

TREATISE ON
INVERTEBRATE PALEONTOLOGY

Part E

PORIFERA

Revised

Volume 2:
Introduction to the Porifera

J. KEITH RIGBY, COORDINATING AUTHOR

by R. M. FINKS, R. E. H. REID, and J. K. RIGBY

*Prepared under Sponsorship of
The Geological Society of America, Inc.*

*The Paleontological Society
The Palaeontographical Society*

*SEPM (Society for Sedimentary Geology)
The Palaeontological Association*

RAYMOND C. MOORE
Founder

ROGER L. KAESLER
Editor

JILL HARDESTY, JANE KERNS
MICHAEL CORMACK
Assistant Editors and Editorial Staff

THE GEOLOGICAL SOCIETY OF AMERICA, INC.
and
THE UNIVERSITY OF KANSAS
BOULDER, COLORADO, and LAWRENCE, KANSAS
2003

© 2003 BY THE GEOLOGICAL SOCIETY OF AMERICA, INC.

AND

THE UNIVERSITY OF KANSAS

ALL RIGHTS RESERVED

Library of Congress Catalogue Card Number 53-12913

ISBN 0-8137-3130-5

Distributed by the Geological Society of America, Inc., P.O. Box 9140, Boulder, Colorado 80301, www.geosociety.org, from which current price lists of parts in print may be obtained and to which all orders and related correspondence should be directed. Editorial office of the *Treatise*: Paleontological Institute, The University of Kansas, 1475 Jayhawk Blvd., Room 121, Lawrence, Kansas 66045-7613, www.ku.edu/~paleo.

Citation information: Kaesler, R. L., ed. 2003. *Treatise on Invertebrate Paleontology, Part E (Revised), Porifera, vol. 2*. The Geological Society of America & The University of Kansas. Boulder & Lawrence. xxvii + 349 p., 135 fig., 10 tables.

The *Treatise on Invertebrate Paleontology* has been made possible by (1) funding principally from the National Science Foundation of the United States in its early stages, from The Geological Society of America through the bequest of Richard Alexander Fullerton Penrose, Jr., and from The Kansas University Endowment Association through the bequest of Raymond C. and Lillian B. Moore; (2) contribution of the knowledge and labor of specialists throughout the world, working in cooperation under sponsorship of The Geological Society of America, the Paleontological Society, the SEPM (Society for Sedimentary Geology), the Palaeontographical Society, and the Palaeontological Association; (3) acceptance by The University of Kansas of publication without any financial gain to the University; and (4) generous contributions by our individual and corporate sponsors.

PART E, Revised

PORIFERA

VOLUME 2:

INTRODUCTION TO THE PORIFERA

R. M. FINKS, R. E. H. REID, and J. K. RIGBY

CONTENTS

INFORMATION ON <i>TREATISE</i> VOLUMES	viii
EDITORIAL PREFACE (Roger L. Kaesler)	x
STRATIGRAPHIC DIVISIONS	xxiii
COORDINATING AUTHOR'S PREFACE (J. Keith Rigby)	xxiv
REPOSITORIES AND THEIR ABBREVIATIONS	xxvi
GENERAL FEATURES OF THE PORIFERA (R. E. H. Reid)	1
Introduction	1
Anatomy and Histology	1
Spicules	5
Spongin	8
Other Skeletal Characteristics	9
Form and Attachment	11
Individuality	11
Appendix: Terminology	11
CLASSIFICATION (J. K. Rigby)	13
CLASS DEMOSPONGEA: GENERAL MORPHOLOGY AND CLASSIFICATION (R. E. H. Reid)	15
Soft parts	16
Influence of Soft Parts on the Skeleton	17
Spicules	18
Tetraxons and Triaxons	27
Microscleres	29
Distribution of Microscleres	36
Spicular Ontogeny and Phylogeny	37
Megaspiculation: 1. Choristids	38
Megaspiculation: 2. Monaxonids	42
Megaspiculation: 3. Lithistids and Sublithistids	47
Nomenclature and Classification	51
Keratose Sponges	61
Other Demospongia	62
PALEOZOIC DEMOSPONGEA: MORPHOLOGY AND PHYLOGENY (Robert M. Finks)	63
Introduction	63
Skeletal Morphology	63
POST-PALEOZOIC DEMOSPONGEA (R. E. H. Reid)	81
Introduction	81
Classification	88

Status of Phylogenetic Concepts	89
Criteria of Classification	90
Names of Taxa	90
Ranks of Taxa	91
Subclasses	91
Alternative Classes or Subclasses	100
Skeletal Evolution	102
Phylogeny	110
DEMOSPONGE PHYLOGENY (R. E. H. Reid)	113
Introduction	113
Nonlithistid Problems	113
Historical Background	117
Conclusions	125
HEXACTINELLIDA: GENERAL MORPHOLOGY AND CLASSIFICATION (R. E. H. Reid)	127
Introduction	127
Hexactinellida and Hyalosponges	127
Soft Parts	127
Spicules	129
Megascleres	131
Microscleres	132
Classification	133
PALEOZOIC HEXACTINELLIDA: MORPHOLOGY AND PHYLOGENY (Robert M. Finks)	135
Organization of the Paleozoic Reticulosid Skeleton	135
Specialized Spicules	138
Evolutionary Relationships and Classification	143
POST-PALEOZOIC LYSSACINOSA (R. E. H. Reid)	155
WORKING KEYS TO SOME LYSSACINOSID FAMILIES (R. E. H. Reid)	160
DICTYONINE HEXASTEROPHORA (R. E. H. Reid)	162
Introduction	162
Habitus and General Skeletal Morphology	162
Hexactinosa	166
Lychniscosa	170
Phylogeny	174
GLOSSARY OF MORPHOLOGICAL TERMS (R. E. H. Reid & J. K. Rigby)	177
Introduction	177
Glossary	177
REPRODUCTION AND DEVELOPMENT (Robert M. Finks)	191
Reproduction	191
Development	191
Asexual Reproduction	199
PHYSIOLOGY (Robert M. Finks)	201
Feeding Mechanism	201
Food Substances	203
Digestion and Excretion	204
Transport of Metabolites	205
Irritability and Behavior	205

Respiration	206
Chemical Composition	207
Life Span	210
FUNCTIONAL MORPHOLOGY AND ADAPTATION (Robert M. Finks)	211
Introduction	211
Hydraulic System	211
Surface Area	213
Mechanical Support	214
Protection	215
Adaptations to Rough or Quiet Water	216
Adaptations to Suspended Sediment	218
Stabilization	218
Modes of Growth	221
VARIABILITY AND VARIATION (Robert M. Finks)	223
Introduction	223
Skeletal Treatment	223
External Form	224
Temporal Variation	228
Spicules	231
Skeletal Net	239
Aquiferous System	239
Conclusion	241
ECOLOGY AND PALEOECOLOGY OF SPONGES (Robert M. Finks)	243
Introduction	243
Ecology of Sponges	243
Ecological Distribution of Sponges	245
Silica and Sponge Ecology	252
Infaunal Sponges	253
Sponges Incorporating Sand in their Bodies	254
Predation on Sponges	255
Other Organisms in Sponges	255
Substrate	260
Light	260
Salinity	260
Temperature	260
EVOLUTION AND ECOLOGIC HISTORY OF SPONGES DURING PALEOZOIC TIMES (Robert M. Finks)	261
GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION (Robert M. Finks & J. Keith Rigby)	275
Holocene Distributions	275
Bathymetry	275
Origin of the Abyssal Sponge Fauna	279
History of Depth Distributions	282
Holocene Sponge Faunal Provinces	286
Geographic Distribution in the Past	287
Determinants of Sponge Distribution	292
TECHNIQUES OF STUDY (Robert M. Finks)	297
Introduction	297

Field Observations	297
Laboratory Study	297
Examination and Documentation	299
REFERENCES CITED	301
INDEX	345

INFORMATION ON *TREATISE* VOLUMES

Parts of the *Treatise* are distinguished by assigned letters with a view to indicating their systematic sequence while allowing publication of units in whatever order each is made ready for the press. Copies can be obtained from the Publication Sales Department, The Geological Society of America, 3300 Penrose Place, P.O. Box 9140, Boulder, Colorado 80301, www.geosociety.org.

