Treatise on Invertebrate Paleontology

Part H

Brachiopoda

Revised

Volume 1: Introduction

ALWYN WILLIAMS, C. H. C. BRUNTON, and S. J. CARLSON with
FERNANDO ALVAREZ, A. D. ANSELL, P. G. BAKER, M. G. BASSETT, R. B. BLODGETT,
A. J. BOUCOT, J. L. CARTER, L. R. M. COCKS, B. L. COHEN, PAUL COPPER, G. B. CURRY,
MAGGIE CUSACK, A. S. DAGYS, C. C. EMIG, A. B. GAWTHROP, REMY GOURVENNEC,
R. E. GRANT, D. A. T. HARPER, L. E. HOLMER, HOU HONG-FEI, M. A. JAMES, JIN YU-GAN,
J. G. JOHNSON, J. R. LAURIE, STANISLAV LAZAREV, D. E. LEE, SARAH MACKAY,
D. I. MACKINNON, M. O. MANCEÑIDO, MICHAL MERGL, E. F. OWEN, L. S. PECK,
L. E. POPOV, P. R. RACHEBOEUF, M. C. RHODES, J. R. RICHARDSON, RONG JIA-YU,
MADIS RUBEL, N. M. SAVAGE, T. N. SMIRNOVA, SUN DONG-LI, DEREK WALTON,
BRUCE WARDLAW, and A. D. WRIGHT

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, KAREN RENTERIA ELIZABETH BROSIUS, JACK KEIM, JANE KERNS Assistant Editors and Editorial Staff

THE GEOLOGICAL SOCIETY OF AMERICA, INC. and
THE UNIVERSITY OF KANSAS
BOULDER, COLORADO, and LAWRENCE, KANSAS
1997

© 1997 by The University of Kansas

AND

THE GEOLOGICAL SOCIETY OF AMERICA, INC.

ALL RIGHTS RESERVED

Library of Congress Catalogue Card Number 53–12913 ISBN 0-8137-3108-9

Distributed by the Geological Society of America, Inc., P.O. Box 9140, Boulder, Colorado 80301, 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, 121 Lindley Hall, the University of Kansas, Lawrence, Kansas 66045.

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 H, Revised

BRACHIOPODA

VOLUME 1

ALWYN WILLIAMS, M. A. JAMES, C. C. EMIG, SARAH MACKAY, M. C. RHODES, B. L. COHEN, A. B. GAWTHROP, L. S. PECK, G. B. CURRY, A. D. ANSELL, MAGGIE CUSACK, DEREK WALTON, C. H. C. BRUNTON, D. I. MACKINNON, and J. R. RICHARDSON

CONTENTS

Information on Treatise volumes	vi
Editorial Preface	vii
Stratigraphic Divisions	XX
Coordinating Author's Preface (Alwyn Williams)	1
Anatomy (Alwyn Williams, M. A. James, C. C. Emig, Sarah Mackay, and M. C. Rhodes) General Characters Mantles and Body Walls Pedicle Coelomic and Circulatory System Muscular System Digestive System Excretory System The Lophophore Nervous and Sensory System Reproduction Embryology and Development	125
THE BRACHIOPOD GENOME (B. L. Cohen and A. B. Gawthrop) Structure, Composition, and Organization of the Nuclear and Mitochondrial Genomes Toward a Genealogical Classification of the Brachiopoda Implications of the SSU rRNA Gene Comparison Results for Brachiopod Systematics Future Prospects Acknowledgments	189 189 191 208 209
Physiology (L. S. Peck, M. C. Rhodes, G. B. Curry, and A. D. Ansell) Introduction Sensory and Neuromuscular Physiology and Behavior Body Size and Composition Feeding Digestion Respiration Excretion Metabolic Pathways	213 214 215 222 228 229 233

