

PALAEOBIOLOGY  
A SYNTHESIS



An ichthyosaur embryo (skull length 6.5 cm) discovered in 1985 by collectors Robert and Peter Langham; from the Lower Lias (Lower Jurassic) of the Somerset coast, U.K. On display at City of Bristol Museum & Art Gallery, U.K. (Photograph courtesy of Dept. of Geology, University of Bristol).

# PALAEOBIOLOGY

## A SYNTHESIS

EDITED BY

DEREK E. G. BRIGGS

*Department of Geology  
University of Bristol  
Queen's Road  
Bristol BS8 1RJ*

AND

PETER R. CROWTHER

*Department of Geology  
Bristol City Museums and  
Art Gallery  
Queen's Road  
Bristol BS8 1RL*

ON BEHALF OF

THE PALAEOONTOLOGICAL ASSOCIATION



**Blackwell  
Science**

© 1990 by  
Blackwell Science Ltd  
Editorial Offices:  
Osney Mead, Oxford OX2 0EL  
25 John Street, London WC1N 2BL  
23 Ainslie Place, Edinburgh EH3 6AJ  
350 Main Street, Malden  
MA 02148 5018, USA  
54 University Street, Carlton  
Victoria 3053, Australia

Other Editorial Offices:  
Blackwell Wissenschafts-Verlag GmbH  
Kurfürstendamm 57  
10707 Berlin, Germany

Blackwell Science KK  
MG Kodenmacho Building  
7-10 Kodenmacho Nihombashi  
Chuo-ku, Tokyo 104, Japan

All rights reserved. No part of this publication may be reproduced, stored in a retrieval system, or transmitted, in any form or by any means, electronic, mechanical, photocopying, recording or otherwise, except as permitted by the UK Copyright, Designs and Patents Act 1988, without the prior permission of the copyright owner.

First published 1990  
Paperback reissue with corrections 1992  
Reprinted with further corrections 1993,  
1995, 1997

Set by Setrite Typesetters Ltd,  
Hong Kong  
Printed and bound in Great Britain  
at the University Press, Cambridge

The Blackwell Science logo is a  
trade mark of Blackwell Science Ltd,  
registered at the United Kingdom  
Trade Marks Registry

#### DISTRIBUTORS

Marston Book Services Ltd  
PO Box 269  
Abingdon, Oxon OX14 4YN  
(Orders: Tel: 01235 465500  
Fax: 01235 465555)

#### USA

Blackwell Science, Inc.  
Commerce Place  
350 Main Street  
Malden, MA 02148 5018  
(Orders: Tel: 800 759 6102  
617 388 8250  
Fax: 617 388 8255)

#### Canada

Copp Clark Professional  
200 Adelaide Street West, 3rd Floor  
Toronto, Ontario M5H 1W7  
(Orders: Tel: 416 597-1616  
800 815-9417  
Fax: 416 597-1617)

#### Australia

Blackwell Science Pty Ltd  
54 University Street  
Carlton, Victoria 3053  
(Orders: Tel: 3 9347 0300  
Fax: 3 9347 5001)

#### British Library

Cataloguing in Publication Data

Palaeobiology: A Synthesis

1. Palaeobiology

I. Briggs, D.E.G. II. Crowther, P.R.  
560

ISBN 0-632-02525-5 (Hbk)

ISBN 0-632-03311-8 (Pbk)

#### Library of Congress

Cataloguing-in-Publication Data

Palaeobiology: A Synthesis.

Includes index.

1. Palaeobiology

I. Briggs, D.E.G. II. Crowther, P.R.

QE721.E53 1989 560'.3'21 88-35060

ISBN 0-632-02525-5 (Hbk)

ISBN 0-632-03311-8 (Pbk)

