

TREATISE ON INVERTEBRATE PALEONTOLOGY

Part V

HEMICHORDATA

Second Revision

Including Enteropneusta, Pterobranchia (Graptolithina)

by DENIS E. B. BATES, ELENA BELL, EDSSEL D. BRUSSA,
CHRISTOPHER B. CAMERON, ROGER A. COOPER, PAUL GONZALEZ,
ANNA KOZŁOWSKA, ALFRED C. LENZ, DAVID K. LOYDELL, SUE RIGBY,
JOHN F. RIVA, MICHAEL STEINER, BLANCA A. TORO, ALFONS H. M.
VANDENBERG, JAN ZALASIEWICZ, and YUANDONG ZHANG

JÖRG MALETZ
Coordinating Author

Prepared under Sponsorship of

The Paleontological Society
The Palaeontographical Society

SEPM (Society for Sedimentary Geology)
The Palaeontological Association

RAYMOND C. MOORE
Founder

PAUL A. SELDEN and WILLIAM I. AUSICH
Editors

ELIZABETH BLACK, MICHAEL CORMACK, DENISE MAYSE
Assistant Editor and Editorial Staff

THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL INSTITUTE
LAWRENCE, KANSAS
2023

© 2023 BY

THE UNIVERSITY OF KANSAS PALEONTOLOGICAL INSTITUTE

ALL RIGHTS RESERVED

Library of Congress Catalogue Card Number 53-12913
ISBN 978-0-99003621-3-5

Distributed by the Paleontological Institute, The University of Kansas, 1475 Jayhawk Blvd., Room 119, Lawrence, Kansas 66045-7594, USA, www.paleo.ku.edu, 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 119, Lawrence, Kansas 66045-7594, USA, www.paleo.ku.edu.

Citation information: Selden, Paul A. & William I. Ausich, eds. 2023. *Treatise on Invertebrate Paleontology. Part V, Second Revision, Hemichordata*. The University of Kansas Paleontological Institute. Lawrence, Kansas. xxx + 548 p., 310 fig.

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 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 V
HEMICHORDATA

Including Enteropneusta, Pterobranchia (Graptolithina)

Second Revision

JÖRG MALETZ, Coordinating Author

CONTENTS

INFORMATION ON <i>TREATISE</i> VOLUMES.....	viii
EDITORIAL PREFACE (Paul A. Selden and William I. Ausich).....	xi
CONTRIBUTORS.....	xxiv
REPOSITORIES AND THEIR ABBREVIATIONS.....	xxv
ORIGINAL PUBLICATION IN <i>TREATISE ONLINE</i>	xxvii
COORDINATING AUTHOR'S PREFACE (Jörg Maletz).....	xxix
INTRODUCTION TO PHYLUM HEMICHORDATA.....	1
INTRODUCTION TO THE CLASS ENTEROPNEUSTA.....	5
Morphology.....	5
Development and Reproduction.....	7
Life Habits.....	10
Evolution.....	11
Paleontology.....	14
Future Research.....	15
INTRODUCTION TO THE CLASS PTEROBRANCHIA.....	17
Evolutionary Origins.....	17
Pterobranch Zooids.....	19
Ontogeny and Astogeny.....	23
Lifestyle.....	25
The Fossil Record.....	26
MORPHOLOGY OF THE PTEROBRANCH TUBARIUM.....	29
Tubarium Construction.....	29
Colony Shapes.....	30
Thecal Wall Formation.....	33
Ultrastructure.....	36
Chemical Composition of the Tubarium.....	39
Ontogeny and Astogeny.....	40
Sicular Ontogeny.....	40
Thecal Ontogenies.....	47
The Stolon System.....	56
Colonial Astogeny.....	57
Branching.....	62
Extrathecal Developments.....	69
Late-Stage and Gerontic Modifications.....	76
HEMICHORDATA TAPHONOMY.....	81
Preservational Potential.....	81
Decay.....	83

Deposition and Burial	84
Post-Burial Modifications	86
Deformation and Retrodeformation	88
Weathering	89
PALEOECOLOGY OF THE PTEROBRANCHIA	91
Life Mode	91
Locomotion	92
Feeding	93
Parasites, Epibionts, and Predators	94
Life History Strategies	95
Species Associations and Local Populations	97
Patterns of Facies Occurrence	97
Graptoloid Biofacies and Biotopes	99
BIOSTRATIGRAPHY	103
The Fossil Record of the Hemichordata	103
Graptolite Biostratigraphy	103
Ordovician	105
Silurian	110
Devonian	115
The Duration of Graptolite Biozones	115
PALEOGEOGRAPHY OF THE HEMICHORDATA	119
Extant Hemichordata	119
Fossil Hemichordata	120
Biogeography	121
Historical Biogeography	124
GEOLOGICAL APPLICATIONS	127
Dating of Rock Sequences	127
Structural Geology and Basin Reconstruction	127
Economic Geology	130
Biosequence Stratigraphy	133
EVOLUTIONARY HISTORY	135
Evolutionary Interpretations	136
Origination, Extinction, and Diversity	138
Evolutionary Trends	140
GRAPTOLITE PREPARATION AND ILLUSTRATION TECHNIQUES	147
Collecting Graptolites	147
Physical Preparation of Graptolites	148
Chemical Isolation of Graptolites	152
Illustrations	156
Drawings	157
Visible Light, Ultra-Violet, and Infrared Photography	157
Scanning Electron Microscopy	160
Transmission Electron Microscopy	163
GLOSSARY OF THE HEMICHORDATA	165
THE HISTORY OF GRAPTOLITE CLASSIFICATION	181