Energy Partitioning	. 240
SHELL BIOCHEMISTRY (Maggie Cusack, Derek Walton, and G. B. Curry) Introduction Amino Acids in Brachiopod Shells Proteins Lipids in Brachiopod Valves Carbohydrates in Brachiopod Valves Immunology of Brachiopod Shell Macromolecules	243245250255260
SHELL STRUCTURE (Alwyn Williams) Introduction Periostraca Primary Layer Secondary Layer Tertiary Layer Shell Perforations	. 267. 269. 271. 275. 293
MORPHOLOGY (Alwyn Williams, C. H. C. Brunton, and D. I. MacKinnon) Shell Form Ornamentation Modifications of Pedicle Opening Articulation Brachidia Musculature Mantle Canal Systems	 321 329 347 360 372 385
Morphological and Anatomical Terms Applied to Brachiopods (Alwyn Williams and C. H. C. Brunton)	
Ecology of Articulated Brachiopods (J. R. Richardson)	
Substrate Relationships Distribution Demography Predation and Parasitism	. 451 . 457
Distribution	. 451 . 457 . 460 . 463 . 464
Distribution Demography Predation and Parasitism BIOGEOGRAPHY OF ARTICULATED BRACHIOPODS (J. R. Richardson) Factors Concerning Distribution Distribution of Families	. 451 . 457 . 460 . 463 . 464 . 470 . 473 . 473
Distribution Demography Predation and Parasitism BIOGEOGRAPHY OF ARTICULATED BRACHIOPODS (J. R. Richardson) Factors Concerning Distribution Distribution of Families Family Origins and Paths of Dispersal ECOLOGY OF INARTICULATED BRACHIOPODS (C. C. Emig) Introduction Behavior	. 451 . 457 . 460 . 463 . 464 . 473 . 473 . 473 . 497 . 497
Distribution Demography Predation and Parasitism BIOGEOGRAPHY OF ARTICULATED BRACHIOPODS (J. R. Richardson) Factors Concerning Distribution Distribution of Families Family Origins and Paths of Dispersal ECOLOGY OF INARTICULATED BRACHIOPODS (C. C. Emig) Introduction Behavior Ecology BIOGEOGRAPHY OF INARTICULATED BRACHIOPODS (C. C. Emig) Introduction Patterns in Distribution	. 451 . 457 . 460 . 463 . 464 . 470 . 473 . 473 . 482 . 497 . 497

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.

VOLUMES ALREADY PUBLISHED

- Part A. Introduction, xxiii + 569 p., 371 fig., 1979.
- Part C. Protista 2 (Sarcodina, Chiefly "Thecamoebians" and Foraminiferida), xxxi + 900 p., 5,311 fig., 1964.
- Part D. Protista 3 (Chiefly Radiolaria, Tintinnina), xii + 195 p., 1,050 fig., 1954.
- Part E. Archaeocyatha, Porifera, xviii + 122 p., 728 fig., 1955.
- Part E, Revised. Archaeocyatha, Volume 1, xxx + 158 p., 871 fig., 1972.
- Part F. Coelenterata, xvii + 498 p., 2,700 fig., 1956.
- Part F. COELENTERATA, Supplement 1 (Rugosa and Tabulata), xl + 762 p., 3,317 fig., 1981.
- Part G. Bryozoa, xii + 253 p., 2,000 fig., 1953.
- Part G, Revised. BRYOZOA, Volume 1 (Introduction, Order Cystoporata, Order Cryptostomata), xxvi + 626 p., 1,595 fig., 1983.
- Part H. Brachiopoda, xxxii + 927 p., 5,198 fig., 1965.
- Part I. Mollusca 1 (Mollusca General Features, Scaphopoda, Amphineura,
 - Monoplacophora, Gastropoda General Features, Archaeogastropoda, Mainly Paleozoic Caenogastropoda and Opisthobranchia), xxiii + 351 p., 1,732 fig., 1960.
- Part K. MOLLUSCA 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea), xxviii + 519 p., 2,382 fig., 1964.
- Part L. Mollusca 4 (Ammonoidea), xxii + 490 p., 3,800 fig., 1957.
- Part L, Revised. MOLLUSCA 4, Volume 4 (Cretaceous Ammonoidea), xx + 362 p., 2,070 illus. on 216 fig., 1996.
- Part N. Mollusca 6 (Bivalvia), Volumes 1 and 2 (of 3), xxxvii + 952 p., 6,198 fig., 1969; Volume 3, iv + 272 p., 742 fig., 1971.
- Part O. ARTHROPODA 1 (Arthropoda General Features, Protarthropoda, Euarthropoda General Features, Trilobitomorpha), xix + 560 p., 2,880 fig., 1959.
- Part O, Revised. ARTHROPODA 1 (Introduction, Order Agnostida, Order Redlichiida), xxiv + 530 p., 309 fig., 1997.
- Part P. Arthropoda 2 (Chelicerata, Pycnogonida, Palaeoisopus), xvii + 181 p., 565 fig., 1955.
- Part Q. Arthropoda 3 (Crustacea, Ostracoda), xxiii + 442 p., 3,476 fig., 1961.
- Part R. ARTHROPODA 4, Volumes 1 and 2 (Crustacea Exclusive of Ostracoda, Myriapoda, Hexapoda), xxxvi + 651 p., 1,762 fig., 1969.
- Part R. ARTHROPODA 4, Volumes 3 and 4 (Hexapoda), xxii + 655 p., 1,489 fig., 1992.
- Part S. ECHINODERMATA 1 (Echinodermata General Features, Homalozoa, Crinozoa, exclusive of Crinoidea), xxx + 650 p., 2,868 fig., 1967 [1968].
- Part T. Echinodermata 2 (Crinoidea), Volumes 1–3, xxxviii + 1,027 p., 4,833 fig., 1978.
- Part U. Echinodermata 3 (Asterozoans, Echinozoans), xxx + 695 p., 3,485 fig., 1966.
- Part V. Graptolithina, xvii + 101 p., 358 fig., 1955.
- Part V, Revised. Graptolithina, xxxii + 163 p., 507 fig., 1970.
- Part W. MISCELLANEA (Conodonts, Conoidal Shells of Uncertain Affinities, Worms, Trace Fossils, Problematica), xxv + 259 p., 1,058 fig., 1962.

