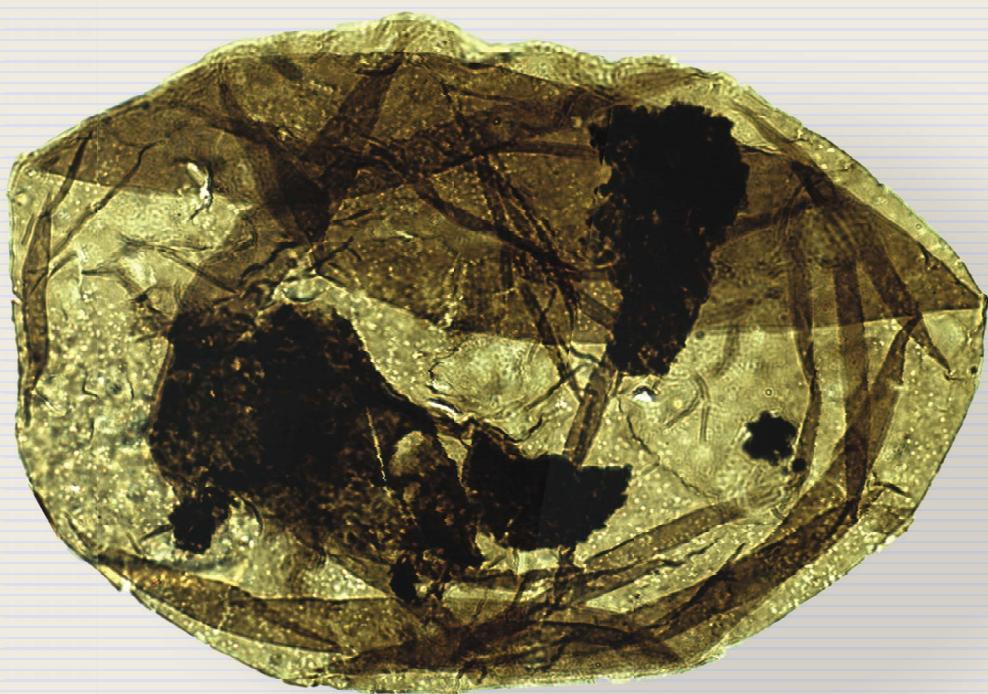


JOURNAL of PALEONTOLOGY



VOL 90 | NO 5 | 2016



CAMBRIDGE
UNIVERSITY PRESS



OFFICERS AND EDITORS OF THE PALEONTOLOGICAL SOCIETY



President

STEVE HOLLAND,
Univ. of Georgia
stratum@uga.edu

President-Elect

ARNOLD I. MILLER,
Univ. of Cincinnati
Arnold.miller@uc.edu

Past President

SANDRA J. CARLSON,
Univ. of California–Davis
sjcarlson@ucdavis.edu

Secretary

MARGARET M. YACOBUCCI,
Bowling Green State Univ.
mmyacob@bgsu.edu

Treasurer

PETER J. HARRIES,
North Carolina State
pjharrie@ncsu.edu

JP Editors

BRENDA R. HUNDA,
Cincinnati Museum Center
BHunda@cincymuseum.org

JISUO JIN,
Univ. of Western Ontario
jjin@uwo.ca

JP Managing Editor

SARA A. MARCUS,
journalofpaleontology@cambridge.org

JP Associate Editors
NICHOLAS BUTTERFIELD,
Cambridge Univ.

STYLIANOS CHATZIMANOLIS,
Univ. Tennessee–Chattanooga

TOM CRONIN,
USGS

WILLIAM A. DiMICHELE,
Smithsonian Institution

ROBERT J. ELIAS,
Univ. of Manitoba

NADIA FRÖBISCH,
Museum für Naturkunde

FOREST J. GAHN,
Brigham Young Univ., Idaho

JOSEPH HANNIBAL,
Cleveland Museum of Natural History

PETER J. HARRIES,
North Carolina State

JOACHIM HAUG,
Univ. of Greifswald

MICHAEL HAUTMANN,
Univ. of Zurich

MARTIN J. HEAD,
Brock Univ.

SAMANTHA HOPKINS,
Univ. of Oregon

NIGEL HUGHES,
UC Riverside

DANIEL KSEPKA,
Bruce Museum

MAX LANGER,
Universidade de São Paulo

STEPHEN A. LESLIE,
James Madison Univ.

BRUCE LIEBERMAN,
Univ. of Kansas

STEVEN LoDUCA,
Eastern Michigan Univ.

RICK LUPIA,
Oklahoma Museum

GABRIELA MÁNGANO,
Univ. Saskatchewan

MALGORZATA MOCZYDŁOWSKA-
VIDAL, Uppsala Univ.

ALISON MURRAY,
Univ. of Alberta

PAULA NOBLE,
Univ. of Nevada

BRIAN PRATT,
University of Saskatchewan

IMRAN RAHMAN,
Oxford University Museum of Natural
History, England

ERIC SCOTT,
San Bernardino Co. Museum

MARY SILCOX,
Univ. of Toronto Scarborough

HANS-DIETER SUES,
Smithsonian Institution

COLIN SUMRALL,
Univ. of Tennessee

LEIF TAPANILA,
Idaho State Univ.