The Early Years.....	181
1850–1865.....	182
1866–1880.....	183
1880–1918.....	185
The Twentieth Century.....	186
Cladistics.....	186
CLASSIFICATION OF THE HEMICHORDATA (chart).....	188
SYSTEMATIC DESCRIPTIONS	
Phylum HEMICHORDATA.....	189
Class PLANCTOSPHAEROIDEA.....	189
Class ENTEROPNEUSTA.....	190
Stem Group Taxa (no family assignment).....	190
Crown Group Taxa.....	191
Family HARRIMANIIDAE.....	191
Family SPENGELIDAE.....	192
Family PTYCHODERIDAE.....	192
Family TORQUARATORIDAE.....	193
Class PTEROBRANCHIA.....	194
Subclass CEPHALODISCIDA.....	197
Family CEPHALODISCIDAE.....	200
Subclass GRAPTOLITHINA.....	205
Family RHABDOPLEURIDAE.....	206
Family WIMANICRUSTIDAE.....	215
Family CYSTICAMARIDAE.....	221
Family DITHECODENDRIDAE.....	224
Family CYCLOGRAPTIDAE.....	226
Order DENDROIDEA.....	233
Family DENDROGRAPTIDAE.....	236
Family CALLOGRAPTIDAE.....	241
Family MASTIGOGRAPTIDAE.....	247
Order GRAPTOLOIDEA.....	253
Suborder GRAPTODENDROIDINA.....	253
Family ANISOGRAPTIDAE.....	254
Suborder SINOGRAPTINA.....	265
Family SIGMAGRAPTIDAE.....	266
Family SINOGRAPTIDAE.....	276
Family ABROGRAPTIDAE.....	280
Family THAMNOGRAPTIDAE (Suborder Uncertain).....	282
Suborder DICHOGRAPTINA.....	285
Family DICHOGRAPTIDAE.....	290
Family PHYLLOGRAPTIDAE.....	296
Family DIDYMOGRAPTIDAE.....	300
Family PTEROGRAPTIDAE.....	305
Suborder GLOSSOGRAPTINA.....	309
Family ISOGRAPTIDAE.....	310
Family GLOSSOGRAPTIDAE.....	319
Suborder AXONOPHORA.....	329

Infraorder DIPLOGRAPTINA.....	334
Stem Group DIPLOGRAPTINA.....	335
Family DIPLOGRAPTIDAE.....	336
Family LASIOGRAPTIDAE.....	344
Family CLIMACOGRAPTIDAE.....	349
Family DICRANOGRAPTIDAE.....	356
Infraorder NEOGRAPTINA.....	367
Stem Group NEOGRAPTINA.....	369
Family NORMALOGRAPTIDAE.....	372
Superfamily RETIOLITOIDEA.....	381
Family NEODIPLOGRAPTIDAE.....	381
Family RETIOLITIDAE.....	387
Subfamily PETALOLITHINAE.....	390
Subfamily RETIOLITINAE.....	395
Superfamily MONOGRAPTOIDEA.....	419
Family DIMORPHOGRAPTIDAE.....	419
Family MONOGRAPTIDAE.....	427
Subfamily Pernerograptinae.....	432
‘Streptograptines’.....	437
Subfamily Monograptinae.....	440
Subfamily Pristiograptinae.....	448
Subfamily Linograptinae.....	454
UNCERTAIN GENERA.....	461
REFERENCES.....	473
INDEX.....	538

INFORMATION ON TREATISE VOLUMES

The *Treatise on Invertebrate Paleontology* is published by the University of Kansas Paleontological Institute, www.paleo.ku.edu. The *Treatise* is organized in lettered Parts (A–W) to indicate their systematic sequence but also allowing publication of units in whatever order each is finalized. It is published in three formats. Individual chapters are published when completed in the *Treatise Online* series. When a volume is complete, it is published both as a book and as an online volume in the *Digital Treatise* series. In addition, *Paleontological Institute Special Publications* series are published periodically. The web address above provides information for ordering *Treatise* publications. Please encourage academic libraries to subscribe to all Paleontological Institute publications.

