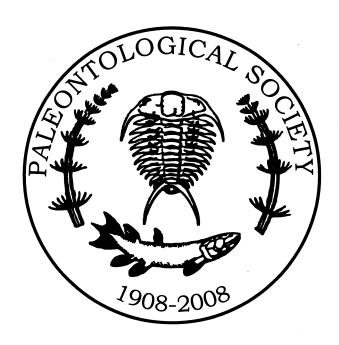


FROM EVOLUTION TO GEOBIOLOGY

Research Questions Driving Paleontology at the Start of a New Century



Patricia H. Kelley and Richard K. Bambach Editors

The Paleontological Society Papers
Volume 14 October 2008

COVER

Cover art designed by Peter Lang and Jennifer McElwain

Bottom right

Raymondicrinus oregonensis (Moore & Vokes)

Oligocene, Keasey Formation, Oregon

Photo credit: Hans Hess, Natural History Museum Basel Copyright: Hans Hess, Natural History Museum Basel

Originally published in black and white in "Fossil Crinoids" (Hess et al., 1999, Cambridge University Press)

Bottom left

Skeleton of the pantolestid Palaeosinopa

Late early Eocene, Green River Shale, Wyoming

Photo credit: Georg Oleshinsky, Institut fur Palaontologie, Bonn, Germany

Permission: Ken Rose, John Hopkins University.

Originally published in Rose, K. D., and W. v. Koenigswald. 2005. An exceptionally complete skeleton of *Palaeosinopa* (Mammalia, Cimolesta, Pantolestidae) from the Green River Formation, and other postcranial elements of the Pantolestidae from the Eocene of Wyoming USA). Palaeontographica Abteilung A, 273:55-96.

Center page, right

Meghystrichosphaeridium

Ediacaran, Doushantuo Formation (constrained between 635 and 551 Ma), Weng'an, South China

Photo: Shuhai Xiao, Virginia Polytechnic Institute and State University

Center page, left

Molecular Paleobiology - DNA strand wrapped around the bryozoan Archimedes

Archimedes - Carboniferous, Kinderhook Formation, Indiana

Photo credit: Craig Layne, Dartmouth College Courtesy: Kevin Peterson, Dartmouth College

Background

Demosponge *Choia*Middle Cambrian Wheeler Shale, western Utah

Photo credit: Stephen B. Church Copyright: Stephen B. Church

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Presented as a Paleontological Society Short Course at the
Annual Meeting of the Geological Society of America
Houston, Texas

October 4, 2008

Convened by
Patricia H. Kelley
Richard K. Bambach

A Publication of the Paleontological Society

Series Editor

Susan H. Butts
Peabody Museum of Natural History
Yale University
170 Whitney Avenue
New Haven, CT 06520-8118

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ISSN 1089-3326

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Printed by Yale University Printing and Publishing Services.

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AUTHORS

Abigail C. Allwood

California Institute of Technology Jet Propulsion Laboratory 4800 Oak Grove Drive Pasadena, CA, 91109 abigail.c.allwood@jpl.nasa.gov

Richard K. Bambach

Department of Paleobiology Smithsonian Institution, National Museum of Natural History MRC – 121 NMNH Washington DC 20013–7012 richard.bambach@verizon.net

C. Kevin Boyce

Department of the Geophysical Sciences University of Chicago 5734 S. Ellis Ave., HGS 267 Chicago, IL 60637 ckboyce@uchicago.edu

Andrew M. Bush

Department of Ecology and Evolutionary Biology and Center for Integrative Geosciences University of Connecticut 75 North Eagleville Road Storrs, CT 06269-3043 andrew.bush@uconn.edu

Christopher A. Brochu

Department of Geoscience University of Iowa Iowa City, IA 52242 christopher-brochu@Uiowa.edu

Gwen M. Daley

Department of Chemistry, Physics, and Geology Winthrop University Rock Hill, SC 29733 daleyg@winthrop.edu

Gregory P. Dietl

Paleontological Research Institution 1259 Trumansburg Road Ithaca, NY 14850 gpd3@cornell.edu

E. Grosjean

Petroleum and Marine Division Geoscience Australia Canberra, ACT 2601 Australia Emmanuelle.Grosjean@ga.gov.au

Gene Hunt

Department of Paleobiology National Museum of Natural History Smithsonian Institution NHB, MRC 121, P.O. Box 37012 Washington, DC 20013-7012 hunte@si.edu

Patricia H. Kelley

Department of Geography and Geology University of North Carolina Wilmington 601 South College Road Wilmington, NC 28403-5944 kelleyp@uncw.edu

Rowan Lockwood

Department of Geology The College of William and Mary P.O. Box 8795 Williamsburg, VA 23187 rxlock@wm.edu

