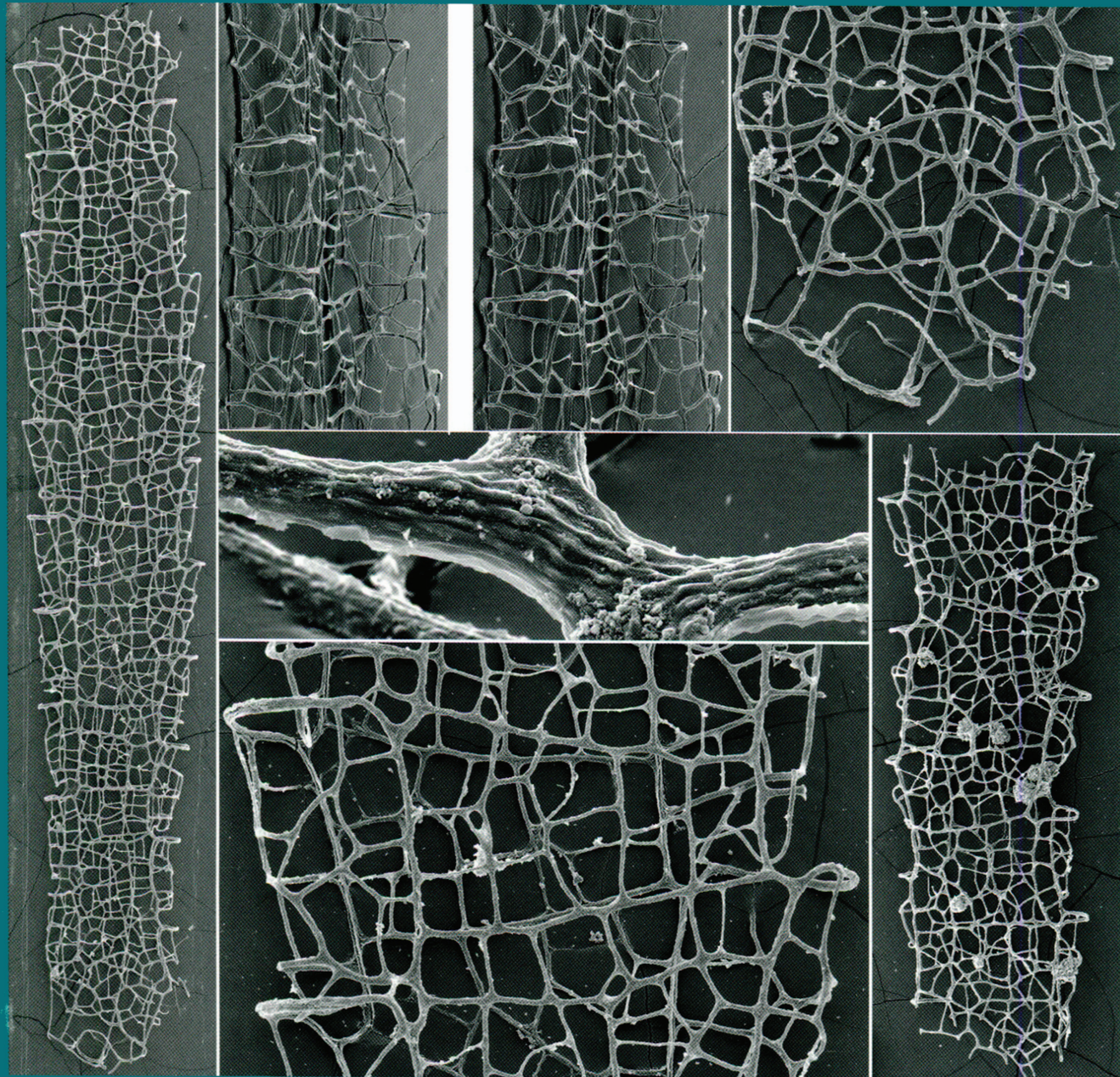


# JOURNAL

OF

# PALAEONTOLOGY



VOL 80 ■ No 4 ■ JULY 2006 ■ THE PALEONTOLOGICAL SOCIETY





## OFFICERS AND EDITORS OF THE PALEONTOLOGICAL SOCIETY

### President

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

### President-Elect

DEREK E. G. BRIGGS, New Haven, CT  
derek.briggs@yale.edu

### Past-President

WILLIAM I. AUSICH, Columbus, OH  
ausich.1@osu.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, University of Calgary  
LAURIE C. ANDERSON, Louisiana State University  
DAVID S. BERMAN, Carnegie Museum  
of Natural History  
DANIEL B. BLAKE, University of Illinois  
ROBERT L. CARROLL, McGill University  
KEITH DEWING, Geological Survey of Canada  
WILLIAM A. DIMICHELE, National Museum of  
Natural History  
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 J. HEAD, Brock University  
ERIC HILTON, Field Museum of Natural History  
STEPHEN A. LESLIE, University of Arkansas  
RICHARD LUPIA, University of Oklahoma  
MIKE MELCHIN, St. Francis Xavier University, Canada  
BRIAN PRATT, University of Saskatchewan  
ERIC SCOTT, San Bernardino County Museum  
JAMES SPRINKLE, University of Texas  
STEPHEN R. WESTROP, University of Oklahoma  
MICHAEL O. WOODBURNE, Museum of  
Northern Arizona  
DAVID M. WORK, Maine State Museum