PUBLISHED VOLUMES

- Part A. INTRODUCTION: Fossilization (Taphonomy), Biogeography, and Biostratigraphy, xxiii + 569 p., 169 fig., 1979.
- Part C. PROTISTA 2 (Sarcodina, Chiefly "Thecamoebians" and Foraminiferida), Volumes 1 and 2, xxxi + 900 p., 653 fig., 1964.
- Part D. PROTISTA 3 (Protozoa: Chiefly Radiolaria, Tintinnina), xii + 195 p., 92 fig., 1954.
- Part E. ARCHAEOCYATHA and PORIFERA, xviii + 122 p., 89 fig., 1955.
- Part E, Revised. ARCHAEOCYATHA, Volume 1, xxx + 158 p., 107 fig., 1972.
- Part F. COELENTERATA, xx + 498 p., 358 fig., 1956.
- Part F. COELENTERATA, Supplement 1 (Rugosa and Tabulata), Volumes 1 and 2, xl + 762 p., 462 fig., 1981.
- Part G. BRYOZOA, xiii + 253 p., 175 fig., 1953.
- Part G, Revised. BRYOZOA, Volume 1 (Introduction, Order Cystoporata, Order Cryptostomata), xxvi + 625 p., 295 fig., 1983.
- Part H. BRACHIOPODA, Volumes 1 and 2, xxxii + 927 p., 746 fig., 1965.
- Part H, Revised. BRACHIOPODA, Volume 1 (Introduction), xx + 539 p., 417 fig., 40 tables, 1997.
- Part H, Revised. BRACHIOPODA, Volumes 2 and 3 (Linguliformea, Craniiformea, Rhynchonelliformea [part]), xxx + 919 p., 616 fig., 17 tables, 2000.
- Part H, Revised. BRACHIOPODA, Volume 4 (Rhynchonelliformea [part]), xxxix + 768 p., 484 fig., 3 tables, 2002.
- Part I. MOLLUSCA 1 (Mollusca General Features, Scaphopoda, Amphineura, Monoplacophora, Gastropoda General Features, Archaeogastropoda, Mainly Paleozoic Caenogastropoda and Opisthobranchia), xxiii + 351 p., 216 fig., 1960.
- Part K. MOLLUSCA 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea), xxviii + 519 p., 361 fig., 1964.
- Part L. MOLLUSCA 4 (Cephalopoda: Ammonoidea), xxii + 490 p., 558 fig., 1957.
- Part L, Revised. MOLLUSCA 4, Volume 4 (Cretaceous Ammonoidea), xx + 362 p., 216 fig., 1996.
- Part N. MOLLUSCA 6 (Bivalvia), Volumes 1 and 2 (of 3), xxxvii + 952 p., 613 fig., 1969.
- Part N. MOLLUSCA 6 (Bivalvia), Volume 3, iv + 272 p., 153 fig., 1971.
- Part O. ARTHROPODA 1 (Arthropoda General Features, Protarthropoda, Euarthropoda General Features, Trilobitomorpha), xix + 560 p., 415 fig., 1959.
- Part O, Revised. ARTHROPODA 1 (Trilobita: Introduction, Order Agnostida, Order Redlichiida), xxiv + 530 p., 309 fig., 1997.

- Part P. ARTHROPODA 2 (Chelicerata, Pycnogonida, Palaeoisopus), xvii + 181 p., 123 fig., 1955 [1956].
- Part Q. ARTHROPODA 3 (Crustacea, Ostracoda), xxiii + 442 p., 334 fig., 1961.
- Part R. ARTHROPODA 4, Volumes 1 and 2 (Crustacea Exclusive of Ostracoda, Myriapoda, Hexapoda), xxxvi + 651 p., 397 fig., 1969.
- Part R. ARTHROPODA 4, Volumes 3 and 4 (Hexapoda), xxii + 655 p., 265 fig., 1992.
- Part S. ECHINODERMATA 1 (Echinodermata General Features, Homalozoa, Crinozoa, exclusive of Crinoidea), Volumes 1 and 2, xxx + 650 p., 400 fig., 1968 [1967].
- Part T. ECHINODERMATA 2 (Crinoidea), Volumes 1–3, xxxviii + 1,027 p., 619 fig., 1978.
- Part U. ECHINODERMATA 3 (Asterozoans, Echinozoans), xxx + 695 p., 534 fig., 1966.
- Part V. GRAPTOLITHINA, xvii + 101 p., 72 fig., 1955.
- Part V, Revised. GRAPTOLITHINA, xxxii + 163 p., 109 fig., 1970.
- Part W. MISCELLANEA (Conodonts, Conoidal Shells of Uncertain Affinities, Worms, Trace Fossils, Problematica), xxv + 259 p., 153 fig., 1962.
- Part W, Revised. MISCELLANEA, Supplement 1 (Trace Fossils and Problematica), xxi + 269 p., 110 fig., 1975.
- Part W, Revised. MISCELLANEA, Supplement 2 (Conodonta), xxviii + 202 p., frontis., 122 fig., 1981.

THIS VOLUME

- Part E, Revised. Porifera, Volume 2 (Introduction to the Porifera), xxvii + 349 p., 135 fig., 10 tables, 2003.

VOLUMES IN PREPARATION

- Part B. PROTISTA 1 (Chryomonadida, Coccolithophorida, Charophyta, Diatomacea, etc.).
- Part E, Revised. PORIFERA (additional volumes).
- Part F, Revised. CNIDARIA (Scleractinia).
- Part G, Revised. BRYOZOA (additional volumes).
- Part H, Revised. BRACHIOPODA (additional volumes).
- Part K, Revised. MOLLUSCA 3 (Nautiloidea).
- Part L, Revised. MOLLUSCA 4 (Ammonoidea) (additional volumes).
- Part M. MOLLUSCA 5 (Coleoidea).
- Part O, Revised. ARTHROPODA 1 (Trilobita) (additional volumes).
- Part Q, Revised. ARTHROPODA 3 (Ostracoda).
- Part R, Revised. ARTHROPODA 4 (Crustacea Exclusive of Ostracoda).
- Part T, Revised. ECHINODERMATA 2 (Crinoidea).
- Part V, Revised. GRAPTOLITHINA.
- Part W, Revised. TRACE FOSSILS.

EDITORIAL PREFACE

ROGER L. KAESLER

[The University of Kansas]

From the outset the aim of the *Treatise on Invertebrate Paleontology* has been to present a comprehensive and authoritative yet compact statement of knowledge concerning groups of invertebrate fossils. Typically, preparation of early *Treatise* volumes was undertaken by a small group with a synoptic view of the taxa being monographed. Two or perhaps three specialists worked together, sometimes co-opting others for coverage of highly specialized taxa. Recently, however, both new *Treatise* volumes and revisions of existing ones have been undertaken increasingly by teams of specialists led by a coordinating author. This volume, Part E Revised, Porifera, Volume 2, has been prepared by such a team. In the early stages of the work, R. M. Finks and R. E. H. Reid worked together on the volume. Final preparation of this volume was coordinated by J. K. Rigby, working with manuscript that was submitted previously by both Finks and Reid. Editorial matters specific to this volume are discussed near the end of this editorial preface.

ZOOLOGICAL NAMES

Questions about the proper use of zoological names arise continually, especially questions regarding both the acceptability of names and alterations of names that are allowed or even required. Regulations prepared by the International Commission on Zoological Nomenclature (ICZN) and published in 1999 in the *International Code of Zoological Nomenclature*, hereinafter referred to as the *Code*, provide procedures for answering such questions. The prime objective of the *Code* is to promote stability and universality in the use of the scientific names of animals, ensuring also that each generic name is distinct and unique, while avoiding unwarranted restrictions on freedom of

thought and action of systematists. Priority of names is a basic principle of the *Code*; but, under specified conditions and by following prescribed procedures, priority may be set aside by the Commission. These procedures apply especially where slavish adherence to the principle of priority would hamper or even disrupt zoological nomenclature and the information it conveys.

The Commission, ever aware of the changing needs of systematists, revised the *Code* in 1999 to enhance further nomenclatorial stability, specifying that the revised *Code* should take effect at the start of 2000. In spite of the revisions, the nomenclatorial tasks that confront zoological taxonomists are formidable and have often justified the complaint that the study of zoology and paleontology is too often merely the study of names rather than the study of animals. It is incumbent upon all systematists, therefore, at the outset of their work to pay careful attention to the *Code* to enhance stability by minimizing the number of subsequent changes of names, too many of which are necessitated by insufficient attention to detail. To that end, several pages here are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise*, especially in this volume. Terminology is explained, and examples are given of the style employed in the nomenclatorial parts of the systematic descriptions.

