

Volume 274, Number 5, May 2013

JOURNAL OF

morphology

ISSN 0362-2525



WILEY Blackwell

Editor: J. Matthias Starck

JOURNAL OF MORPHOLOGY welcomes articles of original research in cytology, protozoology, embryology, general, comparative and functional morphology. Preliminary notices or articles of a purely taxonomic or ecological nature are not included. No paper which has already appeared will be accepted nor will simultaneous publications elsewhere be allowed. Manuscripts may now be submitted online via Manuscript Central at <http://mc.manuscriptcentral.com/jmor>.

© 2013 Wiley Periodicals, Inc., a Wiley company. All rights reserved. No part of this publication may be reproduced in any form or by any means, except as permitted under section 107 or 108 of the 1976 United States Copyright Act, without either the prior written permission of the publisher, or authorization through the Copyright Clearance Center, 222 Rosewood Drive, Danvers, MA 01923, (978) 750-8400, fax (978) 750-4470. Such permission requests and other permission inquiries should be addressed to the Permissions Department, c/o John Wiley & Sons, Inc., 111 River Street, Hoboken, NJ 07030, (201) 748-6011, fax (201) 748-6008, or visit <http://www.wiley.com/go/permissions>

JOURNAL OF MORPHOLOGY, (Print ISSN 0362-2525), is published monthly by Wiley Periodicals, through Wiley Subscription Services, Inc., a Wiley Company, 111 River St., Hoboken, NJ 07030-5774. ©2013 Wiley Periodicals, Inc. Periodicals postage paid at Hoboken, NJ, and at additional mailing offices. **Postmaster:** Send all address changes to **JOURNAL OF MORPHOLOGY**, Journal Customer Services, John Wiley & Sons Inc., 350 Main St., Malden, MA 02148-5020. **Information for subscribers:** **JOURNAL OF MORPHOLOGY** is published in 12 issues per year. Institutional subscription prices for 2013 are: Print & Online: US\$8,758 (US), US\$8,926 (Canada and Mexico), £4,621 (UK), €5,843 (Europe), US\$9,010 (Rest of World). Prices are exclusive of tax. Asia-Pacific GST, Canadian GST and European VAT will be applied at the appropriate rates. For more information on current tax rates, please go to wileyonlinelibrary.com/tax-vat. The price includes online access to the current and all online back files to January 1st 1997, where available. For other pricing options, including access information and terms and conditions, please visit www.wileyonlinelibrary.com/access. **Back issues:** Single issues from current and recent volumes are available at the current single issue price from cs-journals@wiley.com. Earlier issues may be obtained from Periodicals Service Company, 11 Main Street, Germantown, NY 12526, USA. Tel: +1 518 537 4700, Fax: +1 518 537 5899, Email: psc@periodicals.com. **Delivery Terms and Legal Title:** Prices include delivery of print journals to the recipient's address. Delivery terms are Delivered at Place (DAP); the recipient is responsible for paying any import duty or taxes. Legal title passes to the customer on dispatch by our distributors. **Journal Customer Services:** For ordering information, claims and any enquiry concerning your journal subscription please go to wileyonlinelibrary.com/support or contact your nearest office: Americas: Email: cs-journals@wiley.com; Tel: +1 781 388 8598 or +1 800 835 6770 (Toll free in the USA & Canada). Europe, Middle East and Africa: Email: cs-journals@wiley.com; Tel: +44 (0) 1865 778315. Asia Pacific: Email: cs-journals@wiley.com; Tel: +65 6511 8000. Visit our Online Customer Self-Help available in 7 languages at <http://onlinelibrary.custhelp.com>. Claims for undelivered copies will be accepted only after the following issue has been received. Please enclose a copy of the mailing label or cite your subscriber reference number in order to expedite handling. Missing copies will be supplied when losses in transit and where reserve stock permits. If claims are not resolved satisfactorily, please write Journal Customer Services. **Advertising:** contact Advertising Sales Manager, 111 River Street, Hoboken, NJ 07030, Tel: +1 201 748-8832; Fax: +1 201 748-6207. **Commercial Reprints:** E-mail: corporatesalesusa@wiley.com; corporatesalesusa@wiley.com; or corporatesalesaustralia@wiley.com. **Author Reprints (50-500 copies):** Order online: <http://www.sheridanreprints.com/orderForm.html>. E-mail: cjones@tsp.sheridan.com. **Note to NIH Grantees:** Pursuant to NIH mandate, Wiley-Blackwell will post the accepted version of contributions authored by NIH grant-holders to PubMed Central upon acceptance. This accepted version will be made publicly available 12 months after publication. For further information, see www.wiley.com/go/nihmandate. For submission instructions, subscription and all other information visit: wileyonlinelibrary.com/jmor.