PUBLISHED VOLUMES

- Part A. INTRODUCTION: Fossilization (Taphonomy), Biogeography, and Biostratigraphy, xxiii + 569 p., 169 fig., 1979.
- Part B. PROTOCTISTA 1 (Charophyta), xvi + 170 p., 79 fig., 9 tables, 2005.
- Part B. PROKARYOTA (Bacteria and Archaea), xvii + 179 p., 48 fig., 3 tables, 2023.
- 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 E, Revised. PORIFERA, Volume 2 (Introduction to the Porifera), xxvii + 349 p., 135 fig., 10 tables, 2003.
- Part E, Revised. PORIFERA, Volume 3 (Demospongiae, Hexactinellida, Heteractinida, Calcareia), xxxi + 872 p., 506 fig., 1 table, 2004.
- Part E, Revised. PORIFERA, Volume 4 and 5 (Hypercalcified Porifera), liii + 1223 p., 665 fig., 42 tables, 2015.
- 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 H, Revised. BRACHIOPODA, Volume 5 (Rhynchonelliformea [part]), xlvi + 631 p., 398 fig., 2006.
- Part H, Revised. BRACHIOPODA, Volume 6 (Supplement), l + 906 p., 461 fig., 38 tables, CD of compiled references from volumes 1–6, 2007.
- 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 2 (Carboniferous and Permian Ammonoidea), xxix + 258 p., 139 fig., 1 table, 2009.
- 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; 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., 1967 [1968].
- Part T. ECHINODERMATA 2 (Crinoidea), Volumes 1–3, xxxviii + 1,027 p., 619 fig., 1978.
- Part T, Revised. ECHINODERMATA 2 (Crinoidea), Volume 3, xxix + 261 p., 112 fig., 2011.
- 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 V, Second Revision. Hemichordata (incl. Graptolithina), xxx + 548 p., 310 fig., 2023.

VOLUMES IN PREPARATION

- Part B. PROTISTA 1 (Chryomonadida, Coccolithophorida, Diatomacea).
- Part E, Revised. PORIFERA (additional volumes).
- Part F, Revised. CNIDARIA (Scleractinia).
- Part G, Revised. BRYOZOA (additional volumes).
- Part K, Revised. MOLLUSCA 3 (Nautiloidea).
- Part L, Revised. MOLLUSCA 4 (Ammonoidea) (additional volumes).
- Part M. MOLLUSCA 5 (Coleoidea).
- Part N, Revised. MOLLUSCA 6 (Bivalvia), Volume 1.
- Part O, Revised. ARTHROPODA 1 (Trilobita) (additional volumes).
- Part P, Revised. ARTHROPODA 2 (Chelicerata).

Part Q, Revised. ARTHROPODA 3 (Ostracoda).

Part R, Revised. ARTHROPODA 4 (Crustacea Exclusive of Ostracoda).

Part T, Revised. ECHINODERMATA 2 (Crinoidea) (additional volumes).

Part W, Revised. TRACE FOSSILS.

EDITORIAL PREFACE

PAUL A. SELDEN¹ and WILLIAM I. AUSICH²

[¹Director 2007–2020, ²Interim Director 2020–2022]

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 V, Hemichordata (Second Revision of Graptolithina) has been guided by Coordinating Author Jörg Maletz. The *Treatise* editor for the project was also a team effort. The planning and most of the text was submitted, edited, and published online during the editorship of Paul Selden. After Paul retired in 2020, William Ausich took up the mantle as interim editor. 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 the *International Code of Zoological Nomenclature* (4th edition, 1999), 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 restric-

tions 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 *Code* is updated periodically and is now available online [www.iczn.org/the-code/the-international-code-of-zoological-nomenclature/the-code-online]. A significant recent change to nomenclatorial practice is that new nomenclatorial acts must be registered on Zoobank [zoobank.org] for recognition by the ICZN. Zoobank is the official register of the ICZN and includes registry of nomenclatorial acts of genera and species, authors, publications, and type specimens.

Among other requirements, the revised *Code* is clear that the type genus of family-level taxa must be specified. In this volume we have continued the practice that has characterized most previous volumes of the *Treatise*, namely that the type genus of all family-level taxa is the first listed and diagnosed. 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 on 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*.

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 also 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 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 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 may be classified 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 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 on 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 estab-

lished 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 correctae* 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 & LYDEKKE, 1889, p. 297]

Family PALAEOCORPIDAE
Lehmann, 1944

[*nom. correct.* PETRUNKEVITCH, 1955, p. 73, *pro* Palaescorpionidae
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*, because 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 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. 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 -oidea, -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, because 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 because 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 ser-ratocarinatus* 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 except that diacritical marks have been removed. Where other mandatory changes are required, 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.*].

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 witnessed the last of such change as new, so-called republics continue to spring up around the globe. One expects confusion among readers in the future as they try to decipher such geographical terms as USSR, 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 use *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 Chinese authors have used in each of their publications rather than attempting to adopt a common spelling to be used in all citations of their 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 reference section.

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.

In previous *Treatise* volumes, traditional Chinese name order was followed when citing a Chinese language publication, in an attempt to list authors as they appear in the source being cited. However, the increasingly global nature of scientific publishing has rendered this past *Treatise* policy cumbersome and prone to error. Therefore, starting with this volume, *Treatise* is using the Western name order style for all authors, regardless of country of origin or language of publishing. The aim is for consistency and should not imply disrespect for Chinese tradition.

In this volume, we also use the full given name for Chinese authors rather than initials when the name is known (Yuandong Zhang instead of Y.-D. Zhang). Some authors cited in this volume share both a family name and the same initials with another cited author.

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

Authorship entails both credit and responsibility. As the knowledge of paleontology grows and paleontologists become more specialized, preparation of *Treatise* volumes must necessarily involve larger and larger teams of researchers, each focusing on increasingly narrow aspects of the higher taxon under revision. In this volume, we have taken special pains to acknowledge authorship of small subsections. Readers citing the volume are encouraged to pay close attention to the actual authorship of a section or subsection.

Stratigraphic nomenclature in the *Treatise* follows that recommended by the International Commission of Stratigraphy, which updates their International Chronostratigraphic Chart periodically (www.stratigraphy.org).