G. D. Love

Department of Earth Sciences University of California, Riverside Riverside, CA 92521 glove@ucr.edu

W. Meredith

School of Chemical, Environmental and Mining Engineering University of Nottingham University Park, Nottingham NG7 2RD UK William.Meredith@nottingham.ac.uk

Ryosuke Motani

Department of Geology University of California, Davis One Shields Avenue Davis, CA 95616 motani@geology.ucdavis.edu

Shanan E. Peters

Department of Geology & Geophysics University of Wisconsin-Madison 1215 W. Dayton St. Madison, WI 53706 peters@geology.wisc.edu

Kevin J. Peterson

Department of Biological Sciences Dartmouth College Hanover, NH 03755 USA Kevin.J.Peterson@Dartmouth.edu

David Sepkoski

History Department University of North Carolina, Wilmington Wilmington, NC 28403 sepkoskid@uncw.edu

C. E. Snape

School of Chemical, Environmental and Mining Engineering University of Nottingham University Park, Nottingham NG7 2RD UK Colin.Snape@nottingham.ac.uk

C. Stalvies

School of Civil Engineering and Geosciences University of Newcastle upon Tyne Newcastle upon Tyne NE1 7RU UK farliec@hotmail.com

Alycia L. Stigall

Department of Geological Sciences and OHIO Center for Ecology and Evolutionary Studies
Ohio University
316 Clippinger Laboratories
Athens, OH 45701
stigall@ohio.edu

Colin D. Sumrall

Department of Earth and Planetary Sciences University of Tennessee Knoxville, TN 37996 csumrall@utk.edu

Leif Tapanila

Department of Geosciences Idaho State University 921 S. 8th Ave. Pocatello, ID 83209-8072 tapaleif@isu.edu

Peter Wilf

Department of Geosciences Pennsylvania State University 537 Deike Building University Park, PA 16802 pwilf@psu.edu

Shuhai Xiao

Department of Geosciences Virginia Polytechnic Institute and State University 3061B Derring Hall Blacksburg, VA 24061 xiao@vt.edu

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PREFACE

On December 30, 1908, thirty-four paleontologists met at Johns Hopkins University and signed a document indicating their intent to form a professional society with the purpose of "the promotion of the Science of Paleontology" (as stated in our first Constitution; Cleland, 1910, p. 77). One hundred years later, we celebrate the birthday of a Society that has changed in many ways, yet remains vibrant and strong.

Four years ago, in anticipation of this occasion, the Paleontological Society Incoming Council appointed Patricia Kelley and Richard Bambach as organizers of the Centennial Short Course. Although anniversaries are typically times for looking backwards, we quickly decided on a different approach for the Centennial Short Course. Certainly, history is important; after all, the past is the key to the present (to invert a phrase), but rather than focusing on reviewing and celebrating our past achievements we have chosen to look toward the future. Thus our aim for this Centennial program has been to look at a wide spectrum of large-scale research questions that are motivating the rising leaders in our profession. In short, we wish to provide a picture of where the profession is headed, not concentrate on where we have been.

Rather than recruit "the usual suspects" of established senior experts to pontificate, we asked younger scholars of high repute to fill our program. We are all familiar with what the established senior citizens of our profession find interesting, but we are not always aware of what is motivating those who will be the senior leaders at the 125th anniversary of our society. We selected general areas of study (e.g., evolution, paleoecology, geobiology), sought prominent workers in those areas who are still in the early or middle stages of their careers, and let them designate their own specific topics for discussion. They represent the research directions in which the profession is headed.

We asked those who accepted our invitation to (a) frame a large-scale question related to the general topic that fit their research goals and (b) prepare their presentation to both discuss the significance of the question and illustrate how we can address that question with some actual results from finished or ongoing research. Thus we asked each contributor to touch on general theory and concepts, but also to present specific, data-driven or concrete information. After all, research results are what bring general questions to life. They are necessary to give perspective on where we are in fulfilling our overarching research agendas.

We attempt to touch on the full spectrum of intellectual activity in the profession, with scholars drawn from all the general subdisciplines of paleontology (micropaleontology, invertebrate paleontology, vertebrate paleontology, paleobotany) who also represent a cross-section of research approaches (from systematics to ichnology to biogeography). The contributions range across the geologic time scale, from the Archean to the Recent, and we also worked for a demographic balance among the participants (in terms of institutional pedigree, geographic region, gender, type of institution). We recognize that our coverage of the discipline of paleontology is necessarily incomplete. (At one time we thought of asking PS Council if we could have two weeks for this short course, rather than a day!) Nevertheless, we are excited about the diverse group of contributors we have assembled, and the range of topics they cover. No matter what your own specialty is, we believe you will learn something interesting from the program about what paleontology is and can be. It is not a short course in the traditional sense; it is a short course on what is going on in the discipline as a whole.