# Contents

List of Contributors, ix

Foreword, xiii

L. R. M. COCKS

## 1 Major Events in the History of Life

- 1.1 Origin of Life, 3  
C. R. WOESE & G. WÄCHTERSHÄUSER
- 1.2 Precambrian Evolution of Prokaryotes and Protists, 9  
A. H. KNOLL
- 1.3 Precambrian Metazoans, 17  
M. A. FEDONKIN
- 1.4 Origin of Hard Parts — Early Skeletal Fossils, 24  
B. RUNNEGAR & S. BENGTSON
- 1.5 Late Precambrian—Early Cambrian Metazoan Diversification, 30  
S. CONWAY MORRIS
- 1.6 Evolutionary Faunas, 37  
J. J. SEPKOSKI, Jr
- 1.7 Early Diversification of Major Marine Habitats
  - 1.7.1 Infauna and Epifauna, 41  
W. I. AUSICH & D. J. BOTTJER
  - 1.7.2 Plankton, 49  
R. B. RICKARDS
  - 1.7.3 Reefs, 52  
C. T. SCRUTTON
- 1.8 Terrestrialization
  - 1.8.1 Soils, 57  
V. P. WRIGHT
  - 1.8.2 Plants, 60  
D. EDWARDS & N. D. BURGESS
  - 1.8.3 Invertebrates, 64  
P. A. SELDEN
  - 1.8.4 Vertebrates, 68  
A. C. MILNER
- 1.9 Flight
  - 1.9.1 Arthropods, 72  
R. J. WOOTTON
  - 1.9.2 Vertebrates, 75  
K. PADIAN
- 1.10 Angiosperms, 79  
M. E. COLLINSON
- 1.11 Grasslands and Grazers, 84  
J. R. THOMASSON & M. R. VOORHIES

1.12 Hominids, 88

R. L. SUSMAN

## 2 The Evolutionary Process and the Fossil Record

- 2.1 Molecular Palaeontology, 95  
G. B. CURRY
- 2.2 Speciation, 100  
B. CHARLESWORTH
- 2.3 Microevolution and the Fossil Record, 106  
P. R. SHELDON
- 2.4 Heterochrony, 111  
K. J. McNAMARA
- 2.5 Red Queen Hypothesis, 119  
M. J. BENTON
- 2.6 Hierarchy and Macroevolution, 124  
N. ELDREDGE
- 2.7 Patterns of Diversification, 130  
P. W. SIGNOR
- 2.8 Coevolution, 136  
S. CONWAY MORRIS
- 2.9 Adaptation, 139  
P. W. SKELTON
- 2.10 Evolution of Large Size, 147  
M. J. BENTON
- 2.11 Rates of Evolution — Living Fossils, 152  
D. C. FISHER
- 2.12 Mass Extinction: Processes
  - 2.12.1 Earth-bound Causes, 160  
A. HALLAM
  - 2.12.2 Extra-terrestrial Causes, 164  
D. JABLONSKI
  - 2.12.3 Periodicity, 171  
J. J. SEPKOSKI, Jr
- 2.13 Mass Extinction: Events
  - 2.13.1 Vendian, 179  
M. A. S. McMENAMIN
  - 2.13.2 End-Ordovician, 181  
P. J. BRENCHLEY
  - 2.13.3 Frasnian—Famennian, 184  
G. R. MCGHEE, Jr
  - 2.13.4 End-Permian, 187  
D. H. ERWIN
  - 2.13.5 End-Triassic, 194  
M. J. BENTON

- 2.13.6 Cretaceous–Tertiary (Marine), 198  
F. SURLYK
- 2.13.7 Cretaceous–Tertiary (Terrestrial), 203  
L. B. HALSTEAD
- 2.13.8 Pleistocene, 207  
E. L. LUNDELIUS, Jr

### 3 Taphonomy

- 3.1 Decay Processes, 213  
P. A. ALLISON
- 3.2 The Record of Organic Components and the Nature of Source Rocks, 217  
P. FARRIMOND & G. EGLINTON
- 3.3 Destructive Taphonomic Processes and Skeletal Durability, 223  
C. E. BRETT
- 3.4 Transport — Hydrodynamics
  - 3.4.1 Shells, 227  
J. R. L. ALLEN
  - 3.4.2 Plant Material, 230  
R. A. SPICER
  - 3.4.3 Bones, 232  
A. K. BEHRENSMEYER
- 3.5 Fossil Concentrations and Life and Death Assemblages, 235  
F. T. FÜRSICH
- 3.6 Ostracod Deposits, 239  
C. E. BRETT
- 3.7 Flattening, 244  
D. E. G. BRIGGS
- 3.8 Diagenesis
  - 3.8.1 Skeletal Carbonates, 247  
M. E. TUCKER
  - 3.8.2 Carbonate Nodules and Plattenkalks, 250  
P. A. ALLISON
  - 3.8.3 Pyrite, 253  
P. A. ALLISON
  - 3.8.4 Phosphate, 256  
L. PRÉVÔT & J. LUCAS
- 3.9 Taphofacies, 258  
C. E. BRETT & S. E. SPEYER
- 3.10 Anatomical Preservation of Fossil Plants, 263  
A. C. SCOTT
- 3.11 Taphonomy of Fossil-Lagerstätten
  - 3.11.1 Overview, 266  
A. SEILACHER
  - 3.11.2 Burgess Shale, 270  
S. CONWAY MORRIS
  - 3.11.3 Upper Cambrian 'Orsten', 274  
K. J. MÜLLER
  - 3.11.4 Hunsrück Slate, 277  
J. BERGSTRÖM
  - 3.11.5 Mazon Creek, 279  
G. C. BAIRD