Unlike other volumes, stratigraphic ranges are listed herein to the level of biozones, due to the unique role graptolites play in determining ages and ranges.

Few authors, including in the *Treatise*, consistently provide the names and publication dates of sources that first declared a name to be a synonym of another genus or type species. This is surprising because such information is an important part of the history of a taxon. Identifying synonyms is particularly of crucial importance in the study of graptolites because fossils from as early as the Cambrian are often fragments, and reclassification is common. Graptolite family, genera, and species names have been in flux for centuries. In the interest of being as thorough as possible, the authors of this volume have endeavored to note author, date, and page numbers of researchers first synonymizing a name. We list such sources, identified as “synonymized by...” (abbreviated to “syn. by”). Therefore entries might read:

...[=*Prochnygraptus* PRIBYL, & ŠTORCH, 1985, p. 159 (type, *Monograptus singularis* TÖRNQUIST, 1892, p. 22, OD); syn. by ZALASIEWICZ, 1995, p. 34]

...[=*Dibranchiograptus* HUNDT, 1949a, p. 19 (type, *D. bibrachiatus*, OD), syn., herein]

All sections in this volume first appeared as chapters in *Treatise Online*, published between 2014 and 2022. This presents new dilemmas. For instance, credits for previously published figures are identified by publication and date at the end of figure captions; “new” is used if a figure is being published for the first time. In that regard, we treat *Treatise Online* and *Treatise* (the printed volume) as the same entity, therefore “new” will appear herein, even if technically published online earlier.

Authors who wish to cite *Treatise* material may choose to cite the online publication, which is the earliest date—often referred to in the text as “originally published as...” (a listing of all Part V *Treatise Online* chapters are on p. xxvii). Please note that editorial changes have been made subsequent to *Treatise Online* versions. Therefore, the printed

volume represents the most accurate and up-to-date information.

ACKNOWLEDGMENTS

This second revision of Part V began under the supervision of the late Assistant Editor, Jill Hardesty and Editor and Director Paul Selden. Assistant Editor Elizabeth Black took on the task in 2016 in the early stages of submission of manuscripts. As chapters were finished, they were made available to the community in *Treatise Online*. Becoming the Interim Director as the project was in its final phases, William Ausich took on the formidable task of moving this volume through the various stages of final editing and into production. In this, able assistance was provided by other members of the editorial team, including Denise Mayse, Office Manager and Copy Editor, with her excellent attention to detail while proofing, checking the references, and various other tasks, and Mike Cormack with his outstanding computer skills and management of subscriptions and *Treatise Online*. Six months before this volume went to the printer, Bruce Lieberman became Director

and Editor, and his input was invaluable in the last stages.

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, Richard A. Robison, and the late Roger L. Kaesler. We are indebted to them for preparing earlier prefaces and for the leadership they have provided in bringing the *Treatise* project to its present status.

Paul Selden
William Ausich

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

CONTRIBUTORS

Jörg Maletz

Coordinating Author

Institut für Geologische Wissenschaften, Freie
Universität Berlin, Malteserstrasse 74-100, D-12249,
Berlin, Germany
Yorge@zedat.fu-berlin.de

Denis E. B. Bates

86 Maesceinion, Waunfawr, Aberystwyth,
Ceredigion SY23 3QQ, UK
denisebbates@gmail.com

Elena Beli

Département de sciences biologiques, University of
Montreal, C.P. 6128, Succursale Centre-ville, Mon-
tréal, Quebec, H3C 3J7, Canada
elena.beli@umontreal.ca

²Dipartimento di Scienze e Tecnologie Biologiche ed
Ambientali, Università del Salento, Provinciale
Lecce-Monteroni 73100, Lecce, Italy

Edsel D. Brussa

Deceased, formerly of Departamento de Ciencias
Naturales, Universidad Nacional de La Pampa, Santa
Rosa, Argentina

Christopher B. Cameron

Département de sciences biologiques, Université
de Montréal, Montréal, Quebec, Canada, H3C 3J7
c.cameron@umontreal.ca

Roger A. Cooper

Deceased, formerly of GNS Science, Lower Hutt,
New Zealand.

Paul Gonzalez

National Human Genome Research Institute,
National Institutes of Health, Computational
Genomics Unit, NIH Bethesda Campus, Building
50, Rm. 5222, 50 South Dr., Bethesda, Maryland
20892, USA
paul.gonzalez@nih.gov

Anna Kozłowska

Institute of Paleobiology, Polish Academy of Sciences,
ul. Twarda 51/55, Warsaw, 00-818, Poland
akd@twarda.pan.pl

Alfred C. Lenz

Department of Earth Sciences, University of
Western Ontario, London N6A 5B7, Canada
aclenz@uwo.ca

David K. Loydell

School of the Environment, Geography and Geosci-
ences, University of Portsmouth, Burnaby Road,
Portsmouth, PO1 3QL, UK
david.loydell@port.ac.uk

Sue Rigby

Bath Spa University, Department of Paleontology,
Newton St Loe, Bath BA2 9BN, UK
vice-chancellor@bathspa.ac.uk

John F. Riva

Deceased, formerly of INRS Centre Eau, Terre, Envi-
ronnement, Québec, Canada.