Part W, Revised. MISCELLANEA, Supplement 1 (Trace Fossils and Problematica), xxi + 269 p., 912 fig., 1975.

Part W, Revised. MISCELLANEA, Supplement 2 (Conodonta), xxviii + 202 p., frontis., 858 fig., 1981.

THIS VOLUME

Part H, Revised. Brachiopoda (Introduction), xx + 539 p., 417 fig., 40 tables, 1997.

VOLUMES IN PREPARATION

Part B. Protista 1 (Chrysomonadida, Coccolithophorida, Charophyta, Diatomacea, etc.).

Part E, Revised. PORIFERA. Volume 2.

Part G, Revised. BRYOZOA (additional volumes).

Part H, Revised. Brachiopoda (additional volumes).

Part I. Introduction to MOLLUSCA (part).

Part J. Mollusca 2 (Caenogastropoda, Streptoneura exclusive of Archaeogastropoda, Euthyneura).

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).

EDITORIAL PREFACE

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 H, Brachiopoda 1, Revised, the first of a series of volumes on the brachiopods, has been prepared by such a team of specialists whose work was coordinated by Sir Alwyn Williams. 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 1985 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, is undertaking a revision of the Code that will further enhance nomenclatorial stability. Nevertheless, 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 nomenclature, 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 in 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; and they call for correction. For example, 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 propose of zoological nomenclature as an information retrieval system. One looks forward with hope to a revised 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; 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, p. 73), 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 nomen-

clature, 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 preexisting available name (Code, Article 13a), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (Code, Article 13b). 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 genusgroup 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.

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 often to be made 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* specifies the endings only for subfamily (-inae) and family (-idae) names, but all family-group taxa are defined as coordinate (*Code*, Article 36, p. 77): "A name established for a taxon at any rank in the family group is deemed to be simultaneously established with the same author and date for taxa based upon the same name-bearing

type (type genus) at other ranks in the family group, with appropriate mandatory change of suffix [Art. 34a]." Such changes of rank and concomitant changes of endings as elevation of a tribe to subfamily rank or of a subfamily to family rank, if introduced subsequent to designation of a subfamily or family 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.

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*. The latter is merely the individual who first defined some lowerranked, 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.

Superfamily AGNOSTOIDEA M'Coy, 1849

[nom. transl. Shergold, Laurie, & Sun, 1990, p. 32, ex Agnostinae M'Coy, 1849, p. 402]

Family-group Names: Use of *nomen* correctum

Valid name changes classed as *nomina* correcta 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 family and subfamily, 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 familygroup 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, p. 79), in which case "... it must be replaced either by the next oldest available name from among its synonyms, including those of its subordinate taxa, or, if there is no such name, by a new replacement 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 (p. 81), however, specifies that for subsequent application of the rule of priority, the family-group name "... should be cited with its own author and date, followed by the date of the replaced name 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 11f). 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 lowerrank categories: subspecies to superfamily. Suprafamilial categories (suborder to phylum) are either not mentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoological 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, thoroughly discussed 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. 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, respectively, 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 Bellerophontacea 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 33a and Glossary, p. 254) 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 *Trea*tise 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 also is given, 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, 1964, 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 except that diacritical marks have been removed. Where other mandatory changes are required, these are introduced later in the text, typically in a figure caption.