- 3.11.6 Holzmaden, 282  
R. WILD
- 3.11.7 Solnhofen Lithographic Limestones, 285  
G. VIOHL
- 3.11.8 Grube Messel, 289  
J. L. FRANZEN
- 3.11.9 Baltic Amber, 294  
T. SCHLÜTER
- 3.12 Completeness of the Fossil Record, 298  
C. R. C. PAUL

### 4 Palaeoecology

- 4.1 Morphology, 307  
L. LUGAR
- 4.2 Composition and Growth of Skeleton, 314  
B. RUNNEGAR
- 4.3 Biomechanics, 318  
P. A. SELDEN
- 4.4 Hydrodynamics, 322  
M. LaBARBERA
- 4.5 Populations, 326  
G. B. CURRY
- 4.6 Coloniality, 330  
B. R. ROSEN
- 4.7 Stromatolites, 336  
S. M. AWRAMIK
- 4.8 Reefs and Carbonate Build-ups, 341  
B. R. ROSEN
- 4.9 Encrusters, 346  
P. D. TAYLOR
- 4.10 Reconstructing Ancient Plant Communities, 351  
A. C. SCOTT
- 4.11 Trace Fossils, 355  
S. G. PEMBERTON, R. W. FREY & T. D. A. SAUNDERS
- 4.12 Evidence for Diet, 362  
J. E. POLLARD
- 4.13 Predation
  - 4.13.1 Marine, 368  
C. E. BRETT
  - 4.13.2 Terrestrial, 373  
J. A. MASSARE & C. E. BRETT
- 4.14 Parasitism, 376  
S. CONWAY MORRIS
- 4.15 Palaeopathology, 381  
L. B. HALSTEAD
- 4.16 Trophic Structure, 385  
J. A. CRAME
- 4.17 Evolution of Communities, 391  
A. J. BOUCOT
- 4.18 Biofacies, 395  
P. J. BRENCHLEY
- 4.19 Fossils as Environmental Indicators
  - 4.19.1 Climate from Plants, 401  
R. A. SPICER

- 4.19.2 Temperature from Oxygen Isotope Ratios, 403  
T. F. ANDERSON
- 4.19.3 Salinity from Faunal Analysis and Geochemistry, 406  
J. D. HUDSON
- 4.19.4 Oxygen Levels from Biofacies and Trace Fossils, 408  
D. J. BOTTJER & C. E. SAVRDA
- 4.19.5 Depth from Trace and Body Fossils, 411  
G. E. FARROW

## 5 Taxonomy, Phylogeny, and Biostratigraphy

- 5.1 Rules of Nomenclature
  - 5.1.1 International Codes of Zoological and Botanical Nomenclature, 417  
M. E. TOLLITT
  - 5.1.2 Disarticulated Animal Fossils, 419  
R. J. ALDRIDGE
  - 5.1.3 Disarticulated Plant Fossils, 421  
B. A. THOMAS
  - 5.1.4 Trace Fossils, 423  
S. R. A. KELLY
- 5.2 Analysis of Taxonomy and Phylogeny
  - 5.2.1 Overview, 425  
R. A. FORTEY
  - 5.2.2 Cladistics, 430  
P. L. FOREY
  - 5.2.3 Evolutionary Systematics, 434  
A. J. CHARIG
  - 5.2.4 Stratophenetics, 437  
P. D. GINGERICH
  - 5.2.5 Problematic Fossil Taxa, 442  
S. BENGTSON
- 5.3 Analysis of Taxonomic Diversity, 445  
A. B. SMITH
- 5.4 Vicariance Biogeography, 448  
L. GRANDE
- 5.5 Palaeobiogeography, 452  
C. R. NEWTON
- 5.6 Biostratigraphic Units and the Stratotype/Golden Spike Concept, 461  
C. H. HOLLAND
- 5.7 Zone Fossils, 466  
M. G. BASSETT
- 5.8 International Commission on Stratigraphy, 468  
M. G. BASSETT
- 5.9 International Geological Correlation Programme, 469  
J. W. COWIE