Michael Steiner

Institut für Geologische Wissenschaften, Freie
Universität Berlin, Malteserstrasse 74-100, D-12249,
Berlin, Germany
Michael.Steiner@fu-berlin.de

Blanca A. Toro

Facultad de Ciencias Exactas, Físicas y Naturales,
Universidad Nacional de Córdoba, Vélez Sarsfield
1611, Ciudad Universitaria, Córdoba, X5016CGA,
Argentina.
btorogr@mendoza-conicet.gob.ar

Alfons H. M. Vandenberg

6 Frew Ave., Frankston, VIC 3199, Victoria, Australia
fvandenberg@mail.com

Yuandong Zhang

State Key Laboratory of Palaeobiology and
Stratigraphy, Nanjing Institute of Geology and
Palaeontology, Chinese Academy of Sciences,
Nanjing, China
ydzhang@nigpas.ac.cn

Jan Zalasiewicz

School of Geography, Geology and the Environment,
University of Leicester, University Road,
Leicester, LE1 7RH, UK
Jaz1@leicester.ac.uk

REPOSITORIES AND THEIR ABBREVIATIONS

Institutional acronyms for the repositories of specimens mentioned and illustrated in this volume:

- AMF:** Australian Museum, Sydney, Australia
AMNH: American Museum of Natural History, New York City, New York, USA
BAF: Palaeontological collection, Department of Geology, TU Bergakademie Freiberg, Germany
BB: Bedřich Bouček collection, Czech Geological Survey, Prague, Czech Republic
BELUM: Ulster Museum, Belfast, Northern Ireland
BGR: Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany
BGS GSM: British Geological Survey, Geological Survey Museum, Keyworth, Nottingham, UK
BSPGM: Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany
BU: Lapworth Museum, Birmingham University, Birmingham, UK
CCG: Changchun College of Geology, Changchun, Jilin Province, China
CGS: Czech Geological Survey, Prague, Czech Republic
CGM: Central Geological Museum named after F. N. Tchernyshev, St. Petersburg, Russia
CMC: Cincinnati Museum Center, Cincinnati, Ohio, USA (collection formerly at University of Minnesota)
CNIGR: Museum of the A. P. Karpinsky All-Union Geological Research Institute (VSEGEI), St. Petersburg, Russia
CPC: Commonwealth Palaeontological Collections, Geoscience Australia, Canberra, Australia (previously Bureau of Mineral Resources, BMR)
CSGM: Central Siberian Geological Museum, Novosibirsk, Russia (see **IGiG**)
DPI: La Plata Museum, La Plata, Argentina
DPM: Departamento de Paleontología, Universidad Complutense, Madrid, Spain
FGWG: Universität Greifswald, Institut für Geographie und Geologie, Greifswalder Geologische Sammlungen, Greifswald, Germany
FMNH: Field Museum, Chicago, Illinois, USA
GIT: Tallinn University of Technology, Geoscience collections of Estonia, Tallinn, Estonia
GLAHM: Hunterian Museum, University of Glasgow, Glasgow, UK
GM: Geological Museum, K. I. Satpayev Institute of Geological Sciences, Almaty, Kazakhstan
GMCH: Geological Museum of China, Beijing, China
GPIT: Geologisch-Paläontologisches Institut der Universität Tübingen, Tübingen, Germany
GSC: Geological Survey of Canada, Ottawa, Canada
GSE: Geological Survey Museum (British Geological Survey), Keyworth, Nottingham, UK
GSM: Geological Survey Museum, London, UK
IGiG: Central Siberian Geological Museum, Novosibirsk, Russia
i751: Museo Civico di Storia Naturale di Milano, Milano, Italy
KR: TU Clausthal, Institut für Geologie und Paläontologie, Clausthal-Zellerfeld, Germany
LO: Lunds Originale, Department of Geology, Lund University, Lund, Sweden
MB.G.: Museum für Naturkunde, Berlin, Germany
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MGM: Museo Geominero, Spanish Geological Survey (IGME), Madrid, Spain
MGUH: Geological Museum of the University of Copenhagen, Copenhagen, Denmark
MNHN: Muséum National d'Histoire Naturelle, Paris, France
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NHMUK: The Natural History Museum, London, UK (formerly BMNH)
NMG: Naturkundemuseum, Gera, Germany
NM: National Museum, Department of Paleontology, Prague, Czech Republic
NMV: Museums Victoria, Melbourne, Australia
NMW: National Museum of Wales, Cardiff, UK
NRM: Naturhistoriska Riksmuseet Stockholm, Stockholm, Sweden
NYSM: New York State Museum, Albany, New York, USA
OMR: B. Horák Museum, Rokychany, Czech Republic
OSU: Orton Geological Museum, Ohio State University, Columbus, Ohio, USA
OU: Otago University, Department of Geology, Geology Museum, Dunedin, New Zealand
PMO: Natural History Museum, Paleontological Type collections, University of Oslo, Oslo, Norway
PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Uppsala, Sweden
PMU: Palaeontological Collections, Museum of Evolution, Uppsala University, Uppsala, Sweden (previously UM)
PKUM: Geological Museum of Peking University, Beijing, China
ROM: Royal Ontario Museum, Toronto, Canada