DAVID VARRICCHIO,
Montana State Univ.

PETER WAGNER,
Smithsonian Institution

STEVE WESTROP,
Oklahoma Museum

DAVID M. WORK,
Maine State Museum

PATRICK WYSE JACKSON,
Trinity College Dublin

MARGARET M. YACOBUCCI,
Bowling Green State Univ.

SAMUEL ZAMORA,
Geological Survey of Spain

RENBIN ZHAN,
Nanjing Institute of Geology and
Palaeontology,
Chinese Academy of Sciences

Paleobiology Senior Editor
CATHERINE BADGLEY,
Univ. of Michigan

Paleobiology Co-Editors
CARLOS A. JARAMILLO,
Smithsonian Tropical Research
Institute

MICHAEL KOWALEWSKI,
Univ. of Florida

SHUHAI XIAO,
Virginia Polytechnic Institute

Editor of Special Publications
SARA A. MARCUS,
Oregon Inst. Of Technology
sara.marcus@oit.edu

Communications Officer
LEIF TAPANILA,
Idaho State Univ.
tapleif@isu.edu

Program Coordinator
MATTHEW CLAPHAM
Univ. of California, Santa Cruz
mclapham@ucsc.edu

Education/Outreach Coordinator

MARGRET FRAISER,
Univ. of Wisconsin,
Milwaukee
mfraiser@uwm.edu

Councilors
LAUREL COLLINS,
Florida International Univ.
collinsl@fiu.edu

KATE BULINSKI,
Bellarmine University
kbulinski@bellarmine.edu

Student Representative
LUCY CHANG,
Univ. California, Berkeley
luchang@berkeley.edu

SHARON McMULLEN,
Univ. of Wisconsin–Madison
skmcullen@wisc.edu

Section Chairs
Cordilleran:
NICOLE BONUSCO,
CA State Univ. Fullerton
nbonuso@fullerton.edu

North Central:
REBECCA FREEMAN,
Univ. of Kentucky
rebecca.freeman@uky.edu

Northeastern:
ALEXANDER J. BARTHOLOMEW,
SUNY–New Paltz
barthola@newpaltz.edu

Rocky Mountain:
LEIF TAPANILA,
Idaho State Univ.
tapaleif@isu.edu

Southeastern:
CHRISTY VISAGGI,
Georgia State Univ.
cvisaggi@gsu.edu

Editor – Priscum
MATT POWELL,
Juniata College
powell@juniata.edu

Editor – Social Media
PHOEBE COHEN,
Williams College
Phoebe.A.Cohen@williams.edu

Cover illustration: The acritarch *Leiosphaeridia tenuissima* from the mid-Neoproterozoic Alinya Formation, Officer Basin, Australia. Riedman and Porter, Fig. 11.12, p. 870.

ISSN 0022-3360

Copyright © 2016 The Paleontological Society. All rights reserved.

SUBSCRIPTION INFORMATION

The *Journal of Paleontology* [ISSN 0022-3360] is published bimonthly (January, March, May, July, September, and November) by Cambridge University Press for the Paleontological Society. Members of the Paleontological Society automatically receive electronic subscriptions to the *Journal of Paleontology* and *Paleobiology* as a benefit of membership. Institutional subscriptions can be purchased direct from Cambridge University Press or through any major subscription agent. Print-only, online-only and bundled print and online prices are all available, and subscription prices are tiered according to institution type and size.

Please contact Cambridge University Press for further details:

For customers in North America

Email: subscriptions_newyork@cambridge.org;
Phone: (800) 872-7423, option 4

For customers outside of North America

Email: journals@cambridge.org;
Phone: +44 (0)1223-32-6070; Fax: +44 (0)1223-32-5150

Downloads of individual articles are available on <http://journals.cambridge.org/JPA>.

Reprints of individual articles may be ordered. For information on reprints, please contact Cambridge University Press.

Archives of previous issues are available on <http://journals.cambridge.org/JPA>.

Permissions All rights reserved. Permissions and reproduction policies, request forms, and contacts are available at: <http://www.cambridge.org/uk/information/rights/permission.htm>

ADVERTISING

To advertise in the journal please email USAAdSales@cambridge.org or telephone +1(212) 337-5053 in the USA, Canada, or Mexico; email ad_sales@cambridge.org or telephone +44 (1223) 325083 in the rest of the world.

ABSTRACTING AND INDEXING

Articles published in the *Journal of Paleontology* are indexed by De Gruyter Saur, EBSCOhost, Elsevier BV, Gale, GeoScienceWorld, MetaPress, National Library of Medicine, Ovid, ProQuest, and Thomson Reuters.

POSTAL INFORMATION

Periodicals postage rate paid at New York, NY, and at additional mailing offices. POSTMASTER: Send address changes in the USA, Canada, and Mexico to: *Journal of Paleontology*, Cambridge University Press, Journals Fulfillment Department, One Liberty Plaza, 20th Floor, New York, NY 10006. Send address changes elsewhere to the *Journal of Paleontology*, Cambridge University Press, Journals Fulfillment Department, UPH, Shaftesbury Road, Cambridge CB2 8BS, England.

Copyright © 2016 The Paleontological Society. All rights reserved.

Printed in the United States of America