We hope to avoid the peculiar feeling of datedness common when one reads most anniversary reviews. The Journal of Paleontology editors asked Raymond C. Moore to review "the general status of paleontology near the three-fourths mark in the 20th century" (Moore et al., 1968, p. 1327), and he recruited 48 colleagues to write brief essays on the developments in their specialty areas covering the previous half century and looking ahead, too. It is curious now to look at that compilation (Moore et al., 1968). Of the fifty brief essays, only two are conceptually based; the remainder are descriptive of techniques and methods, discuss work done in particular geographic regions, or (thirty-seven of the fifty) deal with particular taxonomic groups. Many of the authors were obvious senior leaders in the profession at the time (including all the winners of the Paleontological Society Medal up to that time, eleven who subsequently received the award, and numerous distinguished foreign scholars). However, very few of the younger scholars who were shaping the "paleobiology revolution" at that time are represented. Although several of the essays make comments that accurately forecast the direction the field moved in the coming years (those by Axelrod, Schindewolf, Newell, and Simpson are particularly forward looking), the overall impression is that this is the field as it had been, not the field that was developing into modern paleontology. It will be interesting in the future to see how closely today's program connects to the developments in paleontology in our second century.

The program does begin with some history. The two "old fogeys" on the program (Kelley, Bambach) give us some background on the development of the profession, and then a younger historian of science with a personal connection to paleontology (Sepkoski) examines how the fossil record has been regarded as a source of evolutionary data from Darwin's time to the near present. The topical paleontological presentations start with evolution in deep time (Allwood on Archaean stromatolites, Love on molecular biomarkers, Xiao on Ediacaran events, and Peterson on possible connections between genetics and the nature of the Cambrian Explosion). Evolution remains on stage as Hunt considers evolution within lineages, Boyce deals with the evolution of plant physiology from the leaf record, and Motani follows the evolution of functional morphology in ichthyosaurs. Systematics and phylogeny link up in the papers by Sumrall and Brochu. Large-scale patterns in the fossil record get their due from Lockwood on the role of extinctions in the history of life, Stigall on relationships between paleobiogeography, paleoecology and macroevolution, and Peters on the role of macrostratigraphy in paleobiology. Aspects of paleoecology are dealt with by Tapanila on the direct evidence of symbiosis using trace fossils, Bush on comparative paleoecology of fossil assemblages, and Wilf on leaves as environmental recorders. Dietl ends the program by discussing innovative applications of evolutionary and ecological principles to societal issues.

Our hope is that this wide-ranging suite of conceptual discussions will provide insight into the direction in which paleontological thinking is developing as the Paleontological Society embarks on its second century.

REFERENCES

CLELAND, H. F. 1910. Proceedings of the preliminary meeting of the Paleontological Society, held at Baltimore, Maryland, December 30, 1908, and also proceedings of the first annual meeting held at Cambridge, Massachusetts, December 29, 1909. Geological Society of America Bulletin, 21:69-86.

MOORE, R. C., and 48 other authors. 1968. Developments, trends, and outlooks in paleontology. Journal of Paleontology, 42:1327–1377.

ACKNOWLEDGMENTS

Many individuals, as well as the Paleontological Society Council, provided input to us as we developed our ideas for organizing this short course. We are particularly grateful to the following individuals for their feedback as our plans were developing: Bill Ausich, Dave Bottjer, Matt Carrano, Steve Culver, Greg Dietl, Bill DiMichele, Doug Erwin, Andy Knoll, Charles Marshall, Anne Raymond, and Donna Surge. It was a pleasure working with the Short Course Series Editor, Susan Butts, and we thank her for her hard work in producing this volume on a short time line. The following reviewers gave us constructive comments on particular papers and we thank them for their time, attention, and willingness to help: Bill Ausich, Dave Bottjer, Sandy Carlson, Bill DiMichele, Phil Donoghue, Mary Droser, Doug Erwin, Seth Finnegan, Woody Fischer, Mike Foote, Andy Knoll, Michal Kowalewski, Charles Marshall, Frank O'Keefe, Kevin Padian, John Pojeta, Anne Raymond, Jim Valentine, Geerat Vermeij, Mark Wilson, and Scott Wing. Most participants in the short course also provided reviews of one or more contributions to this volume. We are grateful to these "internal reviewers" for helping to improve each manuscript. Finally, we thank all the contributors for providing high-quality manuscripts that will spur us all to think in new ways about our science.

Patricia Kelley and Richard Bambach

Conveners