GROUPS OF TAXONOMIC CATEGORIES

Each taxon belongs to a category in the Linnaean hierarchical classification. The *Code* recognizes three groups of categories, a species-group, a genus-group, and a family-group. Taxa of lower rank than subspecies are excluded from the rules of zoological no-

menclature, and those of higher rank than superfamily are not regulated by the *Code*. It is both natural and convenient to discuss nomenclatorial matters in general terms first and then to consider each of these three recognized groups separately. Especially important is the provision that within each group the categories are coordinate, that is, equal in rank, whereas categories of different groups are not coordinate.

FORMS OF NAMES

All zoological names can be considered on the basis of their spelling. The first form of a name to be published is defined as the original spelling (*Code*, Article 32), and any form of the same name that is published later and is different from the original spelling is designated a subsequent spelling (*Code*, Article 33). Not every original or subsequent spelling is correct.

ORIGINAL SPELLINGS

If the first form of a name to be published is consistent and unambiguous, the original is defined as correct unless it contravenes some stipulation of the *Code* (Articles 11, 27 to 31, and 34) or unless the original publication contains clear evidence of an inadvertent error in the sense of the *Code*, or, among names belonging to the family-group, unless correction of the termination or the stem of the type genus is required. An original spelling that fails to meet these requirements is defined as incorrect.

If a name is spelled in more than one way in the original publication, the form adopted by the first reviser is accepted as the correct original spelling, provided that it complies with mandatory stipulations of the *Code* (Articles 11 and 24 to 34).

Incorrect original spellings are any that fail to satisfy requirements of the *Code*, represent an inadvertent error, or are one of multiple original spellings not adopted by a first reviser. These have no separate status in zoological nomenclature and, therefore, cannot enter into homonymy or be used as replacement names. They call for correction. For ex-

ample, a name originally published with a diacritical mark, apostrophe, dieresis, or hyphen requires correction by deleting such features and uniting parts of the name originally separated by them, except that deletion of an umlaut from a vowel in a name derived from a German word or personal name unfortunately requires the insertion of *e* after the vowel. Where original spelling is judged to be incorrect solely because of inadequacies of the Greek or Latin scholarship of the author, nomenclatorial changes conflict with the primary purpose of zoological nomenclature as an information retrieval system. One looks forward with hope to further revisions of the *Code* wherein rules are emplaced that enhance stability rather than classical scholarship, thereby facilitating access to information.

SUBSEQUENT SPELLINGS

If a subsequent spelling differs from an original spelling in any way, even by the omission, addition, or alteration of a single letter, the subsequent spelling must be defined as a different name. Exceptions include such changes as an altered termination of adjectival specific names to agree in gender with associated generic names (an unfortunate impediment to stability and retrieval of information); changes of family-group names to denote assigned taxonomic rank; and corrections that eliminate originally used diacritical marks, hyphens, and the like. Such changes are not regarded as spelling changes conceived to produce a different name. In some instances, however, species-group names having variable spellings are regarded as homonyms as specified in the *Code* (Article 58).

Altered subsequent spellings other than the exceptions noted may be either intentional or unintentional. If “demonstrably intentional” (*Code*, Article 33), the change is designated as an emendation. Emendations may be either justifiable or unjustifiable. Justifiable emendations are corrections of incorrect original spellings, and these take the authorship and date of the original

spellings. Unjustifiable emendations are names having their own status in nomenclature, with author and date of their publication. They are junior, objective synonyms of the name in its original form.

Subsequent spellings, if unintentional, are defined as incorrect subsequent spellings. They have no status in nomenclature, do not enter into homonymy, and cannot be used as replacement names.

AVAILABLE AND UNAVAILABLE NAMES

Editorial prefaces of some previous volumes of the *Treatise* have discussed in appreciable detail the availability of the many kinds of zoological names that have been proposed under a variety of circumstances. Much of that information, while important, does not pertain to the present volume, in which authors have used fewer terms for such names. The reader is referred to the *Code* (Articles 10 to 20) for further details on availability of names. Here, suffice it to say that an available zoological name is any that conforms to all mandatory provisions of the *Code*. All zoological names that fail to comply with mandatory provisions of the *Code* are unavailable and have no status in zoological nomenclature. Both available and unavailable names are classifiable into groups that have been recognized in previous volumes of the *Treatise*, although not explicitly differentiated in the *Code*. Among names that are available, these groups include inviolate names, perfect names, imperfect names, vain names, transferred names, improved or corrected names, substitute names, and conserved names. Kinds of unavailable names include naked names (see *nomina nuda* below), denied names, impermissible names, null names, and forgotten names.

Nomina nuda include all names that fail to satisfy provisions stipulated in Article 11 of the *Code*, which states general requirements of availability. In addition, they include names published before 1931 that were unaccompanied by a description, definition,

or indication (*Code*, Article 12) and names published after 1930 that (1) lacked an accompanying statement of characters that differentiate the taxon, (2) were without a definite bibliographic reference to such a statement, (3) were not proposed expressly as a replacement (*nomen novum*) of a pre-existing available name (*Code*, Article 13.1), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (*Code*, Article 13.2). *Nomina nuda* have no status in nomenclature, and they are not correctable to establish original authorship and date.

VALID AND INVALID NAMES

Important considerations distinguish valid from available names on the one hand and invalid from unavailable names on the other. Whereas determination of availability is based entirely on objective considerations guided by articles of the *Code*, conclusions as to validity of zoological names may be partly subjective. A valid name is the correct one for a given taxon, which may have two or more available names but only a single correct, hence valid, name, which is also generally the oldest name that it has been given. Obviously, no valid name can also be an unavailable name, but invalid names may be either available or unavailable. It follows that any name for a given taxon other than the valid name, whether available or unavailable, is an invalid name.

One encounters a sort of nomenclatorial no-man's land in considering the status of such zoological names as *nomina dubia* (doubtful names), which may include both available and unavailable names. The unavailable ones can well be ignored, but names considered to be available contribute to uncertainty and instability in the systematic literature. These can ordinarily be removed only by appeal to the ICZN for special action. Because few systematists care to seek such remedy, such invalid but available names persist in the literature.

NAME CHANGES IN RELATION TO GROUPS OF TAXONOMIC CATEGORIES SPECIES-GROUP NAMES

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here, both because the topic is well understood and relatively inconsequential and because the *Treatise* deals with genus-group names and higher categories. When the form of adjectival specific names is changed to agree with the gender of a generic name in transferring a species from one genus to another, one need never label the changed name as *nomen correctum*. Similarly, transliteration of a letter accompanied by a diacritical mark in the manner now called for by the *Code*, as in changing originally *bröggeri* to *broeggeri*, or eliminating a hyphen, as in changing originally published *cornu-oryx* to *cornuoryx*, does not require the designation *nomen correctum*. Of course, in this age of computers and electronic databases, such changes of name, which are perfectly valid for the purposes of scholarship, run counter to the requirements of nomenclatorial stability upon which the preparation of massive, electronic databases is predicated.

GENUS-GROUP NAMES

Conditions warranting change of the originally published, valid form of generic and subgeneric names are sufficiently rare that lengthy discussion is unnecessary. Only elimination of diacritical marks and hyphens in some names in this category and replacement of homonyms seem to furnish basis for valid emendation. Many names that formerly were regarded as homonyms are no longer so regarded, because two names that differ only by a single letter or in original publication by the presence of a diacritical mark in one are now construed to be entirely distinct (but see *Code*, Article 58).

As has been pointed out above, difficulty typically arises when one tries to decide

whether a change of spelling of a name by a subsequent author was intentional or unintentional, and the decision has to be made often arbitrarily.

FAMILY-GROUP NAMES

Family-Group Names: Authorship and Date

All family-group taxa having names based on the same type genus are attributed to the author who first published the name of any of these groups, whether tribe, subfamily, or family (superfamily being almost inevitably a later-conceived taxon). Accordingly, if a family is divided into subfamilies or a subfamily into tribes, the name of no such subfamily or tribe can antedate the family name. Moreover, every family containing differentiated subfamilies must have a nominate subfamily (*sensu stricto*), which is based on the same type genus as the family. Finally, the author and date set down for the nominate subfamily invariably are identical with those of the family, irrespective of whether the author of the family or some subsequent author introduced subdivisions.

Corrections in the form of family-group names do not affect authorship and date of the taxon concerned, but in the *Treatise* recording the authorship and date of the correction is desirable because it provides a pathway to follow the thinking of the systematists involved.

