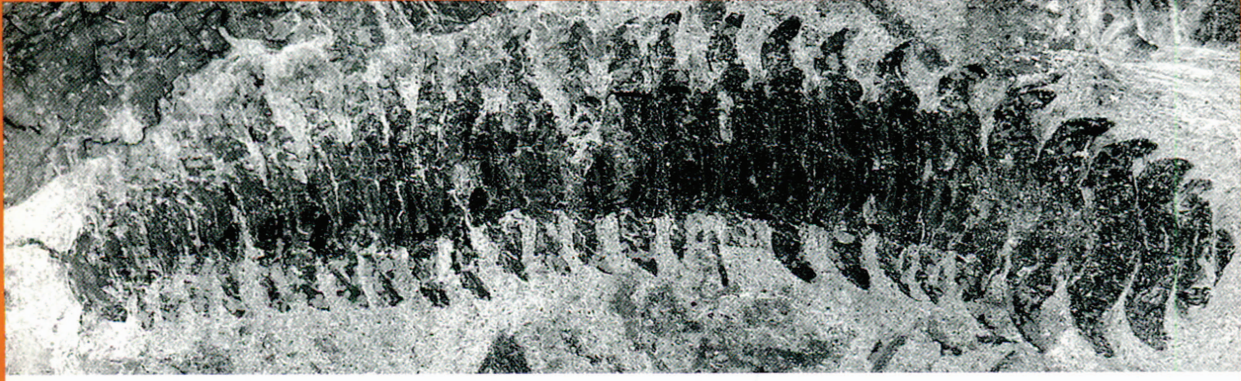


JOURNAL

OF

PALAEONTOLOGY



VOL 79 ■ No 4 ■ JULY 2005 ■ THE PALEONTOLOGICAL SOCIETY



OFFICERS AND EDITORS OF THE PALEONTOLOGICAL SOCIETY

President

WILLIAM I. AUSICH, Columbus, OH
ausich.1@osu.edu

President-Elect

DAVID J. BOTTJER, Los Angeles, CA
dbottjer@usc.edu

Past-President

PATRICIA H. KELLEY, Wilmington, NC
kelley@uncwil.edu

Secretary

ROGER D. K. THOMAS
Department of Earth and Environment
Franklin & Marshall College
P.O. Box 3003
Lancaster, PA 17604-3003
roger.thomas@fandm.edu

Treasurer

MARK E. PATZKOWSKY
Dept. of Geosciences
Pennsylvania State University
506 Deike Bldg.
University Park, PA 16802
brachio@geosc.psu.edu

Program Coordinator

MARK A. WILSON, Wooster, OH
mwilson@wooster.edu

JP Editors

JONATHAN M. ADRAIN, Iowa City, IA
CHRISTOPHER A. BROCHU, Iowa City, IA
ANN F. BUDD, Iowa City, IA

JP Production Editor

LORI VERMAAS, Iowa City, IA

JP Associate Editors

JASON S. ANDERSON, Western University
of Health Sciences
LAURIE C. ANDERSON, Louisiana State University
DANIEL B. BLAKE, University of Illinois
MATTHEW CARRANO, National Museum of
Natural History
ROBERT L. CARROLL, McGill University
RICHARD CIFELLI, University of Oklahoma
KEITH DEWING, Geological Survey of Canada
WILLIAM A. DIMICHELE, Natural Museum of
Natural History
WILLIAM P. ELDER, Lafayette, California
ROBERT J. ELIAS, University of Manitoba
MICHAEL ENGEL, University of Kansas
JOHN R. GROVES, University of Northern Iowa
STEVEN J. HAGEMAN, Appalachian State University
PETER J. HARRIES, University of South Florida
MARTIN HEAD, University of Cambridge
ERIC HILTON, Field Museum of Natural History
PETER JELL, Queensland Museum, Australia
STEPHEN A. LESLIE, University of Arkansas
RICHARD LUPIA, University of Oklahoma
MIKE MELCHIN, St. Francis Xavier University, Canada
MOLLY F. MILLER, Vanderbilt University
BRIAN PRATT, University of Saskatchewan
PETER ROOPNARINE, California Academy of Sciences
ERIC SCOTT, San Bernardino County Museum
JAMES SPRINKLE, University of Texas
STEVE WESTROP, University of Oklahoma
DAVID M. WORK, Maine State Museum
SHUHAI XIAO, Virginia Polytechnic Institute
Paleobiology Co-Editors
WILLIAM 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
LISA E. PARK, Akron, OH