### Paleobiology Co-Editors

TOMASZ K. BAUMILLER, ROBYN J. BURNHAM,  
and PHILIP D. GINGERICH, Ann Arbor, MI

### Editor Special Publications

SUSAN H. BUTTS, New Haven, CT

### Education Coordinator

MICHAEL A. GIBSON, Martin, TN

### Councilors

JENNIFER C. McELWAIN, Chicago, IL  
ANNE L. RAYMOND, College Station, TX

### Student Representative

JOCELYN SESSA, University Park, PA

### Section Chairs

Cordilleran: ROBERT B. BLODGETT,  
Anchorage, AK  
North-Central: LISA E. PARK,  
Akron, OH  
Northeastern: LISA AMATI  
Potsdam, NY  
Rocky Mountain: FORREST J. GAHN,  
Washington, DC  
Southeastern: COLIN D. SUMRALL,  
Knoxville, TN  
South-Central: ELIZABETH A. HEISE,  
Brownsville, 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: Lenz and Kozłowska, 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](mailto: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.

### Submit manuscripts online at <http://journalofpaleontology@allentrack.net>

Associate editors are: Jason S. Anderson, University of Calgary; Laurie C. Anderson, Louisiana State University, [laurie@geol.lsu.edu](mailto:laurie@geol.lsu.edu); David S. Berman, Carnegie Museum of Natural History, [bermand@carnegiemn.org](mailto:bermand@carnegiemn.org); Daniel B. Blake, University of Illinois, [dblake@uiuc.edu](mailto:dblake@uiuc.edu); Robert L. Carroll, McGill University, [robert.carroll@mcgill.ca](mailto:robert.carroll@mcgill.ca); Keith Dewing, Geological Survey of Canada, [kdewing@NRCan.gc.ca](mailto:kdewing@NRCan.gc.ca); William A. DiMichelle, National Museum of Natural History, [Dimichelle.Bill@NMNH.SI.EDU](mailto:Dimichelle.Bill@NMNH.SI.EDU); Robert J. Elias, University of Manitoba, [eliasrj@Ms.UManitoba.CA](mailto:eliasrj@Ms.UManitoba.CA); Michael Engel, University of Kansas, [msengel@ku.edu](mailto:msengel@ku.edu); John R. Groves, University of Northern Iowa, [John.Groves@uni.edu](mailto:John.Groves@uni.edu); Steven J. Hageman, [hagemansj@appstate.edu](mailto:hagemansj@appstate.edu); Peter J. Harries, University of South Florida, [harries@chuma.cas.usf.edu](mailto:harries@chuma.cas.usf.edu); Martin J. Head, Brock University, [mjhead@brocku.ca](mailto:mjhead@brocku.ca); Eric Hilton, Field Museum of Natural History, [ehilton@fieldmuseum.org](mailto:ehilton@fieldmuseum.org); Stephen A. Leslie, University of Arkansas, [saleslie@ualr.edu](mailto:saleslie@ualr.edu); Richard Lupia, University of Oklahoma, [rlupia@ou.edu](mailto:rlupia@ou.edu); Mike Melchin, St. Francis Xavier University, Canada, [mmelchin@stfx.ca](mailto:mmelchin@stfx.ca); Brian Pratt, University of Saskatchewan, [brian.pratt@usask.ca](mailto:brian.pratt@usask.ca); Eric Scott, San Bernardino County Museum, [escott@sbcm.sbcounty.gov](mailto:escott@sbcm.sbcounty.gov); James Sprinkle, University of Texas, [echino@mail.utexas.edu](mailto:echino@mail.utexas.edu); Stephen R. Westrop, University of Oklahoma, [swestrop@ou.edu](mailto:swestrop@ou.edu); Michael O. Woodburne, Museum of Northern Arizona, [mikew@npgcable.com](mailto:mikew@npgcable.com); David M. Work, Maine State Museum; [david.work@maine.gov](mailto:david.work@maine.gov).

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

Copyright © 2006, 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.

## 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 and geologic sections, 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 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. 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.

Digital photographs are encouraged. Figures may be submitted in JPEG only during online submission (highly recommended if the manuscript includes a large number of figures); however, authors will need to use other formats later on to secure acceptance for publication, primarily TIFF and EPS formats—which may also be used during online submission. Line art should be submitted in bitmap mode, with an ideal resolution of 1,200 ppi and a minimum resolution of 600 ppi; use Illustrator, CorelDRAW, or Canvas. For color photos, use CMYK mode, ideal resolution 350 ppi, minimum 200 ppi; for B/W halftone (black and white photo, or vector art not limited to black and white), grayscale mode, ideal 350 ppi, minimum 200 ppi; for line/halftone combination, grayscale mode, ideal 600 ppi, minimum 200 ppi.