Family-Group Names: Use of *nomen translatum*

The *Code* (Article 29.2) specifies the suffixes for tribe (-ini), subfamily (-inae), family (-idae) and superfamily (-oidea), the formerly widely used ending (-acea) for superfamily having been disallowed. All these family-group categories are defined as coordinate (*Code*, Article 36.1): "A name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at other ranks in the family group; all these taxa have the same type genus, and their names are

formed from the stem of the name of the type genus [Art. 29.3] with appropriate change of suffix [Art. 34.1]. The name has the same authorship and date at every rank.” Such changes of rank and concomitant changes of endings as elevation of a subfamily to family rank or of a family to superfamily rank, if introduced subsequent to designation of the original taxon or based on the same nominotypical genus, are *nomina translata*. In the *Treatise* it is desirable to distinguish the valid alteration in the changed ending of each transferred family-group name by the term *nomen translatum*, abbreviated to *nom. transl.* Similarly for clarity, authors should record the author, date, and page of the alteration, as in the following example.

Family HEXAGENITIDAE
Lameere, 1917

[*nom. transl.* DEMOULIN, 1954, p. 566, ex Hexagenitinae LAMEERE, 1917, p. 74]

This is especially important for superfamilies, for the information of interest is the author who initially introduced a taxon rather than the author of the superfamily as defined by the *Code*. For example:

Superfamily AGNOSTOIDEA
M’Coy, 1849

[*nom. transl.* SHERGOLD, LAURIE, & SUN, 1990, p. 32, ex Agnostinae M’COY, 1849, p. 402]

The latter is merely the individual who first defined some lower-ranked, family-group taxon that contains the nominotypical genus of the superfamily. On the other hand, the publication that introduces the superfamily by *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the taxon.

Family-Group Names:
Use of *nomen correctum*

Valid name changes classed as *nomina correctata* do not depend on transfer from one category of the family group to another but most commonly involve correction of the stem of the nominotypical genus. In addition,

they include somewhat arbitrarily chosen modifications of endings for names of tribes or superfamilies. Examples of the use of *nomen correctum* are the following.

Family STREPTELASMATIDAE
Nicholson, 1889

[*nom. correct.* WEDEKIND, 1927, p. 7, pro Streptelasmidae NICHOLSON in NICHOLSON & LYDEKKER, 1889, p. 297]

Family PALAEOSCORPIDAE
Lehmann, 1944

[*nom. correct.* PETRUNKEVITCH, 1955, p. 73, pro Palaeoscorpionidae LEHMANN, 1944, p. 177]

Family-Group Names:
Replacements

Family-group names are formed by adding combinations of letters, which are prescribed for all family-group categories, to the stem of the name belonging to the nominotypical genus first chosen as type of the assemblage. The type genus need not be the first genus in the family to have been named and defined, but among all those included it must be the first published as name giver to a family-group taxon. Once fixed, the family-group name remains tied to the nominotypical genus even if the generic name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* requires replacement of a family-group name only if the nominotypical genus is found to have been a junior homonym when it was proposed (*Code*, Article 39), in which case “. . . it must be replaced either by the next oldest available name from among its synonyms [Art. 23.3.5], including the names of its subordinate family-group taxa, or, if there is no such synonym, by a new name based on the valid name . . . of the former type genus.” Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family-group name. Recommendation 40A of the *Code*, however, specifies that for subsequent application of the rule of priority, the family-group name “. . . should be cited

with its original author and date (see Recommendation 22A.2.2), followed by the date of its priority as determined by this Article; the date of priority should be enclosed in parentheses.” Many family-group names that have been in use for a long time are *nomina nuda*, since they fail to satisfy criteria of availability (*Code*, Article 11.7). These demand replacement by valid names.

The aim of family-group nomenclature is to yield the greatest possible stability and uniformity, just as in other zoological names. Both taxonomic experience and the *Code* (Article 40) indicate the wisdom of sustaining family-group names based on junior subjective synonyms if they have priority of publication, for opinions of the same worker may change from time to time. The retention of first-published, family-group names that are found to be based on junior objective synonyms, however, is less clearly desirable, especially if a replacement name derived from the senior objective synonym has been recognized very long and widely. Moreover, to displace a widely used, family-group name based on the senior objective synonym by disinterring a forgotten and virtually unused family-group name based on a junior objective synonym because the latter happens to have priority of publication is unsettling.

A family-group name may need to be replaced if the nominotypical genus is transferred to another family group. If so, the first-published of the generic names remaining in the family-group taxon is to be recognized in forming a replacement name.

SUPRAFAMILIAL TAXA: TAXA ABOVE FAMILY-GROUP

International rules of zoological nomenclature as given in the *Code* affect only lower-rank categories: subspecies to superfamily. Suprafamilial categories (suborder to kingdom) are either not mentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoo-*

logical Nomenclature (1953, Articles 59 to 69) proposed adopting rules for naming suborders and higher taxa up to and including phylum, with provision for designating a type genus for each, in such manner as not to interfere with the taxonomic freedom of workers. Procedures were outlined for applying the rule of priority and rule of homonymy to suprafamilial taxa and for dealing with the names of such taxa and their authorship, with assigned dates, if they should be transferred on taxonomic grounds from one rank to another. The adoption of terminations of names, different for each category but uniform within each, was recommended.

The Colloquium on Zoological Nomenclature, which met in London during the week just before the 15th International Congress of Zoology convened in 1958, discussed thoroughly the proposals for regulating suprafamilial nomenclature, as well as many others advocated for inclusion in the new *Code* or recommended for exclusion from it. A decision that was supported by a wide majority of the participants in the colloquium was against the establishment of rules for naming taxa above family-group rank, mainly because it was judged that such regulation would unwisely tie the hands of taxonomists. For example, a class or order defined by an author at a given date, using chosen morphologic characters (e.g., gills of bivalves), should not be allowed to freeze nomenclature, taking precedence over another class or order that is proposed later and distinguished by different characters (e.g., hinge teeth of bivalves). Even the fixing of type genera for suprafamilial taxa would have little, if any, value, hindering taxonomic work rather than aiding it. Beyond mere tidying up, no basis for establishing such types and for naming these taxa has yet been provided.

The considerations just stated do not prevent the editors of the *Treatise* from making rules for dealing with suprafamilial groups of animals described and illustrated in this

publication. Some uniformity is needed, especially for the guidance of *Treatise* authors. This policy should accord with recognized general practice among zoologists; but where general practice is indeterminate or nonexistent, our own procedure in suprafamilial nomenclature needs to be specified as clearly as possible. This pertains especially to decisions about names themselves, about citation of authors and dates, and about treatment of suprafamilial taxa that, on taxonomic grounds, are changed from their originally assigned rank. Accordingly, a few rules expressing *Treatise* policy are given here, some with examples of their application.

1. The name of any suprafamilial taxon must be a Latin or Latinized, uninominal noun of plural form or treated as such, with a capital initial letter and without diacritical mark, apostrophe, diaeresis, or hyphen. If a component consists of a numeral, numerical adjective, or adverb, this must be written in full.

2. Names of suprafamilial taxa may be constructed in almost any manner. A name may indicate morphological attributes (e.g., Lamellibranchiata, Cyclostomata, Toxoglossa) or be based on the stem of an included genus (e.g., Bellerophontina, Nautilida, Fungiina) or on arbitrary combinations of letters (e.g., Yuania); none of these, however, can end in -idae or -inae, which terminations are reserved for family-group taxa. No suprafamilial name identical in form to that of a genus or to another published suprafamilial name should be employed (e.g., order Decapoda LATREILLE, 1803, crustaceans, and order Decapoda LEACH, 1818, cephalopods; suborder Chonetoidea MUIR-WOOD, 1955, and genus *Chonetoidea* JONES, 1928). Worthy of notice is the classificatory and nomenclatorial distinction between suprafamilial and family-group taxa that are named from the same type genus, since one is not considered to be transferable to the other (e.g., suborder Bellerophontina ULRICH & SCOFIELD, 1897 is not coordinate with superfamily Bellerophontoidea MCCOY,

1851 or family Bellerophontidae MCCOY, 1851).

3. The rules of priority and homonymy lack any force of international agreement as applied to suprafamilial names, yet in the interest of nomenclatorial stability and to avoid confusion these rules are widely applied by zoologists to taxa above the family-group level wherever they do not infringe on taxonomic freedom and long-established usage.