Student Representative

LEIF TAPANILA, Salt Lake City, UT

Section Chairs

Cordilleran: REX ALAN HANGER,
Whitewater, WI
North-Central: CHRISTOPHER JOHN CROW,
Fort Wayne, IN
Northeastern: NEIL E. TIBERT,
Fredericksburg, VA
Rocky Mountain: SCOTT M. RITTER,
Provo, UT
Southeastern: CRAIG W. OYEN,
Shippensburg, PA
South-Central: THOMAS OLSZEWSKI,
College Station, TX

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: Wilson et al., Fig. 4.

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 \$86 per year. Institutional Subscription price is \$165 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 fax: (785)843-1274, jps@allenpress.com. 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: Roger D.K. Thomas, Department of Earth and Environment, Franklin & Marshall College, Lancaster, PA 17604-3003.

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

Associate editors are: Laurie C. Anderson, Louisiana State University, laurie@geol.lsu.edu; Daniel B. Blake, University of Illinois, dblake@ux1.cso.uiuc.edu; Matthew Carrano, National Museum of Natural History, carrano.matthew@nmnh.si.edu; Robert L. Carroll, McGill University, robert.carroll@mcgill.ca; Richard Cifelli, University of Oklahoma, rlc@ou.edu; Keith Dewing, Geological Survey of Canada, kdewing@NRCCan.gc.ca; William A. DiMichelle, Natural Museum of Natural History, Dimichelle.Bill@NMNH.SI.EDU; William P. Elder, Lafayette, California, chronovision@attbi.com; Robert J. Elias, University of Manitoba, eliasrj@Ms.UManitoba.CA; Michael Engel, University of Kansas, msengel@ku.edu; John R. Groves, University of Northern Iowa, John.Groves@uni.edu; Steven J. Hageman, hagemansj@appstate.edu; Peter J. Harries, University of South Florida, harries@chuma.cas.usf.edu; Martin J. Head, University of Cambridge, mh300@hermes.cam.ac.uk; Eric Hilton, Field Museum of Natural History, ehilton@fieldmuseum.org; Peter Jell, Queensland Museum, Australia, Peter@qm.qld.gov.au; Stephen A. Leslie, University of Arkansas, saleslie@ualr.edu; Richard Lupia, University of Oklahoma, rlupia@ou.edu; Mike Melchin, St. Francis Xavier University, Canada, mmelchin@stfx.ca; Molly F. Miller, Vanderbilt University, MillerMF@ctr.vax.vanderbilt.edu; Brian Pratt, University of Saskatchewan, brian.pratt@usask.ca; Peter Roopnarine, California Academy of Sciences, proopnarine@calacademy.org; Eric Scott, San Bernardino County Museum, escott@sbc.m.sbccounty.gov; James Sprinkle, University of Texas, echino@mail.utexas.edu; Steve Westrop, University of Oklahoma, swestrop@ou.edu; David M. Work, Maine State Museum; david.work@maine.gov; Shuhai Xiao, Virginia Polytechnic Institute, xiao@vt.edu.

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

Copyright © 2005, 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.

JOURNAL POLICY

The *Journal of Paleontology* publishes original articles and notes on the systematics of fossil organisms and the implications of systematics to all aspects of paleobiology and stratigraphic paleontology. It emphasizes specimen-based research and features high quality illustrations. Comments on articles and replies are considered for publication. Manuscripts should be submitted to the office of the Editors, which handles the review process. The Associate Editors work with authors to produce final copy, and they return manuscripts to the Editors for final processing. Manuscripts submitted elsewhere should not be submitted to the *Journal*.