RPM: Redpath Museum, McGill University,
Montreal, Québec, Canada

SGU: Sveriges Geologiska Undersökning, Uppsala,
Sweden

SM: Sedgwick Museum of Earth Sciences,
Cambridge, UK

SMF: Senckenberg Forschungsinstitut und
Naturmuseum, Frankfurt am Main, Germany

SNOMNH: Sam Noble Oklahoma Museum of Natu-
ral History, Norman, Oklahoma, USA

SVEGEI: F. N. Tchernyshev Central Geological
Museum, St. Petersburg, Russia

T: West Bohemian Museum, Pilsen, Czech Republic

TUG: University of Tartu, Natural History Museum,
Tartu, Estonia

UM: Ulster Museum, Belfast, UK

UMMP: University of Michigan, Museum of
Paleontology, Ann Arbor, Michigan, USA

USNM: US National Museum of Natural History,
Washington, DC, USA

UQ: Queensland Museum, South Brisbane,
Queensland, Australia

UUG: Czech Geological Survey (Česká geologická
služba), Prague, Czech Republic

UWO: University of Western Ontario, London,
Ontario, Canada

VU: Geological Museum, Department of Geology
and Mineralogy, Vilnius University, Vilnius,
Lithuania

ZPAL: Institute of Palaeobiology, Polish Academy of
Sciences, Warsaw, Poland (older ZPAL materials
do not have type numbers)

ORIGINAL PUBLICATION IN *TREATISE ONLINE*

All content in this volume was originally published online. Below are the relevant *Treatise Online* chapters with their original titles in the order reflected in this volume (not in date order). Authors wishing to cite the online published material, may follow the suggested citations below. They may be accessed at paleo.ku.edu/treatiseonline. The Reference Section also cites online chapters by authors where relevant.

Chapter 1: Introduction to the Hemichordata.

Maletz, Jörg, & Christopher B. Cameron 2021. Part V, Second Revision, Chapter 1: Introduction to the Hemichordata. *Treatise Online* 157:1–9, 2 fig.

Chapter 2. Class Enteropneusta:

Cameron, Christopher B. 2018. Part V, Second Revision, Chapter 2: Class Enteropneusta: Introduction, morphology, life habits, systematic descriptions, and future research. *Treatise Online* 109:1–22, 8 fig.

Chapter 3: Introduction to the class Pterobranchia.

Maletz, Jörg, & Christopher B. Cameron. 2016. Part V, Second Revision, Chapter 3: Introduction to the class Pterobranchia Lankester, 1877. *Treatise Online* 82:1–15, 8 fig.

Chapter 4: Morphology of the Pterobranch Tubarium.

Maletz, Jörg, Alfred C. Lenz, & Denis E. B. Bates. 2016. Part V, Second Revision, Chapter 4: Morphology of the Pterobranch Tubarium. *Treatise Online* 76:1–63, 44 fig.

Chapter 5: Hemichordate taphonomy.

Maletz, Jörg. 2018. Part V, Second Revision, Chapter 5: Hemichordate taphonomy. *Treatise Online* 110:1–15, 5 fig.

Chapter 6: Paleocology of the Pterobranchia.

Cooper, Roger A., Sue Rigby, Denis E. B. Bates, & Jörg Maletz. 2017. Part V, Second Revision, Chapter 6: Paleocology of the Pterobranchia (Cephalodiscida and Graptolithina). *Treatise Online* 86:1–16, 9 fig.

Chapter 7: Biostratigraphy.

Maletz, Jörg. 2021. Part V, Second Revision, Chapter 7: Biostratigraphy. *Treatise Online* 146:1–22, 7 fig.

Chapter 8: Paleogeography of the Hemichordata.

Maletz, Jörg. 2020. Part V, Second Revision, Chapter 8: Paleogeography of the Hemichordata. *Treatise Online* 133:1–12, 4 fig.

Chapter 9: Geological applications.

Maletz, Jörg, & Alfons H. M. VandenBerg. 2021. Part V, Second Revision, Chapter 9: Geological applications. *Treatise Online* 155:1–12, 3 fig.

Chapter 10: Evolutionary history.

Maletz, Jörg. 2020. Part V, Second Revision, Chapter 10: Evolutionary history. *Treatise Online* 143:1–16, 6 fig.

Chapter 11: Graptolite Preparation and Illustration Techniques.

Denis E. B. Bates, Jörg Maletz, & Jan Zalasiewicz. 2015. Part V, Revised, Volume 1, Chapter 11: Graptolite Preparation and Illustration Techniques. *Treatise Online* 65:1–20, 17 fig.

Chapter 12: Glossary of the Hemichordata.

Jörg Maletz, Denis E. B. Bates, Edsel D. Brussa, Roger A. Cooper, Alfred C. Lenz, John F. Riva, Blanca A. Toro, & Yuandong Zhang. 2014. Part V, Revised

Chapter 12: Glossary of the Hemichordata. *Treatise Online* 62:1–23, 6 fig.

Chapter 13: The history of graptolite classification.

Maletz, Jörg. 2017. Part V, Second Revision, Chapter 13: The history of graptolite classification. *Treatise Online* 88:1–11, 4 fig., 1 table.

Chapter 14: Order Cephalodiscida.

Maletz, Jörg, & Paul Gonzalez. 2017. Part V, Second Revision, Chapter 14: Order Cephalodiscida: Introduction and systematic descriptions. *Treatise Online* 100:1–8, 4 fig.