4. Authors who accept priority as a determinant in nomenclature of a suprafamilial taxon may change its assigned rank at will, with or without modifying the terminal letters of the name, but such changes cannot rationally be judged to alter the authorship and date of the taxon as published originally. A name revised from its previously published rank is a transferred name (*nomen translatum*), as illustrated in the following.

Order CORYNEXOCHIDA Kobayashi, 1935

[*nom. transl.* MOORE, 1959, p. 217, ex suborder Corynexochida KOBAYASHI, 1935, p. 81]

A name revised from its previously published form merely by adoption of a different termination without changing taxonomic rank is a *nomen correctum*.

Order DISPARIDA Moore & Laudon, 1943

[*nom. correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, pro order Disparata MOORE & LAUDON, 1943, p. 24]

A suprafamilial name revised from its previously published rank with accompanying change of termination, which signals the change of rank, is recorded as a *nomen translatum et correctum*.

Order HYBOCRINIDA Jaekel, 1918

[*nom. transl. et correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, ex suborder Hybocrinites JAEKEL, 1918, p. 90]

5. The authorship and date of nominate subordinate and supraordinate taxa among

suprafamilial taxa are considered in the *Treatise* to be identical since each actually or potentially has the same type. Examples are given below.

Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* TEICHERT in TEICHERT & others, 1964, p. 128, *ex order* Endoceroidea TEICHERT, 1933, p. 214]

Order ENDOCERIDA Teichert, 1933

[*nom. correct.* TEICHERT in TEICHERT & others, 1964, p. 165, *pro order* Endoceroidea TEICHERT, 1933, p. 214]

TAXONOMIC EMENDATION

Emendation has two distinct meanings as regards zoological nomenclature. These are alteration of a name itself in various ways for various reasons, as has been reviewed, and alteration of the taxonomic scope or concept for which a name is used. The *Code* (Article 33.1 and Glossary) concerns itself only with the first type of emendation, applying the term to intentional, either justified or unjustified changes of the original spelling of a name. The second type of emendation primarily concerns classification and inherently is not associated with change of name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleontologists, who have emended zoological names refer to what they consider a material change in application of the name such as may be expressed by an importantly altered diagnosis of the assemblage covered by the name. The abbreviation *emend.* then must accompany the name with statement of the author and date of the emendation. On the other hand, many systematists think that publication of *emend.* with a zoological name is valueless because alteration of a taxonomic concept is introduced whenever a subspecies, species, genus, or other taxon is incorporated into or removed from a higher zoological taxon. Inevitably associated with such classificatory expansions and restrictions is

some degree of emendation affecting diagnosis. Granting this, still it is true that now and then somewhat more extensive revisions are put forward, generally with a published statement of the reasons for changing the application of a name. To erect a signpost at such points of most significant change is worthwhile, both as an aid to subsequent workers in taking account of the altered nomenclatorial usage and to indicate where in the literature cogent discussion may be found. Authors of contributions to the *Treatise* are encouraged to include records of all especially noteworthy emendations of this nature, using the abbreviation *emend.* with the name to which it refers and citing the author, date, and page of the emendation. Examples from *Treatise* volumes follow.

Order ORTHIDA Schuchert & Cooper, 1932

[*nom. transl. et correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 220, *ex suborder* Orthoidea SCHUCHERT & COOPER, 1932, p. 43; *emend.*, WILLIAMS & WRIGHT, 1965, p. 299]

Subfamily ROVEACRININAE Peck, 1943

[Roveacrininae PECK, 1943, p. 465; *emend.*, PECK in MOORE & TEICHERT, 1978, p. 921]

STYLE IN GENERIC DESCRIPTIONS

CITATION OF TYPE SPECIES

In the *Treatise* the name of the type species of each genus and subgenus is given immediately following the generic name with its accompanying author, date, and page reference or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names of this species is cited, accompanied by an asterisk (*), with notation of the author, date, and page of original publication, except if the species was first published in the same paper and by the same author as that containing definition of the genus of which it is the type. In this instance, the initial letter of the generic name followed

by the trivial name is given without repeating the name of the author and date. Examples of these two sorts of citations follow.

Orionastraea SMITH, 1917, p. 294 [**Sarcinula phillipsi* MCCOY, 1849, p. 125; OD].

Schoenophyllum SIMPSON, 1900, p. 214 [**S. aggregatum*; OD].

If the cited type species is a junior synonym of some other species, the name of this latter is given also, as follows.

Actinocyathus D'ORBIGNY, 1849, p. 12 [**Cyathophyllum crenulate* PHILLIPS, 1836, p. 202; M; =*Lonsdaleia floriformis* (MARTIN), 1809, pl. 43; validated by ICZN Opinion 419].

In some instances the type species is a junior homonym. If so, it is cited as shown in the following example.

Prionocyclus MEEK, 1871b, p. 298 [**Ammonites serratocarinatus* MEEK, 1871a, p. 429, non STOLICZKA, 1864, p. 57; =*Prionocyclus wyomingensis* MEEK, 1876, p. 452].

In the *Treatise* the name of the type species is always given in the exact form it had in the original publication. Where mandatory changes are required, such as removal of diacritical marks or hyphens, these are introduced later in the text, typically in the description of a figure.

Fixation of Type Species Originally

It is desirable to record the manner of establishing the type species, whether by original designation (OD) or by subsequent designation (SD). The type species of a genus or subgenus, according to provisions of the *Code*, may be fixed in various ways in the original publication; or it may be fixed subsequently in ways specified by the *Code* (Article 68) and described in the next section. Type species fixed in the original publication include (1) *original designation* (in the *Treatise* indicated by OD) when the type species is explicitly stated or (before 1931) indicated by n. gen., n. sp. (or its equivalent) applied to a single species included in a new genus, (2) defined by use of *typus* or *typicus* for one of the species included in a new genus (adequately indicated in the *Treatise* by the

specific name), (3) established by *monotypy* if a new genus or subgenus has only one originally included species (in the *Treatise* indicated as M), and (4) fixed by *tautonymy* if the genus-group name is identical to an included species name not indicated as the type.

Fixation of Type Species Subsequently

The type species of many genera are not determinable from the publication in which the generic name was introduced. Therefore, such genera can acquire a type species only by some manner of subsequent designation. Most commonly this is established by publishing a statement naming as type species one of the species originally included in the genus. In the *Treatise* such fixation of the type species by subsequent designation in this manner is indicated by the letters SD accompanied by the name of the subsequent author (who may be the same person as the original author) and the publication date and page number of the subsequent designation. Some genera, as first described and named, included no mentioned species (for such genera established after 1930, see below); these necessarily lack a type species until a date subsequent to that of the original publication when one or more species is assigned to such a genus. If only a single species is thus assigned, it becomes automatically the type species. Of course, the first publication containing assignment of species to the genus that originally lacked any included species is the one concerned in fixation of the type species, and if this publication names two or more species as belonging to the genus but did not designate a type species, then a later SD designation is necessary. Examples of the use of SD as employed in the *Treatise* follow.

Hexagonaria GURICH, 1896, p. 171 [**Cyathophyllum hexagonum* GOLDFUSS, 1826, p. 61; SD LANG, SMITH, & THOMAS, 1940, p. 69].

Mesephemera HANDLIRSCH, 1906, p. 600 [**Tineites lithophilus* GERMAR, 1842, p. 88; SD CARPENTER, herein].

Another mode of fixing the type species of a genus is through action of the International

Commission of Zoological Nomenclature using its plenary powers. Definition in this way may set aside application of the *Code* so as to arrive at a decision considered to be in the best interest of continuity and stability of zoological nomenclature. When made, it is binding and commonly is cited in the *Treatise* by the letters ICZN, accompanied by the date of announced decision and reference to the appropriate numbered opinion.

Subsequent designation of a type species is admissible only for genera established prior to 1931. A new genus-group name established after 1930 and not accompanied by fixation of a type species through original designation or original indication is invalid (*Code*, Article 13.3). Effort of a subsequent author to validate such a name by subsequent designation of a type species constitutes an original publication making the name available under authorship and date of the subsequent author.

HOMONYMS

Most generic names are distinct from all others and are indicated without ambiguity by citing their originally published spelling accompanied by name of the author and date of first publication. If the same generic name has been applied to two or more distinct taxonomic units, however, it is necessary to differentiate such homonyms. This calls for distinction between junior homonyms and senior homonyms. Because a junior homonym is invalid, it must be replaced by some other name. For example, *Callophora* HALL, 1852, introduced for Paleozoic trepostomate bryozoans, is invalid because Gray in 1848 published the same name for Cretaceous–Holocene cheilostomate bryozoans. Bassler in 1911 introduced the new name *Hallophora* to replace Hall's homonym. The *Treatise* style of entry is given below.