- 5.10 Global Boundary Stratotypes
  - 5.10.1 Overview, 471  
J. W. COWIE
  - 5.10.2 Precambrian–Cambrian, 475  
J. W. COWIE
  - 5.10.3 Ordovician–Silurian, 478  
C. R. BARNES & S. H. WILLIAMS
  - 5.10.4 Silurian–Devonian, 480  
C. H. HOLLAND
- 5.11 Fossils and Tectonics, 482  
R. A. FORTEY & L. R. M. COCKS

## 6 Infrastructure of Palaeobiology

- 6.1 Computer Applications in Palaeontology, 493  
J. A. KITCHELL
- 6.2 Practical Techniques
  - 6.2.1 Preparation of Macrofossils, 499  
P. J. WHYBROW & W. LINDSAY
  - 6.2.2 Extraction of Microfossils, 502  
R. J. ALDRIDGE
  - 6.2.3 Photography, 505  
D. J. SIVETER
  - 6.2.4 Electron Microscopy, 508  
D. CLAUGHER & P. D. TAYLOR
  - 6.2.5 Determination of Thermal Maturity, 511  
J. E. A. MARSHALL
- 6.3 Museology
  - 6.3.1 Collection Care and Status Material, 515  
P. R. CROWTHER
  - 6.3.2 Collection Management and Documentation Systems, 517  
P. R. CROWTHER
  - 6.3.3 Exhibit Strategies, 519  
R. S. MILES
- 6.4 Societies, Organizations, Journals, and Collections, 522  
J. NUDDS & D. PALMER
- 6.5 History of Palaeontology
  - 6.5.1 Before Darwin, 537  
J. C. THACKRAY
  - 6.5.2 Darwin to Plate Tectonics, 543  
P. J. BOWLER
  - 6.5.3 Plate Tectonics to *Paleobiology*, 547  
J. W. VALENTINE
  - 6.5.4 The Past Decade and the Future, 550  
A. HOFFMAN

Index, 557





## List of Contributors

- R. J. ALDRIDGE *Department of Geology, University of Leicester, Leicester LE1 7RH, U.K.*
- J. R. L. ALLEN *Postgraduate Research Institute for Sedimentology, University of Reading, Reading RG6 2AB, U.K.*
- P. A. ALLISON *Postgraduate Research Institute for Sedimentology, University of Reading, Reading RG6 2AB, U.K.*
- T. F. ANDERSON *Department of Geology, University of Illinois, Urbana, Illinois 61801, U.S.A.*
- W. I. AUSICH *Department of Geological Sciences, Ohio State University, Columbus, Ohio 43210, U.S.A.*
- S. M. AWRAMIK *Department of Geological Sciences, University of California, Santa Barbara, California 93106, U.S.A.*
- G. C. BAIRD *Department of Geosciences, State University of New York College: Fredonia, Fredonia, New York 14063, U.S.A.*
- C. R. BARNES *School of Earth and Ocean Sciences, University of Victoria, P.O. Box 3055, Victoria, British Columbia V8W 3P6, Canada.*
- M. G. BASSETT *Department of Geology, National Museum of Wales, Cathays Park, Cardiff CF1 3NP, U.K.*
- A. K. BEHRENSMEYER *Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, U.S.A.*
- S. BENGTON *Institute of Palaeontology, University of Uppsala, Box 558, S-751 22 Uppsala, Sweden.*
- M. J. BENTON *Department of Geology, University of Bristol, Queen's Road, Bristol BS8 1RJ, U.K.*
- J. BERGSTRÖM *Swedish Museum of Natural History, Section of Palaeozoology, PO Box 50007, S-104 05 Stockholm, Sweden.*
- D. J. BOTTJER *Department of Geological Sciences, University of Southern California, Los Angeles, California 90089, U.S.A.*
- A. J. BOUCOT *Department of Zoology, Oregon State University, Corvallis, Oregon 97331, U.S.A.*
- P. J. BOWLER *Department of Social Anthropology, Queen's University, Belfast BT7 1NN, U.K.*
- P. J. BRENCHLEY *Department of Earth Sciences, University of Liverpool, PO Box 147, Liverpool L69 3BX, U.K.*
- C. E. BRETT *Department of Geological Sciences, University of Rochester, Rochester, New York 14627, U.S.A.*
- D. E. G. BRIGGS *Department of Geology, University of Bristol, Queen's Road, Bristol BS8 1RJ, U.K.*
- N. D. BURGESS *Royal Society for the Protection of Birds, Sandy, Bedfordshire SG19 2DL, U.K.*
- A. J. CHARIG *c/o Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- B. CHARLESWORTH *Department of Ecology and Evolution, University of Chicago, 1103 East 57th Street, Chicago, Illinois 60637, U.S.A.*
- D. CLAUGHER *Department of Mineralogy, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- L. R. M. COCKS *Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- M. E. COLLINSON *Department of Geology, Royal Holloway & Bedford New College, University of London, Egham Hill, Egham, Surrey TW20 0EX, U.K.*
- S. CONWAY MORRIS *Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, U.K.*
- J. W. COWIE *Department of Geology, University of Bristol, Queen's Road, Bristol BS8 1RJ, U.K.*
- J. A. CRAME *British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, U.K.*
- P. R. CROWTHER *Bristol City Museums & Art Gallery, Queen's Road, Bristol BS8 1RL, U.K.*