Chapter 15: Subclass Graptolithina and incertae sedis family Rhabdopleuridae.

Maletz, Jörg, & Elena Beli. 2018. Part V, Second Revision, Chapter 15: Subclass Graptolithina and *incertae sedis* family Rhabdopleuridae: Introduction and systematic descriptions. *Treatise Online* 101:1–14, 8 fig.

Chapter 16: Order Graptolithina, uncertain families.

Maletz, Jörg. 2019. Part V, Second Revision, Chapter 16: Order Graptolithina, uncertain families: Introduction, morphology, and systematic descriptions. *Treatise Online* 122:1–19, 12 fig.

Chapter 17: Order Dendroidea.

Maletz, Jörg. 2020. Part V, Second Revision, Chapter 17: Order Dendroidea: Introduction, morphology, and systematic descriptions. *Treatise Online* 139:1–23, 12 fig.

Chapter 18: Order Graptoloidea and Family Anisograptidae.

Maletz, Jörg, Blanca A. Toro, & Yuandong Zhang. 2017. Part V, Second Revision, Chapter 18: Order Graptoloidea and Family Anisograptidae: Introduction, morphology, and systematic descriptions. *Treatise Online* 85:1–14, 9 fig.

Chapter 19: Suborder Sinograptina.

Maletz, Jörg, Yuandong Zhang, & Alfons H. M. VandenBerg. 2018. Part V, Second Revision, Chapter 19: Suborder Sinograptina: Introduction, morphology, and systematic descriptions. *Treatise Online* 107:1–23, 17 fig.

Chapter 20: Suborder Dichograptina.

Maletz, Jörg, Blanca A. Toro, Yuandong Zhang, & Alfons H. M. VandenBerg. 2018. Part V, Second Revision, Chapter 20: Suborder Dichograptina: Introduction, morphology, and systematic descriptions. *Treatise Online* 108:1–28, 19 fig.

Chapter 21: Suborder Glossograptina.

Maletz, Jörg, & Yuandong Zhang. 2016. Part V, Second Revision, Chapter 21: Suborder Glossograptina: Introduction, Morphology, and Systematic Descriptions. *Treatise Online* 79:1–22, 20 fig.

Chapter 22: Suborder Axonophora, Infraorder Diplograptina I.

Maletz, Jörg. 2019. Part V, Second Revision, Chapter 22: Suborder Axonophora, Infraorder Diplograptina I

(Diplograptidae, Lasiograptidae): Introduction, morphology, and systematic descriptions. *Treatise Online* 127:1–26, 14 fig.

Chapter 23: Suborder Axonophora, Infraorder Diplograptina II.

Maletz, Jörg. 2020. Part V, Second Revision, Chapter 23: Suborder Axonophora, Infraorder Diplograptina II (Climacograptidae, Dicranograptidae): Introduction, morphology, and systematic descriptions. *Treatise Online* 129:1–20, 10 fig.

Chapter 24: Infraorder Neograptina and family Normalograptidae.

Maletz, Jörg. 2019. Part V, Second Revision, Chapter 24: Infraorder Neograptina and family Normalograptidae: Introduction, morphology, and systematic descriptions. *Treatise Online* 116:1–15, 8 fig.

Chapter 25: Superfamily Retiolitoidea and family Neodiplograptidae.

Maletz, Jörg. 2019. Part V, Second Revision, Chapter 25: Superfamily Retiolitoidea and family Neodiplograptidae: Introduction, morphology, and systematic descriptions. *Treatise Online* 117:1–8, 4 fig.

Chapter 26: Family Retiolitidae.

Lenz, Alfred C., Denis E. B. Bates, Anna Kozłowska, and Jörg Maletz. 2018. Part V, Second Revision, Chapter 26: Family Retiolitidae: Introduction, morphology, and systematic descriptions. *Treatise Online* 114:1–37, 24 fig.

Chapter 27: Superfamily Monograptioidea and family Dimorphograptidae.

Maletz, Jörg. 2017. Part V, Second Revision, Chapter 27: Superfamily Monograptioidea and family Dimorphograptidae: Introduction, morphology, and systematic descriptions. *Treatise Online* 87:1–9, 6 fig.

Chapter 28: Family Monograptidae.

Maletz, Jörg, & David K. Loydell. 2021. Part V, Second Revision, Chapter 28: Family Monograptidae: Introduction, morphology, and systematic descriptions. *Treatise Online* 156:1–43, 19 fig.

Chapter 29: Uncertain genera.

Maletz, Jörg, & Michael Steiner. 2021. Part V, Second Revision, Chapter 29: Uncertain genera. *Treatise Online* 152:1–17, 3 fig.

COORDINATING AUTHOR'S PREFACE

Jörg Maletz

INTRODUCTION

This Second Revision of the Part V *Treatise on Invertebrate Paleontology*, dealing with the phylum Hemichordata, is a considerably extended version of the Graptolite Treatises of BULMAN (1955, 1970), which primarily covered the Graptolithina, at the time interpreted as an extinct class of the Hemichordata. With the recognition of the Graptolithina as fossil members of the Pterobranchia and the identification of the benthic colonial pterobranch *Rhabdopleura* as an extant graptolite (MITCHELL & others, 2013), the focus in this volume is extended to include the record of fossil Hemichordata and to also examine the soft-body anatomy in more detail. Zooidal anatomy is important for the interpretation of the fossil graptolites and their life style and points to the importance of modern biology in understanding the fossil record.