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 automatically becomes 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 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 13b). 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-to-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 of the existence of a junior homonym generally is made.

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 separately published, 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 ar-

ranged 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.

Mackenziephyllum 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 [*Strepte-lasma 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.

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, might also be spelled 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, recently 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, and his subsequent bibliographic citations are listed

as Chang, Yi-Maw. The *Treatise* staff has adopted the convention of listing family names first, inserting a comma, and following this with given names or initials. We do this even for Chinese authors who have not reversed their names in the Western fashion.

Several systems exist for transliterating the Cyrillic alphabet into the roman alphabet. 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

This volume is unlike most previous volumes of the *Treatise* in one important respect: it is devoted entirely to introductory material, having no systematic paleontology. This is true of Part A, Introduction (Robison & Teichert, eds., 1979), the introduction to the entire series. It is also true of Part T, Echinodermata 2(1), the first of three volumes on the crinoids, which, unlike the present series on brachiopods, were published simultaneously (Moore & Teichert, eds., 1978). All other volumes have included systematic paleontology, and this is the first so-called systematic volume to contain no systematics.

Each group of organisms, it seems, lends itself to different kinds of investigations or has attracted groups of investigators with special interests. The brachiopods are no exception. In spite of the fact that more than 95 percent of the brachiopod genera are extinct, the community of brachiopod specialists has made unprecedented progress in understanding the functional morphology, genetics, embryology, and anatomy of brachiopods, all topics that are discussed in detail in this introductory volume.

ACKNOWLEDGMENTS

The Paleontological Institute's Assistant Editor for Text, Jill Hardesty, and the Assistant Editor for Illustrations, Karen Renteria, 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 members of the other editorial team, Liz Brosius and Jane Kerns; by Jack Keim with photography; and by Jean Burgess with general support. Jill Krebs, the remaining member of the Paleontological Institute staff, is involved with preparation of PaleoBank, the paleontological database for future *Treatise* volumes, and has not been closely involved with the brachiopod *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, I am pleased to extend on behalf of the members of the staff of the Paleontological Institute, both past and present, our most sincere thanks to Sir Alwyn Williams for the unwavering scholarship, dedication to the task, and scrupulous attention to detail that have marked his involvement with this project from the outset and, indeed, his entire career as a specialist on the Brachiopoda.

REFERENCES

Moore, R. C., and C. Teichert. 1978. Treatise on Invertebrate Paleontology. Part T, Echinodermata 2(1). The University of Kansas and Geological Society of America. Lawrence & Boulder. 401 p.

Ride, W. D. L., C. W. Sabrosky, G. Bernardi, and R.
V. Melville, eds. 1985. International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature. University of California Press. Berkeley & Los Angeles. 338 p.

Robison, R. A., and C. Teichert. 1979. Treatise on Invertebrate Paleontology. Part A, Introduction. The University of Kansas and Geological Society of America. Lawrence & Boulder. 569 p.

Roger L. Kaesler Lawrence, Kansas July 15, 1997

STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well established throughout the world, but minor divisions (e.g., substages, stages, and subseries) are more likely to be provincial in application. The stratigraphical units listed here represent an authoritative version of the stratigraphic column for all taxonomic work relating to revision of Part H. They are adapted from the International Union of Geological Sciences 1989 Global Stratigraphic Chart, compiled by J. W. Cowie and M. G. Bassett.

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

Upper Permian Series Lower Permian Series

Carboniferous System

Upper Carboniferous Subsystem

Stephanian Series Westphalian Series

Namurian Series (part)

Lower Carboniferous Subsystem

Namurian Series (part)

Visean Series

Tournaisian Series

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 Subsystem Cincinnatian Series Champlainian Series (part)

Lower Ordovician Subsystem Champlainian Series (part)

Canadian Series

Cambrian System

Lower Cambrian Series Middle Cambrian Series Upper Cambrian Series