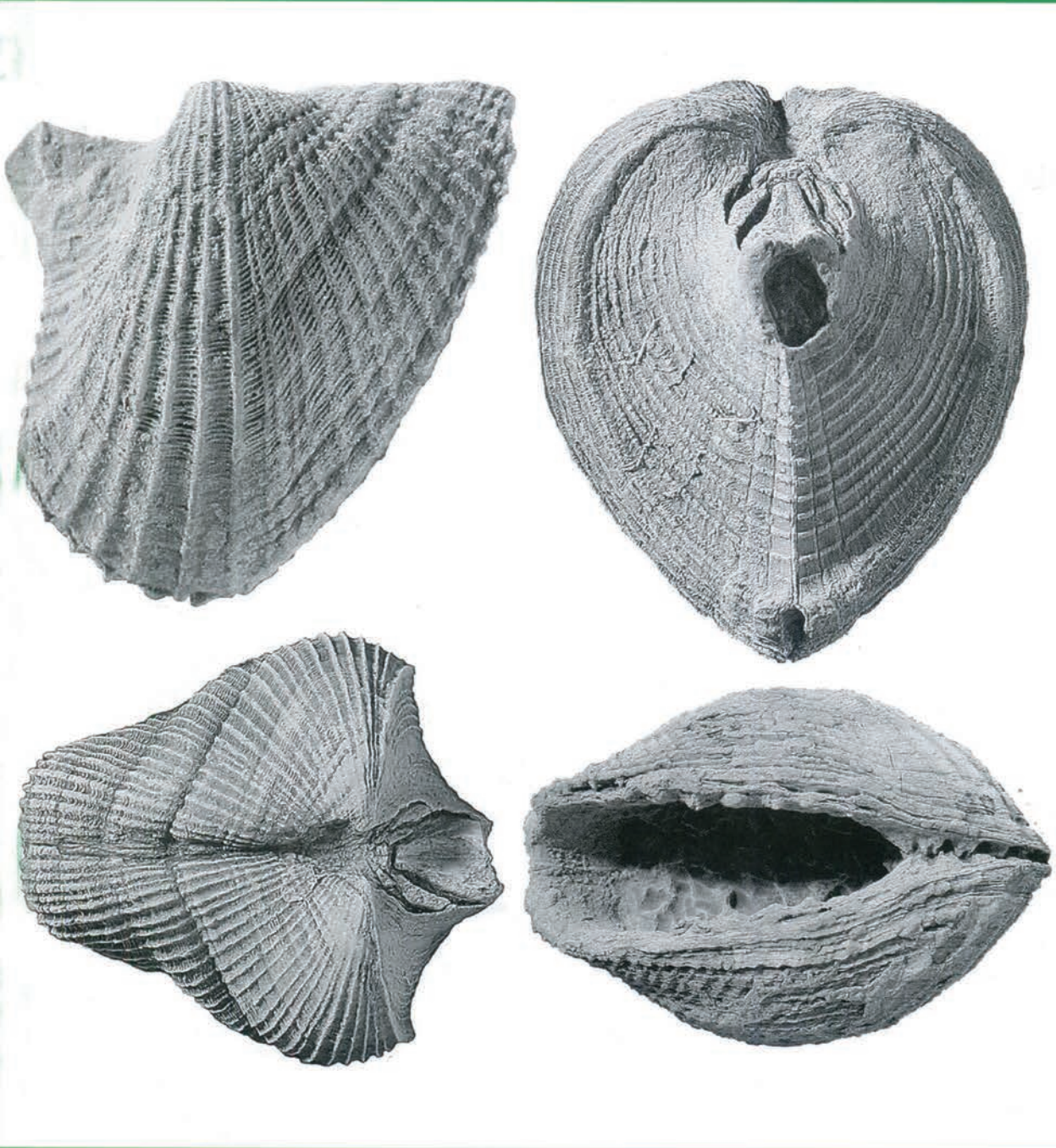


# JOURNAL

OF

# PALEONTOLOGY



VOL 77 □ No 4 □ JULY 2003 □ THE PALEONTOLOGICAL SOCIETY



## OFFICERS AND EDITORS OF THE PALEONTOLOGICAL SOCIETY

### *President*

WILLIAM I. AUSICH, Columbus, OH

### *President-Elect*

DAVID BOTTJER, Los Angeles, CA

### *Past-President*

PATRICIA H. KELLEY, Wilmington, NC

### *Secretary*

CARL W. STOCK

Department of Geological Sciences  
University of Alabama  
Box 870338  
Tuscaloosa, AL 35487-0338