The two editions of BULMAN'S *Treatise* (1955, 1970) have been the standard for graptolite research for seven decades, but their precursor in the *Handbuch der Paläozoologie* (BULMAN, 1938) seems to be nearly forgotten and is difficult to obtain. This volume could be regarded as the first version of the Graptolite Treatise, because it covers in a similar manner all the main aspects of graptolite taxonomy and its understanding at the time of publication and was obviously the basic source for the later versions. Unfortunately, it was published at the wrong time and in the wrong country. BULMAN (1938) established all the basic taxonomic concepts in the volume, even introducing a number of new taxa.

BULMAN'S work on the graptolites and their taxonomy in the two previous *Treatise* volumes is neither the only one nor the first attempt at a general overview of graptolites. However, most general treatments did not attain the influence and acceptance in the in-

ternational scientific community, either due to the language in which they were published or the time of publication. HALL (1868) and FRECH (1897) provided an understanding of graptolite research during their times and achieved important and valuable insights. General overviews by DAWYDOFF (1948), WATERLOT (1953), MÜNCH (1952), MU and LEE (1960), and OBUT (1957, 1964) had less impact due to the language barriers (published in French, German, Chinese, and Russian, respectively), but nevertheless they were important in shaping the opinions of generations of researchers.

Discussions to produce a new Graptolite *Treatise* began more than 20 years ago, with Chuck Mitchell and Mike Melchin initiating the first steps with then *Treatise* Editor Roger Kaessler. Along the way, there were meetings in Prague (1999, 2008), Nanjing (2007), and Sardinia (2009). Twelve years into the project, I became Coordinating Author when Chuck Mitchell was unable to continue due to other commitments. I began producing a newsletter in 2010 to track progress and keep in touch with authors.

SCOPE OF THE VOLUME

This volume is aimed at providing the most complete and up-to-date information on the fossil Hemichordata, their taxonomy, and their use in the geological sciences. The inclusion of not only the Pterobranchia (Graptolithina) but also the Enteropneusta shows our increased knowledge of the relationships of this fascinating fossil group with extant groups of organisms. This approach connects the fossil graptolites with their closest relatives, largely known from extant organisms.

Graptolites, the main focus of this volume, have been used successfully in the understanding of lithostratigraphic succes-

sions, unraveling structural complexities in geology and, thus, are important biological objects enabling numerous geological interpretations, as detailed on p. 127–134 (first published as MALETZ & VANDENBERG, 2021, *Treatise Online*). LAPWORTH (1878) first used graptolites to decipher the tectonic complexities in the succession of the Moffat Series, a milestone in graptolite research (FORTEY, 1993; HAMILTON, 2001) and a first hint on the importance of graptolite research to applied geology. Graptolite fusellum has been used to determine temperature and burial histories of Paleozoic sediments (e.g., GOODARZI & NORFORD, 1985). Graptolite research, thus, goes far beyond the identification of taxa and the relative dating of successions that included graptolites as index fossils. It is not just a discipline for taxonomists and fossil collectors; the geological application of graptolites is still developing and modern data collection and database interpretations may infuse new life into graptolite research. In recent years, paleodiversity studies using graptolite faunas have become the focus of research on extinction and origination intervals in Earth's history (e.g., CRAMPTON & others, 2020).

The Enteropneusta, unfortunately, have been neglected in the past because so few fossil ones were recognized, and even the extant enteropneusts were rarely investigated in much detail. Only through the renewed interest in the Burgess Shale biota and their preservation, fossil Enteropneusta have gained more interest. As a result, new fossil taxa have been studied and described, including ones that are tubicolous (e.g., CARON, CONWAY MORRIS, & CAMERON, 2013; NANGLU, CONWAY MORRIS, & CAMERON, 2016; CAMERON, 2018) and one with tentaculate

arms (NANGLU, CARON, & CAMERON, 2020), two characteristics that were previously regarded as restricted to the Pterobranchia.

ADDITIONAL INFORMATION

Color versions of many of the specimens and illustrations in this volume are available in *Treatise Online*. A reference to a color version is included in captions when color contributes vital information.

The systematic description section, which begins on p. 189, also includes additional introductory information and morphology details for each taxon group.

ACKNOWLEDGEMENTS

As the coordinating author of this volume, I wish to thank all my co-authors (listed on p. xxiv) and also all specialists who provided information, illustrations, and reviews of the individual chapters. I should not forget the hard working team at the *Treatise* office in Kansas who were essential to the production of this volume—Director Paul Selden, who supervised the project from 2007 to mid-2020, Assistant Editor Elizabeth Black who handled all but the first two chapters submitted; Michael Cormack for *Treatise Online* support; Denise Mayse, whose copyediting and proofing was essential; and Interim Editor William Ausich, who shepherded the project through its final stages.

Unfortunately, a number of our colleagues have left us during this long process, and we will always remember their input. Thus, a special thank you goes to Edsel D. Brussa (1961–2008), Roger A. Cooper (1939–2020), John F. Riva (1929–2020) and also to Assistant Editor Jill Hardesty (1965–2015), who initially supervised the editorial work for this *Treatise* volume.