- G. B. CURRY *Department of Geology & Applied Geology, University of Glasgow, Glasgow G12 8QQ, U.K.*
- D. EDWARDS *Department of Geology, University of Wales College of Cardiff, Cathays Park, Cardiff CF1 3YE, U.K.*
- G. EGLINTON *Organic Geochemistry Unit, School of Chemistry, University of Bristol, Bristol BS8 1TS, U.K.*
- N. ELDREDGE *Department of Invertebrates, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, U.S.A.*
- D. H. ERWIN *Department of Palaeobiology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, U.S.A.*
- P. FARRIMOND *The Organic Geochemistry Unit, The University, Newcastle upon Tyne NE1 7RU, U.K.*
- G. E. FARROW *19 Glenburn Road, Bearsden, Glasgow G61 4PT, U.K.*
- M. A. FEDONKIN *Palaeontological Institute, U.S.S.R. Academy of Sciences, Moscow 117321, U.S.S.R.*
- D. C. FISHER *Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.*
- P. L. FOREY *Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- R. A. FORTEY *Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- J. L. FRANZEN *Forschungsinstitut Senckenberg, Senckenberganlage 25, D-6000 Frankfurt am Main 1, Germany.*
- R. W. FREY *Deceased.*
- F. T. FÜRSICH *Institut für Paläontologie der Universität, Pleicherwall 1, D-8700 Würzburg, Germany.*
- P. D. GINGERICH *Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.*
- L. GRANDE *Department of Geology, Field Museum of Natural History, Chicago, Illinois 60605, U.S.A.*
- A. HALLAM *School of Earth Sciences, University of Birmingham, PO Box 363, Birmingham B15 2TT, U.K.*
- L. B. HALSTEAD *Deceased.*
- A. HOFFMAN *Deceased.*
- C. H. HOLLAND *Department of Geology, Trinity College, Dublin, Ireland.*
- J. D. HUDSON *Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, U.K.*
- D. JABLONSKI *Department of the Geophysical Sciences, University of Chicago, 5734 S. Ellis Avenue, Chicago, Illinois 60637, U.S.A.*
- S. R. A. KELLY *British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, U.K.*
- J. A. KITCHELL *Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.*
- A. H. KNOLL *Department of Organismic & Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.*
- M. LaBARBERA *Department of Anatomy, University of Chicago, 1025 East 57th Street, Chicago, Illinois 60637, U.S.A.*
- W. LINDSAY *Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- J. LUCAS *Institut de Géologie, Université Louis Pasteur, 1 rue Blessig, Strasbourg 67084, France.*
- L. LUGAR *Department of Geology, Franklin & Marshall College, Lancaster, Pennsylvania 17604, U.S.A.*
- E. L. LUNDELIUS, Jr *Department of Geological Sciences, University of Texas, Austin, Texas 78713, U.S.A.*
- J. E. A. MARSHALL *Department of Geology, The University, Highfield, Southampton SO9 5NH, U.K.*
- J. A. MASSARE *Department of Geological Sciences, University of Rochester, Rochester, New York 14627, U.S.A.*
- G. R. MCGHEE, Jr *Department of Geological Sciences, Rutgers University, New Brunswick, New Jersey 08903, U.S.A.*
- M. A. S. McMENAMIN *Department of Geology & Geography, Mount Holyoke College, South Hadley, Massachusetts 01075, U.S.A.*
- K. J. McNAMARA *Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia.*