Hallophora BASSLER, 1911, p. 325, *nom. nov. pro Callophora* HALL, 1852, p. 144, *non* GRAY, 1848.

In like manner, a replacement generic name that is needed may be introduced in the *Treatise* (even though first publication of generic names otherwise in this work is generally

avoided). An exact bibliographic reference must be given for the replaced name as in the following example.

Mysterium DE LAUBENFELS, herein, *nom. nov. pro Mystrium* SCHRAMMEN, 1936, p. 183, *non* ROGER, 1862 [**Mystrium porosum* SCHRAMMEN, 1936, p. 183; OD].

Otherwise, no mention is made generally of the existence of a junior homonym.

Synonymous Homonyms

An author sometimes publishes a generic name in two or more papers of different date, each of which indicates that the name is new. This is a bothersome source of errors for later workers who are unaware that a supposed first publication that they have in hand is not actually the original one. Although the names were published separately, they are identical and therefore definable as homonyms; at the same time they are absolute synonyms. For the guidance of all concerned, it seems desirable to record such names as synonymous homonyms. In the *Treatise* the junior of one of these is indicated by the abbreviation *jr. syn. hom.*

Not infrequently, identical family-group names are published as new names by different authors, the author of the name that was introduced last being ignorant of previous publication(s) by one or more other workers. In spite of differences in taxonomic concepts as indicated by diagnoses and grouping of genera and possibly in assigned rank, these family-group taxa, being based on the same type genus, are nomenclatorial homonyms. They are also synonyms. Wherever encountered, such synonymous homonyms are distinguished in the *Treatise* as in dealing with generic names.

A rare but special case of homonymy exists when identical family names are formed from generic names having the same stem but differing in their endings. An example is the family name Scutellidae RICHTER & RICHTER, 1925, based on *Scutellum* PUSCH, 1833, a trilobite. This name is a junior homonym of Scutellidae GRAY, 1825, based on the echinoid genus *Scutella* LAMARCK, 1816.

The name of the trilobite family was later changed to Scutelluidae (ICZN, Opinion 1004, 1974).

SYNONYMS

In the *Treatise*, citation of synonyms is given immediately after the record of the type species. If two or more synonyms of differing date are recognized, these are arranged in chronological order. Objective synonyms are indicated by accompanying designation *obj.*, others being understood to constitute subjective synonyms, of which the types are also indicated. Examples showing *Treatise* style in listing synonyms follow.

Mackenziophyllum PEDDER, 1971, p. 48 [**M. insolitum*; OD] [= *Zonastraea* TSYGANKO in SPASSKIY, KRAVTSOV, & TSYGANKO, 1971, p. 85, *nom. nud.*; *Zonastraea* TSYGANKO, 1972, p. 21 (type, *Z. graciosa*, OD)].

Kodonophyllum WEDEKIND, 1927, p. 34 [**Streptelasma Milne-Edwardsi* DYBOWSKI, 1873, p. 409; OD; = *Madrepora truncata* LINNE, 1758, p. 795, see SMITH & TREMBERTH, 1929, p. 368] [= *Patrophontes* LANG & SMITH, 1927, p. 456 (type, *Madrepora truncata* LINNE, 1758, p. 795, OD); *Codonophyllum* LANG, SMITH, & THOMAS, 1940, p. 39, *obj.*].

Some junior synonyms of either the objective or the subjective sort may be preferred over senior synonyms whenever uniformity and continuity of nomenclature are served by retaining a widely used but technically rejectable name for a genus. This requires action of the ICZN, which may use its plenary powers to set aside the unwanted name, validate the wanted one, and place the concerned names on appropriate official lists.

OTHER EDITORIAL MATTERS BIOGEOGRAPHY

Purists, *Treatise* editors among them, would like nothing better than a stable world with a stable geography that makes possible a stable biogeographical classification. Global events of the past few years have shown how rapidly geography can change, and in all likelihood we have not seen the last of such change as new, so-called republics continue to spring up all over the globe. One expects confusion among readers in the future as

they try to decipher such geographical terms as U.S.S.R., Yugoslavia, or Ceylon. Such confusion is unavoidable, as books must be completed and published at some real time. Libraries would be limited indeed if publication were always to be delayed until the political world had settled down. In addition, such terms as central Europe and western Europe are likely to mean different things to different people. Some imprecision is introduced by the use of all such terms, of course, but it is probably no greater than the imprecision that stems from the fact that the work of paleontology is not yet finished, and the geographical ranges of many genera are imperfectly known.

Other geographic terms can also have varying degrees of formality. In general, *Treatise* policy is to use adjectives rather than nouns to refer to directions. Thus we have used *southern* and *western* in place of *South* and *West* unless a term has been formally defined as a geographic entity (e.g., South America or West Virginia). Note that we have referred to western Texas rather than West Texas, which is said to be not a state but a state of mind.

NAMES OF AUTHORS: TRANSLATION AND TRANSLITERATION

Chinese scientists have become increasingly active in systematic paleontology in the past two decades. Chinese names cause anguish among English-language bibliographers for two reasons. First, no scheme exists for one-to-one transliteration of Chinese characters into roman letters. Thus, a Chinese author may change the roman-letter spelling of his name from one publication to another. For example, the name Chang, the most common family name in the world reportedly held by some one billion people, has been spelled more recently Zhang. The principal purpose of a bibliography is to provide the reader with entry into the literature. Quite arbitrarily, therefore, in the interest of information retrieval, the *Treatise* editorial staff has decided to retain the roman spelling

that a Chinese author has used in each of his publications rather than attempting to adopt a common spelling of an author's name to be used in all citations of his work. It is entirely possible, therefore, that the publications of a Chinese author may be listed in more than one place under more than one name in the bibliography.

Second, most but by no means all Chinese list their family name first followed by given names. People with Chinese names who study in the West, however, often reverse the order, putting the family name last as is the Western custom. Thus, for example, Dr. Yi-Maw Chang, formerly of the staff of the Paleontological Institute, was Chang Yi-Maw when he lived in Taiwan. When he came to America, he became Yi-Maw Chang. In the *Treatise*, authors' names are used in the text and listed in the references as they appear in the source being cited.

Several systems exist for transliterating the Cyrillic alphabet into the roman alphabet. On the recommendation of skilled bibliographic librarians, we have adopted the American Library Association/Library of Congress romanization table for Russian and other languages using the Cyrillic alphabet.

MATTERS SPECIFIC TO THIS VOLUME

Some languages, in this volume most notably the Polish and Czech languages, are enriched with the use of diacritical marks that provide enhanced alphabetical diversity. While celebrating diversity, we have nevertheless elected to omit such marks from Polish and Czech geographical terms used in the *Treatise*. We continue to insert diacritical marks in authors' names. Two factors have led us to this editorial decision. First, we in the *Treatise* editorial office typeset electronically all the pages, and such diacritical marks must be inserted by hand into the final computer-prepared pages. This is a costly and time-consuming operation that is fraught with the possibility of introducing errors. Second, in the burgeoning informa-

tion age of the new millennium, databases and schemes for information retrieval will be of critical importance in managing paleontological information. Stability and uniformity of terminology are requisites of database-management systems, and the use of diacritical marks and computer technology are likely to remain incompatible for some time to come. We hope that linguistic purists will be tolerant of this transgression, which we have undertaken solely in the interest of expediency, consistency, and information retrieval.

In this volume we have taken special pains to acknowledge authorship of chapters and subsections. Readers citing the volume are encouraged to pay close attention to the actual authorship of a chapter or subsection.

Stratigraphic ranges of taxa have been compiled from the ranges of lower taxa. In all instances, we have used the *range-through* method of describing ranges. In instances, therefore, where the work of paleontology is not yet finished, some ranges of higher taxa will not show gaps between the ranges of their subtaxa and may seem to be more complete than the data warrant.

ACKNOWLEDGMENTS

The Paleontological Institute's Assistant Editor for Text, Jill Hardesty, and the Assistant Editor for Illustrations, Jane Kerns, have faced admirably the formidable task of moving this volume through the various stages of editing and into production. In this they have been ably assisted by other members of the editorial team including Jack Keim with photography and computer graphics, Mike Cormack with his outstanding computer skills, Mary Huyck with her work on illustrations, and Denise Mayse and Jean Burgess with general support. Jill Krebs, the remaining member of the Paleontological Institute editorial staff, is involved with preparation of PaleoBank, the paleontological database for future *Treatise* volumes, and has not been closely involved with this volume.