### *Treasurer*

MARK E. PATZKOWSKY

Department of Geosciences  
Pennsylvania State University  
5086 Deike Building  
University Park, PA 16820

### *Program Coordinator*

MARK A. WILSON, Wooster, OH

### *JP Managing Editors*

ANN F. BUDD, Iowa City, IA

BRIAN J. WITZKE, Iowa City, IA

JULIA GOLDEN, Iowa City, IA

JONATHAN ADRAIN, Iowa City, IA

### *JP Associate Editor*

TIMOTHY HAZEN, Iowa City, IA

### *JP Technical Editors*

LAURIE C. ANDERSON, Baton Rouge, LA

GORDON C. BAIRD, Fredonia, NY

ROBERT L. CARROLL, Montréal, Quebec

WILLIAM P. ELDER, Lafayette, CA

ROBERT J. ELIAS, Winnipeg, Manitoba

JOHN R. GROVES, Cedar Falls, IA

THOMAS E. GUENSBURG, Rockford, IL

PETER J. HARRIES, Tampa, FL

MARTIN J. HEAD, Cambridge, UK

RICHARD D. HOARE, Bowling Green, OH

PETER JELL, Queensland, Australia

JOANNE K. KLUESSENDORF, Urbana, IL

THOMAS M. LEHMAN, Lubbock, TX

STEVEN LODUCA, Ypsilanti, MI

ROSALIE F. MADDOCKS, Houston, TX

MIKE MELCHIN, Antigonish, NS

CARL MENDELSON, Beloit, WI

DONALD G. MIKULIC, Champaign, IL

MOLLY F. MILLER, Nashville, TN

P. DAVID POLLY, London, UK

BRIAN R. PRATT, Saskatoon, Saskatchewan

JOHN M. RENSBERGER, Seattle, WA

HOLMES A. SEMKEN, Iowa City, IA

DAVID M. WORK, Augusta, ME

### *JP Book Editor*

ALAN TURNER, Iowa City, IA

### *Paleobiology Co-Editors*

WILLIAM D. DIMICHELE and JOHN PANDOLFI,  
Washington, DC

### *Editor Special Publications*

RUSSELL D. (TIM) WHITE, New Haven, CT

### *Education Coordinator*

DALE A. SPRINGER, Bloomsburg, PA

### *Councilors*

ROBERT A. GASTALDO, Waterville, ME

STEVE M. HOLLAND, Athens, GA

### *Student Representative*

ALYCIA RODE, Lawrence, KS

### *Section Chairs*

Cordilleran: RALPH HITZ, Tacoma, WA

North-Central: DANITA BRANDT,

East Lansing, MI

Northeastern: MARK LECKIE,

Amherst, MA

Rocky Mountain: MICHAEL WILSON, New

Westminster, BC

Southeastern: REESE BARRICK,

Raleigh, NC

South-Central: LANCE L. LAMBERT,

San Antonio, TX

### *Patrons*

ARTHUR J. and BARBARA P. BOUCOT

JAMES C. BROWER

PETER R. CRANE

KARL W. FLESSA

BRIAN F. GLENISTER

PATRICIA H. KELLEY

N. GARY LANE

WILLIAM A. OLIVER, JR.