- R. S. MILES *Department of Public Services, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- A. C. MILNER *Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- K. J. MÜLLER *Rheinische F.-W. Universität, Institut für Paläontologie, Nussallee 8, D-5300 Bonn 1, Germany.*
- C. R. NEWTON *Department of Geology, Syracuse University, Syracuse, New York 13244, U.S.A.*
- J. NUDDS *Manchester Museum, University of Manchester, Oxford Road, Manchester M13 9PL, U.K.*
- K. PADIAN *Department of Paleontology, University of California, Berkeley, California 94720, U.S.A.*
- D. PALMER *Department of Geology, National Museum of Wales, Cathays Park, Cardiff CF1 3NP, U.K.*
- C. R. C. PAUL *Department of Earth Sciences, University of Liverpool, PO Box 147, Liverpool L69 3BX, U.K.*
- S. G. PEMBERTON *Department of Geology, University of Alberta, Edmonton, Alberta T6G 2E3, Canada.*
- J. E. POLLARD *Department of Geology, University of Manchester, Oxford Road, Manchester M13 9PL, U.K.*
- L. PRÉVÔT *Centre de Géochimie, CNRS, 1 rue Blessig, Strasbourg 67084, France.*
- R. B. RICKARDS *Department of Earth Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EQ, U.K.*
- B. R. ROSEN *Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- B. RUNNEGAR *Institute of Geophysics & Planetary Physics and Department of Earth & Space Sciences, University of California, 405 Hilgard Avenue, Los Angeles, California 90024, U.S.A.*
- T. D. A. SAUNDERS *Department of Geology, University of Alberta, Edmonton, Alberta T6G 2E3, Canada.*
- C. E. SAVRDA *Department of Geology, Auburn University, Auburn, Alabama 36849, U.S.A.*
- T. SCHLÜTER *Department of Geology, Makerere University, PO Box 7062, Kampala, Uganda.*
- A. C. SCOTT *Department of Geology, Royal Holloway & Bedford New College, University of London, Egham Hill, Egham, Surrey TW20 0EX, U.K.*
- C. T. SCRUTTON *Department of Geological Sciences, University of Durham, Durham DH1 3LE, U.K.*
- A. SEILACHER *Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Sigwartstrasse 10, D-7400 Tübingen 1, Germany, and Kline Geology Laboratory, Yale University, New Haven, Connecticut 06511, U.S.A.*
- P. A. SELDEN *Department of Geology, University of Manchester, Oxford Road, Manchester M13 9PL, U.K.*
- J. J. SEPKOSKI, Jr *Department of the Geophysical Sciences, University of Chicago, 5734 S. Ellis Avenue, Chicago, Illinois 60637, U.S.A.*
- P. R. SHELDON *Department of Earth Sciences, Open University, Walton Hall, Milton Keynes MK7 6AA, U.K.*
- P. W. SIGNOR *Department of Geology, University of California, Davis, California 95616, U.S.A.*
- D. J. SIVETER *Geology Collections, University Museum, Parks Road, Oxford OX1 3PW, U.K.*
- P. W. SKELTON *Department of Earth Sciences, Open University, Walton Hall, Milton Keynes MK7 6AA, U.K.*
- A. B. SMITH *Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- S. E. SPEYER *Department of Geology, Arizona State University, Tempe, Arizona 85287-1404, U.S.A.*
- R. A. SPICER *Department of Earth Sciences, University of Oxford, Parks Road, Oxford OX1 3PR, U.K.*
- F. SURLYK *Geological Institute, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.*
- R. L. SUSMAN *Department of Anatomical Sciences, State University of New York, Stony Brook, Long Island, New York 11794, U.S.A.*
- P. D. TAYLOR *Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- J. C. THACKRAY *Archivist, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- B. A. THOMAS *Department of Botany, National Museum of Wales, Cathays Park, Cardiff CF1 3NP, U.K.*
- J. R. THOMASSON *Department of Biology and Allied Health, Fort Hays State University, Hays, Kansas 67601, U.S.A.*

