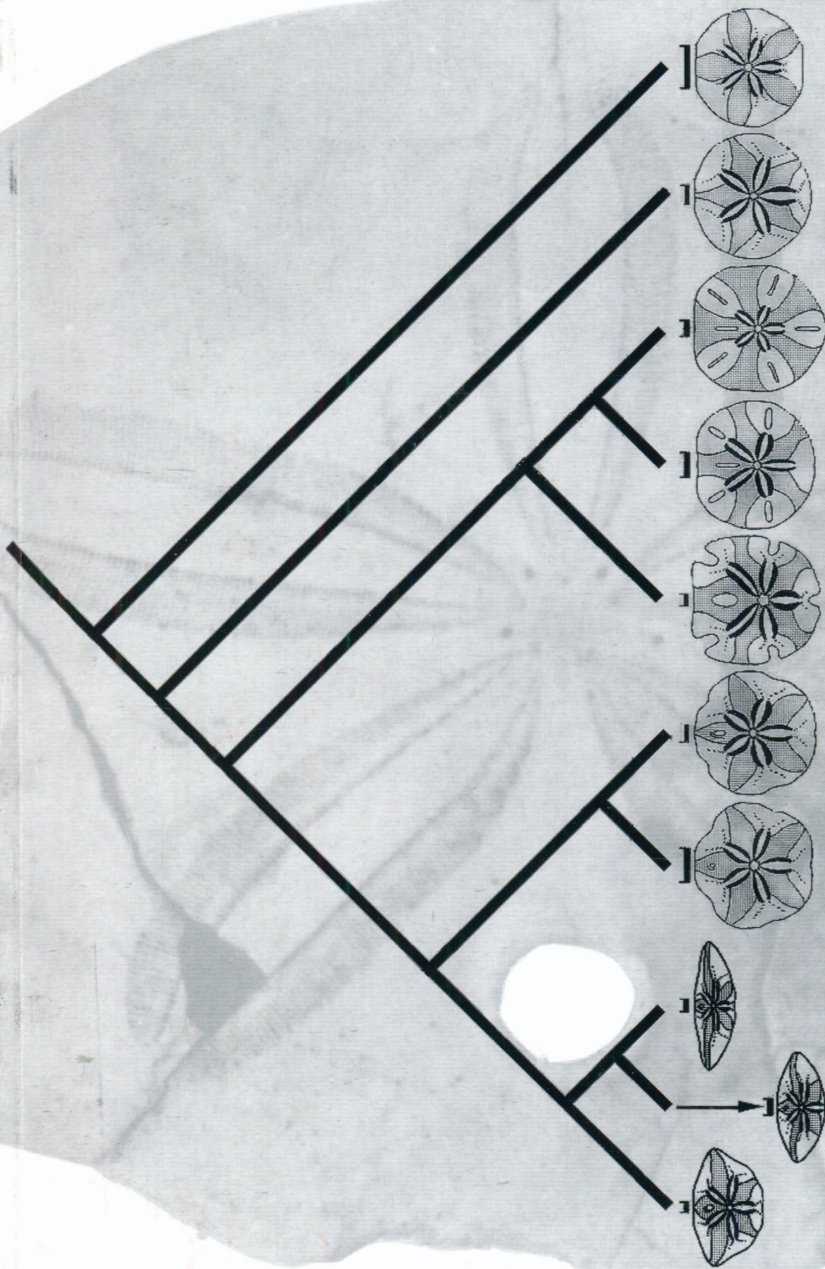


JOURNAL

OF

P
A
L
E
O
N
T
O
L
O
G
Y



VOL 74 ■ No 2 ■ MAR 2000 ■ THE PALEONTOLOGICAL SOCIETY



OFFICERS AND EDITORS OF THE PALEONTOLOGICAL SOCIETY

President

PETER R. CRANE, Chicago, IL

President-Elect

PATRICIA H. KELLEY, Wilmington, NC

Past-President

KARL W. FLESSA, Tucson, AZ

Secretary

CARL W. STOCK

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

Treasurer

THOMAS W. KAMMER,

Dept. of Geology and Geography
West Virginia University
P.O. Box 6300
Morgantown, WV 26506-6300