ALLISON R. (PETE) PALMER

JUNE R. P. and CHARLES A. ROSS

HELEN TAPPAN-LOEBLICH

JOHNNY A. WATERS

SCOTT L. WING

### **Cover illustration:** Rogalla et al., Figure 1.

The JOURNAL OF PALEONTOLOGY (ISSN 0022-3360) is published bimonthly by The Paleontological Society, 810 East 10th St., Lawrence, KS 66044, USA. Dues and subscriptions for members of The Paleontological Society are \$74 per year. Subscription price is \$128 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to The Paleontological Society, 810 East 10th St., Lawrence, KS 66044. For information on prices of back issues of the JOURNAL, please contact: SEPM Business Office, 1731 East 71st St., Tulsa, OK 74136-5108, for volumes 1 (1927) through 59 (1985) or The Paleontological Society Business Office, P.O. Box 1897, 810 East 10th St., Lawrence, KS 66044-8897, for volumes 60 (1986) and following.

Communications about the JOURNAL, notices, subscriptions, rates, changes of address, and nonreceipt of preceding numbers should be addressed to: JOURNAL OF PALEONTOLOGY Subscriptions Office, P.O. Box 1897, 810 East 10th St., Lawrence, KS 66044-8897, USA. Claims for nonreceipt of preceding numbers must be submitted within three months (six months if foreign) of the date of publication in order to be filled gratis. Communications about membership and requests for blanks for nomination of new members in The Paleontological Society should be directed to the Secretary: Carl W. Stock, Department of Geological Sciences, University of Alabama, Tuscaloosa, AL 35487-0338.

### Address manuscripts to:

Editors, Journal of Paleontology, Department of Geology, 121 Trowbridge Hall, University of Iowa, Iowa City, IA 52242-1379, USA, fax: 319-335-1821, e-mail: fossils@uiowa.edu

Technical editors are: Laurie C. Anderson, Department of Geology and Geophysics, Louisiana State University, Baton Rouge, LA 70803; Gordon C. Baird, Department of Geology, State University of New York, Fredonia, NY 14063; Robert L. Carroll, Redpath Museum, McGill University, Montréal, Quebec, H3A 2K6; William P. Elder, 3252 Camino Diablo, Lafayette, CA 94549; Robert J. Elias, Department of Geological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2; John R. Groves, Department of Earth Science, University of Northern Iowa, Cedar Falls, IA 50614; Thomas E. Guensburg, Division of Physical Sciences, Rock Valley College, Rockford, IL 61111; Peter J. Harries, Department of Geology, University of South Florida, Tampa, FL 33620; Martin J. Head, Department of Geography, University of Cambridge, Cambridge CB2 3EN, UK; Richard D. Hoare, Department of Geology, Bowling Green State University, Bowling Green, OH 43403; Joanne K. Kluesendorf, Department of Geology, University of Illinois, Urbana, IL 61801; Thomas M. Lehman, Department of Geosciences, Texas Tech University, Lubbock, TX 79409; Steven LoDuca, Department of Geology and Geography, Eastern Michigan University, Ypsilanti, MI 48197; Rosalie F. Maddocks, Department of Geosciences, University of Houston, Houston, TX 77204; Mike Melchin, Department of Geology, St. Francis Xavier University, Antigonish, NS B2G 2W5; Carl Mendelson, Department of Geology, Beloit College, Beloit, WI 53511; Donald G. Mikulic, Illinois State Geological Survey, Champaign, IL 61820; Molly F. Miller, Geology Department, Vanderbilt University, Nashville, TN 37235; P. David Polly, School of Biological Sciences, University of London, London E1 4NS, UK; Brian R. Pratt, Department of Geological Sciences, University of Saskatchewan, Saskatoon SK S7N 5E2; John M. Rensberger, Department of Geology, University of Washington, Seattle, WA 98195; Holmes A. Semken, Department of Geology, University of Iowa, Iowa City, IA 52242; David M. Work, Maine State Museum, Augusta, ME 04333.

The JOURNAL OF PALEONTOLOGY is printed offset by Allen Press, Inc., Lawrence, KS 66044.

Copyright © 2003, The Paleontological Society  
ALLEN PRESS, INC., LAWRENCE, KANSAS

Visit The Paleontological Society website at  
[paleosoc.org](http://paleosoc.org)

### COPYRIGHT STATEMENT

The appearance of 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 or internal use, or for the personal or internal 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., P.O. Box 765, Schenectady, New York 12301, for copying beyond that permitted by Sections 107 or 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.