Contributors should read the "Preparation of Manuscripts," below; more detailed "Instructions for Authors" were published in the November, 1998 issue (72:1087–1092) and are available on the World Wide Web at <http://www.journalofpaleontology.org>. Manuscripts not adhering to format will be returned to authors for correction before entering the editorial process. Cost of *Journal* publication is taken entirely from membership dues in The Paleontological Society and voluntary page contributions. Authors are charged for changes they make during the proof stage and also for their original mistakes that must be corrected during this stage. A limit of 25 published pages is placed on all papers within the *Journal*; limited excess pages might be accepted but their cost will be charged to the author. Longer manuscripts must be submitted to the memoir series; all publication costs for memoirs must be paid by authors.

PREPARATION OF MANUSCRIPTS

GENERAL

Important references for format preparation are: 1) The *Journal of Paleontology* Instructions for Authors (Volume 72, pages 1087–1092) (<http://www.journalofpaleontology.org>); 2) *Suggestions to Authors of the Reports of the United States Geological Survey* (seventh edition) 1991; and 3) *The Chicago Manual of Style* (fourteenth edition) 1993. Where there is conflict, current *Journal* style prevails; any recent issue provides a useful guide, but note changes with the 72:1087–1092 "Instructions for Authors."

All copy must be submitted on either 21.5 × 28.0 cm (8½ × 11 in.) or A4 standard-weight paper. Submit three copies. Manuscripts must be laser printed or letter-quality typed; dot-matrix printing is not acceptable. Avoid small font sizes; 12-point Times or 10-point Helvetica are appropriate. Double-space throughout, including references and table and figure descriptions; provide ample margins. Submitted copies need not include original illustrations, but they should be of very high quality; originals may be requested if submitted figures are not of adequate quality. Use metric measurements. A 7.5–10.0 cm heading is left on the first page above the title. First-page format should follow published examples.

TEXT

ABSTRACT—An abstract of 250 or fewer words is required for articles; abstracts do not accompany notes or other comments. The heading for the abstract is not indented; it is capitalized throughout, and it is followed by two hyphens but no period.

Headings.—Two grades of headings are almost always sufficient. Primary headings are centered and typed in all capital letters. Secondary headings are indented, underlined, and followed by a period and two hyphens. The first two words of the introduction are capitalized and abut the left margin. Do not end manuscript lines with hyphens.

Systematics.—Format for arrangement of systematic paleontology can be found in current issues of the *Journal*. All descriptions of new taxa must be accompanied by a diagnosis, an indication of type specimens and repository, stratigraphic and geographic data, and specific reference to illustrations of the taxon. Particularly note the format, punctuation, and capitalization conventions used in the synonymy.

REFERENCES

Particular care should be given to reference format. The "Instructions for Authors" provides many examples.

ILLUSTRATIONS

Figures.—All illustrations, including maps, geologic sections, and halftone illustrations, must be numbered in the sequence of their first appearance in the text. "Figure" is used rather than "Plate," and therefore line drawing and photographic figures are numbered in sequence. All illustrations, including review copies, must be submitted at publication size. These sizes are: full page, 18.3 × 23.3 cm; double-column, 18.3 cm; single column, 9.0 cm. Halftone illustrations must be original photographs mounted on black or white cardboard. Photographic subjects must be illuminated from the upper left, or evenly illuminated. A photograph of a montage is not acceptable. Each illustration must be identified by a numeral, but typewritten numbering is not acceptable. Press-on lettering is acceptable, but it readily breaks from the original and therefore much care must be used. Line drawings may be either an original or a glossy print mounted on white cardboard. Allow 1.5 cm at top of figure for a printer's label. Review copies of photographic figures should be similar in quality to the original. Standard photocopies are not acceptable.

Digital photographs are encouraged. 450 dpi is best. TIFF and EPS file formats preferred. Submit good quality printouts with review copies. For more information, see www.journalofpaleontology.org.