Program Coordinator

MARY L. DROSER, Riverside, CA

Managing Editors

ANN F. BUDD, Iowa City, IA
BRIAN J. WITZKE, Iowa City, IA
JULIA GOLDEN, Iowa City, IA

Associate Editor

TIMOTHY HAZEN, Iowa City, IA

Technical Editors

LAURIE C. ANDERSON, Baton Rouge, LA
WILLIAM I. AUSICH, Columbus, OH
GORDON C. BAIRD, Fredonia, NY
JAMES E. DAY, Normal, IL
WILLIAM P. ELDER, Lafayette, CA
ROBERT J. ELIAS, Winnipeg, Manitoba
JOHN R. GROVES, Houston, TX
THOMAS E. GUENSBURG, Rockford, IL
MARTIN J. HEAD, Cambridge, UK
RICHARD D. HOARE, Bowling Green, OH
NIGEL C. HUGHES, Riverside, CA
PATRICIA H. KELLEY, Wilmington, NC
JOANNE K. KLUESSENDORF, Urbana, IL
H. RICHARD LANE, Arlington, VA
THOMAS M. LEHMAN, Lubbock, TX
STEVEN LODUCA, Ypsilanti, MI
ROSALIE F. MADDOCKS, Houston, TX
CARL MENDELSON, Beloit, WI
DONALD G. MIKULIC, Champaign, IL
MOLLY F. MILLER, Nashville, TN
MATTHEW H. NITECKI, Chicago, IL
JOHN M. RENSBERGER, Seattle, WA
HOLMES A. SEMKEN, Iowa City, IA

Paleobiology Co-Editors

DOUGLAS H. ERWIN and SCOTT L. WING,
Washington, DC

Editor Special Publications

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

Education Coordinator

DALE A. SPRINGER, Bloomsburg, PA

Councilors

WILLIAM I. AUSICH, Columbus, OH

Student Representative

KATE LYONS, Chicago, IL

Section Chairs

Cordilleran: CAROL M. TANG,
Tempe, AZ and LIZ NESBITT, Seattle, WA
North-Central: DON MIKULIC, Champaign, IL
Northeastern: CYNTHIA G. FISHER,
West Chester, PA
Rocky Mountain: ROBERT C. THOMAS,
Dillon, MT
Southeastern: DAVID SCHWIMMER,
Columbus, GA
South-Central: WALTER L. MANGER,
Fayetteville, AK

Patrons

ARTHUR J. and BARBARA P. BOUCOT
JAMES C. BROWER
PETER R. CRANE
KARL W. FLESSA
BRIAN F. GLENISTER
STEPHEN JAY GOULD
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: Mooi et al., composite.

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 \$67 per year. Subscription price is \$113 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; William I. Ausich, Department of Geology, The Ohio State University, Columbus, OH 43210; Gordon C. Baird, Department of Geology, State University of New York, Fredonia, NY 14063; James E. Day, Department of Geology, Illinois State University, Normal, IL 61761; 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, Amoco Production Company, P.O. Box 3092, Houston, TX 77253; Thomas E. Guensburg, Division of Physical Sciences, Rock Valley College, Rockford, IL 61111; 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; Nigel C. Hughes, Department of Earth Sciences, University of California, Riverside, CA 92521; Patricia H. Kelley, Department of Earth Sciences, University of North Carolina at Wilmington, Wilmington, NC 28403; Joanne K. Kluesendorf, Department of Geology, University of Illinois, Urbana, IL 61801; H. Richard Lane, National Science Foundation, 4201 Wilson Boulevard, Arlington, VA 22230; 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; 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; Matthew H. Nitecki, Department of Geology, Field Museum of Natural History, Chicago, IL 60605; 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.

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

Copyright © 2000, The Paleontological Society
ALLEN PRESS, INC., LAWRENCE, KANSAS

Visit The Paleontological Society website at
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.