Abstracted/indexed by: BIOBASE • Biological Abstracts® • CAB Abstracts® • Cambridge Scientific Abstracts • Chemical Abstracts Service/SciFinder • Current Awareness in Biological Sciences • Current Contents®/Life Sciences • Index Medicus/MEDLINE/PubMed • Reference Update • Science Citation Index® • Science Citation Index Expanded™ • SCOPUS • VINITY.

Wiley's Corporate Citizenship initiative seeks to address the environmental, social, economic, and ethical challenges faced in our business and which are important to our diverse stakeholder groups. We have made a long-term commitment to standardize and improve our efforts around the world to reduce our carbon footprint. Follow our progress at www.wiley.com/go/citizenship.

Printed in Singapore by Markono Print Media Pte Ltd.

morphology

FOUNDED BY C.O. WHITMAN, 1887
Originally Founded by the Wistar Institute

Editor

J. Matthias Starck

Department of Biology II, University of Munich (LMU) – Biocenter,
Planegg-Martinsried, Germany
E-mail: starck@uni-muenchen.de

Editor Emeritus

Frederick W. Harrison

191 Wildwood Drive, Sylva, North Carolina
mmmorph@aol.com

Senior Advisory Board

William M. Kier

Department of Biology
University of North Carolina
Chapel Hill, NC
billkier@bio.unc.edu

Reinhardt Møbjerg Kristensen

Zoological Museum and
Arctic Station
University of Copenhagen
Copenhagen, Denmark
rmkristensen@snm.ku.dk

Peter Wainwright

Department of Evolution &
Ecology
University of California
Davis, CA
PCWainwright@ucdavis.edu

Marvalee H. Wake

Department of Integrative
Biology
University of California
Berkeley, CA
mhwake@socrates.berkeley.edu

Associate Editors

Gerd Alberti

Ernst Moritz Arndt Universität Greifswald
GERMANY

George V. Lauder

Harvard University
Cambridge, Massachusetts

James R. Stewart

East Tennessee State University
Johnson City, Tennessee

Burton J. Bogitsh

Vanderbilt University
Nashville, Tennessee

Paul F. A. Maderson

Quakertown, Pennsylvania

Volker Storch

Rupert-Karls-Universität Heidelberg
GERMANY

Shaun P. Collin

University of Queensland
Brisbane, AUSTRALIA

Shunsuke F. Mawatari

Hokkaido University
JAPAN

Adam P. Summers

University of California–Irvine
Irvine, California

Takahiro Fujino

Yamagata University
JAPAN

Christopher R. Murphy

The University of Sydney
AUSTRALIA

Sharon Swartz

Brown University
Providence, Rhode Island

Theodore Garland, Jr.

University of California
Riverside, California

R. Glenn Northcutt

University of California
La Jolla, California

Linda Trueb

The University of Kansas
Lawrence, Kansas

Alfred Goldschmid

University of Salzburg
AUSTRIA

Fernando Pardos

Universidad Complutense
Madrid, SPAIN

Janice Voltzow

University of Scranton
Scranton, Pennsylvania

Stanislav Gorb

University of Kiel
Deutschland, GERMANY

Steven F. Perry

Universität Bonn, Poppelsdorfer
Schloss, GERMANY

Norimitsu Watabe

University of South Carolina
Columbia, South Carolina

James Hanken

Harvard University
Cambridge, Massachusetts

F. James Rohlf

Stony Brook University
Stony Brook, New York

Robert M. Woollacott

Harvard University
Cambridge, Massachusetts

Susan W. Herring

University of Washington
Seattle, Washington

David M. Sever

Southeastern Louisiana University
Hammond, Louisiana

Jens T. Hoeg

University of Copenhagen
DENMARK

Tracy L. Simpson

University of Hartford
West Hartford, Connecticut