Many of the illustrations in this volume were prepared a number of years ago by the

late Roger B. Williams, who served the Paleontological Institute as assistant editor for illustrations until shortly before his death. We remain indebted to him for his dedication to the *Treatise* project, his very high standards, and his synoptic view of the *Treatise*.

This editorial preface and other, recent ones are extensive revisions of the prefaces prepared for previous *Treatise* volumes by former editors, including the late Raymond C. Moore, the late Curt Teichert, and Richard A. Robison. I am indebted to them for preparing earlier prefaces and for the leadership they have provided in bringing the *Treatise* project to its present status.

Finally, on behalf of the members of the staff of the Paleontological Institute and the other authors of this volume, I am pleased to have the opportunity to extend our sincere thanks to Professor J. Keith Rigby for helping us bring this volume to publication.

Throughout his career, his work has been marked by scrupulous scholarship, complete dedication to the task, and unwavering attention to detail. He has brought the same approach to this project, and we are grateful to him for all he has done.

REFERENCES

- International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, 4th edition. International Trust for Zoological Nomenclature. London. 306 p.
- Moore, R. C., and C. Teichert. 1978. *Treatise on Invertebrate Paleontology. Part T, Echinodermata* 2(1). The Geological Society of America and The University of Kansas. Boulder & Lawrence. 401 p.
- Robison, R. A., and C. Teichert. 1979. *Treatise on Invertebrate Paleontology. Part A, Introduction*. The Geological Society of America and The University of Kansas. Boulder & Lawrence. 569 p.

Roger L. Kaesler
Lawrence, Kansas
October 27, 2003

STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well established throughout the world, but minor divisions (e.g., subseries, stages, and substages) are more likely to be provincial in application. The stratigraphic units listed here represent an authoritative version of the stratigraphic column for all taxonomic work relating to the revision of Part E. They are adapted from the International Union of Geological Sciences 2000 International Stratigraphic Chart, compiled by Jürgen Remane, Chairman of the International Commission on Stratigraphy (ICS), with the collaboration of all ICS Subcommissions. A copy of the chart can be obtained at the following website: <http://www.iugs.org/iugs/pubs/intstratchart.htm>.

Cenozoic Erathem

Quaternary System

- Holocene Series
- Pleistocene Series

Neogene System

- Pliocene Series
- Miocene Series

Paleogene System

- Oligocene Series
- Eocene Series
- Paleocene Series

Mesozoic Erathem

Cretaceous System

- Upper Cretaceous Series
- Lower Cretaceous Series

Jurassic System

- Upper Jurassic Series
- Middle Jurassic Series
- Lower Jurassic Series

Triassic System

- Upper Triassic Series
- Middle Triassic Series
- Lower Triassic Series

Paleozoic Erathem

Permian System

- Lopingian Series
- Guadalupian Series
- Cisuralian Series

Carboniferous System

- Pennsylvanian Subsystem
- Mississippian Subsystem

Devonian System

- Upper Devonian Series
- Middle Devonian Series
- Lower Devonian Series

Silurian System

- Pridoli Series
- Ludlow Series
- Wenlock Series
- Llandovery Series

Ordovician System

- Upper Ordovician Series
- Middle Ordovician Series
- Lower Ordovician Series

Cambrian System

- Upper Cambrian Series
- Middle Cambrian Series
- Lower Cambrian Series

COORDINATING AUTHOR'S PREFACE

J. KEITH RIGBY
[Brigham Young University]

This volume is the first to revise and update the Porifera section of the 1955 pioneer volume of *The Treatise of Invertebrate Paleontology, Part E*, by M. W. de Laubenfels. That significant work helped initiate renewed interest in the sponges among the next generation of researchers, an interest also prompted, in part, by the focused studies of N. D. Newell and G. A. Cooper and their students and coworkers on the faunas and facies of the Permian reefs of Texas and New Mexico.

The current work includes this introductory volume and, to follow soon after, a systematic part concerned largely with those forms that have been traditionally included in the Porifera. An additional volume is in preparation documenting those groups relatively newly included in the phylum, such as the stromatoporoids, chaetetids, and sclerosponges. Some minor overlap of these two efforts is inevitable, particularly where taxonomic limits are blurred in the gray area established between categories.

Sponges are relatively simple animals with a long and incomplete geologic record, for many taxa likely left no readable record of their organic skeleton or skeletons of easily disassembled elements, although they contributed to cherty units and spiculites throughout the geologic record. Sponges are common animals in modern seas, yet relatively few paleontologists have focused research efforts on fossil sponges and their geologic record, possibly because of their perceived limited value as time-stratigraphic index fossils and also because their selective preservation of biologic information has made use of classifications of living forms difficult for fossils in some instances because of limitation of what can be seen in the fossils. As a result, records of sponges with solid skeletons, such as the lithistid demosponges or groups of calcareous sponges, have been

overplayed because of their ease of preservation compared to the probably large and diverse populations of sponges with easily disarticulated or organic skeletons that are undocumented. Nonetheless more than 1,200 genera of fossil sponges have been described and illustrated here, representing numerous families and orders in each of the traditional classes of the Porifera.

Investigations of fossil Porifera have had cycles of interest when numbers of investigators and, as a consequence, numbers of publications increased and decreased, as documented in the extensive bibliography compiled for the volumes. Peaks of activity were recorded in the 1870–1890s and 1960–1990s, but comparatively few papers were published in the mid-1800s, the 1900–1920s, and during the immediate past few years.

This revision of the Porifera volume is largely the result of three specialists: Robin E. H. Reid, Robert M. Finks, and J. Keith Rigby. Reid and Finks began their compilations and manuscript preparation in the 1970s at the invitation of R. C. Moore, with Reid focusing on Mesozoic and Cenozoic hexactinellid and demosponge taxa and Finks on Paleozoic taxa and the heteractinid and calcareous sponges. Both of them completed manuscripts on several chapters of the introduction and made preliminary compilations on some systematic sections. Reid completed manuscripts on Mesozoic and Cenozoic demospongiid and hexactinellid taxa by the late 1970s but shifted his research interests some time later to work on vertebrate fossils. I became officially involved in 1987 after it became apparent that preparation of manuscripts and illustrations for the fossil sponges needed renewed efforts to complete and update earlier compilations and descriptions, and to include descriptions and illustrations of the various taxa added to

the geologic record since the period of active involvement of the first two authors. Numerous colleagues have contributed much and willingly helped with literature and locality and distribution data. They have assisted in helping to settle many problems satisfactorily.

Appreciation is expressed to colleagues for their assistance in preparation of the manuscript and illustrations for this volume of the *Treatise of Invertebrate Paleontology*. In particular I would like to thank Baba Senowbari-Daryan, Institute für Paläontologie, Universität Erlangen-Nürnberg; Andrzej Pisera, Polska Akademia Nauk, Warsaw; Diego Garcia-Bellido Capdevila, Universidad Complutense, Madrid; Loren Babcock, Ohio State University; Dorte Mehl-Janussen, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; Fan Jiasong, Institute of Geology, Beijing; Wu Xichun, Chengdu Institute of Geology, China; Rachel Wood, University of Cambridge; Andrey Yu. Zhuravlev, Palaeontological Institute, Russian Academy of Sciences, Moscow; V. J. Goryansky, Leningrad; Barry D. Webby, University of Sidney; and John Pickett, Geological Survey of New South Wales. Appreciation is also extended to Robert B. Blodgett, Oregon State University; Robert E. Sloan and Penny Krosch, University of Minnesota; Wilbert R. Danner, University of British Columbia; Karl W. Flessa, University of Arizona; Fred D.

Bosworth, Johns Hopkins University; Carl W. Stock, University of Alabama; Colin W. Stearn, McGill University; Robert J. Elias, University of Manitoba; Françoise Debrenne, Laboratoire de Paléontologie, Paris; Björn E. E. Neuman, University of Bergen; Tomasz Wrzolek, Silesian University, Poland; Daniel C. Fisher, Museum of Paleontology, University of Michigan; Thomas E. Bolton, Geological Survey of Canada, Ottawa; and Desmond H. Collins, Royal Ontario Museum.