- M. E. TOLLITT *Department of Public Services, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- M. E. TUCKER *Department of Geological Sciences, University of Durham, Durham DH1 3LE, U.K.*
- J. W. VALENTINE *Department of Geological Sciences, University of California, Santa Barbara, California 93106, U.S.A.*
- G. VIOHL *Jura Museum, Willibaldsburg, D-8078 Eichstatt, Germany.*
- M. R. VOORHIES *University of Nebraska State Museum, University of Nebraska, Lincoln, Nebraska 68588, U.S.A.*
- G. WÄCHTERSCHÄUSER *Tal 29, D-8000 München 2, Germany.*
- P. J. WHYBROW *Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.*
- R. WILD *Staatliches Museum für Naturkunde, Rosenstein 1, D-7000 Stuttgart 1, Germany.*
- S. H. WILLIAMS *Department of Earth Sciences, Memorial University, St John's, Newfoundland A1B 3X5, Canada.*
- C. R. WOESE *Department of Microbiology, University of Illinois, 131 Burrill Hall, 407 South Goodwin Avenue, Urbana, Illinois 61801, U.S.A.*
- R. J. WOOTTON *Department of Biological Sciences, University of Exeter, Prince of Wales Road, Exeter EX4 4PS, U.K.*
- V. P. WRIGHT *Postgraduate Research Institute for Sedimentology, University of Reading, Reading RG6 2AB, U.K.*

# Foreword

L. R. M. COCKS

*President of the  
Palaeontological Association  
1986–1988*

Scientists, both professional and amateur, have been describing fossils for over 200 years and the fruits of their labours make long library shelves groan with monographs and periodicals. These fruits have been distilled many times into the varied palaeontological textbooks and other encyclopaedic essays, which, in the case of the most common fossils, the invertebrate animals, have culminated in the many volumes of the *Treatise on Invertebrate Paleontology*. It is not our aim to compete with them. This is not an encyclopaedia of palaeontology.

Why then another book? In fact the very virtues and comprehensiveness of the *Treatise* and other compilations have enabled many scientists to add extra dimensions to their studies over the past 20 years, and it is the fruits of this vintage crop which are assembled here. Palaeobiology has come to encompass the heady topics of evolution, ecology and the subsequent taphonomy of extinct animals and plants, and articles on these are gathered here in over 120 contributions by leading workers from a variety of countries. General descriptions of the morphology of fossils are omitted, but the book includes background sections on general taxonomy, biostratigraphy and techniques, and a tantalizing group of essays in which the historical background to our science is placed in perspective. Each of the contributions reflects the individuality of its authors, but we trust that each article is complete in itself (and many will no doubt directly refresh a continuing lecture course).

For over 30 years the Palaeontological Association has been the focal point in Britain for studies on fossils. This book is not merely sponsored by the Association, but was generated in outline round its Council table. It forms one of a line of continuing substantial publications by the Association in ad-

dition to its twin periodicals *Palaeontology* and *Special Papers in Palaeontology*, and we are particularly pleased at the international response to our call for contributions, all of which have been received within a very tight timetable.

However, the Association's most particular and special thanks must go to Derek Briggs and Peter Crowther, who, from the twin venues of the University and City Museum at Bristol, have cheerfully and enthusiastically master-minded the whole project from its inception. Their contributions of time and effort, willingly given at the Association's request, have culminated so effectively in the present volume. Blackwell Scientific Publications have also proved excellent partners, and have brought all their renowned publishing expertise into the production of this book.

I cannot close without reiterating what a challenging and exciting time this is for palaeontology. During the nineteenth century the dating of rocks by fossils was at the very leading edge of geological studies, but for the middle years of this century it was displaced from that central position as the new generation of machine-led scientists made qualitative comparisons of fossils seem old-fashioned and peripheral. However, this very volume demonstrates how that latter position has changed, and that palaeontological and palaeobiological studies are now at the heart of a host of scientific themes ranging from evolutionary biology, through the disposition of continental plates in ancient oceans, to direct use in the search for oil. These changes have been accompanied by much quantitative reassessment of biotas and much new machinery. Individual palaeontologists have responded vigorously to these challenges and our horizons are already expanding in all dimensions into the next century.