I thank the faculty and staff of the Department of Geology, Brigham Young University, for their support and continuing interest, and thank personnel of the Interlibrary Loan Office of the Harold B. Lee Library, also at Brigham Young University, for their invaluable assistance. I also express gratitude for secretarial help in preparation of final versions of manuscripts at Brigham Young University, some of which was partially funded by a grant from The Paleontological Institute, University of Kansas, which also funded translation by Dmitri Slinkov of critical Russian literature for the compilation. The continued interest and support of editors and the staff of The Paleontological Institute, University of Kansas, through the long process of preparation and production of the manuscript and illustrations, editing the compilations, and, finally, publication of the volume is also much appreciated.

REPOSITORIES AND THEIR ABBREVIATIONS

Abbreviations and locations of museums and institutions holding type material, which are used throughout the volume, are listed below.

AGE: Archiv für Geschiebekunde, Geologisch-Paläontologisches Institut, Hamburg, Germany
AI: Institute of Geological Sciences, Polish Academy of Sciences, Kraków, Poland
AMNH: American Museum of Natural History, New York City, New York, USA
AM or AMu: Australian Museum, Sydney, Australia
BM: Berlin Museum, Berlin, Germany
BMNH: British Museum (Natural History), London, United Kingdom
BMS: Buffalo Museum of Science, Buffalo, New York, USA
BSPGM: Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany
BYU: Geology Department, Brigham Young University, Provo, Utah, USA
CCG: Chengdu College of Geology (now Chengdu University of Technology), Chengdu, Sichuan, China
CEGH-UNC: Cátedra de Estratigrafía y Geología Histórica, Universidad Nacional de Córdoba, Córdoba, Argentina
CSGM: Central Siberian Geological Museum, United Institute of Geology, Geophysics, & Mineralogy, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia
CU: University of Cincinnati, Cincinnati, Ohio, USA
CUG: Colgate University, Geology Department Collections, Hamilton, New York, USA
CPC: Bureau of Mineral Resources, Canberra, Australia
CRICYT: Centro Regional de Investigaciones Científicas y Tecnológicas, Mendoza, Argentina
FEGI: Far East Geological Institute, Russian Academy of Sciences, Vladivostok, Russia
FM: Field Museum (Natural History), Chicago, Illinois, USA
GII: Institut für Geologie und Paläontologie der Universität Innsbruck, Innsbruck, Austria
GIK: Geologisch-Paläontologisches Institut, Universität zu Köln, Köln, Germany
GPIMH: Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, Hamburg, Germany
GSC: Geological Survey of Canada, Ottawa, Canada
GSM: British Geological Survey (formerly Geological Survey Museum; Institute of Geological Sciences, London), Keyworth, Nottinghamshire, United Kingdom

GSS: Geological Survey of Scotland, Edinburgh, United Kingdom
GSWA: Geological Survey of Western Australia, East Perth, Australia
HM: Hunterian Museum, University of Glasgow, Glasgow, United Kingdom
IGASB: Institute of Geology, Academia Sinica, Beijing, China
IGPTU: Institut und Museum für Geologie und Paläontologie, Tübingen Universität, Tübingen, Germany
IPFUB: Institut für Paläontologie, Freie Universität, Berlin, Germany
IPPAS: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland
IPM: Institut de Paléontologie du Muséum national d'Histoire naturelle de Paris, Paris, France
IPUB: Institut für Paläontologie, Universität Bonn, Bonn, Germany
IPUM: Instituto di Paleontologia, Università di Modena, Modena, Italy
IRSNB: Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium
ISM: Illinois State Geological Survey, Urbana, Illinois, USA, formerly at Illinois State Museum, Springfield, Illinois, USA
IU: Indiana University, Bloomington, Indiana, USA
JPI: Jiangnan Petroleum Institute, Jingsha, Hubei, China
KUMIP: University of Kansas, Lawrence, Kansas, USA
LGI: Leningrad Mining Institute, Leningrad, Russia
MCCA: Museo Comunale in Cortina d'Ampezzo, Cortina d'Ampezzo, Italy
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MFGI: Museum Far Eastern Geological Institute, Vladivostok, Russia
MHGI: Museum of the Hungarian Geologic Institute, Budapest, Hungary
MIGT: Museum, Institute of Geology, Dushambe, Tajikistan
MMMN: Manitoba Museum of Man and Nature, Winnipeg, Canada
MMF: Geological and Mining Museum, Sydney, Australia
MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN: Muséum National d'Histoire Naturelle de Paris, Paris, France
MUZ IG: Museum of the State Geological Institute, Warsaw, Poland
NIUPGAS: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NMV: National Museum of Victoria, Melbourne, Australia
NRM: Naturhistoriska Riksmuseet (Swedish Museum of Natural History), Stockholm, Sweden
NYSM: New York State Museum, Albany, New York, USA

- ODM:** Old Dominion College, Norfolk, Virginia, USA
- OSU:** Ohio State University, Department of Geology, Columbus, Ohio, USA
- OUZC:** Ohio University Zoological Collections, Athens, Ohio, USA
- PDMNH-P:** Paleontological Department of the National Museum, Museum of Natural History, Prague, Czech Republic
- PIUB:** Paleontological Institute of the University of Bonn, Bonn, Germany
- PIUBF:** Paläontologisches Institut, Freie Universität Berlin, Berlin, Germany
- PIUW:** Paläontologischen Instituts, Universität Wien, Vienna, Austria
- PIUZ:** Paleontological Institute, University of Zürich, Zürich, Switzerland
- PIW:** Institut für Paläontologie der Universität Würzburg, Würzburg, Germany
- P-MD:** Provincial Museum of Danzig, Danzig, Germany
- PRM:** Peter Redpath Museum, Montreal, Canada
- PU:** Princeton University, Princeton, New Jersey, USA
- ROM:** Royal Ontario Museum, Toronto, Canada
- SAM:** South Australian Museum, Adelaide, Australia
- SGIP:** Sammlung des Geologisch-Paläontologischen Institutes der Universität Palermo, Palermo, Italy
- SMF:** Natur-Museum und Forschungs-Institut, Senckenberg, Germany
- SPIE:** Sammlung des Institut für Paläontologie, Universität Erlangen-Nürnberg, Erlangen, Germany
- SPIML:** Sammlung des Paläontologischen Institutes der Universität Marburg, Lahn, Germany
- SPIT:** Sammlung des Paläontologischen Institutes der Universität Tübingen, Tübingen, Germany
- SSPHG:** Staatliches Sammlung für Paläontologie und historische Geologie, München, Germany
- SSSBGF:** Stratigraphische Sammlung der Sektion Geowissenschaften der Bergakademie Freiberg, Freiberg, Germany
- SUP:** Sydney University, Department of Geology, Sydney, Australia
- TMM:** Texas Memorial Museum, University of Texas, Austin, Texas, USA
- TsNIGER:** Ts NIGER Museum, Russia
- UA:** University of Alberta, Edmonton, Alberta, Canada
- UAF:** University of Alaska, Fairbanks, Alaska, USA
- UC:** University of Cincinnati, Cincinnati, Ohio, USA
- UCC:** Chicago Natural History Museum, formerly in Walker Museum, Chicago, Illinois (see also FM), USA
- UCM:** Universidad Complutense de Madrid, Madrid, Spain
- UG:** University of Göttingen, Göttingen, Germany
- UL:** Lodz University, Institute of Geography, Lodz, Poland
- UM:** University of Minnesota, Minneapolis, Minnesota, USA
- UMG:** University of Montana, Department of Geology, Missoula, Montana, USA
- UNE:** University of New England, Armidale, New South Wales, Australia
- UPLGS:** Université de Paris, Laboratoire de Géologie de la Sorbonne, Paris, France
- U-SK:** Universitäts-Sammlung zu Kiel, Germany
- UTBEG:** University of Texas, Bureau of Economic Geology, Austin, Texas, USA
- VK:** Theo Van Kemper Collection, Amsterdam, The Netherlands
- WAGS:** Western Australia Geological Survey, Perth, Australia
- WAM:** Western Australia Museum, Perth, Australia
- WIF:** Wadi Institute of Himalayan Geology, Dehra Dun, India
- WMC:** Woodwardian Museum, University of Cambridge, Cambridge, United Kingdom
- WMNM:** Wesfälisches Museum für Naturkunde, Münster, Germany
- YaFAN:** Institute of Geology, Yakut Branch, Siberian Division AN SSR, Yakutsk, Russia
- YPM:** Yale Peabody Museum, New Haven, Connecticut, USA
- ZPAL:** Institute of Paleobiology, Warsaw, Poland